

This is the accepted manuscript made available via CHORUS. The article has been published as:

## Hamiltonian dynamics for complex food webs

Vladimir Kozlov, Sergey Vakulenko, and Uno Wennergren

Phys. Rev. E **93**, 032413 — Published 21 March 2016

DOI: [10.1103/PhysRevE.93.032413](https://doi.org/10.1103/PhysRevE.93.032413)

# Hamiltonian dynamics for complex food-webs

Vladimir Kozlov\*

*Dept. of Mathematics, University of Linköping, 58183, Linköping, Sweden*

Sergey Vakulenko

*Institute for Mechanical Engineering Problems, Russian Academy of Sciences, Saint Petersburg, Russia and  
Saint Petersburg National Research University of Information Technologies, Mechanics and Optics. Saint Petersburg, Russia*

Uno Wennergren

*Dept. of Ecology, University of Linköping, 58183, Linköping, Sweden*

(Dated: February 26, 2016)

We investigate stability and dynamics of large ecological networks by introducing classical methods of dynamical system theory from physics, including Hamiltonian and averaging methods. Our analysis exploits the topological structure of the network, namely the existence of strongly connected nodes (hubs) in the networks. We reveal new relations between topology, interaction structure and network dynamics. We describe mechanisms of catastrophic phenomena leading to sharp changes of dynamics and hence completely alters the ecosystem. We also show how these phenomena depend on the structure of interaction between species. We can conclude that a Hamiltonian structure of biological interactions leads to stability and large biodiversity.

## I. INTRODUCTION

In this paper, we consider the dynamics of food-web networks with complex topology. By classical methods of hamiltonian mechanics we show how the network structure and topology affect dynamics and that, even in a permanent network, there are possible complicated effects: multistability, resonances, quasiperiodic dynamics, and chaos.

The last decade, the topological structure of biological networks and, in particular, ecological networks (food webs) has been received great attention (see [1–5]). Different indices have been introduced and studied in detail for empirical models and random assembled networks (see for an overview [6]). These indices are connectance, cluster coefficients, degree distribution, number of compartments, and many others [6]. They reflect important topological properties of networks, for example, the degree distribution indicates that the ecological networks contain a few number of strongly connected species, while the compartment number describes the species decomposition into compartments of subset of species [5]. The networks can contain different substructures (for example, when a guild of species contains specialists with few links and generalists with many links). Many works have investigated a connection between the network structure and fragility (see, for example, [7, 8]). Great efforts has been done to reveal connections between the network topological structure and their robustness [2, 6, 9].

One of the key problems is to find a qualitative description of the dynamics generated by a network of a given topological structure. This analysis of the dynamics generally boils down to an analysis of either local or global stability of the networks. Until May’s seminal works [10, 11], ecologists believed that huge complex ecosystems, involving a larger number of species and connections, are more stable

[12]. May [10, 11] considered a community of  $S$  species with connectance  $C$  that measures the number of realized links with respect to the number of possible links. By using local stability analysis he showed that the instability will increase with respect to  $C$ . More connected communities would therefore be more unstable. These ideas were developed in [9], where networks consisting of predator-prey modules were studied. It is shown that if predator-prey interactions are prevalent, then the complex community is locally stable. This local stability approach was also used in [13, 14], where more complicated networks with interactions of different types (predator-prey, amensalism, mutualism, competition) were studied. This technique, used in [9–11, 13, 14], only allows us to study local stability of equilibria. More general and overarching results achieved by analysis of global stability are scarce, yet some important ones exist on few species system [15] by applying the Lyapunov function method.

All these aforementioned results, however, say us nothing about multistationary, transient dynamics and other possible complex effects. Therefore, many intriguing questions are still open, for example, can food-webs exhibit a complicated behaviour with complex transient dynamics being nonetheless stable? Does it exist chaos, periodical oscillations, bursts and transient phenomena, connected with multistability, and how do these effects depend on network topology?

In this paper, we briefly describe a “physical” approach to these problems based on hamiltonian methods. We consider a class of Lotka-Volterra systems consisting of two groups of species and where the interactions only exist between these groups. This is a likely generalization of the classical prey-predator model with two species and under some natural assumptions such systems are reduced to Hamiltonian ones (for brevity, we refer to them as HLV systems). Note that our models lie in a large class of Lotka-Volterra systems introduced in [16], which admit a special Hamiltonian representation involving a skew-product Poisson matrix depending on species abundances.

A simple example of the HLV system appears if we con-

---

\* vladimir.kozlov@liu.se

sider a community consisting of a predator species feeding on a number of prey-species. In such a system the interaction graph is a star with the predator in the center interacting with all its prey. Such star structures often appear as a motif in ecological webs [1]. In fact, the interaction graphs of many real food-webs have scale-free structure [4, 7], thus, large networks contain many species being a generalist by interacting with a number of other species. Another example is a set of consumers feeding on the same resource (for example, plankton being fed on by several species ranging from very small to very large).

In this paper, we use Hamiltonian representations of the HLV based on canonical variables ([17], where a class of Lotka-Volterra systems with Hamiltonian dynamics on an attractor is found). Such canonical structure simplifies an analysis of dynamics and facilitates the use of classical perturbation methods [18, 19].

The main results are as follows. We have developed Hamiltonian approaches of [16] and [17] in two directions. The first main result is given by the two theorems V.3 and V.5 on permanence of large random Lotka-Volterra systems, which are small perturbations of HLV's. Permanence does not exclude existence of complex transient dynamics. The second part of results is based on the canonical Hamiltonian structure and concerns the asymptotic description of such dynamics. By these asymptotics we can obtain a very short description of these complex systems. This description is particularly simple for star systems. Neglecting species competition and self-limitation effects, we obtain that the star subsystem can be described by Hamiltonians. In canonical variables, these ecological Hamiltonians correspond to nonlinear oscillators, which can be described by two canonical variables only and such phenomenon is well studied in physics and mechanics. Therefore, all results for such simple food-web can be obtained by a translation from physical interpretation to an ecological understanding. We show, by this analogy, that this dynamics is integrable and exhibits interesting phenomena, for example, kink and soliton solutions. We find a dependence of solution types on ecological interactions involved in the system. An interesting effect, which does not exist in mechanics but arises in ecology, is a domino effect. In star systems an extinction of a single species, often denoted keystone species, may lead to extinction of all species. We can show what structure of interactions that defines such a keystone species. Note that, from a dynamical point of view, solitons correspond to so-called homoclinic curves [20]. This implies an important consequence. Namely, if we consider a weakly perturbed star-system, this homoclinic structure can generate chaos, an effect well studied in several mechanical and physical applications. Another interesting effect is that in ecology, in contrast to mechanics and physics, the Hamiltonians of star systems involve some positive constants which are defined by initial data. This means that the dynamics of star system has a "memory". The solution form and period depend on these initial conditions.

The case of large food-webs is particularly interesting. Numerical results of [21] show that food web stability is enhanced when species at a high trophic level feed on multiple prey species or species at an intermediate trophic level are fed

upon by multiple predator species. This means that generalist species increase stability. Note that they play a main role in our approach since potential energy in our Hamiltonians is defined via generalist species' abundances.

In order to study realistic and large food-webs, we use an asymptotic approach, which allows us to investigate dynamics of weakly perturbed HLV systems. This approach is based on methods, developed in the theory and mechanics of Hamiltonian systems [18–20, 22]. The canonical structure for the HLV that we use in this paper makes it simpler to apply these methods.

By assuming that the food-web of generalist species have random scale free topology we can use perturbation methods and find a simplified description of the food-web dynamics. Scale free topology may occur in food webs, for example in systems with fairly low connectance [4, 7]. As an example, let us consider a predator species feeding on a number of prey-species. They form a star subsystem in the food web. If we consider this star subsystem as a separate unit (niche), we can study dynamics of this subsystem in the case of weak self-limitation and competition. The important observation is that different star subsystems (niches) are weakly overlapping in foodwebs with random scale-free topology, therefore, such webs can be viewed as unions of almost independent weakly perturbed integrable Hamiltonian subsystems. So, we obtain a system, which is a classical object of Hamiltonian theory, a weakly perturbed integrable multidimensional Hamiltonian system.

Different types of perturbations are possible in these systems. One type of perturbation can be generated by a variable environment, for example by climate change. Another type of perturbation is due to a topological structure (niche overlapping). At last, if we take into account weak self-limitation or species competition, we obtain a third type of perturbation. These perturbations can be purely dissipative (for instance, if we are dealing with self-limitation effects), Hamiltonian, or antidissipative.

The dynamics of such weakly perturbed integrable Hamiltonian systems can be described by averaging methods [19, 22]. The main equations describing perturbation effects have a transparent physical interpretation. The state of  $i$ -th star subsystem is defined by an averaged "energy"  $E_i$ . We obtain a system of equations for these energies. By an analysis of this system we find that there are possible different interesting effects such as existence of bursts, chaos and quasiperiodic solutions, and resonances. The resonance effects appear if different niches interact (overlap), and even a weak interaction can lead to chaos or resonances. Resonances can also provoke instability. The weak resonance effect can be repressed by a self-limitation. Note that for two species systems resonances induced by a periodic oscillations of system parameters is considered in [23].

The advantage of the proposed approach becomes evident when we analyze the effect of the environment or study transient dynamics. In the Hamiltonian case it is sufficient to investigate a "potential energy" in canonical variables associated with star subunits. The form of this potential energy depends on the network topology and interconnection forces. An

analysis of the energy form allows us to find possible kinds of transient dynamics in the system, i.e. what can happen in this network: oscillations, bursts, or sharp transitions, and also to check the stability. We show that the evolution of energy can lead to a sharp change of solution form, for example, there are possible transitions from periodical solutions to solitons, and vice versa. It is important to note that the union of weakly interacting star subsystems is ecologically stable (permanent) if predator-prey interactions are prevalent in the star subsystems and that weak self-limitation exists in the system. These results, which are consistent and expand the results from local stability analysis [13, 21], has a transparent physical interpretation. Each separate star predator-prey subsystem has a globally stable equilibrium corresponding to a minimum of the energy. Thus, the potential energy of the union of star subsystems also has a global minimum. A weak self-limitation effect repress possible resonances providing permanence of the whole complex food-web (note that for a purely Hamiltonian system permanence is impossible, for details see [24]).

In the next section II, we formulate the Lotka-Volterra model with self-limitation describing interaction of two species communities (for example, plants and pollinators, or preys and predators).

The investigation of ecological stability is based on a reduction of the problem to a Hamiltonian system, which is presented in sections III and IV. Namely, we transform equations to another system and obtain, under some ecologically relevant assumptions, a Hamiltonian formulation of these equations. In Sect. VI star systems are considered. Sect. VII concern the case of varying environment, which is modeled by an ecological system consisting of one generalist species and several specialist species with time dependent interactions. We also include weak self-limitation in the model.

A resonance analysis for ecological system consisting of two generalist species and several specialist species is performed in Sect. VIII.

## II. STATEMENT OF PROBLEM

### A. Topology of networks

We consider the following Lotka-Volterra system describing an interaction between two groups of species  $x$  and  $v$ :

$$\frac{dx_i}{dt} = x_i(-r_i + \sum_{k=1}^M a_{ik}v_k - \sum_{j=1}^N \gamma_{ij}x_j), \quad (1)$$

$$\frac{dv_j}{dt} = v_j(\bar{r}_j - \sum_{l=1}^N b_{jl}x_l - \sum_{k=1}^M d_{jk}v_k), \quad (2)$$

where  $i = 1, \dots, N$ ,  $j = 1, \dots, M$  and  $N + M$  is the total number of species with abundances  $x_i$  and  $v_j$ . The coefficients  $r_i$  and  $\bar{r}_j$  are intrinsic growth (or decay) rates for species  $x_i$  and  $v_j$ , respectively. The matrices  $\mathbf{A}$  and  $\mathbf{B}$  with the entries  $a_{ij}$  and  $b_{ij}$ , respectively, determine an interaction between two groups of species, whereas the matrices  $\gamma$  with entries  $\gamma_{ij}$  and  $\mathbf{D}$  with

entries  $d_{ij}$  correspond to self-limitation. This model describes an ecological system with two trophic levels.

The topological structure of the networks is defined by a directed graph  $(V, E)$ , where  $V$  is a set of vertices and  $E$  is a set of edges (links). We distinguish two types of nodes,  $V_1 = \{1, 2, \dots, N\}$  and  $V_2 = \{1, 2, \dots, M\}$ . Thus,  $V = V_1 \cup V_2$ .

The edge  $e = \{i, j\}$  belongs to  $E$  if one of the alternatives is fulfilled: a)  $a_{ij} \neq 0$  when  $i \in V_1$  and  $j \in V_2$ ; b)  $\gamma_{ij} \neq 0$  when  $i \in V_1$  and  $j \in V_1$ ; c)  $b_{ij} \neq 0$  when  $i \in V_2$  and  $j \in V_2$ ; d)  $d_{ij} \neq 0$  when  $i \in V_2$  and  $j \in V_2$ .

Connectance  $\mathcal{C}$  is an important characteristic of the network and it is defined as the number of the ecological links divided by the number of all possible links:

$$\mathcal{C} = 2|E|/(N+M)(N+M-1), \quad (3)$$

where  $|E|$  is the number of edges.

In the scale-free networks the degree distribution of a node is

$$Pr_k = Ck^{-s} \quad (4)$$

(see [1]), where  $Pr_k$  is the probability for a node to have  $k$  adjacent nodes and the exponent  $s$  lies within the interval  $(2, 3)$ . The networks with such property usually have a low number of strongly connected nodes (hubs) whereas the remaining ones are weakly connected. In our case this means that we have several species-generalists and many species-specialists. Each generalist (hub) is a center of a "star subsystem" consisting of many species. We study the dynamics of such subsystems in Sect. VI.

Some species corresponds to nodes adjacent to two different hubs. This means that two star subsystems are overlapping, or, in biological terms, two different predators are feeding on the same prey. Numerical simulations, where scale-free networks were generated by the standard preferential attachment algorithm, show that this overlapping is small, the number of nodes sharing two different centers  $\ll N + M$ .

### B. Dynamics

We consider system (1), (2) in the positive cone  $\mathbf{R}_{>}^{N+M} = \{x = (x_1, \dots, x_N), v = (v_1, \dots, v_M) : x_i > 0, v_j > 0\}$ . This cone is invariant under dynamics (1), (2) and we assume that initial data always lie in this cone:

$$x(0) = \phi \in \mathbf{R}_{>}^N, \quad v(0) = \psi \in \mathbf{R}_{>}^M. \quad (5)$$

We distinguish the following main cases:

**PP** (predator-prey). If  $v_j$  are preys and  $x_i$  are predators, then

$$a_{il} \geq 0, \quad b_{jk} \geq 0, \quad r_i > 0, \quad \bar{r}_j > 0; \quad (6)$$

**MF** (facultative mutualism)

$$a_{il} \geq 0, \quad b_{jk} \leq 0, \quad r_i < 0, \quad \bar{r}_j > 0; \quad (7)$$

**MO** (obligatory mutualism)

$$a_{il} \geq 0, \quad b_{jk} \leq 0, \quad r_i > 0, \quad \bar{r}_j < 0; \quad (8)$$

and

**C** (competition)

$$a_{il} \leq 0, \quad b_{jk} \geq 0, \quad r_i > 0, \quad \bar{r}_j > 0. \quad (9)$$

Note that, if  $a_{il} \leq 0$ ,  $b_{jk} \leq 0$ ,  $r_i < 0$ ,  $\bar{r}_j < 0$ , then we are dealing with the **PP** case, where  $v_j$  are predators and  $x_i$  are preys.

Systems, where we observe a generalist species and a number of specialist species (for example,  $M = 1$  and  $N \gg 1$ , or  $N = 1$  and  $M \gg 1$ ) are omnipresented in real food-webs and they are important structural elements (substructures) in ecological networks. The topology of these substructures is defined by star graphs consisting of a single central vertex and a number of satellites.

We have a pure star structure if all products  $a_i b_i$  are of the same sign. The case  $a_i b_i > 0$  corresponds to an **M** - star structure, and the case  $a_i b_i < 0$  corresponds to a **P** - star structure. Dynamics of these star networks is quite different. We also consider mixed structures, where  $a_i b_i$  may have different signs.

On coefficients  $d_{ij}$  and  $\gamma_j$  we assume that they are non-negative. Our asymptotical results hold under the condition that they are small.

In subsequent sections we describe the dynamics of large ecological networks/foodwebs. We consider networks consisting of weakly interacting star structures. We change the old principle "divide and rule" on "divide and analyze". First, we investigate dynamical properties of a single star system, and then, using weak overlapping property, we develop a perturbation approach for weakly interacting star systems.

An interesting situation, when the idea "divide and analyze" may be useful, arises when we analyze consequences of habitat destruction [25, 26]. What can happen when an ecosystem will be separated by a new highway? We can consider the new system as a union of two almost independent, weakly interacting subsystems.

### III. TRANSFORMATION OF LOTKA-VOLTERRA SYSTEMS

To study oscillations in the food-webs (where  $M \leq N$ ), we make a transformation of equations (1), (2) to another system with respect to variables  $q = (q_1, \dots, q_M) \in \mathbf{R}^M$  and  $C = (C_1, \dots, C_N) \in \mathbf{R}_>^N$ , which is defined as follows:

$$\frac{dC_i}{dt} = V_i(C, q), \quad (10)$$

$$\frac{d^2 q_j}{dt^2} = \left( \frac{dq_j}{dt} + \mu_j \right) \left( F_j(C, q) - \sum_{k=1}^M d_{jk} \left( \frac{dq_k}{dt} + \mu_k \right) \right), \quad (11)$$

where  $i = 1, \dots, N$ ,  $j = 1, \dots, M$ ,

$$V_i(C, q) = C_i \left( \bar{\gamma}_i - \sum_{k=1}^N \gamma_{ik} C_k \exp(\mathbf{A}_k \cdot q) \right), \quad (12)$$

$$F_j(C, q) = \bar{r}_j - \sum_{k=1}^N b_{jk} C_k \exp(\mathbf{A}_k \cdot q), \quad (13)$$

and

$$\bar{\gamma}_i = -r_i + \sum_{m=1}^M a_{im} \mu_m. \quad (14)$$

Here  $\mu_1, \dots, \mu_M$  are positive constants and  $\mathbf{A}_i \cdot q = \sum_{k=1}^M a_{ik} q_k$ . The we obtain that the following.

Let  $q$  and  $C$  be a solution to (10) and (11) with initial data

$$q_k(0) = \alpha_k, \quad q'_k(0) = \beta_k, \quad k = 1, \dots, M \quad \text{and} \quad C_i(0) = C_i^0,$$

where  $i = 1, \dots, N$  and  $\beta_k > -\mu_k$ ,  $k = 1, \dots, M$ . Then the functions

$$x_i(t) = C_i \exp\left(\sum_{k=1}^M a_{ik} q_k(t)\right), \quad v_k = \frac{dq_k}{dt} + \mu_k, \quad (15)$$

solve system (1), (2) with the initial conditions

$$x_i(0) = C_i^0 \exp\left(\sum_{k=1}^M a_{ik} \alpha_k\right),$$

Moreover, all solutions to system (1), (2) can be obtain by solving (10) and (11) with appropriate initial conditions.

System (10) and (11) can be reduced to a first order system if we introduce the new variables  $p_j$  by

$$\frac{dq_j}{dt} + \mu_j = \exp(p_j), \quad j = 1, \dots, M.$$

We obtain then

$$\frac{dq_j}{dt} = \exp(p_j) - \mu_j \quad (16)$$

and

$$\frac{dp_j}{dt} = F_j(C, q) - \sum_{l=1}^M d_{jl} \exp(p_l), \quad (17)$$

where  $j = 1, \dots, M$ .

### IV. HAMILTONIAN

#### A. Reduction to a Hamiltonian system

Equation (10) takes a particularly simple form when  $\gamma_j = 0$  and  $\bar{\gamma}_i = 0$ . Then the right-hand side in (10) equals zero and hence  $C_i$  is a constant. Therefore, if  $p$  and  $q$  solve system (16), (17) supplied with the initial conditions

$$q_k(0) = \alpha_k \quad \text{and} \quad p_k(0) = \log(\beta_k + \mu_k), \quad k = 1, \dots, M,$$

then the corresponding solution to (1), (2) is given by (15).

We assume additionally that  $d_{jl} = 0$ . Then system (16), (17) can be rewritten as a Hamiltonian system provided the matrices **A** and **B** satisfy the relations

$$\sigma_l b_{lk} = \rho_k a_{kl}, \quad k = 1, \dots, N, \quad l = 1, \dots, M, \quad (18)$$

where  $\rho_l$  and  $\sigma_l \neq 0$  are real numbers [16](for biological interpretation of this condition see the remark at the end of this section). Indeed, let

$$\tilde{p}_j = p_j \text{ and } \tilde{q}_j = \sigma_j q_j.$$

Then relations (16) and (17) imply

$$\frac{d\tilde{p}_j}{dt} = F_j(C, \tilde{q}) \quad (19)$$

and

$$\frac{d\tilde{q}_j}{dt} = \sigma_j(\exp(\tilde{p}_j) - \mu_j), \quad j = 1, \dots, M. \quad (20)$$

We introduce two functions

$$\Phi(C, \tilde{q}) = \sum_{k=1}^N \rho_k C_k \exp\left(\sum_{l=1}^M a_{kl} \sigma_l^{-1} \tilde{q}_l\right) - \sum_{k=1}^M \tilde{r}_k \tilde{q}_k$$

and

$$\Psi(\tilde{p}) = \sum_{k=1}^M \sigma_k(\exp(\tilde{p}_k) - \mu_k \tilde{p}_k).$$

One can verify that

$$\frac{\partial \Phi(C, \tilde{q})}{\partial \tilde{q}_j} = -F_j, \quad \frac{\partial \Psi(\tilde{p})}{\partial \tilde{p}_j} = \sigma_j(\exp(\tilde{p}_j) - \mu_j).$$

Thus, system (19), (20) takes the form

$$\frac{d\tilde{p}_j}{dt} = -\frac{\partial H(C, \tilde{p}, \tilde{q})}{\partial \tilde{q}_j} \quad (21)$$

and

$$\frac{d\tilde{q}_j}{dt} = \frac{\partial H(C, \tilde{p}, \tilde{q})}{\partial \tilde{p}_j}, \quad j = 1, \dots, M, \quad (22)$$

where

$$H(C, \tilde{p}, \tilde{q}) = \Phi(C, \tilde{q}) + \Psi(\tilde{p}). \quad (23)$$

Relation (18) admits a biological interpretation. Consider, for example, a predator-prey system. Then condition (18) means that the coefficients  $a_{kl}$  and  $b_{lk}$  are proportional to the frequency of meetings between  $k$ -th predator and  $l$ -th prey, when the predator-species is feeding on the prey-species. Note that if  $M = 1$  or  $N = 1$ , this condition is fulfilled. It corresponds to the case of a star structure, which we study in coming section.

## V. PERMANENCE OF DYNAMICS

Although many Lotka-Volterra systems are permanent [15] and even globally stable [27], nonetheless there exist large classes of Lotka-Volterra systems, which can exhibit a complex dynamics (multistability [28] or chaos [24]). To understand which phenomena are more common, we must define a measure on the set of system parameters and to estimate the probability to obtain, say, a permanent Lotka-Volterra system. In this section we realize this idea for systems close to HLTV.

### A. Strong persistence and permanence

Let us remind definitions of permanency and strong persistence. The general Lotka-Volterra system

$$\frac{dy_i}{dt} = y_i(-R_i + \sum_{k=1}^N W_{ik} y_k), \quad i = 1, \dots, N, \quad (24)$$

is said to be permanent if there exist  $\delta > 0$  and  $D > 0$  independent of the initial data such that

$$\liminf_{t \rightarrow +\infty} y_i(t) \geq \delta, \quad (25)$$

$$\limsup_{t \rightarrow +\infty} y_i(t) \leq D \quad (26)$$

for every solution to (24) (see [15]). The system is strongly persistent, if  $\delta$  and  $D$  in (25) and (26) may depend on initial data.

The strong persistence property means that the system is ecologically stable and all species coexist. System (24) can be strongly persistent only if the corresponding linear system

$$WY = R \quad (27)$$

has a positive solution (i.e., all  $Y \in \mathbb{R}_{>0}^N$ ) [15]. Here  $W$  is the matrix with the entries  $w_{ij}$ , and  $R, Y$  are vectors with components  $R_i, Y_i$ , respectively.

Let us present some necessary and sufficient conditions of boundedness of trajectories of system (21), (22) (we omit the sign of tilde to simplify notation). The trajectories  $q(t)$  are bounded under the following conditions:  $\sigma_n > 0$ ,  $n = 1, \dots, M$ , and

$$\lim \Phi(C, q) = +\infty \quad \text{as } |q| \rightarrow +\infty, \quad q \in \mathbb{R}^N. \quad (28)$$

In the next assertion we present some conditions, which guarantee the asymptotic property (28).

**Theorem V.1.** Assume that

$$\rho_k > 0, \quad k = 1, \dots, N. \quad (29)$$

Then (28) is equivalent to the following: the rank of matrix  $\{b_{jl}\}$  is  $M$  and there exists a vector  $z = (z_1, \dots, z_N) \in \mathbb{R}_{>0}^N$  such that

$$\tilde{r}_l = \sum_{j=1}^N b_{lj} z_j, \quad l = 1, \dots, M. \quad (30)$$

*Proof.* Let  $\mathbb{K}$  be the closed convex set

$$\mathbb{K} = \{\eta \in \mathbb{R}^M : \eta_l = \sigma_l^{-1} \sum_{k=1}^N a_{kl} z_k, \quad z_l \geq 0, l = 1, \dots, N\}.$$

Since all numbers  $\rho_k$  and  $C_k$  are positive, the property (i) is equivalent to

$$q \in \mathbb{K}^* \implies \tilde{r} \cdot q < 0,$$

where

$$\mathbb{K}^* = \{\xi \in \mathbb{R}^M : \xi \cdot \eta \leq 0 \text{ for all } \eta \in \mathbb{K}\}.$$

The last property can be also formulated as  $\bar{r}$  belongs to the interior of  $((\mathbb{K})^*)^*$ . Using that  $((\mathbb{K})^*)^* = \mathbb{K}$ , we obtain (28) is equivalent to  $\bar{r} \in$  the interior of  $\mathbb{K}$ , which is exactly the assertion of Theorem due to (18).  $\square$

The conditions  $\bar{\gamma}_i = 0, i = 1, \dots, N$  and (30) means that system (1), (2) has a positive equilibrium in  $\mathbb{R}_{>}^{N+M}$ . So, we obtain

**Corollary V.2.** *Let  $d_{kl} = \gamma_{ij} = 0$  in (1), (2) and let relation (18) be fulfilled with positive  $\rho_k$  and  $\sigma_l$ . Then system (1), (2) is strongly persistent if and only if the rank of the matrix  $A$  is  $M$  and algebraic systems*

$$\sum_{k=1}^M a_{ik} v_k = r_i, \quad (31)$$

$$\sum_{l=1}^N b_{jl} x_l = \bar{r}_j \quad (32)$$

have positive solutions.

The next theorem deals with a general Lotka-Volterra system

$$\frac{dx_i}{dt} = x_i(-r_i + \sum_{j=1}^M (a_{ij} + A_{ij})v_j - \sum_{l=1}^N \gamma_{il}x_l), \quad (33)$$

$$\frac{dv_j}{dt} = v_j(\bar{r}_j - \sum_{i=1}^N (b_{ji} + B_{ji})x_i - \sum_{k=1}^M d_{jk}v_k), \quad (34)$$

where, as before,  $i = 1, \dots, N$  and  $j = 1, \dots, M$ . We denote by  $\mathbf{a}, \mathbf{A}, \boldsymbol{\gamma}, \mathbf{b}, \mathbf{B}$  and  $\mathbf{d}$  the matrices with entries  $a_{ij}, A_{ij}, \gamma_{il}, b_{ji}, B_{ji}$  and  $d_{jk}$  respectively and introduce the block-matrix

$$\mathfrak{M} = \begin{pmatrix} \boldsymbol{\gamma} & -\mathbf{A} \\ \mathbf{B} & \mathbf{d} \end{pmatrix} \begin{pmatrix} \boldsymbol{\rho}^{-1} & 0 \\ 0 & \boldsymbol{\sigma}^{-1} \end{pmatrix},$$

where  $\boldsymbol{\rho}^{-1}$  and  $\boldsymbol{\sigma}^{-1}$  are diagonal matrices with the entries  $\rho_1^{-1}, \dots, \rho_N^{-1}$  and  $\sigma_1^{-1}, \dots, \sigma_M^{-1}$  on the diagonal, respectively.

**Theorem V.3.** *We assume that system (33), (34) has a positive equilibrium. Let the matrices  $\mathbf{a}$  and  $\mathbf{b}$  satisfy condition (18) with positive  $\rho_i$  and  $\sigma_j$ . If the matrix  $\mathfrak{M}$  is positive definite, i.e.*

$$(\xi, \eta) \mathfrak{M} (\xi, \eta)^T > 0$$

for all  $\xi \in \mathbb{R}^N$  and  $\eta \in \mathbb{R}^M$  such that  $|\xi| + |\eta| \neq 0$  then system (33), (34) is permanent.

**Proof.** First let us make a change of variables  $X_i = \rho_i x_i, i = 1, \dots, N$ , and  $X_{N+j} = \sigma_j v_j, j = 1, \dots, M$ . Then we obtain the system

$$\frac{dX_m}{dt} = X_m(-R_m - \sum_{k=1}^{N+M} (\mathfrak{A}_{mk} + \mathfrak{M}_{mk})X_k), \quad m = 1, \dots, N+M, \quad (35)$$

where  $R = (r_1, \dots, r_N, \bar{r}_1, \dots, \bar{r}_M)$  and

$$\mathfrak{A} = \begin{pmatrix} 0 & -\mathbf{a} \\ \mathbf{b} & 0 \end{pmatrix} \begin{pmatrix} \boldsymbol{\rho}^{-1} & 0 \\ 0 & \boldsymbol{\sigma}^{-1} \end{pmatrix}.$$

System (35) has a positive equilibrium and it is permanent if the matrix  $\mathfrak{A} + \mathfrak{M}$  is positive definite. the last is equivalent to positive definiteness of the matrix  $\mathfrak{M}$  due to (18).

According to Theorem V.3 even small self-limitation and concurrence can stabilize a system with a Hamiltonian structure. In this case an elementary analysis (see subsection VIC) shows that, in an equilibrium state, all the species co-exist. This means that ecological systems with weakly perturbed Hamiltonian structure can have large biodiversity. If the Hamiltonian condition (18) is violated then for small  $\lambda_g$  and  $\lambda_d$  the competition exclusion principle shows that only a single species can survive.

Let us consider perturbed Hamiltonian systems. Note that these perturbations can be connected with more complicated interaction topology and violations of condition (18). In the Hamiltonian case we have the square interaction matrix  $W = W_H$  of the size  $N + M$ , which can be decomposed in 4 blocks

$$\begin{bmatrix} 0 & A \\ B & 0 \end{bmatrix}$$

that corresponds to 2 trophic levels. Moreover, matrices  $A$  and  $B$  are connected via condition (18). Let us consider the perturbed interaction matrix  $W = W_H + \tilde{W}$ . Let us define the vector  $d$  with  $N + M$  components by  $d = (\rho_1, \dots, \rho_N, \sigma_1, \dots, \sigma_M)$ .

Consider the matrix  $\tilde{W}^{(d)}$  with the entries

$$\tilde{W}_{kl}^{(d)} = d_k d_l^{-1} \tilde{W}_{kl}, \quad k, l = 1, \dots, N + M.$$

If the matrix  $\tilde{W}^{(d)}$  is negatively defined and for system (24) there exists a positive equilibrium, then system (24) is permanent. It can be shown by the same arguments as in the proof of Theorem V.3.

## B. Case of large number of species

We start this section by showing that the Lotka-Volterra system (24) of a random structure has no positive equilibria. Consider the set of all  $N \times N$  matrices  $A$  with entries  $a_{ij}$  uniformly bounded by a constant

$$|A_{ij}| < K,$$

such that each row of  $A$  is non-zero and contains at most  $M_r$  non-zero entries and each column is also non-zero and contains at most  $M_c$  non-zero entries. Using the standard Lebesgue measure  $\mu$  defined on  $\mathbb{M}_{K,N}$ , for any measurable  $C$  we introduce the probability  $P(C) = \mu(C)/\mu(\mathbb{M}_{K,N})$ .

**Theorem V.4.** *Let  $B$  be a vector with  $N$  components and  $A \in \mathbb{M}_{K,N}$ . Then the probability  $P_N$  that the linear equation  $AY = B$  has a positive solution  $Y$  tends to zero as  $N \rightarrow +\infty$ .*

**Proof.** Let  $Y = (y_1, \dots, y_N)$  be a positive solution of (27). We can assume that all row and columns of  $A$  contain at least non-zero entries (probability to have a matrix with a zero row or column is 0). Let us change a sign of  $k$ -th row in  $A$  that gives a matrix  $A^{(k)}$ . Equation  $A^{(k)}Y = B$  has the solution  $Y = (x_1, \dots, -x_k, \dots, x_N)$ , which is not positive. So, each matrix  $A$ , for which  $AY = B$  has a positive solution, corresponds at least  $N$  different matrices, for which these solutions are not positive. Therefore,  $P_N \leq 1/N$ .

This result admits an ecological interpretation. Consider a random large ecological network. Assume that the connectance of this network is bounded. If we have no restrictions on ecological interactions, such network has no positive stationary states and thus it is not ecologically stable with a probability close to 1. A possible variant of such a restriction can be a sign restrictions on the coefficients of the system or condition (18), which leads to a Hamiltonian structure.

The next example demonstrates that the notion of structural stability for large Lotka-Volterra system must be used with discretion.

**Example.** Consider the general Lotka-Volterra system (24) where  $A$  is the identity matrix. Then the matrix  $A$  has the eigenvalue 1 only. Consider the matrix  $A_\varepsilon = A - \varepsilon B$  where  $B$  is the  $N \times N$  matrix with all elements equal 1. If we take the sum of all rows we get that it is equal to  $1 - N\varepsilon$ . Therefore, if  $\varepsilon = 1/N$  the matrix  $A_\varepsilon$  has zero eigenvalue.

The following theorem says that the conditions proved in Theorem V.1 which are equivalent to (28) are satisfied with probability close to 1 for large  $N$ .

**Theorem V.5.** *Let  $M$  be fixed and let  $\bar{r}_j$ ,  $j = 1, \dots, M$ , be random numbers mutually independent and normally distributed according to standard normal law  $\mathbf{N}(r_0, \sigma^2)$ , where  $\sigma \neq 0$  and  $r_0 > 0$ . Let also coefficients  $b_{jk}$ ,  $j = 1, \dots, M$  and  $k = 1, \dots, N$ , be mutually independent random numbers subjected to the normal law  $\mathbf{N}(0, 1)$ . Then condition (30) is fulfilled and the matrix  $B$  has rank  $M$  with probability  $1 - \varepsilon_N$ , where  $\varepsilon_N \rightarrow 0$  as  $N \rightarrow +\infty$ .*

*Proof.* Let  $B_j = \{b_{1j}, \dots, b_{Mj}\}$  and  $R = (r_1, \dots, r_M)$ ,  $j = 1, \dots, N$ . To prove Theorem it is sufficient to show that the vector  $R$  belongs to the convex cone, which coincides with all linear combinations with positive coefficients of  $M$  vectors from the set  $\{B_j\}_{j=1}^N$  and these vectors are linear independent with probability  $\geq 1 - \varepsilon_n$ , where  $\varepsilon_n \rightarrow 0$  as  $N \rightarrow \infty$ .

We identify vectors  $B_j$  and  $R$  with points  $B_j/|B_j|$  and  $R/|R|$  respectively on the sphere

$$S_M = \{w : w = (w_1, \dots, w_M) : |w| = (w_1^2 + \dots + w_M^2)^{1/2} = 1\}.$$

Let us introduce the sets

$$S_m^\pm(\varepsilon) = \{w \in S_M : |w \pm e^m| < \varepsilon\}, \quad m = 1, \dots, M,$$

where  $e^m$  the unit vectors with components  $e_k^m = \delta_k^m$ ,  $k = 1, \dots, M$ . Let also

$$S(\varepsilon) = \{w \in S_M : |w_k \pm 1| > 2\varepsilon, \quad k = 1, \dots, M\}.$$

One can check the following properties:

- (1) Probability that the number  $R/|R|$  lies in  $S(\varepsilon)$  can be estimated from below by  $1 - C\varepsilon$ , where  $C > 0$  is a constant;
- (2) Probability that at least one of vectors  $B_j/|B_j|$ ,  $j = 1, \dots, N$  belongs to  $S_m^\pm(\varepsilon)$ ,  $m = 1, \dots, M$ , can be estimated from below by

$$1 - M \left(1 - \frac{|S_m(\varepsilon)|}{|S_M|}\right)^{N-1},$$

where  $|S|$  is the measure of  $S$ ;

- (3) If  $S_m^\pm(\varepsilon)$ ,  $m = 1, \dots, M$ , contains at least one vector  $B_j$  and the vector  $R$  belongs to  $S(\varepsilon)$  then it is inside the convex cone of certain  $M$  vectors from different  $S_m^\pm(\varepsilon)$ .

These properties prove the theorem.  $\square$

Consider some biological corollaries and interpretations of these results, in particular, Theorems V.1, V.5 and corollary V.2. Mathematically, persistence follows from existence of positive solutions of systems (31) and (32). Let  $M \ll N$ , and all interactions are random. Theorem V.5 asserts that then the second system has a solution with a probability close to 1. However, the same arguments, as in the proof this theorem, show then that system (31) has a positive solution with probability close to 0.

To overcome this difficulty and understand origins of large system stability, one can suppose that real ecological systems can use an *adaptive strategy*. Indeed, let us recall that fundamental relation (18) admits an interpretation by meeting frequencies between predators and preys (see the end of section IV). This frequencies are defined by the coefficients  $\sigma_k$  and  $\rho_i$ . Using this fact, we rewrite (31) as follows:

$$\sum_{k=1}^M \sigma_k b_{ki} v_k = \rho_i r_i, \quad i = 1, \dots, N. \quad (36)$$

For fixed  $\sigma_k$  and  $\rho_i$  this system has a solution with a small probability for large  $N$ . However, let us suppose that predator-species and prey-species can change the meeting frequency (i.e., adjust  $\sigma_k$  and  $\rho_i$ ) (this means, biologically, existence of adaptive behaviour). Then these coefficients become unknowns and now (36) always has a solution if we assume that the signs of coefficients are preserved under their random choice.

Finally, Theorem V.5 shows that in the Hamiltonian case the ecological stability can be reinforced by an increase of  $N$  and an adaptive strategy. Nonetheless, many ecological networks may be unstable and a transient dynamics or catastrophic phenomena are possible. In the next sections we study mechanisms of such phenomena by the Hamiltonian methods.

## VI. STAR STRUCTURES

In the case of the Hamiltonian structure we can develop a general approach that allows us to describe transient dynamics and catastrophic phenomena. If a Hamiltonian system has a single positive equilibrium, then all level sets  $H(p, q) = E$  have the same topological structure. Catastrophic phenomena appear if topology of these level sets changes depending on  $E$ .

We start with the simplest case, when we are dealing with a star structure.

### A. Star structures without self-limitation

As in the previous section, we assume that  $\gamma_{ij} = 0, d_{jl} = 0$  in system (16), (17) and condition (14) holds. These assumptions guarantee, in particular, that  $C_i$  are constants. Let  $M = 1$ , i.e., we deal with a star structure. Then condition (14) becomes

$$r_i = a_{i1}\mu_1, \quad i = 1, \dots, N \quad (37)$$

for some positive  $\mu_1$ . Note that this condition is very restrictive for large  $N$  but one can show that such relation can be explained from an evolutionary point of view (this issue will be discussed in the future publications). Moreover, a positive equilibrium with  $x_i > 0$  exists only if this condition holds.

We set  $a_i = a_{i1}, b_j = b_{j1}$  and  $q = q_1, p = p_1$ . Let us denote  $\bar{r} = \bar{r}_1$ . System (16), (17) takes the form

$$\frac{dq}{dt} = \exp(p) - \mu_1, \quad \frac{dp}{dt} = f(C, q), \quad (38)$$

where

$$f(C, q) = - \sum_{j=1}^N b_j C_j \exp(a_j q) + \bar{r}. \quad (39)$$

This is a Hamiltonian system with the Hamiltonian

$$H(q, p) = \Psi(p) + \Phi(q), \quad (40)$$

where

$$\Psi(p) = \exp(p) - \mu_1 p, \quad (41)$$

is a "kinetic energy", and

$$\Phi(C, q) = \sum_{j=1}^N \rho_j C_j \exp(a_j q) - \bar{r} q \quad (42)$$

is a "potential" energy. Here  $\rho_j = b_j/a_j$  and  $\sigma_j = 1$ . The function  $\Psi$  is convex, goes to  $+\infty$  as  $|p| \rightarrow \infty$ , and has a minimum, which is  $\mu_1(1 - \log \mu_1)$  and is attained at  $p = \log \mu_1$ .

System (38) has the energy integral

$$\Psi(p) + \Phi(C, q) = E = \text{const}. \quad (43)$$

Proceeding as in [29], we can describe solution of (38) in terms of the function  $\Phi(C, q)$  and the energy level  $E$ . The values of  $q$  satisfying (43) lie in the set

$$D(E) = \{q : \Phi(q) \leq E - \min \Psi(p) = E - \mu_1(1 - \log \mu_1)\}.$$

This set is a union of intervals, which can be bounded or unbounded. The ends of these intervals are defined by

$$\Phi(C, q) = E - \mu_1(1 - \log \mu_1). \quad (44)$$

After finding  $q$  the component  $p$  can be reconstructed from (43).

### B. Oscillations, solitons and kinks

Let us consider some important typical situations. In this section,  $a_i$  and  $b_i$  are arbitrary.

(i) If equation (44) has a unique root or it has no roots, then the corresponding interval is infinite, and we have non-periodic solutions  $(q(t), p(t))$ , which are unbounded in  $q$ . Then some of  $x_i(t)$  go to 0 or  $+\infty$  as  $t \rightarrow \infty$  and the original system is not ecologically stable;

(ii) If (44) has two non-degenerate roots  $q_- < q_+$  and  $\Phi(C, q) < E - \mu_1(1 - \log \mu_1)$  for all  $q \in (q_-, q_+)$  then  $(q(t, C, E), p(t, C, E))$  is a periodic solution of the amplitude  $A = q_+ - q_-$  (see Fig.1). The period  $T$  is defined by

$$T = \int_0^T dt = \int_{q_-}^{q_+} \left( \frac{dq}{dt} \right)^{-1} dq = \int_{q_-}^{q_+} (\exp(p(q)) - \mu_1)^{-1} dq, \quad (45)$$

where  $p(q)$  can be found from (43). The period  $T$  depends on  $E$  and  $C$ . For example, we have only periodic solutions for the **PP** case (see Fig. 1).

(iii) If  $\Phi(C, q)$  has a local maximum at  $q = q_+$ , which is  $E - \mu_1(1 - \log \mu_1)$ , and the second root in (44) is non-degenerate, (see Fig. 2), we obtain a soliton. Its graph has a local burst in time, and  $q(t) \rightarrow q_+$  as  $t \rightarrow \infty$ .

(iv) The kink solution corresponds to the case when  $\Phi$  has two local maxima at  $q_{\pm}$  such that  $\Phi(q_-) = \Phi(q_+) = E - \mu_1(1 - \log \mu_1)$ . The kink describes a jump in  $t$  that can correspond to a sharp change of ecological behaviour.

The kink solutions are unstable under a small perturbation of  $\Phi(C, q)$ , whereas solitons are stable under such perturbations. When the parameter  $E$  changes, we observe a transition (via solitons or kinks) between different periodic solutions and transitions from a periodic solution to unbounded in time solution and vice versa. Solitons and kinks appear only if we have a star system with different signs  $a_i b_i$  (for example, a combination of **PP** and **C**).

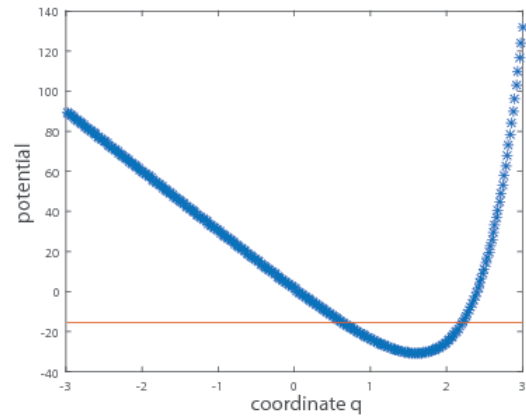


FIG. 1: The graph of the potential  $\Phi$  for case **PP** and small values of  $\bar{r}$

Let us formulate conditions providing that  $\Phi(q) \rightarrow +\infty$  as  $|q| \rightarrow +\infty$  in the case of arbitrary  $a_i$  and  $b_i$ . Then  $|q(t)|$  is bounded uniformly in  $t$  and hence the population abundances

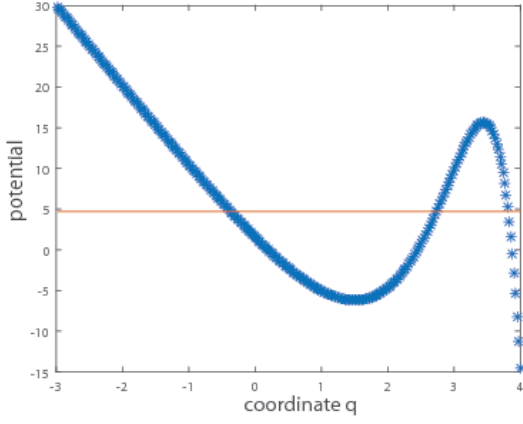


FIG. 2: The graph of the potential  $\Phi$  for the case when **PP** and **C** interactions coexist,  $N > 1$

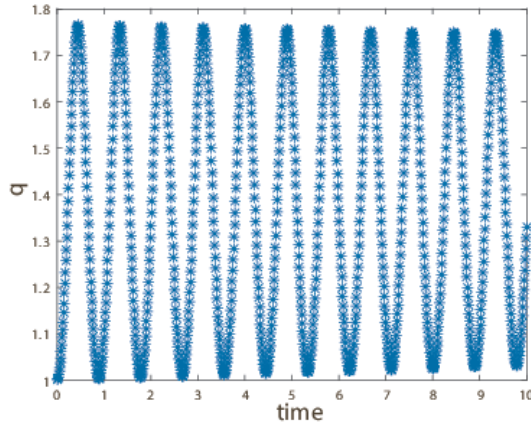


FIG. 3: The plot of a periodic solution  $q(t)$

$x_i$  are separated from 0 and  $+\infty$ . Therefore, then system (1), (2) is strongly persistent.

(PI) Assume that all  $a_i$  are positive. Let  $i_+$  be the index corresponding to the largest  $a_i$ . Condition  $b_{i_+} > 0$  and  $\bar{r} > 0$  is equivalent to persistency of our system. In this case  $\Phi(q) \rightarrow +\infty$  as  $q \rightarrow \infty$  and according to (44),  $|q(t)|$  is bounded;

(PII) Assume that all  $a_i$  are negative. Let  $i_-$  be the index that corresponds to the largest value of  $-a_i$ . If  $b_{i_-} < 0$  and  $\bar{r} > 0$ , then  $|q(t)|$  is bounded and the system is persistent (and vice versa).

(PIII) Let  $a_i$  may have different signs. Let  $i_{\pm}$  be the indices corresponding to the maximal values of  $\pm a_i$ , respectively. If  $b_{i_+} > 0$  and  $b_{i_-} < 0$ , then the system is persistent.

To conclude this section, let us describe some effects. First, condition (PIII) shows that there is possible a *domino* effect, when an extinction of a species leads to instability of all species in the foodweb.

Indeed, let us assume that if  $a_j > 0$  for  $j \neq i_+$  the coefficient  $b_j < 0$ . Then extinction of the  $i_+$ -th species leads to instability of the whole system of species.

The second effect is a noise-induced transition [30]. Assume that the potential energy  $\Phi(q)$  has a local maximum  $\Phi_+$ , and  $\Phi(q) \rightarrow +\infty$  as  $q \rightarrow \pm\infty$ . Then  $\Phi$  has at least two local

minima (two potential wells) and, according to (iii), a soliton exists. If the network environment is random, its fluctuations can generate random transitions between the potential wells even if  $E < \Phi_+$ . Such transitions provoke ecological catastrophes.

### C. Hamiltonians via $x, v$ and perturbations

Hamiltonians in variables  $(q, p)$  can be represented as functions of species abundances  $x_i$  and  $v$ . Let  $m_i$  be positive numbers such that  $\sum_{i=1}^N m_i = 1$ . By elementary transformations we obtain that functions

$$E(x, v, m) = v - \mu \ln(v) + \sum_{i=1}^N \rho_i x_i - \bar{r} m_i a_i^{-1} \ln(x_i) \quad (46)$$

are motion integrals, i.e., conserve on the system trajectories. If we consider these functions as Hamiltonians, then, in order to write the equations in a Hamiltonian form, we must use a special representation involving a skew-product Poisson matrix depending on species-abundances [16]. We have thus a whole family of motion integrals. There is an interesting property: if all  $\rho_i$  and  $a_i$  are positive, then the minimum of the function  $E(x, v, m)$  gives us an equilibrium  $(\bar{v}, \bar{x})$  of the Hamiltonian star system defined by

$$\bar{v} = \mu, \quad \bar{x}_i = \bar{r} m_i (\rho_i a_i)^{-1}.$$

Different choices of weights  $m_i$  correspond to different positive equilibria.

Consider some properties of the Hamiltonian and non-Hamiltonian star systems with weak competition and self-limitation. Let  $M = 1$  and  $N > 1$ . We assume, to simplify calculations, that  $\gamma_{ij} = \gamma_i \delta_{ij}$ , where  $\delta_{ij}$  is the Kronecker delta. Let us consider equations (1) and (2), which can be written down then as follows:

$$\frac{dx_i}{dt} = x_i(-r_i + a_i v - \gamma_i x_i), \quad (47)$$

$$\frac{dv}{dt} = v(\bar{r} - \sum_{l=1}^N b_l x_l - dv). \quad (48)$$

where  $i = 1, \dots, N$ . Let us denote  $\mu_i = r_i/a_i$  and  $\theta_i = b_i a_i \gamma_i^{-1}$ . A positive equilibrium is defined by relations

$$\bar{x}_i = \gamma_i^{-1} a_i (v - \mu_i), \quad (49)$$

$$\bar{v} = \frac{\bar{r} + \sum_{i=1}^N \mu_i \theta_i}{d + \sum_{i=1}^N \theta_i}, \quad (50)$$

provided that  $v > \mu_i$ ,  $i = 1, \dots, N$ . One can check that for small  $\gamma_i, d > 0$  this condition holds only for the Hamiltonian case, i.e., when  $\mu_i = \mu$  for all  $i$ .

Another interesting fact is that if in the relation for the Hamiltonian (46) we put  $m_i = \bar{x}_i(\gamma)$  and  $\mu = \bar{v}$ , then  $E(x, v)$  becomes a Lyapunov function decreasing along trajectories of the corresponding Lotka-Volterra system.

## VII. VARYING ENVIRONMENT

Consider system (1),(2) assuming that  $M = 1$  and that  $a_i, b_i, r_i$  and  $\bar{r}$  can depend on  $t$ . The dependence on  $t$  describes an influence of a varying environment.

System (1),(2) takes the form

$$\frac{dx_i}{dt} = x_i(-r_i(t) + a_i(t)v - \sum_{j=1}^N \gamma_{ij}x_j), \quad (51)$$

$$\frac{dv}{dt} = v(\bar{r}(t) - \sum_{j=1}^N b_j(t)x_j - d_{11}v). \quad (52)$$

Suppose that there exist constants  $\bar{\gamma}_i > 0$  and  $\mu$  such that

$$r_j(t) - a_j(t)\mu = -\bar{\gamma}_j, \quad j = 1, \dots, N, \quad (53)$$

Similar to Section III, we put

$$x_i = C_i \exp(a_i q), \quad dq/dt + \mu = v.$$

After some transformations (compare with Sect. III), we obtain the following system for  $C_i, q$  and  $p$ :

$$\frac{dC_i}{dt} = C_i(\bar{\gamma}_i - \sum_{j=1}^N \gamma_{ij}C_j \exp(a_j q) - q \frac{da_i}{dt}), \quad (54)$$

$$\frac{dq}{dt} = \exp(p) - \mu, \quad (55)$$

$$\frac{dp}{dt} = \bar{r}(t) - d_{11} \exp(p) - \sum_{j=1}^N b_j C_j \exp(a_j q), \quad (56)$$

which is equivalent to (51) and (52). We investigate this system in the next subsection.

### A. Weak self-limitation and slowly varying environment

Let the coefficients  $a_k, b_k, r_k$  and  $\bar{r}$  be functions of the slow time  $\tau = \varepsilon t$ , where  $\varepsilon > 0$  is a small parameter. We assume that

(I) self-limitations are small, i.e.,  $d_{11} = \varepsilon \bar{d}$ , where  $\bar{d} > 0$  and  $\gamma_{ij} = \kappa \gamma_i \delta_{ij}$ , where  $\gamma_i > 0$  and  $\kappa > 0$ ;

(II)  $\bar{\gamma}_i = \kappa \hat{\gamma}_i$ , where  $\hat{\gamma}_i > 0$ .

Under these assumptions, system (54), (56) lies in the class of well studied weakly perturbed Hamiltonian systems [18, 19]. Equations (55) and (56) take the following form:

$$\frac{dq}{dt} = \exp(p) - \mu, \quad \frac{dp}{dt} = f(C(t), q(t), \tau) + \varepsilon g(p(t)), \quad (57)$$

where  $g = -\bar{d} \exp(p)$  is a term associated with self-limitation effects for  $v$ , and

$$f(C, q, \tau) = - \sum_{j=1}^N b_j(\tau) C_j \exp(a_j(\tau) q) + \bar{r}(\tau). \quad (58)$$

Equation (54) for  $C_i(t)$  becomes

$$\frac{dC_i}{dt} = \varepsilon \tilde{W}_i(C, q, \tau), \quad (59)$$

where

$$\tilde{W}_i(C, q, \tau) = \beta C_i \left( \hat{\gamma}_i(\tau) - \gamma_i C_i \exp(a_i(\tau) q) - q \frac{da_i}{d\tau} \right) \quad (60)$$

and  $\beta = \kappa/\varepsilon$ .

System (57), (59) can be resolved by the averaging method (see [22]), which gives rigorous results for time intervals of order  $O(\varepsilon^{-1})$ . According to this method, we can represent  $C(t)$  as

$$C(t) = \bar{C}(\tau) + O(\varepsilon),$$

where an equation for  $\bar{C}(\tau)$  will be written below. The  $q$  and  $p$  variables can be represented in the following multiscale form:

$$q = Q(t, \tau, E(\tau)) + O(\varepsilon), \quad p = P(t, \tau, E(\tau)) + O(\varepsilon), \quad (61)$$

where the leading terms  $Q$  and  $P$  can be found from the system

$$\frac{dQ}{dt} = \exp(P) - \mu, \quad \frac{dP}{dt} = f(\bar{C}(\tau), Q, \tau), \quad (62)$$

analogous to (38). Here  $f$  is given by (39), where  $C, b_j$  and  $\bar{r}$  depend on the parameter  $\tau$ . This system is Hamiltonian and the corresponding energy integral is defined by (43). Taking into account the dependence of  $f$  on  $\tau$  in (62) we write the energy integral as

$$\Psi(P) + \Phi(\bar{C}(\tau), Q, \tau) = E(\tau) \quad (63)$$

for each fixed  $\tau$  and  $E$ . The properties of solutions  $Q(t, \tau, E(\tau))$  can be described as in Sect. VI. We seek periodic in  $t$  solutions  $Q, P$  of system (62), (63) assuming that  $\tau$  and hence  $\bar{C}, E$  are parameters. System (62) should be supplemented by the equation describing behaviour of  $E(\tau)$  and  $\bar{C}(\tau)$  as functions of  $\tau$  (it appears that these equations are coupled). In the multiscale procedure, the equation for  $E$  guarantees the boundedness of corrections to the leading terms  $Q$  and  $P$  on the time intervals of length  $O(\varepsilon^{-1})$ .

The equation for the unknown function  $E(\tau)$  can be derived as follows. Let

$$\langle z(\cdot, \tau) \rangle = T^{-1} \int_0^T z(t, \tau) dt$$

be the average of a function  $z(t, \tau)$  over the period  $T(E)$ . Using Theorem 3 from [22], one has

$$\frac{dE}{d\tau} = S_1(E, \bar{C}, \tau) + S_2(E, \bar{C}, \tau) + S_3(E, \bar{C}, \tau), \quad (64)$$

where

$$S_1 = \langle g(P(\cdot, \tau))(\exp(P(\cdot, \tau, E)) - \mu) \rangle$$

gives the contribution of self-limitation effects,

$$S_2 = \langle \Phi_\tau(\bar{C}(\tau), Q(\cdot, \tau, E), \tau) \rangle$$

is the term determining a direct dependence of  $\Phi$  on  $\tau$  and

$$S_3 = \left\langle \sum_{i=1}^N \Phi_{\bar{C}_i}(\bar{C}(\tau), Q(\cdot, \tau, E), \tau) \bar{W}_i(\bar{C}(\tau), Q(\cdot, \tau, E), \tau) \right\rangle$$

is the term coming from the dependence of  $\Phi$  on  $C_i$ .

For  $\bar{C}_i$  we have [22]

$$\frac{d\bar{C}_i}{d\tau} = W_i(\bar{C}_i, E, \tau), \quad (65)$$

where

$$W_i(\bar{C}, E, \tau) = \bar{C}_i(\bar{\gamma}_i - \gamma_i \bar{C}_i \theta_i(\bar{C}, E) - \frac{da_i}{d\tau} \langle Q \rangle), \quad (66)$$

and  $\theta_i(C, E) = \langle \exp(a_i Q) \rangle$ .

Thus, we have obtained equations (65) and (64) for  $\bar{C}_i(\tau)$  and  $E$ , respectively. These equations and (62), (63) give us the complete system that allows to describe dynamics for time intervals of length  $O(\varepsilon^{-1})$ . Note that first two equations (62), (63) contain the derivatives with respect to  $t$ , while eqs. (65) and (64) involve the slow time  $\tau$  only.

The hamiltonian  $H$  depends on the parameter  $\mu$  introduced in (53). The averaging allows us to find this parameter. For periodic solutions relation (62) implies

$$\langle f(\bar{C}(\tau), Q, \tau) \rangle = \sum_{k=1}^N b_k \bar{C}_k \langle \exp(a_k Q) \rangle - \bar{r} = 0. \quad (67)$$

It is natural to choose  $\mu$  in such a way that (65) has a stationary solution. This solution is defined by

$$\bar{C}_k = \bar{\gamma}_k (\gamma_k \langle \exp(a_k Q) \rangle)^{-1}. \quad (68)$$

Substituting (68) into (67) and using the definition of  $\bar{\gamma}_k$ , one has the following relation

$$\sum_{k=1}^N b_k (r_k - a_k \mu) \gamma_k^{-1} = 0. \quad (69)$$

One can verify that  $\mu = \bar{v} > 0$ , where  $\bar{v}$  is the  $v$ -component of an equilibrium solution  $(\bar{x}, \bar{v})$  of system (1), (2) in the case  $M = 1$ ,  $\mathbf{D} = \mathbf{0}$  and  $\gamma$  is a diagonal matrix.

One can show that solutions of this "averaged" system (62), (63), (64), (65) are close to the solutions of the original system (57), (59) on a time interval of length  $O(\varepsilon^{-1})$ . Equation (64) expresses an "averaged" energetic balance: three factors define evolution of averaged energy, namely, the evolution of  $\bar{C}$ , the dependence of the parameters on  $\tau$  and self-limitation effects.

### B. Main effects: irregular bursts, quasiperiodic solutions and chaos

To proceed with a qualitative analysis of solutions to system (57), (59), we assume that

$$\Phi(C, q) \rightarrow +\infty \quad \text{as } q \rightarrow \pm\infty. \quad (70)$$

This relation holds for random  $a_j$  and  $b_j$  if  $a_j/b_j = \rho_j > 0$ . Let  $q_j^*(C)$  be local extrema of  $\Phi$  for a given  $C$ . Let us put  $\Phi_j = \Phi(q_j^*(C))$ .

Energetic relation (64) allows us to find interesting phenomena. In fact, if  $\Phi_j$  is a local maximum, then evolution of  $E$  can lead to special periodic solutions in  $q$ , when  $E$  approaches the value  $\Phi_j$ . These solutions can be represented as periodic sequences of bursts separated by large time intervals  $T_0(E, \tau)$  (see Fig.4). If  $E = \Phi_j$ , we have a single burst (soliton) and  $T_0 = \infty$ . Note that Fig. VII B illustrates the case of fixed  $\tau$  and  $E$  ( $\varepsilon = 0$ ). For  $E$  close to  $\Phi_j$  and small  $\varepsilon > 0$  the time behaviour of  $q(t, \tau)$  exhibits a chain of slightly different bursts separated by different large time intervals (see Fig. 5). Existence of solitons means that there is a homoclinic structure in the unperturbed Hamiltonian dynamics, and therefore, this sequence of bursts can be chaotic as a result of  $\tau$ -evolution [19, 201].

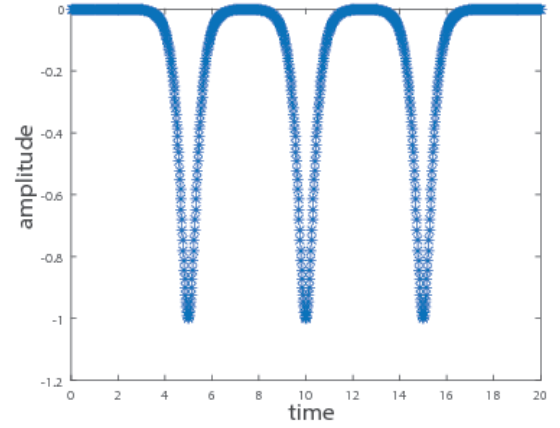


FIG. 4: The plot of a periodic solution  $q(t)$  with a large period  $T$  for  $\varepsilon = 0$

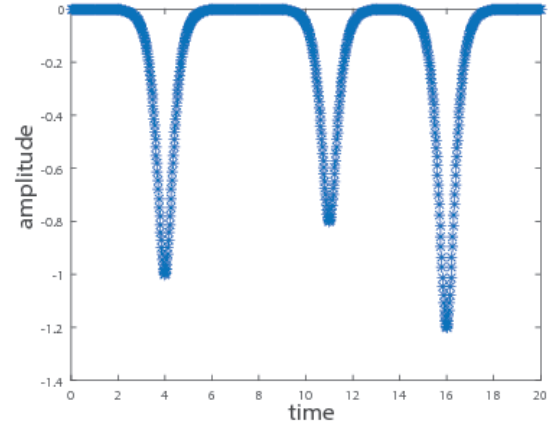


FIG. 5: The plot of a solution  $q(t)$  close to a sequence of the bursts for small  $\varepsilon$

The following picture of the time evolution of solutions  $q(t)$  can be observed. For  $E$  close to a local minimum of  $\Phi$  we have periodic oscillations with an amplitude and a period, which slowly evolve in  $t$ . When  $E$  approaches a local maximum of

$\Phi$ , we obtain a irregular chain of rare bursts. Such a picture is observed in macroscopic ecological dynamics (see [31]).

The following effects can occur here:

(Ai) Let  $E(0) > \Phi_l^*$  for some  $l$ . The value  $E(\tau)$  does not meet values  $\Phi_l^*$  for all  $\tau$ . Then we deal with only periodical solutions with a period and an amplitude depending on  $\tau$ . This means that the environment stabilizes the population against self-limitation;

(Aii) The value  $E(\tau)$  passes through  $\Phi_l^*$  for some  $\tau$ , then we have an ecological burst;

(Aiii) An ecological burst is also possible when  $E(0) < \Phi_l^*$  for all  $l$  and  $S_2$  is more than  $|S_1|$ . Then we observe that the environment destabilizes the population against self-limitation.

So, the climate and seasonal oscillations can stabilize ecological dynamics in certain cases.

Consider more complicated situations. A system of equations similar to (65) and (64) can be derived (at least, formally) in the general multidimensional case  $M > 1$  if the parameters  $\tilde{\gamma}_i$  (defined by (14)) are small, and the potential energy  $\Phi(q)$  satisfies some conditions. Indeed, the behaviour of solutions of non-perturbed Hamiltonian system is defined by the energy  $E$ . If  $E$  is close to a local minimum of  $\Phi$ , then, at least for some values of  $E$ , we have quasiperiodic solutions that follows from the KAM theory (see [18, 19]). Then the averaging procedure leads to a system analogous to (65) and (64). In the multidimensional case effects (Ai)- (Aiii) are also possible if the potential energy  $\Phi$  has local minima and saddle points. All these effects are induced by non-Hamiltonian perturbations.

Other interesting situations appear for an ecological system decomposed into  $n > 1$  weakly interacting compartments, which are star systems with  $M = 1$  and  $N > 1$ . Let us assume that self-limitation is absent:  $\tilde{\gamma}_i = 0$ ,  $\gamma_i = 0$  and  $\mathbf{D} = 0$ . In this case the Hamiltonian  $H(C, q, p)$  can be represented as

$$H = H_0(C, q, p) + \kappa \tilde{\Phi}(C, q), \quad (71)$$

where

$$H_0 = \sum_{l=1}^n \Psi(C, p_l) + \Phi(C, q_l).$$

The system with the Hamiltonian  $H_0$  is a completely integrable Hamiltonian one. The small contribution  $\kappa \tilde{\Phi}$  describes weak interactions between compartments (niches). For example, such situation can occur if we have  $n$  preys and  $Nn$  of predators. Each predators usually eats some special types of prey, but sometimes (with a small frequency  $\kappa > 0$ ) different predators share the same prey. A similar decomposition into weakly interacting parts can be applicable when we investigate food webs living in industrial landscapes [26].

## VIII. RESONANCES

The main idea is as follows. The networks with the scale-free topology contains a number of hubs, strongly connected nodes. In ecosystems, the hubs correspond to species-generalists. Each species-generalist interacts with many species-specialists forming a star subsystem. The different

star subsystems weakly overlapped in randomly constructed webs. We consider networks consisting of weakly overlapped star systems. Therefore, such webs can be viewed as sets of weakly interacting integrable Hamiltonian systems. Thus, the whole food-web becomes classical object of Hamiltonian theory, since we are dealing with a weakly perturbed integrable multidimensional Hamiltonian system.

### A. Two interacting star systems

The resonance analysis is important in the Hamiltonian dynamics investigation, since resonances can lead to instabilities, periodical oscillations, chaos, and other interesting effects in systems with many variables. These effects are important for mechanical and physical applications. However, resonances have not been considered yet for large ecological webs. For example, work [23] considered the case of two species predator-prey systems perturbed by small time periodic climate variations. In opposite to [23], we consider internal resonances, when there are no external variations and the resonance effect is generated by system interactions. We show that in ecological networks such internal resonance effects exist and can provoke instabilities.

Let us consider two star subsystems, the first one involves variables  $v$  and  $x_i$ ,  $i = 1, \dots, N_1$ , while the second subsystem involves abundances  $w$  and  $y_j$ ,  $j = 1, \dots, N_2$ . System of equations describing a weak interaction between these subsystems can be written in the following form:

$$\frac{dx_i}{dt} = x_i(-r_i^{(1)} + a_i^{(1)}v + \kappa \tilde{a}_i^{(1)}w - \gamma_i^{(1)}x_i), \quad (72)$$

$$\frac{dv}{dt} = v(\bar{r}_i^{(1)} - \sum_{i=1}^{N_1} b_i^{(1)}x_i - \kappa \sum_{j=1}^{N_2} \tilde{b}_j^{(1)}y_j - \varepsilon d_1v), \quad (73)$$

$$\frac{dy_j}{dt} = y_j(-r_j^{(2)} + a_j^{(2)}w + \kappa \tilde{a}_j^{(2)}v - \gamma_j^{(2)}y_j), \quad (74)$$

$$\frac{dw}{dt} = w(\bar{r}_i^{(2)} - \sum_{j=1}^{N_2} b_j^{(2)}y_j - \varepsilon \sum_{i=1}^{N_1} \tilde{b}_i^{(2)}x_i - \varepsilon d_2w). \quad (75)$$

Here  $\kappa > 0$  and  $\varepsilon > 0$  are small parameters such that  $\kappa \gg \varepsilon$ . The terms proportional to  $\kappa$  describe a weak interaction of two subpopulations with star structures. The terms proportional to  $\varepsilon$  correspond to self-limitation effects. We assume that

$$r_i^{(k)} - \mu_k a_i^{(k)} = -\varepsilon \tilde{\gamma}^{(k)}, \quad k = 1, 2,$$

and introduce variables  $q_1$  and  $q_2$  (see Sect. III) by

$$\frac{dq_1}{dt} + \mu_1 = v, \quad \frac{dq_2}{dt} + \mu_2 = w,$$

and

$$x_i = C_i^{(1)} \exp(a_i^{(1)} q_1), \quad y_j = C_j^{(2)} \exp(a_j^{(2)} q_2), \quad (76)$$

where  $C_i^k$  are unknowns. Let us define  $p_i$  by

$$\frac{dq_i}{dt} = \exp(p_i) - \mu_i, \quad i = 1, 2. \quad (77)$$

Then  $p_1$  and  $p_2$  satisfy

$$\frac{dp_1}{dt} = -\Phi_q^{(1)}(q_1) + \kappa g_1(q_2) - \varepsilon d_1 \exp(p_1), \quad (78)$$

$$\frac{dp_2}{dt} = -\Phi_q^{(2)}(q_2) + \kappa g_2(q_1) - \varepsilon d_2 \exp(p_2), \quad (79)$$

where

$$\Phi^{(1)}(q_1) = \sum_{i=1}^{N_1} \frac{C_i^{(1)} b_i^{(1)}}{a_i^{(1)}} \exp(a_i^{(1)} q_1) - \bar{r}^{(1)} q_1,$$

$$\Phi^{(2)}(q_2) = \sum_{i=1}^{N_2} \frac{C_i^{(2)} b_i^{(2)}}{a_i^{(2)}} \exp(a_i^{(2)} q_2) - \bar{r}^{(2)} q_2,$$

$$g_1(q_2) = \sum_{j=1}^{N_2} \tilde{b}_j^{(1)} C_j^{(2)} \exp(a_j^{(2)} q_2),$$

$$g_2(q_1) = \sum_{i=1}^{N_1} \tilde{b}_i^{(2)} C_i^{(1)} \exp(a_i^{(1)} q_1).$$

For fixed  $C_i^k$  we obtain the weakly perturbed Hamiltonian system, defined by equations (77), (78) and (79). We suppose that for  $\kappa = \varepsilon = 0$  this system has an equilibrium solution

$$q_1(t) \equiv \bar{q}_1, \quad q_2(t) \equiv \bar{q}_2 \quad (80)$$

and periodical solutions oscillating around this equilibrium.

### B. Asymptotic analysis

To simplify the statement, we consider the case of small periodic oscillations near equilibrium (80). Then we keep only quadratic terms in the Taylor expansion of  $\Phi^k$ , i.e.

$$\Phi^1(q_1) = \omega_1^2 \tilde{q}_1^2, \quad \Phi^2(q_2) = \omega_2^2 \tilde{q}_2^2, \quad \tilde{q}_i = q_i - \bar{q}_i.$$

The functions  $g_i$  can be approximated by linear terms as follows:

$$g_1(q_2) = g_1 + g_{12} \tilde{q}_2 + O(\tilde{q}_2^2), \quad g_2(q_1) = g_2 + g_{21} \tilde{q}_1 + O(\tilde{q}_1^2),$$

where

$$g_{12} = \frac{dg_1(q)}{dq}(\bar{q}_1), \quad g_{21} = \frac{dg_2(q)}{dq}(\bar{q}_2).$$

In the case of small oscillations system (77), (78) and (79) can be written as a linear system of second order

$$\frac{d^2 \tilde{q}_1}{dt^2} + \omega_1^2 \tilde{q}_1 = \kappa g_{12} \tilde{q}_2 - \varepsilon d_1 \left( \frac{d\tilde{q}_1}{dt} + \mu_1 \right), \quad (81)$$

$$\frac{d^2 \tilde{q}_2}{dt^2} + \omega_2^2 \tilde{q}_2 = \kappa g_{21} \tilde{q}_1 - \varepsilon d_2 \left( \frac{d\tilde{q}_2}{dt} + \mu_2 \right). \quad (82)$$

The resonance case occurs if

$$\omega_1 = \omega_2 = \omega.$$

If  $|\omega_1 - \omega_2| \gg \kappa$ , then system (81), (82) can be resolved in a simple way and the solutions are small regular perturbations of periodic limit cycles. Let us consider the resonance case.

To resolve system (81), (82), we apply a standard asymptotic method. Let us introduce a slow time  $\tau = \kappa t$ . We are looking for asymptotic solutions in the form

$$\tilde{q}_k = A_k(\tau) \sin(\omega t + \phi_k(\tau)) + \kappa S_k(t, \tau) + \dots, \quad k = 1, 2 \quad (83)$$

where  $A_k$  and  $\phi_k$  are new unknown functions of  $\tau$ ,  $S_k(t, \tau)$  are corrections of the main terms. Here  $A_k$  define slowly evolving amplitudes of the oscillations whereas  $\phi_k$  describe phase shifts. Differentiating (83) with respect to  $t$  and substituting the relations obtained into (81) and (82), we have

$$\frac{\partial^2 S_k}{\partial t^2} + \omega^2 S_k = F_k(A_1, A_2, \phi_1, \phi_2, t), \quad (84)$$

where

$$F_1 = -(2\omega \frac{dA_1}{d\tau} + \bar{\varepsilon} d_1 \omega A_1) \cos(\omega t + \phi_1) +$$

$$+ 2\omega A_1 \frac{d\phi_1}{d\tau} \sin(\omega t + \phi_1) + g_{12} A_2 \sin(\omega t + \phi_2) + \tilde{\mu}_1 + O(\kappa^2),$$

$$F_2 = -(2\omega \frac{dA_2}{d\tau} + \bar{\varepsilon} d_2 \omega A_2) \cos(\omega t + \phi_2) +$$

$$+ 2\omega A_2 \frac{d\phi_2}{d\tau} \sin(\omega t + \phi_2) + g_{21} A_1 \sin(\omega t + \phi_1) + \tilde{\mu}_2 + O(\kappa^2).$$

Here  $\bar{\varepsilon} = \varepsilon / \kappa$  and  $\tilde{\mu}_k = \bar{\varepsilon} \mu_k d_k$ .

We seek solutions  $S_k$  of (84), which are  $O(1)$  as  $\kappa \rightarrow 0$ . Such solutions exist if and only if the following relations hold:

$$\int_0^T F_k(A_1, A_2, \phi_1, \phi_2, t) \sin(\omega t + \phi_k) dt = 0, \quad (85)$$

$$\int_0^T F_k(A_1, A_2, \phi_1, \phi_2, t) \cos(\omega t + \phi_k) dt = 0, \quad (86)$$

where  $T = 2\pi / \omega$ . Evaluation of the integrals in (85), (86) gives the following system for the amplitudes  $A_k$  and the phases  $\phi_k$ :

$$2\omega \frac{dA_1}{d\tau} = -\bar{\varepsilon} d_1 \omega A_1 + b_{12} A_2 \sin(\phi_2 - \phi_1), \quad (87)$$

$$2\omega \frac{dA_2}{d\tau} = -\bar{\varepsilon} d_2 \omega A_2 + b_{21} A_1 \sin(\phi_2 - \phi_1), \quad (88)$$

$$\omega A_1 \frac{d\phi_1}{d\tau} = -b_{12} A_2 \cos(\phi_2 - \phi_1), \quad (89)$$

$$\omega A_2 \frac{d\phi_2}{d\tau} = b_{21} A_1 \cos(\phi_2 - \phi_1), \quad (90)$$

where  $b_{12} = g_{12}$ ,  $b_{21} = -g_{21}$ . We refer to these equations as *resonance system*.

### C. Investigation of the resonance system

The resonance system can be studied analytically in some cases. Let  $\phi_2(0) - \phi_1(0) = (2n+1)\pi/2$ , where  $n$  is an integer. Then equations (89), (90) show that  $\phi_2(\tau) - \phi_1(\tau) = (2n+1)\pi/2$  for all  $\tau \geq 0$  and thus  $\sin(\phi_2(\tau) - \phi_1(\tau)) = \pm 1$ . As a result, we reduce (87), (88) to the linear system

$$2\omega \frac{dA_1}{d\tau} = -\bar{\epsilon}d_1\omega A_1 \pm b_{12}Q_2, \quad (91)$$

$$2\omega \frac{dA_2}{d\tau} = -\bar{\epsilon}d_2\omega A_2 \pm b_{21}Q_1. \quad (92)$$

If  $\bar{\epsilon} \gg 1$ , i.e., the self-limitation is stronger than the interaction, then solutions of this system are exponentially decreasing and we have stability. If  $\bar{\epsilon} \ll 1$ , then solutions of this system are exponentially increasing and we have instability under condition  $b_{21}b_{12} > 0$ , i.e.

$$R = \frac{dg_1(q)}{dq}(\bar{q}_1) \frac{dg_2(q)}{dq}(\bar{q}_2) < 0. \quad (93)$$

We see that if  $a_i^{(k)}, \tilde{b}_i^{(k)} > 0$  for all  $i$ , then  $R > 0$  and we have a stable dynamics ( $Q_i$  are exponentially decreasing).

This relation leads to the following biological conclusion. Instability occurs as a result of resonances only if prey-predator interactions are mixed with other kinds of interactions, which may perturb prey-predator system (even if these perturbations are small).

### IX. CONCLUSIONS

The Hamiltonian approach to food-webs presented here have revealed that large complex ecological foodwebs can exhibit different complicated dynamic phenomena: quasiperiodic oscillations, chaos, multistationarity and internal resonances. The hamiltonian methods also allows us to describe

how variable environment (for example, climate), weak self-limitation, and weak competition may affect large foodwebs. By averaging methods, we obtain that the typical dynamics of a system, where different interactions coexist, is as follows. There exist periodic or quasiperiodic oscillations. The periods and the forms of these oscillations slowly evolve in time. After a long time evolution, these periodic oscillations can be transformed to a chaotic chain of rare bursts. Mathematically, these bursts are connected with some special solutions like solitons and kinks in physics. In ecology these phenomenon of rare bursts or transition have been observed and discussed both theoretically and empirically [11, 26]. A slowly varying environment can also provoke a chaos, but in some cases it can repress bursts and stabilizes dynamics. So, the climate may sometimes increase ecological system stability and in other cases have the completely opposite effect by inducing chaos.

Note that, in large foodwebs, internal resonances can arise due to their topological structure. Such resonance effects can result in ecological catastrophes. In particular, it is possible that large ecological system can collapse without any explicit external cause as a result of an internal resonance between two weakly connected subsystems. It is shown that these effects can arise as a result of mixed interactions in the web (for example predator-prey plus some weak competition).

Finally, an asymptotic description of complex dynamical phenomena is possible for large food-webs. This description uses classical methods of hamiltonian mechanics and physics and the scale-free structure of these webs.

### X. ACKNOWLEDGEMENTS

The authors are grateful to anonymous Referees for useful comments and remarks. This second author was financially supported by Linköping University, Government of Russian Federation, Grant 074-U01 and by grant 16-01-00648 of Russian Fund of Basic Research. Also he was also supported in part by grant RO1 OD010936 (formerly RR07801) from the US NIH.

- 
- [1] R. Albert R. and A. L. Barabási, *Rev. Modern Physics*, **74**, 47 (2002).
  - [2] J. Bascompte, *Basic and Applied Ecology*, **8**, 485 (2007).
  - [3] J. Bascompte, J., P. Jordano, C. J. Melian, and J.M. Olesen, *Proceedings of the National Academy of Sciences*, **100**, 9383 (2003).
  - [4] J.A. Dunne, R.J. Williams, and N.D. Martinez, *Proceedings of the National Academy of Sciences* **99**, 12917 (2002).
  - [5] A.E. Krause, K.A. Frank, D.M. Mason, R. E. Ulanowicz, and W.W. Taylor, *Nature*, **426** 282 (2003).
  - [6] C. F. Dormann, J. Fruend, N. Bluthgen and B. Gruber, *The Open Ecology Journal* **2**, 7 (2009).
  - [7] J. Montoya, S. Pimm, and R. Sole, *Nature* **442**, 259 (2006).
  - [8] S.L. Pimm, *Nature*, **307**, 321 (1984).
  - [9] S. Allesina and M. Pascual, *Theor. Ecol* **1**, 55 (2008).
  - [10] R. May, *Nature(London)* **238**, 413 (1972).
  - [11] R. May, *Stability and complexity in model ecosystems* (Princeton Univ. Press, 1974).
  - [12] G. E. Hutchinson, *Americ. Naturalist*, **93**, 145 (1959).
  - [13] S. Allesina and Si Tang, *Nature*, **483**, 205 (2012).
  - [14] S. Allesina, *Nature*, **487**, 175, (2012).
  - [15] J. Hofbauer and K. Sugmund, *Evolutionary games and population dynamics*, (Cambridge University Press, Cambridge, 1988).
  - [16] M. Plank, *J. Math. Phys.* **36** (7), 3520 (1995).
  - [17] W. M. Oliva, *Publ. Mat.*, **58**, 421-452, (2014).
  - [18] J. Poschel, *Proceedings of Symposia in Pure Mathematics (AMS)* **69**, 707, (2001).
  - [19] V.I. Arnol'd, *Geometric methods in Theory of Ordinary Differential Equations*, ( 2nd ed. Springer, New York, 1988).
  - [20] C. Robinson, *Dynamical systems: stability, symbolic dynamics and chaos*, ( CRC Press, 1999).

- [21] T. Gross, L. Rudolf, S. Levin and U. Dieckmann, *Science*, **325**, 747 (2009).
- [22] T. Sari, Preprint RR-4374, Inria-00072214, (2002).
- [23] A. A. King and W. M. Schaffer, *J. Math. Biol.*, **39**, 439 (1999).
- [24] V. Kozlov, S. Vakulenko and U. Wennergren, New perspectives: stability and complex dynamics of food webs via Hamiltonian methods, arXiv:1510.00558
- [25] S. Gudmundson, A. Eklof, and U. Wennergren, *Proceedings of the Royal Society B*. **282**, (2015).
- [26] P. Kareiva and U. Wennergren, *Nature* **373**, 299 (1995).
- [27] D. O. Logofet, *Linear Algebra and its Applications*, **398**, 75 (2005).
- [28] M.E Gilpin, T. J. Case, Multiple domains of attraction in competition communities, *Nature*, **261**, 40, 1976.
- [29] G.B. Whitham, *Linear and Nonlinear Waves*, (John Wiley and Sons Inc., New-York London Sidney Toronto, 1974)
- [30] W. Horsthemke, R. Lefever, *Noise-Induced Transitions*(Springer, Berlin, Heidelberg, New-York, 2006).
- [31] Uyeda J. C., Thomas F. Hansen, Stevan J. Arnold, and Jason Pienaar, *PNAS*, **Vol. 108**, No. 8, 2011.