Techniques of spatially explicit individual-based models: construction, simulation, and mean-field analysis

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Abstract

The main focus of this article is to present and relate four different frameworks in which spatially explicit individual-based models (IBMs) can be defined. These frameworks differ in the way space and time are modeled; each can be treated either discretely or continuously. The emphasis is put on constructing and simulating one of the simplest single-species IBMs in each spatio-temporal framework, discussing some of their technical subtleties, and deriving corresponding mean-field models when the homogeneous mixing conditions are assumed to hold. The four frameworks are more supplements than competitors. Since at almost every step of IBM construction several alternatives are a priori plausible I discuss the most important ones in more details. This article seems to be the first attempt to collect and synthesize information of this kind that is scattered over the literature. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Not only the 'What to study?' and 'What has been found?' questions are vital for a good scientific work. Rather, the 'How to solve the problem under consideration?' question forms the inevitable 'how' bones for the 'what' flesh. Appropriate methodology may reveal important insights into a seemingly banal problem. On the other hand, techniques that are not adequate enough may drown topics of prime importance.

Individual-based approach to modeling population dynamics, one of the main streams of today's theoretical ecology, has already been reviewed many times (Huston et al., 1988; Hogeweg and Hesper, 1990; Lomnicki, 1992; DeAngelis et al., 1994; Judson, 1994; Uchmanski and Grimm, 1996; Grimm, 1999). The point of interest in all these works has been either the role of individual-based models (IBMs) in ecology as a whole or an attempt to discuss potentials and summarize predictions of the existing IBMs. The present article aims at reviewing fundamental techniques underlying construction, simulation, and mean-field analysis of spatially explicit IBMs, including

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means of summarizing and visualizing vast amount of model data generated. Non-spatial IBMs also exist (Botkin et al., 1972; DeAngelis et al., 1979; Grist and des Clers, 1999) but are not the subject of this article.

Spatially explicit models of population dynamics can be classified according to whether population sizes, space, and time are treated as discrete or continuous entities (Table 1). For the purposes of this review, I define IBMs as such models in which a discrete individual that has at least one feature unique is the fundamental modeling unit. This is the case of the last four groups enlisted in Table 1; the feature that makes each individual unique is simply at least its spatial location. I refer to just these four model types as the spatially explicit IBMs. There is some controversy in the literature about what should be considered the IBM par excellence (Murdoch et al., 1992; Uchmanski and Grimm, 1996; Grimm, 1999). The IBM definitions and underlying arguments proposed in these articles are philosophical; tech-

niques used to build and work with such models are not affected by them at all. I note here that the concept of 'individual' need not always coincide with that of 'individual organism'. Models with more general population units such as local populations (Dytham, 1994), ant colonies (Britton et al., 1996), and bird flocks (Fahse et al., 1998) do not differ technically from models treating individual organisms.

Time seems to be mature enough to collect and synthesize chips of information scattered over a multitude of articles, and review techniques underlying spatially explicit IBMs. In all four model groups of interest the methodologies are relatively well established though elaborated to various degrees. They have been used to address both theoretical and practical aspects of population dynamics, working with both single-species and multi-species populations of both motile and sessile organisms. I aim at extracting their common conceptual and methodological background. This may help to reveal artifacts of particular modeling

Table 1
Eight possibilities of how spatially explicit models can be classified according to whether population size (P), space (S), and time (T) are treated as discrete (D) or continuous (C) entities

P	S	T	Common label	Formulation	References
C	D	D	Coupled map lattices[a]	System of difference eq.	Hassell et al. (1991), Kaneko, 1998
C	D	C	Reaction-dispersal networks	System of ODEs	Levin, 1974; Takeuchi, 1996
C	C	D	Reaction-dispersal models	Integrodifference eq.	Neubert et al., 1995; Kot et al. (1996), Veit and Lewis, 1996
C	C	C	Reaction-dispersal models[b]	PDEs, integrodifferential eq.	Okubo, 1980; Britton, 1986; Murray, 1990; Wilson, 1998
D	D	D	Individual-based models[c]	Set of rules	de Roos, McCauley and Wilson; see the next section
D	D	C	Interacting particle systems	Set of rules	Durrett and Levin; see the next section
D	C	D	Neighborhood models	Set of rules	Pacala and Silander; see the next section
D	C	C	Spatial point processes	Set of rules	Bolker and Pacala; see the next section

Abbreviations, eq., equations; ODEs, ordinary differential equations; PDEs, partial differential equations.

[a] Coupled map lattices can also be considered discrete-space IBMs under specific conditions, e.g. when the value at each site represents mass of the plant individual present (Hendry et al., 1996); they are used to evolve individuals' characteristics rather than their spatial distribution.

[b] Reaction–dispersal models defined in continuous time cover widely used reaction-diffusion models.

[c] Some instances of individual-based models are sometimes referred to as (probabilistic) cellular automata or artificial ecologies.

approaches as well as areas of particular model group applicability. Further on, unless specified otherwise, I refer to the spatially explicit individual-based models as IBMs or simply models.

The comparison studies that have been published and involved IBMs (DeAngelis and Rose, 1992; Durrett and Levin, 1994a; Wilson, 1998) exclusively concentrated on, say, an inter-approach comparison (*i*-state distribution versus *i*-state configuration models in DeAngelis and Rose, 1992; mean-field models, patch models, reaction–diffusion models, and interacting particle systems in Durrett and Levin, 1994a; IBMs, deterministic and stochastic reaction–dispersal models in Wilson, 1998). I propose an intra-approach comparison study, contrasting different methodologies used to formulate IBMs, and want to focus on technical means needed to run and analyze them.

This article is intended as the first one in a series of three. The next article that is currently under preparation should review techniques (both statistical and analytical) used to analyze IBMs when the homogeneous mixing conditions underlying mean-field models do not hold. The final article should present some of the software packages available that were developed to simulate myriads of interacting organisms of various species sharing the common environment, and discuss some IBM representatives found in the literature in view of the techniques reviewed in the first two papers.

2. Simple single-species IBMs

All four spatio-temporal frameworks of IBMs, listed in the last four rows of Table 1, have more or less established methodologies. In other words, for each framework there is a series of articles in which modeling aspects, that is, issues of model construction, simulation, and analysis, are at least as important as ecological problems studied. These series are due to de Roos, McCauley and Wilson (D-space, D-time IBMs; de Roos et al., 1991; McCauley et al., 1993; Wilson et al., 1993, 1995; McCauley et al., 1996; Wilson, 1996, 1998), Durrett and Levin (D-space, C-time IBMs; Dur-

rett, 1988, 1993; Durrett and Levin, 1994a,b, 1998; Durrett, 1999), Pacala and Silander (C-space, D-time IBMs; Pacala and Silander, 1985; Pacala, 1986, 1987; Pacala and Silander, 1990), and Bolker and Pacala (C-space, C-time IBMs; Bolker and Pacala, 1999; Bolker et al., 2000). The respective methodologies have been motivated by various ecological problems and elaborated to various degrees. To introduce them in a concise and unified manner, I first construct and simulate probably one of the simplest IBMs of single-species population growth in a two-dimensional habitat in each spatio-temporal framework, and then attempt at making (some) general comments. I (subjectively) order the frameworks so that their technical complexity increases. Sets of rules describe performance and thus determine the fate of every single individual. The processes of mortality, reproduction (including offspring dispersal and establishment), and movement (in case of motile organisms) drive evolution of population size (temporal pattern) and distribution (spatial pattern) in the environment.

2.1. D-space, D-time

The two-dimensional, physically homogeneous environment is modeled as a lattice of $M \times N$ identical square sites, with periodic boundary conditions (BC; the left and right edges and the top and bottom edges of the lattice are joined together so that it forms the surface of a torus). Time runs in discrete steps. At any time step, at most one individual is allowed to occupy each site. Initially, x_0 ($\leq M \times N$) individuals are scattered uniformly randomly over the lattice. The processes that determine the fate of each individual are as follows.

2.1.1. Mortality
Every time step, each individual dies with a probability P_m (density-independent, uniform mortality).

2.1.2. Reproduction
Every time step, each individual gives birth to one offspring with a probability P_r (asexual reproduction).

2.1.2.1. Offspring dispersal and establishment. Respecting BC, the conceived offspring is instantaneously and equiprobably placed to a site in a square neighborhood (excluding the original site) of side $2e + 1$ ($e = 1, 2, …$) centered at its parent's site, and is discarded provided that an adult individual occupies the selected site. If two or more offspring attempt to recruit to the same adult-free site at the same time step, only one of them is uniformly randomly chosen and allowed to do it, the rest discarded. Thus, reproduction is density dependent. Any established offspring becomes the adult able of reproduction at the next time step.

2.1.3. Movement

Every time step, respecting BC, each individual moves equiprobably to a site in a square neighborhood (including the original site) of side $2d + 1$ ($d = 0, 1, 2, …$) centered at its current site unless another individual occupies the selected site. In case the individual cannot move it remains in its original site. The order in which individuals attempt to move is modeled as uniform random. For sessile species, one may formally set $d = 0$.

I order the demographic processes concurrently in the actual IBM implementation. That is, the mortality and reproduction rules are applied independently to each adult individual: the reproduction rule takes place before the dead individuals are removed from the lattice, and the established offspring are not subject to the mortality rule at the actual time step. Bookkeeping is then made by superposing the lattices of newborns and surviving adults. Finally, the movement rule is applied to each individual of the updated population. The reproduction rule includes the so-called 'collision rule' which determines what happens if two or more events try to simultaneously influence a site.

2.2. D-space, C-time

The introductory assumptions are identical to the above model, yet time is considered to run continuously now. The model rules differ in their formulation and are as follows.

2.2.1. Mortality

Each individual dies at a rate m (density-independent, uniform mortality).

2.2.2. Reproduction

Each individual gives birth to one offspring at a rate r (asexual reproduction).

2.2.2.1. Offspring dispersal and establishment. Respecting BC, the conceived offspring instantaneously disperses equiprobably to a site in a square neighborhood (excluding the original site) of side $2e + 1$ ($e = 1, 2, …$) centered at its parent's site, and is discarded provided that another adult individual occupies the selected site. Thus, reproduction is density dependent. Any established offspring immediately becomes the adult able to reproduce.

2.2.3. Movement

Respecting BC, each individual moves at a rate w equiprobably to a site in a square neighborhood (including the original site) of side $2d + 1$ ($d = 0, 1, 2, …$) centered at its current site unless another individual occupies the selected site. In case the individual cannot move it remains in its original site. For sessile species, one may formally set $w = 0$ and/or $d = 0$.

There is no place for explicit ordering of mortality and reproduction rules in this model. Rather, the ordering is determined by the actual occurrence of particular events. In this way, even the movement rule is mingled with the others. The rules are more concise now as at each continuous-time instant at most one event takes place (with probability one) and no 'collision rules' are thus required.

I make a few notes concerning the actual computer implementation of the model. First, events are said to occur at a rate a if the occurrence times are described by a Poisson process with the parameter a; see, for example, Mangel and Clark (1988) for details. The important consequence is that the time intervals τ between the occurrence of two successive events are independent and identically exponentially distributed random variables: $P[\tau < t] = 1 - \exp(-at)$,

where $P[A]$ stands for a probability of an event A. Second, the above rules prescribe that three Poisson processes should run for each individual (mortality, reproduction, and movement); three running processes vanish when an individual dies, and three new processes appear when an offspring is successfully established on the lattice. Although using techniques of object-oriented programming would enable one to keep track of multiple Poisson processes for each individual, it is unnecessary and would introduce unnecessary overhead. Instead, the so-called 'thinning of Poisson processes' technique can be applied which keeps one background Poisson process only (Durrett, 1995). This single process generates time instants at which events may occur. Let $S = MN$ be the number of lattice sites and let the background Poisson process generate time instants at a rate cS, where $c \geq m + r + w$. Upon each time instant generated a lattice site is uniformly randomly chosen; if occupied the individual dies with the probability m/c, gives birth to one offspring with the probability r/c, attempts to move with the probability w/c, and does nothing with the probability $1 - (m + r + w)/c$. If the chosen site is empty, nothing happens to the lattice configuration at that time instant. Thus, each site is independently trying to change at the rate c, as $cS \times 1/S = c$, $1/S$ being the probability that a particular site is uniformly randomly selected.

In the literature, one can find at least some of the rules defined from different viewpoints. For example, in the above single-species model one may use the viewpoint of either an individual (above) or a vacant site (Durrett, 1999) to specify the reproduction rule. The latter gives the following rule: vacant sites become occupied at a rate $r \times f$, where f is the fraction of occupied neighbors. Note that when individuals give birth at a rate r, vacant sites are filled at a rate at most r, since births onto occupied sites are discarded. Simulation of this rule works as follows. Upon a time instant generated by the background Poisson process a lattice site is uniformly randomly chosen and if vacant one of its neighbors is picked at random; if this neighbor is occupied (this event has the probability f) the vacant site is made occupied with the probability r/c. Analogous rule

duality can be found in an example from epidemics. Sites can be vacant or occupied by susceptibles or infecteds. The local disease transmission rule can be defined as: (i) infecteds emit disease at a rate r equiprobably to a nearest neighbor and if that site is occupied by a susceptible, it becomes infected, otherwise nothing happens, or (ii) susceptible individuals become infected at a rate $r \times f$, where f is the fraction of nearest neighbors occupied by infecteds. Such rules are substitutes and use of one or another has no simulation or analytical consequences. Rather, the choice is more a matter of biological plausibility and interpretation.

2.3. C-space, D-time

The two-dimensional, physically homogeneous environment is modeled as a continuous plot of size $M \times N$, with periodic BC. Time runs in discrete steps. Initially, x_0 individuals (now not limited a priori) are scattered uniformly randomly over the plot. The processes that determine the fate of each individual are as follows.

2.3.1. Mortality
Every time step, each individual dies with a probability P_m.

2.3.2. Reproduction
Every time step, each individual gives birth to one offspring with a probability P_r.

2.3.2.1. Offspring dispersal and establishment. The conceived offspring instantaneously disperses to a position generated by an offspring dispersal kernel, specified by a probability density function (pdf). In the physically homogeneous environment, this pdf is typically radial and non-increasing with increasing distance between the new offspring position (x', y') and its parent's position (x, y). I assume here that this pdf is uniform on a circle of radius ε centered at the parent's position. That is, I generate a point u from the uniform pdf on $(0, \varepsilon]$ and a point ϕ from the uniform pdf on $[0, 2\pi)$, and set:

$$x' = x + u \cos \phi, \qquad y' = y + u \sin \phi, \tag{1}$$

respecting BC. The offspring dispersal kernel is supplemented by an establishment probability determining whether the offspring is actually established in the selected position or is discarded. I assume that this probability depends on the number n of individuals located in a circle of radius e centered at (x', y'), decreases linearly from unity at $n = 0$ to zero at some $n = E$, and stays zero for all $n > E$. The newborns are not counted to n. Any established offspring becomes the adult able of reproduction at the next time step.

2.3.3. Movement

Every time step, each individual moves to a position generated by a movement kernel. I assume here that this kernel is specified by the uniform pdf on a circle of radius δ centered at the current individual's position (x, y). That is, I generate a point z from the uniform pdf on $[0, \delta]$ and a point ξ from the uniform pdf on $[0, 2\pi)$, and set:

$$x' = x + z \cos \xi, \qquad y' = y + z \sin \xi \qquad (2)$$

respecting BC. The movement kernel is supplemented by a movement probability determining, for $z > 0$, whether the individual actually moves to the selected position or remains in the original one. I assume that this probability depends on the number n of individuals in a circle of radius d centered at (x', y'), decreases linearly from unity at $n = 0$ to zero at some $n = D$, and stays zero for all $n > D$. If an individual moves, only its new position counts to n. The order in which individuals attempt to move is implemented as uniform random. For sessile species, one may formally set $\delta = 0$.

As time is considered discrete and all individuals act at once, the ordering of mortality and reproduction processes has to be specified externally. I assume they are ordered concurrently as in the 'D-space, D-time' case. The movement rule is applied after mortality and reproduction rules are accomplished. No 'collision rules' are required here as at each time step each location is affected (with probability one) by at most one event.

The uniform random initial distribution of x_0 individuals in the plot implies that the number $0 \leq n \leq x_0$ of individuals located in a region of area $0 \leq A \leq S \,(= MN)$ is binomially distributed with the event probability A/S,

$P[\text{there are } n \text{ individuals in an area } A]$

$$= \binom{x_0}{n} \left(\frac{A}{S}\right)^n \left(1 - \frac{A}{S}\right)^{x_0 - n} \qquad (3)$$

This probability distribution is valid no matter what the shape of the region is and where the region is located within the plot. If $S \to \infty$ and $x_0 \to \infty$ so that x_0/S is (or converges to) a constant, then $A/S \to 0$ for a fixed A, and the probability that a region of area $A \geq 0$ contains $n \geq 0$ individuals is Poisson distributed in this limit:

$P[\text{there are } n \text{ individuals in an area } A]$

$$= \frac{\lambda^n}{n!} \exp(-\lambda), \quad \lambda = v_0 A, \qquad (4)$$

where $v_0 = x_0/S$ has the meaning of initial population density.

An important technical problem in model implementation is to identify each individual's neighbors in a relatively short time; Pacala and Silander (1985) suggested a very efficient data structure to achieve this goal.

2.4. C-space, C-time

The introductory assumptions are identical to the previous model, yet time is considered to run continuously now. The model rules differ in their formulation and are as follows.

2.4.1. Mortality
Each individual dies at a rate m.

2.4.2. Reproduction
Each individual gives birth to one offspring at a rate r.

2.4.2.1. Offspring dispersal and establishment. Respecting BC, the produced offspring instantaneously disperses to a position generated by an offspring dispersal kernel, and an establishment probability is used to decide whether the offspring is actually established in that position or is discarded. I assume both the kernel and the probability to be the same as in the previous model.

Any established offspring immediately becomes the adult able to reproduce.

2.4.3. Movement

Respecting BC, each individual moves at a rate w into a position generated by a movement kernel, and stays there with a movement probability; otherwise, it remains in its original position. Both the kernel and the probability are assumed to be the same as in the previous model. Bolker et al. (2000) simulated plant population growth (no movement) as follows. 'Starting with a random initial distribution of individuals, the simulator takes small time steps to approximate a continuous-time process. In each time step, the simulator picks pseudo-random numbers to see if each plant has died or reproduced. If it has reproduced, the simulator picks a random point from the dispersal kernel to see where its offspring disperses to. It then calculates the local density around that point to determine the offspring's establishment probability, and picks another random number to see if it establishes'.

There is no a priori need to approximate continuous time by discrete steps. Last but not least, the model then looses its explicit 'C-time' character. One may rigorously simulate this IBM by running a background Poisson process with density-dependent rate $x(m + r + w)$, x being the actual population size at the time an event is expected to occur. Once a time instant is generated an individual is uniformly randomly chosen: it dies with the probability $m/(m + r + w)$, gives birth to one offspring with the probability $r/(m + r + w)$, and attempts to move with the remaining probability $w/(m + r + w)$. Reproduction/movement event is followed by generating a position in the environment according to the respective kernel where the offspring disperses/adult moves. Finally, local density around the landing point determines the offspring establishment/adult movement probability.

2.5. Output visualization

An appropriate summarization and visualization of the large amount of model data generated by IBMs is important to a priori assess popula-

tion dynamics and, in turn, formulate and test hypotheses and/or select adequate tools for a more rigorous analysis. An obvious entity to look at is temporal course of population size. Spatially explicit models are appreciated for generating spatial patterns which evolve in time. These patterns can be seen by taking snapshots of the environment at either all times population size changes or at specific times a distance apart; see Wilson et al. (1995), Berec et al. (2001). A kind of picture being somewhere in between these two extremes and created for 'D-space, D-time' systems, is the *xt*-plot of Wilson (1998); it is built up by appending a fixed but uniformly randomly chosen row of the lattice to the bottom of the picture each time step. Analogous 'spatio-temporal' pictures can be developed for the other frameworks, too. For 'C-space, D-time' systems, one may superimpose a lattice on the continuous plot and follow the *xt*-plot technique, with different numbers of individuals in discrete sites corresponding to different levels of grey color. 'C-time' IBMs may be sampled at regular time instants, for example.

To show how model outcomes depend on various parameter values, one may exploit diagrams of Fryxell and Lundberg (1994). A grid of points is laid on a two-dimensional parameter space and the model is run for each of the selected combinations. Different marking of the grid points can be used to distinguish different types of model behavior (e.g. highly probable extinction, moderately probable extinction, lowly probable extinction (Berec et al., 2001), Grimm (1999) used a slight generalization of this type of picture in which the same marks were of different sizes depending on the strength of the observed phenomenon (e.g. probability of extinction in the 'moderately probable extinction' group).

2.6. A short discussion

At the qualitative level, all model formulations and simulation outputs are essentially the same. The models describe behavior of each individual organism in a spatially explicit habitat, and include the fundamental processes. Fig. 1 shows sigmoidal population growth under all four spatio-temporal frameworks. The most rapid growth
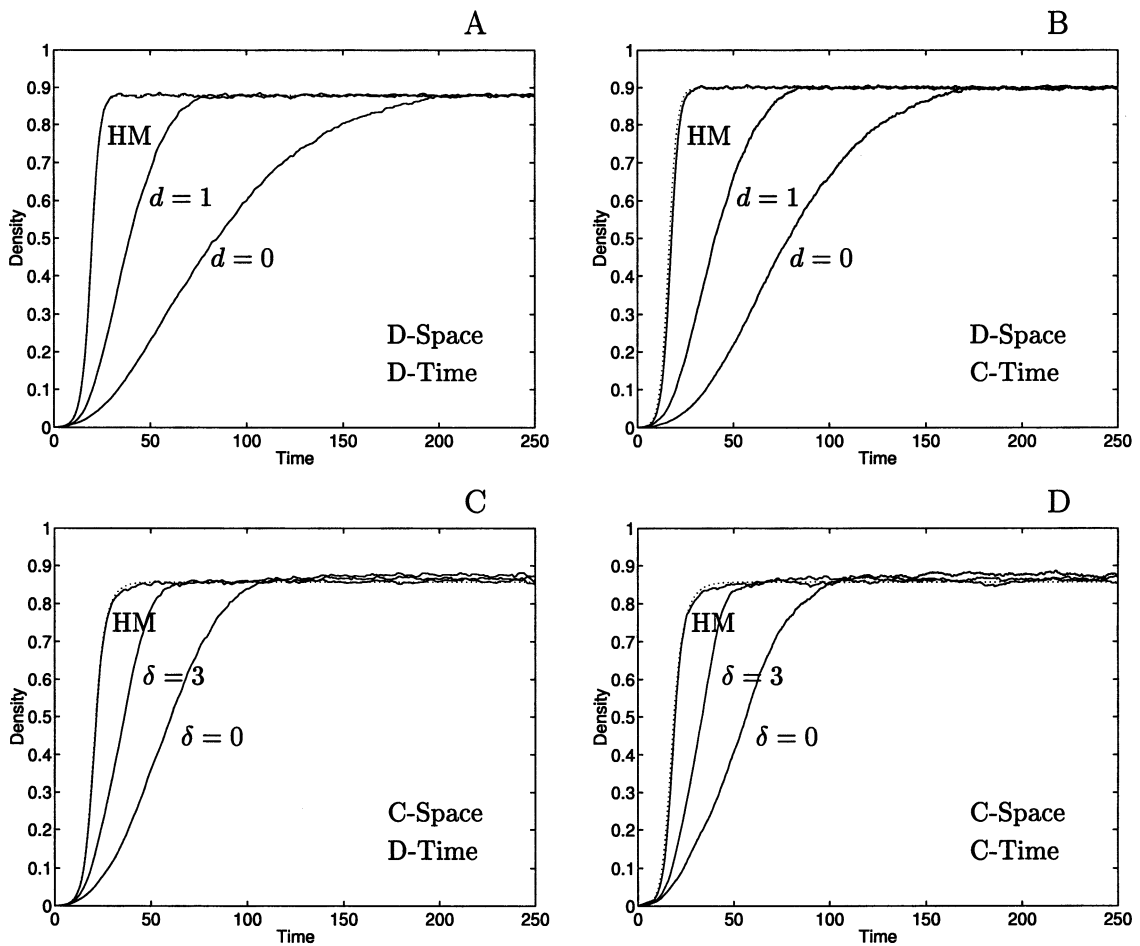
Fig. 1. Single-species population growth curves corresponding to the four spatio-temporal frameworks. (A). D-space, D-time; $M = 128$, $N = 128$, $x_0 = 10$, $P_m = 0.05$, $P_r = 0.5$, $e = 1$; simulation under the homogeneous mixing conditions (HM) virtually coincides with the solution of the mean-field model (5) (dotted line). (B). D-space, C-time; $M = 128$, $N = 128$, $x_0 = 10$, $m = 0.05$, $r = 0.5$, $w = 1$, $c = 1.6$, $e = 1$; HM virtually coincides with the solution of the mean-field model (8) (dotted line). (C). C-space, D-time; $M = 128$, $N = 128$, $x_0 = 10$, $P_m = 0.05$, $P_r = 0.5$, $\varepsilon = 3$, $e = 2$, $E = 11$, $d = 2$, $D = 11$; HM virtually coincides with the solution of the mean-field model (9) (dotted line). (D). C-space, C-time; $M = 128$, $N = 128$, $x_0 = 10$, $m = 0.05$, $r = 0.5$, $w = 1$, $\varepsilon = 3$, $e = 2$, $E = 11$, $d = 2$, $D = 11$; HM virtually coincides with the solution of the mean-field model (12) (dotted line).

is achieved under the homogeneous mixing conditions (see the next section), and the rate of approach of the 'stable' population size decreases with decreasing the movement rate of individuals. The explanation for this behavior is as follows. The slower is the movement the closer offspring stay relative to their parents. As a consequence, spatial clustering evolves in the environment which results in a decreased reproductive success within the clusters due to overcrowding. The re-

productive success on the cluster boundaries is higher and the clusters grow. Eventually, the habitat is filled and the number of individuals 'stabilized' at a carrying capacity. Pacala (1986), Tilman et al. (1997), and others reported a decrease in 'equilibrium' population size for small movement rates. Law and Dieckmann (2000) demonstrated that the carrying capacity may be larger or smaller than that obtained under the homogeneous mixing conditions, and that it de-

pends on an intricate interplay between intraspecific competition and movement in single-species models. I observed an increase in the 'equilibrium' population size with respect to the mean-field carrying capacity with decreasing movement rate in both 'C-space' models.

At the technical level, no two models are the same. Table 2 summarizes the fundamental technical differences between 'D-time' and 'C-time' modeling frameworks. I used the concurrent ordering of demographic processes, followed by movement, in the above 'D-time' IBMs. There are alternative possibilities. The processes of mortality, reproduction, and movement may be ordered in any sequential manner, and the ordering even made independent for each individual. I discuss this issue in more details below.

Likewise, Table 3 summarizes the technical differences between the 'D-space' and 'C-space' frameworks. The 'interaction' characteristic deserves some explanation. In 'D-space' models covering more individual types (such as predators and prey in de Roos et al. (1991) or males and females in Berec et al. (2001)) the interaction is often direct: individuals of both types have to occupy the same site for the interaction to take place. In analogous 'C-space' models an interaction neighborhood has to be defined (indirect interaction) as two individuals occupy the same position with zero probability. In the above single-species IBMs, offspring establishment and adult movement demonstrate direct interaction between individuals in 'D-space' models and indirect interaction in 'C-space' models.

Table 2
A technical comparison of 'D-time' and 'C-time' IBMs

Characteristic	D-time ($t = 0,1,2, ...$)	C-time ($t \geq 0$)
Formulation	Relatively simple	More difficult
'Dynamic' parameters	Probabilities	Rates
Analysis	More difficult (more complex dynamics)	Simpler
Mean-field model	Difference equations	Ordinary differential equations
Updating	Synchronous (all sites updated at once)	Asynchronous (one site updated at a time)
System state	Changes abruptly	Changes gradually
Process ordering	External	Internal

Table 3
A technical comparison of 'D-space' and 'C-space' IBMs

Characteristic	D-space (lattice)	C-space (plot)
Individual volume	Finite	Infinitesimal
Smallest heterogeneity level	Finite	Infinitesimal
Interaction	Possibly direct	Indirect

3. Mean-field analysis

Apart from their significant contribution to the issues of spatial pattern formation, IBMs provide a way to determine population-level consequences of specific individual-level behavior. In order to be reliable, computer simulations must be run repeatedly to provide information about average, or typical, population responses. Given often a large dimensionality of model parameter space, computer simulations are more suitable to address specific questions about the model rather than uncover complete model behavior. Mean-field models reside on the other side of the individually oriented modeling spectra: they are analytical models that take no account at all of space and possible individual variability. As such, construction of mean-field models forces one to admit assumptions about individual biology that are rarely plausible in natural systems; I formulate these 'homogeneous mixing conditions' in this section. Mean-field models take the form of (a system of) ordinary differential/difference equations (ODEs). This brings at least one advantage of building them: an agreement between mean-field models and IBMs simulated under the homogeneous mixing conditions provides an important starting point from which to explore complexities brought about by assumptions destroying these

conditions. Moreover, information obtained from a stability analysis of mean-field models allows one to choose parameter values for IBMs that yield stable or unstable population dynamics under the homogeneous mixing conditions, and to see whether these features change when these assumptions are not met. Still the mean-field models are rather regular companions to the published IBMs. That is why I now review rigorous techniques of mean-field model construction in each spatio-temporal framework.

3.1. D-space, D-time

I show in Appendix A that if v and v' represent population densities at the beginning and at the end of a time step, respectively, the rigorous mean-field model corresponding to the above 'D-space, D-time' IBM is:

$$v' = v(1 - P_{\mathrm{m}}) + (1 - v)\left[1 - \left(1 - v\frac{P_{\mathrm{r}}}{N}\right)^N\right] \quad (5)$$

For small enough P_{r} or v the expression in square brackets can be well approximated by the term $P_{\mathrm{r}} v$, giving:

$$v' = v(1 - P_{\mathrm{m}}) + vP_{\mathrm{r}}(1 - v) = v + rv\left(1 - \frac{v}{K}\right) \quad (6)$$

which is a discrete-time version of the Verhulst logistic equation, with the intrinsic growth rate $r = P_{\mathrm{r}} - P_{\mathrm{m}}$ and the carrying capacity (with respect to the maximal admissible density $v = 1$) $K = 1 - P_{\mathrm{m}}/P_{\mathrm{r}}$. For large enough N one may approximately write

$$v' = v(1 - P_{\mathrm{m}}) + (1 - v)(1 - \mathrm{e}^{-vP_{\mathrm{r}}}), \quad (7)$$

as $\lim_{N \to \infty} (1 + z/N)^N = \mathrm{e}^z$ for any real number z.

To be precise, mean-field model (5) assumes that individuals are,

- identical in their parameters;
- uniformly randomly distributed on the lattice (each site has an equal probability of being occupied by an individual);
- members of an infinite population (thus living on an infinite lattice).

These assumptions are called the 'homogeneous mixing conditions' in the literature. In other words, if individuals are more or less iden-

tical in their relevant characteristics, more or less uniformly randomly distributed on the lattice at each time instant, and forming a relatively large population, difference Eq. (5), and possibly Eq. (6), is a good approximation of the population density evolving according to the above defined IBM with discrete space and discrete time. In simulations, the lattice size is always finite. The first assumption is guaranteed here by the simplicity of IBM rules. For motile species, the middle assumption can be technically approached by giving individuals a high movement rate (large d) and/or letting the offspring disperse over large neighborhoods (large e). The assumption is exactly fulfilled by taking up all individuals at the end of each time step and scattering them uniformly randomly over the lattice, under the constraint that at most one individual lands in a site. For sessile species, uniform random initial distribution and uniform random offspring dispersal guarantee the middle assumption at each time step, with large e approximating it quite well.

3.2. D-space, C-time

I show in Appendix B that the rigorous mean-field model corresponding to the above 'D-space, C-time' IBM is:

$$\dot{v} = rv(1 - v) - mv = \tilde{r}v\left(1 - \frac{v}{K}\right) \quad (8)$$

This is the well-known Verhulst logistic equation describing single-species population growth, with the intrinsic growth rate $\tilde{r} = r - m$ and the carrying capacity (with respect to the maximal admissible density $v = 1$) $K = 1 - m/r$.

To be precise, mean-field model (8) assumes that individuals are subject to the homogeneous mixing conditions specified above. All the comments are valid here, too, with the high movement rate characterized by large d or w much greater than r. If the alternative rule for reproduction is applied (see above), one arrives at the same mean-field model (8) since the fraction of occupied neighbors f becomes the mean fraction of occupied neighbors x/S under the homogeneous mixing conditions.

3.3. *C-space, D-time*

I show in Appendix C that the rigorous mean-field model corresponding to the above 'C-space, D-time' IBM is:

$$
v' = v(1 - P_m)
$$
$$
+ vP_r \left[P_L \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA) \left[1 - \frac{n+1}{E} \right]_+ \right.
$$
$$
\left. + (1 - P_L) \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA) \left[1 - \frac{n}{E} \right]_+ \right] \quad (9)
$$

P_L is the probability that if an offspring lands in a distance from its parent, the latter lies within the establishment neighborhood of the former ($P_L = e/\varepsilon$ if $e < \varepsilon$ and $P_L = 1$ otherwise); for a real number z, $[z]_+ = z$ if $z > 0$ and zero otherwise. Provided that v is small in the course of time and/or E is large, Eq. (9) will not stay far from that in which $[z]_+$ is replaced just by z (for a real number z). The latter sums to:

$$
v' = v + rv \left(1 - \frac{v}{K} \right) \quad (10)
$$

which is a discrete-time version of the Verhulst logistic equation, with the intrinsic growth rate $r = P_r(1 - P_L/E) - P_m$ and the carrying capacity (with respect to the maximal admissible density $v = 1$):

$$
K = \frac{E - P_L}{A} \left(1 - \frac{P_m}{P_r(1 - P_L/E)} \right) \quad (11)
$$

To be precise, mean-field model (9) assumes that individuals are subject to the homogeneous mixing conditions that are just 'C-space' analogues of those specified for the 'D-space' cases,
- identical in their parameters;
- uniformly randomly distributed on the plot;
- members of an infinite population living in an infinite plot.

In other words, if individuals are more or less identical in their relevant characteristics, more or less uniformly randomly distributed on the plot at each time instant, and forming a relatively large population, the ordinary difference Eq. (9) is a good approximation of the population density evolving according to the above defined IBM with continuous space and discrete time. In simulations, the plot size is always finite. The first assumption is guaranteed here by the simplicity of IBM rules. For motile species, the middle assumption can be technically approached by giving individuals a high movement rate (large δ) and/or letting the offspring disperse over large neighborhoods (large ε). The assumption is exactly fulfilled by taking up all individuals at the end of each time step and scattering them randomly over the plot. For sessile species, uniform random initial distribution and uniform random landing of the offspring guarantee the middle assumption at each time step, with large ε approximating it quite well.

3.4. *C-space, C-time*

I show in Appendix D that the rigorous mean-field model corresponding to the above 'C-space, C-time' IBM is:

$$
\dot{v} = -mv
$$
$$
+ rv \left[P_L \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA) \left[1 - \frac{n+1}{E} \right]_+ \right.
$$
$$
\left. + (1 - P_L) \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA) \left[1 - \frac{n}{E} \right]_+ \right] \quad (12)
$$

Analogously to the previous case, if v is small in the course of time and/or E is large, Eq. (12) will not stay far from that in which $[z]_+$ is replaced just by z (for a real number z). The latter sums to:

$$
\dot{v} = \tilde{r}v \left(1 - \frac{v}{K} \right), \quad (13)
$$

which is the Verhulst logistic equation, with the intrinsic growth rate $\tilde{r} = P_r(1 - P_L/E) - P_m$ and the carrying capacity (with respect to the maximal admissible density $v = 1$):

$$
K = \frac{E - P_L}{A} \left(1 - \frac{P_m}{P_r(1 - P_L/E)} \right) \quad (14)
$$

To be precise, mean-field model (12) assumes that individuals are subject to the homogeneous mixing conditions specified for the 'C-space, D-time' case. All the comments are valid here, too, with the high movement rate characterized by large δ or w much greater than r.

3.5. A short discussion

Formally, mean-field models are systems of ordinary differential equations (C-time) or difference equations (D-time) that describe temporal dynamics generated by the IBM rules under the homogeneous mixing conditions. These conditions do not differ in principle for the four spatiotemporal model frameworks and can be generally formulated as follows: (i) populations are to be divided into a finite number of groups within which individuals are supposed to be identical (averaging over individuals within respective groups), (ii) populations are well-mixed so that any individual may equally interact with any other (averaging over space), and (iii) populations are sufficiently large so that individuals respond only to means (averaging over system realizations).

Any deviation from the homogeneous mixing conditions causes that the mean-field (non-spatial, population-level) models have only an approximate power. Pair and moment approximations that are going to be reviewed in the next article are promising alternatives as better analytical IBM counterparts (Bolker et al., 2000; Law and Dieckmann, 2000; van Baalen, 2000).

In small populations (relaxation of the condition (iii)) at least variance starts to play a role, too. IBM simulations then may demonstrate strong demographic stochasticity that always gives a population a chance to go extinct at any time instant. If interactions are only local (relaxation of the condition (ii)) due to, for example, slow movement or small interaction neighborhoods, clusters of individuals are usually formed in the environment. Spatial pattern of individuals is then no more uniform random. Condition (i) may be relaxed by enabling model parameters to vary with individuals; then, parameter variance and higher moments start to play the role in mean-field models. This influence can be diminished by forming a larger number of groups and averaging the parameters within them. The more groups we form, however, the more we deviate from the condition (iii) within the individual groups.

As for the simple IBMs formulated and analyzed in this article, their rigorous mean-field models take forms of different complexity. Nevertheless, under some mild assumptions, all these forms are well approximated by the Verhulst logistic model of single-species population growth, showing that even at this level the four spatiotemporal frameworks are more alternatives rather than competitors.

4. Alternatives and complexities

The use of spatially explicit IBMs demands description of the environment and each individual living in it, together with its individual–individual and individual–environment interactions. At (almost) every step of this description at least a few alternatives are a priori plausible. Some make the models possibly more realistic yet probably more complex to formulate, simulate and analyze. Others are just technical alternatives. Knowledge of whether and how a choice from among the alternatives changes spatio-temporal patterns should help to separate effects of model artifacts and biological processes. Some authors claimed that IBMs are rather robust against at least some of these alternatives (Durrett and Levin, 1994b; McGlade, 1999; Wilson et al., 1999), causing no qualitative change in population-level behavior, but a few works only addressed these questions explicitly (McCauley et al., 1993; Wilson et al., 1993).

One may ask whether a (discrete) lattice should be modeled as regular or irregular, and in the former case if it should be composed of squares, triangles or hexagons. Environment can be assumed homogeneous or heterogeneous in its physical characteristics, movement may be directed as opposed to diffusive, initial population distribution may be random or admit a specific spatial pattern, etc. Individuals need not be identical in their behavior; IBM rules may (and usually do) depend on various individual characteristics such as age, size, sex, genotype, etc. In particular, in evolutionary models different genotypes may have different parameter values, leading to differences in their respective reproductive success (Keeling
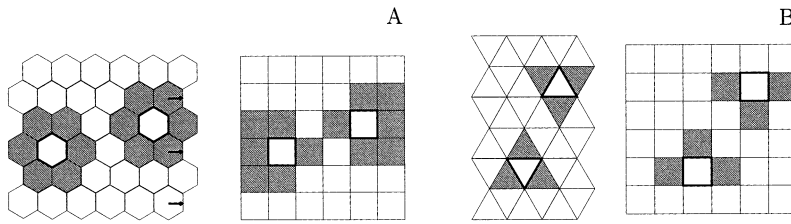
Fig. 2. (A) Projection of a hexagonal lattice and the nearest neighbors of its two sites onto a square lattice. (B) Projection of a triangular lattice and the nearest neighbors of its two sites onto a square lattice.

and Rand, 1995). This section discusses these and other model features in more details.

Finally, I note that most published IBMs are problem-specific, and applied issues often drive the choice of an appropriate alternative. For example, particular BC are used to study specific habitable environments, specific initial conditions allow for a study of species invasions, and particular spatio-temporal variations in environmental conditions can be used to investigate effects of harvesting and habitat degradation.

4.1. Discrete space topology

Any habitat is characterized by its shape and size (see below). Additionally, 'D-space' environments require a topology, regular lattices made up of squares being by far the most common choice. The fundamental reason is no doubt their easy computer implementation (the lattice sites are simply represented as pairs of non-negative integers). Nevertheless, the lattices composed of hexagons (which probably capture better an idea of circular individual neighborhood) or triangles can be technically represented as square lattices, with properly transformed interaction neighborhoods. As an example, consider an individual that interacts with its nearest neighbors only (Fig. 2). For the hexagonal lattice with six nearest neighbors, an equivalent square lattice may be obtained by shifting hexagon rows half the hexagon diameter (Fig. 2A). Note that there are two types of neighborhoods, and no one is of the von Neumann type (i.e. containing four square-lattice nearest neighbors). Triangular lattices may be transformed analogously (Fig. 2B). In fact, even irregular space tessellation's can be projected onto

square lattices, with interaction neighborhoods generally differing for each site. To summarize, though the a priori lattice choice should always respect specific system properties, its subsequent computer coding and formal treatment can be done via a square lattice with adequate (possibly site-specific) interaction neighborhoods. In this way, one may formally view the study of impacts of various space tessellation's on population dynamics as covered by the study of influences of various interaction neighborhoods (see below).

4.2. Boundary conditions

The assumption of an infinite habitat simplifies derivation of many mathematical results (Durrett and Levin, 1994b). However, finite habitats are what one encounters in applications and computer simulations. BC are then a necessary component of IBM formulation; they describe the fate of an individual that hits the habitat boundary. The individual 'leaving' the habitat may be 'lost' and thus reduce the population size (a phenomenon termed the boundary effect) or may 'reappear' elsewhere in the habitat. Also, an individual that is located near the boundary may have incomplete interaction neighborhoods and thus tend to have fewer neighbors than it would have in the middle of the habitat (a phenomenon termed the edge effect); this effect is often a model artifact which may result in higher survivorship and fecundity of annual plants (Pacala and Silander, 1985) and faster tree growth (Moravie et al., 1997) than actually observed.

Absorbing, reflecting, and periodic BC have been proposed in the literature. Under absorbing BC, individuals can step off the habitat and be

removed from the system. Absorbing BC do not deal with the boundary and edge effects at all, and do not allow for immigration. To reduce the effects one typically focuses on population dynamics in a central portion of a model environment (Pacala and Silander, 1985). Under reflecting BC, individuals that hit the boundary ricochet back into the habitat in a random or determinate direction. Keitt (1997) implemented them in such a way that no movement occurred when an individual attempted to move off the lattice. Reflecting BC are realistic, for example, for ground animals living on an island or water animals living in a pond. They seem unrealistic, e.g. for plant seeds unless one interprets the 'reflected' seed as another seed that 'immigrates' into the studied area. Therefore, reflecting BC remove the boundary effect (do not change the population size), but do not modify the edge effect. Pacala and Silander (1985) claimed that in the examples they considered the dynamics on small habitats with reflecting BC are very similar to the dynamics on small portions that are embedded in large habitats with absorbing BC. In this way one may considerably lessen computational costs as computer runs for small habitats are relatively inexpensive. However, before this strategy is adopted one has to exemplify a congruence between results of these two approaches for the system under study. Under periodic BC, the opposite edges of the habitat are connected together (the form of the habitat has to allow for such a wrapping). There is no system with periodic BC in nature. The only plausible argument for their use is just the same as for plant seeds and reflecting BC: an individual returning from the other side of the habitat is another individual; this may mimic dynamics in large habitats. Periodic BC have, however, nice technical properties: they remove the boundary effect, remove the edge effect (interaction neighborhoods are always complete), and above all they are easily implementable in computers. That is why they are by far the most used BC in IBMs. Britton et al. (1996) got similar results with periodic and reflecting BC. One could probably notice that the choice of BC (and in fact of any other IBM attribute) for a given application is always a trade-off between realism and computational simplicity.

4.3. Scales

An important question in any modeling effort is that of scales. In spatially explicit IBMs, size of the time step in 'D-time' models, size of the site in 'D-space' models (with regular lattices), and size of the habitat (lattice/plot) are of a primary interest. All these scales are strongly influenced by biological questions being addressed, modeled processes, and information available as model input. In many IBMs describing actual ecosystems scales naturally follow from the interactions studied and life histories of species involved; models of population dynamics of army ants (Britton et al., 1996), red grouse (Hendry et al., 1997), and wild daffodils (Durrett and Levin, 1994b) are just a few examples. In IBMs describing artificial ecologies where the stress is put on interactions in general, these scales should be considered model parameters; in other words, it is important to view the system at all admissible scales.

Problem to be addressed, scale of spatial heterogeneity in physical characteristics, area covered by or under control of an individual, and computational simplicity all play a role in choosing an adequate size of the lattice site (Keeling, 1999). Systems to be modeled are so diverse that it is virtually impossible to formulate any general rule. Any lattice site should be physically homogeneous; hence its size should be smaller than the smallest scale of relevant heterogeneities. It should be large enough to contain at least one individual (often just a single individual) or an area under its direct control (such as its territory); the latter is often related to the movement rate of motile organisms and the size of time step in 'D-time' IBMs. A balance must be struck between too fine a scale in which case the model will be computationally intensive, and too coarse a scale in which relevant heterogeneities or interactions may be ignored. The choice is less clear and more intricate if two or more individual types with different spatial characteristics are considered, such as in many predator–prey and host–parasitoid systems. Use of separate lattices for each type, with rules that relate them, is probably an appropriate way. In some systems, where one individual type is very small with respect to the

other, a continuous plot could even be considered for the former. Last but not least, the question of the size of each site is tightly linked to the range over which spatial interactions take place. For simplicity of model formulations and speed of computations the best way is to only allow interactions in small neighborhoods, but this may be in a direct conflict with taking a small enough scale, so these two factors need to be balanced (see below for more on interaction neighborhoods).

Once a 'D-space' topology and a site size are fixed, or when one decides to use 'C-space' models, the question of habitat size arises. Smaller habitats support smaller populations in which demographic stochasticity as well as individual mixing are stronger. As a result, spatially homogeneous distributions and rapid extinctions are often observed in IBMs with small habitats. On the other hand, if the habitat is too large, interesting dynamics may be averaged out (Keeling, 1999). Spatial patterns are commonly observed for larger (and even physically homogeneous; see below) environments (Wilson et al., 1995). Moreover, de Roos et al. (1991) demonstrated stabilization of temporal population dynamics in a two-dimensional, predator–prey system. Where lies the border between these types of model behavior? Some authors have already tried to address this question, with a characteristic length scale as an emergent, system-specific scale at which system dynamics are most informative (de Roos et al., 1991; Keeling, 1999).

The choice of a time step in 'D-time' models is not so important in artificial ecologies. It is intimately related to life cycle details that are modeled, and respective model parameters. For many time-step dependent parameters, such as the probability of death or reproduction of an individual per time step, doubling the time step virtually means doubling these probabilities. The care has to be taken to keep these probabilities in between zero and one. Also, keeping these probabilities low may enable one to use simplifying assumptions in mean-field model derivation (see 'D-space, D-time' framework above). Last but not least, use of large time steps may lead to ignorance of important processes and interactions that possibly take place within them.

4.4. Initial conditions

Knowledge of initial population sizes is not sufficient to uniquely determine outcomes of spatially explicit IBMs. Rather, complete spatial distribution of involved populations is required. This issue has a strong practical appeal and can be exemplified on a problem of species (re)introduction or invasion. What consequences has a release of a number of individuals from a point source and how they differ if this number is divided and multiple releases made from different spatial points? Imagine, for example, a population that demonstrates the Allee effect, with a negative per capita growth rate at low sizes (Stephens et al., 1999). Then, a threshold population size exists such that below it the probability of population extinction is inproportionately higher than above the threshold (Dennis, 1989). Population dynamic consequences of such a system could be totally different provided that the point source size is above this threshold while all the multiple source local sizes fall below it; see Groom (1998) for a real example. Silvertown et al. (1992) explored effects of various initial distributions in five-species plant community on outcomes of interspecific competition. Although the ultimate fate of the community did not depend on the order of plants in the initial patterns with different species arranged in monospecific bands, transient dynamics differed significantly.

An important question is how to define initial conditions for established populations. Technically, the easiest way is to assume that individuals are uniformly randomly distributed in their habitat, and this choice is by far the most common in the literature. This case can easily be set up in laboratory experiments; it may also be observed at the beginning of some ecological successions and for trees in older forest stands (Szwagrzyk and Czerwczak, 1993). When this assumption does not hold, populations may be clustered or overdispersed in space. Then, for 'C-space' IBMs initial conditions may be generated from appropriate spatial point process models. Cressie (1993)

made a review of such models and methods of their estimation from the observed patterns of individuals. These models also cover situations in which non-uniform characteristics such as age and size have to be assigned to each individual at the start of simulations. Lepš and Kindlmann (1987) suggested a flexible generator of clustered patterns in a 'C-space, D-time' IBM. If the number of lattice sites is sufficiently large these methods can be used (as an approximation at least) to gain an insight into 'D-space' IBMs, too, as exemplified by Wiegand et al. (1998).

4.5. Environmental heterogeneity

Spatial and/or temporal heterogeneity in environmental characteristics is one of the principal determinants of observed spatio-temporal population patterns. One may distinguish heterogeneity in physical characteristics of the environment as opposed to that in biological characteristics where non-random spatial patterns of individuals are formed in the environment that is physically homogeneous (McCauley et al., 1993; Keeling, 1999; Herben et al., 2000). Patterns due to the former type are imposed via extrinsic factors such as temperature, moisture, light, nutrients, topographic heterogeneity, and habitat unsuitability or destruction; spatial heterogeneity in physical characteristics of the environment can be described either phenomenologically (describing a cumulative effect of all potential sources of heterogeneity) or mechanistically (separately describing individual sources). Patterns due to the latter type are emergent via intrinsic factors such as limited dispersal and local interactions of the studied populations; although these patterns are hard to detect in natural systems, Wilson et al. (1999) suggest its presence in a system composed of western tussock moth feeding on perennial lupines in coastal California.

Influence of individuals and the environment is mutual. The latter determines vital rates of populations while the former contribute to the spatial heterogeneity by influencing, for example, dynamics of resource renewal and depletion. Britton et al. (1996) constructed a 'D-space, D-time' IBM in which army ant colonies exploited patches of food, thus reducing their efficiency for and growth rate of other colonies; left exploited patches recovered in a number of time steps. Doi et al. (1998) considered an IBM of a microorganic closed ecosystem where each individual consumes a nutrient from the environment and excretes its metabolic products to the environment as detritus. Models of forest growth that are intended to have a high predictive power describe spatial heterogeneity in a big detail (Busing, 1991; Pacala et al., 1996).

In 'D-space' IBMs, spatial heterogeneity in physical characteristics of the environment is easily modeled by defining a variable giving each site a value of its state. Britton et al. (1996) gave this variable a meaning of the state of recovery of the site after a recent army ant raid. Dytham (1994) and Keitt (1997) distinguished destroyed and habitable sites in a two-species competition system and a general food web, respectively. In 'C-space' IBMs, a variable describing physical state of a location is spatially continuous and hence more difficult to define and handle. Pacala (1987) presented two ways of dealing with it in one-dimensional environments of a finite length: the environment is divided into a finite number of connected intervals (patches), and physical characteristics of these patches are either fixed or vary stochastically with time. In two-dimensional systems a question arises how to handle possibly non-rectangular patches. A possible solution seems to be a use of a Geographic Information System (GIS) model as a background description of the physical environment. The statistical method of kriging can also be exploited in 'C-space' models; it estimates a spatially continuous distribution of an environmental variable from a finite number of measured samples (Cressie, 1993). Interpolation of environmental variables in 'C-space' IBMs can also be coupled with GIS (Briggs et al., 1997).

4.6. Process ordering

In 'D-time' models ordering of acting processes is not implied by them but has to be specified externally. Yet it is not always obvious how the processes should be ordered in a time step. Move-

ment (for motile organisms) is mostly separated from mortality and reproduction processes in the literature, and put at the end (or equivalently at the beginning) of the time step. I distinguish three cases concerning ordering of mortality and reproduction in the above single-species, 'D-time' IBMs, and give them the following labels, CC for concurrent ordering (individuals reproduce and die simultaneously, newborns cannot die nor establish to the sites occupied by actually deceased adults, individuals that are marked dead may still reproduce in the current time step); RM for reproduction preceding mortality (population first reproduces, then all individuals (including newborns) are exposed to death); and MR for reproduction following mortality (individuals are first exposed to death and those that die removed from the habitat, only surviving individuals are able to reproduce); see Fig. 3.

Which ordering to choose for a particular system? This issue is by no means a mere technical detail, since it can profoundly alter population dynamics by introducing specific density-dependent relationships and/or by modifying parameter values. McCauley et al. (1993) showed that for a 'D-space, D-time', predator–prey IBM prey growth is a function of prey density if the process ordering is concurrent, but that it depends on the predator density as well provided that the demographic processes and predation are ordered in a sequential way. Hence, an assumption made in this regard is important. In some systems such as plants reproducing by seeds and animals with non-overlapping generations or short reproductive periods, mortality and reproduction are more or less temporally separated processes. The RM and MR cases are equivalent if applied to sessile species. On the other hand, if movement is added at the end of each time step it is placed in qualitatively different points of the RM and MR loops (Fig. 3); as movement may considerably modify spatial patterns of individuals in the habitat, the RM and MR cases may now produce different results. Concurrent ordering is a way to model situations where mortality and reproduction processes overlap. Some examples of process ordering in more complex IBMs can be found in McCauley et al. (1993) for predator-prey systems and in Durrett and Levin (1994b) for competition among plants.

For a more quantitative insight, I now derive mean-field models for the CC, RM, and MR
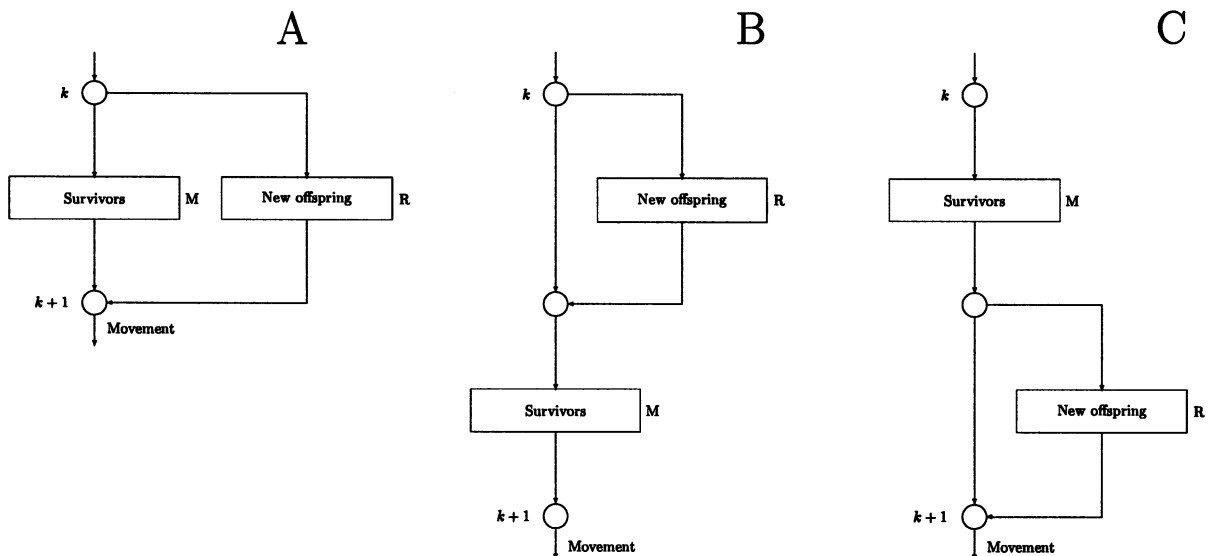

Fig. 3. Ordering of mortality (M) and reproduction (R) processes in a time step. (A) Concurrent ordering. (B) Reproduction preceding mortality. (C) Reproduction following mortality.
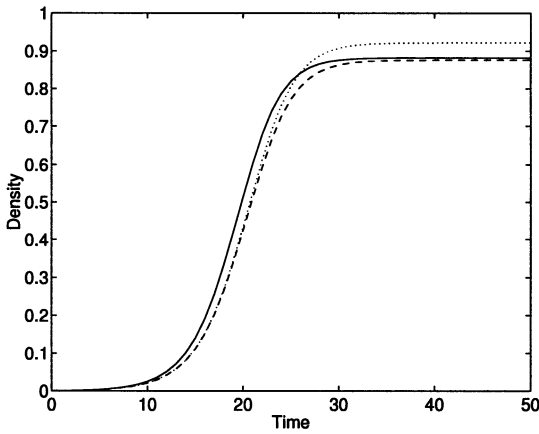
Fig. 4. Effects of ordering of mortality and reproduction processes in a time step on mean-field model dynamics in the 'D-space, D-time' framework. Concurrent ordering (Eq. (20); solid line), reproduction preceding mortality (Eq. (21); dashed line), reproduction following mortality (Eq. (22); dotted line). Parameter values: $S = 128 \times 128$, $P_r = 0.5$, $P_m = 0.05$, $N = 4$, $x_0 = 10$, $v_0 = x_0/S$.

scenarios in the above 'D-space, D-time' IBM. Analogous, yet slightly more laborious calculations can be made for the 'C-space, D-time' case. The CC case has been analyzed above; the mortality and reproduction processes are independent events starting with the same number of individuals. Under the homogeneous mixing conditions, this implies (see above):

$$E(X'|X = x) = x(1 - P_m)$$
$$+ (S - x)\left[1 - \left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N\right] \quad (15)$$

In the RM case, in order to be counted in the next generation, offspring has to be conceived, placed successfully on the lattice, and survive to the end of the time step. The adult survival and offspring establishment processes are still independent events. Therefore:

$$E(X'|X = x) = x(1 - P_m)$$
$$+ (S - x)\left[1 - \left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N\right]$$
$$(1 - P_m) \quad (16)$$

The MR case is the most complex as the adult survival and offspring establishment processes are

no more independent events. In particular, adults that currently die enable offspring to be established in the respective emptied sites. Consequently, two expectation equations have to be composed:

$$E(\tilde{X}|X = x) = x(1 - P_m),$$
$$E(X'|\tilde{X} = \tilde{x}, X = x)$$
$$= x(1 - P_m) + (S - \tilde{x})\left[1 - \left(1 - \frac{\tilde{x}}{S}\frac{P_r}{N}\right)^N\right]$$
$$(17)$$

where $\tilde{X}$ is a random variable giving the number of surviving adults before reproduction starts. One may be tempted to combine these equations to get:

$$E(X'|X = x) = x(1 - P_m)$$
$$+ (S - x(1 - P_m))$$
$$\left[1 - \left(1 - \frac{x}{S}(1 - P_m)\frac{P_r}{N}\right)^N\right] \quad (18)$$

This is, however, not correct mathematically. It can be easily shown that:

$$E(X'|X = x) = E[E(X'|\tilde{X} = \tilde{x}, X = x)|X = x] \quad (19)$$

and unless one assumes that $P(\tilde{x}|x) = \delta(\tilde{x} - x(1 - P_m))$, where $P(\cdot|\cdot)$ is a pdf and $\delta(\cdot)$ the Dirac delta function, that is, unless the mortality process is deterministic, the combined expectation in Eq. (18) does not hold. Yet it may be a good approximation if variance of $\tilde{X}$ is small, such as in large populations. Going through the same steps as when deriving the mean-field model within the 'D-space, D-time' framework, one may get the following equations for the evolution of populations densities,

$$v' = v(1 - P_m) + (1 - v)\left[1 - \left(1 - v\frac{P_r}{N}\right)^N\right] \quad CC$$
$$(20)$$

$$v' = v(1 - P_m) + (1 - v)\left[1 - \left(1 - v\frac{P_r}{N}\right)^N\right]$$
$$(1 - P_m) \quad RM \quad (21)$$

$$v' = v(1 - P_m)$$
$$+ (1 - v(1 - P_m))\left[1 - \left(1 - v(1 - P_m)\frac{P_r}{N}\right)^N\right]$$
$$MR \quad (22)$$

Typical behavior of these three mean-field models is shown in Fig. 4. Note that the MR model attains the highest carrying capacity, the CC model demonstrates the most rapid growth, and the RM and MR models coincide for low population densities.

All the above orderings can be referred to as temporal as they define an order of demographic processes in a time step. Ruxton (1996) and above all Ruxton and Saravia (1998) pointed out that an order in which sites are processed in 'D-space' models (spatial ordering) may also affect model output. In particular, they considered random site processing order and 'top-left to bottom-right' site processing order in precisely the above 'D-space, D-time' IBM with $e = 1$ and $d = 0$ (no movement), together with a triplet of temporal process orderings (including the above MR case). Moreover, they compared the 'time type' scenarios in which changes in the states of the lattice sites were registered immediately or at the end of a time step. Based on a couple of simulation experiments they came with a hierarchical classification of these ordering alternatives: temporal ordering had the most pronounced effect, followed by time type and finally spatial ordering. Although this ranking can be model specific, the important consideration is that the model output depends critically on assumptions made about process ordering. Ruxton and Saravia (1998) ended up with two general warnings: first, spatio-temporal ordering must be carefully selected to match the biological characteristics of the system to be modeled rather than led by programming expediency, and second, a complete description of the details of this ordering should be specified in the publications using IBMs.

4.7. Interaction neighborhoods

The interaction neighborhood is an area about an individual circumscribing a part of the habitat (possibly containing some other individuals) that influences its current behavior. In the above single-species IBMs, I defined such neighborhoods for the processes of offspring establishment and individual movement. Mortality and/or reproduction probabilities could also be made neighborhood dependent (see below).

Interaction neighborhoods may be formulated as regular or irregular. In the former case, one may adopt $\|z\|$ as a distance function and let $N = \{z : \|z\| \leq r\}$ be the set of sites or locations within a distance r from the origin. The interaction neighborhood for a process and an individual located at x is then the set $\{x + z : z \in N\}$. The functions $\|z\|_1 = |z_1| + |z_2|$ and $\|z\|_\infty = \max\{|z_1|, |z_2|\}$, $z = (z_1, z_2)$, probably most suit to two-dimensional 'D-space' IBMs with lattices composed of squares, giving diamond- and square-shaped neighborhoods, respectively (Durrett and Levin, 1994b); the most popular von Neumann (or nearest neighbor) and Moore neighborhoods can be expressed as $N = \{z : \|z\|_1 = 1\}$ and $N = \{z : \|z\|_\infty = 1\}$, respectively. For two-dimensional 'D-space' IBMs with hexagonal and triangular lattices one usually formulates regular interaction neighborhoods in terms of rings of nearest neighbors, second-nearest neighbors etc. (Tilman et al., 1997). When these lattices are projected onto square lattices, these neighborhoods have to be transformed accordingly (see above). For two-dimensional 'C-space' IBMs, circular neighborhoods due to the Euclidean norm $\|z\|_2 = (|z_1|^2 + |z_2|^2)^{1/2}$ are probably the most common choice.

Durrett and Levin (1994a) claimed that 'one should not worry too much about what neighborhood to choose. In most cases the qualitative behavior of the model does not depend on the neighborhood used'. This statement concerns neighborhood shape but not its size. The observations from many IBMs show and the above mean-field model derivations confirm that when the interaction neighborhoods increase in size the system behaves more and more like a well-mixed system: spatial distribution of individuals resembles the uniform random distribution and temporal evolution of density approaches mean-field model dynamics.

An important question concerns choice of neighborhood sizes for the system under study. Generally, the adequate choice depends on the individual life history and physiology. For 'D-space' IBMs this question is intimately related to the site size. In 'D-time' IBMs the time step is also important. Britton et al. (1996) derived the move-

ment neighborhood size of the army ant colonies from the actual observations of distances crossed per defined time step. Pacala and Silander (1985), Silander and Pacala (1985), Pacala and Silander (1990) touched this problem in a 'C-space' IBM of plant communities. Their seed set (or fecundity) predictor and survivorship predictor relate the average number of seeds per plant and the probability of reaching adulthood from seed, respectively, to a number of neighbor plants in respective circular neighborhoods. The 'best' neighborhood sizes were estimated by fitting the predictors evaluated for a finite number of neighborhood radii to the observed data on seed sets and survivorship, and choosing such a radius for each predictor that minimizes residual variance.

4.8. Life cycles

No two individuals are the same. Rather, they differ in age, size, stage, sex, genotype, and many other physiological and behavioral traits. The above simple, single-species IBMs do not take this uniqueness into account; various individuals differ just by their location in space. Some of these traits can be technically considered as system states and the model parameters (such as reproduction and mortality probabilities/rates) or even the whole model rules made dependent on them; in other words, the same local environment may have different effects on the individual performance depending on its state. One may also be interested in the population-level distribution of these states (mostly age, size and sex) and its temporal dynamics. Evolutionary models assume that different genotypes may have different parameter values, which leads to differences in their respective reproductive success (Keeling and Rand, 1995). Temporal variation may be included in IBMs by altering the model rules from time to time (e.g. from generation to generation in annual plants).

Almost all published IBMs assume that movement is local but diffusive (equiprobable in all directions). Yet often it may be directed: actively to water, sexual partner, sward etc. passively by wind or river stream (Fahse et al., 1998; Berec et al., 2001). A predator may direct its movement to

areas with a higher local density of prey; likewise, a prey may direct it to areas with a lower predator density.

Although the vast majority of theoretical studies considers the same mortality risk for each individual, non-uniform mortality scenarios are more the rule than an exception in nature. Adverse environmental conditions, density dependence, and starvation are just a few forces determining the unique mortality probability/rate for each individual. As opposed to the above IBMs, Law and Dieckmann (2000) considered density-independent reproduction and density-dependent mortality in single-species populations in the 'C-time, C-space' framework. Dieckmann and Law (2000) modeled both processes as density dependent. Starvation component of reproduction and mortality has been considered, for example, by Wilson and Keeling (2000).

Models may be constructed that allow for non-zero ('C-time') and non-unit ('D-time') development times for juveniles or production of two or more offspring per reproductive event, that describe 'C-space' individuals with a volume or at least an area so that they could not overlap, and that enable more than one 'D-space' individual occupy a site. Such realistic features are even a necessity in many applied issues.

Last but not least, no population lives alone in its habitat, but rather interacts with other populations. Spatially explicit IBMs can also be constructed for multi-species systems such as predator–prey systems (McCauley et al., 1993), competition systems (Durrett and Levin, 1998; Pacala, 1986), or one-predator two-prey optimal foraging systems (Berec, 2000; Berec and Křivan, 2000). In such systems, a number of alternatives can also be considered to model inter-population interactions.

5. Conclusions

This article reviews spatially explicit IBMs from a methodological point of view. My focus is primarily on showing technical as well as conceptual differences between the four frameworks for such models, differing by whether time and space are

each modeled discretely or continuously. For each of these frameworks I formulate one of the simplest single-species IBMs and discuss its simulation subtleties and mean-field analysis. All four mean-field models resemble the Verhulst logistic model of single-species population grow and are exact under the homogeneous mixing conditions. These conditions can be generally formulated as follows: (i) populations are to be divided into a finite number of groups within which individuals are supposed to be identical (averaging over individuals within respective groups), (ii) populations are well-mixed so that any individual may equally interact with any other (averaging over space), and (iii) populations are sufficiently large so that individuals respond only to means (averaging over system realizations). No one can probably claim that one framework is better than another. This article shows that they are more supplements than competitors, and probably any system can be described in any of the frameworks. Yet for a given system, some frameworks may perhaps be more suitable for implementing a given rule or feature than the others.

I also discuss some alternatives in construction of IBMs in more details. Some of them are just technical but some make the model more complex yet possibly more realistic. One should note at this point that finding an appropriate level of aggregation in a model is a decisive part of modeling procedure. This is exactly the reason why Murdoch et al. (1992) suggested building a suite of models with increasing complexity and hence deciding on the adequate model resolution for a given purpose.

Finally, I cannot forbear one specific note. The only complete description of any IBM is its computer code. Its publication inside any article is impossible, yet any conceptual description of model rules is, due to an effort to save an expensive space, in most cases incomplete, particularly in more complex systems. Hendry et al. (1997) published at least a flow chart of their model, but even this practice is, in my opinion, unsatisfactory. Any modeller may implement the flow chart differently and when the system is at least a bit more complex, the probability of making an error increases. Moreover, every reader should be allowed to check published simulations. I am fully aware that there are many possible computer languages available, some of them even specific to some model environments. But no reader should be a priori disallowed to view the code. Imagine how many of us have to code the same or at least quite similar IBMs simultaneously. Sharing our codes would make the modeling much more effective, even though not always. Last but not least, this would force modelers to write clear, understandable codes, and possibly create standardized model outputs, which is useful by itself. That is why I suggest to describe models roughly by words in the articles, putting stress on the most important parameters and interactions, and enable anyone downloading of IBM codes from authors' web pages or at least sending the codes on request by e-mail. I do this just now. Anyone can download the codes of the above single-species IBMs, implemented in C-language, from my personal web page http://www.entu.cas.cz/berec/ibm.html I hope this helps.

Some more issues have to be addressed to make IBM analysis more reliable, i.e. able to satisfactorily describe systems even when the homogeneous mixing conditions do not hold. These include,

- statistical descriptions of spatial population patterns;
- non-spatial, population-level models that track temporal population dynamics;
- spatial, population-level models that track spatio-temporal dynamics, etc.;

These issues are going to be reviewed in the next article.

Acknowledgements

Appendix A. Mean-field model derivation in the 'D-space, D-time' case

Let X' and X be random variables representing numbers of occupied lattice sites at the beginning and at the end of a time step, respectively (note that the model rules are stochastic). Let X_s and X_r be two more random variables, representing numbers of survived adult individuals and newly established offspring, respectively, at the end of the time step. Obviously, $X' = X_s + X_r$. Hence:

$$E(X'|X=x) = E(X_s|X=x) + E(X_r|X=x), \quad (23)$$

where I denote by $E(Y|X=x)$ the mean value of a random variable Y conditioned on the event $X = x$. Clearly:

$$E(X_s|X=x) = x(1 - P_m) \quad (24)$$

as the number of individuals that die every time step is binomially distributed. Similarly:

$$E(X_r|X=x) = x P_r P \text{ [conceived offspring is estab-lished on the lattice]} \quad (25)$$

Yet I use an alternative expression for $E(X_r|X=x)$ as the involved probability is easier to evaluate:

$$E(X_r|X=x) = (S - x)P \text{ [site that is vacant now becomes occupied at the next time step]}, \quad (26)$$

where $S - x$ is the current number of vacant sites. Provided that the individuals are uniformly randomly distributed on the lattice, it is:

$$P \text{ [site that is vacant now becomes occupied at the next time step]} = 1 - \left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N, \quad (27)$$

where $N = (2e + 1)^2 - 1$ is the number of sites in the establishment neighborhood. Eq. (27) is due to the fact that each neighbor of the vacant site independently sends an individual with the probability that the neighbor site is occupied (x/S) times the probability that the individual present there reproduces (P_r) times the probability that it sends offspring to the focal vacant site ($1/N$). To sum up:

$$E(X'|X=x) = x(1 - P_m)$$
$$+ (S - x)\left[1 - \left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N\right] \quad (28)$$

Due to the concurrent ordering of mortality and reproduction rules, X_s and X_r are independent random variables. Hence, variance in the number of individuals at the end of the time step is:

$$\text{Var}(X'|X=x) = \text{Var}(X_s|X=x) + \text{Var}(X_r|X=x) \quad (29)$$

with (binomial distributions):

$$\text{Var}(X_s|X=x) = x(1 - P_m)P_m \quad (30)$$

and:

$$\text{Var}(X_r|X=x) = (S - x)\left[1 - \left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N\right]$$
$$\left(1 - \frac{x}{S}\frac{P_r}{N}\right)^N \quad (31)$$

Now, divide Eq. (29) by S^2 and send $x \to \infty$ and $S \to \infty$ so that x/S remains (or converges to) a constant v. Hence:

$$\text{Var}(V'|V=v) \to 0 \quad (32)$$

where the random variable $V = X/S$ stands for the population density. This implies:

$$v' = E(V'|V=v) \quad (33)$$

in the limit, with v' being the actual population density at the end of the time step. Consequently:

$$v' = v(1 - P_m) + (1 - v)\left[1 - \left(1 - v\frac{P_r}{N}\right)^N\right] \quad (34)$$

in the above limit. Eq. (34) can be alternatively derived by means of the (strong) law of large numbers.

Appendix B. Mean-field model derivation in the 'D-space, C-time' case

Through the technique of thinning of Poisson processes, one background Poisson process is made running at a rate cS, $c \geq m + r + w$ (Durrett, 1995). Lengths of intervals between two successive event times are thus independent and identically

exponentially distributed random variables with parameter cS. At every event time generated, a site is uniformly randomly chosen and if occupied a random number is picked uniformly from the interval [0, 1] to decide on the particular event: death, birth, movement (for motile organisms) or nothing (see above).

Consider a small time interval h. By definition, probability that just one event time is generated in h is $cSh + o(h)$ as $h \to 0$ (probability that two or more event times are generated in h is $o(h)$, probability that no event time is generated in h is $1 - cSh + o(h)$; the term $o(h)$ has a precise mathematical meaning and for practical purposes can be treated as a quantity that is negligible in comparison with h), and probability that the chosen site is occupied is x/S, provided that individuals are uniformly randomly distributed on the lattice. The particular event may result in the increase of population by one individual (birth and successful offspring establishment), the decrease by one individual (death), or no change in abundance (no event, reproduction but unsuccessful offspring establishment, or movement [with uniform random positioning of the individual]). Also, an empty site may be chosen or no event time generated in h. The event of birth and successful offspring establishment takes place with the probability $r/c(1 - x/S)$, while the event of death with the probability m/c. To sum up, the mean change in the number of individuals in a small time interval h is:

$$
\dot{v} = rv(1-v) - mv = \tilde{r}v\left(1 - \frac{v}{K}\right) \tag{37}
$$

Appendix C. Mean-field model derivation in the 'C-space, D-time' case

With the notation established for the 'D-space, D-time' case,

$$
E(X_s|X = x) = x(1 - P_m), \tag{38}
$$

and similarly:

$$
E(X_r|X = x) = xP_rP \quad \text{[conceived offspring is established on the plot]} \tag{39}
$$

The probability that the conceived offspring is established on the plot depends on the place it lands and the number of neighbors around that place. The probability $P_E(n)$ of successful establishment given n neighbors is:

$$
P_E(n) = \left[1 - \frac{n}{E}\right]_+ \equiv \begin{cases} 1 - n/E & \text{if } n \le E, \\ 0 & \text{if } n > E. \end{cases} \tag{40}
$$

If the offspring lands in such a distance from its parent so that the latter lies within the establishment neighborhood of the former (an event with the probability P_L, $P_L = e/\varepsilon$ if $e < \varepsilon$ and $P_L = 1$ otherwise), the parent influences the establishment

$$
\begin{aligned}
E(X(t+h)|X(t) = x) &= x + (-1)\left[cSh \frac{x}{S} \frac{m}{c}\right] + 1\left[cSh \frac{x}{S} \frac{r}{c}\left(1 - \frac{x}{S}\right)\right] + 0 \\
&\times \left[cSh \frac{x}{S}\left[\frac{1 - (m + r + w)}{c} + \frac{r}{c}\frac{x}{S} + \frac{w}{c}\right] + cSh\left(1 - \frac{x}{S}\right) + (1 - cSh)\right] + o(h) \\
&= x + \left[rx\left(1 - \frac{x}{S}\right) - mx\right]h + o(h) \quad \text{as } h \to 0
\end{aligned} \tag{35}
$$

By computing variance in the number of individuals and letting $h \to 0$, $S \to \infty$, and $x \to \infty$ so that x/S is (or converges to) a constant v, one may show that:

$$
\text{Var}(V(t+h)|V(t) = v) \to 0 \quad \text{as} \quad h \to 0 \tag{36}
$$

Time evolution of the population density v thus converges to the solution of ODE:

probability of its offspring. Therefore, one may write:

P[conceived offspring is established on the plot]

$$
= P_L \sum_{n=0}^{x-1} P_N(n, x-1, e, \tilde{\varepsilon})P_E(n+1)
$$

$$
+ (1 - P_L) \sum_{n=0}^{x} P_N(n, x, e, \tilde{\varepsilon})P_E(n) \tag{41}
$$

where $P_N(m, y, e, \tilde{\varepsilon})$ is the probability that the offspring located at $\tilde{\varepsilon}$ has m adult neighbors out of y possible in its e-neighborhood, and equals:

$$P_N(m, y, e, \tilde{\varepsilon}) = \binom{y}{m}\left(\frac{A}{S}\right)^m\left(1 - \frac{A}{S}\right)^{y-m} \tag{42}$$

under the assumption of uniform random distribution of the individuals on the plot, with $A = \pi e^2$. One may easily show that for $x \to \infty$ and $S \to \infty$ ($S = MN$, the plot size) such that x/S is (or converges to) a constant v variance Var $(V'|V = v) \to 0$, which implies $v' = E(V'|V = v)$ in the limit. Moreover, the binomial terms P_N converge to the Poisson counterparts with the parameter vA. Hence:

$$v' = v(1 - P_m)$$
$$+ vP_r\left[P_L \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA)\left[1 - \frac{n+1}{E}\right]_+\right.$$
$$\left. + (1 - P_L) \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA)\left[1 - \frac{n}{E}\right]_+\right] \tag{43}$$

Appendix D. Mean-field model derivation in the 'C-space, C-time' case

The background Poisson process is made running at the rate $x(m + r + w)$, x being the current population size. Mean-field model derivation is a combination of the 'D-space, C-time' and 'C-space, D-time' cases. In particular, consider a small time interval of length h, starting at time t at which $X(t) = x$. The probability that just one event time is generated within this interval is $x(m + r + w)h + o(h)$ as $h \to 0$. Provided it is generated, an individual is uniformly randomly selected; it dies with the probability $m/(m + r + w)$, reproduces with the probability $r/(m + r + w)$, and moves with the probability $w/(m + r + w)$. The mean change in the number of individuals in h is:

$$E(X(t+h)|X(t) = x) = x + (-1)$$
$$\times \left[x(m + r + w)h\frac{m}{m + r + w}\right]$$
$$+ 1 \times \left[x(m + r + w)h\frac{r}{m + r + w}P \text{ [conceived off-}\right.$$
$$\left.\text{spring is established on the plot]}\right]$$
$$+ 0 \times \left[x(m + r + w)h\left(\frac{w}{m + r + w} + \frac{r}{m + r + w}\right.\right.$$
$$(1 - P \text{ [conceived offspring is established on}$$
$$\left.\left.\text{the plot])}\right)\right.$$
$$+ (1 - x(m + r + w)h)] + o(h) = x + [rxP$$
$$\text{[conceived offspring is established on the plot]}$$
$$- mx]h + o(h) \text{ as } h \to 0, \tag{44}$$

where:

P [conceived offspring is established on the plot $P_L = \sum_{n=0}^{x-1} P_N(n, x - 1, e, \tilde{\varepsilon})P_E(n+1)$

$$+ (1 - P_L) \sum_{n=0}^{x} P_N(n, x, e, \tilde{\varepsilon})P_E(n) \tag{45}$$

Meaning of the involved probabilities in the last expression is exactly the same as in the 'C-space, D-time' case. One may show that for $h \to 0$, $x \to \infty$ and $S \to \infty$ such that x/S is (or converges to) a constant v variance Var $(V'|V = v) \to 0$, which implies $v' = E(V'|V = v)$ in the limit. Altogether, time evolution of the population density v thus converges to the solution of ODE:

$$\dot{v} = -mv$$
$$+ rv\left[P_L \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA)\left[1 - \frac{n+1}{E}\right]_+\right.$$
$$\left. + (1 - P_L) \sum_{n=0}^{+\infty} \frac{(vA)^n}{n!} \exp(-vA)\left[1 - \frac{n}{E}\right]_+\right] \tag{46}$$

References

Berec, L., 2000. Mixed encounters, limited perception and optimal foraging. Bulletin of Mathematical Biology 62, 849–868.

Berec, L., Křivan, V., 2000. A mechanistic model for partial preferences. Theoretical Population Biology 58, 279–289.

Berec, L., Boukal, D.S., Berec, M., 2001. Linking the Allee effect, sexual reproduction and temperature-dependent sex determination via spatial dynamics. American Naturalist 157, 217–230.

Bolker, B.M., Pacala, S.W., 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. American Naturalist 153, 575–602.

Bolker, B.M., Pacala, S.W., Levin, S.A., 2000. Moment methods for ecological processes in continuous space. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 388–411.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60, 849–872.

Briggs, D.J., Collins, S., Elliott, P., Fischer, P., Kingham, S., Lebret, E., Pryl, K., VanReeuwijk, H., Smallbone, K., VanderVeen, A., 1997. Mapping urban air pollution using GIS: a regression-based approach. International Journal of Geographical Information Science 11, 699–718.

Britton, N.F., 1986. Reaction–Diffusion Equations and Their Applications to Biology. Academic Press, London.

Britton, N.F., Partridge, L.W., Franks, N.R., 1996. A mathematical model for the population dynamics of army ants. Bulletin of Mathematical Biology 58, 471–492.

Busing, R.T., 1991. A spatial model of forest dynamics. Vegetatio 92, 167–179.

Cressie, N.A.C., 1993. Statistics for Spatial Data. Wiley, New York.

de Roos, A.M., McCauley, E., Wilson, W.G., 1991. Mobility versus density-limited predator–prey dynamics on different scales. Proceedings of the Royal Society of London B 246, 117–122.

DeAngelis, D.L., Rose, K.A., 1992. Which individual-based approach is most appropriate for a given problem. In: DeAngelis, D.L., Gross, L.J. (Eds.), Individual-Based Models and Approaches in Ecology—Populations, Communities and Ecosystems. Chapman & Hall, New York, pp. 67–87.

DeAngelis, D.L., Cox, D.K., Coutant, C.C., 1979. Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. Ecological Modelling 8, 133–148.

DeAngelis, D.L., Rose, K.A., Huston, M.A., 1994. Individual-oriented approaches to modeling ecological populations and communities. In: Levin, S. (Ed.), Frontiers in Mathematical Biology. Springer, Berlin, pp. 390–410.

Dennis, B., 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resource Modeling 3, 481–538.

Dieckmann, U., Law, R., 2000. Relaxation projections and the method of moments. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 412–455.

Doi, M., Sakashita, T., Fuma, S., Takeda, H., Miyamto, K., Nakamura, Y., 1998. Computer simulation of microorganic ecology (microcosm) as a self-sustaining system of complexity. In: Inaba, J., Nakamura, Y. (Eds.), Comparative Evaluation of Environmental Toxicants. National Institute of Radiological Sciences, Japan, pp. 289–290.

Durrett, R., 1988. Crabgrass, measles, and gypsy moths: an introduction to interacting particle systems. Mathematical Intelligence 10, 37–47.

Durrett, R., 1993. Stochastic models of growth and competition. In: Levin, S.A., Powell, T.M., Steele, J.H. (Eds.), Patch Dynamics. Springer, Berlin, pp. 176–183.

Durrett, R., 1995. Ten lectures on particle systems. In: Dold, F.T.A. (Ed.), Lecture Notes in Mathematics, vol. 1068. Springer, New York, pp. 97–201.

Durrett, R., 1999. Stochastic spatial models. SIAM Review 41, 677–718.

Durrett, R., Levin, S.A., 1994a. The importance of being discrete (and spatial). Theoretical Population Biology 46, 363–394.

Durrett, R., Levin, S.A., 1994b. Stochastic spatial models: a user's guide to ecological applications. Philosophical Transactions of the Royal Society of London B 343, 329–350.

Durrett, R., Levin, S.A., 1998. Spatial aspects of interspecific competition. Theoretical Population Biology 53, 30–43.

Dytham, C., 1994. Habitat destruction and competitive coexistence: a cellular model. Journal of Animal Ecology 63, 490–491.

Fahse, L., Wissel, C., Grimm, V., 1998. Reconciling classical and individual-based approaches in theoretical population ecology: a protocol for extracting population parameters from individual-based models. American Naturalist 152, 838–852.

Fryxell, J.M., Lundberg, P., 1994. Diet choice and predator–prey dynamics. Evolutionary Ecology 8, 407–421.

Grimm, V., 1999. Ten years of individual-based modeling in ecology: what have we learned and what could we learn in the future. Ecological Modelling 115, 129–148.

Grist, E.P.M., des Clers, S., 1999. Seasonal and genotypic influences on life cycle synchronization: further insights from annual squid. Ecological Modelling 115, 149–163.

Groom, M.J., 1998. Allee effects limit population viability of an annual plant. American Naturalist 151, 487–496.

Hassell, M.P., Comins, H.N., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. Nature 353, 255–258.

Hendry, R.J., McGlade, J.M., Weiner, J., 1996. A coupled map lattice model of the growth of plant monocultures. Ecological Modelling 84, 81–90.

Hendry, R., Bacon, P.J., Moss, R., Palmer, S.C.F., McGlade, J., 1997. A two-dimensional individual-based model of territorial behavior: possible population consequences of kinship in red grouse. Ecological Modelling 105, 23–39.

Herben, T., During, H.J., Law, R., 2000. Spatio-temporal patterns in grassland communities. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 48–64.

Hogeweg, P., Hesper, H., 1990. Individual-oriented modelling in ecology. Mathematical and Computer Modelling 13, 105–116.

Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. BioScience 38, 682–691.

Judson, O.P., 1994. The rise of the individual-based model in ecology. Trends in Ecology and Evolution 9, 9–14.

Kaneko, K., 1998. Diversity, stability, and metadynamics: remarks from coupled map studies. In: Bascompte, J., Solé, R. (Eds.), Modeling Spatiotemporal Dynamics in Ecology. Springer, Berlin, pp. 27–45.

Keeling, M., 1999. Spatial models of interacting populations. In: McGlade, J.M. (Ed.), Advanced Ecological Theory. Blackwell Science, Oxford, pp. 64–99.

Keeling, M.J., Rand, D.A., 1995. A spatial mechanism for the evolution and maintenance of sexual reproduction. Oikos 74, 414–424.

Keitt, T.H., 1997. Stability and complexity on a lattice: coexistence of species in an individual-based food web model. Ecological Modelling 102, 243–258.

Kot, M., Lewis, M.A., van den Driessche, P., 1996. Dispersal data and the spread of invading organisms. Ecology 77, 2027–2042.

Law, R., Dieckmann, U., 2000. Moment approximations of individual-based models. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 252–270.

Lepš, J., Kindlmann, P., 1987. Models of the development of spatial pattern of an even-aged plant population over time. Ecological Modelling 39, 45–57.

Levin, S.A., 1974. Dispersion and population interactions. American Naturalist 108, 207–228.

Lomnicki, A., 1992. Population ecology from the individual perspective. In: DeAngelis, D.L., Gross, L.J. (Eds.), Individual-based Models and Approaches in Ecology–Populations, Communities and Ecosystems. Chapman & Hall, New York, pp. 3–17.

Mangel, M., Clark, C.W., 1988. Dynamic Modeling in Behavioral Ecology. Princeton University Press, Princeton, NJ.

McCauley, E., Wilson, W.G., de Roos, A.M., 1993. Dynamics of age-structured and spatially structured predator–prey interactions: individual-based models and population-level formulations. American Naturalist 142, 412–442.

McCauley, E., Wilson, W.G., de Roos, A.M., 1996. Dynamics of age-structured predator–prey populations in space: asymmetrical effects of mobility in juvenile and adult predators. Oikos 76, 485–497.

McGlade, J.M., 1999. Individual-based models in ecology. In: McGlade, J. (Ed.), Advanced Ecological Theory. Blackwell Science, Oxford, pp. 1–22.

Moravie, M.A., Pascal, J.-P., Auger, P., 1997. Investigating canopy regeneration processes through individual-based spatial models: application to a tropical rain forest. Ecological Modelling 104, 241–260.

Murdoch, W.W., McCauley, E., Nisbet, R.M., Gurney, W.S.C., de Roos, A.M., 1992. Individual-based models: combining testability and generality. In: De Angelis, D.L.,

Gross, L.J. (Eds.), Individual-Based Models and Approaches in Ecology-Populations, Communities and Ecosystems. Chapman & Hall, New York, pp. 18–35.

Murray, J.D., 1990. Mathematical Biology. Springer, Berlin.

Neubert, M.G., Kot, M., Lewis, M., 1995. Dispersal and pattern formation in a discrete-time predator–prey model. Theoretical Population Biology 48, 7–43.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer, Berlin.

Pacala, S.W., 1986. Neighborhood models of plant population dynamics. 2. Multi-species models of annuals. Theoretical Population Biology 29, 262–292.

Pacala, S.W., 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. Theoretical Population Biology 31, 359–392.

Pacala, S.W., Silander, J.A. Jr, 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. American Naturalist 125, 385–411.

Pacala, S.W., Silander, J.A., 1990. Field tests of neighborhood population dynamic models of two annual weed species. Ecological Monographs 60, 113–134.

Pacala, S.W., Canham, C.D., Saponara, J., Silande, J.A. Jr, Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66, 1–43.

Ruxton, G.D., 1996. Effects of the spatial and temporal ordering of events on the behavior of a simple cellular automaton. Ecological Modelling 84, 311–314.

Ruxton, G.D., Saravia, L.A., 1998. The need for biological realism in the updating of cellular automata models. Ecological Modelling 107, 105–112.

Silander, J.A., Pacala, S.W., 1985. Neighborhood predictors of plant performance. Oecologia 66, 256–263.

Silvertown, J., Holtier, S., Johnson, J., Dale, P., 1992. Cellular automaton models of interspecific competition for space—the effect of pattern on process. Journal of Ecology 80, 527–534.

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect. Oikos 87, 185–190.

Szwagrzyk, J., Czerwczak, M., 1993. Spatial patterns of trees in natural forests of East-Central Europe. Journal of Vegetation Science 4, 469–476.

Takeuchi, Y., 1996. Global dynamical properties of Lotka–Volterra systems. World Scientific Publishing Company, Singapore.

Tilman, D., Lehman, C.L., Kareiva, P., 1997. Population dynamics in spatial habitats. In: Tilman, D., Kareiva, P. (Eds.), Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions (Monographs in population biology, No. 30). Princeton University Press, Princeton, NJ, pp. 3–20.

Uchmanski, J., Grimm, V., 1996. Individual-based modelling in ecology: what makes the difference. Trends in Ecology and Evolution 11, 437–441.

van Baalen, M., 2000. Pair approximations for different spatial geometries. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 359–387.

Veit, R.R., Lewis, M.A., 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. American Naturalist 148, 255–274.

Wiegand, T., Moloney, K.A., Milton, S.J., 1998. Population dynamics, disturbance, and pattern evolution: identifying the fundamental scales of organization in a model ecosystem. American Naturalist 152, 321–337.

Wilson, H.B., Keeling, M.J., 2000. Spatial scales and low-dimensional dynamics. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, pp. 209–226.

Wilson, W.G., 1996. Lotka's game in predator–prey theory: linking populations to individuals. Theoretical Population Biology 50, 368–393.

Wilson, W.G., 1998. Resolving discrepancies between deterministic population models and individual-based simulations. American Naturalist 151, 116–134.

Wilson, W.G., de Roos, A.M., McCauley, E., 1993. Spatial instabilities within the diffusive Lotka–Volterra system: individual-based simulation results. Theoretical Population Biology 43, 91–127.

Wilson, W.G., McCauley, E., de Roos, A.M., 1995. Effect of dimensionality on Lotka–Volterra predator–prey dynamics: individual based simulation results. Bulletin of Mathematical Biology 57, 507–526.

Wilson, W.G., Harrison, S.P., Hastings, A., McCann, K., 1999. Exploring stable pattern formation in models of tussock moth populations. Journal of Animal Ecology 68, 94–107.