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Forwards Attractor Structures in a Planar Cooperative Non-autonomous Lotka–Volterra System

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Abstract

The global attractor of a dissipative dynamical system provides the necessary information to understand the asymptotic dynamics of all the system's solutions. A crucial question consists in finding the structure of this set. In this paper we provide a full characterization of the structure of attractors for a planar non-autonomous Lotka–Volterra cooperative system. We show sufficient conditions for the existence of forward attractors and give a full description of them by proving the existence of such bounded global solutions that all bounded global solutions join them, i.e. converge towards them when time tends to plus and minus infinity. These results generalize those known in an autonomous framework. The case of particular interest in our work is the situation where globally forward-stable non-autonomous solutions have both coordinates strictly positive. We study this case in detail and obtain sufficient conditions that the problem parameters must satisfy in order to obtain various structures of non-autonomous attractors. This allows us to understand different paths of the solutions towards the unique globally stable one.

1 Introduction

In the analysis of dissipative dynamical systems, the concept of a global attractor plays a fundamental role as it encompasses the time-asymptotic behavior of all the solutions.

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A global attractor is a compact invariant set which attracts all the solutions, allowing us to describe all the essential dynamics of the system. In particular, if the system has a gradient-like structure, the global attractor contains all the unstable equilibria and heteroclinic connections between them, and, in general, all invariant and bounded structures of the system. The concept of a global attractor has been generalized to non-autonomous problems, where the attractors become time-dependent [9, 16]. Still, for the gradient-like case, such as the one we consider in this paper, certain globally bounded solutions play the role of stable and unstable equilibria, which are connected by solutions approaching them backward and forwards in time [10].

The first step in the analysis of a model from population dynamics is finding the globally stable solutions. However, in order to gain a full understanding of the system, one needs to find other unstable and saddle-node equilibria (or in the non-autonomous case, time-dependent hyperbolic global solutions which play their role [9]), and describe the full characterization of how all equilibria are connected to each other. For example, we usually find situations where, for different values of the model parameters, we get globally stable solutions having the same nonzero elements, but the path followed by a trajectory towards these solutions can be different, because the global attractor structure is not the same [11, 18].

Consider an autonomous generalized Lotka–Volterra system

$$u_i' = u_i\left(a_i - b_{ii}u_i - \sum_{\substack{j=1\\ j\neq i}}^{n} b_{ij}u_j\right) \quad \text{for } i \in \{1, \ldots, n\}. \tag{1}$$

This system is common in population dynamics to characterize the interactions between species and their time dependent behavior in the ecosystems. The system consists of n ODEs, where the unknown variable u_i represents the density of the i-th species, the vector parameter $(a_i)_{i=1}^n$ represents the intrinsic species growth rate, and the inter-species interactions are represented by the off-diagonal terms of the matrix $(b_{ij})_{i,j=1}^n$.

We study dynamics with the coefficients a_i depending on time and constant b_{ij}. Our standing assumption is the condition (H) which asserts the diagonal dominance of the matrix $B = (b_{ij})_{i,j=1}^n$. Under such strong stability condition, the dynamics for the autonomous case is gradient-like, i.e. every solution converges to an equilibrium as $t \to \infty$ [22]. We fully characterize the non-autonomous dynamics in the planar case under general assumptions on time-dependent a_i, which are not necessarily small perturbations of a constant. Essentially, our non-autonomous dynamics remains gradient-like. Note that for non diagonally-dominant case the problem may have periodic solutions, such as in the classical predator–prey model. Then small non-autonomous periodic perturbations lead to more complicated dynamics, where the cycle is replaced by the torus on which the solutions evolve [15, 20].

The authors in [11], extending the results of [22] (who considered only the globally stable solution), provide different conditions for the vector $a = (a_i)_{i=1}^n$ leading to the existence of a globally stable solution with all positive coordinates. However, in each case the global attractor is composed of a different number of semistable equilibria

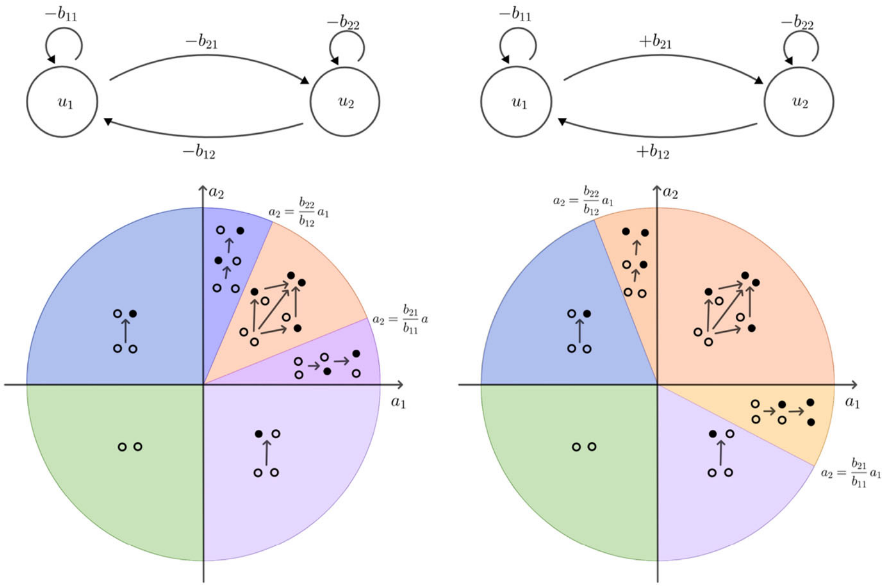

Fig. 1 Attractor structures configuration for a $2D$ Lotka–Volterra system, with inter and intraspecific parameters as drawn. Left, competitive case. Right, cooperative case. The orange cones are the regions of maximal biodiversity in both cases. Observe in the cooperative case the orange cone is splitted in three regions, each one corresponding to a different attractor structure. This does not happen in the smaller orange cone for the competitive framework (Color figure online)

with varying compositions of zero and nonzero coordinates and different connections between them.

On the other hand, the nature of interactions plays also a crucial role in the description of the attractor structure. Indeed, observe in Fig. 1 the situation in the planar case for competitive and cooperative scenarios, highlighting important and crucial differences. In the competitive case, we observe that the presence of a positive stationary point is confined to an internal cone within the positive quadrant, determined by the intrinsic growth rates. Meanwhile, in the cooperative case, the cone of maximal biodiversity also extends to the second and fourth quadrants, enlarging the zone for the robustness and resilience of both species. Moreover, within this extended cone we observe different attractor configurations, while there is only one in the competitive case. Specifically, the cone of maximal biodiversity for which each species exists independently on the other coincides with the entire first quadrant in the cooperative case, whereas in the competitive case it is limited to the interior range within this quadrant. Furthermore, the role of cooperation demonstrates its strength in the cooperative case, where we observe the existence of two subcones within the cone of maximal biodiversity, indicating that the existence of a second species is closely intertwined with the existence of the first one.

However, the descriptive power of the autonomous model is insufficient to reflect the modeled reality, so that we may need to treat the parameters present in the equations as functions of time. This necessitates a non-autonomous theory which becomes significantly richer and more difficult to work with. The first difficulty arises at the level of the attractor generalization, and, in fact, there are several nonequivalent definitions available [5, 9, 16].

The study of the non-autonomous Lotka–Volterra model was initiated by Gopalsamy [12, 13], and further developed by Ahmad and Lazer [1], and Redheffer [19]. Although these authors significantly developed the techniques for studying dynamics, their primary focus was on characterizing time dependent globally asymptotically stable solutions. In [10], for the first time, we characterized the full attractor for a Lotka–Volterra system with time dependent parameters. The results therein provide conditions on the time dependent vector of intrinsic growth rates $(a_i(t))_{i=1}^n$ and the matrix $(b_{ij}(t))_{i,j=1}^n$ that ensure the existence of semistable solutions (which are stable solutions for the subsystems of the problem), a comprehensive characterization of asymptotic behavior including species permanence and extinction for different initial data, as well as the heteroclinic connections. Thus, the complete structure of non-autonomous attractor has been described. However, the conditions proposed in [10] are not sufficiently general to encompass situations where several different attractor structures occur with the same species present in the globally stable solution. In particular, the conditions in [10] only allow for the description of the case in the first quadrant with a full attractor characterization (all the nodes present), thus failing to describe intertwined phenomena in biodiversity as depicted in Fig. 1.

In the present article we generalize the picture in Fig. 1 to a non-autonomous framework. For clarity, we will reduce the complexity of the model, and we fix the matrix $(b_{ij})_{i,j=1}^d$ as time independent, while the time dependence occurs only in the vector of intrinsic growth rates. Our work is inspired by the articles of Ahmad and Lazer [2, 3], who impose the conditions on the time averages of the intrinsic growth rates $(a_i(t))_{i=1}^n$ and prove that the solution for the planar case with positive initial conditions will not tend to zero in any of the variables as time grows. As in their work, we define the following quantities for a continuous function $f : \mathbb{R} \to \mathbb{R}$ which is bounded from above and below:

$$m[f] = \lim_{n\to\infty} \inf_{t-s\geq n} \left\{ \frac{1}{t-s} \int_s^t f(\tau)\, d\tau \right\},$$
$$M[f] = \lim_{n\to\infty} \sup_{t-s\geq n} \left\{ \frac{1}{t-s} \int_s^t f(\tau)\, d\tau \right\},$$

and

$$f_M = \sup_{t\in\mathbb{R}} f(t) \;\;\&\;\; f_L = \inf_{t\in\mathbb{R}} f(t).$$

Since the set $\{\frac{1}{t-s}\int_s^t f(\tau)\, d\tau \,|\, t-s \geq n\}$ gets smaller as n increases, the limits exist. Furthermore, we have the following inequalities

$$f_L \leq m[f] \leq M[f] \leq f_M.$$

In this work, we enhance the concept of permanence as discussed in [2, 3], and we establish, under their conditions, the existence of a global solution, i.e., the one that exists and remains bounded for every $t \in \mathbb{R}$ with all coordinates positive, and attracts any other solution with positive initial conditions forward in time. We obtain this result, first for the logistic equation in Sect. 3.1, and for the Lotka–Volterra planar model in the cooperative case in Sect. 4.1. Additionally, we complement these findings by providing conditions under which we obtain the existence of a global forward attractive solution in which the species become asymptotically extinct. In Sect. 3.2 we consider the one dimensional case, and in Sects. 4.2 and 4.3 we extend this analysis to the case of two dimensions, considering scenarios where both or one of the species become extinct.

As we stressed before, however, the global attractor for the considered system is more than a global attractive solution. Actually, the whole global attractor except this solution is not attracting any solution. Hence as in [10], but under the condition that involves only the averaged non-autonomous terms, we construct, for all cases that we consider, the heteroclinic connections between the globally stable solution and the unstable and semistable ones. In case of permanence for the Lotka–Volterra model we prove the occurrence of an interesting event: keeping the same conditions for the existence of a global positive attracting solution, depending on the signs of the averaged intrinsic growth rates $a_i(t)$, we obtain in Sect. 4.1.2 different structures for the attractor.

In cases where $a_i(t)$ are not periodic in time, there may be a gap between their upper and lower averages, denoted by $m[a_i]$ and $M[a_i]$, respectively. Consequently, we cannot provide results which fully cover the parameter space. However, if the upper and lower averages coincide, which occurs when $a_i(t)$ are periodic, we partition the space $\mathbb{R}^2$ of averaged intrinsic growth rates into regions associated with a particular attractor structure. A comprehensive description of this partitioning is given in Sect. 4.4.

While the system we study is planar, and the non-autonomous dynamics we investigate is gradient-like, there exist various related models whose detailed study of non-autonomous dynamics has been only partially understood. We highlight, as especially interesting, the 3D Lotka–Volterra system, where one may observe the occurrence of heteroclinic 3-cycles in the May–Leonard model. Recent results on non-autonomous perturbations of such models can be found in [17, 23]. It is, in our opinion, an intriguing open question to characterize the non-autonomous May–Leonard type dynamics which is not merely a small perturbation of the autonomous problem. Another class of models, interesting both from the point of view of applications and underlying mathematics, are epidemiological models, where the non-autonomous terms naturally appear due to the seasonality of viral outbreaks. Relevant articles include [4, 7, 8, 24, 26], and the monograph [21] provides related results on such models.

2 General Results for *n*-Dimensional Lotka–Volterra System

We consider the following Lotka–Volterra system of ordinary differential equations

$$u_i' = u_i \left(a_i(t) - b_{ii}u_i - \sum_{\substack{j=1 \\ j\neq i}}^{n} b_{ij}u_j \right) \quad \text{for } i \in \{1, \ldots, n\}, \tag{2}$$

where $a_i(\cdot)$ are continuous real-valued functions and b_{ij} are real constants. Throughout all the article we always assume that $b_{ii} > 0$ and $b_{ij} < 0$ for $i \neq j$, and $i, j = 1, \ldots, n$, meaning that the problem is cooperative. Moreover, we make the following standing assumption on the column diagonal dominance,

$$c_j b_{jj} + \sum_{\substack{i=1 \\ j\neq i}}^{n} c_i b_{ij} > 0 \quad \text{for } j = 1, \ldots, n, \tag{H}$$

for some positive constants $\{c_i\}_{i=1}^n$. From [19] we obtain the following result

Lemma 2.1 *Let $u, v : \mathbb{R} \to \mathbb{R}^n$ be two solutions of* (2) *satisfying $\bar{\sigma} \leq u(t), v(t) \leq \sigma$ for positive constants $\bar{\sigma}, \sigma$. Assume* (H)*, then*

$$\bar{\sigma}|u(t) - v(t)| \leq \sigma|u(t_0) - v(t_0)|e^{-\bar{\sigma}\delta(t-t_0)} \quad \textit{for every} \quad t \geq t_0,$$

and for a positive constant δ depending only on the matrix $(b_{ij})_{i,j=1}^n$ and the constants $(c_i)_{i=1}^n$.

As a straightforward consequence of the above lemma we get the following result.

Corollary 2.2 *Assume* (H)*. If there exists a solution $u^* : \mathbb{R} \to \mathbb{R}^n$ of* (2) *such that $0 < \bar{d} \leq u^*(t) \leq d < \infty$ for every $t \in \mathbb{R}$, then this is the unique solution of* (2) *which is bounded away from zero and infinity.*

We denote

$$\overline{C}_+ = \{x = (x_1, \ldots, x_n) \in \mathbb{R}^n : x_i \geq 0 \text{ for } i \in \{1, \ldots, n\}\},$$

and

$$C_+ = \text{int}\,\overline{C}_+ = \{x = (x_1, \ldots, x_n) \in \mathbb{R}^n : x_i > 0 \text{ for } i \in \{1, \ldots, n\}\}.$$

We now recall the definition of a global attractor:

Definition 2.3 Let X be a metric space and let $S(t) : X \to X$ be a semigroup of mappings parameterized by $t \geq 0$. The set $\mathcal{A} \subset X$ is called a global attractor for $\{S(t)\}_{t\geq 0}$ if it is nonempty, compact, invariant (i.e. $S(t)\mathcal{A} = \mathcal{A}$ for every $t \geq 0$), and it attracts all bounded sets of X (i.e. if $B \subset X$ is nonempty and bounded then $\lim_{t\to\infty} \operatorname{dist}(S(t)B, \mathcal{A}) = 0$, where $\operatorname{dist}(C, D) = \sup_{x\in C} \inf_{y\in D} d(x, y)$ is the Hausdorff semidistance between sets $C, D \subset X$).

In our (autonomous) framework, $X = \overline{C}_+$ and $S(t)u_0 = u(t; u_0)$, with $u(t; u_0)$ the solution to (2) with initial data u_0.

2.1 Exponential Dichotomies and Linearization

In this section we remind some properties of non-autonomous linear systems of ODEs. The key concept here will be exponential dichotomy. If a system has such dichotomy, then one can construct local stable and unstable manifolds, which are later crucial to obtain the connections between the non-autonomous equilibria. The results of this section are based on [6], and can be also found in [10].

We will consider the following linear nonautonomous system of ODEs

$$x'(t) = D(t)x(t), \tag{3}$$

where $D : \mathbb{R} \to \mathbb{R}^{n\times n}$ is continuous and bounded, i.e. $\sup_{t\in\mathbb{R}} \|D(t)\| \le M$, where M is a positive constant. The fundamental matrix of this system is given by $M_D(t, t_0)$. Then, the solution with the initial condition $x(t_0) = x_0$ is given by $x(t) = M_D(t, t_0)x_0$. We denote $M_D(t) = M_D(t, 0)$.

Definition 2.4 Let $I \subset \mathbb{R}$ be a time interval, where either $I = \mathbb{R}$, or $I = \mathbb{R}^+$ or $I = \mathbb{R}^-$. We say that the system (3) has an exponential dichotomy on I with the projection $P : I \to \mathbb{R}^{n\times n}$, constant $k \ge 1$ and exponents $\alpha, \beta > 0$ if the following property holds

$$P(t)M_D(t, s) = M_D(t, s)P(s) \ \text{ for every } \ t, s \in I, \tag{4}$$

and we have the inequalities

$$\|M_D(t, s)P(s)\| \le ke^{-\alpha(t-s)} \ \text{ for every } \ s \le t \in I, \tag{5}$$

$$\|M_D(t, s)(I - P(s))\| \le ke^{\beta(t-s)} \ \text{ for every } \ t \le s \in I. \tag{6}$$

Note that from (4) it follows that $P(t) = M_D(t)P(0)M_D(t)^{-1}$, so it is enough to define $P(0)$ in order to determine $P(t)$ for other times. We will denote $P(0) = P$.

We briefly recall the results of [6] on dichotomies for block upper triangular systems, which have the form

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix}' = \begin{pmatrix} A(t) & C(t) \\ 0 & B(t) \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \end{pmatrix}, \tag{7}$$

where $A(t), B(t), C(t)$ are bounded and continuous in time. The following result, cf. [6, Corollary 1], relates the case where two smaller systems with $A(t)$ and $B(t)$ have exponential dichotomies with the dichotomy of the whole system (7).

Corollary 2.5 *Assume that the linear systems $x'(t) = A(t)x(t)$ and $y'(t) = B(t)y(t)$ have exponential dichotomies on $\mathbb{R}$, where $A(t) \in \mathbb{R}^{d\times d}$ and $B(t) \in \mathbb{R}^{(n-d)\times(n-d)}$, and $C(t)$ is piecewise continuous and bounded $d \times (n-d)$ matrix. Then (7) has the exponential dichotomy on $\mathbb{R}$.*

The result [6, Theorem 1] gives the following formulas for P for (7) on $\mathbb{R}^-$ and $\mathbb{R}^+$,

$$P^+ = \begin{pmatrix} P^A & L^+P^B \\ 0 & P^B \end{pmatrix} \text{ on } \mathbb{R}^+ \qquad P^- = \begin{pmatrix} P^A & L^-(I_{n-d} - P^B) \\ 0 & P^B \end{pmatrix} \text{ on } \mathbb{R}^-, \tag{8}$$

where P^A is the projection for the system with $A(t)$ and P^B for $B(t)$. The matrices L^+, L^- are defined by

$$L^+ = -\int_0^\infty M_A(s)^{-1}(I_d - P^A(s))C(s)M_B(s)\,ds,$$
$$L^- = \int_{-\infty}^0 M_A(s)P^A(s)C(s)M_B(s)^{-1}\,ds.$$

The projection P which gives the dichotomy of (7) on the whole $\mathbb{R}$ is defined in such a way, that it is a uniquely defined projection whose kernel coincides with the kernel of P^- and whose range coincides with the range of P^+.

3 Dynamics of the Non-autonomous Logistic Equation

We consider the logistic equation

$$u' = u(a(t) - bu), \tag{9}$$

and we assume that $|a(\cdot)|$ is bounded and $b > 0$. We will prove that if $m[a] > 0$ then all positive solutions are permanent, i.e., they are attracted by a certain strictly positive solution. On the other hand, if $M[a] < 0$, then every solution tends to zero, i.e. the species becomes extinct.

Assuming that $m[a] = M[a]$, this constant can be interpreted as the time averaged multiplication rate of the population at low density. If it is positive, then the birth rate, in average, exceeds the death rate, or, in other words, an average individual produces more than one offspring during its lifetime which allows the species to persist. Thus $m[a]$ is linked with the basic reproduction number R_0, a threshold parameter crucial in many epidemiological and ecological models. This parameter denotes the average number of offsprings that one individual produces during lifetime, and in the logistic case, it is given as ratio of the averaged birth rate to death rate [14]. Note, that in order to be consistent with two-dimensional models whose analysis is a main topic of this paper, we consider only time dependent a and b is a constant. We refer to [26] where an analysis of a logistic model with both time dependent parameters is presented together with its link to the SIR epidemic model for the time-periodic case.

3.1 The Case of Permanence

We assume that

$$m[a] > 0. \tag{10}$$

Lemma 3.1 *For every solution $u(t)$ of (9) such that $u(t_0) > 0$, it holds*

$$\sup_{t\in[t_0,\infty)} u(t) = \max\left\{u(t_0), \frac{a_M}{b}\right\}.$$

Proof If $u(t_0) > \frac{a_M}{b}$, then for every $t \geq t_0$ such that the inequality $u(t) > \frac{a_M}{b}$ holds we have

$$u' = u(a(t) - bu) \leq u\left(a(t) - b\frac{a_M}{b}\right) = u(a(t) - a_M) \leq 0,$$

so, the function u is nonincreasing. If $u(t_0) \leq \frac{a_M}{b}$, then suppose that for the time $t^* \geq t_0$ we have $u(t^*) = \frac{a_M}{b}$. Then we have again

$$u'(t^*) = u(t^*)\left(a(t^*) - b\frac{a_M}{b}\right) \leq 0,$$

so, $u(t) \leq \frac{a_M}{b}$ for every $t \geq t_0$. □

Ahmad and Lazer proved in [3], that, under certain conditions on the average of a, the infimum of any solution with a positive initial condition is positive. Additionally, they showed that any two solutions with positive initial conditions converge forward in time to each other. In our case, to establish the permanence, we require the existence of one globally bounded solution separated from zero and attracting all remaining solutions with positive initial conditions. In the following theorem, we prove, under the same conditions as Ahmad and Lazer, the existence of such solution, thus improving their results.

Theorem 3.2 *We consider (9) and we assume (10), then we have the following results:*

1. *For every $t_0 \in \mathbb{R}$ and every solution of (9) with $u(t_0) > 0$, it holds that $\inf_{t\in[t_0,\infty)} u(t) > 0$.*
2. *For every solution u, v of (9) such that $u(t_0), v(t_0) > 0$, $\lim_{t\to\infty} |u(t)-v(t)| = 0$.*
3. *There exists a solution u^*, bounded away from zero and infinity in $\mathbb{R}$ which is the unique solution bounded away from zero and infinity in the sense of Corollary 2.2.*

Proof The proof of 1. follows the lines of the proof of item (b) in [2, Theorem 2.5] for the one dimensional case. Now, 2. follows from Lemma 2.1. To prove 3. first note that if we take some positive $\delta < m[a]$, then there exists n_0 such that for every $n \geq n_0$, if $t, s \in \mathbb{R}$ are such that $t - s \geq n$, then

$$\frac{1}{t-s}\int_s^t a(\tau)d\tau > \delta.$$

We take $t \in \mathbb{R}$, and $0 < u_0 = \frac{\delta}{b} < \frac{a_M}{b}$. We are going to prove that $\liminf_{t_0 \to -\infty} u(t, t_0, u_0) > 0$. Suppose the contrary, then we can take $t_0 < t$, and a solution u such that

$$u(t, t_0, u_0) \le \frac{\delta}{n_0 b} e^{-n_0 r} = \bar{d}$$

where $r > 0$ and

$$-r \le a(t) - bu(t) \quad \text{for every } t \ge t_0,$$

since $|a|$ is bounded and u is a bounded function in $[t_0, \infty)$ by Lemma 3.1. Then, we can find some $t_0 < s < t$ such that

$$u(s, t_0, u_0) = \frac{\delta}{n_0 b},$$

and for every $\tau \in [s, t]$, $u(\tau) \le \frac{\delta}{bn_0}$. By the argument of [3, Lemma 2.4] we see that $t - s \ge n_0$, and then

$$\delta < \frac{1}{t-s} \int_s^t a(\tau) d\tau = \frac{1}{t-s} \log\left(\frac{u(t)}{u(s)}\right) + \frac{b}{t-s} \int_s^t u(\tau) d\tau \le \frac{1}{t-s}(t-s)\frac{\delta}{n_0},$$

which leads to a contradiction.

We take the sequence of solutions $\{u_m\}_{m\in\mathbb{N}}$ with initial condition $u_m(-m) = \frac{\delta}{b}$. If we take a time $t \in \mathbb{R}$, then the solutions u_m on the interval $I_1 = [t-1, t]$ are bounded by $\bar{d} \le u \le d$. Moreover, the coefficients of (9) are continuous and bounded, so the sequence $\{u_m\}_{m\in\mathbb{N}}$ is equicontinuous in I_1, and then, by the Arzelà-Ascoli theorem, there exists a subsequence $\{v_{m,1}\}_{m\in\mathbb{N}}$ which converges to some function $\bar{d} \le u^*(t) \le d$ in I_1. Furthermore, we can select a subsequence $\{v_{m,2}\}_{m\in\mathbb{N}}$ of the previous subsequence $\{v_{m,1}\}_{m\in\mathbb{N}}$ that converges in the interval $I_2 = [t-2, t]$ to a solution u^*, bounded away from zero and infinity. Repeating this process for every interval $I_j = [t-j, t]$, we choose the diagonal sequence $\{v_{m,m}\}_{m\in\mathbb{N}}$ that converges in every interval I_m, and we obtain the solution u^*. The uniqueness of u^* is given directly from Corollary 2.2. □

Now, we prove that the results of [10, Lemma 5.2] for the scalar problem also hold with the new conditions (Fig. 2).

Lemma 3.3 *Let $u : \mathbb{R} \to \mathbb{R}$ be a solution to (9) with $u(t_0) \ge 0$. If we assume (10), then exactly one of the four possibilities below holds*

(a) $u \equiv 0$,
(b) $u \equiv u^*$,
(c) *if* $u(t_0) \in (0, u^*(t_0))$ *then* $\lim_{t\to-\infty} u(t) = 0$ *and* $\lim_{t\to\infty} |u^*(t) - u(t)| = 0$,
(d) *if* $u(t_0) > u^*(t_0)$ *then* $\lim_{t\to-\infty} u(t) = \infty$ *and* $\lim_{t\to\infty} |u^*(t) - u(t)| = 0$.

Fig. 2 Dynamics in case of the existence of an attracting global solution bounded away from zero and infinity for (9). The forward attractor (in red) is composed by the zero solution, the global solution u^*, and the heteroclinic connections between them (Color figure online)

Proof If $u(t_0) \in (0, u^*(t_0))$, it is evident that $u(t) < u^*(t)$ for $t \in \mathbb{R}$. By Corollary 2.2, u^* is the unique solution bounded away from zero and infinity, and by $\lim_{t\to\infty} |u^*(t) - u(t)| = 0$, then $\liminf_{t\to-\infty} u(t) = 0$. We suppose that $\limsup_{t\to-\infty} u(t) = \gamma > 0$. Let r be such that

$$-r \leq a(t) - bu(t) \quad \text{for every} \quad t \in \mathbb{R}.$$

Then for every $n \in \mathbb{N}$, we can take times $s, t \in \mathbb{R}$, $s < t$

$$u(s) = \frac{\gamma}{n}, u(t) = \frac{\gamma}{n} e^{-rn} \quad \& \quad \max_{\tau \in [s,t]} u(\tau) = \frac{\gamma}{n},$$

then it is easy to see that $t - s \geq n$. With the same process as in Theorem 3.2 we arrive at a contradiction, and $u(t) \xrightarrow{t\to-\infty} 0$.

If $u(t_0) > u^*(t_0)$, then, by the same approach as before, we know that $\limsup_{t\to-\infty} u(t) = \infty$, so there exists a sequence $\{t_n\}_{n\in\mathbb{N}}$ such that $t_n \xrightarrow{n\to\infty} -\infty$, and an n_0, such that for every $n \geq n_0$, $u(t_n) > \frac{a_M}{b}$. As we have seen in Lemma 3.1, in the intervals (t_{n+1}, t_n), the function u is non-increasing for $n \geq n_0$, so, $\lim_{t\to-\infty} u(t) = \infty$. □

The following lemma will be later useful to establish the connections in the planar case.

Lemma 3.4 *There exist $\delta > 0$ and $M > 0$ such that if $w : \mathbb{R} \to \mathbb{R}$ solves the following one-dimensional problem linearized around u^**

$$w'(t) = w(t)(a(t) - 2b(t)u^*(t)),$$

then we have

$$|w(t)| \leq M|w(t_0)|e^{-\delta(t-t_0)} \quad \text{for every} \quad t \geq t_0.$$

Proof The proof follows from [2, Lemma 3.6]. □

3.2 The Case of Extinction

Theorem 3.5 *Consider (9) and assume $M[a] < 0$. Then, for every solution with $u(t_0) > 0$ we have $u(t) \xrightarrow{t\to\infty} 0$. Also, these solutions are unbounded in the past. As a consequence, the global attractor for (9) is $\{0\}$ (Fig. 3).*

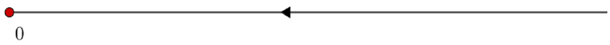

Fig. 3 Dynamics of (9) in case for which every solution decays to zero forward in time

Proof We write the explicit form of every solution of (9)

$$u(t) = u(t_0)e^{\int_{t_0}^{t} a(s)-bu(s)ds}.$$

As

$$M[a] = \delta < 0,$$

we have that

$$\int_{t_0}^{t} a(s)ds \leq (t - t_0)\delta \xrightarrow{t\to\infty} -\infty.$$

So, since $u(t) > 0$ for every $t \geq t_0$ we have

$$u(t) \leq u(t_0)e^{\int_{t_0}^{t} a(s)ds} \xrightarrow{t\to\infty} 0.$$

To prove the second statement, observe that either the solution blows up backwards in finite time, or, otherwise, with the same inequality we obtain

$$u(t_0) \geq u(t)e^{-\int_{t_0}^{t} a(s)ds} \xrightarrow{t_0\to-\infty} \infty.$$

□

4 Dynamics of Planar Lotka–Volterra Problem

We consider the following Lotka–Volterra non-autonomous model

$$\begin{cases} u_1' = u_1(a_1(t) - b_{11}u_1 - b_{12}u_2) \\ u_2' = u_2(a_2(t) - b_{21}u_1 - b_{22}u_2) \end{cases}, \tag{LV-2D}$$

where $b_{11}, b_{22} > 0, b_{12}, b_{21} < 0$, and a is a vector of bounded functions $a_{iL} \leq a_i(t) \leq a_{iM}$ for every $t \in \mathbb{R}$. We assume that the matrix $(b_{ij})_{i,j=1}^{2}$ is column diagonally dominant, that is, there exist $c_1, c_2 \in \mathbb{R}_{>0}$ such that the following inequalities hold

$$c_1b_{11} > -c_2b_{21} \ \ \& \ \ c_2b_{22} > -c_1b_{12}. \tag{H$_{2D}$}$$

In this section we will treat (H_{2D}) as the standing assumption.

Lemma 4.1 *We suppose that u is a solution of* (LV-2D). *Then, there exist numbers $d_1, d_2 \in \mathbb{R}_{>0}$ such that if $u_1(t_0) \leq d_1$ and $u_2(t_0) \leq d_2$, then $u_i(t) \leq d_i$ for $t \geq t_0$ and $i = 1, 2$. Furthermore, if for some $i \in \{1, 2\}$ we have $u_i(t_0) > d_i$, then* $\limsup_{t\to\infty} u_i(t) \leq d_i$.

Proof First, we denote $\overline{a_{iM}} = a_{iM} + C_i$ for some $C_i \geq 0$, chosen such that $\overline{a_{iM}} > 0$. We formulate and solve the following linear system of equations

$$\begin{cases} \overline{a_{1M}} = b_{11}d_1 + b_{12}d_2 \\ \overline{a_{2M}} = b_{21}d_1 + b_{22}d_2 \end{cases} . \tag{11}$$

Its solutions are given by

$$d_1 = \frac{\overline{a_{1M}}b_{22} - \overline{a_{2M}}b_{12}}{b_{11}b_{22} - b_{12}b_{21}} \;\; \& \;\; d_2 = \frac{\overline{a_{2M}}b_{11} - \overline{a_{1M}}b_{21}}{b_{11}b_{22} - b_{12}b_{21}}. \tag{12}$$

By (H_{2D}) we obtain that $d_1, d_2 > 0$. Since $a_i(t) \leq \overline{a_{iM}} = b_{ii}d_i + b_{ij}d_j$ for every $t \in \mathbb{R}$, we obtain applying [19, Lemma 5] that $\limsup_{t\to\infty} u_i(t) \leq d_i$ if the inequality $u_i(t_0) > d_i$ holds. On the other hand, by [19, Lemma 1], we obtain the first assertion of the lemma. □

The following corollary is a simple consequence of the above lemma.

Corollary 4.2 *Let u be a solution of* (LV-2D)*, such that $u_i(t_0) \geq 0$, then $\sup_{t\in[t_0,\infty)} u_i(t) < \infty$ for $i = 1, 2$.*

4.1 The Case of the Permanence of Both Species

4.1.1 Existence of a Positive Attracting Solution

We will first study the case in which there exists a unique globally attracting solution with both species positive and separated from zero and infinity. The existence of such solution will require the following assumption

$$m[a_1] > \frac{b_{12}}{b_{22}} m[a_2] \;\; \& \;\; m[a_2] > 0. \tag{A}$$

Theorem 4.3 *Assume* (A). *The following assertions hold.*

1. *For every $t_0 \in \mathbb{R}$ and for every solution of* (LV-2D) *with $u(t_0) > 0$, it holds that* $\inf_{t\in[t_0,\infty)} u(t) > 0$.
2. *For every solution u, v of* (LV-2D) *such that $u(t_0), v(t_0) > 0$ we have* $\lim_{t\to\infty} |u(t) - v(t)| = 0$.
3. *There exists a global in time solution $u^* = (u_1^*, u_2^*)$, bounded away from zero and infinity in $\mathbb{R}$, which is the unique solution bounded away from zero and infinity in the sense of Corollary* 2.2.

Proof Exactly as in Theorem 3.2, the proof of 1. follows the lines of the proof of item (b) in [2, Theorem 2.5]. Now, the assertion 2. follows from Lemma 2.1. The proof of 3. follows by a similar argument as the corresponding proof of Theorem 3.2. To this end, we take a positive constant $0 < \delta < m[a_1] - \frac{b_{12}}{b_{22}} m[a_2]$. There exists a number n_0 such that for every $n \geq n_0$, if $t, s \in \mathbb{R}$ are such that $t - s \geq n$, then

$$\frac{1}{t-s} \int_s^t a_1(\tau) d\tau > \frac{b_{12}}{b_{22}} m[a_2] + \delta.$$

Firstly, we will prove that there exists $\gamma_1, \gamma_2 > 0$, such that fixing t and taking $u(t_0) = (\gamma_1, \gamma_2)$, we have that $\lim_{t_0 \to -\infty} u(t, t_0; u_0) > 0$. Since

$$u_2' = u_2(a_2(t) - b_{21}u_1 - b_{22}u_2) \geq u_2(a_2(t) - b_{22}u_2),$$

and $m[a_2] > 0$ we already know by the argument of Theorem 3.2 that $\liminf_{t_0 \to -\infty} u_2(t, t_0; u_0) > 0$. By contradiction, let us suppose that $\liminf_{t_0 \to -\infty} u_1(t, t_0; u_0) = 0$. For every $n \geq n_0$, there exists a time t_0 such that $u_1(t, t_0; u_0) \leq \frac{\gamma_1}{n} e^{-nr}$, where

$$-r \leq a_1(t) - b_{11}u_1(t) - b_{12}u_2(t).$$

Moreover, there exists $s \in (t_0, t)$ such that $u_1(s, t_0; u_0) = \frac{\gamma_1}{n}$ and for every $\tau \in [s, t]$ we have $u_1(\tau, t_0; u_0) \leq \frac{\gamma_1}{n}$. Again it is easy to see that $t - s \geq n$. We take a number n such that

$$\frac{1}{t-s} \int_s^t a_2(\tau) d\tau > m[a_2] - \frac{\gamma_1}{2}$$

for $t - s \geq n$. Moreover,

$$\frac{1}{t-s} \log\left(\frac{u_2(t)}{u_2(s)}\right) < \frac{\gamma_1}{2}.$$

The above inequality holds for appropriately large $t - s$ because u_2 is bounded above and below by positive constants for any initial time. Hence,

$$\begin{aligned} \frac{b_{22}}{t-s} \int_s^t u_2(\tau) d\tau &= \frac{1}{t-s} \int_s^t a_2(\tau) d\tau - \frac{b_{21}}{t-s} \int_s^t u_1(\tau) d\tau - \frac{1}{t-s} \log\left(\frac{u_2(t)}{u_2(s)}\right) \\ &\geq m[a_2] - \gamma_1. \end{aligned} \tag{13}$$

Then

$$\begin{aligned} \frac{1}{t-s} \int_s^t a_1(\tau) d\tau &= \frac{1}{t-s} \log\left(\frac{u_1(t)}{u_1(s)}\right) + \frac{b_{11}}{t-s} \int_s^t u_1(\tau) d\tau + \frac{b_{12}}{t-s} \int_s^t u_2(\tau) d\tau \\ &\leq \frac{b_{11}\gamma_1}{n} + \frac{b_{12}}{b_{22}} m[a_2] - \frac{b_{12}\gamma_1}{b_{22}}. \end{aligned} \tag{14}$$

We need to take

$$\gamma_1 = \frac{\delta}{\frac{b_{11}}{n_0} - \frac{b_{12}}{b_{22}}},$$

whence we obtain $m[a_1] \leq \frac{b_{12}}{b_{22}} m[a_2] + \delta$ which leads to a contradiction.

Following the same process as Theorem 3.2 which uses the Arzelà–Ascoli lemma and the diagonal argument, we obtain the existence of a global solution u^* in $\mathbb{R}$ bounded away from zero and infinity. We obtain the uniqueness of u^* directly from Corollary 2.2. □

4.1.2 Structure of the Attractors

We consider two separate assumptions which allow us to distinguish between the two situations with different structures of the attractors.

In the first case we will assume that

$$m[a_1] > 0, \tag{E$_1$}$$

in which the solution of type $(\widehat{u}_1, 0)$ with $\widehat{u}_1$ bounded away from zero and infinity exists. The second case will rely on the assumption that

$$M[a_1] < 0, \tag{E$_2$}$$

in which such solution does not exist. Note that although our argument is fairly general, it still does not cover all possibilities, it can hold that $m[a_1] \leq 0$ and, simultaneously $M[a_1] \geq 0$, we do not study such a case, which can occur if for instance there is a gap between $m[a_1]$ and $M[a_1]$ or $m[a_1] = M[a_1] = 0$.

The argument will lead to different structures of the attractors depending on the conditions (E_1) and (E_2) on the function a_1. With the first condition we have the existence of a global solution $(\widehat{u}_1, 0)$ given by Theorem 3.2, where $\widehat{u}_1$ is bounded away from zero and infinity. However, if we consider (E_2) and assume (A), then such solution $(\widehat{u}_1, 0)$ does not exist by Theorem 3.5. In both cases, the solution (u_1^*, u_2^*) is globally stable, but our key observation is, that the structure of the attractor of the system is different for the above two cases.

Theorem 4.4 *Assume* (A). *There exists a global solution of* (LV-2D) *denoted by* $z = (z_1, z_2) : \mathbb{R} \to \mathbb{R}^2$ *such that*

$$\lim_{s \to -\infty} |(z_1(s), z_2(s)) - (0, \widehat{u}_2(s))| = 0$$

and

$$\lim_{s \to \infty} |(z_1(s), z_2(s)) - (u_1^*(s), u_2^*(s))| = 0.$$

If (E_1) *holds, the analogous result also holds for* $(\widehat{u}_1, 0)$.

Proof Note that (A) implies the existence of solution $(0, \widehat{u}_2)$ with $\widehat{u}_2$ separated from zero and infinity. We prove that the solution $(0, \widehat{u}_2)$ is locally unstable, i.e. its non-autonomous unstable manifold is nonempty and intersects the interior of the positive quadrant. We have seen in Theorem 4.3 that the permanent solution $(u_1^*(s), u_2^*(s))$ attracts forwards in time every solution with initial data in this quadrant, so this will ensure the existence of the connection. We start by proving the existence of the non-autonomous local unstable manifold following the lines of [10, Theorem 6.3], so we study the system linearized around $(0, \widehat{u}_2)$. We write

$$w(t) = u(t) - \widehat{u}(t)$$

where $\widehat{u}(t) = (0, \widehat{u}_2(t))$, and $u(t)$ is a solution with initial condition in a neighborhood of $\widehat{u}$. Then

$$\begin{aligned} w'(t) &= \begin{pmatrix} a_1(t) - b_{12}\widehat{u}_2(t) & 0 \\ -b_{21}\widehat{u}_2(t) & a_2(t) - 2b_{22}\widehat{u}_2(t) \end{pmatrix} w(t) \\ &\quad + \begin{pmatrix} -b_{11}(t)w_1(t)^2 - b_{12}(t)w_1(t)w_2(t) \\ -b_{21}(t)w_1(t)w_2(t) - b_{22}(t)w_2(t)^2 \end{pmatrix}. \end{aligned} \tag{15}$$

The linearized system has the following form

$$\left\{ \begin{pmatrix} v_2'(t) \\ v_1'(t) \end{pmatrix} = \begin{pmatrix} a_2(t) - 2b_{22}\widehat{u}_2(t) & -b_{21}\widehat{u}_2(t) \\ 0 & a_1(t) - b_{12}\widehat{u}_2(t) \end{pmatrix} \begin{pmatrix} v_2(t) \\ v_1(t) \end{pmatrix} = \begin{pmatrix} A(t) & C(t) \\ 0 & B(t) \end{pmatrix} \begin{pmatrix} v_2(t) \\ v_1(t) \end{pmatrix}, \right. \tag{16}$$

where $A(t) = a_2(t) - 2b_{22}\widehat{u}_2(t)$, $C(t) = -b_{21}\widehat{u}_2(t)$ and $B(t) = a_1(t) - b_{12}\widehat{u}_2(t)$. By Lemma 3.4, we know that $w_2'(t) = A(t)w_2(t)$ has an exponential dichotomy with projection $P_A = I_{1\times 1}$. We study the equation $v_1'(t) = B(t)v_1(t)$, for which

$$v_1(t) = v_1(s)e^{\int_s^t a_1(r) - b_{12}\widehat{u}_2(r)ds}, \tag{17}$$

for every $t \geq s$. Since $\widehat{u}_2$ is the unique bounded solution of the logistic equation $u_2'(t) = u_2(a_2(t) - b_{22}u_2)$, we have that

$$\begin{aligned} \int_s^t \widehat{u}_2(\tau)d\tau &= \frac{1}{b_{22}}\left(\int_s^t a_2(\tau)d\tau - \log\left(\frac{\widehat{u}_2(t)}{\widehat{u}_2(s)}\right)\right) \\ &\geq \frac{1}{b_{22}}\left(\int_s^t a_2(\tau)d\tau - \log\left(\frac{\widehat{u}_{2M}}{\widehat{u}_{2L}}\right)\right). \end{aligned}$$

We substitute the above estimate in (17), whence

$$v_1(t) \geq M_1 v_1(s) e^{\int_s^t a_1(r)d\tau - \frac{b_{12}}{b_{22}}\int_s^t a_2(\tau)d\tau},$$

where $M_1 = e^{\frac{b_{12}}{b_{22}} \log(\frac{\widehat{u}_{2M}}{\widehat{u}_{2L}})}$. By (A), we know that for an $0 < \delta < m[a_1] - \frac{b_{12}}{b_{22}} m[a_2]$, there exists a number n_0 such that for every $t - s \geq n_0$ we have

$$\begin{aligned}\frac{1}{t-s} \int_s^t a_1(\tau) d\tau - \frac{b_{12}}{b_{22}(t-s)} \int_s^t a_2(\tau) d\tau \\ \geq \inf_{t-s \geq n_0} \frac{1}{t-s} \int_s^t a_1(\tau) d\tau - \frac{b_{12}}{b_{22}} \inf_{t-s \geq n_0} \frac{1}{t-s} \int_s^t a_2(\tau) d\tau > \delta.\end{aligned}$$

Hence, we deduce that

$$v_1(t) \geq M_1 v_1(s) e^{\delta(t-s)}.$$

It remains to see what happens if $t - s < n_0$. Let $r = n_0 + s$. Then we have

$$\begin{aligned}v_1(t) &\geq M_1 v_1(s) e^{\int_s^r a_1(\tau) - \frac{b_{12}}{b_{22}} a_2(\tau) d\tau} e^{-\int_t^r a_1(\tau) - \frac{b_{12}}{b_{22}} a_2(\tau) d\tau} \\ &\geq M_1 v_1(s) e^{(r-s)\delta} e^{-(r-t)(a_{1M} - \frac{b_{12}}{b_{22}} a_{2M})} = M_1 v_1(s) e^{(t-s)\delta} e^{(r-t)(\delta - (a_{1M} - \frac{b_{12}}{b_{22}} a_{2M}))},\end{aligned}$$

since $a_{1\,M} - \frac{b_{12}}{b_{22}} a_{2\,M} \geq m[a_1] - \frac{b_{12}}{b_{22}} m[a_2] > \delta$, we have that

$$v_1(t) \geq \bar{M} v_1(s) e^{\delta(t-s)},$$

where

$$\bar{M} = M_1 e^{n_0(\delta - (a_{1M} - \frac{b_{12}}{b_{22}} a_{2M}))}.$$

We have proved that for every $t \geq s$ we have that

$$v_1(t) \geq \bar{M} v_1(s) e^{\delta(t-s)}.$$

Therefore, $v_1'(t) = B(t) v_1(t)$ has an exponential dichotomy with projection $P = 0$. Moreover, $C(t)$ is a bounded function, so Corollary 2.5 gives us the projections

$$P^+ = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} \text{ on } \mathbb{R}^+ \text{ and } P^- = \begin{pmatrix} 1 & L^- \\ 0 & 0 \end{pmatrix} \text{ on } \mathbb{R}^-.$$

The projection

$$P = P^- = \begin{pmatrix} 1 & L^- \\ 0 & 0 \end{pmatrix}$$

has the same range as P^+ and hence the system (16) has exponential dichotomy with the projection P for every time $t \in \mathbb{R}$ the associated time-dependent projection is given by

$$P(t) = \begin{pmatrix} 1 & L(t) \\ 0 & 0 \end{pmatrix},$$

for certain bounded function $L(t)$. To see that the unstable manifold intersects the positive quadrant, which implies that every point from it is attracted towards (u_1^*, u_2^*) forward in time, we follow the proof of [10, Theorem 6.3]. □

In the next theorem we establish the existence of heteroclinic connection from (0, 0) to the solution with both coordinates positive.

Theorem 4.5 *Assume* (A) *and* (E_1). *There exists the solution of* (LV-2D) *denoted by* $y = (y_1, y_2) : \mathbb{R} \to \mathbb{R}^2$ *such that*

$$\lim_{s\to-\infty}((y_1(s), y_2(s)) = (0, 0)$$

and

$$\lim_{s\to\infty} |(y_1(s), y_2(s)) - (u_1^*(s), u_2^*(s))| = 0.$$

Proof The linearized system around (0, 0) is

$$\begin{cases} v'(t) = \begin{pmatrix} a_2(t) & 0 \\ 0 & a_1(t) \end{pmatrix} v(t). \end{cases} \tag{18}$$

We take δ such that $\delta < \min\{m[a_1], m[a_2]\}$. Repeating the same argument as Theorem 4.4, there exists a number n_0 such that

$$\int_s^t a_1(\tau)d\tau > (t-s)\delta \;\; \& \;\; \int_s^t a_2(\tau)d\tau > (t-s)\delta,$$

for every $t - s \geq n_0$. Alternatively, if $t - s \leq n_0$, we take $r = s + n_0$ and we obtain for $i = 1, 2$

$$v_i(t) = v_i(s)e^{\int_s^r a_i(\tau)d\tau} e^{-\int_t^r a_i(\tau)d\tau} \geq v_i(s)e^{(r-s)\delta} e^{-(r-t)a_{iM}} \geq \bar{M}_i v_i(s)e^{\delta(t-s)},$$

where $\bar{M}_i = e^{n_0(\delta - a_{iM})}$. Then, the system (18) has an exponential dichotomy with the projection $P(t) \equiv 0$. Following [10, Theorem 6.4], we obtain the existence of the unstable manifold of zero that enters in the positive quadrant, and then it is attracted by (u_1^*, u_2^*). □

The next result summarizes the dynamics of the whole problem if we assume (A) and (E_1) (Fig. 4).

Theorem 4.6 *Assume* (A) *and* (E_1). *The system* (LV-2D) *has the following solutions* $u : \mathbb{R} \to \mathbb{R}^2$ *bounded both in the past and in the future:*

(a) $u(t) = (0, 0)$ *for* $t \in \mathbb{R}$,
(b) $u(t) = (\widehat{u}_1(t), 0)$ *and* $u(t) = (0, \widehat{u}_2(t))$, *corresponding to the unique solutions for one-dimensional subproblems bounded away from zero and infinity, given in Theorem 3.2.*
(c) *Solutions of type* $u(t) = (u_1(t), 0)$ *with initial condition* $0 < u_1(t_0) < \widehat{u}_1(t_0)$, *where* $\lim_{t\to-\infty} u_1(t) = 0$ *and* $\lim_{t\to\infty}(u_1(t) - \widehat{u}_1(t)) = 0$, *given in Lemma 3.3. Analogously,* $u(t) = (0, u_2(t))$ *with initial condition* $0 < u_2(t_0) < \widehat{u}_2(t_0)$, *where* $\lim_{t\to-\infty} u_2(t) = 0$ *and* $\lim_{t\to\infty}(u_2(t) - \widehat{u}_2(t)) = 0$.
(d) $u(t) = (u_1^*(t), u_2^*(t))$ *the unique solution with both nonzero coordinates bounded away from zero and infinity given in Theorem 4.3.*
(e) *Solutions of type* $u(t) = (u_1(t), u_2(t))$ *such that* $\lim_{t\to-\infty}(u_1(t), u_2(t)) = (0, 0)$ *and* $\lim_{t\to\infty}(u_1(t) - u_1^*(t), u_2(t) - u_2^*(t))$, *given in Theorem 4.5.*
(f) *Solutions of type* $u(t) = (u_1(t), u_2(t))$ *such that* $\lim_{t\to-\infty}(u_1(t), u_2(t)) = (\widehat{u}_1(t), 0)$ *and* $\lim_{t\to\infty}(u_1(t) - u_1^*(t), u_2(t) - u_2^*(t))$, *given in Theorem 4.4. Analogously,* $u(t) = (u_1(t), u_2(t))$ *such that* $\lim_{t\to-\infty}(u_1(t), u_2(t)) = (0, \widehat{u}_2(t))$ *and* $\lim_{t\to\infty}(u_1(t) - u_1^*(t), u_2(t) - u_2^*(t)) = 0$.

Moreover any solution of (LV-2D) *which is bounded both in the past and in the future is one of the solutions described in items (a)-(f).*

Proof We only need to prove the last assertion, that items (a)-(f) saturate all possibilities. By Theorem 4.3 we know that (u_1^*, u_2^*) is the unique solution bounded away from zero and infinity, so, if u is a solution that it is bounded in $\mathbb{R}$ and none of its coordinates equals zero, then in at least one of the coordinates $u_1(t)$ or $u_2(t)$ there has to exist a sequence $t_n \to -\infty$, such that $u_1(t_n) \xrightarrow{n\to\infty} 0$, or $u_2(t_n) \xrightarrow{n\to\infty} 0$. If we suppose that it happens for u_1, by (E_1) and analogously with the proof of item (c) of Lemma 3.3, we see that $u_1(t) \xrightarrow{t\to-\infty} 0$. We suppose now that both u_1 and u_2 do not converge backwards to 0, for example $u_1(t) \xrightarrow{t\to-\infty} 0$, and $u_2(t)$ is separated from zero, then the argument that

$$\lim_{t\to-\infty} |u_2(t) - \widehat{u}_2(t)| = 0$$

follows the lines of [10, Theorem 6.5]. Analogously we obtain that $\lim_{t\to-\infty} |u_1(t) - \widehat{u}_1(t)| = 0$ when $u_2(t) \xrightarrow{t\to-\infty} 0$ and $u_1(t)$ is separated from zero. □

Remark 1 With this last result, we establish that the forward attractor of (LV-2D) is composed of bounded solutions. Moreover, following the lines of Lemma 4.1, it can be proved that $\lim_{t_0\to-\infty} u_i(t, t_0; u_0) \le d_i$, for $i = 1, 2$. That implies that the compact set $[0, d_1] \times [0, d_2]$ is pullback attractive. Consequently, from [5, Theorem 6.13], we deduce the existence of a pullback attractor, which is equal to the set of bounded orbits of the system. Therefore, we have constructed a model where the pullback and forward attractors of the system coincide. This also applies to the other attractor structures of the planar Lotka–Volterra model studied later in this paper, and to the logistic model discussed in the previous section.

We pass to the situation where (E_2) holds. The next result characterizes the backwards dynamics of solutions for such case.

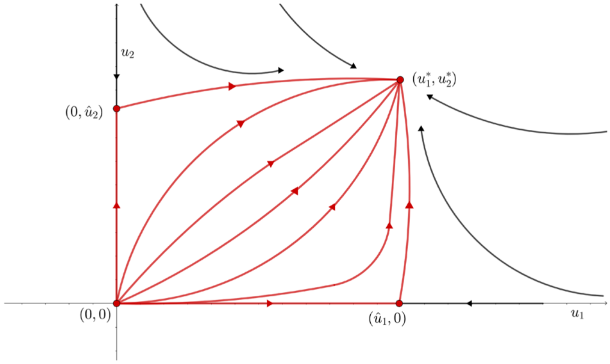

Fig. 4 Dynamics of (LV-2D) in case of the existence of an attracting global solution bounded away from zero and infinity for both coordinates, and the solutions $(\widehat{u}_1, 0)$ and $(0, \widehat{u}_2)$. The forward attractor (in red) is composed by the solutions $(0, 0)$, $(\widehat{u}_1, 0)$ and $(0, \widehat{u}_2)$, the solution (u_1^*, u_2^*), and the heteroclinic connections between them (Color figure online)

Lemma 4.7 *Assume that* (E_2) *holds. If* u *is a solution such that* $u(t_0) > 0$ *and there exists a sequence* $t_n \to -\infty$ *such that* $u_2(t_n) \to 0$ *then* $u_2(t) \xrightarrow{t\to-\infty} 0$ *and* $u_1(t) \xrightarrow{t\to-\infty} \infty$

Proof The proof that $u_2(t) \to 0$ as $t \to -\infty$ follows the lines of the argument in item (c) of Lemma 3.3. We take

$$M[a_1] = \delta_1 < 0.$$

Since $u_2(t) \xrightarrow{t\to-\infty} 0$, we can take t^* such that for every $t \le t^*$,

$$u_2(t) \le \delta_2 < \frac{\delta_1}{b_{12}}.$$

Then, we fix $t \le t^*$. For $s < t$ such that $t - s \ge n$ we have

$$\begin{aligned} u_1(s) &\ge u_1(t)e^{-\int_s^t a_1(\tau)-b_{12}u_2(\tau)d\tau} \ge u_1(t)e^{-\int_s^t a_1(\tau)d\tau+b_{12}\delta_2(t-s)} \\ &\ge u_1(t)e^{(t-s)(b_{12}\delta_2-\delta_1)} \xrightarrow{s\to-\infty} \infty, \end{aligned}$$

and the proof is complete. □

The above result is enough to characterize the dynamics of the whole problem if we assume (A) and (E_2) (Fig. 5).

Theorem 4.8 *Assume* (A) *and*(E_2). *The system* (LV-2D) *has the following solutions* $u : \mathbb{R} \to \mathbb{R}^2$ *bounded both in the past and in the future*

(a) $u(t) = (0, 0)$ *for* $t \in \mathbb{R}$,
(b) $u(t) = (0, \widehat{u}_2(t))$, *corresponding to the unique solutions for one-dimensional subproblem bounded away from zero and infinity, given in Theorem 3.2.*

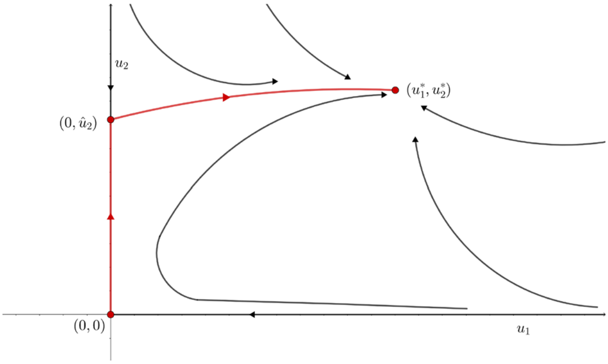

Fig. 5 Dynamics of (LV-2D) in case of the existence of an attracting global solution bounded away from zero and infinity for both coordinates, but the solution $(\widehat{u}_1, 0)$ does not exist. The forward attractor (in red) is composed by the solutions $(0, 0)$, $(0, \widehat{u}_2)$, (u_1^*, u_2^*), and the heteroclinic connections between them(Color figure online)

(c) *Solutions of type* $u(t) = (0, u_2(t))$ *with initial condition* $0 < u_2(t_0) < \widehat{u}_2(t_0)$, *where* $\lim_{t\to-\infty} u_2(t) = 0$ *and* $\lim_{t\to\infty}(u_2(t) - \widehat{u}_2(t)) = 0$, *given in Lemma* 3.3.
(d) $u(t) = (u_1^*(t), u_2^*(t))$ *the unique solution with both nonzero coordinates bounded away from zero and infinity given in Theorem* 4.3.
(e) *Solutions of type* $u(t) = (u_1(t), u_2(t))$ *such that* $\lim_{t\to-\infty}(u_1(t), u_2(t)) = (0, \widehat{u}_2(t))$ *and* $\lim_{t\to\infty}(u_1(t) - u_1^*(t), u_2(t) - u_2^*(t)) = 0$ *given in Theorem* 4.4.

All other solutions different that the ones named in $(a)-(e)$ *are backward unbounded. Moreover,*

(f) *Solutions of type* $u(t) = (u_1(t), 0)$ *with initial condition* $u_1(t_0) > 0$, *satisfies* $\lim_{t\to\infty} u_1(t) = 0$ *and* $\lim_{t\to-\infty} u_1(t) = -\infty$, *given by Theorem* 3.5.

4.2 Extinction of One Species

We have characterized the situation where the globally asymptotically solution both species are nonzero. We pass to the analysis of the case when one of the species becomes, in the limit, extinct. To this end, we need to impose the following assumption

$$M[a_1] < \frac{b_{12}}{b_{22}} M[a_2] \quad \& \quad m[a_2] > 0. \tag{B}$$

Theorem 4.9 *We assume* (B), *then for every solution such that* $u(t_0) > 0$ *we have* $u_1(t) \xrightarrow{t\to\infty} 0$.

Proof Since $M[a_1] < \frac{b_{12}}{b_{22}} M[a_2]$, we can take a number $\varepsilon > 0$, such that for some n_0 and for every $t - s \geq n_0$ we have that

$$\frac{1}{t-s} \int_s^t a_1(\tau) d\tau < \frac{b_{12}}{b_{22}} M[a_2] - \varepsilon.$$

Since $m[a_2] > 0$ and

$$u_2' = u_2(a_2(t) - b_{22}u_2 - b_{21}u_1) \geq u_2(a_2(t) - b_{22}u_2),$$

we know by comparison with the solution of the logistic equation of Theorem 3.2 that $\inf_{t \geq t_0} u_2(t) = \delta_2 > 0$. Furthermore, u_2 is bounded from above by Lemma 4.1, so

$$\frac{b_{22}}{t-s}\int_s^t u_2(\tau)d\tau \leq \frac{1}{t-s}\int_s^t a_2(\tau)d\tau - \frac{b_{21}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{M_2}{t-s}, \tag{19}$$

where $M_2 = \log\left(\frac{u_{2L}}{u_{2M}}\right)$.

We suppose first that $\inf_{t \geq t_0} u_1(t) = \delta_1 > 0$. Then, by (19), and since u_1 is bounded from above

$$\begin{aligned}
\frac{1}{t-s}\int_s^t a_1(\tau)d\tau &= \frac{1}{t-s}\log\left(\frac{u_1(t)}{u_1(s)}\right) + \frac{b_{11}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{b_{12}}{t-s}\int_s^t u_2(\tau)d\tau \\
&\geq \frac{M_1}{t-s} + \frac{b_{11}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{b_{12}}{b_{22}}\left(\frac{1}{t-s}\int_s^t a_2(\tau)d\tau\right. \\
&\quad \left. - \frac{b_{21}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{M_2}{t-s}\right) \\
&\geq \frac{b_{12}}{b_{22}}\frac{1}{t-s}\int_s^t a_2(\tau)d\tau + \frac{M_1 + \bar{M}_2}{t-s} + \left(b_{11} - \frac{b_{12}b_{21}}{b_{22}}\right)\delta_1,
\end{aligned}$$

where $M_1 \in \mathbb{R}$ and $\bar{M}_2 = \frac{b_{12}}{b_{22}}M_2$. We can take $t-s$ large enough to have

$$\frac{1}{t-s}\int_s^t a_2(\tau)d\tau < M[a_2] - \frac{b_{22}}{b_{12}}\frac{\varepsilon}{2}$$

and

$$\frac{M_1 + \bar{M}_2}{t-s} + \left(b_{11} - \frac{b_{12}b_{21}}{b_{22}}\right)\delta_1 > -\frac{\varepsilon}{2},$$

so

$$\frac{1}{t-s}\int_s^t a_1(\tau)d\tau \geq \frac{b_{12}}{b_{22}}\frac{1}{t-s}\int_s^t a_2(\tau)d\tau - \frac{\varepsilon}{2} > \frac{b_{12}}{b_{22}}M[a_2] - \varepsilon.$$

We have arrived at a contradiction which means that $\inf_{t \geq t_0} u_1(t) = 0$. Since the initial condition $u_1(t_0)$ is positive, it must be that $u_1(t) > 0$ for every $t > t_0$. Then $\liminf_{t\to\infty} u_1(t) = 0$. We suppose now that $\limsup_{t\to\infty} u_1(t) = \gamma_1 > 0$. For every $n \geq n_0$, there exist times $t > s \geq t_0$, such that

$$u_1(t) = \frac{\gamma_1}{n}, u_1(s) = \frac{\gamma_1}{n}e^{-Rn} \;\;\&\;\; \min_{\tau\in[s,t]} u_1(\tau) = \frac{\gamma_1}{n}e^{-Rn},$$

where $R > 0$ and

$$a_1(t) - b_{11}u_1(t) - b_{12}u_2(t) \leq R \text{ for every } t \geq t_0.$$

Since

$$u_1(t) = u_1(s)e^{\int_s^t a_1(\tau)-b_{11}u_1(\tau)-b_{12}u_2(\tau)d\tau},$$

is easy to see that $t - s \geq n$. Then, using (19) again, and by the fact that $\log(u_1(t)/u_1(s)) \geq 0$, we obtain

$$\begin{aligned}\frac{1}{t-s}\int_s^t a_1(\tau)d\tau &\geq \frac{b_{11}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{b_{12}}{b_{22}}\left(\frac{1}{t-s}\int_s^t a_2(\tau)d\tau - \frac{b_{21}}{t-s}\int_s^t u_1(\tau)d\tau + \frac{M_2}{t-s}\right)\\ &\geq \frac{b_{12}}{b_{22}}\frac{1}{t-s}\int_s^t a_2(\tau)d\tau + \frac{\bar{M}_2}{t-s} + \left(b_{11} - \frac{b_{12}b_{21}}{b_{22}}\right)\frac{\gamma_1}{n}e^{-Rn}.\end{aligned}$$

We can take $t - s$ large enough to have

$$\frac{1}{t-s}\int_s^t a_2(\tau)d\tau < M[a_2] - \frac{b_{22}}{b_{12}}\frac{\varepsilon}{2},$$

and

$$\frac{\bar{M}_2}{t-s} + \left(b_{11} - \frac{b_{12}b_{21}}{b_{22}}\right)\frac{\gamma_1}{n}e^{-Rn} > -\frac{\varepsilon}{2}.$$

Hence

$$\frac{1}{t-s}\int_s^t a_1(\tau)d\tau \geq \frac{b_{12}}{b_{22}}\frac{1}{t-s}\int_s^t a_2(\tau)d\tau - \frac{\varepsilon}{2} > \frac{b_{12}}{b_{22}}M[a_2] - \varepsilon,$$

and we arrive again at a contradiction, then $\lim_{t\to\infty} u_1(t) = 0$. □

Lemma 4.10 *Assume (B). The solution $\widehat{u} = (0, \widehat{u}_2)$ is locally stable, where $\widehat{u}_2$ is the solution of*

$$u' = u(a_2(t) - b_{22}u)$$

that is bounded away from zero and infinity given by Theorem 3.2.

Proof To study the local stability of the solution $(0, \widehat{u}_2)$, we prove the existence of an exponential dichotomy around such solution with projection $P(t) = I_{2\times 2}$ in the sense of Definition 2.4. This makes it possible to use the result in [9, Theorem 8.5] to obtain the required local nonlinear stability. Hence, we study the system linearized around $(0, \widehat{u}_2)$. To this end we write

$$w(t) = u(t) - \widehat{u}(t),$$

where $u(t)$ is a solution with the initial condition in a neighborhood of $\widehat{u}$. We formulate the linearized system as in (16). For the system $v_1'(t) = B(t)v_1(t)$ we have an exponential dichotomy with the projection $P = I_{1\times 1}$. We study the one dimensional linear ODE with $A(t)$. To this end first observe that for $\widehat{u}_2$ we have

$$\int_s^t \widehat{u}_2(\tau)d\tau = \frac{1}{b_{22}}\left(\int_s^t a_2(\tau)d\tau - \log\left(\frac{\widehat{u}_2(t)}{\widehat{u}_2(s)}\right)\right)$$
$$\leq \frac{1}{b_{22}}\left(\int_s^t a_2(\tau)d\tau - \log\left(\frac{\widehat{u}_{2L}}{\widehat{u}_{2M}}\right)\right),$$

and we substitute this formula in (17) to obtain

$$v_1(t) \leq M_1 v_1(s) e^{\int_s^t a_1(r)d\tau - \frac{b_{12}}{b_{22}}\int_s^t a_2(\tau)d\tau},$$

where $M_1 = e^{\frac{b_{12}}{b_{22}}\log\left(\frac{\widehat{u}_{2L}}{\widehat{u}_{2M}}\right)}$.

Now, by (B), we know that for a $0 > -\delta > M[a_1] - \frac{b_{12}}{b_{22}}M[a_2]$, there exists a number n_0 such that for every $t - s \geq n_0$

$$\frac{1}{t-s}\int_s^t a_1(\tau)d\tau - \frac{b_{12}}{b_{22}(t-s)}\int_s^t a_2(\tau)d\tau$$
$$\leq \sup_{t-s\geq n_0}\frac{1}{t-s}\int_s^t a_1(\tau)d\tau - \frac{b_{12}}{b_{22}}\sup_{t-s\geq n_0}\frac{1}{t-s}\int_s^t a_2(\tau)d\tau < -\delta.$$

Then, if $t - s \geq n_0$, it is easy to see that

$$v_1(t) \leq M_1 v_1(s) e^{-\delta(t-s)}.$$

We suppose that $t - s \leq n_0$. Let $r = n_0 + s$. We have

$$v_1(t) \leq M_1 v_1(s) e^{\int_s^r a_1(\tau) - \frac{b_{12}}{b_{22}}a_2(\tau)d\tau} e^{-\int_t^r a_1(\tau) - \frac{b_{12}}{b_{22}}a_2(\tau)d\tau}$$
$$\leq M_1 v_1(s) e^{-(r-s)\delta} e^{-(r-t)(a_{1L} - \frac{b_{12}}{b_{22}}a_{2L})} = M_1 v_1(s) e^{(t-s)\delta} e^{(r-t)(-\delta-(a_{1L} - \frac{b_{12}}{b_{22}}a_{2L}))}.$$

Since $a_{1\,L} - \frac{b_{12}}{b_{22}}a_{2\,L} \leq M[a_1] - \frac{b_{12}}{b_{22}}M[a_2] < -\delta$, we have that

$$v_1(t) \leq \bar{M} v_1(s) e^{-\delta(t-s)},$$

where

$$\bar{M} = M_1 e^{n_0(-\delta-(a_{1L} - \frac{b_{12}}{b_{22}}a_{2L}))}.$$

Hence, for every $t \geq s$ we have

$$v_1(t) \leq \bar{M} v_1(s) e^{-\delta(t-s)}.$$

Therefore, $v_1'(t) = B(t)v_1(t)$ has an exponential dichotomy with projection $P = I_{1\times 1}$. It follows that the linearized system around $(0, \widehat{u}_2)$, has an exponential dichotomy with projection $P = I_{2\times 2}$, so the solution is locally stable. □

Once we have the local stability, the proof of the global asymptotic stability of the solution $(0, \widehat{u}_2)$ follows from [2, Theorem 2.3] thanks to the attractivity and positively invariance of the set $S = \{(x_1, x_2) \in \mathbb{R}^2_{\geq 0} \mid x_i \leq d_i \text{ for } i = 1, 2\}$ from Lemma 4.1. Hence, we have the following theorem.

Theorem 4.11 *Assume* (B). *Let u be a solution of* (LV-2D) *such that* $u(t_0) > 0$, *then* $u_1(t) \xrightarrow{t\to\infty} 0$ *and*

$$\lim_{t\to\infty} |u_2(t) - \widehat{u}_2| = 0.$$

We have obtained enough information for full characterization of the dynamics in the case (B) (Fig. 6).

Theorem 4.12 *Assume* (B). *The system* (LV-2D) *has the following solutions* $u : \mathbb{R} \to \mathbb{R}^2$ *bounded both in the past and in the future*

(a) $u(t) = (0, 0)$ *for* $t \in \mathbb{R}$,
(b) $u(t) = (0, \widehat{u}_2(t))$, *corresponding to the unique solutions for one-dimensional subproblem bounded away from zero and infinity, given in Theorem* 3.2.
(c) *Solutions of type* $u(t) = (0, u_2(t))$ *with initial condition* $0 < u_2(t_0) < \widehat{u}_2(t_0)$, *where* $\lim_{t\to-\infty} u_2(t) = 0$ *and* $\lim_{t\to\infty}(u_2(t) - \widehat{u}_2(t)) = 0$, *given in Lemma* 3.3.

All other solutions different from the ones listed in items (a)–(c) are backward unbounded. Moreover,

(d) *Solutions of type* $u(t) = (u_1(t), 0)$ *with initial condition* $u_1(t_0) > 0$, *satisfies* $\lim_{t\to\infty} u_1(t) = 0$ *and* $\lim_{t\to-\infty} u_1(t) = \infty$, *given by Theorem* 3.5.
(e) *Solutions of type* $u(t) = (0, u_2(t))$ *with initial condition* $u_2(t_0) > \widehat{u}_2(t_0)$, *satisfies* $\lim_{t\to-\infty} u_2(t) = \infty$ *and* $\lim_{t\to\infty}(u_2(t) - \widehat{u}_2(t)) = 0$, *given in Lemma* 3.3.

Proof We take a solution u such that $u(t_0) > 0$, and we supppose that $u_2(t)$ is backward bounded. If $\inf_{(-\infty,t_0]} u_2(t) = 0$, it is easy to see with the techniques used up to now that $u_2(t) \xrightarrow{t\to-\infty} 0$, and following Lemma 4.7, we see that $u_1(t) \xrightarrow{t\to-\infty} \infty$. We suppose then that $\inf_{t\in(-\infty,t_0]} u_2(t) > 0$. By (19) and (B) we have that

$$\begin{aligned}
&\int_s^t a_1(\tau)d\tau - b_{11}\int_s^t u_1(\tau)d\tau - b_{12}\int_s^t u_2(\tau)d\tau \\
&\quad \leq \int_s^t a_1(\tau)d\tau - \frac{b_{12}}{b_{22}}\int_s^t a_2(\tau)d\tau \\
&\qquad - \left(b_{11} - \frac{b_{21}b_{12}}{b_{22}}\right)\int_s^t u_1(\tau)d\tau + \frac{M_2 b_{12}}{b_{22}} \\
&\quad \leq -(t-s)\varepsilon - C.
\end{aligned}$$

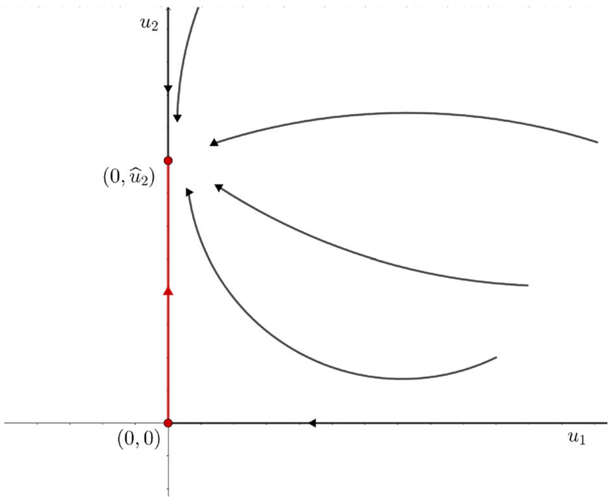

Fig. 6 Dynamics of (LV-2D) in case of the existence of an attracting global solution with one coordinate, u_2, bounded away from zero and infinity. The forward attractor (in red) is composed by the solutions $(0, 0)$, $(0, \widehat{u}_2)$, and the heteroclinic connections between them (Color figure online)

Using the explicit formula for the solution of u_1 we have that

$$u_1(s) = u_1(t)e^{-(\int_s^t a_1(\tau)d\tau - b_{11}\int_s^t u_1(\tau)d\tau - b_{12}\int_s^t u_2(\tau)d\tau)} \geq u_1(t)e^{(t-s)\epsilon}K \xrightarrow{s\to-\infty} \infty.$$

□

4.3 Extinction of Both Species

The remaining case in the 2D Lotka–Volterra model is the one for which there occurs the extinction of both species. The conditions that we need for that situation are the following

$$M[a_1] < 0 \quad \& \quad M[a_2] < 0. \tag{C}$$

Theorem 4.13 *Assuming* (C), *the solution* $u \equiv (0, 0)$ *is the unique trajectory of* (LV-2D) *bounded both in the future and in the past. Futhermore, for every solution such that* $u(t_0) \geq 0$, *it holds* $\lim_{t\to\infty}(u_1(t), u_2(t)) = (0, 0)$.

4.4 Periodic Case

We will now assume that the functions a_i are periodic with periods T_i. Such assumption has the justification in applications, for example by the periodicity of the seasons. If it holds, then

$$[a_i] = M[a_i] = m[a_i] = \frac{1}{T_i} \int_0^{T_i} a_i(\tau) d\tau.$$

Hence, $m[a_i]$ and $M[a_i]$ coincide. We denote their common value by $[a_i]$. In fact the results of this section are valid whenever we have such coincidence, and the periodicity is not necessary, only a sufficient condition. Using the previous results such assumption allows us to split the plane of the averaged coefficients $([a_1], [a_2])$ into the disjoint subregions with each subregion representing one particular structure of non-autonomous attractor. Summarizing all the above results, in the following table we depict which parameter values guarantee the existence of each of four types of globally stable solutions.

Conditions on $[a_1]$, $[a_2]$	Globally stable solution
$[a_1] > \frac{b_{12}}{b_{22}}[a_2]$ & $[a_2] > \frac{b_{21}}{b_{11}}[a_1]$	(u_1^*, u_2^*)
$[a_1] > 0$ & $[a_2] < \frac{b_{21}}{b_{11}}[a_1]$	$(\widehat{u}_1, 0)$
$[a_2] > 0$ & $[a_1] < \frac{b_{12}}{b_{22}}[a_2]$	$(0, \widehat{u}_2)$
$[a_1] < 0$ & $[a_2] < 0$	$(0, 0)$

If the averages of $[a]$ belong to each of the regions $\mathbb{R}^2$, we obtain, a particular form of globally stable solution consisting of zeros and nonzero values. For autonomous case, it has been proved in [18] that the regions of parameters a (which are constant in time) corresponding to the particular form of the globally stable solution can be split further into subregions that correspond to the particular structures of global attractor. They are then distinguished by particular unstable equilibria and the heteroclinic connections.

These are the findings, which, for the planar case, we adapt for the non-autonomous theory. In the region

$$[a_1] > \frac{b_{12}}{b_{22}}[a_2] \quad \& \quad [a_2] > \frac{b_{21}}{b_{11}}[a_1], \tag{20}$$

the globally stable solution is permanent, that is there exists the solution $(u_1^*(\cdot), u_2^*(\cdot))$ such that $u_i^*(t) > 0$ for $i = 1, 2$ and every $t \in \mathbb{R}$. We have seen in Sect. 4.1.2, however, that the structure of the forward attractor of the system varies depending on the signs of $[a_1]$ and $[a_2]$. When both are positive, then the solutions consisting of a zero and a strictly positive function on another variable always exist for both variables. Then the structure of global solutions and their connections follows the scheme depicted in Fig. 7.

When $[a_1]$ is, however, negative, but the permanence condition (20) still holds, then the structure of the attractor is given in Fig. 8.

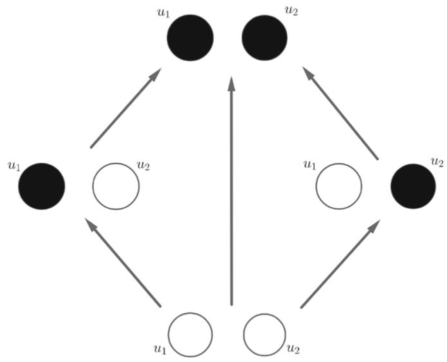

Fig. 7 Structure of the forward attractor when both $[a_1]$ and $[a_2]$ are positive. The black dots in the above figure represent the coordinates for which the solution is strictly positive, and the white dots correspond to the coordinates that are identically equal to zero

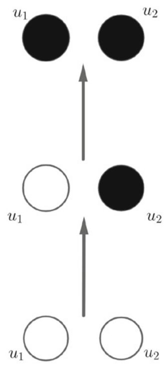

Fig. 8 Structure of the forward attractor when $[a_1]$ is negative, but it holds (20)

Summarizing, we have three subregions of the region given by (20). So, depending on the location of the vector $([a_1], [a_2])$ there may occur one of the six possible structures of the non-autonomous attractor. Particular regions and the structures to which they correspond are depicted in Fig. 9.

The only difficulty concerns the attractor structure on the boundaries between the regions, i.e. the case when the nonsharp inequalities hold in the above table. We leave open the question of this structure for nonsharp inequalities—its answer would shed light on the understanding of non-autonomous attractor bifurcation. Some partial answers, however, are already available. In particular in [25] the author proves that for the logistic equation (9), if $[a] \leq 0$ (not only $[a] < 0$), for every solution u with positive initial condition we have $u(t) \xrightarrow{t\to\infty} 0$. Moreover in [25] it is proved, for the planar case of competitive coexistence if the coefficients satisfy

$$[a_1] \leq \frac{b_{12}}{b_{22}}[a_2] \quad \& \quad [a_2] > 0,$$

then for any solution u with initial positive conditions we have that $\lim_{t\to\infty}(u_1, u_2 - \widehat{u}_2) = (0, 0)$. Still the question of cooperative case, as well as the results on unbounded

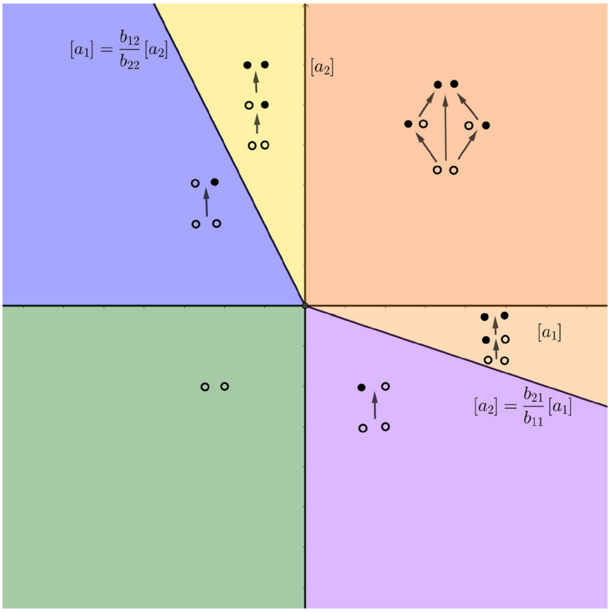

Fig. 9 Split of the space of $\mathbb{R}^2$ for the space of values $([a_1], [a_2])$

backward behavior, which would be needed for the characterization of the attractor structure, are, according to our knowledge, not yet available.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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