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Evolution of dietary diversity and a starvation driven cross-diffusion system as its singular limit

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Abstract

We rigorously prove the passage from a Lotka-Volterra reaction-diffusion system towards a cross-diffusion system at the fast reaction limit. The system models a competition of two species, where one species has a more diverse diet than the other. The resulting limit gives a cross-diffusion system of a starvation driven type. We investigate the linear stability of homogeneous equilibria of those systems and rule out the possibility of cross-diffusion induced instability (Turing instability). Numerical simulations are included which are compatible with the theoretical results.

Keywords. Cross-diffusion, starvation-driven diffusion, entropy, Turing instability.
2010 Mathematics Subject Classification. Primary : 35B25, 35B40, 35K57, 35Q92, 92D25. Secondary 35B45, 35K45

1 Introduction

1.1 Problem setting

We consider a semilinear reaction-diffusion system that models a competition dynamics when two species have partially different diets. The population densities of the two species are denoted by $u = u(t,x)$ and $v = v(t,x)$. The species u has a more diverse diet and is divided into two substates $u_a = u_a(t,x)$ and $u_b = u_b(t,x)$ so that $u = u_a + u_b$. The system is parametrized by a small parameter $\varepsilon > 0$ and written as

$$\begin{cases} \partial_t u_a^\varepsilon = d_a \Delta u_a^\varepsilon + f_a(u_a^\varepsilon) + \dfrac{1}{\varepsilon} Q(u_a^\varepsilon,\, u_b^\varepsilon,\, v^\varepsilon\,), & \text{in } (0,+\infty)\times\Omega, \\ \partial_t u_b^\varepsilon = d_b \Delta u_b^\varepsilon + f_b(u_b^\varepsilon,\, v^\varepsilon) - \dfrac{1}{\varepsilon} Q(u_a^\varepsilon,\, u_b^\varepsilon,\, v^\varepsilon\,), & \text{in } (0,+\infty)\times\Omega, \\ \partial_t v^\varepsilon = d_v \Delta v^\varepsilon + f_v(u_b^\varepsilon,\, v^\varepsilon), & \text{in } (0,+\infty)\times\Omega, \end{cases} \tag{1.1}$$

where $\Omega \subset \mathbb{R}^{\mathrm{N}}$, $\mathrm{N} \geq 1$, is a bounded domain with a smooth boundary, and d_a, d_b and d_v are diffusivities for the three populations. The unknown solutions depend

on the parameter ε and we denote it explicitly if needed. The above system is complemented with nonnegative initial data

$$u_a^\varepsilon(0,x) = u_a^{\rm in}(x)\,, \quad u_b^\varepsilon(0,x) = u_b^{\rm in}(x)\,, \quad v^\varepsilon(0,x) = v^{\rm in}(x)\,, \quad x \in \Omega\,, \tag{1.2}$$

and zero flux boundary conditions,

$$d_a \nabla u_a^\varepsilon \cdot \sigma = d_b \nabla u_b^\varepsilon \cdot \sigma = d_v \nabla v^\varepsilon \cdot \sigma = 0\,, \quad \text{on } (0,+\infty) \times \partial\Omega\,, \tag{1.3}$$

where σ denotes the outward unit normal vector on the boundary $\partial\Omega$.

In this paper, we explore the effect of diet diversity in a competition context and show the emergence of cross-diffusion triggered by the different substates u_a and u_b, as $\varepsilon \to 0$. The competition dynamics is given in the reaction terms. The reaction terms of order one are given by

$$\begin{aligned} f_a(u_a) &:= \eta_a u_a \Big(1 - \frac{u_a}{a}\Big), \\ f_b(u_b, v) &:= \eta_b u_b \Big(1 - \frac{u_b + v}{b}\Big), \\ f_v(u_b, v) &:= \eta_v v \Big(1 - \frac{u_b + v}{b}\Big)\,, \end{aligned} \tag{1.4}$$

where $a, b > 0$ are carrying capacities supported by two different groups of resources and η_a, η_b, and $\eta_v > 0$ are the intrinsic growth rates of u_a, u_b, and v, respectively. The competition of the two species, u and v, is for the resource b. However, the species u has a diverse diet and can survive by consuming the other resource a without competition. To model such a competition using a Lotka-Volterra type system, the species u is divided into two substates u_a and u_b depending on their diets. In the above reaction terms, u_a takes a logistic equation type reaction, and u_b and v take Lotka-Volterra competition equations type reactions as given in (1.4). Since competition exists only partially for the species u, the competition is weak for u. However, the species v competes with u for all of its resources and hence the competition is not weak in general and the competition result may depend on the parameter ε (see Sections 4 and 5).

The individuals of the species u may freely change the type of food depending on the availability, which is modelled by the fast reaction term of order ε^{-1},

$$\frac{1}{\varepsilon}\, Q(u_a, u_b, v) := \frac{1}{\varepsilon}\left[\phi\Big(\frac{u_b + v}{b}\Big)\, u_b - \psi\Big(\frac{u_a}{a}\Big)\, u_a\right], \qquad \varepsilon > 0\,. \tag{1.5}$$

In this reaction term, $\epsilon^{-1}\,\phi\Big(\dfrac{u_b + v}{b}\Big)$ is the conversion rate for individuals in the state u_b which switch to the other state u_a, and $\epsilon^{-1}\,\psi\Big(\dfrac{u_a}{a}\Big)$ is the conversion rate in the other direction. The conversion rate $\phi\big(\frac{u_b+v}{b}\big)$ is assumed as a function of the starvation measure $\frac{u_b+v}{b}$ for the populations u_b and v. If the resource b dwindles or the population $u_b + v$ increases, the resource b becomes scarce relatively, and more individuals of population u_b will convert to u_a and consume the other resource a. Hence, we assume that ϕ is an increasing function of the starvation measure (see [22] for more discussion on the starvation measure). In the same way, the conversion rate ψ is a function of the starvation measure $\frac{u_a}{a}$ for the population u_a and is assumed to be increasing. For this reason, it makes sense to call the conversion dynamics given by (1.5) a starvation-driven conversion, which eventually results in the starvation-driven cross-diffusion after taking the limit $\varepsilon \to 0$ (see [8, 9]). More specifically, we assume the following starvation-driven conversion hypothesis

(H1) ϕ and ψ in (1.5) are increasing functions belonging to $C^1([0,+\infty))$; in addition, there exist strictly positive constants δ_ψ, δ_ϕ, $M_{\phi'}$, and $M_{\psi'}$ such that, for all $x \geq 0$,

$$\psi(x) \geq \delta_\psi > 0, \quad \phi(x) \geq \delta_\phi > 0, \quad \phi'(x) \leq M_{\phi'}, \quad \text{and} \quad \psi'(x) \leq M_{\psi'}.$$

The main result of the paper is that, as $\varepsilon \to 0$, the (unique) solution $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ of the initial boundary value problem (1.1)–(1.5) converges to a limit (u_a, u_b, v) and this limit is a weak solution of the reaction cross-diffusion system

$$\begin{cases} \partial_t u = \Delta(d_a u_a + d_b u_b) + f_a(u_a) + f_b(u_b, v), & \text{in } (0,+\infty) \times \Omega, \\ \partial_t v = d_v \Delta v + f_v(u_b, v), & \text{in } (0,+\infty) \times \Omega, \end{cases} \tag{1.6}$$

where u_a and u_b are (uniquely) determined by the nonlinear system

$$u_a + u_b = u \quad \text{and} \quad Q(u_a, u_b, v) = 0, \tag{1.7}$$

complemented by the initial data,

$$u(0,x) = u^{\text{in}}(x) := u_a^{\text{in}}(x) + u_b^{\text{in}}(x)\,, \quad v(0,x) = v^{\text{in}}(x)\,, \quad x \in \Omega\,, \tag{1.8}$$

and the zero flux boundary condition,

$$\nabla(d_a u_a + d_b u_b) \cdot \sigma = d_v \nabla v \cdot \sigma = 0\,, \qquad \text{in } (0,+\infty) \times \partial\Omega\,. \tag{1.9}$$

Note that the zero flux boundary conditions in (1.3) are equivalent to the homogeneous Neumann boundary conditions,

$$\nabla u_a^\varepsilon \cdot \sigma = \nabla u_b^\varepsilon \cdot \sigma = \nabla v^\varepsilon \cdot \sigma = 0\,, \quad \text{on } (0,+\infty) \times \partial\Omega$$

(see [20] for similar diffusion operator for a single species with two phenotypes). However, after taking the singular limit, we obtain the zero flux boundary conditions (1.9), but not the homogeneous Neumann boundary conditions.

If $d_a = d_b$, the diffusion for the species u given in (1.6) is the homogeneous linear diffusion. However, the diffusivity of a species usually depends on its food (or prey) and $d_a \neq d_b$ in general. In that case ($d_a \neq d_b$), the diffusion for the total population in (1.6) contains cross-diffusion dynamics depending on the distribution of the three populations groups, u_a, u_b and v, through the relations in (1.7). This explains the starvation-driven diffusion for the specific case of the paper, a concept formally introduced by Cho and Kim [7]. Funaki *et al.* [18] derived a macroscopic cross-diffusion model from a system of two phenotypes and a signaling chemical in the context of chemotaxis.

The proof of the convergence as $\varepsilon \to 0$ is rigorously obtained via *a priori* estimates for $u_a^\varepsilon, u_b^\varepsilon$, and v^ε. The main tool is the energy (or entropy) functional

$$\mathcal{E}(u_a, u_b, v) := \int_\Omega h_1(u_a)\,dx + \int_\Omega h_2(u_b, v)\,dx\,, \tag{1.10}$$

where

$$h_1(u_a) := \int_0^{u_a} \psi\Big(\frac{z}{a}\Big)\,z\,dz, \quad \text{and} \quad h_2(u_b, v) := \int_0^{u_b} \phi\Big(\frac{z+v}{b}\Big)\,z\,dz\,. \tag{1.11}$$

Notice here that the assumption (H1) implies that h_1 is positive, increasing, and convex, and that h_2 is positive, increasing in both variables, and convex with respect to the first variable. Therefore, the name entropy for the function given in (1.10) is justified. We refer to [10] and [15] for the use of such entropies in the context of triangular cross-diffusion systems (that is, systems in which only one of the two equations includes a cross-diffusion term). For more general systems, we refer to [5, 6, 12, 14, 21, 2] among other works.

Then, by invoking the *Aubin-Lions Lemma*, we pass to the limit along a subsequence and conclude that the limit is a weak solution of (1.6)–(1.9). To use the energy estimate, we take initial values with bounded energy, which is our second hypothesis

(H2) $u_a^{\text{in}} \in L^1_+(\Omega)$, $u_b^{\text{in}} \in L^1_+(\Omega)$, $v^{\text{in}} \in L^\infty_+(\Omega)$, and $\mathcal{E}(u_a^{\text{in}}, u_b^{\text{in}}, v^{\text{in}}) < \infty$.

Remark 1. *Under Hypothesis (H2), the initial data $u_a^{in}, u_b^{in}, v^{in}$ for the reaction diffusion system (1.1) do not satisfy a priori the nonlinear equation $Q(u_a^{in}, u_b^{in}, v^{in}) = 0$ in (1.7). Thus, the appearance of an initial layer is expected (see also Section 5).*

We conclude this introduction proposing a formal derivation of (1.1) out of a microscopic system. We shall consider problems left open here (such as regularity, uniqueness, stability and long time asymptotic behaviour of the macroscopic solutions) in a forthcoming paper, where a more general class of cross-diffusion system is analysed.

The rest of the paper is organised as follows. *Section 2* is devoted to the statement of the existence result. In *Section 3.1*, we prove a priori estimates, which are the preliminary ingredients for the proof of the existence result obtained in *Section 3.2*. The paper concludes with the existence and linear stability analysis of trivial and non-trivial spatially homogeneous steady states, in *Section 4* and *Appendix A*, with a particular emphasis put on the coexistence state. Some numerical tests in *Section 5* illustrate the linear stability analysis. The discussion in *Section 6* completes the article.

1.2 Formal derivation of the reaction-diffusion system with fast switching

We explain here how the mesoscopic scale model (1.1) is obtained at a formal level from a microscopic scale model in which the resources inducing the competition explicitly appear. Consider

$$\begin{cases} \partial_t s_1 = \dfrac{1}{\delta}\Big[r_1 s_1\Big(1 - \dfrac{s_1}{A_1}\Big) - p_1 s_1 U_1\Big] \\ \partial_t s_2 = \dfrac{1}{\delta}\Big[r_2 s_2\Big(1 - \dfrac{s_2}{A_2}\Big) - p_2 s_2 U_2 - p_V s_2 V\Big] \\ \partial_t U_1 = D_1 \Delta U_1 + k_1 p_1 s_1 U_1 + \dfrac{1}{\varepsilon}\Big[\Phi\Big(\dfrac{p_2 U_2 + p_V V}{s_2}\Big) U_2 - \Psi\Big(\dfrac{p_1 U_1}{s_1}\Big) U_1\Big] \\ \partial_t U_2 = D_2 \Delta U_2 + k_2 p_2 s_2 U_2 - \dfrac{1}{\varepsilon}\Big[\Phi\Big(\dfrac{p_2 U_2 + p_V V}{s_2}\Big) U_2 - \Psi\Big(\dfrac{p_1 U_1}{s_1}\Big) U_1\Big] \\ \partial_t V = D_V \Delta V + k_V p_V s_2 V, \end{cases} \tag{1.12}$$

where $\delta > 0$ is the microscopic reaction time scale and ε is the mesoscopic one (hence $\delta \ll \varepsilon \ll 1$). These equations describe the time evolution of a small ecosystem with

two prey population densities (or vegetal resources), s_1 and s_2, and two predator population densities (or harvesters of the vegetal resources), U and V. Moreover, the population U is composed of two subpopulations U_1 and U_2 depending on the prey they consume, i.e., s_1 and s_2, respectively. The prey species s_i follows the logistic dynamics with a carrying capacity A_i and an intrinsic growth rate r_i. The predator species consume a certain amount of preys which is proportional to the prey density with proportionality factors p_1, p_2 and p_V. The harvested prey mass is converted to the predator mass with conversion rates k_1, k_2 and k_V. The subpopulations U_1 and U_2 convert to each other depending on the availability of the prey. The two functions Φ and Ψ are the conversion rates which are respectively increasing functions of the starvation measures $\frac{p_2U_2+p_VV}{s_2}$ and $\frac{p_1U_1}{s_1}$. The other species V consumes only the second prey s_2. Hence, the active competition is only between V and U_2, while U_1 competes with V passively (via conversion). Finally, since the dispersal rate of a predator species usually depends on the nature of its prey, $D_1 \neq D_2$ in general.

Remark 2. *The expression (1.12) has no diffusion terms for the prey species s_1 and s_2. Since growth is the dominant factor for plant species and their dispersal is negligible, this is especially relevant when the prey species are vegetal resources. Mathematically, this choice yields an explicit form in the singular limits $\delta \to 0$, see (1.13). Adding diffusion terms in the prey species equations could result in a less explicit formulas.*

The mescoscopic system with fixed $\varepsilon > 0$ is obtained in the limit $\delta \to 0$. This is to say that the time-scale for the reaction of the resources s_1 and s_2 is much faster than all other processes. In simple predator-prey models this corresponds to a fast dynamics of the prey which has been studied more carefully in [30, 24, 28].

In this formal limit $\delta \to 0$, we find

$$s_1\Big(r_1 - \frac{r_1 s_1}{A_1} - p_1U_1\Big) = 0 \implies s_1 = 0 \ \text{ or } \ s_1 = A_1\Big(1 - \frac{p_1U_1}{r_1}\Big),$$

and

$$s_2\Big[r_2\big(1 - \frac{s_2}{A_2}\big) - p_2U_2 - p_VV\Big] = 0 \implies s_2 = 0 \ \text{ or } \ s_2 = A_2\Big(1 - \frac{p_2U_2 + p_VV}{r_2}\Big).$$

Only the nontrivial case, $s_1 \neq 0 \neq s_2$, is meaningful (since $s_1 = 0$ and $s_2 = 0$ correspond to unstable equilibria), and we obtain two relations

$$\frac{p_1U_1}{s_1} = \frac{r_1}{s_1} - \frac{r_1}{A_1} \quad \text{and} \quad \frac{p_2U_2 + p_VV}{s_2} = \frac{r_2}{s_2} - \frac{r_2}{A_2}.$$

Therefore, the last three equations in (1.12) turn into

$$\begin{cases} \partial_t U_1 = D_1\Delta U_1 + A_1k_1p_1U_1\big(1 - \frac{p_1U_1}{r_1}\big) + \dfrac{1}{\varepsilon}\big[\Phi U_2 - \Psi U_1\big] \\ \partial_t U_2 = D_2\Delta U_2 + A_2k_2p_2U_2\,\big(1 - \frac{p_2U_2+p_VV}{r_2}\big) - \dfrac{1}{\varepsilon}\big[\Phi U_2 - \Psi U_1\big] \\ \partial_t V \ = D_V\Delta V + A_2k_Vp_VV\,\big(1 - \frac{p_2U_2+p_VV}{r_2}\big), \end{cases} \tag{1.13}$$

where the conversion rates Φ and Ψ read as

$$\Phi = \Phi\Big(\frac{r_2}{s_2} - \frac{r_2}{A_2}\Big) \quad \text{and} \quad \Psi = \Psi\Big(\frac{r_1}{s_1} - \frac{r_1}{A_1}\Big),$$

and the Lotka-Volterra reaction dynamics of competition type naturally appears.

Now we consider the relationship between the variables in (1.1) and in (1.13). First, we define

$$u_a^\varepsilon := U_1,\ u_b^\varepsilon := U_2,\ v^\varepsilon := \frac{p_V}{p_2} V\,,$$

and keep the same diffusivity coefficients

$$d_a := D_1,\ d_b := D_2,\ d_v := D_V\,.$$

Then, the coefficients in the Lotka-Volterra type competition dynamics, f_a, f_b and f_v, are given as

$$\eta_a := p_1 A_1 k_1, \quad \eta_b := p_2 A_2 k_2, \quad \eta_v := p_V A_2 k_V, \quad a := \frac{r_1}{p_1}, \quad b := \frac{r_2}{p_2}. \tag{1.14}$$

Finally, the mesoscopic conversion rates are as follows

$$\phi(x) := \Phi\Big(\frac{r_2}{A_2}\frac{x}{1-x}\Big), \quad \psi(x) := \Psi\Big(\frac{r_1}{A_1}\frac{x}{1-x}\Big). \tag{1.15}$$

After replacing variables, coefficients and functions with the above new ones, system (1.13) becomes our system (1.1).

Remark 3. *(i) The conversion rates of the microscopic model, Φ and Ψ, are functions of the starvation measures $\frac{p_2U_2+p_VV}{s_2}$ and $\frac{p_1U_1}{s_1}$, instead of simply $\frac{U_2+V}{s_2}$ and $\frac{U_1}{s_1}$, in order to take into account the difference in the harvesting rates p_2 and p_V. (ii) The mesoscopic conversion rates ϕ and ψ in (1.15) are increasing functions, since Φ and Ψ are chosen to be increasing functions. (iii) It is worth noticing that the carrying capacities a and b for the predator species are proportional to the growth rates r_i's of the prey species and that the prey carrying capacities A_i's are also involved in deciding ϕ and ψ (see (1.14) and (1.15)). (iv) The macroscopic system reduces to the classical Lotka-Volterra system of competition type with linear diffusion, whenever the conversion rates ϕ and ψ are both constant, (see the discussion section 6).*

2 Statement of the main result

Before stating our main result in Theorem 2.2 below, we introduce some notations that will be used in the sequel, and the definition of the very weak solutions of (1.6)–(1.9), with the reaction terms in (1.4).

We denote

$$\begin{aligned} C_c^k &:= C_c^k([0,+\infty)\times\bar\Omega) \\ &:= \Big\{u = u(t,x) : \exists\, T>0 \text{ s.t. } u\in C^k\big([0,T)\times\bar\Omega\big) \ \text{ and } \ \operatorname{supp} u \Subset [0,T)\times\bar\Omega\Big\}, \end{aligned}$$

and, for all $p\in[1,+\infty)$,

$$L^p_{loc} := L^p_{loc}((0,+\infty)\times\Omega) := \Big\{u = u(t,x) : \forall\, T>0\,, u\in L^p(\Omega_T)\Big\}\,,$$

with $\Omega_T := (0,T)\times\Omega$. Similarly, for $p=+\infty$,

$$L^\infty_{loc} := L^\infty_{loc}((0,+\infty)\times\Omega) := \Big\{u = u(t,x) : \forall\, T>0\,,\ \operatorname*{ess\,sup}_{(t,x)\in\Omega_T} |u(t,x)| < +\infty\Big\}\,.$$

It is worth noticing here that, due to hypothesis (H1), the function

$$q(u_b, u, v) := Q(u - u_b, u_b, v) = \phi\Big(\frac{u_b + v}{b}\Big)u_b - \psi\Big(\frac{u - u_b}{a}\Big)(u - u_b)\,, \tag{2.1}$$

defined for $(u_b, u, v) \in [0, u] \times (0, +\infty) \times (0, +\infty)$, satisfies (for given $u > 0, v > 0$)

$$\partial_{u_b} q(u_b, u, v) = \phi\Big(\frac{u_b + v}{b}\Big) + \frac{u_b}{b}\phi'\Big(\frac{u_b + v}{b}\Big) + \psi\Big(\frac{u - u_b}{a}\Big) + \frac{u - u_b}{a}\psi'\Big(\frac{u - u_b}{a}\Big) > 0$$

and

$$q(0, u, v) < 0\,, \qquad q(u, u, v) > 0\,.$$

Hence, for any given $(u, v) \in \mathbb{R}^2_+$, there exists a unique $u_b^*(u, v) \in (0, u)$ zero of q, and thus a unique solution of the nonlinear system (1.7) is well-defined. Furthermore, the implicit function theorem guarantees the continuity (and even the C^1 character) of u_b^* with respect to (u, v).

Definition 2.1. *Let Ω be a smooth bounded domain of $\mathbb{R}^{\mathrm{N}}$, $\mathrm{N} \geq 1$. Assume $u^{in} \in L^1_+(\Omega)$, and $v^{in} \in L^\infty_+(\Omega)$ be nonnegative initial densities. We say that the pair of nonnegative functions (u, v) is a* ***very weak solution*** *of (1.6)–(1.9) over $(0, +\infty) \times \Omega$, with reaction terms (1.4), if the following conditions are satisfied*

- *(u, v) belongs to $L^2_{loc} \times L^\infty_{loc}$,*
- *for all test functions $\xi_1, \xi_2 \in C^2_c$, with $\nabla\xi_1 \cdot \sigma = \nabla\xi_2 \cdot \sigma = 0$ on $[0, +\infty) \times \partial\Omega$, and for u_a, u_b defined as the unique solution of (1.7), a.e. on $(0, +\infty) \times \Omega$, it holds*

$$-\int_0^{+\infty}\int_\Omega (\partial_t\xi_1)u\,dxdt - \int_\Omega \xi_1(0, \cdot)u^{in}dx - \int_0^{+\infty}\int_\Omega \Delta\xi_1\big(d_a u_a + d_b u_b\big)dxdt$$
$$= \int_0^{+\infty}\int_\Omega \xi_1\big(f_a(u_a) + f_b(u_b, v)\big)\,dx\,dt\,, \tag{2.2}$$

and

$$-\int_0^{+\infty}\int_\Omega (\partial_t\xi_2)\,v\,dxdt - \int_\Omega \xi_2(0, \cdot)\,v^{in}\,dx - d_v\int_0^{+\infty}\int_\Omega \Delta\xi_2\,v\,dxdt$$
$$= \int_0^{+\infty}\int_\Omega \xi_2\,f_v(u_b, v)\,dxdt\,. \tag{2.3}$$

We observe that all terms in (2.2)–(2.3) are well-defined thanks to the assumptions (H2) on the initial densities $u^{\mathrm{in}}, v^{\mathrm{in}}$, to the L^2 integrability of the subpopulation densities u_a, u_b and to the L^∞ bound for v. Remember that the logistic structure of the reaction functions f_a, f_b, f_v involves at most quadratic nonlinearities.

Theorem 2.2. *Let Ω be a smooth bounded domain of $\mathbb{R}^{\mathrm{N}}$, $\mathrm{N} \geq 1$. Assume (H1) and (H2) on parameters and initial data $u_a^{in}, u_b^{in}, v^{in}$, respectively. We denote $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ the unique global strong (for $t > 0$) solution of system (1.1)–(1.3) with those initial data. Then, the triplet $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ converges a.e. $(t, x) \in (0, +\infty) \times \Omega$ (up to extraction of a subsequence) towards a nonnegative triplet (u_a, u_b, v), as $\varepsilon \to 0$.*

Moreover, the functions $u := u_a + u_b$, v satisfy the nonlinear system (1.7), for a.e. $(t,x) \in (0,+\infty) \times \Omega$, and the following bounds: $u \in L^q(\Omega_T)$ for $q = 2 + 2/\mathrm{N}$ if $\mathrm{N} \geq 3$, $q < 3$ if $\mathrm{N} = 2$ and $q = 3$ if $\mathrm{N} = 1$; $v \in L^\infty(\Omega_T)$; $|\nabla u| \in L^2(\Omega_T)$; and for the same previous q, $|\nabla v| \in L^{2q}(\Omega_T)$; $\partial_{x_i,x_j} v, \partial_t v \in L^q(\Omega_T)$, $i,j = 1,\dots,\mathrm{N}$. Finally, (u,v) is a very weak solution of the macroscopic system (1.6)–(1.9) with the reaction terms (1.4), in the sense of Definition 2.1.

3 Proof of the main Theorem

We first recall that for any $\varepsilon > 0$, there exists a unique global strong (for $t > 0$) solution $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ solution to system (1.1)–(1.3), under the assumption on the initial data of Theorem 2.2. We refer for example to [13, 29] for obtaining such a result.

3.1 A priori estimates

In this section we shall obtain *a priori* estimates on the subpopulation densities $u_a^\varepsilon, u_b^\varepsilon$, on the total population densities $u^\varepsilon := u_a^\varepsilon + u_b^\varepsilon$ and v^ε, and on $Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$. More specifically, we take advantage of the triangular structure of the system that give us *a priori* estimates on the density v^ε and its derivatives (see Lemma 3.1). The reaction functions f_a and f_b of competition type allow us to control the total mass $\int_\Omega u^\varepsilon(t)\,dx$, and to get an $L^2(\Omega_T)$ estimate on u^ε (see Lemma 3.2). The latter will be employed in Lemma 3.3 to obtain estimates on ∇u_a^ε, ∇u_b^ε and $Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$, through the use of the energy functional (1.10)–(1.11). In addition, the triplet $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ will be shown to have finite energy $\mathcal{E}(T)$ as well, for all $T > 0$.

Hereafter, all constants C and C_T are strictly positive and may depend on Ω, the initial data $u_a^{\mathrm{in}}, u_b^{\mathrm{in}}, v^{\mathrm{in}}$, the coefficients in system (1.1), the transition functions ϕ, ψ and on T, but never on ε. They may change also from line to line in the computations.

Lemma 3.1. *Under the hypothesis of Theorem 2.2, the following statements hold:*

(i) there exists a constant $C > 0$ such that for all $\varepsilon > 0$

$$\|v^\varepsilon\|_{L^\infty((0,+\infty)\times\Omega)} \leqslant C\,; \tag{3.1}$$

(ii) for all $q \in (1,+\infty)$ there exists a constant $C(q) > 0$ such that, for all $\varepsilon > 0$, $T > 0$ and all $i,j = 1,..,\mathrm{N}$,

$$\|\partial_t v^\varepsilon\|_{L^q(\Omega_T)} + \|\partial_{x_i,x_j} v^\varepsilon\|_{L^q(\Omega_T)} \leqslant C(q)(1 + \|u_b^\varepsilon\|_{L^q(\Omega_T)})\,; \tag{3.2}$$

(iii) for all $q \in (1,+\infty)$ there exist $C(q,\mathrm{N}) > 0$ and $C(q) > 0$ such that, for all $\varepsilon > 0$ and all $T > 0$,

$$\|\nabla v^\varepsilon\|^{2q}_{L^{2q}(\Omega_T)} \leq C(q,\mathrm{N})(1 + \|u_b^\varepsilon\|^q_{L^q(\Omega_T)}) + C(q)\,T. \tag{3.3}$$

Remark 4.
In the sequel, the value of q in (3.2)–(3.3) will be first chosen equal to 2 (see Lemma 3.2), and then to a different number after Corollary 3.4.

Proof. It is easily seen that

$$0 \leqslant v^\varepsilon(t,x) \leqslant K := \max\left\{ \|v^{\rm in}\|_{L^\infty(\Omega)} \,;\, b\right\}, \quad \text{for a.e.} \quad (t,x) \in (0,+\infty)\times\Omega\,. \tag{3.4}$$

Indeed, by the existence result of strong solution for (1.1), we know that the nonnegativity of v^ε is preserved in time. Concerning the upper bound in (3.4), it is obtained by multiplying the equation for v^ε in (1.1) by $(v^\varepsilon - K)^+ := \max\{0, v^\varepsilon - K\}$ and integrating over Ω, to obtain for all $t > 0$,

$$\int_\Omega (v^\varepsilon(t) - K)_+^2 \, dx \leq \int_\Omega (v^{{\rm in},\varepsilon} - K)_+^2 \, dx = 0\,.$$

Next, by the maximal regularity property of the heat equation (see [25] and the references therein), for all $q \in (1,+\infty)$ there exists a strictly positive constant C, which only depends on Ω and q, such that for all $i,j = 1,..,\mathrm{N}$,

$$\begin{aligned} \|\partial_t v^\varepsilon\|_{L^q(\Omega_T)} + \|\partial_{x_i,x_j} v^\varepsilon\|_{L^q(\Omega_T)} &\leq C(\|f_v(u_b^\varepsilon, v^\varepsilon)\|_{L^q(\Omega_T)} + \|v^{\rm in}\|_{L^q(\Omega)}) \\ &\leq C\big(1 + \|u_b^\varepsilon\|_{L^q(\Omega_T)}\big), \end{aligned} \tag{3.5}$$

so that estimate (3.2) holds. Then, thanks to the Gagliardo-Nirenberg inequality [27], for all $q \in (1,+\infty)$, there exists $C(q) > 0$, such that, for all $t > 0$ and $i = 1,\dots \mathrm{N}$, we have

$$\|\partial_{x_i} v^\varepsilon(t)\|_{L^{2q}(\Omega)} \leq C(q) \sum_{j=1}^{\mathrm{N}} \|\partial_{x_i,x_j} v^\varepsilon(t)\|_{L^q(\Omega)}^{1/2} \|v^\varepsilon(t)\|_{L^\infty(\Omega)}^{1/2} + C(q)\|v^\varepsilon(t)\|_{L^\infty(\Omega)}\,.$$

Integrating the above inequality over $(0,T)$ and using (3.1) and (3.5), we get estimate (3.3). □

Lemma 3.2. *Under the hypothesis of Theorem 2.2, for all $T > 0$ there exists $C_T > 0$ such that for all $\varepsilon > 0$ the following estimates hold:*

$$\sup_{t\,\in\,[0,T]} \int_\Omega (u_a^\varepsilon + u_b^\varepsilon)(t)\, dx \leq C_T \qquad \textit{and} \qquad \|u_a^\varepsilon + u_b^\varepsilon\|_{L^2(\Omega_T)} \leq C_T\,. \tag{3.6}$$

Proof. Adding the first two equations in (1.1) and using the positivity of $u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon$, we get

$$\partial_t(u_a^\varepsilon + u_b^\varepsilon) \leq d_a \Delta u_a^\varepsilon + d_b \Delta u_b^\varepsilon + \eta_a u_a^\varepsilon \left(1 - \frac{u_a^\varepsilon}{a}\right) + \eta_b u_b^\varepsilon \left(1 - \frac{u_b^\varepsilon}{b}\right) \tag{3.7}$$

$$\leq d_a \Delta u_a^\varepsilon + d_b \Delta u_b^\varepsilon + \frac{1}{4}\,(a\eta_a + b\eta_b)\,. \tag{3.8}$$

Then, integrating (3.8) over Ω, the inequality becomes

$$\frac{d}{dt} \int_\Omega \big(u_a^\varepsilon + u_b^\varepsilon\big)(t)\, dx \leq C\,,$$

implying, for all t in $[0,T]$, that

$$\|u_a^\varepsilon(t) + u_b^\varepsilon(t)\|_{L^1(\Omega)} \leq \|u_a^{\rm in} + u_b^{\rm in}\|_{L^1(\Omega)} + C\,T\,. \tag{3.9}$$

In order to obtain the $L^2(\Omega_T)$ estimate for $u_a^\varepsilon + u_b^\varepsilon$, we integrate inequality (3.7) first over Ω and then over $(0,t)$, for $t \in (0,T)$, to obtain

$$\int_\Omega (u_a^\varepsilon + u_b^\varepsilon)(t)\,dx + \frac{\eta_a}{a}\int_{\Omega_t} (u_a^\varepsilon)^2\,dx\,dt + \frac{\eta_b}{b}\int_{\Omega_t} (u_b^\varepsilon)^2\,dx\,dt \\ \leq \|u_a^{\text{in}} + u_b^{\text{in}}\|_{L^1(\Omega)} + C\|u_a^\varepsilon + u_b^\varepsilon\|_{L^1(\Omega_T)}\,.$$

The second estimate in (3.6) follows, using the first one. □

Lemma 3.3. *Under the hypothesis of Theorem 2.2, for all $T > 0$, there exists $C_T > 0$ such that, for all $\varepsilon > 0$, the global solution of (1.1) satisfies*

$$\mathcal{E}(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)(T) + \|\nabla u_a^\varepsilon\|^2_{L^2(\Omega_T)} + \|\nabla u_b^\varepsilon\|^2_{L^2(\Omega_T)} + \frac{1}{\varepsilon}\|Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)\|^2_{L^2(\Omega_T)} \\ \leq C_T\,. \tag{3.10}$$

Proof. We shall analyse the evolution of $\mathcal{E}$, along the trajectories of the solution of (1.1). Thus, from the first equation in (1.1) and assumption (H1), we have

$$\begin{aligned}
\frac{d}{dt}\int_\Omega h_1(u_a^\varepsilon)\,dx &= \int_\Omega (\partial_t u_a^\varepsilon)\,u_a^\varepsilon\,\psi\Big(\frac{u_a^\varepsilon}{a}\Big)\,dx \\
&= -d_a\int_\Omega \Big[\psi\Big(\frac{u_a^\varepsilon}{a}\Big) + \frac{u_a^\varepsilon}{a}\,\psi'\Big(\frac{u_a^\varepsilon}{a}\Big)\Big]|\nabla u_a^\varepsilon|^2\,dx \\
&\quad + \int_\Omega u_a^\varepsilon\,f_a(u_a^\varepsilon)\,\psi\Big(\frac{u_a^\varepsilon}{a}\Big)\,dx + \frac{1}{\varepsilon}\int_\Omega u_a^\varepsilon\,\psi\Big(\frac{u_a^\varepsilon}{a}\Big)\,Q_\varepsilon\,dx \\
&\leq -d_a\delta_\psi\int_\Omega |\nabla u_a^\varepsilon|^2\,dx \\
&\quad + C\int_\Omega (u_a^\varepsilon)^2\Big(1 - \frac{u_a^\varepsilon}{a}\Big)\mathbb{1}_{\{u_a^\varepsilon \leq a\}}dx + \frac{1}{\varepsilon}\int_\Omega u_a^\varepsilon\psi\Big(\frac{u_a^\varepsilon}{a}\Big)Q^\varepsilon dx.
\end{aligned} \tag{3.11}$$

Concerning the second term in the energy (1.10), we see that

$$\begin{aligned}
&\frac{d}{dt}\int_\Omega h_2(u_b^\varepsilon, v^\varepsilon)\,dx \\
&\quad = \int_\Omega (\partial_t u_b^\varepsilon)\,u_b^\varepsilon\,\phi\Big(\frac{u_b^\varepsilon + v^\varepsilon}{b}\Big)dx + \int_\Omega (\partial_t v^\varepsilon)\partial_v h_2(u_b^\varepsilon, v^\varepsilon)\,dx \\
&\quad =: I_1 + I_2\,.
\end{aligned} \tag{3.12}$$

Using the second equation in (1.1), I_1 rewrites as follows

$$\begin{aligned}
I_1 \leq &-d_b\int_\Omega |\nabla u_b^\varepsilon|^2\left[\phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) + \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right)\right]dx \\
&- d_b\int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right)\nabla u_b^\varepsilon\cdot\nabla v^\varepsilon\,dx \\
&+ C\int_\Omega (u_b^\varepsilon)^2\left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right)\mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \leq b\}}\,dx \\
&- \frac{1}{\varepsilon}\int_\Omega u_b^\varepsilon\,\phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right)\,Q^\varepsilon\,dx\,.
\end{aligned} \tag{3.13}$$

On the other hand, observing that

$$\partial_v h_2(u_b, v) = \int_0^{u_b} \frac{z}{b}\,\phi'\left(\frac{z+v}{b}\right) dz = u_b\phi\left(\frac{u_b+v}{b}\right) - \int_0^{u_b} \phi\left(\frac{z+v}{b}\right) dz\,, \quad (3.14)$$

the positivity of ϕ' implies that $\partial_v h_2$ is positive and

$$\begin{aligned}
&\int_\Omega \partial_v h_2(u_b^\varepsilon, v^\varepsilon)\, f_v(u_b^\varepsilon, v^\varepsilon)\, dx \\
&\le \eta_v \int_\Omega \partial_v h_2(u_b^\varepsilon, v^\varepsilon)\, v^\varepsilon \left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \le b\}}\, dx \\
&\le \eta_v \int_\Omega u_b^\varepsilon \phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) v^\varepsilon \left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \le b\}}\, dx\,.
\end{aligned}$$

Therefore, we obtain

$$\begin{aligned}
I_2 \le &-d_v \int_\Omega \partial_{vv} h_2(u_b^\varepsilon, v^\varepsilon)\, |\nabla v^\varepsilon|^2\, dx - d_v \int_\Omega \partial_{vu_b} h_2(u_b^\varepsilon, v^\varepsilon)\, \nabla u_b^\varepsilon \cdot \nabla v^\varepsilon\, dx \\
&+ \eta_v \int_\Omega u_b^\varepsilon \phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) v^\varepsilon \left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \le b\}}\, dx\,.
\end{aligned} \quad (3.15)$$

Computing from (3.14)

$$\partial_{vu_b} h_2(u_b, v) = \frac{u_b}{b}\,\phi'\left(\frac{u_b+v}{b}\right),$$

and plugging estimates (3.13) and (3.15) into (3.12), we end up with the estimate

$$\begin{aligned}
\frac{d}{dt}\int_\Omega h_2(u_b^\varepsilon, v^\varepsilon)\, dx \le &- d_b \int_\Omega \left[\phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) + \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right)\right] |\nabla u_b^\varepsilon|^2\, dx \\
&- d_v \int_\Omega \partial_{vv} h_2(u_b^\varepsilon, v^\varepsilon) |\nabla v^\varepsilon|^2\, dx \\
&- (d_b + d_v) \int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \nabla u_b^\varepsilon \cdot \nabla v^\varepsilon\, dx \\
&+ C \int_\Omega (u_b^\varepsilon)^2 \left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \le b\}}\, dx \\
&+ \eta_v \int_\Omega u_b^\varepsilon \phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) v^\varepsilon \left(1 - \frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \mathbb{1}_{\{u_b^\varepsilon + v^\varepsilon \le b\}}\, dx \\
&- \frac{1}{\varepsilon} \int_\Omega u_b^\varepsilon\, \phi\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) Q^\varepsilon\, dx\,.
\end{aligned} \quad (3.16)$$

Next, using the positivity of ϕ' again, we estimate the third term in (3.16) with a weight $\eta > 0$ as

$$\begin{aligned}
&- (d_b + d_v) \int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) \nabla u_b^\varepsilon \cdot \nabla v^\varepsilon\, dx \\
&\le (d_b + d_v) \frac{\eta}{2} \int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) |\nabla u_b^\varepsilon|^2\, dx + \frac{d_b + d_v}{2\eta} \int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon + v^\varepsilon}{b}\right) |\nabla v^\varepsilon|^2\, dx.
\end{aligned}$$

Thus, choosing $\eta \in (0, 2d_b(d_b+d_v)^{-1})$, gives $C(\eta) := (d_b - (d_b+d_v)\frac{\eta}{2}) > 0$, and inequality (3.16) becomes

$$\begin{aligned}\frac{d}{dt}\int_\Omega h_2(u_b^\varepsilon, v^\varepsilon)\,dx \le & -d_b\delta_\phi \int_\Omega |\nabla u_b^\varepsilon|^2\,dx - d_v\int_\Omega \partial_{vv}h_2(u_b^\varepsilon, v^\varepsilon)|\nabla v^\varepsilon|^2\,dx \\ & - C(\eta)\int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon+v^\varepsilon}{b}\right)|\nabla u_b^\varepsilon|^2\,dx \\ & + \frac{(d_b+d_v)}{2\eta}\int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon+v^\varepsilon}{b}\right)|\nabla v^\varepsilon|^2\,dx \\ & + C - \frac{1}{\varepsilon}\int_\Omega u_b^\varepsilon\,\phi\left(\frac{u_b^\varepsilon+v^\varepsilon}{b}\right)Q^\varepsilon\,dx\,.\end{aligned} \tag{3.17}$$

Finally, by assumption (H1), the derivative

$$\begin{aligned}\partial_{vv}h_2(u_b, v) &= \frac{u_b}{b}\,\phi'\left(\frac{u_b+v}{b}\right) - \left[\phi\left(\frac{u_b+v}{b}\right) - \phi\left(\frac{v}{b}\right)\right] \\ &= \int_v^{u_b+v}\left[\phi'\left(\frac{u_b+v}{b}\right) - \phi'\left(\frac{z}{b}\right)\right]\frac{dz}{b}\end{aligned}$$

satisfies

$$|\partial_{vv}h_2(u_b, v)| \le 2\,M_{\phi'}\frac{u_b}{b}\,.$$

Therefore, adding (3.11) and (3.17), and using the boundedness of ϕ' again, we arrive at the following estimate for the time derivative of the energy

$$\begin{aligned}\frac{d}{dt}\mathcal{E}(u_a^\varepsilon(t), u_b^\varepsilon(t), v^\varepsilon(t)) \le & -d_a\delta_\psi\int_\Omega |\nabla u_a^\varepsilon|^2\,dx - d_b\delta_\phi\int_\Omega |\nabla u_b^\varepsilon|^2\,dx \\ & - C(\eta)\int_\Omega \frac{u_b^\varepsilon}{b}\,\phi'\left(\frac{u_b^\varepsilon+v^\varepsilon}{b}\right)|\nabla u_b^\varepsilon|^2\,dx \\ & + C\|u_a^\varepsilon + u_b^\varepsilon\|_{L^2(\Omega)}\|\nabla v^\varepsilon\|^2_{L^4(\Omega)} - \frac{1}{\varepsilon}\int_\Omega (Q_\varepsilon)^2 dx + C.\end{aligned} \tag{3.18}$$

Integrating in time over $[0, T]$ the latter inequality, estimate (3.10) is proved by the means of Lemma 3.1 (with $q = 2$), Lemma 3.2 and the boundedness of the initial energy. □

We conclude this section by giving improved estimates from interpolation arguments.

Corollary 3.4. *Under the hypothesis of Theorem 2.2, for all $T > 0$, the following estimates hold:*

$$\|u_a^\varepsilon + u_b^\varepsilon\|_{L^2\left([0,T];\,H^1(\Omega)\right)} \leqslant C_T\,, \tag{3.19}$$

and

$$\|u_a^\varepsilon + u_b^\varepsilon\|_{L^q(\Omega_T)} \leqslant C_T\,, \tag{3.20}$$

where

$$q := \begin{cases} 2 + 2/\mathrm{N} & \text{if } \mathrm{N} > 2, \\ 3, & \text{if } \mathrm{N} = 1. \end{cases} \tag{3.21}$$

and $q < 3$ if $\mathrm{N} = 2$.

Proof. The following argument is performed for the subpopulation u_a^ε. It can be applied similarly to u_b^ε and thus to $u_a^\varepsilon + u_b^\varepsilon$.

Lemma 3.2 and 3.3 give that u_a^ε is bounded in $L^2([0,T];\, H^1(\Omega))$. Thus, by the Sobolev embedding theorem, we have that u_a^ε is bounded in $L^2([0,T];\, L^{\mathrm{N}^*}(\Omega))$, with $\mathrm{N}^* = \frac{2\mathrm{N}}{\mathrm{N}-2}$ if $\mathrm{N} > 2$, $\mathrm{N}^* \in [2, +\infty)$ if $\mathrm{N} = 2$ and $\mathrm{N}^* = \infty$ if $\mathrm{N} = 1$. Since we also know that u_a^ε is bounded in $L^\infty([0,T];\, L^1(\Omega))$, by interpolation we obtain that u_a^ε is bounded in $L^q(\Omega_T)$, with q as in (3.21). □

Remark 5. *At this point, using Lemma 3.1 again, we see that $\partial_t v^\varepsilon$ and $\nabla\nabla v^\varepsilon$ are bounded in $L^q(\Omega_T)$.*

3.2 End of the proof of the main result

End of the proof of Theorem 2.2. The proof is divided in four steps and uses compactness to identify limits along subsequences. The first and the second one focus on the identification of the limit (as $\varepsilon \to 0$) of the densities v^ε and $u^\varepsilon = u_a^\varepsilon + u_b^\varepsilon$, a.e. in $[0,T] \times \Omega$, respectively. In the third step we obtain the a.e. convergence of the subpopulation densities $u_a^\varepsilon, u_b^\varepsilon$ and we identify the obtained limit as the unique solution of the nonlinear system (1.7). The convergence argument is also extended globally in time by a diagonal argument. Finally, the proof is concluded in the fourth step, taking the limit as ε tends to zero, in the very weak formulation of the system satisfied by $u^\varepsilon = u_a^\varepsilon + u_b^\varepsilon$ and v^ε.

First step. Let $T > 0$ be arbitrarily fixed. Thanks to the control of the density v^ε given in Lemma 3.1 and to the boundedness of $u_a^\varepsilon + u_b^\varepsilon$ in $L^2(\Omega_T)$ obtained in Lemma 3.2, we have that $(v^\varepsilon)_\varepsilon$ is bounded in $L^4([0,T]; W^{1,4}(\Omega))$ and $(\partial_t v^\varepsilon)_\varepsilon$ is bounded in $L^2([0,T]; L^2(\Omega))$. Therefore, by applying Rellich's Theorem, there exists a subsequence, still denoted v^ε, and $v \in L^4(\Omega_T)$ such that, as $\varepsilon \to 0$,

$$v^\varepsilon(t,x) \longrightarrow v(t,x)\,, \qquad \text{a.e. on } [0,T] \times \Omega\,. \tag{3.22}$$

Moreover,

$$\nabla v^\varepsilon \rightharpoonup \nabla v \qquad \text{in } L^4(\Omega_T), \tag{3.23}$$

and due to Lemma 3.1 again, v is nonnegative and belongs to $L^\infty(\Omega_T)$, while ∇v lies in $L^4(\Omega_T)$.

Second step. We rewrite the parabolic equation satisfied by the density $u^\varepsilon = u_a^\varepsilon + u_b^\varepsilon$ as

$$\partial_t u^\varepsilon = \Delta(d_a\, u_a^\varepsilon + d_b\, u_b^\varepsilon) + f_a(u_a^\varepsilon) + f_b(u_b^\varepsilon, v^\varepsilon)\,. \tag{3.24}$$

Thanks to Corollary 3.4, we see that $(u^\varepsilon)_\varepsilon$ is uniformly bounded in $L^2([0,T]; H^1(\Omega))$ and in $L^{2+2\delta}(\Omega_T)$ for some $\delta > 0$, so that the reaction term in (3.24) is uniformly bounded in $L^{1+\delta}(\Omega_T)$. Then $(\partial_t(u_a^\varepsilon + u_b^\varepsilon))_\varepsilon$ is uniformly bounded in $L^{1+\delta}([0,T]; W^{-1,1+\delta}(\Omega))$. Thus, Aubin-Lions' lemma (cf. [26]) yields a subsequence (still denoted u^ε), and a function $u \geq 0$, $u \in L^2(\Omega_T)$, such that, as $\varepsilon \to 0$,

$$u^\varepsilon(t,x) = u_a^\varepsilon(t,x) + u_b^\varepsilon(t,x) \longrightarrow u(t,x)\,, \qquad \text{a. e. in } \Omega_T\,, \tag{3.25}$$

where the nonnegativity of u follows from that of u^ε. Furthermore,

$$\nabla u^\varepsilon \rightharpoonup \nabla u \qquad \text{in } L^2(\Omega_T)\,, \tag{3.26}$$

and

$$\|u\|_{L^2(\Omega_T)} = \lim_{\varepsilon\to 0} \|u_a^\varepsilon + u_b^\varepsilon\|_{L^2(\Omega_T)} \leqslant C_T\,,$$
$$\|\nabla u\|_{L^2(\Omega_T)} \leq \liminf_{\varepsilon\to 0} \|\nabla u^\varepsilon\|_{L^2(\Omega_T)} \leqslant C_T\,.$$

Third step. The energy estimate (3.10) yields the estimate

$$\Big\|\phi\Big(\frac{u_b^\varepsilon + v^\varepsilon}{b}\Big)u_b^\varepsilon - \psi\Big(\frac{u_a^\varepsilon}{a}\Big)u_a^\varepsilon\Big\|_{L^2(\Omega_T)} \leq \sqrt{\varepsilon}\,C_T\,. \tag{3.27}$$

Therefore, $Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ converges to zero in $L^2(\Omega_T)$, as $\varepsilon \to 0$, and (up to extraction of a subsequence)

$$\phi\Big(\frac{u_b^\varepsilon + v^\varepsilon}{b}\Big)u_b^\varepsilon - \psi\Big(\frac{u_a^\varepsilon}{a}\Big)u_a^\varepsilon \longrightarrow 0, \qquad \text{a.e. in } \Omega_T\,. \tag{3.28}$$

It remains to prove the existence of the a.e. limit of subsequences of $(u_a^\varepsilon)_\varepsilon, (u_b^\varepsilon)_\varepsilon$ and to obtain that this limit is, a.e. over Ω_T, the unique solution of (1.7), corresponding to the functions u and v obtained in (3.25) and (3.22), respectively.

Let us denote $\big(u_a^*(u,v), u_b^*(u,v)\big)$ the unique solution of (1.7). Then, using the function q defined in (2.1), we get

$$\begin{aligned} Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon) &= Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon) - Q(u_a^*(u^\varepsilon, v^\varepsilon), u_b^*(u^\varepsilon, v^\varepsilon), v^\varepsilon) \\ &= q(u_b^\varepsilon, u^\varepsilon, v^\varepsilon) - q(u_b^*(u^\varepsilon, v^\varepsilon), u^\varepsilon, v^\varepsilon) \\ &= \partial_{u_b} q(\zeta, u^\varepsilon, v^\varepsilon)\,(u_b^\varepsilon - u_b^*(u^\varepsilon, v^\varepsilon))\,, \end{aligned}$$

for some intermediate value ζ between u_b^ε and $u_b^*(u^\varepsilon, v^\varepsilon)$. Hence by hypothesis (H1) we obtain

$$|Q(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)| \geq (\delta_\phi + \delta_\psi)|u_b^\varepsilon - u_b^*(u^\varepsilon, v^\varepsilon)|\,.$$

Thus by (3.28), $|u_b^\varepsilon - u_b^*(u^\varepsilon, v^\varepsilon)| \to 0$ as $\varepsilon \to 0$, a.e. in Ω_T. Finally, the proved convergence (3.25) and (3.22) and the continuity of u_b^* with respect to its arguments, yields the desired result, i.e.,

$$u_b^\varepsilon \to u_b^*(u,v)\,, \quad u_a^\varepsilon = u^\varepsilon - u_b^\varepsilon \to u_a^*(u,v)\,, \quad \varepsilon \to 0\,, \qquad \text{a.e. in } \Omega_T\,.$$

To conclude, let us remark that all the a.e. convergence results obtained so far have been performed on $[0,T]$, for any arbitrary $T > 0$. Since $(u_a^\varepsilon, u_b^\varepsilon, v^\varepsilon)$ is defined on $[0,+\infty)$, by extracting subsequences, these arguments can be replicated in the time intervals $[0,2T]$, $[0,3T]$, and so on. Then by Cantor's diagonal argument, the convergences (3.22), (3.25) and (3.28), and the convergence of the pair $(u_a^\varepsilon, u_b^\varepsilon)$ towards the solution of (1.7) are verified a.e. in $(0,+\infty)\times\Omega$.

Fourth step. We shall prove now that (u,v) is a weak solution of (1.6), in the sense of Definition 2.1. For this purpose, let us consider two test functions ξ_1, ξ_2 in C_c^2, satisfying $\nabla\xi_1\cdot\sigma = \nabla\xi_2\cdot\sigma = 0$, on $[0,T]\times\partial\Omega$. Multiplying the equation satisfied by $u_a^\varepsilon + u_b^\varepsilon$ by ξ_1 and the third equation of (1.1) by ξ_2 and integrating over $(0,+\infty)\times\Omega$, we get,

$$\begin{aligned} &-\int_0^\infty\int_\Omega (\partial_t\xi_1)\,(u_a^\varepsilon + u_b^\varepsilon)\,dx\,dt - \int_\Omega \xi_1(0)\,\big(u_a^{\mathrm{in},\varepsilon} + u_b^{\mathrm{in},\varepsilon}\big)\,dx = \\ &\int_0^\infty\int_\Omega \Delta\xi_1\,\big(d_a u_a^\varepsilon + d_b u_b^\varepsilon\big)\,dx\,dt + \int_0^\infty\int_\Omega \xi_1\big(f_a(u_a^\varepsilon) + f_b(u_b^\varepsilon, v^\varepsilon)\big)\,dx\,dt\,, \end{aligned} \tag{3.29}$$

and

$$
\begin{aligned}
-\int_0^\infty \int_\Omega (\partial_t \xi_2\,)\, v^\varepsilon \, dx\, dt - \int_\Omega \xi_2(0)\, v^{\mathrm{in},\varepsilon}\, dx = \\
d_v \int_0^\infty \int_\Omega \Delta \xi_2\, v^\varepsilon \, dx\, dt + \int_0^\infty \int_\Omega \xi_2\, f_v(u_b^\varepsilon, v^\varepsilon)\, dx\, dt\,.
\end{aligned}
\tag{3.30}
$$

Concerning the equation (3.29), the convergence results obtained in the previous steps and the estimates in (3.6) allow us to pass to the limit as $\varepsilon \to 0$, in all the terms of the equation, using Lebesgue's dominated convergence theorem, thus obtaining (2.2).

The same conclusion holds for equation (3.30). Indeed, the boundedness of v^ε and its convergence (3.22), together with the estimates in (3.6), allow us to pass to the limit in all terms of (3.30), using Lebesgue's dominated convergence theorem again, thus obtaining (2.3). The proof of Theorem 2.2 is now completed. □

4 Linear stability analysis

In this section, we investigate the linear stability of spatially homogeneous steady states of the macroscopic system (1.6)–(1.9), with reaction and fast reaction functions given by (1.4) and (1.5), respectively. We shall also see the relationship between the linear stability of the coexistence steady state at the mesoscopic and macroscopic scale, as $\varepsilon \to 0$.

Let ψ and ϕ be conversion rates satisfying assumption (H1). We introduce the following few notations for later use,

$$
\psi_1 = \psi(1), \qquad \phi_1 = \phi(1)\,,
$$

and the parameter providing a criterion for the linear stability (see *Theorem 4.1* and *Proposition 4.2*),

$$
\alpha := \frac{\psi_1}{\phi_1}\,\frac{a}{b} > 0\,. \tag{4.1}
$$

The pair $(\bar u, \bar v) \in \mathbb{R}^2_+$ is a spatially homogeneous steady state of the macroscopic system if and only if $\bar u = \bar u_a + \bar u_b$ and the triplet $(\bar u_a, \bar u_b, \bar v)$ satisfy the nonlinear system

$$
f_a(\bar u_a) + f_b(\bar u_b, \bar v) = f_v(\bar u_b, \bar v) = Q(\bar u_a, \bar u_b, \bar v) = 0\,. \tag{4.2}
$$

Extinction of u. From $Q(\bar u_a, \bar u_b, \bar v) = 0$ and the strict positivity of ϕ and ψ, we see that $\bar u_a = 0$ if and only if $\bar u_b = 0$: no extinction of a single subpopulation of the species u is admitted. Thus, for $\bar u_a = \bar u_b = 0$, we obtain the trivial and semi-trivial steady states

$$
(\bar u_1, \bar v_1) = (0, 0) \qquad \text{and} \qquad (\bar u_2, \bar v_2) = (0, b)\,, \tag{4.3}
$$

corresponding to the total extinction of the two species in the ecosystem and to a partial extinction, respectively.

Survival of u and extinction of v. The other steady states with $\bar u_a \neq 0$ and $\bar u_b \neq 0$ are of main interest. The first case is with $\bar v = 0$. Denoting $\bar u_a = \lambda\, a$ and $\bar u_b = \sigma\, b$, for $\lambda, \sigma > 0$, system (4.2) reduces to

$$
\eta_a a\, \lambda(1-\lambda) + \eta_b b\, \sigma(1-\sigma) = 0\,, \qquad \frac{\lambda \psi(\lambda)}{\sigma \phi(\sigma)} = \frac{b}{a}\,. \tag{4.4}
$$

Such a semi-trivial state always exists but the uniqueness is non-trivial. Indeed, the second equation in (4.4) can be written equivalently as

$$\frac{\sigma\phi(\sigma)}{\phi_1} = \alpha\,\frac{\lambda\psi(\lambda)}{\psi_1}\,. \tag{4.5}$$

Due to assumption (H1), the functions $\Lambda(\lambda) := \lambda\psi(\lambda)/\psi_1$ and $\Sigma(\sigma) := \sigma\phi(\sigma)/\phi_1$ are strictly increasing functions from 0 to $+\infty$. Hence, for every $\lambda > 0$ there exists a unique $\sigma(\lambda) > 0$ solving (4.5) and given by

$$\sigma(\lambda) = \Sigma^{-1}(\alpha\Lambda(\lambda))\,. \tag{4.6}$$

Plugging (4.6) into the left hand side equation in (4.4), the stationary states correspond to the zeros of the function F below

$$F(\lambda) := \eta_a a\,\lambda(1-\lambda) + \eta_b b\,\sigma(\lambda)(1-\sigma(\lambda))\,. \tag{4.7}$$

Furthermore, by the competition structure, it follows that F is positive for small enough λ and $F(\lambda) \to -\infty$ as $\lambda \to +\infty$. Thus, the macroscopic system (1.4)–(1.7) admits at least one semi-trivial equilibrium

$$(\bar{u}_3, \bar{v}_3) = (a\lambda + b\sigma, 0)\,, \tag{4.8}$$

solution of system (4.4), with $\sigma = \sigma(\lambda)$ uniquely determined by (4.6). Moreover, if the equilibrium is unique, F is decreasing around the corresponding λ, i.e. $F'(\lambda) < 0$.

In general it is possible to have several semi-trivial states of type (4.8). As an example, take

$$a = b = 1, \quad \eta_a = 0.2, \quad \eta_b = 1, \quad \phi \equiv 1, \quad \psi(x) = \begin{cases} 0.1 & \text{if } x \le 1.6, \\ 0.3 & \text{otherwise.} \end{cases} \tag{4.9}$$

The corresponding $F(\lambda)$ is shown in Figure 1, from where we see that there exist three semi-trivial states.

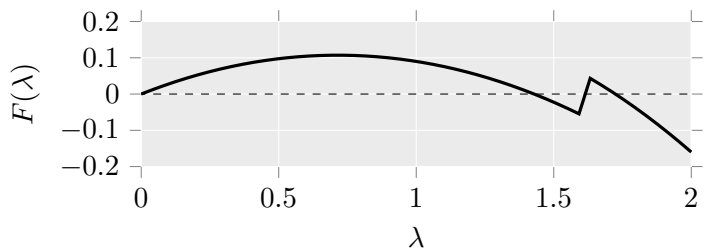

Figure 1: Reaction term $F(\lambda)$ for the example (4.9).

We will discuss the uniqueness issue in *Proposition* 4.2, where a sufficient condition for uniqueness of (4.8) is given, and *Proposition* 4.3, where we exhibit a family of conversion rates functions ϕ, ψ for which uniqueness of (4.8) holds true.

Coexistence of u and v. Finally, if $\bar{u}_a \neq 0$, $\bar{u}_b \neq 0$, $\bar{v} \neq 0$, from $f_v(\bar{u}_b, \bar{v}) = 0$ we get $\bar{u}_b + \bar{v} = b$ and thus $\bar{u}_a = a$. Then, from $Q(\bar{u}_a, \bar{u}_b, \bar{v}) = 0$ and the definition

of α it follows that $\bar{u}_b = b\alpha$. Therefore, system (4.2) has a unique totally nontrivial solution given by

$$(\bar{u}_4, \bar{v}_4) = (a + b\alpha, b(1-\alpha))\,, \tag{4.10}$$

provided that $\alpha < 1$.

We shall see in the following subsection (see *Theorem* 4.1) that the stationary states (4.3) are unstable, so that the total extinction of the species u never occurs. The species u always survives and its coexistence with the species v is conditioned by the switching strategy that the subpopulations u_a and u_b adopt when both resources run out, quantified through the parameter α. Indeed, the coexistence occurs if the switch from the state u_b to the state u_a is faster than the opposite switch, i.e. $\alpha < 1$. On the other hand, v goes extinct only if $\alpha > 1$.

The relationship between the linear stability of the mesoscopic and macroscopic coexistence steady states, as $\varepsilon \to 0$, is seen in *Subsection 4.3*.

4.1 Linear stability analysis for the cross-diffusion system

Let us consider the partial starvation measures

$$\lambda = \frac{\bar{u}_a}{a} \geq 0\,, \qquad \sigma = \frac{\bar{u}_b}{b} \geq 0\,, \qquad \delta = \frac{\bar{v}}{b} \in \{0, 1-\sigma\}\,,$$

so that each of the above steady states can be identified with the triplet $(\lambda, \sigma, \delta)$ and written as

$$\bar{P} = (\bar{u}, \bar{v}) = \big(\lambda a + \sigma b, \delta b\big)\,. \tag{4.11}$$

Linearizing around $\bar{P}$ the ODEs system associated to (1.4)–(1.7), in the sense of small perturbation τ, $|\tau| \ll 1$, i.e.

$$\begin{aligned} &u_a = \bar{u}_a + \tau\,\tilde{u}_a \quad \text{and} \quad u_b = \bar{u}_b + \tau\,\tilde{u}_b \\ &u = u_a + u_b = (\bar{u}_a + \bar{u}_b) + \tau(\tilde{u}_a + \tilde{u}_b) = \bar{u} + \tau\,\tilde{u}, \\ &v = \bar{v} + \tau\tilde{v}, \end{aligned} \tag{4.12}$$

we obtain

$$\begin{cases} \dot{\tilde{u}} = \eta_a(1-2\lambda)\tilde{u}_a + \eta_b(1-2\sigma-\delta)\tilde{u}_b - \eta_b\sigma\,\tilde{v} + o(1), \\ \dot{\tilde{v}} = -\eta_v\delta\,\tilde{u}_b + \eta_v(1-\sigma-2\delta)\tilde{v} + o(1). \end{cases} \tag{4.13}$$

Moreover, from the linearization of $Q(u_a, u_b, v)$ around $(\bar{u}_a, \bar{u}_b, \bar{v})$, we have

$$\partial_1\bar{Q}\,\tilde{u}_a + \partial_2\bar{Q}\,\tilde{u}_b + \partial_3\bar{Q}\,\tilde{v} + o(1) = 0, \tag{4.14}$$

where $\partial_j\bar{Q} = \partial_j Q(\bar{u}_a, \bar{u}_b, \bar{v})$ and

$$\begin{aligned} &\partial_1\bar{Q} = -\psi(\lambda) - \lambda\psi'(\lambda) =: -\beta(\lambda) < 0\,, \\ &\partial_2\bar{Q} = \phi(\sigma+\delta) + \sigma\phi'(\sigma+\delta) =: \gamma(\sigma,\delta) > 0\,, \\ &\partial_3\bar{Q} = \sigma\phi'(\sigma+\delta) =: \theta(\sigma,\delta) > 0\,. \end{aligned} \tag{4.15}$$

Using $\tilde{u} = \tilde{u}_a + \tilde{u}_b$, from (4.14) we obtain $\tilde{u}_a$ and $\tilde{u}_b$ in terms of $\tilde{u}$ and $\tilde{v}$ as follows

$$\tilde{u}_a = \frac{1}{r}\,\gamma(\sigma,\delta)\,\tilde{u} + \frac{1}{r}\,\theta(\sigma,\delta)\,\tilde{v} + o(1)\,, \qquad \tilde{u}_b = \frac{1}{r}\,\beta(\lambda)\,\tilde{u} - \frac{1}{r}\,\theta(\sigma,\delta)\,\tilde{v} + o(1)\,, \tag{4.16}$$

where $r = r(\lambda, \sigma, \delta) := \partial_2 \bar{Q} - \partial_1 \bar{Q} = \beta(\lambda) + \gamma(\sigma, \delta) > 0$. Thus, system (4.13) becomes

$$\dot{\tilde{w}} = \bar{M}\,\tilde{w} + o(1), \qquad \tilde{w} := \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix},$$

and the matrix $\bar{M} = M(\bar{P})$ has the following entries

$$\begin{aligned} M_{11}(\bar{P}) &= \frac{\eta_a}{r}(1-2\lambda)\gamma(\sigma,\delta) + \frac{\eta_b}{r}(1-2\sigma-\delta)\beta(\lambda)\,, \\ M_{12}(\bar{P}) &= \frac{\eta_a}{r}(1-2\lambda)\theta(\sigma,\delta) - \frac{\eta_b}{r}(1-2\sigma-\delta)\theta(\sigma,\delta) - \eta_b\sigma\,, \\ M_{21}(\bar{P}) &= -\frac{\eta_v}{r}\delta\,\beta(\lambda)\,, \\ M_{22}(\bar{P}) &= \frac{\eta_v}{r}\delta\,\theta(\sigma,\delta) + \eta_v(1-\sigma-2\delta)\,. \end{aligned} \tag{4.17}$$

Next, for u_a and u_b as in (4.12), using (4.16) again, the linearization of the cross-diffusion operator in (1.6) reads as

$$\Delta\big(d_a u_a + d_b u_b\big) = \tau\Big(d_a \frac{\gamma(\sigma,\delta)}{r} + d_b \frac{\beta(\lambda)}{r}\Big)\Delta\tilde{u} + \tau(d_a - d_b)\frac{\theta(\sigma,\delta)}{r}\Delta\tilde{v} + o(\tau),$$

and the linearized cross-diffusion macroscopic system writes

$$\partial_t \tilde{w} = \bar{J}\Delta\tilde{w} + \bar{M}\tilde{w} + o(1)\,, \qquad \nabla(\tilde{w} + o(1)) \cdot \sigma = 0, \tag{4.18}$$

with

$$\bar{J} := \begin{bmatrix} d_a \frac{\gamma(\sigma,\delta)}{r} + d_b \frac{\beta(\lambda)}{r} & (d_a - d_b)\frac{\theta(\sigma,\delta)}{r} \\ 0 & d_v \end{bmatrix}.$$

The homogeneous (up to a $o(1)$ term) Neumann boundary conditions for $\tilde{w}$ in (4.18) follow by the no flux boundary condition (1.9) and (4.16).

Neglecting the $o(1)$ terms, the stability of the linearized system (4.18) can be analysed decomposing $\tilde{w}(t,x)$ as

$$\tilde{w}(t,x) = \sum_{n\in\mathbb{N}} \tilde{w}_n(t)\, e_n(x)\,,$$

where $(e_n)_{n\in\mathbb{N}}$ is the orthogonal eigenbasis of $-\Delta$ on Ω with Neumann boundary conditions. Denoting $0 = \lambda_0 < \lambda_1 \le \cdots \le \lambda_n \le \cdots$ the corresponding eigenvalues, the projection coefficients $\tilde{w}_n(t)$ evolve independently according the equations

$$\partial_t \tilde{w}_n(t) = (-\lambda_n \bar{J} + \bar{M})\tilde{w}_n(t)\,, \qquad n \in \mathbb{N}\,.$$

Thus, for the stability analysis it suffices to consider the stability of the matrix $N_n := -\lambda_n \bar{J} + \bar{M}$, i.e.

$$N_n = \begin{bmatrix} -\frac{1}{r}\big(d_a\,\gamma + d_b\beta\big)\lambda_n + M_{11} & -\frac{1}{r}(d_a - d_b)\theta\,\lambda_n + M_{12} \\ M_{21} & -d_v\lambda_n + M_{22} \end{bmatrix}, \tag{4.19}$$

with $M_{ij} = M_{ij}(\bar{P})$ defined in (4.17).

Theorem 4.1. *Let ψ and ϕ be conversion rates satisfying assumption (H1) and $\alpha > 0$ defined as in (4.1). Then, the following holds true.*

(i) The trivial and semi-trivial steady states $(\bar{u}_1, \bar{v}_1) = (0,0)$ *and* $(\bar{u}_2, \bar{v}_2) = (0, b)$ *are linearly unstable.*

(ii) The family of semi-trivial steady states $(\bar{u}_3, \bar{v}_3) = (a\lambda + b\sigma, 0)$ *satisfies*

$$\sigma = \lambda = 1\,, \qquad \text{if } \alpha = 1\,, \tag{4.20}$$

$$0 < \sigma < 1 < \lambda < \frac{1}{2} + \frac{1}{2}\sqrt{1 + \frac{b\eta_b}{a\eta_a}}\,, \qquad \text{if } \alpha < 1\,, \tag{4.21}$$

and the swapped relation

$$0 < \lambda < 1 < \sigma < \frac{1}{2} + \frac{1}{2}\sqrt{1 + \frac{a\eta_a}{b\eta_b}}\,, \qquad \text{if } \alpha > 1\,. \tag{4.22}$$

Furthermore, they are linearly unstable if $\alpha \le 1$*, and if* $\alpha > 1$*, they are linearly stable if and only if the function* F *in* (4.7) *is strictly decreasing around* λ*, i.e.* $F'(\lambda) < 0$*.*

(iii) If $\alpha < 1$*, there exists a unique strictly positive steady state given by* $(\bar{u}_4, \bar{v}_4) = (a + b\alpha, b(1-\alpha))$ *and it is linearly stable.*

Proof. *(i)* From (4.17) and (4.15), we have

$$M(0,0) = \operatorname{diag}\Big\{\frac{\eta_a\phi(0) + \eta_b\psi(0)}{\phi(0) + \psi(0)}, \eta_v\Big\} \qquad \text{and} \qquad M(0,b) = \begin{bmatrix} \frac{\eta_a\phi_1}{\phi_1+\psi(0)} & 0 \\ -\frac{\eta_v\psi(0)}{\phi_1+\psi(0)} & -\eta_v \end{bmatrix},$$

implying that the steady states $(0,0)$ and $(0,b)$ are linearly unstable, both for the macroscopic system and for the associated diffusion-less one, because of the zero eigenvalue of the Laplacian.

(ii) In order to proceed with the investigation of the family of steady states $(\bar{u}_3, \bar{v}_3) = (a\lambda + b\sigma, 0)$, let us observe that from the first equation in (4.4), we have

$$(1-\lambda)(1-\sigma) < 0 \quad \text{or} \quad \lambda = \sigma = 1\,. \tag{4.23}$$

Thus, according to the value of α, we get from (4.5): if $\alpha > 1$, then $\lambda \in (0,1)$ and $\sigma > 1$, i.e. $\bar{u}_a < a$ and $\bar{u}_b > b$; if $\alpha < 1$, then $\lambda > 1$ and $\sigma \in (0,1)$, i.e. $\bar{u}_a > a$ and $\bar{u}_b < b$; if $\alpha = 1$, then $\lambda = \sigma = 1$ giving the optimal selection case $\bar{u}_a = a, \bar{u}_b = b$.

Next, let us rewrite the left equation in (4.4) as

$$\sigma(1-\sigma) = \frac{\eta_a a}{\eta_b b}\lambda(\lambda - 1) =: K(\lambda)\,. \tag{4.24}$$

If $\alpha > 1$, as $\lambda \in (0,1)$, it follows that $K(\frac{1}{2}) \le K(\lambda) < 0$ and σ is upper bounded by the positive root of the above equation with $\lambda = \frac{1}{2}$. Hence, (4.22) follows. If $\alpha < 1$, swapping the role between λ and σ, we obtain (4.21).

Furthermore, the entries (4.17) of the matrix $M(\bar{P}) = M(a\lambda + b\sigma, 0)$ are now

$$\begin{aligned}
M_{11}(\bar{P}) &= \eta_a(1-2\lambda)\frac{\gamma}{r} + \eta_b(1-2\sigma)\frac{\beta}{r}\,,\\
M_{12}(\bar{P}) &= \big(\eta_a(1-2\lambda) - \eta_b(1-2\sigma)\big)\frac{\theta}{r} - \eta_b\,\sigma\,,\\
M_{21}(\bar{P}) &= 0\,,\\
M_{22}(\bar{P}) &= \eta_v(1-\sigma)\,.
\end{aligned}$$

As $M_{21} = 0$, the steady state is linearly stable for the diffusionless macroscopic system if and only if $M_{11} < 0$ and $M_{22} < 0$. Hence, $\sigma > 1$ is a necessary condition for the linear stability, and it holds only if $\alpha > 1$.

In the case $\alpha = 1$, giving the optimal selection case $\lambda = \sigma = 1$, $M(a+b,0)$ has a zero eigenvalue, so that the equilibrium is a non hyperbolic equilibrium. The contribution of the cross-diffusion term does not change the nature of the equilibrium because of the zero eigenvalue of the Laplacian.

Let $\alpha > 1$. The steady states under consideration satisfy $Q(\lambda a, \sigma(\lambda)b, 0) = 0$, where $\sigma(\lambda)$ is defined in (4.6). Taking the derivative with respect to λ and using (4.15), we obtain

$$a\partial_1 Q(\lambda a, \sigma(\lambda)b, 0) + b\,\sigma'(\lambda)\partial_2 Q(\lambda a, \sigma(\lambda)b, 0) = -\beta(\lambda)a + \gamma(\sigma(\lambda), 0)b\,\sigma'(\lambda) = 0\,.$$

Thus

$$\sigma'(\lambda) = \frac{a}{b}\frac{\beta(\lambda)}{\gamma(\sigma(\lambda), 0)}\,.$$

Plugging $\sigma'(\lambda)$ into the derivative of F

$$F'(\lambda) = \eta_a a(1-2\lambda) + \eta_b b\,\sigma'(\lambda)(1-2\sigma(\lambda))\,, \tag{4.25}$$

we now find

$$F'(\lambda) = \eta_a a(1-2\lambda) + \eta_b a\frac{\beta(\lambda)}{\gamma(\sigma(\lambda), 0)}(1-2\sigma(\lambda)) = \frac{a}{\gamma(\sigma(\lambda), 0)}\,rM_{11}(\bar{P}).$$

Hence, M_{11} is negative if and only if $F'(\lambda)$ is negative, which implies (ii) for the diffusionless macroscopic system and for the cross-diffusion one.

(iii) Let $\alpha < 1$. Since now $(\lambda, \sigma, \delta) = (1, \alpha, 1-\alpha)$, from (4.17), we have

$$M(\bar{u}_4, \bar{v}_4) = -\frac{1}{r}\begin{bmatrix} \eta_a\gamma + \eta_b\alpha\beta & \eta_a\theta + \eta_b\alpha(r-\theta) \\ \eta_v(1-\alpha)\beta & \eta_v(1-\alpha)(r-\theta) \end{bmatrix}. \tag{4.26}$$

As $r - \theta > 0$, it holds

$$\mathrm{tr}M < 0\,. \tag{4.27}$$

By $r = \beta + \gamma$ and $\gamma - \theta = \phi_1$, we have

$$\begin{aligned} \det M &= \frac{\eta_v(1-\alpha)}{r^2}\big[(\eta_a\gamma + \eta_b\alpha\beta)(r-\theta) - \eta_a\theta\beta - \eta_b\alpha\beta(r-\theta)\big] \\ &= \frac{\eta_a\eta_v(1-\alpha)}{r^2}\big[\gamma(r-\theta) - \theta\beta\big] = \frac{\eta_a\eta_v(1-\alpha)}{r}\,\phi_1 > 0, \end{aligned} \tag{4.28}$$

i.e. the equilibrium $(\bar{u}_4, \bar{v}_4)$ is stable for the diffusionless macroscopic system.

The expression form (4.26) for M implies for N_n, $n \in \mathbb{N}$, by (4.19), that

$$\mathrm{tr}\ N_n < 0\,,$$

and

$$\det N_n = A\lambda_n^2 + B\lambda_n + C\,,$$

with

$$\begin{aligned} A &:= d_v\frac{d_a\gamma + d_b\beta}{r} > 0, \\ B &:= \frac{(d_a - d_b)\theta}{r}M_{21} - \frac{d_a\gamma + d_b\beta}{r}M_{22} - d_v M_{11}, \\ C &:= \det M > 0. \end{aligned} \tag{4.29}$$

Furthermore, using the definition of r and the strict negativity of all the entries of $M(\bar{u}_4, \bar{v}_4)$, we find for B in (4.29)

$$\begin{aligned} B &= -(d_a - d_b)\frac{\eta_v \theta\beta(1-\alpha)}{r^2} + (d_a\gamma + d_b\beta)\frac{\eta_v(r-\theta)(1-\alpha)}{r^2} - d_v M_{11} \\ &= \frac{\eta_v(1-\alpha)}{r^2}\Big(- d_a\theta\beta + d_a r\gamma - d_a\theta\gamma + d_b r\beta\Big) - d_v M_{11} \\ &= \frac{\eta_v(1-\alpha)}{r}(d_a\phi_1 + d_b\beta) - d_v M_{11} > 0, \end{aligned}$$

which implies that $\det N_n > 0$, for all $n \in \mathbb{N}$. Therefore, the equilibrium $(\bar{u}_4, \bar{v}_4)$ remains linearly stable by adding the cross-diffusion terms. □

4.2 Uniqueness of semi-trivial states with extinction of v

One possibility to ensure uniqueness of the steady state $(\bar{u}_3, \bar{v}_3) = (a\lambda + b\sigma, 0)$ is to impose, in the case $\alpha > 1$, that the net flux of the individuals of the species u goes from the state u_b to the state u_a, when the population u_b reached the capacity of its resource and the population u_a has only halved the capacity of its resource. When $\alpha < 1$, the opposite switching mechanism has to be imposed. A precise version is the following.

Proposition 4.2. *Consider $\Lambda(\lambda) = \lambda\psi(\lambda)/\psi_1$ and $\Sigma(\sigma) = \sigma\phi(\sigma)/\phi_1$, with ϕ, ψ satisfying assumption (H1). Assume that*

$$\alpha\Lambda(1/2) \le 1\,, \qquad \text{if} \qquad \alpha > 1\,, \tag{4.30}$$

and

$$\alpha^{-1}\Sigma(1/2) \le 1\,, \qquad \text{if} \qquad \alpha < 1\,. \tag{4.31}$$

Then, there exists a unique solution of (4.4). Furthermore, the corresponding steady state (4.8) is linearly stable if $\alpha > 1$, and unstable if $\alpha < 1$.

Proof. Let $\alpha > 1$. For the proof recall the function $\lambda \mapsto \sigma(\lambda)$ from (4.6). Then, $\sigma(0) = 0$, while the increasing behaviour of Λ and Σ together with condition (4.30) imply that, for $\lambda \in (0, 1/2]$,

$$\sigma(\lambda) \le \Sigma^{-1}(\alpha\Lambda(1/2)) \le \Sigma^{-1}(1) = 1\,.$$

Hence, for $\lambda \in (0, 1/2]$, the function F from (4.7) is strictly positive.

Now, let $\bar{\lambda}$ be the smallest zero of F, so that $(a\bar{\lambda} + b\sigma(\bar{\lambda}), 0)$ is one of the steady states under consideration. By the above argument $\bar{\lambda} > 1/2$, and by *Theorem* 4.1, $\alpha > 1$ implies that $\sigma(\bar{\lambda}) > 1$. Therefore, the monotonicity of $\lambda \mapsto \sigma(\lambda)$ again implies that $\sigma(\lambda) > 1$, for any $\lambda \ge \bar{\lambda}$.

Finally, we find from (4.25) that $F'(\lambda) < 0$, for all $\lambda \ge \bar{\lambda}$. Hence there exists a unique stationary state and the claimed stability follows from *Theorem* 4.1.

The case $\alpha < 1$ follows changing the role between the variables λ and σ and between the functions Λ and Σ, i.e. defining $\lambda(\sigma) := \Lambda^{-1}(\alpha^{-1}\Sigma(\sigma))$ and analyzing the behaviour of $G(\sigma) := \eta_a a\lambda(\sigma)(1 - \lambda(\sigma)) + \eta_b b\sigma(1 - \sigma)$, instead of $F(\lambda)$. The claimed instability follows again by *Theorem* 4.1. □

Conditions (4.30) and (4.31) can be rephrased in terms of the ratio $\frac{b}{a}$, respectively as

$$\frac{\frac{1}{2}\psi(\frac{1}{2})}{\phi_1} \leq \frac{b}{a} < \frac{\psi_1}{\phi_1} \qquad \text{and} \qquad \frac{\psi_1}{\phi_1} < \frac{b}{a} \leq \frac{\psi_1}{\frac{1}{2}\phi(\frac{1}{2})}\,.$$

They are not necessary conditions. Indeed, we provide below a family of conversion rates ψ, ϕ, for which the uniqueness of the stationary states (4.8) holds true, whatever is $\frac{b}{a}$. For that family of conversion rates, some numerical test are shown in *Section* 5.

Since the population densities u_a and u_b are of the same species, it is natural to expect that the conversion dynamics from u_a to u_b is similar to that from u_b to u_a. So, in order to be consistent with the modelling considerations in *Subsection* 1.2, (see (1.15)), we choose

$$\psi(x) = \omega_1 \phi(\omega_2 x), \qquad \omega_1 > 0\,, \omega_2 \geq 0\,, \tag{4.32}$$

and we prove the following.

Proposition 4.3. *Consider ψ as in (4.32) and*

$$\phi(x) = \theta_1 x + \theta_2, \qquad \theta_1 \geq 0\,, \theta_2 > 0\,, \tag{4.33}$$

Then there exists a unique stationary state $(\bar{u}_3, \bar{v}_3) = (a\lambda + b\sigma, 0)$. It is linearly stable if $\frac{b}{a} < \omega_1\phi(\omega_2)/\phi_1$, and unstable otherwise.

Proof. Let $\sigma(\lambda)$ be as in (4.6). As observed previously, the stationary states (4.8) corresponds to the zeros of the function $F(\lambda)$ in (4.7). Taking the second derivative of F, gives

$$F''(\lambda) = b\,\eta_b\big[\sigma''(\lambda) - 2(\sigma'(\lambda))^2 - 2\sigma(\lambda)\sigma''(\lambda)\big] - 2a\,\eta_a\,. \tag{4.34}$$

By (4.33) and (4.32), we have

$$\frac{\sigma\phi(\sigma)}{\phi_1} = \bar{\theta}\sigma^2 + (1-\bar{\theta})\sigma\,, \qquad \bar{\theta} = \frac{\theta_1}{\theta_1+\theta_2}\,,$$

and

$$\frac{\lambda\psi(\lambda)}{\psi_1} = \bar{\omega}\lambda^2 + (1-\bar{\omega})\lambda\,, \qquad \bar{\omega} = \frac{\omega_2\theta_1}{\omega_2\theta_1+\theta_2}\,.$$

Hence, equation (4.5) reads as

$$\bar{\theta}\sigma^2(\lambda) + (1-\bar{\theta})\sigma(\lambda) = \alpha[\bar{\omega}\lambda^2 + (1-\bar{\omega})\lambda] =: W(\lambda)\,, \tag{4.35}$$

and

$$\sigma(\lambda) = \frac{\bar{\theta}-1}{2\bar{\theta}} + \frac{1}{2\bar{\theta}}[(\bar{\theta}-1)^2 + 4\bar{\theta}\,W(\lambda)]^{\frac{1}{2}}\,.$$

Furthermore, deriving twice (4.35) with respect to λ, we obtain the identity

$$2(\sigma'(\lambda))^2 + 2\sigma(\lambda)\sigma''(\lambda) = 2\alpha\frac{\bar{\omega}}{\bar{\theta}} + (1-\frac{1}{\bar{\theta}})\sigma''(\lambda)\,.$$

Plugging the latter into (4.34), we end up with

$$F''(\lambda) = \frac{b\,\eta_b}{\bar{\theta}}\sigma''(\lambda) - (2\alpha\frac{\bar{\omega}}{\bar{\theta}}b\,\eta_b + 2a\,\eta_a)\,.$$

Finally, observing that $W'^2 - 2W\,W'' = \alpha^2(1-\bar\omega)^2$, we compute

$$\sigma''(\lambda) = \left(\frac{W'(\lambda)}{[(\bar\theta-1)^2+4\bar\theta\,W(\lambda)]^{\frac12}}\right)' = \frac{W''[(\bar\theta-1)^2+4\bar\theta\,W] - 2\bar\theta W'^2}{[(\bar\theta-1)^2+4\bar\theta\,W]^{\frac32}}$$

$$= \frac{2\alpha\bar\omega(\bar\theta-1)^2 - 2\bar\theta(W'^2-2W\,W'')}{[(\bar\theta-1)^2+4\bar\theta\,W]^{\frac32}} = 2\alpha\frac{\bar\omega(1-\bar\theta)^2-\alpha\bar\theta(1-\bar\omega)^2}{[(\bar\theta-1)^2+4\bar\theta\,W(\lambda)]^{\frac32}}\,.$$

If $\bar\omega(1-\bar\theta)^2-\alpha\bar\theta(1-\bar\omega)^2 \le 0$, the function F is strictly concave and therefore has a unique zero. If $\bar\omega(1-\bar\theta)^2-\alpha\bar\theta(1-\bar\omega)^2 > 0$, then $\sigma''(\lambda)$ is a strictly positive decreasing function that converge to 0 as $\lambda \to +\infty$, and consequently F has at most one inflection point and a unique zero. Moreover, F is decreasing around its unique zero. So that it gives a stable stationary point if $\alpha > 1$. □

4.3 Linear stability analysis for the mesoscopic system

A triple $(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon)$ is a homogeneous stationary solutions of the mesoscopic scale problem (1.1) if and only if

$$f_a(\bar u_a^\varepsilon) + \frac{1}{\varepsilon}Q(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon) = f_b(\bar u_b^\varepsilon, \bar v^\varepsilon) - \frac{1}{\varepsilon}Q(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon) = f_v(\bar u_b^\varepsilon, \bar v^\varepsilon) = 0.$$

If $\bar v^\varepsilon = 0$, then either $\bar u_a^\varepsilon = \bar u_b^\varepsilon = 0$, which gives the totally trivial steady state corresponding to the trivial macroscopic one $(\bar u_1, \bar v_1)$, or $\bar u_a^\varepsilon \neq 0$ and $\bar u_b^\varepsilon \neq 0$. In the second case the triplet $(\bar u_a^\varepsilon, \bar u_b^\varepsilon, 0)$ satisfies the system

$$\begin{cases} \eta_a \bar u_a^\varepsilon(1-\dfrac{\bar u_a^\varepsilon}{a}) + \dfrac{1}{\varepsilon}\big[\phi(\dfrac{\bar u_b^\varepsilon}{b})\,\bar u_b^\varepsilon - \psi(\dfrac{\bar u_a^\varepsilon}{a})\,\bar u_a^\varepsilon\big] = 0, \\ \eta_b \bar u_b^\varepsilon(1-\dfrac{\bar u_b^\varepsilon}{b}) - \dfrac{1}{\varepsilon}\big[\phi(\dfrac{\bar u_b^\varepsilon}{b})\,\bar u_b^\varepsilon - \psi(\dfrac{\bar u_a^\varepsilon}{a})\,\bar u_a^\varepsilon\big] = 0, \end{cases}$$

it can be non unique, as in the macroscopic case, and it converges to a macroscopic equilibrium $(\bar u_3, \bar v_3)$, in the limit $\varepsilon \to 0$.

If $\bar v^\varepsilon \neq 0$, then from $f_v(u_b, v) = 0$ we have $\bar u_b^\varepsilon + \bar v^\varepsilon = b$. Hence, for all $\varepsilon > 0$, $f_b(\bar u_b^\varepsilon, \bar v^\varepsilon) = Q(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon) = 0$ and we obtain the two stationary states $(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon) = (0, 0, b)$ and

$$(\bar u_a^\varepsilon, \bar u_b^\varepsilon, \bar v^\varepsilon) = (a, b\alpha, b(1-\alpha))\,, \tag{4.36}$$

provided that $\alpha < 1$. These equilibria do not depend on $\varepsilon > 0$, so that we shall drop the ε exponent in the sequel. In the limit $\varepsilon \to 0$, they correspond to the linearly unstable equilibrium $(\bar u_2, \bar v_2)$ and to the positive linearly stable equilibrium $(\bar u_4, \bar v_4)$, respectively.

Hereafter, we focus on the totally nontrivial spatially homogeneous steady (4.36), and we see that, for all $\varepsilon > 0$, it is also stable for the mesoscopic system (1.1) and the corresponding ODEs system. Indeed, setting

$$u_a^\varepsilon = \bar u_a + \tau\tilde u_a^\varepsilon \qquad u_b^\varepsilon = \bar u_b + \tau\tilde u_b^\varepsilon, \qquad v^\varepsilon = \bar v + \tau\tilde v^\varepsilon, \qquad |\tau| \ll 1,$$

the linearization of (1.1) around $(\bar u_a, \bar u_b, \bar v)$ writes as

$$\partial_t \tilde w^\varepsilon = \mathrm{diag}\{d_a, d_b, d_v\}\Delta\tilde w^\varepsilon + M^\varepsilon \tilde w^\varepsilon + o(1), \qquad \tilde w^\varepsilon := \big(\tilde u_a^\varepsilon, \tilde u_b^\varepsilon, \tilde v^\varepsilon\big)^{\mathrm T},$$

with

$$M^\varepsilon := \begin{bmatrix} -\eta_a + \frac{1}{\varepsilon}\partial_1\bar{Q} & \frac{1}{\varepsilon}\partial_2\bar{Q} & \frac{1}{\varepsilon}\partial_3\bar{Q} \\ -\frac{1}{\varepsilon}\partial_1\bar{Q} & -\eta_b\alpha - \frac{1}{\varepsilon}\partial_2\bar{Q} & -\eta_b\alpha - \frac{1}{\varepsilon}\partial_3\bar{Q} \\ 0 & -\eta_v(1-\alpha) & -\eta_v(1-\alpha) \end{bmatrix}.$$

Again, we need to analyse the stability of the matrix M^ε above and N_n^ε below

$$N_n^\varepsilon := -\lambda_n \mathrm{diag}\{d_a, d_b, d_v\} + M^\varepsilon,$$

i.e.

$$N_n^\varepsilon = \begin{bmatrix} -d_a\lambda_n - \eta_a + \frac{1}{\varepsilon}\partial_1\bar{Q} & \frac{1}{\varepsilon}\partial_2\bar{Q} & \frac{1}{\varepsilon}\partial_3\bar{Q} \\ -\frac{1}{\varepsilon}\partial_1\bar{Q} & -d_b\lambda_n - \eta_b\alpha - \frac{1}{\varepsilon}\partial_2\bar{Q} & -\eta_b\alpha - \frac{1}{\varepsilon}\partial_3\bar{Q} \\ 0 & -\eta_v(1-\alpha) & -d_v\lambda_n - \eta_v(1-\alpha) \end{bmatrix}.$$

For that, we apply the Routh-Hurwitz criterion [19] and we obtain the result below, proved in Appendix A.

Proposition 4.4. *Under the assumption $\alpha < 1$, for all $\varepsilon > 0$ and $\lambda_n \geq 0$, the matrices M^ε and N_n^ε are stable, i.e. all their eigenvalues have negative real part.*

To complete the analysis, we shall see below how the previous linear stability property is preserved in the limit as $\varepsilon \to 0$. Indeed, two eigenvalues of N_n^ε converge to those of N_n in (4.19), while the third one goes to $-\infty$.

Let us denote

$$D^\varepsilon(\mu) := N_n^\varepsilon - \mu I_3,$$

where I_3 stands for the 3×3 identity matrix. The goal of the computations below is to compute $|D^\varepsilon| = \det D^\varepsilon(\mu)$, (see also [20]).

First, adding the second row of D^ε to the first one, we get

$$|D^\varepsilon| = \begin{vmatrix} -(d_a\lambda_n + \eta_a + \mu) & -(d_b\lambda_n + \eta_b\alpha + \mu) & -\eta_b\alpha \\ -\frac{1}{\varepsilon}\partial_1\bar{Q} & -(d_b\lambda_n + \eta_b\alpha + \mu) - \frac{1}{\varepsilon}\partial_2\bar{Q} & -\eta_b\alpha - \frac{1}{\varepsilon}\partial_3\bar{Q} \\ 0 & -\eta_v(1-\alpha) & -\big(d_v\lambda_n + \eta_v(1-\alpha) + \mu\big) \end{vmatrix}.$$

Recalling from (4.15) that $r = \partial_2\bar{Q} - \partial_1\bar{Q}$ and $\partial_3\bar{Q} = \sigma\,\phi'(\sigma+\delta)$, we find for $\sigma = \alpha$ and $\delta = 1-\alpha$ that

$$\partial_3\bar{Q} + (\partial_1\bar{Q} - \partial_2\bar{Q})\frac{\alpha\phi_1'}{r} = 0.$$

Adding to the third column the difference between the first and the second column, both multiplied by $\frac{\alpha\phi_1'}{r}$, we thus obtain

$$|D^\varepsilon| = \begin{vmatrix} -(d_a\lambda_n + \eta_a + \mu) & -(d_b\lambda_n + \eta_b\alpha + \mu) & N_{12} \\ -\frac{1}{\varepsilon}\partial_1\bar{Q} & -(d_b\lambda_n + \eta_b\alpha + \mu) - \frac{1}{\varepsilon}\partial_2\bar{Q} & d_{23} \\ 0 & -\eta_v(1-\alpha) & N_{22} - \mu \end{vmatrix},$$

with N_{ij} the entries of the matrix N_n in (4.19) and

$$d_{23} := (d_b\lambda_n + \eta_b\alpha + \mu)\frac{\alpha\phi_1'}{r} - \eta_b\,\alpha.$$

Furthermore, as by (4.15) it follows

$$\partial_1\bar{Q}(\alpha\phi_1' + \phi_1) + \partial_2\bar{Q}\beta = 0\,,$$

adding the second column, multiplied by $\frac{\beta}{r}$, to the first one, multiplied by $\frac{\alpha\phi_1'+\phi_1}{r}$, we get

$$(1-\frac{\beta}{r})|D^\varepsilon| = \begin{vmatrix} N_{11}-\mu & -(d_b\lambda_n+\eta_b\alpha+\mu) & N_{12} \\ -(d_b\lambda_n+\eta_b\alpha+\mu)\frac{\beta}{r} & -(d_b\lambda_n+\eta_b\alpha+\mu)-\frac{1}{\varepsilon}\partial_2\bar{Q} & d_{23} \\ N_{21} & -\eta_v(1-\alpha) & N_{22}-\mu \end{vmatrix}.$$

Finally, subtracting the first column to the second one, multiplied by $\frac{\beta}{r}$, we have

$$\frac{\beta}{r}(1-\frac{\beta}{r})|D^\varepsilon| = \begin{vmatrix} N_{11}-\mu & d_{12} & N_{12} \\ d_{21} & -\frac{1}{\varepsilon}\frac{\beta}{r}\partial_2\bar{Q} & d_{23} \\ N_{21} & 0 & N_{22}-\mu \end{vmatrix}, \tag{4.37}$$

with

$$\begin{aligned} d_{12} &:= \mu\Big(1-\frac{\beta}{r}\Big) - \big(d_b\lambda_n+\eta_b\alpha\big)\frac{\beta}{r} - N_{11}, \\ d_{21} &:= -(d_b\lambda_n+\eta_b\alpha+\mu)\frac{\beta}{r}\,. \end{aligned}$$

Thus, (4.37) rewrites as

$$\frac{\beta}{r}(1-\frac{\beta}{r})\,|D^\varepsilon(\mu)| = -\frac{1}{\varepsilon}\,\beta\left(1-\frac{\beta}{r}\right)\,\det(N_n-\mu\,I_2) + R(\mu)\,,$$

where

$$R(\mu) = -\frac{\beta}{r}\Big(1-\frac{\beta}{r}\Big)\,\mu^3 + p(\mu)\,,$$

with $p(\mu)$ a polynomial function of degree two that does not depend on ε. Consequently

$$|D^\varepsilon(\mu)| = -\mu^3 - \frac{r}{\varepsilon}\det(N_n-\mu\,I_2) + \frac{r^2}{\beta(r-\beta)}p(\mu)\,, \tag{4.38}$$

with

$$\det(N_n-\mu\,I_2) = \mu^2 - (trN_n)\mu + \det N_n\,. \tag{4.39}$$

Let γ_i, $i=1,2$ denote the eigenvalues of N_n and let μ_i^ε denote the eigenvalues of N_n^ε, $i=1,2,3$. It has been shown that $\Re(\gamma_i)<0$ and $\Re(\mu_i^\varepsilon)<0$. Moreover, observe that μ_i^ε is a root of (4.38) if and only if it is a root of

$$-\varepsilon\mu^3 - r\det(N_n-\mu\,I_2) + \varepsilon\frac{r^2}{\beta(r-\beta)}p(\mu)\,. \tag{4.40}$$

Plugging in (4.40) the simple asymptotic expansion in ε of $\mu_i^\varepsilon = \nu_0^i+\varepsilon\nu_1^i+\varepsilon^2\nu_2^i+\cdots$, the zero order terms gives $-r\det(N_n-\nu_0^i\,I_2)=0$. Therefore,

$$\mu_i^\varepsilon = \gamma_i + O(\varepsilon)\,, \qquad i=1,2\,, \tag{4.41}$$

and

$$\mu_1^\varepsilon + \mu_2^\varepsilon = \text{tr } N_n + O(\varepsilon),$$
$$\mu_1^\varepsilon \mu_2^\varepsilon = \det N_n + O(\varepsilon)\,.$$

On the other hand, writing $|D^\varepsilon(\mu)| = -(\mu-\mu_1^\varepsilon)(\mu-\mu_2^\varepsilon)(\mu-\mu_3^\varepsilon)$, from (4.38)–(4.39), we deduce the identities below

$$\mu_1^\varepsilon + \mu_2^\varepsilon + \mu_3^\varepsilon = -\frac{r}{\varepsilon} + O(1),$$
$$\mu_1^\varepsilon \mu_2^\varepsilon + \mu_3^\varepsilon(\mu_1^\varepsilon + \mu_2^\varepsilon) = -\frac{r}{\varepsilon}\text{tr } N_n + O(1),$$
$$\mu_1^\varepsilon \mu_2^\varepsilon \mu_3^\varepsilon = -\frac{r}{\varepsilon}\det N_n + O(1)\,,$$

so that,

$$\mu_3^\varepsilon = -\frac{r}{\varepsilon} + O(1)\,.$$

5 Numerical simulations

For the numerical simulations we consider the linear conversion rates

$$\phi(x) = x + \delta \qquad \text{and} \qquad \psi(x) = \theta x + \gamma\,, \tag{5.1}$$

with $\delta = 0.5$, $\theta = 5$ and $\gamma = 1$, together with the growth rates

$$\eta_a = 3, \qquad \eta_b = 2, \qquad \eta_v = 40\,. \tag{5.2}$$

Depending on the choice of a and b we consider two cases: the v extinction case

$$a = 1.5, \quad b = 6, \quad \Rightarrow \alpha = 1, \tag{5.3}$$

and the coexistence case

$$a = 1.5, \quad b = 8, \quad \Rightarrow \alpha < 1. \tag{5.4}$$

In the case of the ODE system associated to the mesoscopic system (1.1) with (1.4) and (5.1), the numerical solution is illustrated in Figure 2 ($\alpha = 1$) and Figure 4 ($\alpha < 1$). The expected initial layer for the subpopulations u_a^ε and u_b^ε can be observed in Figure 3 and 5 (see Remark 1).

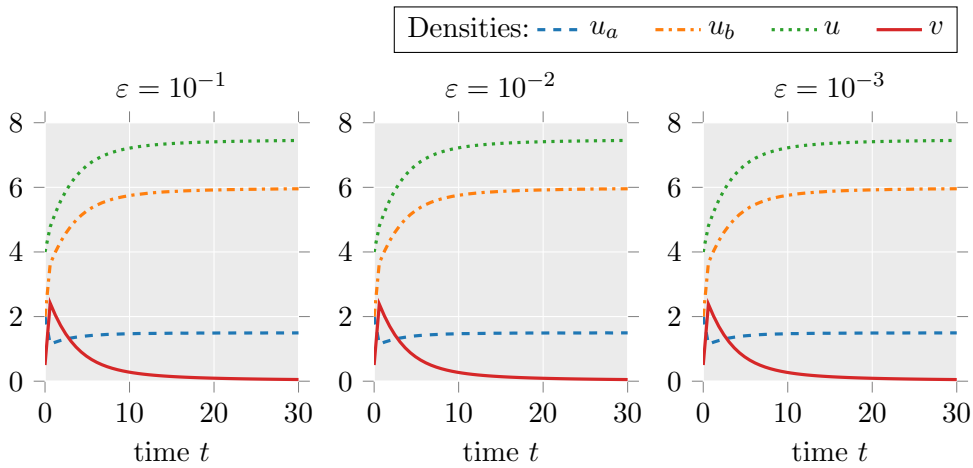

Figure 2: $\alpha = 1$. Solution of the mesoscopic ODE system with parameters given in (5.1),(5.2) and (5.3), for $\varepsilon = 10^{-1}, 10^{-2}, 10^{-3}$ (from left to right), with extinction of v^ε, and convergence of $u^\varepsilon = u_a^\varepsilon + u_b^\varepsilon$ towards $a + b$. Here the maximal time is $T = 30$.

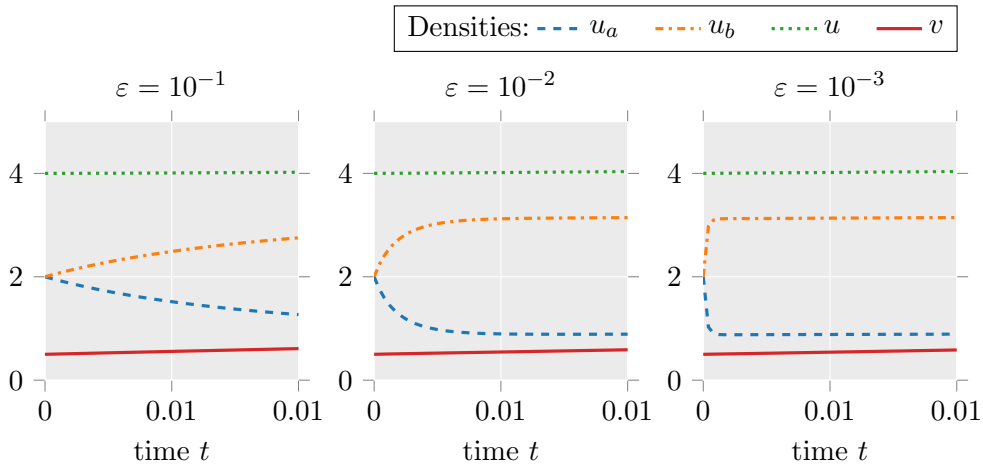

Figure 3: $\alpha = 1$. Zoom of the solution in Figure 2 in a right neighbourhood of $t = 0$ for $\varepsilon = 10^{-1}, 10^{-2}, 10^{-3}$ (from left to right).

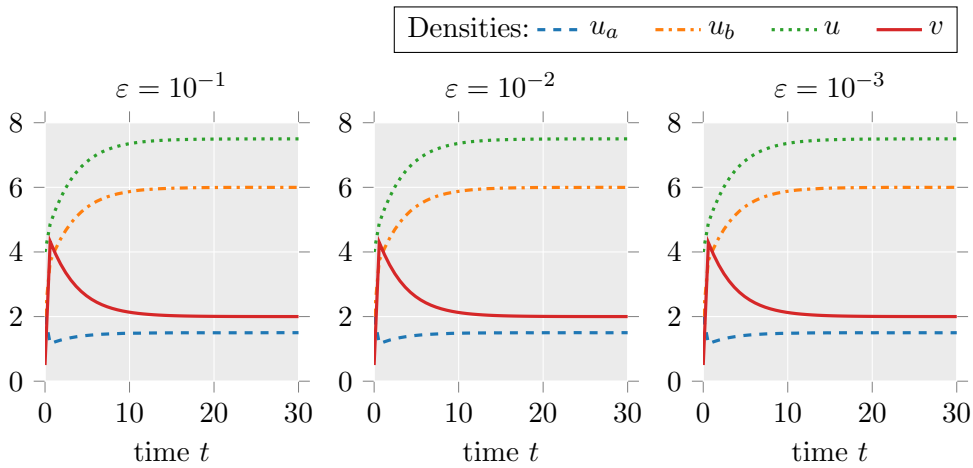

Figure 4: $\alpha < 1$. Solution of the mesoscopic ODE system with parameters given in (5.1),(5.2) and (5.4), for $\varepsilon = 10^{-1}, 10^{-2}, 10^{-3}$ (from left to right), with convergence of $(u^\varepsilon, v^\varepsilon) = (u_a^\varepsilon + u_b^\varepsilon, v^\varepsilon)$ towards $(a + b\alpha, b(1-\alpha))$. Here the maximal time is $T = 30$.

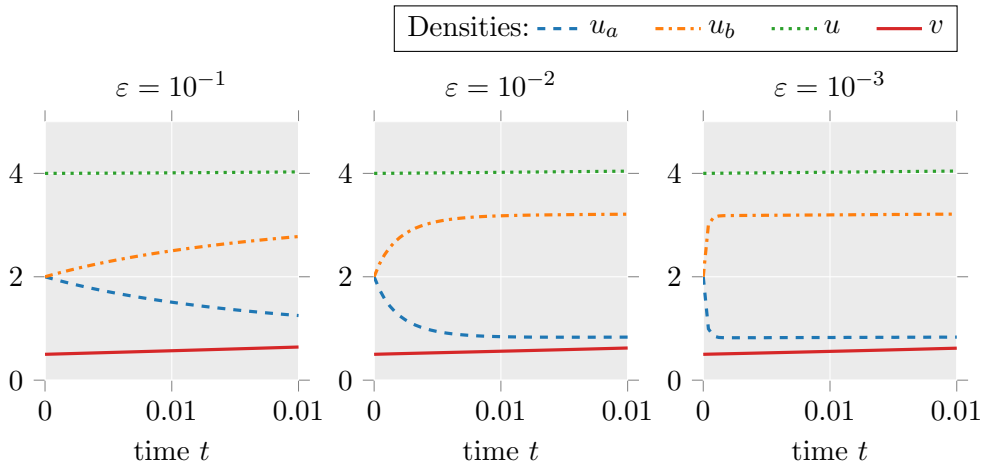

Figure 5: $\alpha < 1$. Zoom of the solution in Figure 4 in a right neighbourhood of $t = 0$ for $\varepsilon = 10^{-1}, 10^{-2}, 10^{-3}$ (from left to right).

The effect of the spatial dispersal of the species by diffusion is shown in Figure 6 ($\alpha = 1$) and Figure 7 ($\alpha < 1$) below, in the case of the one dimensional spatial domain $[0, 1]$. Additionally, we provide videos in the supplements along with the used code. All the parameters are kept as in the previous computations and the diffusion coefficients are

$$d_a = 2, \qquad d_b = 0.1, \qquad d_v = 0.1\,,$$

and the initial conditions has been chosen as

$$u_a^{\text{in}}(x) = \cos(4\pi x) + 4\,, \qquad u_b^{\text{in}}(x) = (x-1)\sin(4\pi x^2) + 2\,,$$
$$v^{\text{in}}(x) = \cos(4\pi x) + \cos(2\pi x) + 2.5\,.$$

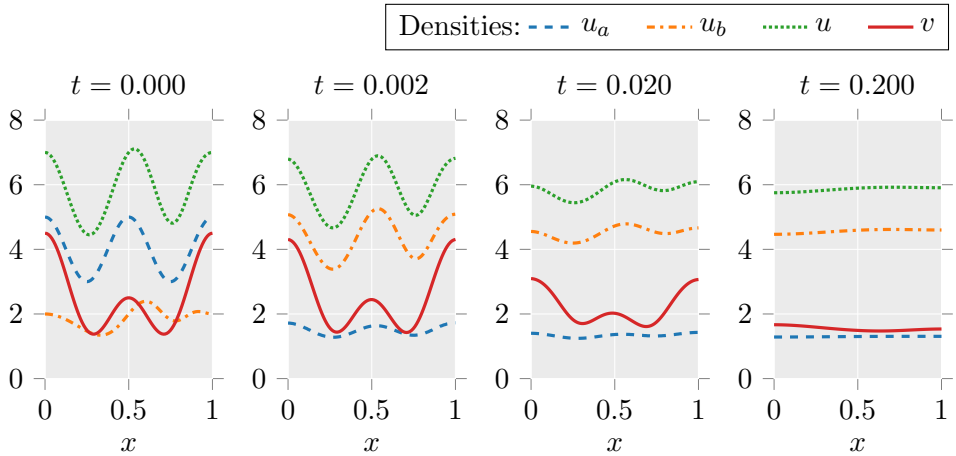

Figure 6: $\alpha = 1$. Solution of the mesoscopic PDE system (1.1) in the extinction case.

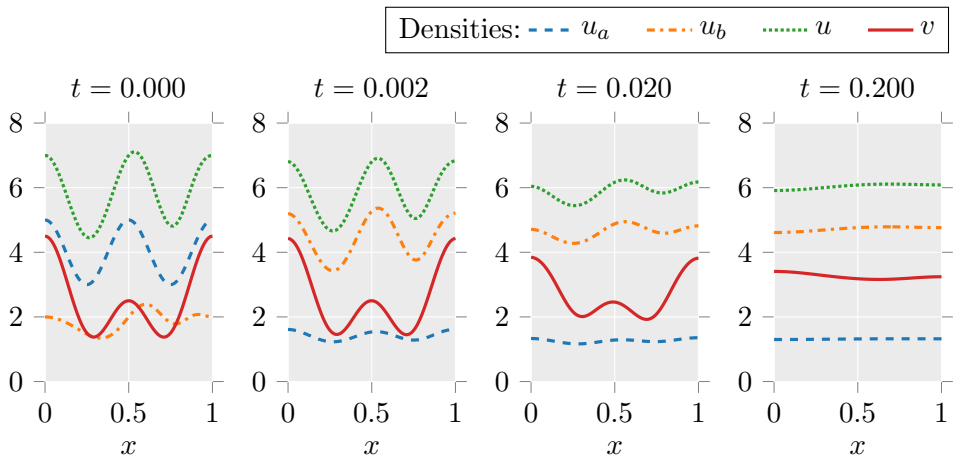

Figure 7: $\alpha < 1$. Solution of the mesoscopic PDE system (1.1) in the coexistence case.

6 Concluding remarks and discussion

In this paper we derive a (macroscopic) reaction-cross-diffusion system with no flux boundary conditions for two species u and v in competition for resources, from a (mesoscopic) diffusion system with slow and fast reaction terms and homogeneous

Neumann boundary conditions. At the mesoscopic scale, the fast reaction term governs the switching of the individuals of two sub-populations u_a and u_b of the species u, into each other, a strategy to optimise the two available ressources consumed by u. The individuals of the species v follow a monodiet and evolve competing solely with u_b. As a consequence, no cross-diffusion term appears in the macroscopic equation for v. In other words, the reaction-cross-diffusion system is triangular.

Examples of cross-diffusion systems (triangular and not) derived by taking a fast-reaction limit can be found in [10, 15, 5, 6, 12, 14, 21, 2]. A different but equally popular approach for the derivation of cross-diffusion systems (not pursued in this paper) is the mean-field limit of interacting particles, e.g. [17, 11, 4, 16].

For the mathematical analysis, a cross-diffusion term can break general parabolic estimates including the maximum principle, so only local existence results are usually obtained [1]. For global existence, one needs for instance an entropy functional to get a priori estimates and construct a weak solution [14, 21, 16]. Uniqueness is a major problem as well. The key mathematical contribution of this paper is the identification of the entropy functional (1.10), which behaves well under diffusion *and* the fast-reaction term (1.5). By the obtained control, we are able to undergo the fast reaction limit, to identify the limit densities u and v and prove along this way that (u, v) is a global in time weak solution. Further studies for the regularity and uniqueness of the solution of a larger class of triangular cross-diffusion systems, including (1.6), are the objects of future works.

An interesting mathematical issue left open in this paper is the discrepancy between the boundary conditions for the mesoscopic and macroscopic systems: for the mesoscopic system (1.1), the no-flux and the Neumann boundary conditions are equivalent, but for the limit system (1.6) we naturally obtain no-flux boundary conditions (1.9). Formally, the no-flux boundary conditions (1.9) are

$$\left[d_a + (d_b - d_a)\partial_1 u_b^*\right] \nabla u \cdot \sigma + \left[(d_b - d_a)\partial_2 u_b^*\right] \nabla v \cdot \sigma = 0 \qquad \text{and} \qquad \nabla v \cdot \sigma = 0,$$

where $u_b^* = u_b^*(u, v)$ is the unique solution to (1.7) for given u and v. Differentiating the condition $Q(u - u_b^*(u, v), u_b^*(u, v), v) = 0$ with respect to u yields

$$\partial_1 u_b^* = \frac{\psi\left(\frac{u-u_b^*}{a}\right) + \frac{u-u_b^*}{a}\psi'\left(\frac{u-u_b^*}{a}\right)}{\phi\left(\frac{u_b^*+v}{b}\right) + \frac{u_b^*}{b}\phi'\left(\frac{u_b^*+v}{b}\right) + \psi\left(\frac{u-u_b^*}{a}\right) + \frac{u-u_b^*}{a}\psi'\left(\frac{u-u_b^*}{a}\right)}.$$

Hence by our assumptions $\partial_1 u_b^* \in (0, 1)$, which implies $\left[d_a + (d_b - d_a)\partial_1 u_b^*\right] > 0$. Therefore, the no-flux boundary condition is formally equivalent to the Neumann boundary condition. It would be interesting to see whether singularities can break this equivalence.

From a modelling point of view, we show that the competition between u and v described above, can be modelled by a Lotka-Volterra competitive type system, with competitive coefficients derived by the population dynamics. To the best of the author's knowledge, the meaning of the classical Lotka-Volterra competition system is only abstract, and connecting the system coefficients to specific situations is rarely been done. We are able to answer to this fundamental question in the specific model of the paper. Indeed, dropping the diffusion terms, the competition system (1.6)–

(1.7) reads as

$$\begin{cases} \partial_t u = \eta_a u_a \left(1 - \dfrac{u_a}{a}\right) + \eta_b u_b \left(1 - \dfrac{u_b + v}{b}\right), \\ \partial_t v = \eta_v v \left(1 - \dfrac{u_b + v}{b}\right), \end{cases} \tag{6.1}$$

and

$$u = u_a + u_b, \quad \phi\Big(\frac{u_b + v}{b}\Big) u_b = \psi\Big(\frac{u_a}{a}\Big) u_a \,. \tag{6.2}$$

Let

$$r_a(u_a, u_b, v) := \left(1 + \frac{\psi(\frac{u_a}{a})}{\phi(\frac{u_b+v}{b})}\right)^{-1} \quad \text{and} \quad r_b(u_a, u_b, v) := \left(1 + \frac{\phi(\frac{u_b+v}{b})}{\psi(\frac{u_a}{a})}\right)^{-1}. \tag{6.3}$$

Then, it holds

$$u_a = r_a u, \quad u_b = r_b u, \quad r_a + r_b = 1, \quad 0 < r_a, r_b < 1,$$

and the system can be rewritten in terms of u and v, as the following Lotka-Volterra system

$$\begin{cases} u_t = \eta_u (1 - b_{11} u - b_{12} v) u, \\ v_t = \eta_v (1 - b_{21} u - b_{22} v) v, \end{cases} \tag{6.4}$$

where the competition coefficients are given by

$$b_{11} = \frac{\eta_a r_a^2/a + \eta_b r_b^2/b}{\eta_a r_a + \eta_b r_b}, \quad b_{12} = \frac{\eta_b r_b/b}{\eta_a r_a + \eta_b r_b}, \quad b_{21} = \frac{r_b}{b}, \quad b_{22} = \frac{1}{b}, \tag{6.5}$$

and the growth rates are

$$\eta_u = \eta_a r_a + \eta_b r_b \qquad \text{and} \qquad \eta_v \,. \tag{6.6}$$

The fundamental difference between the classical Lotka-Volterra competition system and our model (6.4)-(6.6) is in the solution dependency of the coefficients r_a and r_b in (6.3) and thus of the b_{ij}'s. Our understanding is that the classical Lotka-Volterra competition system with constant coefficients b_{ij} should be considered locally, where the coefficients variation is small, while (6.4)-(6.6), can be considered globally. In this viewpoint, we can still call the competition modelled by system (6.4)-(6.6) a strong competition if $b_{12}/b_{11} > 1$ and $b_{21}/b_{22} > 1$ for all solutions.

A systematic study on the derivation of advection and cross-diffusion terms from a given population dynamics with meaningful parameter regimes is performed in [9, Section 4].

Again from a modelling perspective, a motivation to consider reaction-cross-diffusion systems is the possibility to find instabilities due to the cross-diffusion, where a normal diffusion cannot induce instabilities. The identification of these cross-diffusion induced instabilities is a very active research area [20, 31, 3]. This has been the motivation of our investigation of spatially homogeneous stationary states and their linear stability in *Section* 4. For semi-trivial stationary states with $v = 0$, we see that the fast-reaction term can lead to non-trivial behaviour (lack of uniqueness), see also [23]. On the other hand, the totally non-trivial homogeneous steady state (coexistence state) is unique and linearly stable. Thus, the possibility of cross-diffusion induced instability is ruled out in that case.

The existence of heterogeneous steady states of the macroscopic system is not discarded, and it will be analyzed in a forthcoming paper.

A Proof of Proposition 4.4

Proof. The Routh matrix associated to M^ε writes as (see [19])

$$R_{M^\varepsilon} := \begin{bmatrix} 1 & \det_2 M^\varepsilon \\ -\mathrm{tr} M^\varepsilon & -\det M^\varepsilon \\ \dfrac{(\det_2 M^\varepsilon)(\mathrm{tr} M^\varepsilon) - \det M^\varepsilon}{\mathrm{tr} M^\varepsilon} & 0 \\ -\det M^\varepsilon & 0 \end{bmatrix},$$

with

$$\det_2 M^\varepsilon := [M^\varepsilon]_{11} + [M^\varepsilon]_{22} + [M^\varepsilon]_{33},$$

and where $[M^\varepsilon]_{ii}$ are the following minors:

$$[M^\varepsilon]_{11} := \begin{vmatrix} M^\varepsilon_{22} & M^\varepsilon_{23} \\ M^\varepsilon_{32} & M^\varepsilon_{33} \end{vmatrix}, \qquad [M^\varepsilon]_{22} := \begin{vmatrix} M^\varepsilon_{11} & M^\varepsilon_{13} \\ M^\varepsilon_{31} & M^\varepsilon_{33} \end{vmatrix}, \qquad [M^\varepsilon]_{33} := \begin{vmatrix} M^\varepsilon_{11} & M^\varepsilon_{12} \\ M^\varepsilon_{21} & M^\varepsilon_{22} \end{vmatrix}.$$

By the Routh-Hurwitz criterion [19], M^ε is stable if and only if there are no sign variations in the first column entries of R_{M^ε}, i.e., if and only if M^ε satisfies

$$\begin{cases} \mathrm{tr} M^\varepsilon < 0, \\ (\det_2 M^\varepsilon)(\mathrm{tr} M^\varepsilon) - \det M^\varepsilon < 0, \\ \det M^\varepsilon < 0. \end{cases} \tag{A.1}$$

From the expression of M^ε, we get

$$\mathrm{tr}\ M^\varepsilon = -\eta_a - \eta_b \alpha - \eta_v (1-\alpha) - \frac{r}{\varepsilon} < 0,$$

and

$$\begin{aligned} [M^\varepsilon]_{11} &= \eta_v \frac{1-\alpha}{\varepsilon} \phi_1 > 0, \\ [M^\varepsilon]_{22} &= \eta_v (1-\alpha)\Big(\eta_a + \frac{\beta}{\varepsilon}\Big) > 0, \\ [M^\varepsilon]_{33} &= \eta_a \eta_b \alpha + \frac{1}{\varepsilon}\eta_a (r-\beta) + \frac{1}{\varepsilon}\eta_b \alpha \beta > 0, \end{aligned}$$

which imply

$$\det_2 M^\varepsilon > 0.$$

Furthermore,

$$\det M^\varepsilon = \Big(-\eta_a + \frac{1}{\varepsilon}\partial_1 \bar{Q}\Big)[M^\varepsilon]_{11} - \frac{\eta_v}{\varepsilon}\partial_1 \bar{Q} \frac{1-\alpha}{\varepsilon}(\partial_2 \bar{Q} - \partial_3 \bar{Q}) = -\frac{\eta_a \eta_v \phi_1}{\varepsilon}(1-\alpha) < 0\,.$$

It remains to check the second inequality in (A.1), that is a consequence of the previous computations and of the identity

$$\det M^\varepsilon = -\eta_a [M^\varepsilon]_{11}\,.$$

Indeed,

$$\begin{aligned} (\det_2 M^\varepsilon)(\mathrm{tr}\ M^\varepsilon) - \det M^\varepsilon &= \big([M^\varepsilon]_{11} + [M^\varepsilon]_{22} + [M^\varepsilon]_{33}\big)\mathrm{tr}\ M^\varepsilon + \eta_a [M^\varepsilon]_{11} \\ &= \big([M^\varepsilon]_{22} + [M^\varepsilon]_{33}\big)\mathrm{tr}\ M^\varepsilon - [M^\varepsilon]_{11}\Big(\eta_b \alpha + \eta_v (1-\alpha) + \frac{r}{\varepsilon}\Big) < 0\,. \end{aligned}$$

Thus, M^ε is stable for all $\varepsilon > 0$.

Concerning the matrix N^ε, we define the quantities

$$D_1 := d_a + d_b + d_v > 0\,, \quad D_2 := d_a d_v + d_b d_v + d_a d_b > 0\,, \quad D_3 := d_a d_b d_v\,, \tag{A.2}$$

and

$$\begin{aligned} A &:= d_a(M^\varepsilon_{22} + M^\varepsilon_{33}) + d_b(M^\varepsilon_{11} + M^\varepsilon_{33}) + d_v(M^\varepsilon_{11} + M^\varepsilon_{22}) < 0, \\ B &:= d_b d_v M^\varepsilon_{11} + d_a d_v M^\varepsilon_{22} + d_a d_b\, M^\varepsilon_{33} < 0, \\ C &:= d_a\,[M^\varepsilon]_{11} + d_b[M^\varepsilon]_{22} + d_v[M^\varepsilon]_{33} > 0\,. \end{aligned} \tag{A.3}$$

Thus, using the previous computations, we obtain

$$\mathrm{tr}\ N^\varepsilon = \mathrm{tr}\ M^\varepsilon - D_1\lambda_n < 0\,,$$

$$\det{}_2\, N^\varepsilon = \det{}_2\, M^\varepsilon + D_2\,\lambda_n^2 - A\,\lambda_n > 0,$$

and

$$\det N^\varepsilon = \det M^\varepsilon - D_3\,\lambda_n^3 + B\,\lambda_n^2 - C\,\lambda_n < 0\,.$$

To conclude, it remains to check the sign of the quantity below:

$$\begin{aligned} (\det{}_2\, N^\varepsilon)(\mathrm{tr}\ N^\varepsilon) - \det N^\varepsilon = {} & (\det{}_2\, M^\varepsilon)(\mathrm{tr}\ M^\varepsilon) - \det M^\varepsilon \\ & + \lambda_n^3(-D_1D_2 + D_3) + \lambda_n^2(D_2 \mathrm{tr}\, M^\varepsilon + AD_1 - B) \\ & + \lambda_n(-D_1 \det{}_2\, M^\varepsilon - A\,\mathrm{tr}\, M^\varepsilon + C)\,. \end{aligned}$$

The latter is indeed strictly negative, using again the negativity of the entries of M^ε, the positivity of the minors $[M^\varepsilon]_{ii}$, definitions (A.2) and (A.3) and

$$-D_1D_2 + D_3 < 0\,, \qquad AD_1 - B < 0\,, \qquad -D_1 \det{}_2\, M^\varepsilon + C < 0\,.$$

Then, by the Routh-Hurwitz criterion again, N^ε is stable for all strictly positive ε. □

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