# **Competitive exclusion in a two-species chemotaxis model**

**C. Stinner · J. I. Tello · M. Winkler**

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**Abstract** We consider a mathematical model for the spatio-temporal evolution of two biological species in a competitive situation. Besides diffusing, both species move toward higher concentrations of a chemical substance which is produced by themselves. The resulting system consists of two parabolic equations with Lotka–Volterratype kinetic terms and chemotactic cross-diffusion, along with an elliptic equation describing the behavior of the chemical. We study the question in how far the phenomenon of competitive exclusion occurs in such a context. We identify parameter regimes for which indeed one of the species dies out asymptotically, whereas the other reaches its carrying capacity in the large time limit.

**Keywords** Chemotaxis · Stability of solutions · Asymptotic behavior · Competitive exclusion

**Mathematics Subject Classification (2010)** 92C17 · 35K55 · 35B35 · 35B40

## **1 Introduction**

We consider two biological species which compete for the resources and migrate towards a higher concentration of a chemical produced by themselves. Here the movement of the two populations is governed by diffusion and chemotaxis. We further

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assume that the populations proliferate, that the mutual competition between them takes place according to the classical Lotka–Volterra dynamics and that the chemical signal diffuses much faster than the two populations. Denoting the population densities by  $u(x, t)$  and  $v(x, t)$  and the concentration of the chemoattractant by  $w(x, t)$ , classical models (see [Murray 1993](#page-18-0)) lead to the system

$$
\begin{cases}\nu_t = d_1 \Delta u - \chi_1 \nabla \cdot (u \nabla w) + \mu_1 u (1 - u - a_1 v), & x \in \Omega, \ t > 0, \\
v_t = d_2 \Delta v - \chi_2 \nabla \cdot (v \nabla w) + \mu_2 v (1 - v - a_2 u), & x \in \Omega, \ t > 0, \\
-\Delta w + \lambda w = ku + v, & x \in \Omega, \ t > 0,\n\end{cases}
$$
\n(1.1)

<span id="page-1-0"></span>under homogeneous Neumann boundary conditions

$$
\frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial w}{\partial \nu} = 0, \quad x \in \partial \Omega, \ t > 0,
$$
\n(1.2)

<span id="page-1-1"></span>and initial conditions

$$
u(x, 0) = u_0(x), \qquad v(x, 0) = v_0(x), \qquad x \in \Omega,
$$
\n(1.3)

in a bounded domain  $\Omega \subset \mathbb{R}^n$ ,  $n \geq 1$ , with smooth boundary, where  $d_i$ ,  $\chi_i$ ,  $\mu_i$ ,  $a_i$  ( $i =$ 1, 2),  $\lambda$  and *k* are positive parameters.

In order to describe the competition of two species, the associated Lotka–Volterra ODE system

$$
\begin{cases} u' = \mu_1 u (1 - u - a_1 v), & t > 0, \\ v' = \mu_2 v (1 - v - a_2 u), & t > 0, \end{cases}
$$

<span id="page-1-2"></span>has been studied extensively. It is well-known that if

$$
a_1 > 1 > a_2 \ge 0 \tag{1.4}
$$

and both species are initially positive then the second population outcompetes the first in the sense that  $u(t) \to 0$  and  $v(t) \to 1$  as  $t \to \infty$ . A proof of this result and of extensions to systems with more populations is given in [\(Zeeman 1995](#page-19-0), Theorem 2.1). It is the objective of the present work to investigate in how far this phenomenon, usually referred to as *competitive exclusion*, can be observed also in cases when both species move towards increasing concentrations of a signal which they produce themselves.

The influence of chemotaxis on the dynamics of biological species competing for res[ources](#page-18-1) [like](#page-18-1) [nutrients](#page-18-1) [or](#page-18-1) [space](#page-18-1) [is](#page-18-1) [for](#page-18-1) [instance](#page-18-1) [pointed](#page-18-1) [out](#page-18-1) [in](#page-18-1) Celani and Vergassola [\(2010\)](#page-18-1), [Hawkins](#page-18-2) [\(2011](#page-18-2)), [Hibbing](#page-18-3) [\(2010\)](#page-18-3) and [Tindall](#page-19-1) [\(2008](#page-19-1)). Particular fields of relevance include economically important situations when different bacteria interact with crop plants, where beyond standard kinetics, the respective overall competitive fitnesses are crucially affected by chemotaxis and motility, see [Brencic and Winans](#page-18-4) [\(2005\)](#page-18-4), [Vande Broek and Vanderleyden](#page-19-2) [\(1995](#page-19-2)) and [Yao and Allen](#page-19-3) [\(2006](#page-19-3)). Derivations of related mathematical models can be found in [Kelly et al.](#page-18-5) [\(1988\)](#page-18-5), [Lauffenburger](#page-18-6) [\(1991\)](#page-18-6), [Painter and Sherratt](#page-18-7) [\(2003](#page-18-7)) and some basic mathematical aspects such as the global existence of solutions to models which involve both chemotaxis and competition are addressed in [Kuiper](#page-18-8) [\(2001](#page-18-8)), [Zhang](#page-19-4) [\(2006\)](#page-19-4). Moreover, for some particular models the existence and stability of steady states reflecting either competitive exclusion or coexistence have already been studied analytically, see [Dung](#page-18-9) [\(2000\)](#page-18-9), [Dung and Smith](#page-18-10) [\(1999\)](#page-18-10), [Wang and Wu](#page-19-5) [\(2002](#page-19-5)) and [Zhang](#page-19-4) [\(2006\)](#page-19-4); however, to the best of our knowledge the literature does not provide any qualitative information on the solution behavior in the context of competitive exclusion when chemotaxis as well as competitive terms involving both species are present.

Concerning the problem considered in this paper, in case of  $a_1, a_2 \in [0, 1)$  it has been shown in [Tello and Winkler](#page-19-6) [\(2012](#page-19-6)) that [\(1.1\)](#page-1-0)–[\(1.3\)](#page-1-1) possesses a unique positive steady state and conditions on the parameters  $\mu_i$  and  $\chi_i$  are established which ensure its global asymptotic stability. In contrast to this result of coexistence of the species we shall show here that in presence of [\(1.4\)](#page-1-2) competitive exclusion will take place, provided that the influence of chemotaxis is sufficiently small.

<span id="page-2-1"></span>In order to state our results in this direction, let us introduce the ratios

$$
q_1 := \frac{\chi_1}{\mu_1}
$$
 and  $q_2 := \frac{\chi_2}{\mu_2}$ . (1.5)

It turns out that in our analysis, besides the number *k* these parameters will play the role of key parameters with regard to the effect in question. In particular, we shall see that if both  $q_1$  and  $q_2$  are sufficiently small then competitive exclusion occurs for any solution  $(u, v, w)$  with  $v \neq 0$ .

<span id="page-2-2"></span>More precisely, in addition to [\(1.4\)](#page-1-2) our overall assumptions are

k, 
$$
q_1
$$
 and  $q_2$  are nonnegative and such that  $q_1 \le a_1$ ,  $q_2 < \frac{1}{2}$  and  
\n $kq_1 + \max \left\{ q_2, \frac{a_2 - a_2 q_2}{1 - 2q_2}, \frac{kq_2 - a_2 q_2}{1 - 2q_2} \right\} < 1.$  (1.6)

<span id="page-2-0"></span>Observe that these can be rewritten in separate conditions for  $k$ ,  $q_2$  and  $q_1$  in such a way that we require

$$
k \ge 0,
$$
  
\n
$$
q_2 \in \left[0, \frac{1}{2}\right) \text{ is such that } q_2 < \begin{cases} \frac{1-a_2}{2-a_2} & \text{if } k \le \frac{a_2(2-a_2)}{1-a_2}, \\ \frac{1}{2-a_2+k} & \text{if } k > \frac{a_2(2-a_2)}{1-a_2}, \end{cases}
$$
  
\n
$$
q_1 \in [0, a_1] \text{ satisfies } kq_1 < 1 - \max\left\{q_2, \frac{a_2 - a_2q_2}{1 - 2q_2}, \frac{kq_2 - a_2q_2}{1 - 2q_2}\right\}. \quad (1.7)
$$

<span id="page-2-3"></span>Here, the latter hypothesis [\(1.7\)](#page-2-0) itself is equivalent to saying that  $kq_1 + q_2 < 1$  and

$$
\begin{cases}\n kq_1 + (2 - a_2)q_2 + a_2 - 2kq_1q_2 < 1 \quad \text{if } kq_2 < a_2, \\
 kq_1 + (2 - a_2 + k)q_2 - 2kq_1q_2 < 1 \quad \text{if } kq_2 \ge a_2.\n\end{cases}
$$
\n
$$
(1.8)
$$

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<span id="page-3-2"></span>Prescribing the above conditions, we obtain the following main result on competitive exclusion.

**Theorem 1.1** *Assume* [\(1.4\)](#page-1-2), *and suppose that k and the numbers q*<sup>1</sup> *and q*<sup>2</sup> *defined in* [\(1.5\)](#page-2-1) *satisfy* [\(1.6\)](#page-2-2)*. Then for any choice of nonnegative initial data*  $u_0 \in C^0(\overline{\Omega})$ *and*  $v_0 \in C^0(\overline{\Omega})$  *satisfying*  $v_0 \neq 0$ *, the problem* [\(1.1\)](#page-1-0)–[\(1.3\)](#page-1-1) *possesses a uniquely determined global-in-time classical solution*  $(u, v, w)$  *such that*  $u > 0, v > 0$  *and*  $w > 0$  in  $\overline{\Omega} \times (0, \infty)$  and

$$
u(\cdot, t) \to 0
$$
,  $v(\cdot, t) \to 1$  and  $w(\cdot, t) \to \frac{1}{\lambda}$  as  $t \to \infty$ , (1.9)

<span id="page-3-3"></span>*uniformly with respect to*  $x \in \Omega$ *. Moreover, either*  $u \equiv 0$  *in*  $\overline{\Omega} \times [0, \infty)$  *or*  $u > 0$  *in*  $\overline{\Omega}\times(0,\infty)$  *is satisfied.* 

Let us illustrate how the condition  $(1.6)$  becomes easier to handle in some special cases.

*Remark* (i) In the prototypical case when  $\chi_1 = \chi_2 \equiv \chi$  and  $\mu_1 = \mu_2 \equiv \mu$ , [\(1.6\)](#page-2-2) reduces to the condition that  $q := \frac{\chi}{\mu}$  satisfies  $q < \frac{1}{k+1}$  and

$$
q < \begin{cases} \frac{2+k-a_2-\sqrt{(k+2-a_2)^2-8k(1-a_2)}}{4k} & \text{if } a_2 > kq \\ \frac{2+2k-a_2-\sqrt{(2k+2-a_2)^2-8k}}{4k} & \text{if } a_2 \le kq. \end{cases} \tag{1.10}
$$

<span id="page-3-0"></span>(ii) If in the above case we moreover have  $k = 1$  then  $(1.10)$  becomes

$$
q < \begin{cases} \frac{4 - a_2 - \sqrt{8 - 8a_2 + a_2^2}}{4} & \text{if } a_2 \le q \\ \frac{1 - a_2}{2} & \text{if } a_2 > q. \end{cases} \tag{1.11}
$$

<span id="page-3-1"></span>We observe that the first case can only occur if  $a_2 < \frac{4-a_2-\sqrt{8-8a_2+a_2^2}}{4}$  is satisfied, which is equivalent to  $a_2 < \frac{1}{3}$  in view of  $a_2 \in [0, 1)$ . Hence, the first case in  $(1.11)$  is equivalent to

$$
a_2 < \frac{1}{3}
$$
 and  $a_2 \le q < \frac{4 - a_2 - \sqrt{8 - 8a_2 + a_2^2}}{4}$ .

The second case in  $(1.11)$  is equivalent to

$$
q < \min\left\{a_2, \frac{1-a_2}{2}\right\} = \begin{cases} a_2 & \text{if } a_2 < \frac{1}{3} \\ \frac{1-a_2}{2} & \text{if } a_2 \in \left[\frac{1}{3}, 1\right). \end{cases}
$$

Combining both cases we conclude

$$
q < \begin{cases} \frac{4 - a_2 - \sqrt{8 - 8a_2 + a_2^2}}{4} & \text{if } a_2 < \frac{1}{3} \\ \frac{1 - a_2}{2} & \text{if } a_2 \in \left[\frac{1}{3}, 1\right). \end{cases} \tag{1.12}
$$

(iii) In the limit case  $k = 0$ , [\(1.10\)](#page-3-0) requires that

<span id="page-4-0"></span>
$$
q < \frac{1 - a_2}{2 - a_2} \tag{1.13}
$$

(iv) Finally, in the borderline case  $a_2 = 0$ , [\(1.13\)](#page-4-0) reads

$$
q < \frac{1}{2} \tag{1.14}
$$

and is thus consistent with the conditions already found in [\(Tello and Winkler](#page-19-7) [2007,](#page-19-7) Theorem 5.1).

*Remark* The global existence statement in Theorem [1.1](#page-3-2) remains valid if [\(1.7\)](#page-2-0) is replaced with the weaker requirement that  $kq_1 + q_2 < 1$ . In fact, Lemma [2.2](#page-6-0) below will show that in this case the interplay of diffusion and kinetics in  $(1.1)$  is strong enough to overbalance chemotactic cross-diffusion in such a way that all solutions are global and remain bounded.

The plan of this paper is as follows. In Sect. [2](#page-4-1) we show the local existence of a solution along with its positivity properties and prove the existence of a global bounded solution once  $kq_1 + q_2 < 1$  is satisfied. Section [3](#page-8-0) contains relations between the possible limits of  $u$  and  $v$  which are established by using comparison methods in combination with some algebraic inequalities. In particular we show that  $v(t) \rightarrow 1$ if  $u(t) \rightarrow 0$  is satisfied. In Sect. [4](#page-13-0) we then prove that *u* converges to 0 in the cases  $kq_2 < a_2$  and  $kq_2 > a_2$ , respectively, and complete the proof of Theorem [1.1.](#page-3-2) The final Sect. [5](#page-17-0) contains our conclusions and a discussion.

### <span id="page-4-1"></span>**2 Preliminaries: boundedness**

In this section we state some basic properties of the solutions to  $(1.1)$ – $(1.3)$  and give a criterion for their boundedness. We start with the local existence of a solution and its positivity properties.

<span id="page-4-3"></span>**Lemma 2.1** *Suppose that*  $u_0, v_0 \in C^0(\overline{\Omega})$  *are nonnegative such that*  $v_0 \neq 0$ *. Then there exists*  $T_{max} \in (0, \infty]$  *and a unique classical solution*  $(u, v, w)$  *of*  $(1.1)$ – $(1.3)$ *which is nonnegative and belongs to*  $C^0(\bar{\Omega} \times [0, T_{max})) \cap C^{2,1}(\bar{\Omega} \times (0, T_{max}))$ *. Moreover,*  $v > 0$  *and*  $w > 0$  *in*  $\Omega \times (0, T_{max})$  *and either*  $u \equiv 0$  *in*  $\Omega \times (0, T_{max})$  *or*  $u > 0$  *in*  $\Omega \times (0, T_{max})$  *are satisfied. Furthermore, we have the following extensibility criterion:*

<span id="page-4-2"></span>
$$
If T_{max} < \infty, \text{ then } \limsup_{t \nearrow T_{max}} \left( \|u(\cdot, t)\|_{L^{\infty}(\Omega)} + \|v(\cdot, t)\|_{L^{\infty}(\Omega)} \right) = \infty. \tag{2.1}
$$

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*Proof* The local existence and regularity of the solution as well as the extensibility criterion  $(2.1)$  can be proved by a slight adaption of well-known methods. We thus may confine ourselves with an outline of the proof and refer the reader e.g. to [Winkler](#page-19-8) [\(2010\)](#page-19-8), where details are given in a closely related situation.

For small  $T \in (0, 1)$ , in the space

$$
X := C^{0}([0, T]; C^{0}(\bar{\Omega})) \times C^{0}([0, T]; C^{0}(\bar{\Omega}))
$$

we consider the closed set

$$
S := \Big\{ (u, v) \in X \; \Big| \; \|u\|_{L^{\infty}((0,T);L^{\infty}(\Omega))} \le R + 1 \text{ and } \|v\|_{L^{\infty}((0,T);L^{\infty}(\Omega))} \le R + 1 \Big\},
$$

where  $R := ||u_0 + v_0||_{L^{\infty}(\Omega)}$ . For  $(u, v) \in S$ , we introduce a mapping  $\Phi$  on *S* by letting  $w \in \bigcap_{1 \le p \le \infty} L^{\infty}((0, T); W^{2, p}(\Omega))$  denote the (weak) solution of

$$
\begin{cases}\n-\Delta w + \lambda w = ku + v, & x \in \Omega, \\
\frac{\partial w}{\partial v} = 0, & x \in \partial \Omega,\n\end{cases}
$$
\n(2.2)

<span id="page-5-0"></span>and then defining

$$
\Phi(u, v)(t) := \begin{pmatrix} \Phi_1(u, v)(t) \\ \Phi_2(u, v)(t) \end{pmatrix}
$$
  
\n:= 
$$
\begin{pmatrix} \int_{0}^{t} e^{d_1(t-s)} \Phi_1(-s) \Phi_2(-\chi_1 \nabla \cdot (u \nabla w) + f_1(u, v)](s) ds \\ \int_{0}^{t} e^{d_2(t-s)} \Phi_1(-\chi_2 \nabla \cdot (v \nabla w) + f_2(u, v)](s) ds \\ 0 \end{pmatrix}
$$

for  $t \in [0, T]$ , where  $(e^{\tau \Delta})_{\tau > 0}$  denotes the Neumann heat semigroup, and where

$$
f_1(u, v) := \mu_1 u (1 - u - a_1 v)
$$
 and  $f_2(u, v) := \mu_2 v (1 - v - a_2 u)$ ,  $u \in \mathbb{R}$ ,  $v \in \mathbb{R}$ .

Then by a straightforward reasoning involving standard elliptic regularity properties and known smoothing estimates for the heat semigroup [\(Quittner and Souplet 2007](#page-18-11)), it is possible to show that if  $T = T(R)$  is sufficiently small then  $\Phi$  is a contraction on *S*. The accordingly existing fixed point  $(u, v)$  of  $\Phi$ , along with w as gained from [\(2.2\)](#page-5-0), can then, again by standard regularity arguments, shown to be smooth in  $\Omega \times (0, T)$ and continuous in  $\Omega \times [0, T]$  in all its components, and to solve [\(1.1\)](#page-1-0) classically in  $\Omega \times (0, T)$ . Since the choice of *T* depends on *R* only, [\(2.1\)](#page-4-2) is now immediate.

An application of the strong maximum principle to the first and second equation of  $(1.1)$  implies the claim concerning the positivity of *u* and *v*. Hence,  $ku + v$  is positive in  $\overline{\Omega} \times (0, T_{max})$  and the strong elliptic maximum principle applied to the third equation of  $(1.1)$  yields positivity also of w.

Finally, taking differences  $U := u_1 - u_2$  and  $V := v_1 - v_2$  of two supposedly existing solutions  $(u_i, v_i, w_i)$  in  $\Omega \times (0, T)$  for some  $T > 0$ ,  $i \in \{1, 2\}$ , upon testing the equations for *U* and *V* obtained from  $(1.1)$  by *U* and *V*, respectively, in a straightforward manner one can derive an inequality of the form

$$
\frac{1}{2}\frac{d}{dt}\left\{\int\limits_{\Omega}U^2+\int\limits_{\Omega}V^2\right\}\leq C(T')\left\{\int\limits_{\Omega}U^2+\int\limits_{\Omega}V^2\right\}\quad\text{for all }t\in(0,T'),
$$

valid for any fixed  $T' \in (0, T)$  and some  $C(T') > 0$  depending on the bounded quantities  $||u_i||_{L^{\infty}(\Omega \times (0,T'))}$  and  $||v_i||_{L^{\infty}(\Omega \times (0,T'))}$ ,  $i \in \{1, 2\}$ . This clearly implies uniqueness.

We now let  $\mathcal{L}_j = \mathcal{L}_j(x, t)$ ,  $j \in \{1, 2\}$ , the parabolic operators

$$
\mathcal{L}_j \varphi := d_j \Delta \varphi - \chi_j \nabla w(x, t) \cdot \nabla \varphi, \quad (x, t) \in \Omega \times (0, T_{max}), \tag{2.3}
$$

<span id="page-6-1"></span>for  $\varphi \in C^2(\Omega)$ . Then the first and third equation of [\(1.1\)](#page-1-0) show that

<span id="page-6-4"></span>
$$
u_t - \mathcal{L}_1 u = u \cdot \{ -\chi_1 \Delta w + \mu_1 (1 - u - a_1 v) \}
$$
  
=  $u \cdot \{ \mu_1 - (\mu_1 - k\chi_1)u - (a_1\mu_1 - \chi_1)v - \lambda\chi_1 w \}$  in  $\Omega \times (0, T_{max})$ . (2.4)

Similarly, the second and third equation of  $(1.1)$  imply

<span id="page-6-5"></span>
$$
v_t - \mathcal{L}_2 v = v \cdot \{-\chi_2 \Delta w + \mu_2 (1 - v - a_2 u)\}
$$
  
= 
$$
v \cdot \{\mu_2 - (\mu_2 - \chi_2)v + (k\chi_2 - a_2\mu_2)u - \lambda\chi_2 w\} \text{ in } \Omega \times (0, T_{max}).
$$
 (2.5)

<span id="page-6-0"></span>The final result of this section asserts boundedness of the solution once the ratios *q*<sup>1</sup> and  $q_2$  defined in  $(1.5)$  are small enough.

**Lemma 2.2** *Assume that*

$$
kq_1 + q_2 < 1. \tag{2.6}
$$

<span id="page-6-2"></span>*Then*  $T_{max} = \infty$  *and both u and v are bounded in*  $\Omega \times (0, \infty)$ *.* 

<span id="page-6-3"></span>*Proof* According to the fact that *u*, *v* and *w* are all nonnegative by Lemma [2.1,](#page-4-3) we have

$$
\mathcal{P}_1 u := u_t - \mathcal{L}_1 u - u \cdot \{\mu_1 - (\mu_1 - k\chi_1)u + \chi_1 v\} \le 0 \quad \text{in } \Omega \times (0, T_{max}) \quad \text{and}
$$
\n
$$
\mathcal{P}_2 v := v_t - \mathcal{L}_2 v - v \cdot \{\mu_2 - (\mu_2 - \chi_2) v + k\chi_2 u\} \le 0 \quad \text{in } \Omega \times (0, T_{max}),
$$
\n(2.7)

where  $\mathcal{L}_1$  and  $\mathcal{L}_2$  are defined in [\(2.3\)](#page-6-1). We now observe that [\(2.6\)](#page-6-2) is equivalent to

$$
(\mu_1 - k\chi_1)(\mu_2 - \chi_2) > k\chi_1\chi_2
$$

and hence to

$$
\frac{\mu_1-k\chi_1}{\chi_1}>\frac{k\chi_2}{\mu_2-\chi_2}.
$$

<span id="page-7-0"></span>We can thus pick  $\xi > 0$  large enough such that

$$
\xi \ge \max\left\{ \|u_0\|_{L^{\infty}(\Omega)}, \frac{\mu_2 - \chi_2}{k\chi_2} \|v_0\|_{L^{\infty}(\Omega)} \right\}
$$
(2.8)

and that

$$
\frac{\mu_1 - k\chi_1 - \frac{\mu_1}{\xi}}{\chi_1} > \frac{k\chi_2 + \frac{\mu_2}{\xi}}{\mu_2 - \chi_2},
$$

which enables us to find  $A > 0$  fulfilling

$$
\frac{\mu_1 - k\chi_1 - \frac{\mu_1}{\xi}}{\chi_1} > A > \frac{k\chi_2 + \frac{\mu_2}{\xi}}{\mu_2 - \chi_2}.
$$
 (2.9)

<span id="page-7-1"></span>Then the constant functions defined by

$$
\overline{u}(x, t) := \xi
$$
 and  $\overline{v}(x, t) := A\xi$ ,  $(x, t) \in \overline{\Omega} \times [0, T_{max})$ ,

satisfy

<span id="page-7-2"></span>
$$
\overline{u}(x,0) = \xi \ge u_0(x) \quad \text{and} \quad \overline{v}(x,0) = A\xi > \frac{k\chi_2}{\mu_2 - \chi_2} \cdot \xi \ge v_0(x) \quad \text{for all } x \in \Omega
$$
\n(2.10)

by  $(2.8)$ . Moreover,  $(2.9)$  warrants that

$$
\mathcal{P}_1 \overline{u} = -\xi \cdot \{\mu_1 - (\mu_1 - k\chi_1)\xi + \chi_1 \cdot A\xi\} > 0 \quad \text{in } \Omega \times (0, T_{\text{max}})
$$

and

$$
\mathcal{P}_2\overline{v}=-A\xi\cdot\{\mu_2-(\mu_2-\chi_2)\cdot A\xi+k\chi_2\xi\}>0\quad\text{in }\Omega\times(0,T_{max}).
$$

In view of  $(2.7)$  and  $(2.10)$ , the comparison principle for cooperative reaction–diffusion systems (see for instance [Quittner and Souplet 2007,](#page-18-11) Proposition 52.22) allows us to conclude that  $u \leq \overline{u}$  and  $v \leq \overline{v}$  in  $\Omega \times (0, T_{max})$ , which by Lemma [2.1](#page-4-3) entails that  $T_{max} = \infty$  and that *u* and *v* are globally bounded.

#### <span id="page-8-0"></span>**3 Some technical inequalities**

<span id="page-8-4"></span>According to the above boundedness result, under the assumption [\(1.6\)](#page-2-2) we know that

$$
L_1 := \limsup_{t \to \infty} \left( \max_{x \in \overline{\Omega}} u(x, t) \right),
$$
  
\n
$$
L_2 := \limsup_{t \to \infty} \left( \max_{x \in \overline{\Omega}} v(x, t) \right),
$$
 and  
\n
$$
l_2 := \liminf_{t \to \infty} \left( \min_{x \in \overline{\Omega}} v(x, t) \right)
$$
(3.1)

define finite real numbers satisfying

$$
L_1 \ge 0 \quad \text{and} \quad 0 \le l_2 \le L_2.
$$

<span id="page-8-5"></span>Proving Theorem [1.1](#page-3-2) then amounts to verifying that  $L_1 = 0$  and  $L_2 = l_2 = 1$ , because the large time behavior of  $w$  is then uniquely determined according to the following.

<span id="page-8-1"></span>**Lemma 3.1** *For each*  $t \in (0, T_{max})$ *, we have* 

$$
\min_{y \in \overline{\Omega}} v(y, t) \le \lambda w(x, t) \le k \cdot \max_{y \in \overline{\Omega}} u(y, t) + \max_{y \in \overline{\Omega}} v(y, t) \text{ for all } x \in \overline{\Omega}. \tag{3.2}
$$

*Proof* The proof repeats a standard elliptic comparison argument: If  $\varphi \in C^2(\overline{\Omega})$ denotes an arbitrary function satisfying  $\frac{\partial \varphi}{\partial v} < 0$  on  $\partial \Omega$ , then for any  $\varepsilon > 0$ , at each point  $x_0 \in \overline{\Omega}$  where  $z := w(\cdot, t) + \varepsilon \varphi$  attains its maximum we necessarily have  $x_0 \in \Omega$  and hence  $\Delta z(x_0) \leq 0$ . Since  $\Delta z = \lambda z - ku - v + \varepsilon(\Delta \varphi - \lambda \varphi)$ , this implies that

$$
\lambda z(x) \leq \lambda z(x_0) \leq ku(x_0, t) + v(x_0, t) - \varepsilon (\Delta \varphi - \lambda \varphi)(x_0)
$$
  
 
$$
\leq k \cdot \max_{y \in \bar{\Omega}} u(y, t) + \max_{y \in \bar{\Omega}} v(y, t) + \varepsilon \cdot \max_{y \in \bar{\Omega}} |\Delta \varphi(y) - \lambda \varphi(y)|.
$$

Taking  $\varepsilon \searrow 0$  we arrive at the right inequality in [\(3.2\)](#page-8-1), whereas the left can be seen similarly on dropping the nonnegative term  $k \cdot \min_{y \in \overline{\Omega}} u(y, t)$ .  $\Box$ 

<span id="page-8-6"></span>A first trivial observation linking the asymptotic of  $(u, v, w)$  to  $L_1, L_2$  and  $l_2$  then is the following.

<span id="page-8-2"></span>**Lemma 3.2** *Assume* [\(2.6\)](#page-6-2)*. Then for all*  $\varepsilon > 0$  *there exists*  $t_{\varepsilon} > 0$  *such that* 

$$
u(x,t) \le L_1 + \varepsilon \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_{\varepsilon}, \tag{3.3}
$$

<span id="page-8-3"></span>*that*

$$
l_2 - \varepsilon \le v(x, t) \le L_2 + \varepsilon \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_{\varepsilon}, \tag{3.4}
$$

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<span id="page-9-0"></span>*and that*

$$
l_2 - \varepsilon \le \lambda w(x, t) \le k(L_1 + \varepsilon) + (L_2 + \varepsilon) \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_\varepsilon. \tag{3.5}
$$

*Proof* That [\(3.3\)](#page-8-2) and [\(3.4\)](#page-8-3) can be achieved for suitably large  $t_{\varepsilon}$  is an immediate consequence of the definitions in [\(3.1\)](#page-8-4). Then applying Lemma [3.1](#page-8-5) for fixed  $t \ge t_{\varepsilon}$  we readily obtain  $(3.5)$ .

<span id="page-9-3"></span>Next we compare *u* with a suitable spatially homogeneous function and obtain an upper bound for  $L_1$  in terms of  $l_2$ .

**Lemma 3.3** Assume [\(1.6\)](#page-2-2). Then the numbers  $L_1$  and  $l_2$  defined in [\(3.1\)](#page-8-4) fulfill the *relation*

$$
(1 - kq_1)L_1 \le (1 - a_1l_2)_+.
$$
\n(3.6)

<span id="page-9-1"></span>*Proof* If  $u \equiv 0$  in  $\overline{\Omega} \times [0, \infty)$ , then [\(3.6\)](#page-9-1) is fulfilled in view of  $L_1 = 0$ . Otherwise, according to  $(2.4)$ , taking  $\mathcal{L}_1$  as in  $(2.3)$  we recall that

$$
u_t = \mathcal{L}_1 u + u \cdot \{ \mu_1 - (\mu_1 - k\chi_1)u - (a_1\mu_1 - \chi_1)v - \lambda\chi_1w \} \text{ in } \Omega \times (0, \infty),
$$

where [\(1.6\)](#page-2-2) ensures that  $a_1\mu_1 - \chi_1 \ge 0$ . Thus, if for fixed  $\varepsilon > 0$  we take  $t_{\varepsilon}$  as given by Lemma  $3.2$ , then  $(3.4)$  and  $(3.5)$  yield

$$
-(a_1\mu_1 - \chi_1)v \leq -(a_1\mu_1 - \chi_1) \cdot (l_2 - \varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty)
$$

and

$$
-\lambda \chi_1 w \leq -\chi_1 \cdot (l_2 - \varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty),
$$

and therefore we obtain

$$
u_t \leq \mathcal{L}_1 u + u \cdot \{\mu_1 - (\mu_1 - k\chi_1)u - a_1\mu_1(l_2 - \varepsilon)\} \quad \text{in } \Omega \times (t_{\varepsilon}, \infty).
$$

Since  $\mathcal{L}_1$  annihilates spatially homogeneous functions, a parabolic comparison argument hence implies that

$$
u(x, t) \le \overline{u}(t) \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_{\varepsilon}, \tag{3.7}
$$

<span id="page-9-2"></span>where  $\bar{u}$  denotes the solution of the initial-value problem

$$
\begin{cases} \overline{u}' = \overline{u} \cdot {\mu_1 - (\mu_1 - k\chi_1)\overline{u} - a_1\mu_1(l_2 - \varepsilon)}, & t > t_{\varepsilon}, \\ \overline{u}(t_{\varepsilon}) = \max_{x \in \overline{\Omega}} u(x, t_{\varepsilon}). \end{cases}
$$

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Since  $u(\cdot, t_{\varepsilon})$  is positive in  $\overline{Q}$  by Lemma [2.1,](#page-4-3) it is clear that

$$
\overline{u}(t) \to \max \left\{ 0, \frac{\mu_1 - a_1 \mu_1 (l_2 - \varepsilon)}{\mu_1 - k \chi_1} \right\}
$$
 as  $t \to \infty$ ,

which in conjunction with  $(3.7)$  yields the inequality

$$
\limsup_{t\to\infty}\left(\max_{x\in\bar{\Omega}}u(x,t)\right)\leq \max\left\{0,\frac{\mu_1-a_1\mu_1(l_2-\varepsilon)}{\mu_1-k\chi_1}\right\}.
$$

Taking  $\varepsilon \searrow 0$  now shows that indeed [\(3.6\)](#page-9-1) must be valid.

In order to study the large time behavior of  $v$  we need to distinguish two cases depending on the sign of  $kq_2 - q_2$ . We again use comparison arguments involving spatially homogeneous functions and first give the result for  $kq_2 < a_2$ .

<span id="page-10-3"></span><span id="page-10-1"></span>**Lemma 3.4** *Suppose that* [\(1.6\)](#page-2-2) *holds*, *and that*  $kq_2 < a_2$ *. Then* 

$$
(1 - q_2)L_2 \le (1 - q_2 l_2)_+ \tag{3.8}
$$

<span id="page-10-2"></span>*and*

$$
(1 - q_2)l_2 \ge 1 - a_2 L_1 - q_2 L_2. \tag{3.9}
$$

*Proof* The procedure is similar to that in Lemma [3.3:](#page-9-3) Given  $\varepsilon > 0$ , we take  $t_{\varepsilon} > 0$  as provided by Lemma  $3.2$ . We recall that by  $(2.5)$  we have

<span id="page-10-0"></span>
$$
v_t = \mathcal{L}_2 v + v \cdot \{ \mu_2 - (\mu_2 - \chi_2)v - (a_2\mu_2 - k\chi_2)u - \lambda\chi_2w \} \quad \text{in } \Omega \times (0, \infty)
$$
\n(3.10)

with  $\mathcal{L}_2$  given by [\(2.3\)](#page-6-1). Since  $a_2\mu_2 - k\chi_2$  is nonnegative according to our hypothesis  $kq_2 < a_2$ , using that  $u \ge 0$  we can estimate

$$
-(a_2\mu_2 - k\chi_2)u \le 0 \quad \text{in } \Omega \times (0, \infty),
$$

whereas by  $(3.5)$ ,

$$
-\lambda \chi_2 w \leq -\chi_2 \cdot (l_2 - \varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty).
$$

Thus, [\(3.10\)](#page-10-0) implies that

$$
v_t \leq \mathcal{L}_2 v + v \cdot \{\mu_2 - (\mu_2 - \chi_2)v - \chi_2(l_2 - \varepsilon)\} \quad \text{in } \Omega \times (t_{\varepsilon}, \infty),
$$

whence by comparison we find that

$$
v(x, t) \le \overline{v}(t) \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_{\varepsilon},
$$

if we let  $\overline{v}$  denote the solution of

$$
\begin{cases} \overline{v}' = \overline{v} \cdot \{\mu_2 - (\mu_2 - \chi_2)\overline{v} - \chi_2(l_2 - \varepsilon)\}, & t > t_{\varepsilon}, \\ \overline{v}(t_{\varepsilon}) = \max_{x \in \overline{\Omega}} v(x, t_{\varepsilon}). \end{cases}
$$

In light of the long time asymptotics of  $\overline{v}$ , this entails that

$$
\limsup_{t \to \infty} \left( \max_{x \in \overline{\Omega}} v(x, t) \right) \le \max \left\{ 0, \frac{\mu_2 - \chi_2(l_2 - \varepsilon)}{\mu_2 - \chi_2} \right\}
$$

for any  $\varepsilon > 0$  and hence

$$
L_2 \leq \max\left\{0, \frac{\mu_2 - \chi_2 l_2}{\mu_2 - \chi_2}\right\},\,
$$

which proves  $(3.8)$ .

Similarly,  $(3.9)$  can be obtained by going back to  $(3.10)$  and using  $(3.3)$  and  $(3.5)$ to estimate

$$
-(a_2\mu_2 - k\chi_2)u \ge -(a_2\mu_2 - k\chi_2) \cdot (L_1 + \varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty)
$$

and

$$
-\lambda \chi_2 w \geq -\chi_2 \cdot (kL_1 + L_2 + (k+1)\varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty),
$$

again because  $k \chi_2 \leq a_2 \mu_2$ . We thereupon obtain

$$
v_t - \mathcal{L}_2 v \ge v \cdot {\mu_2 - (\mu_2 - \chi_2)v - (a_2\mu_2 - k\chi_2) \cdot (L_1 + \varepsilon) - \chi_2(kL_1 + L_2 + (k+1)\varepsilon)}
$$
  
=  $v \cdot {\mu_2 - (\mu_2 - \chi_2)v - a_2\mu_2 \cdot (L_1 + \varepsilon) - \chi_2(L_2 + \varepsilon)}$   
in  $\Omega \times (t_{\varepsilon}, \infty)$ ,

whence

$$
v(x, t) \ge \underline{v}(t) \quad \text{for all } x \in \overline{\Omega} \text{ and } t \ge t_{\varepsilon}, \tag{3.11}
$$

by the comparison principle, where

$$
\begin{cases}\n\underline{v}' = \underline{v} \cdot \{\mu_2 - (\mu_2 - \chi_2)\underline{v} - a_2\mu_2(L_1 + \varepsilon) - \chi_2(L_2 + \varepsilon)\}, & t > t_\varepsilon, \\
\underline{v}(t_\varepsilon) = \min_{x \in \Omega} v(x, t_\varepsilon).\n\end{cases} \tag{3.12}
$$

<span id="page-11-0"></span>Now an important observation, singling out the particular steady state solution  $(\tilde{u}, \tilde{v}, \tilde{w}) \equiv (1, 0, \frac{1}{\lambda})$  for which [\(3.9\)](#page-10-2) does not hold, is that  $\underline{v}(t_{\varepsilon})$  is positive thanks to the positivity of v in  $\overline{Q} \times (0, \infty)$  asserted by Lemma [2.1.](#page-4-3) Consequently, v again approaches the larger of the equilibria of  $(3.12)$ , that is, we have

$$
\underline{v}(t) \to \max\left\{0, \frac{\mu_2 - a_2\mu_2(L_1 + \varepsilon) - \chi_2(L_2 + \varepsilon)}{\mu_2 - \chi_2}\right\} \text{ as } t \to \infty,
$$

which in the limit  $\varepsilon \searrow 0$  clearly implies [\(3.9\)](#page-10-2).

In case of  $kq_2 \geq a_2$  we proceed in a similar way.

<span id="page-12-3"></span><span id="page-12-0"></span>**Lemma 3.5** *Assume* [\(1.6\)](#page-2-2), *and suppose that*  $kq_2 \geq a_2$ *. Then* 

$$
(1 - q_2)L_2 \le (1 + (kq_2 - a_2)L_1 - q_2l_2)_+ \tag{3.13}
$$

<span id="page-12-2"></span>*and*

$$
(1 - q_2)l_2 \ge 1 - kq_2L_1 - q_2L_2. \tag{3.14}
$$

*Proof* Again using [\(2.5\)](#page-6-5) as a starting point, given  $\varepsilon > 0$  we take  $t_{\varepsilon} > 0$  as given by Lemma [3.2](#page-8-6) and estimate

$$
(k\chi_2 - a_2\mu_2)u \le (k\chi_2 - a_2\mu_2) \cdot (L_1 + \varepsilon) \quad \text{in } \Omega \times (t_\varepsilon, \infty)
$$

and

$$
-\lambda \chi_2 w \leq -\chi_2 \cdot (l_2 - \varepsilon) \quad \text{in } \Omega \times (t_\varepsilon, \infty).
$$

<span id="page-12-1"></span>We thereupon obtain from the identity

$$
v_t = \mathcal{L}_2 v + v \cdot \{ \mu_2 - (\mu_2 - \chi_2)v + (k\chi_2 - a_2\mu_2)u - \lambda\chi_2 w \} \text{ in } \Omega \times (0, \infty),
$$
\n(3.15)

as obtained in [\(2.5\)](#page-6-5), that

$$
v_t \leq \mathcal{L}_2 v + v \cdot \{ \mu_2 - (\mu_2 - \chi_2)v + (k\chi_2 - a_2\mu_2)(L_1 + \varepsilon) - \chi_2(l_2 - \varepsilon) \}
$$
  
in  $\Omega \times (t_{\varepsilon}, \infty)$ .

By comparison with spatially homogeneous ODE solutions in the same manner as in Lemma [3.4,](#page-10-3) we thereby derive the inequality

$$
\limsup_{t\to\infty}\left(\max_{x\in\bar{\Omega}}v(x,t)\right)\leq \max\left\{0,\frac{\mu_2+(k\chi_2-a_2\mu_2)(L_1+\varepsilon)-\chi_2(l_2-\varepsilon)}{\mu_2-\chi_2}\right\},\,
$$

which on taking  $\varepsilon \searrow 0$  yields [\(3.13\)](#page-12-0).

Similarly, inserting the lower estimates

$$
(k\chi_2 - a_2\mu_2)u \ge 0 \quad \text{in } \Omega \times (0, \infty)
$$

and

$$
-\lambda \chi_2 w \ge -\chi_2 \cdot (kL_1 + L_2 + (k+1)\varepsilon) \quad \text{in } \Omega \times (t_{\varepsilon}, \infty)
$$

into  $(3.15)$  shows that

$$
v_t \geq \mathcal{L}_2 v + v \cdot \{ \mu_2 - (\mu_2 - \chi_2)v - \chi_2(kL_1 + L_2 + (k+1)\varepsilon) \} \quad \text{in } \Omega \times (t_{\varepsilon}, \infty),
$$

which on comparison entails that

$$
\liminf_{t \to \infty} \left( \min_{x \in \overline{\Omega}} v(x, t) \right) \ge \frac{\mu_2 - \chi_2(kL_1 + L_2 + (k+1)\varepsilon)}{\mu_2 - \chi_2}
$$

and thereby proves [\(3.14\)](#page-12-2).

<span id="page-13-3"></span>Using the estimates shown in this section, we are now able to prove that  $v(t) \rightarrow 1$ in  $L^{\infty}(\Omega)$  as  $t \to \infty$  if we assume  $L_1 = 0$ .

**Lemma 3.6** Assume that [\(1.6\)](#page-2-2) holds, and suppose that  $L_1 = 0$ . Then  $L_2 = l_2 = 1$ .

*Proof* We first observe that  $q_2 l_2 \leq 1$ , for otherwise by either [\(3.8\)](#page-10-1) or by [\(3.13\)](#page-12-0) in combination with  $L_1 = 0$  we would have  $L_2 = 0$  and hence could draw the conclusion that  $l_2 = 0$  which is absurd in view of  $(3.9)$  and  $(3.14)$ .

Accordingly, in light of the hypothesis  $L_1 = 0$ , Lemma [3.4](#page-10-3) and Lemma [3.5](#page-12-3) show that in both cases  $kq_2 < a_2$  and  $kq_2 \ge a_2$ , the inequalities

$$
(1 - q_2)L_2 \le 1 - q_2 l_2 \tag{3.16}
$$

<span id="page-13-2"></span><span id="page-13-1"></span>and

$$
(1 - q_2)l_2 \ge 1 - q_2 L_2 \tag{3.17}
$$

hold, which on subtraction imply

$$
(1 - q_2)(L_2 - l_2) \le q_2(L_2 - l_2).
$$

Since [\(1.6\)](#page-2-2) implies that  $q_2 < \frac{1}{2}$ , this asserts that  $L_2 \leq l_2$  and hence  $L_2 = l_2$ . Therefore, once more applying  $(3.16)$  shows that  $L_2 \le 1$ , while similarly  $(3.17)$ entails that  $l_2 \geq 1$ . This completes the proof.

#### <span id="page-13-0"></span>**4 Asymptotic behavior**

According to Lemmas [2.1,](#page-4-3) [2.2,](#page-6-0) [3.2](#page-8-6) and [3.6,](#page-13-3) in order to prove Theorem [1.1](#page-3-2) it remains to show that  $L_1 = 0$  is indeed valid. This will be done by considering again two cases depending on the sign of  $kq_2 - a_2$ .

$$
\qquad \qquad \Box
$$

## 4.1 The case  $kq_2 < a_2$

Combining Lemmas [3.3](#page-9-3) and [3.4,](#page-10-3) we complete the proof of Theorem [1.1](#page-3-2) for  $kq_2 < a_2$ .

**Lemma 4.1** *Suppose that* [\(1.6\)](#page-2-2) *holds as well as kq*<sub>2</sub>  $\lt a_2$ *. Then*  $L_1 = 0$ *.* 

<span id="page-14-2"></span>*Proof* Let us suppose on the contrary that  $L_1$  be positive. Then Lemma [3.3](#page-9-3) says that

<span id="page-14-0"></span>
$$
(1 - kq_1)L_1 \le 1 - a_1l_2 \tag{4.1}
$$

and hence

$$
l_2 < \frac{1}{a_1}.\tag{4.2}
$$

Here we observe that by [\(4.2\)](#page-14-0) we also have  $1 - q_2 l_2 > 1 - \frac{q_2}{q_1} \ge 1 - \frac{1}{q_1} > 0$  due to the fact that [\(1.6\)](#page-2-2) entails that  $q_2 \leq 1$ . Consequently, Lemma [3.4](#page-10-3) asserts that

$$
(1 - q_2)L_2 \le 1 - q_2 l_2 \tag{4.3}
$$

<span id="page-14-3"></span>and

$$
(1 - q_2)l_2 \ge 1 - a_2 L_1 - q_2 L_2. \tag{4.4}
$$

<span id="page-14-1"></span>Now combining  $(4.4)$  with  $(4.1)$  yields

$$
q_2L_2 \ge 1 - a_2L_1 - (1 - q_2)l_2
$$
  
\n
$$
\ge 1 - a_2 \cdot \frac{1 - a_1l_2}{1 - kq_1} - (1 - q_2)l_2
$$
  
\n
$$
= 1 - \frac{a_2}{1 - kq_1} + \left(\frac{a_1a_2}{1 - kq_1} - 1 + q_2\right) \cdot l_2,
$$

which in light of  $(4.3)$  shows that

$$
\frac{1-q_2}{q_2} \cdot \left\{ 1 - \frac{a_2}{1-kq_1} + \left( \frac{a_1a_2}{1-kq_1} - 1 + q_2 \right) \cdot l_2 \right\} \le (1-q_2)L_2 \le 1-q_2l_2.
$$

Thus, necessarily

$$
\frac{1-q_2}{q_2} \cdot \left(1 - \frac{a_2}{1-kq_1}\right) - 1 \le \left\{-\frac{1-q_2}{q_2} \cdot \left(\frac{a_1a_2}{1-kq_1} - 1 + q_2\right) - q_2\right\} \cdot l_2,
$$

<span id="page-14-4"></span>which on multiplication by  $(1 - kq_1)q_2$  can be seen to be equivalent to

$$
\begin{aligned} \{1 - a_1 a_2 - k q_1 - (2 - a_1 a_2) q_2 + 2k q_1 q_2 \} \cdot l_2 &\ge 1 - a_2 \\ -k q_1 - (2 - a_2) q_2 + 2k q_1 q_2. \end{aligned} \tag{4.5}
$$

Since according to [\(1.8\)](#page-2-3),

$$
I := 1 - a_2 - kq_1 - (2 - a_2)q_2 + 2kq_1q_2
$$

is positive,  $(4.5)$  is thus only possible if also

$$
J := 1 - a_1 a_2 - k q_1 - (2 - a_1 a_2) q_2 + 2k q_1 q_2
$$

is positive. Therefore, [\(4.5\)](#page-14-4) implies that

$$
l_2\geq \frac{I}{J},
$$

which in conjunction with  $(4.2)$  says that  $a_1 I < J$ , that is,

$$
a_1 - a_1 a_2 - a_1 k q_1 - a_1 (2 - a_2) q_2 + 2 a_1 k q_1 q_2 < 1
$$
\n
$$
-a_1 a_2 - k q_1 - (2 - a_1 a_2) q_2 + 2 k q_1 q_2.
$$

A simple rearrangement thus yields

$$
(a_1 - 1) \cdot (1 - kq_1 - 2q_2 + 2kq_1q_2) < 0,
$$

which is incompatible with the assumption  $I > 0$ , because  $a_1 > 1$  and

$$
1 - kq_1 - 2q_2 + 2kq_1q_2 = I + a_2(1 - q_2) \ge I > 0
$$

thanks to the fact that  $q_2 < 1$  by [\(1.6\)](#page-2-2). This contradiction shows that actually  $L_1$  must vanish.

4.2 The case  $kq_2 \geq a_2$ 

Finally, a combination of Lemmas [3.3](#page-9-3) and [3.5](#page-12-3) completes the proof of Theorem [1.1](#page-3-2) also for  $kq_2 \geq a_2$  like in the preceding section. The details of the proof are given in the following Lemma.

**Lemma 4.2** *Let* [\(1.6\)](#page-2-2) *hold, and assume that*  $kq_2 \geq a_2$ *. Then*  $L_1 = 0$ *.* 

*Proof* If *L*<sup>1</sup> was positive, again Lemma [3.3](#page-9-3) would yield

<span id="page-15-0"></span>
$$
l_2 < \frac{1}{a_1} \tag{4.6}
$$

<span id="page-15-1"></span>and

$$
L_1 \le \frac{1 - a_1 l_2}{1 - k q_1}.\tag{4.7}
$$

On the other hand, since [\(4.6\)](#page-15-0) and  $kq_2 \ge a_2$  imply  $1 + (kq_2 - a_2)L_1 - q_2l_2 >$  $1 - \frac{q_2}{q_1} \ge 1 - \frac{1}{q_1} > 0$ , Lemma [3.5](#page-12-3) says that

$$
(1 - q2)L2 \le 1 + (kq2 - a2)L1 - q2l2, \t\t(4.8)
$$

<span id="page-16-0"></span>which combined with  $(4.7)$  implies

$$
(1 - q_2)L_2 \le 1 + (kq_2 - a_2) \cdot \frac{1 - a_1l_2}{1 - kq_1} - q_2l_2
$$
  
= 
$$
\left(1 + \frac{kq_2 - a_2}{1 - kq_1}\right) - \left\{\frac{a_1(kq_2 - a_2)}{1 - kq_1} + q_2\right\} \cdot l_2,
$$
 (4.9)

because  $kq_2 \geq a_2$ . Moreover, the second statement in Lemma [3.5](#page-12-3) asserts that

$$
(1 - q_2)l_2 \ge 1 - kq_2L_1 - q_2L_2,
$$

which in view of  $(4.7)$  and  $(4.9)$  becomes

$$
(1 - q_2)l_2 \ge 1 - kq_2 \cdot \frac{1 - a_1l_2}{1 - kq_1} - \frac{q_2}{1 - q_2} \cdot \left(1 + \frac{kq_2 - a_2}{1 - kq_1}\right) + \frac{q_2}{1 - q_2} \cdot \left\{\frac{a_1(kq_2 - a_2)}{1 - kq_1} + q_2\right\} \cdot l_2.
$$

When multiplied by  $(1 - kq_1)(1 - q_2)$ , this yields

$$
{(1 - kq1)(1 - q2)2 - a1kq2(1 - q2) - a1q2(kq2 - a2) - q22(1 - kq1)} \cdot l2\n\ge (1 - kq1)(1 - q2) - kq2(1 - q2) - (1 - kq1)q2 - q2(kq2 - a2),
$$

which can be simplified so as to become

$$
J\cdot l_2\geq I,
$$

where

$$
I := 1 - kq_1 - (2 + k - a_2)q_2 + 2kq_1q_2
$$

is positive thanks to  $(1.8)$ , and hence also

$$
J := 1 - kq_1 - (2 - a_1a_2 + ka_1)q_2 + 2kq_1q_2
$$

must be positive. We thus have  $l_2 \geq \frac{I}{J}$ , whence we may conclude using [\(4.6\)](#page-15-0) that  $a_1 I < J$ , that is,

$$
a_1 - a_1kq_1 - (2a_1 + ka_1 - a_1a_2)q_2 + 2a_1kq_1q_2 < 1 - kq_1
$$
\n
$$
-(2 - a_1a_2 + ka_1)q_2 + 2kq_1q_2.
$$

However, this is equivalent to

$$
(a_1 - 1)(1 - kq_1)(1 - 2q_2) < 0,
$$

which contradicts [\(1.6\)](#page-2-2), because clearly  $kq_1 < 1$  and  $q_2 < \frac{1}{2}$ .  $\frac{1}{2}$ .

#### <span id="page-17-0"></span>**5 Conclusions and discussion**

In this paper we have considered two biological species which compete for the same resources and migrate chemotactically towards a higher concentration of a chemical substance, which they produce. The problem is modeled by using a system of three partial differential equations: two nonlinear parabolic equations to describe the evolution of the biological species and a linear PDE to model the behavior of the chemical. This chemical diffuses considerably faster than the living organism, and it is thus assumed that the evolution of the chemical signal is governed by an elliptic equation.

The system contains several parameters which measure different aspects in the system: chemotaxis effects, competition, diffusion, chemical production and decay. In the case when competition is absent, it is known that due to chemotaxis, the considered system may produce finite-time blow-up [\(Espejo et al. 2010](#page-18-12)), while if on the other hand chemotactic effects are blinded out, then the competitive terms keep the solution bounded and guarantee their global existence. A natural and challenging question has been posed in the literature for such systems: Which are the constraints and the threshold values that decide between driving the system toward global existence, or enforcing blow-up? This question remains open even in the case of a single species. In that case [the](#page-19-7) [competitive](#page-19-7) [term](#page-19-7) [is](#page-19-7) [simplified](#page-19-7) [to](#page-19-7) [a](#page-19-7) [logistic](#page-19-7) [growth](#page-19-7) [function](#page-19-7) [\(cf.](#page-19-7) Tello and Winkler [2007](#page-19-7) for partial results).

A second question concerns the influence of chemotaxis effects on the stability of the homogeneous steady states determined by the competitive terms. The presence of a large number of parameters in the system makes this question difficult to answer. In the case where the competitive terms are weak in the sense that in  $(1.1)$  we have  $a_i \in [0, 1)$  for  $i = 1, 2$ , a partial answer is given in [Tello and Winkler](#page-19-6) [\(2012\)](#page-19-6) within some range of the chemotactic parameters. In this paper we have studied the problem under the assumption that when compared to the latter setting, one of the species is significantly more aggressive in terms of competition.

In this framework, characterized by the assumption  $(1.4)$ , we have seen that if in [\(1.5\)](#page-2-1), both ratios  $q_i$ ,  $i = 1, 2$ , between the chemotactic sensitivities  $\chi_i$  and the competition parameters  $\mu_i$  are suitably small then all nontrivial solutions will be global in time and bounded, and that they approach the homogeneous steady state in which the aggressive subpopulation is at its carrying capacity and the less aggressive species has died out. This inter alia shows that the phenomenon of (asymptotic) extinction of one species, known to be valid for the associated Lotka–Volterra ODE system without diffusion and chemotaxis, persists also in such systems with chemotactic interaction, provided the latter is sufficiently weak. Global existence of solutions is obtained under the assumption  $q_1k + q_2 < 1$ . In that case competition prevents blow-up but extra assumptions are required to prove the stability claim in [\(1.9\)](#page-3-3).

We do not know in how far the set  $(1.6)$  of hypotheses under which our results have been derived is optimal. After all, in some known borderline cases our approach yields requirements which are consistent with assumptions made in the literature for correspondingly simplified models (cf. the discussion in the remark following Theorem [1.1\)](#page-3-2). In light of results from the literature on corresponding single-species systems, it seems natural to conjecture that for suitably large values of  $q_i$ , solutions may exhibit more colorful dynamics. Indeed, in such a setting numerical simulations indicate that chaotic behavior may occur [\(Painter and Hillen 2011](#page-18-13)). It is conceivable that some solutions may even blow up in finite time, but a substantial influence of the space dimension *n* on the occurrence of such explosion phenomena is most likely to be expected: In the single-species case, for instance, although some examples of high-dimensional blow-up phenomena despite logistic-type growth restrictions have been found for  $n \geq 5$  [\(Winkler 2011](#page-19-9)), it is known that blow-up never occurs when  $n \leq 2$  [\(Tello and Winkler 2007](#page-19-7)). In particular, the detection of explosions must thus be restricted to the case  $n > 3$  in which even numerical approaches seem delicate. As opposed to this, our assumptions in this paper are completely independent of *n*, and moreover they are fully explicit; thereby our results reveal, in a quantitative manner, a stability feature of the competitive exclusion phenomenon with respect to chemotactic interaction.

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