Stability and Oscillations in Spatially-extended Models of Population Interaction

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Abstract

Conditions for species coexistence in a simple patch-occupancy metapopulation model are derived. The model is described by a system of ordinary differential equations. The ecological stability of the community is interpreted in terms of conservation of species composition in the model. The limits for the stability are related to the boundness of the model solutions in phase space. Analytical results show that there are regions in the parameter space where the species coexistence can occur depending on characteristics of competing species interaction and structure of the links connecting isolated patches.

1 Introduction

This paper presents the investigation of oscillations and nonlinear dynamics of models of ecological systems with spatial heterogeneity. Understanding the abundance of natural populations is the central task confronting the quantitative ecology. Many conceptual and theoretical models of how predators influence lower levels have been developed to explain the observed structure of food webs [1]. Ecologists have hypothesized that regional recovery from large disturbance should occur more rapidly in species with widespread dispersal than in species with more limited dispersal [2]. Ecological theory predicts that any mechanisms that reduce isolation among patches with uniform distribution assist to evolution of organisms. Modeling results can prove that spatial variability in the abundance of species will change little over time organisms with restricted dispersal will become more uniformly distributed over time. Orbit structure of dynamical system is applied to stable structures definition in generalized models of population dynamics.

The application of non-linear dynamics analysis methods allows to gain model explanation of some effects observed in natural ecosystems. The orbit structure of a dynamical system is applied to spatio-temporal evolution of the model expressed in the from of ordinary differential equations. It is so-called Lagrange stability that serves as a formal analogy of ecological stability defined in terms of conservation of species number in biological community. The dynamics of coupled oscillators is proved to be relevant in the study of pattern generation of a biological system. Patterns of Hopf bifurcation started with Turing model have

been an active subject of research recent years [3]. Dynamics of nets of coupled oscillators is applied to definition of oscillations in spatially extended systems.

Global bifurcation phenomena associated with networks of identical oscillators are reviewed in [4]. As an application global bifurcation of phase locked oscillators is applied to migratory effects investigation in specially-discrete models of trophic chains.

2 Lagrange Stability and Method of its Definition

> "...It is precisely astronomy that showed us
> what general appearances of natural phenomena are".
> H. Pouncare. "Revue de Metaphysique et de Morale".

Conservation of the number of species in a biological community can be considered as a characteristic of its stability. The ecological stability is a concept which requires all of the species in the community to be preserved for a sufficiently long time, i.e. the population size of any species should not tend to zero or take close to zero values.

The concept of ecological stability has proven to be a formal analogue of Lagrange stability [5]. The ecological system can be regarded as stable, when model equations possess periodic solutions even if the equilibrium is unstable. Let us suppose that model equations has several equilibrium states. The concept of Lagrange stability is associated with the boundness of solutions in the phase space.

Let's suppose that dynamics of a biological community is described by the following system of ordinary differential equations:

$$\frac{dN_i}{dt} = F_i(N_i, \ldots, N_n), \qquad i = \overline{1, n} \tag{1}$$

with initial conditions $N_i(0) = N_i(0) - N_i(t)$ is the number of i-th population.

Two closed finite domains Ω_0^n and Ω^n are defined in phase space P^n. The formal expression for the region of ecostability is given by notation:

$$\forall N^0 \in \Omega_0^n \ \exists \Omega^n(\Omega_0^n) \subset Int P^n : \forall t > 0 \ N(t) \in \Omega_n$$

where

$$N^0 = \{N_1^0, \ldots, N_n^0\} \in \Omega_0^n,$$
$$N(t) = \{N_1(t), \ldots, N_n(t)\} \in \Omega^n$$

The method for Lagrange's stability investigation, based on the reduction of the initial problem to the problem concerning the stability of trivial solution of a certain subsystem of equations at permanent perturbations has been advanced by D. O. Logofet, Yu. M. Svirezhev [5]. By substitution $\xi_i = \ln(\frac{N_0}{N_i^0})$, $i = \overline{1, n}$ in (1) the original model is brought to the system.

$$\frac{d\xi_i}{dt} = \phi_i(\xi_1, \ldots, \xi_n; N_1^0, \ldots N_n^0), \ \ i = \overline{1, n}, \tag{2}$$

with initial conditions $\xi_1(0) = 0$. Further transformation is defined to bring the system of equations (1) to the form

$$\frac{d\xi_i}{dt} = \psi_i(\xi_1, \ldots, \xi_n; N_1^0, \ldots N_n^0) + B_i, \ \ i = \overline{1, n}, \tag{3}$$

where

$$\psi_i = \phi_i(\xi_1, \ldots, \xi_n; N_1^0, \ldots, N_n^0) - \phi_i(0, \ldots, 0; N_0^0, \ldots, N_n^0),$$

$$B_i = \phi(0, \ldots, 0; N_1^0, \ldots, N_n^0),$$

It is obvious that $\xi_i^* = 0$, $i = \overline{1,n}$ is the solution of the system $\frac{d\xi_i}{dt} = \phi_i$, $i = \overline{1,n}$ henceforth referred as the reduced system. The stability of the trivial solution $\xi_i^* = 0$, $i = \overline{1,n}$ under constant perturbation B_i defines the region in the space of parameters $\{N_1^0, \ldots, N_n^0\}$ for the region of ecostability. According to the Chetaev-Malkin theorem, the trivial solution $\xi_i^* = 0$, $i = \overline{1,n}$ is stable by Lyapunov, if the solution is asymptotically stable for the reduced system and B_i are sufficiently small. The last condition is vague, as there are no tools to estimate the smallness of B_i. A number of other results exist for the definition of stability of the trivial solution for reduced system under constant perturbations.

3   Trophic Chain as a Generalized Oscillator

The structure of a community with n species hierarchically connected with prey-predator relationship is called a trophic chain. The equation for the dynamics of an arbitrary population in the structure except the lowest and the upper ones must include the term for a biomass loss due predation. The equations of model of almost Volterra type model for trophic chain are described by the following system:

$$N_0' = Q - V_0(N_0)N_1, \qquad i = \overline{1,n}$$
$$N_i' = k_i V_{i-1}(N_{i-1})N_i - V_i(N_i)N_i - m_i N_i \tag{4}$$

where, the sign "$\prime$" is denotation for the first derivative by time i.e. variable t, variables N_i are used for biomasses or densities of interacting population, n is the length of the chain. The external resource inflow is described by N_0 on the lowest level of the structure. The speed Q of an external resource is assumed constant or it is reasonable to regard N_0 linearly dependent on the external energy input. The factors k_i are assumed to describe the part of energy gained with consumption by a single predator population which is transformed to its own biomass increase and m_i are mortality rates. A functional response, denoted by $V_i(x)$, defines the relationship between the numbers of prey attacked per predator at different prey densities.

Trophic chains present natural generalization to multidimensional case the original equations of Lotka-Volterra. The length of chain in ecological systems is usually 4 -- 5, though the existence of chains with length 7 was observed [1]. Tropic chains are rather well-studied objects in ecology. Several types of nonlinear functions for the functional response were proposed. We will outline the presentation of trophic chain in the form of a generalized oscillator [6].

Trophic chains naturally are ecosystem structures with hierarchically coupled "prey-predator" systems. By application of Lagrange stability investigation method the system (4) is transformed to the following:

$$\frac{d\xi_0}{dt} = \left[\frac{Q}{N_0^0 e^{\xi_0}} - \frac{Q}{N_0^0}\right] + N_1^0 \left[\omega_0(0, N_0^0) - \omega_0(\xi_0, N_0^0)e^{\xi_1}\right],$$
$$\frac{d\xi_0}{dt} = k_i N_{i-1}^0 \left[\omega_{i-1}(\xi_{i-1}, N_{i-1}^0)e^{\xi_{i-1}} - \omega_{i-1}(0, N_{i-1}^0)\right] + \tag{5}$$
$$+ N_{i-1}^0 \left[\omega_i(0, N_i^0) - \omega_i(\xi_i^0)e^{\xi_{i-1}}\right] + B_i,$$

Here $\xi_i = \ln(N_i/N_i^0)$, N_i^0-initial conditions of the system (4):

$$\omega_i(\xi_i, N_i) = \frac{V(N_i^0 e^{\xi_i})}{N_i^0 e^{\xi_i}},$$

$$B_0 = \frac{Q}{N_0^0} - \omega_0(0, N_0^0)N_1^0.$$

$$B_i = k_i \omega_{i-1}(0, N_{i-1}) - \omega_i(0, N_i^0) N_{i+1}^0 m_i.$$

The function $\omega_i(\xi_i, N_i)$ is called a specific trophic function further.

Let us denote $\omega_i(\xi_0, N_i)$ at $\xi_i = 0$ α_i^0 and derivatives of specific trophic function by $\alpha_i^{(e)}$, where i-is the order of derivative.

Hopf bifurcation for two spices describes the bifurcation of time-periodic solutions with parameter $\alpha = \omega'(0, N_1^0)$ where $\alpha = \partial\omega(\xi_1, N_1^0)/\partial\xi_1$ are evaluated at $\xi_i = 0$. For a multidimensional case we must require following conditions:

$$\frac{Q}{N_0^0} = -N_1^0 \alpha_0$$

$$\alpha_i^{(0)} \rightarrow \alpha_{i\,max}, \qquad |\alpha_i| > \epsilon, \epsilon > 0, i = \overline{1, n} \tag{6}$$

where $\alpha_{i\,max}$ is the value of a specific trophic function in the point of maximum, i.e. $w' = 0$.

The solutions of the whole model and the corresponding dynamics in the neighborhood of the saturation point for all species of the chain can be described as almost periodic with the number of basic frequencies $n/2$. The behavior of a system of coupled oscillators is classified by commensurability of the relationships among these frequencies. If the difference between two of them can become equal or close to some integer m, this number is called the order of resonance. Resonances up to the forth order are important in dynamics investigation. The case of even n requires special consideration.

Equation (2) describe predator's effect on lower trophic levels through direct consumption. The speed of external resource Q is assumed to be sufficient. In this model we can define the values of Q in term of parameters of trophic chains. The other restrictions for parameter values are defined from the condition of smallness on B_i. The explicit expressions are given in [6].

Forcing oscillations in an ecological system is restricted due the spatio-temporal distribution and delay in population increase in response to environmental condition improvement. A single population must possess the ability to increase biomass or density to respond excess resource availability. It is well-known that only species with small body size can demonstrate such feature. The interpretation of two phenomena is based on the application of dynamics of coupled oscillators. The first is the question of energy limitation and length of trophic chain. The amount of resource for the chains of the same length depends on features of species in it . Let suppose that the speed of external resource input is limited only by producers on the first level. After some accumulation of biomass the increase of fluctuations can cause additional production.

The variation of parameters can return the system to equilibrium, but increase in biomass during such process intensification can make worse the conditions of habitats. After dumping of oscillations the extinction of one of the species in the community is possible. Even it could be stable but it is the other structure with some different relationships.

As in general, when a system has come to a transient state no prediction of further transition to one of a few possible transient states is valid. The sensitivity points of a food chain can be defined as such structure is hierarchical and in a bounded system the compensation effect of spatial distribution on the stabilization is not taken into account.

4 Rings of coupled oscillators as models of spatially discrete communities with circular placement of habitats

Migration is one of the mechanisms recognized by ecologists as a stabilizing factor of community with spatial heterogeneity. The model of a trophic chain based on the assumption that effects of predators occur through direct consumption of prey. Trophic chains are considered as ecosystem structures with a "predator-prey" type of species interaction, dead biomass transfer not being taken into account.

The impact of migration on the stability of n communities with the same set of p species was studied in [7]. The equations of the system with components connected by migration flows are the following:

$$\frac{dN_i^k}{dt} = f_i^k[N_1^k, \ldots, N_p^k] + \sum_{s=1}^{n}(N_i^s m_i^{ks} - N_i^k m_i^{sk}),$$

$$i = \overline{1,p}, \; k,s = \overline{1,n} \tag{7}$$

where m_i^{ks} is an instant rate of the migration intensity of the i-th species on the route from s habitat to k-th. We will treat system (7) as a discrete model of a spatially heterogeneous community, where the trophic chains describe dynamics of components. The equations of joint community are interpreted as coupled oscillators. Coupled oscillators exhibit a great range of interesting phenomena and provide models for many situations in biology. We will describe global bifurcations of phase-locked and synchronous oscillations studied for coupled chemical oscillators by J. C. Alexander and G. Auchmuty [8].

Let $u_i^j(t)$ be the density of i-th population in j-th trophic chain.

If the speed of migration is linear the coupled system obeys

$$\frac{du_i^j}{dt} = d_{-1,i}u_i^{j-1} - d_{0,i}u_i^j + d_{1,i}u_i^{j+1} + f_i(u^j; \mu) \tag{8}$$

Here $1 \le i \le m$, $1 \le j \le N$ and $u_i^0 = u_i^N$, $u_i^1 = u_i^{N+1}$ for all i, where dynamics of components are equations of trophic chains and hence μ-is interpreted as parameter of bifurcation in (5). It depends on variation of specific trophic functions $\omega_i(\xi_i, N_i)$. Isolated chains can be called cells and the density of a population is associated with the concentration of the species in a chemical system.

In vector form (8) may be written

$$\frac{d}{dt} = \begin{bmatrix} u^1 \\ u^2 \\ u^3 \\ \ldots \\ u^N \end{bmatrix} =$$

$$= \begin{bmatrix} -D_0 & D_1 & 0 & \cdots & 0 & D_{-1} \\ D_{-1} & -D_0 & D_1 & \cdots & 0 & 0 \\ 0 & D_{-1} & -D_0 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ D_1 & 0 & 0 & \cdots & D_{-1} & -D_0 \end{bmatrix} \times$$

$$\times \begin{bmatrix} u^1 \\ u^2 \\ u^3 \\ \ldots \\ u^N \end{bmatrix} + \begin{bmatrix} f(u^1; \mu) \\ f(u^2; \mu) \\ f(u^3; \mu) \\ \ldots \\ f(u^N; \mu) \end{bmatrix} \tag{9}$$

Here each u_i is an m-vector and each D_k, $k = 0, \pm 1$ is a diagonal $m \times m$ matrix with entries d_{ki} on the diagonal (8) will be written as

$$\frac{d\mu}{dt} = D\nu + F(\nu; \mu) \tag{10}$$

where μ is a vector with mN components and D is the $mN \times mN$ matrix in (9).

Equations (8) do not require the couplings forward and backward to be equal. if they are, then

$$D_1 = D_{-1}$$

One often assumes that there is no change in total concentration of the i-th species solely due to the transport mechanism. this implies

$$D_0 = D_1 + D_{-1}$$

When (10) holds, then a steady state of the coupled system (8) is

$$\nu_\mu = (u_\mu, u_\mu, \ldots, u_\mu)^T.$$

In general, if there is a steady state for (8) which has the same concentration, u_μ in every place, then u_μ must obey

$$(D_0 - D_1 - D_{-1})u = f(u; \mu)$$

and thus the coupling will change the steady state in each habitat whenever (10) does not hold. Oscillators in (8) are assumed identical and functions f are written without indices.

Suppose the system (8) has a periodic solution of the form

$$u_i(t) = p(t) \tag{11}$$

$$u_j(t) = p(t - z_j T), \qquad 2 \le j \le N$$

Here $p(t)$ is a non-trivial, vector-valued periodic function of least period $T > 0$. Such a solution is called a phase-locked solution of (8). Essentially the oscillation in each cell of ring is described by the function p. Adjacent cells, however, may be out of phase by the phase difference $z_j = \chi_{j+1} - \chi_1$, and we assume $\chi_0 = 0$. Phase-locked oscillates occur when all the oscillators are in phase.

Let us consider the equation of an oscillators for a pair of predator-prey, obtained from (5) when $n = 2$

$$\xi = -y_0 w'(0, x_0)\xi - y_0 w(0, x_0)\eta - y_0 \mu \xi \eta^2 \tag{12}$$

$$\eta = k x_0 [w''(0, x_0) + w(0, x_0)]\xi$$

where ξ, η are densities of prey and predator in transformed system, x_0, y_0 are initial values of population sizes. The solution $\xi^* = \eta^* = 0$ is asymptotically stable under condition $\omega'(0, x_0) > 0$, $\omega'(0, x_0) = d\omega(\xi, x_0)/d\xi$ evaluated $\xi = 0$.

Let us denote $\mu = \omega'(0, x - 0)$. In dimensionless variables defined by division on

$$a = \sqrt{k x_0 [w'_0(0, x_0) + \omega(0, x_0)] y_0 \omega(0, x_0)}$$

the system (12) can be brought to a Van der Pol oscillator, which in variables u_i is written as

$$\frac{d}{dt} = \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} u_2 & 0 & 0 \\ -u_1 & -\mu(u_1^2 - 1) & u_2 \end{bmatrix} \tag{13}$$

where $u_1 = \eta$, $u_2 = \xi$. The limits for variation of parameter μ are given by the inequality $|\omega'(0, x_0)| < \omega(0, x_0)$. We will consider a coupled ring of $n = 4M$ van der Pol oscillators with

$$D_1 = D_{-1} = \begin{bmatrix} d_1 & 0 \\ 0 & d_2 \end{bmatrix} \qquad d_2 \ge 0, d_1 \ge 0, D_0 = 2D_1.$$

Suppose that $0 \le d_1 < 0.5$, $0 \le \chi < 1$.

By applying the theorem of phase locked solutions bifurcation of $n = 4M$ Van der Pol oscillators we will obtain, that there is a branch of solutions of form (13) bifurcating from $(0, \mu_0, V_0)$ with $\mu_0 = 2(d_1 + d_2)$, $V_0 = \sqrt{1 - 4d_1^2}$.

The conditions that required by global bifurcation theorem for phase-locked solutions are straight-forward to verify for particular example. But the question of which branches bifurcate first and which ones are stable depends on the details of coupling and dynamics of isolated system. To study a system of trophic chains it is necessary to require limit cycle bifurcation of component.

5 Ecological interpretation of some results.

In many ecological situations the assumption of being well-mixed does not hold and a spatial model with local interactions is more appropriate and can result in predictions that differ from well-mixed case. The models of this type do not include explicitly distances between sites, no change of population on migration path resulting from mortality rate change is taken into account as well. The united system of trophic chains is more stable if the frequencies range is less than in the point case. The synchronization arising between nearest neighbors in the cycle of coupled oscillators can provide explanation for stability mechanism. The increase of emigration in natural communities rate often causes increasing rate of death among migrants. Such effects are not taken into account in the model under investigation.

Migration either of diffusion type or in the form of imposed flow can bring to synchronous oscillations of species in case of a closed system. The impact of conservative migration, i.e. without loss of species on the route of migration, is equal to decrease of species productivity.

Migration cannot stabilize the unstable prey-predator system. However if the intensities of species migration are sufficiently high, then all cells composing the network can be regarded as one cell. The oscillations become asynchronous when either prey or predator move to more dense populations of their kind.

The increase of the migration intensity has the qualitative impact similar with impact from change of predation intensity.

6 Conclusion

The study of nonlinear phenomena has applied motivation in providing the concepts for some generalizations of ecological models. To obtain the models based on more realistic hypotheses about natural system behavior it is possible to lean upon well-known mathematical concepts. A trophic chain with nonlinear functions describing prey-predator interaction is one of the examples of such generalizations. The application of the ecological stability concept allows gaining model explanations of some observation and effects that did not have interpretation in the frame of existing mathematical theory. Models of spatially heterogeneous system can be interpreted by net of trophic chains, interconnected by migration flows. Oscillations in a joint system are applied to ecosystem dynamics investigations.

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Կենսաբանական համակեցությունների մոդելների կայունությունը անհամասեռ միջավայրում

Ն. Ա. Աջաբյան

Ամփոփում

Առտածված են պայմաններ ոչ համասեռ միջավայրում պարզ ընդհանրացված կենսահամնրության տեսակների գոյատևման համար։ Ֆազային տարածությունում մոդելի լուծումների սահմանափակության պայմաններով են արտահայտվում էկոլոգիական կայունության սահմանները։