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# Spatial simulation: A spatial perspective on individual-based ecology—a review

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A B S T R A C T

Spatial Simulation is a spatially explicit, bottom-up modelling approach that includes individual-based models and cellular automata. While spatial heterogeneity and individual variation have been considered as noise in the past, this is exactly what has become the centre of interest of the individual-based paradigm in ecology. According to Individual-based Ecology, the interaction and behaviour of individual organisms leads to the emergence of macro-level patterns on the system scale. Although individual-based models have almost always been spatially explicit, the focus was commonly given to temporal processes and behavioural rules over spatial aspects. Today, the wide availability of spatial data and ever increasing computational power together with a strive for realistic models has renewed the attention to spatial aspects in simulation modelling. This review provides an overview of the state of the art of Spatial Simulation modelling in Ecology, reviews its limitations and open issues and it discusses future research avenues by taking an explicit geospatial perspective. The main avenues that are discussed revolve around the role of spatial context to determine the structure of living systems, potentials of hybrid top-down/bottom-up model designs to integrate hierarchical, spatial and temporal scales of ecological systems, and current trends in the representation and analysis of simulated spatio-temporal (big) data.



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## 1. Introduction

The geospatial context has been recognised as a key to understanding how individual-based processes can manifest in macro-level patterns (Tilman and Kareiva, 1997; Manson and O'Sullivan, 2006). Whereas in the past, spatial heterogeneity was merely considered as noise in ecological data-series, Individual-based Ecology understands heterogeneity as the cradle of emergence in complex systems (Grimm and Railsback, 2005).

Spatial Simulation is an umbrella term for spatially-explicit simulation models including Cellular Automata, Agent-based and Individual-based models, as well as Microsimulation. These models rely on an iterative recalculation of the modelled system state, which is based on individual entities or individual regions that are located in space (O'Sullivan and Perry, 2013). Spatial Simulation is thus an approach that closely relates to the Individual-based research paradigm in Ecology (Judson, 1994; DeAngelis and Mooij, 2005; Grimm and Railsback, 2005). In a retrospective on the past four decades of individual-based modelling in ecology, DeAngelis and Grimm (2014) observed a rapid increase of individual-based models in the 1990ies towards an ubiquitous use today.

Dieckmann and Law, (2000) identified four reasons for the wide adoption of the individual-based paradigm in the ecological community: (1) computer power, (2) for most academics rules are more accessible than the formal mathematical language of traditional models, (3) complex system structures cannot be adequately represented in traditional models, and (4) observed phenomena cannot be reproduced satisfactorily with traditional models. Furthermore, a decisive advantage of Individual-based Ecology lies in its structural realism. This allows for more reliable predictions under changing conditions compared to models that rely on empirical relationships (Stillman et al., 2015).

Spatial Simulation models have been developing from building on abstract, computer-generated spatial contexts to application on specific geographic datasets (Stanilov, 2012). This evolution towards realism is accompanied by an increasing interest in spatial aspects (Brown et al., 2005). Not least facilitated by increased computer power and abundance of spatial data, a multitude of realistic Spatial Simulation models are being developed, including forest models (Parrott and Lange, 2004; Shugart et al., 2015), wildlife ecology and management (McLane et al., 2011), land-use and land-cover change (Matthews et al., 2007; Brown et al., 2012), socio-ecological systems (Bennett and McGinnis, 2008; An, 2012; Filatova et al., 2013) and population dynamics (Martin et al., 2013).

In this review, the conceptual backgrounds of Spatial Simulation modelling in Individual-based Ecology are reflected and by taking an explicitly spatial perspective, possible ways ahead are discussed. The paper aims to provide a synopsis of 1) conceptual views of Spatial Simulation from contributing fields, primarily ecology, complexity theory and GIScience, and 2) methodological research in the related fields of individual-based modelling and geocomputation. In the following section, an overview of the state of the art of Spatial Simulation modelling is provided, Section 3 summarises open issues, and Section 4 discusses how the 'spatial view' in the way of geospatial concepts and methods can contribute to the field.

## 2. Spatial simulation in ecology

### 2.1. Roots in complexity science

Spatial Simulation methods have their roots in the theory of complex systems. This makes these models specifically apt for use in ecology, which is a system science at its very core (Jørgensen et al., 2011). According to systems theory, a system is more than the sum of its parts. It views systems in a holistic way in contrast to traditional approaches in science that focus on reductionism, i.e. the in-depth analysis of simpler system parts (Gallagher et al., 1999). In Complexity Theory a system emerges from adaptive, 'bottom-up' interactions of its individual entities (Holland, 1992). The study of complex systems essentially relies on computer models that represent the interaction of system entities, most often in a spatially explicit way (Batty and Torrens, 2005). Complex system analysis involves Spatial Simulation modelling and related methods such as genetic algorithms, and artificial intelligence.

According to the individual-based paradigm in ecology, the logical entities to represent an ecological system from bottom-up are individual organisms. The related modelling approach is termed 'individual-based modelling' in the ecological domain (Huston et al., 1988; Grimm and Railsback, 2005), which is essentially synonymous to the term 'agent-based modelling' used in geography and the social sciences (Torrens, 2010; Heppenstall et al., 2011; Wilensky and Rand, 2015). Depending on the context, these terms are used synonymously in this paper. The environmental context is usually represented as a grid, where dynamic processes are modelled by means of cellular automata. Cellular automata are also a bottom-up simulation modelling method that is based on cells as 'individual' entities (Gardner, 1970; Wolfram, 1986; Batty et al., 1999; Torrens and Benenson, 2005). Microsimulation relies on demographic data for its parameterisation and is thus mainly applied to human systems (O'Donoghue et al., 2014) or for socio-ecological systems (Svoray and Benenson, 2009). For a review of microsimulation and further methods to model complex systems see Birkin and Wu (2012).

### 2.2. The role of space in ecological systems

The spatial context matters greatly in ecological systems. A number of landmark publications laid the foundation of what is today known as Spatial Ecology (Kareiva, 1994; Tilman and Kareiva, 1997). Huffaker (1958) proved in his experiment with phytophagous and predatory mites the grand importance of spatial heterogeneity for the stability of predator-prey systems. MacArthur and Wilson (1967) showed that the spatial configuration of patches in a landscape impact the number of species that can live in this landscape. Turner (1989) studied the effect of landscape patterns on ecological processes. Tilman and Kareiva (1997) discussed the role of space in population dynamics. Spatial Simulation modelling has been widely adopted as a methodological approach to study these ecological systems in a spatially explicit way.

Goodchild (2001) defined a model to be *spatially explicit* according to the following four criteria: (1) the model represents the location of its components (2) the model design includes spatial concepts such as spatial configuration and neighbourhood, (3) the outcome differs if the model is relocated, and (4) the spatial structure of the input differs from the output.

Ecology traditionally had an emphasis on the process dynamics over spatial patterns. However, in recent years temporal and spatial approaches have been converging in ecological modelling by explicit consideration of both temporal dynamics and spatial contexts. Fig. 1 shows the trend in references to either the spatial or the temporal domain in the journal Ecological Modelling since its foundation in 1975. From around the early 2000 s both dimensions seem to receive a similar share of research interest in the journal.

### 2.3. Linking pattern with process

One of the intriguing strengths of Spatial Simulation models is that they can link process and patterns by establishing causal relations across spatial scales (An et al., 2009). The approach of Spatial

Simulation complements descriptive analysis of static spatial (landscape) models, by testing hypotheses on how patterns are