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On chaos in Lotka–Volterra systems: an analytical approach

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Abstract
In this paper, we study Lotka–Volterra systems with N species and n resources. We show that the long time dynamics of these systems may be complicated. Depending on parameter choice, they can generate all types of hyperbolic dynamics, in particular, chaotic ones. Moreover, Lotka–Volterra systems can generate Lorenz dynamics. We state the conditions on the strong persistence of Lotka–Volterra systems when the number of resources is less than the number of species.

Mathematics Subject Classification: 37D05, 37D10, 37D45, 92D25, 92D40

1. Introduction

In this paper, we consider the Lotka–Volterra system for N species and n resources. This system is an important model for population dynamics and ecology, describing species concurrence and interactions. According to the Poincaré–Bendixon theory, the chaotic behaviour in Lotka–Volterra systems may occur only for $N \geqslant 3$. There is numerical evidence of the existence of chaotic motion for $N \geqslant 3$ (see [1], and [11, 37] and references therein), but as far as we know there is no analytical proof of this fact. For competitive Kolmogorov systems (which are much more general than Lotka–Volterra ones), it was shown by Smale (see [36]) that any type of dynamics can be realized there when the number of species is sufficiently large.

The large time behaviour of solutions is relatively well understood for gradient and monotone dissipative systems (see, for example, [9, 10, 24]). We use the so-called method of realization of vector fields (RVF) proposed by Poláčik [26] for partial differential equations (see also [27, 28, 32, 38, 39]). This method allows us to show that a family of semiflows realizes systems of ordinary differential equations on some invariant manifolds. In certain cases, this method can be used to prove the existence of chaotic large time behaviour. Notice that in the pioneering book [25] it was shown that all autonomous systems of first order ordinary differential equations with polynomial right-hand sides can be realized by large Lotka–Volterra systems. However, [25] contains no results on invariant manifolds, persistence and chaos.

Another aspect treated in the paper is the influence of resources on the dynamics of the system. The case of one resource has already been investigated by Volterra [41]. He proved that under certain conditions only one species survives. Other examples of such an influence can be found in [11, 37]. The competitive exclusion principle [8] predicts that N species cannot exist on fewer than N resources, although, in some realistic natural situations, many species will share a few resources. This dilemma is the so-called paradox of plankton [14]. Chaotic dynamics have been proposed as an answer to this paradox in [12, 13], where a model (more complicated than the Lotka–Volterra system) with 3 resources was studied numerically.

The main result of this paper is the existence of chaotic behaviour for Lotka–Volterra dynamics with few resources and many species. We also show that for any prescribed finite family of hyperbolic (possibly, chaotic) dynamics, there is a Lotka–Volterra system generating this family of dynamics. Moreover, this Lotka–Volterra system can be chosen to be strongly persistent. This means that species abundances $x_i(t)$ do not vanish as $t \to +\infty$ and $|x_i(t)|$ are bounded for all times $t > 0$. We find a class of Lotka–Volterra systems with $n < N$ resources, which are strongly persistent. Certainly, the conditions for the exclusion principle (see [11], section 5.4) are violated here.

The paper is organized as follows. In section 2 we state the Lotka–Volterra model for N species and n resources. An important change of variables, which reduces the initial system to a system of n differential equations, is presented in section 3. This transformation is analogous to the change of variables suggested in [4–6] for a generalized Lotka–Volterra model.

In section 4.1 we study the family $\mathcal{G}$ of the vector fields G in $\boldsymbol{R}^n = \{q : q = (q_1, \dots, q_n)\}$ resulting from the above change of variables. We show that the family $\mathcal{G}$ contains all polynomials of exponential functions $\exp(\lambda_k q_k)$. Using a classical theorem on approximation of functions by exponential polynomials (see theorem 18 from [18]), we present conditions on exponents λ_k, which guarantee the density of corresponding exponential polynomials in the space of continuous functions on a ball.

Section 4.2 contains the main results on chaotic behaviour in Lotka–Volterra systems. If a finite family of hyperbolic dynamics is given, a sufficiently large Lotka–Volterra model with an appropriate choice of parameters can generate this family by variation of the initial data only.

In section 5, we investigate the plankton paradox problem: how many species can share a bounded number of resources? Mathematically, it concerns the important concepts of *permanency* and *strong persistency*, introduced by Schuster, Sigmund and Wolf and Freedman and Waltman, respectively (see [7, 33], for an overview see [11, 37]). Strong persistency is weaker than permanency and means that, for each individual trajectory $x(t)$ (an individual life history, from the biological point of view), the abundance of all species does not tend to 0 as time t goes to $+\infty$. We describe the construction of strongly persistent Lotka–Volterra systems, which have chaotic behaviour.

A biological interpretation of these results can be found in the final section.

2. Statement of problem

The Lotka–Volterra system reads as follows:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i \left(r_i - \sum_{j=1}^{N} K_{ij} x_j \right), \tag{1}$$

where $i = 1, \ldots, N$, and in which N species with population x_i for $i = 1$ to N compete for bounded resources, the coefficient r_i is the intrinsic growth (or decay) rate for ith species. The matrix $\boldsymbol{K}$ with the entries K_{ij} determines an interaction between species. We consider this system in the positive cone $\boldsymbol{R}^N_> = \{x = (x_1, \ldots, x_N) : x_i > 0\}$, which is invariant under dynamics (1). Below we assume that the initial data for (1) always lie in this cone:

$$x(0) = \phi \in \boldsymbol{R}^N_>. \tag{2}$$

Our key assumptions are as follows. Suppose that the interaction matrix can be factorized

$$\boldsymbol{K} = \boldsymbol{A}\boldsymbol{B},$$

where $\boldsymbol{A}$, $\boldsymbol{B}$ are matrices of size $N \times n$ and $n \times N$ respectively, i.e.

$$K_{ij} = \sum_{s=1}^{n} A_{is} B_{sj}. \tag{3}$$

Here $1 \leqslant n \leqslant N$. Notice that each matrix $\boldsymbol{K}$ of the rank n admits such factorization and the matrices $\boldsymbol{A}$, $\boldsymbol{B}$ depend continuously on $\boldsymbol{K}$. We also assume

$$r_i = \sum_{k=1}^{n} A_{ik} \mu_k \tag{4}$$

for certain μ_k, $k = 1, \ldots, n$. If $\boldsymbol{K}$ is represented by (3) and rank $\boldsymbol{K} = n$, assumption (4) is necessary for strong persistence, we discuss this question in more detail in section 5.1 and also present a biological interpretation.

Under the above assumptions, (1) can be represented as a model with n resources:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i S_i(x), \qquad i = 1, \ldots, N, \tag{5}$$

where

$$S_i(x) = \sum_{k=1}^{n} A_{ik} R_k(x), \qquad R_k(x) = \mu_k - \sum_{l=j}^{N} B_{kj} x_j. \tag{6}$$

This means that all growth coefficients S_i depend on resources $R_j(x)$, which are linear functions of x. Notice that R_j can be negative. In this case they can be interpreted as production rates.

3. Change of variables

Let $q = (q_1, \ldots, q_n) \in \boldsymbol{R}^N$. We define a family of vector fields depending on parameters $\boldsymbol{A}$, $\boldsymbol{B}$, μ and N by

$$G_k(q) = G_k(q, \mu, \boldsymbol{A}, \boldsymbol{B}, C, N) = -\mu_k + \sum_{l=1}^{N} B_{kl} C_l \exp(-\sum_{j=1}^{n} A_{lj} q_j), \tag{7}$$

where $C = (C_1, \ldots, C_N) \in \boldsymbol{R}^N_>$ and $k = 1, \ldots, n$. Here $\boldsymbol{A}$ and $\boldsymbol{B}$ are the same matrices as in the previous section and the vector parameter C plays a special role. Namely, it determines a connection between the initial condition (2) for system (1) and the initial conditions for the transformed system from the following proposition, where a reduction of system (1) to a $n \times n$-system of differential equations is described.

Proposition 3.1.

(i) *Assume* $p \in \mathbf{R^n}$. *Let* q *be a solution to the Cauchy problem*

$$\frac{\mathrm{d}q_k}{\mathrm{d}t} = G_k(q, \mu, \boldsymbol{A}, \boldsymbol{B}, C, N), \qquad q(0) = p, \tag{8}$$

where $k = 1, \ldots, n$. *Then the functions*

$$x_i = C_i \exp(-\sum_{j=1}^{n} A_{ij} q_j), \qquad i = 1, \ldots, N, \tag{9}$$

satisfy (1) *and the Cauchy data* (2) *with*

$$\phi_i = C_i \exp(-\sum_{j=1}^{n} A_{ij} p_j), \qquad i = 1, \ldots, N. \tag{10}$$

(ii) *Let* x *be a solution to the Cauchy problem* (1), (2). *If* q *solves* (8) *with* C *and* p *satisfying* (10) *then* x *and* q *are connected by* (9).

Proof.

(i) Differentiating (9) and using (8), we get

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i\Big(- \sum_{j=1}^{n} A_{ij}(-\mu_j + \sum_{m=1}^{N} B_{jm} C_m \exp(-\sum_{k=1}^{n} A_{mk} q_k)\Big),$$

which implies (1). Relation (10) follows from (9).

(ii) Let x be a solution to (1), (2). If we take q as solution to (8), where C and p are subject to (10), we observe that vector function (9) also solves (1), (2). This proves the assertion.

□

Remark 1. From relation (10) it follows that the constants C and p are defined non-uniquely. This is connected with the following fact. If q is a solution to (8) with certain C and p, then the vector function $q + \alpha = (q_1 + \alpha_1, \ldots, q_n + \alpha_n)$ solves (8) with C_j replaced by $C_j \exp(-\sum_{k=1}^{n} A_{ik}\alpha_k)$ and p_k by $p_k + \alpha_k$. This means that there is a natural isomorphism between systems satisfying (10) for a fixed ϕ.

We denote by $\mathcal{G}(\boldsymbol{A}, \boldsymbol{B}, N, \mu)$ the family of vector fields defined by (7) for all possible $C \in \boldsymbol{R}^N_>$. Let $\mathcal{Q}_n(C)$ be the set of points $x \in \boldsymbol{R}^N_>$ defined by (9), where $q \in \boldsymbol{R}^n$. Then $\mathcal{Q}_n(C)$ is a manifold of dimension n, which is invariant with respect to the semiflow generated by (1).

4. Main results

4.1. Properties of fields from $\mathcal{G}$

Let M be a positive integer and $\boldsymbol{D}$ be a $M \times n$ matrix with real entries. We write $\boldsymbol{M}^n = \{1, \ldots, M\}^n$ and consider the class $\mathcal{E}(\boldsymbol{D}, M, n)$ consisting of vector fields $F = (F_1, \ldots, F_n)$ with components

$$F_k(q) = -\mu_k + \sum_{i \in M^n} b_{ki} \exp\left(\sum_{j=1}^{n} D_{i_j j} q_j\right), \qquad k = 1, \ldots, n. \tag{11}$$

Here $\boldsymbol{i} = (i_1, \ldots, i_n)$ is a multi-index, b_{mi} are arbitrary coefficients and μ_l, $l = 1, \ldots, n$, are fixed constants the same as in (4).

In order to explain the introduction of this class of fields, let us consider the following example. As is known the functions

$$\sum_{i=1}^{M} a_i^{(j)} \exp(\lambda_i^{(j)} q_j),$$

where j is fixed, are dense in the space $C^1[r_0, r_1]$, $r_0 < r_1$ provided the exponents $\lambda_i^{(j)}$ satisfy a certain growth condition (see appendix and [18]). Therefore, the linear combinations of the functions

$$a_{k_1}^{(1)} a_{k_2}^{(2)} \ldots a_{k_n}^{(n)} \exp(\lambda_{k_1}^{(1)} q_1 + \cdots + \lambda_{k_n}^{(n)} q_n)$$

are dense in $(C^1[r_0, r_1])^n$. But these combinations are the same as those in (11).

The connection between classes $\mathcal{E}(\boldsymbol{D}, M, n)$ and $\mathcal{G}$ is given by the following.

Proposition 4.1. *For every integer $M > 0$ and $M \times n$ matrix $\boldsymbol{D}$ there exist a positive integer N and matrices $\boldsymbol{A}$ and $\boldsymbol{B}$ of the sizes $N \times n$ and $n \times N$ respectively such that*

$$\mathcal{E}(\boldsymbol{D}, M, n) \subset \mathcal{G}(\boldsymbol{A}, \boldsymbol{B}, N, \mu).$$

Proof. Let $N = 2M^n n$. First, we will use the multi-index $\boldsymbol{i} = (i_1, \ldots, i_n) \in \boldsymbol{M}^n$ instead of the index $m = 1, \ldots, M^n$, for this purpose we assume that an isomorphism $m = m(\boldsymbol{i})$ is fixed. Second, every index $l = 1, \ldots, 2M^n n$ can be represented as $l = (2m-2)n + s$ or $l = (2m-1)n + s$, with certain $m = 1, \ldots, M^n$ and $s = 1, \ldots, n$. Then, by this notation, sum (7) can be rewritten as

$$G_k = -\mu_k + S_1 + S_2, \tag{12}$$

where

$$S_2 = \sum_{m=1}^{M} \sum_{s=1}^{M-1} B_{k,(2m-2)n+s} C_{(2m-2)n+s} \exp(-\sum_{j=1}^{n} A_{(2m-2)n+s,j} q_j),$$

$$S_1 = \sum_{m=1}^{M} \sum_{s=1}^{M-1} B_{k,(2m-1)n+s} C_{(2m-1)n+s} \exp(-\sum_{j=1}^{n} A_{(2m-1)n+s,j} q_j).$$

Let us set

$$A_{(2m-2)n+s,j} = A_{(2m-1)n+s,j} = D_{i_j,j}, \tag{13}$$

where $\boldsymbol{i} = \boldsymbol{i}(m)$ is a multi-index corresponding to m, and

$$B_{k,(2m-2)n+s} = \kappa_{km}^{(0)} \delta_{k,s}, \qquad B_{k,(2m-1)n+s} = \kappa_{km}^{(1)} \delta_{k,s}, \qquad \kappa_{km}^{(0)} \kappa_{km}^{(1)} < 0 \tag{14}$$

for all $s, j, k = 1, \ldots, n$ and $m = 1, \ldots, M^n$. Here $\delta_{s,k}$ is the Kronecker delta and i_j is the jth component of $\boldsymbol{i}$, $m = m(\boldsymbol{i})$. Then formula (12) becomes

$$G_k = -\mu_k + \sum_{i \in M^n} \widetilde{C}_{k,m(i)} \exp(-\sum_{j=1}^{n} D_{i_j,j}\, q_j), \tag{15}$$

where

$$\widetilde{C}_{k,m} = \kappa_{km}^{(0)} C_{(2m-2)n+k} + \kappa_{km}^{(1)} C_{(2m-1)n+k}.$$

This implies that the constants $\widetilde{C}_{k,1}, \ldots, \widetilde{C}_{k,m}$ run all values in $\boldsymbol{R}^N$ as C runs all values in $\boldsymbol{R}^N_>$, $N = M^n$ for every k. The proof of the assertion is complete.

Let us consider the family $\mathcal{P}_{k,n}$ of polynomial vector fields $H = (H_1, \dots, H_n)$ of order k, i.e.,

$$H_m(z) = \sum_{|i| \leqslant k} a_{m,\mathbf{i}} z_1^{i_1} z_2^{i_2} \dots z_n^{i_n}, \qquad m = 1, \dots, n, \tag{16}$$

where $\boldsymbol{i} = (i_1, \dots, i_n)$, $|\boldsymbol{i}| = i_1 + i_2 + \dots + i_n$ and $z_j \in \boldsymbol{R}_+$ are real positive numbers.

Proposition 4.2. *For given positive integers k and n there exist a number N, a $n \times N$ matrix $\boldsymbol{A}$, a $N \times n$ matrix $\boldsymbol{B}$ and a vector $\mu \in \boldsymbol{R}^n$, such that for each polynomial field $H \in \mathcal{P}_{k,n}$ there are coefficients C_i such that system (8) reduces to the system*

$$\frac{\mathrm{d}z_m}{\mathrm{d}t} = H_m(z), \qquad m = 1, \dots, n \tag{17}$$

by the change of variables

$$z_m = \exp(q_m). \tag{18}$$

Proof. Consider the system

$$\frac{\mathrm{d}q_m}{\mathrm{d}t} = F_m(q), \tag{19}$$

where F_m are defined by (11) with $\mu_k = 0$. The change of variables (18) transforms (19) to the following system:

$$\frac{\mathrm{d}z_m}{\mathrm{d}t} = \tilde{H}_m = \sum_{|\boldsymbol{i}| \in \boldsymbol{M}^n} b_{m,\mathbf{i}} z_1^{D_{i_1,1}} z_2^{D_{i_2,2}} \dots z_n^{D_{i_n,n}} z_m, \tag{20}$$

where $M = k + 2$. Taking

$$D_{sj} = s - 2, \qquad s \in \{1, \dots, k + 2\},$$

we have

$$\tilde{H}_m = \sum_{|\boldsymbol{i}| \in \boldsymbol{M}^n} b_{m,i} z_1^{i_1 - 2} z_2^{i_2 - 2} \dots z_n^{i_n - 2} z_m, \qquad m = 1, \dots, n. \tag{21}$$

In general, $\tilde{H}_m$ is not a polynomial, because the monomials in the right-hand side of (21) can contain some terms with negative exponents, z_j^{-1}. However, by a choice of $b_{m,i}$ we transform $\tilde{H}_m$ to polynomials. In fact, let

$$b_{m,i} = 0, \qquad \text{if } i_j = 1 \quad \text{for some } j \neq m.$$

and

$$b_{m,i} = 0, \qquad \text{if any } i_j = k + 2.$$

Then (21) is a polynomial of degree k and all polynomials from $\mathcal{P}_{k,n}$ can be obtained in (21) by an appropriate choice of $b_{m.i}$. The proof is complete.

In the appendix we prove the following assertion.

Proposition 4.3. *Assume a field $F \in \mathcal{G}(\boldsymbol{A}, \boldsymbol{B}, N, \mu)$ has a stable hyperbolic rest point. Then ω-limit set of (5) has the fractal and Hausdorff dimension $d \geqslant N - n$.*

By B_n we denote the closed ball of radius 1 in $\boldsymbol{R}^n$ centred at 0. Let $\bar{D}(K, n)$ be the class of infinite matrices $\boldsymbol{D} = \{D_{ij}\}$, $i \in \boldsymbol{N}$ and $j \in \{1, \ldots, n\}$ such that

$$| D_{ij}| < K, \qquad i = 1, 2, \ldots, \qquad j = 1, \ldots, n. \tag{22}$$

If $\boldsymbol{D} \in \bar{D}(K, n)$ and $\bar{M}$ is a positive integer, then by $\boldsymbol{D}^{(\bar{M})}$ we denote a $\bar{M} \times n$-matrix with the entries

$$D_{ij}^{(\bar{M})} = D_{ij}, \qquad i = 1, \ldots, \bar{M}, \quad j = 1, \ldots, n. \tag{23}$$

The matrix $\boldsymbol{D}^{(\bar{M})}$ will be called $\bar{M}$*-truncation* of $\bar{D}$.

Proposition 4.4. *Let us fix an integer $n > 0$. For any $K > 0$ there exists a matrix $\boldsymbol{D} \in \bar{D}(K, n)$ such that the space of all vector fields $\cup_{M=1}^{\infty} \mathcal{E}(\boldsymbol{D}^{(M)}, M, n)$ is dense in the set of all C^1-smooth vector fields on B_n.*

The proof uses a technical lemma and can be found in the appendix. Inequality (22) has a transparent biological interpretation: interactions K_{ij} between species can be chosen *a priori* bounded. In fact, the boundedness of $\boldsymbol{D}$ in (11) and the boundedness of b_{ki} imply that K_{ij} are bounded as $N \to \infty$.

4.2. Chaos in the Lotka–Volterra model with n resources

Let us recall some facts from the theory of dynamical systems which we will use below. Assume a semiflow on B_n has a compact invariant hyperbolic set $\mathcal{I}$ (we refer to the definition of compact invariant hyperbolic sets in [15, 29, 31]). The simplest hyperbolic sets are hyperbolic rest points and limit cycles. Famous examples of hyperbolic sets with chaotic dynamics are the Smale horseshoe and Anosov flows [2, 29]. Chaotic dynamics on the compact invariant hyperbolic set $\mathcal{I}$ is transitive and has sensitive dependence on the initial conditions (see [31, p 41], [29, p 40 and p 86]). A flow S^t is transitive on $\mathcal{I}$ provided the orbit of some point $p \in \mathcal{I}$ is dense in $\mathcal{I}$. The flow S^t on the set $\mathcal{I} \subset B_n$ is said to have a sensitive dependence on the initial conditions provided there is an $r > 0$ (independent of the point) such that for each point $x \in \mathcal{I}$ and for each $\epsilon > 0$ there is a point $y \in \mathcal{I}$ with $|x - y| < \epsilon$ and a time moment $T \geqslant 0$ such that $|S^T x - S^T y| > r$ [29]. Recall that a trajectory of a semiflow S^t is the map $t \to x(t) = S^t x(0)$, where $t \in (0, +\infty)$ and the orbit is the union of the trajectory points $x(t)$.

Consider a Cauchy problem

$$\frac{\mathrm{d}q}{\mathrm{d}t} = F(q), \qquad q(0) = p, \tag{24}$$

where $q, p \in B_n \subset \boldsymbol{R}^n$ and $F = (F_1, \ldots, F_n) \in C^1(B_n)$. Assume that F is directed inward on the boundary ∂B_n, then system (24) generates a global semiflow. Assume this semiflow has a compact hyperbolic invariant set $\mathcal{I}$. Clearly, it must lie at a positive distance from ∂B_n. Let us consider a vector field $\tilde{F}$, which is sufficiently close to F in C^1-norm, i.e.

$$|\tilde{F} - F|_{C^1(B_n)} < \epsilon \tag{25}$$

for a sufficiently small $\epsilon > 0$. Then the perturbed dynamics

$$\frac{\mathrm{d}q}{\mathrm{d}t} = \tilde{F}(q) \tag{26}$$

also has a compact invariant hyperbolic set $\tilde{\mathcal{I}}$ close to $\mathcal{I}$ (see [31], section 15, and [15], theorem 18.2.3). Flows, generated by (24) and (26), and restricted to $\mathcal{I}$ and $\tilde{\mathcal{I}}$, respectively, are topologically orbitally equivalent (on this equivalence, see [29], section 4.7.). This entails, in particular, that there is a homeomorphism $h : \mathcal{I} \to \tilde{\mathcal{I}}$, which tends to the identity as

$|\tilde{F} - F|_{C^1(B_n)} \to 0$. Moreover, this homeomorphism maps the orbits of (24), restricted to $\mathcal{I}$ onto the orbits of (26), restricted to $\tilde{\mathcal{I}}$ (notice that these orbits are images of trajectories defined for all $t \in (-\infty, +\infty)$).

We denote by $S^t_{\tilde{F}}$ the global semiflow on B_n, generated by (26). If this semiflow has a compact invariant set $\mathcal{I}$, then we denote by $S^t_{\tilde{F}}|_{\mathcal{I}}$ a flow which is the restriction of $S^t_{\tilde{F}}$ to $\mathcal{I}$. We denote by S^t_{LV} a semiflow generated by system (5), and the corresponding restriction to an invariant set K, by $S^t_{LV}|_K$.

Now we can formulate the main theorem.

Theorem 4.5. *Let $F^{(l)}$, $l = 1, \ldots, p$, be C^1-vector fields on B_n directed inward on ∂B_n and having compact invariant hyperbolic sets $\mathcal{I}^{(l)}$. Then there exists a positive integer N, $\mu \in \boldsymbol{R}^n$, matrices $\boldsymbol{A}, \boldsymbol{B}$ of sizes $N \times n$ and $n \times N$ respectively and $C^{(l)} \in \boldsymbol{R}^N_>$ such that system (5) has compact invariant sets $\mathcal{K}(C^{(l)}) \subset \mathcal{Q}_n(C^{(l)})$, which are homeomorphic to $\mathcal{I}^{(l)}$. These sets are hyperbolic for the flow $S^t_{LV}|_{\mathcal{K}(C^{(l)})}$ and, moreover, the flows $S^t_{LV}|_{\mathcal{K}(C^{(l)})}$ and $S^t_{F^{(l)}}|_{\mathcal{I}^{(l)}}$ are orbitally topologically equivalent.*

In other words, if a finite family of hyperbolic dynamics is given, a sufficiently large Lotka–Volterra model with appropriate parameters can generate this family by variation of the initial data. These hyperbolic dynamics may be chaotic.

Proof. We derive this theorem from propositions 3.1 and 4.4. According to proposition 4.4, for each $\epsilon > 0$ there exist a matrix $\boldsymbol{D} \in \bar{D}(K, n)$, a number M and vector fields $\tilde{F}^{(l)} \in \mathcal{E}(\boldsymbol{D}^{(M)}, M, n)$, $l = 1, \ldots, p$ such that

$$|\tilde{F}^{(l)} - F^{(l)}|_{C^1(B_n)} < \epsilon. \tag{27}$$

These estimates imply the existence of compact invariant hyperbolic sets $\tilde{\mathcal{I}}^{(l)}$ for the dynamics

$$\frac{\mathrm{d}q}{\mathrm{d}t} = \tilde{F}^{(l)}(q),$$

together with homeomorphisms $h^{(l)} : \mathcal{I}^{(l)} \to \tilde{\mathcal{I}}^{(l)}$, which map orbits of $\mathcal{I}^{(l)}$ onto orbits of $\tilde{\mathcal{I}}^{(l)}$ and define topological orbital equivalencies, provided that $\epsilon > 0$ is a sufficiently small number.

By proposition 4.1 we can find matrices $\boldsymbol{A}, \boldsymbol{B}$ and vectors $C^{(l)} \in \boldsymbol{R}^{N_l}_>$ such that

$$\tilde{F}^l_k = \sum_{m=1}^{N} B_{km} \tilde{C}^{(l)}_m \exp(-\sum_{j=1}^{n} A_{mj} q_j). \tag{28}$$

Then the compact invariant sets $\mathcal{K}(C^{(l)})$ are images of $\tilde{\mathcal{I}}^{(l)}$ under the map $q \to x(q)$ from B_n to $\boldsymbol{R}^N_>$ defined by relation (9). □

The proof is complete.

Remarks.

(i) For C sufficiently close to $C^{(l)}$, the manifold $\mathcal{Q}_n(C)$ also contains a compact hyperbolic invariant set $\mathcal{K}(C)$ homeomorphic to $\mathcal{I}^{(l)}$.

(ii) Since the matrix $\bar{D}$ can be chosen to be uniformly bounded (see proposition 4.4), the entries of the matrices $\boldsymbol{A}, \boldsymbol{B}$ (and hence the coefficients K_{ij}) are also uniformly bounded with respect to N. From the biological point of view, this means that one can generate complicated dynamics within a large population with restricted species interactions.

4.3. Lotka–Volterra systems generating Lorenz dynamics

As is known, the Lorenz system

$$\frac{dx_1}{dt} = \sigma(x_2 - x_1), \qquad \frac{dx_2}{dt} = x_1(r - x_3) - x_2, \qquad \frac{dx_3}{dt} = x_1x_2 - \beta x_3, \tag{29}$$

with an appropriate choice of constants r, σ, β, has trajectories with chaotic behaviour. This system is polynomial, but the trajectory may leave the cone $x_i > 0, i = 1, 2, 3$, whereas the polynomial system (17) is defined on this cone. We can, however, circumvent this difficulty by a shift of the variables x_i. Notice that the Lorenz system (29) has an absorbing set A_R defined by

$$A_R = \{x : \; x_1^2 + x_2^2 + (x_3 - \sigma - r)^2 < R^2\},$$

where R is large enough. The attractor of the Lorenz system lies in this set $B_{R,\sigma,r}$. Therefore, we can restrict $x = (x_1, x_2, x_3)$ to this domain in (29). After the change of variables $z_i = x_i + R_i$, where $R_1, R_2 > R$ and $R_3 > \sigma + r + R$, we have $z_i \geqslant \delta > 0$ on A_R. With the new variables the Lorenz system takes the form

$$\frac{dz_1}{dt} = \sigma(z_2 - z_1) + \sigma(R_1 - R_2), \tag{30}$$

$$\frac{dz_2}{dt} = (r + R_3)z_1 + R_1z_3 - z_1z_3 - z_2 - R_3R_1 - R_1r + R_2, \tag{31}$$

$$\frac{dz_3}{dt} = z_1z_2 - \beta z_3 - R_2z_1 - R_1z_2 + R_1R_2 + \beta R_3. \tag{32}$$

According to proposition 4.2, this system can be obtained from a Lotka–Volterra system with 3 resources and $2 \times M^3 \times n = 162$ species, since here $M = n = 3$. However, one can find a realization of the Lorenz system by (1) involving only 10 species. To show this we note that for sufficiently large $R > R_0(R_1, R_2, r_3, \sigma, r, \beta)$, system (30)–(32) has the absorbing set

$$\tilde{A}_R = \{z : \; (z_1 - R_1)^2 + (z_2 - R_2)^2 + (z_3 - R_3 - \sigma - r)^2 < R^2\},$$

which is the shift of the absorbing set A_R for the Lorenz system. Assuming that

$$R_2 \gg R_1, R_3, r$$

and making the change of variables $z_i = \exp(q_i)$, we write system (30)–(32) as

$$\frac{dq_1}{dt} = \sigma(\exp(q_2 - q_1) - 1) + \sigma(R_1 - R_2)\exp(-q_1), \tag{33}$$

$$\begin{aligned}\frac{dq_2}{dt} &= (r + R_3)\exp(q_1 - q_2) + R_1\exp(q_3 - q_2) - \exp(q_1 + q_3 - q_2) \\ &\quad - 1 + (-R_3R_1 - R_1r + R_2)\exp(-q_2),\end{aligned} \tag{34}$$

$$\begin{aligned}\frac{dq_3}{dt} &= \exp(q_1 + q_2 - q_3) - \beta - R_2\exp(q_1 - q_3) \\ &\quad - R_1\exp(q_2 - q_3) + (R_1R_2 + \beta R_3)\exp(-q_3).\end{aligned} \tag{35}$$

In order to represent the right-hand side of this system in the form

$$G_k(q_1, q_2, q_3) = -\mu_k + \sum_{l=1}^{10} B_{kl}C_l \exp\Big(-\sum_{j=1}^{3} A_{lj}q_j\Big), \qquad k = 1, 2, 3, \tag{36}$$

we take $\mu_1 = \sigma, \quad \mu_2 = 1, \quad \mu_3 = \beta$ and $C_1 = C_2 = \cdots = C_{10} = 1$. Furthermore, we choose

$$A_{11} = 1, \qquad A_{12} = -1, \qquad A_{13} = 0, \qquad A_{21} = 1, \qquad A_{22} = A_{23} = 0,$$

and

$$B_{11} = \sigma,\ B_{12} = \sigma(R_1 - R_2), \qquad B_{13} = \cdots = B_{1,10} = 0.$$

For $k = 2$ we set

$$A_{32} = A_{52} = A_{62} = A_{42} = 1, \qquad A_{33} = A_{41} = A_{61} = A_{63} = 0,$$
$$A_{31} = A_{43} = A_{51} = A_{53} = -1,$$

and

$$B_{21} = B_{22} = 0, \qquad B_{23} = r + r_3, \qquad B_{24} = R_1, \qquad B_{25} = -1,$$
$$B_{26} = -R_3 r_1 - r_1 r + R_2.$$

Finally, for $k = 3$, let us take

$$A_{71} = A_{72} = A_{10,3} = A_{82} = A_{93} = 1, \qquad A_{81} = A_{73} = A_{92} = -1,$$
$$A_{91} = A_{83} = A_{10,1} = A_{10,2} = 0,$$

and

$$B_{31} = \cdots = B_{36} = 0, \qquad B_{37} = 1, \qquad B_{38} = -R_2, \qquad B_{39} = -R_1,$$
$$B_{3,10} = R_1 R_2 + \beta R_3.$$

As a result, we obtain that system $\mathrm{d}q_k/\mathrm{d}t = G_k(q_1, q_2, q_3)$ coincides with system (33)–(35). Now, we can choose σ, β, r in such a way that the corresponding Lorenz system has a chaotic attractor.

Note that when we vary the parameters β, r, σ, the Lorenz systems demonstrate different transitions and dynamical effects: Andronov–Hopf and pitchfork bifurcations, transient chaos and bifurcations to strange attractors. Let us fix $\beta = 8/3$ and $\sigma = 10$ in (29). It is well know that for $r < 1$ the point $x = (0, 0, 0)$ is a rest point attractor for the Lorenz system, thus, $z = (R_1, R_2, R_3)$ is a globally attracting rest point for (33)–(35). For $r = 1$ we have saddle-node bifurcation, for large r we obtain Andronov–Hopf bifurcations, intermittency and the strange attractor for $r > r_0$, where $r_0 \approx 24.06$. The same effects can be observed in Lotka–Volterra dynamics due to its equivalence to the Lorenz system.

Let us consider two more examples corresponding to $p = 2$ in theorem 4.5. We start with two classical systems with chaotic behaviour, the Ueda system

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = x_2, \qquad \frac{\mathrm{d}x_2}{\mathrm{d}t} = -ax_1^3 - bx_2 + c_0 \sin(\omega t), \tag{37}$$

and the Rossler system

$$\frac{\mathrm{d}x_1}{\mathrm{d}t} = -x_2 - x_3, \qquad \frac{\mathrm{d}x_2}{\mathrm{d}t} = x_1 + \mathrm{d}x_2, \qquad \frac{\mathrm{d}x_3}{\mathrm{d}t} = e + x_3(x - c_1). \tag{38}$$

Since $\sin(\omega t)$ is a solution of system $\mathrm{d}x_3/\mathrm{d}t = \omega x_4$, $\mathrm{d}x_4/\mathrm{d}t = -\omega x_3$, we can treat (37) as a part of 4×4 polynomial system. The vector fields, which define the right-hand sides (37) and (38), can be included in the following parametric family of fields in $\boldsymbol{R}^4$:

$$F_1 = \alpha_{10} + \alpha_{12}x_2 + \alpha_{13}x_3, \qquad F_3 = \alpha_{30} + \alpha_{31}x_1 + \alpha_{32}x_2 + \alpha_{33}x_3, \tag{39}$$

$$F_2 = \alpha_{20} + \alpha_{21}x_1 + \alpha_{22}x_2 + \alpha_{23}x_3 + +\beta_{21}x_1^2 + \beta_{22}x_1^3, \qquad F_4 = \alpha_{40} + \alpha_{43}x_3. \tag{40}$$

This family is invariant with respect to the shift $x_i \to x_i + R_i$. We can use the same realization procedure as for the case of the Lorenz system. Since expressions (39) and (40) contain 15 parameters, it is sufficient to use the Lotka–Volterra system for 30 species and with 4 resources in order to realize both the Ueda and Rössler systems.

As was pointed by one of the referees, these embeddings of polynomial systems of ordinary differential equations into Lotka–Volterra systems require a dimension increase. The 3×3 Lorenz system can be realized by a Lotka–Volterra system for 10 species and with 3 resources. As a result, this Lotka–Volterra system does not have a chaotic/transitive attractor, but a 7-parameter family of chaotic invariant sets (equivalent to Lorenz attractors). One can show that small perturbations of the interaction matrix in the corresponding Lotka–Volterra system will destroy this unstable structure.

5. Persistence

5.1. Permanency and strong persistence

We say that the Lotka–Volterra dynamics (5) is strongly persistent if each trajectory $x(t)$ has a ω-limit set, which is a compact in $\boldsymbol{R}^N_>$ (see [7]).

If the ω-limit sets of all trajectories are contained in a compact subset of $\boldsymbol{R}^N_>$, we say that system (5) is permanent (see [11]). Strong persistency is weaker then permanency. Permanency and persistence are important concepts of mathematical ecology and have received a great deal of attention over the past few decades, see the monographs [11, 37]. In the work [3], the permanency, partial permanency and global stability of rest points in Lotka–Volterra systems were studied. Some general sufficient conditions for permanency were found by Schreiber, [35]. These conditions are not satisfied in our case because of (4). When relation (4) is not valid, it is shown in [11] that at least one of $x_i(t)$ tends to 0 or ∞ as $t \to +\infty$. In fact, let us consider equation (1) with the matrix $\boldsymbol{K}$ with entries (3). Then there is a vector $h \neq 0$ such that $h^T \boldsymbol{A} = 0$. Thus (1) gives

$$\frac{\mathrm{d} \sum_{i=1}^N h_i \log x_i h_i}{\mathrm{d}t} = \sum_{i=1} h_i r_i = \bar{r}(h).$$

If the Lotka–Volterra system is permanent, then $\bar{r}(h) = 0$. But if it holds for all $h \in Ker A$, we obtain that r_i can be presented by (4).

To see a biological sense of relation (4), let us recall some results of Volterra on the so-called *competition exclusion* principle. This principle asserts that, in a population consisting of N species sharing a single resource, only a single *dominant* species survives. To describe this phenomenon in more detail, let us consider the following Lotka–Volterra system with a single resource:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i(r_i - A_i \sum_{j=1}^N B_j x_j), \qquad i = 1, \dots, N. \tag{41}$$

Assume that $r_N/A_N > r_{N-1}/A_{N-1} > \dots > r_1/A_1$ and $A_i, B_i > 0$ for all i. These conditions mean that the N-th species is dominant. Volterra proved that the solutions of (41) satisfy $x_i(t) \to 0$ and $x_N(t) \to r_N/(A_N B_N)$ as $t \to +\infty$. For $n = 1$, condition (4) implies

$$r_i/A_i = \mu,$$

which means that there are no dominant species within the population when (4) is valid.

Below we describe some effects that can appear in Lotka–Volterra dynamics with few resources.

I. *The case $n = 1$, a single resource.* Let us consider the function $G(q) = G_1(q, \mu, \boldsymbol{A}, \boldsymbol{B}, C, N)$ defined by (7). To simplify the notation, let us set

$$q_1 = q \in \boldsymbol{R}, \qquad A_{m1} = -a_m, \qquad B_{1m} = b_m, \qquad \mu_1 = \mu.$$

Then

$$G(q) = -\mu + \sum_{m=1}^{N} b_m C_m \exp(a_m q). \tag{42}$$

We introduce the quantities $a_+ = \max\{a_m\}$ and $a_- = \min\{a_m\}$ and denote by m_+, m_- the corresponding indices, i.e., $a_{m_\pm} = a_\pm$. Let us set $b_\pm = b_{m_\pm}$. To simplify our analysis, we suppose that

$$a_- < a_j < a_+, \qquad j \neq m_- \quad \text{and} \quad j \neq m_+.$$

It is straightforward to check the following assertions on large time behaviour for $q(t)$ and $x_i = C_i \exp(a_i q)$.

(1) $a_+ > 0,\ b_+ > 0$. Here we have the blow-up effect for trajectories with sufficiently large $q_{m_+}(0)$, i.e., $q(t) \to +\infty$ as $t \to t_0$ for a finite t_0. The species number tends to infinity as $t \to t_0$.
(2) $a_- < 0, b_- < 0$. We have the blow-up effect $\boldsymbol{a}$ for trajectories with sufficiently large $-q(0)$, i.e. $q(t) \to -\infty$ as $t \to t_0$. In this case x_{m_-} tends to zero as $t \to t_0$.
(3) $a_+ > 0,\ b_+ < 0$ and $a_- < 0, b_- > 0$. The Lotka–Volterra system is strongly persistent.

5.2. *Strong persistency and chaos*

In this subsection we show that, for any N and $n > 2$, there are Lotka–Volterra systems with N species and n resources, which are strongly persistent and, at the same time, exhibit chaotic behaviour.

Theorem 5.1. *Let $F^{(l)}$, $l = 1, \ldots, p$ be C^1-vector fields on B_n directed inward on ∂B_n and having compact invariant hyperbolic sets $\mathcal{I}^{(l)}$. Then there exists a positive integer N, $\mu \in \boldsymbol{R}^n$, and matrices $\boldsymbol{A}, \boldsymbol{B}$ of sizes $N \times n$ and $n \times N$ respectively such that the dynamics defined by system (1) satisfies all conclusions of* theorem 4.5 *and additionally, this dynamics is strongly persistent.*

Proof. We take the number N, the matrices $\boldsymbol{A}, \boldsymbol{B}$ and the vector μ as in theorem 4.5. We modify system (8) in the following way:

$$\frac{\mathrm{d}q_k}{\mathrm{d}t} = G_k(q, \mu, \boldsymbol{A}, \boldsymbol{B}, C, N) + \epsilon(C_{N+2k} \exp(-bq_k) - C_{N+2k-1} \exp(bq_k)), \tag{43}$$

where $k = 1, \ldots, n$, $\epsilon > 0$ is a small parameter, b is a sufficiently large positive parameter, $C_{N+1}, \ldots, C_{N+2n} > 0$. Since each function G_k is a linear combination of the exponents $\exp(-\sum_{j=1}^{n} A_{mj} q_j)$, we choose b to satisfy $b > 2 \max_m\{\sum_{j=1}^{n} |A_{mj}|\}$. Consider the domain $\Pi_a = \{q : -a < q_i < a\}$. Assuming that $q(0) \in \Pi_a$, one can show that, for some sufficiently large $a = a(\epsilon, C_{N+1}, \ldots, C_{N+2n})$, the corresponding trajectory $q(t, q(0))$ of system (43) cannot leave Π_a.

Let us consider a Lotka–Volterra system (1) with n resources and with some new $\tilde{\boldsymbol{A}}, \tilde{\boldsymbol{B}}$ and a new species number $\tilde{N} = N + 2n$ for which equations (43) become (8) (see proposition 3.1). Since all trajectories of system (43) are bounded, this new Lotka–Volterra system is persistent. On the other hand, if $q \in B_n$, and $C_{N+1}, \ldots, C_{N+2n} < 1$, the vector field in (43) is a small smooth perturbation of the vector field in system (8). Therefore, for sufficiently small ϵ, the property of structural stability of the hyperbolic sets proves the assertion.

In the following example we demonstrate that a variation of the initial conditions for system (1) can lead to a qualitative change in the behaviour of trajectories, from, for example, boundedness for large t to blow-up at a finite time.

Let $n = 1$ (a single resource) and $q = q_1 \in \boldsymbol{R}$. Consider the following equation for q:

$$\frac{\mathrm{d}q}{\mathrm{d}t} = -\mu + f(q), \tag{44}$$

where

$$f(q) = G_1(q) = \kappa C_1 \exp(-\lambda q) - \tilde{\kappa}(C_3 - C_2)\exp(\tilde{\lambda} q), \tag{45}$$

Here $N = 3$ and

$$\kappa, \tilde{\kappa}, \lambda, \tilde{\lambda} > 0.$$

If $C_3 > C_2$ and μ is sufficiently small, then the dynamics (44), (45) has a rest point as a global attractor. If $C_3 < C_2$ we have a blow-up. If the third species is removed from the population, i.e., $C_3 = 0$, we also obtain a blow-up.

6. Discussion and concluding remarks

We have studied Lotka–Volterra systems with N species and n resources. One of the main results of this paper is an analytical proof of the coexistence of many hyperbolic dynamics on some invariant sets in the same Lotka–Volterra system (the entries of the interaction matrix of these systems can be chosen to be uniformly bounded as $N \to \infty$). This allows one, in particular, to prove the existence of chaotic behaviour for certain Lotka–Volterra systems. These Lotka–Volterra dynamics exhibit the main feature of chaos, namely, sensitive dependence on initial conditions and transitivity. The ω-limit sets can have a large dimension ($\geqslant N - n$), and the model dynamics in the whole $\boldsymbol{R}^N_>$ can have a long, non-fading memory. We also present an example of a Lotka–Volterra system with $N = 10$ species and $n = 3$ resources that has Lorenz dynamics. This example shows that in Lotka–Volterra systems we can observe different bifurcations resulting from variations of the interaction matrix $\boldsymbol{K}$.

Let us compare these Lotka–Volterra systems with the Hopfield model of attractor neural networks with N neurons. This system is also defined by interaction matrices $\mathbf{K}$. Similar to (9), substitution allows one to show that the Hopfield system can generate different hyperbolic dynamics for appropriate $\boldsymbol{K}$ and large N [39]. These Hopfield systems have global attractors of dimension $\leqslant n$. Moreover, in the Hopfield systems, in order to obtain a prescribed hyperbolic set, we have to vary N and $\boldsymbol{K}$. In contrast to this, some Lotka–Volterra systems with appropriate parameters can realize large classes of hyperbolic dynamics *only by variation of the initial data* (see proposition 4.4 and theorem 4.5). However, in general, these Lotka–Volterra systems have no global attractor.

The second question treated here is the persistence of Lotka–Volterra systems with n resources. The investigation of the dynamics of systems of many species, exploiting a few resources, is an important ecological problem [8, 14]. The competitive exclusion principle asserts that many species cannot survive together on few resources. Concepts of permanency and persistence were proposed in order to mathematically formulate what the survival of all species means [7, 33]. In nature we observe that a number of species can share the same resources and survive all together (as an example, phytoplankton can be considered). We have presented a general method that allows one to find different examples of persistent Lotka -Volterra systems. It is shown that, under some conditions, the Lotka–Volterra model with n resources and $N > n$ species exhibits a complicated large time behaviour and, at the same time, this dynamics is strongly persistent. Therefore, large ecosystems may be stable, exhibit many kinds of chaotic behaviour and have a long memory.

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Appendix.

A.1. Proof of proposition 4.4

The following assertion is a consequence of theorem 18, section 7, chapter 4 in [18].

Proposition A.1. *Let λ_k, $k = 1, \ldots$, be an infinite sequence of real numbers. Assume that*

$$0 < R < \frac{1}{e} \limsup_{k \to \infty} \frac{k}{|\lambda_k|}. \tag{A.1}$$

Then the set of linear combinations of the function $\exp(\lambda_k x)$ *is dense in* $C^1([-R, R])$.

Now let us choose a matrix D_{ji}, $j = 1, \ldots,$ and $i = 1, \ldots, n$ such that for each $i = 1, \ldots$ the sequences $D_{j,i}$, $j = 1, 2, \ldots$, are infinite, subject to (22) and satisfy the relation

$$\limsup_{j \to \infty} \frac{j}{|D_{j,i}|} = \infty.$$

Then according to proposition A.1 sums (11) are dense in $C^1(B_n)$. This proves proposition 4.4.

A.2. Proof of proposition 4.3

Let the matrices $\boldsymbol{A}$, $\boldsymbol{B}$ and the number N be fixed in (8) and let $q^* = q^*(C^{(0)})$ be a hyperbolic rest point of (8) for a certain $C^{(0)}$. Then there is a hyperbolic rest point for system (8) for C subject to $|C - C^{(0)}| \leqslant \delta$ with some positive δ. The image

$$X = \left\{ x = (x_1, \ldots, x_N) : x_i = C_i \exp\left(-\sum_{j=1}^{n} A_{ij} q_j^*(C) \right) \right\}$$

is an invariant set for system (1). Let us estimate its dimension. We have

$$\frac{\partial x_i}{\partial C_k} = \left(\delta_{ik} - C_i \sum_{j=1}^{n} A_{ij} \frac{\partial q_j^*(C)}{\partial C_k} \right) h_i,$$

where $h_i = \exp(-\sum_{j=1}^{n} A_{ij} q_j^*(C))$. The dimension of the set of vectors $\xi = (\xi_1, \ldots, \xi_N)$ satisfying

$$\sum_{k=1}^{N} \frac{\partial q_j^*(C)}{\partial C_k} \xi_k = 0, \qquad j = 1, \ldots, n,$$

is $\geqslant N - n$ and for such ξ

$$\sum_{k=1}^{N} \frac{\partial x_i}{\partial C_k} \xi_k = h_i \xi_i \qquad \text{for each } i = 1, \ldots, N.$$

Therefore, the dimension of the set of $\eta = (\eta_1, \ldots, \eta_N)$ satisfying

$$\sum_{k=1}^{N} \frac{\partial x_i}{\partial C_k} \xi_k = 0 \qquad \text{for each } i = 1, \ldots, N$$

is $\leqslant n$. Thus the matrix

$$\left\{ \frac{\partial x_i}{\partial C_k} \right\}_{i,k=1}^{N}$$

has at least $N - n$ non-zero eigenvalues and consequently $\dim X \geqslant N - n$, that completes the proof.

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