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Review

Simulation modelling of ecological hierarchies in constructive dynamical systems

Cédric Ratzé [a,b], *François Gillet* [c,*], *Jean-Pierre Müller* [a], *Kilian Stoffel* [b]

[a] *CIRAD TA 60/15, 73 ave. Jean-Félix Breton, 34398 Montpellier Cedex 5, France*
[b] *University of Neuchâtel, Institut Interfacultaire d'Informatique, rue Emile-Argand 13, 2007 Neuchâtel, Switzerland*
[c] *EPFL, Ecole Polytechnique Fédérale de Lausanne, Ecological Systems Laboratory, Station 2, 1015 Lausanne, Switzerland*

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ABSTRACT

Organized complexity is a characteristic feature of ecological systems with heterogeneous components interacting at several spatio-temporal scales. The hierarchy theory is a powerful epistemological framework to describe such systems by decomposing them vertically into levels and horizontally into holons. It was at first developed in a temporal and functional perspective and then, in the context of landscape ecology, extended to a spatial and structural approach. So far, most ecological applications of this theory were restricted to observational purposes, using multi-scale analysis to describe hierarchies. In spite of an increasing attention to dynamics of hierarchically structured ecological systems, current simulation models are still very limited in their representation of self-organization in complex adaptive systems. An ontological conceptualization of the hierarchy theory is outlined, focusing on key concepts, such as levels of organization and the compound and component faces of the holons. Various existing formalisms are currently used in simulation modelling, such as system dynamics, discrete event and agent based paradigms. Their ability to express the hierarchical organization of dynamical ecological systems is discussed. It turns out that a multi-modelling approach linking all these formalisms and oriented toward the specification of a constructive dynamical system would be able to express the dynamical structure of the hierarchy (creation, destruction and change of holons) and the functional and structural links between levels of organization.

Contents

* Corresponding author.
E-mail address: francois.gillet@epfl.ch (F. Gillet).
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1. Introduction

An important form of complexity can be found in so-called 'self-organized systems' or 'complex adaptive systems' in which the dynamics and the emergent properties are consequences of interactions between heterogeneous components at different spatio-temporal scales (Cowan et al., 1994; Levin, 1999; Wu and Marceau, 2002; Patten et al., 2002). Complexity in ecological systems is typically a kind of 'organized complexity' (Weinberg, 1975; O'Neill et al., 1986), characterized by intermediate numbers of heterogeneous components (e.g., organisms belonging to different species) and structured interrelationships among these components, including nested structures (e.g., biological communities, ecosystems).

The only possibility to understand and to model such complex systems is to exhibit some organizational principles behind the apparent inextricability. The hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986) allows a decomposition of this kind of systems that could improve our understanding of the underlying dynamical processes. Conceived by its authors as an epistemology, this theory has the important property to emphasize on both top-down and bottom-up perspectives (Wu and David, 2002). Formally, it is a view of ecological systems, which takes the scales of observation explicitly into account and which tries to conceptualize the phenomena at their proper scale. Hierarchical organization simply means that, at a given level of resolution, a system is composed of interacting components (i.e., lower-level entities) and is itself a component of a larger system (i.e., higher-level entity) (O'Neill et al., 1989). The hierarchy theory assumes that ecological systems are near-decomposable vertically into levels of organization and horizontally into holons. Most ecological hierarchies are nested hierarchies: in such a 'holarchy' (Koestler, 1968), holons of the higher level are composed of and actually contain the lower-level holons. A holarchically integrated system is a dynamic and adaptive entity, reflecting in its own functioning the patterns of change over all levels of the system (Li, 2000).

The dynamics of hierarchically organized ecological systems has received increasing attention from the end of the 1980's, as shown by a search on ISI Web of Science (Fig. 1). Scientific journals in the field of ecology have furnished an important contribution to this topic. However, the modelling aspects have not been extensively developed so far. The focus on modelling became less important since 1996, probably because of the difficulty in translating the dynamical concepts of the hierarchy theory into mathematical or computational models. Therefore, hierarchy theory has been largely used in an observational and descriptive perspective but few of these descriptions have been developed so that to be simulatable. In this direction, a lot of work remains to be done. Simulations exhibiting multiple scales or even a hierarchical structure are rare and most of them were built on a case-by-case basis (e.g., Luan et al., 1996; Wu and Levin, 1997; Mäkelä, 2003; Bragg et al., 2004; Gillet, 2005; Li et al., 2006). Wu and David (2002) proposed a multi-scale modelling methodology and a modelling platform (HPD-MP) designed to facilitate the development of such spatial hierarchical models. To go a step further, we need to introduce a more conceptualised and unified modelling and simulation approach.

Our goal is to build formal tools allowing the specification of models of dynamical systems suited for the constructive expression of the concepts of the hierarchy theory. Being relatively new, a good part of the terminology of hierarchy theory used in ecology is very general and can hide differences in the actual meaning and use of its basic concepts. In this

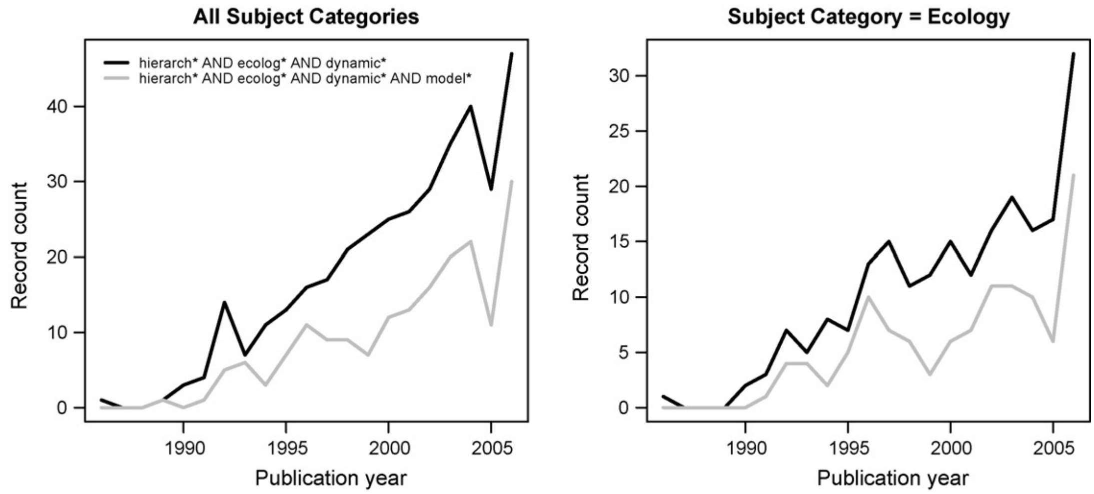

Fig. 1 – Results of a search on ISI web of science (December 2, 2006).

paper, we thus begin with a critical review of the main concepts of the hierarchy theory, in order to extract their operational meaning in a dynamic modelling perspective. Thereafter, we review the existing formalisms which have been proposed for modelling complex systems and we evaluate their ability at expressing explicitly these concepts. Finally, we discuss the possible ways to combine heterogeneous formalisms in a multi-modelling framework using the holon concept, which we advocate as being central for successful modelling of complex ecological systems.

2. Key concepts of the hierarchy theory

Following the epistemological perspective of the hierarchy theory, all concepts discussed below are only convenient representations of real natural systems, which may help at interpreting the features and understanding the mechanisms of organized complexity.

2.1. *The concept of scale*

Despite the growing importance of scale in ecology, this notion is used based on different definitions (Hay et al., 1997; Marceau and Hay, 1999) and can lead to some confusion (Marceau, 1999). In a recent review, Dungan et al. (2002) identified three dimensions of the scale concepts in a spatial context: phenomenon, sampling and analysis. In our modelling perspective, we will outline three important meanings of the notion of spatio-temporal scale: (i) an observational meaning, (ii) an ontological meaning and (iii) a representational meaning.

(i) In the observational meaning, scale conceptually represents a filter or a window of perception through which the world is quantified (Hay et al., 2002). This observation scale is not a property of the world, but is generated by the sampling of an external observer (Allen and Hoekstra, 1992; Blaschke and Petch, 1999). This conception of scale is defined by two combined characteristics (Marceau and Hay, 1999; Dungan et al., 2002): the observation grain is the smallest space and time unit used in the sampling or the smallest distinguishable information that can be obtained; the observation extent is the total space-time span over which the observations with this grain are made. For an external observer, meaningful entities and phenomena only exist over a specific range of observation scales (Hay et al., 2002). For example, while no relationship is observable at the traditional week-long sampling interval between phytoplankton and zooplankton biomass in a lake, a negative relationship exists at finer temporal scale (2- to 3-day interval) and a positive one at coarser scale (10- to 14-day interval) (Carpenter, 1989).

(ii) The ontological meaning of scale refers to the notion of characteristic (or inherent or intrinsic) scale of an object (entity, process or phenomenon), i.e. to the effective size or measure of the object and/or its properties and attributes (Marceau and Hay, 1999). For example, properties such as size, mass, volume of entities such as cell, leaf or tree remain scale invariant when multiplying the observations in their specific scale domain, before disappearing outside of the scale domain. The intrinsic scale of existence of an entity determines its proper window of interaction within its environment. The phenomenon grain corresponds to the minimum spatio-temporal size at which an object reacts to the external dynamics, and the extent as the reach or span of its interactions (Burnett and Blaschke, 2003). For example, the spatial and temporal scales of biological activity in aquatic systems are tightly coupled to the scales of physical phenomena such as thermoclines, currents, or gyres (Meentmeyer and Box, 1987; Steele, 1989). For Allen and Starr (1982), the scale is the period of time and space over which signals are integrated or smoothed to give a message. In this perspective, objects of interest are intrinsically linked to the particular scale at which they can be distinguished and defined (Marceau, 1999).

(iii) The representational meaning of scale is of particular importance because modelling implies the representation of a world with some limited precision. The scale of representation may be chosen independently of the intrinsic scale of existence of an entity and of the scale at which it is observed, by applying scaling operations. Scaling refers to the transfer of information or data from one scale to another. When scaling up, information is taken at one scale to derive information at a larger scale. Inversely when scaling down, the information obtained at one scale is applied to components at a finer scale (Marceau, 1999). Difficulties arise in scaling up, as illustrated by the 'modifiable area unit problem' (Jelinski and Wu, 1996): many different ways exist to aggregate a study area into coarser spatial units, which are arbitrary and have no intrinsic meaning.

A constructive simulation of hierarchical systems should be able to account for the intrinsic scale of the entities and to express both scaling-up and scaling-down operations.

2.2. *The concept of level of organization*

2.2.1. *Scale domains and scale thresholds*

The central idea of the hierarchy theory is to derive the hierarchical organization from differences in temporal and spatial scales between the phenomena of interest. In empirical studies, some analytical methods (e.g., plot of power spectrum or fractal dimension versus scale) revealed the existence of thresholds in the continuum of possible scales of observations (Turner et al., 1989), which correspond to boundaries between distinct levels of organization (Marceau, 1999). Two complementary concepts are important to understand the link between scales and levels of organization: the scale domain and the scale threshold. The scale domain is a region of the scale spectrum over which the structure and the functional relationships between variables describing a particular object of interest (process, entity, phenomenon) do not change or change monotonically (in an easily predictable way) with change in scale. Such domains are separated by thresholds that are relatively sharp transitions or critical points along the scale continuum where a shift in the relative importance of variables influencing a process occurs (Marceau, 1999). The relatively isolated levels of organization correspond to scale domains, and interactions tend to be stronger and more frequent within a domain of scale than among them (Hay et al., 2002).

Many studies have shown the effect of scale change on the explanatory power of different sets of variables. For example, at the scale of individual leaf surfaces, evapotranspiration is mainly influenced by stomatal mechanisms, while at the canopy or regional scales, climate becomes the driving force (Jarvis and McNaughton, 1986); the mortality of oak seedlings decreases with increasing precipitation at the local scale of forest stands, whereas at regional scale it is lower in drier climatic regions (Neilston and Wulstein, 1983).

2.2.2. *Functional and structural boundaries between levels*

At the beginning (Allen and Starr, 1982; O'Neill et al., 1986), hierarchy theory in ecology has focused on temporal and functional aspects of ecosystems: the hierarchical levels were defined by different characteristics of the processes (e.g., behavioural frequencies, relaxation time, cycle time or response time). In the spatial context of landscape ecology, a more structural approach has emerged that integrates the spatial aspects in the so-called 'hierarchical patch dynamics' (HPD) paradigm (Wu and Levin, 1994, 1997; Wu and Loucks, 1995; Reynolds and Wu, 1999; Burnett and Blaschke, 2003). Basically, the landscape is decomposed into a hierarchy of patch mosaics to relate functional processes with structural spatial properties across scales. As observed at a given scale based on a given criterion, each patch is homogeneous in its interior and relatively heterogeneous in comparison to its exterior. For example, to understand effects of urbanization on landscape dynamics, Wu and David (2002) used a three-level hierarchy: the regional landscape with patches characterized by dominant biome and land use pattern, local landscape (e.g., urban or rural) and local ecosystem composed of relatively homogeneous vegetation-soil complexes.

2.2.3. *Relating patterns and processes across hierarchical levels*

The next problem is to find appropriate scaling laws to relate information across a wide range of scales. A variety of mathematical tools exist for up- or down-scaling (Turner et al., 1989). However, it appears that such techniques can only be appropriate when applied within the relevant scale domains of the phenomena under investigation (Wiens, 1989). Extension across the scale thresholds may be difficult or impossible because (i) of the instability in the dynamics of the transition zone between two domains of scale (Marceau, 1999), and (ii) of changes in spatial heterogeneity (Turner et al., 1989). The presence of different dominant processes at different scales means that as a scaling method attempts to span a wider range of scales, it needs to incorporate the effects of an increasing number of processes (Peterson, 2000).

It is therefore of crucial importance to identify these scale thresholds and to derive the appropriate laws governing the interactions within and between levels of organization. If entities and relationships between variables emerge at specific scales, there must be a way to define and relate them across discrete levels of organization (Marceau, 1999).

In a constructive modelling perspective, the purpose is to express a hierarchically structured virtual world in a simulator effectively functioning with various explicit levels of organization based on multiple scale domains of description and interaction, which can be used to assess the consequences of the organizational principles of the hierarchy theory. It turns out that one of the greatest challenges for mechanistic ecological modelling is to meaningfully connect the levels of organization. However, it is impossible to reduce the higher level to the lower because each has its own unique scale-dependent qualities: the whole and the parts are both valid objects of intellectual pursuit. When scale and levels of organization are articulated into a hierarchical organization, they can be used to develop models with considerable predictive value. Bragg et al. (2004) defined a hierarchical model as an integrated, systematic approach for approximating ecological behaviour across organization levels. They argued that an explicitly hierarchical model should be a notable improvement over designs that are more rigid.

2.3. *The concept of holon*

2.3.1. *Functional and structural boundaries between subsystems*

Within a same level of organization, some of the components will interact weakly and others strongly, creating boundaries around strongly interacting components regarding their surrounding components. This is a functional, spatial and temporal way to delimit the subsystems at a given level of the hierarchy.

From these considerations, it is possible to describe an upper level of organization which is also composed of components or patches but interacting at slower rate, each of which representing a subsystem at its intrinsic scale. Introduced by Koestler (1968), the notion of holon is defined as being both a component and a compound. For example, a leaf can be simultaneously seen as either an atomic part of a plant interacting with its environment or as a composed whole integrating its cells. As such, this notion implies to articulate a subsystem as a set of strongly interacting components at a given level of organization, that is a composed whole, and its representation as an atomic part at the next upper level of organization (Fig. 2).

In vegetation ecology, different nested integration levels are considered, and in each of them holons can be recognized. (i) The lower level is the synusia (Gillet and Gallandat, 1996), composed of plants of similar size and sharing a same local habitat (e.g., the short herb layer of a forest understorey, or a patch of tall forbs in a clearing); frequent and direct plant interactions (e.g., competition) occur within each synusial community, which is delimited as a holon. (ii) At a higher level, the phytocoenosis (e.g., a forest) integrates tree, shrub, herb and moss synusiae in which plants belonging to different synusiae have no direct interactions, but some synusiae influence each other in a complex way (e.g., the tree synusia modifies the climate inside the forest, and some herb synusiae play an important role in the initial stages of tree regeneration). As a holon, a forest phytocoenosis tends to develop its boundaries (canopy, forest edges) to protect its components against external disturbances. (iii) Phytocoenoses interact through their boundaries (ecotones) in the landscape at a third organization level.

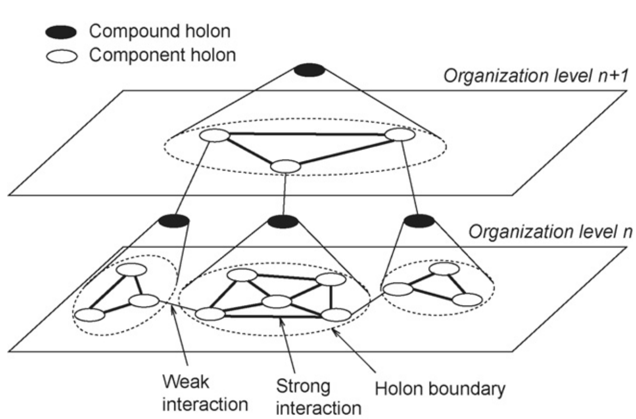

Fig. 2 – The holons for articulating organizational levels.

2.3.2. *Component and compound holon*

The holon can also naturally scale up and down the information between the two levels of organization it relates, taking into account the representational meaning of scale. For uniformity, we will consider that any component at any level of description is a holon, being an entity potentially or effectively decomposable into a subsystem at the lower level of organization. Therefore, the term "holon" will be used uniformly thereafter making the distinction between atomic or "component holons" when talking about the interacting components and "compound holons" when talking about the subsystems.

2.4. *The concept of constraint*

The behaviour of an ecological system is dynamically limited to a subset of the set of possibilities, on one hand by the potential behaviour of its components, and on the other hand by the environmental constraints imposed by higher levels (O'Neill et al., 1989). For example, limiting climatic factors, such as temperature, impose constraints on plant growth. In the famous example of spruce budworm dynamics (Ludwig et al., 1978; Allen and Hoekstra, 1992), avian predation controls the growth of the budworm population when its density is low, but at a critical stage the population can reach a high enough density so as to escape this predation constraint and to increase uncontrolled until the pest eats itself out of its resources: this switch in constraints is responsible for the cyclic epidemic outbreaks observed in spruce forests.

According to the hierarchy theory, the relationships between levels are asymmetric: the constrained processes have a lower influential power on the dynamics of the upper level than the constraining process has on the dynamics of the lower level. Taking into account this notion of constraint, we have to define the holons so that the asymmetry between the component- and the compound-holon actually occurs in the simulations.

An important consequence of this organizational principle is that the dynamics of the system at a given focal level is not only dependent on the interactions between components at the lower level (bottom-up integration) but also to the constraints imposed by the higher level (top-down influences). Therefore, any model of a hierarchical system should consider at least three levels of organization, involving a triadic view of causalities (Salthe, 1985; Ulanowicz, 1997).

2.5. *Interactions between hierarchies*

Additionally, a given hierarchy derives from a given perspective or point of view on the system. The hierarchy theory considers the dynamics of an ecological system as resulting from the interplay of different hierarchically structured perspectives (O'Neill et al., 1986). Various thematic points of view (e.g., population, ecosystem) can lead to different organizations that are interacting at different levels of organization. Therefore, the hierarchy theory will encompass all the thematic points of view interacting in the ecological system.

3. Review of the existing modelling formalisms

Various formalisms or modelling approaches are extensively used in ecological modelling. Each of them is based on some assumptions and hypotheses. It is probably possible to express or to represent any kind of system in each of these formalisms, but it turns out that each formalism is more or less suitable for the expression of certain categories of models including the choice between continuous or discrete time or states, explicit or implicit space, structural and qualitative aspects or functional and quantitative aspects, dynamical or fixed structure, single or multiple levels of organization. For our purpose, two criteria are critical: the expression of (i) dynamical structure and of (ii) hierarchical organization. A comparison of the various formalisms in regard to these two model features is given in Table 1. We shall discuss each approach in turn.

3.1. *System dynamics models*

3.1.1. *Ordinary differential equations*

Most of the modelling formalisms used so far in ecology are the ordinary differential equations (ODEs), suited to express continuous dynamical systems. A model of this kind is a system of coupled state variables, each describing a continuous quantity, such as population density or average biomass, evolving smoothly in a time continuum. The ODEs give implicitly all the possible trajectories of the state variables depending on the other variables taken in consideration on their infinitesimal linear variation of trajectory in the phase space. The structure of interaction (that is the reciprocal influences of the coupled variables) is given once and for all by the coupled equations. The simulation phase consists in solving numerically, with a given precision, the system of equations with the parameters and the initial conditions appropriate to a particular empirical case. To solve differential equations numerically, any computer simulation must achieve a discretization of time by means of various integration methods (e.g., explicit or implicit Euler, Runge-Kutta). The theoretical assumption of this kind of mathematical model is that natural systems generally tend to evolve asymptotically toward single or multiple stable equilibria (either punctual, cyclic or strange). This equilibrium paradigm leads to studies of the long-term, asymptotic behaviour of ecological systems by searching for attractors and bifurcations (Coquillard and Hill, 1997; Bousquet and Le Page, 2004). However, recent work has emphasized the importance of short-term, transient dynamics in ecological systems and models (Hastings, 2004), including transient chaos and saddle nodes.

It is possible to express different time scales for the state variables in a system of ODEs in which differences in rates are explicitly exhibited. The dynamics of such a slow-fast system is dominated by the slow variables, with the fast variables simply following along. Furthermore, the fast variables are supposed to rapidly reach a steady state, which can be used as an approximated constant parameter only influencing statically the global dynamics. Such dynamics can be analyzed by the geometric singular perturbation approach (Rinaldi and Scheffer, 2000). Translated into the hierarchical terminology, the slower components belong to a higher level and impose constraint on the dynamics of the faster components (O'Neill et al., 1986). The system may pass several transient phases in which both fast and slow variables play alternatively the

Table 1 – Comparison of modelling formalisms

Modelling approaches	Entities; formalisms	Dynamical structure	Hierarchical organization
System dynamics paradigm			
Differential equations	Physical state variables; ODE, PDE, continuous time and space	No	In the singular perturbation theory: fast and slow variables give different temporal scales
Compartment models	Aggregated state variables, stock-flow diagrams, feedback loops, difference equations, implicit spatial structure	No	By structural abstraction, but not so expressive as the notion of level in hierarchy theory
Discrete event paradigm			
Cellular automata	Neighbouring cells in a fixed lattice; state-transition rules, discrete time and space	No	One level of interaction in the model, and a second emergent global implicit level for the external observer
DEVS	Passive objects; flowcharts	Only DS-DEVS	By structural and behavioural abstraction, but the levels are not explicitly ordered by temporal scales
Agent based paradigm			
Individual-based models	Particles, moving individuals; individual behaviour rules	Only in i-state configuration models	No
Multi-agent systems	Active objects (reactive and proactive agents); interaction rules in a changing environment	Yes, by reciprocal situation in an (explicit or not) interaction space	Often only one emergent global implicit level for an external observer. In some cases, emergent bottom-up construction of levels

major role (O'Neill et al., 1989). Due to switches between different constraints, fast variables may exhibit periodically catastrophic shifts, as illustrated by the famous example of spruce budworm outbreaks (Ludwig et al., 1978).

Auger (Auger and Poggiale, 1998; Auger et al., 2000) used aggregation methods to simplify systems of ODEs with several time scales and proposed to define a level of organization as a level of invariance and conservation.

3.1.2. Compartment models

The compartment models, or box models, are a particular representation of ODEs, where the semantic interpretation refers explicitly to the theory of system dynamics and systems thinking (Forrester, 1961; Richmond, 2001). Compartment models are integrated and spatially implicit, which means that they are designed to describe the time development of average properties in implicitly defined spaces (Eriksson, 1971), following the mean-field assumption. A compartment model is composed of a finite set of state variables describing some average characteristics of discrete, structural entities statically linked together by a network of flows and controls (Godfrey, 1983). Differential (continuous time) or difference (discrete time) equations are used to calculate flows. Some compartments can be merged in a new one to abstract the complexity of the functioning and structure of the interior of a compartment to the others, allowing some modularity and nestedness. They were at first designed to describe physiological processes depending on local mass balance conditions (Jacquez and Simon, 1993). They are specifically adapted to the modelling of transfers and exchanges of matter or energy between compartments representing stocks or reservoirs.

3.1.3. Partial differential equations

Partial differential equations (PDEs) can be used for the explicit expression of a continuous space in the model. Here the coupled state variables are dependent on both time and space coordinates. Generally the PDEs are more difficult to solve than ODEs and can be very heavy to simulate. Here again, the computer simulation needs to discretize the space, e.g. by finite element methods (Lewis and Ward, 1991).

Using nonlinear stochastic PDEs, an interdisciplinary field of research called synergetics (Haken, 1997) has investigated the emergence of spatial, temporal and functional structures in physical self-organizing systems, with possible applications to landscape ecology (Li, 2000).

3.2. Discrete event models

3.2.1. Discrete event specification systems

An automaton is defined by its sets of inputs, outputs, and internal states, a transition function from an input and state to a new state and an output function. As such, automata are discrete in time even if the dates of input/output/transition occurrences can be either at fixed time steps or arbitrary. The DEVS (discrete event specification system) was developed by Zeigler et al. (2000) in the context of the theoretical foundations of the simulation and modelling of discrete event dynamical systems and adapted to the coupling of systems through encapsulation.

An atomic DEVS model is an automaton structure with the addition of an internal transition function and a time advance function for spontaneous state transitions. An atomic model is like a compartment or black box with input and output ports, where the input and output events are received or sent, and an internal state which can transit to a new state for two possible reasons: (i) an external event occurred at the input part of the box; (ii) an internal transition occurred when the box was in its current state for an elapsed time corresponding to the result of the time advance function applied to this state. If the natural duration of the current state is equal to infinity, then no internal transition can occur. Some extensions have been defined to break out some limitations. For example, the DEVS models were originally asynchronous, so that if two external events occurred simultaneously at the input port of a basic DEVS model, it was necessary to specify a priority of treatment of these events in the DEVS coupled model. This limitation does not exist anymore in parallel-DEVS (Zeigler et al., 2000) for which an abstract simulator (Chow et al., 1994) has been defined.

A coupled DEVS model is defined as the specification of a new box with input and output ports and including a finite set of basic DEVS models (i.e., atomic or other coupled DEVS models), which are statically interconnected. A coupled DEVS model has an external behaviour equivalent to an atomic model, allowing to using it as a new atomic model for another coupled model. This feature of DEVS is called closure under coupling and permits to recursively build more and more complex models in a hierarchical and modular manner. However, the decomposition achieved in the DEVS formalism is functional and not spatial.

3.2.2. Cellular automata

To explicitly express spatially located interactions, the cellular automaton (CA) introduced by von Neumann (1963) is widely used. A CA is a finite set of interconnected automata or cells, which represent discrete spatial domains. The connectivity reflects the local interactions between the states of neighbouring cells. Different types of connectivity are possible, such as the von Neumann connectivity, where each cell has four direct neighbours, or the De Moore connectivity with eight neighbours. Regarding time and simulation, a CA is a synchronous model evolving step by step following a discrete-time dynamics: each cell evolves simultaneously with the others in function of its current state and the current state of its neighbours. An extension of DEVS called Cell-DEVS (Wainer and Giambiasi, 2001) has been developed to specify CA.

In the context of ecological modelling, Phipps (1992) argued that many ecological problems related to spatial heterogeneity and patchiness can be formalized with CA. More generally, they are well suited to mimic systems with strong local interactions. However, a CA does not take into account various scales of space and time. Only two levels are considered: the global or macro-level of the whole cell grid and the local or micro-level of each individual cell. But the interactions themselves stay on one single level, the second level being only present for the observation and analysis of the possible relations between the local rules and the emergent global pattern resulting from the local interactions.

Furthermore, as for the classical PDE models of systems dynamics, the connectivity does not evolve over time, the lattice being fixed once for all. However, the definition of the parallel dynamic structure discrete event system specification (DS-DEVS), again as an extension of DEVS, allows the possibility to both dynamically change the network of connections between atomic models and create or destroy some atomic models of any coupled model (Barros, 1996, 1998).

3.3. Agent based models

The power of the classical system dynamics models is the abstraction of objects by taking average quantities or measures to represent them, but it is also their weakness. If the object is constant, it is a good approximation to describe it with only some state variables. However, if it has a complex and changing internal structure, then we cannot only extract some quantities from the object's structure to represent the object itself. We have to build a calculus on objects, i.e. on the structures that link the variables, by building a constructive dynamical system (CDS). An important property of a CDS is the possibility of dynamical creation or destruction of some objects in the system (Fontana and Buss, 1996). Furthermore, changes in the structure influence both the dynamics of the variables and the structure of their relationships; it is a case of dynamical system with dynamical structure (Giavitto et al., 2002). Individual-based models and multi-agent systems were proposed for considering structural dynamics.

3.3.1. Individual-based models

The essence of the individual-based model (IBM) approach is to derive properties of ecological systems from the properties of the biological organisms constituting the system (Lomnicki, 1992; Bousquet and Le Page, 2004). The two main reasons given to justify IBMs were the need to consider (i) the genetic uniqueness of the individuals and (ii) the fact that their spatial location implies local interactions with the environment (Huston et al., 1988).

In fact there are two schools of thought about the notion of individual in the IBM approach (DeAngelis and Rose, 1992). The 'i-state distribution models' consider inter-individual variability due to heterogeneity in the internal structure (sizes, ages, and others characteristics) of populations and communities. This methodology relies on analytic tools such as Leslie matrices or difference equations that can deal with distributions of characteristics in populations. By contrast, the 'i-state configuration models' represent each individual as a discrete entity with unique characteristics and a specific history. This methodology is based on the simulation of interacting individual entities. Furthermore the social aspects can be represented by individuals perceiving the system and deciding to change the organization. This second approach goes clearly in the direction of more individual autonomy and is closer to the multi-agent system approach.

Applied to plant populations and communities, the IBM approach suffers from important theoretical limitations due (i) to the difficulty to apply the notion of biological individual to clones and (ii) to its underlying reductionist viewpoint ignoring the reality of high-level entities and hierarchical structures (Gillet et al., 2002).

3.3.2. Multi-agent systems

Basically, a multi-agent system (MAS) is a dynamical collection of interacting agents (Ferber, 1999). An agent is an autonomous discrete entity acting on its local environment and interacting with other agents (see the influence-reaction model in Ferber and Müller, 1996), in a way chosen by itself (autonomy) and based on some knowledge of its own state and of the state of its local environment (other agents and objects of different kinds). In many cases of spatially explicit multi-agent systems, space is represented by a cellular automaton, in which the agents are situated (e.g., Bousquet et al., 1998).

The most crucial properties of the MAS are: (i) the locality of the interactions between the agents and their environment; (ii) the possibility for the agents to move in this environment, i.e. to change the local environment of interactions and consequently the structure of the relational network; (iii) the autonomy of the agents, which is a choice governed by the local situation; (iv) the possibility of dynamical creation or destruction of the agents.

Contrary to ODE, PDE, CA and DEVS formalisms, the MAS approach has the disadvantage to be not exhaustively and commonly formalized. However some recent contributions tried to improve this situation by defining some specification methodologies (e.g., A-UML, Odell et al., 2000) or by building abstract machines specifically designed for MAS simulation using DEVS formalism (Schattenberg and Uhrmacher, 2001; Uhrmacher, 2001).

The MAS community distinguishes between the agent-centred and the organization-centred MAS. The concept of organization was first introduced to better structure the MAS in the specification phase, in a static way (Durand, 1996). It refers to a structured set of possibly interacting roles, where each role corresponds to a recurrent behaviour played by an agent in the organization. For example, a simple organization of biomass exchange can be composed of two roles, the role of biomass consumer and the role of biomass producer, and one recurrent interaction of biomass consumption between these roles. Instantiated in a grazing system, a cow agent plays the role of biomass consumer while a plant agent plays the role of biomass producer. Later on, this concept was used to structure dynamically the community of agents in the system, such as in agent-group-role (Gutknecht, 2001) or in MOCA (Amiguet, 2002; Amiguet and Müller, 2002a,b; Amiguet et al., 2002). Following this organization concept, the system is partitioned into overlapping groups of agents where an agent can play the different roles defined in a group. This conception can be useful to represent the multiplicity of thematic points of view on a system and their articulations. In the grazing system example, the same cow can play simultaneously a role of nutrient source for the plant. In all cases, the system remains partially flat, because the organization is not structured with multiple explicit levels.

In the direction of expressing hierarchies is the idea of the dynamical reification of a group of agents as a new agent. Servat (Servat et al., 1998; Servat, 2000) made an important contribution in this direction, which corresponds in terms of the hierarchy theory to the dynamical emergence of a new holon with agents as interacting component-holons and group of agents as compound-holon. He observed that in traditional MAS models, an external observer can observe global emergent phenomena; but this macro level is not part of the model and needs, after the simulation, some analysis to be caught. He proposed first to internalise the external observer with an automatic dynamical detection of stable emergent structures in the agent population and to give them some visibility as observable groups of agents with integrated observation variables. The second important step is to give to the emergent agent group the possibility to play a role as an actor in the dynamics of the model. This step needs the reification of the group as a new agent, which implies specifying the rules of interaction between agents, between groups and between agents and external groups, and also between a group and its agents. Showed in the hierarchy theory perspective, Servat's approach remains relatively flat in the sense that the groups are always interacting at the same explicit level of interaction than the other entities, so that agents can directly interact with external groups. Servat applied these mechanisms to a hydro-dynamical model for runoff, erosion and infiltration processes where the agents are water drops grouping into rivers and ponds. Rivers as stable flowing water paths and ponds as stagnating water zones obey to different behavioural laws and evolve according to coarser time and space scales than single water droplets. Translated into holonic concepts, water droplets represent component-holons at a low level of organization and rivers and ponds component-holons at the upper level. To link the two levels, a compound-holon represents the integration of a group of component-holons of the low level to build the component-holons of the upper level. Thus, a level of organization represents the horizontal dynamical structure of interaction between component-holons, while a compound-holon represents the vertical dynamical structure of composition of the holons. The lower level of organization can also serve to detect stable groups of water drops and to dynamically create, destroy or change the rivers and ponds composition. This clearly advocates for the ability of expressing a dynamical structure in a hierarchical system model.

Another interesting attempt in the same direction is the use of MAS to represent water flow as collection of vortex particles (Tranouez et al., 2001). Here the vortex agents having a similar vorticity can aggregate together locally to constitute a vortex of higher level, which is reified by the creation of a new vortex agent with a higher volume but the same internal rules. This process of dynamical scale change is recursive and the vortices interact both with lower level particles and other vortices, the last type of interaction leading to the creation of vortices of higher level. Here the levels are not strictly delineated and the vertical hierarchy is not explicitly represented.

3.4. *Multi-modelling and multi-formalism*

3.4.1. *Structural versus behavioural abstraction*

One important issue with the DEVS recursive model structure is to represent hierarchies in which the components in each level are partly dependent on the next lower level: it is thus impossible to simulate each level independently. To solve this problem, Lee and Fishwick (1996) distinguished between two kinds of abstraction: structural and behavioural abstraction. The structural abstraction corresponds to the decomposition of the system in subsystems or components and is equivalent to multi-modelling. Behavioural abstraction is the replacement of a component with its specific internal structure by a more generic component which produces a similar behaviour. This kind of decomposition is more vertically structured and is not well suited to easily represent horizontal interactions with dynamical structure of interaction between components at each level.

3.4.2. *Coupling system dynamics and discrete event formalisms*

Zeigler et al. (2000) have formally developed a similar approach, which they called multi-formalism, for the case of discrete event simulation. They defined different specification formalisms: DTSS for discrete time specified systems, DESS for differential equation specified systems and DEVS. Furthermore, DEVS can used as a relatively universal formalism, by either mapping other existing formalisms in an equivalent DEVS model or wrapping other formalisms by a DEVS interface for input and output. The use of coupled DEVS models enables the coupling of different kinds of formalisms.

For example to simulate on digital computers systems of differential equations, for which the traditional methods are based on the discretization of time, one may discretize the phase space by the definition of thresholds, obtaining so a transformation of the ODE system into a quantized-state system, which can be exactly represented in a DEVS model (Kofman and Junco, 2001; Kofman et al., 2001).

GDEVS (Giambiasi et al., 2000) is a generalisation of DEVS and an interesting way to hybrid continuous time dynamics with discrete event systems. Basically, a DEVS relies always on piecewise constant functions. GDEVS generalizes the input and output functions to piecewise polynomial functions of a given fixed order.

It is also possible to combine some advantages of CA and ODE by coupling or integrating them together. This solution is implemented in the Spatial Modeling Environment (Costanza and Voinov, 2004), a generic tool to build spatially explicit models of populations, ecosystems and landscapes. The landscape at any point in time is described using a raster (cell based) representation. In each cell, a same compartment model describes the local internal dynamics by a system of difference equations. The neighbouring cells can then be connected by horizontal fluxes of material and information. Such models allow simulating dynamics at two spatial scales (cell and landscape), or even more if a modular structure is used within the cell unit model, the lower scale being in this case only implicit (functional disaggregation). The spatial disaggregation of a compartment model is also implemented in the Simile visual modelling environment (Muetzelfeldt and Massheder, 2003), using a declarative representation of model structure. An original feature of this approach is the conditional existence of some part of the model and a high flexibility in the specification of submodels, allowing a hierarchical model structure and the combination of various formalisms, including individual-based models.

3.4.3. *Coupling agent-based and system dynamics formalisms*

More specifically oriented toward modelling of an ecological system with multiple scales, Duboz (Duboz et al., 2003; Duboz,

2004) gave an important contribution to the combination of different formalisms. He argued that the micro- and macro-levels are better modelled with different formalisms, and thus he coupled the formalism suited for the macro-level (ODE) with a MAS for the micro-level in the concrete case of a marine ecosystem with copepod as predator and phytoplankton as prey. A reactive agent model (MAS) was used to model the impact of the heterogeneity of the distribution of individual prey particles on the dynamics at the population level expressed by a predator-prey model (ODE system of Holling–Tanner). The strong coupling was achieved by cycles of bottom-up emergent computation and top-down parameterization. Such coupling is an operational way to do a scale transfer (Fig. 3): (i) in the bottom-up direction, at each integration step of the ODE, the averaged ingestion rate parameter is replaced by an instantaneous value calculated by the MAS; (ii) in the top-down direction, the population state variables calculated by the ODE at every time step of the upper level serve as initialisation parameters for the MAS. At the MAS level, no continuity was assumed between two adjacent cycles, because the role of each MAS simulation on the ODE was to give an instantaneous ingestion rate of the copepods which is density and heterogeneity dependent. The two coupled models operate at two different time scales. Also important is the fact that the upper macro-model is deterministic and continuous whereas the lower micro-model is stochastic and discrete. To have more stability against the stochastic nature of the micro-model the MAS simulation was replicated with the same initialisation parameters but different initial conditions, to get an averaged computational trace of the simulations.

Recent developments of simulation tools such as AnyLogic™ (Borshchev and Filippov, 2004), VLE (Quesnel et al., 2005) or Mimosa (Müller, 2004; Müller et al., 2005) make it possible weak or strong coupling of several modelling approaches.

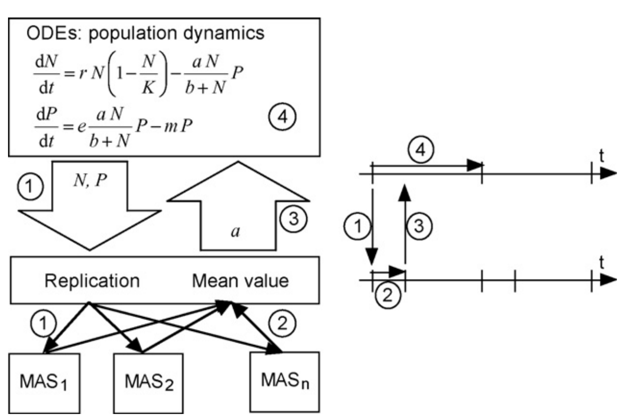

Fig. 3 – Example of ODE and MAS strong coupling (after Duboz et al., 2003 and Duboz, 2004). *N*: density of the prey population; *P*: density of the predator population; *K*: carrying capacity of the prey population; *r*: intrinsic net growth rate of the prey; *a*: maximum ingestion rate of the predators; *b*: half-saturation constant of the functional response of the predators; *e*: transformation coefficient of prey to predator; *m*: predator death rate. (1) MAS initialised with fixed values for N and P from the ODE; (2) MAS simulations; (3) transmission of the average value of the *a* parameter; (4) ODE simulation for one integration step.

4. Conclusion and perspectives

Although they bring some ad hoc propositions for combining two levels or several heterogeneous formalisms, none of the above mentioned approaches can tackle the problem of modelling all aspects of the dynamics of hierarchical systems as described by the hierarchy theory. In particular, the evolutionary, developmental aspect of hierarchical organization (Holling, 1994; Salthe, 2005) has been poorly investigated in ecological models. Too often, the emergence of hierarchies is described as a bottom-up process, in which the integration of components is considered the major determinant (e.g., Kolasa, 2005).

In ecology, low-level fast processes are better understood than high-level slow processes, (i) because observations and experiments are mainly carried out at fine grain and small extent in space and time, and (ii) because the most familiar and established theories rely on population biology. This explains the recent trend to develop detailed, process-based, micro-models, and to infer from them aggregated, phenomenological macro-models for landscapes simulations, by means of various ad-hoc upscaling techniques and modelling formalisms (review in Urban, 2005). This meta-modelling approach has proved to be tactically efficient, but it is strategically questionable: it does not explain how and why hierarchical levels emerge and interact in ecological systems, by ignoring the triadic causality emphasized by the hierarchy theory. Such considerations could however be critical in the future development of systems ecology to cope with issues and problems associated with human-environment interactions (Müller and Li, 2004).

The way out seems to start from generalized DEVS taking advantage of its already proposed extensions to represent multiple formalisms and dynamical structures, and to extend it towards multi-agent systems and explicit representation of holons. To represent and simulate adaptive evolution of complex systems, the concept of holon, which is central to hierarchy theory, has been successfully used in holon network models (Honma et al., 1998) and in holonic MAS models (e.g., Rodriguez et al., 2006), but these approaches seem to have passed unnoticed in ecology so far.

From our critical review of the existing formalisms used in dynamical modelling, we have emphasized the notion of constructive dynamical system. We have also pointed out the interest of articulating different formalisms, in particular with discrete and continuous dynamics and with different time representations. This last articulation will be possible in the context of an ontology of time for modelling and simulation of dynamical systems we have proposed in another paper (Müller and Ratzé, 2004).

The next step is to represent the revisited key concepts of the hierarchy theory in a modelling and simulation framework, leading to the construction of an architecture of specifiable formal machines based on both the MAS approach and the generalized DEVS formalism. For each key concept of the hierarchy theory, we will design a specific kind of machine with a particular role in the architecture: a component-holon will be represented by an entity-machine, a compound-holon by a group-machine, and a level of organization by a level-machine. Each machine will be structured as an automaton with a particular explicit time management.

The critical points of such a conceptualization of the hierarchy theory are: (i) the explicit expression of the concept of level of organization, with a formal distinction between the level of abstraction for the structural part and the level of detail for the functional part; (ii) the articulation between the level of organization and the scale domain; (iii) the representation of the holon as two linked faces: the holon as a component and the holon as a compound, which allows more flexibility in the expression of the structural dynamics and the articulation of the levels of detail; (iv) a categorization of the possible bottom-up and top-down articulations within a holon.

The main challenges will be: (i) to represent functional dynamics of states, such that we can manipulate different time representations, hybrid continuous and discrete dynamics and different articulated degrees of detail; (ii) to manage the simulation with a coherent time advance following the principle of causality and such that we can construct step by step in a distributed manner the different state trajectories.

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