Competitive exclusion and coexistence in a model with age-structured resource

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Abstract

In this paper, we introduce and analyse a model in which a shared, age-structured resource is exploited by two competing populations through age-dependent interaction kernels. It provides a general framework for studying resource-mediated competition in epidemiology, immunology and ecology.

We use integrated semigroups theory to establish the well-posedness of the model and its fundamental properties, including positivity and the existence of a global attractor. Then, by means of Lyapunov functionals, persistence results and generalised LaSalle principle, we fully characterize the asymptotic dynamics in terms of the competitors's basic reproduction numbers and invasive fitnesses.

Our results demonstrate that in addition to the classical competitive exclusion, the system can exhibit globally asymptotically stable coexistence, an outcome allowed by a mechanism of age-mediated niche partitioning.

Keywords: Global asymptotic stability; Lyapunov functionals; Integrated semigroups theory; Niche partitioning; Competitive exclusion; Coexistence.

1 Introduction

Understanding the outcome of competition for a shared resource is a recurrent question in biological fields such as ecology, epidemiology or immunology. In this context, the competitive exclusion principle, or Gause's principle, states that only the strongest competitor, typically characterized by the largest basic reproduction number, survives while all others go extinct.

This principle faces limitations, as coexistence is frequently observed in real biological systems and is often explained by niche partitioning mechanisms, whereby competitors adopt different strategies to exploit the resource. These include spatial or temporal separation of predation, or specialization on distinct subsets of the resource [5, 14, 21]. These observations have motivated the development of numerous mathematical models to identify which mechanisms may relax competitive exclusion. Many of them are extensions of the Kermack–McKendrick epidemiological model or of the competitive Lotka-Volterra equations [22, Sections 3.5 and 10] incorporating various sources of variability such as interaction terms that do not obey the law of mass action [3–5], spatial heterogeneity through diffusion and/or advection [1, 26, 30], time delay [8] or an effect of seasonality [2, 17].

In this paper, we investigate the effect of age-structure of the resource population, motivated by the idea that specialization of competitors for different ages of the resource might allow for competitors coexistence [6]. We consider the following model, in which two populations, y_1 and y_2, compete for the same age-structured resource x:

$$\begin{cases} \partial_t x(t,a) + \partial_a x(t,a) &= -\mu_x(a)x(t,a) - x(t,a)(\beta_1(a)y_1(t) + \beta_2(a)y_2(t)), \\ y_1'(t) &= y_1(t)c_1\int_0^\infty \beta_1(a)x(t,a)da - \mu_1 y_1(t), \\ y_2'(t) &= y_2(t)c_2\int_0^\infty \beta_2(a)x(t,a)da - \mu_2 y_2(t), \\ x(t,0) &= \Lambda, \\ (x(0,\cdot), y_1(0), y_2(0)) &= (x_0, y_{1,0}, y_{2,0}) \in L^1(\mathbb{R}_+,\mathbb{R}_+)\times\mathbb{R}_+^2. \end{cases} \tag{1}$$

Death rates are described by the parameters μ_i. The functions β_i are age-dependent interaction kernels, allowing each competitive population to exploit different segments of the structured resource. This heterogeneity captures biological situations where the resources differ in accessibility and suitability across their life cycle. In ecological systems, this corresponds for instance to predators specializing on juvenile versus adult prey, or plants versus fruits; in epidemiology or immunology, it reflects the spread of two strains among susceptible individuals or immune cells, where the infection probability is age or stage dependent.

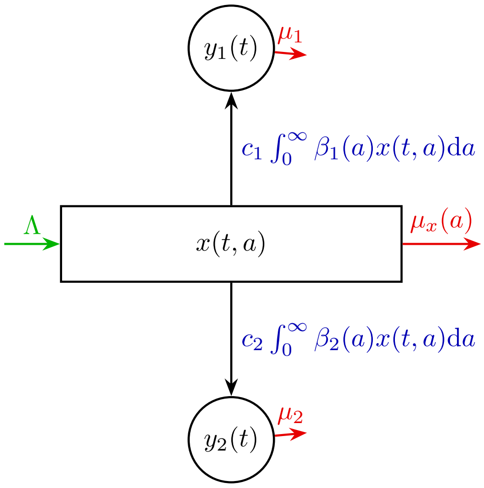

Figure 1: Graphical representation of model (1)

Unlike epidemiological models, where interactions induce a direct transfer from the susceptible to the infected class, ecological predation involves losses that are not fully converted into predator growth. This is embedded in the conversion factors c_1 and c_2, as in the Lotka-Volterra equations, which are set to 1 in epidemiological context.

An assumption of the model is that the influx of resources of age 0 is constant, *i.e.* $x(t,0) = \Lambda$, rather than linear in the density of resources. This assumption is standard in mathematical immunology and epidemiology [18]. While less common in ecology, it is relevant in situations involving allochthonous resources [12, 23], *i.e.* resources that originate from a place other than where they will live, such as algae dragged by a river to the shore, seeds spread by the wind or by animals. It also makes sense when the resource is a product of human activity, such as breeding, plantation, or industrial byproduct. It is also appropriate for competitive species in a chemostat [8], where the controlled resource supply is constant.

The problem of competition for the same age-structured resource with a linear source term has, to our knowledge, not been investigated. Only the case of a single (unstructured) predator hunting an age-structured prey has been analysed in [25] (see also the references therein), then generalising the predator-prey Lotka-Volterra equations to age-structured prey. The authors show that not only this system can produce periodic solution (as in the Lotka-Volterra ODE system), but also extinction of both population, convergence to a positive equilibrium or unbounded solutions.

In [7], Djidjou-Demasse et al. proposed a within-host competition model in which a population of red blood cells (the resource) can be infected by multiple *Plasmodium* strains. The resource is discretely structured into three stages, while the parasite populations are structured by a continuous age variable. Moreover, infection is mediated by the release of merozoites and thus deviates from the mass-action assumption. Although this modeling framework is tailored to a specific biological system, it addresses similar questions to those we are considering here. In particular, the authors show that stable coexistence may occur under explicit conditions on the parameters, a feature that we also recover in our more general setting.

Models with structures closely related to (1) have been considered in which the competitors are age-structured while the resource is not and with $c_i = 1$. First Magal, McCluskey and Webb [15] analyzed the single-strain case, later extended to multiple strains by Martcheva and Li [19], and further refined in [27], for the two strains case, in which the degenerate situation where two strains sharing equal reproduction numbers is considered. In a recent work [9], we completed this line of research by treating the case of an arbitrary number of strains where the maximal reproduction number can be shared by several strains. These works consistently show that age-structure in the competitors alone does not allow for robust coexistence: competitive exclusion holds generically while coexistence can only occur for singular parameter values, resulting in a continuum of equilibria.

Instead, in this paper we show that considering age-structure in the resource has a fundamentally different effect, as it allows for structurally stable coexistence under suitable conditions on the kernels β_i. In particular, a necessary condition is that β_2 and β_1 are not proportional, which is consistent with the concept of niche partitioning.

This paper is organized as follows. We first establish the well-posedness of the model using integrated semi-group theory and the method of characteristics. We characterize the omega-limit sets of each initial condition and prove the existence of an asymptotically stable global attractor. Then we state the conditions of existence of equilibria in terms of basic and invasion reproduction numbers.

Next, we define candidate Lyapunov functionals. Those functions are not defined on the whole phase space. We prove that, thanks to the regularization induced by the boundary condition, they are defined and differentiable along all complete orbits included in suitable invariant subsets, and conclude that they are valid Lyapunov functionals on those subsets. In particular, the proof that those functions are well defined on the omega-limit sets requires to demonstrate the uniform persistence of the flow, using criteria from [11, 28] based on the behaviour of the flow near the equilibria included in the boundary.

Finally, we compute the basin of attraction of each equilibrium and prove its stability. This is achieved by considering that, under suitable conditions, *i)* the omega-limit set of each compact set is attractive, *ii)* a Lyapunov functional is defined on this set and *iii)* this omega-limit set contains an equilibrium. Using a generalisation of the LaSalle invariance principle [28, Theorem 2.52], we conclude that each omega-limit set actually reduces to a single equilibrium.

2 Framework and preliminary results

We begin this section by introducing the framework and the different notations. Then we establish several properties of the semiflow, such as its well-posedness, positivity, dissipativity as well as the existence of a global attractor. Finally we state the fundamental properties of the omega-limit sets.

2.1 Assumptions and notations

Throughout this article, we consider that the following assumption is satisfied.

Assumption 2.1. *We suppose that:*

- μ_x, β_1 *and* β_2 *are in* $L^\infty(\mathbb{R}_+, \mathbb{R}_+)$,
- Λ, μ_1 *and* μ_2 *are in* $\mathbb{R}_+^*$,
- *there exists* $\mu_0 > 0$ *such that* $\mu_x(a) \geq \mu_0$ *a.e.* $a \geq 0$.

We introduce the notations $\underline{\mu} = \min\{\mu_0, \mu_1, \mu_2\}$, $\overline{\mu} = \max\{\|\mu_x\|_{L^\infty}, \mu_1, \mu_2\}$, $\underline{c} = \min\{1, c_1, c_2\}$ and $\overline{c} = \max\{1, c_1, c_2\}$.

Let us define, $X_+ = L^1(\mathbb{R}_+, \mathbb{R}_+) \times \mathbb{R}_+^2$ and, for $i \in \{1, 2\}$, the sets $X_i = \{(x, y_1, y_2) \in X_+ : y_i > 0\}$ and $\partial X_i = \{(x, y_1, y_2) \in X_+ : y_i = 0\}$.

Definition 2.2. *Let* $\Phi : \mathbb{R}_+ \times X_+ \to X_+$ *be a semiflow. A set* $S_1 \subset X_+$ *is said to attract a set* $S_2 \subset X_+$ *if* $S_1 \neq \emptyset$ *and*

$$d(\Phi_t(S_2), S_1) := \sup_{s_2 \in S_2} \inf_{s_1 \in S_1} ||\Phi_t(s_2) - s_1||_X \underset{t \to +\infty}{\to} 0.$$

2.2 Qualitative properties of the semiflow

We first use the theory of integrated semigroups to assess the existence of a unique mild (integrated) solution to system (1) for any initial condition $(x_0, y_{1,0}, y_{2,0}) \in X_+$. We use the notations and definitions from [16, 28] and introduce the linear operator $A : D(A) \subset \mathcal{X} \to \mathcal{X}$ by

$$A \begin{pmatrix} \begin{pmatrix} 0 \\ x \end{pmatrix} \\ y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} -x(0) \\ -x' - \mu_x x \end{pmatrix} \\ -\mu_1 y_1 \\ -\mu_2 y_2 \end{pmatrix}$$

where $D(A) = (\{0\} \times W^{1,1}(\mathbb{R}_+, \mathbb{R})) \times \mathbb{R}^2$ and $\mathcal{X} = (\mathbb{R} \times L^1(\mathbb{R}_+, \mathbb{R})) \times \mathbb{R}^2$. We also define $\mathcal{X}_0 = \overline{D(A)} = (\{0\} \times L^1(\mathbb{R}_+, \mathbb{R})) \times \mathbb{R}^2$ and its positive cone $\mathcal{X}_{0+} = (\{0\} \times L^1(\mathbb{R}_+, \mathbb{R}_+)) \times \mathbb{R}_+^2$. We introduce A_0, the part of A on $\mathcal{X}_0$, *i.e.* the restriction of A to

$$D(A_0) = \{x \in D(A) \ : \ Ax \in \overline{D(A)}\}.$$

Finally, we define the non-linear function $F : \mathcal{X}_0 \to \mathcal{X}$ by

$$F \begin{pmatrix} \begin{pmatrix} 0 \\ x \end{pmatrix} \\ y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} \Lambda \\ -y_1 \beta_1 x - y_2 \beta_2 x \end{pmatrix} \\ c_1 y \int_0^\infty \beta_1(a) x(a) \mathrm{d}a \\ c_2 z \int_0^\infty \beta_2(a) x(a) \mathrm{d}a \end{pmatrix}.$$

Then system (1) can be rewritten as the following abstract semilinear Cauchy problem with $u(t) = ((0, x(t, \cdot)), y_1(t), y_2(t))$

$$\forall t \geq 0, \quad u'(t) = Au(t) + F(u(t)) \ ; \ u(0) = u_0 \in \mathcal{X}_{0+}. \tag{2}$$

Since $\mathcal{X}_0 = \overline{D(A)} \subsetneq \mathcal{X}$, *i.e.* A is a non-densely defined operator, integrated solutions of (2) will belong to $\mathcal{X}_0$. Moreover, the non-linear operator $A + F$ satisfies the following properties.

Lemma 2.3.

1. *A is a Hille-Yosida operator, with $(-\underline{\mu}, +\infty) \subset \rho(A)$, where $\rho(A)$ denotes the resolvent set of A, A is resolvent positive (i.e. $\forall \lambda \in \rho(A)$, $(\lambda I - A)^{-1}\mathcal{X}_+ \subset \mathcal{X}_+$) and*

$$\|(\lambda I - A)^{-n})\|_{\mathcal{L}(\mathcal{X})} \leq \frac{1}{(\lambda + \underline{\mu})^n}, \ \forall \lambda > -\underline{\mu}, \ \forall n \geq 1.$$

2. *F is a locally Lipschitz continuous function: $\forall r > 0$, $\exists K_r > 0$ such that*

$$\|F(u_0) - F(\tilde{u}_0)\|_{\mathcal{X}} \leq K_r \|u_0 - \tilde{u}_0\|_{\mathcal{X}}$$

for every $(u_0, \tilde{u}_0) \in (\mathcal{X}_0 \cap \mathcal{B}_{\mathcal{X}}(0, r))^2$ where $\mathcal{B}_{\mathcal{X}}(0, r)$ is the ball of $\mathcal{X}$ centered at $0_{\mathcal{X}}$ with radius r.

Proof. 1. Let $\lambda \in \mathbb{R}$, $((0, x), y_1, y_2) \in D(A)$ and $(\alpha, \varphi, c, d) \in \mathcal{X}$. Then

$$(\lambda I_{D(A)} - A) \begin{pmatrix} \begin{pmatrix} 0 \\ x \end{pmatrix} \\ y_1 \\ y_2 \end{pmatrix} = \begin{pmatrix} \begin{pmatrix} \alpha \\ \varphi \end{pmatrix} \\ c \\ d \end{pmatrix} \Leftrightarrow \left\{ \begin{array}{rcl} x(0) & = & \alpha \\ x' & = & -(\lambda + \mu_x)x + \varphi \\ y_1 & = & \frac{c}{\lambda + \mu_1} \\ y_2 & = & \frac{d}{\lambda + \mu_2} \end{array} \right.$$

where the first two equations are equivalent to $x(a) = \alpha e^{-\int_0^a \lambda + \mu_x(s)\mathrm{d}s} + \int_0^a \varphi(s) e^{-\int_s^a \lambda + \mu_x(r)\mathrm{d}r}\mathrm{d}s$ for a.e. $a \geq 0$. Then for any $\lambda > \underline{\mu}$, $(\lambda I_{D(A)} - A)$ is a bijection from $D(A)$ to $\mathcal{X}$ and A is resolvent positive. Moreover, the previous expression of x leads, for any $\lambda > \underline{\mu}$ and any $V = (\alpha, \varphi, c, d) \in \mathcal{X}$, to

$$||(\lambda I_{D(A)} - A)^{-1} V||_{\mathcal{X}} \leq \frac{\alpha + ||\varphi||_{L^1}}{\lambda + \underline{\mu}} + \frac{c}{\lambda + \mu_1} + \frac{d}{\lambda + \mu_2} \leq \frac{||V||_{\mathcal{X}}}{\lambda + \underline{\mu}}$$

and then, as the operator norm is sub-multiplicative, for any $n \geq 1$, to

$$||(\lambda I_{D(A)} - A)^{-n}||_{\mathcal{L}(\mathcal{X})} \leq ||(\lambda I_{D(A)} - A)^{-1}||^n_{\mathcal{L}(X)} = \sup_{V \in \mathcal{X}, ||V||_{\mathcal{X}} = 1} ||(\lambda I_{D(A)} - A)^{-1} V||^n_X \leq \frac{1}{(\lambda + \underline{\mu})^n}.$$

2. Standard computations show that F is locally Lipschitz continuous, where the local Lipschitz constant can be chosen as $K_r = r \sum_{i=1}^2 ||\beta_i||_{L^\infty}(1 + c_i)$.

□

Proposition 2.4. 1. *For any $u_0 \in \mathcal{X}_{0+}$, there exists a unique non-negative maximal integrated solution u to (2), i.e. $u \in \mathcal{C}([0, t_{max}(u_0)), \mathcal{X}_{0+})$ such that*

$$\int_0^t u(s) \in D(A), \quad \forall t \in [0, t_{\max}(u_0))$$

and

$$u(t) = u_0 + A \int_0^t u(s)\mathrm{d}s + \int_0^t F(u(s))\mathrm{d}s, \quad \forall t \in [0, t_{\max}(u_0)). \tag{3}$$

2. *This solution is global in time, i.e. $t_{\max}(u_0) = +\infty$ and it defines a continuous semiflow $U : \mathbb{R}_+ \times \mathcal{X}_{0+} \to \mathcal{X}_{0+}$, $(t, u_0) \longmapsto u(t)$. Moreover, for any $t \geq 0$ and any $u_0 \in \mathcal{X}_{0+}$, the total mass $||u(t)||_{\mathcal{X}}$ of system (1) satisfies, for all $t \geq 0$:*

$$||u(t)||_{\mathcal{X}} \leq \overline{c}||u_0||_{\mathcal{X}} e^{-\underline{\mu}t} + \frac{\overline{c}\Lambda}{\underline{\mu}}(1 - e^{-\underline{\mu}t}) \leq \overline{c} \max\left(||u_0||_{\mathcal{X}}, \frac{\overline{c}\Lambda}{\underline{\mu}}\right). \tag{4}$$

3. *The trivial bijection from $\mathcal{X}_{0+}$ to X_+, obtained by removing the first coordinate, defines a contiuous semiflow for (1)*

$$\Phi : \mathbb{R}_+ \times X_+ \to X_+, \quad v = (x_0, y_{1,0}, y_{2,0}) \longmapsto \Phi_t(v) = (\Phi_t^x, \Phi_t^1, \Phi_t^2)(v) = (x(t, .), y_1(t), y_2(t)).$$

For all $t \geq 0$ and $v = (x_0, y_{1,0}, y_{2,0}) \in X_+$, the semiflow satisfies $\Phi_t^x(v)(a) = \widetilde{\Phi_t^x}(v)(a) + \widehat{\Phi_t^x}(v)(a)$ with, a.e. $a \geq 0$,

$$\left\{ \begin{array}{rcl} \widetilde{\Phi_t^x}(v)(a) & = & x_0(a - t) e^{-\int_{a-t}^a \left(\mu_x(s) + \sum_{i=1}^2 \beta_i(s) \Phi^i_{s-a+t}(v)\right)\mathrm{d}s} \chi_{[t,\infty)}(a), \\ \widehat{\Phi_t^x}(v)(a) & = & \Lambda e^{-\int_0^a \left(\mu_x(s) + \sum_{i=1}^2 \beta_i(s) \Phi^i_{t-a+s}(v)\right)\mathrm{d}s} \chi_{[0,t)}(a). \end{array} \right. \tag{5}$$

4. *The semiflow Φ is bounded-dissipative on X_+, i.e. there exists a bounded subset that attracts each bounded subset of X_+.*

5. *The semiflow Φ is asymptotically smooth, i.e. for every non-empty, bounded and positively invariant set $B \subset X_+$, there exists a compact set $K \subset B$ such that K attracts B.*

6. *The semiflow Φ is state-continuous, uniformly in finite time, i.e. for every $(t,v) \in \mathbb{R}_+ \times X_+$ and every $\varepsilon > 0$, there exists $\delta > 0$ such that*

$$\forall (s,\tilde{v}) \in [0,t] \times X_+ : \|v - \tilde{v}\|_X \leq \delta \Longrightarrow \|\Phi_s(v) - \Phi_s(\tilde{v})\|_X \leq \varepsilon.$$

Proof. 1. From Lemma 2.3, A is a Hille-Yosida operator, so it generates a locally Lipschitz continuous integrated semigroup $\{S_A(t)\}_{t\geq 0}$ on $\mathcal{X}$ ([13, Theorem 2.4] or [16, Proposition 3.4.3, p.116]). Moreover, Kellermann-Hieber theorem ([13] or [16, Theorem 3.6.2, p.133]) states that for any $\tau > 0$ and any $f \in L^1((0,\tau),\mathcal{X})$, the maps $t \longmapsto (S_A * f)(t)$ are continuously differentiable on $(0,\tau)$, where $*$ denotes the convolution product:

$$(S_A * f)(t) = \int_0^t S_A(t-s) f(s) ds$$

and for all $t \in [0,\tau]$

$$\|u_f(t)\| := \left\| \frac{d}{dt}(S_A * f)(t) \right\| \leq \int_0^t e^{-\underline{\mu}(t-s)} \|f(s)\| \mathrm{d}s. \tag{6}$$

If in particular $f \in \mathcal{C}((0,\tau),\mathcal{X})$, then $\|u_f(t)\| \leq \delta_A(t) \sup_{s\in[0,t]} ||f(s)||$ where $\delta_A(t) = t$ converges to 0 as $t \to 0$ and Assumption 5.1.2 from [16] applies. Since we proved that F is locally Lipschitz continuous, [16, Theorem 5.2.7, p.226] states that there exists a unique maximal integrated solution $U(.)u_0 \in \mathcal{C}([0,t_{\max}),\mathcal{X}_0)$ (with $t_{\max} \leq +\infty$) to problem (2) for each initial condition $u_0 \in \mathcal{X}_0$. This solution satisfies:

$$U(t)u_0 = T_{A_0}(t)u_0 + \frac{d}{dt}\left(S_A * (F \circ U(.)u_0)(t)\right) \tag{7}$$

where $\{T_{A_0}\}_{t\geq 0}$ is the $\mathcal{C}_0$-semigroup on $\mathcal{X}_0$ generated by A_0. The existence of $\{T_{A_0}\}_{t\geq 0}$ on $\overline{D(A_0)}$ comes from the Hille-Yosida Theorem [16, Lemma 2.4.5] while Lemma 2.2.11 from [16] implies that $\overline{D(A_0)} = \mathcal{X}_0$.

For any $\gamma \leq 0$, the operator $A - \gamma I$ is resolvent positive, as a direct consequence of A beeing resolvent positive. Moreover, for any $r > 0$ and any $u_0 \in \mathcal{X}_{0+}$ such that $\|u_0\|_{\mathcal{X}} \leq r$, $F(u_0) + \gamma_r u_0 \in \mathcal{X}_+$, where $\gamma_r = 2r(\|\beta_1\|_{L^\infty} + \|\beta_2\|_{L^\infty})$. Then [16, Theorem 5.3.2] states that the integrated solution is non-negative.

2. From (3), the mild solution of (2) is such that, for any $u_0 = ((0,x_0),y_{1,0},y_{2,0}) \in \mathcal{X}_{0+}$ and any $t \in [0,t_{\max})$,

$$x(t,.) = x_0(.) - \int_0^t \partial_a x(s,.)\mathrm{d}s - \int_0^t \mu_x(.)x(s,.)\mathrm{d}s - \sum_{i=1}^{2} y_i(s) \int_0^t \beta_i(.)x(s,.)\mathrm{d}s \tag{8}$$

$$y_i(t) = y_{i,0} - \mu_i \int_0^t y_i(s)\mathrm{d}s + c_i \int_0^t y_i(s) \int_0^\infty \beta_i(a)x(s,a)\mathrm{d}a\mathrm{d}s, \quad \forall i \in \{1,2\}. \tag{9}$$

Set $N(t) = \bar{c}\int_0^\infty x(t,a)\mathrm{d}a + \sum_{i=1}^2 y_i(t)$, then $N(0) = \bar{c}||x_0||_{L^1} + \sum_{i=1}^2 y_{i,0}$. Using the integrated expressions (8)-(9):

$$N(t) = N(0) + \bar{c}\Lambda t - \int_0^t \bar{c}\int_0^\infty \mu_x(a)x(s,a)\mathrm{d}a\mathrm{d}s - \sum_{i=1}^{2}\left(\mu_i \int_0^t y_i(s)\mathrm{d}s + (c_i - \bar{c})\int_0^t y_i(s)\int_0^\infty \beta_i(a)x(s,a)\mathrm{d}a\mathrm{d}s\right)$$

where we used the following equation since $\int_0^t x(s,.)\mathrm{d}s \in W^{1,1}(\mathbb{R}_+,\mathbb{R})$

$$\int_0^t \int_0^\infty \partial_a x(s,a)\mathrm{d}a\mathrm{d}s = -\int_0^t \Lambda \mathrm{d}s = -\Lambda t.$$

Then

$$N'(t) = \bar{c}\Lambda - \bar{c}\int_0^\infty \mu_x(a)x(t,a)\mathrm{d}a - \sum_{i=1}^{2}\left(\mu_i y_i(t) + (c_i - \bar{c})\int_0^\infty y_i(t)\beta_i(a)\mathrm{d}a\right).$$

By using the definition of $\underline{\mu}$ and truncating the $(c_i - \overline{c})$ negative contribution we obtain $N'(t) \leq \overline{c}\Lambda - \underline{\mu}N(t)$. It follows that

$$||u(t)||_{\mathcal{X}} = \int_0^\infty x(t,a)\mathrm{d}a + \sum_{i=1}^2 y_i(t) \leq N(t) \leq N(0)e^{-\underline{\mu}t} + \frac{\overline{c}\Lambda}{\underline{\mu}}(1 - e^{-\underline{\mu}t})$$

by using Gronwall's lemma which leads to (4) since $N(0) \leq \overline{c}||u_0||_{\mathcal{X}}$. In particular, $t \longmapsto ||u(t)||_{\mathcal{X}}$ is bounded on $[0, t_{\max}(u_0))$, then $t_{\max} = +\infty$.

3. Formula (5) are derived from the method of characteristics (or Duhamel's formula).
4. From (4), for any bounded set $B \subset X_+$, $\lim_{t\to+\infty} ||\Phi_t(v)||_{\mathcal{X}} \leq \frac{\overline{c}\Lambda}{\underline{\mu}}$ uniformly in $v \in B$, then the closed ball of X_+ centered at 0_X with radius $\frac{\overline{c}\Lambda}{\underline{\mu}}$ attracts all bounded sets of X_+.
5. We prove the asymptotic smoothness of Φ using Lemma 3.2.6 from [10] (see also [28, Theorem 2.46]). For any $t \in \mathbb{R}_+$, the semiflow Φ_t decomposes as $\Phi_t = (\widetilde{\Phi_t^x}, 0, 0) + (\widehat{\Phi_t^x}, \Phi_t^1, \Phi_t^2)$.

   First, equation (5) implies that the function $\delta : R_+ \times \mathbb{R}_+ \ni (t,r) \longmapsto re^{-\mu_0 t} \in \mathbb{R}_+$ is such that, for any $r > 0$, $t \geq 0$ and $v \in X_+$ such that $||v||_X \leq r$ then $||(\widetilde{\Phi_t^x}(v), 0, 0)||_X \leq \delta(t,r)$ with $\lim_{s\to+\infty} \delta(s,r) = 0$.

   Next we prove that, for any fixed $t \geq 0$, $(\widehat{\Phi_t^x}, \Phi_t^1, \Phi_t^2)$ is a compact operator on any bounded subset of X_+, that is for any bounded set $B \subset X_+$, $(\widehat{\Phi_t^x}, \Phi_t^1, \Phi_t^2)(B)$ is a precompact set of X_+, *i.e.* $\widehat{\Phi_t^x}(B)$ is a precompact set of $L^1(\mathbb{R}_+, \mathbb{R}_+)$.

   It remains to prove the three assumptions of the Fréchet-Kolmogorov theorem [33, Theorem X.1, p. 275]. Let $r > 0$ and $B \subset \mathcal{B}_{X_+}(0, r)$, the ball of X_+ centered at 0_X with radius r.

   i) The boundedness of $\widehat{\Phi_t^x}(B)$ is given by equation (4), which readily implies that for any $v \in B$

   $$||\widehat{\Phi_t^x}(v)||_{L^1} \leq ||\Phi_t(v)||_{X_+} \leq \overline{c}\max\left(r, \frac{\Lambda}{\underline{\mu}}\right) =: M_r.$$

   ii) For any $v \in B$, the equitightness property $\lim_{d\to+\infty} \int_{a>d} \widehat{\Phi_t^x}(v)(a)\mathrm{d}a = 0$ uniformly on $\widehat{\Phi_t^x}(B)$ is also readily satisfied because $\widehat{\Phi_t^x}(v)(a) = 0$ for $a > t$ (independently of $v \in B$).

   iii) It remains to prove that for any $t \geq 0$, $\lim_{h\to 0} \int_{\mathbb{R}} |\widehat{\Phi_t^x}(v)(a+h) - \widehat{\Phi_t^x}(v)(a)|\mathrm{d}a = 0$, uniformly in $v \in B$. From (5), for any $v \in B$ and any $t, a \geq 0$, $\widehat{\Phi_t^x}(v)(a) = \Lambda e^{A_{t,v}(a)}\chi_{[0,t)}(a)$, where

   $$A_{t,v} : a \longmapsto -\int_0^a \left(\mu_x(s) + \sum_{i=1}^2 \beta_i(s)\Phi_{t-a+s}^i(v)\right)\mathrm{d}s.$$

   If $t = 0$, the integral is readily zero. Let $v \in B$, $t > 0$ and $h \in (0, t]$. Since $\widehat{\Phi_t^x}(v)(a+h) = 0$ if $a > t - h$ and $\widehat{\Phi_t^x}(v)(a) = 0$ if $a > t$, then

   $$\begin{aligned}&\int_{\mathbb{R}} |\widehat{\Phi_t^x}(v)(a+h) - \widehat{\Phi_t^x}(v)(a)|\mathrm{d}a \\ &= \int_{-h}^0 \widehat{\Phi_t^x}(v)(a+h)da + \int_0^{t-h} |\widehat{\Phi_t^x}(v)(a+h) - \widehat{\Phi_t^x}(v)(a)|\mathrm{d}a + \int_{t-h}^t |\widehat{\Phi_t^x}(v)(a)|\mathrm{d}a\end{aligned}$$

   The first and third terms are clearly bounded by Λh. The second term is controlled by using the mean value inequality $|e^{-a} - e^{-b}| \leq e^{-\min(a,b)}|a - b| \leq |a - b|$ for any $a, b > 0$:

   $$\begin{aligned}&|\widehat{\Phi_t^x}(v)(a+h) - \widehat{\Phi_t^x}(v)(a)| \leq \Lambda|A_{t,v}(a+h) - A_{t,v}(a)| \\ &\leq \Lambda\int_a^{a+h} \left(\mu_x(s) + \sum_{i=1}^2 \beta_i(s)\Phi_{t-a+s}^i(v)\right)\mathrm{d}s + \Lambda\sum_{i=1}^2 \int_0^a \beta_i(s)\left|\Phi_{t-a-h+s}^i(v) - \Phi_{t-a+s}^i(v)\right|\mathrm{d}s.\end{aligned}$$

   From (4) and the boundedness of B, there exist constants $C_0, C_1, C_2 > 0$ such that

   $$\int_a^{a+h} \left(\mu_x(s) + \sum_{i=1}^2 \beta_i(s)\Phi_{t-a+s}^i(v)\right)\mathrm{d}s \leq C_1 h$$

and, using the integrated expression (9),

$$\beta_i(s)|\Phi^i_{t-a-h+s}(v)-\Phi^i_{t-a+s}(v)| = \beta_i(s)\left|c_i\int_{t-a-h+s}^{t-a+s}\Phi^i_\sigma(v)\left(\int_0^\infty\beta_i(\alpha)\Phi^x_\sigma(v)(\alpha)\mathrm{d}\alpha-\mu_i\right)\mathrm{d}\sigma\right|$$
$$\leq ||\beta_i||_{L^\infty}c_iM_r(||\beta_i||_{L^\infty}M_r+\mu_i)h \leq C_ih.$$

Finally,

$$\int_0^{t-h}|\widehat{\Phi^x_t}(v)(a+h)-\widehat{\Phi^x_t}(v)(a)|\mathrm{d}a \leq (t-h)\Lambda(\sum_{i=0}^2 C_i)h$$

and then

$$\int_0^\infty|\widehat{\Phi^x_t}(v)(a+h)-\widehat{\Phi^x_t}(v)(a)|\mathrm{d}a \leq \Lambda\left(2+(t-h)(\sum_{i=0}^2 C_i)\right)h$$

converges to 0 as $h\to 0$, uniformly on $v\in B$.

Consequently, the Fréchet-Kolmogorov theorem states that $\widehat{\Phi^x_t}(B)$ is a precompact set of $L^1(\mathbb{R}_+,\mathbb{R}_+)$, then the set $(\widehat{\Phi^x_t},\Phi^1_t,\Phi^2_t)(B)$ is precompact in X_+ and this achieves the proof.

6. Let $u_0\in\mathcal{X}_{0+}$, $t\geq 0$, $\varepsilon>0$ and set

$$r=\overline{c}\max\left(\frac{\Lambda}{\underline{\mu}},\|u_0\|_\mathcal{X}+\varepsilon\right),\qquad \delta=\varepsilon e^{-K_rt}$$

where K_r is the Lipschitz constant from Lemma 2.3. Let $\tilde{u}_0\in\mathcal{X}_{0+}$ such that $\|u_0-\tilde{u}_0\|_\mathcal{X}\leq\delta$. Since $U(.)u_0$, $U(.)\tilde{u}_0$ and F are continuous, then $F\circ U(.)u_0-F\circ U(.)\tilde{u}_0$ belong to $\in\mathcal{C}(\mathbb{R}_+,\mathcal{X})\subset L^1([0,t],\mathcal{X})$. Moreover, since $\|\tilde{u}_0\|_\mathcal{X}\leq\delta+\|u_0\|_\mathcal{X}\leq r$, we know from (4) that for every $s\in[0,t]$, $(U(s)u_0,U(s)\tilde{u}_0)\in(\mathcal{X}_{0+}\cap B_\mathcal{X}(0,r))^2$. From (7), it comes for any $s\in[0,t)$:

$$U(s)\tilde{u}_0-U(s)u_0=T_{A_0}(s)(\tilde{u}_0-u_0)+\frac{d}{dt}\left(S_A*((F\circ U(.)\tilde{u}_0)-(F\circ U(.)u_0))(s)\right).$$

Then the Hille-Yosida Theorem applied to A_0 (notice that $\rho(A_0)=\rho(A)$ by [16, Lemma 2.2.10]) states that

$$\|T_{A_0}(s)(\tilde{u}_0-u_0)\|_\mathcal{X}\leq e^{-\underline{\mu}s}\|\tilde{u}_0-u_0\|_\mathcal{X}\leq\delta,\ \forall s\in[0,t].$$

Finally, equation (6) with $f=F\circ U(.)u_0-F\circ U(.)\tilde{u}_0$ rewrites as

$$\|U(s)\tilde{u}_0-U(s)u_0\|_\mathcal{X}\leq\delta+\int_0^s\|F(U(\xi)\tilde{u}_0)-F(U(\xi)u_0)\|_\mathcal{X}d\xi\leq\delta+K_r\int_0^s\|U(\xi)\tilde{u}_0-U(\xi)u_0\|_\mathcal{X}d\xi,\quad\forall s\in[0,t]$$

which leads by means of Gronwall's inequality to

$$\|U(s)\tilde{u}_0-U(s)u_0\|_\mathcal{X}\leq\delta e^{K_rs}\leq\varepsilon,\quad\forall s\in[0,t],$$

which is the expected bound, where v and $\tilde{v}$ are obtained from u_0 and $\tilde{u}_0$ by removing the first coordinate.

□

Corollary 2.5. *There exists a unique compact attractor of bounded set $\mathcal{A}\subset X_+$, that is $\mathcal{A}$ is a non-empty, compact and invariant subset that attracts every bounded subsets of X_+. This attractor satisfies $\mathcal{A}\subset B_{X_+}(0,\frac{\overline{c}\Lambda}{\mu_0})$. Moreover, the set $\mathcal{A}$ is locally asymptotically stable (LAS), i.e. for every neighborhood $\mathcal{V}$ of $\mathcal{A}$, there exists a neighborhood $\mathcal{W}\subset\mathcal{V}$ of $\mathcal{A}$ such that $\Phi_t(\mathcal{W})\subset\mathcal{V}$ for every $t\geq 0$.*

Proof. The existence of a unique compact attractor $\mathcal{A}$ is given by [28, Theorem 2.33] (or [10, Theorem 3.4.6]) as a consequence of Φ being asymptotically smooth and bounded-dissipative. Since Φ is also state-continuous, uniformly in finite time, [28, Theorem 2.39] states that $\mathcal{A}$ is locally asymptotically stable. □

For each $v\in X_+$, we denote by $\mathcal{O}_v=\{\Phi_t(v),t\geq 0\}$ the positive orbit starting from v and

$$\omega(v)=\bigcap_{\tau\geq 0}\overline{\{\Phi_t(v),t\geq\tau\}}$$

the ω-limit set of v.

Lemma 2.6 (Properties of omega-limit set). *For every $v \in X_+$,*

- *$\omega(v)$ is non-empty, compact and connected,*
- *$\omega(v)$ is invariant under Φ_t,*
- *$\omega(v)$ attracts v, i.e. $\lim_{t\to\infty} d(\Phi_t(v), \omega(v)) = 0$.*

Proof. Under the hypotheses already checked to prove the asymptotic smoothness of the semiflow, [32, Proposition 3.13, p.100] states that for every $v \in X_+$, the orbit $\mathcal{O}_v \subset X_+$ is relatively compact ($\overline{\mathcal{O}_v}$ is compact). Then [10, Lemma 3.1.1 and 3.1.2, p. 36] (or [31, Thm 4.1, p. 167]) give the conclusions of the Lemma. □

3 Main results on asymptotic dynamics

In this section, we identify the equilibria of (1) in X_+. In particular, we interpret the conditions for existence of positive coexistence equilibria (i.e. in $X_1 \cap X_2$) from a biological point of view. Next, we state the main results of this paper, which give en exhaustive characterisation of the attractivity and stability of equilibria, their proofs are deferred to Section 5.

3.1 Existence of equilibria

Proposition 3.1 (Equilibria in the boundary $\partial X_1 \cup \partial X_2$).

1. *There exists a trivial equilibrium E_0, with no competitor, defined by*
$$E_0 = (x_0^*, 0, 0) = (\Lambda e^{-\int_0^\cdot \mu_x(s)ds}, 0, 0).$$
2. *When they exist, the equilibria with a single competitor are denoted by $E_1 = (x_1^*, y_1^*, 0) \in X_1 \cap \partial X_2$ and $E_2 = (x_2^*, 0, y_2^*) \in X_2 \cap \partial X_1$. For each $i, j \in \{1, 2\}$ with $i \neq j$, E_i exists if and only if $\mathcal{R}_{0,i} > 1$, where $\mathcal{R}_{0,i}$ is the basic reproduction number*
$$\mathcal{R}_{0,i} = \frac{\Lambda c_i}{\mu_i} \int_0^\infty \beta_i(a) e^{-\int_0^a \mu_x(s)ds} da = \frac{c_i}{\mu_i} \int_0^\infty \beta_i(a) x_0^*(a) da, \quad \forall i \in \{1, 2\}. \tag{10}$$
In this case we have
$$x_i^*(a) = \Lambda e^{-\int_0^a \mu_x(s)ds} e^{-y_i^* \int_0^a \beta_i(s)ds}$$
where $y_i^* > 0$ is implicitly defined by
$$\frac{c_i}{\mu_i} \int_0^\infty \beta_i(a) x_i^*(a) \mathrm{d}a = 1. \tag{11}$$

Proof. Let $i \in \{1, 2\}$, then E_i satisfies
$$(x_i^*)'(a) = -\mu_x x_i^*(a) - x_i^*(a)\beta_i(a) y_i^*$$
which integrates as stated in the proposition. □

The search of coexistence equilibria in $\mathcal{X}_1 \cap X_2$, that is equilibria for which all components are positive, is more complicated. Indeed, a point $(\overline{x}, \overline{y_1}, \overline{y_2}) \in X_+$ with $\overline{y_1} > 0, \overline{y_2} > 0$ is an equilibrium if and only if it satisfies the following system:
$$\begin{cases} T_k(\overline{y_1}, \overline{y_2}) &= 1, & \forall k \in \{1, 2\} \\ \overline{x}(a) &= \Lambda e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-\sum_{i=1}^2 \overline{y}_i \int_0^a \beta_i(s)\mathrm{d}s}, & \forall a \geq 0 \end{cases} \tag{12}$$
where, for each $k \in \{1, 2\}$,
$$T_k(y_1, y_2) = \frac{\Lambda c_k}{\mu_k} \int_0^\infty \beta_k(a) e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-\sum_{i=1}^2 y_i \int_0^a \beta_i(s)\mathrm{d}s} \mathrm{d}a.$$
Clearly $T_1 < \mathcal{R}_{0,1}$ and $T_2 < \mathcal{R}_{0,2}$ on $(\mathbb{R}_+^*)^2$, then it follows from the first condition in (12) that there is no positive equilibrium if $\mathcal{R}_{0,1} \leq 1$ or $\mathcal{R}_{0,2} \leq 1$. To investigate the possibility of equilibrium if $\mathcal{R}_{0,1} > 1$ and $\mathcal{R}_{0,2} > 1$, observe that $T_1(0, 0) = \mathcal{R}_{0,1}$ and $T_1(y_1^*, 0) = 1$ while $T_2(0, 0) = \mathcal{R}_{0,2}$ and $T_2(0, y_2^*) = 1$. We then define
$$\begin{aligned} \gamma_{2\to1} = T_1(0, y_2^*) = \tfrac{\Lambda c_1}{\mu_1} \int_0^\infty \beta_1(a) e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-y_2^* \int_0^a \beta_2(s)\mathrm{d}s} \mathrm{d}a = \tfrac{c_1}{\mu_1} \int_0^\infty \beta_1(a) x_2^*(a) \mathrm{d}a, \\ \gamma_{1\to2} = T_2(y_1^*, 0) = \tfrac{\Lambda c_2}{\mu_2} \int_0^\infty \beta_2(a) e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-y_1^* \int_0^a \beta_1(s)\mathrm{d}s} \mathrm{d}a = \tfrac{c_2}{\mu_2} \int_0^\infty \beta_2(a) x_1^*(a) \mathrm{d}a. \end{aligned} \tag{13}$$

Remark 3.2. *Let $(i,j) \in \{1,2\}^2$, $i \neq j$, then $\gamma_{i\to j}$ is defined if and only if $\mathcal{R}_{0,i} > 1$. Moreover, $\gamma_{i\to j} \leq \mathcal{R}_{0,j}$, with strict inequality if and only if $\|\beta_j\|_{L^1} > 0$.*

Those quantities are known as *invasion fitnesses* or *invasion reproduction numbers* and can be explained as in adaptive dynamics where we consider that populations are at equilibrium E_1 (respectively E_2) and we want to know if newly introduced competitor y_2 (resp. y_1) can invade.

Lemma 3.3. *Assume that $\mathcal{R}_{0,1} > 1$ and $\mathcal{R}_{0,2} > 1$, then the following assumptions are equivalent:*

1. *$\gamma_{1\to 2} = \gamma_{2\to 1} = 1$.*
2. *$y_2^*\beta_2(a) = y_1^*\beta_1(a)$ almost everywhere $a \geq 0$.*
3. *$c_2\mu_1\beta_2(a) = c_1\mu_2\beta_1(a)$ almost everywhere $a \geq 0$.*

The proof of this Lemma will be handled in Section 4.

Proposition 3.4 (Positive equilibria)**.** *Suppose that $\mathcal{R}_{0,1} > 1$ and $\mathcal{R}_{0,2} > 1$, then*

1. *If $\gamma_{1\to 2} > 1$ and $\gamma_{2\to 1} > 1$ there exists a unique positive equilibrium $E_3 = (\overline{x}, \overline{y_1}, \overline{y_2})$. Moreover E_3 is such that $0 < \overline{y_1} \leq y_1^*$ and $0 < \overline{y_2} \leq y_2^*$ and $(\overline{y_1}, \overline{y_2}) \neq (y_1^*, y_2^*)$.*
2. *If $\gamma_{1\to 2} = \gamma_{2\to 1} = 1$, then $x_1^* = x_2^*$ and there is a continuum E_∞ of positive equilibria, given by*
$$E_\infty = \{E_{1+\sigma} \ : \ \sigma \in (0,1)\} \text{ where } E_{1+\sigma} = (1-\sigma)E_1 + \sigma E_2 = (x_1^*, (1-\sigma)y_1^*, \sigma y_2^*),$$
i.e. E_∞ is the segment joining E_1 to E_2. There is no positive equilibrium outside of E_∞.
3. *Otherwise, there is no positive equilibrium.*

We will later show (Proposition 5.3) that the case $\max\{\gamma_{i\to j}, \gamma_{j\to i}\} < 1$ and the case $\gamma_{i\to j} = 1$, $\gamma_{j\to i} < 1$ $(i,j \in \{1,2\},\ i \neq j)$ never happen. Consequently, the third item actually states that there is no positive equilibrium when $\gamma_{j\to} > 1$ and $\gamma_{i\to j} \leq 1$. This is a direct consequence of the global attractivity of E_i in $X_1 \cap X_2$, which will be stated in Theorem 3.11.

In this section, we only prove the existence statement of the first item, as well as the second item. The uniqueness of E_3 will be proven later (Lemma 4.3.3).

Proof of Proposition 3.4. 1. Suppose that $\gamma_{1\to 2} > 1$ and $\gamma_{2\to 1} > 1$. First we note that the functions $\mathbb{R}_+ \ni z \longmapsto T_1(z, y_2)$ and $\mathbb{R}_+ \ni z \longmapsto T_2(y_1, z)$ are decreasingly going to zero as z goes to $+\infty$. Let us define the two following assumptions:
$$\inf(\operatorname{supp}(\beta_2)) \geq \sup(\operatorname{supp}(\beta_1)) \tag{14}$$
and
$$\inf(\operatorname{supp}(\beta_1)) \geq \sup(\operatorname{supp}(\beta_2)). \tag{15}$$
We readily see that those two conditions are not compatible since it would lead to $\beta_1 = \beta_2 \equiv 0$ and then $\mathcal{R}_{0,1} = \mathcal{R}_{0,2} = 0$ that is absurd.

Suppose now that (14) holds then the function $\mathbb{R}_+ \ni z \longmapsto T_1(y_1, z)$ is constant implying that $T_1(y_1^*, y_2) = 1$ for every $y_2 \geq 0$. Since (15) does not hold then the function $\mathbb{R}_+ \ni z \longmapsto T_2(z, y_2)$ is decreasingly going to zero as z goes to $+\infty$ for every $y_2 \geq 0$. It follows from $T_2(y_1^*, 0) = \gamma_{1\to 2} > 1$ that $y_1 \longmapsto T_2(y_1, 0) - 1$ has exactly one root $\widehat{y_1} > y_1^*$. Consequently, the level curve $\{(y_1, y_2) \in \mathbb{R}_+^2 : T_2(y_1, y_2) = 1\}$ continuously joins $(0, y_2^*)$ and $(\widehat{y_1}, 0)$ while $\{(y_1, y_2) \in \mathbb{R}_+^2 : T_1(y_1, y_2) = 1\} = \{(y_1^*, y_2), y_2 \geq 0\}$. It then readily follows that there exists $(\overline{y_1}, \overline{y_2})$ such that $(\overline{x}, \overline{y_1}, \overline{y_2})$ is an equilibrium, where $\overline{x}$ is defined by (12) and $\overline{y_1} = y_1^*$. The monotony of T_2 also implies that $0 < \overline{y_2} < y_2^*$ and the equilibrium is unique in this case.

The case where (15) holds but not (14) is similar and leads to a unique coexistence equilibrium $(\overline{x}, \overline{y_1}, y_2^*)$ with $0 < \overline{y_1} < y_1^*$ by monotony of T_1 and $\overline{x}$ is given by (12).

Finally, in the case where neither (15) nor (14) hold, we see that the functions $y_1 \longmapsto T_2(y_1, 0) - 1$ and $y_2 \longmapsto T_1(0, y_2) - 1$ have exactly one root $\widehat{y_1} > y_1^*$ and $\widehat{y_2} > y_2^*$ respectively. Consequently, the level curve $\{(y_1, y_2) \in \mathbb{R}_+^2 : T_1(y_1, y_2) = 1\}$ continuously joins $(0, \widehat{y_2})$ and $(y_1^*, 0)$, while the level curve $\{(y_1, y_2) \in \mathbb{R}_+^2 : T_2(y_1, y_2) = 1\}$ continuously joins $(0, y_2^*)$ and $(\widehat{y_1}, 0)$. It then readily follows that there exists $(\overline{y_1}, \overline{y_2})$ such that $(\overline{x}, \overline{y_1}, \overline{y_2})$ is an equilibrium, where $\overline{x}$ is defined by (12). The monotony of T_1 and T_2 also implies that $0 < \overline{y_1} < y_1^*$ and $0 < \overline{y_2} < y_2^*$.

2. If $\gamma_{1\to 2} = \gamma_{2\to 1} = 1$, then Lemma 3.3 readily implies that $T_1 = T_2$ and that for all $\sigma \in (0,1)$, $T_1((1-\sigma)y_1^*, \sigma y_2^*) = 1$. Moreover, formula (12) implies that if there exists $\sigma \in (0,1)$ such that $y_1 = (1-\sigma)y_1^*$ and $y_2 = \sigma y_2^*$ then (x^*, y_1^*, y_2^*) is an equilibrium if and only if

$$x^*(a) = \Lambda e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{(1-\sigma)y_1^* \int_0^a \beta_1(s)\mathrm{d}s - \sigma y_2^* \int_0^a \beta_2(s)\mathrm{d}s}.$$

Then Lemma 3.3 implies that $x^* = x_1^* = x_2^*$.

Since $(y_1, y_2) \longmapsto T_1(y_1, y_2)$ is a decreasing function with respect to both y_1 and y_2 on $\mathbb{R}_+^2$, then $T_1(y_1, y_2) < 1$ (resp > 1) on the right (resp. left) side of the segment joining $(y_1^*, 0)$ to $(0, y_2^*)$, so there is no other positive equilibrium. $\square$

Remark 3.5. *It is worth noticing that if $\beta_2 = c\beta_1$ for some $c \in \mathbb{R}_+^*$, then equations (11) and (13) readily imply that $\gamma_{2\to 1} = 1/\gamma_{1\to 2}$. Consequently, in this case, either there is a continuum of equilibria (in the critical and structurally unstable case $c = c_1\mu_1/c_2\mu_2$ which, from Lemma 3.3, implies $\gamma_{2\to 1} = \gamma_{1\to 2} = 1$), or there is no positive equilibrium and one competitor goes extinct. This is consistent with the belief that niche differentiation is necessary to avoid competitive exclusion.*

Remark 3.6. *Since x_1^* is a decreasing function of a, then the definition of $\gamma_{1\to 2}$ implies that in the situation where the environment is occupied by single population y_1 (considered at its equilibrium E_1), the best competitive strategy for a newly introduced population y_2 to challenge the resident population y_1 (i.e. the β_2 shape that maximizes $\gamma_{1\to 2}$, as we will see with Theorem 3.11 that the survival of y_2 depends on $\gamma_{1\to 2}$) is such that β_2 in concentrated near the age $a = 0$ (optimally, a Dirac distribution in 0). Indeed, since the resource influx is constant, then there is no need for the competitors to preserve the resource sustainability (as it would have been in the case of a linear birth rate). Consequently the best strategy is to be the first competitor to collect enough resource.*

3.2 Attractivity, stability and basins of attraction

We investigate the stability and attractiveness of every equilibrium, depending on the values of the basic reproduction numbers and invasion fitnesses $R_{0,i}$ and $\gamma_{i\to j}$ $(i, j \in \{1, 2\})$. For the sake of clarity, we gathered hereunder the main results on equilibria attractivity and stability, which are proved in Section 5.

Proposition 3.7 (Positive invariance of sets)**.** *For $i \in \{1,2\}$, the sets X_i and ∂X_i are positively invariant, that is, for all $t \geq 0$ $\Phi_t(X_i) \subset X_i$ and $\Phi_t(\partial X_i) \subset \partial X_i$.*

Proof. For any $i \in \{1,2\}$, any initial condition $v = (x_0, y_{1,0}, y_{2,0}) \in X_1$ and any $t \geq 0$, $y_i'(t) \geq -\mu_i y_i(t)$, then $y_i(t) \geq y_{i,0}e^{-\mu_i t} > 0$. The positive invariance of ∂X_i is straightforward. $\square$

A consequence of Proposition 3.7 is that if there exists $i \in \{1,2\}$ such that $v \in \partial X_i$ then the model (1) reduces to a single predator model.

Theorem 3.8 (Asymptotic stability of E_0)**.** *Suppose that one of the following assumptions holds:*

1. $\max\limits_{i\in\{1,2\}} \{\mathcal{R}_{0,i}\} \leq 1$ *and* $S = X_+$
2. $\mathcal{R}_{0,1} \leq 1$ *and* $S = \partial X_2$
3. $\mathcal{R}_{0,2} \leq 1$ *and* $S = \partial X_1$
4. $S = \bigcap\limits_{i\in\{1,2\}} \partial X_i$

then $\{E_0\}$ is globally asymptotically stable in S.

Remark 3.9. *More precisely, one can note that the equilibrium E_0 is globally exponentially stable in $\bigcap_{i\in\{1,2\}} \partial X_i$. Indeed, consider the initial condition $v = (x_0, 0, 0) \in \bigcap\limits_{i\in\{1,2\}} \partial X_i$. Then (5) rewrites as*

$$x(t,a) = \begin{cases} x_0(a-t)e^{-\int_{a-t}^a \mu_x(s)ds} & \text{if } a \geq t, \\ x_0^*(a) & \text{if } t \geq a. \end{cases}$$

Moreover, for $0 \leq t < a$, then $x_0^*(a) = \Lambda e^{-\int_0^a \mu_x(s)\mathrm{d}s} = \Lambda e^{-\int_0^{a-t} \mu_x(s)\mathrm{d}s} e^{-\int_{a-t}^a \mu_x(s)\mathrm{d}s} = x_0^*(a-t)e^{-\int_{a-t}^a \mu_x(s)\mathrm{d}s}$. We deduce that $\|x(t,.) - x_0^*\|_{L^1} = \int_t^\infty |(x_0(a-t) - x_0^*(a-t))|e^{-\int_{a-t}^a \mu_x(s)ds}da \leq \|x_0 - x_0^*\|_{L^1}e^{-\mu_0 t} \underset{t\to+\infty}{\longrightarrow} 0.$

Theorem 3.10 (Asymptotic stability with only one non-trivial equilibrium)**.** *Let $(i,j)\in\{1,2\}^2, j\neq i$, and assume that $\mathcal{R}_{0,i}>1$. Then:*

1. *E_i is globally asymptotically stable in $S=X_i\cap\partial X_j$.*
2. *If moreover $\mathcal{R}_{0,j}\leq 1$ then E_i is globally asymptotically stable in $S=X_i$.*

Theorem 3.11 (Asymptotic stability with two non-trivial equilibria : non-critical case)**.** *Let $i,j\in\{1,2\}$, $i\neq j$ and suppose $\min_{k\in\{1,2\}}\{\mathcal{R}_{0,k}\}>1$.*

1. *Suppose that $\gamma_{j\to i}>1$ and $\gamma_{i\to j}\leq 1$ then E_i is globally asymptotically stable in $S=\cap_{k\in\{1,2\}}X_k$.*
2. *Suppose that $\min_{k\in\{1,2\}}\{\gamma_{j\to i}\}>1$, then E_3 is globally asymptotically stable in $S=\cap_{k\in\{1,2\}}X_k$.*

Theorem 3.12 (Asymptotic stability with two non-trivial equilibria : critical case)**.** *Suppose $\min_{k\in\{1,2\}}\{\mathcal{R}_{0,k}\}>1$ and $\gamma_{1\to 2}=\gamma_{2\to 1}=1$. Then the continuum set of equilibria E_∞ (defined in Proposition 3.4) is globally asymptotically stable in $S=\cap_{k\in\{1,2\}}X_k$. Moreover, for any $v=(x_0,y_{1,0},y_{2,0})\in\mathcal{X}_1\cap X_2$, $\Phi_t(v)$ converges to $E_{1+\sigma}:=(1-\sigma)E_1+\sigma E_2$ where σ is the only solution in $(0,1)$ of*

$$(1-\sigma)y_1^*=\frac{y_{1,0}}{y_{2,0}}(\sigma y_2^*)^{\mu_1/\mu_2}.$$

One can note that the statements in Theorems 3.8, 3.10, 3.11 and 3.12 could actually be rewritten in a stronger sense since in the proofs we show that the mentionned attractor E ($E=E_i$ with $i=0,1,2,3$ or ∞ depending on the statement) actually attracts every compact subset K of S, which is equivalent ([28, Lemma 2.6]) to the fact that $d(\Phi_t(x),\{E\})\to 0$ as $t\to+\infty$ uniformly for $x\in K$.

We can also note that if each competitor is able to survive in the absence of the other ($\mathcal{R}_{0,i}>1$ for $i\in\{1,2\}$), then at least one competitor always survive, *i.e.* the competition cannot drive both population to extinction.

Those results are summarized in Tables 1 and 2.

	$\partial X_1\cap\partial X_2$	$\partial X_1\cap X_2$	$X_1\cap\partial X_2$	$X_1\cap X_2$
$\max\{\mathcal{R}_{0,1},\mathcal{R}_{0,2}\}\leq 1$	E_0	E_0	E_0	E_0
$\mathcal{R}_{0,1}>1\geq\mathcal{R}_{0,2}$	E_0	E_0	E_1	E_1
$\mathcal{R}_{0,1}\leq 1<\mathcal{R}_{0,2}$	E_0	E_2	E_0	E_2
$\min\{\mathcal{R}_{0,1},\mathcal{R}_{0,2}\}>1$	E_0	E_2	E_1	see table 2

Table 1: Convergence of the solution of (1) depending on the basic reproduction numbers and the subset of initial conditions in X_+. Results come from Theorems 3.8 and 3.10.

	$\gamma_{1\to 2}<1$	$\gamma_{1\to 2}=1$	$\gamma_{1\to 2}>1$
$\gamma_{2\to 1}<1$			E_2
$\gamma_{2\to 1}=1$		$E_{1+\sigma}\in E_\infty$	E_2
$\gamma_{2\to 1}>1$	E_1	E_1	E_3

Table 2: Convergence of the solution of (1) from any initial condition in $X_1\cap X_2$ in the case $\min\{\mathcal{R}_{0,1},\mathcal{R}_{0,2}\}>1$. Attractor results come from Theorems 3.11 and 3.12, while Proposition 5.3 states that three grayed-out configurations are never met.

3.3 Examples and numerical simulations

Example 3.13. *We assume that $\mu_1=\mu_2=\mu$, $c_1=c_2=c$,*

$$\beta_1(a)=\mathbf{1}_{[\underline{\beta},\overline{\beta}]}(a)\widetilde{\beta}(a),\quad \beta_2(a)=\beta_1(a+\alpha),\quad a.e.\ a\geq 0$$

where $0\leq\underline{\beta}<\overline{\beta}$, $\alpha\in(-\infty,\underline{\beta})$ and $\widetilde{\beta}\in L^1_+(\mathbb{R}_+)$. Then we can compute with (10) the quantities

$$\mathcal{R}_{0,1}=\frac{\Lambda c}{\mu}\int_{\underline{\beta}}^{\overline{\beta}}\widetilde{\beta}(a)e^{-\int_0^a\mu_x(s)\mathrm{d}s}\mathrm{d}a,\quad \mathcal{R}_{0,2}(\alpha)=\frac{\Lambda c}{\mu}\int_{\underline{\beta}}^{\overline{\beta}}\widetilde{\beta}(a)e^{-\int_0^{a-\alpha}\mu_x(s)\mathrm{d}s}\mathrm{d}a.$$

It follows that the function $\alpha \longmapsto \mathcal{R}_{0,2}(\alpha)$ is increasing, with $\mathcal{R}_{0,2}(0) = \mathcal{R}_{0,1}$. From (11) we see that

$$\frac{\Lambda c}{\mu}\int_0^\infty \beta_1(a)e^{-\int_0^a \mu_x(s)\mathrm{d}s}e^{-y_1^*\int_0^a \beta_1(s)\mathrm{d}s}\mathrm{d}a = 1 = \frac{\Lambda c}{\mu}\int_0^\infty \beta_2(a)e^{-\int_0^a \mu_x(s)\mathrm{d}s}e^{-y_2^*(\alpha)\int_0^a \beta_2(s)\mathrm{d}s}\mathrm{d}a$$

which is equivalent to

$$\int_{\underline{\beta}}^{\overline{\beta}} \widetilde{\beta}(a)e^{-\int_0^a \mu_x(s)\mathrm{d}s}e^{-y_1^*\int_{\underline{\beta}}^a \widetilde{\beta}(s)\mathrm{d}s}\mathrm{d}a = \int_{\underline{\beta}}^{\overline{\beta}} \widetilde{\beta}(a)e^{-\int_0^{a-\alpha} \mu_x(s)\mathrm{d}s}e^{-y_2^*(\alpha)\int_{\underline{\beta}}^a \widetilde{\beta}(s)\mathrm{d}s}\mathrm{d}a.$$

Since the function $\alpha \longmapsto e^{-\int_0^{a-\alpha}\mu_x(s)\mathrm{d}s}$ is increasing for every $a \geq 0$ then the function $\alpha \longmapsto y_2^*(\alpha)$ is necessarily increasing, with $y_2^*(0) = y_1^*$. Finally (13) allows us to compute

$$\gamma_{2\to1}(\alpha) = \frac{\Lambda c}{\mu}\int_{\underline{\beta}}^{\overline{\beta}} \widetilde{\beta}(a)e^{-\int_0^a \mu_x(s)\mathrm{d}s}e^{-y_2^*(\alpha)\int_{\underline{\beta}}^a \widetilde{\beta}(s)\mathrm{d}s}\mathrm{d}a$$

hence the function $\alpha \longmapsto \gamma_{2\to1}(\alpha)$ is decreasing and

$$\gamma_{1\to2}(\alpha) = \frac{\Lambda c}{\mu}\int_{\underline{\beta}}^{\overline{\beta}} \widetilde{\beta}(a)e^{-\int_0^{a-\alpha} \mu_x(s)\mathrm{d}s}e^{-y_1^*(\alpha)\int_{\underline{\beta}}^{\min\{a-\alpha,\overline{\beta}\}} \widetilde{\beta}(s)\mathrm{d}s}\mathrm{d}a$$

so the function $\alpha \longmapsto \gamma_{1\to2}(\alpha)$ is increasing, with $\gamma_{1\to2}(0) = \gamma_{2\to1}(0) = 1$.

This example proves that if β_1 and β_2 differ only by a translation, then only the first competitor to reach the resource can survive. Precisely, we see that if $\mathcal{R}_{0,1} > 1$ then when $\alpha = 0$ we are in the case of Theorem 3.12, that is the continuum set of equilibria E_∞ exists and is GAS in $X_1 \cap X_2$. When $\alpha > 0$, then $\gamma_{1\to2}(\alpha) > 1 > \gamma_{2\to1}(\alpha)$ leading to the first case of Theorem 3.11 that is E_2 is GAS in $X_1 \cap X_2$. On the contrary, if $\alpha < 0$ then $\gamma_{1\to2}(\alpha) < 1 < \gamma_{2\to1}(\alpha)$ that is E_1 is GAS in $X_1 \cap X_2$. Also, there exists $\underline{\alpha} < 0$ such that for every $\alpha \leq \underline{\alpha}$ then $\mathcal{R}_{0,2}(\alpha) \leq 1$ and E_2 ceases to exist.

Example 3.14. *This example illustrates (numerically) a case where the globally asymptotically stable (attractive in $X_1 \cap X_2$) steady state bifurcate from E_1 to E_3 and then to E_2. As in the previous example, we assume that the two competitors differ only in their respective function β_i, $i = 1, 2$, defined as*

$$\beta_1(a) = \frac{1}{5}\mathbf{1}_{[2,7]}(a), \quad \beta_2(a) = \frac{1}{10}\left(\mathbf{1}_{[0,\alpha]}(a)\frac{a}{\alpha} + \mathbf{1}_{(\alpha,20]}(a)\left(\frac{20-a}{20-\alpha}\right)\right), \quad a.e.\ a \geq 0 \tag{16}$$

where $\alpha \in [0, 30]$. That is, β_1 and β_2 both have unit L^1-norm, with β_1 being a gate function while β_2 is a triangle shaped function with mode α.

As illustrated on Figures 2 and 3, as the mode α of β_2 varies, system (1) successively undergoes two transcritical bifurcations where E_2 and E_1 respectively merge and exchange their stability with E_3 at $\alpha \approx 9.6$ and 11.8 respectively, while E_3 leaves the positive cone before and after those bifurcations.

4 Lyapunov functionals

In this section, we introduce candidate Lyapunov functionals, that will be used in the next Section. Those functionals are not defined on the whole X_+ space, yet we prove that they are well-defined on all complete orbits (hence all invariant subsets) included in suitable sets and that they are valid Lyapunov functionals.

4.1 Definitions

We first define the key function $g : \mathbb{R}_+^* \to \mathbb{R}_+$ by $g(z) = z - \ln(z) - 1$, known as the Volterra Lyapunov function. Note that $g(z) = 0$ if $z = 1$ and $g(z) > 0$ otherwise. Then we formally introduce the following functionals

$$L_0(x, y_1, y_2) = \int_0^\infty x_0^*(a)g\left(\frac{x(a)}{x_0^*(a)}\right)da + \frac{y_1}{c_1} + \frac{y_2}{c_2},$$

$$L_i(x, y_1, y_2) = \int_0^\infty x_i^*(a)g\left(\frac{x(a)}{x_i^*(a)}\right)da + \frac{y_i^*}{c_i}g\left(\frac{y_i}{y_i^*}\right) + \frac{y_j}{c_j}, \quad \forall i, j \in \{1, 2\},\ j \neq i. \tag{17}$$

In the case $\min(\mathcal{R}_{0,1}, \mathcal{R}_{0,2}) > 1$ and $\min(\gamma_{2\to1}, \gamma_{1\to2}) > 1$, we know from Proposition 3.4 (first item) that there exists a positive equilibrium $E_3 = (\overline{x}, \overline{y_1}, \overline{y_2})$. We define the associated functional

$$L_3(x, y_1, y_2) = \int_0^\infty \overline{x}(a)g\left(\frac{x(a))}{\overline{x}(a)}\right)\mathrm{d}a + \sum_{i=1}^2 \frac{\overline{y_i}}{c_i}g\left(\frac{y_i}{\overline{y_i}}\right).$$

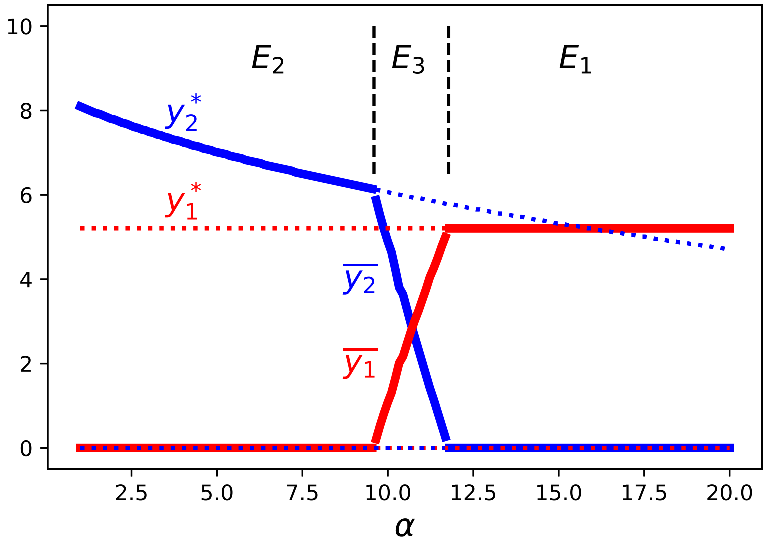

Figure 2: Bifurcation diagram for Example 3.14. Only the y_1 (red) and y_2 (blue) coordinates are depicted. wide and thin lines correspond to stable and unstable equilibrium coordinates. The upper vertical dotted lines separate three intervals for α in which the global attractor in $X_1 \cap X_2$ is E_2, E_3 or E_1. Parameters are (arbitrarily) set as follow : $c_1 = c_2 = \Lambda = 1$, $\mu_1 = \mu_2 = 0.1$ and $\mu_x \equiv 0.1$.

The domain of definition D_{L_0}, D_{L_1}, D_{L_2} and D_{L_3} of those functionals will be investigated in Lemma 4.3. We remind the following definition

Definition 4.1 (Lyapunov functional)**.** *Let S be a forward invariant subset of X_+. A function $L : S \to \mathbb{R}$ is called a Lyapunov functional on S if:*

- *L is continuous on S;*
- *the function $\mathbb{R}_+ \ni t \longmapsto L(\Phi_t(v))$ is non-increasing for every $v \in S$.*

If moreover $E = \{v \in S \ : \ \mathbb{R}_+ \ni t \longmapsto L(\Phi_t(v))$ is constant $\} \neq \emptyset$, we say that L is strict for E.

Definition 4.2 (Complete orbit)**.** *A set $\gamma \subset X_+$ is called a complete orbit for system* (1) *if there exists $\Psi : \mathbb{R} \to X_+$ such that $\gamma = \{\Psi(s),\ s \in \mathbb{R}\}$ and $\forall (t, s) \in \mathbb{R}_+ \times \mathbb{R}$, $\Phi_t(\Psi(s)) = \Psi(t + s)$. If $\eta \in \gamma$, we say that γ is a complete orbit through η and, without loss of generality, we can consider that $\Psi(0) = \eta$.*

Moreover, if $\{\Psi(s),\ s \in \mathbb{R}\}$ is a complete orbit through η, we define the set

$$\alpha(\eta) = \bigcap_{\tau \geq 0} \overline{\{\Psi(-t),\ t \geq \tau\}}.$$

4.2 Well-posedness of Lyapunov functionals

For L_0, L_1, L_2 and L_3 to be well defined and to be Lyapunov functionals, the components (x, y_1, y_2) must satisfy positive and regularity properties. The following lemma states that those properties are typically satisfied on complete orbits, since it imposes that the characteristic solution originates from the positive boundary condition. It will be used in Section 5 to prove the well-posedness of each functional L_i for $i \in [\![0, 3]\!]$ on omega-limit sets (Propositions 5.2 and 5.3) and to characterize the basins of attraction of all equilibria.

Lemma 4.3 (Well-posedness of Lyapunov functionals on bounded complete orbits)**.**

1. *Denote $\mathcal{O}_+$ the set of all bounded and complete orbits included in X_+, then $\mathcal{O}_+ \subset D_{L_0}$, in particular $E_0 \in D_{L_0}$. Moreover, suppose that one of the following assumptions hold :*

   (a) $\max(\mathcal{R}_{0,1}, \mathcal{R}_{0,2}) \leq 1$, $S = X_+$,

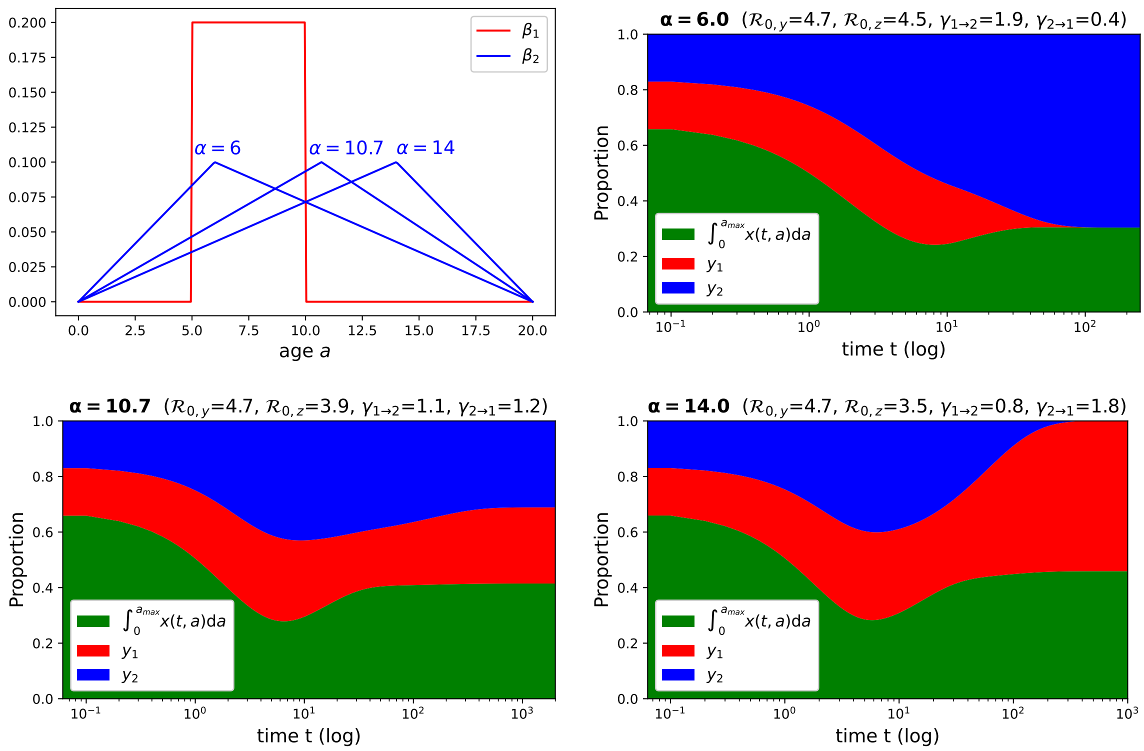

Figure 3: Top left) graphs of the functions β_1 and β_2 as defined in (16) for $\alpha = 6,\ 10.7$ and 14, corresponding to three areas of the bifurcation diagram in Figure 2. Top right, bottom left and right) Numerical simulations for $\alpha = 6,\ \alpha = 10.7$ and $\alpha = 14$ of the relative proportions of y_1, y_2 and $\int_0^{a_{\max}} x(t,a)\mathrm{d}a$, with $a_{\max} = 20$, $x_0 = e^{-0.05a}$ and $y_0 = z_0 = 3$.

   (b) $\mathcal{R}_{0,1} \leq 1$ *and* $S = \partial X_2$,

   (c) $\mathcal{R}_{0,2} \leq 1$ *and* $S = \partial X_1$,

   (d) $S = \partial X_1 \cap \partial X_2$,

   then L_0 *is a Lyapunov functional on* $\mathcal{O}_+ \cap S$*, strict for* $\{E_0\}$.

2. *Let* $i, j \in \{1, 2\}$ *with* $i \neq j$. *Denote* $\mathcal{O}_i$ *the set of all bounded and complete orbits included in* X_i. *If* $\mathcal{R}_{0,i} > 1$, *then* $\mathcal{O}_i \subset D_{L_i}$. *In particular,* $E_i \in D_{L_i}$. *Moreover, suppose that one of the following assumptions holds :*

   (a) $\gamma_{i\to j} < 1$ *and* $S = X_i$,

   (b) $S = X_i \cap \partial X_j$,

   (c) $\mathcal{R}_{0,j} > 1$, $\gamma_{i\to j} = 1$, $\gamma_{j\to i} \neq 1$ *and* $S = X_i$,

   (d) $\mathcal{R}_{0,j} > 1$, $\gamma_{i\to j} = \gamma_{j\to i} = 1$ *and* $S = X_i$,

   then L_i *is a Lyapunov functional on* $\mathcal{O}_i \cap S$ *and* L_i *is strict for* $\{E_i\}$ *if* (*a*), (*b*) *or* (*c*) *is true and strict for* $E_\infty \cup \{E_i\}$ *if* (*d*) *is true.*

3. *If* $\min(\mathcal{R}_{0,1}, \mathcal{R}_{0,2}) > 1$, $\gamma_{2\to1} > 1$ *and* $\gamma_{1\to2} > 1$, *then* E_3 *(as defined in Proposition 3.4) is the only equilibrium in* $X_1 \cap X_2$ *and* L_3 *is a well-defined Lyapunov functional on* $\mathcal{O}_1 \cap \mathcal{O}_2 \subset D_{L_3}$*, strict for* $\{E_3\}$.

Remark that, from (13), the assumption $\gamma_{i\to j} < 1$ in Lemma 4.3 is always satisfied if $\mathcal{R}_{0,j} \leq 1$. To prove Lemma 4.3 we need to introduce the following Lemma.

Lemma 4.4 (Differentiability of the semi-flow along the complete orbits)**.** *If there exists a complete orbit through* $v \in X_+$, *then* $t \longmapsto \Phi_t(v) \in C^1(\mathbb{R}_+, X)$, *i.e. is continuously differentiable in* X.

Proof of Lemma 4.4. Set $v = (x, y_1, y_2) \in X_+$ and $\tilde{v} = ((0, x), y_1, y_2) \in \mathcal{X}_{0+}$. [16, Theorem 5.6.6, p. 242] states that if $\tilde{v} \in D(A)$ and $A\tilde{v} + F(\tilde{v}) \in \mathcal{X}_0$, then $t \longmapsto \Phi_t(v)$ is continuously differentiable in $L^1(\mathbb{R}_+, \mathbb{R}_+) \times \mathbb{R}^2_+$. This theorem also requires F to be continuously differentiable, which is readily verified as each term in the expression of F is a bilinear form.

Here, we prove that if there exists a complete orbit $\Psi = (\Psi^x, \Psi^1, \Psi^2)$ through v, then necessarily $\tilde{v} \in D(A)$ and $A\tilde{v} + F(\tilde{v}) \in \mathcal{X}_0$. Indeed, let Ψ be a complete orbit through v, such that $\Psi(0) = v$, then for $a \geq 0$ the method of characteristics implies that

$$x(a) = \Psi^x(0)(a) = \Lambda e^{-G(a)}, \text{ with } G(a) := \int_0^a \mu_x(s) + \sum_{i=1}^{2} \beta_i(s)\Psi^i(s-a)\mathrm{d}s.$$

Consequently, $x(a) \leq \Lambda e^{-a\mu_0}$, so $x \in L^1(\mathbb{R}_+, \mathbb{R}_+)$. Moreover, since F is positive and absolutely continuous and since $t \longmapsto e^{-t}$ is Lipschitz continuous on $\mathbb{R}_+$, x is also absolutely continuous, then differentiable almost everywhere. Finally, x is clearly decreasing, then

$$\int_0^{+\infty} |x'(a)| da = -\int_0^{+\infty} x'(a)\mathrm{d}a = \lim_{a\to+\infty} x(0) - x(a) = \Lambda < +\infty.$$

We just proved that $x \in W^{1,1}(\mathbb{R}_+)$, then $\tilde{v} \in D(A)$. Finally, $x(0) = \Lambda$ is readily verified, so $A\tilde{v} + F(\tilde{v}) \in \mathcal{X}_0$. $\square$

Now we can prove Lemma 4.3.

Proof of Lemma 4.3.

1. First we show that L_0 is well defined on $\mathcal{O}_+$.

   Let $v \in X_+$ such that there exists a bounded and complete orbit $\Psi = (\Psi^x, \Psi^1, \Psi^2)$ which satisfies $\Psi(0) = v$.

   For any $a \geq 0$, if $t > a$, then $\Psi^x(t)(a) = \Phi^x_t(\Psi(0)) = \Phi^x_t(v)$. If $t \leq a$, then for any $b > a - t$, $\Psi^x(t)(a) = \Phi^x_{t+b}(\Psi(-b))(a)$. In both cases, formula (5) and the boundedness of Ψ implies

   $$0 < \Lambda e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-a\|\beta_i\|_{L^\infty}\|\Psi^i\|_{L^\infty(\mathbb{R})}} < \Psi^x(t)(a) = \Lambda e^{-\int_0^a \mu_x(s)+\sum_{i=1}^2 \beta_i(s)\Psi^i(t-a+s)\mathrm{d}s} \leq \Lambda e^{-a\mu_0}$$

   so that for any $t \in \mathbb{R}$, $a \longmapsto x_0^*(a) g(\Psi^x(t)(a)/x_0^*)$ is well defined on $\mathbb{R}_+$. From Assumption 2.1, simple comparisons prove that the integral of the latter function, that appears in the definition of L_0, is well defined.

   Next we prove the Lyapunov decreasing property. Let $t \geq 0$ and set $(x(t,\cdot), y_1(t), y_2(t)) = \Phi_t(v)$. From Lemma 4.4, we can compute the following derivative

   $$\begin{aligned}\frac{dL_0}{dt}(\Phi_t(v)) &= \int_0^\infty \left(1 - \frac{x_0^*(a)}{x(t,a)}\right) \partial_t x(t,a)\mathrm{d}a + \sum_{i=1}^{2} \frac{y_i'(t)}{c_i} \\ &= -\int_0^\infty \left(1 - \frac{x_0^*(a)}{x(t,a)}\right) \left(\partial_a x(t,a) + (\mu_x(a) + \sum_{i=1}^{2} \frac{y_i(t)}{c_i}\beta_i(a))x(t,a)\right) \mathrm{d}a \\ &\quad + \sum_{i=1}^{2} y_i(t) \left(\int_0^\infty \beta_i(a)x(t,a)\mathrm{d}a - \frac{\mu_i}{c_i}\right).\end{aligned}$$

   We use the fact that

   $$x_0^*(a)\frac{dg}{da}\left(\frac{x(t,a)}{x_0^*(a)}\right) = \left(1 - \frac{x_0^*(a)}{x(t,a)}\right)\left(\partial_a x(t,a) - \frac{x(t,a)x_0^{*\prime}(a)}{x_0^*(a)}\right) = \left(1 - \frac{x_0^*(a)}{x(t,a)}\right)(\partial_a x(t,a) + \mu_x(a)x(t,a))$$

   whence

   $$\begin{aligned}\frac{dL_0}{dt}(\Phi_t(v)) &= -\int_0^\infty x_0^*(a)\frac{\mathrm{d}g}{\mathrm{d}a}\left(\frac{x(t,a)}{x_0^*(a)}\right)\mathrm{d}a - \int_0^\infty (x(t,a) - x_0^*(a))\sum_{i=1}^{2} y_i(t)\beta_i(a)\mathrm{d}a \\ &\quad + \sum_{i=1}^{2} y_i(t)\left(\int_0^\infty \beta_i(a)x(t,a)\mathrm{d}a - \frac{\mu_i}{c_i}\right) \\ &= -\int_0^\infty \mu_x(a)x_0^*(a)g\left(\frac{x(t,a)}{x_0^*(a)}\right)da + \sum_{i=1}^{2} y_i(t)\left(\int_0^\infty \beta_i(a)x_0^*(a)\mathrm{d}a - \frac{\mu_i}{c_i}\right).\end{aligned}$$

We finally end up with

$$\frac{dL_0}{dt}(\Phi_t(v)) = -\int_0^\infty \mu_x(a)x_0^*(a)g\left(\frac{x(t,a)}{x_0^*(a)}\right)\mathrm{d}a + \sum_{i=1}^2 \frac{\mu_i}{c_i}y_i(t)(\mathcal{R}_{0,i}-1) \tag{18}$$

and we can actually show that

$$\frac{dL_0}{dt}(\Phi_t(v)) \le -\int_0^\infty \mu_x(a)x_0^*(a)g\left(\frac{x(t,a)}{x_0^*(a)}\right)da \le 0.$$

Indeed, it is clear if $\max_{i\in\{1,2\}}\{\mathcal{R}_{0,i}\} \le 1$, which proves case (a). Finally (b), (c) and (d) are direct consequences of the positive invariance of ∂X_i for $i \in \{1,2\}$ (Proposition 3.7) so that for any $i \in \{1,2\}$ and initial condition in ∂X_i, $y_i(t) = 0$ for all $t \ge 0$.

Finally, suppose that $t \longmapsto L_0(\Phi_t(v))$ is constant on $\mathbb{R}_+$. Then from equation (18), $\forall t \ge 0,\ x(t,.) = x_0^*$. If moreover $R_{0,i} < 1$ for some $i \in \{1,2\}$, then $y_i \equiv 0$. Otherwise, if $R_{0,i} = 1$, then injecting the relation $\forall t \in \mathbb{R}_+,\ x(t,.) = x_0^*$ in the first equation of (1) leads for every $t \in \mathbb{R}_+$ and a.e. $a \ge 0$ to $\beta_1(a)y_1(t) + \beta_2(a)y_2(t) = 0$.

Since $\beta_i \equiv 0$ would be a contradiction with $R_{0,i} = 1$, we can conclude that $y_i \equiv 0$.

Consequently, $t \longmapsto L_0(\Phi_t(v))$ is constant on $\mathbb{R}_+$ if and only if $v = E_0$.

2. Let $v \in X_1$ such that there is a bounded and complete orbit $\{\Psi(t), t \in \mathbb{R}\}$ through v (such a v exists, since the constant orbit $\{E_1\}$ is one). We prove just as above that if $\mathcal{R}_{0,1} > 1$, then for any $t \in \mathbb{R}$, $a \longmapsto x_1^*(a)g(\Psi^x(t)(a)/x_1^*)$ is well defined on $\mathbb{R}_+$ and is in $L^1(\mathbb{R}_+,\mathbb{R}_+)$. The term $g(\Psi^1(t)/y_1^*)$ is also well defined since X_1 is invariant. So, for all $t \in \mathbb{R},\ L_1(\Psi(t))$ is well defined.

   Denote $(x(t,\cdot), y_1(t), y_2(t)) = \Phi_t(v)$ and let $t \ge 0$, then from Lemma 4.4 we can compute the following derivative:

$$\begin{aligned}
\frac{dL_1}{dt}(\Phi_t(v)) &= -\int_0^\infty \left(1-\frac{x_1^*(a)}{x(t,a)}\right)\left(\partial_a x(t,a) + x(t,a)\left(\mu_x(a) + \sum_{i=1}^2 y_i(t)\beta_i(a)\right)\right)\mathrm{d}a + \left(1-\frac{y_1^*}{y_1(t)}\right)\frac{y_1'(t)}{c_1} + \frac{y_2'(t)}{c_2}\\
&= -\int_0^\infty x_1^*(a)\frac{dg}{da}\left(\frac{x(t,a)}{x_1^*(a)}\right)\mathrm{d}a - \int_0^\infty \left(1-\frac{x_1^*(a)}{x(t,a)}\right)(\beta_1(a)(y_1(t)-y_1^*) + y_2(t)\beta_2(a))x(t,a)\mathrm{d}a\\
&\quad + \frac{(y_1(t)-y_1^*)}{c_1}\left(c_1\int_0^\infty \beta_1(a)x(t,a)\mathrm{d}a - \mu_1\right) + \frac{z(t)}{c_2}\left(c_2\int_0^\infty \beta_2(a)x(t,a)\mathrm{d}a - \mu_2\right)\\
&= -\int_0^\infty (\mu_x(a) + y_1^*\beta_1(a))\,x_1^*(a)g\left(\frac{x(t,a)}{x_1^*(a)}\right)\mathrm{d}a + (y_1(t)-y_1^*)\left(\int_0^\infty \beta_1(a)x_1^*(a)da - \frac{\mu_1}{c_1}\right)\\
&\quad + y_2(t)\left(\int_0^\infty \beta_2(a)x_1^*(a)\mathrm{d}a - \frac{\mu_2}{c_2}\right)\\
&= -\int_0^\infty (\mu_x(a) + y_1^*\beta_1(a))\,x_1^*(a)g\left(\frac{x(t,a)}{x_1^*(a)}\right)da + y_2(t)\frac{\mu_2}{c_2}(\gamma_{1\to 2} - 1),
\end{aligned} \tag{19}$$

   where we used the equalities

$$\begin{aligned}
x_1^*(a)\frac{dg}{da}\left(\frac{x(t,a)}{x_1^*(a)}\right) &= \left(1-\frac{x_1^*(a)}{x(t,a)}\right)\left(\partial_a x(t,a) - \frac{x(t,a)x_1^{*\prime}(a)}{x_1^*(a)}\right)\\
&= \left(1-\frac{x_1^*(a)}{x(t,a)}\right)(\partial_a x(t,a) + (\mu_x(a) + \beta_1(a)y_1^*)x(t,a))
\end{aligned}$$

   and

$$c_1\int_0^\infty \beta_1(a)x_1^*(a)da = \mu_1, \qquad c_2\int_0^\infty \beta_2(a)x_1^*(a)da = \mu_2\gamma_{1\to 2}.$$

   We first consider the case $\gamma_{1\to 2} < 1$. Remember that $g(x/x_1^*) = 0$ if and only if $x = x_1^*$, so

$$\frac{dL_1}{dt}(\Phi_t(v)) \le 0,$$

   with equality if and only if $x(t,\cdot) = x_1^*$ and $y_2(t) = 0$, in particular $\frac{dL_1}{dt}(\Phi_t(E_1)) = 0$.

   Note that if $x(t,\cdot) = x_1^*$, $y_2(t) = 0$ and $y_1(t) \ne y_1^*$, then $\partial_t x(t,a) \ne 0$ so there is no $v \in X_+\backslash\{E_1\}$ such that for all $t \ge 0$, $\frac{dL_1}{dt}(\Phi_t(v)) = 0$. We then deduce (a) and (b).

Now we consider the case $\mathcal{R}_{0,2} > 1, \gamma_{1\to 2} = 1$ and $\gamma_{2\to 1} \neq 1$. In this case, L_1 is constant on the positive orbit $\{\Phi_t(v), t \geq 0\}$ if and only if $x(t,\cdot) \equiv x_1^*$. Then the two first equations in (1), along with (11), lead, for all $t \geq 0$ and a.e. $a \geq 0$, to

$$y_2(t)\beta_2(a) = (y_1^* - y_1(t))\beta_1(a) \quad \text{ and } \quad y_1'(t) = 0.$$

In particular, y_1 is constant. Note that $\beta_2 \not\equiv 0$, otherwise it would be a contradiction with $\gamma_{1\to 2} = 1$, then y_2 is also constant. Consequently, either for all $t \geq 0$, $y_1(t) = y_1^*$ and $y_2(t) = 0$, then $\{\Phi_t(v), t \geq 0\} = \{E_1\}$ is the only orbit on which L_1 is constant and the proof is complete, or for all $t \geq 0$, $y_1(t) \neq y_1^*$. The latter case implies that for all $t \geq 0$ and $a \geq 0$,

$$\beta_1(a) = \delta\beta_2(a) \text{ where } \delta = \frac{y_2(t)}{y_1^* - y_1(t)} \text{ is constant.}$$

Moreover $\delta \neq 0$, otherwise we would have $\beta_1 \equiv 0$, which is not compatible with $\mathcal{R}_{0,1} > 1$.

Since $\gamma_{1\to 2} = 1$ and $\beta_1 = \delta\beta_2$, the definition of $\gamma_{1\to 2}$ in (13) and equation (11) lead to $\delta = \frac{\mu_1 c_2}{\mu_2 c_1}$.

Injecting the relation $\beta_1 = \mu_1\beta_2/\mu_2$ into the definition of $\gamma_{2\to 1}$ ultimately gives $\gamma_{2\to 1} = 1$, which is absurd. Then $\Phi_t(v) \equiv E_1$.

Finally, consider the case (d) with $\mathcal{R}_{0,j} > 1$ and $\gamma_{i\to j} = \gamma_{j\to i} = 1$. Just as above, L_1 is constant on the positive orbit $\{\Phi_t(v), t \geq 0\}$ if and only if $x(t,\cdot) \equiv x_1^*$. Remember that $x_1^* = x_2^*$ when $\gamma_{1\to 2} = \gamma_{2\to 1} = 1$ (by Proposition 3.4). Then injecting (11) in (1) implies that for all $t \in \mathbb{R}$, $y_1'(t) = y_2'(t) = 0$. Consequently γ is a constant orbit in X_1, *i.e.* a positive equilibrium, then belongs to $E_\infty \cup \{E_1\}$.

This achieves the proof, and the same applies for the L_2 case.

3. The existence of an equilibrium $E_3 = (\overline{x}, \overline{y_1}, \overline{y_2}) \in \cap_{k\in\{1,2\}} X_k$ has been established in Section 3.1. The well-posedness of L_3 on $\mathcal{O}_1 \cap \mathcal{O}_2$ is obtained exactly as above for the one of L_1 and L_2. Let $v \in X_1 \cap X_2$ such that there exists a bounded and complete orbite through v (such a v exists as the constant orbit $\{E_3\}$ is one). Denote $(x(t,\cdot), y_1(t), y_2(t)) = \Phi_t(v)$ and let $t \geq 0$, then from Lemma 4.4, we can compute the following derivative.

   If $v = E_3$, then $t \longmapsto L_3(\Phi_t(V))$ is readily constant, it remains to prove that the reciprocal is true.

   Indeed, differentiating as in the proof of the second item leads to

$$\frac{\mathrm{d}L_3}{\mathrm{d}t}(\Phi_t(v)) = -\int_0^\infty \left(\mu_x(a) + \sum_{k\in\{1,2\}} \beta_k(a)\overline{y_k}\right) \overline{x}(a) g\left(\frac{x(t,a)}{\overline{x}(a)}\right) \mathrm{d}a \leq 0.$$

   Assume $t \longmapsto L_3(\Phi_t(v))$ is constant on $\mathbb{R}_+$. Then the previous derivaritives implies that for any $t \geq 0$, $\Phi_t^x(v) = \overline{x}$. Moreover, the definition of $\overline{x}$ (equation (12)) implies that, for any $k \in \{1,2\}$,

$$c_k \int_0^\infty \beta_k(a)\overline{x}(a)\mathrm{d}a = \mu_k.$$

   Consequently, system (1), implies that y_1 and y_2 are constant and that, for any $a \geq 0$,

$$\sum_{k\in\{1,2\}} y_k(t)\beta_k(a) = \sum_{k\in\{1,2\}} \overline{y_k}\beta_k(a).$$

   Suppose that $y_1 \not\equiv \overline{y_1}$. Then for any $a \geq 0$,

$$\beta_1(a) = \delta\beta_2(a) \text{ with } \delta = -\frac{y_2 - \overline{y_2}}{y_1 - \overline{y_1}}.$$

   Note that $\gamma_{2\to 1} > 1$ implies that $\delta \neq 0$. Indeed, otherwise we would have $\beta_1 \equiv 0$ and then $\gamma_{2\to 1} = 0$.

   Injecting this relation in the definition (13) of $\gamma_{2\to 1}$ leads to

$$\gamma_{2\to 1} = \frac{c_1\delta}{\mu_1}\int_0^\infty \beta_2(a)x_2^*(a)\mathrm{d}a = \frac{c_1\mu_2}{c_2\mu_1}\delta$$

   where the last equality results from the definition (11) of y_2^*. Similarly $\gamma_{1\to 2} = \dfrac{c_2\mu_1}{c_1\mu_2}\dfrac{1}{\delta} = 1/\gamma_{2\to 1}$. Consequently $\gamma_{1\to 2}\gamma_{2\to 1} = 1$, which is absurd and then $t \longmapsto L_3(\Phi_t(v))$ is constant if and only if $v = E_3$.

   Consequently, the only positive orbit on which $t \longmapsto L_3(\Phi_t)$ is constant is $\{E_3\}$, that is, L_3 is a Lyapunov functional on $\omega(v)$, strict for E_3.

   Since a positive equilibrium is, in particular, a positive orbit, the former proof also implies that E_3 is the only equilibrium in $X_1 \cap X_2$.

□

5 Global analysis and proof of the main results

In this section we handle the attractivity of the equilibria and compute their basin of attraction. To prove the stability, we will actually prove that $\{E_i\}$ not only attracts the points, but also the compact sets in their basin. We proved in Lemma 2.6 that for any $v \in X_+$, $\Phi_t(v)$ converges to $\omega(v)$. In this section, we prove that, under suitable conditions, each compact set K is attracted by an invariant and compact set $\omega(K)$, on which the Lyapunov functionals L_i (for $i \in [\![0,3]\!]$) are well-defined, and which contains their critical point E_i. In particular, this requires to prove the uniform persistence of the flow to guarantee that y_i does not vanish on $\omega(K)$, so that $\omega(K)$ belongs to the suitable subset identified in Lemma 4.3.

It may be tempting to conclude that $\omega(K) = \{E_i\}$ once one has shown that $\omega(w) = \{E_i\}$ for every $w \in \omega(K)$, however this is not true in general. In other words, the convergence to $\omega(K)$ and then to $\omega(w)$ is not transitive as we only get $\omega(w) \subset \omega(K)$, even if $\omega(K)$ is compact and invariant (see [29, Example p.224] for a simple counter-example). Instead, if we can define a Lyapunov functional on $\omega(K)$, strict for $\{E_i\}$, then $\omega(K)$ reduces to $\{E_i\}$. This is a special case of Theorem 2.52 from [28], which generalises the LaSalle invariance principle and implies that a strict Lyapunov functional cannot be defined on an invariant compact set larger than the singleton reduced to its critical point.

5.1 Proof of Lemma 3.3

Proof of (3) $\Rightarrow$ (1)**.** This is a straightforward consequence of the definition of y_1^* and y_2^*.

Proof of (1) $\Rightarrow$ (2)**.** Let $v = (x_0, y_{1,0}, y_{2,0}) \in X_1 \cap X_2$ where for all $a \geq 0$, $x_0(a) = \Lambda e^{-a}$. Then straightforward calculations prove that L_1 and L_2 are well-defined in v and on the positive orbit starting from $\{v\}$. Since x_0 is, in particular, in $W^{1,1}(\mathbb{R}_+)$ then [16, Theorem 5.6.6, p. 242] applies and we can differentiate $t \longmapsto L_1(\Phi_t(v))$ as is the proof of Lemma 4.3. It follows from (19) that $t \longmapsto L_1(\Phi_t(v))$ is decreasing, then converges, so its derivative converges to 0, that is $\Phi_t^x(v)$ converges to x_1^* in $L^1(\mathbb{R}_+, \mathbb{R}_+)$. The same arguments applied to L_2 show that $\Phi_t^x(v)$ converges to x_2^* in $L^1(\mathbb{R}_+, \mathbb{R}_+)$. Consequently $x_1^* = x_2^*$ in $L^1(\mathbb{R}_+)$, that is, for a.e. $a \geq 0$:

$$\Lambda e^{-\int_0^a \mu_x(s)ds} e^{-y_1^* \int_0^a \beta_1(s)\mathrm{d}s} = \Lambda e^{-\int_0^a \mu_x(s)ds} e^{-y_2^* \int_0^a \beta_2(s)\mathrm{d}s}$$

then

$$y_1^* \int_0^a \beta_1(s)\mathrm{d}s = y_2^* \int_0^a \beta_2(s)\mathrm{d}s$$

and finally $y_1^* \beta_1(a) = y_2^* \beta_2(a)$ a.e. $a \geq 0$.

Proof of (2) $\Rightarrow$ (3)**.** Equation (11) with $i = 1$ states that

$$c_1 \int_0^\infty \beta_1(a) x_1^*(a)\mathrm{d}a = c_1 \Lambda \int_0^\infty \beta_1(a) e^{-\int_0^a \mu_x(s)\mathrm{d}s} e^{-y_1^* \int_0^a \beta_1(s)\mathrm{d}s}\mathrm{d}a = \mu_1.$$

With the second item of Lemma 3.3, it rewrites as

$$\frac{c_1 \Lambda y_2^*}{y_1^*} \int_0^\infty \beta_2(a) e^{-\int_0^a \mu_x(s)ds} e^{-y_2^* \int_0^a \beta_2(s)\mathrm{d}s}\mathrm{d}a = \frac{c_1 \Lambda y_2^*}{y_1^*} \int_0^\infty \beta_2(a) x_2^*(a)\mathrm{d}a = \mu_1$$

Using equation (11), now with $i = 2$, we obtain

$$c_1 y_2^* \mu_2 = c_2 \mu_1 y_1^*.$$

Since $y_2^* \beta_2(a) = y_1^* \beta_1(a)$ almost everywhere $a \geq 0$, multiplying each side by β_2 leads to the third item of Lemma 3.3. □

5.2 Proof of Theorem 3.8 : Attractivity of E_0

We introduce the local notations $L_* = L_0$ and $E_* = E_0$, so that the same proof can be reused later for different settings.

The proof proceed in two steps. First we prove that every compact set $K \in S$ is attracted by a compact subset of $\omega(K) \subset S$. The second step basically follows the proof of [28, Theorem 2.52] to prove that $\omega(K)$ reduces to E_*

Let $K \subset S$ be a compact set. From Proposition 2.4 Φ is asymptotically smooth on X_+. From equation (4), $t \longmapsto \|\Phi_t(K)\|_X$ is bounded on $\mathbb{R}_+$ (in the vocabulary of [28], Φ is eventually bounded on K). Then [28, Proposition 2.27] states that $\omega(K) := \cap_{t\geq 0}\overline{\{\Phi_s(K), s\geq t\}}$ is a compact invariant set that attracts K. Moreover, since S is invariant and closed, then $\omega(K)\subset S$.

Next, we prove that $\omega(K)=\{E_*\}$. Since $\omega(K)$ is invariant and compact, there exists a bounded and complete orbit through any element of it. Then we know from Lemma 4.3 that L_* is a well defined Lyapunov functional on $\omega(K)$. Let $v\in\omega(K)$ and $\gamma(v)=\{\Psi(t), t\in\mathbb{R}\}\subset\omega(K)$ be a complete and bounded orbit through v. The compactness of $\omega(K)$ implies that $\omega(v)\subset\omega(K)$ and $\alpha(v)\subset\omega(K)$. It follows from [28, Proposition 2.51] that L_* is constant on the invariant sets $\alpha(v)$ and $\omega(v)$, in particular $t\longmapsto L_*\circ\Phi_t(u)$ is constant for any $u\in\alpha(v)\cup\omega(v)$. Then Lemma 4.3 implies that necessarily $u\in\{E_*\}$, so that $\omega(v)=\alpha(v)=\{E_*\}$, in particular $\{E_*\}\subset\omega(K)$. Consequently $\lim_{t\to-\infty}L_*(\Psi(t))=\lim_{t\to+\infty}L_*(\Psi(t))=L_*(E_*)$. This implies that $v=E_*$, indeed $t\longmapsto L_*\circ\Phi_t(u)$ is decreasing for any $u\in\omega(K)\backslash\{E_*\}$ (Lemma 4.3). Then $\omega(K)=\{E_*\}$. We proved that $\{E_*\}=\omega(K)$ attracts K, then $\{E_*\}$ attracts every compact set of S.

We just proved that $\{E_*\}$ is a compact attractor of compact sets (in particular, an attractor of points) in S. Since Φ is also state-continuous, uniformly in finite time (Proposition 2.4), [28, Theorem 2.39] states that $\{E_*\}$ is stable. $\square$

5.3 Proof of Theorem 3.10 : case with only one non-trivial equilibrium

We characterise the attractivity of E_1 and E_2 in the case where only one of them exists (*i.e.* $\mathcal{R}_{0,1}>1\geq\mathcal{R}_{0,2}$ or $\mathcal{R}_{0,2}>1\geq\mathcal{R}_{0,1}$), or when we restrict the dynamics to a one-predator model (*i.e.* to the boundary ∂X_1 or ∂X_2).

Definition 5.1 (persistence [28]). *Let $\rho: X_+\to\mathbb{R}_+$. The semiflow Φ is uniformly weakly $\rho-$persistent if there exists $\varepsilon>0$ such that*

$$u\in X_+, \rho(u)>0\Longrightarrow \limsup_{t\to+\infty}\rho(\Phi_t(u))\geq\varepsilon.$$

If we can replace $\limsup$ *with* $\liminf$ *in the former, then Φ is said to be uniformly $\rho-$persistent.*

We want to show that under suitable conditions, for any $v\in X_i$ with $i\in\{1,2\}$ then $\omega(v)\subset X_i$, so that Lemma 4.3 implies that the appropriate Lyapunov functional is well defined on $\omega(v)$. To do so, we make use of [28, Theorem 8.20, p.189] (see also [11]) to conclude on the uniform persistence of the flow based only on its behaviour on the boundary set $\rho^{-1}(\{0\})$ (here ∂X_1 and ∂X_2) and near the attractor included in this set.

Proposition 5.2 (Well-posedness of Lyapunov functional on omega-limit sets : case with only one non trivial equilibrium)**.** *Let $(i,j)\in\{1,2\}^2, j\neq i$ and suppose that $\mathcal{R}_{0,i}>1$. Define $\rho_i: X_+\to\mathbb{R}_+$, $(x,y_1,y_2)\longmapsto y_i$. Then the restriction of the semiflow Φ to the invariant set ∂X_j is uniformly ρ_i-persistent. If moreover $\mathcal{R}_{0,j}\leq 1$ then Φ is uniformly ρ_i-persistent.*

Proof. We only provide a proof for the uniform persistence on X_+ when $\mathcal{R}_{0,i}>1$ and $\mathcal{R}_{0,j}\leq 1$. The other case is similar.

From Theorem 3.8, $\{E_0\}$ is globally attractive in ∂X_i (since $\mathcal{R}_{0,j}\leq 1$) and consequently $\bigcup_{u\in\partial X_i}\omega(u)=\{E_0\}$. Below, we prove the four required assumptions to apply [28, Theorem 8.20], which states that Φ is uniformly weakly ρ_i-persistent.

1) $\{E_0\}$ **is trivially compact and invariant.**

2) E_0 **is isolated in** ∂X_i**,** *i.e.* the maximal compact invariant set of a neighborhood of itself in ∂X_i. Actually we already proved in the proof of Theorem 3.8 the stronger property that $\{E_0\}$ is the only compact invariant set in ∂X_i.

3) $\{E_0\}$ **is acyclic in** ∂X_i**,** *i.e.* apart from the constant orbit $\{E_0\}$, there is no complete orbit $\gamma\subset\partial X_i$ connecting $\{E_0\}$ to itself (a homoclinic loop). Indeed, consider $u\in\partial X_i$, $u\neq E_0$ and $\gamma(u)$ a homoclinic loop through u in ∂X_i. Then the proof from the previous point applies and $\gamma(u)=\{E_0\}$.

4) $\{E_0\}$ **is uniformly weakly repelling in** X_i**,** *i.e.* $\exists\ \varepsilon>0$ such that $\limsup_{t\to+\infty}\|E_0-\Phi_t(u)\|_X\geq\varepsilon$ for any $u\in X_i$. Indeed, let $u\in X_i$ and denote $\Phi_t(u)=(x(t),y_1(t),y_2(t))$, then for any $t\geq 0$:

$$\begin{aligned} y_i'(t)=&y_i(t)\left(c_i\int_0^\infty\beta_i(a)(x(t,a)-x_0^*(a))\mathrm{d}a+c_i\int_0^\infty\beta_i(a)x_0^*(a)\mathrm{d}a-\mu_i\right)\\ =&y_i(t)\left(c_i\int_0^\infty\beta_i(a)(x(t,a)-x_0^*(a))\mathrm{d}a+\mu_i(\mathcal{R}_{0,i}-1)\right).\end{aligned}$$

Set $\varepsilon=\frac{\mu_i(\mathcal{R}_{0,i}-1)}{2c_i||\beta_i||_{L^\infty}}$ and assume that $\limsup_{t\to+\infty}\|E_0-\Phi_t(u)\|_X<\varepsilon$. Then $\exists\ T>0$, $\forall t\geq T$, $|x(t,\cdot)-x_0^*|_{L^1}<\varepsilon$ implying that $\forall t\geq T$, $y_i'(t)>y_i(t)\left(\mu_i(\mathcal{R}_{0,i}-1)-c_i||\beta_i||_{L^\infty}\varepsilon\right)$, with $\mu_i(\mathcal{R}_{0,1}-1)-c_i||\beta_i||_{L^\infty}\varepsilon>0$. We would get $\lim_{t\to+\infty}y_i(t)=+\infty$, which contradicts $\limsup_{t\to+\infty}\|E_0-\Phi_t(u)\|_X<\varepsilon$.

Then Φ is uniformly weakly ρ_i-persistent and the existence of a global attractor (by corollary 2.5) implies that it is actually uniformly ρ_i-persistent ([28, Theorem 5.2 and hypothesis H0 p.125]). $\square$

Proposition 5.2 allows to conclude on the attractivity of positive equilibrium in the special case where there exists only one non-trivial equilibrium, or when we restrict the dynamics to a one-predator model, as stated in Theorem 3.10 proved below.

Proof of Theorem 3.10. The proof proceeds exactly as for Theorem 3.8, with $L_* = L_i$ and $E_* = E_i$, except that here S is not closed. In this case, the inclusion $\omega(K) \subset S$ is obtained because S is invariant and Φ is uniformly ρ_i-persistent (Proposition 5.2), so that for any compact $K \subset S$, $\omega(K) \subset \{(x, y_1, y_2) \in S \ : \ y_i \geq \varepsilon\} \subset S$, where ε is the one from the definition 5.1 of the uniform persistence.

Note that for the second item, one requires the additional hypothesis $\gamma_{i\to j} < 1$ to guarantee that L_* is a Lyapunov functional, strict for $\{E_i\}$, on the compact invariant set $\omega(K) \subset S = X_i$ (Lemma 4.3.2.a). This is readily satisfied since $\mathcal{R}_{0,i} > 1$ implies that $\|\beta_i\|_{L^1} > 0$, then $\gamma_{i\to j} < \mathcal{R}_{0,j} \leq 1$ (Remark 3.2). □

5.4 Proofs of Theorems 3.11 and 3.12 : case with two non-trivial equilibria

In this case, at least two non-trivial equilibria exist and the following proposition takes the role of Proposition 5.2

Proposition 5.3 (Well-posedness of Lyapunov functional on omega-limit sets : case with multiple non trivial equilibria)**.**

Let $(i,j) \in \{1,2\}^2$, $i \neq j$ and suppose $\min\limits_{i\in\{1,2\}} \{\mathcal{R}_{0,i}\} > 1$. Define $\rho_i : X_+ \to \mathbb{R}_+$, $(x, y_1, y_2) \longmapsto y_i$, $\rho_{1,2} : X_+ \to \mathbb{R}_+$, $(x, y_1, y_2) \longmapsto \min(y_1, y_2)$ and $\rho_{1+2} : X_+ \to \mathbb{R}_+$, $(x, y_1, y_2) \longmapsto y_1 + y_2$. Then :

1. *$\gamma_{j\to i} \geq 1$ or $\gamma_{i\to j} \geq 1$.*
2. *If $\gamma_{j\to i} = 1$, then $\gamma_{i\to j} \geq 1$.*
3. *If $\gamma_{j\to i} > 1$ then the semiflow Φ is uniformly ρ_i-persistent.*
4. *If $\gamma_{j\to i} > 1$ and $\gamma_{i\to j} > 1$ then the semiflow Φ is uniformly $\rho_{1,2}$-persistent.*
5. *If $\gamma_{1\to 2} = \gamma_{2\to 1} = 1$, then the semiflow Φ is uniformly ρ_{1+2}-persistent.*

Proof.

1. Suppose that $\gamma_{j\to i} < 1$ and $\gamma_{i\to j} < 1$, then, exactly as for the case $\gamma_{j\to i} > 1$ and $\gamma_{i\to j} > 1$ (see Proposition 3.4.1), there would exist at least one equilibrium $E_3 \in \cap_{k\in\{1,2\}} X_k$. Moreover, since $\{E_3\}$ is a complete orbit included in $\cap_{k\in\{1,2\}} X_k \subset X_i$, Lemma 4.3 states that L_i is well defined on $\{E_3\}$. Since E_3 is an equilibrium, the function $t \longmapsto L_i(\Phi_t(E_3))$ is constant. On the other hand, since $\gamma_{i\to j} < 1$, L_i is a Lyapunov functional on the complete (and constant) orbit through E_3, strict for E_i, and then $t \longmapsto L_i(\Phi_t(E_3))$ is decreasing. This is absurd, then it is not possible that $\gamma_{j\to i} < 1$ and $\gamma_{i\to j} < 1$.

2. Suppose that $\gamma_{j\to i} = 1$ and $\gamma_{i\to j} < 1$. Set $v = (x_0, y_{1,0}, y_{2,0}) \in \cap_{k\in\{1,2\}} X_k$ where for all $a \geq 0$, $x_0(a) = \Lambda e^{-a}$. Then, exactly as in the proof of Lemma 3.3, we conclude that $\Phi^x_t(v)$ converges to $x_i^* = x_j^*$ on $L^1(\mathbb{R}_+, \mathbb{R}_+)$, that $t \longmapsto L_j(\Phi_t(v))$ and $t \longmapsto L_i(\Phi_t(v))$ are decreasing and that their derivatives converge to zero. In particular, the latter implies that $\Phi^j_t(v)$ converges to zero (equation (19)). In turn, this would imply that $\lim_{t\to+\infty} L_j(\Phi_t(v)) = +\infty$, by definition of L_j in (17), which is absurd since $t \longmapsto L_j(\Phi_t(v))$ is decreasing.

3. Let $v \in X_i$. We use again [28, Theorem 8.20] to prove that $\omega(v) \subset X_i$.

   From Theorem 3.10, we have $\bigcup\limits_{u\in\partial X_i} \omega(u) = \{E_0, E_j\}$ and we prove the following statements

   1) $\{E_0\}$ **and** $\{E_j\}$ **are trivially two disjoint, compact and invariant sets.**

   2) $\{E_0, E_j\}$ **is acyclic in** ∂X_i**,** *i.e.* :

   - Apart from the constant orbit $\{E_0\}$, there is no complete orbit $\gamma \subset \partial X_i$ connecting $\{E_0\}$ to itself (a homoclinic loop). Indeed, otherwise we would have $\gamma \subset \cap_{k\in\{1,2\}} \partial X_k$ since $\{E_j\}$ is globally attractive in $\partial X_i \cap X_j$ (Theorem 3.10). Moreover, $\cap_{k\in\{1,2\}} \partial X_k$ is invariant and equation (5) induces that the singleton orbit $\{E_0\}$ is the only complete orbit in $\cap_{k\in\{1,2\}} \partial X_k$.
   - Let $\gamma = \{\Psi(t), t \in \mathbb{R}\} \subset \partial X_i$ be a homoclinic loop connecting E_j to itself. We prove that necessarily $\gamma = \{E_j\}$. We know that $E_j \in X_j$ and $\partial X_i \cap X_j$ is invariant. Since $\{E_0\}$ is globally attractive in $\partial X_i \cap \partial X_j$ (Theorem 3.8) then $\gamma \subset \partial X_i \cap X_j$. Moreover, by definition of γ, $\lim_{t\to-\infty} L_j(\Psi(t)) = \lim_{t\to+\infty} L_j(\Psi(t)) = L_j(E_j)$. Since L_j is a Lyapunov functional on γ strict for $\{E_j\}$ (Lemma 4.3.2.b), then $\gamma = \{E_j\}$, otherwise L_j would have been decreasing along γ.

- There is no cycle formed by two complete orbits in ∂X_i connecting $\{E_0\}$ to $\{E_j\}$ and $\{E_j\}$ to $\{E_0\}$. Indeed, since $E_j \in X_j$ and is attractive on $\partial X_i \cap X_j$ (Theorem 3.10), there is no complete orbit connecting E_j to E_0 in ∂X_i.

3) $\{E_0\}$ **is isolated in** ∂X_i**.** Let V be a neighborhood of E_0 in ∂X_i such that $E_j \notin V$ and let $K \subset V$ be a compact invariant set. Since E_j is globally attractive in $\partial X_i \cap X_j$ (Theorem 3.10.1) and $E_j \notin K$, then $K \subset \cap_{k\in\{1,2\}} \partial X_k$. Since K is compact and invariant, through any $u \in K$ there is a bounded and complete orbit $\gamma(u) \subset K$. Since the constant orbit $\{E_0\}$ is the only complete orbit included in $\cap_{k\in\{1,2\}} \partial X_k$, it follows that $K = \{E_0\}$.

4) $\{E_j\}$ **is isolated in** ∂X_i**.** Suppose $V \subset \partial X_i \cap X_j$ is a neighborhood of E_j and $K \subset V$ is a compact invariant set such that $E_j \in K$. Since K is compact and invariant, for any $u \in K$ there is a bounded and complete orbit $\gamma(u) \subset K$ through u. Then from Lemma 4.3, L_j is a Lyapunov functional on K and, for any $u \in K$, L_j is constant on $\gamma(u)$ if and only if $u = E_j$. Then [28, Theorem 2.52] implies that $K = \{E_j\}$. If $K' \subset V$ is a compact and invariant set such that $E_j \notin K'$, one can repeat the previous argument with $K = K' \cup \{E_j\}$, then conclude that $K = \{E_j\}$, so $K' = \emptyset$.

5) $\{E_0\}$ **is uniformly weakly repelling in** X_i**.** See the proof of Proposition 5.2.

6) $\{E_j\}$ **is uniformly weakly repelling in** X_i**.** The proof is identical to the latter point (see Proposition 5.2) after replacing $\mathcal{R}_{0,i}$, E_0 and x_0^* respectively by $\gamma_{j\to i}$, E_j and x_j^*.

Then Φ is uniformly weakly ρ_i-persistent and the existence of a global attractor (corollary 2.5) implies that it is actually uniformly ρ_i-persistent ([28, Theorem 5.2 and hypothesis H0 p.125]).

4. This a direct consequence of the uniform ρ_i-persistence for $i \in \{1,2\}$ stated in item 3.

5. We have $\rho_{1+2}^{-1}(\{0\}) = \partial X_1 \cap \partial X_2$ and $\bigcup\limits_{u\in\partial X_1\cap\partial X_2} \omega(u) = \{E_0\}$ (by Theorem 3.8). Then we can prove, exactly as in the proof of Proposition 5.2, than $\{E_0\}$ is compact, invariant, isolated and acyclic in $\partial X_1 \cap \partial X_2$ and uniformly weakly repelling in $X_1 \cup X_2$. We conclude that Φ is uniformly weakly ρ_{1+2}-persistence, and the existence of a global attractor (corollary 2.5) implies that it is actually uniformly ρ_{1+2}-persistent ([28, Theorem 5.2 and hypothesis H0 p.125]).

□

We can now compute the basin of attraction of each equilibrium, by means of the LaSalle invariance principle [20, Theorem 2.52].

Proof of Theorem 3.11. The proof proceeds exactly as for Theorem 3.8 (with $L_* = L_i$ and $E_* = E_i$ for item 1 and $L_* = L_3$ and $E_* = E_3$ for item 2), except that here S is not closed. In this case, the inclusion $\omega(K) \subset S$ is obtained because S is invariant and Φ is uniformly ρ_i-persistent for item 1 or $\rho_{1,2}$-persistant for item 2 (Proposition 5.3, items 3 and 4 respectively). □

The critical case $\gamma_{1\to2} = \gamma_{2\to1} = 1$ is handled by Theorem 3.12.

Proof of Theorem 3.12. The proof proceeds in three steps. First we prove that $E_\infty \cup \{E_1, E_2\}$ is a compact attractor of compact sets in $\cup_{k\in\{1,2\}} X_k$ and is stable. Then we prove thate E_∞ is an attractor of points in $\mathcal{X}_1 \cap X_2$. Finally we prove the formula limit of $\Phi_t(v)$.

1. Let $K \subset X_1 \cup X_2$ be a compact set. Exactly as in the proof of Theorem 3.8, we know that K is attracted by a compact invariant set $\omega(K)$. It comes from the uniform ρ_{1+2}-persistence (Proposition 5.3) that $\omega(K) \subset X_1 \cup X_2$ and from Lemma 4.3 that for any $i \in \{1,2\}$, L_i is a Lyapunov functional on $\omega(K) \cap X_i$ (if it is not empty), strict for $E = E_\infty \cup (\{E_i\} \cap \omega(K))$.

   Let $v \in \omega(K)$. Since $\omega(K)$ is invariant and compact, there exists a bounded and complete orbit $\gamma(v) = \{\Psi(t), t \in \mathbb{R}\} \subset \omega(K)$ through v. The compactness of $\omega(K)$ implies that $\omega(v) \subset \omega(K)$ and $\alpha(v) \subset \omega(K)$.

   If $v \in X_i \cap \partial X_j$ for $i, j \in \{1,2\}$, $i \neq j$, then the invariance of ∂X_j and the fact that $\omega(v) \cup \alpha(v) \subset \omega(K) \subset X_1 \cup X_2$ implies that $\omega(v) \cup \alpha(v) \subset X_i \cap \partial X_j \cap \omega(K)$. Then we conclude as in the proof of Theorem 3.8 that $v = \{E_i\}$. In particular, $\omega(K) \cap X_i \cap \partial X_j$ is either empty, or reduces to $\{E_i\}$.

   If $v \in X_1 \cap X_2$, then both L_1 and L_2 are well defined Lyapunov function on $\gamma(v)$ (Lemma 4.3). Moreover, since $\alpha(v) \subset \omega(K)$, the previous paragraph implies that either $\alpha(v) \subset X_1 \cap X_2$, or there exists $i \in \{1,2\}$ such that $E_i \in \alpha(v)$, and the same applies for $\omega(v)$.

   Suppose that $E_i \in \alpha(v)$, *i.e.* $\exists (t_n)_{n\in\mathbb{N}} \in \mathbb{R}_+^{\mathbb{N}}$ such that $\lim_{n\to+\infty} t_n = +\infty$ and $\lim_{n\to+\infty} \Psi(-t_n) = E_i$. We know that $L_i(E_i) = 0$ and $t \longmapsto L_i(\Psi(t))$ is a non-increasing non-negative function, then it comes that $L_i(\Phi(t)) = 0$ for all $t \in \mathbb{R}$, so $\gamma(v) = \{E_i\}$. In particular $v = E_i$, which is absurd. Then $E_i \notin \alpha(v)$. Similarly, $E_i \notin \omega(v)$ because $t \longmapsto L_j(\Psi(t))$ (with $j \in \{1,2\}$, $j \neq i$) is a non-increasing function and $\lim_{\Psi(t)\to E_i} L_j(\Psi(t)) = +\infty$. We just proved that $\alpha(v) \cup \omega(v) \subset X_1 \cap X_2$.

We know that L_1 and L_2 are constant on the invariant sets $\alpha(v)$ and $\omega(v)$ ([28, Proposition 2.51]). In particular, for any $i \in \{1,2\}$ and any $u \in \alpha(v) \cup \omega(v)$, $t \longmapsto L_i \circ \Phi_t(u)$ is constant. Then Lemma 4.3 implies that $u \in E_\infty$, so that $\omega(v) \subset E_\infty$ and $\alpha(v) \subset E_\infty$.

Now we prove that $\omega(v)$ and $\alpha(v)$ are singletons. Indeed, Proposition 3.4 states that $x_1^* = x_2^*$ and that $E_\infty = \{E_{1+\sigma} := (1-\sigma)E_1 + \sigma E_2 \ : \ \sigma \in (0,1)\}$. Computing the values of L_1 and L_2 alongside this parametrization leads to

$$L_1(E_{1+\sigma}) = 0 + \frac{y_1^*}{c_1} g(1-\sigma) + \sigma \frac{y_2^*}{c_2}, \quad L_2(E_{1+\sigma}) = 0 + \frac{y_2^*}{c_2} g(\sigma) + (1-\sigma)\frac{y_1^*}{c_1}, \qquad \forall \sigma \in (0,1).$$

Since g is a decreasing function on $(0,1)$, then $\sigma \longmapsto L_1(E_{1+\sigma})$ and $\sigma \longmapsto L_1(E_{1+\sigma})$ are respectively increasing and decreasing functions on $(0,1)$. In particular, the only subsets of E_∞ on which L_1 or L_2 are constant are its singletons. Since L_1 and L_2 are constant on the invariant sets $\alpha(v)$ and $\omega(v)$, then they both reduce to singletons, say $\alpha(v) = E_\alpha$ and $\omega(w) = E_\omega$.

We prove that $E_\alpha = E_\omega$. Indeed, assume that $E_\alpha \neq E_\omega$, then the opposite monotonicities of L_1 and L_2 restricted to E_∞ imply that either $L_1(E_\alpha) < L_1(E_\omega)$ or $L_2(E_\alpha) < L_2(E_\omega)$. On the other hand, for any $i \in \{1,2\}$, the Lyapunov functional L_i is non-increasing along the complete orbit $\gamma(v)$, then $L_i(E_\alpha) = \lim_{t\to-\infty} L_i(\Psi(t) \geq \lim_{t\to+\infty} L_i(\Psi(t) = L_i(E_\omega)$. This is absurd, so $\alpha(v) = \omega(v)$ and reduces to a singleton $\{E_{1+\sigma_v}\} \subset E_\infty$.

Then $\gamma(v)$ is a homoclinic loop connecting $E_{1+\sigma_v}$ to itself and we can conclude, as in the proof of Theorem 3.8, that $\gamma(v)$ reduces to $\omega(v)$, *i.e.* $\{v\} = \omega(v) \subset E_\infty$.

We proved that $\omega(K) \subset E_\infty \cup \{E_1, E_2\}$, *i.e.* $E_\infty \cup \{E_1, E_2\}$ is a compact attractor of the compact sets of $X_1 \cup X_2$. Since Φ is also state-continuous, uniformly in finite time, [28, Theorem 2.39] states that $E_\infty \cup \{E_1, E_2\}$ is also stable.

2. Now we prove that E_∞ is globally attractive in $\mathcal{X}_1 \cap \mathcal{X}_2$. Let $v = (x_0, y_{1,0}, y_{2,0}) \in \mathcal{X}_1 \cap X_2$, and denote, for all $t \geq 0$, $\Phi_t(v) = (x(t,.), y_1(t), y_2(t))$. The third item of Lemma 3.3 implies that

$$\frac{y_1'(t)}{y_1(t)} = \frac{\mu_1 y_2'(t)}{\mu_2 y_2(t)}, \text{ that is } (\ln \circ y_1)'(t) = \frac{\mu_1}{\mu_2}(\ln \circ y_2)'(t).$$

After integration, it comes that y_1 and y_2 are linked by the following algebraic relation

$$y_1(t) = \frac{y_{1,0}}{y_{2,0}} y_2(t)^{\frac{\mu_1}{\mu_2}} \tag{20}$$

Suppose that $\liminf_{t\to+\infty} y_1(t) = 0$, then there exists $(t_n)_{n\in\mathbb{N}}$ such that $t_n \underset{n\to+\infty}{\to} +\infty$ and $y_1(t_n) \underset{n\to+\infty}{\to} 0$. Then, from equation (20), $y_2(t_n) \underset{n\to+\infty}{\to} 0$. From Lemma 2.6, $\omega(v)$ is a non empty attractor of v, then there exists $\tilde{x} \in L^1(\mathbb{R}_+, \mathbb{R}_+)$ such that $(\tilde{x}, 0, 0) \in \omega(v)$, otherwise the sequence $(x(t_n), y_1(t_n), y_2(t_n))$ would not belong to any neighborhood of $\omega(v)$. This is absurd as we proved that $E_\infty \cup \{E_1, E_2\}$ is an attractor of the compact sets of $X_1 \cup X_2$, in particular $\omega(\{v\}) \subset E_\infty \cup \{E_1, E_2\}$, while $(\tilde{x}, 0, 0) \notin E_\infty \cup \{E_1, E_2\}$ for any $\tilde{x} \in L^1(\mathbb{R}_+, \mathbb{R}_+)$.

Then we proved that $\omega(v) \subset E_\infty$, so E_∞ is an attractor of points in $X_1 \cap X_2$ and its stability is directly inherited from the stability of $E_\infty \cup \{E_1, E_2\}$ in $X_1 \cup X_2$.

3. We proved that $E_\sigma := \omega(v) \subset E_\infty$. Let $\sigma \in (0,1)$ such that $E_{1+\sigma} = (x_1^*, (1-\sigma)y_1^*, \sigma y_2^*) \in \omega(v)$. Then there exists $(t_n)_{n\in\mathbb{N}} \in \mathbb{R}_+^{\mathbb{N}}$ such that $\lim_{n\to+\infty} t_n = +\infty$ and $\lim_{n\to+\infty}(y_1(t_n), y_2(t_n)) = ((1-\sigma)y_1^*, \sigma y_2^*)$. Consequently, equation (20) implies that

$$(1-\sigma)y_1^* = \frac{y_{1,0}}{y_{2,0}}(\sigma y_2^*)^{\mu_1/\mu_2}. \tag{21}$$

This equation admits at least one solution since $\omega(v) \neq \emptyset$, and at most one because its left-hand side is a decreasing function of σ while its right-hand side is an increasing one.

□

Remark 5.4. *We could actually note that the set E_∞ is the attractor of compact sets in $X_1 \cap X_2$. This comes from the fact that for any compact set $K \subset X_1 \cap X_2$, then the function $K \ni v := (x_0, y_{1,0}, y_{2,0}) \longmapsto \sigma \in (0,1)$ is continuous, where σ is the unique solution of (21). Consequently this function attains its bounds $0 < \sigma_1 < \sigma_2 < 1$ and $\omega(K) \subset \{(x, y_1, y_2) \in X : y_1 \geq (1-\sigma_1)y_1^*, y_2 \geq \sigma_1 y_2^*\} \subset X_1 \cap X_2$. The first item of the latter proof can then be used similarly.*

6 Discussion

In this work, we have shown that introducing age-structure in a resource population shared by two competitors can fundamentally alter the outcome of competition. In contrast with models where only the competitors are structured, for which competitive exclusion generically prevails, we prove that heterogeneity in the interaction kernels may allow for stable coexistence. We give necessary and sufficient conditions for existence, attractivity and stability of equilibria, including in the critical case where a continuum of infinite number of equilibria exists.

From a biological perspective, our results support the idea that specialization with respect to resource age can act as a mechanism of niche partitioning. The condition that the interaction kernels should not be proportional for stable coexistence (Remark 3.5) reflects the need for *sufficiently* distinct competitive strategies.

This study could be generalized to $n > 2$ competitors, with most of the proofs being barely affected. The major difficulty would lie in determining the conditions for the existence of equilibria with more that two competitors.

As pointed out in Remark 3.6, considering a constant influx of resources of age 0 implies that the best competitive strategy is to focus on the youngest resources. This was illustrated in Example 3.13, where the two predators differ only in their interaction term by a translation factor.

However, feeding partly on the youngest resources is not enough to ensure survival. As shown numerically in Example 3.14, a generalist population y_2 feeding on resources of all ages may not survive against a specialist population y_1 that feeds (exlusively) on resources within a specific age range. From an epidemiological perspective, this can be interpreted as different *Plasmodium* species competing for red blood cells, where *P. vivax* and *P. ovale* preferentially invade reticulocytes (young red blood cells), *P. malariae* primarily targets mature cells, whereas *P. falciparum* can infect cells across all age classes [24].

This radical optimal competitive strategy could be altered when considering two alternative assumptions that we are exploring in ongoing works. First one can consider the case of linear birth rate (*i.e.* $x(t,0) = \int_0^\infty \lambda(a)x(t,a)\mathrm{d}a$), so that the competitors need to preserve the sustainability of the resource. Alternatively, in an ecological setting, one could reasonably hypothesize that the nutritive value of a prey depends on its age (*i.e.* non-constant functions c_1 and c_2), this would change the picture in a non trivial way, as predators would face contradictory interests : being the first to reach the prey while waiting for it to grow before hunting it.

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