

A DISCRETE MODEL OF COMPETING SPECIES SHARING A PARASITE

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ABSTRACT. In this work we develop a discrete model of competing species affected by a common parasite. We analyze the influence of the fast development of the shared disease on the community dynamics. The model is presented under the form of a two time scales discrete system with four variables. Thus, it becomes analytically tractable with the help of the appropriate reduction method. The 2-dimensional reduced system, that has the same asymptotic behaviour as the full model, is a generalization of the Leslie-Gower competition model. It has the unfrequent property in this kind of models of including multiple equilibrium attractors of mixed type. The analysis of the reduced system shows that parasites can completely alter the outcome of competition depending on the parasite's basic reproductive number R_0 . In some cases, initial conditions decide among several exclusion or coexistence scenarios.

1. Introduction. Already in the classic experiment of Park [19] in the 1940s, the influence of parasites on species competition was experimentally demonstrated. The presence of the sporozoan parasite *Adelina tribolii* can change the competition outcome of flour beetles *Tribolium confusum* and *Tribolium castaneum*. In the absence of the pathogen, *Tribolium confusum* is the superior competitor whilst in the presence of the pathogen it becomes outcompeted by *Tribolium castaneum*. The fact that parasites can alter competitive relationships between host species implies that they can play keystone roles in ecological communities [14]. They can alter the outcome of an interaction, mediating coexistence or exclusion. They can also make use of some host species as reservoirs to infect other species in which the parasite is more virulent.

The effects of parasites on competition can be classified into those affecting population densities and those modifying the competitive abilities of hosts. For the first case it is used the term *parasite-mediated competition* and, for the second,

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parasite-modified competition. Both are important for host population dynamics and community structure. It is more common that models incorporate parasite-mediated competition considering an increased mortality as the main effect of parasitism. Nevertheless, parasite-modified competition as an example of trait-mediated indirect interaction (TMII) also has significant effects on community dynamics [22].

A general parasitism-competition model needs to include intraspecific competition, interspecific competition and a parasite affecting the two hosts both in their reproduction/survival rates and in their competitive capabilities [14].

In [4], two discrete time models encompassing competition influenced by a parasite were presented. The first one corresponds to the case of one parasite affecting demography and intraspecific competition in a single host. The second one considers a direct competition between two different species with one of them being the parasite's host. In this work we extend the study to the case in which the parasite is shared by both competing species.

As it is justified in [4], the use of time scales in this kind of models is relevant and it is endowed with a certain novelty. It is well known that TMII's act on a shorter time scale than demographic effects [2, 13]. This important issue is reflected in our model by assuming that the transitions between infected and noninfected individuals are faster than their demographic counterparts.

In discrete time models that encompass various processes it is usual to consider them as taking place sequentially [15]. This fact suggests a way of introducing the separation of time scales in the construction of the model. We assume that a large number k of infection-recovery episodes take place between two demographic-competition steps. In [20, 3] it is shown how to construct this kind of discrete time models with two time scales. At the same time, a reduction method is proposed that helps to carry out the analytical study of the model. In this way we can circumvent the characteristic difficulty of analysis of complete eco-epidemic competition models (see [14] box 2.3 and references therein).

The proposed full model is represented by a 4-dimensional discrete system whose states variables are the number of susceptible and infected individuals in each of the two competing species. The reduction method applied to the full model builds up a reduced 2-dimensional system approximately describing the dynamics of the total number of individuals of both species. Then, the asymptotic analysis of the full model can be known by studying the asymptotic behavior of this reduced system. It turns out to be a competitive planar discrete system [21] with all its non-negative solutions tending to non-negative equilibria. A model with the same form appears in a different context in [18], where a local stability analysis of some particular cases is performed.

In the full model, the representation of competition is based upon the discrete Leslie-Gower model [16], that replicates in discrete time the competition outcomes of the classical Lotka-Volterra competition model [9] through three possible scenarios: a globally attracting coexistence equilibrium, a globally attracting exclusion equilibrium and, finally, two attracting exclusion equilibria. The resulting reduced system can be thought as a generalization of the Leslie-Gower model. Nevertheless, it displays a far richer dynamics that can include multiple equilibrium attractors of mixed type [8], i.e., at least one coexistence equilibrium and at least one exclusion equilibrium. In fact, there are cases whose attractors are one coexistence and one exclusion equilibria and others with one coexistence and two exclusion equilibria. On the other hand, some cases can be found presenting two different coexistence

equilibria as the only attractors. The existence of multiple equilibrium attractors of mixed type has been proved in structured competition models like LPA [11] and in a non-structured Leslie-Gower competition model with Allee effects [6]. The reduced model obtained in this work could explain, through simple nonlinearities and without introducing structure in the populations, the observed case of multiple mixed-type attractors in Park experiments.

The analysis of the reduced system gives insights about the possible effects of the parasite on the competition community. It is shown that a parasite with a large enough basic reproductive number R_0 can completely alter the outcome of competition. It is also proved that the final situation can be dependent on initial conditions with up to three different attracting equilibria and their associated basins of attraction.

This work is organized as follows: In Section 2 it is presented the model of species competition sharing a parasite with the parasite transmission-recovery dynamics acting faster than the demographic dynamics. Assuming equal transmission and recovery coefficients in both species, Section 3 deals with the study of the model with the help of an appropriate reduction technique. In Section 4 different scenarios corresponding to the parasite affecting either species growth or species competitive abilities are discussed. The conclusions in Section 5 and the Appendix with the proof of the mathematical results complete the manuscript.

2. The model. We consider two species that compete and a parasite that infects both of them. We assume that the disease acts on a shorter time scale than the demographic dynamics. To include two time scales in a discrete model, the time unit of the system should be the one associated with the slow process [3, 20], in this case demography. Thus, during one time unit we can assume that a single episode of demographic change occurs following a number k of disease infection-recovery cycles. In this way, we intend to represent the fact that pathogens exhibit outbreaks on short time scales, days or weeks, in comparison to demographic changes that might be considered annual.

To represent the competition, intra and inter-species, we generalize the well-known Leslie-Gower model [16] that, for two species N^1 and N^2 , reads as follows

$$\begin{aligned} N^1(t+1) &= \frac{b^1 N^1(t)}{1 + c^{11} N^1(t) + c^{12} N^2(t)} \\ N^2(t+1) &= \frac{b^2 N^2(t)}{1 + c^{21} N^1(t) + c^{22} N^2(t)}, \end{aligned} \quad (1)$$

where parameters $b^i > 0$ are the inherent growth rates and $c^{ij} > 0$ the competition coefficients. In [9] it is proved that this model exhibits the same four dynamic scenarios as the classical continuous Lotka-Volterra competition model, provided that both species have inherent growth rates larger than one. They are characterized through the following two parameters:

$$D^1 = \frac{b^1 - 1}{c^{11}} - \frac{b^2 - 1}{c^{21}}, \quad D^2 = \frac{b^2 - 1}{c^{22}} - \frac{b^1 - 1}{c^{12}} \quad (2)$$

1. Species 1 out-competes species 2: $D^1 > 0$ and $D^2 < 0$.
2. Species 2 out-competes species 1: $D^1 < 0$ and $D^2 > 0$.
3. Coexistence of both species: $D^1 < 0$ and $D^2 < 0$.
4. Exclusion of species either 1 or 2 depending on initial conditions: $D^1 > 0$ and $D^2 > 0$.

The effect of the parasite is reflected in the model by distinguishing susceptible and infected individuals in both competing species. Let N_S^1 , N_I^1 , N_S^2 and N_I^2 denote the corresponding state variables. The proposed extension of the Leslie-Gower model is

$$\begin{aligned} N_S^1(t+1) &= \frac{b_S^1 N_S^1(t)}{1 + c_{SS}^{11} N_S^1(t) + c_{SI}^{11} N_I^1(t) + c_{SS}^{12} N_S^2(t) + c_{SI}^{12} N_I^2(t)} \\ N_I^1(t+1) &= \frac{b_I^1 N_I^1(t)}{1 + c_{IS}^{11} N_S^1(t) + c_{II}^{11} N_I^1(t) + c_{IS}^{12} N_S^2(t) + c_{II}^{12} N_I^2(t)} \\ N_S^2(t+1) &= \frac{b_S^2 N_S^2(t)}{1 + c_{SS}^{21} N_S^1(t) + c_{SI}^{21} N_I^1(t) + c_{SS}^{22} N_S^2(t) + c_{SI}^{22} N_I^2(t)} \\ N_I^2(t+1) &= \frac{b_I^2 N_I^2(t)}{1 + c_{IS}^{21} N_S^1(t) + c_{II}^{21} N_I^1(t) + c_{IS}^{22} N_S^2(t) + c_{II}^{22} N_I^2(t)}, \end{aligned} \quad (3)$$

where all parameters are positive with parameters b representing growth rates and c competition coefficients. All parameters, those representing growth as well as those related to competition, depend on infection status. This means that we include in the model both parasite-mediated and parasite-modified competition.

System (3) represents the episode of demographic change. To build up the complete model we still need to define the action of the disease infection-recovery cycles. In order to do it we extend the discrete-time SIS epidemic model studied in [1] to the case of two species sharing the same parasite. Denoting $\mathbf{N} = (N_S^1, N_I^1, N_S^2, N_I^2)$, the associated map is

$$\mathbf{F}(\mathbf{N}) = (F_S^1(\mathbf{N}), F_I^1(\mathbf{N}), F_S^2(\mathbf{N}), F_I^2(\mathbf{N})), \quad (4)$$

where

$$\begin{aligned} F_S^1(\mathbf{N}) &= N_S^1 - \frac{N_S^1 (\beta_{11} N_I^1 + \beta_{12} N_I^2)}{N_S^1 + N_I^1 + N_S^2 + N_I^2} + \gamma_1 N_I^1 \\ F_I^1(\mathbf{N}) &= N_I^1 + \frac{N_S^1 (\beta_{11} N_I^1 + \beta_{12} N_I^2)}{N_S^1 + N_I^1 + N_S^2 + N_I^2} - \gamma_1 N_I^1 \\ F_S^2(\mathbf{N}) &= N_S^2 - \frac{N_S^2 (\beta_{21} N_I^1 + \beta_{22} N_I^2)}{N_S^1 + N_I^1 + N_S^2 + N_I^2} + \gamma_2 N_I^2 \\ F_I^2(\mathbf{N}) &= N_I^2 + \frac{N_S^2 (\beta_{21} N_I^1 + \beta_{22} N_I^2)}{N_S^1 + N_I^1 + N_S^2 + N_I^2} - \gamma_2 N_I^2, \end{aligned}$$

where parameters β , representing the transmission coefficients, and parameters γ , the recovery rates, are all positive.

As the working set we consider the possible (non-negative) population values for which there is at least one infected individual, i.e., the set

$$\Omega := \{(N_S^1, N_I^1, N_S^2, N_I^2) \in \mathbb{R}_+^4 : N_I^1 + N_I^2 > 0\}, \quad (5)$$

where \mathbb{R}_+^4 denotes the closed non-negative cone. For the transformation to make sense in this context, the condition $\mathbf{F}(\Omega) \subset \Omega$ must hold. In the next section we give necessary and sufficient conditions for this to hold in the case that we will deal with.

The full model combining the demographic and the disease processes is defined by composing the k -th iterate $\mathbf{F}^{(k)}$ of map \mathbf{F} (4), and the map \mathbf{S} associated to system (3):

$$\mathbf{N}(t+1) = (\mathbf{S} \circ \mathbf{F}^{(k)}) (\mathbf{N}(t)). \quad (6)$$

To study this model we proceed in the next section to perform its reduction into a 2-dimensional competition system with the total population of the two species as state variables. The reduction method can be found in [20, 3]. Roughly, the reduction is based on the fact that the infectious process rapidly attains an equilibrium with fixed proportions of susceptible and infected individuals in each species.

3. Analysis of the reduced model with homogeneous disease transmission and recovery. The reduction of system (6) in its general form is too involved if not impossible to carry out, and so we will address a particular case that yields interesting enough insights to be worth studying.

We assume that both species are equal in terms of disease transmission and recovery:

$$\beta := \beta_{11} = \beta_{12} = \beta_{21} = \beta_{22} \text{ and } \gamma := \gamma_1 = \gamma_2.$$

Moreover, in order for map \mathbf{F} to be properly defined and for the disease to attain an endemic equilibrium, we also assume the following hypothesis:

Hypothesis 1: $0 < \gamma < \beta \leq 1$.

In Appendix A it is proved that, under the previous hypothesis, the disease process associated to map \mathbf{F} satisfies $\mathbf{F}(\Omega) \subset \Omega$, leaves invariant the total population of each species $N^1 := N_S^1 + N_I^1$ and $N^2 := N_S^2 + N_I^2$, and attains an equilibrium of the form:

$$(\nu N^1, (1 - \nu)N^1, \nu N^2, (1 - \nu)N^2) \tag{7}$$

expressed in terms of the inverse of the parasite R_0 :

$$\nu := \frac{\gamma}{\beta} = \frac{1}{R_0} \tag{8}$$

The reduction procedure for system (6) is carried out by assuming that this equilibrium is attained. Then it is straightforward to write the following 2-dimensional reduced system whose state variables are the total populations N^1 and N^2 :

$$\begin{aligned} N^1(t + 1) &= \frac{r_S^1 N^1(t)}{1 + c_{S1}^1 N^1(t) + c_{S2}^1 N^2(t)} + \frac{r_I^1 N^1(t)}{1 + c_{I1}^1 N^1(t) + c_{I2}^1 N^2(t)} \\ N^2(t + 1) &= \frac{r_S^2 N^2(t)}{1 + c_{S1}^2 N^1(t) + c_{S2}^2 N^2(t)} + \frac{r_I^2 N^2(t)}{1 + c_{I1}^2 N^1(t) + c_{I2}^2 N^2(t)}, \end{aligned} \tag{9}$$

where for $i, j = 1, 2$

$$r_S^i := b_S^i \nu, \quad r_I^i := b_I^i (1 - \nu), \quad c_{Sj}^i := \nu c_{SS}^{ij} + (1 - \nu) c_{SI}^{ij}, \quad c_{Ij}^i := \nu c_{IS}^{ij} + (1 - \nu) c_{II}^{ij}.$$

This system generalizes the classical Leslie-Gower competition model, since it coincides with it when $\nu = 1$.

In Appendix A it is proved that the analysis of stability of the equilibria and periodic solutions of system (6) can be performed by carrying out the corresponding analysis in system (9).

In order to carry out the mathematical treatment of system (9) we express it in the form

$$(N^1(t + 1), N^2(t + 1)) = H(N^1(t), N^2(t)), \tag{10}$$

where H is the map defined by

$$H(x_1, x_2) = (H_1(x_1, x_2), H_2(x_1, x_2)) = (\phi_1(x_1, x_2)x_1, \phi_2(x_1, x_2)x_2),$$

and

$$\phi_i(x_1, x_2) := \frac{r_S^i}{1 + c_{S1}^i x_1 + c_{S2}^i x_2} + \frac{r_I^i}{1 + c_{I1}^i x_1 + c_{I2}^i x_2}, \quad i = 1, 2.$$

Note that all the parameters of the model are positive except possibly r_1^1 and r_1^2 that are non-negative.

As we will see, the numbers

$$\phi_i(0, 0) = r_S^i + r_I^i = b_S^i \nu + b_I^i (1 - \nu), \quad i = 1, 2$$

will play an important role in the dynamics of the system.

Let $A_1 = \{(x_1, 0) : x_1 > 0\}$ and $A_2 = \{(0, x_2) : x_2 > 0\}$ be the positive axes. It is immediate to realize that the sets \mathbf{R}_+^2 , $\mathring{\mathbf{R}}_+^2$ and A_i , $i = 1, 2$ are forward invariant by H . In the sequel, unless otherwise stated, we will always assume that we are working on Ω (5).

Let us study the isoclines of the system, i.e., the sets defined by $x_1 = H_1(x_1, x_2)$ and $x_2 = H_2(x_1, x_2)$. Clearly, besides the x_1 -axis (resp. x_2 -axis) in which the variable x_2 (resp. x_1) is constant, the isoclines are the curves S_i defined by $\phi_i(x_1, x_2) = 1$ for $i = 1, 2$. The following Lemma presents their main properties:

Lemma 3.1. *Let $i \in \{1, 2\}$ be fixed. The set $S_i := \{(x_1, x_2) \in \mathbb{R}^2 : \phi_i(x_1, x_2) = 1\}$ is a hyperbola that degenerates if and only if $c_{S1}^i c_{I2}^i = c_{S2}^i c_{I1}^i$, in which case it becomes two parallel lines. In addition, S_i intersects $\mathring{\mathbf{R}}_+^2$ if and only if $\phi_i(0, 0) > 1$ and, in that case (a) only one of its branches intersects $\mathring{\mathbf{R}}_+^2$ and (b) S_i intersects both the positive axes A_1 and A_2 , being the intercepts defined by*

$$R_{ij} = \frac{1}{2c_{Sj}^i c_{Ij}^i} \left(\alpha_j^i + \sqrt{(\alpha_j^i)^2 + 4c_{Sj}^i c_{Ij}^i (r_S^i + r_I^i - 1)} \right), \quad j = 1, 2, \quad (11)$$

where $\alpha_j^i := r_S^i (c_{Ij}^i - 1) + r_I^i (c_{Sj}^i - 1)$, $j = 1, 2$. Moreover, for each $i = 1, 2$, $\Gamma_i := S_i \cap \mathbf{R}_+^2$ can be written in the form $x_2 = \Phi_i(x_1)$, $x_1 \in [0, R_{i1}]$, where Φ_i is a strictly decreasing convex function.

Proof. See Appendix B. □

In what follows we will write $(x_1, x_2) \leq (x'_1, x'_2)$ (resp. $(x_1, x_2) < (x'_1, x'_2)$) to denote that $x_1 \leq x'_1$ and $x_2 \leq x'_2$ (resp. $x_1 < x'_1$ and $x_2 < x'_2$). Similarly, we define the K -order in the following way: we write $(x_1, x_2) \leq_K (x'_1, x'_2)$ (resp. $(x_1, x_2) <_K (x'_1, x'_2)$) to denote that $x_1 \leq x'_1$ and $x_2 \geq x'_2$ (resp. $x_1 < x'_1$ and $x_2 > x'_2$).

Proposition 1. *Let us consider system (10):*

a. *All solutions in \mathbf{R}_+^2 are forward bounded, and more specifically*

$$H(\mathbf{R}_+^2) \subset S := \left[0, \frac{r_S^1}{c_{S1}^1} + \frac{r_I^1}{c_{I1}^1} \right) \times \left[0, \frac{r_S^2}{c_{S2}^2} + \frac{r_I^2}{c_{I2}^2} \right) \quad (12)$$

b. *H is strongly competitive in \mathbf{R}_+^2 , i.e., if $x, x' \in \mathbf{R}_+^2$ are distinct points with $x \leq_K x'$ it follows that $H(x) <_K H(x')$ [21].*

c. *All orbits in \mathbf{R}_+^2 are eventually componentwise monotone, i.e., for each $(N^1(0), N^2(0)) \in \mathbf{R}_+^2$, the corresponding solution $(N^1(t), N^2(t))$ satisfies that $N^i(t)$ is eventually monotone for each $i = 1, 2$. Moreover, all orbits tend to an equilibrium as $t \rightarrow \infty$.*

Proof. See Appendix B. □

Let us now consider the existence of equilibria for system (10). Note that $E_0^* := (0, 0)$ is an equilibrium point for all values of the parameters. Using Lemma 3.1 we conclude:

- For each $i = 1, 2$, there exists a semitrivial equilibrium point E_i^* on the positive axis A_i if and only if $\phi_i(0, 0) > 1$. In that case the semitrivial equilibrium is unique.
- A necessary condition for the existence of a positive equilibrium is that $\phi_i(0, 0) > 1$ for both $i = 1, 2$.

The next result analyzes the global behavior of solutions of system (10) except in the case in which $\phi_i(0, 0) > 1, i = 1, 2$:

Theorem 3.2. *Let us consider system (10):*

- For each $i = 1, 2$, if $\phi_i(0, 0) \leq 1$ then for any initial value on \mathbf{R}_+^2 species i tends to extinction as $t \rightarrow \infty$.*
- If $\phi_i(0, 0) \leq 1$ for $i = 1, 2$, all orbits in \mathbf{R}_+^2 tend to E_0^* , and if the inequalities are strict then E_0^* is hyperbolic. If $\phi_i(0, 0) > 1$ for $i = 1, 2$, then E_0^* is a repeller and therefore no orbit can converge to E_0^* .*
- If $\phi_1(0, 0) > 1$ and $\phi_2(0, 0) \leq 1$ then (1) all orbits with $N^1(0) = 0$ tend to E_0^* and (2) all orbits with $N^1(0) > 0$ tend to E_1^* .*
- If $\phi_2(0, 0) > 1$ and $\phi_1(0, 0) \leq 1$ then (1) all orbits with $N^2(0) = 0$ tend to E_0^* and (2) all orbits with $N^2(0) > 0$ tend to E_2^* .*

Proof. See Appendix B. □

Let us now consider the case in which $\phi_i(0, 0) > 1$ for $i = 1, 2$. The positive equilibria of the system are the number of (positive) intersections of Γ_1 and Γ_2 . In the first place, since the isoclines are hyperbolas they can intersect in four points at most, and so there can be at most four positive equilibria. It is easy to find parameter values for which there are zero, one, two or three positive equilibria. After extensive numerical simulations we have not been able to find any case for which there are four positive intersections, and so we will not treat that case in the following discussion.

In order to study the behavior of solutions, we consider the different generic cases based on the relative position of the intercepts R_{ij} (11) of Γ_1 and Γ_2 , and on the number (up to three) of positive equilibria. Specifically, we distinguish several scenarios, that we denote with a letter, which correspond to the relative position of the intercepts R_{ij} and a subindex that denotes the number of positive equilibria. We only consider the generic cases, i.e., we omit the cases in which the isoclines are tangent at an equilibrium point:

- **Case A.** $R_{11} < R_{21}, R_{12} > R_{22}$. There can be one (**Case A₁**) or three (**Case A₃**) positive equilibria.
 - **Case B.** $R_{11} > R_{21}, R_{12} < R_{22}$. There can be one (**Case B₁**) or three (**Case B₃**) positive equilibria.
 - **Case C.** $R_{11} > R_{21}, R_{12} > R_{22}$. There can be zero (**Case C₀**) or two (**Case C₂**) positive equilibria.
 - **Case D.** $R_{11} < R_{21}, R_{12} < R_{22}$. There can be zero (**Case D₀**) or two (**Case D₂**) positive equilibria.
- (13)

Taking into account Lemma 3.1, the isoclines divide \mathbf{R}_+^2 in a finite number of open connected and disjoint sets in which x_i is either strictly increasing or strictly decreasing for each $i = 1, 2$. To describe the kind of monotonicity in each region we use arrows, in such a way that, for example, the situation in which x_1 decreases and

x_2 increases corresponds to a horizontal arrow pointing to the left and a vertical arrow pointing up.

Figure 1 shows the different configurations described in (13).

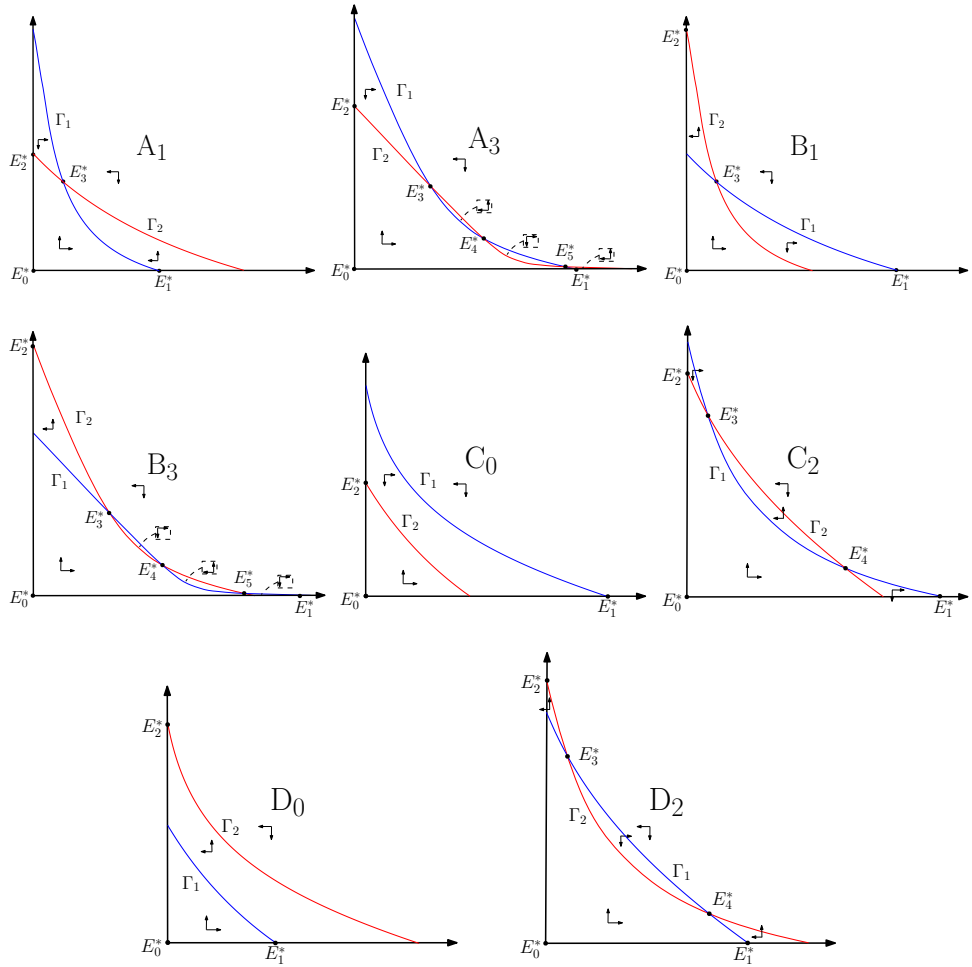


FIGURE 1. Different configurations of system (10) when $\phi_i(0, 0) > 1$ for $i = 1, 2$, in terms of the relative position of the intercepts of isoclines, R_{ij} (11) and the number of positive equilibria, as described in (13)

The following result deals, on the one hand, with the stability of the semitrivial and of the positive equilibria in the different scenarios described in (13). On the other hand, it characterizes the global dynamics on the positive axes and studies the behavior of solutions for positive initial conditions:

Theorem 3.3. *Let us consider system (10) and assume that $\phi_i(0, 0) > 1$ for $i = 1, 2$.*

1. Semitrivial equilibria and behavior on the positive axes.

- a. All orbits starting on the positive i -axis A_i converge to E_i^* , $i = 1, 2$.

b. Let $i = 1, 2$ be fixed. If $\phi_j(E_i^*) < 1$ for $j \neq i$, then E_i^* is hyperbolic and attracting. If $\phi_j(E_i^*) > 1$ for $j \neq i$ then E_i^* is hyperbolic and unstable.

2. Position of the equilibria. Let us assume that there exist $s \geq 0$ positive equilibria that we denote E_{2+i}^* , $i = 1, \dots, s$. Then they can be ordered using the K -order in such a way that

$$E_2^* <_K E_3^* <_K \dots <_K E_{2+s}^* <_K E_1^*$$

and in the sequel we assume that they are ordered in this way.

3. Stability of equilibria and behavior of solutions for positive initial conditions. Let us consider cases **A**, **B**, **C** and **D** as described in (13):

- **Case A.** E_1^* and E_2^* are hyperbolic and unstable.
 - In case **A**₁, the (unique) positive equilibrium E_3^* is hyperbolic and attracting. All orbits starting on $\mathring{\mathbf{R}}_+^2$ converge to E_3^* .
 - In case **A**₃, E_3^* and E_5^* are hyperbolic and attracting and E_4^* is a hyperbolic saddle. Moreover E_4^* cannot attract any open set and therefore almost all orbits starting in $\mathring{\mathbf{R}}_+^2$ converge to either E_3^* or E_5^* .
- **Case B.** E_1^* and E_2^* are hyperbolic and attracting.
 - In case **B**₁, the (unique) positive equilibrium E_3^* is a hyperbolic saddle. Moreover E_3^* cannot attract any open set and therefore almost all orbits starting in $\mathring{\mathbf{R}}_+^2$ converge to either E_1^* or E_2^* .
 - In case **B**₃, E_3^* and E_5^* are hyperbolic saddles and E_4^* is hyperbolic and attracting. Moreover E_3^* and E_5^* cannot attract any open set and therefore almost all orbits starting in $\mathring{\mathbf{R}}_+^2$ converge to either E_1^* , E_2^* or E_4^* .
- **Case C.** E_1^* is hyperbolic and attracting and E_2^* is hyperbolic and unstable.
 - In case **C**₀ all orbits starting on $\mathring{\mathbf{R}}_+^2$ converge to E_1^* .
 - In case **C**₂ no orbits starting in $\mathring{\mathbf{R}}_+^2$ can converge to E_2^* . Besides, E_3^* is hyperbolic and attracting and E_4^* is hyperbolic and a saddle. Moreover, E_4^* cannot attract any open set and therefore almost all orbits starting in $\mathring{\mathbf{R}}_+^2$ converge to either E_1^* or E_3^* .
- **Case D.** E_2^* is hyperbolic and attracting and E_1^* is hyperbolic and unstable.
 - In case **D**₀ all orbits starting on $\mathring{\mathbf{R}}_+^2$ converge to E_2^* .
 - In case **D**₂ no orbits starting in $\mathring{\mathbf{R}}_+^2$ can converge to E_1^* . Besides, E_4^* is hyperbolic and attracting and E_3^* is hyperbolic and a saddle. Moreover, E_3^* cannot attract any open set and therefore almost all orbits starting in $\mathring{\mathbf{R}}_+^2$ converge to either E_2^* or E_4^* .

Proof. See Appendix B. □

4. Parasite-mediated and parasite-modified competition. In this section we discuss the effects of parasitism on the competition community, system (6), with the help of the analysis of system (9) performed in Section 3. The results on approximate aggregation in [3, 20] guarantee, loosely speaking, that when a solution of the reduced system (9) with initial condition $(N^1(0), N^2(0))$ tends to a hyperbolic equilibrium (N^{1*}, N^{2*}) then, for k large enough, any positive solution of system (6) satisfying $N_S^1(0) + N_I^1(0) = N^1(0)$ and $N_S^2(0) + N_I^2(0) = N^2(0)$ tends to an equilibrium which is approximately

$$(\nu N^{1*}, (1 - \nu) N^{1*}, \nu N^{2*}, (1 - \nu) N^{2*}),$$

with ν given by (8).

We recall that the Leslie-Gower competition model presents the same four dynamic scenarios as the continuous Lotka-Volterra competition model: 1. Species 1 out-competes species 2; 2. Species 2 out-competes species 1; 3. Coexistence; 4. Exclusion of either species 1 or 2. These four scenarios are also among the options described in Theorem 3.3 for system (9). Case C_0 corresponds to 1., case D_0 to 2., case A_1 to 3. and case B_1 to 4..

The existence of a parasite affecting one of the competing species [4] makes a new scenario appear consisting in either exclusion of the uninfected species or species coexistence, i.e., parasite mediated coexistence. The cases C_2 and D_2 in Theorem 3.3 also exhibit this dichotomy between exclusion of one of the species and coexistence depending on initial conditions. The remaining two cases in Theorem 3.3, A_3 and B_3 , are specific consequences of the existence of a parasite shared by two competing species. They add two new dynamic scenarios due to the existence of three positive equilibria. In case A_3 , two of them are asymptotically stable whereas the intermediate one is a saddle, and so for most initial conditions the long term output of competition is one of those two different levels of stable coexistence. Finally, in case B_3 , it is the intermediate equilibrium that is asymptotically stable together with the two exclusion equilibria. We note that in this latter case all three possibilities of exclusion can be attained. It suffices to start dynamics in the corresponding basin of attraction, see Figure 2, to get species 2 excluded ($B(E_1^*)$), to get species 1 excluded ($B(E_2^*)$) or to obtain coexistence ($B(E_4^*)$).

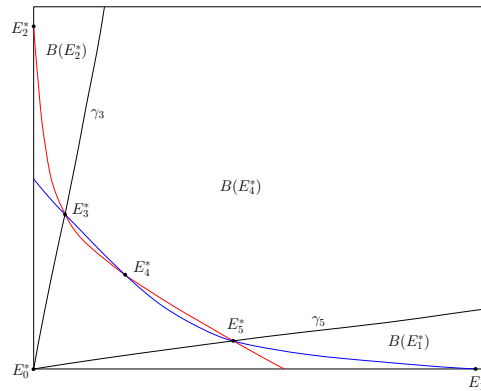


FIGURE 2. Basins of attraction $B(E_1^*)$, $B(E_2^*)$ and $B(E_4^*)$ of equilibria E_1^* , E_2^* and E_4^* and separatrix curves γ_3 and γ_5 for system (9) for parameters values: $\nu = 0.5$, $b_S^1 = 13$, $b_I^1 = 3.6$, $b_S^2 = 3.4$, $b_I^2 = 8$, $c_{SS}^{11} = c_{SI}^{11} = 0.9$, $c_{IS}^{11} = c_{II}^{11} = 0.1$, $c_{SS}^{12} = c_{SI}^{12} = 1.1$, $c_{IS}^{12} = c_{II}^{12} = 5$, $c_{SS}^{21} = c_{SI}^{21} = 6$, $c_{IS}^{21} = c_{II}^{21} = 0.3$, $c_{SS}^{22} = c_{SI}^{22} = 0.2$, $c_{IS}^{22} = c_{II}^{22} = 0.8$.

The effects of parasite on competition are classified [14] into parasite-mediated competition and parasite-modified competition. The first one refers to parasites influencing the competitive relationship by altering host densities through changes in either parasite-induced mortality or fecundity. On the other hand, the term parasite-modified competition is used for the case of parasites altering the competitive abilities of individuals of both species.

To illustrate the parasite-mediated competition we assume that parasites do not affect competitive abilities. Competition coefficients do not depend on individuals

being infected or uninfected. To be precise, we consider in system (6) four different competition coefficients just depending on the species involved: c^{11} , c^{12} , c^{21} and c^{22} . The sixteen competition coefficients appearing in (6) satisfy:

$$c_{SS}^{ij} = c_{SI}^{ij} = c_{IS}^{ij} = c_{II}^{ij} = c^{ij}, \text{ for } i, j \in \{1, 2\}.$$

Concerning the growth rates we generally assume that they are reduced by parasites:

$$b_I^i < b_S^i, \text{ for } i \in \{1, 2\}.$$

The competition model without parasites has the following Leslie-Gower form (1):

$$N_S^1(t+1) = \frac{b_S^1 N_S^1(t)}{1 + c^{11} N_S^1(t) + c^{12} N_S^2(t)}, \quad N_S^2(t+1) = \frac{b_S^2 N_S^2(t)}{1 + c^{21} N_S^1(t) + c^{22} N_S^2(t)}. \quad (14)$$

The reduced model (9) also has a Leslie-Gower form:

$$N^1(t+1) = \frac{(\nu b_S^1 + (1 - \nu)b_I^1) N^1(t)}{1 + c^{11} N^1(t) + c^{12} N^2(t)}, \quad N^2(t+1) = \frac{(\nu b_S^2 + (1 - \nu)b_I^2) N^2(t)}{1 + c^{21} N^1(t) + c^{22} N^2(t)}, \quad (15)$$

the only change concerning the growth rates. In the uninfected community they are b_S^1 and b_S^2 and when the parasite is taken into account they become

$$b^1 := \nu b_S^1 + (1 - \nu)b_I^1 \text{ and } b^2 := \nu b_S^2 + (1 - \nu)b_I^2.$$

An immediate conclusion is that the parasite can drive extinct any of the species. Indeed, a necessary condition for the species i to get extinct by the effect of the parasite is $b^i < 1$. If this is the case, a large enough R_0 yields

$$b^i = \nu b_S^i + (1 - \nu)b_I^i = \frac{1}{R_0} b_S^i + \left(1 - \frac{1}{R_0}\right) b_I^i < 1,$$

and then Theorem 3.2 implies the long-term extinction of species i .

We next assume that, independently of the size of R_0 , the parasite cannot drive extinct any of the two species, i.e., $b_I^1, b_I^2 > 1$. The outcome of competition in the Leslie-Gower system (15) depends (see (2)) on the signs of coefficients

$$\begin{aligned} \bar{D}^1 &= \frac{\nu b_S^1 + (1 - \nu)b_I^1 - 1}{c^{11}} - \frac{\nu b_S^2 + (1 - \nu)b_I^2 - 1}{c^{21}}, \\ \bar{D}^2 &= \frac{\nu b_S^2 + (1 - \nu)b_I^2 - 1}{c^{22}} - \frac{\nu b_S^1 + (1 - \nu)b_I^1 - 1}{c^{12}}, \end{aligned}$$

that can be expressed in the following form:

$$\begin{aligned} \bar{D}^1 &= \left(1 - \frac{1}{R_0}\right) \left(\frac{b_I^1 - 1}{c^{11}} - \frac{b_I^2 - 1}{c^{21}}\right) + \frac{1}{R_0} \left(\frac{b_S^1 - 1}{c^{11}} - \frac{b_S^2 - 1}{c^{21}}\right), \\ \bar{D}^2 &= \left(1 - \frac{1}{R_0}\right) \left(\frac{b_I^2 - 1}{c^{22}} - \frac{b_I^1 - 1}{c^{12}}\right) + \frac{1}{R_0} \left(\frac{b_S^2 - 1}{c^{22}} - \frac{b_S^1 - 1}{c^{12}}\right). \end{aligned}$$

A straightforward conclusion of these expressions is that, for large enough R_0 , their signs coincide with those of parameters

$$\bar{D}_I^1 := \frac{b_I^1 - 1}{c^{11}} - \frac{b_I^2 - 1}{c^{21}}, \quad \bar{D}_I^2 := \frac{b_I^2 - 1}{c^{22}} - \frac{b_I^1 - 1}{c^{12}},$$

and are independent of those of parameters

$$\bar{D}_S^1 := \frac{b_S^1 - 1}{c^{11}} - \frac{b_S^2 - 1}{c^{21}}, \quad \bar{D}_S^2 := \frac{b_S^2 - 1}{c^{22}} - \frac{b_S^1 - 1}{c^{12}}.$$

Therefore, an endemic parasite establishing a large enough fraction of infected individuals in the population can modify any outcome of competition and yield any other. Indeed, the outcome of system (14) plays no role in the outcome of system (15), which would coincide with that of the following system

$$N^1(t+1) = \frac{b_I^1 N^1(t)}{1 + c^{11} N^1(t) + c^{12} N^2(t)}, \quad N^2(t+1) = \frac{b_I^2 N^2(t)}{1 + c^{21} N^1(t) + c^{22} N^2(t)}.$$

Let us now illustrate how parasite-modified competition can yield a rich variety of different outcomes. For that we develop a particular case of system (6). In Figure 3 we show the cases described in Theorem (3.3) that correspond to different values of parameter $\nu = 1/R_0 \in (0, 1)$ and parameter $b_S^1 \in [2, 20]$ setting the following fixed values for the rest of parameters: $b_I^1 = 2$, $b_S^2 = 4.4$, $b_I^2 = 9$, $c_{SS}^{11} = 1.3$, $c_{SI}^{11} = 0.5$, $c_{IS}^{11} = c_{II}^{11} = 0.1$, $c_{SS}^{12} = 1$, $c_{SI}^{12} = 0.05$, $c_{IS}^{12} = 8$, $c_{II}^{12} = 3$, $c_{SS}^{21} = 6$, $c_{SI}^{21} = c_{IS}^{21} = c_{II}^{21} = 0.3$, $c_{SS}^{22} = c_{SI}^{22} = 0.2$, $c_{IS}^{22} = c_{II}^{22} = 0.8$. We have chosen the parameters values so that the competitive abilities of infected individuals are less than or equal to those of uninfected individuals in the same circumstances, i.e., $c_{AI}^{ij} \leq c_{AS}^{ij}$ for $A \in \{S, I\}$ and $i, j \in \{1, 2\}$.

The corresponding reduced system (9) is

$$\begin{aligned} N^1(t+1) &= \frac{b_S^1 \nu N^1(t)}{1 + (1.3\nu + 0.5(1-\nu)) N^1(t) + (\nu + 0.05(1-\nu)) N^2(t)} \\ &\quad + \frac{2(1-\nu) N^1(t)}{1 + (0.1\nu + 0.1(1-\nu)) N^1(t) + (8\nu + 3(1-\nu)) N^2(t)}, \\ N^2(t+1) &= \frac{4.4\nu N^1(t)}{1 + (6\nu + 0.3(1-\nu)) N^1(t) + (0.2\nu + 0.2(1-\nu)) N^2(t)} \\ &\quad + \frac{9(1-\nu) N^1(t)}{1 + (0.3\nu + 0.3(1-\nu)) N^1(t) + (0.8\nu + 0.8(1-\nu)) N^2(t)}. \end{aligned} \quad (16)$$

When there is no parasite (in the limit when ν tends to 1) we find two different scenarios. If $b_S^1 \in [2, 18)$ the corresponding case is B_1 (see Figure 1 to follow the cases) that entails an exclusion situation of one of the species depending on initial conditions. For $b_S^1 > 18$ the new scenario is case C_0 in which species 1 out-competes species 2. The influence of parasites can now be followed by moving backward from ν close to 1 ($R_0 = 1$) to $\nu = 0$ ($R_0 \rightarrow \infty$) in the bifurcation diagram (Figure 3).

Low values of b_S^1 imply, as R_0 increases, moving from case B_1 , exclusion, to case D_0 in which species 2 out-competes species 1. We see that in this example the parasite favours the second species.

The intermediate values of b_S^1 yield the same beginning and end of the dynamic scenario, B_1 and D_0 , though going first through case B_3 and then case D_2 . In case B_3 , apart from the two exclusion options included in case B_1 , it appears the possibility, all three depending on initial conditions (see Figure 1), of coexistence. This is a neat example of parasite mediated coexistence. The transition from case B_3 to D_0 is done through D_2 where the option of species 1 excluding species 2 has disappeared.

High values of b_S^1 , the growth rate of non-infected individuals of species 1, entail a transition from case C_0 , species 1 out-competes species 2, to D_0 , species 2 out-competes species 1, as R_0 increases. This transition is done through case C_2 , that encompasses species 2 exclusion and coexistence, followed by case A_1 , that represent global coexistence.

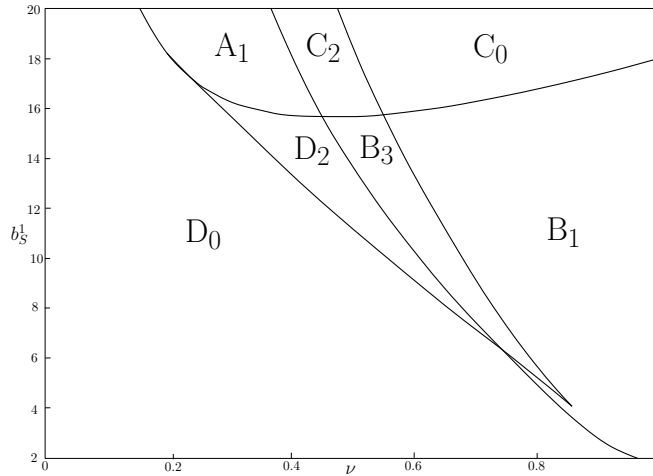


FIGURE 3. Asymptotic behaviour cases of solutions of system (9) (Th. (3.3)) for parameters values: $\nu \in (0, 1)$, $b_S^1 \in [2, 20]$, $b_I^1 = 2$, $b_S^2 = 4.4$, $b_I^2 = 9$, $c_{SS}^{11} = 1.3$, $c_{SI}^{11} = 0.5$, $c_{IS}^{11} = c_{II}^{11} = 0.1$, $c_{SS}^{12} = 1$, $c_{SI}^{12} = 0.05$, $c_{IS}^{12} = 8$, $c_{II}^{12} = 3$, $c_{SS}^{21} = 6$, $c_{SI}^{21} = c_{IS}^{21} = c_{II}^{21} = 0.3$, $c_{SS}^{22} = c_{SI}^{22} = 0.2$, $c_{IS}^{22} = c_{II}^{22} = 0.8$.

These transitions from a scenario to another one as ν decreases from one to zero can even present a more complex pattern. For example, for a value of b_S^1 around 16, the dynamic scenario goes through the following six cases in order: B_1 , C_0 , C_2 , A_1 , D_2 and D_0 . Similarly, for values of b_S^1 close to 15.7, the sequence of cases is: B_1 , B_3 , C_2 , A_1 , D_2 and D_0 .

5. Conclusion. In this work we have extended a previous eco-epidemic model [4] that filled a gap in the existent literature due to being in discrete time and having the parasite dynamics occurring on a shorter time scale than the competition interactions. In the model studied here we have introduced the three ingredients demanded by general parasitism-competition modules [14]: intraspecific host competition, interspecific competition between hosts and a parasite capable of infecting both hosts. Whereas in [4] the parasite affected only one the two competing species, the contribution of this work is analysing the effect of a shared parasite affecting the competition community.

After the general presentation of the model in Section 2, we have assumed in Section 3 homogeneous disease transmission and recovery to keep this work simple enough to be analytically tractable. In this way we have been able to apply a reduction technique that allows one to find analytic results stressing the effects of the disease on the community. In spite of this simplifying assumption, the mathematical analysis of the model reveals a number of interesting long term scenarios that were not exhibited in previous models [4]. There are two new situations in which three different positive equilibria exist. They are called, see Figure 1, cases A_3 and B_3 in Section 3.

Case A_3 is a notable example of coexistence of non-Lotka-Volterra type. Two positive equilibria out of three are asymptotically stable, whereas the third, the intermediate one, is a saddle whose stable manifold serves as separatrix curve of

the basins of attraction of the first two. The two exclusion equilibria are also saddles. Thus, we have that different positive initial conditions lead to one of the two different stable coexistence equilibria.

Case B_3 is another example of coexistence of non-Lotka-Volterra type. In this case, the intermediate equilibrium is asymptotically stable and the two other positive equilibria are saddles (see Figure 2). The two exclusion equilibria are asymptotically stable. The stable manifolds of the saddles are the boundary of the three basins of attraction included in the positive quadrant. Now different positive initial conditions lead to one of the three exclusion possibilities: species 1 is the superior competitor; species 2 is the superior competitor; species coexist. In [17] it is described a competition experiment in which varying the initial conditions two *Tribolium* species could coexist though in most cases exclusion was the outcome. The attempt to interpret these results in terms of the classical Lotka-Volterra scenario, or rather of its discrete counterpart, the Leslie-Gower model, failed. These results were reviewed in [12]. An explanation of both species exclusion and species coexistence was provided through the discrete non-linear stage-structured model for flour beetles [7] extended to include two interacting species [10]. The case B_3 of the simple planar system (9) offers an alternative explanation in a non-structured setting in terms of the simplified action of a shared parasite.

The results in Section 4 show that parasites can reverse the effects of direct competition between the hosts. System (14), competition without parasite, can yield one of the species as superior competitor whereas the outcome of system (15), competition with parasite only affecting growing terms, can be the exclusion of this same species provided that the R_0 of the parasite is large enough. In the same direction, it is illustrated in the example corresponding to system (16) that the species 2, favoured by the parasite, can overcome the growing advantage of the species 1 as the parasite R_0 increases. From a community ecology perspective, these results confirm the extended opinion [14] that parasites can act as keystone species. A preferential application of this fact is to biological control. The insights gained with the analysis of this kind of models can lead to the fruitful use of parasites in biological control. A more detailed analysis of the model in cases relevant to specific situations and data sets, could be a sound perspective of this work.

Appendix

Appendix A. Disease dynamics in the case $\beta_{ij} = \beta$ and $\gamma_i = \gamma$ for $i, j = 1, 2$, and reduction results. The disease dynamics keeps constant the total population of both species

$$N^1 := F_S^1(\mathbf{N}) + F_I^1(\mathbf{N}) = N_S^1 + N_I^1, \quad N^2 := F_S^2(\mathbf{N}) + F_I^2(\mathbf{N}) = N_S^2 + N_I^2.$$

Thus

$$N_S^1 = N^1 - N_I^1 \quad \text{and} \quad N_S^2 = N^2 - N_I^2,$$

and the disease dynamics, for fixed N^1 and N^2 , is completely defined in terms of variables N_I^1 and N_I^2 . The maps updating the values of these variables in the particular case of equal transmission and recovery parameters are the following :

$$\begin{aligned} f(N_I^1, N_I^2) &:= F_I^1(N^1 - N_I^1, N_I^1, N^2 - N_I^2, N_I^2) \\ &= (1 - \gamma)N_I^1 + \frac{\beta(N^1 - N_I^1)(N_I^1 + N_I^2)}{N^1 + N^2} \end{aligned}$$

$$g(N_I^1, N_I^2) := F_I^2(N^1 - N_I^1, N_I^1, N^2 - N_I^2, N_I^2) \\ = (1 - \gamma)N_I^2 + \frac{\beta(N^2 - N_I^2)(N_I^1 + N_I^2)}{N^1 + N^2}.$$

As we noted when introducing the disease dynamics, we must impose some conditions on parameters β and γ so that $\mathbf{F}(\Omega) \subset \Omega$ (5). In the first place we impose the condition $\mathbf{F}(\mathbb{R}_+^4) \subset \mathbb{R}_+^4$. This is equivalent to making functions f and g satisfy $f([0, N^1] \times [0, N^2]) \subset [0, N^1]$ and $g([0, N^1] \times [0, N^2]) \subset [0, N^2]$, respectively, for any nonnegative N^1 and N^2 :

- A first necessary condition is that $f(N^1, N_I^2) \geq 0$, i.e., $(1 - \gamma)N^1 \geq 0$, which implies that $\gamma \in (0, 1]$.
- We also need that $f(0, N^2) \leq N^1$, i.e., $\frac{\beta N^1 N^2}{N^1 + N^2} \leq N^1$ for all $N^1, N^2 \geq 0$. Since the limit of the second term when N^2 tends to infinity is βN^1 , we also assume that $\beta \in (0, 1]$.

These two necessary conditions turn out to be also sufficient for $\mathbf{F}(\mathbb{R}_+^4) \subset \mathbb{R}_+^4$. Indeed, let

$$\gamma, \beta \in (0, 1] \tag{17}$$

and $(N_I^1, N_I^2) \in [0, N^1] \times [0, N^2]$. Then

$$f(N_I^1, N_I^2) = (1 - \gamma)N_I^1 + \frac{\beta}{N^1 + N^2} (N^1 - N_I^1) (N_I^1 + N_I^2) \geq 0,$$

and

$$f(N_I^1, N_I^2) \leq N_I^1 + \beta(N^1 - N_I^1) \leq N_I^1 + (N^1 - N_I^1) = N^1,$$

as we wanted. An analogous reasoning proves that also g satisfies the required conditions.

Now, given the above conditions, it is immediate to check that $\mathbf{F}(\Omega) \subset \Omega$.

The asymptotic behaviour of the solutions of systems (6) and (9) can be related by making use of results in [20] regarding approximate reduction techniques. The condition for the results to hold is that $\mathbf{F}^{(k)}$ converges to a map $\bar{\mathbf{F}}$ uniformly on compact sets of Ω and the same happens with their differentials, i.e., $\lim_{k \rightarrow \infty} D\mathbf{F}^{(k)}(N_S, N_I) = D\bar{\mathbf{F}}(N_S, N_I)$ uniformly on compact sets.

To find map $\bar{\mathbf{F}}$ we study the long term behaviour of the 2-dimensional system describing the dynamics of infected individuals of both species, N_I^1 and N_I^2 :

$$N_I^1(t + 1) = f(N_I^1(t), N_I^2(t)), \quad N_I^2(t + 1) = g(N_I^1(t), N_I^2(t))$$

Its equilibrium points are the disease free equilibrium $E_0 = (0, 0)$ and, if $\beta > \gamma$, a positive equilibrium representing the disease endemicity

$$E_+ = \left((1 - \frac{\gamma}{\beta})N^1, (1 - \frac{\gamma}{\beta})N^2 \right)$$

that we could also express in terms of ν (8), or R_0 ,

$$E_+ = ((1 - \nu)N^1, (1 - \nu)N^2) = \left((1 - \frac{1}{R_0})N^1, (1 - \frac{1}{R_0})N^2 \right).$$

By linearization it is easy to prove that E_0 is A.S. if $\beta < \gamma$ and E_+ is A.S. if $\beta > \gamma$. Henceforth we assume Hypothesis 1: $0 < \gamma < \beta \leq 1$.

Now, we define our candidate to be $\bar{\mathbf{F}}$ as

$$\bar{\mathbf{F}}(N_S^1, N_I^1, N_S^2, N_I^2) = (\nu(N_S^1 + N_I^1), (1 - \nu)(N_S^1 + N_I^1), \nu(N_S^2 + N_I^2), (1 - \nu)(N_S^2 + N_I^2)).$$

We restrict our attention to the case in which there are infected individuals in the initial population, i.e., we work in the set Ω (5) which is positively invariant for \mathbf{F} .

Next we prove the required convergence results of $\mathbf{F}^{(k)}$ to $\bar{\mathbf{F}}$.

Proposition 2. *Let \mathbf{F} be the map defined in (4) with $\beta_{ij} = \beta$ and $\gamma_i = \gamma$ for $i, j = 1, 2$, and let Hypothesis 1 hold. Then the following two limits exist uniformly on compact sets of Ω (5):*

1. $\lim_{k \rightarrow \infty} \mathbf{F}^{(k)}(N_S^1, N_I^1, N_S^2, N_I^2) = \bar{\mathbf{F}}(N_S^1, N_I^1, N_S^2, N_I^2)$.
2. $\lim_{k \rightarrow \infty} D\mathbf{F}^{(k)}(N_S^1, N_I^1, N_S^2, N_I^2) = D\bar{\mathbf{F}}(N_S^1, N_I^1, N_S^2, N_I^2)$.

Proof. In order to prove the result we define the sets

$$V_i := \{(N_S^1, N_I^1, N_S^2, N_I^2) \in \Omega : N_S^i + N_I^i = 0\}, \quad i = 1, 2,$$

$$\hat{\Omega} := \{(N_S^1, N_I^1, N_S^2, N_I^2) \in \Omega : N_S^1 + N_I^1 > 0, N_S^2 + N_I^2 > 0\}.$$

To carry out the proof we will show that $\lim_{k \rightarrow \infty} \mathbf{F}^{(k)} = \bar{\mathbf{F}}$ and that $\lim_{k \rightarrow \infty} D\mathbf{F}^{(k)} = D\bar{\mathbf{F}}$ uniformly on compact sets of V_1 (*), on compact sets of V_2 (***) and on compact sets of $\hat{\Omega}$.

On V_1 (resp. V_2) map \mathbf{F} has the form $\mathbf{F}(\mathbf{N}) = (0, 0, \hat{\mathbf{F}}(N_S^2, N_I^2))$ (resp. $\mathbf{F}(\mathbf{N}) = (\hat{\mathbf{F}}(N_S^1, N_I^1), 0, 0)$) where

$$\hat{\mathbf{F}}(x_1, x_2) = \left(x_1 - \beta \frac{x_1 x_2}{x_1 + x_2} + \gamma x_2, x_2 + \beta \frac{x_1 x_2}{x_1 + x_2} - \gamma x_2 \right)$$

and therefore in order to prove (*) and (***) it suffices to show that $\lim_{k \rightarrow \infty} \hat{\mathbf{F}}^{(k)} = \bar{\hat{\mathbf{F}}}$ and that $\lim_{k \rightarrow \infty} D\hat{\mathbf{F}}^{(k)} = D\bar{\hat{\mathbf{F}}}$ on compact sets of $\{(x_1, x_2) : x_2 > 0, x_1 + x_2 > 0\}$, where

$$\bar{\hat{\mathbf{F}}}(x_1, x_2) = (\nu(x_1 + x_2), (1 - \nu)(x_1 + x_2))$$

This result was proved in Lemma A.1 of [5].

Now we turn our attention to the uniform convergence in compact sets of $\hat{\Omega}$. We begin by making a change of variables and expressing the map \mathbf{F} in terms of new variables: $x := N_I^1 + N_I^2$ the total number of infected individuals, $y := \frac{N_I^1}{N_S^1 + N_I^1} - \frac{N_I^2}{N_S^2 + N_I^2}$ the difference between the fraction of infected individuals in the first and the second species, $z := N^1 = N_S^1 + N_I^1$ the total population of the first species, and $w := N^2 = N_S^2 + N_I^2$ the total population of the second species.

Let G denote the map associated to this change of variables:

$$(x, y, z, w) = G(N_S^1, N_I^1, N_S^2, N_I^2) := \left(N_I^1 + N_I^2, \frac{N_I^1}{N_S^1 + N_I^1} - \frac{N_I^2}{N_S^2 + N_I^2}, N_S^1 + N_I^1, N_S^2 + N_I^2 \right),$$

and let G^{-1} be its inverse map.

Map \mathbf{F} in the new variables is easily found to be

$$\mathbf{H}(x, y, z, w) := G(\mathbf{F}(G^{-1}(x, y, z, w))) = \left(\left(1 + \beta - \gamma - \frac{\beta x}{z + w}\right)x, \left(1 - \gamma - \frac{\beta x}{z + w}\right)y, z, w \right).$$

Therefore we need to prove the uniform convergence on compact sets of $G(\hat{\Omega})$ of its iterates $\mathbf{H}^{(k)}$ to map $\bar{\mathbf{F}}$ expressed in terms of the new variables, that we denote $\bar{\mathbf{H}}$:

$$\bar{\mathbf{H}}(x, y, z, w) := G(\bar{\mathbf{F}}(G^{-1}(x, y, z, w))) = ((1 - \nu)(z + w), 0, z, w).$$

The uniform convergence of the differentials of $\mathbf{H}^{(k)}$ to the differential of $\bar{\mathbf{H}}$ should also be proved.

With the help of the function

$$\phi(x) := (1 + \beta - \gamma - \beta x)x,$$

we can express \mathbf{H} in the following form

$$\mathbf{H}(x, y, z, w) = \left((z + w)\phi\left(\frac{x}{z + w}\right), (1 - \gamma - \frac{\beta x}{z + w})y, z, w \right),$$

and its k -th iterate as

$$\mathbf{H}^{(k)}(x, y, z, w) = \left((z + w)\phi^{(k)}\left(\frac{x}{z + w}\right), y \prod_{i=0}^{k-1} \left(1 - \gamma - \beta\phi^{(i)}\left(\frac{x}{z + w}\right)\right), z, w \right).$$

Note that in $G(\hat{\Omega})$ we have $0 < x \leq z + w$. Let $K \subset G(\Omega)$ be a compact set. Then there exist numbers

$$M_K = \max_K(z + w), \quad a_K = \min_K\left(\frac{x}{z + w}\right) > 0 \quad \text{and} \quad b_K = \left(\max_K \frac{x}{z + w}\right) \leq 1. \quad (18)$$

Function ϕ satisfies that $\phi((0, 1]) \subset (0, 1]$ and so

$$\left|1 - \gamma - \beta\phi^{(i)}\left(\frac{x}{z + w}\right)\right| \leq \max\{1 - \gamma, |1 - \gamma - \beta|\} =: c < 1, \quad (19)$$

where in the last inequality we have used Hypothesis 1. Then we have

$$\begin{aligned} & \max_K \|\mathbf{H}^k(x, y, z, w) - \bar{\mathbf{H}}(x, y, z, w)\|_1 = \\ & \max_K \left(\left| (z + w)\left(\phi^{(k)}\left(\frac{x}{z + w}\right) - (1 - \nu)\right) \right| + |y| \prod_{i=0}^{k-1} \left| 1 - \gamma - \beta\phi^{(i)}\left(\frac{x}{z + w}\right) \right| \right) \leq \\ & M_K \max_K \left(\phi^{(k)}\left(\frac{x}{z + w}\right) - (1 - \nu) \right) + c^k. \end{aligned}$$

where we have used that one has $|y| \leq 1$ in $G(\hat{\Omega})$. Now it is straightforward to see that the solutions of the scalar difference equation $x(t + 1) = \phi(x(t))$ with initial conditions $x(0) \in [a_K, b_K] \subset (0, 1]$ converge monotonically and, therefore, uniformly on $[a_K, b_K]$, to $1 - \nu$. Therefore we have proved the uniform convergence of $\mathbf{H}^{(k)}$ to $\bar{\mathbf{H}}$ on compact sets of $G(\hat{\Omega})$.

To prove the uniform convergence of the differential of $\mathbf{H}^{(k)}$ we start by expressing $D\mathbf{H}^{(k)}$ in terms of the derivatives of ϕ^k :

$$\begin{aligned} & D\mathbf{H}^{(k)}(x, y, z, w) \\ & = \begin{pmatrix} (\phi^{(k)})'\left(\frac{x}{z + w}\right) & 0 & d_{13} & d_{14} \\ d_{21} & \prod_{i=0}^{k-1} \left(1 - \gamma - \beta\phi^{(i)}\left(\frac{x}{z + w}\right)\right) & d_{23} & d_{24} \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}, \quad (20) \end{aligned}$$

with

$$d_{13} = d_{14} = \phi^{(k)}\left(\frac{x}{z + w}\right) - \frac{x}{z + w}(\phi^{(k)})'\left(\frac{x}{z + w}\right),$$

$$d_{21} = y \sum_{j=0}^{k-1} \left(-\frac{\beta}{z+w} (\phi^{(j)})' \left(\frac{x}{z+w} \right) \prod_{i=0, i \neq j}^{k-1} \left(1 - \gamma - \beta \phi^{(i)} \left(\frac{x}{z+w} \right) \right) \right),$$

and

$$d_{23} = d_{24} = y \sum_{j=0}^{k-1} \left(\frac{\beta x}{(z+w)^2} (\phi^{(j)})' \left(\frac{x}{z+w} \right) \prod_{i=0, i \neq j}^{k-1} \left(1 - \gamma - \beta \phi^{(i)} \left(\frac{x}{z+w} \right) \right) \right).$$

Now we want to show that the following limit is uniform on compact sets of $(0, 1]$

$$\lim_{k \rightarrow \infty} (\phi^k)'(x) = 0.$$

Since $|\phi'(1-\nu)| < 1$, there exist $\alpha < 1$ and a neighbourhood $I \subset (0, 1]$ of $1-\nu$ such that for every $x \in I$ we have $|\phi'(x)| < \alpha$. The uniform convergence to $1-\nu$ of the solutions of the scalar difference equation $x(t+1) = \phi(x(t))$ with initial conditions $x_0 \in (0, 1]$ together with the chain rule to obtain $(\phi^k)'(x) = \prod_{i=0}^{k-1} \phi'(\phi^{(i)}(x))$ yield the result.

This last result, together with (18), (19) and (20) straightforwardly imply the uniform convergence on compact sets of $D\mathbf{H}^{(k)}(x, y, z, w)$ to

$$D\bar{\mathbf{H}}(x, y, z, w) = \begin{pmatrix} 0 & 0 & 1-\nu & 1-\nu \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}.$$

□

The next theorem relates the asymptotic behavior of systems (6) and (9) for large enough values of parameter k when the hypotheses of Proposition 2 hold.

Theorem A.1. *Let the hypotheses of Proposition 2 hold. Let (N^{1*}, N^{2*}) be a hyperbolic equilibrium point of (9). Then there exists $k_0 \in \mathbb{N}$ such that for each $k \geq k_0$ there exists a hyperbolic equilibrium point $(N_{S,k}^{1*}, N_{I,k}^{1*}, N_{S,k}^{2*}, N_{I,k}^{2*})$ of (6) satisfying*

$$\lim_{k \rightarrow \infty} (N_{S,k}^{1*}, N_{I,k}^{1*}, N_{S,k}^{2*}, N_{I,k}^{2*}) = (\nu N^{1*}, (1-\nu)N^{1*}, \nu N^{2*}, (1-\nu)N^{2*}).$$

Moreover, let $k \geq k_0$ be fixed:

1. If (N^{1*}, N^{2*}) is asymptotically stable (resp. unstable) then $(N_{S,k}^{1*}, N_{I,k}^{1*}, N_{S,k}^{2*}, N_{I,k}^{2*})$ is asymptotically stable (resp. unstable).
2. In the case of (N^{1*}, N^{2*}) being asymptotically stable, if $(N_S^1(0) + N_I^1(0), N_S^2(0) + N_I^2(0))$ is in the basin of attraction of (N^{1*}, N^{2*}) , then $(N_S^1(0), N_I^1(0), N_S^2(0), N_I^2(0))$ is in the basin of attraction of $(N_{S,k}^{1*}, N_{I,k}^{1*}, N_{S,k}^{2*}, N_{I,k}^{2*})$.

Analogous results hold for periodic solutions.

Proof. It is a direct consequence of the results in [20] and Proposition 2. □

Appendix B. Dynamics of the reduced system. The proof of Lemma 3.1, Proposition 1 and Theorems 3.2 and 3.3 follows reasonings very similar to those of Lemma 2, Propositions 3 and 5, and Theorems 4 and 6 in [4]. In that reference, the system under analysis (Eq. (20) in that reference) is a particular case of system (10) corresponding to making $r_I^2 = 0$. As a consequence, here both isoclines are hyperbolas whereas in [4] Γ_1 is a hyperbola and Γ_2 is a straight line. Therefore, in the proofs below we concentrate on the differences with [4] and refer the reader to that reference for those reasonings that are identical.

Proof of Lemma 3.1. This is essentially Lemma 2 in [4] except for the fact that here we apply the reasonings therein to both S_1 and S_2 and not only to S_1 . We also need to give conditions for the isoclines S_i to be degenerate which are not studied in that reference. From the classical theory of conics one has that the two discriminants for S_i are

$$\begin{aligned} \delta_i &:= \det \begin{pmatrix} c_{S_1}^i c_{I_1}^i & \frac{1}{2} (c_{S_1}^i c_{I_2}^i + c_{S_2}^i c_{I_1}^i) \\ \frac{1}{2} (c_{S_1}^i c_{I_2}^i + c_{S_2}^i c_{I_1}^i) & c_{S_2}^i c_{I_2}^i \end{pmatrix} = -\frac{1}{4} (c_{S_1}^i c_{I_2}^i - c_{S_2}^i c_{I_1}^i)^2 \leq 0 \\ \Delta_i &:= \det \begin{pmatrix} c_{S_1}^i c_{I_1}^i & \frac{c_{S_1}^i c_{I_2}^i + c_{S_2}^i c_{I_1}^i}{2} & -\frac{c_{S_1}^i (r_I^i - 1) + c_{I_1}^i (r_S^i - 1)}{2} \\ \frac{c_{S_1}^i c_{I_2}^i + c_{S_2}^i c_{I_1}^i}{2} & c_{S_2}^i c_{I_2}^i & -\frac{c_{S_2}^i (r_I^i - 1) + c_{I_2}^i (r_S^i - 1)}{2} \\ -\frac{c_{S_1}^i (r_I^i - 1) + c_{I_1}^i (r_S^i - 1)}{2} & -\frac{c_{S_2}^i (r_I^i - 1) + c_{I_2}^i (r_S^i - 1)}{2} & 1 - r_S^i - r_I^i \end{pmatrix} \\ &= \frac{1}{4} r_S^i r_I^i (c_{S_1}^i c_{I_2}^i - c_{S_2}^i c_{I_1}^i)^2 \geq 0 \end{aligned}$$

It is well known that hyperbola S_i is degenerate if and only if $\delta_i = 0$, i.e., if and only if $c_{S_1}^i c_{I_2}^i = c_{S_2}^i c_{I_1}^i$ and, in that case, $\Delta_i = 0$ and therefore it corresponds to two parallel lines.

Proof of Proposition 1. The proof of (a) is straightforward. Regarding (b), it is immediate to check that, for $i, j \in \{1, 2\}$, $i \neq j$, the map $H_i(x_1, x_2)$ is strictly increasing as a function of x_i and strictly decreasing as a function of x_j . Therefore it follows trivially that if $x, x' \in \mathbf{R}_+^2$ are distinct points with $x \leq_K x'$ then $H(x) <_K H(x')$.

(c) Let us consider map $H : \bar{S} \rightarrow \bar{S}$, where S is defined in (12):

(i) It is immediate to check that \bar{S} contains order intervals [21, p. 345] and is \leq_K -convex [21, p. 339].

(ii) In order to show that $\det DH(x_1, x_2) > 0$ for $(x_1, x_2) \in \bar{S}$, where D denotes differential, we have made use of Matlab Symbolic Math Toolbox, and obtained that the resulting expression is the product of a number of factors all of which are strictly positive in \bar{S} .

(iii) Direct calculations prove that $DH(x_1, x_2)$ is K -positive in \bar{S} [21, p. 338], i.e., $\frac{\partial H_1}{\partial x_1} > 0$, $\frac{\partial H_2}{\partial x_2} > 0$, $\frac{\partial H_1}{\partial x_2} \leq 0$ and $\frac{\partial H_2}{\partial x_1} \leq 0$ en \bar{S} .

(iv) Finally, it is immediate to check that \bar{S} is compact and connected and that $H^{-1}(0, 0)$ is a single point.

Using the properties (i) through (iv) above, [21, Lemma 4.3] guarantees that H satisfies property (O+) [21, p. 343]. Now, using (a) and (b) and property (O+) we can apply Theorem 4.2 in [21] so that all orbits in \mathbf{R}_+^2 are eventually componentwise monotone and converge to an equilibrium.

Proof of Theorem 3.2. It corresponds to Proposition 5 in [4]. The reasonings to carry out its proof are literally identical to the ones used in that reference.

Proof of Theorem 3.3. Part 1 of this result corresponds to Proposition 5 in [4] and the reasonings therein can be translated literally to this case. Part 2 is immediate taking into account that the positive equilibria are the intersections of Γ_1 and Γ_2 and both are the graphs of strictly decreasing functions of x_1 .

Let us consider part 3, in which the eight different cases described in (13) are studied. To start with, we point out that Lemmas A.1. and A.2. in [4] translate directly to our setting. Indeed, the first one hinges in the properties proved in Proposition 1, whereas the second is a consequence of the facts that $\frac{\partial H_1}{\partial x_2} < 0$ and $\frac{\partial H_1}{\partial x_1} < 0$ in $\mathring{\mathbf{R}}_+^2$ and that $\det DH(x_1, x_2) > 0$ for $(x_1, x_2) \in \bar{S}$. Using Lemma A.2. and the fact that isoclines are not tangent at equilibria, it follows that all the positive equilibria are hyperbolic.

Now, the statement regarding our scenarios \mathbf{A}_1 , \mathbf{B}_1 , \mathbf{C}_0 , \mathbf{C}_2 and \mathbf{D}_0 , correspond, respectively, to the statements for cases \mathbf{A} , \mathbf{B} , \mathbf{C}_{1a} , \mathbf{C}_{1b} and \mathbf{C}_2 in Theorem 6 in [4], the only difference being that in that reference isocline Γ_2 is a straight line instead of a hyperbola. This does not alter in any way the reasonings carried out therein and so they translate literally to our setting.

Regarding our case \mathbf{D}_2 , it is the reciprocal of case \mathbf{C}_2 interchanging x_1 with x_2 , E_1^* with E_2^* , and E_3^* with E_4^* , and so the proof for this case follows from the one corresponding to \mathbf{C}_2 .

Let us turn prove the statements regarding the only remaining cases, \mathbf{A}_3 and \mathbf{B}_3 , in which there are three positive equilibria. Let us consider the six open connected regions in which Γ_1 and Γ_2 divide \mathbb{R}_+^2 in cases (see Figure 1) \mathbf{A}_3 and \mathbf{B}_3 . Let us define U_0 as the region whose adherence contains the origin, U_∞ as the only unbounded region, U_{23} as the region limited by Γ_1 and Γ_2 whose adherence contains equilibria E_2^* and E_{3j}^* and similarly for U_{34} , U_{45} and U_{51} . We have then that $\mathbb{R}_+^2 = U_0 \cup U_\infty \cup \bar{U}_{23} \cup \bar{U}_{34} \cup \bar{U}_{45} \cup \bar{U}_{51}$. We can divide \mathbb{R}_+^2 into the four disjoint sets

$$\begin{aligned} W &:= \{x \in \mathbf{R}_+^2 : H(x) \leq_K x\}, \quad W' := \{x \in \mathbf{R}_+^2 : H(x) \geq_K x\} \\ T &:= \{x \in \mathbf{R}_+^2 : H(x) < x\}, \quad T' := \{x \in \mathbf{R}_+^2 : H(x) > x\}. \end{aligned}$$

Let us consider case \mathbf{A}_3 . Using the monotonicity of the two components of map H (see Figure 1), we have that in this case $W = \bar{U}_{34} \cup \bar{U}_{51}$, $W' = \bar{U}_{23} \cup \bar{U}_{45}$, $T = U_\infty$ and $T' = U_0$. Using Lemma A.1. in [4] it follows that $\bar{U}_{34} \cup \bar{U}_{51}$ and $\bar{U}_{23} \cup \bar{U}_{45}$ are forward invariant for H , that orbits starting in U_0 cannot enter U_∞ and that orbits starting in U_∞ cannot enter U_0 . Since $\bar{U}_{23} \cup \bar{U}_{45}$ is forward invariant, $E_3^* \in \bar{U}_{23}$ is a fixed point and \bar{U}_{23} is connected, $H(\bar{U}_{23})$ cannot intersect \bar{U}_{45} and therefore \bar{U}_{23} must be forward invariant. A similar reasoning proves that \bar{U}_{45} , \bar{U}_{34} and \bar{U}_{51} are forward invariant.

By the monotonicity of H in the different regions we have that orbits starting in U_{34} , U_{45} , U_{23} and U_{51} respectively, cannot converge to E_4^* , E_4^* , E_2^* and E_1^* , respectively and using that each orbit must converge to a fixed point we have that they must converge, respectively, to E_3^* , E_5^* , E_3^* and E_5^* . In particular E_4^* is unstable. Let us now show that E_3^* is attracting. Let $\varepsilon > 0$ be small enough, let $B(E_3^*, \varepsilon)$ be the open ball with center E_3^* and radius ε and let $x \in B(E_3^*, \varepsilon)$, so that x must belong to one and only one of the sets \bar{U}_{23} , \bar{U}_{34} , U_0 and U_∞ . Let us consider in turn the three following possibilities: (i) $x \in \bar{U}_{23} \cup \bar{U}_{34}$, (ii) $x \in U_0$ and (iii) $x \in U_\infty$.

In scenario (i) we have already shown that the corresponding orbit converges to E_3^* . (ii) We have proved that the corresponding orbit $H^{(n)}(x)$ cannot enter U_∞ and so either $H^{(n)}(x)$ enters $\bar{U}_{23} \cup \bar{U}_{34}$ for a certain n , and in that case we already know that the orbit must converge to E_3^* or, on the contrary, $H^{(n)}(x)$ remains in U_0 for all $n \geq 0$. In this latter case the fact that x is ε -close to E_3^* and the monotonicity in this region precludes convergence of the orbit to E_1^* , E_2^* , E_3^* or to E_5^* , and so it must necessarily converge to E_3^* . (iii) In this case we can carry out a reasoning completely analogous to that of (ii). As a conclusion we have that E_3^* attracts the open ball $B(E_3^*, \varepsilon)$ and so it is attracting. The proof that E_5^* is attracting is carried out similarly. In order to show that E_4^* is a saddle, because it attracts points different from itself and cannot attract any open set, we can use the same reasonings carried out for E_4^* in case \mathbf{C}_{1b} of Theorem 6 in [4]. Finally, the monotonicity of H in the neighbourhood of E_1^* and of E_2^* precludes the convergence of any orbit to these two points and, therefore, except for the orbits that converge to the saddle E_4^* , the rest of the orbits in \mathbf{R}_+^2 converge to E_3^* or to E_5^* .

Regarding the statements for case \mathbf{B}_3 , they are proved analogously to those of case \mathbf{A}_3 .

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