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How environmental noise can contract and destroy a persistence zone in population models with Allee effect

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ABSTRACT

A problem of the analysis of the noise-induced extinction in population models with Allee effect is considered. To clarify mechanisms of the extinction, we suggest a new technique combining an analysis of the geometry of attractors and their stochastic sensitivity. For the conceptual one-dimensional discrete Ricker-type model, on the base of the bifurcation analysis, deterministic persistence zones are constructed in the space of initial states and biological parameters. It is shown that the random environmental noise can contract, and even destroy these persistence zones. A parametric analysis of the probabilistic mechanism of the noise-induced extinction in regular and chaotic zones is carried out with the help of the unified approach based on the sensitivity functions technique and confidence domains method.

1. Introduction

A clarification of underlying mechanisms of the diversity in the population systems dynamics is a challenging problem of the modern theoretical biology. Even small variations in the population size and biological parameters can initiate essential changes in dynamic regimes and cause qualitative shifts and ecological catastrophes (Scheffer et al., 2001; Rietkerk et al., 2004). In the population dynamics, a study of regimes of the stable existence (persistence) and extinction is a problem of a high importance. A presence of these contrary regimes in population systems is often attributed to the Allee effect (Allee, 1931; Dennis, 1989; Stephens et al., 1999; Schreiber, 2003).

In general, in systems with Allee effect, there is a threshold level of the population size (or density) below which the population goes to the extinction. This threshold level is a border separating persistence and extinction zones. Possible biological mechanisms that cause Allee effects are quite diverse. A detailed review of these mechanisms can be found in Courchamp et al. (2008) and Kramer et al. (2009).

Mathematically, the Allee effect means that the population system is at least bistable, when along with a nontrivial attractor respective to the regime of the persistence, there is a trivial attractor corresponding to the extinction. A separatrix between basins of attraction of these attractors plays a role of the Allee threshold. At present, in the population dynamics, a wide range of continuous and discrete-time mathematical models with the Allee effect is known. For the analysis of such models, a modern mathematical theory of local and global bifurcations is actively used (see, e.g. Kuznetsov and Rinaldi, 1996; Bazykin, 1998; van Voorn et al., 2007; Cai et al., 2013). A new direction is formed by investigations of reaction–diffusion and delayed population models with Allee effect (see, e.g. Méndez et al., 2011; Biswas et al., 2015).

Discrete-time mathematical models with Allee effect were studied by many authors (Schreiber, 2003; Li et al., 2007; Duarte et al., 2012; Assas et al., 2015; Elaydi and Sacker, 2010). One of the attractive features of discrete models is the fact that these models, even in one-dimensional case, exhibit both regular and chaotic behavior. Here, Ricker model is a classic example (Ricker, 1954). The initial Ricker model has no Allee effect, but there is a simple modification with embedded Allee effect (Elaydi and Sacker, 2010; Avilés, 1999). Using this conceptual one-dimensional population model, one can study the main regimes of the persistence and extinction. In this paper, to study an impact of noise, we use this Ricker-type model with Allee effect as a deterministic skeleton.

It is well known that the random noise in population systems can drastically change its dynamics (Scheffer et al., 2001; May, 1973; Chesson, 1991; Lande, 1993; Lande et al., 2003; Blasius et al., 2007; Allen and van den Driessche, 2013). In particular, random disturbances in systems with Allee effect can lead to the noise-induced extinction. An interplay of the stochasticity and Allee effect in the analysis of the population persistence was

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studied for various dynamic models (Lande, 1998; Allen et al., 2005; Dennis, 2002), including Ricker-type models (Roth and Schreiber, 2014). The recent paper (Dennis et al., 2015) provides an excellent overview of the impact of Allee effects in stochastic populations, and probabilistic methods of its analysis on examples of continuous-time one-dimensional systems. A constructive method of the analysis of the noise-induced extinction for two-dimensional systems with Allee effect has been proposed in Bashkirtseva and Ryashko (2011).

In this paper, we study Ricker-type discrete model in the corporation of Allee effect and random environmental noise. A resilience of the population system is characterized by a size of the persistence zone. Traditionally, the persistence zone is considered as a set of initial values of the population size. This set is defined as a basin of attraction of the nontrivial attractor corresponding to the stable existence of the population.

In one-dimensional continuous-time systems, where such nontrivial attractor is a stable equilibrium, the Allee threshold specifies only the lower border of the persistence zone. In the one-dimensional unimodal discrete population models, along with the traditionally discussed lower border, an upper border of the persistence zone also exists. Thus, the Allee effect in such systems restricts the persistence zone by some finite interval. This interval is the area of the sustainable existence of the population. A strengthening of Allee effect implies a decrease of the length of this interval, and hence the reduction of the persistence zone. As a rule, such study of the Allee effect is realized for the variation of the initial data only, under fixed values of other biological parameters. However, to understand the possible qualitative changes in the behavior of the population system, one has to take into account not only the changes of initial states, but also a variation of other biological parameters of the population system. Indeed, an important consequence of Allee effect is an appearance of restrictions on other population system parameters. These restrictions define additional borders of the persistence zone. An exit beyond these borders also leads to the extinction of the population. Thus, a complete mathematical description of the persistence domain should include the limited areas in the extended space of the variables (x_0, μ), with both initial states x_0, and biological parameters μ of the system.

In Section 2, on the base of the conceptual deterministic Ricker-type model with Allee effect, a description of persistence zones in the extended space of the variables (x_0, μ) is given. Note that these zones cover both regular (equilibrium, periodic) and chaotic dynamics regimes. To find borders of persistence zones, we suggest and apply analytical methods. It is also demonstrated how an amplifying Allee effect changes these zones.

In Section 3, an influence of random perturbations on the persistence zones of the stochastic Ricker model is studied. It is shown that under the increasing noise, these zones are compressed, and can disappear when the noise intensity exceeds some threshold value. Here, we also discuss changes in the internal dynamics of stochastic flows accompanying by transitions from order to chaos, and from chaos to order.

In the parametric analysis of noise-induced phenomena in the population dynamics, the elaboration of constructive analytical methods is a problem of a high importance. Full mathematical description of the stochastic dynamics is given by probability density functions. In continuous-time systems, these functions are solutions of the Fokker–Planck–Kolmogorov equation (Gardiner, 1983; Horsthemke and Lefever, 1984). In one-dimensional case, the stationary Fokker–Planck–Kolmogorov equations have analytical solutions. In Dennis et al. (2015), it is shown how probability density functions found analytically can be effectively used for the constructive parametric analysis of the phenomena of the noise-induced extinction in one-dimensional population models. For discrete-time systems, the probability density functions

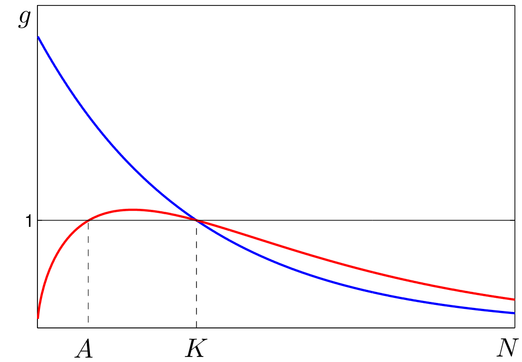

Fig. 1. Intrinsic growth rate function $g(N)$ without Allee effect (blue) and with Allee effect (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

are governed by Frobenius–Perron equations (Lasota and Mackey, 1994; Inoue et al., 2001). An analytical solution of these functional equations is difficult even for the one-dimensional case. In these circumstances, for the description of probabilistic distributions around deterministic attractors, a constructive method of the analytical approximation based on the stochastic sensitivity functions technique (Bashkirtseva et al., 2010; Bashkirtseva and Ryashko, 2013, 2015) can be used.

In Section 4, it is shown how the stochastic sensitivity functions technique and method of confidence domains can be applied to the parametric analysis of the noise-induced extinction for the Ricker-type model with Allee effect in zones of equilibrium, periodic, and chaotic regimes.

2. Analysis of persistence zones in the deterministic population model

Consider a one-dimensional discrete population model

$$N_{t+1} = g(N_t)N_t, \tag{1}$$

where N is a size of the population, $g(N)$ is a per capita intrinsic growth rate function. The function $g(N)$ defines the population dynamics. For $g > 1$, the population grows, for $g < 1$ the population decreases. The equation $g(N) = 1$ defines the nontrivial equilibria of Eq. (1).

In this paper, we consider Ricker-type functions

$$g(N) = N^{\alpha-1}\exp\left[r\left(1 - \frac{N}{K}\right)\right], \tag{2}$$

where r is an intrinsic growth rate, K is a carrying capacity, $\alpha \geq 1$ is a cooperation parameter (Avilés, 1999). The system (1), (2) has a nontrivial equilibrium $N = K$. In the classical Ricker model, the parameter $\alpha = 1$. A variation of the parameter α essentially changes a form of the function $g(N)$ (see Fig. 1), and consequently, the dynamics of system (1). This class of Ricker-type population models is quite representative for the study of changes of persistence and extinction zones in systems with Allee effect. In system (1), (2), the coefficient α is a tuning parameter that regulates a strength of the Allee effect.

For $\alpha = 1$ (see $g(N)$ shown by blue in Fig. 1), the population grows in the zone $0 < N < K$, and decreases for $N > K$. For $\alpha > 1$, one more equilibrium, $N = A$ appears, and the zone of the growth is reduced to $0 < A < N < K$. A typical plot of the function $g(N)$ is shown in Fig. 1 by red for $\alpha = 1.6$. If the initial size of the population $N_0 < A$, then the population is extinct. This phenomenon is called Allee effect, and A is an Allee threshold. So, the Ricker system with $\alpha = 1$ has no Allee effect, and for $\alpha > 1$, this is the system with Allee effect.