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Spatiotemporal complexity of biological invasion in a space- and time-discrete predator–prey system with the strong Allee effect

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A B S T R A C T

Understanding dynamical complexity of alien species invasion is an important and timely issue as it is believed that identification of possible invasion scenarios may result in a more effective invasive species management and control. To address this issue, mathematical modeling is widely recognized as a convenient theoretical tool as it often helps to reveal generic tendencies in a situation when it would hardly be possible otherwise. However, although much attention has been paid to spatially continuous models of biological invasion, spatially discrete models have remained outside of the mainstream. Meanwhile, species habitat is often distinctly patchy or even fragmented, and then spatially discrete models seems to be the most appropriate modeling framework. In this paper, we consider invasion scenarios in a space- and time-discrete system described by a coupled map lattice. The alien species is assumed to be affected by the strong Allee effect and by a specialist predator. We first consider the stage of species introduction and obtain analytical conditions to distinguish between invasion success and invasion failure. We then focus on species spatial spread. By means of extensive computer simulations, we identify the main scenarios of species spread (e.g. patchy invasion and multiple traveling bands) and reveal the corresponding structure of the parameter space. Counter-intuitively, we have found that alien species can invade over the whole domain even in the case when its local persistence would not be possible.

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1. Introduction

Biological invasions have been attracting considerable attention over the last few decades as they have a significant impact on biodiversity, agriculture, forestry and fishery all over the world (Pimentel, 2002). Understanding of typical invasion scenarios, revealing relevant inter- and intra-specific interactions and identification of the factors affecting the rate and the pattern of species spread are important issues both for theoretical and practical ecology. In a somewhat more general context, biological invasion is a factor related to ecosystems complexity, although its effect can be controversial. One the one hand, since invasion can follow a complicated dynamical scenario (cf. Petrovskii et al., 2005a,b), it apparently makes ecosystem dynamics more complex. On the other hand, on a longer time-scale, invasion tends to simplify the ecosystem structure by reducing its biodiversity.

A regular empirical study of biological invasion (which implies replicated experiments) is, for obvious reasons, rarely possible. A typical field study is reduced to observation and data collection which, although being a source of important information (e.g., see Fagan and Bishop (2000)), rarely makes it possible to reveal general tendencies. In this situation, mathematical modeling and simulations provide a convenient virtual laboratory and may be regarded, to a certain extent, as a substitute to a real experiment. Indeed, a lot of important insights into invasion properties have been made by considering the properties of relevant mathematical models (Shigesada and Kawasaki, 1997; Owen and Lewis, 2001).

In the previous studies, the choice of the model to describe biological invasion has been somewhat biased towards space-continuous models such as diffusion-reaction systems (Shigesada and Kawasaki, 1997; Petrovskii and Li, 2006) or integro-difference systems (e.g., Kot and Schaffer, 1986; Kot et al., 1996). Meanwhile, the environment properties are often patchy and sometimes can even be regarded as discontinuous (e.g., in case of a fragmented habitat). Correspondingly, it should be described more adequately by a space discrete system. However, space- and time-discrete models of invasion have rarely been considered systematically and the understanding of their properties is largely lacking.
In this paper, we provide a thorough investigation of biological invasion in space- and time-discrete settings. The corresponding model is given by a coupled map lattice (Kaneko, 1986; Hassell et al., 1991; Comins et al., 1992; White and White, 2005). We assume that the alien species is affected by the strong Allee effect, which is known to be typical in ecological populations (Dennis, 1989; Courchamp et al., 1999, 2008) and was proved to be especially important in biological invasions (Taylor and Hastings, 2005). We also assume that the alien species is affected by predation and hence can be regarded as a 'prey.' We first consider the "problem of critical aggregation" (Lewis and Kareiva, 1993; Kot et al., 1996; Petrovskii and Li, 2006) to show that successful invasion is only possible if the prey size in the initially infested site exceeds a certain threshold value. The value of the threshold is found analytically.

In case the initial size of the alien species is overcritical, the species starts spreading over space. By performing extensive computer simulations we show that, depending on parameter values, there can be a variety of invasion scenarios. Interestingly and rather counter-intuitively, the discreteness of the system has little effect and most of the invasion scenarios are qualitatively similar to those earlier observed in space-continuous systems such as, for instance, propagation of a traveling front with formation of chaotic pattern in the wake (cf. Sherratt et al., 1997) and species spread by means of 'traveling bands,' i.e. by formation of expanding ring-like structures (Petrovskii et al., 2002b; also see Malchow et al. (2008)). In particular, for the parameters' range for which the species would not be viable in the non-spatial case, on a 2D lattice we observe "patchy invasion" (Petrovskii et al., 2002a, 2005b; Morozov et al., 2006) when the spread is not preceded by the propagation of a continuous population front.

The paper is organized as follows. In Section 2, we briefly revisit the properties of the corresponding non-spatial model. Although the spatiotemporal dynamics of the system can by no means be reduced to the properties of the non-spatial one, the latter provides an important 'skeleton' which helps to understand and to explain the behavior of the spatially extended system. In Section 3, we consider the early stages of invasion, i.e. species introduction and establishment, and show that, apart of the above-mentioned criticality, the system exhibits a complicated dependence on dispersal rates so that invasion failure and invasion success may alternate. In Section 4, we reveal typical scenarios of alien species spread for different initial conditions. Finally, in Section 5 we discuss ecological implications of our results.

2. Model

We consider a two-dimensional rectangular lattice where to each node (or 'site') of the lattice we ascribe two real numbers, i.e. the prey size and the predator size. These numbers can change in the course of the system dynamics due to the local inter- and intra-specific interactions such as birth, death and predation, and due to migration between different sites.

The dynamics at each discrete step from to to + 1 consists of two distinctly different stages, i.e. the dispersal stage and the 'reaction' stage. The dispersal stage is described by the following equations:

\[ N'_{xy,t} = (1 - \mu_N)N_{xy,t} + \sum_{(i,j) \in V_{xy}} \frac{\mu_N}{4} N_{ij,t} \]  

\[ P'_{xy,t} = (1 - \mu_P)P_{xy,t} + \sum_{(i,j) \in V_{xy}} \frac{\mu_P}{4} P_{ij,t} \]  

where \( N_{xy,t} \) and \( P_{xy,t} \) are the prey and predator sizes, respectively, at site \((x, y)\) at time \(t\) (where \(x, y\) and \(t\) are integer numbers), \( N'_{xy,t} \) and \( P'_{xy,t} \) are the sizes after dispersal. The dispersal rates \( \mu_N \) and \( \mu_P \) give the populations fractions of the prey and predator, respectively, that, at each time step, migrate or disperse to other sites of the lattice. We assume that dispersal occurs only to the four nearest sites (in particular, neglecting the contribution of long-jump dispersal), so that the 'dispersal stencil' is given as \( V_{xy} = \{(x-1,y), (x+1,y), (x,y-1), (x,y+1)\} \).

In its turn, the reaction stage is described as

\[ N_{xy,t+1} = f(N_{xy,t}P_{xy,t}) \]  

\[ P_{xy,t+1} = g(N_{xy,t}P_{xy,t}) \]  

where \( f \) and \( g \) take into account the specifics of the interactions.

2.1. Local population dynamics

We first briefly consider the properties of the corresponding nonspatial model, i.e. \( N_{t+1} = f(N_tP_t) \) and \( P_{t+1} = g(N_tP_t) \). The focus of this paper is on the population dynamics subject to the strong Allee effect. The Allee effect has been shown to be very common in population dynamics (Dennis, 1989; Stephens and Sutherland, 1999; Courchamp et al., 1999, 2008); therefore, a model taking it into account is expected to provide a more realistic description of many processes going on in an ecosystem.

We assume that the Allee effect affects the growth of prey so that the dependence of \( f \) on \( N_t \) can be described by an S-shaped curve. For the impact of predation on the prey growth, we use a standard Nicholson–Bailey-type model. Correspondingly, we consider the following equation for the prey:

\[ n_{t+1} = \alpha(n_t)^2 \exp(-\gamma n_t/\beta) \]  

where \( n \) and \( p \) are the prey and predator sizes, respectively, \( \alpha \) is the prey intrinsic growth rate and \( \gamma \) is the predator efficiency. Note that \( 1/\beta \) has the meaning of the prey density when its per capita growth rate reaches its maximum value.

For the predator dynamics, we focus on the case when the predator is a specialist predator, so that it cannot survive in the absence of its prey and use the simplest parametrization:

\[ p_{t+1} = \delta n_t p_t \]  

where \( \delta \) is the predator growth rate.

For convenience, we scale the population sizes as

\[ N_t = \delta n_t \]  

\[ P_t = \gamma p_t \]  

so that, in the new variables, Eqs. (5) and (6) takes the following form:

\[ N_{t+1} = \frac{r(N_t)^2}{1 + b(N_t)^2} \exp(-P_t) \]  

\[ P_{t+1} = N_t P_t \]  

where \( r = \alpha/\delta \) and \( b = (\beta/\gamma)^2 \) are new dimensionless parameters. Since Eqs. (8) and (9) correspond to the 'reaction' stage of the system dynamics, in the following we will call \( b \) and \( r \) the reaction parameters.

It is readily seen (for details, see Rodrigues et al., in press) that the system ((8) and (9)) has at most four steady states, i.e., the extinction state \((0,0)\), two 'prey-only' states \((N_1, 0)\) and \((N_2, 0)\) and the coexistence state \((N^*, P^*)\) where

\[ N_1 = \frac{r - \sqrt{r^2 - 4b}}{2b}, \quad N_2 = \frac{r + \sqrt{r^2 - 4b}}{2b} \]  

A predator–prey system subject to a weak Allee effect has been studied in our recent work; see Rodrigues et al. (2011).
\[ (N^*, P^*) = \left( 1.1 \ln \left( \frac{r}{b+1} \right) \right). \]  

(11)

While \((0, 0)\) always exists, the boundary states \((N^*_1, 0)\) and \((N^*_2, 0)\) are only feasible for \(r > 2\sqrt{b}\). They merge for \(r = 2\sqrt{b}\) and disappear for \(r < 2\sqrt{b}\). The coexistence state \((N^*, P^*)\) is feasible for \(b + 1 < r\).

\[ r < r_{cr} = (b + 1) \exp \left( \frac{b - 1}{b + 1} \right). \]  

(12)

Applying the linear stability analysis, it is readily seen that \((0, 0)\) is always stable. \((N^*_1, 0)\) is always unstable while \((N^*_2, 0)\) is stable for \(2 < r < b + 1\). Correspondingly, \((N^*_2, 0)\) can only be stable for \(b > 1\). The coexistence state appears to be stable for \(r < r_{cr} = (b + 1) \exp \left( \frac{b - 1}{b + 1} \right)\).

The corresponding structure of the parameter plane \((b, r)\) is shown in Fig. 1 and the results about the steady states, existence and stability are summarized in Table 1. The coexistence equilibrium is feasible and stable for parameters from domain A. The solid curve in Fig. 1 corresponds to \(r = r_{cr}\), see (13), where \((N^*, P^*)\) loses its stability through the Hopf bifurcation. On this line, the determinant of the Jacobian matrix at the coexistence equilibrium is equal to one; see Allen (2007) for details. Inside domain B the local dynamics is oscillatory according to the (multipoint) limit cycle. When crossing the long-dashed curve (obtained numerically), the limit-cycle disappears so that, for parameters from domain C, the only attractor is the extinction state. The straight dotted line corresponds to \(r = b + 1\), cf. (12); therefore, for domains D, E and F the coexistence state does not exist. In particular, in domain E, the only steady state is \((0, 0)\), and in domains D and F (above the short-dashed curve which corresponds to \(r = 2\sqrt{b}\)) also the two ‘prey only’ states exist. The prey only equilibrium \((N^*_1, 0)\) is never stable while \((N^*_2, 0)\) is stable for parameter values inside region F. We therefore observe that in regions A and F the system exhibit bistability; see Table 1.

### 3. Species introduction and establishment

It is well known that biological invasion consists of three distinctly different stages such as (i) alien species introduction, (ii) establishment and (iii) spatial spread (Shigesada and Kawasaki, 1997). Not every introduction results in successful invasion. Especially when the population growth is affected by the strong Allee effect, successful establishment (and, eventually, spread) is only possible when the initial population size is above a certain critical value. While this problem is relatively well understood in space-continuous systems (Lewis and Kareiva, 1993; Kot et al., 1996; Petrovskii and Li, 2006), no work has been done to reveal the conditions of successful/unsuccessful alien species establishment in discrete systems. This problem is addressed in this section.

#### 3.1. Single species invasion

We begin with a simpler case when the impact of predation on the introduced species can be neglected. In order to make the problem analytically tractable, instead of the true prey growth function \(f(N)\), we use its piecewise-constant caricature:

\[ \hat{f}(N) = \begin{cases} N^2 - H(N - N^*_1) & \text{for } N < H(N - N^*_1) \\ \text{constant} & \text{for } N \geq H(N - N^*_1) \end{cases} \]  

(14)

(cf. Kot et al., 1996) where \(H(x)\) is the Heaviside step function; see Fig. 2.

The corresponding population dynamics is thus described by the following system:

\[ N_{x,y,t} = (1 - \mu_N)N_{x,y,t} + \sum_{(x',y') \in V} \frac{\mu_N}{4} N_{x',y',t}, \]  

(15)

\[ N_{x,y,t+1} = \hat{N}_H(N_{x,y,t} - N^*_1). \]  

(16)

### Table 1

<table>
<thead>
<tr>
<th>Domain</th>
<th>((0, 0))</th>
<th>((N^*_1, 0))</th>
<th>((N^*_2, 0))</th>
<th>((N^<em>, P^</em>))</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Stable</td>
<td>Unstable</td>
<td>Unstable</td>
<td>Stable</td>
</tr>
<tr>
<td>B</td>
<td>Stable</td>
<td>Unstable</td>
<td>Unstable</td>
<td>Unstable</td>
</tr>
<tr>
<td>C</td>
<td>Stable</td>
<td>Unstable</td>
<td>Unstable</td>
<td>Unstable</td>
</tr>
<tr>
<td>D</td>
<td>Stable</td>
<td>Unstable</td>
<td>Unstable</td>
<td>Unstable</td>
</tr>
<tr>
<td>E</td>
<td>Stable</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>F</td>
<td>Stable</td>
<td>Unstable</td>
<td>Stable</td>
<td>-</td>
</tr>
</tbody>
</table>

*means that the state is not feasible.

**Fig. 1.** The structure of the reaction parameters’ space for the system (8) and (9); see details in the text.
It is readily seen that the population growth during the ‘reaction stage’ will lead to \( N_{x,y,t+1,1} = 0 \) for \( N_{x,y,t} < N_1 \) and it will lead to \( N_{x,y,t+1} = N_2 \) for \( N_{x,y,t} \geq N_1 \).

We consider the case that the alien species is initially released, at its carrying capacity \( N_2 \), in a single site \( p \) which we assume to be sufficiently away from the domain boundary in order to exclude the effect of boundary conditions. As a result of the dispersal, the species spreads into the four neighboring sites. Since these sites are identical, it is sufficient to consider the evolution of the population size only in one of them, which we denote as site \( q \).

The spread into site \( q \) will be successful if and only if the density after dispersal exceeds the Allee threshold:

\[
N_q' = \frac{\mu_N}{4} N_2 > N_1, \tag{17}
\]

that is,

\[
\mu_N > \frac{4N_1}{N_2}. \tag{18}
\]

After the first step, all four neighbors \( q \) of the site \( p \) are invaded. It is readily seen that condition (18) is sufficient to ensure that, at the second step, all the neighbors of the sites \( q \) are invaded and, obviously, this process will go on until the spreading species reaches the boundary and the whole domain is occupied. Condition (18) therefore guarantees that species introduction results in its spatial spread.

On the other hand, a successful species establishment at the site \( p \) of initial introduction takes place if and only if the prey size remaining there after dispersal does not fall below the Allee threshold, that is,

\[
N_p' = (1 - \mu_N) N_2 > N_1, \tag{19}
\]

that is,

\[
\mu_N < 1 - \frac{N_1}{N_2}. \tag{20}
\]

Condition (20) thus ensures that species introduction results in its successful establishment but it tells nothing about the possibility of spread.

All possible outcomes from the species introduction can then be obtained by combining conditions (18) and (20); see Fig. 3. For parameters from domains I and III, condition (20) holds, which guarantees that the species establishment will be successful. However, only for parameters from domain I the establishment is followed by the spatial spread. For parameters from domain III, an alien species introduced at a certain site \( p \) will remain confined to this site. This may be regarded as ‘invasion pinning’ due to the inherent heterogeneity of the spatially discrete system (cf. Keitt et al., 2001). Note that this situation is drastically different from the predictions of continuous single-species models (e.g. Petrovskii and Li, 2006) where the alien species either goes extinct or spreads over the whole domain but cannot survive locally.

Apart from domain I, spatial spread takes place also for parameters from domain II. The difference is in the pattern of spread. While for domain I the species distribution in the wake of spread is homogeneous, \( N_{x,y,t} = N_2 \), for domain II oscillations and patterns can be observed.

For parameters from domain IV, neither of conditions (18) and (20) holds and the alien population goes extinct. Note that extinction only becomes possible when \( \kappa = N_1/N_2 > \kappa' \) where \( \kappa' = 1/5 \) is the position of the righthand-side-most point of domain I. We also want to mention that the value of \( \kappa \) depends only on the system’s geometry, i.e. on the ‘dispersal stencil,’ but not on the systems parameters. For instance, \( \kappa' = 1/3 \) in a 1D lattice, and \( \kappa' = 1/9 \) in a 2D lattice where the number of neighbors is increased to eight by including the sites connected with diagonal lines.

Interestingly, for the values of \( \kappa \) just slightly greater than \( \kappa' \), the system dynamics may show a certain ‘intermittency’ with respect to an increase in \( \mu \). For small \( \mu \), introduction results in a successful (local) establishment but not in spread. For intermediate values \( \mu \sim 1 - \kappa' \), introduction results in species extinction. However, for a larger \( \mu \), invasion becomes successful again so that the introduction is followed by a spatial spread. As well as with the invasion pinning, this situation is essentially different from what is observed in continuous single-species models.
We want to emphasize that, for the model with the piecewise constant growth rate (14), the conditions (18) and (20) of successful species spread or establishment are exact. However, it yet remains to find out what may happen in the model with continuous growth rate, i.e. when Eq. (16) is replaced with

\[
N_{x,y,t+1} = \frac{r (N'_{x,y,t})^2}{1 + b (N''_{x,y,t})^2}, \tag{21}
\]

cf. (8). In order to address this issue, the system (15) and (21) was studied in numerical simulations. We used the same initial conditions as above, i.e. that at \( t = 0 \) a single site is invaded with the alien population at its carrying capacity. The results are given in Table 2. We therefore observe that, although the properties are qualitatively similar between the two models (in particular, showing the intermittency in the invasion success and a possibility of the invasion pinning), the value of the critical parameter(s) and the specific succession of regimes are different.

The above results are obtained for the case when introduction takes place in a single site. However, the situation can be somewhat different when more than one site is initially inhabited. In order to address this case, we considered the situation when the alien species is introduced in a square domain of \( n \times n \) sites in the middle of the lattice. Specifically, we considered \( n = 2, n = 3 \) and \( n = 4 \). We consider the growth function as given by (21) with parameters \( r = 4.8 \) and \( b = 2.7 \), which corresponds to the second row in Table 2. Since this problem is not analytically solvable, we studied it through simulations. We obtained that the introduction results in spatial spread for \( \mu_N \geq 0.2 \), but the alien population remained confined (pinned) in its initial region for \( \mu_N \leq 0.1 \). A generic conclusion is therefore that the success of the invasion depends on the size of the initially inhabited region, the larger is the region the more likely invasion to be successful. The situation is thus similar to what is known as a "problem of critical aggregation" in continuous systems (Lewis and Kareiva, 1993; Kot et al., 1996; Petrovskii and Li, 2006).

We also want to mention that, obviously, for the model with the piecewise constant population growth the rate of the population spread\(^1\) is exactly one, i.e. one site per time-step. However, the rate of spread can be lower in the model with the continuous growth rate function \( f(N) \).

### 3.2. Effect of predation

Understanding of the conditions of successful establishment and spread of alien species becomes much more difficult when the species is affected by predation. Even in the simplest case of the piecewise growth of prey, the analytical expressions appear to be bulky and not instructive, in particular, because they now contain more equations and more parameters. Since the main goal of this paper is to identify the main scenarios of species spread, we therefore avoid considering this issue in detail and provide only a brief overview of the general tendencies induced by the impact of predation. We consider the situation when the predator is introduced at the same site as the (alien) prey and soon after the introduction of the alien species (which, in practical terms, may be regarded as biological control strategy) so that at \( t = 0 \) both species are present. Dispersal takes place as described by the Eqs. (1) and (2).

We have observed that the presence of predator tends to decrease the size of the parameter range where the successful establishment and/or spread takes place. Generally, the invading prey has the less chances to succeed the larger is the initial size of the predator population for the apparent reason that the impact of predation put an additional pressure on the prey population that can push its size below the Allee threshold. Intermittency with respect to different parameters has been observed so that the parameter ranges corresponding to successful invasion are separated by the range(s) where invasion fails. Successful establishment without spread (invasion pinning) can happen either for both species or for prey only: in the latter case the predator goes extinct. We also want to mention here that, since we consider a specialist predator, extinction of prey inevitably results in extinction of predator.

### 4. Regimes of spatial spread

Once the impact of the Allee effect and/or predation is not strong enough to ensure the alien species extinction or pinning, the species starts spreading over the space. Now we proceed to analysis of regimes of spread in the system described by Eqs. (1)–(4) with (8) and (9). The system is studied by means of extensive numerical simulations in a square \( 100 \times 100 \) domain for different reaction parameters \( r \) and \( b \) and different dispersal rates \( \mu_N \) and \( \mu_P \). At the domain boundary, the no-flux conditions are used.

The system’s dynamics depends to a certain extent on the choice of the initial conditions. Therefore, in order to gain a broader view of the system properties, we consider two somewhat different types of the initial species distribution, which we will call Type I and Type II initial condition, accordingly. The main difference is the presence or absence of symmetry. For symmetric Type I initial condition, we consider that the prey population is at its equilibrium, \( N_{2x} \), in the \( 3 \times 3 \) square domain at the center of the habitat, while the predator is released only in the central site with the population size \( P \). For asymmetric Type II initial condition, prey population initially occupies the rectangle \( 48 \leq x < 53 \) and \( 47 \leq y < 55 \) at its equilibrium value \( N_{2x} \), while predator is initially present inside the rectangle \( 48 \leq x < 51 \) and \( 47 \leq y < 50 \) at \( P \). Note that, since the focus of this section is on the regimes of spatial spread, for both types of the initial conditions we avoid the situations when invasion is terminated due to either insufficient initial prey size or excessive predator size.

For the sake of brevity, in most of the figures below, we only show the snapshots of the prey distribution as the spatial distribution of predator exhibits qualitatively similar features.
4.1. Type I: symmetric initial condition

We begin with a general observation that the regime of species spread depends significantly on the properties of the corresponding non-spatial system, i.e. on the value of parameters $r$ and $b$. It can also depend on dispersal rates $\mu_N$ and $\mu_P$. Correspondingly, we performed simulations for parameters chosen from different regions of the system’s $(b, r)$ parameter plane, see Fig. 1, and for different combinations of $\mu_N$ and $\mu_P$.

We first consider parameter region A where the coexistence state is stable, and choose $r = 4.8$ and $b = 2.7$. The general tendency that we observe in simulation results is that both populations remain confined in the prey original range for sufficiently small $\mu_N$. In particular, for $\mu_N = 0.1$ we observe invasion pinning occurring for any $0 < \mu_P < 1$. However, for a larger value of $\mu_N$ invasion success depends also on the predator dispersal rate. In particular, for $\mu_N = 0.2$, invasion pinning is observed for $\mu_P \leq 0.4$. For $\mu_N = 0.2$ and $\mu_P \geq 0.5$, the initially occupied region increases slightly, then resulting in the invasion pinning.

For $\mu_N \geq 0.3$, the species spread occurs for any value of $\mu_P$. The spread takes place through the propagation of a traveling front; see Fig. 4a and b. The corresponding total population size of prey and predator is shown in Fig. 5a. We observed that the speed of the front depends on the dispersal rate of both species so that it increases with an increase in the prey dispersal rate and decreases slightly with an increase in the predator dispersal rate.

We now proceed to parameter region B of Fig. 1 where the dynamics of the nonspatial system is oscillatory due to the existence of a stable multipoint limit cycle. Specifically, we choose $r = 4.5$ and $b = 2$. The two regimes of the system dynamics that we observe in simulations are (i) the invasion pinning with the population densities in the inhabited area exhibiting oscillations and (ii) species spread through the propagation of a population front with oscillations in its wake. The general tendency remains similar to that observed above for parameters from region A, i.e. the invasion is typically pinned for small $\mu_N$ and the spread occurs more often for large $\mu_N$. In particular, for $\mu_N \leq 0.2$, both species remain confined for any value of $\mu_P$. The initially inhabited area can grow slightly (e.g. as observed for $\mu_N = 0.2$ and $\mu_P \geq 0.3$) but the species do not succeed to spread.

For $\mu_N \geq 0.3$ both species invade the habitat exhibiting oscillations in the wake of the invasion. Figs. 4c and d show, respectively, the prey and predator spatial distribution obtained for $r = 4.5$, $b = 2$, $\mu_N = 0.4$ and $\mu_P = 0.8$. The corresponding total population size of prey and predator is shown in Fig. 5b. We mention here that the speed of the propagating population front appears to be approximately proportional to $\mu_N$ (being approximately equal to $1/3\mu_N$ for the given $r$ and $b$) but shows only insignificant dependence on $\mu_P$.

Note that the pattern in the wake of invasion front can change significantly if the dispersal rates satisfy the condition of the Turing diffusive instability on the lattice (White and White, 2005; Rodrigues et al., 2011), which normally implies that either $\mu_N\mu_P < 1$ or $\mu_N/\mu_P > 1$. Following Neubert et al. (1995), we distinguish between the so called “plus-one” and “minus-one” Turing bifurcations as, indeed, the dynamics can sometimes be
different for these two cases (Rodrigues et al., in press). Since the corresponding analysis is rather long and bulky, we are not able to give the mathematical details for these bifurcations and an interested reader is advised to check the existing literature; e.g. see Neubert et al. (1995), White and White (2005), Rodrigues et al. (2011). For the reaction parameters in region A and dispersal rates in the region of the “plus-one” Turing bifurcation (which, for the system (1)-(4) with (8) and (9), requires that \( \mu_N/\mu_P \gg 1 \), the propagating invasion front is followed by the formation of stable heterogeneous structures; see Fig. 6a and b obtained for \( r = 3.5, b = 2.0, \mu_N = 0.9 \) and \( \mu_P = 0.01 \). Once the species occupy the whole domain, the resulting spatial distribution of prey and predator is heterogeneous and stationary; see Fig. 6c. Fig. 6d shows how the corresponding total population size of prey and predator changes with time. The situation is similar in the case the dispersal rates are in the region of “minus-one” Turing bifurcation (which requires \( \mu_N/\mu_P \ll 1 \); we do not show it here for the sake of brevity. The situation becomes qualitatively different when the reaction parameters are in region B and dispersal rates are in the region of the plus-one Turing bifurcation. In this case, in the wake of the traveling population front an oscillating heterogeneous pattern emerges (see Fig. 7 obtained for \( r = 4.5, b = 2, \mu_N = 0.9 \) and \( \mu_P = 0.002 \)), which eventually occupies the whole domain (Fig. 7c). Fig. 7d shows the corresponding total population size of prey and predator over time. The combination of the distinctly irregular, non-stationary spatial pattern with the irregular oscillations in time (cf. Fig. 7c and d) points out at the spatiotemporal chaos. Situation appears to be similar when the dispersal rates are in the region of the minus-one Turing bifurcation; we do not show it here for the sake of brevity.

The spatiotemporal dynamics becomes more complicated for parameters from region C. For a hypothetical choice of parameters as \( r = 4.2 \) and \( b = 0.7 \), a variety of different regimes is found for different choice of the dispersal rates; see Figs. 8–10.

Fig. 8 shows the pulse-like regime of invasion (obtained for \( \mu_N = 0.8 \) and \( \mu_P = 0.5 \)) which we also call the regime of traveling band. The prey is concentrated inside a narrow ring-shaped region, the radius of the ring growing with time. The predator exhibits a similar pattern forming a ring of a slightly smaller radius as a result of their pursuit of prey. Interestingly, this regime of spread finally
results in invasion failure. Once the rings are, eventually, pushed to the domain boundary (Fig. 8e, f), both species go extinct. Since the domain boundary is impenetrable (due to the no-flux condition) and the prey pulse is followed by the pulse of predators, there is no way to escape, so that finally all prey population is consumed which, in its turn, leads to the extinction of their specialist predator. The corresponding total population size over time is shown in Fig. 12a.

A completely different regime of species spread is shown in Fig. 9 (obtained for $\mu_N = 0.5$ and $\mu_P = 0.8$). In this case, no continuous traveling front is formed and the spread takes place through formation and movement of separate patches of high population density. Correspondingly, we will call this regime the “patchy invasion” (cf. Petrovskii et al., 2002a, 2005b; Morozov et al., 2006). The patch dynamics follows a complicated scenario: the patches can move, split, merge and split again, eventually
resulting in an intricate spatial pattern. The size of the invaded region grows with time so that finally the species invade over the whole domain proving the invasion success. The total population of prey and predator can be seen in Fig. 12b. Note that, since the initial conditions are symmetric, the corresponding solution of our system (1)–(4) is symmetric as well.

Interestingly, although at each moment the spatial pattern exhibits a high degree of regularity, the total population size shows irregular oscillations indicating chaotic dynamics. This result is in a good agreement with our earlier work on continuous systems (see Morozov et al., 2004) where it was shown that, in the case when the prey is hampered by the strong Allee effect, the predator–prey system may show a chaotic temporal dynamics but possesses a very simple spatial structure.

The system’s dynamics becomes different again for $\mu_N = 0.7$ and $\mu_P = 0.8$; see Fig. 10. In this case, the species spread by means of propagating continuous traveling front followed by pattern formation in the wake. The corresponding prey and predator total population sizes are shown in Fig. 12c.

Note that it does not always seem possible to unambiguously distinguish between the traveling fronts with patterns in the wake and the patchy invasion; see Fig. 11 obtained for $\mu_N = 0.4$ and $\mu_P = 0.5$. For instance, the continuous front can be (almost) absent at some moments (e.g. Fig. 11e) but re-appear at later moments, the system thus showing an intermittent behavior. At some other moments (or for somewhat different parameter values), a distinct patchy structure can be observed inside a continuous envelope (e.g. see Fig. 11f). For convenience, we will refer to these regimes as

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**Fig. 9.** Spatial distribution of prey at different moments: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 100$, (e) $t = 200$ and (f) $t = 235$ obtained for $r = 4.2$, $b = 0.7$, $\mu_N = 0.5$ and $\mu_P = 0.8$.

**Fig. 10.** Spatial distribution of prey at different moments: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 75$, (e) $t = 90$ and (f) $t = 100$ obtained for $r = 4.2$, $b = 0.7$, $\mu_N = 0.7$ and $\mu_P = 0.8$. 
transitional’ between the patchy spread and the more conventional traveling front scenario.

The above results obtained for parameters $r = 4.2$ and $b = 0.7$ from domain C (cf. Fig. 1) are summarized in Fig. 13 showing the structure of the dispersal rates parameter plane. Here different symbols correspond to different regimes. Diamonds (empty and filled) and crosses represent extinction of both species, the difference being explained below. Filled squares stand for patchy invasion. Empty squares correspond to traveling fronts with pattern formation in the wake. Half-filled squares stand for the transitional regimes between patchy invasion and invasion fronts with patterns in the wake. We want to recall here that, for parameters from domain C, species persistence is not possible in the non-spatial system as the only attractor is the extinction state. In the spatial system, however, species can coexist and even invade over space (we observe from Fig. 13 that it can only happen when the dispersal rates are on the same order). Obviously, species persistence becomes possible due to formation of a distinctly heterogeneous, non-equilibrium spatiotemporal patterns.

However, in case $\mu_N$ and $\mu_P$ are significantly different, the species go extinct also in the spatial system. The extinction may follow different scenarios. One of them has already been shown before, see Fig. 8, when species spread does not result in successful invasion; this regime is shown in Fig. 13 by empty diamonds.

Alternatively, for small values of $\mu_N$ and high values of $\mu_P$, both populations rapidly break down soon after the introduction. For some parameter values it happens straightforwardly, i.e. without forming any pattern; for other parameter values, short-living patterns similar to either traveling band or to patchy spread may emerge first. However, in the latter case, these patterns are not

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**Fig. 11.** Spatial distribution of prey at different moments: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 75$, (e) $t = 100$ and (f) $t = 180$ obtained for $r = 4.2$, $b = 0.7$, $\mu_N = 0.4$ and $\mu_P = 0.5$.

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**Fig. 12.** Total population size of prey (solid curve) and predator (dashed curve) vs time as obtained for $r = 4.2$, $b = 0.7$ and different dispersal rates: (a) $\mu_N = 0.8$ and $\mu_P = 0.5$, (b) $\mu_N = 0.5$ and $\mu_P = 0.8$, (c) $\mu_N = 0.7$ and $\mu_P = 0.8$ and (d) $\mu_N = 0.4$ and $\mu_P = 0.5$, i.e. for the regimes shown in Figs. 8, 9, 10 and 11, respectively.
Fig. 13. The structure of the dispersal rates parameter plane ($\mu_N, \mu_P$) obtained for reaction parameters $r = 4.2$, $b = 0.7$ and for the Type I initial conditions. Different symbols represent different patterns of invasion.

Fig. 14. Spatial distribution of prey at different moments: (a) $t = 20$, (b) $t = 50$, (c) $t = 80$, (d) $t = 90$, (e) $t = 100$ and (f) $t = 120$ obtained for $r = 4.2$, $b = 0.7$, $\mu_N = 0.8$ and $\mu_P = 1$. 
self-sustained and disappear promptly. In Fig 13, this type of extinction is shown by filled diamonds.

A curious scenario is observed for a marginal case of $\mu_P = 1$ and intermediate values of $\mu_N$. Species introduction then results in formation of a checkboard-like pattern, likely as a result of the Turing instability (cf. Fig. 6). The pattern grows in size eventually occupying the whole domain (cf. Fig. 14a–c), which seems to signify invasion success. However, it appears that, unlike the case shown in Fig. 6, for the reaction parameters from domain C the pattern is not self-sustainable. Interaction of the growing pattern with the domain boundary has a detrimental effect. The wave of advance is reversed so that the pattern starts shrinking (see Fig. 14d and e), which finally results in the species extinction. This scenario is shown by a cross.

A closer look at the structure of the $(\mu_N, \mu_P)$ diagram shown in Fig. 13 immediately reveals the impact of predation on the invasion success. We first mention that, for the reaction parameters of Fig. 13, an introduction of the alien prey alone (i.e., as described by the Type I initial conditions but without predator) with dispersal rate $\mu_N \geq 0.1$ always leads to a species spread over the entire domain, hence resulting in a successful invasion. Therefore, all cases of species extinction observed for $\mu_N \geq 0.1$ (as marked with filled diamonds, crosses and empty diamonds) should be attributed solely to the impact of predation.

4.2. Type II: asymmetric initial condition

The results of the previous section demonstrated that the system’s dynamics is inherently richer for parameters from

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4 Note that this does not contradict to the results shown in Table 2 because the initial conditions are now different.
domain C (see Fig. 1) than for those from domains A or B. In particular, the impact of space was shown to play a highly non-trivial role and appears to be crucial for species survival in domain C because, since the extinction state (0, 0) is the only attractor there, in the corresponding non-spatial system extinction would be the only outcome.

Now we are going to consider the model (1)–(4), (8) and (9) for the asymmetric Type II initial condition. For the above reasons, since one of the goals of this paper is to reveal the dynamical complexity associated with alien species invasion, in this section we focus on the scenarios of species spread for parameters from domain C. We pay special attention to the possibility of the patchy spread as this seems to be not only the most interesting and counter-intuitive invasion regime from the theoretical point of view but also the one that may have important implications for practice (cf. Petrovskii and McKay, 2010). We make simulations for different dispersal rates in order to identify typical invasion patterns and to reveal the corresponding parameter plane structure.

Figs. 15 to 19 shows the simulation results obtained for parameters $r = 4.2$ and $b = 0.7$ (i.e. the same as in the previous section). Since the predator spatial distribution is qualitatively similar to that of prey, for the sake of brevity we only show the distribution of prey.

Fig. 15 shows snapshots of prey distribution at different time obtained for $\mu_N = 0.3$ and $\mu_P = 0.5$. The species invasion apparently follows the patchy spread scenario. Note that, contrary to what was observed for the symmetric initial conditions, now the population distribution is lacking any sign of symmetry. The corresponding time-dependence of the total prey and predator sizes is shown in Fig. 19a.

Fig. 17. Spatial distribution of prey at different moments: (a) $t = 25$, (b) $t = 35$, (c) $t = 50$, (d) $t = 75$, (e) $t = 90$ and (f) $t = 125$ for $r = 4.2$, $b = 0.7$, $\mu_N = 0.5$ and $\mu_P = 0.5$.

Fig. 18. Spatial distribution of prey at different moments: (a) $t = 15$, (b) $t = 25$, (c) $t = 35$, (d) $t = 50$, (e) $t = 125$ and (f) $t = 150$ for $r = 4.2$, $b = 0.7$, $\mu_N = 0.6$ and $\mu_P = 0.5$. 

Fig. 19. Total populations size of prey (solid curve) and predator (dashed curve) for \( r = 4.2, b = 0.7 \) and: (a) \( \mu_N = 0.3 \) and \( \mu_p = 0.5 \), (b) \( \mu_N = 0.4 \) and \( \mu_p = 0.5 \), (c) \( \mu_N = 0.5 \) and \( \mu_p = 0.5 \) and (d) \( \mu_N = 0.6 \) and \( \mu_p = 0.5 \).

For a greater value of \( \mu_N \), the absence of the continuous envelope becomes less obvious and, indeed, it can be seen for most of the time. The continuous envelope can break at some moments as in the patchy spread but it would re-appear at later time. As above, we call this pattern of spread ‘transitional’. An example is shown in Fig. 16 obtained for \( \mu_N = 0.4 \) and \( \mu_p = 0.5 \). In the wake of the traveling envelope, a distinct patchy structure is formed. The corresponding total prey and predator sizes oscillate irregularly (see Fig. 19b).

A further increase in \( \mu_N \) restores the traveling front completely, see Fig. 17 obtained for parameters \( \mu_N = 0.5 \) and \( \mu_p = 0.5 \). In the wake of the front, the formation of a dynamic spatiotemporal pattern takes place. However, contrary to the transitional scenario of spread, the pattern in the wake looks considerably different, making worm-like structures rather than patches. The corresponding total population sizes vs time are shown in Fig. 19c.

For a still larger value of \( \mu_N \), traveling bands are observed, see Fig. 18 obtained for \( \mu_N = 0.6 \) and \( \mu_p = 0.5 \). An essential difference from the case of the symmetric initial conditions is that now species introduction can result in multiple bands, not just in a single ring (cf. Fig. 8). The corresponding total population sizes show regular, approximately periodic oscillations with time (see Fig. 19d). The rings/bands are generated by a ‘pacemaker’ situated in the center of the domain, i.e. at the place of species introduction. Correspondingly, in case of asymmetric initial conditions, this regime of multiple traveling bands does not result in invasion failure.

For a larger value of \( \mu_N \), the multiple bands eventually give way to the single band scenario, which finally lead to invasion failure when the expanding ring is pushed to the domain boundary and disappear; see the comments to Fig. 8.

An interesting question is how the invasion rate, i.e. the rate at which the invaded domain grows with time, depends on the pattern of spread. Fig. 20 shows the radius of the invaded area vs time as obtained for the regimes shown in Figs. 15–18. The invasion rate is given by the slope of the lines, it is readily seen that it decreases with a decrease in \( \mu_N \). The largest invasion rate is therefore observed for the multiple traveling band scenario, while lowest invasion rate is observed for the patchy spread; the latter being in a good agreement with predictions of continuous models (Morozov et al., 2006).

Thus, a successful invasion following different scenarios of species spread is observed when the dispersal rates are on the same order. Recall that the corresponding non-spatial system has species extinction as the only possible outcome. The successful invasion and the subsequent population persistence in the spatially explicit system is therefore a highly non-trivial fact. However, species can go extinct in the spatial system as well in the case that their dispersal rates are significantly different. The extinction then takes place following scenario(s) similar to what was observed for the Type I initial conditions, and hence we do not further discuss it here.

Our simulation results obtained for \( r = 4.2 \) and \( b = 0.7 \) and different dispersal rates are summarized in Fig. 21a which shows the structure of the dispersal rates’ parameter plane with regard to different invasion scenarios. Filled squares stand for patchy invasion. Empty squares correspond to traveling fronts with pattern formation in the wake. Half-filled squares stand for the transitional regimes between patchy invasion and invasion fronts with patterns in the wake. Empty circles stand for multiple traveling bands. Empty diamonds stand for invasion failure after propagating of a single population band. Filled diamonds mark the parameters when species go extinct promptly after their introduction, without forming any clear pattern.

![Fig. 19. Total populations size of prey (solid curve) and predator (dashed curve) for r = 4.2, b = 0.7 and: (a) \( \mu_N = 0.3 \) and \( \mu_p = 0.5 \), (b) \( \mu_N = 0.4 \) and \( \mu_p = 0.5 \), (c) \( \mu_N = 0.5 \) and \( \mu_p = 0.5 \) and (d) \( \mu_N = 0.6 \) and \( \mu_p = 0.5 \).](image1)

![Fig. 17 obtained for parameters \( \mu_N = 0.5 \) and \( \mu_p = 0.5 \).](image2)

![Fig. 18 obtained for \( \mu_N = 0.6 \) and \( \mu_p = 0.5 \).](image3)

![Fig. 20 shows the radius of the invaded area vs time as obtained for the regimes shown in Figs. 15–18.](image4)
In order to give a broader view of the system properties, simulations were performed, and the structure of the \((\mu_N, \mu_P)\) plane was revealed accordingly, for two other parameter sets, specifically, for \(r = 6\) and \(b = 1.5\) (see Fig. 21b) and for \(r = 2.5\) and \(b = 0.5\) (see Fig. 21c). The meaning of the symbols is the same as above. It is readily seen that all the main scenarios of spread are present, although their position in the parameter plane is somewhat different. In particular, for the larger value of \(r\) (Fig. 21b), the patchy spread can only be observed at small values of \(\mu_N\) and the most common pattern of spread is the traveling front with patterns in the wake. For the smaller \(r\) (Fig. 21c), invasion success appears to be possible only if the prey dispersal rate \(\mu_N\) is sufficiently large; then the regime of multiple bands becomes rather common but the traveling front with patterns in the wake can only be observed for \(\mu_N \approx 1\).

The question still remains as to how the system's dynamics may change if \(r\) and/or \(b\) vary in a broader range. Since constructing a diagram like those shown in Fig. 21 requires a considerable time and effort, it is hardly possible to give a truly comprehensive account of the system's properties by obtaining a similar diagram for many different values of \(r\) and \(b\). Therefore, in order to provide an insight into this issue, we use a different approach. We fix the dispersal rates at certain hypothetical values and consider what is the domain in the \((b, r)\) parameter plane corresponding to a given invasion scenario. Here we focus on the patchy invasion. Fig. 22 (obtained for \(\mu_N = 0.3\) and \(\mu_P = 0.5\) and the Type II initial conditions) shows the sub-domain \(G\) of domain \(C\) where the patchy spread is observed. Existence of the patchy spread therefore depends strongly on the value of \(b\), being possible only in a relatively narrow range of values, but less so on \(r\). Interestingly, since \(b\) may be regarded as a certain measure of the strength of the Allee effect,\(^6\) this result is in a good agreement with the properties of continuous models (cf. Petrovskii and McKay, 2010).

5. Discussion and conclusions

Patterns of alien species invasion have been a focus of considerable interest for at least two decades (Andow et al., 1990; Sherratt et al., 1995; Shigesada et al., 1995; Johnson et al., 2006). Their understanding is thought to be important both for theoretical and practical reasons. Identification of principal invasion scenarios and possible transitions between them as a result of response to a change in environmental conditions and/or to a human intervention can be used to develop a more efficient strategy of invasive species management and control (Fagan et al., 2002; Taylor and Hastings, 2005).

Mathematical modeling of biological invasions has long been recognized as a powerful research approach (Okubo et al., 1989; Shigesada and Kawasaki, 1997; Owen and Lewis, 2001) that makes it possible to reveal generic properties of different invasion stages, especially in a situation when replicated field experiments are hard to make or are not possible at all. Interestingly, although much attention has been paid to invasion modeling using space-continuous models (such as diffusion-reaction equations or integro-difference equations), space-discrete models have remained outside of the mainstream. Meanwhile, in many cases, the environment shows a considerable spatial variability which is best taken into account by the spatially-discrete approach (Comins et al., 1992; White and White, 2005).

In this paper, we considered scenarios of biological invasion in a spatially-discrete system described by a coupled map lattice. We first considered the stage of species introduction and establishment and showed that there can be three qualitatively different outcomes of the species introduction such as species extinction, species spread and a successful local establishment without further spread, i.e. 'invasion pinning.' Which of these option is going to take place depends on the species dispersal rate and on the details of its growth rate (e.g. the strength of the Allee effect). For a special case of a stepwise growth rate (Kot et al., 1996), we

\(^6\) For a given \(r\), the larger is \(b\) the stronger is the Allee effect; see Eq. (10) and the comments after Eq. (11). The Allee effect becomes the strongest when \(b\) approaches the critical value \(r^2/4\).
obtained exact analytical conditions to distinguish between the different cases.

We then considered patterns of species spatial spread. We assumed that the invading species is affected by a specialist predator. Existence of such predator can be a feature of biological control strategy when a specially chosen predatory species is introduced in the wake of the spreading prey (Berryman, 1991; Kenis and Vaaamonde, 1998; Petrovskii et al., 2005b). By means of performing extensive numerical simulations, we identified the typical patterns of spread that appeared to be significantly different for different values of the species’ dispersal rates and also depending significantly on the properties of the corresponding non-spatial predator–prey system.

Regarding the patterns of spread, our main findings are as follows:

- we found a few qualitatively different scenarios of spatial spread in the predator–prey model with strong Allee effect for the prey. In particular, we found traveling fronts with spatiotemporal patterns in the wake, solitary and multiple traveling bands (rings) and patchy spread without a traveling front at all. We have shown that these scenarios of spread are typical in the sense that they are observed for different parameter values and for different initial conditions;
- we found that the spatial aspect is crucial for the invasion success and/or species persistence. In particular, the regimes of patchy invasion, multiple traveling bands and traveling front with pattern formation in its wake were shown to make it possible for the species to invade over the space (and, consequently, to persist over the whole domain) for parameters where the alien population would not be viable in the corresponding homogeneous (non-spatial) system. It means that a spatially homogeneous population would inevitably go extinct, and species persistence only becomes possible due to the formation of distinctly heterogeneous spatiotemporal patterns;

With regard to the diagrams shown in Figs. 13 and 21, we want to mention that, for technical reasons, we only identified the regimes of spread on a certain ‘grid’ of values $\mu_0$ and $\mu_P$ such as $\mu_N = 0.1, 0.2, \ldots, 1.0$ and $\mu_P = 0.1, 0.2, \ldots, 1.0$. In reality, however, dispersal rates can of course be given by any real number between 0 and 1. Therefore, we cannot draw the exact boundary between different regimes. Moreover, generally speaking, we cannot exclude existence of other regimes for some ‘sub-grid’ values of the dispersal rates, although the parameter range for such regimes should likely be rather narrow.

Note that the results of our study have clear ecological implications:

1. the biocontrol strategy based on the introduction of a specialist predator is generally successful as it can turn the otherwise successful invasion to failure (e.g. see the comment at the end of Section 4.1);
2. rather counter-intuitively, biocontrol is predicted to be least effective when the predator’s dispersal rate is in the intermediate range, i.e. not too small and not too large. Indeed, an increase in $\mu_P$ turns invasion failure to invasion success, but a further increase can turn success to failure. Consider, for instance, the diagram shown in Fig. 21a. Consider $\mu_N = 0.5$. Prey invasion is successful for $0.3 \leq \mu_P \leq 0.7$ but fails for $\mu_P \leq 0.2$ and for $0.8 \leq \mu_P \leq 1$;
3. the biocontrol strategy has more chances to be successful in the case of a more efficient predator. This is clearly seen from the diagrams of Fig. 21. Indeed, recalling the definition of parameters $r$ and $b$ (see the line below Eq. (9)), it is readily seen that smaller values of $r$ and/or $b$ correspond to a larger $\delta$ where $\delta$ quantifies predation efficiency. The succession of the diagrams as $(b) \rightarrow (a) \rightarrow (c)$ then corresponds to an increase in predation efficiency, and also to a clear increase in the parameter range of species extinction (shown by the filled diamonds).

In conclusion, we want to mention that the properties of spatially-discrete and spatially-continuous systems are usually believed to be qualitatively different, and they can indeed be rather different in some cases (e.g. Keitt et al., 2001). This is often used as an argument for choosing an adequate modeling framework, especially in practical applications (cf. Kot, 2001). Surprisingly, however, we found a considerable agreement between the properties of the time- and space-discrete coupled map lattice and those of continuous diffusion-reaction models. In particular, we found that all typical invasion scenarios observed in continuous systems (such as simple traveling fronts with a homogeneous population density in the wake, traveling fronts with patterns in the wake, propagating bands or rings [either solitary or multiple], and the patchy invasion) can be observed as well in the discrete system. Moreover, we found very few artifacts of the regular lattice structure (e.g. a checkerboard pattern like those in the middle of the domain in Figs. 6b, c or the corners in the otherwise circular front in Fig. 10). These observations lead to a somewhat controversial conclusion: The so much debated suggestion that the choice of the model is largely a matter of technical convenience can in fact be true, provided the population dynamics is parameterized appropriately.

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