Stochastic sensitivity technique in a persistence analysis of randomly forced population systems with multiple trophic levels

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A B S T R A C T

Motivated by important ecological applications we study how noise can reduce a number of trophic levels in hierarchically related multidimensional population systems. A nonlinear model with three trophic levels under the influence of external stochastic forcing is considered as a basic conceptual example. We analyze a probabilistic mechanism of noise-induced extinction of separate populations in this "prey-predator-top predator" system. We propose a new general mathematical approach for the estimation of the proximity of equilibrium regimes of this stochastic model to hazardous borders where abrupt changes in dynamics of ecological systems can occur. Our method is based on the stochastic sensitivity function technique and visualization method of confidence domains. Constructive abilities of this mathematical approach are demonstrated in the analysis of different scenario of noise-induced reducing of the number of trophic levels.

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1. Introduction

Currently, in the ecology, one can observe a distinct trend of the transition from the study of individual isolated communities to the study of highly organized hierarchically related population systems [10]. It is well-known that reducing the number of trophic levels, or removing predator species, implies a biodiversity loss, and as a consequence, abrupt shifts in ecosystem-level processes [15,32,33,35]. To understand the internal mechanisms of such shifts observed in the real nature, it is necessary to take into account the relationships between interacting populations, the interspecies and age diversity, multi-level food chains, etc. In such systems, often even small quantitative changes in one hierarchical level can cause radical changes in the subsystems located on other levels of hierarchy. The mathematical description of such complex ecosystems leads to the necessity to develop methods for analyzing nonlinear dynamic models of high dimension [11,24]. A transition to multi-dimensional models essentially complicates this analysis. Indeed, even in three-dimensional models, along with well-studied equilibria and periodic regimes, quasi-periodic and chaotic dynamics can be observed [12,14,21].

Now, in the study of ecological systems, it is generally accepted to take into account the impact of unavoidable random pertur-

bations [2,5,13,25,26]. In nonlinear systems, even small noise can cause unexpected stochastic phenomena: noise-induced transitions [6,23,30], stochastic resonance [17,28], noise-induced chaos [9,18]. In models of interacting populations, random disturbances can transform system from persistence to extinction [1,3,4,22,29,31]. Until now, a direct numerical simulation of random trajectories is a main tool in the study of stochastic effects in population systems. In parametric analysis, this method is extremely time-consuming. In the investigations of stochastic nonlinear dynamics, analytical techniques based on the direct use of Fokker–Planck–Kolmogorov equation are limited mainly by one- or two-dimensional systems. In these circumstances, the development of constructive approximation methods in stochastic analysis of probabilistic phenomena in the multidimensional nonlinear population models attracts a common interest. In present paper, we use a new approach based on the stochastic sensitivity functions technique and confidence domains method [7,8]. A novelty of this study is connected with the extension of the stochastic sensitivity theory and confidence domains method to the multidimensional case. We demonstrate the universality of this new general approach in the probabilistic analysis of population systems with multiple trophic levels.

In systems of interacting populations, a deterministic persistence analysis is usually reduced to the study of attractors of corresponding dynamic models. In this analysis, Lyapunov exponents of attractors are the defining characteristics. But in the study of the influence of inevitable random disturbances, it is not sufficient to consider these exponents only. In the analysis of the persistence of stochastic population models, one should take into account three

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additional factors. First, an important thing is a type of noises, namely, what parameters and equations are forced, and what are intensities of these noises. The second factor is a stochastic sensitivity of attractors. Along with the first factor, the stochastic sensitivity defines a dispersion of random states of the forced system around the deterministic attractor. The third factor is a distance between attractor and hazardous borders beyond which the system dynamics abruptly changes, for example, some of the trophic levels become extinct. Here, from ecological point of view, one of the most important questions is how noise can reduce a number of trophic levels.

Undoubtedly, a mathematical analysis of the interaction of these three factors for many-dimensional population models describing multiple trophic levels is a challenging problem of the modern stochastic dynamics. In present paper, we focus on this problem for the case of the many-dimensional stochastic systems modeling the dynamics of populations in equilibrium modes. As a conceptual example, we consider a three-dimensional food chain model of the interacting prey, predator and top predator [36,37,40].

In Section 2, we give a brief review of dynamic regimes of this system in the deterministic case. A diversity of equilibrium modes is studied in dependence of the prey rate parameter.

In Section 3, it is shown how to study a stochastic sensitivity of equilibria in many-dimensional population models analytically. A simple geometrical description of the random states dispersion around the equilibrium is given in a form of the confidence domains (intervals, ellipses, ellipsoids).

An application of this mathematical theory of the stochastic sensitivity to the constructive analysis of different scenaria of the noise-induced extinction in systems with different number of trophic levels is given in Section 4.

2. Deterministic model

Consider the three-species food chain dynamic model [36–39]

$$
\begin{aligned}
\dot{x} &= ax - bx^2 - \frac{w_0 xy}{x + d_0}, \\
\dot{y} &= -cy + \frac{w_1 xy}{x + d_1} - \frac{w_2 yz}{y + d_2}, \\
\dot{z} &= dz^2 - \frac{w_3 z^2}{y + d_3},
\end{aligned}
\tag{1}
$$

where x, y, and z represent the population densities of prey, predator and top predator respectively (for example, rodent-snake-peacock). All parameters are positive, and the functional responses of Holling-type II with parameters w_i, d_i ($i = 0, 1, 2, 3$) are used. In the first equation, the parameter a stands for the prey intrinsic growth rate, and b measures the competition of preys. In the second equation, the parameter c is a mortality of the predator y. In the third equation, the parameter d describes the growth rate of z in the assumption that the densities of males and females of top predator are equal.

This system has six equilibria:

$M_0(0, 0, 0)$,
$M_1\left(\frac{a}{b}, 0, 0\right)$,
$M_2\left(\frac{cd_1}{w_1 - c}, \frac{1}{w_0}\left(ad_0 + (a - bd_0)\frac{cd_1}{w_1 - c} - b\left(\frac{cd_1}{w_1 - c}\right)^2\right), 0\right)$
$M_{3,4}(\bar{x}_{3,4}, \bar{y}_{3,4}, \bar{z}_{3,4})$,
$M_5\left(0, \frac{w_3}{d} - d_3, -\frac{c}{w_2}\left(\frac{w_3}{d} - d_3 + d_2\right)\right)$.
Here,
$\bar{x}_{3,4} = \frac{a - bd_0}{2b} \pm \frac{1}{2b}\sqrt{(bd_0 + a)^2 - 4b\left(\frac{w_0 w_3}{d} - w_0 d_3\right)}$,
$\bar{y}_{3,4} = \frac{w_3}{d} - d_3$,
$\bar{z}_{3,4} = \left(-c + \frac{w_1 \bar{x}_{3,4}}{\bar{x}_{3,4} + d_1}\right)\frac{\bar{y}_{3,4} + d_2}{w_2}$.

a is a bifurcation parameter	$b = 0.06$	$w_0 = 1$	$d_0 = 10$
$c = 1$	$w_1 = 2$	$d_1 = 10$	$w_2 = 0.405$	$d_2 = 10$
$d = 0.038$	$w_3 = 1$	$d_3 = 20$	

Table 2
Eigenvalues of Jacobi matrices of equilibria.

Equilibrium	λ_1	λ_2	λ_3
M_0	a	-1	0
M_1	$-a$	$\frac{a - 0.6}{a + 0.6}$	0
M_2 $0.6 < a$	$0.25a - 0.45 \pm 0.5\sqrt{0.25a^2 - 1.1a - 0.39}$		0
M_3 $0.9158 < a < 1.2966$	$-$	$-$	$-$

Following [27], we fix all parameters except the control parameter a (see the Table 1).

For this set of parameters, points M_4 and M_5 do not belong to the first octant. So, it what follows, we consider only four equilibria:

$$
M_0(0, 0, 0), \quad M_1\left(\frac{a}{0.06}, 0, 0\right), \quad M_2(10, 20a - 12, 0),
$$
$$
M_3(\bar{x}_3, \bar{y}_3, \bar{z}_3).
\tag{2}
$$

Here,

$$
\bar{x}_3 = \frac{a}{0.12} - 5 + \frac{1}{0.12}\sqrt{(a + 0.6)^2 - 1.52}, \quad \bar{y}_3 = 6.31579,
$$

$$
\bar{z}_3 = -40.3 + 80.6\frac{\bar{x}_3}{\bar{x}_3 + 10}.
$$

Note that the equilibrium M_2 has positive coordinates for $a > a_1 = 0.6$, and the equilibrium M_3 has positive coordinates for $a > a_2 = 0.9158$. The equilibrium M_3 loses its stability at the Andronov-Hopf bifurcation point $a_3 = 1.2966$.

In the Table 2, eigenvalues of the Jacobi matrices of system (1) for all these equilibria are shown. In the range $a_2 < a < a_3$, all eigenvalues of the Jacobi matrix of the equilibrium M_3 have negative real parts.

So, in system (1), in dependence of the rate a, three dynamic regimes can be observed.

1) For $0 < a < a_1$, the system (1) has two equilibria: M_0 with the basin of attraction $B_0 = \{(x, y, z)|x = 0, y \geq 0, z \geq 0\}$; M_1 with $B_1 = \{(x, y, z)|x > 0, y \geq 0, z \geq 0\}$.
2) For $a_1 < a < a_2$, the system possesses three equilibria: M_0 with the same basin B_0; M_1 with new basin $B_1 = \{(x, y, z)|x > 0, y = 0, z \geq 0\}$; M_2 with the basin $B_2 = \{(x, y, z)|x > 0, y > 0, z \geq 0\}$;
3) For $a_2 < a < a_3$, there are four equilibria: M_0 with the same basin of attraction B_0; M_1 with $B_1 = \{(x, y, z)|x > 0, y = 0, z \geq 0\}$; M_2 with the new basin $B_2 = \{(x, y, z)|x > 0, y > 0, z = 0\}$, and the non-singular equilibrium M_3 with the basin of attraction $B_3 = \{(x, y, z)|x > 0, y > 0, z > 0\}$.

If the initial state of system (1) is non-singular, i.e. belongs to the set $\{(x, y, z)|x > 0, y > 0, z > 0\}$, then the trajectory tends to M_1, or to M_2, or to M_3 depending on the parameter a. Coordinates of attracting points as a function of the parameter a are plotted in Fig. 1. Here, one can see that in the first zone $0 < a < a_1$, the point M_1 is attracting, so predators' populations y and z are extinct, and only the prey x thrives. Note that the increasing a implies a natural growth of the equilibrium values of prey.

In the second zone $a_1 < a < a_2$, trajectories tend to M_2 that corresponds to the extinction of the predator z and coexistence of