Discrete and continuous time simulations of spatial ecological processes predict different final population sizes and interspecific competition outcomes

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A B S T R A C T

Cellular automata (CAs) are commonly used to simulate spatial processes in ecology. Although appropriate for modelling events that occur at discrete time points, they are also routinely used to model biological processes that take place continuously. We report on a study comparing predictions of discrete time CA models to those of their continuous time counterpart. Specifically, we investigate how the decision to model time discretely or continuously affects predictions regarding long-run population sizes, the probability of extinction and interspecific competition. We show effects on predicted ecological outcomes, finding quantitative differences in all cases and in the case of interspecific competition, additional qualitative differences in predictions regarding species dominance. Our findings demonstrate that qualitative conclusions drawn from spatial simulations can be critically dependent on the decision to model time discretely or continuously. Contrary to our expectations, simulating in continuous time did not incur a heavy computational penalty. We also raise ecological questions on the relative benefits of reproductive strategies that take place in discrete and continuous time.

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1. Introduction

Cellular automata (CAs) are commonly used to simulate dynamic spatial processes in ecology, contributing to developments in both applied and theoretical research. In a simple CA model of birth-death processes, individuals inhabit discrete sites, usually organised in a grid formation. Time progresses in discrete steps and an *update scheme* specifies how individuals die or give birth into neighbouring sites at each step. For example, in the applied literature CAs have been used to simulate the spatial distribution of insect colonies (Perfecto and Vandermeer, 2008; Vandermeer et al., 2008) and the effect of plant-soil feedbacks on relative tree abundance (Mangan et al., 2010), while in microbial ecology, Fox et al. (2008) used a CA to investigate the way in which plasmids invade bacterial populations. In contrast, Laird and Schamp (2008) used a CA to explore theoretical questions relating to differences between interspecific competition in spatial and non-spatial (homogeneous mixing) contexts while Roxburgh et al.

(2004) investigated mechanisms leading to long-term species coexistence in the context of the intermediate disturbance hypothesis. In addition, CAs have been used to validate simplifications required to solve models analytically, such as in the theoretical work on population self-structuring reviewed in Lion and van Baalen (2008), as well as in a range of publications on the evolution host–parasite interactions (see e.g. Kamo and Boots, 2004; Best et al., 2011, for parasite virulence and host resistance, respectively), the evolution of altruism (e.g. Lion and van Baalen, 2007) and the evolution of reproductive effort (Lion, 2010).

Among the assumptions embodied in CA models is that of discrete time. This in turn introduces the need to make additional assumptions in the form of modelling decisions regarding the *update scheme* used to govern the order in which sites are considered and events take place. When these modelling decisions are made carefully, CAs can form appropriate models for discrete time spatial processes. However, they are often employed to simulate continuous time ecological processes or models, frequently without acknowledgement that this introduces an additional layer of approximation. Fortunately, these continuous processes can be simulated directly using a discrete space version of the Gillespie algorithm (Gillespie, 1977). Following this algorithm, time is continuous in the sense that it progresses in arbitrarily small steps, the length of which varies according to event rates, and these are limited only by the precision of the computer on which it

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is implemented. Although a little more mathematically involved than discrete time approaches, the implementation of this algorithm reduces the number of modelling decisions and thus allows a stronger focus on the biology while enhancing comparability between studies. Once understood, the approach can also be applied to non-spatial and continuous space problems, as well as to evolutionary problems (see e.g. Meier et al., 2011).

Decisions about whether to simulate in continuous or discrete time, and in the latter case which update scheme to use, are not simply technical but should be made in direct relation to the dynamics of the biological system under study. In order to compare studies and make informed decisions about which approach to use, it is important to understand any disparities in predictions between continuous and discrete time simulations, especially in the case where CAs are used to model continuous time processes. Although it is known that CA update schemes (the order in which events are considered) can affect ecological dynamics (Ruxton and Saravia, 1998), differences in ecologically meaningful predictions between CAs and corresponding continuous time simulation approaches have never been tested.

In this paper, we assume stochastic real world processes that occur in continuous time with exponentially distributed waiting times between events, taking as a case study the asymmetric logistic model of population growth on a lattice (Matsuda et al., 1992). We regard this model as our benchmark and consider discrete time CA simulations as approximations to this model. Specifically, we simulate this model stochastically in continuous time and compare outcomes with those of simulations conducted using two probabilistic CA update schemes, a range of time step sizes and two methods for converting between the rates used in continuous time models and probabilities required for discrete time simulation. We conduct two experiments, focusing in the first on a single species and in the second on competition between two species. In both experiments, we report long-run population sizes, and in the context of interspecific competition, also predictions regarding coexistence and competitive exclusion, using these outcomes to highlight disparities between discrete and continuous time.

In the following sections we consider some of the modelling decisions that need to be made when using CAs, emphasising the conversion from rates to probabilities required to approximate continuous processes. We describe our experimental protocol, provide findings from our two experiments and conclude with modelling recommendations.

2. Modelling decisions of cellular automata

Provided that time steps are chosen carefully so that they match the periodicity of real ecological events, discrete time simulations can be appropriate when simulating ecological processes that occur synchronously (e.g. reproductive cycles in cicadas) or where there are strong cyclical patterns (e.g. due to seasonality). Their use becomes more difficult to justify when modelling continuous processes (e.g. disease transmission) or to validate analytic simplifications in continuous time models. Nonetheless, justifications for employing discrete time simulations, decisions regarding particular choices of update scheme and method of converting rates to probabilities are rarely reported (although see Best et al., 2011; Ovaskainen and Hanski, 2003, for articles including this information). This makes replication almost impossible, as well as hindering comparisons between studies and the interpretation of any conflicting findings. In this study, we investigate the extent of these problems by simulating the same system in continuous and discrete time, taking a continuous time model as our benchmark. We limit our discussion to one or

more species living on a finite grid, and assume ecological processes that take place continuously according to a well-understood model.

Simple CA models of ecological processes are usually constructed in the following way: organisms live on a grid of sites; time progresses in discrete time steps and at each iteration individuals persist, die, or give birth into *neighbouring* sites according to a set of *local transition rules*. In probabilistic models, event probabilities are often dependent on the configuration of occupied and empty sites in the neighbourhood. CAs are relatively straightforward to implement, requiring limited mathematical or modelling knowledge (Berec, 2002; Breckling et al., 2011) but their very ease of implementation belies a range of complexities. Specifically, important modelling decisions arise as a result of the discrete nature of time: these concern the order in which events are executed and the way in which event rates are converted to probabilities.

The issue of event ordering arises because in discrete time, events may occur simultaneously at the same site (e.g. two births into the same site) and decisions thus need to be made about the order in which events should take place and how to resolve competition. An *update scheme* is therefore used to determine event ordering. A large number of schemes have been proposed and comparisons between these in the computing science, theoretical physics and ecological literature demonstrate important differences in dynamics and steady state outcomes (e.g. Manzoni, 2012; Ingerson and Buvel, 1984; Lumer and Nicolis, 1994; Schönfisch and de Roos, 1999; Cornforth et al., 2002; Ruxton and Saravia, 1998).

Event frequency in continuous time is typically characterised by event rates and the assumption that waiting times between events are exponentially distributed. For use in CA models, these rates must be converted into event probabilities. We use two different approaches in our study, one that allows for multiple events and one that allows only a single event per time step Δ_t. In the first, we make use of the fact that for a process with exponentially distributed waiting times, the number of events within a specified time window follows a Poisson distribution. Thus, we sample the number of events from a Poisson distribution with parameter $r\Delta_t$ where r is the instantaneous rate (note that this only makes sense for births). When discrete time is viewed as an approximation to a continuous process, this is similar to the τ-leaping idea proposed by Gillespie (2001). The second conversion is a cruder approximation that allows a maximum of one event per time step, bringing the simulation into line with most common CA approaches (see e.g. Best et al., 2011, for a study where this conversion is described explicitly). Probabilities in this approach are computed from rates as described in Section 3.3. System dynamics are expected to differ between conversion approaches and although it is known that reducing the time step should limit this effect (see e.g. Schönfisch and de Roos, 1999), it is unclear how small Δ_t needs to be before particular qualitative and quantitative properties of ecological models are indistinguishable.

3. Experimental protocol

Following Ruxton and Saravia's (1998) comparison of CA update schemes, we take as a case study one of the simplest spatial models, the asymmetric logistic model of population growth on a lattice. We simulate a stochastic version of this model for different birth and death rates using a model with exponentially distributed waiting times between events. This is compared to simulations using two CA update schemes, a range of time steps and two methods used to convert from rates to probabilities. In our analysis, we consider the continuous time simulation as our benchmark and the discrete time simulations as approximations to this. In Experiment