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

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ABSTRACT

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

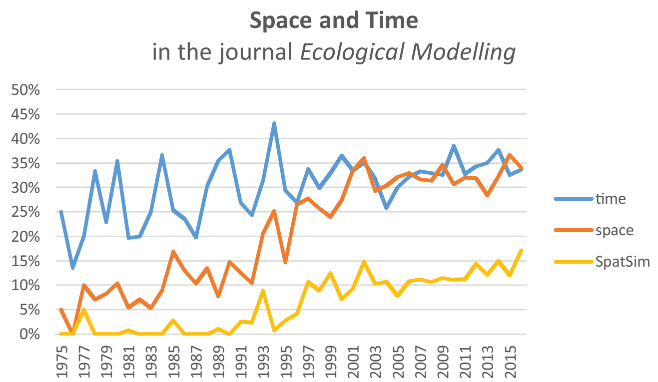

Fig. 1. Explicit reference to space (search terms: "space" or "spatial*") and time ("time" or "temporal*") in the title, abstract or keywords in the Ecological Modelling journal in percent of all papers published. The yellow line shows the share of Spatial Simulation models (search terms: "Spatial Simulation", "individual-based", "agent-based", "cellular automata" in Scopus). The categorisation of papers is not mutually exclusive: the same paper may be counted in one, two or all three categories. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

generated. Brown et al. (2006) therefore argued that generative landscape sciences based on Spatial Simulation models are an important research frontier in landscape ecology.

Although the pattern-process relationship is primarily attributed to landscape ecology, it is a common theme in most ecological domains. However, in the wider field of ecology, patterns are not necessarily spatial, but relate to any aggregate feature. Movement ecology is based on movement patterns emerging from behaviour in response to internal states, external factors, motion capacities, and navigation capacities (Tischendorf, 1997; Nathan et al., 2008; Hooten et al., 2010; Tang and Bennett, 2010). Population ecology assumes that temporal persistence, age structure, and spatial distribution of a population emerge from the properties of its individuals (Lomnicki, 2001; Clutton-Brock and Sheldon, 2010). Fluxes in ecosystem ecology not least arise from how individuals interact with each other and their environment (Grimm and Railsback, 2005; Breckling et al., 2006). Plant ecology rests on an understanding of the competition between plants to predict responses of ecological systems to environmental change (Berger et al., 2008). Finally, environmental management and conservation planning heavily relies on modelling that is based on process understanding rather than empirically determined rates in order to be able to project the future scenarios under changing environmental conditions (Stillman et al., 2015).

2.4. Representation of space and time

Three types of spatial features typically compose a Spatial Simulation model: (1) individual organisms or agents, (2) their interaction neighbourhood, and (3) the environment. Agents are represented as discrete vector features that can freely move over continuous vector space. Usually, agents are modelled as points, but other vector data types as for example lines or polygons are conceptually possible. To this end, Hammam et al. (2007) implemented a prototypic example for an agent-based model with vector agents that can grow, move and change their shape over time. However, agents with changing polygon boundaries remained a challenge (Stanilov, 2012). The first modelling platform that supports the representation of vector agents is GAMA (GIS Agent-based Modeling Architecture) (Grignard et al., 2013b). Interaction neighbourhoods are usually defined as part of an agent's behaviour, which is given by the distance of its sensory capacities and eventually a view angle.

The environment is commonly modelled as a grid-based Cellular Automaton. For computational reasons a cellular automaton grid usually is implemented on a regular raster with quadratic cells. However, this square matrix can cause geometric artefacts, which can be partly avoided by hexagons or irregular grids. Birch et al. (2007) therefore postulated to make the choice of the grid type an explicit decision in the model design. Alternatively, the environment could be represented as a discretised space by means of a coverage, which is the collection of all environmental features in a topological vector representation. However, the computation of geometric change in coverages is demanding. More importantly, coverages lack the elegance of complex dynamics that rest on simple, generic rules as in Cellular Automata. Apart from these alternatives for a 2D representation of the environment, other representations are possible and may also be more suitable. For example, birds or fish may be more adequately simulated in a fully 3D space, whereas migrating animals may be aptly restricted to network space.

The temporal dynamics in Spatial Simulation models is governed by iterated rules, either behavioural rules for agents or transition rules for cells in cellular automata. To categorise these processes Brown et al. (2005) borrow from fluid dynamics: Lagrangian processes are object-centric and describe a process from the perspective of a moving object, whereas the Eulerian view describes change at a fixed location. Agent-centric representations are Lagrangian and well suited to model living, actively moving organisms. Location-centric processes are Eulerian, which ideally represent continuous, physical phenomena. Spatial Simulation models often combine these process perspectives as a natural way to represent biotic systems that interact with the physical environment.

2.5. Scale

The use of terms to refer to "small" and "large" spatial scales is complete opposite in ecology and geography (Withers and Meentemeyer, 1999; Jenerette and Wu, 2000). In geography, scale is described in reference to the ratio of map distance to earth distance, whereas in ecology scale refers to the extent of the studied system. Consequently, in ecology small-scale refers to a small study area, which is large-scale in geography. This ambiguity is a serious issue in research fields at the interface of these two communities such as Spatial Simulation. To avoid confusion, it has been suggested to use the terms of fine and broad scale in interdisciplinary communication (Turner, 1989), which is also adopted in this review.

It is widely acknowledged, that both components of scale—resolution and extent—have significant effects on the outcomes in static landscape analysis (Wu, 2004). For Spatial Simulation, scale dependence of model outcomes is also prominently acknowledged in the standard ODD (=Overview, Design concepts, Detail) protocol (Grimm et al., 2010). However, only few studies have explored this effect explicitly. Shook and Wang (2015) presented a systematic study on spatial and temporal resolutions of an agent-based model, where they showed that a spread process slowed down at coarser temporal and finer spatial resolutions. Wallentin and Loidl (2015) demonstrated a significant effect of the extent on simulation outcomes in a transport microsimulation model.

Beyond the consideration of just one scale, Wiens (1989) elaborated in his seminal paper on "Spatial Scaling in Ecology" on the concept of a multiple scales in the organisation of ecological systems. At about the same time Huston et al. (1988) enthusiastically titled "New computer models unify ecological theory". He argued that these individual-based models would facilitate the representation of various levels of hierarchical organisation in a synergistic way, integrating multiple strains of ecology from population to community and ecosystem ecology. However, although Spatial Simulation by definition involves at least two scales—the individual and the system scale—examples that explicitly address multiple scales are rare (e.g. Evans and Kelley, 2004; Cabecinha et al., 2009; Koniak and Noy-Meir, 2009; Cilfone et al., 2015).

2.6. Spatial simulation modelling software

In reference to Dysons's (2012) argument that scientific progress is not only driven by ideas but also by tools, the question arises whether current tools are adequate to implement the concepts of spatially explicit simulation modelling discussed so far. The challenge lies in the integration of two complementary toolsets: agent-based modelling toolkits and Geographic Information Systems (GIS) (Crooks and Castle, 2012). In practice, Spatial Simulation workflows often make use of GIS in the preparation of spatial input data and the analysis and geovisualisation of simulation outcomes, whereas the simulation model handles process dynamics by means of iterated rulesets.

In the past, several attempts were made to fully integrate simulation modelling with GIS software to make use of the rich functionalities of a GIS in terms of spatial data handling, analysis and visualisation at runtime (Batty, 1994; Maguire, 2005; Parker, 2005). Brown et al. (2005) provided an extensive review on the alternatives to couple spatial data models with agent-based process models. The most promising project for tight integration was termed "Agent Analyst", an identity-based middleware coupling of ArcGIS and the agent-based modelling environment Repast (Johnston, 2013). However, the application did not support essential features of spatial simulation such as visualisation at runtime, connection to geodatabases or network datasets (Groff, 2007). It failed to attract a wider user community and it has not been further maintained.

Today, Spatial Simulation modelling frameworks themselves have advanced capabilities to represent, manipulate, analyse and visualise geographic data (Crooks and Castle, 2012). For instance, the GIS extension of the widely used agent-based modelling software NetLogo (Russell and Wilensky, 2008) makes use of the GIS library from My World GIS and the Java Topology Suite (JTS), while the Repast GIS plugin exploits functions from the Java libraries GeoTools, JTS and OpenMap (North et al., 2013). Finally, GAMA builds on a number of Java projects that together offer the richest functionality in terms of GIS data representation, spatial analysis and geovisualisation (Grignard et al., 2013b). GIS capabilities such as coordinate transformation, distance measurement, buffering, network centrality measures or shortest path algorithms are thus available through the modelling software. Additionally, these applications can schedule events and processes, and handle context aware behaviour and interaction of individual entities. With respect to their functionality in handling the spatial dimension, simulation modelling tools have become temporally enabled Geographical Information Systems (GIS).

3. Open issues in spatial simulation

Despite being promising in many aspects, Spatial Simulation has also received significant criticism. A fundamental question asked, was whether the world is entirely organised as a bottom-up, emergent system and hence whether (or when) Spatial Simulation is an adequate way of modelling it (O'Sullivan and Haklay, 2000). Further, Couclelis (2001) argued in her publication "why I no longer work with agents" that Spatial Simulation models are too complex to learn from them anything useful. In direct response to this criticism, O'Sullivan et al. (2012) made reference to the theoretical groundings of Spatial Simulation in complexity science. They identified three criteria that need to be met to justify their use: (1) heterogeneity of the decision-making context of agents, (2) importance of interaction effects (Holland, 1992), and (3) a 'mid-numbered' size and organisation of the system (Weaver, 1948) that excludes mathematical tractability of low numbered systems and statistical averaging of high numbered system. Given the general applicability of a Spatial Simulation approach for a specific question, a number of further challenges has been identified and discussed in the literature (Table 1). The debated issues can be clustered into the three main topics discussed below.

3.1. Contribution to theory

Despite the large number of published models, a repeatedly formulated concern is that it is unclear how model designs and expected insights relate and contribute to ecological theory. A phenomenon that O'Sullivan et al. (2015) termed YAAWN syndrome ("yet another ABM ... whatever ... never mind"). With regards to model design, Crooks et al. (2008) observe that many models lack an explicit foundation in theory and instead are built on a multitude of ad-hoc assumptions. In terms of insights that are expected from modelling, Grimm (1999) distinguished between pragmatic and paradigmatic motivation to individual-based modelling. A pragmatic motivation is to use the most adequate method for the question at hand. The paradigmatic motivation however uses individual-based modelling to critically review and rethink paradigms in ecology. DeAngelis and Mooij (2005) agree that paradigmatic models can tackle fundamentally different questions as compared to traditional approaches. They see the interface between aggregate versus individual-based models as a source of creativity for ecological research and they expect a synthesis between bottom up and top down approaches.

Recently, the focus of the debate seems to have shifted. Although there is now an agreement on the potential of agent-based models to contribute to theory, the degree of theory-led research is perceived differently. Whereas O'Sullivan et al. (2015) still observe that most agent-based models in land systems science are specific to individual case studies, DeAngelis and Grimm (2014) identified a gradual increase in paradigmatic models and see the need for a merger with pragmatic models. This merger should not only construct, but also deconstruct model outcomes to filter out essential processes and features. Along the same lines, Van Nes and Scheffer (2005) proposed a workflow of scrutinising, simplifying, synthesising models in order to link to theory. Optimistically, Grimm (2016) concluded that individual-based modelling is finally reaching its goal to unify ecological theory, after having overcome three legacies: the demographic legacy (behaviour imposed instead of emergent), the no-prediction legacy (testable outcomes considered less important than conceptual understanding), the single pattern legacy (theories focused on explaining single rather than multiple patterns). A recent example of the grounding of Spatial Simulation models in theory is the application of dynamic energy budgets (Kooijman, 2010) and the metabolic theory of ecology (Brown et al., 2004) to individual-based models (Sibly et al., 2013).

However, in a pointed comment Dragicevic (2016) posed the question whether anyone ever has asked how much regression analysis has contributed to a generalised knowledge? This question aptly points out that the debate only at the first sight relates to Spatial Simulation as a methodological approach. Looking at it more profoundly, it addresses the fundamental question on the epistemology of systems thinking and complex system modelling (Winsberg, 2010). Given that the key objective of Spatial Simulation is to gain a better understanding of spatial processes, the problem arises that processes are latent phenomena that only manifest as patterns. Deductive approaches to the scientific process need to rely on hypothesised patterns that can be tested against the observed

Table 1
Literature overview of open issues that have been identified, the related directions for further research, and the respective reference.

Identified issue	*Way ahead*	*reference*
Models are not linked to theory	Integration of bottom-up with top-down approaches is needed	Grimm (1999)
Are all systems emergent?	Recognise the dual bottom-up and top-down structure of a system.	O'Sullivan and Haklay (2000)
Models are too complex	Don't use agent-based models	Couclelis (2001)
Too complex to make sense of	Apply criteria to justify use of agent-based models ■ Heterogeneity ■ Interaction effects ■ Mid-numbered system	(O'Sullivan et al., 2012) in reply to (Couclelis, 2001)
YAAWN syndrome ("yet another ABM . . . whatever . . . never mind")	Strategic directions to avoid YAAWN ■ Validation of model structure, ■ hybrid modelling, ■ participatory approaches, and ■ theoretical engagement	O'Sullivan et al. (2015)
Agent-based modelling raises as many challenges as it seeks to resolve.	7 challenges need to be addressed ■ scientific purpose and value often unclear ■ *ad hoc* assumptions cover theory-base ■ context-specific models are hard to replicate, ■ complete validation against data is unlikely ■ dealing with the sheer number of agents ■ tools that allow focus on research rather than programming, ■ adequate communication of model structure for participatory development	Crooks et al. (2008)
Too complex to be validated	3 legacies have to be overcome ■ the demographic legacy ■ the no-prediction legacy ■ the single pattern legacy	Grimm (2016)
40 years of Individual-based modelling in Ecology	■ standardization of submodels, ■ merger of the pragmatic and paradigmatic perspective by including a deconstruction after the construction phase to identify essential processes and features	DeAngelis and Grimm (2014)

Advanced topics	■ new ways of model design (participatory simulation; or extract rules by machine learning)
	■ design: simple (theory-based) vs. realistic (data-driven) to be determined by:
	  ■ Medawar zone (Grimm and Railsback, 2005)
	  ■ "full spectrum modelling" (Rand and Wilensky, 2007)
	  ■ Iterative modelling (Wilensky and Rand, 2015)
	■ use for education & communication
	■ integration with the real world (humans, robots)
	■ hybrid models
	■ use of advanced data sources (e.g. GIS & social network analysis)
		Wilensky and Rand (2015)

reality, such as in pattern oriented modelling (Grimm et al., 2005). Manson and O'Sullivan (2006) argue that such traditional theory-led approaches make patterns instead of processes the primary object of study. They discuss narrative-oriented and qualitative ways of linking patterns and processes as complementary strategies in the scientific process of making sense of complex system models. Along the same lines, a new 'generative' science epistemology (Epstein, 1999; Brown et al., 2006; Millington et al., 2012) was proposed in addition to the traditional notions of inductive and deductive research: "If you didn't grow it, you didn't explain its emergence" (Epstein, 1999).

3.2. Model validation

Model validation has been acknowledged as a grand challenge to Spatial Simulation models by many researchers. The problem arises from the very nature of individual-based models, that disregards the principle of parsimony (Batty and Torrens, 2005). O'Sullivan et al. (2015) pointed out that besides commonly adopted sensitivity analysis, there is a need for methods that assess structural validity. Comprehensive overviews of available methods for the evaluation of environmental models are provided by Rykiel (1996) and more recently by Bennett et al. (2013).

In general, three approaches to validation can be distinguished, which are not necessarily mutually exclusive.

[3.]

1. Confrontation with data. Traditionally, models are confronted with data for validation. A widely adopted approach is pattern-oriented modelling proposed by Grimm et al. (2005). This approach builds on the idea that a model that predicts multiple patterns simultaneously is very likely to be structurally valid. Building on this multiple-pattern strategy, Kubicek et al. (2015) suggested a hierarchically structured approach, in which each hierarchical level of organisation is evaluated independently. Finally, (Wilensky and Rand, 2015) introduced full spectrum modelling to find an optimal level of model detail.
2. Exploratory and model-centric validation. There is a growing consensus that the individual-based modelling paradigm cannot be treated (only) with conventional strategies of model validation against data (Batty and Torrens, 2005). Full validation against data is unlikely to be ever achieved for Spatial Simulation, because there will hardly ever be enough data (independent variables) to account for the number of assumptio ns (dependent variables) (Batty et al., 2006; Crooks et al., 2008). Moreover, with the increasing number of explaining variables, the potential of wrongly identifying meaningless variables as significant predictors also increases (Comber et al., 2016). Denz (2014) therefore suggests concentrating more on exploratory in contrast to confirmatory approaches, with the added benefit to be able to tackle previously unknown aspects of the studied system. Complementary to conventional validation approaches, which treat the model as a black box and only focus on the outcomes, model-centric approaches focus on the modelling cycle workflow (Wallentin and Car, 2012; Augusiak et al., 2014).
3. Confrontation with data is not necessary or not meaningful. Some researchers do not see the confrontation with data as mandatory to work with and learn from models. The question has been raised, whether data-driven validation of patterns is the adequate metric to assess the validity of processes. Bennett et al. (2011) argued that complex systems are inherently multifinal (a process can manifest in multiple patterns) and equifinal (the same pattern can result from multiple alternative processes). The accurate prediction of land use patterns can thus be conceptually impossible, regardless the modelling method. They further argue that understanding land use pattern generation through modelling is a valid research goal in itself. Brown et al. (2006) shared this view and suggested to complementing pattern-oriented landscape ecology with process-oriented generative landscape science. Finally, MacPherson and Gras (2016) argue against mandatory confrontation of models with data, because they feel that Spatial Simulation models used in theoretical ecology are experimental systems in their own right. Towards this end, Field (2015) postulates to explore measures for the usefulness instead of the validity of a model.

3.3. Model communication

Model communication most importantly needs to address the intended audience. Cartwright et al. (2016) thereby distinguish peer researchers, stakeholders and the lay public. In the communication within the scientific community, a lot has been achieved by introducing the ODD protocol (Grimm et al., 2006; Grimm et al., 2010), which has become a widely accepted standard. Further, the provision of model source codes is increasingly seen as a best-practice standard to ensure full transparency and repeatability (Polhill and Edmonds, 2007; Ellison, 2010; Müller et al., 2014; Rollins et al., 2014).

In contrast to scientific (one-way) reporting, model communication with stakeholders is a two-way communication process. Effective participatory modelling needs to trade-off comprehensiveness and level of complexity in the communication of the model structure and of the uncertainty of its outcomes (O'Sullivan et al., 2015). Although, there is no comparable standard to the ODD protocol, recent reviews of the model communication with stakeholders provide guidance (Cartwright et al., 2016; Voinov et al., 2016). From an educational perspective, Wilensky and Papert (2010) and Wilensky and Rand (2015) argued that rule-based simulation models are much more accessible to students than mathematical treatment of systems and thus fundamentally can change learning of complex phenomena. Regardless the audience, a number of researchers suggested to complement quantitative reporting with a qualitative, narrative approach as an effective communication strategy to link patterns to the processes that have formed them (Manson and O'Sullivan, 2006; Reitsma, 2010; Millington et al., 2012).

4. Ways ahead from a spatial perspective

In this section, I take an explicitly spatial perspective to revisit the three open issues discussed in the previous section, i.e. con-

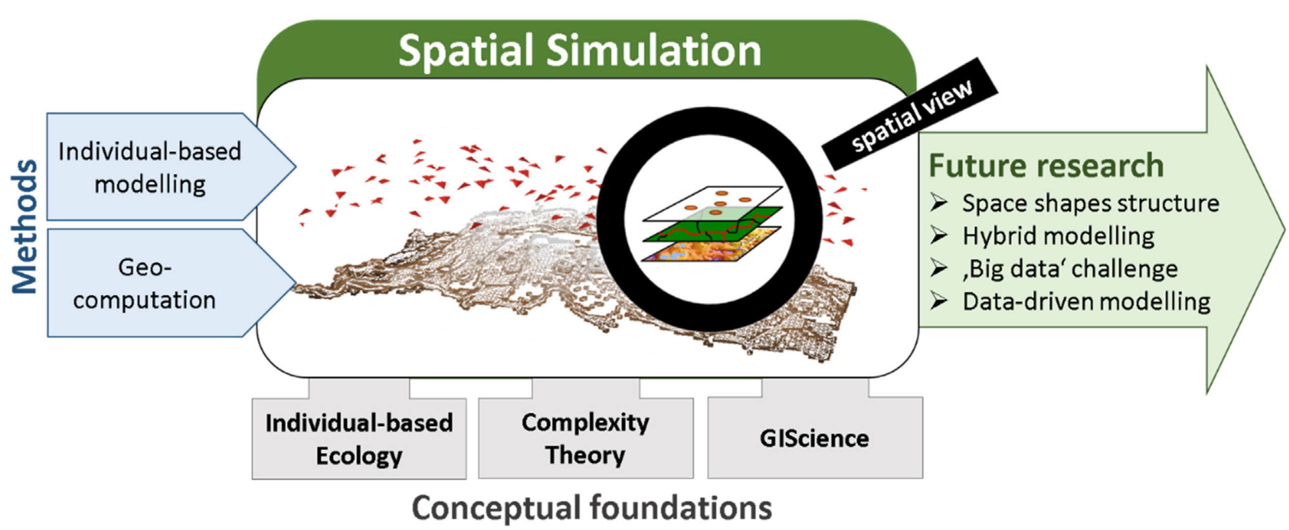

Fig. 2. Spatial Simulation is at the interface of Individual-based Ecology, Complexity Theory and GIScience. Viewing the field through a 'spatial lens' highlights a number of promising topics for further research, which are expected to cross-fertilise the contributing domains.

tribution to theory, model validation and model communication. I argue that in addition to linking to ecological theory, Spatial Simulation can also benefit from and contribute to the body of geospatial theories, most importantly concepts of GIScience, including Time Geography (Hägerstrand, 1970) and geocomputation. Fig. 2 provides an overview of the field of Spatial Simulation and four avenues for further research, which are discussed in more detail below.

4.1. Spatial structure shapes ecological systems

The increasing recognition that paradigmatic individual-based models are adequate tools to test and advance ecological theory gives way to use spatial simulation for further exploring spatial aspects of ecology. Although bottom-up ecological models are essentially spatial, the spatial dimension is often not in the foreground of model building and analysis. In the spirit of systems thinking Commoner (1971) stated the first law of ecology “everything is connected to everything else”. At about the same time Tobler (1970) formulated the first law of geography, which resembles the first law of ecology, but adds an important clause: “everything is related to everything else, but nearer things are more related than distance things”. Again referring to systems theory, this ‘spatial addition’ to the ecological law is a decisive one. Even if all individuals in a system had equal attributes and equal behaviour, the unique spatial context in a heterogeneous environment would differentiate them and ultimately lead to emergence. Thus, heterogeneous geographic space structures connections between individuals in complex living systems.

Specifically, the spatial context shapes an agent’s neighbourhood for sensing (“field of view”) and interaction (“zone of influence”). For pragmatic reasons, these neighbourhoods are commonly modelled as circular or angular buffers. Within these buffers an agent often has the unbounded potential to sense, act and react based on the assumption of homogeneous space and random walk (Stoll and Weiner, 2000). However, spatial heterogeneity such as a topographic gradient may lead to a different ”zone of influence” geometry with significant impacts on the model structure (Bradshaw and Fortin, 2000). Fig. 3 exemplifies how heterogeneous space shapes the geometry and the structure of local neighbourhoods for sensing and action and how this can affect simulation results.

Today, geospatial context is incorporated into individual-based models in increasingly rich ways. An example are Brownian bridges that can represent a probability surface of home ranges between subsequent locations of a moving individual (Horne et al., 2007; Wells et al., 2014). However, the underlying assumption of Brownian bridge models is random movement, which again assumes homogeneous space. Only recently, the use of context-aware ‘geospatial’ Brownian bridges has been proposed (Dodge, 2015; Ahearn et al., 2016; Long, 2016). Further examples for geospatially rich models relate to the integration of large amounts of geographic data under a spatial simulation framework (Minelli et al., 2016) or the representation of three dimensional neighbourhoods (Grignard et al., 2013b).

However, less focus is given to the relation between spatial heterogeneity of local neighbourhoods and the system structure as defined by the connections between individuals. Whereas spatially homogeneous neighbourhoods allow accommodating a maximum number of interaction partners, this number is likely to decrease in more realistic geospatial settings. In the above example only a tenth

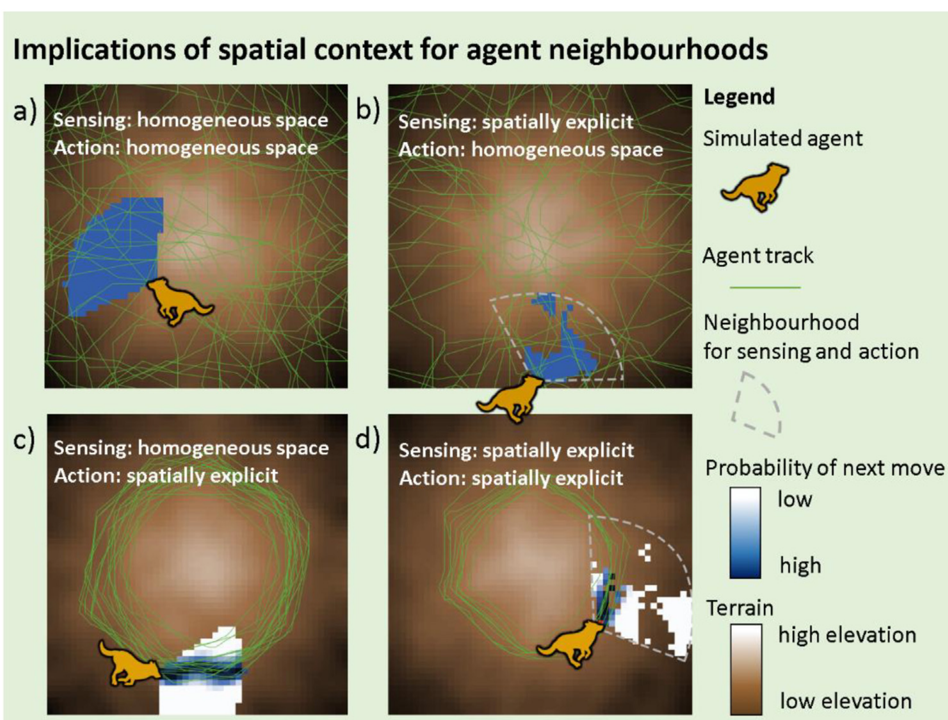

Fig. 3. Four scenarios of a simple model that simulates an agent that moves on a hilly landscape. The scenarios represent increasing consideration of the spatial context in the agent’s neighbourhood.
a) Assumption of homogenous space for sensing and movement results in unrestricted sight and a random walk pattern.
b) Assumption of heterogeneous space for sensing and homogeneous space for movement leads to partly blocked lines of sight, which enforces walk patterns along well visible landforms.
c) Assumption of homogeneous space for sensing and heterogeneous space for movement (with a preference for staying at the same elevation to optimise use of energy) results in circular movement around the hill.
d) Assumption of spatial heterogeneity for both, sensing and movement considerably restricts an agent’s room for manoeuvre and thus slows down movement and can lead to 180° turns (e.g. Fig. 3d, top left).

of the maximum neighbourhood is available for action in heterogeneous space (Fig. 3d). The spatial context thus is an essential aspect in the attempt to design structurally realistic models. Full understanding of how shape and spatial configuration of neighbourhoods affect model structures is expected to more closely integrate concepts of Spatial Ecology into Individual-based Ecology. A systematic analysis for various ecological systems thus holds great promise for further research.

4.2. Hybrid designs to merge bottom-up with top-down processes

A further strain of research that holds the potential of advancing ecological theory is hybrid modelling. Hybrid models provide feedbacks between spatial scales (Yu and Bagheri, 2016) and across hierarchical levels that capture bottom-up as well as top-down drivers in socio-ecological systems (Parrott, 2011). Two main motivations of hybrid modelling can be ascribed to first, computational performance restrictions that bottom-up models pose by the sheer number of individuals (Crooks et al., 2008) and second, the consideration that no single approach is 'best suited' to gain a holistic understanding of a system (O'Sullivan et al., 2015). This latter integration of bottom-up approaches with top-down methods can provide appropriately integrated views of hierarchically organised ecological systems. Hybrid models can thus be a key to operationalise the long-lasting whish for a merger to 'unify ecological theory' (Huston et al., 1988; DeAngelis and Grimm, 2014; Grimm et al., 2017), which currently is bound to single levels of organisation: population ecology, community ecology and ecosystem ecology.

Multiple 'top-down' approaches have been proposed as candidate methods for integration into a hybrid model, e.g. regression models (O'Sullivan et al., 2015), multi-criteria decision analysis (Bone et al., 2011), machine learning (Laskowski, 2013; Wilensky and Rand, 2015), and system dynamics (Vincenot et al., 2011; O'Sullivan et al., 2015; Wilensky and Rand, 2015). A modeller's challenge is to find the most appropriate model design for a given system part that reconciles respective strongpoints and limitations of each approach (O'Sullivan et al., 2015; Wilensky and Rand, 2015). A fuller exploration of hybrid model structures thus has been identified as promising direction for further research (O'Sullivan et al., 2015). Especially dynamically switching models that automatically adapt to systems states and emergence have been highlighted to be worth for further exploration (Vincenot et al., 2011; Gray and Wotherspoon, 2015; Wallentin and Neuwirth, 2017).

4.3. Spatio-temporal data handling to support model communication and validation

Model validation can only be as good as the data that is available for analysis. When a Spatial Simulation model is executed, it can produce large amounts of data, which potentially provides a rich source for model analysis and validation. However, the structured representation of these data remains a challenge and no generally applicable spatio-temporal data models are in place (O'Sullivan, 2005; Gebbert and Pebesma, 2014; Jin et al., 2016; Jjumba and Dragicevic, 2016). Consequently, modelling workflows rely on run-time aggregation of data into state variables to describe a set of expected patterns. However, this common practice dramatically reduces the richness and complexity of the simulated data and it impedes searching for unexpected patterns by means of exploratory analysis and pattern mining. Three approaches can potentially tackle this problem and help to leverage the full potential of simulated data:

First, development of new spatio-temporal data models that facilitate the storage, query, analysis and visualisation of large amounts of simulated data. In GIScience there is a large body of literature on data models to represent spatio-temporal systems (Langran and Chrisman, 1988; Peuquet and Duan, 1995; Worboys, 2005). O'Sullivan (2005) provided a well readable overview of modelling concepts for spatio-temporal data that explicitly relate to Spatial Simulation. In a nutshell, there are two widely used data models. Field-based data models represent phenomena that continuously vary over space, and are thus well suited in handling outcomes of cellular automata. Object-based data models in contrast, associate change in attributes, location or shape to a specific object, which makes them a natural representation of agent-based simulation model outcomes. However, neither of these data models facilitates representation of complex systems that commonly exhibit both object and field-based behaviour. Recent research on integrated data models that overcome the restrictions of the field-object duality include the voxel automata model presented by Jjumba and Dragicevic (2016), and spatio-temporal graph models (Del Mondo et al., 2013; Yi and Xiao, 2015; Wachowicz, 2016). However, until today no adequate spatio-temporal data model has been implemented in an agent-based environment for operational testing.

Second, exploratory analysis of simulated data streams. Increasingly detailed input data, an ever finer spatial and temporal resolution of simulation outputs and the necessity of conducting Monte Carlo analyses may produce data in such large amounts that conventional analysis at the end of a simulation fails. These models are better suited for streaming data processing workflows (Wachowicz et al., 2016). Methods and tools to analyse and visualise data as the model runs make use of distributed, cloud-based storage and computing platforms that can handle massive amounts of unstructured data and support exploratory data stream analysis (e.g. Jin et al., 2016). Frameworks for exploratory spatial data analysis (Anselin, 1999; Anselin et al., 2006), exploratory spatio-temporal data analysis (Andrienko et al., 2003; Andrienko et al., 2010) and exploratory spatio-temporal data mining and visualisation (Compieta et al., 2007) provide linked views on data in the form of tables, charts and maps that can be interactively queried and analysed by the user. Dynamic exploratory analysis of data streams allows for dynamic aggregation of spatio-temporal simulation data to provide multiple views on the simulation at runtime (Grignard et al., 2013a). These approaches combine the strengths of human intuition and pattern recognition with computational data processing. Demšar et al. (2015b) provided an overview on applications in movement ecology (home ranges, movement patterns, detecting behaviour from movement, linking movement and spatial context) and the related methods (geometrical analysis of trajectories, similarity and clustering, visual analytics). An overview of spatio-temporal data statistics and mining is provided by Cressie and Wikle (2015) and methods for movement analysis were reviewed by Ranacher and Tzavella (2014). Besides being an analytical method, exploratory data visualisation is an interactive way for model communication. Visualisation techniques for spatio-temporal data include spatio-temporal density mapping (Peters and Meng, 2014), visualisation in a space-time cube (Demšar et al., 2015a) and map animation (Maggi et al., 2016). Although real-time exploratory tools can greatly support intuitive understanding of model outcomes, they have been integrated into simulation modelling workflows and tools only recently (Breslav et al., 2015; Jin et al., 2016). Further research is expected to help optimising algorithmic support for a modeller to efficiently and effectively explore, validate and communicate data-rich model outcomes.

Third, shifting from phenomenological data models to process data models. In an effort to bring the focus back from a descriptive analysis of spatio-temporal pattern to its underlying process O'Sullivan and Perry (2013) offered an intriguingly clear and simple classification of spatial processes. They described three process categories: aggregation-segregation, movement, percolation and growth. It is the first structured description of emergent spatial processes in complex systems. This categorisation reaches beyond phenomenological description of spatio-temporal phenomena and may be counted as a first step towards the definition of spatial process data models. Although, it remains an open question, whether it is feasible to formalise process data models, these would represent the information encoded in spatio-temporal data and thus are expected to greatly support spatial simulation modelling.

4.4. The end of theory? Spatial simulation in the era of big (spatial) data

The large amounts of available data not only pose a methodological challenge for spatial simulation, but have much more fundamental, epistemological implications (Winsberg, 2010). If patterns and relations can be detected automatically from petabytes of data that allow predicting future system states more accurately than ever: what is the value of theory? Towards this end, Anderson (2008) proclaimed the end of theory: “faced with massive data, this approach to science—hypothesize, model, test—is becoming obsolete”. Indeed, ecology transitions into an increasingly data-rich era with data originating from a multitude of different automatic data collection platforms, sensors, satellites and monitoring systems (Callebaut, 2012; Hampton et al., 2013; Soranno and Schimel, 2014). In the domain of numerical modelling, data assimilation is an established set of Bayesian-based techniques to integrate data streams for the improvement of forecast accuracy (Montzka et al., 2012). However, adaptation of the approach to rule-based simulation models has been suggested only recently for discrete event simulations (Xie et al., 2016) and for agent-based models (Ward et al., 2016).

Observation data has been integrated into spatial simulation models by means of genetic algorithms at simulation runtime to iteratively improve calibration (García et al., 2013; Kari et al., 2013; Li et al., 2013; Wallentin and Oloo, 2016; Whitsed and Smallbone, 2016). This method has also been suggested to automatically extract optimised ‘emerging’ rule sets (Wilensky and Rand, 2015). Emerging rule sets qualify as one of the computational methods that have turned the scientific process upside-down from hypothesis-testing to hypothesis-generating (Mazzocchi, 2015). Data-driven Spatial Simulation thus is a promising approach to link ‘big’ sets of observation data back to ecological theory. Further research should develop workflows and algorithms to put the data-driven paradigm of spatial simulation into practice and to further explore the potential and limitations of data driven modelling with respect to its contribution to ecological theory.

5. Conclusions

The individual-based paradigm in ecology and the field of Spatial Ecology have paved the way for an explicit representation of geographic space in ecological simulation models. Individual-based modelling and related bottom-up simulation models under the umbrella of Spatial Simulation have been widely adopted by the ecological community in the past two decades. The integration of geographic space has thereby facilitated the design of much more realistic models. Moreover, Spatial Simulation as methodological approach to the paradigm of Individual-based Ecology facilitates exploration of concepts of emergence in complex systems and causal process-pattern relationships.

Despite its significant contributions and its wide adoption, Spatial Simulation has also received substantial critique. Three main aspects of this debate relate on whether and how much Spatial Simulation models contribute to ecological theory, how these models can be communicated in a transparent way to facilitate repeatability despite their high level of complexity, and whether and how they can or should be fully validated against data.

Taking a geospatial perspective, this review provided a reflection on this debate and discussed what the geospatial perspective may have to offer to advance Spatial Simulation modelling in ecology. The main avenues identified related to (1) how spatial structure shapes ecological systems, (2) hybrid models as merger of bottom-up and top-down processes to potentially unify ecological theory (3) improvements of spatio-temporal data handling to support model validation and communication, and (4) possible contributions of spatial simulation to the epistemological challenges of data-driven science.

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