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Patterns of patchy spread in multi-species reaction–diffusion models

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ABSTRACT

Spread of populations in space often takes place via formation, interaction and propagation of separated patches of high species density, without formation of continuous fronts. This type of spread is called a ‘patchy spread’. In earlier models, this phenomenon was considered to be a result of a pronounced environmental or/and demographic stochasticity. Recently, it was found that a patchy spread can arise in a fully deterministic predator–prey system and in models of infectious diseases; in each case the process takes place in a homogeneous environment. It is well recognized that the observed patterns of patchy spread in nature are a result of interplay between stochastic and deterministic factors. However, the models considering deterministic mechanism of patchy spread are developed and studied much less compared to those based on stochastic mechanisms. A further progress in the understanding of the role of deterministic factors in the patchy spread would be extremely helpful. Here we apply multi-species reaction–diffusion models of two spatial dimensions in a homogeneous environment. We demonstrate that patterns of patchy spread are rather common for the considered approach, in particular, they arise both in mutualism and competition models influenced by predation. We show that this phenomenon can occur in a system without a strong Allee effect, contrary to what was assumed to be crucial in earlier models. We show, as well, a pattern of patchy spread having significantly different speeds in different spatial directions. We analyze basic features of spatio-temporal dynamics of patchy spread common for the reaction–diffusion approach. We discuss in which ecosystems we would observe patterns of deterministic patchy spread due to the considered mechanism.

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1. Introduction

The study of basic mechanisms underlying species spread in space is of central importance in the theory of biological invasions (Mooney and Drake, 1986; Murray, 1989; Shigesada

and Kawasaki, 1997; Fagan et al., 2002). Another important application is the ecological monitoring of those species which are not exotic and always present at low density but cause significant damages during outbreaks. Such population outbreaks occur both in terrestrial (e.g. insect outbreaks, see Clark

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et al., 1967; Berryman, 1978; Casti, 1982) and in aquatic systems (e.g. toxic plankton ‘blooms’, see Pingree et al., 1975; Anderson, 1989; Hallegraeff, 1993).

Although the patterns of spread observed in nature are rather complex and it is difficult to give their strict classification, we can distinguish roughly between the two following scenarios (Hengeveld, 1989; Shigesada and Kawasaki, 1997; Lewis and Pacala, 2000): (1) propagation of continuous traveling population fronts of high species density and (2) spread via formation and movement of patches of high density separated by areas with density close to zero. In this paper, we study the second scenario and call it a ‘patchy spread’.

Patchy spread has been studied and modeled much less than the spread via propagation of continuous traveling fronts, even the origin of this phenomenon is still a subject of discussions (Davis et al., 1998). In earlier models the basic mechanisms underlying the patchy spread were considered to be related to the landscape fragmentation (Murray, 1989; With, 2001) or/and to a pronounced environmental and demographic stochasticity (Lewis, 2000; Lewis and Pacala, 2000).

However, it is to be emphasized that the actual dynamics of species spread is a result of interplay between stochastic and deterministic factors. Stochastic processes would control ecosystem dynamics only when the intensity of noise surpasses a certain critical level; otherwise, the dynamics is governed by deterministic processes (Malchow et al., 2002, 2004). Moreover, the use of deterministic and stochastic approaches in modeling sometimes provides similar patterns of dynamics (Kawasaki et al., 1997; Mimura et al., 2000). Recent conceptual models using reaction–diffusion approach predict that patchy spread arises as well as a result of deterministic processes in predator–prey systems and in models of spread of infectious disease in a fully homogeneous environment (Petrovskii et al., 2002, 2005; Morozov et al., 2006). A crucial factor for realization of deterministic patchy spread in the mentioned works is that the population growth should be damped by a strong Allee effect, i.e. the growth becomes negative at low species densities (see Allee, 1938; Dennis, 1989).

It is certain that in reality we often deal with a species spread in a heterogeneous environment and in fragmental landscape. However, even in this case, a patchy spread might emerge as a result of some deterministic mechanisms prevailing on the environmental (or/and demographic) stochasticity, and an explanation of the observed patterns based only on stochastic mechanism would be too simplistic. Note that models of patchy spread based on deterministic mechanisms are developed and studied much less compared to those dealing with stochastic factors. As such, a further development and study of models providing patterns of deterministic patchy spread are needed; in particular, it would tell us in which ecosystems we should expect to find those patterns.

In this paper, we study patterns of deterministic patchy spread which arise in multi-species reaction–diffusion models and emerge as a result of intrinsic interactions of populations (all processes take place in a fully homogeneous environment). We consider the following three-species population models describing ecologically relevant situations: (i) model of obligate mutualism with an exploiter (Section 2); (ii) two-prey-

one-predator model (Section 3.1); (iii) two-predator-one-prey model (Section 3.2). We show patterns of a patchy spread in each model. We found that patchy spread can occur in a system without strong Allee effect (contrary to what was assumed to be crucial in earlier models). We demonstrate few patterns of population spread that have not been reported before, but which seem to be of importance for the theory of invasions. In particular, we show that the spread may take place via continuous front with highly curvilinear shape. We show, as well, a pattern of patchy spread having significantly different speeds in different spatial directions. We demonstrate different scenarios of transition to the patchy spread from regimes of smooth population fronts, while a control parameter is being varied. Finally, we formulate (Section 4) the basic features of spatiotemporal dynamics of patchy spread obtained in reaction–diffusion models, compare our results with those obtained in earlier simpler models. We discuss in which ecosystems we could observe patterns of deterministic patchy spread due to the considered mechanism.

2. Patchy spread in a model of obligate mutualism

2.1. Model formulation

In this section, we show that patchy spread arises in a model of obligate mutualism; i.e., when mutualism is necessary for the survival of each of mutualistic species (Odum, 1971). The system consists of two obligate mutualistic species and one exploiter (which is an obligate parasite) consuming one of them. Such a situation is rather common in ecology (Holland et al., 2005; Golinski, 2006). Examples include plant–pollinator–exploiter systems. The most known of those systems are (i) communities consisting of yucca trees and pollinating moths in the presence of non-pollinating moths which are, actually, seed parasites (Pellmyr and Leebens-Mack, 1999) and (ii) communities of fig trees with pollinating and non-pollinating wasps (Kerdelhué and Rasplus, 1996; Weiblen et al., 2001).

Let U_1 and U_2 denote the density of mutualists 1 and 2, respectively, and V the density of the exploiter which consumes mutualist 1. The model consists of three coupled reaction–diffusion equations:

$$\frac{\partial U_1(r, T)}{\partial T} = D_1 \Delta U_1(r, T) - AU_1 - E_1 U_1^2 + M_1 \frac{U_1 U_2}{1 + \Omega_1 U_2} - S \times \frac{U_1 V}{1 + \Theta U_1}, \quad (1)$$

$$\frac{\partial U_2(r, T)}{\partial T} = D_2 \Delta U_2(r, T) - BU_2 - E_2 U_2^2 + M_2 \frac{U_1 U_2}{1 + \Omega_2 U_1}, \quad (2)$$

$$\frac{\partial V(r, T)}{\partial T} = D_3 \Delta V(r, T) + kS \frac{U_1 V}{1 + \Theta U_1} - mV, \quad (3)$$

where $r = (X, Y)$ is the location in space; T is time; and D_1, D_2 and D_3 are diffusion coefficients.

To describe local interactions between the mutualists we utilize the minimal model of obligate mutualism given in Bazykin (1998). The terms AU_1 and BU_2 stand for the rate the extinction of each of the species (at low densities) which

would take place in the absence of a partner. The terms $E_1 U_1^2$ and $E_2 U_2^2$ take into account self-inhibition at high densities. The terms $M_i U_i U_j / (1 + \Omega_i U_i)$ ($i, j = 1, 2, i \neq j$) in (1) and (2) describe the mutualistic relationships (or mutual net benefits) of the partners, taking into account saturation effects at high density of the partner (see Holland et al. (2002) for a biological background of this parameterization). Here $M_1, M_2, \Omega_1, \Omega_2$ are positive coefficients.

The consumption of a mutualist by an exploiter (the last term in (1)) is described, for the sake of simplicity, by Holling type II trophic response (but see Morris et al. (2003) for another possibility). Here $1/\theta$ is the half-saturation constant of consumption rate; S characterizes the intensity of consumption; k is the food utilization coefficient; m is the mortality rate of the exploiter.

In order to reduce the number of model parameters we introduce dimensionless variables: $u_1 = U_1 k S/B$, $u_2 = U_2 E_2/B$, $v = VS/B$, $t = TB$, $x = X(B/D_1)^{1/2}$, $y = Y(B/D_1)^{1/2}$.

Then system (1)–(3) can be re-written as:

$$\frac{\partial u_1}{\partial t} = \Delta u_1 - \alpha u_1 - e u_1^2 + \mu_1 \frac{u_1 u_2}{1 + \omega_1 u_2} - \frac{u_1 v}{1 + \gamma u_1}, \quad (4)$$

$$\frac{\partial u_2}{\partial t} = \varepsilon_1 \Delta u_2 - u_2 - u_2^2 + \mu_2 \frac{u_1 u_2}{1 + \omega_2 u_1}, \quad (5)$$

$$\frac{\partial v}{\partial t} = \varepsilon_2 \Delta v + \frac{u_1 v}{1 + \gamma u_1} - \delta v, \quad (6)$$

where $\alpha = (A/B)$, $e = E_1(kS)$, $\mu_1 = M_1/E_2$, $\mu_2 = M_2/(kS)$, $\delta = m/B$, $\omega_1 = \Omega_1 B/E_2$, $\omega_2 = \Omega_2 B/(kS)$, $\gamma = \theta B/(kS)$, $\varepsilon_1 = D_2/D_1$, $\varepsilon_2 = D_3/D_1$.

We first consider the interactions between the mutualists in absence of the exploiter:

$$\frac{\partial u_1}{\partial t} = \Delta u_1 - \alpha u_1 - e u_1^2 + \mu_1 \frac{u_1 u_2}{1 + \omega_1 u_2}, \quad (7)$$

$$\frac{\partial u_2}{\partial t} = \varepsilon_1 \Delta u_2 - u_2 - u_2^2 + \mu_2 \frac{u_1 u_2}{1 + \omega_2 u_1}. \quad (8)$$

Local dynamics of (7) and (8) is discussed in detail in Bazykin (1998). Here we consider the case when the system is bi-stable; otherwise, the only stationary stable state is a trivial equilibrium. The reciprocal positions of the null-clines and a phase portrait in this case are shown schematically in Fig. 1. There are two stable equilibria: one is characterized by zero densities of both species, the other one has nonzero densities. Note that such bi-stability is a characteristic feature of obligate mutualism and was observed in more complex models (Dean, 1983; Holland et al., 2002; Morris et al., 2003; Wilson et al., 2003).

To study the spatial dynamics of the system we need to provide (7) and (8) with initial conditions. Similarly to Petrovskii et al. (2002) we consider the following initial distributions of species:

$$u_1(x, y, 0) = p_1 \quad \text{if } \left| x - \frac{L}{2} \right| \leq \Delta_{11} \quad \text{and} \quad \left| y - \frac{L}{2} \right| \leq \Delta_{12},$$

otherwise $u_1(x, y, 0) = 0;$ (9)

$$u_2(x, y, 0) = p_2 \quad \text{if } \left| x - \frac{L}{2} \right| \leq \Delta_{21} \quad \text{and} \quad \left| y - \frac{L}{2} \right| \leq \Delta_{22},$$

otherwise $u_2(x, y, 0) = 0;$ (10)

where $p_1, p_2, \Delta_{11}, \Delta_{12}, \Delta_{21}, \Delta_{22}$ are positive parameters. We model the spread of species in a square domain $L \times L$. The choice of initial conditions in form (9) and (10) allows us to study a joint biological invasion of exotic species 1 and 2 related with obligate mutualism.

From now on, we consider the Neumann ‘zero-flux’ boundary conditions for all models that we investigate. Moreover, we take the size of the domain $L \times L$ large enough to minimize a possible influence of boundaries on the system dynamics.

According to the well-known properties of bi-stable systems (see Murray, 1989; Mikhailov, 1990) one would expect two possible scenarios in (7) and (8) with initial distributions (9) and (10): (i) If the sizes of the initially occupied areas and the initial densities p_1, p_2 are sufficiently large (supercritical), then the initial patches will grow in size and invade the whole area (via propagation of smooth traveling waves); the final species densities will correspond to the non-trivial stable stationary state shown in Fig. 1. (ii) If the initial sizes and densities are small (subcritical), then the extinction of both species takes place. Our numerical simulations (including variation of diffusion coefficients) confirm these expectations (no other regimes have been found). Note that the bi-stability of local interactions in (7) and (8) does not automatically imply a bi-stability of the same model with diffusion. For example, if the saddle point (see Fig. 1) is situated too close to the non-trivial stationary state, all initial conditions will be subcritical. Furthermore, we shall consider the situation when there always exist supercritical initial distributions leading to a successful invasion of the mutualists in the absence of the exploiter.

The complexity of spatiotemporal dynamics of the mutualists increases dramatically in the presence of an exploiter, i.e. in the whole model (4)–(6). We assume that the initial distribution of the exploiter is described by a similar expression as those of the mutualists, albeit the centers of

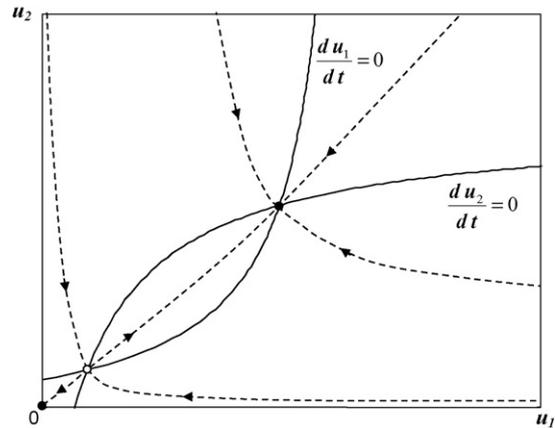


Fig. 1 – Local dynamics of model (7) and (8) of obligate mutualism in the absence of the exploiter. Schematic reciprocal positions of null-clines and phase portrait are shown in case of bi-stability. The two stationary stable states are denoted by black filled circles, each has a domain of attraction.

areas initially occupied by the exploiter and mutualists are shifted:

$$v(x, y, 0) = q \quad \text{if} \quad \left| x - \frac{L}{2} - a \right| \leq \Delta_{31} \quad \text{and} \quad \left| y - \frac{L}{2} - b \right| \leq \Delta_{32},$$

otherwise $v(x, y, 0) = 0$; (11)

where $q, a, b, \Delta_{31}, \Delta_{32}$ are positive parameters.

An important ecological application of model (4)–(6) with (9)–(11) is a biological control of exotic species by intentionally introducing a control agent to stop (or/and to slow) their spread (Fagan and Bishop, 2000; Fagan et al., 2002).

2.2. Transition to patchy spread

Computer experiments show that the spatiotemporal dynamics of (4)–(6) exhibit different complex patterns of species spread. We emphasize that a comprehensive classification of all regimes of the model is not a goal of this paper. Instead, we investigate a possibility of realization of patchy spread and study the transition to this pattern from regimes with continuous traveling population fronts. We chose an ecologically meaningful controlling parameter and follow successions of spread patterns while varying its value. Here we use δ , the mortality rate of exploiter, as the controlling parameter.

Note that for all parameter sets there are some initial conditions (subcritical) which lead to extinction of all species. This is the result of the bi-stability of the obligate mutualism. Adding an exploiter impedes more survival chances for the mutualists. From now on, we shall always assume that initial distributions (9)–(11) are chosen supercritical.

Our simulations have revealed patterns of patchy spread in the considered system. An example of such dynamics is shown in Fig. 2 (for the parameters $\alpha = 0.75, e = 1, \mu_1 = 3, \mu_2 = 3, \gamma = 0.5, \omega_1 = 0.25, \omega_2 = 0.25, \delta = 0.71, e_1 = 2, e_2 = 2$ and the initial conditions (9)–(11) with $p_1 = 5, p_2 = 5, \Delta_{11} = 7.5, \Delta_{12} = 10, \Delta_{21} = 7.5, \Delta_{22} = 10, q = 12, a = 2.5, b = 5, \Delta_{31} = 5, \Delta_{32} = 2.5$). The initial smooth front breaks to pieces, the propagation of species in space takes place via irregular movement of separated patches and groups of patches, and a continuous front never reappears again. The patches move, merge, disappear or produce new patches, etc. After invasion of the whole domain $L \times L$, the spatial distribution of species at any time remains qualitatively similar to the one shown for $t = 400$, although the position and shape of patches vary in the course of time.

We found that a typical scenario of transition to patchy spread, while diminishing δ from large values, is the following: (i) propagation of circular population fronts with stationary spatially homogeneous distributions of species behind the front; (ii) spread of circular traveling fronts with irregular spatiotemporal oscillations in the wake; (iii) propagation of concentric rings with species densities close to zero in the wake of the front; (iv) patchy spread. The patterns (i), (ii), (iii) are well known in literature (Sherratt et al., 1995; Petrovskii and Malchow, 2001; Morozov et al., 2006) and we do not show here the corresponding illustrations. Finally, a further decrease in δ leads to species extinction for all initial distributions, thus overexploitation extinguishes the mutualism. This result is in a good agreement with the field observations (Bull and Rice, 1991; Stanton et al., 1999).

We should emphasize that the parameter set corresponding to the dynamics in Fig. 2 is not unique for the realization of patchy spread, and this pattern can be observed for other parameter sets as well. The dimensionless model (4)–(6) still contains 10 parameters. A thorough analysis of the parameter space (including variation of initial conditions) of this 2D model is virtually impossible. To get insight into the robustness of the phenomenon to a variation of model parameters, we proceed in the following way. We fix four parameters α, e, e_1, e_2 at their original values from Fig. 2 and vary the parameters $\mu_1, \mu_2, \gamma, \omega_1, \omega_2$ within some ranges (we choose the following ranges: $2 < \mu_1, \mu_2 < 3.5, 0.4 < \gamma < 0.75, 0.1 < \omega_1, \omega_2 < 0.45$). For the sake of simplicity, let $\mu_1 = \mu_2, \omega_1 = \omega_2$ and utilize the same initial conditions as before. We take about 100 different sets of $\mu_1, \mu_2, \gamma, \omega_1, \omega_2$ from the above indicated ranges, ‘at random’, making sure that in the absence of the exploiter, the mutualism is bi-stable, and for each fixed parameter set we vary the value of δ as before.

Our analysis showed patterns of patchy spread, while δ is being varied, for most considered combinations of other parameters, albeit for a rather narrow range of δ (compared to domains corresponding to patterns with smooth traveling fronts). Moreover, we found that another scenario of transition to a patchy spread becomes possible (e.g. $\mu_1 = \mu_2 = 3, \gamma = 0.5, \omega_1 = \omega_2 = 0.4$) when transition takes place without formation of concentric rings and occurs via breaking of smooth population fronts (here we do not show snapshots of this scenario for brevity). Note that the transition to extinction from spread with smooth fronts can also take place without appearance of a patchy spread. This is observed when the saddle point in Fig. 1 is situated relatively close to the nontrivial equilibrium.

An important intermediate conclusion can be made here: obligate mutualism combined with exploitation would lead to a patchy spread in a completely homogeneous space.

3. Patchy spread in competition models

3.1. Patchy spread in a one-predator-two-prey model

In this subsection, we consider patterns of spread in a system of a consuming predator and two competitive prey species. One prey is consumed by the predator, the other one is inedible. Important ecological examples include zooplankton grazing on competing algae (Kretzschmar et al., 1993) and competition between edible and inedible terrestrial plants consumed by an herbivorous species (Phillips, 1974; Grover, 1995). Moreover, we should emphasize that this situation is rather typical in ecology. It includes any predator–prey system where the prey is in competition for resources (or territories) with some other species (morphologically different from the prey) which do not serve as a food supply for the predator. It is to be noted that those inedible species can essentially influence the predator–prey interactions. Further (Section 4.3) we discuss a possible application of the model to explain a patchy spread reported for a real ecosystem.

We utilize the model proposed by Kretzschmar et al. (1993). For the sake of simplicity, assume that there is no direct interaction between the predator and the inedible prey. We add diffusion terms into the model and obtain the following equations (for dimensionless densities of species):

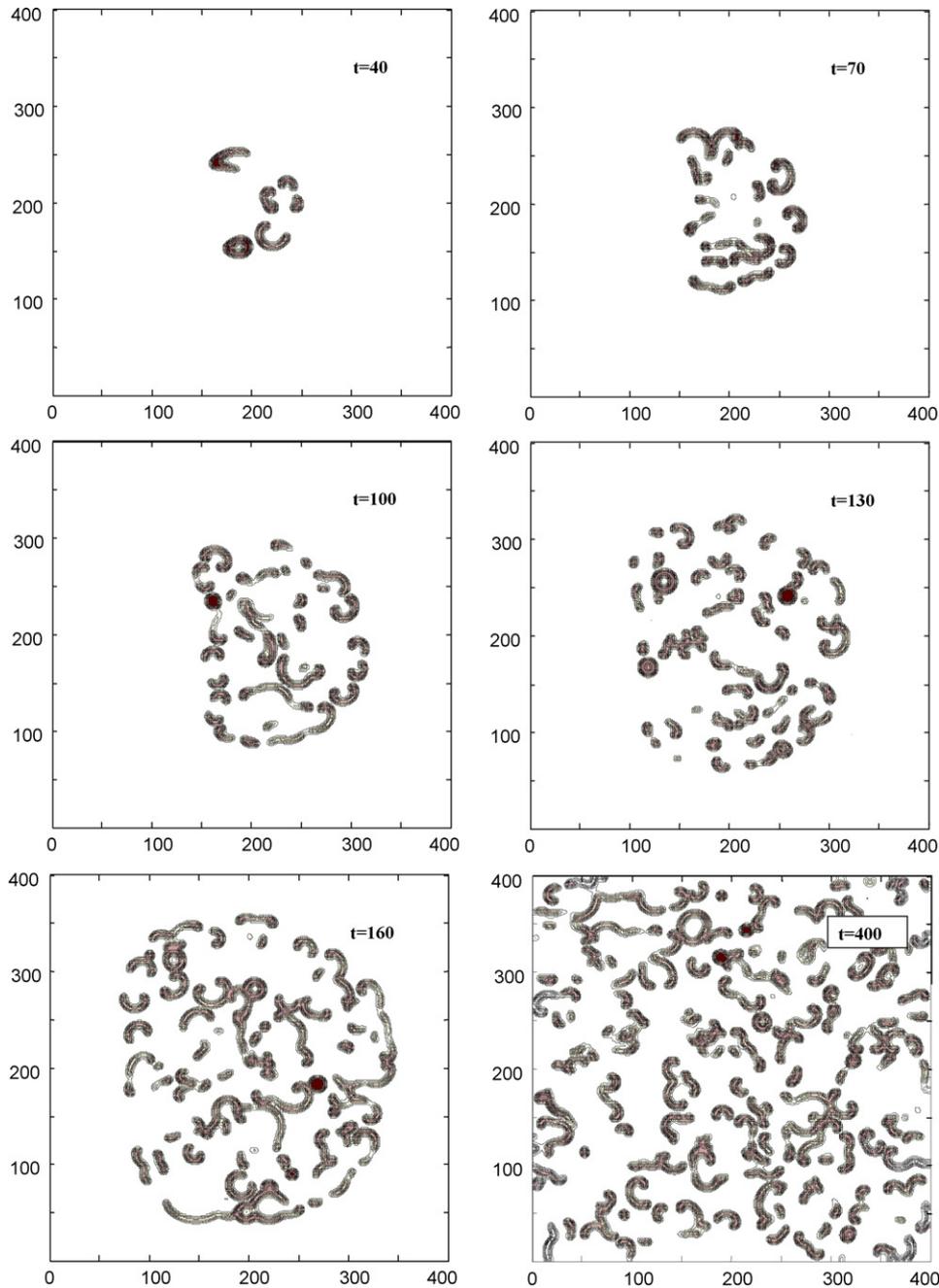


Fig. 2 – Snapshots of the density u_2 of the unexploited mutualist in model (4)–(6) calculated at different moments of time for parameters $\alpha = 0.75$, $e = 1$, $\mu_1 = 3$, $\mu_2 = 3$, $\gamma = 0.5$, $\omega_1 = 0.25$, $\omega_2 = 0.25$, $\delta = 0.71$, $\varepsilon_1 = 2$, $\varepsilon_2 = 2$ and initial conditions (9)–(11) with $p_1 = 5$, $p_2 = 5$, $\Delta_{11} = 7.5$, $\Delta_{12} = 10$, $\Delta_{21} = 7.5$, $\Delta_{22} = 10$, $q = 12$, $a = 2.5$, $b = 5$, $\Delta_{31} = 5$, $\Delta_{32} = 2.5$. Black colors signify high species density; white color signifies densities close to zero. Species spread takes place via movement of separated patches. Distributions of the other species are qualitatively similar.

$$\frac{\partial u_1}{\partial t} = \Delta u_1 + u_1(1 - u_1 - \chi_{12}u_2) - \frac{u_1v}{1 + \gamma u_1}, \tag{12}$$

$$\frac{\partial u_2}{\partial t} = \varepsilon_1 \Delta u_2 + ru_2(1 - u_2 - \chi_{21}u_1), \tag{13}$$

$$\frac{\partial v}{\partial t} = \varepsilon_2 \Delta v + g \frac{u_1v}{1 + \gamma u_1} - \delta v, \tag{14}$$

where u_1 , u_2 , v are the densities of competing preys and predator, respectively, r is the maximal dimensionless growth rate of inedible prey, and χ_{12} , χ_{21} describe the intraspecific competition. The parameters γ , g describe the feeding of the predator (note that the dimensionless parameter g can be greater than 1), δ is the mortality rate of the predator.

In the absence of predator, we arrive at the classical two-species Lotka-Volterra competition model with diffusion

(Murray, 1989; Okubo et al., 1989; Shigesada and Kawasaki, 1997):

$$\frac{\partial u_1}{\partial t} = \Delta u_1 + u_1(1 - u_1 - \chi_{12}u_2), \tag{15}$$

$$\frac{\partial u_2}{\partial t} = \varepsilon_1 \Delta u_2 + r u_2(1 - u_2 - \chi_{21}u_1). \tag{16}$$

The spatiotemporal dynamics of (15) and (16) depend greatly on the dynamics of local species interactions. Following the previous section, we shall consider that the subsystem without predator is locally bi-stable. The species are antagonists ($1/\chi_{12} < 1$ and $1/\chi_{21} < 1$), their stable coexistence is impossible, but each of them can survive by excluding the other one (see Fig. 3).

We consider the following initial spatial distributions of species:

$$u_1(x, y, 0) = \bar{u}_1 \quad \text{if } \left| x - \frac{L}{2} \right| \leq \Delta_{21} \quad \text{and} \quad \left| y - \frac{L}{2} \right| \leq \Delta_{22}, \quad \text{otherwise } u_1(x, y, 0) = 0; \tag{17}$$

$$u_2(x, y, 0) = 1 \quad \text{for all } x, y. \tag{18}$$

By using (17) and (18), we study the invasion of an exotic species into an area initially occupied by a native competitor. This statement of task has numerous practical applications in the theory of biological invasions (Okubo et al., 1989; Shigesada and Kawasaki, 1997; Hosono, 1998). Note, however, that in the mentioned works, the authors only considered analytically the cases when local dynamics correspond either to a stable coexistence of both species or to the situation when only one (and always the same) species wins the competition. The case of local bi-stability was not analyzed.

Simulations show that local bi-stability in (15) and (16) leads to the two scenarios: (i) spread of u_1 followed by the extinction of u_2 via a traveling population front with the final distribution $u_1 = 1$ for all x and y ; and (ii) extinction of the initial

patch of u_1 as a result of competitive exclusion by u_2 . For a successful invasion of u_1 , the sizes of the initial patch and the initial density \bar{u}_1 should be supercritical.

We consider the following initial spatial distribution of the predator:

$$v(x, y, 0) = \bar{v} \quad \text{if } \left| x - \frac{L}{2} - a \right| \leq \Delta_{31} \quad \text{and} \quad \left| y - \frac{L}{2} - b \right| \leq \Delta_{32}, \tag{19}$$

otherwise $v(x, y, 0) = 0$.

Our simulations show that model (12)–(14) exhibits different patterns of patchy spread. It is convenient to take δ again as the controlling parameter. First, we found a similar succession of patterns leading to a patchy spread as in model (4)–(6). For example, for the fixed $r = 2$, $\chi_{12} = 2$, $\chi_{21} = 10$, $\gamma = 2$, $g = 1.1$, $\varepsilon_1 = 1$, $\varepsilon_2 = 2$, the transition to patchy spread from the regimes of smooth fronts takes place via propagation of concentric rings. For the above parameters, the patchy spread is observed for $\delta = 0.094$ and the initial conditions (17)–(19): $\Delta_{11} = 15$, $\Delta_{12} = 15$, $\bar{u}_1 = 1$, $\Delta_{31} = 15$, $\Delta_{32} = 10$, $\bar{v} = 0.5$, $a = 5$, $b = 10$ (see Fig. 4 showing snapshots of u_1). The spatial distribution of v is qualitatively similar to that of u_1 ; on the contrary, the distribution of u_2 is somewhat opposite to that of u_1 , i.e., u_2 reaches its carrying capacity at locations where the density of u_1 is close to zero and vice-versa. For a further decrease in δ extinction of both u_1 and v takes place for all initial distributions.

However, the above-described scenario of transition to a patchy spread is not the only possible one. For smaller values of r , some other scenarios of successions, leading to a patchy spread, take place. A thorough classification of these scenarios will be an issue of our next study. Here we demonstrate a succession of regimes leading to a pattern of patchy spread with a different appearance than the pattern in Fig. 4 and characterized by values of invasion speed essentially different in different space directions.

As before, we keep all model parameters fixed except the predator mortality δ . We choose the following parameter values: $r = 0.75$, $\chi_{12} = 2$, $\chi_{21} = 10$, $\gamma = 2$, $g = 1.1$, $\varepsilon_1 = 1$, $\varepsilon_2 = 2$.

For large values of δ the spread of u_1 and v takes place via propagation of population fronts with the shape close to round. For smaller values of δ , the front is no more circular and gains a pronounced curvilinear shape. Fig. 5 shows an example of this pattern of spread for $\delta = 0.18$, while the initial conditions are the same as in Fig. 4. For a further decrease in δ , the spread becomes cellular-like (see Fig. 6 with $\delta = 0.17$). After the propagation of the fronts of u_1 and v , which have complex structure with sprout-like formations in front of the front, the invaded area becomes divided into a number of ‘cells’ (see Fig. 6 for $t = 3000$). The sides separating the cells are composed by space locations with high densities of u_1 and v ; the positions of the sides change slowly in time. Inside each cell, the densities of u_1 and v are close to zero; on the contrary, the density of u_2 reaches its carrying capacity. Thus, the whole area, initially occupied by the inedible prey, becomes divided in separated patches.

A further decrease in δ results in a patchy spread (in the 1D model we had extinction of u_1 and v). However, this pattern (see Fig. 7 with $\delta = 0.157$) has a different visual appearance compared to the pattern in Fig. 4. This is related to the fact that the mechanism of spatial spread of patches in Fig. 7 is

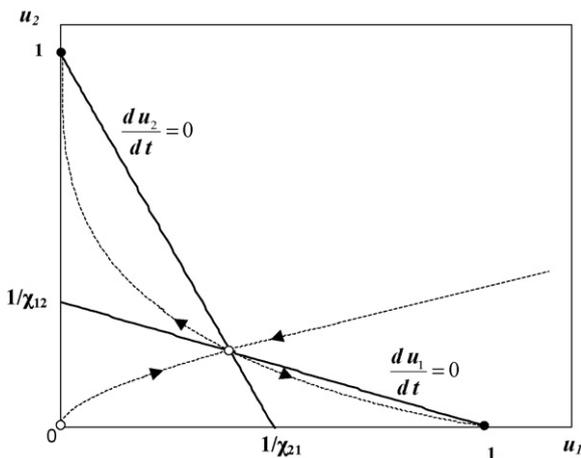


Fig. 3 – Local dynamics of the diffusive Lotka-Volterra competition model (15) and (16). Schematic positions of null-clines and phase portrait are shown in case of bi-stability. Stable stationary states are denoted by black filled circles.

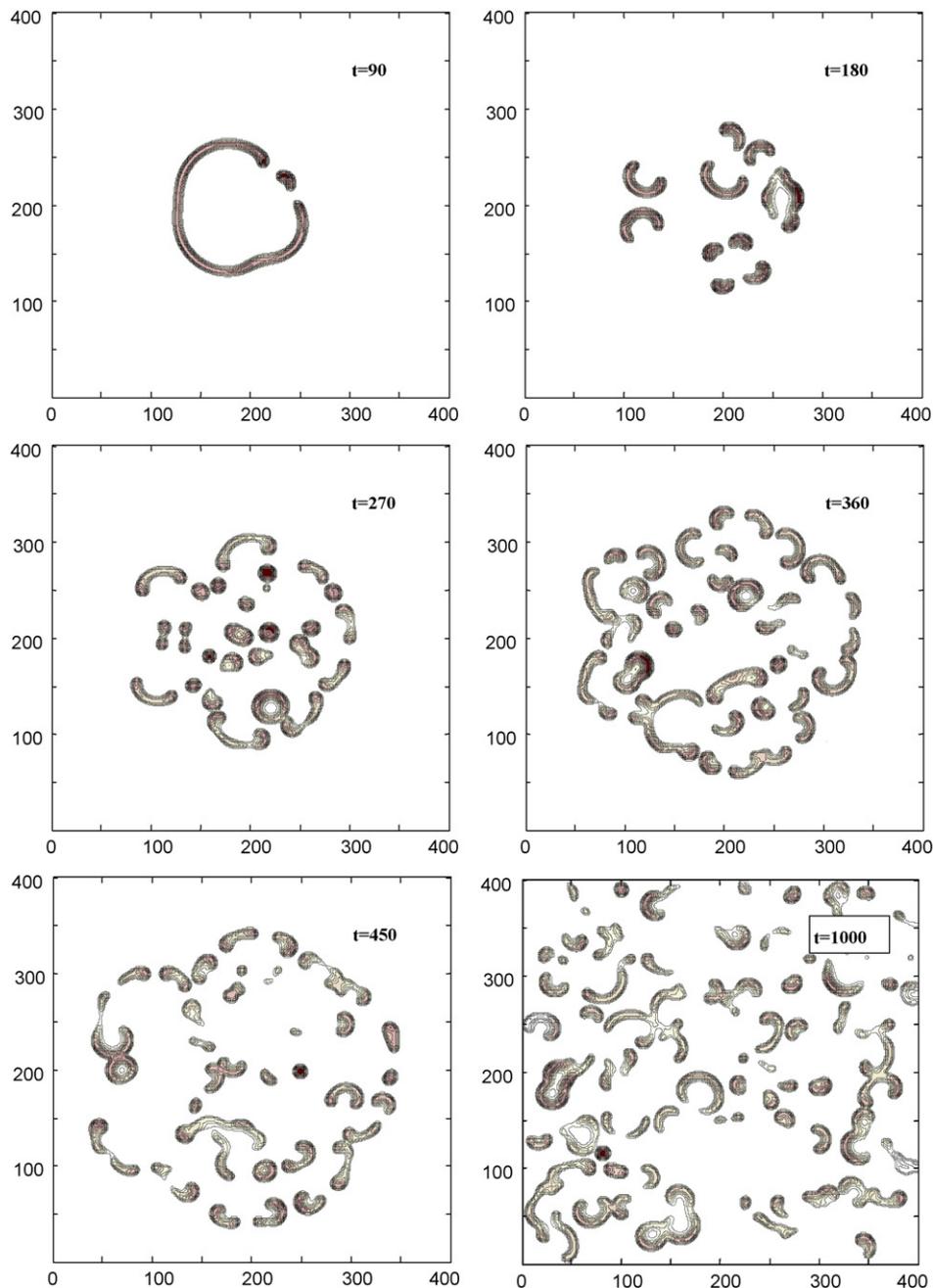


Fig. 4 – Snapshots for density u_1 of the edible prey in the one-predator-two-prey model (12)–(14) calculated at different moments of time for parameters $r = 2$, $\chi_{12} = 2$, $\chi_{21} = 10$, $\gamma = 2$, $e = 1.1$, $\varepsilon_1 = 1$, $\varepsilon_2 = 2$ $\delta = 0.094$ and initial conditions (17)–(19) with $\Lambda_{11} = 15$, $\Lambda_{12} = 15$, $\tilde{u}_1 = 1$, $\Lambda_{31} = 15$, $\Lambda_{32} = 10$, $\tilde{v} = 0.5$, $a = 5$, $b = 10$. Black colors signify high species density; white color signifies densities close to zero. Invasion of the edible prey takes place without forming a smooth front. Distribution of the predator is qualitatively similar, distribution of inedible prey is the opposite to that of the edible prey.

somewhat different from that in Fig. 4 and is closer to the one found in chemical systems (Muratov, 1996). As a result, the speed of spread can be essentially different in different space directions, which can be easily seen from Fig. 7. For a fixed set of model parameters, directions with faster rates of spread are determined only by initial conditions (which should be non-symmetrical). Our estimates show that the discrepancy between speeds in different directions can be as large as five-folds. On the contrary, the patchy spread obtained earlier

for higher values of r , although highly irregular, does not differ essentially in different directions in space, i.e., it can be considered as statistically isotropic. From an ecological point of view, the pattern in Fig. 7 seems to be of significant interest because variation in the invasion speed in different space directions was attributed earlier to an environmental heterogeneity (see Shigesada and Kawasaki, 1997 and references therein) and not to an internal mechanism of system dynamics.

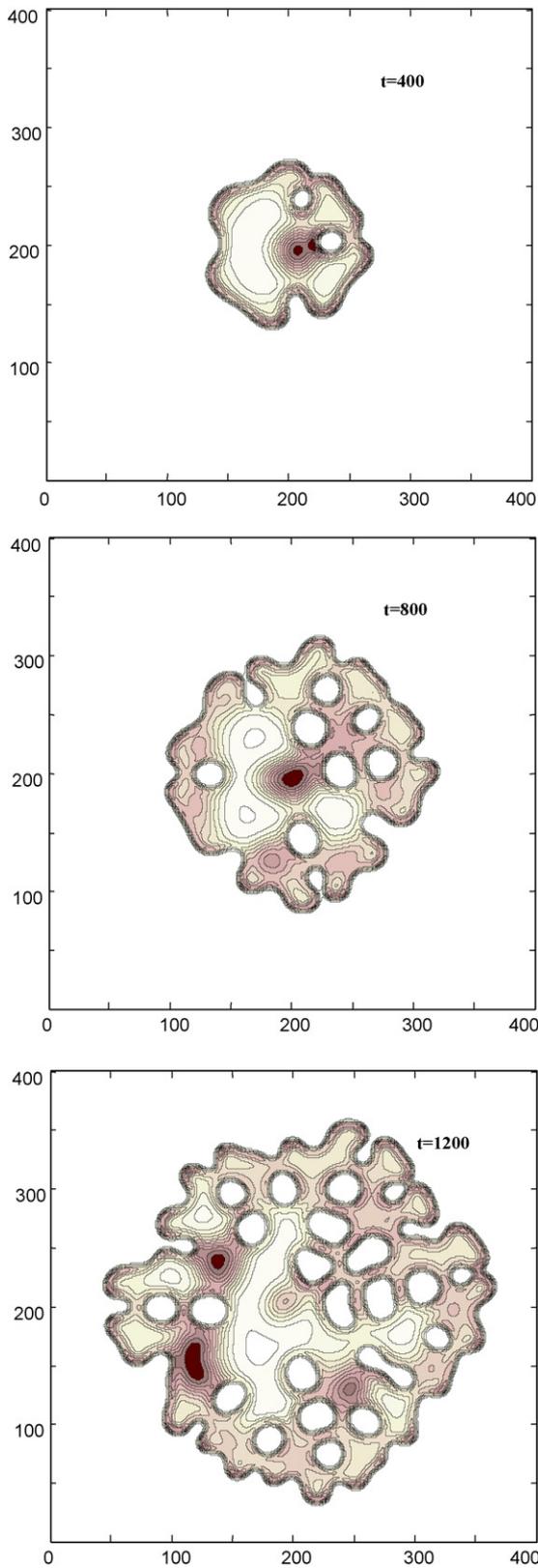


Fig. 5 – Snapshots for density u_1 of the edible prey in the one-predator-two-prey model (12)–(14) calculated at different moments of time for parameters $r = 0.75$, $\chi_{12} = 2$, $\chi_{21} = 10$, $\gamma = 2$, $e = 1.1$, $\varepsilon_1 = 1$, $\varepsilon_2 = 2$, $\delta = 0.18$ and the same initial conditions as in Fig. 4. Black colors signify high species density; white color signifies densities close to

A further decrease in δ leads to the formation of a group of patches of round shape (see Fig. 8, $\delta = 0.145$). After some transient stage ($t \sim 300$) the number of patches does not change. The centers of patches are immobile but their profiles oscillate with time. The number of patches depends on the initial conditions. Finally, for $\delta < 0.144$ extinction of u_1 and v takes place regardless the choice of initial conditions.

We should note that contrary to the patchy spread shown in Fig. 4, the above described scenario of transition to anisotropic patchy spread was found only in case when the dispersal of the predator is faster than that of the prey species (i.e., $\varepsilon_1 < \varepsilon_2$), albeit the ratio $\varepsilon_2/\varepsilon_1$ can be relatively small as in the above example.

3.2. Patchy spread in a two-predator-one-prey model

Here we show that a deterministic patchy spread can arise in a model without Allee effect. We consider a system of two predators competing for a prey in the 2D space (for the brevity sake, already in dimensionless variables):

$$\frac{\partial u}{\partial t} = \Delta u + u - \beta u^2 - \frac{uv}{1 + \gamma_1 u} - \frac{uw}{1 + \gamma_2 u}, \tag{20}$$

$$\frac{\partial v}{\partial t} = \varepsilon_2 \Delta v + \frac{uv}{1 + \gamma_1 u} - \delta_1 v - \tilde{\delta}_1 v^2, \tag{21}$$

$$\frac{\partial w}{\partial t} = \varepsilon_3 \Delta w + \sigma \frac{uw}{1 + \gamma_2 u} - \delta_2 w - \tilde{\delta}_2 w^2, \tag{22}$$

where u, v, w are the densities of prey and predators, respectively, β describes the saturation of the prey growth at high densities, $\gamma_1, \gamma_2, \sigma$ characterize feeding abilities of the predators, and δ_1, δ_2 are the mortality rates of predators at low densities. The terms $\tilde{\delta}_1, \tilde{\delta}_2$ are the so-called ‘closure terms’ describing self-grazing of predators (Steele and Henderson, 1992; Kohlmeier and Ebenhö, 1995).

System (20)–(22) is a generalization of the well-known two-predator-one-prey model (Hsu et al., 1978; Smith, 1982). We added into this model the closure terms to take into account the self-grazing of predators. Such situation is typical for eutrophic plankton communities, where the density of zooplankton species is usually high (Steele and Henderson, 1992; Edwards and Yool, 2000).

Let us first start with the case when the prey is consumed only by one predator:

$$\frac{\partial u}{\partial t} = \Delta u + u - \beta u^2 - \frac{uv}{1 + \gamma_1 u}, \tag{23}$$

$$\frac{\partial v}{\partial t} = \varepsilon_2 \Delta v + \frac{uv}{1 + \gamma_1 u} - \delta_1 v - \tilde{\delta}_1 v^2. \tag{24}$$

Local dynamics of the $u - v$ predator-prey subsystem (23) and (24) are described in detail in Bazykin (1998). For a wide range of parameters, the system exhibits bi-stability and has

zero. The front of invasion of the edible prey has a pronounced curvilinear shape. Distribution of the predator is qualitatively similar; distribution of the inedible prey is the opposite to that of the edible prey.

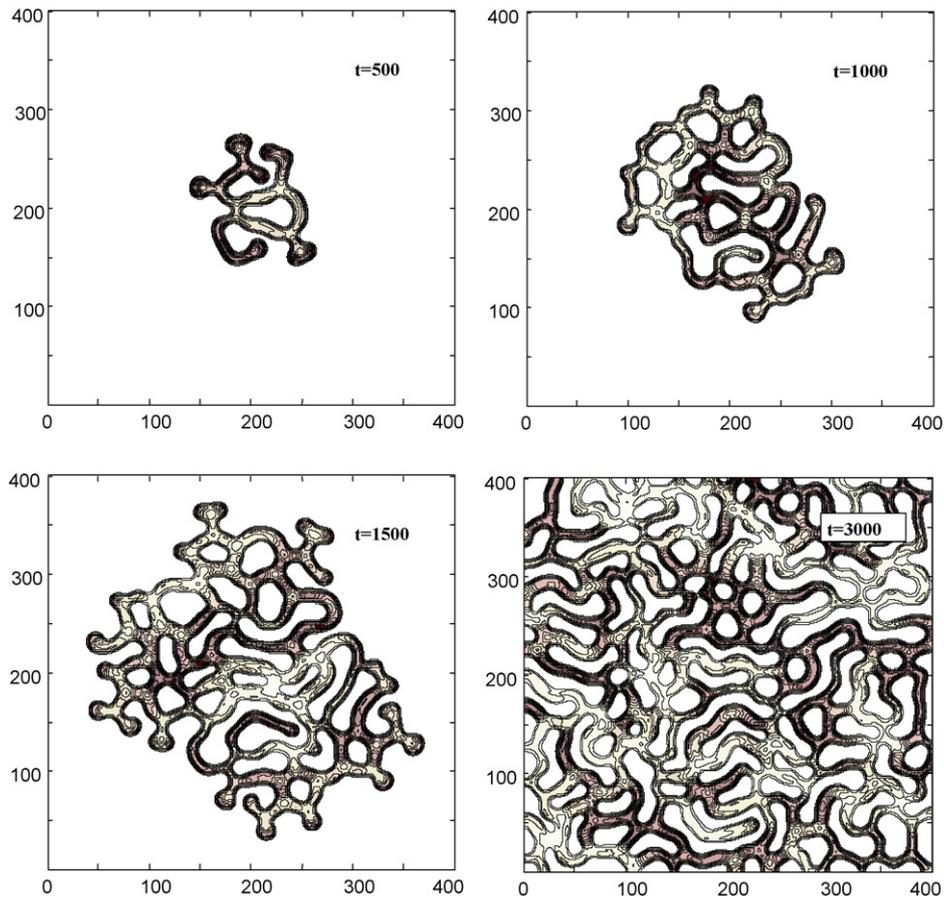


Fig. 6 – Snapshots for density u_1 of the edible prey in the one-predator-two-prey model (12)–(14) calculated at different moments of time for $\delta = 0.17$, other parameters are the same as in Fig. 5. Black colors signify high species density; white color signifies densities close to zero. Invasion of the edible prey takes place via putting out irregular shoots. Distribution of predator is qualitatively similar; distribution of the inedible prey is the opposite to that of the edible prey.

two stable stationary states: the upper (u_1, v_1) and the lower (u_0, v_0) with $u_1 > u_0$ and $v_1 > v_0$, separated by a saddle point. Fig. 9 shows schematically the reciprocal position of the null-lines and a phase portrait in this case. Taking into account the results obtained in the two previous models, we shall optimistically look for patterns of patchy spread in the whole model with two competitive predators when the $u - v$ subsystem exhibits bi-stability.

We shall consider the following initial spatial distributions of u and v :

$$u(x, y, 0) = p \quad \text{if } \left| x - \frac{L}{2} \right| \leq \Delta_{21} \quad \text{and} \quad \left| y - \frac{L}{2} \right| \leq \Delta_{22},$$

$$\text{otherwise } u(x, y, 0) = u_0; \tag{25}$$

$$v(x, y, 0) = v_0 \quad \text{for all } x, y, \tag{26}$$

where u_0, v_0 are the densities corresponding to the lower equilibrium (see Fig. 9, we assume $p > u_0$). Note that, contrary to the previous models dealing with invasion of exotic species, model (23)–(24) with (25)–(26) describes the dynamics of outbreaks of densities of a native species which exists at low density between the outbreaks due to an intensive predator pressure (e.g. plankton blooms and insect outbreaks).

Similar to the previous model (7)–(8) and (15)–(16), bi-stable system (23) and (24) exhibits two qualitatively different types of behaviour: (i) transition to the upper homogeneous stable distribution with $u = u_1$ and $v = v_1$ for $x, y \in L \times L$; (ii) for a subcritical initial perturbation, the species densities relax to the homogeneous distributions u_0 and v_0 .

Let us now consider the whole two-predator-one-prey system. For the initial density of the second predator, we assume that:

$$w(x, y, 0) = p^* \quad \text{if } \left| x - \frac{L}{2} - a \right| \leq \Delta_{31} \quad \text{and} \quad \left| y - \frac{L}{2} - b \right| \leq \Delta_{32},$$

$$\text{otherwise } w(x, y, 0) = 0. \tag{27}$$

Our numerical simulations show that system (20)–(22) provides a variety of regimes of competition between the predators in space leading either to their coexistence or to extinction of one predator. Here we shall restrict ourselves to the case when the second predator is a weaker competitor compared to the first one. Mathematically, we consider the following conditions:

$$\sigma \frac{u_0}{1 + \gamma_2 u_0} - \delta_2 < 0, \tag{28}$$

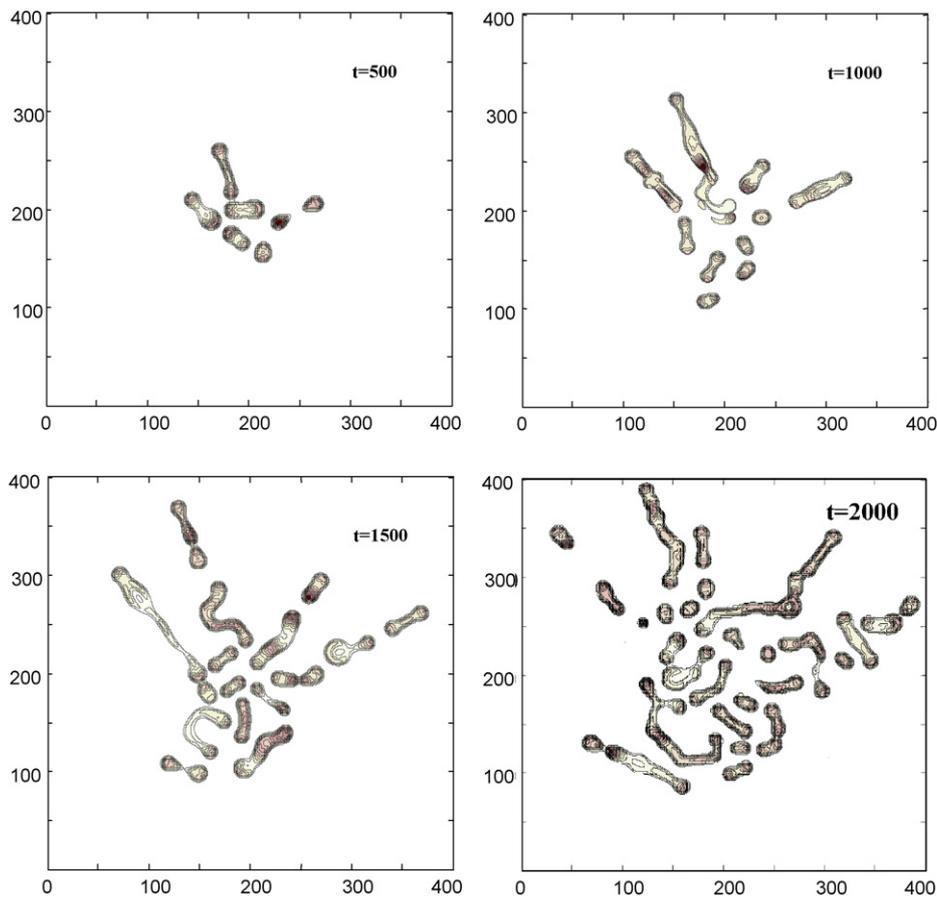


Fig. 7 – Snapshots for density u_1 of the edible prey in the one-predator-two-prey model (12)–(14) calculated at different moments of time for $\delta = 0.157$, other parameters are the same as in Fig. 5. Black colors signify high species density; white color signifies densities close to zero. The rate of spread is essentially different in different directions in space. Distribution of the predator is qualitatively similar; distribution of the inedible prey is the opposite to that of the edible prey.

$$\sigma \frac{u_1}{1 + \gamma_2 u_1} - \delta_2 > 0, \quad (29)$$

where u_0 , u_1 are the lower and the upper stationary stable densities of the prey in the bi-stable $u - v$ subsystem, see Fig. 9.

In this case the homogeneous stationary state with $u = u_0$, $v = v_0$, $w = 0$ ($x, y \in L \times L$) is stable and the homogeneous state $u = u_1$, $v = v_1$, $w = 0$ is unstable with regard to small perturbations. This property is a consequence of stability (or instability) of stationary states for local interactions in (23)–(25) when the $u - v$ subsystem is bi-stable and (28) and (29) holds. Local stability (or instability) will remain for the same model with diffusion when diffusion coefficients are close to each other.

We choose the mortality δ_2 of the second predator as the controlling parameter. For sufficiently large values of δ_2 , spread of the three species takes place via propagation of smooth traveling fronts. For a progressive decrease in δ_2 , smooth population fronts break to pieces and, thus, result into appearance of a patchy spread. Fig. 10 shows snapshots of prey densities obtained for: $\beta = 0.08$, $\sigma = 0.5$; $\gamma_1 = 1$, $\delta_1 = 0.07$, $\tilde{\delta}_1 = 0.23$, $\gamma_2 = 0.8$, $\delta_2 = 0.434$, $\tilde{\delta}_2 = 0.1$, $\varepsilon_1 = \varepsilon_2 = 2$ (this gives $u_0 \approx 0.91$, $v_0 \approx 1.77$) and the initial conditions (25)–(27) with $\Delta_{21} = 25$, $\Delta_{22} = 20$, $\Delta_{31} = 10$, $\Delta_{32} = 15$, $a = 10$, $b = 5$, $p = 5$, $p^* = 0.2$.

A small decrease in δ_2 (beginning with $\delta_2 = 0.427$) leads to extinction of the second predator and relaxation to the homogeneous distributions $u = u_0$, $v = v_0$ for the prey and the first predator respectively (for all initial conditions).

However, surprisingly, a further decrease in δ_2 restores coexistence of the two predators in the model for somewhat smaller values of δ_2 ($\delta_2 < 0.405$). This transition is not associated now with formation of patterns of patchy spread and a single round-shaped patch with oscillating borders is formed, the center of the patch is immobile. Absence of coexistence of the predators for the interval $0.405 < \delta_2 < 0.434$ signifies that for a successful persistence of the second predator its mortality should be either sufficiently small (to provide population survival) or relatively high (to reduce its trophic press on prey and let the prey attain high densities, which, in turn, will allow its own survival). It is interesting to note that within the whole interval $0.405 < \delta_2 < 0.434$, the same model without diffusion terms would predict a coexistence of the three species via stable periodical oscillations. Thus, competition models with and without space dimension may predict completely different outcomes.

Transition to a patchy spread, while varying δ_2 , takes place in a wide range of others model parameters provided that the $u - v$ subsystem is bi-stable (although the range of δ_2 , itself, is

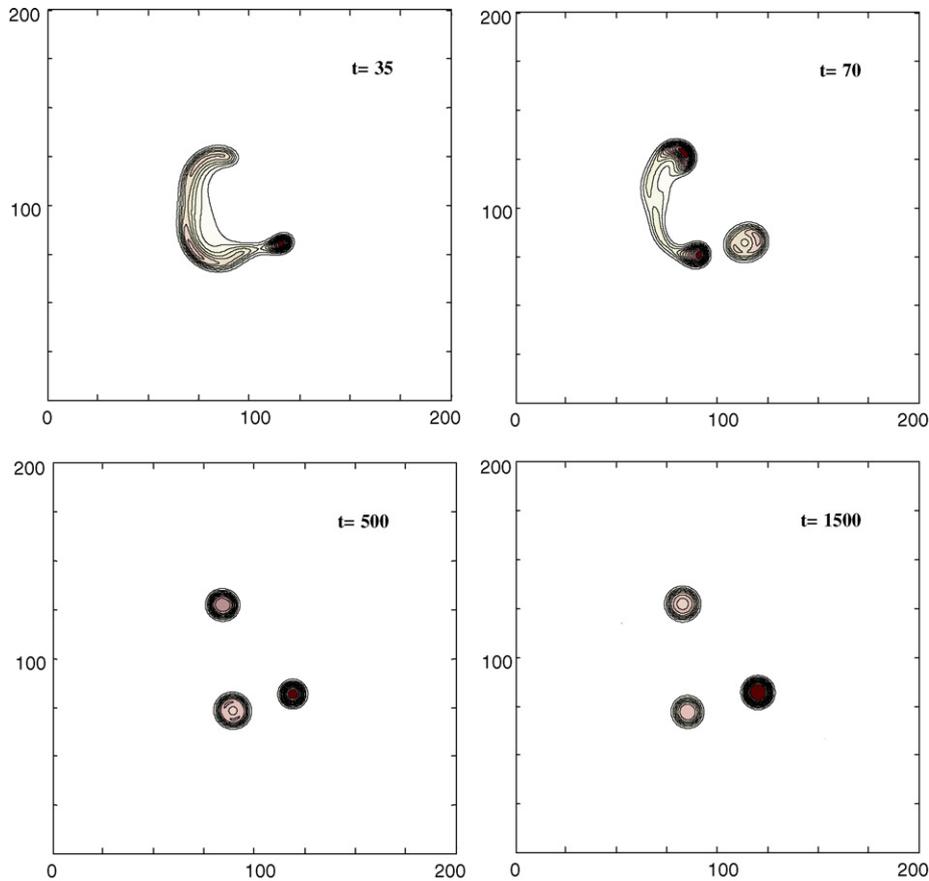


Fig. 8 – Snapshots for density u_1 of the edible prey in the one-predator-two-prey model (12)–(14) calculated at different moments of time for $\delta = 0.145$, other parameters are the same as in Fig. 5. Black colors signify high species density; white color signifies densities close to zero. Introduction of the inedible prey leads to persistence but do not result in a geographic spread. Distribution of the predator is qualitatively similar; distribution of the inedible prey is the opposite to that of the edible prey.

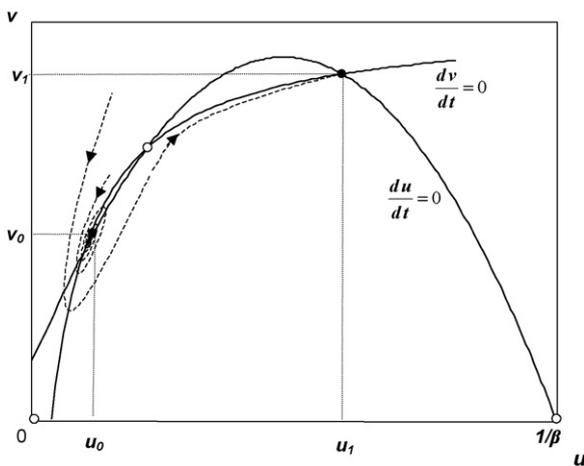


Fig. 9 – Local dynamics of the predator–prey system with closure term for predation (23) and (24). Schematic reciprocal positions of null-clines and phase portrait are shown in case of bi-stability. The two stationary stable states (u_0, v_0) and (u_1, v_1) are denoted by black filled circles, unstable stationary states are denoted by white filled circles.

rather narrow). In addition, we found that patchy spread can occur when $\delta_1 = 0, \delta_2 = 0$ (i.e. in absence of self-grazing in population of the second predator and when self-grazing term for the first predator prevails over its natural mortality). This takes place, for example, for $\sigma = 0.55, \delta_1 = 0.26, \delta_2 = 0.49, (\delta_1 = \delta_2 = 0)$ and other parameters the same as in Fig. 10. Note that a non-zero closure term δ_1 always remains a necessary property for the existence of a patchy spread in (20)–(22).

Thus, the analysis of the two-predator-one-prey model allows us to make an important conclusion: patchy spread is possible in a population model without Allee effect.

4. Discussion

In the previous sections, we showed by means of numerical simulations that patterns of deterministic patchy spatial spread arise in different multi-species reaction–diffusion models, the processes take place in a fully homogeneous environment. In other words, the spread of species via formation and movement of separated patches should not be attributed to a particular system or parameterization of system equations. Comparison of the above three models allows us to mark out some important features that are

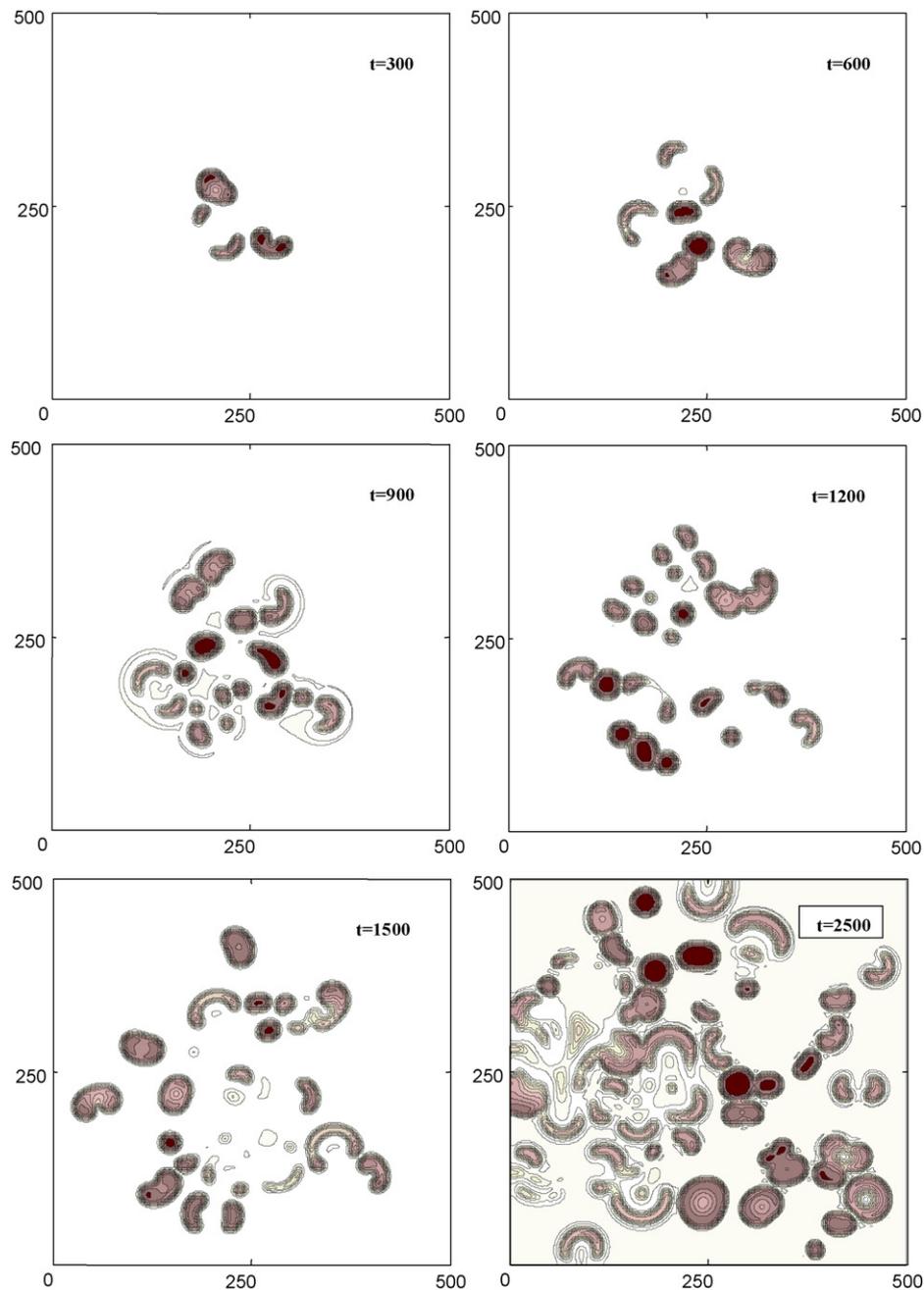


Fig. 10 – Snapshots of the density of the prey in the two-predator-one-prey model (20)–(22) calculated at different moments of time for parameters $\beta = 0.08$, $\sigma = 0.5$, $\gamma_1 = 1$, $\delta_1 = 0.07$, $\tilde{\delta}_1 = 0.23$, $\gamma_2 = 0.8$, $\delta_2 = 0.434$, $\tilde{\delta}_2 = 0.1$, $\varepsilon_1 = \varepsilon_2 = 2$ and initial conditions (25)–(27) with $\Delta_{21} = 25$, $\Delta_{22} = 20$, $\Delta_{31} = 10$, $\Delta_{32} = 15$, $u_0 = 0.91$, $v_0 = 1.77$, $a = 10$, $b = 5$, $p = 5$, $p^* = 0.2$. Black colors signify high species density, bright gray and white colors signify densities close to u_0 . Distribution of predator 1 is qualitatively similar; distribution of predator 2 follows that of the prey, and is close to zero in areas where the prey density is close to u_0 .

common for all models and necessary for the existence of patterns of patchy spread.

4.1. Basic features of dynamics of the patchy spread

In each model, there is a subsystem with a bi-stable dynamics characterized by two homogeneous stationary states. At the lower state, two types of perturbations are possible: transition to the upper state for a supercritical

perturbation and relaxation to the lower state for a subcritical perturbation. In the whole system, the bi-stability of the considered subsystem becomes violated (due to the presence of a predator or exploiter, which is a crucial factor in the models) and the upper homogeneous stable state disappears or loses its stability. On the contrary, the lower stationary homogeneous state persists and remains stable. The stability of the lower homogeneous stationary state becomes of vital importance for the

realization of patchy spread because it ‘absorbs’ all patches with small densities and sizes. Only ‘supercritical’ patches can survive.

Below we formulate some properties of spatiotemporal dynamics of the patchy spread regime which were found in all considered models.

- (1) The patchy spread is a spatiotemporal chaos. (We came to this conclusion by estimating the dominant Lyapunov exponents.)
- (2) For each model the patchy spread is observed for both equal and different diffusion coefficients.
- (3) The transition to patchy spread from regimes of propagation via continuous population fronts, when a model parameter is varied, takes place via different scenarios. In all models, we found the existence of the following succession of regimes: (i) propagation of circular waves with or without oscillations in the wake; (ii) spread of concentric rings; (iii) patchy spread; (iv) species extinction for all initial conditions. This succession takes place both for equal and for different diffusion coefficients. However, when the diffusivity of the predator is higher than that of the prey, some other scenarios become possible (Figs. 5–8 give examples of such a scenario; a thorough classification of patterns of successions leading to patchy spread will be the issue of our next study).
- (4) Transition to patchy spread from the regimes of propagations of smooth traveling fronts leads to an essential drop in the speed of invasion which indicates a transition to a new mechanism of population propagation in space.
- (5) For realization of patchy spread in a 2D system, the corresponding 1D system exhibits extinction regardless the choice of initial conditions (see also Morozov and Li, 2007).

Note that the above results agree with those obtained earlier in a predator–prey system with the Allee effect (Morozov et al., 2006) and in epidemic models (Petrovskii et al., 2005).

4.2. Influence of initial conditions

Initial conditions play an important role in realization of patchy spread in the considered models. For any parameter set, there always exist initial distributions leading to species extinction and only supercritical initial perturbations will result in a patchy spread. Along with the amplitude of initial perturbation, the shape of the initial distribution plays a crucial role. Note that the initial spatial distributions considered in this paper are not always ‘optimal’ to provide a patchy spread.

The point is that a patchy spread can be possible even when species extinction takes place for all parameters in (9)–(11), (17)–(19) and (25)–(27). For example, analysis of model (4)–(6) shows that for all parameters fixed at values as in Fig. 2, extinction takes place for $\delta < 0.698$ when we use initial distributions (9)–(11). However, when we consider initial conditions in the form of two multi-species patches, each of them described by (9)–(11) and separated from the other one by a certain distance, a patchy spread without extinction can be

observed for somewhat lower values of δ (we found patterns of patchy spread till $\delta = 0.696$). Moreover, initial distributions with more complex geometry allow a patchy spread even for smaller values of δ .

To determine when patchy spread and species persistence become impossible for any type of initial conditions, we used the following technique. First, we run simulations for parameters when patchy spread is still realizable for (9)–(11). For a certain moment of time we arrive at a distribution of species qualitatively similar to that from Fig. 2 for $t = 100$. Further, we use the obtained ‘embryo’ of patches as the initial condition for testing a neighbor parameter range (with smaller δ) where the use of initial distributions (9)–(11) leads to extinction. We denote by δ^* the smallest value of δ for which a patchy spread is observed by using the above technique. We obtained $\delta^* = 0.694$.

Another interesting issue is that the initial distributions considered in this paper can still provide patchy spread until δ^* when the environment is slightly heterogeneous in the vicinity of the domain of the original introduction of species. We considered the situation when a small circular area (with the radius about 1/10 of the whole domain) in the vicinity of the initially inhabited domain was characterized by a higher predator mortality (5–10% higher than in the rest of $L \times L$). We found that such environmental heterogeneity promotes formation of irregular embryo patches during the initial stage (regardless the shape of the initially inhabited domain) and it leads to a further patchy spread and species persistence. The considered heterogeneity serves only as a trigger for a further patchy spread since a successful spread takes place even if the heterogeneity is artificially removed later and the environment becomes homogeneous again. In other words, the environmental heterogeneity would enhance the deterministic patchy spread.

4.3. Ecological applications

There is growing evidence that the spread of exotic species often takes place via movement of separated population patches (Hengeveld, 1989; Shigesada and Kawasaki, 1997; Davis et al., 1998; Lewis, 2000; Kolb and Alpert, 2003). We showed that in different ecosystem models patchy spread would arise in a homogeneous environment as a result of a fully deterministic mechanism including a combination of local interactions among populations and a simple Brownian diffusion. The considered models predict that obligate mutualism and competition of native and exotic species are among the factors facilitating this phenomenon. In particular, we obtained that patchy spread can exhibit essentially different rates of invasion in different directions in space, which was earlier attributed only to the influence of environmental heterogeneity and not to some intrinsic mechanisms of population interactions (Shigesada and Kawasaki, 1997).

In the previous models of deterministic patchy spread (Petrovskii et al., 2002, 2005), the crucial factor making this pattern of dynamics possible was the assumption that the prey growth should be damped by the strong Allee effect. Our results confirmed that the Allee effect would enhance a patchy spread in reaction–diffusion models. This is observed in the model of obligate mutualism where the growth rate for each

mutualistic species becomes negative at low density. Also this model demonstrates that an exact expression for parameterization of the Allee effect is not crucial for the realization of a patchy spread. On the other hand, we showed that a patchy spread can be obtained also in a system without an Allee effect (in the two-predator-one-prey model). From this point of view, model (12)–(14) of two-prey-one-predator is of particular interest because it lies between the two mentioned cases.

The point is that model (12)–(14) was analyzed as the result of adding a predator into the diffusive Lotka-Volterra competition model. On the other hand, this model can be regarded as a diffusive predator-prey model (see Sherratt et al., 1995) when interactions take place in a (heterogeneous) dynamical environment constituted by the inedible prey. Although the prey growth is logistic in the initial system, it becomes affected by the strong Allee effect while placed in the environment constituted by the inedible prey (small amounts of edible prey will be eliminated due to competition with the inedible one). This idea seems to be important in ecological applications because it shows that for a realization of patchy spread in predator-prey systems it is not necessary for prey multiplication to be ‘explicitly’ damped by a strong Allee effect.

Note that the above mechanism might be a possible explanation for patchy invasion of tree species and forest mosaic observed in a real ecosystem (see Davis et al., 1998). The point is that along with other factors, the reported patchiness might be a result of interaction between trees and herbivorous. The system consists of hemlock, some other tree species (natural competitors of hemlock) and a predator (white-tailed deer) browsing the trees. Among the most important competitors of hemlock is sugar maple. Hemlock and maple are antagonists and one would replace the other one (Anderson and Loucks, 1979). It is known, as well, that hemlock is highly preferable by deer (Alverson et al., 1988). Thus the one-predator-two-prey model (12)–(14) (with u_1 and u_2 standing for the hemlock and maple densities, and v standing for deer density) can be a possible candidate to explain the observed patchiness.

While studying the persistence of mutualistic species under exploitation, Yu et al. (2001) argued that the spatial dimension can be of vital importance and lamented the lack of mutualist-exploiter models with an explicit space. Wilson et al. (2003) developed a lattice model including environmental stochasticity and studied a possibility of spatial patterns due to the Turing scenario in a mutualist-exploiter (plant-pollinator-exploiter system) system. Our results obtained from a reaction-diffusion mutualism-exploiter model confirmed the conclusion made by Wilson et al. (2003) (coexistence of mutualists and an exploiter, often impossible in a non-spatial model, becomes possible in models with explicit space). However, we predict a formation of patches of high densities of mutualists (see Fig. 2) separated by space with very low densities even for equal dispersal rates of plants, pollinator and exploiter.

Another important application of the paper results concerns the understanding of mechanisms of coexistence of competitive species, which is one of the central problems in ecology (Chesson, 2000). Among important factors facilitating coexistence and preventing extinction is the predation on

competing species, which can result in a ‘predator-mediated coexistence’ (Caswell, 1978; Crowley, 1979). On the other hand, it was demonstrated that the space may be an important factor facilitating coexistence; in particular, a dispersal-mediated coexistence often arises in spatially varying environments (see Holmes et al., 1994 for references). The analysis of (12)–(14) demonstrates that for the parameters corresponding to a patchy spread none of the two mentioned factors alone can lead to a successful coexistence (coexistence becomes impossible both in a nondiffusive system with a predator and in a diffusive system without a predator). However, a combination of the factors makes the coexistence of the three species possible. Another important condition of coexistence is the two-dimensionality of the environment; this factor is not always taken into account while considering competition models in space.

While modeling the coexistence of two predators consuming one prey, we found that the self-grazing of predators allows a stable coexistence of the predators. Earlier models (Hsu et al., 1978; Smith, 1982) show that the only possible coexistence of the predators takes place in an oscillatory regime. Another interesting result is that there is a surprising discrepancy between non-spatial and spatial approaches: for a wide range of parameters providing patterns of coexistence in space, the same system without diffusion often predicts extinction of the second predator. On the contrary, in case when a non-homogeneous coexistence of species (i.e. a coexistence via formation non-homogeneous spatial patterns) is impossible, local dynamics can exhibit stable oscillations of all species (see the end of Section 3.2). Thus, taking into account the space can be crucial for analysis of successful coexistence of the predators.

5. Concluding remarks

The main goal of this paper is to demonstrate that a deterministic patchy spread in homogeneous environment can be found in reaction-diffusion models of ecosystems of different nature. Following this purpose, we were more concerned with showing patterns of patchy spread and did not consider the dynamics of each model in every detail. We are certain that along with the above cases, patterns of the deterministic patchy spread can be easily found in other multi-species models.

However, this paper should not be considered as denying the importance of environmental or/and demographic stochasticity (or landscape fragmentation) in formation of patterns of spatial species spread. It would be unwise to explain such a complex phenomenon as patchy spread as due to realization of only one mechanism or process. Here we show that local population interactions and a simple Brownian diffusion together would lead to patterns of spread (in different ecosystem models), which are similar to those obtained from different assumptions on the environment and species dynamics (cf. Lewis and Pacala, 2000; Lewis, 2000). We argue that while studying an ultimate cause of patchy spread for a particular ecosystem, a comprehensive research should include estimating the impacts of both stochastic and deterministic factors. Such a detailed investigation always requires a

large data set (including spatial distribution of both native species and exotic species) which is not often available. It is certain, however, that only applying such a detailed approach we might be sure about understanding the real causes of spread of patches in every reported case.

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