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Spatiotemporal complexity of patchy invasion in a predator-prey system with the Allee effect.

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Abstract

Invasion of an exotic species initiated by its local introduction is considered subject to predator–prey interactions and the Allee effect when the prey growth becomes negative for small values of the prey density. Mathematically, the system dynamics is described by two nonlinear diffusion–reaction equations in two spatial dimensions. Regimes of invasion are studied by means of extensive numerical simulations. We show that, in this system, along with well-known scenarios of species spread via propagation of continuous population fronts, there exists an essentially different invasion regime which we call a patchy invasion. In this regime, the species spreads over space via irregular motion and interaction of separate population patches without formation of any continuous front, the population density between the patches being nearly zero. We show that this type of the system dynamics corresponds to spatiotemporal chaos and calculate the dominant Lyapunov exponent. We then show that, surprisingly, in the regime of patchy invasion the spatially average prey density appears to be below the survival threshold. We also show that a variation of parameters can destroy this regime and either restore the usual invasion scenario via propagation of continuous fronts or brings the species to extinction; thus, the patchy spread can be qualified as the invasion at the edge of extinction. Finally, we discuss the implications of this phenomenon for invasive species management and control.

Keywords: Biological invasion; Predator–prey system; Patchy spread; Allee effect; Spatiotemporal chaos

1. Introduction

Understanding of patterns and mechanisms of species spatial dispersal is an issue of significant current interest in conservation biology and ecology. It arises from many ecological applications; in particular, it plays a major role in connection to biological invasion and epidemic spread (Drake et al., 1989; Hengeveld, 1989; Murray, 1989; Shigesada and Kawasaki, 1997). A variety of theoretical approaches has been developed and a considerable progress has been made during the last decade. However, many aspects related to species dispersal have never been properly addressed yet.

Regarding the spread of exotic species, a problem of high practical importance is how to create an effective program of management and control of invasive species (Andow et al., 1990; Sakai et al., 2001; Fagan et al., 2002). Such a program must include both good understanding of the mechanisms underlying species spread and an optimal monitoring strategy. In its turn, a relevant strategy is likely to be different for different species (e.g. depending on whether a given species is detectable with satellite-based remote sensing imagery data) and should be also based on the knowledge of the pattern of spread. For instance, in many cases invasion

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of exotic species takes place via propagation of a population front separating the areas where given species is absent, i.e. in front of the front, from the areas where it is present in considerable densities, i.e. in the wake of the front. In this case, under somewhat idealized assumption that the invasion is going isotropically so that its rate does not depend on the direction of spread, the advance of invading species can be monitored using a relatively small number of on-site observers or sampling stations situated along a certain line coming out of the place of original species introduction.

However, reality is often much more complicated. As a result of environmental heterogeneity the rates of invasion can be significantly different in different directions (Shigesada and Kawasaki, 1997). Also, due to the impact of both environmental and biological factors, the pattern of spread can be more complicated than simple population front. There is growing evidence (Davis et al., 1998; Kolb et al., 2004; Swope et al., 2004) that, in some cases, invasion of exotic species takes place through dynamics of separate population patches not preceded by propagation of a continuous population front, see also, Shigesada and Kawasaki (1997), Lewis (2000); and Lewis and Pacala (2000) and the references therein. Below we will call that pattern of spread a patchy invasion. Obviously, in the case of patchy invasion an adequate monitoring strategy should be more complicated and likely include many more observers.

Thus, distinguishing between the situations when species spread takes place via propagation of a continuous population front and when it happens via patchy invasion, as well as identification of factors enhancing or hampering patchy invasion are problems of significant practical and theoretical importance. The origin of patchy invasion is often seen either in environmental heterogeneity (cf. Murray, 1989) or in the impact of stochastic factors (Lewis, 2000; Lewis and Pacala, 2000). Indeed, the whole dynamics of ecological communities appears as a result of interplay between numerous deterministic and stochastic factors. However, the importance of stochasticity should not be overestimated. Sometimes stochastic models and deterministic models lead to qualitatively similar spatiotemporal patterns, although reached through different mechanisms (cf. Kawasaki et al., 1997; Mimura et al., 2000). For a rather general model of marine ecosystem, Malchow et al. (2002) showed that there exists a critical level of noise so that for undercritical noise the system is more driven by deterministic factors. Even in the supercritical case, when noise can change the system dynamics considerably, it was shown that intrinsic spatial scales of the system are still controlled by deterministic mechanisms (Malchow et al., 2004).

Recently, it was shown by Petrovskii et al. (2002a,b) that patchy invasion can arise in a fully deterministic predator–prey system as a result of the Allee effect, i.e. of a threshold phenomenon when the population growth rate becomes negative for low population density (Allee, 1938; Dennis, 1989; Courchamp et al., 1999). Deterministic patchy invasion was shown to correspond to the invasion at the edge of extinction (Petrovskii and Venturino, 2004; Petrovskii et al., 2005c) so that a small finite variation of the system parameters either restores usual population front propagation scenario or brings the species to extinction. Moreover, it was shown that the system dimensionality is a crucial point and the patchy invasion in two spatial dimensions corresponds to species extinction in the corresponding 1D system (Petrovskii and Venturino, 2004; Petrovskii et al., 2005c).

The above papers, however, left many questions open. In this paper, we make a detailed study of the deterministic patchy invasion in a predator–prey system where the prey growth is damped by the Allee effect. In particular, the following issues are addressed: (i) what is the succession of invasion regimes in response to variation of an ecologically meaningful controlling parameter and how the invasion speed depends on the type of spread, (ii) what is the degree of spatiotemporal complexity corresponding to the regime of patchy spread and (iii) what are the ecological implications of the patchy invasion. We show that, although the invasion speed is much lower in the regime of patchy spread than it is in the usual regime(s) of continuous front propagation, the patchy spread provides a scenario of species invasion below the survival threshold. Also, we show that deterministic patchy invasion corresponds to spatiotemporal chaos and estimate the value of the dominant Lyapunov exponent.

2. Mathematical model

We consider 2D dynamics of a predator–prey system described by two partial differential equations of diffusion–reaction type (Nisbet and Gurney, 1982; Murray, 1989; Holmes et al., 1994; Shigesada and Kawasaki, 1997; Medvinsky et al., 2002):

$$\frac{\partial P}{\partial T} = D_1\left(\frac{\partial^2 P}{\partial X^2} + \frac{\partial^2 P}{\partial Y^2}\right) + F(P) - f(P)Z, \quad (1)$$

$$\frac{\partial Z}{\partial T} = D_2\left(\frac{\partial^2 Z}{\partial X^2} + \frac{\partial^2 Z}{\partial Y^2}\right) + kf(P)Z - MZ, \quad (2)$$

Here $P = P(X, Y, T)$ and $Z = Z(X, Y, T)$ are densities of prey and predator, respectively, at moment T and position (X, Y). The function $F(P)$ stands for the intrinsic prey growth, $f(P)$ is the predator trophic