

## The concepts of emergent and collective properties in individual-based models—Summary and outlook of the Bornhöved case studies

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### Abstract

Ecology requires the conceptual and technical ability to analyse complex and dynamic systems consisting of a high and variable number of components and relations. These components are part of a variable interaction structure in a spatially heterogeneous context. The components of ecological interaction networks can give rise to self-organised, and scale-dependent interaction patterns and processes, which are the underlying causes of the overall ecological systems states.

The individual-based modelling approach provides a widely applicable simulation framework based on a ‘hierarchy theory’ view of ecological systems.

Here, we summarise and generalise the theoretical implications of the modelling studies presented in this volume in the field of terrestrial and aquatic, animal and plant ecology. The case studies cover a representative profile of processes related to ecological applications, such as food web interactions, population dynamics, dispersal, energy physiology, nutrient allocation and mutual impact of morphological and physiological development. The generic approach applied in this context allows a hierarchical representation of ecological systems and their components. Model results are obtained as self-organised structural relation networks and as aggregated quantitative states. In order to address different model characteristics we distinguish *collective* and *emergent* properties. Collective properties are those that are attributed equally to different organisation levels of the system. Emergent properties result from the activities of lower level entities on a higher organisation level, while not being present on

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the lower level. They can be subdivided into *aggregational* and *connective* properties. Emergent properties that are aggregational are those which emerge as a result of an aggregation procedure by an observer on the higher level which does not make sense or is not applicable on lower levels. Emergent properties that are connective, however, are based on an interaction network of lower level entities, which brings about the specific system characteristic.

This classification of model results will allow to generalise the achievements and potential of the individual-based modelling approach in ecology.

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## 1. Introduction

Ecological systems are known for the diversity of their complex interrelationships. For structurally diverse and complex systems, it is of crucial importance to adopt the appropriate approach to account for the specific grain and extent of the focused phenomena (Turner and Gardner, 1990; Allen and Hoekstra, 1991). In particular, the conflict between the necessity of abstraction and the menace of neglecting essential details must be dealt with.

Due to the high number of interactions and feedback processes in ecological situations, the extent to which the different mechanisms contribute to particular results often remain unclear. Frequently, there are measurement limitations. Only parts of the entire system are accessible to direct quantification. There are many examples of closely intertwined causal networks, which lead to controversial discussions and often remain unsettled for a long time. A prominent example is the role of driving factors leading to oscillating rodent populations in Northern Scandinavia. This issue has been discussed fiercely for decades (e.g. Elton, 1942; Rosenzweig and Abramsky, 1980; Stenseth, 1999). Comparably complex to deal with are biological invasions, as the invading species sometimes succeed in colonising and dominating a habitat after a long phase of apparently no change with respect to community dynamics or environmental factors (Mack, 1996; Sakai et al., 2001). The relationship between biodiversity and stability (e.g. Lehman and Tilman, 2000; Ives and Hughes, 2002) or ecosystem function (e.g. Mikola and Setälä, 1998; Loreau, 2000; Duffy, 2002) as a currently discussed question, presumably will have no general answer but depends on the specific ecosystem processes

under investigation or even on the current state of the investigated system or on the scale on which processes are observed (Jonsson et al., 2000).

These questions, which are all related to the analysis of causal networks of ecological systems, illustrate the need for methodological repertoires, which are applicable across different organisation levels and system types. This repertoire must allow the investigation of the effects of single inductive processes or entities on the whole system as well as the other way in form of a top-down view analysing the impact of system dynamics and properties onto the subsystems and low level processes as forcing functions or boundary conditions. The widely applied equation-based modelling approach using homogeneous differential equations, descending from classical mechanics (e.g. von Bertalanffy, 1968; Forrester, 1968), is of limited value for representing properties of ecological systems with spatial heterogeneities, with processes including interactions operating across different organisation levels and with the changing composition of components and their interaction structure. Both the theoretical achievements in ecology and the progress in computer science allow a different approach to overcome these limitations (Huston et al., 1988; Levin et al., 1997).

In this paper we will present a generally applicable modelling framework using the individual-based approach, which allows the study of ecological dynamics over several levels of integration. It is based on a hierarchical representation of system structure defined on lower levels, with the properties of higher levels emerging as the result of self-organising processes. The approach allows the investigation of complex interacting causal networks and the analysis of the driving forces responsible for higher level dynamics. Our

generic approach was derived from investigations executed in the context of the Ecosystem Research Project Bornhöved Lakes District (Fränzle, 1998; Fränzle et al., *in press*; Breckling et al., 2005) integrating a wide range of different ecological processes. These Studies using the individual-based modelling approach will be summarised briefly with respect to their basic features and the resulting emergent properties after recalling a few facts on ecological complexity and self-organisation. The central position of the individual organism in this context will be highlighted. The classification of different categories of emerging properties resulting from our simulations constitutes the basis for generalising the potentials of individual-based modelling in analysing ecological processes.

## 2. Theoretical framework: complexity and self-organisation processes

Before exemplifying the ecological interactions depicted in the model systems, we have to state the theoretical concepts on which they are based. The conception has decisive implications for the representation of system properties in conceptual and simulation models and their interpretation, as well as for any extrapolation of the dynamic properties. One of the basic problems in adequately modelling ecological systems is their complexity, which is a result of:

- The high number and variability of components, their context-specific interactions and their diverse structural and functional properties. Identifying functional groups constitutes an approach for reducing complexity, but often species operate on different spatial and temporal scales, which contradicts a full redundancy (Peterson et al., 1998).
- Spatial processes, which have long been neglected in theoretical ecology, as they are regarded as ‘a source of heterogeneity and a source of random deviations away from the well-mixed paradigm’ (O’Neill, 2000).
- Indirect effects, context-sensitive actions or events, non-transitive interrelationships and non-linear dynamics (Werner and Peacor, 2003).
- Rare events and disturbances, which fundamentally change or rearrange the relationship network (Kauffman, 1995).

- Level crossing interactions and feedback-loops (de Roos et al., 2003).

Ecosystem states are the result of specific processes formed by the involved entities. These have to be considered when developing models for analytical purposes that represent more than a mere description of abstract dynamical variables in a specific situation. In this context, ecological models need to consider to what extent details can be ignored without producing results that contradict specific sets of observation, on a particular scale of interest (Levin, 1992). In such an analysis, scales and frequency distributions may emerge, which are essential for understanding how the dynamics of natural systems and the nature of system dynamics relate (Hölker and Breckling, 2002).

In ecology, complex processes result from a wide range of simple and complicated interactions. Simple dynamics may well result from complex networks. Generally, viewing ecosystems as complex systems, describes them as dynamic, constantly evolving systems, which are, from an analytical viewpoint, describable and even to some extent predictable (depending on the level of abstraction). Changes in such systems can be smooth or just as likely, sudden and surprising. Finally, studying complexity means studying rules governing emergence, the constraints affecting self-organisation and general system dynamics in non-linear adaptive interacting systems.

### 2.1. Self-organisation and emergent properties

In the second half of the 20th century a crucial paradigm shift in biological theory (Kratky, 1990) included the perception of ecological systems as being self-organised. This awareness goes along with the insight that the emergence of structure and form, as well as behaviour and dynamical processes of biological entities, are the result of a self-generated circular order of events and not necessarily the result of a structuring external instance. For a detailed definition of the concept of self-organisation and for its ecological relevance (see Müller et al., 1997a; Müller and Nielsen, 2000).

With respect to the model-based representation and analysis of ecological systems, the development of artificial life concepts (Langton, 1988), as well as the theory of the dynamics of complex systems, e.g. the

self-organised criticality (Bak, 1994), the edge of chaos (Kauffman, 1995), and the theory of complex adaptive systems (Gell-Mann, 1994) are conceptual landmarks. The concept of autonomously acting agents in informatics (Laing, 1988; Meyer and Wilson, 1991) and individual-based models (IBMs) (Kaiser, 1979; Hogeweg and Hesper, 1979; Hogeweg, 1980) in ecology illustrate a remarkable parallel development mutually influencing each other. For modelling purposes, aspects of hierarchy and stability are of major importance. As self-organised systems are regulated and coordinated by processes on different spatio-temporal scales with a functional and structural hierarchy of constraints (Allen and Starr, 1982; O'Neill et al., 1996; Hölker and Breckling, 2002), a representation or investigation of one single organisational level will lead to the neglect of crucial causal links. Self-regulation processes can cause persistence and the ability to buffer disturbances below a critical threshold if system dynamics are near the steady state. Larger or repeated disturbances may exceed the buffer capacity. These features of self-organised systems may be used in the modelling context to obtain modelled systems that represent stable dynamics, enabling us to analyse critical situations and conditions.

A corresponding aspect of the self-organisation potential of ecological systems, which focuses on the formation of higher level attributes, are emergent properties. Generally, self-organisation arises as an emergent property. The appearance of cross-level effects and emergent properties is reflected in a vertical hierarchical segmentation of biological systems at different organisation levels due to their spatio-temporal scale. Each level has its specific properties, resulting from interactions of the sub-systems.

Emergent properties are understood as new qualities that appear on higher integration levels and represent more than the sum of the low-level components. They can be explained by introducing component interactions and not solely on the basis of the properties and relationships of the elements (Kueppers and Krohn, 1992, p. 7). As a new dimension of characterisation, emergence provides the potential for investigating causal links across more than one hierarchical level (Breckling and Reuter, 2003) and allows investigation of specific functional characteristics in constitutive nested hierarchies (Mayr, 1982; Hölker and Breckling, 2002).

The important thing about life is that the *local dynamics of a set of interacting entities (e.g. molecules, cells, etc.) support an emergent set of global dynamical structures which stabilize themselves by setting the boundary conditions within which the local dynamics operates*. That is, these global structures can 'reach down' to their own physical bases of support and fine-tune them in the furtherance of their own, global ends. Such local to global back to local, inter-level feedback loops are essential to life, and are the key to understanding its origin, evolution, and diversity (Taylor, 1991).

The theory of emergence is based on the assumption of a hierarchical structure of the natural world and implies that emergent qualities on a higher level of existence require the emergence of new variables describing them. The basic question of functional relationships of the higher level variables with those of the lower levels leads to a fundamental dilemma. If there is no relationship, the new variables are simply epiphenomena; if there is, however, they have to be included into the whole set of variables described by the lower level functional interrelations. Thus, there is either no novelty or it is epiphenomenal.

Following Primas (1977, 1981), the conventional discussion of emergentism and reductionism has been lacking in epistemological clarity, i.e. it has been frequently characterised by a too simply view of the structure of scientific theories. The overwhelming majority of philosophical studies on reductionism and emergentism are based on the concepts of classical physics which notably fails as a foundation of molecular biology, and hence of biology or ecology. In the framework of quantum theory, however, reductionism is in harmony with emergentism and the occurrence of essential novelty is a compelling consequence of the theory.

This kind of emergence results from the existence of incompatible quantities in quantum theory which stresses that microphysical systems have *potential* properties which cannot be revealed simultaneously. Such properties are considered complementary if their actualisations are mutually exclusive and, as such, connected with the impossibility of simultaneous sharp measurements of, e.g. position and momentum. Potential properties that are actualised in each state of the system are *essential* properties and are described by classical observables, i.e. observables commuting with

all others. While in classical physics, where all observables commute, all potential properties *are* essential, and all quantities may (in principle at least) be made subject to sharp simultaneous measurements, it is characteristic for quantum theory that potential properties *can become* actual, which is then a (really) emergent novelty.

Emergence can be viewed both non-temporally as properties of a system not possessed by any of its parts, and in the sense of temporal processes, i.e. the creation of novelty in time or evolutionary emergence. For a mathematical model of the latter one has to specify a system with its properties and its dynamics and to investigate how the essential properties behave in time. In an elegant analysis on the basis of quantum mechanics, Müller-Herold (1984) has pointed out the difference between evolutionary emergent novelty and (mere) evolutionary refinement as associated with ‘dissipative structures’ sensu (Prigogine, 1976). Dissipative structures can be discussed phenomenologically in a purely classical set up, i.e. they do not generate real novelty and must consequently be clearly distinguished from evolutionary emergence. The time-honoured Belousov–Zhabotinsky reaction may serve as an example. It is a dissipative stochastic process associated with a combination of Brownian motion and a set of chemical reactions. When the famous spirals appear in the formerly homogeneous solute system the surface attains a *richer structure*. But the property of *having a shape* remains unchanged. It is only a change of *this type* that would constitute emergent novelty.

## 2.2. Basic entities in ecology

From the above considerations the question arises, how basic levels, which are necessary to model hierarchical ecosystems can be identified. The desired basic level should play a central role in the focused ecological context. In a wide range of ecological questions this applies to the individual organism as a basic level.

Despite the ongoing debate in biological sciences on the concept of the organism (Gutmann and Neumann-Held, 2000; Ruiz-Mirazo et al., 2000) the organisation level of the organisms has to be assigned a keystone importance in ecology. The organism level is not only referred to in most hierarchical systems, but also intersects with ecosystems as well as genetics (Ruiz-Mirazo et al., 2000). The relevance of the organismic level is

based on the fact that organisms are the primary operators of ecological interaction and thus the causal factor for many processes and their resulting dynamics. Evolutionary processes act on individuals and much ecological insight is gained by finding the relevant differences between individuals that lead to differential survival and differential contributions to future generations.

From all ecological units the individual organism possesses the most explicit physical separation from the environment. Due to its morphological manifestation an individual is characterised by a visible and tangible boundary. The single organism represents a coordinating entity that integrates all internal processes into a coherent behavioural and physiological reaction to the environment. The status of (multicellular) organisms in the ecological context is determined by:

- the integration of functionally differentiated delimitable units on the organ and cellular levels including physiological and biochemical processes,
- interaction as a functional unit with the environment,
- the ability to reproduce (unit of reproduction) and
- being the entity of evolutionary processes. It is evaluated for viability, degree of adaptation and fecundity through interaction with its environment (Ruiz-Mirazo et al., 2000).

For modelling purposes, it is important to distinguish between modular and unitary organisms, as some questions cannot be entirely satisfactorily investigated using the individual as the basic unit. This is especially true if specific organismic properties are of explanatory relevance. Basic units are consequently the basic functional entities. This may be single plants or animal organs (modular) or single individuals (unitary). Both types have different developmental and growth forms, distinct life cycles and reaction possibilities to environmental stimuli. The unitary form predominates the zoological sphere with only a few exceptions such as Cnidaria, Bryozoa and Sponges. During ontogenesis the basic form results in a determined process of tissue differentiation leading to the adult form. In the following increase in size, shape and structure basically remain the same after a specific developmental stage. In contrast, modular organisms (mostly plants) grow in a self-repetitive process. Initiated in special tissues (meristems) new specialised modules are gener-



ated during the entire life cycle. This form of growth allows an adaptation to environmental influences involving pronounced modifications of the whole morphological structure (e.g. oversized shoot length in plants deprived of light) and often results in self-similar shapes. The final size and phenotype is not (fully) predetermined.

To model the above specified characteristics may be fulfilled to a wide extent by using the object-oriented programming (OOP) approach as it is applied in most individual-based models (Sequeira et al., 1997; Breckling, 2002). From our experience individual-based models using the OOP approach offer a wide set of possibilities covering the most important ecosystem structures, processes and interaction types (Breckling et al., 2005).

### 3. Emergent properties in model examples from Ecosystems Research in the Bornhöved Lakes District

The model examples from which we derived this general framework on emergence in individual-based models have been developed during the Ecosystem Research Project Bornhöved Lakes District (Fränze, 1998, 2000; Fränze et al., in press; Breckling et al., 2005).

In this project modelling had an important function to link and integrate different spatial and temporal aspects, to develop and test hypotheses and to generalise and extrapolate results. Applications included models on different organisation levels and processes, e.g. fluxes of nutrients, water budgets, climate models and models representing biocoenotic processes (Reiche et al., 2001).

The biocoenotical processes have been mainly analysed using the individual-based modelling approach. These cover a large variety of representative ecological processes like space utilisation, dispersal, energetics, food web interaction, development of morphology and its interaction with physiological processes in plants as well as allocation of nutrients.

A common feature of these models is the representation of level crossing-interactions leading to emergent properties on higher integration levels. This property proved to be essential not only for the representation of central ecological characteristics of the system but

also for analysing networks of causality and for the adaptability of the respective modelling systems and the extrapolation of results (Reuter, 2001).

These models have been presented in detail in the preceding articles of this volume (Jopp and Reuter, 2005; Reuter, 2005; Hölker and Breckling, 2005; Middelhoff and Breckling, 2005; Eschenbach, 2005). Table 1 lists the model topics and the knowledge gaps they intended to close. The quoted 'emerging properties' give an overview of the higher level results which may be achieved by solely using the listed model components and their defined interaction structure.

### 4. A framework to represent emergence in models

An operational specification of emergence and its application in modelling is useful in order to apply new possibilities for analysing ecological interaction structures and dynamics. We intend to set up a framework for emergence to integrate the common features and functionality in the combination of different levels and interactions types in Fig. 1. The figure gives an overview on the ecologically relevant organisation levels, the abiotic influences and the basic processes we used in the individual-based models presented in this volume.

The figure illustrates the nested hierarchy with the *basic functions* as the lowest considered level. These functions constitute the processes directly defined in the model as properties of individuals, plant modules or local environmental sites. They comprise the representation of behavioural and physiological processes such as for example resource capture and use, transport kinetics, reproduction, aging, movement, interaction rules, energy physiology and remineralisation.

Despite the fact that the modules and the individuals constitute the definition level of individual-based models and represent the interacting units, their properties, as well as any property on the higher levels, result from processes that are specified on lower levels. The root:shoot ratio in the plant model (Eschenbach, 2005; Middelhoff and Breckling, 2005) provides a typical example. Root:shoot plasticity is important for plants to adapt to external variation of nutrient and light availability in different habitats and provides a framework for the particular activities of organs. New modules

Table 1

Model overview: topics, basic components knowledge gaps, interaction structure and resulting emergent properties

Type of ecological process	Represented organisms	Knowledge gaps	Model components and structure	Emerging properties
Dispersal and spatial distribution (Jopp and Reuter, 2005)	Carabid beetles: <i>Abax parallelepipedus</i> , <i>Carabus hortensis</i> , <i>C. coriaceus</i>	Dispersal characteristics depending on landscape structure and heterogeneity	Individual arthropods with life cycle and movement algorithm, environment as grid map and with climate data	Dispersal potential, spatial distribution, population size
Energetic gains and activity costs associated with different spatial behaviours and environmental conditions (Hölker and Breckling, 2005)	Fish populations in a lake ( <i>Rutilus rutilus</i> )	Consequences of a trophic bottleneck, relationship between population structure and habitat morphology, size-dependent mortality	Individual fish with movement algorithm, environment as grid map with climate data and food resources, bioenergetic compartments with specific functions to simulate the flow and storage of energy	Spatial behaviour, growth, and food consumption on the individual level, self-sorting of age groups in shoals, consequences of a trophic bottleneck, winter mortality and post-reproductive mortality on the population level
Population dynamics and oscillations (Reuter, 2005)	Small mammal communities (rodents and predators: <i>Clethrionomys</i> , <i>Microtus</i> , <i>Mustela nivalis</i> , <i>Asio otus</i> )	Causal relationships and driving forces for community dynamics of small mammals	Food web interaction, rodents and predators as individual organisms with reproduction, food uptake, movement, rodent food equation-based for small scale landscape elements	Individual life history, population structure and dynamics, community interaction structure, trophic control, spatial distribution of individuals
Tree root system development and plasticity including whole tree and tree stand development (Middelhoff and Breckling, 2005)	Alder trees ( <i>Alnus glutinosa</i> )	Fine root dynamics as a result of above- and below ground processes, uptake and allocation of nutrients and assimilates	Hexagonal grid of soil compartments, coarse and fine root modules, aggregated above ground compartments, process specification for nutrient uptake, nutrient and assimilate transport	Spatial extension and plasticity of root growth, root-shoot ratio, competition and co-existence of neighbouring trees, self-thinning, spatial distribution, nutrient cycle, nutrient storage
Tree growth as affected by physiological and structural traits (single and interaction in tree stands (above ground)) (Eschenbach, 2005)	Alder trees ( <i>Alnus glutinosa</i> )	Allocation of matter in the entire plant (e.g. from the organs of uptake to those of consumption or storage)	Single plant's organs (leaves, internodes, meristems, roots, root tips) with algorithms for uptake, transport, consumption, storage, mobilisation of assimilates (carbon, nutrients). Environment (air and soil segments) as voxels and with climate data	Acclimatisation of the photosynthetic apparatus, tree architecture, exploitation of space, foliage distribution within the crown, lifetime spectrum of organs, and development of sun and shade leaves in the respective crown segments

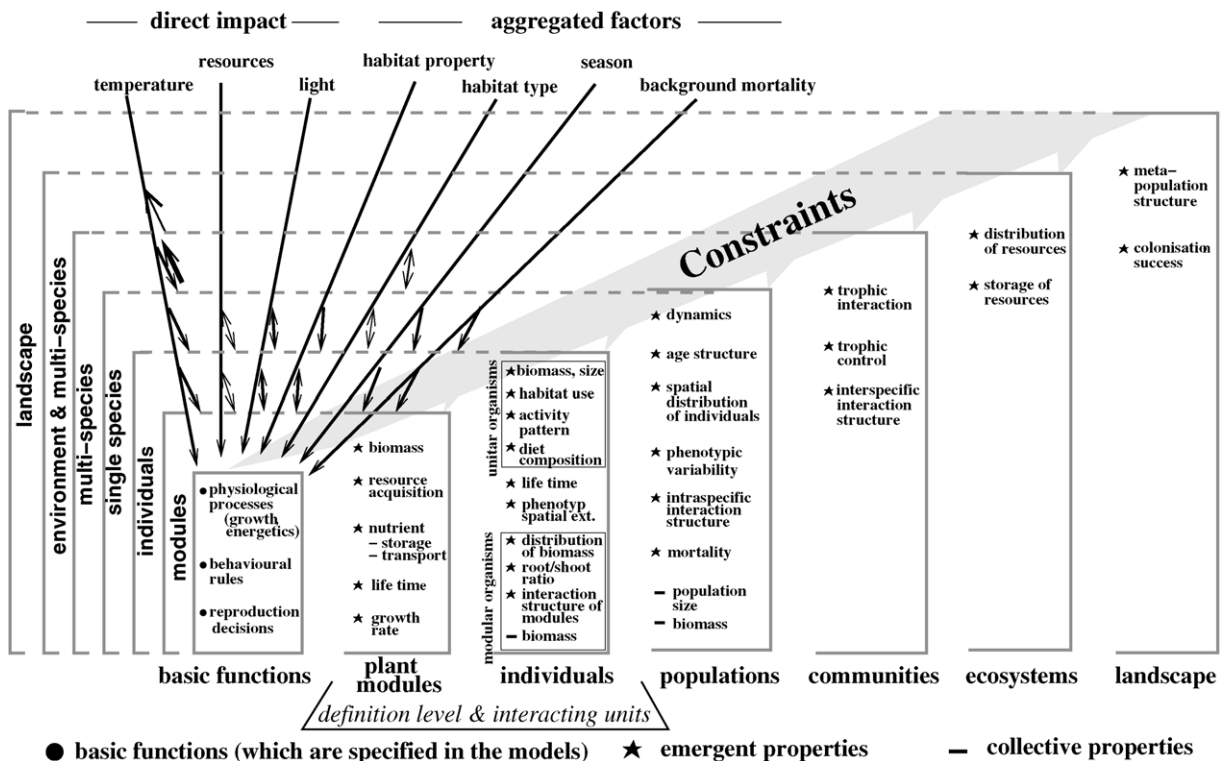


Fig. 1. Level dependent properties in individual-based models. On each organisational level different properties arise. A higher proportion of emergent properties dominates higher levels. External factors in form of constraints set the boundary conditions of possible system states.

(objects, e.g. of the type internodium, root, root-top, leaf) are instantiated depending on the environmental situation and internal condition or are eliminated if necessary. This ensures an appropriate morphological and physiological reaction to essential stimuli. Higher level properties emerge as a result of the interaction of lower level components. Any changes in their properties are not defined on this level in the model. The example of a population also illustrates this successive emergence of properties.

In our models populations basically are an assemblage of individuals (objects in OOP-terminology) of the same type. To obtain the population properties and their dynamics it is necessary to aggregate the properties and changes for each individual. Extrapolation does not use abstract entities but refers to lower levels, e.g. the population number in time by aggregating individuals or their states.

Apart from properties constituting their way upward in the hierarchy, downward directed influences equally exist and give rise to bidirectional driving forces and

level-crossing feedback processes. In Fig. 1 these are indicated by the long grey arrow across all levels. For instance, the reproduction rate in the rodent model depends strongly on the local population density. Similarly in the tree root model, the distribution of nutrients, a property of the ecosystem level, has decisive influence on the growth of the roots and thus on their spatial density.

To complete the overview of the modelling framework we included abiotic influences that normally impact lower levels. Any kind of driving force may be added to these external influences, provided they work uni-directionally (as an external impact).

In order to assess the resulting attributes of the implemented and analysed integration levels we find it essential to classify their properties. It has to be considered to what extent processes should be represented in a model and which properties or levels have to be included to simulate dynamics as a representation of specific causal networks. This helps in interpreting the quality of resulting model properties and to analyse



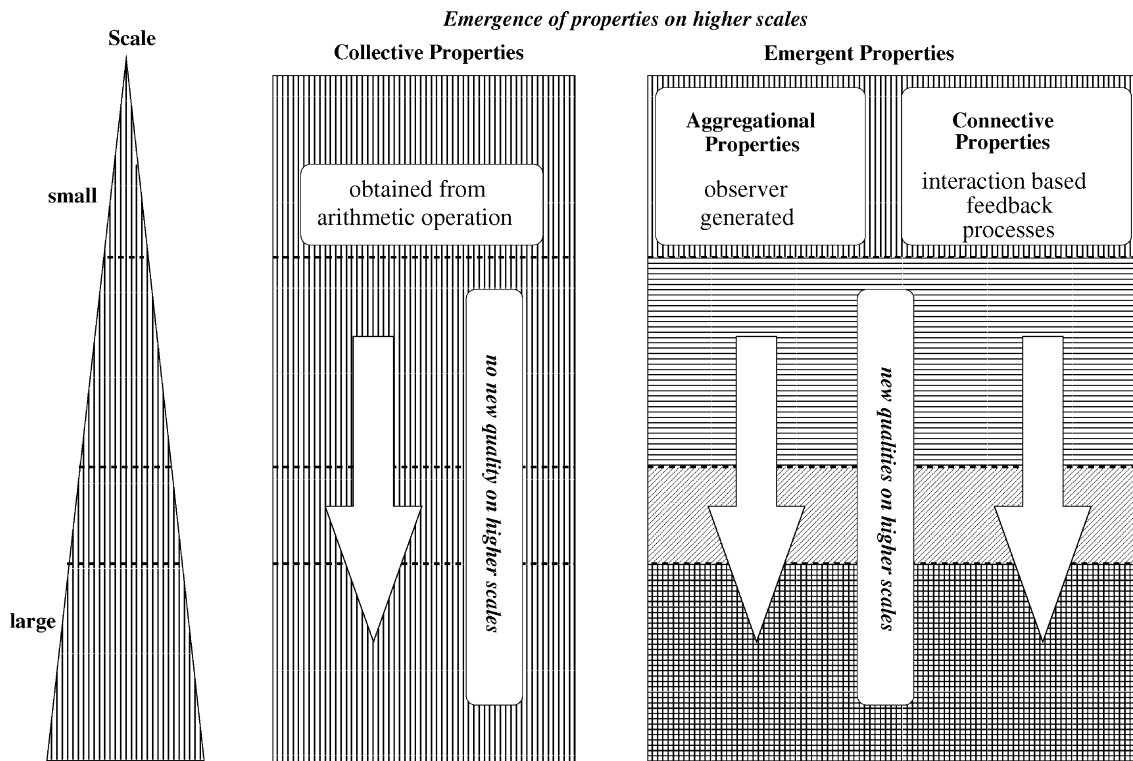


Fig. 2. Categories of properties on higher integrations levels. The main distinction is made between emergent and collective properties. The latter sum up lower level properties on a higher level arithmetically without a change in qualities. Emergent properties are subdivided into the interaction-mediated connective properties and those properties which are specified as a result of an observer's activity (aggregational properties).

the implications for model transfer and adaptation. Müller et al. (1997b) emphasise a classification into collective and emergent properties. In evaluating the self-organising level-specific results of our models we propose a further refinement of categorisation. The additional classification that we propose is based on the processes that are involved in generating a specific property (Fig. 2). Thus, we suggest the following categories:

- *Collective properties* are properties on higher levels, which can be defined as common to lower level entities equally. They result from a simple arithmetic operation regarding lower level entities. No new quality on higher levels is involved, they are only extended quantitatively. For example the total weight of a population is the sum of the biomasses of all individuals and has no new or additional feature.
- *Emergent properties* include all properties, that cannot be linearly reduced to properties on lower levels

or are newly defined on a particular level. As this comprises a wide range of properties, a further division is suggested to denote the different implications for model analyses and the definition of model components and structure.

- *Aggregational properties* can be specified from the perspective of the observer. They primarily denote statistical properties—spatial distributions for instance, or the spatial structure of a population, which are new on the respective level because by definition they cannot exist on the constituent lower level. As their statistical nature implies, these properties result from analytical procedures. Newer considerations evaluating more models lead to the above definition thus extending a former definition (Reuter and Breckling, 1999). We regard it as fundamental to stress the fact that they do not necessarily result from interactions of lower level entities or non-linear feedback processes.

Many model results may be categorised here. The spatial distribution of individuals resulting in the arthropod model (Jopp and Reuter, 2005) is an example for this kind of property as the interaction between individual carabids is limited to a small number of occasions and mainly bases on interactions between the individual and its local environment.

- *Connective properties* are based on the interactions of organisms or their independently modelled components. In the context of our models we denote these properties as features, which exhibit a qualitatively new component on a higher hierarchical level, which cannot be linearly reduced to lower level characteristics of the same quality. These properties necessarily depend on interactions and feedback processes between the represented organisms and between these organisms and their environment. In the rodent community model (Reuter, 2005) the trophic control, which is a genuine attribute of the community, belongs to this category, as it results from complex non-linear interaction across all elements of the represented food web. In the modular plant models growth results from the interaction of plant organs and their environment (Eschenbach, 2005; Middelhoff and Breckling, 2005). Space exploitation is an illustrative example of a connective property in the alder models.

We are aware that sharp borders may not always separate these categories. To some extent they depend on the level of abstraction as well as on the focal level. Despite this fact, the categories have proven to be useful in analysing the driving factors leading to the model results and relating them to real-world findings. We emphasise the possibility of accomplishing this distinction as one of the main analytic potentials provided by the individual-based modelling approach.

## 5. The concept of emergence extends the power of ecological models

The model examples from the ecosystem research project Bornhöved Lakes District illustrate a representative cross-section of the wide application range of individual-based models. Above all they offer many

important possibilities of representing ecological processes and permit a causal analysis of complex interaction networks. The hierarchical set up of the models, which refer to the number of components and their interaction structure, and the emergence of the dynamics of key processes results in a high flexibility in depicting complex ecological processes. The following features can be derived from these models:

- *Plausibility check on several levels:* For individual-based models up to now no generally applicable formal validation method exists. Model validation has to be performed in accordance with model purposes and derived criteria (Mayer and Butler, 1993; Rykiel, 1996). In individual-based models it is possible and necessary to perform plausibility validations on different levels of organisation. Besides, the validation of results – the properties of higher levels – the validation of each single process, module and intermediate level and its accordance with theoretical knowledge on dynamics and expectations is possible. In IBMs validation of all parameter combinations is usually not possible, as the high number of combinations by far exceeds available computing power. By validating each subunit and by a level-dependent validation of aggregational and connective characteristics it is possible to ensure a high degree of reliability that the model representation has been successful and process dynamics closely conform to real world situations. For example, the bioenergetics part of the fish model in Hölker and Breckling (2005) was validated by comparison of the simulated and observed growth under in vivo conditions (aquarium feeding experiments) before the model was adapted to the in situ conditions. With respect to validation this concept can be used to ensure consistency of model structure and results. It follows more the methodology of risk analysis applied to complex technical systems (Breckling and Müller, 2002), which can be evaluated with respect to the parts but not applied to the whole for reasons of practicability.
- *Shift in driving forces:* In our models we state a shift from the mainly parameter-dependent configurations that prevail in equation-based models, to an increasing importance of variable structural elements. The depicted qualitative system structure, the model components and their potential for inter-

active processes dominate the results and decrease the decisive role of parameters to a large extent. As a result we obtain a reduced parameter sensitivity. As parameters in individual-based models usually have a direct biological meaning and do not consist of abstract quantities (Breckling and Reuter, 1996), their variation range is per se restricted. For many IBMs it can be stated that within this range, model behaviour is widely stable with respect to the system representation. Within the context of their rules and structures individual-based models conform to a large extent to self-organising systems. For IBMs one of the main properties results in stable ranges in their non-linear feedback components. Overall changes in system behaviour can thus be traced back to transitions in the respective subsystems. Phase transitions in individual-based models usually relate to either characteristic system behaviour or result from an inappropriate specification of the system structure or the interaction of components. Rule-based models of the discussed type thus do not neglect quantities, but allow the tracking of changes in their dynamics across several organisational levels.

- *Adaptability and transferability of model systems:* The generalisation of model results has to be considered from at least two different viewpoints. For the specific situation for which a model has been developed, IBMs have the potential to be valid for an extended range of applications. As the precise distinction between the representation of the organismic dynamics and the external influences is explicitly implemented (see Fig. 1), modifications of the external conditions are possible without necessarily affecting the definition of internal organismic processes. This allows the adaptation to a changing environmental situation and the transfer of the model to other situations by adapting or exchanging parts of the environmental modules or processes. This discrimination extends extrapolation possibilities as long as it can be ensured that no changes in the reactions of the implemented basic functions have to be considered. The direct transferability of specific models to other biocoenotical components is in most cases only possible after programme adaptation. But through the modular construction of IBMs according to the paradigm of object-oriented programming and the representation of generic processes with a wide validity and distribution, models usually are

adaptable to similar species or situations. For example the Alder model may be adapted to a wide range of trees with a similar morphological organisation and physiology by supplying a pertinent parameterisation file. Similarly, the species dealt with in the small mammal community may be easily replaced by other rodents in order to represent a different community. Considering these aspects and the possibility of exchanging single modules, IBMs exhibit generic features for similar situations and species irrespective of the details represented.

These properties of individual-based models are the results of a representation with object-oriented methods, which allow the self-organisation of interacting objects as well as the generation and deletion of objects. They permit integration of processes and knowledge as components in complex interacting networks from all ecological sub-disciplines ranging from ethology and physiology to landscape ecology.

The general scheme of representing self-organisation processes in ecology and the emergence of higher order phenomena constitutes a new qualitative property of ecological models, thus allowing a considerable extension of the application range of models. The models may be used as virtual laboratories or virtual experimental sites to consider the impact of various parameters in an investigation and to bridge and fill in gaps where empirical findings are not feasible (Kawata and Toquenaga, 1994; Hölker and Breckling, 2002).

The development of individual-based models in general, and specifically the framework presented here, broaden the methodical repertoire that is appropriate for requirements of ecology to analyse complex causality networks across several organisation levels.

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