PERMANENCE AND ASYMPTOTICALLY STABLE COMPLETE TRAJECTORIES FOR NON-AUTONOMOUS LOTKA-VOLTERRA MODELS WITH DIFFUSION

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Abstract. Lotka-Volterra systems are the canonical ecological models used to analyze population dynamics of competition, symbiosis or prey-predator behaviour involving different interacting species in a fixed habitat. Much of the work on these models has been within the framework of infinite-dimensional dynamical systems, but this has frequently been extended to allow explicit time dependence, generally in a periodic, quasiperiodic or almost periodic fashion. The presence of more general non-autonomous terms in the equations leads to non-trivial difficulties which have stalled the development of the theory in this direction. However, the theory of non-autonomous dynamical systems has received much attention in the last decade, and this has opened new possibilities in the analysis of classical models with general non-autonomous terms. In this paper we use the recent theory of attractors for non-autonomous PDEs to obtain new results on the permanence and the existence of forwards and pullback asymptotically stable global solutions associated to non-autonomous Lotka-Volterra systems describing competition, symbiosis or prey-predator phenomena. We note in particular that our results are valid for prey-predator models, which are not order-preserving: even in the 'simple' autonomous case the uniqueness and global attractivity of the positive equilibrium (which follows from the more general results here) is new.

Key words. Lotka-Volterra competition, symbiosis and prey-predator systems, non-autonomous dynamical systems, permanence, attracting complete trajectories.

AMS subject classifications. 35B40, 35K55, 92D25, 37L05.

1. Introduction. Partial differential equations have proved a very useful tool in the modelling of many ecological phenomena related to the dynamics between species interacting in a given habitat. Many authors have allowed explicit dependence on both space and time in the parameters of the equation, a natural way to take into account the spatial and temporal variations that influence real species interactions.

In this paper we consider a non-autonomous model for two species (u and v), evolving within a habitat Ω that is a bounded domain in $\mathbf{R}^N$, $N \geq 1$, with a smooth boundary $\partial\Omega$, of the following type

$$(1.1) \quad \begin{cases} u_t - d_1 \Delta u = u f(t, x, u, v) & x \in \Omega, \ t > s \\ v_t - d_2 \Delta v = v g(t, x, u, v) & x \in \Omega, \ t > s \\ \mathcal{B}_1 u = 0, \ \mathcal{B}_2 v = 0 & x \in \partial\Omega, \ t > s \\ u(s) = u_s, \ v(s) = v_s, \end{cases}$$

where f and g are regular functions, d_1, d_2 are positive constants and $\mathcal{B}_i$ denotes one of the boundary operators

$$(1.2) \qquad \mathcal{B}u = u, \quad \text{or} \quad \mathcal{B}u = \frac{\partial u}{\partial \vec{n}}, \quad \text{or} \quad \mathcal{B}u = d\frac{\partial u}{\partial \vec{n}} + \sigma(x)u,$$

for Dirichlet, Neumann or Robin case, respectively, $\vec{n}$ is the outward normal vector-field to $\partial\Omega$, $\sigma(x)$ a C^1 function. Note that we take diffusion coefficient d_i and boundary potential $\sigma_i(x)$ for the case of Robin boundary condition $\mathcal{B}_i$. Also note that we allow all of the nine possible combinations of boundary conditions in (1.1).

A particularly interesting class of models of the form (1.1) are the non-autonomous Lotka-Volterra models:

$$(1.3) \qquad \begin{cases} u_t - d_1\Delta u = u(\lambda(t,x) - a(t,x)u - b(t,x)v) & x \in \Omega, \ t > s \\ v_t - d_2\Delta v = v(\mu(t,x) - c(t,x)u - d(t,x)v) & x \in \Omega, \ t > s \\ \mathcal{B}_1 u = 0, \ \mathcal{B}_2 v = 0 & x \in \partial\Omega, \ t > s \\ u(s) = u_s, \ v(s) = v_s. \end{cases}$$

We refer for example to [6] for the biological meaning of the parameters d_1, d_2, λ, μ, a, b, c, d involved in (1.3).

In line with the ecological interpretation of these models we will only consider positive solutions, and in the light of this we note here that $u_s, v_s \geq 0$ implies that the solution of (1.1) satisfies $u, v \geq 0$.

Note that our hypotheses on b and c allow different models of population dynamics: competition if $b, c > 0$, symbiosis if $b, c < 0$ and prey-predator if $b > 0$ and $c < 0$, although we do not allow sign changing coeffcients.

Of course, it is an important problem to determine the asymptotic behaviour of solutions of the system (1.1). Since in general this is a very complicated task, one may try to solve simpler problems, e.g. one can try to determine whether or not the two species will survive in the long term or if, on the contrary, one of them will be driven to extinction. Survival of the species has been formalised in the notion of *permanence*, see Hale and Waltman [15] or Hutson and Schmitt [20]. Loosely speaking, the system (1.1) is said to be *permanent* if for any positive initial data u_s and v_s, within a finite time the values of the solution $(u(t, s, x; u_s, v_s), v(t, s, x; u_s, v_s))$, for $x \in \Omega$, enter and remain within a compact set in $\mathbf{R}^2$ that is strictly bounded away from zero in each component. Note, however, that this is an imprecise statement in the presence of Dirichlet boundary conditions.

Note that permanence is a form of *coexistence* of the species, since none is extinguished at any part of the habitat domain at any time.

A related situation, which implies that the system is permanent but gives more detail since it also indicates the expected final state of the system, is when there exists a solution, bounded away from zero, to which all other solutions tend asymptotically.

These two are the main topics with which we are concerned in this paper.

Before going further observe that both (1.1) and (1.3) always posses the *trivial* solution $(0, 0)$ and *semitrivial* solutions of the form $(u, 0)$ and $(0, v)$. In the latter case the non–trivial component satisfies a scalar parabolic problem, of logistic type in the case of (1.3). The dynamics of these solutions have a deep impact on the global dynamics of general solutions. Indeed, if the system is permanent, this implies that semitrivial solutions must be unstable in some sense. On the other hand, if semitrivial solutions are stable, then it can be expected that some solutions of the system exhibit *extinction*, that is, one of the species (or both) approaches asymptotically the value zero.

Some results are already known along these lines. For example in the autonomous case, assume that all the coefficients in (1.3) are constants and consider, for example, the problem with Dirichlet boundary conditions. In this case results about permanence for problem (1.3) depend on the values of λ and μ with respect to the first eigenvalue of certain associated linear elliptic problems, which we now describe. Given $d \in \mathbf{R}$, $d > 0$ and $f \in L^\infty(\Omega)$, we denote by $\Lambda(d, f)$ (we write $\Lambda_0 := \Lambda(d, 0)$) the first eigenvalue of the problem

$$\begin{cases} -d\Delta w = \sigma w + f(x)w & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega, \end{cases}$$

and given $\gamma, \alpha \in \mathbf{R}$ with $\alpha > 0$, we denote by $\omega_{[d,\gamma,\alpha]}$ the unique positive solution of

$$\begin{cases} -d\Delta w = \gamma w - \alpha w^2 & \text{in } \Omega, \\ w = 0 & \text{on } \partial\Omega. \end{cases}$$

If λ and μ satisfy

(1.4) $$\lambda > \Lambda(d_1, -b\omega_{[d_2,\mu,d]}) \quad \text{and} \quad \mu > \Lambda(d_2, -c\omega_{[d_1,\lambda,a]})$$

then the autonomous version of the competition or prey-predator cases of (1.3), with Dirichlet boundary conditions in both components, are permanent and moreover there exists a positive equilibrium solution (Cantrell et al. [4], [6], [7], [8] and López-Gómez [27]).

Although the case of symbiosis, $b, c < 0$, is not treated in these papers, a similar result holds provided that

$$bc < ad,$$

a condition which is used to obtain *a priori bounds* for the solutions (see, for instance, Pao [30] or Theorem 9.8 in Delgado et al. [12], where moreover the coefficients a, b, c and d depend on x).

Note that (1.4) is a condition that expresses the instability of semitrivial solutions.

However, in the competition case it is well-known that if $\lambda \leq \Lambda_0$ or $\mu \leq \Lambda_0$, then one of the two species (or both of them) will be driven to extinction (see López-Gómez and Sabina [29] for an improvement of this result). Similar results can be obtained in the other cases, see [6] and [30]. Note that, in contrast with (1.4), the condition above expresses the stability of either one of the semitrivial solutions.

When non-autonomous terms are allowed in the equations, this is usually done under the assumption of periodicity, quasiperiodicity or almost periodicity, and in this case similar results can be obtained to those for autonomous equations (see Hess [17], Hess and Lazer [18], and Hetzer and Shen [19] and references there in). For the case of periodic coefficients, the use of the Poincaré map implies that the system resembles an autonomous one in many respects.

Cantrell and Cosner [5] assume general non-autonomous terms that are bounded by periodic functions, and using a comparison method give conditions on λ and μ that guarantee that (1.3) is permanent.

Note that most of the references cited in the papers above are concerned (besides periodicity or almost periodicity) with some particular choice of boundary conditions (typically Neumann, or even Dirichlet, in both components) and one of the competition, symbiosis or prey–predator cases. In the first two cases a common tool in the references is the use of order-preserving properties of the Lotka–Volterra system.

For example, in the case of almost periodic time dependence, Hetzer and Shen [19] proved similar results for the competition case, assuming that $d_1 = d_2$ and $\lambda = \mu$ are constant and both components of the system satisfy Dirichlet boundary conditions (no such restrictions are required in the case of Neumann BCs). In that paper, limitation to almost periodic cases is due to the use of skew–product techniques which require, some way or another, some sort of time recurrence in the coefficients of the system.

Note that in [25] Langa et al. studied permanence for the competition case with Dirichlet boundary conditions when only the coefficient a is allowed to depend on time.

In this paper we allow general non-autonomous terms, and do not restrict ourselves to (for example) almost periodic time dependence. As said before, we also consider all nine possible choices of boundary conditions and treat competition, symbiosis and prey–predator models, since we do not rely in monotonicity properties of the system. Note that the only restriction that we impose on the coefficients is that $d_1 = d_2$ in the symbiotic case, a condition that we assume only in order to have explicit upper bounds on the solutions, but not for the permanence results. Also note that as we employ for the solutions of (1.1) or (1.3) the approach of *non–autonomous processes* rather than skew-product techniques, we have to pay attention to both the initial time, s, and the observation time for the solutions, $t > s$. This implies that concepts like permanence, stability, instability and attractivity can be defined and analyzed in both pullback and forwards senses; see Section 2 for further details and also [24]. Observe also that while pullback properties (e.g. permanence, attraction) are usually the most one can expect for general non-autonomous terms, in this case we can also show results on permanence and attractivity also forwards in time; see Langa et al. [25, 23] for cases of pullback but not forwards permanence or attraction in non-autonomous reaction-diffusion equations.

In Section 3, using results for the scalar non–autonomous logistic equations from e.g. [25, 34], which we compile in Section 3.1, we make use of the theory of attractors for non-autonomous PDEs as developed by Chepyzhov and Vishik [9] (see also Crauel et al. [11] or Kloeden and Schmalfuss [21]). Thus, we prove in Section 3.2 that under the assumption s

$$\inf_{\mathbf{R} \times \Omega} a(t,x) > 0 \quad \text{and} \quad \inf_{\mathbf{R} \times \Omega} d(t,x) > 0$$

the system (1.3) has a non–autonomous attractor; see Theorem 3.5. The existence of non–autonomous attractor in this case implies the presence of bounded complete trajectories, i.e. solutions defined for all time.

From here we derive in Section 3.3 some sufficient conditions for the extinction of one (or both) of the species of the system. These conditions are far from optimal but qualitatively describe the stability of semitrivial solutions; see Proposition 3.6.

Then, in Section 3.4 we give sufficient conditions reflecting the instability of semitrivial solutions that guarantee that (1.3) is permanent both in a pullback and in a forwards sense. We want to stress here that these sufficient conditions involve only information about the behaviour of the coefficients of the system at either $t \to -\infty$ or $t \to \infty$. Also, they are given in such a way that the result is robust with respect to perturbations of the coefficients.

The rest of the paper is then devoted to a more detailed analysis of the asymptotic behaviour of the solutions of (1.3). After some preparatory material in Sections 4 and 5, we will prove in Section 6 that under appropriate conditions on the parameters all

non–semitrivial solutions of (1.3) have the same asymptotic behavior as $t \to \infty$. In particular all bounded complete trajectories in the non–autonomous attractor have the same asymptotic behaviour as $t \to \infty$. For this we make use of the permanence results in Section 3.4 and impose a smallness condition on the product of the coupling parameters:

$$\limsup_{t \to \infty} \|b\|_{L^\infty(\Omega)} \limsup_{t \to \infty} \|c\|_{L^\infty(\Omega)} < \rho_0$$

for some suitable constant $\rho_0 > 0$, see Theorem 6.1.

Moreover we show that, under a similar smallness condition on the coupling coefficients, now as $t \to -\infty$, if one of the bounded complete trajectories of (1.3) (which exists from the existence of the non–autonomous attractor) is bounded away from zero at $-\infty$, it is the unique such trajectory, and it also describes the unique pullback asymptotic behavior of all non–semitrivial solutions of (1.3), see Theorem 6.2. When these two theorems can be applied together, there is a unique bounded complete trajectory $(u^*(t), v^*(t))$ that is both forwards and pullback attracting for (1.3), i.e. (u^*, v^*) is a bounded trajectory such that, for any $s \in \mathbf{R}$ and for any positive solution $(u(t, s), v(t, s))$ of (1.3) defined for $t > s$, one has

$$(1.5) \quad (u(t,s) - u^*(t), v(t,s) - v^*(t)) \to (0,0) \qquad \text{as} \quad t \to \infty, \text{ or } \quad s \to -\infty.$$

To obtain these results we need some non trivial machinery for the linear scalar case, Section 4.1, and some perturbation results about the exponential decay for solutions of linear parabolic non–autonomous systems, Section 4.2. In particular, we find conditions guaranteeing that any bounded solution of

$$(1.6) \qquad \begin{cases} u_t - d_1 \Delta u = p(t,x)u \\ v_t - d_2 \Delta v = q(t,x)v \end{cases}$$

gives rise to a solution that tends to zero as $t \to \infty$, when (1.6) is perturbed in a certain way, see Theorem 4.6. It is because we are able to study the linear part of the system in detail that we can obtain results for the nonlinear system.

Since we are able to treat the difference of two solutions of problem (1.3) within this framework, as a consequence of this argument we can apply our results to the Lotka-Volterra model in all three standard cases: competition, symbiosis and prey-predator. It is noteworthy that these different situations are usually studied separately in the literature, but since we do not make any use of monotonicity arguments (which do not apply in the prey-predator case) we are able to give a unified treatment.

We close this paper in Section 7 with a discussion of our results and some possibilities for further developments.

In the case in which all the coefficients are autonomous or periodic, our results in Section 6 that we described above in (1.5), imply the uniqueness of the asymptotic behavior of all non-semitrivial solutions.

Hence, in the autonomous case our results agree with all the classical results of uniqueness and stability of the non-semitrivial steady states of (1.3) for the three cases of competition, symbiosis and prey-predator (see for instance Theorem 4.4 in Furter and López-Gómez [13] and Corollary 4.3 in López-Gómez and Sabina de Lis [29] in the competition case, and Corollary 9.5 in Delgado et al. [12] in the symbiosis case).

Moreover, in the prey-predator case, with (1.5) we are able to conclude the uniqueness and *global stability* of a steady state, solving (for particular ranges of parameter

values) one of the most interesting open problems in this field. We emphasize that this result is new even in the autonomous case, where until now only local stability has been proved, see Theorem 4.1 in Leung [26], see also Lakos [22], López-Gómez and Pardo [28], and Yamada [36].

2. Some notations and preliminaries. In this section we introduce some basic notations and terminology that will be used throughout the rest of the paper. In particular, we make precise the way systems (1.1) or (1.3) are said to be permanent.

2.1. Asymptotic behavior and complete trajectories for nonlinear systems. Note that if the solutions of (1.1) are global, then we can define a non-autonomous nonlinear *process* in some Banach space X appropriate for the solutions, i.e. a family of mappings $\{S(t,s)\}_{t \geq s} : X \to X$, $t, s \in \mathbf{R}$ satisfying:

a) $S(t,s)S(s,\tau)z = S(t,\tau)z$, for all $\tau \leq s \leq t$, $z \in X$,

b) $S(t,\tau)z$ is continuous in $t > \tau$ and z, and

c) $S(t,t)$ is the identity in X for all $t \in \mathbf{R}$.

$S(t,\tau)z$ arises as the value of the solution of our non-autonomous system at time t with initial condition z at initial time τ. For an autonomous system the solutions only depend on $t - \tau$, and we can write $S(t,\tau) = S(t-\tau, 0)$.

In order to describe the asymptotic behavior of non–autonomous systems like (1.1) and (1.3), we rely in the concept of non-autonomous pullback attractor (Chepyzhov and Vishik [9], Kloeden and Schmalfuss [21]), which is the sensible generalization of an attractor for non-autonomous systems. For $A, B \subset X$ we denote the Hausdorff semidistance between A and B by $\mathrm{dist}(A, B) = \sup_{a \in A} \inf_{b \in B} d(a, b)$.

DEFINITION 2.1. *We say that a family of compact sets $\{\mathcal{A}(t)\}_{t \in \mathbf{R}} \subset X$ is a pullback attractor associated to S if*

a) $S(t,\tau)\mathcal{A}(\tau) = \mathcal{A}(t)$, for all $t \geq \tau$ and

b) for all $t \in \mathbf{R}$ and $D \subset X$ bounded

$$\lim_{\tau \to -\infty} dist(S(t,\tau)D, \mathcal{A}(t))) = 0.$$

Observe that the attraction in b) fixes the final time and moves the initial time backwards towards $-\infty$. We are not evolving one trajectory backwards in time, but rather we consider the current state of the system (at the fixed time t) which would result from the same initial condition starting at earlier and earlier times.

To guarantee the existence of such a pullback attractor, one is usually faced with the task of proving the existence of a pullback absorbing family, defined as follows

DEFINITION 2.2. *Given $t_0 \in \mathbf{R}$, we say that $B(t_0) \subset X$ is pullback absorbing at time t_0 if for every bounded $D \subset X$ there exists a $T = T(t, D) \in \mathbf{R}$ such that*

$$S(t_0, \tau)D \subset B(t_0), \ \text{for all } \tau \leq T.$$

A family $\{B(t)\}_{t \in \mathbf{R}}$ is pullback absorbing if $B(t_0)$ is pullback absorbing at time t_0, for all $t_0 \in \mathbf{R}$.

The general result on the existence of non-autonomous pullback attractors is a generalization of the abstract theory for autonomous dynamical systems (Temam [37], Hale [14]):

THEOREM 2.3. *(Crauel et al. [11], Schmalfuss [35])*

Assume that there exists a family of compact pullback absorbing sets. Then, there exists a pullback attractor $\{\mathcal{A}(t)\}_{t \in \mathbf{R}}$ that is minimal in the sense that if $\{C(t)\}_{t \in \mathbf{R}}$ is another family of closed pullback attracting sets, then $\mathcal{A}(t) \subset C(t)$ for all $t \in \mathbf{R}$.

To have a more precise description of the dynamical objects within the pullback attractor, we make the following definition:

DEFINITION 2.4. *Let S be a process. We call the continuous map $w : \mathbf{R} \to X$ a complete trajectory if, for all $s \in \mathbf{R}$,*

$$S(t,s)w(s) = w(t) \qquad for\ all \qquad t \geq s.$$

According to Chepyzhov and Vishik [9], when the family of absorbing sets is uniformly bounded, the pullback attractor can be characterized as

$$(2.1) \qquad \mathcal{A}(t) = \{w(t) : \ w(\cdot) \text{is a bounded complete trajectory for } S\}.$$

2.2. Pullback and forwards permanence for non–autonomous systems.
Consider the nonlinear system (1.1) and assume that f and g are regular functions. Hence, we can assume that for initial data $(u_s, v_s) \in C_{\mathcal{B}_1}(\overline{\Omega}) \times C_{\mathcal{B}_2}(\overline{\Omega})$ there exists a unique (local) smooth solution such that $(u,v) \in C^1_{\mathcal{B}_1}(\overline{\Omega}) \times C^1_{\mathcal{B}_2}(\overline{\Omega})$ for $t > s$, where, for $j = 0, 1$,

$$C^j_{\mathcal{B}}(\overline{\Omega}) = \begin{cases} C^j_0(\overline{\Omega}) & \text{for Dirichlet BCs,} \\ C^j(\overline{\Omega}) & \text{for Neumann or Robin BCs,} \end{cases}$$

with $C^j_0(\overline{\Omega})$ denoting functions in $C^j(\overline{\Omega})$ that are zero on $\partial\Omega$ and $C^0(\overline{\Omega}) = C(\overline{\Omega})$.

Note that in practice we will be interested only in non-negative solutions and that if $u_s \geq 0$ and $v_s \geq 0$ in (1.1), then the local solution satisfies $u, v \geq 0$. In fact, the maximum principle implies that if both $u_s \geq 0$ and $v_s \geq 0$ are non-trivial, then u and v are strictly positive in Ω.

Although at this point we only assume local existence of solutions, it still makes sense to consider complete trajectories of (1.1), which roughly speaking are solutions defined for all times. These objects will play a central role in our analysis below, as can be seen from (2.1). More precisely, a restatement of Definition 2.4 gives

DEFINITION 2.5. *A continuous function $U = \begin{pmatrix} u \\ v \end{pmatrix} : \mathbf{R} \to C_{\mathcal{B}_1}(\overline{\Omega}) \times C_{\mathcal{B}_2}(\overline{\Omega})$ is a complete trajectory of (1.1), if for all $s < t$ in $\mathbf{R}$, $(u(t), v(t))$ is the solution of (1.1) with initial data $u_s = u(s)$, $v_s = v(s)$.*

Now we define several concepts that will help us in making precise the concepts of pullback and forwards permanence for the solutions of (1.1) or (1.3). Note that the concepts below are related to the spaces $C_{\mathcal{B}_i}(\overline{\Omega})$ above. We start with the following

DEFINITION 2.6. *A set of non-negative functions $B \subset C(\overline{\Omega})$ is bounded away from zero, if there exists a non-negative non-trivial continuous function $\varphi_0(x) \geq 0$ in Ω (vanishing on $\partial\Omega$ in case of Dirichlet boundary conditions) such that*

$$u(x) \geq \varphi_0(x) \quad for\ all \quad x \in \Omega, \quad u \in B.$$

The set B is non–degenerate if the function $\varphi_0(x)$ above is in $C^1(\overline{\Omega})$ and $\varphi_0(x) > 0$ in Ω.

Note that φ_0 above can be a positive constant in the case of Neumann or Robin boundary conditions.

Then we have the following definitions for curves in the space of continuous functions.

DEFINITION 2.7. *A positive function with values in $C(\overline{\Omega})$ is non–degenerate at ∞ (respectively $-\infty$) if there exists $t_0 \in \mathbf{R}$ such that u is defined in $[t_0, \infty)$ (respectively $(-\infty, t_0]$) and*

$$\{u(t),\ t \geq t_0\} \quad is\ a\ non\text{–}degenerate\ set$$

(respectively for $t \leq t_0$), that is, there exists a $C^1(\overline{\Omega})$ function $\varphi_0(x) > 0$ in Ω, (vanishing on $\partial\Omega$ in case of Dirichlet boundary conditions), such that

$$u(t, x) \geq \varphi_0(x) \qquad \text{for all} \quad x \in \Omega, \quad t \geq t_0$$

(respectively for all $t \leq t_0$).

A family of curves in $C(\overline{\Omega})$, denoted $\{u_\sigma(t)\}_{\sigma \in \Sigma}$, is non–degenerate at ∞ if there exists $t_0 \in \mathbf{R}$ such that u_σ is defined in $[t_0, \infty)$ and

$$\{u_\sigma(t), \ t \geq t_0, \ \sigma \in \Sigma\} \quad \text{is a non–degenerate set.}$$

Finally, a family of curves in $C(\overline{\Omega})$, denoted $\{u_\sigma(t, s)\}_{\sigma \in \Sigma}$, defined in the intervals $[s, \infty)$ is non–degenerate as $s \to -\infty$ if there exists $s_0 \in \mathbf{R}$ such that for all $s \leq s_0$

$$\{u_\sigma(t), \ s \leq t \leq s_0, \ \sigma \in \Sigma\} \quad \text{is a non–degenerate set}$$

For systems, analogously to Definition 2.6, a set $B \subset (C(\overline{\Omega}))^2$ is bounded away from zero if each projection of B is bounded away from zero in $C(\overline{\Omega})$. In a similar way, as in Definition 2.7, a family of curves $U_\sigma(x, \cdot) \in (C(\overline{\Omega}))^2$, $\sigma \in \Sigma$, is non-degenerate if both components are non-degenerate in $C(\overline{\Omega})$.

Now we can finally define when the system (1.1) or (1.3) is pullback permanent. Observe that we assume here that solutions are globally defined.

DEFINITION 2.8. *We say that system (1.1) is pullback permanent if for any bounded set of intial $B \subset (C(\overline{\Omega}))^2$ bounded away from zero, there exists $t_0 \in \mathbf{R}$ such that for any $t \leq t_0$ the family of solutions*

$$(2.2) \qquad \{\big(u(t, s; u_0, v_0), v(t, s; u_0, v_0)\big), \ s \leq t, \ (u_0, v_0) \in B\}$$

is non–degenerate at $s \to -\infty$.

The system (1.1) is uniformly pullback permanent if it is pullback permament and the functions φ_0 in Definition 2.7 are independent of B.

Note that using the regularizing properties of the solutions of (1.1) or (1.3), if the system is pullback permanent, as defined above, then the set (2.2) is non–degenerate at $s \to -\infty$ for any fixed $t \in \mathbf{R}$.

In an analogous although subtly different way we can define when system (1.1) or (1.3) is forwards permanent

DEFINITION 2.9. *We say that system (1.1) is forwards permanent if for any bounded set of initial $B \subset (C(\overline{\Omega}))^2$ bounded away from zero, and for any $s \in \mathbf{R}$, the family of solutions*

$$(2.3) \qquad \{\big(u(t, s; u_0, v_0), v(t, s; u_0, v_0)\big), \ s \leq t, \ (u_0, v_0) \in B\}$$

is non–degenerate at ∞.

The system (1.1) is uniformly forwards permanent if it is forwards permanent and the functions φ_0 in Definition 2.7 are independent of B.

Note that (1.1) always has the trivial solution $(0, 0)$ as well as semitrivial solutions $(u, 0)$ and $(0, v)$. Hence, if the system is permanent, as defined above, this implies that trivial and semitrivial solutions are unstable in the pullback or forwards sense, see e.g. Langa, Robinson, & Suárez [24]. Also, note that permanence implies coexistence of the species, since the values of the solutions eventually remain far from zero in all points of the domain (except at the boundary in the case of Dirichlet boundary conditions).

In the next section we will give conditions on the coefficients of (1.3) for uniform permanence (both forwards and pullback) which will be moreover robust with respect to suitable perturbations on the coeffcients.

3. Extinction and permanence for non-autonomous Lotka-Volterra equations: competition, symbiosis and prey-predator models. In this section we give results on extinction and pullback and forwards permanence for non-autonomous Lotka-Volterra systems of the type

$$(3.1) \quad \begin{cases} u_t - d_1\Delta u = u\big(\lambda(t,x) - a(t,x)u - b(t,x)v\big), & x \in \Omega, \ t > s \\ v_t - d_2\Delta v = v\big(\mu(t,x) - c(t,x)u - d(t,x)v\big), & x \in \Omega, \ t > s \\ \mathcal{B}_1 u = 0, \ \mathcal{B}_2 v = 0, & x \in \partial\Omega, \ t > s \\ u(s) = u_s \geq 0, \ v(s) = v_s \geq 0, \end{cases}$$

with $d_1, d_2 > 0$; $\lambda, \mu, a, b, c, d \in C^\theta(\overline{Q})$, and $\overline{Q} = \mathbf{R} \times \overline{\Omega}$. Given a function $e \in C^\theta(\overline{Q})$, we define

$$e_L := \inf_{\overline{Q}} e(t,x) \qquad e_M := \sup_{\overline{Q}} e(t,x).$$

We assume from now on that

$$(3.2) \qquad\qquad a_L, d_L > 0$$

and consider the three classical cases depending on the signs of b and c:

1. *Competition*: $b_L, c_L > 0$ in $\overline{Q}$.
2. *Symbiosis*: $b_M, c_M < 0$ in $\overline{Q}$.
3. *Prey-predator*: $b_L > 0$, $c_M < 0$ in $\overline{Q}$.

Also, note that we consider all nine possible choices for $\mathcal{B}_i$ as in (1.2).

Using standard techniques, see for instance Pao [30], it can be shown that given $0 \leq u_s \in C(\overline{\Omega})$, $0 \leq v_s \in C(\overline{\Omega})$ there exists, locally in time, a unique solution of (3.1) which is non-negative, and which we will denote by

$$u = u(t,s,x;u_s,v_s) \geq 0, \quad v = v(t,s,x;u_s,v_s) \geq 0.$$

In fact, due to the strong maximum principle, if $u_s \geq 0$ and $v_s \geq 0$ are both non-trivial then u and v are strictly positive in Ω. Furthermore, if we denote by $\mathcal{C}_i$ and $\text{int}(\mathcal{C}_i)$ for $i = 1, 2$ respectively, the positive cones in $C^1_{\mathcal{B}_i}(\overline{\Omega})$ and their corresponding interior sets, we have

$$\text{int}(\mathcal{C}_i) := \{u \in \mathcal{C}_i : u > 0 \ \text{ in } \Omega, \text{ and } \frac{\partial u}{\partial\vec{n}} < 0 \ \text{ on } \partial\Omega\} \quad \text{if } \mathcal{B}_i u = u$$

and

$$\text{int}(\mathcal{C}_i) := \{u \in \mathcal{C}_i : u \geq \delta > 0, \quad \text{for some } \delta > 0 \ \text{ in } \overline{\Omega}\},$$

if $\mathcal{B}_i u = \frac{\partial u}{\partial\vec{n}}$ or $\mathcal{B}_i u = d_i\frac{\partial u}{\partial\vec{n}} + \sigma_i(x)u$.

Thus, if $u_s \geq 0$ and $v_s \geq 0$ are both non-trivial, then $(u,v) \in \text{int}(\mathcal{C}_1) \times \text{int}(\mathcal{C}_2)$ for $t > s$.

Note also that (3.1) also admits semitrivial solutions of the form $(u,0)$ or $(0,v)$. As indicated in the Introduction, the stability properties of semitrivial solutions play an important role in the global dynamics of (3.1). In fact, extinction requires some semitrivial solution is stable whereas permanence is only possible if semitrivial solutions are somehow unstable.

Thus, we first review some results on the solutions of scalar logistic equations that will be used further below. These results will be used to prove that the local solutions of (3.1) above, are in fact globally defined. Also, they will be crucially used to prove the existence of a pullback attractor as in Section 2.1, and to obtain our results on extinction and permanence as well.

3.1. On the non-autonomous logistic equation. Note that (3.1) always admits semitrivial solutions of the form $(u, 0)$ or $(0, v)$. In this case, when one species is not present, the other one satisfies the non-autonomous logistic equation

$$(3.3) \qquad \begin{cases} u_t - d\Delta u = h(t, x)u - g(t, x)u^2 & \text{in } \Omega, \ t > s \\ \mathcal{B}u = 0 & \text{on } \partial\Omega, \\ u(s) = u_s \geq 0 & \text{in } \Omega, \end{cases}$$

where $d > 0$ and $\mathcal{B}$ as in (1.2), $u_s \in C(\overline{\Omega})$, $h, g \in C^\theta(\overline{Q})$, and

$$g_L > 0 \quad \text{in} \quad \overline{Q}.$$

For $m \in L^\infty(\Omega)$ we denote by $\Lambda_{\mathcal{B}}(d, m)$ the first eigenvalue of

$$(3.4) \qquad \begin{cases} -d\Delta u = \lambda u + m(x)u & \text{in } \Omega, \\ \mathcal{B}u = 0 & \text{on } \partial\Omega. \end{cases}$$

In particular, we denote by $\Lambda_{0,\mathcal{B}}(d) = \Lambda_{\mathcal{B}}(d, 0)$ the first eigenvalue of the operator $-d\Delta$ with boundary conditions $\mathcal{B}$. It is well known that $\Lambda_{\mathcal{B}}(d, m)$ is a simple eigenvalue and a continuous and decreasing function of m. Also note that if m_1 is constant then

$$(3.5) \qquad \Lambda_{\mathcal{B}}(d, m_1 + m_2) = \Lambda_{\mathcal{B}}(d, m_2) - m_1.$$

We write $\varphi_{1,\mathcal{B}}(d, m)$ for the positive eigenfunction associated to $\Lambda_{\mathcal{B}}(d, m)$, normalized such that $\|\varphi_{1,\mathcal{B}}(d, m)\|_{L^\infty(\Omega)} = 1$.

If there is no possible confusion we will suppress the dependence on d and $\mathcal{B}$ in the notations above. When we need to distinguish these quantities with respect to $\mathcal{B}_i$, or d_i, $i = 1, 2$, we will employ superscripts as $\Lambda^i(m)$ or Λ_0^i.

Finally, for $h, g \in L^\infty(\Omega)$ with $g_L > 0$ consider the elliptic equation

$$(3.6) \qquad \begin{cases} -d\Delta u = h(x)u - g(x)u^2 & \text{in } \Omega, \\ \mathcal{B}u = 0 & \text{on } \partial\Omega. \end{cases}$$

The following result is well known (Cantrell and Cosner [6]).

PROPOSITION 3.1. *If $\Lambda(h) \geq 0$, the unique non-negative solution of (3.6) is the trivial one, i.e. $\omega_{[h,g]}(x) = 0$. On the other hand, if $\Lambda(h) < 0$ there exits a unique positive solution of (3.6), which we denote by $\omega_{[h,g]}(x)$. Moreover, $0 < \omega_{[h,g]}(x) \leq \Psi(x)$ in Ω, where*

$$\Psi(x) = \begin{cases} \dfrac{h_M}{g_L} & \text{for Dirichlet or Neumann BCs,} \\ -\dfrac{\Lambda(h)}{\varphi_L g_L}\varphi(x) & \text{for Robin BCs,} \end{cases}$$

with $\varphi = \varphi_{1,\mathcal{B}}(m)$.

The following result will be used in what follows.
LEMMA 3.2. *Assume that $h_n \in L^\infty(\Omega)$ and that*

$$h_n \to h_\infty \quad \text{in } L^\infty(\Omega),$$

with $\Lambda(h_\infty) < 0$. Then, there exist $n_0 \in \mathbb{N}$, and $\varphi \in int(\mathcal{C})$ such that

$$\varphi(x) \leq \omega_{[h_n,g]}(x) \quad \text{in } \Omega, \quad \text{for all } n \geq n_0$$

where $\omega_{[h_n,g]}(x)$ is given by Proposition 3.1.

Proof. Since $\Lambda(h_\infty) < 0$, we can take $\varepsilon > 0$ such that $0 < \varepsilon < -\Lambda(h_\infty)$. For this $\varepsilon > 0$, there exists $n_0 \in \mathbf{N}$ such that for $n \geq n_0$

$$-\varepsilon < h_n - h_\infty < \varepsilon \quad \text{for all } x \in \Omega.$$

Consider $\varphi_\infty \in \text{int}(\mathcal{C})$ the eigenfunction associated to $\Lambda(h_\infty)$ with $\|\varphi_\infty\|_{L^\infty(\Omega)} = 1$. It is not hard to show that $\delta\varphi_\infty$ is subsolution of (3.6) with $h = h_n$ provided that

$$\delta \leq -\frac{\varepsilon + \Lambda(h_\infty)}{g_M}.$$

So, $\delta\varphi_\infty(x) \leq \omega_{[h_n,g]}(x)$ in Ω. This completes the proof. □

In [25] and [34] the following properties of (3.3) were proved.

THEOREM 3.3. *Assume that in (3.3)*

$$h_M < \infty \quad \text{and} \quad g_L > 0 \quad \text{in } \overline{Q}.$$

Then

1. *For every non-trivial $u_s \in C(\overline{\Omega})$, $u_s \geq 0$, there exists a unique positive solution of (3.3) denoted by $\Theta_{[h,g]}(t,s,u_s)$. Moreover,*

   (3.7) $$0 \leq \Theta_{[h,g]}(t,s,u_s) \leq K$$

   where

   $$K := \begin{cases} \max\left\{(u_s)_M, \dfrac{h_M}{g_L}\right\} & \text{for Dirichlet or Neumann BCs,} \\[2ex] \max\left\{(\dfrac{u_s}{\varphi})_M, \dfrac{-\Lambda(h_M)}{\varphi_L g_L}\right\} & \text{for Robin BCs,} \end{cases}$$

   and φ is the positive eigenfunction associated to $\Lambda(h_M)$ with $\|\varphi\|_{L^\infty(\Omega)} = 1$.
2. *For fixed $t > s$, u_s, the map $h \mapsto \Theta_{[h,g]}(t,s,u_s)$ is increasing and $g \mapsto \Theta_{[h,g]}(t,s,u_s)$ is decreasing.*
   For fixed $t > s$, h and g, the map $u_s \mapsto \Theta_{[h,g]}(t,s,u_s)$ is increasing.
3. *Define, for $x \in \Omega$,*

   $$h_0(x) := \inf_{t \in \mathbf{R}} h(t,x), \qquad H_0(x) := \sup_{t \in \mathbf{R}} h(t,x)$$

   and

   $$g_0(x) := \inf_{t \in \mathbf{R}} g(t,x), \qquad G_0(x) := \sup_{t \in \mathbf{R}} g(t,x).$$

   Then, if $u_s \in \text{int}(\mathcal{C})$ and $\Lambda(h_0) < 0$ we have, for any $t > s$,

   (3.8) $$0 < \varepsilon\varphi_1(x) \leq \Theta_{[h,g]}(t,s,x;u_s) \quad \text{in } \Omega,$$

   where φ_1 is the positive eigenfunction associated to $\Lambda(h_0)$ and

   $$\varepsilon = \varepsilon(u_s) := \min\left\{(\frac{u_s}{\varphi_1})_L, \frac{-\Lambda(h_0)}{g_M}\right\}.$$

4. If $\Lambda(H_0) > 0$, then for all initial data $u_s \geq 0$, $\Theta_{[h,g]}(t, s, u_s) \to 0$, in $C^1(\overline{\Omega})$, as $t - s \to \infty$. Moreover the convergence is exponential and uniform for bounded sets of initial data u_s.

5. If $\Lambda(h_0) < 0$ then there exists a unique bounded, complete and non-degenerate trajectory at $\pm\infty$ of (3.3), $\varphi_{[h,g]}$, which moreover satisfies that for all s and any bounded set of non-trivial initial data $u_s \geq 0$, bounded away from 0,

$$\Theta_{[h,g]}(t, s, u_s) - \varphi_{[h,g]}(t) \to 0 \quad as \ t \to \infty.$$

That is, $\varphi_{[h,g]}$ describes the forwards behaviour of all solutions. Also, $\varphi_{[h,g]}$ describes the pullback behaviour of all non-degenerate solutions of (3.3), that is, for each t, if $s \mapsto u_s \geq 0$ is bounded and non-degenerate, then

$$\Theta_{[h,g]}(t, s, u_s) - \varphi_{[h,g]}(t) \to 0 \quad as \ s \to -\infty.$$

Both limits above are taken in $C^1(\overline{\Omega})$. Furthermore for all $t \in \mathbf{R}$, we have

$$\omega_{[h_0, G_0]}(x) \leq \varphi_{[h,g]}(t, x) \leq \omega_{[H_0, g_0]}(x) \quad in \ \Omega.$$

6. If h, g are independent of t and are in $L^\infty(\Omega)$ with $g_L > 0$ and $\Lambda(h) < 0$, then $\varphi_{[h,g]}(t, x) = \omega_{[h,g]}(x)$ is the unique positive solution of (3.6) and for all $t > s$ and u_s

$$\Theta_{[h,g]}(t, s, u_s) = \Theta_{[h,g]}(t - s, u_s) \to \omega_{[h,g]} \quad in \ C^1(\overline{\Omega}) \ as \ t - s \to \infty$$

uniformly for bounded sets of initial data $u_s \geq 0$ bounded away from zero. In particular, there exist $m \leq 1 \leq M$ such that

$$m\omega_{[h,g]} \leq \Theta_{[h,g]}(t, s, u_s) \leq M\omega_{[h,g]},$$

for $t - s$ large.

Moreover in statements 4, 5 and 6 above the convergence as $t \to \infty$ is exponentially fast (see [33]).

3.2. Existence of the pullback attractor and complete trajectories for non-autonomous Lotka–Volterra systems. Our first purpose is to prove the existence of a non-autonomous pullback attractor for (3.1). To do this we will derive suitable estimates on the solutions of (3.1). In doing this we will use the following notation for the solutions of (3.3) with diffusion coefficients d_1 and d_2 and boundary conditions $\mathcal{B}_1$ and $\mathcal{B}_2$ respectively

$$\xi_{[\lambda,a]}(t, s) = \Theta_{[\lambda,a]}(t, s, u_s), \quad \eta_{[\mu,d]}(t, s) = \Theta_{[\mu,d]}(t, s, v_s),$$

where $u_s \geq 0$ and $v_s \geq 0$ in Ω.

THEOREM 3.4. *Provided that $a_L, d_L > 0$, for any solution (u, v) of (3.1), with initial data $u_s \geq 0$, $v_s \geq 0$, the following lower and upper bounds hold:*

1. Competition, $b_L > 0, c_L > 0$:

$$\xi_{[\lambda - b\eta_{[\mu,d]}, a]} \leq u \leq \xi_{[\lambda,a]}, \qquad \eta_{[\mu - c\xi_{[\lambda,a]}, d]} \leq v \leq \eta_{[\mu,d]}.$$

2. Symbiosis, $b_M < 0, c_M < 0$: Assume

(3.9) $$b_L c_L < a_L d_L.$$

Then,

$$\xi_{[\lambda - b\eta_{[\mu,d]},a]} \leq u, \quad \eta_{[\mu - c\xi_{[\lambda,a]},d]} \leq v.$$

Assume furthermore that $d_1 = d_2$ and define

$$\gamma = \max\{\lambda_M, \mu_M\}, \quad M = \frac{a_L - c_L}{d_L - b_L} > 0, \quad K = \frac{a_L d_L - b_L c_L}{d_L - b_L} > 0,$$

and choose w_s such that $w_s \geq \max\{u_s, \frac{1}{M}v_s\}$. Denote by $\Theta_{[\gamma,K]}(t, s, w_s)$ the solution of (3.3) with $d = d_1$ and certain boundary condition that depends on $\mathcal{B}_1$ and $\mathcal{B}_2$ and that will be specifies in the proof. Then, we have the upper bounds

$$u \leq \Theta_{[\gamma,K]}(t, s, w_s), \quad v \leq M\Theta_{[\gamma,K]}(t, s, w_s).$$

3. *Prey-predator, $b_L > 0, c_M < 0$:*

$$\xi_{[\lambda - b\eta_{[\mu - c\xi_{[\lambda,a]},d]},a]} \leq u \leq \xi_{[\lambda - b\eta_{[\mu,d]},a]} \leq \xi_{[\lambda,a]}, \qquad \eta_{[\mu,d]} \leq v \leq \eta_{[\mu - c\xi_{[\lambda,a]},d]}.$$

Proof. 1. Assume that $b_L, c_L > 0$. If we write the equation for u as

$$u_t - d_1\Delta u = u(\lambda - bv) - au^2,$$

then using Theorem 3.3 we get

$$u = \xi_{[\lambda - bv,a]} \leq \xi_{[\lambda,a]},$$

and similarly,

$$v \leq \eta_{[\mu,d]}.$$

Hence, again by Theorem 3.3

$$u = \xi_{[\lambda - bv,a]} \geq \xi_{[\lambda - b\eta_{[\mu,d]},a]}.$$

2. Assume now that $b_M, c_M < 0$. To have the lower bounds it is enough to check that in the equation for u one has

$$\xi_{[\lambda - b\eta_{[\mu,d]},a]}(\lambda - a\xi_{[\lambda - b\eta_{[\mu,d]},a]} - b\eta_{[\mu,d]}) \leq \xi_{[\lambda - b\eta_{[\mu,d]},a]}(\lambda - a\xi_{[\lambda - b\eta_{[\mu,d]},a]} - b\eta_{[\mu - c\xi_{[\lambda,a]},d]}),$$

or equivalently,

$$\eta_{[\mu - c\xi_{[\lambda,a]},d]} \geq \eta_{[\mu,d]},$$

which is true since $c < 0$. Similarly, for the equation for v.

On the other hand, assuming $d_1 = d_2$, define

$$\overline{u} = \Theta_{[\gamma,K]}(t, s, w_s), \quad \overline{v} = M\Theta_{[\gamma,K]}(t, s, w_s)$$

with a suitable boundary condition, $\mathcal{B}$ to be described below. Then using the equations we get that we get that $\overline{u}$ and $\overline{v}$ are supersolutions if

$$-K \geq -a - bM, \qquad -K \geq -dM - c,$$

which is satisfied with the choice of M and K. To compare the solutions with the uppersolutions on the boundary, if either u or v satisfies Dirchlet boundary conditions we take $\mathcal{B}$ the boundary condition of the other component. If both u and v satisfy Robin or Neumann (i.e. $\sigma_i = 0$ in the latter case) boundary conditions we define

$$\sigma = \min\{\sigma_1, \sigma_2\},$$

and $\mathcal{B}u = d_1 \frac{\partial u}{\partial \vec{n}} + \sigma(x)u$.
3. Assume finally that $b_L > 0$, $c_M < 0$, then

$$u \leq \xi_{[\lambda,a]} \quad \text{and} \quad \eta_{[\mu,d]} \leq v.$$

Hence

$$v = \eta_{[\mu-cu,d]} \leq \eta_{[\mu-c\xi_{[\lambda,a]},d]},$$

and then,

$$u = \xi_{[\lambda-bv,a]} \geq \xi_{[\lambda-b\eta_{[\mu-c\xi_{[\lambda,a]},d]},a]}.$$

☐

   With the upper bounds in Theorem 3.4 and using the results for scalar logistic equations in Theorem 3.3, we get the following result.
   THEOREM 3.5. *Under the assumptions in cases 1)-3) of Theorem 3.4, all solutions of (3.1) are global in time and moreover there exists a pullback attractor $\mathcal{A}(t)$ of (3.1), which is bounded for all $t \in \mathbf{R}$. More precisely, we have*

$$\limsup_{t-s\to\infty} u(t,s;u_s,v_s) \leq M_\infty, \quad \limsup_{t-s\to\infty} v(t,s;u_s,v_s) \leq N_\infty,$$

uniformly in Ω and for bounded sets of intial data $u_s, v_s \geq 0$, for some constants $M_\infty \geq 0$ and $N_\infty \geq 0$ that depend on the coefficients of (3.1).

   In particular, there exists at least one complete bounded trajectory $(u^*(t), v^*(t))$, $t \in \mathbf{R}$, for (3.1). Furthermore, all complete bounded trajectories of (3.1) are uniformly bounded by M_∞ and N_∞ and for all $t \in \mathbf{R}$.

   Proof. Thanks to the upper bounds in Theorem 3.4, the positive solutions of (3.1) are always bounded by solutions of the logistic equation of the type (3.3). In particular, all solutions of (3.1) are globally defined.
   Now we use that

$$0 \leq \Theta_{[\alpha,\beta]}(t,s;z) \leq \Theta_{[\alpha_M,\beta_L]}(t-s;z),$$

statements 4)–6) in Theorem 3.3 and that $0 \leq \omega_{[\alpha_M,\beta_L]}(x) \leq \Psi_M$, whith ω and Ψ as in Proposition 3.1, to get the estimates.
   In particular, this implies the existence of bounded pullback absorbing sets for (3.1) in $C(\overline{\Omega}) \times C(\overline{\Omega})$.
   Then following the proof of Section 6 in Langa et al. [25] we can show the existence of a bounded pullback absorbing set in $C^1(\overline{\Omega}) \times C^1(\overline{\Omega})$, and so compact in $C(\overline{\Omega}) \times C(\overline{\Omega})$. Hence, we conclude using Theorem 2.3 the existence of a bounded non-autonomous pullback attractor $\mathcal{A}(t)$ and thus the existence of at least one bounded complete trajectory $(u^*(t), v^*(t))$, $t \in \mathbf{R}$, follows. ☐

3.3. Extinction for non-autonomous Lotka–Volterra systems. Note that with the arguments above there are some cases, when statement 4) in Theorem 3.3 can be used, in which one (or both) constants M_∞ and N_∞ are zero and we have then extinction of one of the species. This implies, in turn, that semitrivial (or the trivial) solutions are stable in a forwards and pullback senses. More precisely, we have the following result. Observe that these sufficient conditions are far from optimal but qualitatively they describe the global stability of trivial or semitrivial solutions.

PROPOSITION 3.6. *With the notations in Theorem 3.4 and 3.5, we have*

1. *Competition, $b_L > 0, c_L > 0$. If*

$$\lambda_M < \Lambda_0^1, \quad then \quad M_\infty = 0,$$

   while if

$$\mu_M < \Lambda_0^2, \quad then \quad N_\infty = 0.$$

2. *Symbiosis, $b_M < 0, c_M < 0$, $d_1 = d_2$ and (3.9), that is $b_L c_L < a_L d_L$. If*

$$\gamma < \Lambda_0^1, \quad then \quad M_\infty = 0,$$

   while if

$$\gamma < \Lambda_0^2, \quad then \quad N_\infty = 0.$$

3. *Prey-predator, $b_L > 0, c_M < 0$. If*

$$\lambda_M < \Lambda_0^1, \quad then \quad M_\infty = 0,$$

   and in this case, if

$$\mu_M < \Lambda_0^2, \quad then \quad M_\infty = 0.$$

   On the other hand, if

$$\Lambda_0^1 < \lambda_M, \quad and \quad \mu_M - c_L \frac{\lambda_M}{a_L} < \Lambda_0^2 \quad then \quad N_\infty = 0.$$

In all the cases, when $M_\infty = 0$ the u component of the solutions of (3.1) extinguishes in pullback and forwards senses, while the v component of the solutions asymptotically follows the dynamics of the scalar logistic equation (3.3) with $h(t, x) = \mu(t, x)$ and $g(t, x) = d(t, x)$ as described in Theorem 3.3.

The case when $N_\infty = 0$ is analogous.

Proof. In fact, in the case of competition we have $0 \le u \le \xi_{[\lambda_M, a_L]}$ and $0 \le v \le \eta_{[\mu_M, d_L]}$. Hence, from statement 4) in Theorem 3.3 and using (3.5), if $\Lambda^1(\lambda_M) = \Lambda_0^1 - \lambda_M > 0$ then $M_\infty = 0$, while $N_\infty = 0$ if $\Lambda^2(\mu_M) = \Lambda_0^2 - \mu_M > 0$.

In the case of symbiosis, assuming $d_1 = d_2$, we have $0 \le u \le \Theta_{[\gamma, K]}(t, s, w_s)$, $0 \le v \le M\Theta_{[\gamma, K]}(t, s, w_s)$. Hence, if $\Lambda^1(\gamma) = \Lambda_0^1 - \gamma > 0$ then $M_\infty = 0$, while $N_\infty = 0$ if $\Lambda^2(\gamma) = \Lambda_0^2 - \gamma > 0$.

Finally, in the case of prey-predator, we have $0 \le u \le \xi_{[\lambda_M, a_L]}$, $0 \le v \le \eta_{[\mu_M - c_L \xi_{[\lambda_M, a_L]}, d_L]}$. Hence, if $\Lambda^1(\lambda_M) = \Lambda_0^1 - \lambda_M > 0$ then $M_\infty = 0$. In this case, $N_\infty = 0$ if $\Lambda^2(\mu_M) = \Lambda_0^2 - \mu_M > 0$.

On the other hand, if $\Lambda_0^1 < \lambda_M$, then for large values of $t - s$ we have $v \le \eta_{[\mu_M - c_L(\omega_{[\lambda_M, a_L]} + \varepsilon), d_L]}$, and then $N_\infty = 0$ if $\Lambda^2(\mu_M - c_L \frac{\lambda_M}{a_L}) = \Lambda_0^2 - \mu_M + c_L \frac{\lambda_M}{a_L} > 0$.

The rest is immediate. ☐

As we are interested in the "permanence" problem for (3.1), we will consider in what follows only the cases in wich $M_\infty > 0$ and $N_\infty > 0$. In particular, note that for sufficiently large values of $\lambda_M > 0$ and $\mu_M > 0$ we can take, for the case of Dirichlet or Neumann boundary conditions in either one of the components u or v,

$$M_\infty = \begin{cases} \frac{\lambda_M}{a_L} & \text{in the competition case} \\ \frac{\gamma}{K} & \text{in the symbiosis case,} \\ \frac{\lambda_M}{a_L} & \text{in the prey-predator case} \end{cases}$$

$$N_\infty = \begin{cases} \frac{\mu_M}{d_L} & \text{in the competition case} \\ M\frac{\gamma}{K} & \text{in the symbiosis case,} \\ \frac{\mu_M - c_L \frac{\lambda_M}{a_L}}{d_L} & \text{in the prey-predator case,} \end{cases}$$

while for Robin boundary conditions we have

$$M_\infty = \begin{cases} \frac{\lambda_M - \Lambda_0^1}{(\varphi^1)_L a_L} & \text{in the competition case} \\ \frac{\gamma - \Lambda_0^1}{(\varphi^1)_L K} & \text{in the symbiosis case,} \\ \frac{\lambda_M - \Lambda_0^1}{(\varphi^1)_L a_L} & \text{in the prey-predator case} \end{cases}$$

$$N_\infty = \begin{cases} \frac{\mu_M - \Lambda_0^2}{(\varphi^2)_L d_L} & \text{in the competition case} \\ M\frac{\gamma - \Lambda_0^2}{(\varphi^2)_L K} & \text{in the symbiosis case,} \\ \frac{\mu_M - c_L \frac{\lambda_M - \Lambda_0^1}{(\varphi^1)_L a_L} - \Lambda_0^2}{(\varphi^2)_L d_L} & \text{in the prey-predator case,} \end{cases}$$

where φ^i denotes the positive eigenfunction associated to Λ_0^i with $\|\varphi^i\|_{L^\infty(\Omega)} = 1$. Note that similar expressions can be given in the remaining five cases for the boundary conditions, although their explicit form becomes more cumbersome.

In fact in the next section we will impose conditions on the coefficients to ensure that the pullback and forwards behaviour of the solutions of (3.1), with non-trivial initial data is far from the semitrivial and the trivial solutions.

3.4. Permanence for non–autonomous Lotka–Volterra systems: non-degeneracy of solutions. Now, using the lower bounds in Theorem 3.4, we will give sufficient conditions for the system (3.1) to be uniformly permanent in pullback and forwards senses, as in Section 2.2. For reasons that will become clear further below, we are interested in obtaining such non-degeneracy in a uniform way with respect to the coefficients λ, μ, a, b, c, d in the system. For this, recall the notations in (3.4) and that we always take non-negative non-trivial initial data u_s, v_s.

Also note that in the results of this section we will use the quantities $\lambda_I \leq \lambda_S$, $\mu_I \leq \mu_S$, $a_I \leq a_S$, $b_I \leq b_S$, $c_I \leq c_S$ and $d_I \leq d_S$, to control the asymptotic sizes of the coefficients λ, μ, a, b, c, d as $t \to \pm\infty$. As all the results will be given in terms of such quantities, the statements below show the robustness of the results with respect to perturbations in the coefficients of the system.

Finally, we stress here once again that the results below imply the instability of trivial and semitrivial solutions.

3.4.1. Competition.

PROPOSITION 3.7. *(Forwards permanence. Competitive case)*
Assume (3.2) and $b_L, c_L > 0$. Then:
  i) If $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_S, d_I]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever

$$\lambda(t,x) \geq \lambda_I, \ \mu(t,x) \leq \mu_S, \ b(t,x) \leq b_S, \ a(t,x) \leq a_S \text{ and } \quad d(t,x) \geq d_I > 0$$

  for all $x \in \Omega$ and $t \geq t_0$, for any $u_s, v_s > 0$, the solution for $t > s \geq t_0$ of
  (3.1) satisfies $\psi_{11}(x) \leq u(t,s,x; u_s, v_s)$ for $t - s$ large enough.
  ii) If $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_S, a_I]})$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda(t,x) \leq \lambda_S, \quad \mu(t,x) \geq \mu_I, \quad a(t,x) \geq a_I > 0, \quad d(t,x) \leq d_S, \quad c(t,x) \leq c_S$$

  for all $x \in \Omega$ and $t \geq t_0$, for any $u_s, v_s > 0$, the solution for $t > s \geq t_0$ of
  (3.1) satisfies $\psi_{22}(x) \leq v(t,s,x; u_s, v_s)$ for $t - s$ large enough.
  Hence, if

$$(3.10) \qquad \lambda_I > \Lambda^1(-b_S \omega_{[\mu_S, d_I]}) \qquad and \qquad \mu_I > \Lambda^2(-c_S \omega_{[\lambda_S, a_I]}),$$

then there exist $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such that for any choice of coefficients that satisfy

$$\lambda_I \leq \lambda(t,x) \leq \lambda_S, \qquad \mu_I \leq \mu(t,x) \leq \mu_S, \qquad 0 < a_I \leq a(t,x) \leq a_S,$$

$$0 < b_I \leq b(t,x) \leq b_S, \quad 0 < c_I \leq c(t,x) \leq c_S, \quad 0 < d_I \leq d(t,x) \leq d_S,$$

for all $x \in \Omega$ and for all $t \geq t_0$, and for all non-trivial $u_s \geq 0$, $v_s \geq 0$ in a fixed bounded set of $C(\overline{\Omega})$ bounded away from 0, the solution (u,v) of (3.1) for $t > s \geq t_0$ is non-degenerate at ∞ and for all $t - s$ large enough

$$u(t,s,x; u_s, v_s) \geq \psi_{11}(x) \quad and \quad v(t,s,x; u_s, v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly forwards permanent.
    Proof. Since $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_S, d_I]})$, by the continuity of $\Lambda^1(m)$ with respect to m, there exists $\varepsilon > 0$ such that

$$\lambda_I > \Lambda^1(-b_S(\omega_{[\mu_S, d_I]} + \varepsilon)) \quad \text{or equivalently by (3.5)} \quad \Lambda^1(\lambda_I - b_S(\omega_{[\mu_S, d_I]} + \varepsilon)) < 0.$$

Using Theorems 3.3 and 3.4, we get, for $t > s \geq t_0$,

$$u(t,s,u_s,v_s) \geq \xi_{[\lambda - b\eta_{[\mu, d]}, a]}(t,s,u_s) \geq \Theta_{[\lambda_I - b_S \eta_{[\mu_S, d_I]}, a_S]}(t - s, u_s).$$

Moreover, $\eta_{[\mu_S, d_I]}(t,s,v_s) \to \omega_{[\mu_S, d_I]}$ in $C^1(\overline{\Omega})$ and uniformly for v_s in bounded sets bounded away from zero, as $t - s \to \infty$, and so

$$(3.11) \ u(t,s,u_s,v_s) \geq \Theta_{[\lambda_I - b_S(\omega_{[\mu_S, d_I]} + \varepsilon), a_S]}(t - s, u_s) \to \omega_{[\lambda_I - b_S(\omega_{[\mu_S, d_I]} + \varepsilon), a_S]}$$

in $C^1(\overline{\Omega})$ and uniformly for u_s in bounded sets bounded away from zero, as $t - s \to \infty$ by Theorem 3.3 and where we have used (3.10). Hence, the result follows for u.
    On the other hand, we have analogously for the v component, for $t > s \geq t_0$,

$$v(t,s,u_s,v_s) \geq \eta_{[\mu - c\xi_{[\lambda, a]}, d]}(t,s,v_s) \geq \Theta_{[\mu_I - c_S \xi_{[\lambda_S, a_I]}, d_S]}(t - s, v_s).$$

Now, from (3.10), $\xi_{[\lambda_S,a_I]}(t,s,u_s) \to \omega_{[\lambda_S,a_I]}$ in $C^1(\overline{\Omega})$ and uniformly for u_s in bounded sets bounded away from zero, as $t-s \to \infty$, and so

$$(3.12) \quad v(t,s,u_s,v_s) \geq \Theta_{[\mu_I - c_S(\omega_{[\lambda_S,a_I]}+\varepsilon),d_S]}(t-s,v_s) \to \omega_{[\mu_I - c_S(\omega_{[\lambda_S,a_I]}+\varepsilon),d_S]}$$

in $C^1(\overline{\Omega})$ and uniformly for v_s in bounded sets bounded away from zero, as $t-s \to \infty$ by Theorem 3.3. □

The same arguments as above, carried in a pullback way lead to the following result. Note that, in particular, this proposition guarantees the equi–non–degeneracy at $-\infty$ of complete non–degenerate trajectories with respect to the coefficients in the system.

PROPOSITION 3.8. *(Pullback permanence. Competitive case)*
Assume (3.2) and $b_L, c_L > 0$. Then:
i) If $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_S,d_I]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever

$$\lambda(t,x) \geq \lambda_I, \quad \mu(t,x) \leq \mu_S, \quad b(t,x) \leq b_S, \quad a(t,x) \leq a_S \quad d(t,x) \geq d_I > 0$$

for all $x \in \Omega$ and $t \leq t_0$ (for some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{11}(x) \leq u(t,s,x;u_s,v_s)$ for $t-s$ large enough. In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $u(t,x) \geq \psi_{11}(x)$ for all $x \in \Omega$ and $t \leq t_0$.
ii) If $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_S,a_I]})$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda(t,x) \leq \lambda_S, \quad \mu(t,x) \geq \mu_I, \quad a(t,x) \geq a_I > 0, \quad d(t,x) \leq d_S, \quad c(t,x) \leq c_S$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{22}(x) \leq v(t,s,x;u_s,v_s)$ for $t-s$ large enough. In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $v(t,x) \geq \psi_{22}(x)$ for all $x \in \Omega$ and $t \leq t_0$.
Hence, if

$$(3.13) \qquad \lambda_I > \Lambda^1(-b_S \omega_{[\mu_S,d_I]}) \qquad and \qquad \mu_I > \Lambda^2(-c_S \omega_{[\lambda_S,a_I]})$$

there exist functions $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda_I \leq \lambda(t,x) \leq \lambda_S, \qquad \mu_I \leq \mu(t,x) \leq \mu_S, \qquad 0 < a_I \leq a(t,x) \leq a_S,$$

$$0 < b_I \leq b(t,x) \leq b_S, \quad 0 < c_I \leq c(t,x) \leq c_S, \quad 0 < d_I \leq d(t,x) \leq d_S,$$

for all $x \in \Omega$ and $t \leq t_0$ (for some $t_0 \in \mathbf{R}$), and for all non-trivial $u_s \geq 0$, $v_s \geq 0$ in a fixed bounded set, B, of $C(\overline{\Omega})$ bounded away from 0, the set of solutions of (3.1) $\{(u,v), \ s < t \leq t_0, \ (u_s,v_s) \in B\}$ is non-degenerate as $s \to -\infty$ and for all $t-s$ large enough

$$u(t,s,x;u_s,v_s) \geq \psi_{11}(x) \quad and \quad v(t,s,x;u_s,v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly pullback permanent and any bounded complete trajectory that is non-degenerate at $-\infty$ satisfies

$$u(t,x) \geq \psi_{11}(x) \quad and \quad v(t,x) \geq \psi_{22}(x) \quad for \ all \ x \in \Omega \ and \ t \leq t_0.$$

Proof. The first part of the statements follow from (3.11) and (3.12), with $t - s \to \infty$ but now $s < t \leq t_0$.

For a complete solution, arguing as in Proposition 3.7 we get for any for $t_0 \geq t > s$,

$$u(t) \geq \xi_{[\lambda - b\eta_{[\mu,d]},a]}(t, s, u(s)) \geq \Theta_{[\lambda_I - b_S \eta_{[\mu_S,d_I]},a_S]}(t - s, u(s)).$$

As v is non-degenerate at $-\infty$, 5) in Theorem 3.3 implies $\eta_{[\mu_S,d_I]}(t, s, v(s)) \to \omega_{[\mu_S,d_I]}(t)$ in $C^1(\overline{\Omega})$ as $s \to -\infty$. Thus, for sufficiently negative s,

$$(3.14) \qquad u(t) \geq \Theta_{[\lambda_I - b_S(\omega_{[\mu_S,d_I]}+\varepsilon),a_S]}(t - s, u(s)) \to \omega_{[\lambda_I - b_S(\omega_{[\mu_S,d_I]}+\varepsilon),a_S]}$$

in $C^1(\overline{\Omega})$ as $s \to -\infty$, because u is non-degenerate at $-\infty$ and 5) in Theorem 3.3 again. Hence the result follows for u.

On other hand, we have analogously for the v component for any for $t_0 \geq t > s$,

$$v(t) \geq \eta_{[\mu - c\xi_{[\lambda,a]},d]}(t, s, v(s)) \geq \Theta_{[\mu_I - c_S \xi_{[\lambda_S,a_I]},d_S]}(t - s, v(s)).$$

Now, $\xi_{[\lambda_S,a_I]}(t, s, u(s)) \to \omega_{[\lambda_S,a_I]}$ in $C^1(\overline{\Omega})$ as $s \to -\infty$, because u is non-degenerate at $-\infty$, and so, for sufficiently negative s,

$$(3.15) \qquad v(t) \geq \Theta_{[\mu_I - c_S(\omega_{[\lambda_S,a_I]}+\varepsilon),d_S]}(t - s, v(s)) \to \omega_{[\mu_I - c_S(\omega_{[\lambda_S,a_I]}+\varepsilon),d_S]}$$

in $C^1(\overline{\Omega})$ as $s \to -\infty$ by Theorem 3.3, because v is non-degenerate at $-\infty$. $\square$

Results for the other cases can be proved analogously, as we now show.

3.4.2. Symbiosis. First for the case of symbiosis, we have the following result. Note that as we make no use here of the upper bound in Theorem 3.4, we do not assume below that $d_1 = d_2$.

PROPOSITION 3.9. *(Forwards permanence. Symbiotic case)*
Assume (3.2), $b_M, c_M < 0$ and (3.9), that is

$$b_L c_L < a_L d_L.$$

Then:

 i) *If $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_I,d_S]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever*

$$\lambda(t, x) \geq \lambda_I, \quad \mu(t, x) \geq \mu_I, \quad b(t, x) \leq b_S < 0, \quad a(t, x) \leq a_S, \quad d(t, x) \leq d_S$$

 for all $x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$ the solution for $t > s \geq t_0$ of (3.1) satisfies $\psi_{11}(x) \leq u(t, s, x; u_s, v_s)$ for $t - s$ large enough.
 ii) *If $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_I,a_S]})$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever*

$$\lambda(t, x) \geq \lambda_I, \quad \mu(t, x) \geq \mu_I, \quad a(t, x) \leq a_S, \quad d(t, x) \leq d_S, \quad c(t, x) \leq c_S < 0$$

 for all $x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$ the solution for $t > s \geq t_0$ of (3.1) satisfies $\psi_{22}(x) \leq v(t, s, x; u_s, v_s)$ for $t - s$ large enough.
Hence, if

$$(3.16) \qquad \lambda_I > \Lambda^1(-b_S \omega_{[\mu_I,d_S]}) \qquad and \qquad \mu_I > \Lambda^2(-c_S \omega_{[\lambda_I,a_S]})$$

then there are functions $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda_I \leq \lambda(t, x), \qquad \mu_I \leq \mu(t, x), \qquad a(t, x) \leq a_S,$$

$$b(t, x) \leq b_S < 0, \quad c(t, x) \leq c_S < 0, \quad d(t, x) \leq d_S$$

$x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), and for all $u_s > 0, v_s > 0$ in a fixed bounded set of $C(\overline{\Omega})$ bounded away from 0, the solution (u, v) of (3.1) for $t > s \geq t_0$ is non-degenerate at ∞, and for all $t - s$ large enough

$$u(t, s; u_s, v_s) \geq \psi_{11}(x) \qquad and \qquad v(t, s; u_s, v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly forwards permanent.

Proof. We proceed as in the Proposition 3.7 using now that, as $t - s \to \infty$,

$$u \geq \xi_{[\lambda - b\eta_{[\mu, d]}, a]} \geq \xi_{[\lambda_I - b_S \eta_{[\mu_I, d_S]}, a_S]} \to \omega_{[\lambda_I - b_S \omega_{[\mu_I, d_S]}, a_S]}$$

and

$$v \geq \eta_{[\mu - c\xi_{[\lambda, a]}, d]} \geq \eta_{[\mu_I - c_S \xi_{[\lambda_I, a_S]}, d_S]} \to \omega_{[\mu_I - c_S \omega_{[\lambda_I, a_S]}, d_S]}.$$

□

On the other hand, for pullback permenence and for complete non-degenerate solutions, we have along the same lines as above

PROPOSITION 3.10. *(Pullback permanence. Symbiotic case)*
Assume (3.2), $b_M, c_M < 0$ and (3.9), that is

$$b_L c_L < a_L d_L.$$

Then:

i) If $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_I, d_S]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever

$$\lambda(t, x) \geq \lambda_I, \quad \mu(t, x) \geq \mu_I, \quad b(t, x) \leq b_S < 0, \quad a(x, t) \leq a_S, \quad d(t, x) \leq d_S.$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{11}(x) \leq u(t, s, x; u_s, v_s)$ for $t - s$ large enough.
In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $u(t, x) \geq \psi_{11}(x)$ for all $x \in \Omega$ and $t \leq t_0$.

ii) If $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_I, a_S]})$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda(t, x) \geq \lambda_I, \quad \mu(t, x) \geq \mu_I, \quad a(t, x) \leq a_S, \quad d(t, x) \leq d_S, \quad c(t, x) \leq c_S < 0,$$

$x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$) for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{22}(x) \leq v(t, s, x; u_s, v_s)$ for $t - s$ large enough.
In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $v(t, x) \geq \psi_{22}(x)$ for all $x \in \Omega$ and $t \leq t_0$.

Hence, if

$$(3.17) \qquad \lambda_I > \Lambda^1(-b_S \omega_{[\mu_I, d_S]}) \qquad and \qquad \mu_I > \Lambda^2(-c_S \omega_{[\lambda_I, a_S]})$$

there exist $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda_I \leq \lambda(t, x), \qquad \mu_I \leq \mu(t, x), \qquad a(t, x) \leq a_S,$$

$$b(t, x) \leq b_S < 0, \quad c(t, x) \leq c_S < 0, \quad d(t, x) \leq d_S.$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$), and for all non-trivial $u_s \geq 0$, $v_s \geq 0$ in a fixed bounded set, B, of $C(\overline{\Omega})$ bounded away from 0, the set of solutions of (3.1)

$\{(u, v), \ s < t \leq t_0, \ (u_s, v_s) \in B\}$ is non-degenerate as $s \to -\infty$ and for all $t - s$ large enough

$$u(t, s, x; u_s, v_s) \geq \psi_{11}(x) \quad and \quad v(t, s, x; u_s, v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly pullback permanent and any bounded complete trajectory that is non-degenerate at $-\infty$ satisfies

$$u(t, x) \geq \psi_{11}(x) \quad and \quad v(t, x) \geq \psi_{22}(x) \quad for \ all \ x \in \Omega \ and \ t \leq t_0.$$

3.4.3. Prey–predator. We also have, for the prey-predator case the following result.

PROPOSITION 3.11. *(Forwards permanence. Prey-predator case)*
Assume (3.2) and $b_L > 0$ and $c_M < 0$. Then:
  i) *If $\lambda_I > \Lambda^1(-b_S\omega_{[\mu_S - c_I\omega_{[\lambda_S, a_I]}, d_I]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever*

$$\lambda_S \geq \lambda(t, x) \geq \lambda_I, \qquad \mu(t, x) \leq \mu_S, \qquad a_S \geq a(t, x) \geq a_I > 0,$$

$$b(t, x) \leq b_S, \qquad c(t, x) \geq c_I, \qquad d(t, x) \geq d_I > 0$$

  for all $x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$ the solution for $t > s \geq t_0$ of (3.1) satisfies $\psi_{11}(x) \leq u(t, s, x; u_s, v_s)$ for $t - s$ large enough.
  ii) *If $\mu_I > \Lambda_0^2$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever*

$$\mu(t, x) \geq \mu_I, \quad d(x, t) \leq d_S$$

  for all $x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$ the solution for $t > s \geq t_0$ of (3.1) satisfies $\psi_{22}(x) \leq v(t, s, x; u_s, v_s)$ for $t - s$ large enough.
  Hence, if

(3.18) $$\lambda_I > \Lambda^1(-b_S\omega_{[\mu_S - c_I\omega_{[\lambda_S, a_I]}, d_I]}) \qquad and \qquad \mu_I > \Lambda_0^2$$

there are are functions $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such that whenever

$$\lambda_I \leq \lambda(t, x) \leq \lambda_S, \qquad \mu_I \leq \mu(t, x) \leq \mu_S, \qquad a_S \geq a(t, x) \geq a_I > 0,$$

$$0 < b_I \leq b(t, x) \leq b_S, \quad c_I \leq c(t, x) \leq c_S < 0, \quad d_S \geq d(t, x) \geq d_I > 0$$

for all $x \in \Omega$ and $t \geq t_0$ (some $t_0 \in \mathbf{R}$), and for all $u_s > 0, v_s > 0$ in a fixed bounded set of $C(\overline{\Omega})$ bounded away from 0, the solution (u, v) of (3.1) for $t > s \geq t_0$ is non-degenerate at ∞ and for all $t - s$ large enough

$$u(t, s, x; u_s, v_s) \geq \psi_{11}(x) \qquad and \qquad v(t, s, x; u_s, v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly forwards permanent.
  Proof. As before, we use now that as $t - s \to \infty$,

$$u \geq \xi_{[\lambda - b\eta_{[\mu - c\xi_{[\lambda, a]}, d]}, a]} \geq \xi_{[\lambda_I - b_S\eta_{[\mu_S - c_I\xi_{[\lambda_S, a_I]}, d_I]}, a_I]} \to \omega_{[\lambda_I - b_S\eta_{[\mu_S - c_I\omega_{[\lambda_S, a_I]}, d_I]}, a_I]}$$

and

$$v \geq \eta_{[\mu, d]} \geq \eta_{[\mu_I, d_S]} \to \omega_{[\mu_I, d_S]}.$$

□

And also
PROPOSITION 3.12. *(Pullback permanence. Prey-predator case)*
Assume (3.2) and $b_L > 0$ and $c_M < 0$. Then:

i) If $\lambda_I > \Lambda^1(-b_S\omega_{[\mu_S-c_I\omega_{[\lambda_S,a_I]},d_I]})$ there exists $\psi_{11} \in int(\mathcal{C}_1)$ such that whenever

$$\lambda_S \geq \lambda(t,x) \geq \lambda_I, \qquad \mu(t,x) \leq \mu_S, \qquad a_S \geq a(t,x) \geq a_I > 0,$$

$$b(t,x) \leq b_S, \qquad\qquad c(t,x) \geq c_I, \qquad d(t,x) \geq d_I > 0.$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t \in \mathbf{R}$), for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{11}(x) \leq u(t,s,x;u_s,v_s)$ for $t - s$ large enough. In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $u(t,x) \geq \psi_{11}(x)$ for all $x \in \Omega$ and $t \leq t_0$.

ii) If $\mu_I > \Lambda_0^2$ there exists $\psi_{22} \in int(\mathcal{C}_2)$ such whenever

$$\mu(t,x) \geq \mu_I, \quad d(x,t) \leq d_S.$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$), for any $u_s, v_s > 0$, the solution for $s < t \leq t_0$ of (3.1) satisfies $\psi_{22}(x) \leq v(t,s,x;u_s,v_s)$ for $t - s$ large enough. In particular, any complete trajectory of (3.1) that is non-degenerate at $-\infty$ satisfies $v(t,x) \geq \psi_{22}(x)$ for all $x \in \Omega$ and $t \leq t_0$.

Hence, if

(3.19) $\lambda_I > \Lambda^1(-b_S\omega_{[\mu_S-c_I\omega_{[\lambda_S,a_I]},d_I]})$ and $\mu_I > \Lambda_0^2,$

there exist functions $\psi_{11} \in int(\mathcal{C}_1)$ and $\psi_{22} \in int(\mathcal{C}_2)$ such whenever

$$\lambda_I \leq \lambda(t,x) \leq \lambda_S, \qquad \mu_I \leq \mu(t,x) \leq \mu_S, \qquad a_S \geq a(t,x) \geq a_I > 0,$$

$$0 < b_I \leq b(t,x) \leq b_S, \quad c_I \leq c(t,x) \leq c_S < 0, \quad d_S \geq d(t,x) \geq d_I > 0,$$

for all $x \in \Omega$ and $t \leq t_0$ (some $t_0 \in \mathbf{R}$), and for all non-trivial $u_s \geq 0$, $v_s \geq 0$ in a fixed bounded set, B, of $C(\overline{\Omega})$ bounded away from 0, the set of solutions of (3.1) $\{(u,v), s < t \leq t_0, (u_s,v_s) \in B\}$ is non-degenerate as $s \to -\infty$ and for all $t-s$ large enough

$$u(t,s,x;u_s,v_s) \geq \psi_{11}(x) \quad and \quad v(t,s,x;u_s,v_s) \geq \psi_{22}(x).$$

In particular, (3.1) is uniformly pullback permanent and any bounded complete trajectory that is non-degenerate at $-\infty$ satisfies

$$u(t,x) \geq \psi_{11}(x) \quad and \quad v(t,x) \geq \psi_{22}(x) \quad for\ all\ x \in \Omega\ and\ t \leq t_0.$$

REMARK 3.13. *Note that in order to apply the previous results one has to check that the assumptions in Propositions 3.7–3.12 are meaningful. Indeed, conditions (3.10), (3.16) and (3.18) must define nonempty sets of coefficients. Here we analyze only Dirichlet or Neumann boundary conditions; Robin ones can be treated in a similar way although the estimates are a little more involved.*

In fact, (3.16) includes all coefficients such that

$$\lambda_I > \Lambda_0^1, \qquad \mu_I > \Lambda_0^2$$

since in this case $\lambda_I > \Lambda_0^1 > \Lambda^1(-b_S\omega_{[\mu_I,d_S]})$ and $\mu_I > \Lambda_0^2$ then $\mu_I > \Lambda^2(-c_S\omega_{[\lambda_I,a_S]})$, see also [12].

However, in order to show that (3.10) defines a non-empty set we must impose some conditions on b or c. If for example $b_S \to 0$ then $\Lambda^1(-b_S \omega_{[\mu_S, d_I]}) \to \Lambda_0^1$. Also, if $c_S \to 0$ then $\Lambda^2(-c_S \omega_{[\lambda_S, a_I]}) \to \Lambda_0^2$. Hence if b_S or c_S are small the conditions in (3.10) can be met, see also [27] and [29].

We analyze condition (3.18) for the prey-predator case in more detail. From Proposition 3.1, in the case of Dirichlet or Neumann boundary conditions, we have $\omega_{[h,g]} \leq h_M/g_L$, and so

$$\omega_{[\lambda_S, a_I]} \leq \frac{\lambda_S}{a_I} \quad \text{and then} \quad \omega_{[\mu_S - c_I \omega_{[\lambda_S, a_I]}, d_I]} \leq \frac{\mu_S - c_I\left(\frac{\lambda_S}{a_I}\right)}{d_I},$$

and then using the monotonicity of $\Lambda(m)$ with respect to m and (3.5), we get

$$\Lambda^1(-b_S \omega_{[\mu_S - c_I \omega_{[\lambda_S, a_I]}, d_I]}) \leq \Lambda^1(-b_S \frac{(a_I \mu_S - c_I \lambda_S)}{a_I d_I}) = \Lambda_0^1 + b_S \frac{(a_I \mu_S - c_I \lambda_S)}{a_I d_I}.$$

Hence, if λ_I and μ_I satisfy

$$\lambda_I > \Lambda_0^1 + \frac{b_S \mu_S}{d_I} + \frac{-b_S c_I}{a_I d_I} \lambda_S, \qquad \mu_I > \Lambda_0^2,$$

then (3.18) defines a non–empty set of parameters.

Observe that the first condition above is a restriction on the oscillation of $\lambda(t,x)$ as $t \to \pm\infty$.

In particular, if $\Lambda_0^1 + \frac{b_S \mu_S}{d_I} > 0$ then a necessary condition is

$$a_I d_I + b_S c_I > 0.$$

In such a case the conditions above can be met.

Now, for reasons that will be apparent in the next sections, we are interested in some uniformity in the previous results with respect to the coefficients $b_I \leq b_S$ and $c_I \leq c_S$. More precisely, we are going to show that the functions $\psi_{11}(x)$ and $\psi_{22}(x)$ in all the previous propositions, can be taken independent of $b(t,x)$ and $c(t,x)$, provided one of the numbers $b_I \leq b_S$ or $c_I \leq c_S$ is sufficiently small. In fact we have the following:

THEOREM 3.14. *i) The competitive case:* $b_L, c_L > 0$. *Assume either*
  1. $\lambda_I > \Lambda_0^1$, $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_S, a_I]})$, and b_S is sufficiently small, or
  2. $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_S, d_I]})$, $\mu_I > \Lambda_0^2$, and c_S is sufficiently small.
Then the functions $\psi_{11}(x)$ *and* $\psi_{22}(x)$ *in Propositions 3.7 and 3.8 can be taken also independent of* b_S *and* c_S.
ii) The symbiotic case: $b_M, c_M < 0$ *and* $b_L c_L < a_L d_L$. *Assume either*
  1. $\lambda_I > \Lambda_0^1$, $\mu_I > \Lambda^2(-c_S \omega_{[\lambda_I, a_S]})$, or
  2. $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_I, d_S]})$, $\mu_I > \Lambda_0^2$.
Then the functions $\psi_{11}(x)$ *and* $\psi_{22}(x)$ *in Propositions 3.9 and 3.10 can be taken also independent of* b_I *and* c_I.
iii) The prey-predator case: $b_L > 0$, $c_M < 0$. *Assume either*
  1. $\lambda_I > \Lambda_0^1$, $\mu_I > \Lambda_0^2$, and b_S is sufficiently small, or
  2. $\lambda_I > \Lambda^1(-b_S \omega_{[\mu_S, d_I]})$, $\mu_I > \Lambda_0^2$, and $|c_I|$ is sufficiently small.
Then the functions $\psi_{11}(x)$ *and* $\psi_{22}(x)$ *in Propositions 3.11 and 3.12 can be taken also independent of* b_S *and* c_I.

Proof. We analyze only the competitive case. By the proof of Proposition 3.7 and Theorem 3.3 statement 6 we get

$$u(t, s, u_s, v_s) \geq \Theta_{[\lambda_I - b_S \eta_{[\mu_S, d_I]}, a_S]}(t - s, u_s) \geq$$
$$\geq \omega_{[\lambda_I - b_S(\omega_{[\mu_S, d_I]} + \varepsilon), a_S]} \geq m\omega_{[\lambda_I - b_S(\omega_{[\mu_S, d_I]} + \varepsilon), a_S]}.$$

It suffices to apply Lemma 3.2 as $b_S \to 0$.

On the other hand,

$$v(t, s, u_s, v_s) \geq \Theta_{[\mu_I - c_S(\omega_{[\lambda_S, a_I]} + \varepsilon), d_S]}(t - s, v_s) \to \omega_{[\mu_I - c_S(\omega_{[\lambda_S, a_I]} + \varepsilon), d_S]},$$

and so taking ε small the result follows.

The other cases can be studied in an analogous way by Propositions 3.9, 3.10, 3.11 and 3.12. □

4. Exponential decay for non-autonomous linear systems. Once the results on permanence of the previous section have been established we turn now our attention to determining ranges of parameters such that there exists some special asymptotically stable trajectories describing the asymptotic behavior of solutions of (3.1), either forwards or in a pullback sense. For this we have to develop some tools on linear systems.

Hence, in this section we give sufficient conditions for certain linear systems to have exponential decay. The results are of a perturbative nature and are based upon results in [33] for scalar equations.

4.1. Preliminary results for the scalar case. We start by recalling some results for the following scalar equation

$$(4.1) \qquad \begin{cases} u_t - d\Delta u = c(t, x)u & x \in \Omega, \ t > s \\ \mathcal{B}u = 0, & x \in \partial\Omega, \ t > s \\ u(s) = u_s. \end{cases}$$

Assume that $d > 0$, $c \in C^\theta(\mathbf{R}, L^p(\Omega))$, with $0 < \theta \leq 1$ and some $p > \max(N/2, 1)$. Then for any $u_s \in X$, where $X = L^q(\Omega)$ with $1 \leq q < \infty$, or $X = C(\overline{\Omega})$, (4.1) has a unique solution given by $u(t, s; u_s)$, which is a strong solution in $L^r(\Omega)$ for any $1 \leq r < p$. This solution can be used to define an order-preserving evolution operator T_c in X via the definition $T_c(t, s)u_s = u(t, s; u_s)$.

Moreover for each q and r with $1 \leq q \leq r \leq \infty$ and $R_0 > 0$ there exist $L_0 = L_0(R_0, r, q) > 0$ and $\delta_0 = \delta(R_0, r, q) > 0$ such that the evolution operator $T_c(t, s)$ satisfies

$$(4.2) \qquad \|T_c(t, s)u_0\|_{L^r(\Omega)} \leq L_0 \frac{e^{\delta_0(t-s)}}{(t - s)^{\frac{N}{2}\left(\frac{1}{q} - \frac{1}{r}\right)}} \|u_0\|_{L^q(\Omega)}, \qquad t > s$$

for every $c \in C^\theta(\mathbf{R}, L^p(\Omega))$, with $0 < \theta \leq 1$ and some $p > N/2$, such that

$$\|c\|_{L^\infty(\mathbf{R}, L^p(\Omega))} \leq R_0.$$

Also, the evolution operator smooths the solutions. More precisely, for every $u_0 \in L^q(\Omega)$ and $t > s$, the map

$$(s, \infty) \ni t \longmapsto u(t, s; u_0) := T_c(t, s)u_0 \in \begin{cases} C_{\mathcal{B}}^\nu(\overline{\Omega}) & \text{if } p > N/2, \\ C_{\mathcal{B}}^{1,\nu}(\overline{\Omega}) & \text{if } p > N, \end{cases}$$

is continuous for some $\nu > 0$. Here

$$C_{\mathcal{B}}^{j,\nu}(\overline{\Omega}) = \begin{cases} C_0^{j,\nu}(\overline{\Omega}) & \text{for Dirichlet BCs,} \\ C^{j,\nu}(\overline{\Omega}) & \text{for Neumann or Robin BCs,} \end{cases}$$

see e.g. Rodríguez-Bernal [32].

The following proposition is taken from Lemma 4.1 in Robinson et al. [31] and Lemma 2.1 in Rodríguez-Bernal [33]:

PROPOSITION 4.1. *Suppose that for some q with $1 \leq q \leq \infty$ there exist $M > 0$ and $\beta \in \mathbf{R}$ such that*

(4.3) $$\|T_c(t,s)\|_{\mathcal{L}(L^q(\Omega))} \leq M\mathrm{e}^{\beta(t-s)} \quad \text{for all} \quad t > s.$$

Then for any $1 \leq r \leq \infty$ there exists a $K \geq 1$ such that

(4.4) $$\|T_c(t,s)\|_{\mathcal{L}(L^r(\Omega))} \leq K\mathrm{e}^{\beta(t-s)} \quad \text{for all} \quad t > s.$$

The constant K can be taken as a continuous function of β, M.

Moreover, for each r with $1 \leq r \leq q \leq \infty$ and for any $\varepsilon > 0$, we have

(4.5) $$\|T_c(t,s)\|_{\mathcal{L}(L^q(\Omega),L^r(\Omega))} \leq M(\beta,\varepsilon)\frac{\mathrm{e}^{(\beta+\varepsilon)(t-s)}}{(t-s)^\delta}, \quad t > s,$$

where $\delta = \frac{N}{2}\left(\frac{1}{r} - \frac{1}{q}\right)$,

(4.6) $$M(\beta,\varepsilon) = \kappa(\beta,M) \begin{cases} \left(\frac{\delta}{\mathrm{e}}\right)^\delta \varepsilon^{-\delta} & \text{if } 0 < \varepsilon < \varepsilon_0 = \frac{\delta}{\mathrm{e}} \\ 1 & \text{if } \varepsilon \geq \varepsilon_0 = \frac{\delta}{\mathrm{e}} \end{cases}$$

and

$$\kappa(\beta,M) = L_0\varepsilon^{\delta_0}\max\{1, M\varepsilon^{-\beta}\}.$$

Note that the constants K and κ in the proposition also depend on q and r but we will not pay attention to this dependence.

Our main argument, further below in the paper, will rely on results of the following type. We start with an evolution operator $T_c(t,s)$ that satisfies the estimate

$$\|T_c(t,s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1 \quad \text{for } t \geq s \text{ and } M_1 > 0$$

for either $s \geq s_0$ or for $t \leq t_0$. Then, we add to $c(t,x)$ a perturbation $p(t,x)$ in the class $C^\theta(\mathbf{R}, L^p(\Omega))$, with $0 < \theta \leq 1$ and some $p > \max(N/2, 1)$, and we want to guarantee that the solutions of the new evolution operator $T_{c+p}(t,s)$ decay exponentially. This means that we want to get estimates of the type

(4.7) $$\|T_{c+p}(t,s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1'\mathrm{e}^{\beta'(t-s)} \quad \text{for all} \quad t > s \quad \text{and some} \quad \beta' < 0$$

and for either $s \geq s_0$ or for $t \leq t_0$. Note also that we can always assume, without loss of generality, that the $L^\infty(\mathbf{R}, L^p(\Omega))$ norms of both $c(t,x)$ and $p(t,x)$ are bounded by R_0, so (4.2) holds for $T_c(t,s)$ and $T_{c+p}(t,s)$.

In this direction, the following important result is a particular case of Corollary 3.3 in Rodríguez-Bernal [33], and it provides sufficient conditions on $p(t,x)$ to ensure that (4.7) holds.

PROPOSITION 4.2. *Assume that*

(4.8) $$\|T_c(t,s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1 \quad \text{for} \quad t \geq s \quad \text{and} \quad M_1 > 0$$

and for either $s \geq s_0$ or for $t \leq t_0$.

Let $p \in C^\theta(\mathbf{R}, L^p(\Omega))$, for some $0 < \theta \leq 1$ and $p > \max(N/2, 1)$, and assume that for $|t|$ sufficiently large, we have $p(t, x) \leq -\varphi(x)$ where

$$\varphi \in C^1(\overline{\Omega}), \quad \varphi \geq 0, \quad and \quad \nabla\varphi \neq 0 \quad at\ the\ points\ at\ which\ \varphi = 0.$$

Then

$$(4.9) \quad \|T_{c+p}(t, s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1' e^{\beta'(t-s)} \quad for\ all \quad t > s \quad and\ some \quad \beta' < 0$$

and for either $s \geq s_0$ or for $t \leq t_0$, with $M_1' = M_1'(M_1, \varphi)$ and $\beta' = \beta'(M_1, \varphi)$.

The constants $M_1' = M_1'(M_1, \varphi)$ and $\beta' = \beta'(M_1, \varphi)$ depend continuously on M_1 and on $\varphi \in C^1(\overline{\Omega})$.

Note that the condition above holds, in particular if $p(t, x) \leq -\delta < 0$ (in which case the constants M_1' and β' can be chosen so that they depend continuously on δ), or if $\varphi \in C_0^1(\overline{\Omega})$ is positive in Ω and $\frac{\partial\varphi}{\partial\vec{n}} < 0$ on $\partial\Omega$. The former is a common situation in the case of Neumann or Robin boundary conditions and the latter in the case of Dirichlet boundary conditions.

In order to apply the above result, we need to show first that (4.8) holds. The next result gives conditions for an evolution operator to have bounds of the type (4.8), see [34], [33]. For this recall the definitions of complete trajectory and of non–degeneracy in Section 2.2, which we apply here to solutions of (4.1). Hence, according to [33], we have

PROPOSITION 4.3. *i) If there exists a positive non-degenerate solution $u(t, s; u_s)$ of (4.1) defined for all $t > s \geq s_0$ such that for some $M > 0$ and some q with $1 \leq q \leq \infty$*

$$\|u(t, s; u_s)\|_{L^q(\Omega)} \leq M,$$

then

$$(4.10) \qquad 0 < M_0 \leq \|T_c(t, s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1 \quad for \quad t \geq s \geq s_0,$$

where M_0, M_1 are independent of t and s and depend continuously on M and $\varphi_0 \in C^1(\overline{\Omega})$.
ii) If there exists a positive complete non-degenerate solution $u(t)$ of (4.1) that is bounded as $t \to -\infty$, i.e.

$$\|u(t)\|_{L^q(\Omega)} \leq M \quad for \quad t \leq t_0$$

then

$$(4.11) \qquad 0 < M_0 \leq \|T_c(t, s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1 \quad for \quad s \leq t \leq t_0$$

where M_0, M_1 are independent of t and s and depend continuously on M and $\varphi_0 \in C^1(\overline{\Omega})$.

4.2. Perturbation and decay of linear systems. In this section we generalize the perturbation result in the previous section to the case of a system of linear equations. The main theorem in this section will be crucial in the analysis of Lotka-Volterra models in the following sections.

Consider the linear coupled non-autonomous system

(4.12)
$$\begin{cases} u_t - d_1\Delta u = a_{11}(t,x)u + a_{12}(t,x)v, & x \in \Omega,\ t > s \\ v_t - d_2\Delta v = a_{21}(t,x)u + a_{22}(t,x)v, & x \in \Omega,\ t > s \\ \mathcal{B}_1 u = 0,\ \mathcal{B}_2 v = 0 \\ u(s) = u_s,\ v(s) = v_s, \end{cases}$$

in $L^q(\Omega, \mathbf{R}^2) \doteq [L^q(\Omega)]^2$. Then define

$$D = \text{diag}(d_1, d_2) \qquad \text{and} \qquad A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

and note that setting $U = \begin{pmatrix} u \\ v \end{pmatrix}$, (4.12) can be written as

$$U_t - D\Delta U = A(t,x)U$$

with boundary conditions $\mathcal{B}U = \begin{pmatrix} \mathcal{B}_1 u \\ \mathcal{B}_2 v \end{pmatrix} = 0$ on the boundary of Ω.

If $A \in C^\theta(\mathbf{R}, L^p(\Omega, \mathbf{R}^4))$, with $0 < \theta \le 1$, $p > N/2$ and $p > q \ge 1$, the existence of a unique solution $U(t, s; U_s)$ of (4.12), in $L^q(\Omega, \mathbf{R}^2)$, can be obtained from Theorems 11.2, 11.3 and 11.4 in Amann [1]. Thus, the time-dependent operator $-D\Delta - A(t,x)$ generates an evolution operator, $T_A(t,s)$, in $L^q(\Omega, \mathbf{R}^2)$ (Theorem 4.4.1 in Amann [2]) via the definition $T_A(t,s)U_s = U(t,s;U_s)$.

The following result, analogous to (4.2), can be proved along the lines of the scalar arguments in Rodríguez-Bernal [33], [32] and Robinson et al. [31].

PROPOSITION 4.4. *For any $1 \le q \le r \le \infty$, and $R_0 > 0$ there exist $L_0 = L_0(R_0, r, q) > 0$ and $\delta_0 = \delta_0(R_0, r, q) > 0$ such that the evolution operator $T_A(t,s)$ satisfies*

(4.13)
$$\|T_A(t,s)U_s\|_{L^r(\Omega,\mathbf{R}^2)} \le L_0 \frac{e^{\delta_0(t-s)}}{(t-s)^{\frac{N}{2}\left(\frac{1}{q} - \frac{1}{r}\right)}} \|U_s\|_{L^q(\Omega,\mathbf{R}^2)},$$

for every $\|A\|_{L^\infty(\mathbf{R}, L^p(\Omega, \mathbf{R}^4))} \le R_0$. In particular, $T_A(t,s)$ extends to an evolution operator in $L^q(\Omega, \mathbf{R}^2)$ for every $1 \le q < \infty$.

Furthermore, the results of Proposition 4.1 for the scalar case remain true for system (4.12).

Along the same lines as for scalar equations, we consider the linear uncoupled system

(4.14)
$$\begin{cases} u_t - d_1\Delta u = q_{11}(t,x)u, & x \in \Omega,\ t > s \\ v_t - d_2\Delta v = q_{22}(t,x)v, & x \in \Omega,\ t > s \\ \mathcal{B}_1 u = 0,\ \mathcal{B}_2 v = 0 \\ u(s) = u_s,\ v(s) = v_s. \end{cases}$$

Observe that with the notations above and setting

$$Q = \text{diag}(q_{11}, q_{22}),$$

then the evolution operator $T_Q(t,s)$ is well defined in $L^q(\Omega, \mathbf{R}^2)$, $1 \le q < \infty$.

Now we assume that each separate equation in (4.14) satisfies

$$\|T_{q_{ii}}(t,s)\|_{\mathcal{L}(L^q(\Omega))} \le M_1, \quad t > s,$$

with M_1 independent of t and s and for either $t \leq t_0$ or $s \geq s_0$. Therefore the evolution operator $T_Q(t, s)$ satisfies (4.8).

Our goal is to give conditions on the coupling perturbations such that the solutions of the perturbed system

$$\begin{cases} u_t - d_1\Delta u = q_{11}(t,x)u + p_{11}(t,x)u + p_{12}(t,x)v, & x \in \Omega,\ t > s \\ v_t - d_2\Delta v = q_{22}(t,x)v + p_{21}(t,x)u + p_{22}(t,x)v, & x \in \Omega,\ t > s \\ \mathcal{B}_1 u = 0,\ \mathcal{B}_2 v = 0 \\ u(s) = u_s,\ v(s) = v_s, \end{cases}$$

decay exponentially. Note that the perturbed system can be written as

$$(4.15) \qquad\qquad U_t - D\Delta U = Q(t,x)U + P(t,x)U$$

with

$$Q = \mathrm{diag}(q_{11}, q_{22}), \quad P = \begin{pmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{pmatrix}, \quad \text{and} \quad U = \begin{pmatrix} u \\ v \end{pmatrix},$$

with $Q, P \in C^\theta(\mathbf{R}, L^p(\Omega, \mathbf{R}^4))$, with $0 < \theta \leq 1$, $p > \max(N/2, 1)$.

Hence our goal is to obtain an estimate of the type

$$(4.16) \quad \|T_{Q+P}(t,s)\|_{\mathcal{L}(L^q(\Omega, \mathbf{R}^2))} \leq M_1' e^{\beta'(t-s)} \quad \text{for all} \quad t > s \text{ and some } \beta' < 0$$

and for either $s \geq s_0$ or for $t \leq t_0$.

Note that again we will assume, without loss of generality, that all the evolution operators considered satisfy (4.13) with the same constants L_0 and δ_0.

In what follows we will make use of the following singular Gronwall lemma (see Henry [16]):

LEMMA 4.5. **(A singular Gronwall lemma)**

Assume that $a \in L^\infty(\tau_0, \infty)$ with $\tau_0 \geq -\infty$ and that $z(t) \geq 0$ is a locally bounded function that for $t \geq s > \tau_0$ satisfies

$$(4.17) \qquad\qquad z(t) \leq A + \int_s^t \frac{a(\tau)}{(t-\tau)^\delta} z(\tau)\,\mathrm{d}\tau$$

with $\delta < 1$. Then we have for $t \geq s > \tau_0$

$$0 \leq z(t) \leq A(\delta)e^{\gamma(t-s)}$$

with $\gamma = \gamma(a, s, \delta) = \left(\|a\|_{L^\infty(s,\infty)}\Gamma(1-\delta)\right)^{1/(1-\delta)}$ and $A(\delta)$ depends only on the constants A and δ but not on the function $a(\cdot)$ or on s, γ or τ_0.

Our next result states that if the diagonal perturbing terms $p_{ii}(t,x)$ are sufficiently strong and the coupling terms $p_{ij}(t,x)$, $i \neq j$, are 'small' at $\pm\infty$, then (4.16) is achieved.

THEOREM 4.6. *With the notations in (4.15), assume that the scalar evolution operators $T_{q_{ii}}(t,s)$ satisfy*

$$(4.18) \qquad\qquad \|T_{q_{ii}}(t,s)\|_{\mathcal{L}(L^q(\Omega))} \leq M_1, \quad t > s,$$

with M_1 independent of t and s and for either $t \leq t_0$ or $s \geq s_0$.

Assume also that $p_{ii}(t,x)$ satisfies $p_{ii}(t,x) \leq -\varphi_{ii}(x)$ with $\varphi_{ii}(x)$ as in Proposition 4.2.

Then there exists a $\rho = \rho(M_1, \varphi_{11}, \varphi_{22}) > 0$ such that if

(4.19) $$\limsup_{|t|\to\infty} \|p_{12}(t)\|_{L^p(\Omega)} \limsup_{|t|\to\infty} \|p_{21}(t)\|_{L^p(\Omega)} \leq \rho^2$$

then

(4.20) $\|T_{Q+P}(t,s)\|_{\mathcal{L}(L^q(\Omega,\mathbf{R}^2))} \leq M_1'' e^{\beta''(t-s)}$ *for all $t > s$ and some $\beta'' < 0$*

and for either $s \geq s_0$ or for $t \leq t_0$, where $M_1'' = M_1''(M_1, \varphi_{11}, \varphi_{22})$ and $\beta'' = \beta''(M_1, \varphi_{11}, \varphi_{22})$.

  The constants ρ, M_1'' and β'' depend continuously on M_1 and $\varphi_{11}, \varphi_{22}$ as in Proposition 4.2.

  Proof. Note that, using Proposition 4.4, we just need to prove the result for some suitably chosen $1 \leq q < \infty$. We proceed in several steps.

  Step 1: If we define

$$P_1 = \left(\begin{array}{cc} p_{11} & 0 \\ 0 & p_{22} \end{array} \right)$$

then Proposition 4.2 applied to each separate equation gives the estimate

(4.21) $\|T_{Q+P_1}(t,s)\|_{\mathcal{L}(L^q(\Omega,\mathbf{R}^2))} \leq M_1' e^{\beta'(t-s)}$ for all $t > s$ and some $\beta' < 0$

and for either $s \geq s_0$ or for $t \leq t_0$, with $M_1' = M_1'(M_1, \varphi_{11}, \varphi_{22})$ and $\beta' = \beta'(M_1, \varphi_{11}, \varphi_{22})$.

  Step 2: We will show that there exists a $\rho = \rho(M_1', \beta')$, which depends continuously on M_1', β', such that if

$$\|p_{12}\|_{L^\infty(\mathbf{R}, L^p(\Omega))} \leq \rho \quad \text{and} \quad \|p_{21}\|_{L^\infty(\mathbf{R}, L^p(\Omega))} \leq \rho$$

then

(4.22) $\|T_{Q+P}(t,s)\|_{\mathcal{L}(L^q(\Omega,\mathbf{R}^2))} \leq M_1'' e^{\beta''(t-s)}$ for all $t > s$ and some $\beta'' < 0$

and for either $s \geq s_0$ or for $t \leq t_0$, with

$$P = P_1 + P_2, \qquad P_2 = \left(\begin{array}{cc} 0 & p_{12} \\ p_{21} & 0 \end{array} \right),$$

where $M_1'' = M_1''(M_1', \beta', \rho)$ and $\beta'' = \beta''(M_1', \beta', \rho)$, depend continuously on M_1', β', ρ.

  In fact, we have, by the variation of constants formula, that for every $U_0 \in L^q(\Omega, \mathbf{R}^2)$ the solution $U(t,s;U_0) = T_{Q+P}(t,s)U_0$ of (4.15) satisfies for $t \geq s$,

$$U(t,s;U_0) = T_{Q+P_1}(t,s)U_0 + \int_s^t T_{Q+P_1}(t,\tau)P_2(\tau)U(\tau,s;U_0)\,d\tau.$$

  Now we choose q such that $p \geq q'$, so that $1/p + 1/q \leq 1$. In what follows we will apply (4.5) with $\frac{1}{r} = \frac{1}{p} + \frac{1}{q}$, and so with $\delta = N/2p$. With this choice, we have (4.21) and from (4.5)

$$\|T_{Q+P_1}(t,s)\|_{\mathcal{L}(L^r(\Omega,\mathbf{R}^2),L^q(\Omega,\mathbf{R}^2))} \leq M(\beta',\varepsilon) \frac{e^{(\beta'+\varepsilon)(t-s)}}{(t-s)^{\frac{N}{2p}}},$$

where $M(\beta', \varepsilon)$ is as in (4.6).

Since $P_2(\tau) \in L^p(\Omega, \mathbf{R}^2)$ and $U(\tau, s; U_0) \in L^q(\Omega, \mathbf{R}^2)$, then the term $P_2(\tau)U(\tau, s; U_0)$ can be estimated, using Hölder's inequality, in $L^r(\Omega, \mathbf{R}^2)$ with $\frac{1}{r} = \frac{1}{p} + \frac{1}{q}$. Thus,

$$\|U(t, s; U_0)\|_{L^q(\Omega, \mathbf{R}^2)} \leq M'_1 e^{(\beta'+\varepsilon)(t-s)}\|U_0\|_{L^q(\Omega, \mathbf{R}^2)} +$$
$$M(\beta', \varepsilon) \int_s^t \frac{e^{(\beta'+\varepsilon)(t-\tau)}}{(t-\tau)^{\frac{N}{2p}}} \|P_2(\tau)\|_{L^p(\Omega, \mathbf{R}^2)} \|U(\tau, s; U_0)\|_{L^q(\Omega, \mathbf{R}^2)} d\tau.$$

Then, multiplying by $e^{-(\beta'+\varepsilon)(t-s)}$, and denoting $A = M'_1\|U_0\|_{L^q(\Omega, \mathbf{R}^2)}$,

$$z(t) = e^{-(\beta'+\varepsilon)(t-s)}\|U(t, s; U_0)\|_{L^q(\Omega, \mathbf{R}^2)}, \quad \text{and} \quad a(\tau) = M(\beta', \varepsilon)\|P_2(\tau)\|_{L^p(\Omega, \mathbf{R}^2)}$$

we get, for all $t \geq s$,

$$z(t) \leq A + \int_s^t \frac{a(\tau)}{(\tau-s)^{\frac{N}{2p}}} z(\tau) \, d\tau.$$

We can apply the singular Gronwall Lemma above with $\delta = \frac{N}{2p} < 1$ and we get,

(4.23) $$\|U(t, s; U_0)\|_{L^q(\Omega, \mathbf{R}^2)} \leq M''_1 e^{(\beta'+\mu(\varepsilon))(t-s)}\|U_0\|_{L^q(\Omega, \mathbf{R}^2)}, \quad t \geq s$$

where

$$\mu(\varepsilon) = \varepsilon + \left(M(\beta', \varepsilon)\Gamma(1-\delta)\|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))}\right)^{\frac{1}{1-\delta}}.$$

Recalling (4.6), we get that

$$\mu(\varepsilon) = \begin{cases} \varepsilon + \varepsilon^{\frac{-\delta}{1-\delta}} A_0 \|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))}^{\frac{1}{1-\delta}} & \text{if } 0 < \varepsilon < \varepsilon_0 = \frac{\delta}{e} \\ \varepsilon + A_1 \|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))}^{\frac{1}{1-\delta}} & \text{if } \varepsilon \geq \varepsilon_0, \end{cases}$$

where

$$A_1 = \left(L_0 e^{\delta_0} \max\{1, M'_1 e^{-\beta'}\}\Gamma(1-\delta)\right)^{1/(1-\delta)}, \quad A_0 = A_1 \left(\frac{\delta}{e}\right)^{\delta/(1-\delta)},$$

and L_0 and δ_0 are the constants in (4.2).

Thus $\mu(0) = \mu(\infty) = \infty$. But the function

$$h(\varepsilon) = \varepsilon + \varepsilon^{\frac{-\delta}{1-\delta}} A_0 \|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))}^{\frac{1}{1-\delta}}$$

has a unique minimum at

$$\varepsilon_1 = (A_0 \frac{\delta}{1-\delta})^{1-\delta} \|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))},$$

and

$$h(\varepsilon_1) = \frac{1}{\delta^\delta}(\frac{A_0}{1-\delta})^{1-\delta} \|P_2\|_{L^\infty((s,\infty),L^p(\Omega,\mathbf{R}^2))}.$$

Therefore, comparing ε_0 and ε_1, and minimizing $\mu(\varepsilon)$ leads to

$$\|U(t, s; U_0)\|_{L^q(\Omega, \mathbf{R}^2)} \leq M''_1 e^{\beta''(t-s)}\|U_0\|_{L^q(\Omega, \mathbf{R}^2)}, \quad t \geq s$$

with

$$\beta'' = \beta' + \min_{\{\varepsilon > 0\}} \mu(\varepsilon) =$$

$$= \beta' + \begin{cases} c_0 \|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))}, & \text{if } \|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))} \leq s^*, \\ c_1 + c_2 \|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))}^{\frac{1}{1-\delta}}, & \text{if } \|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))} \geq s^*, \end{cases}$$

where

$$c_0 = \frac{1}{\delta^\delta} \left(\frac{A_0}{1-\delta}\right)^{1-\delta}, \quad c_1 = \frac{\delta}{e}, \quad c_2 = A_1, \quad s^* = \frac{\delta}{e} \left(\frac{1-\delta}{A_0 \delta}\right)^{1-\delta}.$$

Thus, it is then clear that (4.22) follows, i.e. $\beta'' < 0$, provided that

$$\|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))} < \min\left\{s^*, \frac{-\beta'}{c_0}\right\},$$

which reads

(4.24) $$\|P_2\|_{L^\infty((s,\infty), L^p(\Omega, \mathbf{R}^2))} < \rho := \delta \left(\frac{1-\delta}{\delta A_0}\right)^{1-\delta} \min\left\{-\beta', \frac{1}{e}\right\}.$$

Step 3: Now we show that the result in Step 2 above can be obtained only in terms of $\limsup_{|t|\to\infty} \|P_2(t)\|_{L^p(\Omega, \mathbf{R}^2)}$.

In fact, note that from (4.24), if we take $s \geq s_0$ sufficiently large, the conclusion with $\limsup_{t\to\infty} \|P_2(t)\|_{L^p(\Omega, \mathbf{R}^2)}$ is clear.

On the other hand, observe that we can set $P_2 = 0$ for $t \geq t_0$ and we still have (4.23) for $s \leq t \leq t_0$. Taking then t_0 very negative, (4.24) gives the result for $\limsup_{t\to-\infty} \|P_2(t)\|_{L^p(\Omega, \mathbf{R}^2)}$.

In particular, (4.22) follows, provided that

(4.25) $$\limsup_{|t|\to\infty} \|P_2(t)\|_{L^p(\Omega, \mathbf{R}^2)} < \rho,$$

with ρ as in (4.24).

Step 4: The change of variables

$$U = \begin{pmatrix} u \\ v \end{pmatrix} \to V = \begin{pmatrix} \alpha u \\ \beta v \end{pmatrix}$$

with $\alpha, \beta > 0$, transforms the system (4.15) into

$$V_t - D\Delta V = Q(t,x)V + \tilde{P}(t,x)V$$

with

$$D = \mathrm{diag}(d_1, d_2), \; Q = \mathrm{diag}(q_{11}, q_{22}), \; \tilde{P} = \begin{pmatrix} p_{11} & \frac{\alpha}{\beta} p_{12} \\ \frac{\beta}{\alpha} p_{21} & p_{22} \end{pmatrix}.$$

Hence, we can apply Step 3 provided

$$\frac{\alpha}{\beta} \limsup_{|t|\to\infty} \|p_{12}(t)\|_{L^p(\Omega)} \leq \rho \quad \text{and} \quad \frac{\beta}{\alpha} \limsup_{|t|\to\infty} \|p_{21}(t)\|_{L^p(\Omega)} \leq \rho,$$

with $\rho > 0$ as in (4.24). We can choose α, β such that the above inequalities are satisfied if

$$\limsup_{|t|\to\infty} \|p_{12}(t)\|_{L^p(\Omega)} \limsup_{|t|\to\infty} \|p_{21}(t)\|_{L^p(\Omega)} \leq \rho^2$$

with $\rho > 0$ as in (4.24). $\square$

REMARK 4.7. *Note that (4.24) gives a quantitative threshold for the size of the perturbation. In fact, from (4.24) and the expression of A_0, it can be deduced that*

$$\rho = \rho(M_1', \beta') = \frac{\mathrm{e}^\delta (1-\delta)^{1-\delta}}{\Gamma(1-\delta)} \frac{\min\{-\beta', \frac{1}{\mathrm{e}}\}}{L_0 \mathrm{e}^{\delta_0} \max\{1, M_1' \mathrm{e}^{-\beta'}\}},$$

where M_1', β' are from Step 1.

Observe that Step 4 above is the only place where we used the fact that the system has only two components.

5. Attracting trajectories for general non-autonomous nonlinear systems. In this section we sketch out our approach to the existence of asymptotically stable complete trajectories for Lotka-Volterra systems. The key point is to write the equation satisfied by the difference of two solutions as a perturbation of an associated linear system. Using then the permanence results in Section 3 we can apply Theorem 4.6 to conclude that the difference of two solutions converges to zero as $t \to \infty$. A similar convergence result as the initial time $s \to -\infty$ will imply the uniqueness of complete non–degenerate solutions, which moreover describes the pullback behavior of the system.

First we treat the case of general non-autonomous nonlinear systems, before specializing to Lotka-Volterra models. Consider the general non-autonomous nonlinear system

(5.1)
$$\begin{cases} u_t - d_1 \Delta u = u f(t, x, u, v) & x \in \Omega, \ t > s \\ v_t - d_2 \Delta v = v g(t, x, u, v) & x \in \Omega, \ t > s \\ \mathcal{B}_1 u = 0, \ \mathcal{B}_2 v = 0 & x \in \partial\Omega, \ t > s \\ u(s) = u_s, \ v(s) = v_s, \end{cases}$$

We now sketch our strategy for analyzing the asymptotic behaviour of solutions to (5.1). Consider two different pairs of non-negative initial conditions (u_s^1, v_s^1) and (u_s^2, v_s^2) and consider the corresponding solutions of (5.1), $U_1 = \begin{pmatrix} u_1 \\ v_1 \end{pmatrix}$ and $U_2 = \begin{pmatrix} u_2 \\ v_2 \end{pmatrix}$, respectively. Write $y = u_2 - u_1$ and $z = v_2 - v_1$. Then, (y, z) satisfies

(5.2)
$$\begin{cases} y_t - d_1 \Delta y = q_{11}(t, x) y + p_{11}(t, x) y + p_{12}(t, x) z & x \in \Omega, \ t > s \\ z_t - d_2 \Delta z = q_{22}(t, x) z + p_{21}(t, x) y + p_{22}(t, x) z & x \in \Omega, \ t > s \\ \mathcal{B}_1 y = 0, \ \mathcal{B}_2 z = 0 & x \in \partial\Omega, \ t > s \\ y(s) = y_s, \ z(s) = z_s, \end{cases}$$

with $y_s = u_s^2 - u_s^1$, $z_s = v_s^2 - v_s^1$ and

$$\begin{aligned}
q_{11}(t, x) &= f(t, x, u_2, v_2), & q_{22}(t, x) &= g(t, x, u_2, v_2) \\
p_{11}(t, x) &= u_1 \frac{f(t,x,u_2,v_1) - f(t,x,u_1,v_1)}{u_2 - u_1}, & p_{12}(t, x) &= u_1 \frac{f(t,x,u_2,v_2) - f(t,x,u_2,v_1)}{v_2 - v_1}, \\
p_{21}(t, x) &= v_1 \frac{g(t,x,u_2,v_1) - g(t,x,u_1,v_1)}{u_2 - u_1}, & p_{22}(t, x) &= v_1 \frac{g(t,x,u_2,v_2) - g(t,x,u_2,v_1)}{v_2 - v_1}.
\end{aligned}$$

Most of the analysis that follows in the next section will be based on proving that the following results can be applied. The first one gives sufficient conditions to guarantee that two solutions have the same forwards asymptotic behaviour, while the second gives a criterion to prove the coincidence of two complete trajectories and also describes the pullback behavior of solutions.

THEOREM 5.1. **(Forwards behaviour)**

Assume that both solutions of (5.1), $U_1 = \begin{pmatrix} u_1 \\ v_1 \end{pmatrix}$ and $U_2 = \begin{pmatrix} u_2 \\ v_2 \end{pmatrix}$ are globally defined and bounded in $L^\infty(\Omega, \mathbf{R}^2)$ for $t > s > t_0$. Moreover, suppose that u_1, v_1 are positive in Ω and $U_2(t)$ is positive, non-degenerate for $t > t_0$ and for some $p > \max(N/2, 1)$ and $0 < \theta \le 1$, the coefficients in (5.2) satisfy $p_{ij}, q_{ii} \in C^\theta(\mathbf{R}, L^p(\Omega))$ for $i, j = 1, 2$ and $p_{ii}(t, x) \le -\varphi_{ii}(x)$, for $t > t_0$, with $\varphi_{ii}(x)$ as in Proposition 4.2.

Then there exists a ρ such that if

$$(5.3) \qquad \limsup_{t \to \infty} \|p_{12}(t)\|_{L^p(\Omega)} \limsup_{t \to \infty} \|p_{21}(t)\|_{L^p(\Omega)} \le \rho^2,$$

both solutions have the same forwards asymptotic behaviour, i.e.,

$$U_1(t) - U_2(t) \to 0 \quad \text{exponentially in } C^1_{\mathcal{B}_1}(\overline{\Omega}) \times C^1_{\mathcal{B}_2}(\overline{\Omega}) \quad \text{as} \quad t \to \infty.$$

In particular, $U_1(t)$ is also non-degenerate at $+\infty$.

Proof. Clearly, (5.2) can be written as

$$W_t - D\Delta W = QW + PW$$

where

$$(5.4) \quad D = \text{diag}(d_1, d_2), \ Q = \text{diag}(q_{11}, q_{22}), \ P = \begin{pmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{pmatrix}, \quad W = \begin{pmatrix} y \\ z \end{pmatrix}.$$

Since $U_2 = \begin{pmatrix} u_2 \\ v_2 \end{pmatrix}$ is a positive, bounded and non-degenerate solution, for $t > s > t_0$, of the diagonal system

$$W_t - D\Delta W = QW,$$

it follows from Propositions 4.3 and 4.4 that for any $1 \le q < \infty$,

$$(5.5) \qquad \|T_Q(t, s)\|_{\mathcal{L}(L^q(\Omega, \mathbf{R}^2))} \le M_1, \quad t > s > t_0,$$

with M_1 independent of t and s, $t > s > t_0$.

Then, we apply Theorem 4.6 to obtain that there exists $\rho > 0$ such that if (5.3) holds, then

$$\|T_{Q+P}(t, s)\|_{\mathcal{L}(L^q(\Omega, \mathbf{R}^2))} \le M_1'' e^{\beta''(t-s)} \quad \text{for all} \quad t > s > t_0 \quad \text{and some} \quad \beta'' < 0.$$

Thus, from Proposition 4.4 (see also Proposition 4.1), we have, writing $W_s = (y_s, z_s)$ and for $t > s > t_0$,

$$(5.6) \qquad \|W(t, s; W_s)\|_{L^\infty(\Omega, \mathbf{R}^2)} \le M_2 e^{\beta''(t-s)} \|W_s\|_{L^\infty(\Omega, \mathbf{R}^2)} \to 0, \quad t \to \infty.$$

The uniform forwards convergence of trajectories follows. Standard parabolic regularization implies the $C^1_{\mathcal{B}_1}(\overline{\Omega}) \times C^1_{\mathcal{B}_2}(\overline{\Omega})$ convergence. □

In the following result we use similar arguments to prove the coincidence of complete non-degenerate trajectories, and show that such a trajectory, in case it exists, attracts (in the pullback sense) all bounded positive trajectories. In particular, the following results guarantee the uniqueness of complete non–degenerate solutions.

THEOREM 5.2. **(Coincidence of Complete trajectories and pullback behaviour)**

Assume that $U_1 = \begin{pmatrix} u_1 \\ v_1 \end{pmatrix}$ is a complete trajectory that is bounded in $L^\infty(\Omega, \mathbf{R}^2)$ at $-\infty$, and non-degenerate for $t \leq t_0$. Suppose further that for some $p > \max(N/2, 1)$ and $0 < \theta \leq 1$, the coefficients in (5.2) satisfy $p_{ij}, q_{ii} \in C^\theta(\mathbf{R}, L^p(\Omega))$ for $i, j = 1, 2$ and $p_{ii}(t, x) \leq -\varphi_{ii}(x)$, for $t \leq t_0$, with $\varphi_{ii}(x)$ as in Proposition 4.2.

Then there exists a $\rho > 0$ such that if

$$(5.7) \qquad \limsup_{t \to -\infty} \|p_{12}(t)\|_{L^p(\Omega)} \limsup_{t \to -\infty} \|p_{21}(t)\|_{L^p(\Omega)} \leq \rho^2$$

then:

(i) *$U_1(t)$ is the unique complete trajectory that is bounded in $L^\infty(\Omega, \mathbf{R}^2)$ at $-\infty$, and*

(ii) *if $U_2(s)$ is a family of positive initial data which is bounded in $L^\infty(\Omega, \mathbf{R}^2)$ as $s \to -\infty$ then $U_1(\cdot)$ pullback attracts $S(t, s)U_2(s)$, i.e. for any $t \in \mathbf{R}$*

$$S(t, s)U_2(s) - U_1(t) \to 0 \quad \text{in } C^1_{\mathcal{B}_1}(\overline{\Omega}) \times C^1_{\mathcal{B}_2}(\overline{\Omega}) \quad \text{as} \quad s \to -\infty.$$

Proof.

(i) Let $U_2(t)$ be a complete trajectory bounded in $L^\infty(\Omega, \mathbf{R}^2)$ at $-\infty$. We write (5.2) as

$$W_t - D\Delta W = QW + PW, \qquad W(s) = W_s = U_2(s) - U_1(s)$$

where Q, P and W are defined as in (5.4). Since $U_1 = (u_1, v_1)$ is a complete, positive bounded and non-degenerate solution of the diagonal system

$$W_t - D\Delta W = QW,$$

it follows from Proposition 4.3 that for any $1 \leq q < \infty$, and sufficiently negative t_0,

$$(5.8) \qquad \|T_Q(t, s)\|_{\mathcal{L}(L^q(\Omega, \mathbf{R}^2))} \leq M_1, \quad s < t \leq t_0,$$

with M_1 independent of t and s.

Then, we apply Theorem 4.6 to obtain that there exists $\rho > 0$ such that if (5.7) holds, then

$$\|T_{Q+P}(t, s)\|_{\mathcal{L}(L^q(\Omega, \mathbf{R}^2))} \leq M_1'' e^{\beta''(t-s)} \quad \text{for all } s < t \leq t_0 \quad \text{and some} \quad \beta'' < 0.$$

Thus,

$$\|U_1(t) - U_2(t)\|_{L^q(\Omega, \mathbf{R}^2)} = \|W(t, s; W_s)\|_{L^q(\Omega, \mathbf{R}^2)} \leq M_1'' e^{\beta''(t-s)} \|W_s\|_{L^q(\Omega, \mathbf{R}^2)}.$$
(5.9)

The right hand side tends to zero as $s \to -\infty$ since both complete trajectories are bounded, and the result follows.

(ii) Proceeding as above, we obtain

$$\|U_1(t) - S(t,s)U_2(s)\|_{L^q(\Omega,\mathbf{R}^2)} \leq M_1'' e^{\beta''(t-s)}\|U_1(s) - U_2(s)\|_{L^q(\Omega,\mathbf{R}^2)}.$$

for $s < t \leq t_0$ and some $\beta'' < 0$.

Thus, from Proposition 4.4 (see also Proposition 4.1), we get for $s < t \leq t_0$,

$$\|U_1(t) - S(t,s)U_2(s)\|_{L^\infty(\Omega,\mathbf{R}^2)} \leq M_2 e^{\beta''(t-s)}\|U_1(s) - U_2(s)\|_{L^q(\Omega,\mathbf{R}^2)} \to 0$$

as $s \to -\infty$. Standard parabolic regularization implies the convergence in $C^1_{\mathcal{B}_1}(\overline{\Omega}) \times C^1_{\mathcal{B}_2}(\overline{\Omega})$.

Now for every $\tau \geq t_0$, using the continuity of the nonlinear evolution process, we get, as $s \to -\infty$,

$$U_1(\tau,s) = S(\tau,t)U_1(t,s) \to S(\tau,t)U_2(t).$$

□

The theorems above may perhaps appear more general than they really are. To verify the assumptions involved one must restrict the nonlinearities of the system and carefully choose the classes of solutions being considered. For example the conditions $p_{ii}(t,x) \leq -\varphi_{ii}(x)$ and the smallness conditions on $p_{ij}(t,x)$, $i \neq j$ depend on the particular solutions considered.

Nevertheless, in the next section we will show that the assumptions required can be verified for our example of a general non-autonomous Lotka-Volterra system.

6. Attracting trajectories for non-autonomous Lotka–Volterra systems. As (5.1) is far too general to apply Theorems 5.1 and 5.2 in a straightforward manner, in this section we apply these results to the solutions of (3.1). Note that we handle the three cases, competition, symbiosis and prey-predator, in a unified way.

Then, for the difference of two solutions the coefficients in (5.2) are given by

$$q_{11}(t,x) = \lambda(t,x) - a(t,x)u_2 - b(t,x)v_2, \quad q_{22}(t,x) = \mu(t,x) - c(t,x)u_2 - d(t,x)v_2,$$

$$p_{11}(t,x) = -a(t,x)u_1, \qquad\qquad\qquad p_{12}(t,x) = -b(t,x)u_1,$$

$$p_{21}(t,x) = -c(t,x)v_1, \qquad\qquad\qquad p_{22}(t,x) = -d(t,x)v_1.$$
(6.1)

Hence, to apply Theorems 5.1 or 5.2, since $a_L, d_L > 0$ and $u_1, v_1 \geq 0$, in order to find positive functions $\varphi_{ii}(x)$ such that $p_{ii}(t,x) \leq -\varphi_{ii}(x)$, $i = 1,2$ we need positive functions $\psi_{ii}(x)$ such that $\psi_{11}(x) \leq u_1(t,x)$ and $\psi_{22}(x) \leq v_1(t,x)$, that is, we must consider non–degenerate solutions. The results in Section 3.4 guarantee then that all solutions are non–degenerate.

On the other hand we must show that the product of the coupling terms

$$p_{12}(t,x)p_{21}(t,x)$$

is small at $\pm\infty$. Having obtained bounds on u_1, v_1 this will be achieved by a smallness condition on the coefficients $b(t,x)$ or $c(t,x)$.

But note that the non-degeneracy of solutions above depends on the functions $b(t,x)$ and $c(t,x)$ themselves. Therefore, we will use the results in Section 3.4 which tell that solutions of (3.1) are non-degenerate for all sufficiently small "coupling"

coefficients $b(t, x)$ or $c(t, x)$ and that the functions $\psi_{ii}(x)$, $i = 1, 2$ do not converge to zero as b or c vanish.

We first start with the forwards behaviour in Theorem 5.1. Then we can prove

THEOREM 6.1. *There exists $\rho_0(M_\infty, N_\infty) > 0$, where M_∞ and N_∞ are given in Theorem 3.5, such that if*

$$\limsup_{t \to \infty} \|b\|_{L^\infty(\Omega)} \limsup_{t \to \infty} \|c\|_{L^\infty(\Omega)} < \rho_0(M_\infty, N_\infty),$$

and for some t_0 the coefficients of (3.1) satisfy for $t \geq t_0$ the assumptions of Theorem 3.14, then for any bounded set of positive initial data bounded away from zero, all solutions of (3.1) that start at a sufficiently large $s > t_0$, have the same asymptotic behaviour as $t \to \infty$.

In particular, all complete positive trajectories in the pullback attractor have the same asymptotic behaviour as $t \to \infty$.

Proof. Note that Theorem 3.14 implies that all forwards solutions of (3.1) that start at $s \geq t_0$ are equi-non-degenerate with respect to a bounded set of initial data $u_s > 0$, $v_s > 0$, bounded away from zero, and the coefficients. In particular, from Propositions 4.2 and 4.4 the constant M_1 in (5.5) can be taken independent of such $u_s > 0$, $v_s > 0$ and the coefficients.

Moreover, for such initial data and $t > s \geq t_0$, we have in (6.1)

$$p_{11}(t, x) = -a(t, x)u_1 \leq -a_L \psi_{11}(x) = -\varphi_{11}(x),$$

$$p_{22}(t, x) = -d(t, x)v_1 \leq -d_L \psi_{22}(x) = -\varphi_{22}(x)$$

with $\psi_{11}(x)$ and $\psi_{22}(x)$ independent $u_s > 0$, $v_s > 0$ and of the coefficients. In particular $\varphi_{11}(x)$, $\varphi_{22}(x)$ satisfy the assumptions in Proposition 4.2.

Hence the threshold value $\rho > 0$ in Theorem 5.1 is also uniform for $u_s > 0$, $v_s > 0$ and of the coefficients as in Theorem 3.14.

Now we have in (6.1) $p_{12}(t, x) = -b(t, x)u_1$, $p_{21}(t, x) = -c(t, x)v_1$ and hence (5.3) is satisfied if

$$\limsup_{t \to \infty} \|b\|_{L^\infty(\Omega)} \limsup_{t \to \infty} \|c\|_{L^\infty(\Omega)} < \rho^2(p, \Omega, M_\infty, N_\infty) = \rho_0,$$

where M_∞ and N_∞ are given in Theorem 3.5.

Therefore, from Theorem 5.1, all solutions have the same forwards behaviour. □

Our next result proves that if there is a complete trajectory that is non-degenerate at $-\infty$, then it must be unique and be pullback attracting, as in Theorem 5.2:

THEOREM 6.2. *Assume there exists a complete, bounded solution of (3.1) that is non-degenerate at $-\infty$, $U^*(t)$, $t \in \mathbf{R}$.*

Then there exists $\rho_0(M_\infty, N_\infty) > 0$, where M_∞ and N_∞ are given in Theorem 3.5, such that if

$$\limsup_{t \to -\infty} \|b\|_{L^\infty(\Omega)} \limsup_{t \to -\infty} \|c\|_{L^\infty(\Omega)} < \rho_0(M_\infty, N_\infty),$$

and for some t_0 the coefficients of (3.1) satisfy for $t \leq t_0$ the assumptions of Theorem 3.14, then $U^*(t)$ is the unique bounded complete solution of (3.1) that is non-degenerate at $-\infty$. Moreover, for every $t \in \mathbf{R}$, $U^*(t)$ pullback attracts solutions $U_1(t, s)$ such that $U_1(s)$ are positive and bounded as $s \to -\infty$.

If in addition

$$\limsup_{t\to\infty} \|b\|_{L^\infty(\Omega)} \limsup_{t\to\infty} \|c\|_{L^\infty(\Omega)} < \rho_0(M_\infty, N_\infty),$$

and for some t_1 the coefficients of (3.1) satisfy for $t \geq t_1$ the assumptions of Theorem 3.14, then for any $s \in \mathbf{R}$ and for any positive solution $U(t,s)$ of (3.1) we have

$$U(t,s) - U^*(t) \to 0 \qquad as \quad t \to \infty.$$

Proof. Assume there exists a complete, bounded non-degenerate solution at $-\infty$. Then Theorem 3.14 implies that all bounded non-degenerate solution at $-\infty$ are equi-non-degenerate with respect to the coefficients. In particular, from Propositions 4.2 and 4.4 the constant M_1 in (5.5) can be taken independent of the complete non-degenerate solution under consideration and of the coefficients. Moreover, we have in (6.1)

$$p_{11}(t,x) = -a(t,x)u_1 \leq -a_L \psi_{11}(x) = -\varphi_{11}(x),$$
$$p_{22}(t,x) = -d(t,x)v_1 \leq -d_L \psi_{22}(x) = -\varphi_{22}(x)$$

with $\psi_{11}(x)$ and $\psi_{22}(x)$ independent of the complete non-degenerate solution and of the coefficients. In particular $\varphi_{11}(x)$, $\varphi_{22}(x)$ satisfy the assumptions in Proposition 4.2.

Hence the threshold value $\rho > 0$ in Theorem 5.2 is also independent of the complete non-degenerate solution and of the coefficients.

Now we have in (6.1) $p_{12}(t,x) = -b(t,x)u_1$, $p_{21}(t,x) = -c(t,x)v_1$ and hence (5.7) is satisfied if

$$\limsup_{t\to-\infty} \|b\|_{L^\infty(\Omega)} \limsup_{t\to-\infty} \|c\|_{L^\infty(\Omega)} < \rho^2(p, \Omega, M_\infty, N_\infty) = \rho_0.$$

Therefore, from Theorem 5.2, there exists at most a complete non-degenerate solution at $-\infty$.

To show that $U^*(t)$ is pullback attracting, observe that for sufficiently negative t_0 we can proceed as in the proof of Theorem 5.2 to conclude that $U^*(t)$ pullback attracts solutions $U_1(t,s)$ such that $U_1(s)$ are positive and bounded as $s \to -\infty$.

The rest follows from Theorem 6.1. □

7. Conclusions. We have obtained some results on permanence in non-autonomous Lotka-Volterra models without the assumption of any kind of periodicity. In particular we have found conditions under which there exists at least one complete trajectory, and for which all trajectories convergence together as $t \to +\infty$. The key argument is a perturbation result for an associated linear system satisfied by the difference between two solutions, and using this we have been able to treat all the different classical cases – competition, symbiosis, and prey-predator – in a unified way. While this unified approach has its advantages, our method requires at least one of the coupling parameters in the system to be sufficiently small. Hence, we hope that a more detailed study of each particular situation could lead to some improvements in the conditions imposed on the non-autonomous terms while still using similar techniques.

It is a very interesting open problem to prove, for this Lotka-Volterra example, the existence of a complete trajectory that is non-degenerate at $-\infty$. Given

this non-degeneracy one would get the uniqueness of such a trajectory, and its pull-back attracting property. We believe that use of the concepts of sub- and super-trajectories (cf. Arnold & Chueshov [3] and Chueshov [10]), along with the sub- and super-solutions technique (cf. for example Pao [30]) should be able to provide this, and we intend to pursue this direction in a future paper.

However, it is certainly the case that the hypothesis that the time-dependent terms are bounded is important throughout the literature, as this assumption implies the existence of bounded global solutions, and in particular of bounded attracting trajectories. As the analysis in Langa et al. [23] shows, different kinds of forward asymptotic behaviour, such as the non-existence of asymptotically stable trajectories, is possible if solutions are allowed to be unbounded.

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