



Review

Theoretical considerations on the combined use of System Dynamics and individual-based modeling in ecology

Christian Ernest Vincenot^{a,*}, Francesco Giannino^b, Max Rietkerk^c, Kazuyuki Moriya^a, Stefano Mazzoleni^d

^a Department of Social Informatics, Kyoto University, Yoshida-Honmachi, Sakyo-ku, Kyoto 606-8501, Japan

^b Dipartimento di Ingegneria Agraria e Agronomia del Territorio, Università degli Studi di Napoli Federico II, via Università' 100, Portici 80055, NA, Italy

^c Department of Environmental Sciences, Copernicus Institute, Utrecht University, P.O. Box 80.115, 3508 TC Utrecht, The Netherlands

^d Dipartimento di Arboricoltura, Botanica e Patologia Vegetale, Università degli Studi di Napoli Federico II, via Università' 100, Portici 80055, NA, Italy

ARTICLE INFO

Article history:

Received 16 May 2010

Received in revised form

19 September 2010

Accepted 20 September 2010

Available online 19 October 2010

Keywords:

Agent based

Hybrid model

Modeling scale

Complex system

ABSTRACT

Modeling could be summed up as the task of reproducing the structure and imitating the behavior of complex real-life systems with components interacting with one another at different scales. In many disciplines of ecology, System Dynamics and more recently Individual-Based modeling have emerged as the major tools to support this task. These techniques have usually been considered until now as exclusive alternatives instead of synergistic tools. The present paper starts by presenting the two approaches, and compares them to identify their strong and weak points depending on the type of components constituting the system under consideration. Then we isolate a class of systems difficult or in some cases impossible to model dynamically using any of these approaches alone, because of conceptual limitations. We further point out the usefulness of merging the two paradigms inside of a hybrid modeling framework to handle this class of systems, and present what we consider as the elementary combination patterns of System Dynamics and Individual-Based modeling. Since the power of this promising approach has been unexplored in most fields of ecology, we suggest some possible applications illustrating its usefulness.

© 2010 Elsevier B.V. All rights reserved.

Contents

| | |
|--|-----|
| 1. Introduction..... | 211 |
| 2. Conceptual definition of natural system components..... | 211 |
| 3. Presentation of the main modeling approaches..... | 211 |
| 3.1. System Dynamics..... | 211 |
| 3.2. Individual-Based modeling (IBM)..... | 212 |
| 4. The limitation of single paradigms, and the emergence of a hybrid alternative..... | 212 |
| 5. Reference cases..... | 213 |
| 5.1. Case 1: Individuals interacting with a single SD model..... | 213 |
| 5.2. Case 2: SD submodels embedded in individuals..... | 213 |
| 5.2.1. Independent fixed individuals with dynamic properties..... | 213 |
| 5.2.2. Individuals arranged in a spatial structure and integrating dynamic properties..... | 213 |
| 5.2.3. SD submodel embedded in mobile individuals..... | 214 |
| 5.3. Case 3: Individuals interacting with a space made of SD models..... | 214 |
| 5.3.1. Interaction with a fixed-sized neighborhood..... | 214 |
| 5.3.2. Interaction with a variable zone of influence..... | 215 |
| 5.4. Case 4: SD-IB models swapping..... | 215 |
| 6. Application to complex real-life ecosystems..... | 215 |
| 6.1. Animals living in a dynamic landscape..... | 215 |

* Corresponding author. Tel.: +81 75 753 3136; fax: +81 75 753 3133.

E-mail address: vincenot@bre.soc.i.kyoto-u.ac.jp (C.E. Vincenot).

| | |
|---|-----|
| 6.2. Complex vegetation growth models | 215 |
| 6.3. Epizootic outbreaks, and how to deal with large-amplitude phenomena..... | 216 |
| 7. Conclusion..... | 216 |
| Acknowledgments..... | 216 |
| References | 216 |

1. Introduction

Since the 1960s, ecological modeling has been focused mostly on System Dynamics (SD) modeling, and more generally, coupled differential equations (DE) models. During the past decade, a new approach originating from computer science has increased in popularity: Individual-Based (IB) modeling. SD and IB modeling have traditionally been considered only as competing alternatives (Dyke et al., 1998) differing in most aspects (Osgood, 2007). After a short description of the techniques, we conclude on their respective relative inability to reproduce complex real-life systems alone. We show that a class of systems exists that cannot be modeled dynamically by any of them. Yet the complementarities of the two paradigms lead us to propose the use of a combination of System Dynamics and Individual-Based modeling to solve this issue. The main part of this paper presents the combination patterns between SD and IB that can serve to reproduce the structure and functioning of real-life systems. For each of them, we give some examples of applications in ecology, and finally conclude about the potential use of this technique in this field.

2. Conceptual definition of natural system components

The first issue encountered in the process of modeling is to decide at which level components shall be chosen, and to figure out how they interact with one another to realize the system. This brings back to the fundamental question of knowing what Nature is made of, and how it is organized.

Advances in modern science have favored the theory of reductionism, which has been pushing us to believe that any thing can be described and explained by reducing it to the interactions between its elementary parts (Dawkins, 1996). However, in certain areas of science, phenomena such as emergence cast a doubt on the validity of this philosophy (e.g. symmetry breaking) (Anderson, 1972). Especially in ecology, reductionism is still often challenged due to the complexity and interconnectedness of the non-linear systems studied (Jørgensen, 2002). This issue coupled with the recent development of system thinking has caused a rebirth of interest in holism. This idea, antithetic to reductionism, was summarized by Aristotle as “the whole is more than the sum of its parts”. Holism advocates that natural systems are irreducible and consequently unpredictable through the properties of their parts only. For example, when hydrogen and oxygen unite to form water, properties emerge that are not present in hydrogen and oxygen (Sattler, 2008). The collision of the two theories lead to the creation of hybrid views of Nature. In ontological interpretations such as the holarchic model (Koestler, 1976; Patten, 1978, 1982), systems are composed of entities, which share a dual nature by being simultaneously “wholes” unto themselves while being a “part” of larger systems.

In this paper, we base our reasoning on the latter view and consider that systems encountered in ecology cannot be described effectively in either reductionist or purely holistic terms. From the viewpoint of ecological modeling, this has several direct consequences. First, systems have to be divided in abstract units that we call component here. For example, an arbitrary breakdown of an alpine tundra ecosystem could consist of three components: vegetation, herbivores (e.g. caribous) and predators (e.g. buzzards).

Consequently, by our definition, a component in a system is comparable to a submodel, sector or compartment in a model. Second, for each component, the modeler must decide whether it should be considered as “divisible” or “whole” in the model. It is clear that this choice is dependent on the level of individuality visible among the entities forming the component as well as the scale at which we observe the system. For example, a lake is a body of liquid, which could be decomposed in drops (or further down into molecules), but for most applications in ecology one can consider it as part of a larger ecosystem, thus making useless to further disintegrate this component into an assemblage of drops. Moreover, water molecules do not show much “individuality”. So, for the sake of modeling, this component is most often considered as an indivisible “whole” in ecological models. Depending on scale and individuality, a “whole” component can be disaggregated into individual units by downscaling and, reversely, interacting units of a “divisible” component can be aggregated into a single entity by upscaling (individual plants/animals vs population, organs vs organism, molecules vs matter, etc.).

3. Presentation of the main modeling approaches

3.1. System Dynamics

System Dynamics is based on a formulation of the system in terms of ordinary differential equations (ODEs). It represents the system in a graphical way using two simple building blocks: stocks and flows (Forrester, 1961). This approach greatly simplified the creation and communication of models as shown by its widespread use as an educational tool (Forrester, 1996; Davison and Reimann, 2008), and it also proved to be capable of impressive analytical power (Ford, 1999). In these aspects, SD deviates from simple ODE models by its capacity to represent explicitly dynamics as interlaced feedback loops giving precious information on the system's expectable behavior (Forrester, 1961; Meadows, 2009). Nevertheless, stock-and-flow models have several limitations, the most important one being probably the absence of notion of space, making the design and representation of spatial problems difficult, if not impossible. Therefore spatially explicit problems cannot be addressed by stock-and-flow representation only, which is the core of the SD approach. Instead, for this kind of problems, the use of partial differential equations (PDEs) is the prevailing alternative, providing a mathematical solution, but not a simple and intuitive model representation as it is the case with stock-and-flow models of homogeneous components. In SD, the system is modeled as a single item through state variables, which represent “average” values. Hence, it is suitable for “whole” components, but it is not well-equipped to simulate components with some level of individual-scale heterogeneity. This aggregation comes with a loss of preciseness. Nonetheless, this also enables SD models to be computed fast because the problem can be expressed as simple sets of coupled ODEs only. As this modeling paradigm has been in use for a long time, significant knowledge has been gathered on the methodology to calibrate SD models with real-life data (Luna-Reyes and Andersen, 2003), and numerous study cases are available as reference in ecology (e.g. Faust et al., 2004; Bald et al., 2009).

3.2. Individual-Based modeling (IBM)

Individual-Based (IB) modeling (also referred to more generally as Agent-Based (AB) Modeling) is a bottom-up approach that starts with the ‘parts’ (i.e. individuals/agents) of a system (i.e. population) and then tries to understand how the system’s properties emerge from the interactions among these parts (Grimm, 1999). The behavior of individuals/agents is dictated by algorithmic rules. This permits a great flexibility, while it also makes this approach less accessible to the average user, and the models are typically more difficult to analyze and communicate. IB modeling is particularly useful for spatial problems because individuals/agents are considered as simple entities which can interact dynamically in multidimensional spaces (1D, 2D or 3D) (Kreft et al., 2001). This was well illustrated for instance by the renowned “boids model” (Reynolds, 1987), which showed how the spatial interactions between individuals, each following the same basic set of movement rules, could contribute to the understanding of various open issues in ethology, like the structure and movements of fish schools (Huth and Wissel, 1992, 1994). IB models have often been combined with field data (e.g. Kramer-Schadt et al., 2004; Rossmannith et al., 2007) leading to the development of a strong methodology called Pattern-Oriented Modeling (POM) (Grimm, 1999; Grimm et al., 2005; Kramer-Schadt et al., 2007) for this purpose. Note that the individual-centered paradigm can be seen as conceptually close to Lagrangian methods, although the two modeling approaches are not always considered as equivalent in terms of capabilities (Dembele and Cambier, 2009).

IB models describe a system as a set of individuals that may differ from one another, and each individual is characterized by its inherent dynamic behavior. Since IB modeling relies on this notion of interacting individuals/agents, it needs the component under consideration to be “divisible” into such smaller parts. As a consequence, IB modeling is not adapted to “whole” components, but it is better suited to represent “divisible” components made of interacting parts featuring a significant level of heterogeneity. This form of disaggregation combined with hybrid continuous/discrete time logic (though not present in all IB modeling software) allows to achieve high preciseness and accuracy (Osgood, 2007) (see Dyke et al., 1998, 4.3 and Wilson, 1998 for practical examples). However, IB modeling simulations can easily become intractable, especially when complex inter-individual communications are involved.

4. The limitation of single paradigms, and the emergence of a hybrid alternative

SD and IB modeling have both strong and weak points depending on the type of component under consideration. Hence, previous studies have concluded about the respective suitability of the two approaches to handle diverse types of problems (Dyke et al., 1998; Wakeland et al., 2004, 2005; Marin et al., 2006; Norling, 2006; Rahmandad and Sterman, 2008), or rectify each other’s results (Wilson, 1998). IB modeling has even been used as method to gather fine-grained data to parameterize differential equations (Moorcroft et al., 2001). Besides this, a procedure to convert SD models into IB models has also been described (Borshchev and Filippov, 2004). Some papers illustrate the complementarities of SD and IB modeling in terms of capabilities (Osgood, 2007) or called for the use of SD as an IB modeling platform (Dong-Hwan and Jae-Ho, 1997). However, the advantages of mixing these techniques inside of the same model and the potential use that would emerge from such an interaction have not been stressed enough (Scholl, 2001; Stemate et al., 2007). Moreover, only a few hybrid models merging SD and IB modeling have been produced for scientific purpose, and, to the best of our knowledge, they are limited so far to a few examples

in epidemiology (Bobashev et al., 2007), health science (Schieritz and Milling, 2003; Sadsad and McDonnell, 2007; Wakeland et al., 2007), and economics/management (Schieritz, 2002; Schieritz and Grössler, 2003; Scholl and Phelan, 2004). Many domains, especially environmental sciences, remain mostly unexplored. In ecology, the advantages of an integrated modeling system, capable of combining different approaches and scales, were reported in the context of modeling vegetation dynamics (Mazzoleni and Legg, 1998). A proof of concept was developed to model the effects of grazing animals on vegetation (Legg et al., 1997). In aquatic systems modeling, under the framework of dynamical systems (Wiggins, 2005), some interactively coupled Eulerian–Lagrangian models have been designed during the last decade (Hermann et al., 2001; Goodwin et al., 2006). Typically, in these models, hydrodynamical processes are described using PDEs, while biological components (e.g. zooplanktons or phytoplanktons) are represented by a Lagrangian approach allowing to simulate individual organisms. In other fields of ecology, hybrid solutions have been recently proposed (Bader et al., 2008; Emrich et al., 2008; Manor and Shnerb, 2008), but nothing close to a pure fusion between SD and IB modeling can be found, except a notable undertaking to bridge SME, a spatial modeling environment (Maxwell et al., 2005), and IMPORT/DOME, an IB battlefield simulation environment (Morrison, 1995), to model mobile individuals in dynamic landscapes (Westervelt, 1999).

We assert in the present paper that what have traditionally been seen as antagonistic properties turn out to be powerful synergistic features when the two paradigms are merged. The approaches then become highly complementary and essential to the dynamic modeling of some classes of ecosystems. Particularly in natural sciences, scientists have to study systems formed by several components, and these components can be of different nature. Since each technique is suitable to model a single type of component, it becomes obvious that hybrid modeling is desirable as soon as such a combination of “divisible” and “whole” components occurs in the system, according to the scale of representation. Many real-life systems fall into this class, and the usual workaround to model them using only one paradigm has consisted in having some components not rendered dynamically. In our view, the impossibility to reckon both natures of components may represent a critical failure in the representation of some complex systems, and might explain the recognized difficulty for either modeling paradigms or for hybrid solutions to “unify ecological theory” (Huston et al., 1988).

In some IB models, individuals integrate properties driven by complex internal processes (e.g. energetic balance calculation for animals, or photosynthesis for plants). With this paradigm, such properties and mechanisms are specified respectively by variables and algorithms altering these variables. This form of description can be very hard to understand, analyze, and communicate as visible in an indisputable way throughout the history of software engineering (Eisenstadt, 1993). In this case, the most important factor of problems is the difficulty to create a robust mental model of how an algorithm works (Pennington, 1987; Vessey, 1989). On the other hand, SD is able to represent processes in an intuitive and straightforward way, and hence can be a better choice to describe the above mentioned processes. Likewise, the representation of systems integrating spatial processes is difficult and unintuitive with System Dynamics modeling because of the absence of space. GIS software can efficiently handle static spatial data representation and their integration with SD (Mazzoleni et al., 2003; Ahmad and Simonovic, 2004), but they lack the capability of dealing with PDEs to model spatial processes (e.g. diffusion and propagation) (Mazzoleni et al., 2006). Furthermore these tools do not allow the integration of any sort of IBM approach that would require newly conceived systems. In such a context, IBM individuals could be used to enhance SD models by providing them with a spatial dimension and enabling them to interact in space. Then we suggest that IBM as such can

be used as a spatial modeling platform for SD models as will be exposed later (reference cases 2 and 3).

To sum up, we rationalize that a class of systems exists which cannot be handled in a satisfying way by either SD or IB modeling alone, because of conceptual limitations of each approach. On top of this, the modeling of other classes of systems is also impaired by the restriction to one single approach. Besides the conceptual reasoning reported above, another point to note is that SD and IB modeling differ in terms of CPU time consumption and accuracy. A satisfying trade-off may be found by combining the two techniques (as demonstrated in reference case 4 and in Section 6.3).

We propose here that an advantageous way to solve all of the issues mentioned above would reside in the fusion of SD and IB modeling and suggest that, beside of making the models' structure more natural, it would result in an important gain in modeling capabilities, analytical power, simplicity, and in particular cases, tractability. Incidentally, we can see that software technologies have already started to evolve towards this goal, and some solutions now exist that make it possible to implement hybrid models featuring SD and IB components (Grössler et al., 2003; Borshchev, 2005).

5. Reference cases

When using SD and IB modeling inside of a same modeling framework, typical patterns of combinations appear. Here we explore these “reference cases”, which can be used as examples illustrating the need of hybrid models. For each reference case, we also present some examples of applications in ecology.

5.1. Case 1: Individuals interacting with a single SD model

In the first reference case, individuals act as in a classic IB model, but they interact with an SD model (Fig. 1). This SD model can typically represent dynamic properties of their common environment. A simple illustration would be the system consisting of fishes in a lake. Fishes obviously represent instances of a class of individuals, while the lake can be considered as a whole entity. If we want to model the fishes' spatial behavior depending on the variations in some of the lake's properties (e.g. water level, temperature, turbidity), the most natural way is to choose IB modeling to model the fishes and SD for the lake's dynamic properties. SD alone would be unable to express the fishes' spatial behavior whereas IB modeling could not build a model of the lake's properties using individuals/agents. IBM individuals then behave according to parameters computed by the SD model (e.g. fishes move depending on a home-range influenced by water turbidity), and in return, they can have an impact on the SD model's dynamics (e.g. benthivorous fishes like carps make the water more turbid through their foraging behavior Scheffer et al., 1993).

Also, in some special cases, an IB model could be used to dynamically compute parameters of an SD model. SD models often integrate exogenous variables which represent static parameters,

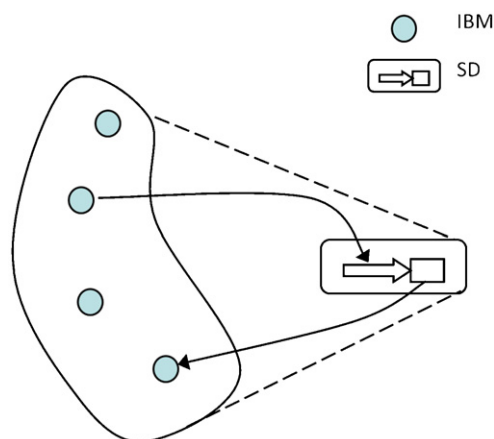


Fig. 1. Reference case 1: IBM individuals communicating with a single SD model. Arrows represent interactions between IBM individuals and components of the SD model (e.g. fishes impacting a lake's turbidity).

the value of which should in fact be dependent on other variables present in the model. An example of such a parameter is the *contact rate* in epidemiological models which is representative of the number of potentially infectious contacts per infected individual. This parameter is obviously dependent on the density of individuals dynamically computed by the model. The same counts for parameters like the *functional response* in predator-prey models which is generally input in a static manner but in fact depends on local interactions between predators and preys (Okuyama, 2009). This reference case aims at calculating such types of parameters using an IB model.

5.2. Case 2: SD submodels embedded in individuals

5.2.1. Independent fixed individuals with dynamic properties

This reference case is adapted to situations in which we have static individuals positioned in space. We can calculate dynamically some of their properties with SD models (Fig. 2a). A simple example of lifeforms that could be simulated by this reference case include sessile aquatic organisms like barnacles or corals (Muko et al., 2001). Organisms can be represented as static individuals, which can reproduce (e.g. through propagule dispersal). The growth and reproduction of each of them can be computed by the SD models, while IB modeling offers the ability to track their dispersal in space.

5.2.2. Individuals arranged in a spatial structure and integrating dynamic properties

It is quite common to have to represent a spatial structure from which some properties change dynamically considering intrinsic variations as well as processes running between some of its parts. A solution to model such a system is to break arbitrarily the spatial structure into basic “nodes” (i.e. regions, parcels, lakes), each represented by an IBM individual including an SD model. These

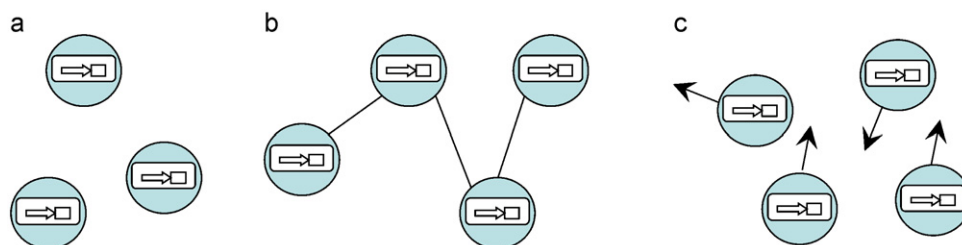


Fig. 2. Reference case 2: SD submodel embedded in individuals. (a) Independent dynamic individuals with fixed spatial location (e.g. sessile aquatic organisms), (b) Network of interacting individuals/systems (e.g. hydrological network), (c) Mobile individuals (dynamic interaction) (e.g. energetic and movement model of birds/molecules/objects).

individuals are then linked with one another in a static network, producing a virtual representation of the wanted spatial structure. While the SD model is continuously computing the node's intrinsic variations, the links between the individuals can be computed by the IB approach to render the processes running between each node (Fig. 2b). In this manner, several SD models can be linked and interact inside of a spatially explicit structure.

Taking advantage of this reference case, an infinity of structures and applications can be imagined. More original than the classic cellular automaton-like grid which can of course also be emulated, a good illustrative example would be the construction of directed graphs. If we want to model the water flow between basins in an hydrological network, we could use this reference case and have one IBM individual assigned per basin. Each individual would include an SD submodel used to continuously compute the basin's intrinsic variations (e.g. water level), and the flows of watercourses between basins could be rendered by inter-individual communications. Using undirected graphs in the same manner, the spread of an epizootic between several locations (i.e. farms, crop fields, etc.) could also be modeled (refer to Fortuna et al., 2009 for an analogous study case on bats). In a similar fashion, the travel of people or animals between spatially fixed and homogeneous locations (i.e. cities, forest patches, etc.) could be simulated (as in Fortuna et al., 2006 for instance). Broadly speaking, the structure depicted here can be seen as an evolution of existing graph-based ecological models (Dale and Fortin, 2010 and the many references therein). As a consequence, uses of this reference case can be sought in the dedicated literature in which different applications can be found with scopes ranging from plant genetics (Dyer and Nason, 2004), biodiversity in food webs (Dunne et al., 2002), landscape fragmentation (Keitt et al., 1997), to marine conservation (Tremblay et al., 2008).

5.2.3. SD submodel embedded in mobile individuals

An SD model is embedded inside of mobile individuals (Fig. 2c) either because it is better suited to handle a given task (e.g. energetic balance calculation) or for the sake of simplicity. The SD model influences the IBM individual, and the other way around. Under this framework, the communications between the two-way interactively coupled submodels can be synchronous or asynchronous. Some applications in ecology are energetic and movement models of foragers, with individuals moving according to rules depending on their energetic status calculated by an SD submodel.

A close example could be the simulation of migration of wolf packs (or any other herds of group-living animals), with IBM individuals representing the packs, and the SD models calculating their respective demography. This could be seen as an advantageous replacement for the conventional *superindividuals* technique (Scheffer et al., 1995; Grimm and Railsback, 2005).

5.3. Case 3: Individuals interacting with a space made of SD models

5.3.1. Interaction with a fixed-sized neighborhood

This reference case is similar to case 1, but features a spatially explicit environment modeled by a grid of interlinked SD submodels. Technically, it features two interacting layers with their own spatial resolution: the layer in which the active individuals evolve (hereafter referred to as "individuals layer"), and the environment layer simulated by a grid of SD submodels (either interacting or not). The latter layer is actually created by "wrapping" SD submodels – each dealing with the simulation of an area of environment – in a second dedicated class of IBM individuals arranged in a grid and used to position the SD models in space and, if needed, to perform data exchanges between them. The individuals layer is conceptually overlaid with the environment layer. Depending on the spatial resolution of both layers, one SD submodel is associated

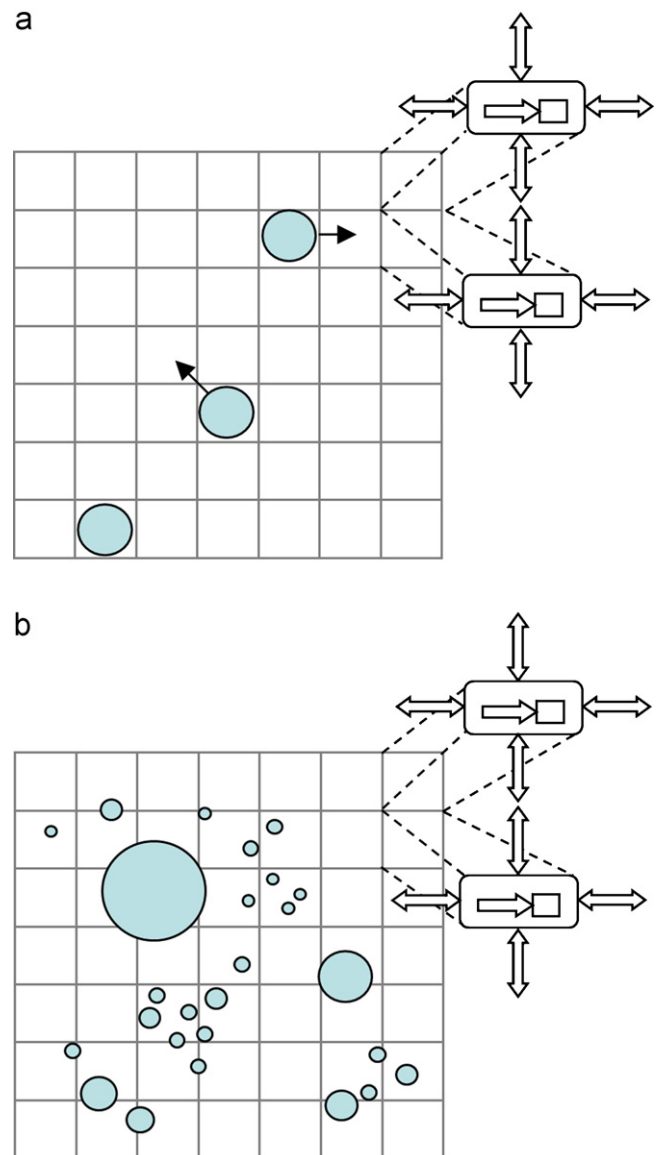


Fig. 3. Reference case 3: Individuals interacting with SD models at different levels of complexity. (a) One to one interactions – individuals moving in a space of fixed SD submodels (e.g. animals grazing a pasture). (b) n to k interactions – differently sized individuals interacting with several SD submodels (e.g. yellow crazy ant colonies altering a variable area of surrounding rain forest, or differently sized plants interacting with diffusion processes in the soil).

with each area of the individuals layer. As a consequence, individuals interact with a different SD submodel depending on their position, thereby enabling them to evolve in a dynamic heterogeneous world (Fig. 3a).

As an illustration, let's consider that we wish to study the impact of the spatial behavior of a frugivorous bird species on the flora of a given region. Modeling the dynamics of the plant community composition in a spatially explicit way can be done in SD using the technique described above. In our environment layer, each SD submodel in the grid computes the evolution of the coverage in its assigned area. In parallel, the birds' behavior is translated into rules in IB modeling. When individuals fly over an area, they can choose to eat some fruits, defecate, or do nothing. Through this dynamic interaction with SD submodels, they impact the survival of plant species by acting as seed disperser. Such a model can be seen as an Individual-Based hybrid version of the insect pollination model presented by Fortuna et al. (2008). A different sort of

modeling issue featuring a system following the structure visible in this reference case resided in the estimation of the viability of endangered tortoises in a military area in the Mojave Desert under different training scenarios affecting the quality of this environment (Westervelt, 1999).

5.3.2. Interaction with a variable zone of influence

The one-to-one (IB-SD space) relation defined above is sometimes too restrictive. Individuals may need to interact with a neighborhood wider than our spatial resolution and sometimes variable in area (depending on the individual's life stage for example). This principle of zone-of-influence (ZOI) or field-of-neighborhood (FON) can be found in the IB modeling literature relevant to plant populations (Wyszomirski et al., 1999; Berger and Hildenbrandt, 2000; Weiner et al., 2001). Nonetheless, it has been formalized for direct inter-individual interactions only, thereby occulting more realistic individual-environment interactions (e.g. plant–soil interactions) that we describe here. Practically, in our hybrid concept, such a mechanism can be obtained by letting one individual interact with more than one SD submodel at a time (Fig. 3b). Modeling the impact of large colonies of animals on their environment requires the use of such a reference case. For example, to see how the spread of colonies of invasive insects is altering the forest structure (e.g. yellow crazy ants on Christmas Island (Abbott, 2005)), we can model colonies as individuals and the forest structure as a space made of SD models. When a colony (i.e. IBM individual) grows in size, it interacts with an increasingly larger area of surrounding forest (i.e. SD submodels). Higher levels of complexity can be captured by including also interactions between neighbor SD models (e.g. diffusion processes between cells).

5.4. Case 4: SD–IB models swapping

As suggested in Section 4, among the differences between SD and IB modeling, computation cost and accuracy are some that justify the need for SD–IB hybrid modeling. The solution presented hereafter is meant to handle specifically such components, which could be modeled using solely SD or IB modeling, but from which the simulation would exhibit difference in either computation time or accuracy depending on the paradigm chosen. SD–IB hybrid modeling offers the possibility to opt for an advantageous compromise, allowing for a component to be modeled with both techniques, but run only in one of them at a given time. A threshold value or a specific event triggers the dynamic change of paradigm at runtime. A typical example is when IB modeling produces finer results but becomes too heavy when the number of individuals is allowed to grow and becomes too important. SD–IB models swapping can make it possible to simulate accurately the component when the number of agents is limited, and then switch to SD when a performance threshold is reached. This use case is frequent when dealing with exponential growth patterns. Examples of application in ecology could be anything dealing with the growth of populations with large amplitude. In demographic models for example, small populations are subject to stochastic behavior best rendered with IB modeling, but population growth quickly makes the number of individuals reach a point at which computation time is strongly impacted and a switch to an SD model would be desirable in terms of performance and without losing much accuracy. This technique could serve as a versatile solution in larger models as will be shown practically in Section 6.3.

6. Application to complex real-life ecosystems

SD–IB hybrid modeling constitutes a solution to describe different types of components inside a single model. This combinatory

approach enables us to simulate complex dynamic ecosystems in a natural way, as illustrated by the following examples.

6.1. Animals living in a dynamic landscape

Understanding the foraging behavior of animals is a complex issue in behavioral ecology. To this end, first, it is essential to consider various biological processes like energy metabolism and foraging cost (Moen et al., 1997), as well as information acquisition (Eliassen et al., 2007). Recently all these aspects have been integrated in a model (Esposito et al., 2010). On top of it, foragers interact with a continuously changing heterogeneous environment, which can also be dynamically simulated (Turner et al., 1995; Westervelt, 1999). In summary, to render precisely this entire system, we first have to include the energetic balance as well as the consequent spatial behavior of individuals in the model. Second, we have to discretize the landscape in smaller homogeneous areas interacting dynamically with one another and with the individuals. SD or IB modeling taken alone would make the task of simulating such a system extremely difficult and the result would be unnatural if not imprecise; merging the two paradigms by combining the different reference cases described above enables us to quickly create a model, the structure of which will be eventually quite simple and easy to handle.

Reference case 2 enables us to compute in a natural way the internal state of IBM individuals, while case 3 shows the ability to engender heterogeneous environments. As a consequence, the creation of a model simulating the described system would sum up in the following steps. First, a stock-and-flow model of the energy budget of the considered animal would be designed. This SD model would then be plugged in a class of IBM individuals conforming to reference case 2c and would impact on this class' movement rules. In parallel, another SD model describing the dynamics of parcels of the environment (e.g. vegetation growth) would be designed. This submodel would be multiplied to form a set of interconnected cells covering the entire space with which the individuals would be interacting with respect to reference case 3a.

As a result of the combination of both reference cases (2c and 3a), spatial heterogeneity of the environment, in which the continuously changing individuals evolve, can be taken into account. Practical real-life examples could include the grazing behavior of cows (or any other herbivorous species) in a dynamic landscape. Applications in marine ecology could focus on the behavior of individual fishes responding to abiotic stimuli (i.e. physical, hydrodynamic, and water quality dynamics) as illustrated by Goodwin et al. (2006) using dynamical systems theory. Extending the model presented here by adding a supplementary class of individuals making use of reference case 2c would also make it possible to render predator–prey behavior in this dynamic landscape.

6.2. Complex vegetation growth models

The spatial modeling of vegetation growth has been the topic of much research effort, centered either exclusively on intra- or inter-specific interactions at the individual level (Winkler and Stocklin, 2002), or on plant–soil interactions at the aggregated level (Eppinga et al., 2009). We show here how, thanks to the reference cases presented previously, this mutual exclusion between the capabilities to model individual growth and plant–soil interactions in multidimensional space could be lifted in an unprecedented manner.

To represent soil water moving laterally in space, water flows would be computed by communicating SD unit models arranged inside of a regular grid. On the other hand, individual plants would take the form of individual agents embedding an SD model. The physical growth of each plant would be represented explicitly, with several plants first sharing a single cell, and some of them growing

in size and starting to draw water from several cells at the same time. One plant individual could then communicate with several cells (i.e. IBM individuals with SD submodels responsible for lateral water flow) at the same time and also influence their dynamics in return. This is accomplished by merging reference case 2c and 3b.

6.3. Epizootic outbreaks, and how to deal with large-amplitude phenomena

Bailey (1975) suggested that large-scale epizootics should be accurately seen as emerging from the transport of infectious individuals between interconnected subpopulations subject to concurrent disease outbreaks. We outline the potential design of such a metapopulation model, which could offer a precise yet tractable deterministic alternative to Watts et al.'s (2005) stochastic formalization of Bailey's view.

The first problem when dealing with the simulation of epizootics' dynamics is their spatial and multiscale nature. To solve this issue, we could make use of reference case 2b, with a graph representing the connections between various sites or subpopulations. On top of this are epizootic outbreaks a classic example of large amplitude phenomena, which generally involve processes acting from very low to very high numbers. Moreover, their behavior differs depending on the stage considered. At the early stage, they involve a low number of individuals and their further evolution is highly dependent on the infected individuals' behavior. When an epizootic is installed, it has reached a high number of individuals and its dynamics is not much impacted by individual behaviors anymore. As a result, if we were to choose IB modeling to model a whole epizootic, it would produce very accurate results at the first stage, but would become way too heavy once the epizootic starts to peak. SD on the opposite would render much too approximately the initial stage, overestimating or underestimating the epizootic's chances of survival, but would compute very fast and with a reasonable margin of error the second stage. Therefore, the application of SD–IB models swapping (reference case 4) would offer an interesting tradeoff to simulate accurately and efficiently the entire phenomenon. Finally, this combination would enable to simulate the spread of a disease spatially, lifting at the same time the usual well-mixed assumption, and with satisfying accuracy and computational cost (similar to Bobashev et al., 2007). Other applications in ecology of the same model structure could be the spread of parasites between crop fields, or in a totally different domain, it would probably also be valuable to create population viability analysis (PVA) models by replacing the idea of spread of pathogenous elements by the demography of a metapopulation distributed in several sites. Stable population sources could run with SD whereas endangered patches could take advantage of the preciseness of IB modeling.

7. Conclusion

In the present paper, we first made the assumption that, from a modeler's viewpoint, components of two different natures can make up a system: "wholes" and "divisibles". We then compared the SD and IB paradigms to establish their strong and weak points, and concluded on their respective inability to model both types of components. Even if the differences between SD and IB modeling were already described in the literature, we went further and pointed out that they could act in a complementary way inside of a same model. Moreover, we observed that real-life systems (e.g. ecosystems) are made of an assemblage of components of different nature ("divisibles" and "wholes"). These two assumptions enabled us to show that SD–IB hybrid modeling is a necessity to handle many complex problems in a realistic and dynamic way. Beside

this, we noted that another advantage of such hybridization is that IB modeling can be seen as a way to give a spatial form and behavior to SD models, while the latter, on top of being a handy and intuitive solution to represent some internal processes of IBM individuals, could also offer in return a nice complementary approach to approximate the results of IB models when they get too heavy in terms of computational cost. A limited number of applied SD–IB hybrid models have already been produced and published in the literature relevant to other fields than ecology, but the different theoretical combination cases of SD and IB modeling have not been so far, to the best of our knowledge, the object of any paper.

Altogether, SD–IB hybrid modeling remains relatively unknown and underused in the modeling community. Yet we believe that it represents a field of research with great latent potential especially in the science of ecology. Accordingly, the further exploration of the blending of the SD and IB paradigms on a theoretical and practical point of view is left to be carried out, and the reference cases described above are meant to serve as test beds for the application of this technical and logical approach to model ecological systems characterized by different levels of complexity.

Acknowledgments

The present project was supported by the National Research Fund, Luxembourg. The authors would like to express their gratitude to two anonymous referees whose constructive and insightful comments contributed to improve substantially the final manuscript.

References

- Abbott, K.L., 2005. Supercolonies of the invasive yellow crazy ant, *Anoplolepis gracilipes*, on an oceanic island: forager activity patterns, density and biomass. *Insectes Sociaux* 52, 266–273.
- Ahmad, S., Simonovic, S.P., 2004. Spatial system dynamics: new approach for simulation of water resources systems. *Journal of Computing in Civil Engineering* 18, 331–340.
- Anderson, P.W., 1972. More is different. *Science* 177, 393–396.
- Bader, M., Rietkerk, M., Bregt, A., 2008. A simple spatial model exploring positive feedbacks at tropical alpine treelines. *Arctic, Antarctic, and Alpine Research* 40, 269–278.
- Bailey, N., 1975. *The Mathematical Theory of Infectious Diseases*, 2nd edition. Hafner, New York.
- Bald, J., Sinquin, A., Borja, A., Caill-Milly, N., Duclercq, B., Dang, C., de Montaudouin, X., 2009. A system dynamics model for the management of the Manila clam, *Ruditapes philippinarum* (Adams and Reeve, 1850) in the Bay of Arcachon (France). *Ecological Modelling* 220, 2828–2837.
- Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecological Modelling* 132, 287–302.
- Bobashev, G.V., Goedecke, D.M., Yu, F., Epstein, J.M., 2007. A hybrid epidemic model: combining the advantages of agent-based and equation-based approaches. In: WSC '07: Proceedings of the 39th Conference on Winter Simulation. IEEE Press, Piscataway, NJ, USA, pp. 1532–1537.
- Borshchev, A., 2005. XJ technologies: Anylogic 6. In: Winter Simulation Conference. ACM, p. 82.
- Borshchev, A., Filippov, A., 2004. From system dynamics and discrete event to practical agent based modeling: reasons, techniques, tools. In: The 22nd International Conference of the System Dynamics Society.
- Dale, M., Fortin, M.-J., 2010. From graphs to spatial graphs. *Annual Review of Ecology, Evolution, and Systematics* 41, 21–38.
- Davison, K., Reimann, P., 2008. System dynamics as a mindtool for environmental education. Australian Association for Research in Education, <http://www.aare.edu.au/05pap/dav05368.pdf>.
- Dawkins, R., 1996. *The Blind Watchmaker: Why the Evidence of Evolution Reveals a Universe without Design*. W.W. Norton & Co.
- Dembele, J.M., Cambier, C., 2009. Improving Lagrangian methods: toward an agent-particle based method. In: Simutools '09: Proceedings of the 2nd International Conference on Simulation Tools and Techniques, ICST, Brussels, Belgium, pp. 1–8.
- Dong-Hwan, K., Jae-Ho, J., 1997. System dynamics as a modeling platform for multi-agent systems. In: The 15th International Conference of the System Dynamics Society.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5, 558–567.
- Dyer, R.J., Nason, J.D., 2004. Population graphs: the graph theoretic shape of genetic structure. *Molecular Ecology* 13, 1713–1727.

- Dyke, V., Savit, R., Riolo, R.L., 1998. Agent-based modeling vs. equation-based modeling: a case study and users' guide. In: MABS, pp. 10–25.
- Eisenstadt, M., 1993. Tales of debugging from the front lines. In: Empirical Studies of Programmers, 5th Workshop, Palo Alto, CA, pp. 86–112.
- Eliassen, S., Jørgensen, C., Mangel, M., Giske, J., 2007. Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. *Oikos* 116, 513–523.
- Emrich, S., Breitenacker, F., Zauner, G., Popper, N., 2008. Simulation of influenza epidemics with a hybrid model – combining cellular automata and agent based features. In: 30th International Conference on Information Technology Interfaces, 2008. ITI 2008, pp. 709–714.
- Eppinga, M.B., de Ruyter, P.C., Wassen, M.J., Rietkerk, M., 2009. Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. *The American Naturalist* 173, 803–818 (PMID: 19371168).
- Esposito, S., Incerti, G., Giannino, F., Russo, D., Mazzoleni, S., 2010. Integrated modelling of foraging behaviour, energy budget and memory properties. *Ecological Modelling* 221, 1283–1291.
- Faust, L.J., Jackson, R., Ford, A., Earnhardt, J.M., Thompson, S.D., 2004. Models for management of wildlife populations: lessons from spectacled bears in zoos and grizzly bears in Yellowstone. *System Dynamics Review* 20, 163–178.
- Ford, A., 1999. Modeling the Environment: an introduction to system dynamics models of environmental systems, 1st edition. Island Press, Covelo, California.
- Forrester, J., 1961. Industrial Dynamics. Productivity Press, Portland, OR.
- Forrester, J., 1996. Road Map 1: System Dynamics and K-12 Teachers. MIT System Dynamics in Education Project, <http://sysdyn.clexchange.org/sdep/Roadmaps/RM1/D-4665-4.pdf>.
- Fortuna, M.A., García, C., Guimarães, P.R., Bascompte, J., 2008. Spatial mating network in insect-pollinated plants. *Ecology Letters* 11, 490–498.
- Fortuna, M.A., Gomez-Rodriguez, C., Bascompte, J., 2006. Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences* 273, 1429–1434.
- Fortuna, M.A., Popa-Lisseanu, A.G., Ibáñez, C., Bascompte, J., 2009. The roosting spatial network of a bird–predator bat. *Ecology* 90, 934–944.
- Goodwin, R.A., Nestler, J.M., Anderson, J.J., Weber, L.J., Loucks, D.P., 2006. Forecasting 3-d fish movement behavior using a Eulerian–Lagrangian-agent method (elam). *Ecological Modelling* 192, 197–223.
- Grimm, V., 1999. Ten years of Individual-Based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115, 129–148.
- Grimm, V., Railsback, S.F., 2005. Individual-Based Modeling and Ecology (Princeton Series in Theoretical and Computational Biology). Princeton University Press, Princeton, pp. 266–268 (Ch. 7.9).
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: lessons from ecology. *Science* 310, 987–991.
- Grössler, A., Stotz, M., Schieritz, N., 2003. A software interface between system dynamics and agent-based simulations: linking vensim and repast. In: Proceedings of the 21st System Dynamics Society International Conference, New York.
- Hermann, A.J., Hinckley, S., Megrey, B.A., Napp, J.M., 2001. Applied and theoretical considerations for constructing spatially explicit Individual-Based models of marine larval fish that include multiple trophic levels. *ICES Journal of Marine Science: Journal du Conseil* 58, 1030–1041.
- Huston, M., Deangelis, D., Post, W., 1988. New computer models unify ecological theory. *BioScience* 38, 682–691.
- Huth, A., Wissel, C., 1992. The simulation of the movement of fish schools. *Journal of Theoretical Biology* 156, 365–385.
- Huth, A., Wissel, C., 1994. The simulation of fish schools in comparison with experimental data. *Ecological Modelling* 75–76, 135–146.
- Jørgensen, S.E., 2002. Integration of Ecosystem Theories: A Pattern, 3rd edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Keitt, T., Urban, D.L., Milne, B.T., 1997. Detecting critical scales in fragmented landscapes. *Ecology and Society* [online] 1. <http://www.ecologyandsociety.org/vol1/iss1/art4/>.
- Koestler, A., 1976. The Ghost in the Machine. Hutchinson.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., Breitenmoser, U., 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology* 41 (13), 711–723.
- Kramer-Schadt, S., Revilla, E., Wiegand, T., Grimm, V., 2007. Patterns for parameters in simulation models. *Ecological Modelling* 204, 553–556.
- Kreft, J.-U., Picioreanu, C., Wimpenny, J.W.T., van Loosdrecht, M.C.M., 2001. Individual-Based modelling of biofilms. *Microbiology* 147, 2897–2912.
- Legg, C., Papanastasis, V., Heathfield, D., Arianoutsou, M., Kelly, A., Muetzelfeldt, R., Mazzoleni, S., 1997. Modelling the impact of grazing on vegetation in the Mediterranean: the approach of the modmed project. In: Papanastasis, V., Peter, D. (Eds.), Ecological Basis of Livestock Grazing in Mediterranean Ecosystems. EC Science and Research Publ. EUR 18308 EN, Brussels, pp. 189–199.
- Luna-Reyes, L.F., Andersen, D.L., 2003. Collecting and analyzing qualitative data for system dynamics: methods and models. *System Dynamics Review* 19, 271–296.
- Manor, A., Shnerb, N.M., 2008. Facilitation, competition, and vegetation patchiness: from scale free distribution to patterns. *Journal of Theoretical Biology* 253, 838–842.
- Marin, M., Zhu, Y., Meade, P.T., Sargent, M., Warren, J., 2006. System dynamics and agent-based simulations for workforce climate. In: WSC '06: Proceedings of the 38th Conference on Winter Simulation, pp. 667–671.
- Maxwell, T., Voinov, A., Costanza, R., 2005. Landscape Simulation Modeling. Springer, pp. 21–42 (Ch. 2).
- Mazzoleni, S., Giannino, F., Colandrea, M., Nicolazzo, M., Massheder, J., 2003. Integration of system dynamics models and geography information systems. In: Di Martino, B., Yang, L., Bobeau, C. (Eds.), Modelling and Simulation' 2003. Eurosis-Eti, pp. 304–306.
- Mazzoleni, S., Giannino, F., Mulligan, M., Heathfield, D., Colandrea, M., Nicolazzo, M., D'Aquino, M., 2006. A new raster-based spatial modelling system: 5D environment. In: Voinov, A., Jakeman, A., Rizzoli, A. (Eds.), In: Summit on Environmental Modelling and Software, vol. 1. International Environmental Modelling and Software Society, Burlington, USA.
- Mazzoleni, S., Legg, C., 1998. Modmed: modelling vegetation dynamics and degradation in Mediterranean ecosystems. In: Mairota, P., Thornes, J., Geeson, N. (Eds.), Atlas of Mediterranean Environments in Europe – The Desertification Context. J. Wiley and Sons.
- Meadows, D., 2009. Leverage points: places to intervene in a system. *Solutions* 1, 41–49.
- Moen, R., Pastor, J., Cohen, Y., 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78, 505–521.
- Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ed). *Ecological Monographs* 71, 557–586.
- Morrison, V.P., 1995. Import/Dome Language Reference Manual. U.S. Army Construction Engineering Research Laboratories, Champaign, Illinois.
- Muko, S., Sakai, K., Iwasa, Y., 2001. Dynamics of marine sessile organisms with space-limited growth and recruitment: application to corals. *Journal of Theoretical Biology* 210, 67–80.
- Norling, E., 2006. Contrasting a system dynamics model and an agent-based model of food web evolution. In: Antunes, L., Takadama, K. (Eds.), MABS. Vol. 4442 of Lecture Notes in Computer Science. Springer, pp. 57–68.
- Okuyama, T., 2009. Local interactions between predators and prey call into question commonly used functional responses. *Ecological Modelling* 220, 1182–1188.
- Osgood, N., 2007. Using traditional and agent based toolsets for system dynamics: present tradeoffs and future evolution. In: The 2007 International Conference of the System Dynamics Society.
- Patten, B.C., 1978. Systems approach to the concept of environment. *The Ohio Journal of Science* 78 (4), 206–222.
- Patten, B.C., 1982. Environs: relativistic elementary particles for ecology. *The American Naturalist* 119 (2), 179–219.
- Pennington, N., 1987. Stimulus structures and mental representations in expert comprehension of computer programs. *Cognitive Psychology* 19, 295–341.
- Rahmandad, H., Sterman, J., 2008. Heterogeneity and network structure in the dynamics of diffusion: comparing agent-based and differential equation models. *Management Science* 54, 998–1014.
- Reynolds, C.W., 1987. Flocks, herds, and schools: a distributed behavioral model. *Computer Graphics* 21, 25–34.
- Rossmannith, E., Blaum, N., Grimm, V., Jeltsch, F., 2007. Pattern-Oriented Modelling for estimating unknown pre-breeding survival rates: the case of the lesser spotted woodpecker (picoides minor). *Biological Conservation* 135, 555–564.
- Sadsad, R., McDonnell, G., 2007. Using multi-scale systems simulation to evaluate health record solutions to improve medication use by the elderly. In: The 25th International Conference of the System Dynamics Society.
- Sattler, R., 2008. Wilber's AQL Map and Beyond. Chapter 1: Hierarchy and Beyond. Printed in Canada. ISBN 978-0-9809417-0-8 <http://www.beyondwilber.ca/AQLmap/bookdwl/files/WAQLMB1.pdf>.
- Scheffer, M., Bavaco, J.M., DeAngelis, D.L., Rose, K.A., van Nes, E.H., 1995. Super-individuals a simple solution for modelling large populations on an individual basis. *Ecological Modelling* 80, 161–170.
- Scheffer, M., Hosper, S., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution* 8, 275–279.
- Schieritz, N., 2002. Integrating system dynamics and agent-based modeling. In: The 20th International Conference of the System Dynamics Society.
- Schieritz, N., Grössler, A., 2003. Emergent structures in supply chains—a study integrating agent-based and system dynamics modeling. In: HICSS'03: Proceedings of the 36th Annual Hawaii International Conference on System Sciences – Track 3.
- Schieritz, N., Milling, P.M., 2003. Modeling the forest or modeling the trees: a comparison of system dynamics and agent-based simulation. In: The 21st International Conference of the System Dynamics Society.
- Scholl, H., 2001. Agent based and system dynamics modeling: a call for cross study and joint research. In: HICSS '01: Proceedings of the 34th Annual Hawaii International Conference on System Sciences, vol. 3. IEEE Computer Society, Washington, DC, USA.
- Scholl, H.J., Phelan, S.E., 2004. Using integrated top-down and bottom-up dynamic modeling for triangulation and interdisciplinary theory integration: the case of long-term firm performance and survival. In: The 22nd International Conference of the System Dynamics Society.
- Stemate, L., Pasca, C., Taylor, I., 2007. A comparison between system dynamics and agent based modeling and opportunities for cross-fertilization. In: WSC '07: Proceedings of the 39th Conference on Winter simulation. IEEE Press, Piscataway, NJ, USA, p. 2376.
- Tremil, E., Halpin, P., Urban, D., Pratson, L., 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology* 23, 19–36.

- Turner, M.G., Arthaud, G.J., Engstrom, R.T., Hejl, S.J., Liu, J., Loeb, S., McKelvey, K., 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5, 12–16.
- Vessey, I., 1989. Toward a theory of computer program bugs: an empirical test. *International Journal of Man-Machine Studies* 30, 23–46.
- Wakeland, W., Fusion, J., Goldstein, B., 2005. A tale of two methods. agent-based simulation and system dynamics. applied in a biomedical context: acute inflammatory response. In: 6th European Congress of Systems Science.
- Wakeland, W., Macovsky, L., An, G., 2007. A hybrid simulation model for studying acute inflammatory response. In: *SpringSim '07: Proceedings of the 2007 Spring Simulation Multiconference*. Society for Computer Simulation International, San Diego, CA, USA, pp. 39–46.
- Wakeland, W.W., Gallaher, E.J., Macovsky, L.M., Aktipis, C.A., 2004. A comparison of system dynamics and agent-based simulation applied to the study of cellular receptor dynamics. In: *HICSS '04: Proceedings of the 37th Annual Hawaii International Conference on System Sciences – Track 3*.
- Watts, D.J., Muhamad, R., Medina, D.C., Dodds, P.S., 2005. Multiscale, resurgent epidemics in a hierarchical metapopulation model. *Proceedings of the National Academy of Sciences of the United States of America* 102, 11157–11162.
- Weiner, J., Stoll, P., Muller Landau, H., Jasentuliyana, A., 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *The American Naturalist* 158, 438–450.
- Westervelt, J., 1999. Modeling mobile individuals in dynamic landscapes. *International Journal of Geographical Information Science* 13, 191–208.
- Wiggins, S., 2005. The dynamical systems approach to Lagrangian transport in oceanic flows. *Annual Review of Fluid Mechanics* 37, 295–328.
- Wilson, W.G., 1998. Resolving discrepancies between deterministic population models and Individual-Based simulations. *The American Naturalist* 151, 116–134.
- Winkler, E., Stocklin, J., 2002. Sexual and vegetative reproduction of *hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Annals of Botany* 89, 525–536.
- Wyszomirski, T., Wyszomirska, I., Jarzyna, I., 1999. Simple mechanisms of size distribution dynamics in crowded and uncrowded virtual monocultures. *Ecological Modelling* 115, 253–273.