This is a postprint version of the paper "A diffusive two predators-one prey model on periodically evolving domains", accepted for the publication in Mathematical Methods in the Applies Sciences.

doi: 10.1002/mma.7323

A diffusive two predators-one prey model on periodically evolving domains

Mirella Cappelletti Montano and Benedetta Lisena

Dipartimento di Matematica, Università degli studi di Bari, 70125 Bari, ITALY

Abstract

The paper deals with a diffusive two predators–one prey model with Holling-type II functional response. We assume that the density of prey and predators are spatially inhomogeneous on a periodically evolving domain and are subject to homogeneous Neumann boundary conditions. We focus on the case in which all populations have periodic logistic growth, if isolated, and no competition occurs between predators.

Our main purpose is to study the asymptotic properties of the solutions of this reaction–diffusion model. More specifically, suitable conditions, depending on the domain evolution function and the space dimension, are introduced leading to the extinction of one predator and the stable coexistence of the surviving predator and its prey. Their density, as time tends to infinity, tends to the periodic solution of the corresponding kinetic predator–prey model. Finally, the autonomous model on a fixed domain is treated.

Keywords. Two predators–one prey model. Diffusion. Evolving domain. Periodicity. Global stability.

2010 Mathematics Subject Classification. 35B40. 35K57. 37N25. 92D25.

1 Introduction

In mathematical ecology, predator–prey models are a topic which has attracted the attention of many researchers starting from the classical predator–prey model independently developed by Lotka and Volterra in the 1920s.

The dynamics of two-species predator–prey systems has been widely studied (see, e.g. [7, 10, 20, 22, 23, 24, 25, 26, 27, 31]). However, the investigation of one prey–two predators systems seems to exhibit much reacher characteristics (see [11, 12, 13, 15, 17, 18, 19, 21, 29]).

In all predator–prey interactions, to represent the average number of prey killed per individual predator, a functional response has been introduced. In particular, the Holling-type II functional response (see [9]) is based on the idea that predators will catch only a limited portion of preys when the prey species is abundant. If the predators and the prey are confined to a bounded domain Ω

with smooth boundary and their densities are spatially inhomogeneous, diffusion terms are added to the reaction terms. Hsiao et al. (see [13]) formulated a one prey–two predators model with Holling-type II functional response in the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u(a_0 - a_1 u) - \dfrac{c_1 uv}{u+m_1} - \dfrac{c_2 uw}{u+m_2} \\ \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + v\left(-b_1 + k_1 \dfrac{c_1 u}{u+m_1}\right) \\ \\ \dfrac{\partial w}{\partial t} = d_3 \Delta w + w\left(-b_2 + k_2 \dfrac{c_2 u}{u+m_2}\right), \\ \end{cases} \tag{1.1}$$

where u, v, w denote the population densities of the prey and the i-th predator ($i = 1,2$), respectively, $\frac{c_i u}{u+m_i}$, $i = 1,2$, is the functional response, d_i, $i = 1,2,3$, is the diffusion coefficient.

In (1.1), the authors only considered intraspecific competition for the prey (represented by the term $-a_1 u$), but not for the two predators. Recently, other authors have supposed both predators and prey intraspecific competition by establishing suitable mathematical models (see, e.g., [12]). Thus, taking intraspecific competition for predators into account, we are addressed to consider the following diffusive model on the domain Ω in $\mathbb{R}^n$

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u\left(a - u - \dfrac{c_1 v}{u+m_1} - \dfrac{c_2 w}{u+m_2}\right) \\ \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + v\left(\dfrac{u}{u+m_1} - b_1 - v\right) \\ \\ \dfrac{\partial w}{\partial t} = d_3 \Delta w + w\left(\dfrac{u}{u+m_2} - b_2 - w\right). \\ \end{cases} \tag{1.2}$$

The parameter a is the intrinsic growth rate of the prey u, b_1, b_2 are the natural death rates of predators v, w in absence of the prey, m_1, m_2 are the so called half saturation coefficients, and c_1, c_2 are the maximal predator per capita consumption rates. All parameters are positive constants. Besides, (1.2) is characterized by no direct interference between rival predators, that is no direct predator competition occurs during the hunting. There exists an indirect competition between the predator species, as they chase the same prey.

Recent advances in mathematical modeling and developmental biology identify the important role of domain evolution. In particular, in population models, the habitat Ω may present periodic variations caused by the seasons effect. Rivers and lakes may change their area and depth. In the summer, the water area becomes larger while in the winter the size of the habitat becomes smaller. In [16] a diffusive logistic equation on periodically evolving domains is investigated showing that the persistence of a species depends on the domain evolution rate. In order to investigate the effects of the domain evolution on the long-time behavior of a model of type (1.2), we study the system

$$\begin{cases} \dfrac{\partial u}{\partial t} + \mathbf{a}\cdot\nabla u + u(\nabla\cdot\mathbf{a}) = d_1(t)\Delta u + u\left(a(t) - u - \dfrac{c_1 v}{u+m_1} - \dfrac{c_2 w}{u+m_2}\right) \\[2ex] \dfrac{\partial v}{\partial t} + \mathbf{a}\cdot\nabla v + v(\nabla\cdot\mathbf{a}) = d_2(t)\Delta v + v\left(\dfrac{u}{u+m_1} - b_1(t) - v\right) \\[2ex] \dfrac{\partial w}{\partial t} + \mathbf{a}\cdot\nabla w + w(\nabla\cdot\mathbf{a}) = d_3(t)\Delta w + w\left(\dfrac{u}{u+m_2} - b_2(t) - w\right), \end{cases} \tag{1.3}$$

on a periodically evolving domain Ω_t, where each solution (u, v, w) depends on position $x(t)$ and time t. By using the same arguments in [16] and the references therein, the domain evolution introduces an advection term $\mathbf{a}\cdot\nabla u$, corresponding to the elemental volumes moving with the flow due to the local growth, and a dilution term $u(\nabla\cdot\mathbf{a})$, due to local volume change. Here $\mathbf{a}$ represents the flow velocity field.

System (1.3) is endowed with initial positive conditions on Ω_0 (the initial domain) and homogeneous Neumann boundary conditions on the boundary Ω_t, $t > 0$. We shall deal with a spatially isotropic and temporally periodic domain Ω_t, whose definition is formulated in the next section. Moreover, we assume that the coefficients $a(t), b_i(t), d_i(t)$, $i = 1, 2$, are periodic in time owing to the seasonal changes of the environment. In (1.3) the functional response has constant coefficients since we assume a negligible effect of the environment variation on this term. To the best of our knowledge, few analytical results are available for ecological system in this setting (see [6, 8, 30]). Even on fixed domains, diffusive predator–prey models, described as non-autonomous systems with periodic coefficients (see [4]), have not been deeply investigated.

In this paper, we are mainly concentrated on diffusive model (1.3), viewing at (1.2) as a simpler case.

We analyze the behavior of the solutions to (1.3) in order to find suitable conditions under which only one predator species survives, while the other one dies out. Then we determine the limiting behavior of the surviving predator and its prey. More precisely, we show that, under suitable assumptions, for any positive solution (u, v, w) to (1.3), we have

$$\lim_{t\to+\infty} w = 0, \quad \lim_{t\to+\infty} |u - u^*| = 0 = \lim_{t\to+\infty} |v - v^*|.$$

Here $(u^*(t), v^*(t))$ is the periodic solution to the kinetic two-species predator–prey model (3.1). Our main tools are comparison results for parabolic equations, the Lyapunov method and the method of invariant regions.

In Section 2, by using standard arguments (see [16, 30] and the reference therein) we transform system (1.3) into the reaction–diffusion system (2.4) on the fixed domain Ω_0, whose new diffusion coefficients and growth rates depend on the domain evolution function $\rho(t)$ (see Section 2) and on the space dimension. In Section 3 we investigate the large time behavior of the kinetic system corresponding to (2.4). Such result appears to be a fundamental step in the investigation developed in Section 4. Its main result, Theorem 4.2, shows that the surviving species tend to spread out in the habitat in a uniform way. Their limiting values are spatially homogeneous and time periodic.

The required assumptions for Theorem 4.2 implicitly depend on the space dimension and on the time evolution of the domain.

In the case of a fixed domain Ω and constant coefficients, our model (1.3) turns into the autonomous predator–prey system (1.2). Section 5 illustrates as the behavior of system (1.2) is influenced by the kinetic two species predator–prey system (5.1) . By the linearized stability technique, in Theorem 5.3, we analyze the local asymptotic stability of the semitrivial solution $(u^*, v^*, 0)$. The global stability result, proved in Theorem 5.5, requires only simple inequalities among the coefficients of system (1.2).

Finally, Section 6 ends the paper with a brief discussion.

2 Preliminaries

Let $\Omega_t \subset \mathbb{R}^n$ $(n \geq 1, t \geq 0)$ be a simply connected bounded evolving domain for all $t \geq 0$, with evolving boundary $\partial\Omega_t$.

Hence we focus on the three-species reaction diffusion system (1.3) acting on the cylinder $\Omega_t \times [0, +\infty[$. We denote by $u(x(t), t)$ the density of the prey and by $v(x(t), t)$, $w(x(t), t)$ the density of the two predators, at time t and position $x(t)$.

System (1.3) can be obtained by applying Reynolds transport theorem (see [1]); in particular, the evolution of Ω_t generates a flow velocity field $\mathbf{a}(x, t)$, that introduces extra advection and dilution terms in the system on a fixed domain.

From now on we assume that the environment is periodic in time and homogeneous in space. The coefficients depending on t are continuous T-periodic functions; in particular, for $i = 1, 2, 3$, $d_i(t) > 0$, $[b_1(t)], [b_2(t)], [a(t)] > 0$. Here, if f is a continuous T-periodic function,

$$[f(t)] = \frac{1}{T} \int_0^T f(t)\, dt$$

denotes the integral average (or mean value) of f.

The remaining coefficients c_1, c_2, m_1, m_2 are strictly positive constants.

We impose self-organization on the system through the Neumann boundary conditions

$$\frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = \frac{\partial w}{\partial \mathbf{n}} = 0 \text{ on } \partial\Omega_t, \quad t > 0,$$

and we consider the initial conditions

$$u(x, 0) = \varphi_1(x),\ v(x, 0) = \varphi_2(x),\ w(x, 0) = \varphi_3(x), \quad x \in \overline{\Omega}_0, \tag{2.1}$$

with $\varphi_i(x) \in C^2(\Omega_0) \cap C(\overline{\Omega}_0)$, $\varphi_i(x) \geq 0$ for every $x \in \overline{\Omega}_0$, but not identically equal to 0, and $i = 1, 2, 3$.

In particular, a solution of (1.3) is said to be positive if the initial data (2.1) satisfy $\varphi_i(x) > 0$, $i = 1, 2, 3$, for all $x \in \Omega_0$.

As a standard assumption in the derivation of reaction–diffusion equations on evolving domains (see [16, 30]) we impose that the flow velocity $\mathbf{a}(x,t)$ coincides with the domain velocity, i.e.,

$$\mathbf{a}(x,t) = (x_1'(t), \dots, x_n'(t)). \tag{H$_1$}$$

Moreover, for analytic convenience, we introduce a transformation that maps (1.3) into a system on the fixed domain Ω_0. A way to achieve this is restricting ourselves to a special class of domain evolution. More precisely, we assume that there exists a C^1, T-periodic function $\rho(t)$ such that $\rho(0) = 1,\ \rho(t) > 0$ for $t > 0$, and, for every $x(t) \in \Omega_t$,

$$(x_1(t), \dots, x_n(t)) = \rho(t)(y_1, \dots, y_n), \quad y = (y_1, \dots, y_n) \in \Omega_0. \tag{H$_2$}$$

Then, under assumptions (H_1) and (H_2), (u, v, w) is mapped into

$$\begin{aligned} \tilde{u}(y_1, \dots y_n, t) &= u(x_1(t), \dots, x_n(t), t) \\ \tilde{v}(y_1, \dots y_n, t) &= v(x_1(t), \dots, x_n(t), t) \\ \tilde{w}(y_1, \dots, y_n, t) &= w(x_1(t), \dots, x_n(t), t). \end{aligned} \tag{2.2}$$

From now on, for simplicity, we shall denote by (u, v, w) the new variables $(\tilde{u}, \tilde{v}, \tilde{w})$ defined in (2.2).

As a matter of fact, under the above transformation, system (1.3) turns into the reaction–diffusion system on a fixed domain

$$\begin{cases} \dfrac{\partial u}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}u = \dfrac{d_1(t)}{\rho^2(t)}\Delta u + u\left(a(t) - u - \dfrac{c_1 v}{u+m_1} - \dfrac{c_2 w}{u+m_2}\right) \\[2ex] \dfrac{\partial v}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}v = \dfrac{d_2(t)}{\rho^2(t)}\Delta v + v\left(\dfrac{u}{u+m_1} - b_1(t) - v\right) \\[2ex] \dfrac{\partial w}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}w = \dfrac{d_3(t)}{\rho^2(t)}\Delta w + w\left(\dfrac{u}{u+m_2} - b_2(t) - w\right), \end{cases} \tag{2.3}$$

where n is the spatial dimension (see [16, 30] for details).

Accordingly, we deal with the resulting model on the fixed domain Ω_0

$$\begin{cases} \dfrac{\partial u}{\partial t} = \dfrac{d_1(t)}{\rho^2(t)}\Delta u + u\left(\gamma(t) - u - \dfrac{c_1 v}{u+m_1} - \dfrac{c_2 w}{u+m_2}\right) \\[2ex] \dfrac{\partial v}{\partial t} = \dfrac{d_2(t)}{\rho^2(t)}\Delta v + v\left(\dfrac{u}{u+m_1} - \delta_1(t) - v\right) \\[2ex] \dfrac{\partial w}{\partial t} = \dfrac{d_3(t)}{\rho^2(t)}\Delta w + w\left(\dfrac{u}{u+m_2} - \delta_2(t) - w\right), \\[2ex] \dfrac{\partial u}{\partial \mathbf{n}} = \dfrac{\partial v}{\partial \mathbf{n}} = \dfrac{\partial w}{\partial \mathbf{n}} = 0 \text{ in } \partial\Omega_0 \times]0, +\infty[, \\[2ex] u(y,0) = \varphi_1(y),\ v(y,0) = \varphi_2(y),\ w(y,0) = \varphi_3(y) \quad y \in \overline{\Omega}_0, \end{cases} \tag{2.4}$$

where

$$\gamma(t) = a(t) - n\frac{\rho'(t)}{\rho(t)}, \quad \delta_i(t) = b_i(t) + n\frac{\rho'(t)}{\rho(t)}, \quad i = 1, 2. \tag{2.5}$$

Therefore we have transformed system (1.3) into a reaction–diffusion system on the fixed domain Ω_0 with diffusion coefficients and growth rates depending on $\rho(t)$. Note that

$$[\gamma(t)] = [a(t)] > 0, \quad [\delta_i(t)] = [b_i(t)] > 0 \text{ for } i = 1, 2. \tag{2.6}$$

3 The kinetic system

We begin our analysis by studying the kinetic two-species predator–prey model

$$\begin{cases} u' = u\left(\gamma(t) - u - \dfrac{c_1 v}{u + m_1}\right) \\ \\ v' = v\left(\dfrac{u}{u + m_1} - \delta_1(t) - v\right). \end{cases} \tag{3.1}$$

Our aim is showing the existence of a global stable, periodic solution $(u^*(t), v^*(t))$ to the above system. Indeed, such a spatially homogeneous solution has a fundamental role to achieve the searched asymptotic properties of the solutions to the reaction–diffusion system (2.4).

From now on, we assume that

$$\left[\frac{u_1(t)}{u_1(t) + m_1}\right] > [\delta_1(t)], \tag{3.2}$$

where we denote by $u_1(t)$ the positive periodic solution to the logistic equation

$$u' = u(\gamma(t) - u)$$

(see [3]). We point out that, if $(u(t), v(t))$ is a positive solution to (3.1), then there exists $t_0 > 0$ such that

$$u(t) \leq u_1(t), \quad t > t_0. \tag{3.3}$$

Indeed, if $u(0) \leq u_1(0)$, from the comparison theorem, it follows that $u(t) \leq u_1(t)$ for every $t > 0$. If, on the other hand, $u(0) > u_1(0)$, by using standard arguments (see, for example, [5]) and taking (3.2) into account, one can prove that (3.3) holds true.

Further, we denote by $v_1(t)$ the positive periodic solution to

$$v' = v\left(\left(\frac{u_1(t)}{u_1(t) + m_1} - \delta_1(t)\right) - v\right). \tag{3.4}$$

Moreover, we suppose that

$$[\gamma(t)] > \frac{c_1}{m_1}[v_1(t)], \tag{3.5}$$

so that the logistic equation

$$u' = u\left(\left(\gamma(t) - \frac{c_1 v_1(t)}{m_1}\right) - u\right) \tag{3.6}$$

admits the positive periodic solution $u_2(t)$.

Finally, assume that

$$\left[\frac{u_2(t)}{u_2(t) + m_1}\right] > [\delta_1(t)], \tag{3.7}$$

and let $v_2(t)$ be the positive periodic solution to

$$v' = v\left(\left(\frac{u_2(t)}{u_2(t) + m_1} - \delta_1(t)\right) - v\right).$$

We set, for $t > 0$,

$$\Sigma(t) = [u_2(t), u_1(t)] \times [v_2(t), v_1(t)]. \tag{3.8}$$

In the next result, we prove that $\Sigma(t)$ is an invariant and attractive region for (3.1); moreover, (3.1) admits a positive periodic solution.

Theorem 3.1. *Under assumptions* (3.2), (3.5), (3.7), *if* $(u(t), v(t))$ *is a positive solution to* (3.1), *there exists* $\bar{t} > 0$ *such that* $(u(t), v(t)) \in \Sigma(t)$ *for every* $t > \bar{t}$. *Moreover, system* (3.1) *admits a positive periodic solution* $(u^*(t), v^*(t))$ *satisfying*

$$(u^*(t), v^*(t)) \in \Sigma(t), \quad t > 0.$$

Proof. Let $(u(t), v(t))$ be a positive solution to (3.1). As (3.3) shows, there exists $t_1 > 0$ such that, for every $t > t_1$, $u(t) \leq u_1(t)$.

From this it follows that, for $t > t_1$,

$$v' \leq v\left(\left(\frac{u_1(t)}{u_1(t) + m_1} - \delta_1(t)\right) - v\right).$$

Hence, there exists $t_2 > t_1$ such that $v(t) \leq v_1(t)$, for $t > t_2$. Moreover,

$$\frac{v(t)}{u(t) + m_1} \leq \frac{v_1(t)}{m_1}, \quad t > t_2;$$

accordingly, for $t > t_2$,

$$u'(t) \geq u\left(\left(\gamma(t) - \frac{c_1 v_1(t)}{m_1}\right) - u\right),$$

so that there exists $t_3 > t_2$ such that $u(t) \geq u_2(t)$ for $t > t_3$.

Finally,

$$v'(t) \geq v\left(\left(\frac{u_2(t)}{u_2(t) + m_1} - \delta_1(t)\right) - v\right),$$

which implies the existence of $\bar{t} > t_3$ such that $v(t) > v_2(t)$ for $t > \bar{t}$.

We pass now to prove the existence of a positive periodic solution to (3.1). To this end, set

$$K = [u_2(0), u_1(0)] \times [v_2(0), v_1(0)]$$

and let $(u(t), v(t))$ be a solution to (3.1) with initial condition $(u(0), v(0)) \in K$. Then

$$u_2(t) \leq u(t) \leq u_1(t), \quad v_2(t) \leq v(t) \leq v_1(t), \qquad \text{for every } t > 0.$$

In particular

$$u_2(0) = u_2(T) \leq u(T) \leq u_1(T) = u_1(0)$$

and

$$v_2(0) = v_2(T) \leq v(T) \leq v_1(T) = v_1(0),$$

so that

$$(u(T), v(T)) \in K. \tag{3.9}$$

Consider the map

$$F : K \longrightarrow K, \quad F(x, y) = (u(T), v(T)),$$

where, for every $(x, y) \in K$, $(u(t), v(t))$ is the solution to (3.1) satisfying $u(0) = x$, $v(0) = y$. F is indeed well-defined, since, by (3.9), $F(x, y) \in K$.

Moreover, F is continuous, so that, thanks to the Brouwer fixed point theorem, there exists a point $(\widehat{u}, \widehat{v}) \in K$ such that

$$F(\widehat{u}, \widehat{v}) = (\widehat{u}, \widehat{v}).$$

By construction, the solution $(u^*(t), v^*(t))$ to (3.1) with initial condition $(\widehat{u}, \widehat{v})$ is T-periodic and, for every $t \in [0, T]$,

$$(u^*(t), v^*(t)) \in \Sigma(t).$$

This completes the proof. □

We note that some of the results in Theorem 3.1 are in accordance with the the ones in [10, Theorem 3.2, Proposition 3.4].

We can now state the following theorem.

Theorem 3.2. *Assume that* (3.2), (3.5), (3.7) *are verified and let* $(u^*(t), v^*(t))$ *be the positive periodic solution to system* (3.1). *Set*

$$\lambda = \left[\frac{m_1 u^*(t)}{u^*(t) + m_1}\right], \quad \mu = [v^*(t)] \tag{3.10}$$

and further suppose that, for each $t \in [0, T]$,

$$\frac{c_1}{u_2(t)+m_1}\left(-\lambda v^*(t)+\mu\frac{m_1 u^*(t)}{u^*(t)+m_1}\right)^2 < 4\lambda\mu\, u^*(t)v^*(t)\left(u_2(t)+m_1-\frac{c_1 v^*(t)}{u^*(t)+m_1}\right). \tag{3.11}$$

Then $(u^*(t), v^*(t))$ *is a globally asymptotically stable solution to* (3.1), *i.e., if* $(u(t), v(t))$ *is a positive solution to* (3.1), *then*

$$\lim_{t\to+\infty}(u(t) - u^*(t)) = 0 = \lim_{t\to+\infty}(v(t) - v^*(t)).$$

Proof. The proof is based on a positive Lyapunov function. Fix a positive solution $(u(t), v(t))$ to system (3.1) and consider the Lyapunov function

$$V(t) = H(t, u(t), v(t)),$$

where

$$H(t,u,v) = \lambda \int_1^{u/u^*(t)} \left(1 - \frac{1}{z}\right) dz + c_1\mu \int_1^{v/v^*(t)} \left(1 - \frac{1}{s}\right) ds.$$

Since, taking Theorem 3.1 into account, for $t > \bar{t}$, the solutions to (3.1) ultimately enter $\Sigma(t)$ (see (3.8)), we restrict the study to this set.

In particular, for $t > \bar{t}$,

$$\begin{aligned} V'(t) &= \lambda \frac{u - u^*(t)}{u} \left(\frac{u}{u^*(t)}\right)' + c_1\mu \frac{v - v^*(t)}{v} \left(\frac{v}{v^*(t)}\right)' \\ &= \lambda \frac{u-u^*(t)}{u^*(t)} \left(\gamma(t) - u - \frac{c_1 v}{u+m_1}\right) - \lambda \frac{u-u^*(t)}{u^*(t)} \left(\gamma(t) - u^*(t) - \frac{c_1 v^*(t)}{u^*(t)+m_1}\right) \\ &+ c_1\mu \frac{v - v^*(t)}{v^*(t)} \left(\frac{u}{u+m_1} - \delta_1(t) - v\right) \\ &- c_1\mu \frac{v - v^*(t)}{v^*(t)} \left(\frac{u^*(t)}{u^*(t)+m_1} - \delta_1(t) - v^*(t)\right) = A(u,v,t) \end{aligned}$$

where, after some computations, we have

$$\begin{aligned} A(u,v,t) &= -\frac{\lambda}{u^*(t)(u+m_1)} \left(u + m_1 - \frac{c_1 v^*(t)}{u^*(t)+m_1}\right) (u - u^*(t))^2 \\ &+ \frac{c_1}{(u+m_1)u^*(t)v^*(t)} \left(-\lambda v^*(t) + \mu \frac{m_1 u^*(t)}{u^*(t)+m_1}\right) (u - u^*(t))(v - v^*(t)) \\ &- \mu \frac{c_1}{v^*(t)} (v - v^*(t))^2. \end{aligned} \tag{3.12}$$

For each fixed t, $A(u, v, t)$ appears as a quadratic form in the variables $(u - u^*(t))$ and $(v - v^*(t))$, so that it is definite negative if and only if

$$\frac{c_1}{u+m_1} \left(-\lambda v^*(t) + \mu \frac{m_1 u^*(t)}{u^*(t)+m_1}\right)^2 < 4\lambda\mu\, u^*(t)v^*(t) \left(u + m_1 - \frac{c_1 v^*(t)}{u^*(t)+m_1}\right). \tag{3.13}$$

Since $u(t) \geq u_2(t)$ for $t > \bar{t}$, hypotesis (3.11) ensures the validity of (3.13). Thus, there exists $k > 0$ such that

$$V'(t) = A(u,v,t) \leq -k((u - u^*(t))^2 + (v - v^*(t))^2);$$

integrating from $\bar{t}$ to t,

$$k \int_{\bar{t}}^{t} ((u - u^*(s))^2 + (v - v^*(s))^2)\, ds \leq V(\bar{t}) - V(t) < V(\bar{t}) < +\infty.$$

Accordingly,

$$\int_{\bar{t}}^{+\infty} ((u - u^*(s))^2 + (v - v^*(s))^2)\, ds < +\infty$$

and this yields (see [31, Lemma 2.1]),

$$\lim_{t\to+\infty} (u - u^*(t))^2 + (v - v^*(t))^2) = 0,$$

so that the global attractivity of $(u^*(t), v^*(t))$ is proved. □

Remark 3.1. *Note that the choice of λ and μ given by* (3.10) *provides that*

$$-\lambda[v^*(t)] + \mu \left[\frac{m_1 u^*(t)}{u^*(t) + m_1}\right] = 0,$$

so that, in the case of an autonomous system, the coefficient of the term $(u - u^*)(v - v^*)$ is zero.

We now consider the kinetic system corresponding to (2.4), that is

$$\begin{cases} u' = u\left(\gamma(t) - u - \dfrac{c_1 v}{u + m_1} - \dfrac{c_2 w}{u + m_2}\right) \\[2ex] v' = v\left(\dfrac{u}{u + m_1} - \delta_1(t) - v\right) \\[2ex] w' = w\left(\dfrac{u}{u + m_2} - \delta_2(t) - w\right). \end{cases} \tag{3.14}$$

We want to determine sufficient conditions in order that (3.14) evolves in time in such a way that one of the predators is driven to extinction.

Theorem 3.3. *Under assumptions* (3.2), (3.5), (3.7), *let $(u^*(t), v^*(t))$ be the periodic positive solution to* (3.1) *and suppose* (3.11) *holds true. Suppose further that*

$$\left[\frac{u_1(t)}{u_1(t) + m_2}\right] < [\delta_2(t)]. \tag{3.15}$$

If $(u(t), v(t), w(t))$ is a positive solution to (3.14), *then*

$$\lim_{t\to+\infty} w(t) = 0 \tag{3.16}$$

and

$$\lim_{t\to+\infty} (u(t) - u^*(t)) = \lim_{t\to+\infty} (v(t) - v^*(t)) = 0. \tag{3.17}$$

Proof. Consider a positive solution $(u(t), v(t), w(t))$ to (3.14) and let $z(t)$ be the solution to

$$\begin{cases} z' = z\left(\left(\dfrac{u_1(t)}{u_1(t) + m_2} - \delta_2(t)\right) - z\right) \\[2ex] z(t_0) = w(t_0); \end{cases}$$

taking (3.3) into account, for $t \geq t_0$,

$$\frac{u_1(t)}{u_1(t)+m_2} - \delta_2(t) \geq \frac{u(t)}{u(t)+m_2} - \delta_2(t)$$

as the function $f(u) = \dfrac{u}{u+m_2}$, $u \geq 0$, is increasing.

Hence,

$$w(t) \leq z(t), \quad t \geq t_0;$$

since (3.15) holds true, it is well known that $\lim\limits_{t\to+\infty} z(t) = 0$ and this yields (3.16).

Since $(u^*(t), v^*(t))$ satisfies the assumptions of Theorem 3.2, it is globally stable for (3.1).

On the other hand, $(u(t), v(t))$ can be viewed a solution to the perturbed system

$$\begin{cases} u' = u\left(\gamma(t) - u - \dfrac{c_1 v}{u+m_1}\right) - \dfrac{c_2 w u}{u+m_2} \\ \\ v' = v\left(\dfrac{u}{u+m_1} - \delta_1(t) - v\right), \end{cases}$$

where the perturbation $q(u,t) = -\frac{c_2 w u}{u+m_2}$ satisfies $\lim\limits_{t\to+\infty} q(u,t) = 0$ uniformly with respect to the first variable, because of (3.16). Taking [2, Theorem 5.5.5] and Theorem 3.2 into account, we conclude that (3.17) holds true. $\square$

4 Main result

In this section, we mainly focus on the diffusive system (2.4). Our first result applies to the bidimensional system

$$\begin{cases} \dfrac{\partial u}{\partial t} = \dfrac{d_1(t)}{\rho^2(t)}\Delta u + u\left(\gamma(t) - u - \dfrac{c_1 v}{u+m_1}\right) \text{ in } \Omega_0 \times [0,+\infty[, \\ \\ \dfrac{\partial v}{\partial t} = \dfrac{d_2(t)}{\rho^2(t)}\Delta v + v\left(\dfrac{u}{u+m_1} - \delta_1(t) - v\right) \text{ in } \Omega_0 \times [0,+\infty[, \\ \\ \dfrac{\partial u}{\partial \mathbf{n}} = \dfrac{\partial v}{\partial \mathbf{n}} = 0 \text{ in } \partial\Omega_0 \times]0,+\infty[, \\ \\ u(y,0) = \varphi_1(y),\ v(y,0) = \varphi_2(y), \quad y \in \overline{\Omega}_0. \end{cases} \tag{4.1}$$

Theorem 4.1. *Under assumptions* (3.2), (3.5), (3.7), *if* $(u(y,t), v(y,t))$ *is a positive solution to* (4.1), *there exists* $\bar{t} > 0$ *such that* $(u(y,t), v(y,t)) \in \Sigma(t)$ *for every* $t > \bar{t}$ *and* $y \in \Omega_0$.

Proof. Take a positve solution $(u(y,t), v(y,t))$ to (4.1) and set $v_0(t) = \min_{y\in\overline{\Omega}_0} v(y,t)$.

Let $\overline{u}(t)$ be the solution to

$$\begin{cases} \overline{u}' = \overline{u}\left(\gamma(t) - \overline{u} - \dfrac{c_1 v_0(t)}{\overline{u} + m_1}\right) \\ \\ \overline{u}(0) = \max_{y\in\overline{\Omega}_0} \varphi_1(y). \end{cases}$$

$\overline{u}(t)$ is a spatially homogeneous solution to

$$\begin{cases} \dfrac{\partial u}{\partial t} = \dfrac{d_1(t)}{\rho^2(t)}\Delta u + u\left(\gamma(t) - u - \dfrac{c_1 v_0(t)}{\overline{u} + m_1}\right) \text{ in } \Omega_0 \times [0, +\infty[\\ \\ \dfrac{\partial u}{\partial \mathbf{n}} = 0 \text{ in } \partial\Omega_0 \times]0, +\infty[, \\ \\ u(y,0) = \max_{y\in\overline{\Omega}_0} \varphi_1(y) \text{ in } \overline{\Omega}_0. \end{cases}$$

By using the comparison theorem for parabolic equations, we get that

$$u(y,t) \le \overline{u}(t), \quad y \in \Omega_0.$$

We first remark that $\lim_{t\to+\infty} v(y,t) > 0$ uniformly with respect to $y \in \Omega_0$ because of (3.2), hence $\lim_{t\to+\infty} v_0(t) > 0$. From this it follows that, reasoning as in Theorem 3.1, for a sufficiently large $t_1 > 0$,

$$\overline{u}(t) \le u_1(t), \qquad t > t_1,$$

and, consequently,

$$u(y,t) \le u_1(t), \qquad t > t_1, y \in \Omega_0.$$

Let now $\overline{v}(t)$ be the solution to

$$\begin{cases} \overline{v}' = \overline{v}\left(\dfrac{\overline{u}(t)}{\overline{u}(t) + m_1} - \delta_1(t) - \overline{v}\right) \\ \\ \overline{v}(t_1) = \max_{y\in\overline{\Omega}_0} v(y, t_1). \end{cases}$$

Then $v(y,t) \le \overline{v}(t)$ for $y \in \Omega_0$.

On the other hand,

$$\frac{\overline{u}(t)}{\overline{u}(t) + m_1} \le \frac{u_1(t)}{u_1(t) + m_1}, \quad t > t_1,$$

and $v_1(t)$ is the periodic solution to the logistic equation (3.4).

Thus, for a sufficiently large $t_2 > t_1$,

$$\overline{v}(t) \leq v_1(t), \quad t > t_2,$$

and, consequently, for $t > t_2$ and $y \in \Omega_0$,

$$v(y,t) \leq v_1(t).$$

Consider now the solution $\underline{u}(t)$ to

$$\begin{cases} \underline{u}' = \underline{u}\left(\gamma(t) - \underline{u} - \dfrac{c_1\overline{v}}{m_1}\right) \\ \\ \underline{u}(t_2) = \min\limits_{y\in\Omega_0} u(y,t_2). \end{cases} \tag{4.2}$$

Then, arguing as before, $\underline{u}(t) \leq u(y,t)$; moreover, since $u_2(t)$ is the periodic solution to the logistic equation (3.6), there exists $t_3 > t_2$ such that for all $t > t_3$ and $y \in \Omega_0$,

$$u(y,t) \geq \underline{u}(t) \geq u_2(t).$$

Reasoning in the same way, we can find $\bar{t} > t_3$ such that, if $t > \bar{t}$ and $y \in \Omega_0$,

$$v(y,t) \geq v_2(t).$$

Hence, the proof is complete. □

We are now ready to prove the main result of the paper, which investigates the asymptotic behavior of (2.4).

Theorem 4.2. *Under assumptions* (3.2), (3.5), (3.7), (3.11) *and* (3.15), *let* $(u^*(t), v^*(t))$ *be the positive periodic solution to* (3.1). *Moreover, assume that, for every* $t \in [0,T]$,

$$\delta_2(t) > \max\left\{1, \frac{m_1}{m_2}\right\} \frac{u^*(t)}{u^*(t) + m_1}. \tag{4.3}$$

If $(u(y,t), v(y,t), w(y,t))$ *is any positive solution of* (2.4) *subject to Neumann boundary conditions, then*

$$\lim_{t\to+\infty} w(y,t) = 0 \tag{4.4}$$

and

$$\lim_{t\to+\infty} |u(y,t) - u^*(t)| = \lim_{t\to+\infty} |v(y,t) - v^*(t)| = 0 \tag{4.5}$$

uniformly with respect to $y \in \Omega_0$.

Proof. Fix a positive solution $(u(y,t), v(y,t), w(y,t))$ to the diffusive system (2.4). Then (4.4) follows from assumption (3.15), Theorem 3.3 and the comparison theorem for parabolic equations.

We now formulate the following claim:

$$\text{there exists } \bar{t} > 0 \text{ such that } u(y,t) \geq u_2(t) \text{ for } t > \bar{t},\ y \in \Omega_0. \tag{4.6}$$

The proof is almost obvious now from previous results in this section and the arguments of Theorem 4.1. Therefore we only make some considerations here.

The inequalities

$$u(y,t) \leq u_1(t), \qquad t > t_1,\ y \in \Omega_0$$
$$v(y,t) \leq v_1(t), \qquad t > t_2 > t_1,\ y \in \Omega_0$$

follow from Theorem 4.1 and the fact that $w(y,t) > 0$.

Put $w_0(t) = \max_{y \in \overline{\Omega_0}} w(y,t)$ and remark that $\lim_{t \to +\infty} w_0(t) = 0$ thanks to (4.4).

The ODE

$$u' = u\left(\left(\gamma(t) - \frac{c_1 v_1(t)}{m_1}\right) - u\right) - c_2 \frac{u w_0(t)}{u + m_2}$$

has the same asymptotic behavior as (3.6), because the perturbation term $\frac{-c_2 u w_0}{u+m_2}$ goes to zero at infinity.

Combining these facts with the arguments in Theorem 3.1 and Theorem 4.1, for a suitable $\bar{t} > 0$, we obtain

$$u(y,t) \geq \underline{u}(t) \geq u_2(t), \quad t > \bar{t},\ y \in \Omega_0,$$

where $\underline{u}(t)$ is the solution to (4.2). Hence inequality (4.6) holds.

At this point, we are able to prove (4.5) by means of the Lyapunov method. Consider the positive function

$$V(t) = \int_{\Omega_0} H(u(y,t), v(y,t), w(y,t))\, dy$$

where

$$H(u(y,t), v(y,t), w(y,t)) = \lambda \int_1^{u/u^*(t)} \left(1 - \frac{1}{z}\right) dz$$
$$+ c_1 \mu \int_1^{v/v^*(t)} \left(1 - \frac{1}{s}\right) ds + c_2 w(y,t),$$

and the constants λ, μ are defined as in (3.10).

Since (u,v,w) verifies (2.4), we infer that, for $t > \bar{t}$,

$$\frac{\partial H}{\partial t} = \lambda \frac{u - u^*(t)}{u} \frac{\partial}{\partial t}\left(\frac{u}{u^*(t)}\right) + c_1 \mu \frac{v - v^*(t)}{v} \frac{\partial}{\partial t}\left(\frac{v}{v^*(t)}\right) + c_2 \frac{\partial w(y,t)}{\partial t}$$
$$= \lambda \frac{d_1(t)}{\rho^2(t) u^*(t)} \left(1 - \frac{u^*(t)}{u}\right) \Delta u + c_1 \mu \frac{d_2(t)}{\rho^2(t) v^*(t)} \left(1 - \frac{v^*(t)}{v}\right) \Delta v + c_2 \frac{d_3(t)}{\rho^2(t)} \Delta w$$
$$+ A(u,v,t) + c_2 w \left(\frac{u + m_1}{u + m_2} \frac{u^*(t)}{u^*(t) + m_1} - \delta_2(t) - w\right),$$

with $A(u,v,t)$ defined as in (3.12).

Hence, taking the no-flux boundary conditions into account, we have

$$
\begin{aligned}
&V'(t) = \int_{\Omega_0} \frac{\partial H}{\partial t}\, dy \\
&= A\frac{d_1(t)}{\rho^2(t)u^*(t)} \int_{\Omega_0} \left(1 - \frac{u^*(t)}{u}\right) \Delta u \, dy + c_1 B \frac{d_2(t)}{\rho^2(t)v^*(t)} \int_{\Omega_0} \left(1 - \frac{v^*(t)}{v}\right) \Delta v \, dy \\
&+ c_2 \frac{d_3(t)}{\rho^2(t)} \int_{\Omega_0} \Delta w \, dy + \int_{\Omega_0} A(u,v,w,y,t)\, dy \\
&= -A\frac{d_1(t)}{\rho^2(t)} \int_{\Omega_0} \frac{|\nabla u|^2}{u^2}\, dy - c_1 B \frac{d_2(t)}{\rho^2(t)} \int_{\Omega_0} \frac{|\nabla v|^2}{v^2}\, dy + \int_{\Omega_0} C(u,v,w,y,t)\, dy \\
&\le \int_{\Omega_0} C(u,v,w,y,t)\, dy
\end{aligned}
$$

where

$$
C(u,v,w,y,t) = A(u,v,t) + c_2 w \left(\frac{u+m_1}{u+m_2} \frac{u^*(t)}{u^*(t)+m_1} - \delta_2(t) - w \right).
$$

Since (3.11) and (4.6) hold true, as in the proof of Theorem 3.2, there exists $k > 0$ such that

$$
A(u,v,t) \le -k((u-u^*(t))^2 + (v-v^*(t))^2).
$$

Consequently,

$$
\begin{aligned}
&C(u,v,w,y,t) \le -\nu((u-u^*(t))^2 + (v-v^*(t))^2 + w^2) \\
&+ c_2 w \left(\frac{u+m_1}{u+m_2} \frac{u^*(t)}{u^*(t)+m_1} - \delta_2(t) \right),
\end{aligned}
\tag{4.7}
$$

where $\nu = \max\{k, c_2\}$.

We claim that, under assumption (4.3),

$$
\frac{u+m_1}{u+m_2} \frac{u^*(t)}{u^*(t)+m_1} - \delta_2(t) < 0.
$$

In fact, if $m_1 \le m_2$, then

$$
\frac{u+m_1}{u+m_2} \frac{u^*(t)}{u^*(t)+m_1} \le \frac{u^*(t)}{u^*(t)+m_1} < \delta_2(t).
$$

On the other hand, if $m_1 > m_2$, then

$$
\frac{u+m_1}{u+m_2} \frac{u^*(t)}{u^*(t)+m_1} < \frac{m_1}{m_2} \frac{u^*(t)}{u^*(t)+m_1} < \delta_2(t).
$$

Summing up, from (4.7) we get that

$$
C(u,v,w,y,t) \le -\nu((u-u^*(t))^2 + (v-v^*(t))^2 + w^2),
$$

so that

$$V'(t) \le -\nu \int_{\Omega_0} ((u-u^*(t))^2 + (v-v^*(t))^2 + w^2)\, dy.$$

Integrating from $\bar{t}$ to t,

$$\nu \int_{\bar{t}}^{t} ds \left(\int_{\Omega_0} ((u-u^*(t))^2 + (v-v^*(t))^2 + w^2)\, dy \right) \le V(\bar{t}) - V(t) < V(\bar{t}) < +\infty;$$

thus

$$\int_{\bar{t}}^{+\infty} ds \left(\int_{\Omega_0} ((u-u^*(t))^2 + (v-v^*(t))^2 + w^2)\, dy \right) < +\infty$$

and, consequently (see [31, Lemma 2.1]),

$$\begin{aligned} &\lim_{t\to+\infty} \|u(\cdot,t) - u^*(t)\|_{L^2(\Omega_0)} = \lim_{t\to+\infty} \|v(\cdot,t) - v^*(t)\|_{L^2(\Omega_0)} \\ &= \lim_{t\to+\infty} \|w(\cdot,t)\|_{L^2(\Omega_0)} = 0. \end{aligned} \tag{4.8}$$

Let $p > \max\{n, 2\}$; then the Sobolev inequality ([28]) yields that, for $(y,t) \in \overline{\Omega}_0 \times \mathbb{R}^+$,

$$\begin{aligned} &|u(y,t) - u^*(t)|^p \le \int_{\Omega_0} |u(y,t) - u^*(t)|^p\, dy + \int_{\Omega_0} |\nabla(u(y,t) - u^*(t))|^p\, dy \\ &\le c_1 \int_{\Omega_0} |u(y,t) - u^*(t)|^2\, dy + c_2 \int_{\Omega_0} |\nabla(u(y,t) - u^*(t))|^2\, dy. \end{aligned} \tag{4.9}$$

Moreover,

$$\lim_{t\to\infty} \int_{\Omega_0} |\nabla(u(y,t) - u^*(t))|^2\, dy = 0;$$

in fact, multiplying by $u - u^*(t)$ the first equation in (2.4) and integrating over Ω_0, there exists $c > 0$ such that

$$\begin{aligned} &\frac{d_1(t)}{\rho^2(t)} \int_{\Omega_0} |\nabla(u(y,t) - u^*(t))|^2\, dy \\ &\le -\frac{1}{2}\frac{d}{dt} \int_{\Omega_0} |u(y,t) - u^*(t)|^2\, dy + c \int_{\Omega_0} |u(y,t) - u^*(t)|^2\, dy. \end{aligned}$$

From this, (4.8) and (4.9), it follows that $\lim_{t\to+\infty} |u(y,t) - u^*(t)| = 0$ uniformly w.r.t. $y \in \Omega_0$. Arguing in the same way, this time multiplying the second equation in (2.4) by $(v - v^*(t))$, one gets $\lim_{t\to+\infty} |v(y,t) - v^*(t)| = 0$ uniformly w.r.t. $y \in \Omega_0$. □

Remark 4.1. *We can use the same methods developed in Sections 3 and 4 to find sufficient conditions in order to achieve the extinction of predator v and the persistence of species u and w.*

5 The autonomous case

We now consider the case of the autonomous system (1.2), acting on a fixed domain Ω. We prove that the general sufficient conditions for the asymptotic behaviour of the solutions introduced in Theorem 4.2 can be replaced by simple inequalities involving the coefficients of the system.

So, from now on, we consider system (1.2) subject to Neumann boundary conditions

$$\frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = \frac{\partial w}{\partial \mathbf{n}} = 0 \text{ in } \partial\Omega\times]0,+\infty[,$$

and initial conditions

$$u(x,0) = \varphi_1(x),\ v(x,0) = \varphi_2(x),\ w(x,0) = \varphi_3(x) \quad x \in \overline{\Omega},$$

where all the coefficients are supposed to be strictly positive constants and $\varphi_i(x) \in C^2(\Omega) \cap C(\overline{\Omega})$, $\varphi_i(x) \geq 0$, but not identically zero, for every $x \in \overline{\Omega}$, $i = 1, 2, 3$.

If $w(x,t) = 0$, then (1.2) turns into

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u\left(a - u - \dfrac{c_1 v}{u + m_1}\right) \\ \\ \dfrac{\partial v}{\partial t} = d_2 \Delta v + v\left(\dfrac{u}{u + m_1} - b_1 - v\right). \end{cases} \tag{5.1}$$

We first focus on the corresponding ODE differential system

$$\begin{cases} u' = u\left(a - u - \dfrac{c_1 v}{u + m_1}\right) \\ \\ v' = v\left(\dfrac{u}{u + m_1} - b_1 - v\right). \end{cases} \tag{5.2}$$

The prey isocline of system (5.2) is the parabole

$$v = \frac{(a-u)(u+m_1)}{c_1}.$$

It has vertex at the point $V\left(\frac{a-m_1}{2}, \frac{(a+m_1)^2}{4c_1}\right)$ and intersects the v-axes at $\frac{am_1}{c_1}$.

The predator isocline is the curve

$$v = \frac{u}{u+m_1} - b_1,$$

which is strictly increasing for $u > 0$.

Under the assumption

$$\frac{a}{a+m_1} > b_1, \tag{5.3}$$

system (5.2) has a unique positive equilibrium (u^*, v^*), $u^* < a$. From now on, we shall assume (5.3) holds true.

Set

$$v_1 = \frac{a}{a+m_1} - b_1,$$

and assume

$$v_1 < \frac{am_1}{c_1}. \tag{5.4}$$

Note that (5.4) obviously holds true if $\frac{am_1}{c_1} \geq 1$ since $v_1 < 1$.

Putting

$$u_1 = a$$

and arguing as in Theorem 3.1, if $(u(t), v(t))$ is a positive solution to (5.2), for sufficiently large t,

$$u(t) \leq u_1 \text{ and } v(t) \leq v_1.$$

Moreover, setting

$$u_2 = a - \frac{c_1 v_1}{m_1} > 0$$

and assuming that

$$\frac{u_2}{u_2 + m_1} > b_1, \tag{5.5}$$

we deduce the existence of $\bar{t} > 0$ such that, for $t > \bar{t}$,

$$u(t) \geq u_2 \text{ and } v(t) \geq v_2,$$

where $v_2 = \frac{u_2}{u_2+m_1} - b_1$.

The next theorem (see Theorem 3.1) shows that assumptions (5.4) and (5.5) ensure the existence of a compact region in the first quadrant of $\mathbb{R}^2$ such that every solution of system (5.2) will eventually enter and stay in that region.

Theorem 5.1. *Under assumptions* (5.4) *and* (5.5)*, the rectangle*

$$\mathcal{R} = [u_2, u_1] \times [v_2, v_1] \tag{5.6}$$

is invariant for (5.2) *and* $(u^*, v^*) \in \mathcal{R}$*. Moreover, for any positive solution* $(u(t), v(t))$ *to* (5.2) *there exists* $\bar{t} > 0$ *such that*

$$(u(t), v(t)) \in \mathcal{R} \text{ for } t > \bar{t}.$$

Our next aim is adding to (5.4) and (5.5) a suitable condition providing the global attractivity of the equilibrium point (u^*, v^*) for the reaction–diffusion system (5.1).

Theorem 5.2. *Assume that* (5.4) *and* (5.5) *hold true and further suppose that*

$$u_2 = a - \frac{c_1 v_1}{m_1} \geq \frac{a - m_1}{2}. \tag{5.7}$$

Then (u^*, v^*) *attracts all positive solutions to* (5.1).

Proof. In order to prove our statement, we use the Lyapunov method.

Let $(u(y,t), v(y,t))$ be a positive solution to (5.1). Consider the Lyapunov function

$$V(t) = \int_\Omega H(u,v)\,dy,$$

where $H(u,v)$ is defined by

$$H(u,v) = \frac{m_1 u^*}{m_1+u^*}\int_1^{u/u^*}\left(1-\frac{1}{z}\right)dz + c_1 v^*\int_1^{v/v^*}\left(1-\frac{1}{s}\right)ds.$$

The rectangle $\mathcal{R}$ (see (5.6)) is an invariant region also for (5.1), since, by Theorem 5.1, it is invariant relative to underlying dynamical system (5.2).

Moreover, as proved in Theorem 4.1, there exists $\bar{t} > 0$ such that, for $t > \bar{t}$, $(u(y,t), v(y,t)) \in \mathcal{R}$. For this reason, we restrict our investigations to this region. In particular, for $t > \bar{t}$,

$$\begin{aligned}\frac{\partial H}{\partial t} &= \frac{m_1}{m_1+u^*}\frac{u-u^*}{u}\frac{\partial u}{\partial t} + c_1\frac{v-v^*}{v}\frac{\partial v}{\partial t}\\ &= \frac{m_1}{m_1+u^*}\frac{u-u^*}{u}\left(d_1\Delta u + u\left(a-u-\frac{c_1 v}{u+m_1}\right)\right)\\ &+ c_1\frac{v-v^*}{v}\left(d_2\Delta v + v\left(\frac{u}{u+m_1}-b_1-v\right)\right).\end{aligned}$$

Hence, by using the Neumann boundary conditions,

$$\begin{aligned}V'(t) &= \frac{m_1 d_1}{m_1+u^*}\int_\Omega\left(1-\frac{u^*}{u}\right)\Delta u\,dy + c_1 d_2\int_\Omega\left(1-\frac{v^*}{v}\right)\Delta v\,dy + \int_\Omega A(y,t)\,dy\\ &= -\frac{m_1 d_1 u^*}{m_1+u^*}\int_\Omega\frac{|\nabla u|^2}{u^2}\,dy - c_1 d_2 v^*\int_\Omega\frac{|\nabla v|^2}{v^2}\,dy + \int_\Omega A(y,t)\,dy,\end{aligned} \tag{5.8}$$

where

$$A(y,t) = \left(\frac{u}{u+m_1}-\frac{u^*}{u^*+m_1}\right)((a-u)(u+m_1)-(a-u^*)(u^*+m_1)) - c_1(v-v^*)^2. \tag{5.9}$$

We claim that

$$\left(\frac{u}{u+m_1}-\frac{u^*}{u^*+m_1}\right)((a-u)(u+m_1)-(a-u^*)(u^*+m_1)) < 0. \tag{5.10}$$

In order to prove (5.10), we point out that, if $u(y,t) < u^*$, we have

$$\frac{u}{u+m_1}-\frac{u^*}{u^*+m_1} < 0 \text{ and } (a-u)(u+m_1)-(a-u^*)(u^*+m_1) > 0$$

while the opposite happens if $u(y,t) > u^*$. In fact, the function

$$x \geq 0 \mapsto \frac{x}{x+m_1}$$

is strictly increasing, and the function

$$x \geq 0 \mapsto (a - x)(x + m_1)$$

is strictly decreasing for $x \geq \dfrac{a - m_1}{2}$. Since (5.7) holds true, by Theorem 5.1, $u(y,t) \geq \frac{a-m_1}{2}$ for all $y \in \Omega_0$ and $t > \bar{t}$, so that (5.10) is verified.

We conclude that (see (5.9)),

$$\int_\Omega A(y,t)\, dy < 0.$$

Taking this and (5.8) into account, we have that $V'(t) < 0$ and this completes the proof (see [14]). □

Remark 5.1. *Condition* (5.7) *in Theorem 5.2 is superfluous whenever* $m_1 \geq a$.

Going back to the diffusive predator–prey system (1.2), we want to answer some biological questions. Under what conditions would only one species of predators survive? How to determine the limiting behavior of the surviving predator and its prey?

The answer to the first question is given by the next theorem, that is a direct consequence of (4.4).

Theorem 5.3. *Let*

$$\frac{a}{a + m_2} < b_2. \tag{5.11}$$

Then any positive solution $(u(y,t), v(y,t), w(y,t))$ *to* (1.2) *satisfies*

$$\lim_{t \to +\infty} w(y,t) = 0 \text{ uniformly with respect to } y \in \Omega.$$

To analyze the local stability of $(u^*, v^*, 0)$, we make use of the linearized stability technique.

Theorem 5.4. *Assume that* (5.11) *holds true. If, in addition,*

$$u^* \geq \frac{a - m_1}{2}, \tag{5.12}$$

then $(u^*, v^*, 0)$ *is an asymptotically stable solution to system* (1.2).

Proof. Let us rewrite system (1.2) in vectorial form as

$$\frac{\partial z}{\partial t} = D \Delta z + F(z),$$

where

$$z = \begin{pmatrix} u \\ v \\ w \end{pmatrix}, \ D = \begin{pmatrix} d_1 & 0 & 0 \\ 0 & d_2 & 0 \\ 0 & 0 & d_3 \end{pmatrix}, \ F(z) = \begin{pmatrix} u\left(a - u - \dfrac{c_1 v}{u + m_1} - \dfrac{c_2 w}{u + m_2}\right) \\ v\left(\dfrac{u}{u + m_1} - b_1 - v\right) \\ w\left(\dfrac{u}{u + m_2} - b_2 - w\right) \end{pmatrix}.$$

It is well known (see [7]) that the solution $(u^*, v^*, 0)$ is asymptotically stable for (1.2) if $z = 0$ is asymptotically stable for the linearized system

$$\frac{\partial z}{\partial t} = D\Delta z + Az, \tag{5.13}$$

where $A = J(u^*, v^*, 0)$ and $J(u^*, v^*, 0)$ denotes the Jacobian matrix of F at $(u^*, v^*, 0)$.

Since

$$\begin{cases} (a - u^*)(u^* + m_1) = c_1 v^* \\ \dfrac{u^*}{u^* + m_1} = b_1 + v^*, \end{cases}$$

we obtain

$$A = \begin{pmatrix} \dfrac{u^*}{u^* + m_1}\left((a - m_1) - 2u^*\right) & -\dfrac{c_1 u^*}{u^* + m_1} & -\dfrac{c_2 u^*}{u^* + m_2} \\ \dfrac{m_1 v^*}{(u^* + m_1)^2} & -v^* & 0 \\ 0 & 0 & \dfrac{u^*}{u^* + m_2} - b_2 \end{pmatrix}.$$

The zero solution is (globally) asymptotically stable for (5.13) if, for every $n \in \mathbb{N}$, the eigenvalues of matrix $A - \lambda_n D$ have negative real parts, where $0 = \lambda_0 < \lambda_1 < \ldots < \lambda_n < \ldots$ are the eigenvalues of $(-\Delta)$ subject to Neumann boundary conditions (see [7]).

We notice that

$$A - \lambda_n D = \begin{pmatrix} \dfrac{u^*}{u^* + m_1}\left((a - m_1) - 2u^*\right) - \lambda_n d_1 & -\dfrac{c_1 u^*}{u^* + m_1} & -\dfrac{c_2 u^*}{u^* + m_2} \\ \dfrac{m_1 v^*}{(u^* + m_1)^2} & -v^* - \lambda_n d_2 & 0 \\ 0 & 0 & \dfrac{u^*}{u^* + m_2} - b_2 - \lambda_n d_3 \end{pmatrix},$$

and its eigenvalues are $\frac{u^*}{u^* + m_2} - b_2 - \lambda_n d_3$ and the eigenvalues of the matrix

$$B_n = \begin{pmatrix} \dfrac{u^*}{u^* + m_1}\left((a - m_1) - 2u^*\right) - \lambda_n d_1 & -\dfrac{c_1 u^*}{u^* + m_1} \\ \dfrac{m_1 v^*}{(u^* + m_1)^2} & -v^* - \lambda_n d_2 \end{pmatrix}.$$

Using (5.11), one gets $\dfrac{u^*}{u^* + m_2} - b_2 - \lambda_n d_3 < 0$. In addition, under assumption (5.12), B_n has negative trace and its determinant

$$\lambda_n^2 d_1 d_2 + \lambda_n \left(d_1 v^* + \frac{d_2 u^*}{u^* + m_1}\left(2u^* - (a - m_1)\right)\right) + \frac{c_1 m_1 u^* v^*}{(u^* + m_1)^3} + \frac{u^* v^* (2u^* - (a - m_1)}{(u^* + m_1)} > 0,$$

so that matrix B_n has eigenvalues with negative real part, and this complete the proof. $\square$

Under assumption (5.11), regarding w as a known function, the system for the components u and v admits as associated limiting system just (5.1). This will be the main argument in next theorem.

Theorem 5.5. *Assume that* (5.4)*,* (5.5)*,* (5.7) *and* (5.11) *hold. Then, for any* $(u(y,t), v(y,t), w(y,t))$ *positive solution to* (1.2)*,*

$$\lim_{t\to+\infty} |u(y,t) - u^*| = \lim_{t\to+\infty} |v(y,t) - v^*| = 0$$

and

$$\lim_{t\to+\infty} w(y,t) = 0$$

uniformly with respect to $y \in \Omega$*.*

Proof. By Theorem 5.3, $w(y,t)$ vanishes at infinity uniformly with respect to $y \in \Omega$. As a consequence, the Neumann problem

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1 \Delta u + u\left(a - u - \dfrac{c_1 v}{u+m_1}\right) - \dfrac{c_2 w u}{u+m_2} \\[2ex] \dfrac{\partial v}{\partial t} = d_2 \Delta v + v\left(\dfrac{u}{u+m_1} - b_1 - v\right) \\[2ex] \dfrac{\partial u}{\partial \mathbf{n}} \mid_{\partial\Omega} = 0 = \dfrac{\partial v}{\partial \mathbf{n}} \mid_{\partial\Omega}, \end{cases}$$

endowed with positive initial conditions, is asymptotically equivalent to (5.1). Hence, applying Therem 5.2, we get the assertion. □

Remarks 5.1.
1. Note that the stability hypothesis (5.12) *is less stringent than inequality* (5.7)*.*
2. Arguing as we have done throughout Section 5, it is easy to determine sufficient conditions that guarantee the extinction of predator v *and the persistence of* u *and* w*.*

6 Conclusion

The paper discusses a predator–prey model consisting of a single prey species u and two predator species v and w with functional response of Holling-type II. We assume that the prey and predators are spatially inhomogeneous and, taking the effect of diffusion into account, we consider a reaction–diffusion system endowed with homogeneous Neumann boundary conditions. This means that there is no population flux across the habitat boundary.

We focus our attention on seasonal changes of the environment taking time-periodic growth rates for the species and periodic diffusion coefficients. The habitat is an evolving domain $\Omega_t \subset \mathbb{R}^n$, $n \geq 1$, which is spatially isotropic and time-periodic with evolution function $\rho(t)$. Note that $\rho(t) = 1$ for fixed domains. This class of evolving domains is described in details in Section 2.

The above features lead to a model in the form

$$\begin{cases} \dfrac{\partial u}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}u = \dfrac{d_1(t)}{\rho^2(t)}\Delta u + uf(t,u,v,w) \\ \\ \dfrac{\partial v}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}v = \dfrac{d_2(t)}{\rho^2(t)}\Delta v + vg(t,u,v) \\ \\ \dfrac{\partial w}{\partial t} + n\dfrac{\rho'(t)}{\rho(t)}w = \dfrac{d_3(t)}{\rho^2(t)}\Delta w + wh(t,u,w), \end{cases}$$

on the domain Ω_t, where n is the spatial dimension. The explicit expression for the functions f, g, h is given in (2.3).

From a mathematical point of view, the effect of an evolving domain (of our type) in place of a fixed domain is concentrated in the link between $a(t)$ and $\gamma(t)$ (growth rate for the prey) and between $b_i(t)$ and $\delta_i(t)$ (growth rates for the predator population), as provided by (2.5).

Indeed, the "new" growth rates depend also on $\rho(t)$, its variation $\rho'(t)$ and the space dimension n. In spite of this relevant modification, the mean values of the growth rates do not change, as pointed out in (2.6).

As a consequence, the periodic solutions $u^*(t)$ and $v^*(t)$, found in Theorem 3.1, can be very different with respect to the case $\rho(t) = 1$, but all the results provided in Section 3, concerning the existence of $u^*(t)$ and $v^*(t)$ and their attractivity, through the presence of an invariant section $\Sigma(t)$, are not deeply influenced by the evolution in time of the domain.

Also, the extinction of the predator species $w(t)$ requires only a condition in average form (inequality (3.15)). On the contrary, hypotheses (3.11) and (4.3) for the global asymptotic stability of the solution $(u^*(t), v^*(t), 0)$ strongly depend on $\rho(t)$, $\rho'(t)$ and n since they have form of pointwise inequalities. Hence our main result, Theorem 4.2, is highly influenced by the domain fluctuation.

The statement of Theorem 4.2 also implies the following property: in system (2.3) the presence of factor $\frac{1}{\rho^2(t)}$ in the diffusion coefficients does not influence the uniform distribution of population, as t goes to infinity.

Finally, the results of Section 5 clearly show how the investigation of a predator–prey model of type (1.2) becomes more demanding when the environment and the habitat are time-dependent as supposed for system (1.3).

Future possible developments in the studies carried out in the present paper could involve different kinds of functional responses, such as the Buddington-DeAngelis functional response, that takes into account the competition between the two predator species. It would also be interesting to apply the methods developed in this work in the context of epidemiological models.

Acknowledgment. This work does not have any conflict of interests. There are no funders to report for this submission.

References

[1] D. Acheson, *Elementary Fluid Dynamics*, Oxford University Press, New York, 1990.

[2] S. Ahmad, M. R. Mohana Rao, *Theory of Ordinary Differential Equations*, Affiliated East–West Press Private Limited, New Delhi, 1999.

[3] S. Ahmad, I. M. Stamova (Eds.) *Lotka–Volterra and Related Systems. Recent Developments in Population Dynamics*, de Gruyter Series in Mathematics and Life Sciences **2**, Walter de Gruyter GmbH, Berlin/Boston, 2013.

[4] M. Cappelletti Montano, B. Lisena, *Diffusive Holling–Tanner predator–prey models in periodic environments*, Applied Math. Letters **87** (1) (2019), 42–49.

[5] M. Cappelletti Montano, B. Lisena, *Global dynamics in periodic Holling–Tanner models with impulses*, Dyn. Contin. Discrete Impuls. Syst. Ser. A Math. Anal. **26** (2019), 329–347.

[6] M. Cappelletti Montano, B. Lisena, *Diffusive Lotka–Volterra competition models on periodically evolving domains*, J. Math. Anal. Appl. **484** (1) (2020), art. 123675.

[7] R. Casten, C. J. Holland, *Stability properties of solutions to systems of reaction–diffusion equations*, SIAM J. Appl. Math. **33** (1977), 353–364.

[8] G. Dal Maso, I. Lucardesi, *The wave equation on domains with cracks growing on a prescribed path: existence, uniqueness, and continuous dependence on the data*, Appl. Math. Res. Express Vol. 2017 (1) (2017), 184–241.

[9] J. H. P. Dawes, M. O. Souza, *A derivation of Holling-type I, II and III functional responses in predator–prey systems*, J. Theor. Biol. **327** (2013), 11–22.

[10] M. Garrione, C. Rebelo, *Persistence in seasonally varying predator–prey systems via basic reproduction number*, Nonlinear Anal.: Real World Appl. **30** (2016), 73–98.

[11] L.-J. Hei, Y. Yu, *Non-constant positive steady state of one resource and two consumers model with diffusion*, J. Math. Anal. Appl. **339** (2008), 566–581.

[12] L. Hsiao, P. de Mottoni, *Persistence in reacting–diffusing systems: interaction of two predators and one prey*, Nonlinear Anal. **11** (8) (1987), 877–891.

[13] L. Hsiao, Y. Su, Z. P. Xin, *On the asymptotic behavior of solutions of a reacting–diffusing system: a two predators–one prey model*, SIAM J. Math. Anal. **18** (3) (1987), 647–669.

[14] S.-B. Hsu, *A survey for constructing Lyapunov functions for mathematical models in population biology*, Taiwanese J. Math. **9** (2) (2005), 151–173.

[15] S.-B. Hsu, T.-W. Hwang, Y. Kuang, *Rich dynamics of a ratio–dependent one–prey two–predators model*, J. Math. Biol. **43** (2001), no. 5, 377–396.

[16] D.-H. Jiang, Z.-C. Wang, *The diffusive logistic equation on periodically evolving domains*, J. Math. Anal. Appl. **458** (2018), 93–111.

[17] W. Ko, I. Ahn, *A diffusive one-prey and two-competing predator system with a ratio-dependent functional response: I, long time behavior and stability of equilibria*, J. Math. Anal. Appl. **397** (2013), 9–28.

[18] W. Ko, K. Ryu, *Analysis of diffusive two competing–prey and one-predator systems with Beddington–DeAngelis functional response*, Nonlinear Anal. **71** (2009), 4185–4202.

[19] B. Lisena, *Asymptotic behaviour in periodic three species predator–prey systems*, Ann. Mat. Pur. Appl. **186** (1) (2007), 85–98.

[20] B. Lisena, *Global stability of a periodic Holling–Tanner predator–prey model*, Math. Meth. Appl. Sci. **41** (2018), n. 9, 3270–3281.

[21] J. Llibre, D. Xiao, *Global dynamics of a Lotka–Volterra model with two predators competing for one prey*, SIAM J. Appl. Math. **74** (2) (2014), 434–453.

[22] J. López-Gómez, R. Ortega, A. Tineo, *The periodic predator–prey Lotka–Volterra model*, Adv. Diff. Eq. **1** (3) (1996), 403–423.

[23] P. Y. H. Pang, M. Wang, *Qualitative analysis of a ratio–dependent predator–prey system with diffusion*, Proc. R. Soc. Edinb. A **133** (2003), no. 4, 919–942.

[24] C. V. Pao, *On nonlinear reaction–diffusion systems*, J. Math. Anal. Appl. **87** (1982), 165–198.

[25] S. Petrovkii, H. Malchow, B.-L. Li, *An exact solution of a diffusive predator–prey system*, Proc. R. Soc. A (2005) **461**, 1029–1053.

[26] F. Rao, C. Castillo-Chavez, Y. Kang, *Dynamics of a diffusion reaction predator–prey model with delay in prey: Effects of delay and spatial components*, J. Math. Anal. Appl. **461** (2018), 1177–1214.

[27] C. Rebelo, C. Soresina, *Coexistence in seasonally varying predator–prey systems with Allee effect*, Nonlinear Anal.: Real World Appl. **55** (2020), art.103140.

[28] J. Smoller, *Shock Waves and Reaction–Diffusion Equations*, Springer–Verlag, New-York, 1983.

[29] T. V. Ton, N. T. Hieu, *Dynamics of species in a model with two predators and one prey*, Nonlinear Anal. **74** (2011), 4868–4881.

[30] C. Venkataraman, O. Lakkis, A. Madzvamuse, *Global existence for semilinear reaction–diffusion systems on evolving domains*, J. Math. Biol. **64** (2012), 41–67.

[31] Q. Wang, M. Fan, K. Wang, *Dynamics of a class of nonautonomous semi–ratio–dependent predator–prey systems with functional responses*, J. Math. Anal. Appl. **278** (2003), 443–471.