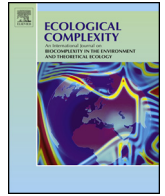




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Original Research Article

Invasive competition with Fokker-Planck diffusion and noise

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ABSTRACT

Species competition in a fluctuating environment is often modelled with stochastic reaction-diffusion equations. In most cases the movement of individuals is described as Fickian diffusion. However, in heterogeneous environments this is not the first choice. Recently, it has been shown that Fokker-Planck diffusion describes the movement of species in a more realistic way. Fickian diffusion always leads to spatially uniform stationary distributions whereas the Fokker-Planck diffusion generates nonuniform solutions according to the heterogeneity of the environment and the corresponding spatial variation of diffusion. Species accumulate in regions of low diffusivity and tend to lower their densities in areas of high diffusivity. In the present paper, the impact of Fokker-Planck diffusion is studied with particular consideration of changing spatio-temporal population patterns during the competitive invasion of a spatially heterogeneous, populated habitat. The standard Lotka-Volterra competition model is applied to describe the resident-invader interaction. The resident is assumed to be adapted to the heterogeneous living conditions, i.e., its motion is modelled as space-dependent Fokker-Planck diffusion. The invader's diffusion is taken as neutral Fickian. Furthermore, it is shown that multiplicative environmental noise can either foster or hinder the invasion.

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1. Introduction

Biological invasions are a growing threat to biodiversity around the world. The spread of alien species can lead not only to the extinction of indigenous species, but also cause considerable economic damage in eco- and agro-ecosystems. These are, contrary to water-air-soil contamination, unfortunately mostly irreparable, since the invasive species constantly reproduce and often have no natural enemies. Well-known examples are the invasion of rabbits (Perrings et al., 2000) and cane toads (Urban et al., 2008) in Australia or the invasion of a Pacific oyster in the Dutch and German Wadden Sea (Diederich et al., 2005). Many of these invasions are caused by anthropogenic effects such as globalized traffic and trade or climate change. On the other hand it might be of interest to reintroduce a species into an ecosystem where it has been eradicated before.

Modelling the invasion process can help to identify mechanisms which foster or hinder successful invasions. Most ecological models on this subject describe species densities on a population

level. Individual movement is often described as diffusive process. In a heterogeneous environment the mathematical formalism which describes this process in a realistic way depends strongly on the respective species abilities.

In a recent publication (Bengfort et al., 2016), different formulations for diffusivities have been assumed purely space-dependent. Spatial patterns may already occur without any interactions. For this setting, the spatially stationary solution has been derived. Furthermore, the speed of diffusive waves of a single logistically growing population has been analytically estimated, and conditions for the formation of spatio-temporal and Turing patterns in an excitable prey-predator system have been given.

Another recent publication (Siekmann and Malchow, 2016) has dealt with the control of invasion of a populated habitat by selective infection of the invader. Furthermore, the area is subject to uncorrelated and/or correlated environmental noise the resident is adapted to but the invading population not.

The present work shall link the two latter approaches. The

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Lotka-Volterra textbook model of the competition of two populations is combined with space-dependent Fokker-Planck diffusion of the residents, Fickian diffusion of the invaders and environmental noise. Two competing species, X_1 and X_2 , are modelled with equal mutual competition rates but different movement abilities. It is assumed that the resident species is adapted to the environmental conditions in its habitat. Favourable regions are characterized by a lower diffusion coefficient whereas it is rather high in unfavourable patches. Hence, the resident species move fast in unfavourable regions and tend to remain in the favoured. On the other hand, the invader's diffusivity is spatially uniform, i.e., it moves independent of the environmental conditions. It will be shown that the spatial heterogeneity modelled by Fokker-Planck diffusion but also the external noise can foster or hinder the invasion.

2. Methods

Interactions and movements of populations in a heterogeneous and variable environment are often modelled with stochastic reaction-diffusion equations. Diffusive fluxes in ecology can differ due to specifics of the population's relationships and environmental heterogeneity. They might be neutral cf. Eq. (1), attractive (2) or repulsive (3), i.e., for N populations

$$\vec{j}_{in} = -D_i(\vec{r}, \mathbf{X}) X_i(\vec{r}, t), \tag{1}$$

$$\vec{j}_{ia} = -D_i^2(\vec{r}, \mathbf{X}) \left[\frac{X_i(\vec{r}, t)}{D_i(\vec{r}, \mathbf{X})} \right] = +X_i(\vec{r}, t) D_i(\vec{r}, \mathbf{X}) - D_i(\vec{r}, \mathbf{X}) X_i(\vec{r}, t), \tag{2}$$

$$\vec{j}_{ir} = -[D_i(\vec{r}, \mathbf{X}) X_i(\vec{r}, t)] = -X_i(\vec{r}, t) D_i(\vec{r}, \mathbf{X}) - D_i(\vec{r}, \mathbf{X}) X_i(\vec{r}, t); \quad i = 1, 2, \dots, N. \tag{3}$$

The usual notation is used: $\mathbf{X}(\vec{r}, t) = \{X_i(\vec{r}, t); \quad i = 1, 2, \dots, N\}$ is the vector of population densities at position $\vec{r} = \{x, y\}$ and time t and $D_i(\vec{r}, \mathbf{X})$ their possibly space- and density-dependent diffusion coefficient. The formulations (1)–(3) have been elaborated by Skellam (1951, 1973), and nicely summarized by Okubo (1980), see also Aronson (1985) and Murray (1989). In order to complete the list of ecodiffusive fluxes in heterogeneous media, one could add the flux in environmental potentials $U(\vec{r})$

$$\vec{j}_{ip} = \vec{j}_{ik} + \gamma_i X_i(\vec{r}, t) U(\vec{r}); \quad i = 1, 2, \dots, N; \tag{4}$$

where γ_i is called the coefficient of affinity of X_i to the environment and index k can be n, a and r respectively, i.e., one of the fluxes (1)–(3) can be applied. The minima of $U(\vec{r})$ correspond to preferable and, therefore, attracting habitats. The latter concept has been derived from the ideas of habitat value and environmental density (Morisita, 1971; Shigesada and Teramoto, 1978).

The neutral diffusion is also called Fickian (Fick, 1855) whereas the repulsive type is named after Fokker (1914) and Planck (1917). For a certain density dependence of diffusion, the latter has been used for modelling the spatial segregation of populations (Shigesada et al., 1979; Mimura and Kawasaki, 1980) as well as the formation of Turing patterns (Malchow, 1988).

2.1. The stochastic competition-diffusion model

The dynamics of resident X_1 and invader X_2 is described by

$$\frac{\partial X_1}{\partial t} = (1 - X_1)X_1 - c_{12}X_1X_2 + d_1 \nabla^2 (X_1 D^*(x, y)) + g_1(X_1) \xi(\vec{r}, t), \tag{5}$$

$$\frac{\partial X_2}{\partial t} = (1 - X_2)X_2 - c_{21}X_1X_2 + d_2 \nabla^2 X_2 + g_2(X_2) \xi(\vec{r}, t). \tag{6}$$

c_{12} and c_{21} are parameters to describe the strength of interspecific competition between X_1 and X_2 , d_1 and d_2 are constant parameters to describe the strength of diffusion. Both species are assumed to grow logistically. The space dependence of the resident's diffusivity is chosen as

$$D^*(x, y) = D_0 + \begin{cases} a \left(\sin \left(\frac{\sqrt{x^2 + y^2}}{3\pi} \right) \right)^m & \text{if } \sqrt{x^2 + y^2} < 3\pi, \\ a \left(\sin \left(\frac{\sqrt{x^2 + y^2}}{3\pi} \right) \right)^m & \text{else.} \end{cases} \tag{7}$$

This spatially varying diffusivity is meant to represent a simple fragmented landscape with a varying habitat quality for species X_1 . The parameter m is an even number which controls the steepness of D^* . Zero-flux boundary conditions are assumed. In order to avoid effects from spatial heterogeneities at the boundaries, D^* is set constant for $\sqrt{x^2 + y^2} < 3\pi$, whereas $x=0, y=0$ defines the center of the landscape.

For simplicity, just uncorrelated white noise $\xi(\vec{r}, t)$ is applied here, i.e.,

$$\langle \xi(\vec{r}, t) \rangle = 0, \langle \xi(\vec{r}_1, t_1) \xi(\vec{r}_2, t_2) \rangle = \delta(\vec{r}_1 - \vec{r}_2) \delta(t_1 - t_2) \tag{8}$$

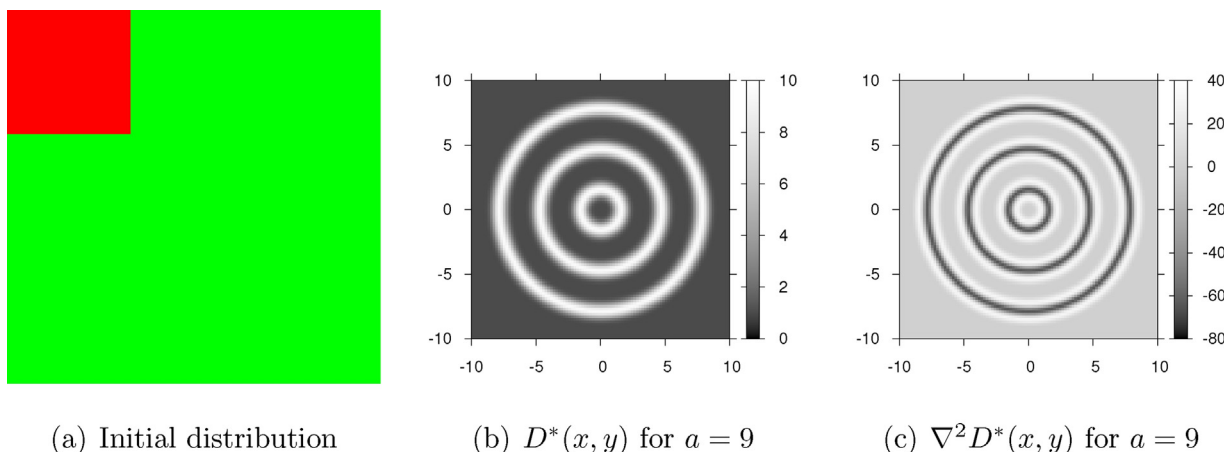


Fig. 1. Initial settings for densities (green = resident, red = invader) and resident's diffusivity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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