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A MATHEMATICAL ANALYSIS OF A PREDATOR–PREY SYSTEM IN A HIGHLY HETEROGENEOUS ENVIRONMENT

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Abstract. We are concerned with the mathematical analysis of a predator–prey system in heterogeneous domains. We first give a global existence result for the problem with spatially variable coefficients. For highly heterogeneous systems, using homogenization techniques we derive a simpler model with constant coefficients yielding the macroscopic dynamic of the predator–prey system. In this process, standard Lotka–Volterra functional responses to predation are preserved, while Holling type II responses are transformed into unusual nonlocal nonlinearities.

1. Introduction

In this paper we are concerned with the mathematical analysis of a predator-prey system in highly heterogeneous habitats or spatial domains.

When spatial structures are ignored our model reduces to a 2×2 system of ordinary differential equations featuring a natural exponential decay for the predator population at a rate $-a$ ($a > 0$), a logistic growth for the prey population with a natural growth rate $r > 0$ and a carrying capacity $K > 0$ and a Holling type II functional response to predation. Let $u = u(t)$ be the density of predators and $v = v(t)$ be the density of prey at time $t \geq 0$; then the predation rate reads $\frac{pv}{1+qv}$ with $\frac{1}{p}$ the time spent by a predator to catch a prey and $\frac{q}{p}$ the manipulation time, offering a saturation effect for large densities of prey when $q > 0$; see Rosenzweig and Mac-Arthur [18]. Last, e being the conversion rate from prey to predator, our model reads

$$\begin{cases} u' = -au + e\frac{pv}{1+qv}u, \\ v' = r(1 - \frac{v}{K})v - \frac{pv}{1+qv}u, \end{cases} \quad u(0) > 0,\ v(0) > 0. \tag{1.1}$$

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Note that for $q = 0$ one retrieves a standard Lotka–Volterra model with a logistic dynamic for prey when $K > 0$ and finite and an exponential growth in the limit $K = +\infty$. The analysis of these models is well documented; see Hsu *et al.* [7], [8], Hsu [9], Cheng [3], Lindstrom [14] and references in Murray [16].

For $q > 0$ and a finite K three outcomes are possible. Set $K^* = \frac{a}{ep-qa}$; then

- when either $ep-qa < 0$ or $ep-qa > 0$ but $K < K^*$, then the predator population goes extinct while the prey population goes back to its carrying capacity K;
- when $ep - qa > 0$ and $K^* < K < 2K^* + \frac{1}{q}$, then the predator population controls the prey population at density $v^* = K^*$ and settles at density $u^* = \frac{re(K-K^*)}{K(ep-qa)}$;
- when $ep - qa > 0$ and $2K^* + \frac{1}{q} < K$ the equilibrium (u^*, v^*) loses its stability; a unique and globally stable periodic solution exists, a Hopf bifurcation taking place at $K = 2K^* + \frac{1}{q}$.

For $q = 0$ and a finite K only the first two cases are possible with identical dynamics.

In the limiting case $K = +\infty$, when isolated from predators the prey population experiences an exponential growth at a rate $r > 0$. For $q > 0$ and $K = +\infty$ only two cases are possible, and predators cannot control the prey population: when $ep - qa < 0$ predators go extinct and prey resume their exponential growth while for $ep - qa > 0$ trajectories are unbounded. For $q = 0$ and $K = +\infty$ the equilibrium $(\frac{r}{p}, \frac{a}{pe})$ is a center.

What we are interested in is to assess the impact of spatial heterogeneities in such a predator–prey system. Hence we consider a spatial and bounded domain Ω in $\mathbb{R}^n$, $n = 1, 2$ or 3 with boundary $\partial\Omega$. Our state variables (u, v) are the space- and time-dependent densities $(u(x,t), v(x,t),\ x \in \Omega,\ t > 0,$ of predators and prey from which we compute the time-dependent densities upon integrating over the spatial domain Ω

$$\int_\Omega u(x,t)dx,\ \ \int_\Omega v(x,t)dx,\ t > 0.$$

We assume the spatial habitat to be sufficiently heterogeneous to locally modify the dynamics of both populations. We are led to consider spatially dependent decay rates $a(x)$ for predators, growth rates $r(x)$ and carrying capacities $K(x)$ for prey. Some subregions of Ω being possibly hostile to predators or favorable to prey the predation rate may also be locally modified yielding a spatially dependent predation rate $\frac{p(x)v}{1+q(x)v}$ as well as a spatially dependent conversion rate $e(x)$.

Next both populations are allowed to disperse in their habitat. We assume that population fluxes obey a Fickian law and are proportional to their respective gradients, say $-d_u(x)\nabla u$ for predators and $-d_v(x)\nabla v$ for prey, where diffusivities $d_u(x) > 0$ and $d_v(x) > 0$ are also spatially dependent and continuous on $\overline{\Omega}$. Then, proceeding as in Murray [16] the dynamics of the predator–prey system is governed by the system of semilinear equations

$$\begin{cases} \dfrac{\partial u}{\partial t} - \operatorname{div}(d_u(x)\nabla u) = -a(x)u + e(x)\dfrac{p(x)v}{1+q(x)v}u, \\ \dfrac{\partial v}{\partial t} - \operatorname{div}(d_v(x)\nabla v) = r(x)(1 - \dfrac{v}{K(x)})v - \dfrac{p(x)v}{1+q(x)v}u, \end{cases} \quad x \in \Omega,\ t > 0. \tag{1.2}$$

We impose no flux boundary conditions on the boundary of Ω

$$d_u(x)\nabla u(x,t)\cdot\eta(x) = d_v(x)\nabla v(x,t)\cdot\eta(x) = 0,\ x \in \partial\Omega,\ t > 0, \tag{1.3}$$

where η is the outward normal to Ω on $\partial\Omega$. Last an initial distribution is assumed at $t = 0$

$$u(x,0) = u_0(x) \geq 0,\ v(x,0) = v_0(x) \geq 0,\ x \in \Omega. \tag{1.4}$$

See also Namba [17], Jansen [11] and Michalski *et al.* [15]. At this level of generality little can be said about the dynamic of the system. From a mathematical point of view (1.2–4) is well posed in the setting of nonnegative and continuous functions (see the proof of Theorem 1 below).

Numerical experiments were performed in Heiser [6] in a one-dimensional environment $\Omega = (0,1)$, $q(x) > 0$ and for simple heterogeneities. As a typical test, $(0,1)$ was split into three subregions with three sets of constant parameters chosen so that the underlying system of ordinary differential equations (1.1) is exhibiting the three different behaviors above depicted; it was generally observed that for small diffusion rates these dynamics were still that of (1.2–4) on the corresponding subdomain with sharp transitions on their common boundaries, while large diffusion rates smoothed out spatial heterogeneities (Ei and Mimura [4]). Next we increased the number of subregions and observed heterogeneous dynamics. We were eventually led to reproduce periodically the original pattern of three subregions with three different behaviors; a spatially homogeneous dynamic emerged as the period was decreasing to 0.

At some level of organization or scaling spatial habitats and heterogeneities can exhibit periodic structures, e.g. from densely inhabited urban areas to sparsely anthropized rural areas or fully isolated ones, trees in an orchard or in a forest. Then it is possible to assume that the domain Ω under consideration is made of more or less identical subdomains Ω_l $(1 \leq l \leq L)$, each of the Ω_l having a heterogeneous structure reproducing that of a basic heterogeneous patch Ω^b. When the number of patches gets large Ω offers highly heterogeneous spatial structures and system (1.2–4) has rapidly oscillating coefficients so that even numerical simulations are not easy to perform; hence the dynamic of the predator–prey system is difficult to analyze in this setting. Similar problems arise in designing composite materials in engineering sciences; homogenization techniques provide useful tools for deriving from a system of partial differential equations with rapidly oscillating coefficients such as (1.2–4) a new system with constant coefficients, or a homogenized system, from which the macroscopic behavior can be analyzed; see Bensoussan *et al.* [2], Jikov *et al.* [12] and their references.

In this work we apply these homogenization techniques to (1.2–4) and derive a simpler homogenized system of partial differential equations; see Subsections 3, 4.2 and 4.3.

It turns out that when $q \equiv 0$ the homogenized system is still a standard Lotka–Volterra system whose coefficients are deduced from the original ones by averaging them (or combination of); see Subsections 3 and 4.4. This suggests that such models are stable with respect to highly spatially heterogeneous environments.

When $q \neq 0$ one finds a homogenized system featuring a nonlocal predation rate; see system (3.5). Strictly speaking the original Holling type II functional response to predation is not preserved in highly spatially heterogeneous environments. However, in the case of a spatially independent conversion rate e from prey to predators, the asymptotic behavior of the homogenized system is similar to the asymptotic behavior of the underlying system with no diffusion, and this asymptotic behavior resembles the asymptotic behavior of a prey–predator system with a Holling type II functional response; see Subsection 4.5.

Notation and basic assumptions are listed in Section 2. In Section 3 we state and discuss our main results. Proofs are supplied in Section 4.

2. Notation and assumptions

Let Ω be a nonempty, bounded, open subset of $\mathbb{R}^n$ with a smooth boundary $\partial\Omega$ so that locally Ω lies on one side of $\partial\Omega$; η is the unit outward normal to Ω on $\partial\Omega$. Next, $|\Omega|$ is the n-dimensional Lebesgue measure of Ω. Last, for

$1 \leq p \leq +\infty$, $\|\|_{p,\Omega}$ is the usual norm in $L^p(\Omega)$ and $\|\|_{p,Q_T}$ is the usual norm in $L^p(Q_T)$ for $Q_T = \Omega \times (0,T)$.

Let $H^1(\Omega)$ be the usual Sobolev space of first order over Ω; we denote by $\langle \cdot, \cdot \rangle$ the duality pairing between $H^1(\Omega)$ and its dual space $\left(H^1(\Omega)\right)^*$. $L^2(U;H)$ is the Hilbert space of those measurable and square-integrable functions $w : U \to H$, and

$$W = \{w \in L^2(0,T;H^1(\Omega)) : \partial_t w \in L^2(0,T;(H^1(\Omega))^*)\}.$$

Let $e_1, \ldots, e_n$ be n independent vectors of $\mathbb{R}^n$; then we may form a parallelogram $\mathbf{Y}$

$$\mathbf{Y} = \Big\{ \sum_{i=1}^{n} t_i \, e_i : 0 < t_1, \ldots, t_n < 1 \Big\}$$

called a periodic cell. A function $f \in L^1_{loc}(\mathbb{R}^n)$ is said to be $\mathbf{Y}$*–periodic* if $f(x) = f(x + e_i)$ for almost all $x \in \mathbb{R}^n$, for all $i = 1, \ldots, n$; we denote by $\mathcal{M}(f)$ the mean value of f on $\mathbf{Y}$,

$$\mathcal{M}(f) = \frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} f(y)dy.$$

Given any $\mathbf{Y}$-periodic function $f : \mathbb{R}^n \to \mathbb{R}$, set $f^\varepsilon(x) = f(\frac{x}{\varepsilon})$, which is an $\varepsilon\mathbf{Y}$*–periodic* function; ε is the period of the structure in all directions.

Definition 1. Let $S_\#$ be the set of all functions $f : \mathbb{R}^n \to \mathbb{R}$ satisfying the following properties:

(i) $f \in L^\infty(\mathbb{R}^n)$; we note $\bar{f} = \|f\|_{\infty,\Omega}$;
(ii) f is $\mathbf{Y}$-periodic;
(iii) there exists a constant $\underline{f} > 0$ such that $\underline{f} < f(y)$ for $y \in \mathbb{R}^n$.

3. Main results

A simple mathematical formulation of a predator–prey system with a Holling type II functional response and spatially periodic coefficients of period $\varepsilon\mathbf{Y}$ in the variable x on $Q_\infty = \Omega \times (0,\infty)$ is

$$\begin{cases} \dfrac{\partial u_\varepsilon}{\partial t} - div(d_u^\varepsilon(x)\, \nabla u_\varepsilon) = -a^\varepsilon(x)\, u_\varepsilon + e^\varepsilon(x)\, \dfrac{p^\varepsilon(x)\, v_\varepsilon}{1 + q^\varepsilon(x)\, v_\varepsilon}\, u_\varepsilon\,, \\ \dfrac{\partial v_\varepsilon}{\partial t} - div(d_v^\varepsilon(x)\, \nabla v_\varepsilon) = r^\varepsilon(x)\, v_\varepsilon(1 - \dfrac{v_\varepsilon}{K^\varepsilon(x)}) - \dfrac{p^\varepsilon(x)\, v_\varepsilon}{1 + q^\varepsilon(x)\, v_\varepsilon}\, u_\varepsilon\,, \end{cases} \tag{3.1}$$

together with homogeneous no-flux boundary conditions on $\partial\Omega \times (0, \infty)$

$$d_u^\varepsilon(x)\frac{\partial u_\varepsilon}{\partial \eta}(x,t) = 0 \ , \ d_v^\varepsilon(x)\frac{\partial v_\varepsilon}{\partial \eta}(x,t) = 0 \ , \ (x,t) \in \partial\Omega \times (0,\infty), \tag{3.2}$$

where η is the unit outward normal to Ω on $\partial\Omega$ and we have nonnegative initial data at $t = 0$

$$\begin{cases} u_\varepsilon(x,0) &= u_0(x) \ , x \in \Omega, \\ v_\varepsilon(x,0) &= v_0(x) \ , x \in \Omega. \end{cases} \tag{3.3}$$

We first give a global existence and uniqueness result for (3.1), (3.2), and (3.3) referred to as problem $(\mathcal{P}_\varepsilon)$; a proof is supplied in Subsection 4.1.

Theorem 1. *Let $d_u, d_v, a, e, p, r \in S_\#$, and assume either $q \in S_\#$ or $q \equiv 0$. For each nonnegative and continuous initial data (u_0, v_0) on $\bar\Omega$, there exists a unique nonnegative and classical solution $(u_\varepsilon, v_\varepsilon)$ of (3.1–3) on $\bar\Omega \times (0,\infty)$, and*

$$\begin{cases} 0 \le \|u_\varepsilon(\cdot,t)\|_{\infty,\Omega}, \|v_\varepsilon(\cdot,t)\|_{\infty,\Omega} \le C_1(u_0,v_0) < +\infty, \ t > 0, \\ \qquad\qquad \text{when } K \in S_\#, \\ 0 \le \|u_\varepsilon(\cdot,t)\|_{\infty,\Omega}, \|v_\varepsilon(\cdot,t)\|_{\infty,\Omega} \le C_2(T,u_0,v_0) < +\infty, \ 0 < t < T, \\ \qquad\qquad \text{when } K = +\infty, \end{cases} \tag{3.4}$$

where $C_1(u_0,v_0)$ and $C_2(T,u_0,v_0)$ are independent of ε for $0 < \varepsilon \le 1$.

The limit as $\varepsilon \to 0^+$ of $(u_\varepsilon, v_\varepsilon)_{0<\varepsilon\le 1}$ is a solution of a somewhat unusual reaction–diffusion system which we now introduce. Set

$$\mathcal{A} = \mathcal{M}(a), \ \mathcal{R} = \mathcal{M}(r), \ \mathcal{K} = \mathcal{M}(r)\left[\mathcal{M}\left(\frac{r}{K}\right)\right]^{-1}.$$

Let D_u and D_v be symmetric positive-definite matrices in $\mathbb{R}^n$. Let $(\mathcal{P})$ be the following reaction–diffusion system with constant coefficients on Q_∞

$$\begin{cases} \dfrac{\partial u}{\partial t} - div(D_u \nabla u) = -\mathcal{A}\, u + \dfrac{1}{|\mathbf{Y}|}\displaystyle\int_{\mathbf{Y}} \frac{e(y)\, p(y)\, v(x,t)}{1+q(y)\, v(x,t)}\, dy\, u(x,t), \\ \dfrac{\partial v}{\partial t} - div(D_v \nabla v) = \mathcal{R}\, v\,(1 - \dfrac{1}{\mathcal{K}}\, v) - \dfrac{1}{|\mathbf{Y}|}\displaystyle\int_{\mathbf{Y}} \frac{p(y)\, u(x,t)}{1+q(y)\, v(x,t)}\, dy\, v(x,t)\,, \end{cases} \tag{3.5}$$

together with homogeneous no-flux boundary conditions on $\partial\Omega \times (0, \infty)$

$$D_u \nabla u \cdot \eta(x,t) = D_v \nabla v \cdot \eta(x,t) = 0 \ , \ (x,t) \in \partial\Omega \times (0,T), \tag{3.6}$$

and the initial data in (3.3).

In Subsection 4.2 we shall prove

Theorem 2. *Let a, e, p and r lie in $S_\#$ and either $K \in S_\#$ or $K = +\infty$. Assume either $q \in S_\#$ or $q \equiv 0$. Let D_u and D_v be symmetric positive-definite matrices.*

For each nonnegative and continuous initial data (u_0, v_0) on $\bar{\Omega}$ there is a unique classical solution (u, v) of problem $(\mathcal{P})$ satisfying $0 \leq u(x,t), v(x,t) \leq C_3(u_0, v_0)$, $x \in \Omega$, $t > 0$ when either $K \in S_\#$ or $K = +\infty$ and $q \equiv 0$, and satisfying $0 \leq u(x,t), v(x,t) \leq C_4(T, u_0, v_0)$, $x \in \Omega$, $0 < t < T$ when $K = +\infty$ and $q \in S_\#$.

We now are ready to describe the limiting behavior of $(u_\varepsilon, v_\varepsilon)_{0<\varepsilon\leq 1}$ as $\varepsilon \to 0^+$.

Theorem 3. *Let d_u, d_v, a, e, p and r lie in $S_\#$ and either $K \in S_\#$ or $K = +\infty$. Assume either $q \in S_\#$ or $q \equiv 0$. There exist symmetric positive-definite matrices D_u and D_v such that the solution $(u_\varepsilon, v_\varepsilon)$ of problem $(\mathcal{P}^\varepsilon)$ satisfies the following: for each fixed $T > 0$*

$$\begin{cases} u_\varepsilon \to u \ \ \textit{strongly in} \ \ L^2(\Omega \times (0,T)), \\ v_\varepsilon \to v \ \ \textit{strongly in} \ \ L^2(\Omega \times (0,T)), \end{cases} \quad \textit{as } \varepsilon \to 0^+, \tag{3.7}$$

where (u, v) is the solution of the corresponding problem $(\mathcal{P})$.

A proof is found in Section 4.3.

Remark. The homogenization process works for any reaction–diffusion system for which uniform bounds independent of ε can be obtained, yielding compactness in L^2 or in some Hölder space.

Homogenized operators. We point out that computation of the homogenized diffusion operators is complicated. However an algorithm using asymptotic expansions appears in [2] and [12].

In the one-dimensional case some simplifications occur, and one has

$$D_w = \Big[\mathcal{M}\Big(\frac{1}{d_w}\Big)\Big]^{-1} w = u, v.$$

In the two-dimensional case one must first compute a set of auxiliary functions, namely $\chi_l^{(w)}$, $\mathbf{Y}$ periodic members of $H^1(\mathbf{Y})$ and solutions of

$$-\operatorname{div}(d_w(y)\nabla\chi_l^{(w)}) = -\frac{\partial d_w(y)}{\partial y_l}, \ w = u, v, \ l = 1, 2.$$

These four functions are uniquely defined up to a constant. The entries of D_w are

$$D_{w,il} = \begin{cases} \mathcal{M}(d_w) + \mathcal{M}(d_w \frac{\partial \chi_i^{(w)}}{\partial y_i}), & \text{for } l = i, \\ \mathcal{M}(d_w \frac{\partial \chi_l^{(w)}}{\partial y_i}), & \text{for } l \neq i, \end{cases}$$

for $w = u, v$; hence these matrices may not be diagonal, but they are symmetric.

In the case of a two-dimensional stratified environment diffusivities and other coefficients are periodic with respect to one of the two coordinates and independent of the second one, say $d_w(y) = d_w(y_1)$, $w = u, v$. Then D_u and D_v are diagonal matrices, and for $w = u, v$

$$D_{w,11} = \Big[\mathcal{M}\Big(\frac{1}{d_w}\Big)\Big]^{-1},\ D_{w,22} = \mathcal{M}(d_w).$$

Large-time behavior. When $q = 0$ the homogenized system (3.5) simplifies and reads

$$\begin{cases} \dfrac{\partial u}{\partial t} - div(D_u \nabla u) = -\mathcal{M}(a)\, u + \mathcal{M}(ep) vu, \\ \dfrac{\partial v}{\partial t} - div(D_v \nabla v) = \mathcal{M}(r)\, v\, (1 - \dfrac{1}{\mathcal{K}}\, v) - \mathcal{M}(p) vu, \end{cases} \tag{3.8}$$

with the initial and boundary conditions from (3.3) and (3.6). This is a standard Lotka–Volterra model with constant coefficients derived from the original spatially heterogeneous and periodic one upon averaging its coefficients. The analysis of the large-time behavior of (3.8) follows from results in Alikakos [1] and is similar to the dynamic of the underlying system of ordinary differential equations

$$\begin{cases} \dfrac{du}{dt} = -\mathcal{M}(a)\, u + \mathcal{M}(ep) vu, \\ \dfrac{dv}{dt} = \mathcal{M}(r)\, v\, (1 - \dfrac{1}{\mathcal{K}}\, v) - \mathcal{M}(p) vu. \end{cases} \tag{3.9}$$

In Subsection 4.4 one shows

Theorem 4. *Assume $\mathcal{K} > 0$. Let (u, v) be the solution of* (3.8), (3.3) *and* (3.6). *Then $\mathcal{M}(a) > \mathcal{M}(ep)\mathcal{K}$ implies $u(\,,t) \to 0$, $v(\,,t) \to \mathcal{K}$; $\mathcal{M}(a) < \mathcal{M}(ep)\mathcal{K}$ implies $u(\,,t) \to \frac{\mathcal{M}(r)}{\mathcal{M}(p)}(1 - \frac{\mathcal{M}(a)}{\mathcal{M}(ep)\mathcal{K}})$, $v(\,,t) \to \frac{\mathcal{M}(a)}{\mathcal{M}(ep)}$, as $t \to +\infty$.*

Assume $\mathcal{K} = +\infty$. Then, for each initial data (u_0, v_0) the solution of (3.8), (3.3) *and* (3.6) *is converging towards a periodic solution of* (3.9).

This result suggests that, to some extent, standard Lotka–Volterra predator–prey models are stable with respect to highly spatially heterogeneous and periodic environments: (3.8) is built upon averaging periodic demographical and predation rates, and the large-time behavior is derived along the same rules.

When $q \neq 0$ the homogenized system (3.5) is featuring a nonlocal predation rate, so the original Holling type II functional response is not preserved in highly spatially heterogeneous environments. However the asymptotic behavior is similar to the one obtained in the case of a Holling type II functional response with constant demographical and predation rates. In Subsection 4.5 one shows that under some hypotheses, the asymptotic behavior of (3.5) is similar to the asymptotic behavior of the underlying system of ordinary differential equations

$$\begin{cases} \dfrac{du}{dt} = -\mathcal{A}\, u + \dfrac{1}{|\mathbf{Y}|} \displaystyle\int_{\mathbf{Y}} \dfrac{e(y)\, p(y)\, v(t)}{1 + q(y)\, v(t)}\, dy\, u(t), \\ \dfrac{dv}{dt} = \mathcal{R}\, v\, (1 - \dfrac{1}{\mathcal{K}}\, v) - \dfrac{1}{|\mathbf{Y}|} \displaystyle\int_{\mathbf{Y}} \dfrac{p(y)\, u(t)}{1 + q(y)\, v(t)}\, dy\, v(t)\ . \end{cases} \tag{3.10}$$

Set $\Phi(\lambda) = \frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \dfrac{e(y)p(y)\,\lambda}{1 + q(y)\,\lambda}\, dy - \mathcal{A}$, $\lambda \geq 0$; then $\lambda \to \Phi(\lambda)$ is increasing with $\Phi(0) = -\mathcal{A}$. Hence there exists a unique $\mathcal{K}^* > 0$, a solution of $\Phi(\lambda) = 0$, or equivalently

$$\frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \frac{e(y)p(y)\,\lambda}{1 + q(y)\,\lambda}\, dy\ = \mathcal{A}$$

if and only if $\lim_{\lambda \to +\infty} \Phi(\lambda) > 0$, say $\mathcal{M}(\dfrac{ep}{q}) > \mathcal{A}$. Set

$$u^* = \frac{\mathcal{R}(1 - \frac{\mathcal{K}^*}{\mathcal{K}})}{\frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \frac{p(y)}{1 + q(y)\,\mathcal{K}^*}\, dy}.$$

In Subsection 4.5.1, we prove the following local asymptotic stability result for (3.10).

Theorem 5. *For each positive initial data* (u_0, v_0)*,* (3.10) *has a unique positive solution* $(u(t), v(t))$ *defined on* $(0, +\infty)$*. Next we have the following:*

(i) $(0, 0)$ *is a saddle point.*

(ii) *If* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *and* $\mathcal{K}^* < \mathcal{K}$*, then* $(0, \mathcal{K})$ *is a saddle point.*

(iii) *If* $\mathcal{M}(\frac{ep}{q}) < \mathcal{A}$ *or* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *but* $\mathcal{K} < \mathcal{K}^*$*, then* $(0, \mathcal{K})$ *is locally stable.*

(iv) *If* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *but* $\mathcal{K}^* < \mathcal{K} < \mathcal{K}^* + \dfrac{\int_{\mathbf{Y}} \frac{p(y)}{(1 + q(y)\,\mathcal{K}^*)}\, dy}{\int_{\mathbf{Y}} \frac{p(y)\, q(y)}{(1 + q(y)\,\mathcal{K}^*)^2}\, dy}$*, then* $(u^*, \mathcal{K}^*)$ *is a nontrivial locally stable admissible steady state.*

We have the following result of global stability for (3.10).

Theorem 6. *Let* (u, v) *be a solution of* (3.10) *with positive initial data. Then*

(i) *When either* $\mathcal{M}(\frac{ep}{q}) < \mathcal{A}$ *or* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$, $\mathcal{K} < \mathcal{K}^*$ *and* $|v_0| < \mathcal{K}$, *then*

$$u(t) \to 0,\ v(t) \to \mathcal{K},\ \ as\ \ t \to +\infty.$$

(ii) *When* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *and* $\mathcal{K}^* < \mathcal{K} < \mathcal{K}^* + \frac{\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\,dy\mathcal{K}^*}{\mathcal{M}(p)-\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\,dy}$, *then*

$$u(t) \to u^*, v(t) \to \mathcal{K}^*\ as\ \ t \to +\infty.$$

We are now ready to analyze the asymptotic behavior of (3.5)

Theorem 7. *Let* (u, v) *be the solution of* (3.5). *Then we have the following:*

(i) *When either* $\mathcal{M}(\frac{ep}{q}) < \mathcal{A}$ *or* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$, $\mathcal{K} < \mathcal{K}^*$ *and* $\|v_0\|_{\infty,\Omega} < \mathcal{K}$, *then the homogenized predator population goes extinct while the homogenized prey population goes to its carrying capacity* $\mathcal{K}$; *i.e., as* $t \to +\infty$, $u(\,,t) \to 0$ *and* $v(\,,t) \to \mathcal{K}$.

(ii) *Assume that the conversion rate from prey to predator* $e(x)$ *is a spatially independent constant. When* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *and* $\mathcal{K}^* < \mathcal{K} < \mathcal{K}^* + \frac{\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\,dy\mathcal{K}^*}{\mathcal{M}(p)-\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\,dy}$, *then the homogenized predator population controls the homogenized prey population at density* $v^* = \mathcal{K}^*$ *and settles at density* u^*; *i.e., as* $t \to +\infty$, $u(\,,t) \to u^*$ *and* $v(\,,t) \to \mathcal{K}^*$.

4. PROOFS

4.1. **A proof of Theorem 1.** The existence of a local unique nonnegative solution for problem $(\mathcal{P}_\varepsilon)$ on $(0, T_{max})$ is derived from classical arguments: Ladyzhenskaya [13] and Smoller [19].

Now, regardless of whether K is a member of $S_\#$ or $K = +\infty$, the right-hand side of the equation for v_ε in (3.1) is bounded from above by $\bar{r}v_\varepsilon$ so that $0 \le v_\varepsilon(x,t) \le \|v_0\|_{\infty,\Omega} \exp(\bar{r}t)$ for $0 < t < T_{max}$. Substituting this in (3.1) the right-hand side of the equation for u_ε is bounded from above by $(-\bar{a} + m(t))\, u_\varepsilon$ for some nondecreasing and continuous function m over $[0, +\infty)$ independent of ε for $0 < \varepsilon \le 1$; hence $0 \le u_\varepsilon(x,t) \le \|u_0\|_{\infty,\Omega}\, M(t)$ for $0 < t < T_{max}$, where M is a nondecreasing and continuous function over $[0, +\infty)$ independent of ε for $0 < \varepsilon \le 1$. Global existence on $\Omega \times (0, +\infty)$, with for each $T > 0$ $L^\infty(Q_T)$ bounds independent of $0 < \varepsilon \le 1$, follows.

Let us now assume that $K \in S_\#$ and derive time-independent L^∞ bounds. From the assumption $d_v \in S_\#$ one has $0 < \underline{\mathrm{d}}_v \le d_v^\varepsilon(x) \le \bar{d}_v,\ x \in \Omega$. By nonnegativity one finds

$$\frac{\partial v_\varepsilon}{\partial t} - div(d_v^\varepsilon(x)\, \nabla v_\varepsilon) \le \bar{r}\, v_\varepsilon - \frac{\underline{\mathrm{r}}}{\bar{K}}\, {v_\varepsilon}^2 \tag{4.1}$$

on $\Omega \times (0, T_{max})$; then a comparison theorem allows us to deduce from (4.1)

$$\sup_{0\le t\le T_{max}} \|v_\varepsilon(\cdot,t)\|_{\infty,\Omega} \le \max(\frac{\bar{K}\,\bar{r}}{\underline{\mathrm{r}}}, \|v_0\|_{\infty,\Omega}). \tag{4.2}$$

Lemma 1. *For* $0 \le t \le T_{\max}$

$$\|u_\varepsilon(\cdot,t)\|_{1,\Omega} \;\le\; \max\{\frac{\bar{r}\,\bar{e}}{\underline{a}}\,|\Omega|\,\max\{\|v_0\|_{\infty,\Omega}, \frac{\bar{K}\,\bar{r}}{\underline{r}}\};\|u_0+\bar{e}\,v_0\|_{1,\Omega}\}. \tag{4.3}$$

Proof. Integrating $u_\varepsilon + \bar{e}v_\varepsilon$ over Ω leads to

$$\begin{aligned}&\frac{d}{dt}\int_\Omega [u_\varepsilon(x,t)+\bar{e}\,v_\varepsilon(x,t)]dx\\ &\le -\int_\Omega a^\varepsilon(x)u_\varepsilon(x,t)\,dx + \int_\Omega r^\varepsilon(x)\bar{e}v_\varepsilon(x,t)\,dx - \int_\Omega \frac{r^\varepsilon(x)\bar{e}}{K^\varepsilon(x)}v_\varepsilon^2(x,t)\,dx.\end{aligned}$$

Set

$$G_\varepsilon(t) = \int_\Omega [u_\varepsilon(x,t)+\bar{e}\,v_\varepsilon(x,t)]dx.$$

Then, either $G_\varepsilon^{'}(t) \le 0$ for $0 \le t \le T_{\max}$, which implies

$$\int_\Omega [u_\varepsilon(x,t)+\bar{e}\,v_\varepsilon(x,t)]dx \;\le\; \int_\Omega [u_0(x)+\bar{e}\,v_0(x)]dx,$$

or there exists a $t_0 > 0$ such that $G^{'}(t_0) > 0$ and at $t = t_0$ one gets

$$\underline{\mathrm{a}}\int_\Omega u_\varepsilon(x,t_0)dx \;\le\; \bar{r}\,\bar{e}\int_\Omega v_\varepsilon(x,t_0)dx.$$

Together with (4.2) these inequalities complete the proof of Lemma 1.

Going back to the right-hand side of (3.1) one finds for $\varepsilon \in (0,1], x \in \Omega$ and $t \in (0, T_{max})$

$$-a^\varepsilon(x) + e^\varepsilon(x)\,\frac{p^\varepsilon(x)\,v_\varepsilon(x,t)}{1+q^\varepsilon(x)\,v_\varepsilon(x,t)} \le c_1, \tag{4.4}$$

with

$$c_1 = \begin{cases} \frac{\bar{e}\bar{p}}{\underline{\mathrm{q}}}, & \text{when } q \in S_\#,\\ \bar{e}\bar{p}\max(\frac{\bar{K}\,\bar{r}}{\underline{\mathrm{r}}}, \|v_0\|_{\infty,\Omega}), & \text{when } q = 0.\end{cases}$$

Now, our objective is to adapt an idea of Alikakos [1]; i.e., when inequality (4.4) holds then an a priori $L^1(\Omega)$ uniform bound of the solutions implies a $L^\infty(\Omega)$ uniform bound.

Multiplying the first equation of (3.1) by $u_\varepsilon^{2^{k-1}}$ and integrating over Ω one has

$$\begin{aligned}&\frac{d}{dt}\Big(\frac{1}{2^k}\int_\Omega u_\varepsilon^{2^k}(x,t)dx\Big)\\ &=\int_\Omega div(d_u^\varepsilon \nabla u_\varepsilon)\, u_\varepsilon^{2^{k-1}}\,dx-\int_\Omega \Big(a^\varepsilon(x)-e^\varepsilon(x)\,\frac{p^\varepsilon(x)\,v_\varepsilon}{1+q^\varepsilon(x)\,v_\varepsilon}\Big)\,u_\varepsilon^{2^k}\,dx \qquad (4.5)\\ &\le -\frac{2^k-1}{2^{2k-2}}\underline{\mathrm{d}}_u\int_\Omega |\nabla u_\varepsilon^{2^{k-1}}|^2\,dx + c_1\int_\Omega u_\varepsilon^{2^k}\,dx.\end{aligned}$$

From this one may reproduce the proof of (Theorem 3.1, p. 208 of [1]) to obtain an $L^\infty(\Omega)$ uniform bound independent of t and of ε for $0<\varepsilon\le 1$.

4.2. **A proof of Theorem 2.** Schauder's fixed-point theorem will supply the existence of a nonnegative solution (u,v) of $(\mathcal{P})$ in any cylinder $\Omega\times(0,T)$. Then a local uniqueness result completes the proof.

4.2.1. *Existence.* Let us fix $T>0$. For any nonnegative $\tilde v\in L^2(\Omega\times(0,T))$ we introduce the system of parabolic equations on $\Omega\times(0,T)$:

$$\begin{cases}\dfrac{\partial u}{\partial t}-div(D_u\nabla u)+\Big(\mathcal{A}+\dfrac{1}{|\mathbf{Y}|}\displaystyle\int_{\mathbf{Y}}\frac{e(y)p(y)\,dy}{q(y)(1+q(y)\tilde v(x,t))}-\mathcal{M}\big(\frac{e\,p}{q}\big)\Big)u=0,\\ \dfrac{\partial v}{\partial t}-div(D_v\,\nabla v)+\Big(\dfrac{\mathcal{R}}{\mathcal{K}}\,v+\dfrac{1}{|\mathbf{Y}|}\displaystyle\int_{\mathbf{Y}}\frac{p(y)u(x,t)}{1+q(y)\,\tilde v(x,t)}dy\;-\mathcal{R}\Big)v=0,\end{cases} \qquad (4.6)$$

together with the boundary conditions (3.6) and the initial conditions (3.3). The first equation in (4.6) is a linear one with bounded coefficients on $\Omega\times(0,T)$; hence it admits a unique nonnegative and bounded solution u defined on $\Omega\times(0,T)$ and

$$\|u(\cdot,t)\|_{\infty,\Omega}\le \|u_0\|_{\infty,\Omega}\,e^{\mathcal{M}(\frac{ep}{q})t},\ 0\le t\le T. \qquad (4.7)$$

Next, $\tilde v$ and u being known and nonnegative, the second equation in (4.6) is a standard semilinear parabolic equation of logistic type when $K\in S_\#$ and a linear equation when $K=+\infty$; hence it admits a unique nonnegative and bounded solution v defined on $\Omega\times(0,T)$ and

$$\|v(\cdot,t)\|_{\infty,\Omega}\le\begin{cases}\max(\mathcal{K},\|v_0\|_{\infty,\Omega}), & K\in S_\#,\\ \|v_0\|_{\infty,\Omega}\,e^{\mathcal{R}t}, & K=+\infty,\end{cases}\quad 0\le t\le T. \qquad (4.8)$$

Set

$$\mathcal{B}=\{v\in L^2(\Omega\times(0,T)),0\le v(x,t)\le \max(\mathcal{K},\|v_0\|_{\infty,\Omega}\,e^{\mathcal{R}T})\}$$

a closed and convex subset of $L^2(\Omega \times (0,T))$. One can define a nonlinear mapping $\Lambda : \mathcal{B} \to \mathcal{B}$ upon setting $\Lambda\tilde{v} = v$ the second component of the solution (u, v) of (4.6).
The mapping

$$\tilde{v} \in \mathbb{R}_+ \to \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)}{q(y)(1+q(y)\,\tilde{v})}dy \, \in \mathbb{R}_+$$

being Lipschitz continuous it follows that the mapping $\tilde{v} \in \mathcal{B} \to u \in L^2(\Omega \times (0,T))$ is also Lipschitz continuous; here u is the first component of the solution (u, v) of (4.6). Then, the mapping

$$(\tilde{v}, u) \in \mathbb{R}_+ \times \mathbb{R}_+ \to \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)u}{q(y)(1+q(y)\,\tilde{v})}dy \, \in \mathbb{R}_+$$

being also Lipschitz continuous, one may conclude that Λ is Lipschitz continuous from $\mathcal{B} \to \mathcal{B}$.
Next we show $\Lambda(\mathcal{B})$ is a relatively compact subset of $\mathcal{B}$. Let us first assume some extra smoothness properties on the initial data (u_0, v_0), i.e.,

$$(u_0, v_0) \in (H^2(\Omega))^2, \quad D_u\nabla u_0 \cdot \eta = D_v\nabla v_0 \cdot \eta = 0 \text{ on } \partial\Omega. \tag{4.9}$$

Multiplying the first equation in (4.6) by $\frac{\partial u}{\partial t}$, the second equation in (4.6) by $\frac{\partial v}{\partial t}$, integrating by parts over $\Omega \times (0,T)$ and using the a priori $L^\infty(\Omega \times (0,T))$ bounds for u and v in (4.7) and (4.8) one arrives at the following: there exists a constant $C_3(T)$, independent of $\tilde{v}$, such that

$$\|\frac{\partial u}{\partial t}\|_{2,\Omega\times(0,T)} + \|\frac{\partial v}{\partial t}\|_{2,\Omega\times(0,T)} + \|\nabla u\|_{2,\Omega\times(0,T)} + \|\nabla v\|_{2,\Omega\times(0,T)} \leq C_3(T).$$

Now, Ω being bounded, $H^1(\Omega \times (0,T))$ is a relatively compact subset of $L^2(\Omega \times (0,T))$, which yields $\Lambda(\mathcal{B})$ relatively compact in $\mathcal{B}$.

As a conclusion, when (4.9) holds one may evoke Schauder's fixed-point theorem to establish the existence of a solution to problem $(\mathcal{P})$ on $\Omega \times (0,T)$. Last, any data (u_0, v_0) is the limit of a sequence of data (u_{0n}, v_{0n}) satisfying (4.9): use cut-off functions and mollifiers. Hence a new limiting process allows us to remove (4.9) and get local existence on small time intervals whose lengths depend only on the right-hand side of (4.7–8) and on the coefficients in (4.6); this follows from the Lipschitz continuity of Λ and Picard's contracting mapping theorem. Local uniqueness yields global existence and uniqueness on $\Omega \times (0,T)$.

Remark. Instead of introducing (4.9), one could as well have introduced a smoothness assumption in some Hölder space $C^{\alpha,\frac{\alpha}{2}}(\bar{\Omega} \times [0,T])$ and get compactness in $C^{\beta,\frac{\beta}{2}}(\bar{\Omega} \times [0,T])$ for some $0 < \beta < \alpha$.

4.2.2. *Local uniqueness.* Uniqueness is a consequence of the Lipschitz continuity of the right-hand side of (3.5) with respect to u and v.

4.2.3. *Uniform L^∞ estimates.* For $K \in S_\#$ the proof is similar to the one in Subsection 4.1.

For $K = +\infty$ and $q \equiv 0$ a proof uses a priori $L^\infty(0,\infty; L^1(\Omega))$ estimates derived from using a suitable Lyapunov function of the form

$$\alpha_u \int_\Omega \big(u(x) - u_h - u_h \ln\big(\frac{u(x)}{u_h}\big)\big)dx + \alpha_v \int_\Omega \big(v(x) - v_h - v_h \ln\big(\frac{v(x)}{v_h}\big)\big)dx,$$

where (u_h, v_h) is the spatially constant stationary solution with positive entries of (3.5) (with $K = +\infty$); see Alikakos [1] for details.

When $K = +\infty$ and $q \in S_\#$ trajectories of the underlying system of ordinary differential equations are not bounded.

4.3. **A proof of Theorem 3.**

4.3.1. *Two technical results.* The following result will be useful. A proof is found in [2].

Lemma 2. *Let $f \in L^\infty(\mathbf{Y})$. Then f can be extended by periodicity to a function belonging to $L^p_{loc}(\mathbb{R}^n)$. Set $f^\varepsilon(x) = f(\frac{x}{\varepsilon})$. Then $f^\varepsilon \rightharpoonup \mathcal{M}(f)$ in a weak * $L^\infty(\Omega)$ sense; i.e.,*

$$\forall \phi \in L^1(\Omega), \int_\Omega f^\varepsilon(x)\phi(x)dx \to \int_\Omega \mathcal{M}(f)\phi(x)dx. \tag{4.10}$$

Next one shall need the following extension of the previous result, whose proof is left to the reader.

Lemma 3. *Let p, q and e lie in $S_\#$. Let v be a nonnegative function continuous with respect to its first component. Then, for $f^\varepsilon = p^\varepsilon$ or $e^\varepsilon p^\varepsilon$ in a weak * $L^\infty(\Omega \times (0,T))$ sense, as $\varepsilon \to 0^+$*

$$\frac{f^\varepsilon}{1 + q^\varepsilon v} \rightharpoonup \frac{1}{\mathbf{Y}} \int_{\mathbf{Y}} \frac{f(y)}{1 + q(y)v(x,t)} dy.$$

4.3.2. *Convergence of* $(u_\varepsilon, v_\varepsilon)$. From Theorem 3.1 and from the Sobolev imbedding $W \subset_{compact} L^2(Q_T)$ one can extract a sequence denoted $(u_{\varepsilon'}, v_{\varepsilon'})$ such that as $\varepsilon' \to 0$

$$(u_{\varepsilon'}, v_{\varepsilon'}) \to (u^o, v^o) \text{ strongly in } L^2(\Omega \times (0,T)) \text{ and a.e. in } \Omega \times (0,T), \quad (4.11)$$

with (u^0, v^0) lying in $L^\infty(\Omega \times (0,T))$.
Let us prove that as $\varepsilon' \to 0$

$$r^{\varepsilon'} v_{\varepsilon'} \rightharpoonup \mathcal{M}(r)\, v^o \text{ weakly in } L^2(\Omega \times (0,T)). \quad (4.12)$$

For each $\phi \in L^2(Q_T)$, after some algebra one finds

$$\begin{aligned} &\Big| \int_{Q_T} (r^{\varepsilon'} v_{\varepsilon'} - \mathcal{M}(r) v^o)\phi \, dx\, dt \Big| && (4.13) \\ &\leq \bar{r} \parallel \phi \parallel_{2,Q_T} \parallel v_{\varepsilon'} - v^o \parallel_{2,Q_T} + \Big| \int_{Q_T} (r^{\varepsilon'} - \mathcal{M}(r)) v^o \phi \, dx\, dt \Big|. \end{aligned}$$

Now ϕv^o lies in $L^1(Q_T)$ so that using Lemma 3.3 and (4.11) one can conclude that (4.12) holds true. In a similar fashion one has $a^{\varepsilon'} u_{\varepsilon'} \rightharpoonup \mathcal{M}(a) u^o$ weakly in $L^2(\Omega \times (0,T))$, as $\varepsilon' \to 0$.
Next, for $\phi \in L^2(Q_T)$ one gets

$$\begin{aligned} &\Big| \int_{Q_T} (\frac{r^\varepsilon}{K^\varepsilon} v_\varepsilon^2 - \mathcal{M}(\frac{r}{K})(v^o)^2)\phi \, dx\, dt \Big| \\ &\leq \frac{\bar{r}}{\underline{\mathrm{K}}} \|\phi\|_{2,Q_T} \|v_\varepsilon - v^0\|_{2,Q_T} \|v_\varepsilon + v^0\|_{\infty,Q_T} && (4.14) \\ &+ \Big| \int_{Q_T} (\frac{r^\varepsilon}{K^\varepsilon} - \mathcal{M}(\frac{r}{K}))(v^o)^2 \phi \, dx\, dt \Big|. \end{aligned}$$

Using (4.11), $(v^o)^2\phi$ a member of $L^1(Q_T)$, the uniform estimates in Theorem 1 and Lemma 2 one can conclude that as $\varepsilon' \to 0$

$$\frac{r^{\varepsilon'}}{K^{\varepsilon'}} v_\varepsilon^2 \rightharpoonup \mathcal{M}(\frac{r}{K})(v^o)^2 \text{ weakly in } L^2(\Omega \times (0,T)). \quad (4.15)$$

Let us now prove that for $f^{\varepsilon'} = p^{\varepsilon'}$ or $e^{\varepsilon'} p^{\varepsilon'}$, then as $\varepsilon' \to 0$

$$\frac{f^{\varepsilon'} v_{\varepsilon'} u_{\varepsilon'}}{1 + q^{\varepsilon'} v_{\varepsilon'}} \rightharpoonup \frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \frac{f(y)\, v^o(x,t)\, u^o(x,t)}{1 + q(y)\, v^o(x,t)} \, dy \text{ weakly in } L^2(\Omega \times (0,T)). \quad (4.16)$$

Adding and subtracting u^0 and v^0 at suitable locations one has

$$\frac{f^{\varepsilon'} v_{\varepsilon'} u_{\varepsilon'}}{1+q^{\varepsilon'} v_{\varepsilon'}} = \frac{f^{\varepsilon'} v_{\varepsilon'}}{1+q^{\varepsilon'} v_{\varepsilon'}}(u_{\varepsilon'} - u^0) + \frac{f^{\varepsilon'} u^0}{1+q^{\varepsilon'} v_{\varepsilon'}}(v_{\varepsilon'} - v^0) + \frac{f^{\varepsilon'} v^0 u^0}{(1+q^{\varepsilon'} v_{\varepsilon'})(1+q^{\varepsilon'} v^0)} q^{\varepsilon'}(v_{\varepsilon'} - v^0) + \frac{f^{\varepsilon'} v^0 u^0}{1+q^{\varepsilon'} v^0}.$$

The first three terms on the right-hand side of this identity are strongly converging to 0 in $L^2(\Omega \times (0,T))$ by (4.11) and the uniform $L^\infty(\Omega \times (0,T))$ estimates in ε, $0 < \varepsilon \leq 1$. To conclude we may deduce from Lemma 3 that as $\varepsilon' \to 0$

$$\frac{f^{\varepsilon'} v^0 u^0}{1 + q^{\varepsilon'} v^0} \rightharpoonup \frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \frac{f(y)\, v^o(x,t)\, u^o(x,t)}{1 + q(y)\, v^o(x,t)}\, dy \text{ weakly in } L^2(\Omega \times (0,T)).$$

Thus for the sequence $(u^{\varepsilon'}, v^{\varepsilon'})$ the right-hand side of (3.1) converges to the corresponding right-hand side of (3.5).

The goal of homogenization techniques is to handle the behavior of such quantities as $-\operatorname{div}\cdot d_u^\varepsilon \nabla u_\varepsilon$ when $\varepsilon \to 0$. Then one can show that there exists a positive-definite symmetric matrix D_u depending solely on d_u, Ω and $\mathbf{Y}$ such that upon extracting further subsequences

$$d_u^{\varepsilon''} \nabla u_{\varepsilon''} \rightharpoonup D_u \nabla u, \text{ weakly in } L^2(\Omega \times (0,T))$$

as $\varepsilon'' \to 0$; see [2] and [12]. Identical arguments work for the equation for v_ε.

At this point the convergence of a suitable subsequence of $(u_\varepsilon, v_\varepsilon)_{0<\varepsilon\leq 1}$ towards a solution of problem $(\mathcal{P})$ is established. A uniqueness argument insures that this subsequential convergence is indeed convergence.

4.4. **A proof of Theorem 4.** Assuming either $\mathcal{K} = \infty$ or $\mathcal{K} > 0$ and $\mathcal{M}(a) < \mathcal{M}(ep)\mathcal{K}$ a proof follows the general methodology devised in [1], using strictly convex Lyapunov functions of the form

$$\alpha_u \int_\Omega \big(u(x) - u_h - u_h \ln\big(\frac{u(x)}{u_h}\big)\big)dx + \alpha_v \int_\Omega \big(v(x) - v_h - v_h \ln\big(\frac{v(x)}{v_h}\big)\big)dx,$$

where (u_h, v_h) is the stationary state with positive entries of (3.9) and (α_u, α_v) suitable positive constants.

When $\mathcal{K} > 0$ and $\mathcal{M}(a) > \mathcal{M}(ep)\mathcal{K}$ one uses comparison results. Going back to the equation for v in (3.8) one finds $0 \leq v(x,t) \leq y(t)$ for $t > 0$ where y is the solution of

$$y' = \mathcal{M}(r)\, y\, (1 - \frac{1}{\mathcal{K}} y),\ y(0) = \|v_0\|_{\infty,\Omega};$$

one observes that $y(t) \to \mathcal{K}$ as $t \to +\infty$ so that for any small and positive δ there exists a $T(\delta)$ such that $0 \leq v(x,t) \leq y(t) \leq \mathcal{K} + \delta$ for $t > T(\delta)$. From the equation for u in (3.8) one has $0 \leq u(x,t) \leq z(t)$ for $t > T(\delta)$ where z is the solution of

$$z' = -\mathcal{M}(a)\, z + \mathcal{M}(ep)\,(\mathcal{K}+\delta)\, z,\ z(T(\delta)) = \|u(\cdot, T(\delta))\|_{\infty,\Omega};$$

choosing δ such that $2\mathcal{M}(ep)\delta = \mathcal{M}(a) - \mathcal{M}(ep)\mathcal{K}$ yields an exponential decay for u towards 0 as $t \to +\infty$. Then, the convergence of v towards $\mathcal{K}$ follows.

4.5. **Asymptotic behavior for the homogenized system (3.3).** As we said before the asymptotic behavior of the system $\mathcal{P}^\varepsilon$ is difficult to derive. By homogenization one can obtain some information about the macroscopic behavior of our problem.

4.5.1. *Steady states and local stability: A proof of Theorem 5.* From (3.10) it is clear that the trivial and semitrivial steady states are $(0,0)$ and $(0,K)$. If $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ the equation $\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)\,\lambda}{1+q(y)\,\lambda}\,dy\ = \mathcal{A}$ admits a unique solution $\lambda = \mathcal{K}^*$ so that when $\mathcal{K}^* < \mathcal{K}$, (u^*, K^*) is a nontrivial steady state. A quick analysis of the Jacobian matrix gives the local stability results of (i)–(iv).

4.5.2. *Global stability: A proof of Theorem 6 and Theorem 7.* When $\mathcal{M}(\frac{ep}{q}) < \mathcal{A}$ we have

$$\frac{\partial u}{\partial t} - div(D_u \nabla u) = -\mathcal{A}u + \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)\,v}{1+q(y)\,v}\,dy\,u,$$

so

$$\frac{\partial u}{\partial t} - div(D_u \nabla u) = (-\mathcal{A} + \mathcal{M}(\frac{ep}{q}))u - \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)}{q(y)}\frac{u}{1+q(y)\,v}\,dy.$$

Then, u being nonnegative, one has

$$\frac{\partial u}{\partial t} - div(D_u \nabla u) \leq (-\mathcal{A} + \mathcal{M}(\frac{ep}{q}))u.$$

Using a comparison result one gets $u(\cdot,t) \to 0$ and $v(\cdot,t) \to \mathcal{K}$ as $t \to +\infty$.

When $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$, $\mathcal{K} < \mathcal{K}^*$, then there exists a positive α such that $\mathcal{K} + \alpha < \mathcal{K}^*$. From comparison theorems we have $0 \leq v(x,t) \leq y(t)$ for $t > 0$, where y is the solution of

$$y' = \mathcal{R}\, y\, (1 - \frac{y}{\mathcal{K}}),\ y(0) = \|v_0\|;$$

one observes that $y(t) \to \mathcal{K}$ as $t \to +\infty$ so that for any small and positive δ there exists a $T(\delta)$ such that $0 \leq v(x,t) \leq y(t) \leq \mathcal{K}+\delta$ for $t > T(\delta)$. From the equation for u in (3.5) or in (3.10) in the case with no diffusion, one has $0 \leq u(x,t) \leq z(t)$ for $t > T(\delta)$ where z is the solution of

$$z' = -\mathcal{A}\, z + \frac{1}{|\mathbf{Y}|} \int_{\mathbf{Y}} \frac{e(y)p(y)\ (\mathcal{K}+\delta)}{1+q(y)\ (\mathcal{K}+\delta)}\, dy\, z,\ z(T(\delta)) = \|u(,T(\delta))\|;$$

choosing $\delta = \alpha$ yields an exponential decay for u towards 0 as $t \to +\infty$. Then, the convergence of v towards $\mathcal{K}$ follows. This achieves the proof of items (i) in Theorem 6 and Theorem 7.

Lemma 4. *Assume* $\mathcal{M}(\frac{ep}{q}) > \mathcal{A}$ *and* $\mathcal{K}^* < \mathcal{K} < \frac{\mathcal{M}(p)\mathcal{K}^*}{\mathcal{M}(p) - \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\, dy}$. *Then the function*

$$V(u,v) = (u-u^*) - u^* \ln(\frac{u}{u^*}) + \int_{\mathcal{K}^*}^{v} \frac{-\mathcal{A} + \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)\,\lambda}{1+q(y)\,\lambda}\, dy}{\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)\,\lambda}{1+q(y)\,\lambda}\, dy}\, d\lambda$$

is a Lyapunov function for (3.10).

Proof of Lemma 4. One has

$$\frac{d}{dt} V(u,v) = \Phi(v)(F(v) - F(\mathcal{K}^*)),$$

where $\Phi(v) = -\mathcal{A} + \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{e(y)p(y)\,v}{1+q(y)\,v}\, dy$ and $F(v) = \frac{\mathcal{R}(1-\frac{v}{\mathcal{K}})}{\frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,v}\, dy}$. First Φ is increasing and $\Phi(\mathcal{K}^*) = 0$. The sign of $F'(v)$ is the same as the sign of $g(v) = -\frac{1}{\mathcal{K}}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,v}\, dy + (1-\frac{v}{\mathcal{K}})\int_{\mathbf{Y}} \frac{p(y)q(y)}{(1+q(y)\,v)^2}\, dy$. If $0 \leq v \leq \mathcal{K}$, then g is decreasing, and if $v \geq \mathcal{K}$, then g is increasing. So one has

- If $v > \mathcal{K}$, then $\Phi(v) > 0$ and $F(v) - F(\mathcal{K}^*) < 0$; so $\frac{d}{dt}V(u,v) < 0$.
- If $\mathcal{K}^* < v < \mathcal{K}$, then $g(v) < g(\mathcal{K}^*)$ and $g(\mathcal{K}^*) \leq 0$ if and only if $\mathcal{K} \leq \mathcal{K}^* + \frac{\int_{\mathbf{Y}} \frac{p(y)}{(1+q(y)\,\mathcal{K}^*)}\, dy}{\int_{\mathbf{Y}} \frac{p(y)\,q(y)}{(1+q(y)\,\mathcal{K}^*)^2}\, dy}$. So $F(v) - F(\mathcal{K}^*) < 0$ and $\frac{d}{dt}V(u,v) < 0$.
- If $0 < v < \mathcal{K}^*$, then $\Phi(v) < 0$ and g is decreasing; so $g(v) < g(0)$.
  - If $\mathcal{K} \leq \frac{\int_{\mathbf{Y}} p(y)\, dy}{\int_{\mathbf{Y}} p(y)q(y)\, dy}$, then $g(0) \leq 0$ so $F(v) - F(\mathcal{K}^*) > 0$ and $\frac{d}{dt}V(u,v) < 0$.
  - If $\mathcal{K} > \frac{\int_{\mathbf{Y}} p(y)\, dy}{\int_{\mathbf{Y}} p(y)q(y)\, dy}$, then $g(0) > 0$, but when $\mathcal{K} \leq \mathcal{K}^* + \frac{\int_{\mathbf{Y}} \frac{p(y)}{(1+q(y)\,\mathcal{K}^*)}\, dy}{\int_{\mathbf{Y}} \frac{p(y)\,q(y)}{(1+q(y)\,\mathcal{K}^*)^2}\, dy}$, $g(\mathcal{K}^*) \leq 0$, and g is decreasing so there exist a unique $\hat{\mathcal{K}}$ in $(0, \mathcal{K}^*)$ such that $g(\hat{\mathcal{K}}) = 0$, and
    - $*$ If $v \in (\hat{\mathcal{K}}, \mathcal{K}^*)$, then $F(v) - F(\mathcal{K}^*) > 0$ and $\frac{d}{dt}V(u,v) < 0$.

∗ If $v \in (0, \hat{\mathcal{K}})$, then $F(v) - F(\mathcal{K}^*) > F(0) - F(\mathcal{K}^*) > 0$ if and only if $\mathcal{K} < \frac{\mathcal{M}(p)\mathcal{K}^*}{\mathcal{M}(p) - \frac{1}{|\mathbf{Y}|}\int_{\mathbf{Y}} \frac{p(y)}{1+q(y)\,\mathcal{K}^*}\,dy}$, and so $\frac{d}{dt}V(u,v) < 0$.

End of the proofs of Theorems 6 and 7. The stability of the nontrivial state of (3.10) follows. Last, if e is a constant, then $\mathcal{V}(u(\cdot,t), v(\cdot,t)) = \int_\Omega V(u(x,t), v(x,t))dx$ is a Lyapunov function for (3.5), and the conclusion is deduced from a result of [1] and [5].

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