CHAPTER 2

Overview of the model types available for ecological modelling

S.E. Jørgensen[1] & T.-S. Chon[2]
[1]*Environmental Chemistry, Copenhagen University, Copenhagen, Denmark.*
[2]*Division of Biological Sciences, Pusan National University, Busan (Pusan), Republic of Korea.*

1 Issues in model development

The take off in ecological modelling occurred in the early 1970s. In this period, ecological models were increasingly used as a computation tool for ecosystem managements, while the journal *Ecological Modelling* was timely published to meet various requirements of model development. At that time, there were mainly only three model types, population dynamic models with age structure, biogeochemical models based on differential equations and static models to describe an extreme or average situation in the system. Occasionally, variations of these model types or even hybrids of two types were also developed for special problems.

Today, models have been greatly improved in various ways in terms of both methodology and implementation. Computation techniques emerge step by step to meet the needs for solving more complex problems presented in ecological processes. Direction of the model development can be addressed in a series of key issues as listed below [1]:

1. *Spatial presentation:* In accordance with development of computational techniques and improvement in data collection in ecology, spatial distribution of the variables has drawn a strong attention from the model users. Spatial information is efficient in elucidating ecological processes in more realistic ways, providing an extra dimension in addressing dynamics of the variables for the model users (e.g. when and where the invading species would outbreak? or how the pollution effects would disperse in ecosystems?). How can we address the problems regarding the spatial distribution which is often crucial to understanding the ecological processes?
2. *Individuality:* Ecosystems are middle number systems [2] in the sense that the number of components are in the magnitudes smaller than the number of atoms in a system. This indicates that individuals could be generated and would be modelled as independent agents in the system. As is well known, all the biological components in ecosystems are different in their attributes. This difference in components (i.e. individual variability) is often important for a proper description of the ecosystem reactions. In addition, emergent or collective

WIT Transactions on State of the Art in Science and Engineering, Vol 34, © 2009 WIT Press
www.witpress.com, ISSN 1755-8336 (on-line)
doi:10.2495/978-1-84564-207-5/02

properties could be produced from interactions among the individuals and would be crucial in determining global properties in the system. How these issues on the individual-individual and individual–population relationships could be addressed in model building?

3. *Adaptation:* The species are adaptable and are able to change their properties in their response to external input that may be produced from forcing functions. The species could be replaced by other species to be better fitted to the changes in forcing functions. Even the networks may be changed if more biological components are replaced with different properties by other species. How to account for the adaptive structural changes in the models?
4. *Biological properties:* In addition to individuality and adaptation listed above, other biological properties have been also applied in model development. Recently, unique characteristics residing in biological/ecological systems such as neural processing or evolutionary mechanism have been efficiently applied to development of algorithms in model building. Calculation methods based on the biological properties were well fit to elucidate complex ecological processes. How can these biological properties be accordingly implemented in model construction?
5. *Data uncertainty:* Ecologists collect and evaluate data from various data sources with either objective (mostly quantitative; e.g. measurements, simulation results), or subjective (often imprecise and qualitative; e.g. subjective estimations from an expert) origins. Due to practical difficulty of surveys and experiments, data collected from various sources, however, have been often limited in terms of quality and quantity. The uncertainty in the data may result from the large size of data sets, heterogeneity and other inherent uncertainties including subjectivity of the information obtained from experts (Salski *et al.*, Chapter 8). Can we model a system that has uncertain observations/data?
6. *Data heterogeneity:* Heterogeneity deserves a special attention in processing and management of ecological data. As is well known, ecological data are frequently collected from ecosystem in different situations. Evaluation of gradually-varying or contrasting ecosystems (e.g. topographic variation, ecosystems with/without disturbing effects from pollutants) provides valuable information for theoretical study and implementation in ecology. Heterogeneity could be originated from various sources such as different data sources, different data types, and different data formats (e.g. time series, spatial data) (Salski *et al.*, Chapter 8). How to develop models if the data base is very heterogeneous from many different ecosystems?
7. *Qualitative data:* Occasionally, qualitative data, rather than quantitative data, are available depending upon experimental conditions. For instance, qualitative judgment could be produced from rating of plant harvest from the experts. These qualitative results need to be used for modelling in ecosystem management. Qualitative models may excel in the situations when theoretical background on the target system is weak, when the problems are ill-defined, or when data are incomplete, uncertain or simply not available (Bredeweg and Salles, Chapter 19). How to develop models of ecosystems, when our knowledge is mainly based on a number of rules/properties/propositions?
8. *Stochastic property:* In ecological data, variability is often observed in the system. The forcing functions and numerous ecological processes are stochastic in nature. The randomness is generated to deal with limitation in our knowledge in revealing natural phenomena in modelling. With randomness residing in the data, deterministic and decisive information cannot be obtained. Instead, we have the probability patterns of variables (e.g. temperature, population density) by accumulating the previous measurements. How to account for probabilistic nature observed in biological and environmental factors in model construction?
9. *Dynamics:* Traditionally models have been developed for provision of either static or dynamic aspects in ecological processes. Dynamic processes have been a key issue regarding

time/space changes in variables, stabilities of the system (e.g. spatial and temporal prey–predator relationships), time-series development (e.g. succession), network (e.g. food), etc. Dynamics need to be developed to elucidate natural and anthropogenic processes more efficiently. How to consider a dynamic transport in different levels in ecosystems, even sometimes in 3D, and to elucidate dynamic aspect of ecological processes?

10. *Network:* Network approach has been utilized as a universal tool to analyze complex biological/ecological data. The complex data structure could be expressed as combinations of nodes and their connecting weights under the network framework. Ecological processes can be efficiently represented in the scheme of network dynamics. How to perform network analyses and network calculations in accordance with the very well developed network theory in presenting ecological systems through modelling?
11. *Toxic effects:* Investigation of effects of toxic substances exposed in environment has been one of the most notable contemporary issues in development of ecological sciences. As a main source of anthropogenic disturbances, toxins are most unique agents in human-dominated ecosystems. In ecological processes, toxin is solely produced by humans and is crucial to ecosystem stability with an extremely small amount, while other disturbing abiological (e.g. flooding, earthquakes) or biological (e.g. disease, invasion of alien species) agents are somehow related to natural processes in some degree with provision of energy subsidy at low levels. Toxin's negative impact, however, is critical in maintaining safety of ecosystems even at minimal levels. Toxic substances affect ecological systems in a complex manner at various hierarchical levels in biological systems: molecular and gene (e.g. chemical toxicology), population (e.g. abnormal mortality and birth rate), community (e.g. species extinction, community change) and ecosystem (e.g. problem in biogeochemical cycle) levels. Toxic effects deserve a special attention in achieving the safety of ecosystems. How to account for the complex relationships of toxins with biological systems in the model? Does development of a toxic substance model require a new type model building?

The 11 issues stated above could be arranged in 4 broad categories in the aspect of model development: presentation of spatial distribution, computational realization of biological properties, revealing environmental factors and data handling. 'Computational realization of biological properties' could be further divided as biological properties used as 'targets' for modelling and biological properties used as 'methods' for model development. The chapters listed in this volume are outlined in Table 1 with objectives, methods and examples for application under the different categories (BT: biological properties used as 'targets' for modelling, BM: biological properties used as 'methods' for modelling, ET: environmental factors used as 'targets' for modelling, DH: data handling and SP: spatial presentation). Some chapters were covered in more than one category according to the scope of modelling and computation methods.

1.1 Presentation of spatial distribution

Along with improvement in modelling capacity (e.g. computation techniques, computer resources) and methods for data collection, the model types were extended to elucidate various ecological processes on spatial domain. The following chapters are related to spatial distribution either directly or indirectly in model presentation (Table 1):

Chapter 5: Ecopath and Ecosim
Chapter 6: Surface modelling
Chapter 7: Individual-based model (IBM)
Chapter 11: Biogeochemical model

Table 1: Summary of the model characteristics listed in different chapters.

Chapter	Title	Category*	Objectives/issues	Computation methods	Examples	Demonstration programs**
5	Ecopath (Ecosim and Ecospace)	BT	Productivity estimation	Mass balance and conservation of energy	Trawling and squid fishery	Ecopath in EwE
		BT	Competition and predation	Mass balance and time dynamics	Trophic relationships	Ecosim in EwE
		BT+SP	Spatial dynamics in population relationships	Mass balance and time/spatial dynamics	Trophic relationships	Ecospace in EwE
6	Surface modelling	SP	Accessibility of location in space	Regular grid system; accessibility related with size and location	Population distribution on the national scale	SMPD
7	Individual-based model	BT	Expression of individuality and group behaviour	Generation of individual attributes; interaction with other individuals; application of local rules; motion of equation	Flocking	FLOCKI
		SP	Spatially explicit presentation	Generation of individual attributes; application of local rules; movement and reproduction	Dispersal of pest insects	POPDIS
8	Fuzzy approach	DH	Solving uncertainty in classification	Fuzzy c-means classification	Classification of wetlands	MATLAB Toolbox
		DH	Solving uncertainty in modelling	Fuzzy knowledge/ data-based models	Cattle grazing	MATLAB Toolbox

9	Ecological informatics	BT	Supervised learning and prediction	Multi-layer perceptron	Plankton dynamics	
		BT	Unsupervised learning and data grouping	Self-organized map	Classification of plankton communities	
		BT	Evolutionary process in ecological informatics	Evolutionary algorithm	Plankton dynamics	
		BT	Object-wise application in data processing	Object-oriented program	Plankton dynamics	SALMO-OO
10	Hybrid model	BT	Highly complex process-based learning	Evolutionary algorithm and object-oriented program	Parameter optimization in plankton dynamics	SALMO-OO
11	Biogeochemical model	ET+SP	Distribution of matter and energy in space and time	Differential equations with compartments	Nutrient cycle in wetland	STELLA[†]
12	Stochastic population dynamics	DH	Solving uncertainty problems	Probability network	Population dynamics in trouts	BayVAM; CATCH-Net
13	Structurally dynamic model	BM	Adaptability in model structure	Expert knowledge; goal function	Optimization in Darwin's finches; ectoparasites–birds interactions	
14	Ecotoxicological model	ET	Measurement of toxic effects	Mass balance; differential equation	Tylosine in agricultural field	EEP[‡]
15	Behavioural methods in ecotoxicology	BT	Detection of complex behavioural data	Multi-perceptron layer; self-organized map; 2D fast Fourier transform	Pattern recognition of the movement tracks	ANNBED
		BT	Revealing gene-individual-population relationships in ecological processes	Individuality implemented to hierarchy of biological systems	Toxic effects on gene, individual and population levels	IGIP

(Continued)

Table 1: Summary of the model characteristics listed in different chapters (Continued).

Chapter	Title	Category*	Objectives/issues	Computation methods	Examples	Demonstration programs**
16	Cellular automata	SP+ET	Spatially explicit presentation	Application of local rules on a lattice space	Species competition in lake	EcoCA-LYC
17	Rule-based system	DH	Derivation of rules from ecological data	Feature and case reasoning; self-organizing feature map; decision tree	Algal biomass in coastal waters	FuzzHab
18	Network calculation	DH	Network analysis in complex data	Langevin equation; Gillespie's stochastic algorithm; network in flow type determination	Energy flow in salt marsh	EcoNet
19	Conceptual knowledge	DH	Mediated conceptual knowledge	Qualitative reasoning; causality relationships; inequality reasoning; correspondences	Binary population interactions; The Ants' Garden; millennium development goals	Garp3
20	Flow pattern and mass distribution	SP+ET	Description of fluid patterns	Navier–Stokes and continuity equations; Eulerian/Lagrangian transport model	Hydrodynamics in estuary	Mohid

* BM: Biological properties as methods for modelling; BT: Biological properties targets for modelling; DH: Data handling; ET: Environmental factors as targets for modelling, and SP: Spatial presentation (See text for detailed information.)
** Some demonstration programs for the models listed are also available from the general tools such as STELLA, MATLAB Toolbox, and so on.
† Software for the development of biogeochemical and population dynamic models. It is based on the conservation principle. See also Chapters 11 and 13.
‡ A program for estimating ecotoxicological parameters.

Chapter 16: Cellular automata (CA)
Chapter 20: Flow pattern and mass distribution

Spatial information provides efficient and realistic views to the model users for implementation to real world (e.g. estimating spatial conformation of invading species, dispersal of pollutants and threshold concentration). In spatial domain, 2D or 3D movement of populations (or invading species), for instance, would provide more realistic data from which the user could forecast for the future or propose more suitable management policies.

Chapter 6 on surface modelling specifically takes the direct issue on how spatial distribution of the variables is addressed in methods and results. The geographic images obtained by satellites could be efficiently used for spatial presentation of ecological processes. Development of Geographic Information System (GIS) has contributed significantly to extend the scope of spatial implementation of the models. The images could be accordingly interpreted to represent the properties of the land use through aerial interpolation. The authors disclose algorithms based on the grid system to reveal spatial distribution of human population in response to environmental conditions on national basis in Chapter 6 (Yue *et al.*).

While Chapter 6 provides information on the spatial distribution of the variables broadly over the space to deliver the large-scale geographic information in general, Chapter 20 illustrates dynamics observed in the fluid patterns specifically in flowing conditions in streams. The chapter is focused on how flow pattern and mass distribution are calculated to reveal spatial patterns of fluids based on the Navier–Stokes and continuity equations ('shallow water equations') in hydrodynamic fields. Along with the transport models with Eulerian and Lagrangian methods, the methods describe the fluid patterns and evolution of water properties (Miranda and Neves, Chapter 20).

Cellular automata (CA) in Chapter 16 (Chen) also elucidates spatial distribution of the variables and is used as a spatially explicit model to illustrate spatial dynamics based on execution of local rules according to pre-determined rules. CA is spatially structured in the sense that the model construction is based on spatial configuration on the relationships between the target and neighbour cells on a lattice space [3, 4]. With the local rules determining the state of the centre cells based on the previous states of the neighbour and centre cells, CA can integrate local processes and consequently reveal global information in the system (Chen, Chapter 16).

Individual-based model (IBM) in Chapter 7 (Chon *et al.*) could also present spatial distribution. IBMs are more emphasized to illustrate variability of individuals in ecological processes, but are similar to CA in the sense that spatially explicit information could be addressed in the model based on local processes. While the generated individuals move around on the lattice space, local information in the neighbourhood of the individuals is collected in an integrative manner to consequently provide information of the population in the system.

In addition, Ecospace [5] discussed in Ecopath in Chapter 5 (Christensen) could present information on dynamics of populations on spatial domain. Ecospace presents a capacity for explicit spatial modelling of ecosystems and can be used for elucidating spatial movement of populations. The traditional biogeochemical models in Chapter 11 (Jørgensen) could also deliver information on distribution of matter and energy in space and time.

1.2 Computational realization of biological properties

Along with concurrent development in computer technologies and biological sciences since the 1980s, complex life phenomena in biological and ecological processes were closely related with development of computation algorithms. On one side, the biological properties were used as

sources for computational techniques. Unique properties such as adaptation and neural processing were used as methods for development of algorithms in modelling. On the other side, biological properties themselves became targets for modelling. Models were designed to efficiently address biological properties residing in biological organisms. Population dynamics, for instance, has been traditionally a popular topic for modelling. Recently, the unique properties such as individuality, behaviours, and toxic effects became objects for modelling. The following chapters are closely related with biological properties used as either methods or targets (Table 1):

As methods for modelling:
Chapter 9: Ecological informatics
Chapter 10: Hybrid models
Chapter 13: Structurally dynamic models (SDM)

As targets for modelling:
Chapter 5: Ecopath and Ecosim
Chapter 7: Individual-based model (IBM)
Chapter 12: Stochastic population dynamics
Chapter 14: Ecotoxicological model
Chapter 15: Behavioural methods in ecotoxicology

As computation capacity increased, biological properties were abstracted by the model developers and were accordingly used as idea for developing new algorithms. Adaptability has been recognized as one of the most unique characteristics in biological properties. The concept of adaptability has been applied to modelling complex phenomena in ecological processes with flexibility. The structurally dynamic model (SDM) in Chapter 13 (Jørgensen) pioneered in using the concept of adaptation in model building. Adaptation allowed the gradual, structural changes in the system in accordance with response to external inputs used in the model. SDM was efficient in addressing life phenomena that could not be readily reflected in the conventional static models. In Chapter 13, SDM was used to demonstrate constant update of the variables and the relationships of the variables by feedbacks towards evolution of higher complexity in ecosystems.

Neural systems also served as conceptual sources for developing learning algorithms and have been efficiently applied to modelling complex ecological phenomena [6, 7]. Chapter 9 on ecological informatics (Recknagel and Cao) deals with artificial neural networks (ANNs) and other bio-inspired models on extracting information from non-linear phenomena. ANNs based on supervised and unsupervised learning were used for forecasting and classification of ecological data. In addition, evolutionary algorithms and object-oriented programming were applied to analysis, synthesis and forecasting in ecological processes. Neural and evolutionary computation allows inducing problem solutions such as patterns, models, and knowledge from complex data. Object-oriented computation facilitates the synthesis of ecosystem simulation models from process-based ecosystem simulation libraries (Recknagel and Cao, Chapter 9).

As computation capacity increased, flexibility in the biologically inspired models allowed combination of two different models to carry out modelling objectives in an integrated manner. By combining different types of models, modelling capacity was greatly enhanced and was selectively more reliable in estimating the variables in the system with complex phenomena from heterogeneous origins. Hybridization of models in Chapter 10 (Cao and Recknagel) demonstrates flexibility in modelling. The methods presenting biological properties were flexible to be combined with other models to produce a more sophisticated model. This type of hybridization was efficient in improving validity of highly complex process-based models. Evolutionary algorithm and object-oriented model were combined to construct a hybrid model in Chapter 10.

In addition to utilization of biological properties as sources of computation methods, modelling has been further developed to address environmental properties in the system. Biogeochemical cycles, for instance, have been traditionally an important object of modelling, while population dynamics and productivity have been conventionally used as targets for modelling in the biological side.

One of the most notable biological properties that have been target for modelling is individuality. IBMs are in general contrasted with the conventional mathematical models that deal with the overall property of population dynamics as a variable (e.g. differential equations for analysing population density). Individuality has been regarded as essential entities in illustrating the complex 'organism–organism' and 'organism–environment' relationships in biological systems in IBMs (Chon *et al.*, Chapter 7). Computational agents were generated to accommodate various attributes in individuals in the model. Properties in individuals have been conveniently accommodated in IBM as attributes (e.g. physiological state, age). Subsequently, complex phenomena expressed through the individual-population relationships in life systems were projected on to a defined space.

Complex processes of reproduction (e.g. mating, fission) could be efficiently elucidated in IBMs, as IBMs are suitable for fabricating the complex inter-individual relationships and for assigning new attributes to progenies. The individual properties could be projected upwards to higher levels at population through various forms of interactions with other individuals: competition, predation, parasitism, etc. The inter-individual relationships can be further extrapolated to larger scales to communities and ecosystems in a hierarchical manner in biological systems [8]. Individual properties could be also efficiently expressed as spatially explicit processes in spatial domain. By integrating information from lower levels, IBMs are efficient in addressing collective and emerging properties at higher levels on a lattice space (Chon *et al.*, Chapter 7).

Another notable issue for the model users in contemporary ecological sciences is modelling toxic effects. Toxic effects are unique in the sense that toxic substances are purely human-originating disturbances and would cause complex responses in biological systems as stated above. Ecotoxicology serves as an entering 'wedge' into the new field of integrative management of ecosystems.

In integrative monitoring of toxic effects, behavioural response has drawn a special attention from the modellers in the field of ecological risk assessment. Behaviours at the individual levels could fill the gaps in measurement scales between the micro-size (e.g. microorganisms, molecular genetics) and macro-size (e.g. community dynamics, ecosystem stability) assessments. Behavioural methods for monitoring of toxic substances were added in this volume (Chon *et al.*, Chapter 15). By linking with ecotoxicological model in Chapter 14 (Jørgensen), modelling of toxic effects could be illustrated in a comprehensive manner across different hierarchical levels in biological systems.

In addition to recent issues in biological properties, the volume provides the chapters on conventionally important topics on population dynamics. Population dynamics is an ideal issue in ecological modelling: population size is suitable for quantification and decisions made on population dynamics are often economically important (e.g. pest management, invading species). Stochastic population dynamics was additionally elucidated in Chapter 12 (Borsuk and Lee), while dynamics in the prey and predator relationships were presented in Ecosim and Ecospace in Chapter 5 (Christensen).

1.3 Revealing environmental factors

As the biological properties such as population dynamics and productivity have been targets to be modelled with, environmental factors have been also an important topic for ecological modelling,

although not as extensive as in biological properties in recent years. The following chapters deal with environmental factors as objects for modelling (Table 1):

Chapter 11: Biogeochemical model
Chapter 14: Ecotoxicological model
Chapter 20: Flow pattern and mass distribution

Biogeochemical models in Chapter 11 (Jørgensen) played an important role in solving numerous problems of ecosystem management in the early period of model development. The models are based on execution of differential equations to provide information on the distribution of matter and energy in space and time according to the conservation principle (Jørgensen, Chapter 11).

Chapter 20 (Miranda and Neves) on flow pattern and mass distribution was discussed in Section 1.1, but is also regarded as the model for illustrating the role of environmental factors in ecological processes. Chapter 19 illustrates the specific patterns of fluids in spatial and time domain in hydrodynamics. The chapter discusses on how water properties change and redistribute due to the flow pattern. The fluid pattern was elucidated according to the Navier-Stokes and continuity equations in the hydrodynamic fields (Miranda and Neves, Chapter 20).

As stated above, toxic substances are one of the most important environmental factors in representing anthropogenic disturbances caused by humans in ecosystems. While other disturbing agents are related with natural processes in some degree, toxin is solely produced by humans and is critical in maintaining safety of ecosystems even with minimal existence in environment. Chapter 14 (Jørgensen) on ecotoxicological models is focused on presence of toxic materials and safety criteria. Toxic substance models may differ from other ecological models in that: (1) being most often more simple (in the conventional models), (2) requiring more parameters, (3) a wider use of parameter estimation methods, (4) a possible inclusion of an effect component [9]. Ecotoxicological models were designed to obtain the best possible knowledge about ecological processes of the considered toxic substances in ecosystem (Jørgensen, Chapter 14).

1.4 Data handling and model construction

Ecological data are collected from various sources from field surveys and from laboratory experiments. The collected data sets could serve as input for modelling and could provide useful information for determining various types of parameters used in the models. More importantly, quality and quantity of the data sets determine the types of models for application. Along with development of computational techniques, handling of ecological data sets has been a key issue in modelling. Due to the difficulties of sampling in field conditions, for instance, there may be uncertainties or heterogeneity in the data. Rules or qualitative properties may be also present in the data. Or network properties need to be addressed when ecological processes are composed of numerous components. The following chapters are related to data handling in this volume (Table 1):

Chapter 8: Fuzzy approach
Chapter 12: Stochastic population dynamics
Chapter 17: Rule-based system
Chapter 18: Network calculation
Chapter 19: Mediating conceptual knowledge using qualitative reasoning

Fuzzy approach is introduced in Chapter 8 (Salski *et al.*) to deal with uncertainty problems and has been used for handling the imprecision of data and vagueness of the expert knowledge. Fuzzy Set Theory was applied to deal with the imprecision of data and vagueness of the expert

knowledge by formulating logical and arithmetical operations for processing information defined in the form of fuzzy sets and fuzzy rules in Chapter 8.

Uncertainty could also be specifically dealt with the stochastic nature in modelling. In Chapter 12 (Borsuk and Lee), probability was used for generating variability in the system. Temporal changes in population status, for instance, can be efficiently covered in stochastic population dynamics. Representations of uncertainty and variability are especially critical for populations at risk of becoming extinct or losing significant genetic resources through declines. Chance occurrences can be catastrophic for species already on the brink of extinction. Chapter 12 on stochastic population dynamics was further discussed in Section 1.2.

Networks are considered as a general property residing in the data structure where many elements are connected in a complex manner in ecological systems. The complex relationships among the components in the system could be conveniently elucidated in the networks. Recently, much interest has been broadly reported on networks and their application to various fields across genome to internet [10]. In Chapter 18 (Kazanci), network calculations were demonstrated to form a set of compartments and flows by using the program EcoNet. Any ecological processes can be represented as a stock-flow diagram in the network framework.

An additional issue in managing ecological data is to find feasibility in expression of qualitative nature in ecological processes. Although ecological processes could be conventionally and simply expressed by differential equations, there are numerous cases where only qualitative data are available. The majority of the reasoning and understandings obtained from ecological data are qualitative rather than quantitative. Consequently, qualitative data are difficult to formulate in the form of differential equations. Chapter 17 (Chen) focuses on the rule-based technique, which derives the rules from the often limited data available from *in situ* measurements, while taking expert knowledge as reference. The rule-based models were demonstrated to derive the rules for reasoning, to produce decision trees and to integrate physically based formulations with empirical rules.

Management of qualitative data was also illustrated in resembling human intelligence. Chapter 19 (Bredeweg and Salles) deals with execution of automated artificial intelligence on computers by mediating conceptual knowledge. Qualitative reasoning investigates how this aspect of human intelligence can be automated on computers [11]. A typical qualitative reasoning engine takes a scenario as input and produces as output a state graph capturing the qualitatively distinct states a system may manifest (Bredeweg and Salles, Chapter 19). The chapter introduces a modelling workbench with a graphical user interface that integrates facilities for model building and for running qualitative simulations. The model uses qualitative reasoning and also efficiently addresses planning of model construction.

2 Increasing number of model types

As a consequence of model development stated above, a number of new types of models have been available recently. To what extent have these new model types been applied in ecological modelling? The question is answered by use of statistics on model papers published in the journal *Ecological Modelling*. The numbers of papers published for the various model types in two periods, the first 7 years of *Ecological Modelling* from 1975 to 1982 and during the last 6 years from year 2000 to 2006 (see Figs 1 and 2).

Although the number of the model papers focusing on the classical model types has increased, the two types of classical models, biogeochemical models and population dynamic models, decreased in percentage because the recently developed model types have relatively increased more in application. For the early period 1975–82, the applications of biogeochemical models

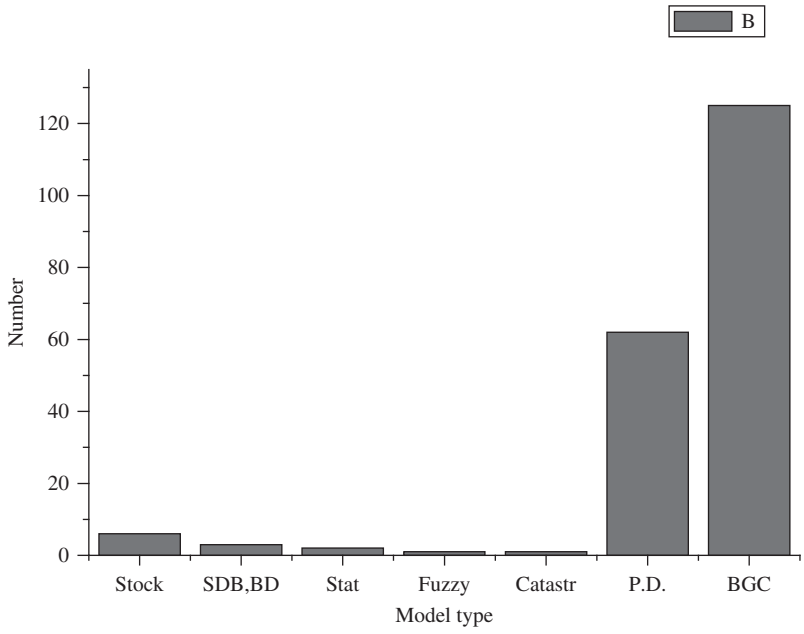

Figure 1: The number of model papers published in the period 1975–82. The statistics of model papers covers from left to right stochastic models, spatial distribution models and structurally dynamic models (SDB), models based on the use of statistics, fuzzy models and models using catastrophe theory, population dynamic models and biogeochemical models.

and population dynamic models were dominant. The proportion of two model types decreased significantly afterwards.

Fuzzy models, spatial distribution models, structurally dynamic models and models using catastrophe theory were used in the period 1975–82, but their application in ecological modelling was very modest. They were new and untested tools in ecological modelling. Recently, however, new models, particularly structurally dynamic models, ANNs and IBMs, have been more extensively applied from 2000 to 2006 (see Fig. 2 and compare with Fig. 1). Fuzzy models and stochastic models seem to also have attracted more modellers most recently. The use of static models – about 20 – in the period 2000–2006 is due to wide application of the software Ecopath (see Chapter 5) that is used particularly for fishery and other implementations for management of aquatic ecosystems.

With the present spectrum of model types, it has been possible to solve the main modelling problems that had been raised already in the 1970s (see the 11 issues on modelling in Section 1). However, it became also clear that all the problems could not be solved completely. We still have a number of problems that may not be possible to solve with the developed models stated above. One alternative for solving the complicated problem could be development of the hybrid models, i.e. by a combination of the here presented single models. Or, newly proposed models would be tested extensively in the coming years. The issues whether we should develop new models or use the established models more accordingly for better results will inevitably come to surface. It is, however, agreeable that we currently have sufficient model types to solve most of ecological modelling problems being faced with us nowadays, although some models still need to be

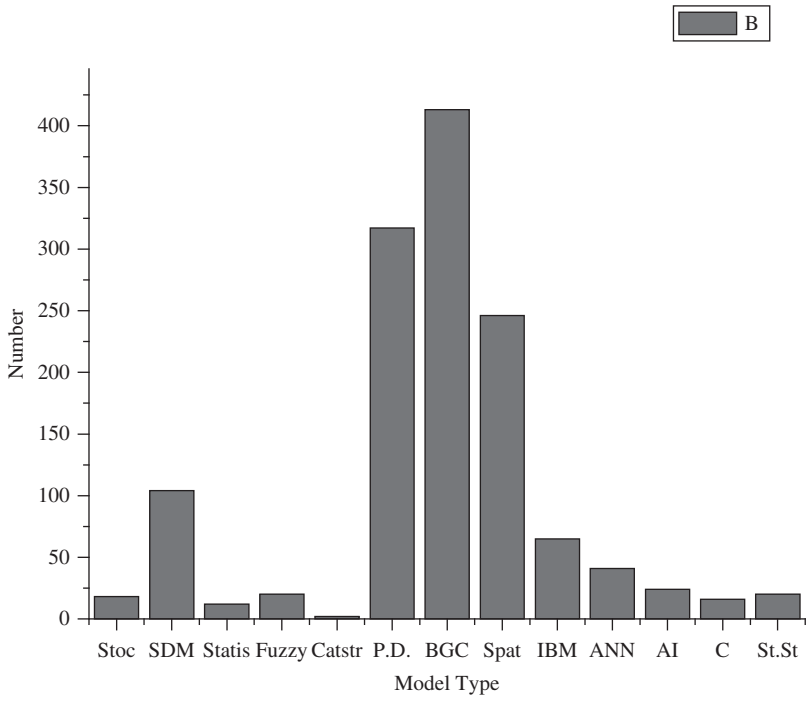

Figure 2: The figure shows the number of model papers published in the period 2000–2006. The statistics cover from left to right stochastic models, structurally dynamic models, statistical models, fuzzy models, models based on the use of catastrophe theory, population dynamic models, biogeochemical models, spatial distribution models, individual based models, artificial neural network models, models developed by the use of artificial intelligence, models using chaos theory and static models.

improved to guarantee their feasibility in real situations. New model types can be further developed in the future and better model results may be obtained either by development of more sophistigate hybrid models or by creation of innovative ones.

3 Characteristics of the model types available today

In Section 1, the contemporary issues in model development were discussed, and the developed model types were outlined depending upon different categories of model characteristics (Table 1). In this section, the models available in this volume are sketched one by one. For all the main model types, the basic points for construction, advantages and disadvantages (mostly expressed as a limitation of the application) and the area of application are described below.

Although the application of theories on catastrophe and chaos were mentioned in the statistical overview of the papers published in *Ecological Modelling* in Section 2, these methods are not covered in this volume. Theories on catastrophe and chaos are basically considered as general mathematical techniques, rather than as the specific, goal-oriented model types being expected in ecological modelling. These mathematical techniques can be applied to development of various model types regardless of model characteristics specified in ecology. Similarly, considering

that the stochastic differential equations (e.g. Fokker–Planck equation) are considered to be a general tool for analysing stochastic processes, the equations are not included in this volume.

Statistical models were neither discussed in this volume because statistic could be also considered as a type of general 'tool' that can be applied to quantitative description of the system based on a certain statistical criterion (e.g. level of significance), while the objective-oriented goals are specifically defined in the input–output relationships in ecological modelling. If a model is based entirely on statistics, it is a so-called black box models, because it does not explicitly provide the causality relationships residing in the input–output variables in ecological systems. Ecological modelling serves as a specific tool in solving the problems in ecosystem management and prediction: the focus more specifically lies on revealing the environment–community causality relationships (e.g. impact of pollution on community dynamics) in real world to a higher extent. The different model types have been extensively applied in environmental management as a powerful tool under various frameworks to understand the reactions of ecosystems to changes in environmental factors and to set up appropriate diagnosing, forecasting and management systems.

3.1 Dynamic models: Chapters 5 and 11

The ecological models have been traditionally developed to provide either static or dynamic aspect in ecological processes. While dynamic models have been efficiently used to illustrate the time-varying processes, static models conveniently provide overall status of ecosystems where static conditions are assumed in the system. Considering that ecological systems are inherently unstable in many cases and are exposed to various (internal or external) disturbing agents, dynamic models were especially useful for elucidating the time- and spatial-development of the variables, for instance, spatial and temporal impact of natural/anthropogenic disturbances on ecosystems, dynamics in bioenergetic and biogeochemical cycles, etc.

Dynamic models have been conventionally covered in several chapters in this volume, including estimation of fishery production with 'Ecopath' in Chapter 5 (Christensen) and mass transfer in biogeochemical cycles in Chapter 11 (Jørgensen). While Chapter 5 reveals biological properties (i.e. productivity) for modelling, Chapter 11 is focused on impact of environmental factors (i.e. nutrients) in ecosystems. The models in two chapters mainly use differential equations to express dynamics of the system. Based on the conservation principles, changes in state variables are expressed as the results of the ingoing minus the outgoing processes. The process equations are usually based on causality.

The model of 'Ecopath' in Chapter 5 has been popular for estimating productivity in fishery. Based on mass–balance equation, the scope of models has been greatly expanded to other fields related to productivity, trophic structure, food web dynamics, etc. in ecological systems (Christensen, Chapter 5). The program in Chapter 5 was provided with the software EwE, which has three main components: Ecopath – a static, mass-balanced snapshot of the system; Ecosim – a time dynamic simulation module for policy exploration; and Ecospace – a spatial and temporal dynamic module primarily designed for exploring impact and placement of protected areas (Christensen, Chapter 5). It is notable that the software has been developed towards spatial presentation with Ecospace (Table 1). Ecospace [5] introduces a capacity for explicit spatial modelling of ecosystems, which have been parameterized through Ecopath and analysed for the time-trends using Ecosim. Integration of Ecospace mapped with commercial GIS formats (using raster format) is also possible. As an exercise, the program for 'trawling cultivation for squid' was provided. Trawling was carried out on shelves to cause removal of macro-algae, sponges, soft-corals and other habitats for juvenile fishes in the area. The habitat changes on shelves

consequently provided favourable environmental conditions for emergence of squid population (Christensen, Chapter 5).

While Chapter 5 mainly deals with biological properties (e.g. productivity, prey-predation), Chapter 11 takes environmental factors (e.g. biogeochemical cycle) as targets for modelling. The biogeochemical models provide both static and dynamic aspects by illustrating distribution patterns of cycling of ecological elements in ecosystems that have been already deeply discussed since the 1970s. We call the type here biogeochemical models, because the type is most frequently applied to the dynamics of mass transfer; but in principle, it could also be applied to bioenergetic transfer. The model type has some clear advantages that make it still attractive to be used for development of many other models. An example of biogeochemical (and ecotoxicological) models was provided regarding estimation of an antibiotic, tylosine. The model focuses on pollution of an agricultural field and has been calibrated and validated for estimation of contamination (Jørgensen, Chapter 11).

Although the biogeochemical models have been traditionally used for a long time, these types of models are still widely applied in modelling nowadays, as can be seen by a comparison of Figs 1 and 2. From 1975 to 1982, the biogeochemical model covered 62.5 % of the total publications in *Ecological Modelling*, whereas it occupied 32% of the publications in the journal from 2000 to 2006.

The advantages of the dynamic models are:

- most often based on causality;
- derived from mass or energy conservation principles;
- easy to understand, interpret and develop;
- software conveniently available, for instance, STELLA;
- easy to use for predictions.

The disadvantages are:

- can hardly be used for heterogeneous data;
- require relatively good data;
- difficult to calibrate when data are complex and contain many parameters;
- cannot account for adaptation and changes in species composition.

3.2 Static models: Chapters 5 and 11

The static models have been traditionally used for estimation of the variables presented in ecosystems and are conveniently described in Chapter 5 (Christensen) and Chapter 11 (Jørgensen). If the seasonal changes are minor, for instance, a static model of the mass flows will often suffice to describe the situation. This model type will be frequently used when a static situation is sufficient to give a proper description of ecological systems or to take environmental management decisions. It can often be used beneficially as a first step towards a dynamic model. However, the models are limited in the sense that the models require assumption of static conditions while in nature the variables are unstable and dynamic in ecological processes.

Due to the limitations of this type of traditional model, it has not been used in more than 1.8% of the publications in *Ecological Modelling* in the last 6 years and the type was not applied from 1975 to 1982. The model type is a biogeochemical dynamic model where the differential equations all are set to zero to obtain the values of the state variables in correspondence to the static situation. Static models can be demonstrated in the similar manner as shown in the examples for the dynamic model provided in the Chapter 5 and Chapter 11.

The advantages of the static models are:

- require smaller databases than for most other model types – particularly less than for dynamic biogeochemical models;
- are excellent to give a worse case or average situation;
- the results are easily validated (and verified).

The disadvantages are:

- do not provide any information about dynamics and changes over time;
- prediction with time as independent variable is not possible;
- can give only average or worse case situations.

3.3 Population dynamic model: Chapter 12

Population dynamics has been one of the most popular objects for modelling, as dynamic natures are quantitatively well expressed in populations in most ecological processes and are important for determination of appropriate population size in implementation for ecosystem management. Changes in population size have been considered as critical issues in ecology, for instance, pest problems, invasion of alien species, conservation of endangered species, etc. The concept of dynamics has been efficiently dealt with in Chapter 12 (Borsuk and Lee). As stated above, biological properties became the objects of the model development. Population dynamic models may also include age structure, which in most cases is based on matrix calculations.

The models of population dynamics are rooted in the Lotka–Volterra model that has been originally developed in the 1920s. Numerous papers have been published about the mathematics behind this model, and a number of deviated models have been introduced to address complex intra- and inter-population relationships. The mathematics of these equation systems seems to have a different focus in presenting population dynamics from an ecological modelling point of view regarding practicality. The focus of the mathematical formulae mainly lies on theoretical description of population growth and the relationships between populations, while the practical aspect (e.g. productivity estimation, pest control, eruption of alien species) in population management is of higher issue in ecological modelling. In real situations, population dynamics has been reported to be related to many other factors (e.g. resource limitation, environmental disturbances), besides the simple theoretical prey–predator relationships. Consequently, the models are expressed in a more complex and integrative manner with other biological or non-biological factors in the system in real situations.

The model of population dynamics is typically used to keep a track of the development of a population. Effects of toxic substances on the development of populations, for instance, can be conveniently covered by increasing the mortality or by decreasing the growth correspondingly. The number of individuals (or density) is the most applied unit, but it can of course easily be translated into biomass. The model type has been extensively used in management such as fishery and national park maintenance. Chapter 12 on stochastic population dynamics (Borsuk and Lee) utilizes probability networks to deal with population density as a principal parameter. The probabilities of catastrophic outcomes or population explosions are efficiently considered using stochastic models that simulate temporal or spatial variation of population size. In this model, probability was also used to allow variability: the densities were randomized with changes in the survival and maturation rates (Borsuk and Lee, Chapter 12). The stochastic aspect is discussed later in Section 3.10.

Example models for stochastic population dynamics were provided with the program 'Bayesian Viability Assessment Module' (BayVAM). The program was used to elucidate population changes in Westslope Cutthroat Trout in the Upper Missouri River Basin, USA. BayVAM is a stochastic, stage-structured demographic model that has been recast as a probability network by incorporating results from many Monte Carlo simulations over all possible combinations of model parameters [12] (Borsuk and Lee, Chapter 12).

In addition, the program, Causal Assessment of Trout Change using a Network model (CATCH-Net), was also provided to show population dynamics of Brown Trout in the Rhine River Basin, Switzerland. CATCH-Net is a probability network model developed to assess the relative importance of different local stress factors in limiting brown trout density in Swiss rivers (Borsuk and Lee, Chapter 12).

Population dynamic models were represented in 31% of the model papers in *Ecological Modelling* in 1975–82, while it was applied in 25% in the period 2000–2006. Although the percentage is decreased, the number of population dynamic papers is, however, five times as much in the latter period than in the former period. This illustrates that ecological modelling has developed significantly from the 1970s to today. The minor reduction in percentage reflects the application of a wider spectrum of different model types today.

The advantages of population dynamic models are:

- fitted to follow the development of a population;
- age structure and impact factors easily considered;
- easy to understand, interpret and develop;
- most often based on causality.

The disadvantages are:

- the conservation principles sometimes not applied;
- limited to population dynamics;
- a good database required for biogeochemical dynamic models;
- difficult in some situations to calibrate;
- require a relatively homogenous database.

3.4 Structurally dynamic models: Chapter 13

After development of conventional types of static and dynamic models, new model development was initiated with introduction of the concept of 'adaptation'. Adaptation could be regarded as gradual internal change in response to external input. Adaptation could be used as a methodology for model development to account for adaptive processes observed in ecology, for instance, physiological acclimation in the laboratory conditions and changes in species composition in the field conditions.

While the model framework was conventionally fixed during modelling procedure in the traditional models, the structural dynamic model (SDM) in Chapter 13 (Jørgensen) allows adaptive changes within the model structure as convergence reached to the final (or optimal) state in the system. This modification in structure through modelling was innovative in the sense that the model utilizes adaptive processes in biological properties. Most often, a goal function is used to direct the changes in the parameters. Eco-exergy, for instance, has been frequently used as goal functions in structurally dynamic models. This model type should be applied whenever it is known that structural changes take place. It is also recommended for models that are used in

environmental management to make prognoses resulting from major changes in the forcing functions (Jørgensen, Chapter 13).

Application of SDM to Darwin's finches [13] is illustrated in Chapter 13 as an example program. The program demonstrates the changes in beak size as a result of climatic changes that influenced availability and quality of food (seeds) for finches. In addition, SDM provides another example. The model of the ectoparasites–birds interactions was provided to show strategy of populations being consistent with an increase in eco-exergy by SDM.

SDMs are applied much more today than 25–30 years ago. In the period 1975–82, only 1.5% of the model papers were about structurally dynamic models, while 8% of the model papers were about structurally dynamic models from 2000 to 2006.

The models in structural dynamics have the following advantages:

- capable of accounting for adaptation;
- capable of accounting for shift in species composition;
- can be used to model biodiversity and ecological niches;
- calibration of parameters (determined by the goal functions) not necessary;
- relatively easy to develop and interpret.

The disadvantages of the model are:

- selection of a goal function needed;
- usually computer time consuming;
- require information about structural changes;
- software not available; programming often needed.

3.5 Fuzzy models: Chapter 8

Due to difficulties of surveys and experiments carried out in ecological sciences, uncertainty may frequently reside in the ecological data. The problems of uncertainties in the collected data may result from various sources, large data sets (spatial data with high resolution, long time series, etc.), heterogeneity obtained from different sources, types, structure and formats in data and inherent uncertainty (Salski *et al*., Chapter 8). Along with the development of computational techniques, however, a significant improvement has been made in handling the problems of ecological data. Fuzzy approach in Chapter 8 was one of the major methods to deal with the problem of uncertainty observed in the data. The approach has been a mostly successful method of dealing with the imprecision of data and vagueness of the expert knowledge. The chapter introduces knowledge-based (i.e. the Mamdani type) or data-based (i.e. the Sugeno type) approaches. Compared with conventional methods of data analysis and modelling, the fuzzy approach enables us to make better use of imprecise ecological data and vague expert knowledge.

The model could be applied when the data set is fuzzy or only semi-quantitative expert knowledge is available, provided of course that the semi-quantitative results are sufficient for the ecological description or the environmental management. Examples in Chapter 8 were presented for fuzzy classification of wetlands for determination of water quality improvement potentials and for a fuzzy and neuro-fuzzy approach to cattle grazing in Western Europe. The model demonstrated usefulness of Fuzzy approach in conservation and in agriculture (Salski *et al.*, Chapter 8).

Fuzzy models were only represented in 0.5% of the model papers in *Ecological Modelling* from 1975 to 1982, while this model type was found in 1.8% of the papers in the period 2000–2006.

Fuzzy models have the following advantages:

- can be applied on a fuzzy data set;
- can be applied on semi-quantitative (linguistic formulations) information;
- can be applied for development of models, where a semi-quantitative assessment is sufficient.

This model type has the following disadvantages:

- can hardly be used for more complex model formulations;
- cannot be used where numeric indications are needed;
- black box models encountered in the Fuzzy model-based data;
- no public software available to run this type of models in ecology, although there are facilities in MatLab to run fuzzy models.

3.6 Models in ecological informatics: Chapter 9

While mathematical methods were used as computation tools in ecological modelling, some properties in biological/ecological processes have been in turn used as algorithms or computation techniques in modelling. As stated above, adaptation was an ideal concept used for development of algorithms in modelling. Additionally other biological properties such as neural processes and evolution have been used as computation sources in the development of machine learning.

The models based on biologically inspired networks are able to provide information on relationships between state variables and forcing functions with heterogeneous database. The models allow to find the relationships and to test the relationships afterwards on an independent data set. It is a black box model and is therefore not based on causality; but, it gives in most cases very useful models that can be applied for prognoses, provided that the model has been based on a sufficient big database. Although direct causality cannot be revealed, the input–output relationships could be illustrated by using sensitivity analyses [6].

In Chapter 9 (Recknagel and Cao), the bio-inspired computation methods such as ANNs, evolutionary algorithms and object-oriented programming used in ecological informatics were discussed for analysis/synthesis and forecasting in ecological processes. Neural and evolutionary computation allows inducing various problem solutions in the types of patterns, models, knowledge from complex data, etc. Whilst traditional techniques solve some particular problem or class of problems 'top–down' by means of *ad hoc* designed statistical or algebraic algorithms, bio-inspired computation is merely based on a loosely connected family of units such as electronic neurons, chromosomes or objects which are continually being modified to improve the computational performance [7]. Bio-inspired algorithms are not rigid, but dynamically evolve 'bottom–up' by means of principles of neuronal learning, natural selection or hierarchical inheritance and have been versatile in learning complex phenomena observed in nature. Application of techniques in ecological informatics would be advantageous where ecological descriptions and understandings are required on the basis of a heterogeneous data base. Although the modellers may consider use of biogeochemical dynamic models due to their causality, ANNs, however, are flexible and faster to use once the network is trained, while the time consuming calibration may be needed for biogeochemical models.

Examples in the bio-inspired networks were provided with the case studies on prediction of plankton populations in Chapter 9. The program SALMO-OO, the core of the lake simulation library, was provided by illustrating processes of algal zooplankton growth. In addition, the object-oriented program was demonstrated with SALMO-OO written by JAVA. SALMO-OO has been

hierarchically modularized into classes and objects that inherit attributes and methods from the next upper level of the hierarchy where a class is defined as a template for the creation (instantiation) of objects that share a common structure and behaviour (Recknagel and Cao, Chapter 9).

ANNs were not published before 1982 in Ecological Modelling, but 3% of the papers covered ANNs in the period 2000–2006. Since 2006, the papers have been published in the new journal of *Ecological Informatics*.

ANNs including self-organizing maps have the following advantages:

- used for analysing non-linear and complex data where other methods must give up;
- easy to apply;
- give a good indication of the certainty due to the application of a test set;
- can be used on a heterogeneous data set;
- providing a close-to-optimum use of the data set.

The disadvantages can be summarized in the following points:

- no causality revealed unless separate computation methods are introduced or a hybrid between ANN and a normal model is applied;
- cannot replace biogeochemical models based on the conservation principles;
- sufficient data sets are required;
- the accuracy of predictions is sometimes limited.

3.7 Individual-based models and cellular automata: Chapters 7 and 16

Individual-based model and CA can be regarded as the models originally motivated through concept of reductionism: the model derives the properties of element from a system and further incorporates the interactions among elements of the system. Regarding interactions among individuals, the models could be viewed in turn as a tool for integrative modelling. Local processes are accordingly accumulated in the system to produce the collective or emergent properties on the global basis.

The model types were developed through adaptive relationships among biological components with different attributes. Within the same species, the differences are minor and are therefore often neglected in the conventional models such as biogeochemical models, but the differences among individuals of the same species may sometimes be important for ecological reactions. For instance, individuals may have different size, which gives different combinations of properties among individuals as it is known from the allometric principles [14]. The right combination may be decisive for growth and/or survival in certain situations, as all modellers know it. Consequently, a model without the differences among individual may give completely different results.

The models of IBMs and CA in Chapter 7 (Chon *et al.*) and Chapter 16 (Chen) are in common in expressing ecological processes in many senses, especially elucidating the local processes in spatial domain in an explicit manner. The space models were constructed to integrate local information to elucidate complex dynamics residing in the relationships between individual and population. CA (or lattice-structured models) and IBM have been commonly utilized for this purpose. While local rules are similarly applied to the neighbour cells for model construction, two models could be differently characterized regarding handling of individuality and spatial information. In IBM, attributes in individuals serve as main variables in model structure, while the variable presents the state of the cells in spatially determined configurations in CA. IBMs focus on variability of attributes in individuals such as physiological status, behaviours, etc. In contrast, the model

construction in CA put more emphasis on spatial conformation of the variables through the rule-based changes in the neighbourhood operation in the spatial domain [15].

In IBMs (Chapter 7), 'individuals' are regarded as essential entities in illustrating the complex 'organism–organism' and 'organism–environment' relationships in biological systems. Properties in individuals have been conveniently accommodated in IBMs. IBMs are, in general, contrasted with the conventional mathematical models that deal with population properties as variables (e.g. differential equations for analysing population density). Various properties can be incorporated to the individuals in the hierarchy of biological systems. First at the individual level, attributes in different regimes in life processes could be addressed such as identification of individuals (e.g. name, position), physiology (e.g. age, health state), morphology (e.g. growth, structure) and ecology (e.g. movement, resource utilization). Individual uniqueness and variation can be efficiently illustrated under the framework of IBMs. In addition, complex processes of reproduction (e.g. mating, fission) could be elucidated in IBMs, as IBMs are suitable for fabricating the complex inter-individual relationships and for assigning new attributes to progenies. Subsequently, the individual properties could be projected upwards to higher levels at population through various forms of interactions with other individuals: competition, predation, parasitism, etc. (Chon *et al.*, Chapter 7). As stated above, the inter-individual relationships can be further extrapolated to larger scales in a hierarchical manner in biological systems [8, 16]. Recently, the protocols [17] and extensive case studies [16] in IBMs have been reported.

Two example studies are provided for demonstrating construction of IBMs in Chapter 7, group behaviour and population dispersal. The demonstration program for demonstrating group behaviour is listed in FLOCKI (Flocking thorough IBM) written with MATLAB to illustrate dynamic processes in chasing and escaping behaviour of preys and predators. Program for demonstrating population dispersal 'POPDIS' written with Visual Basic is provided to simulate dispersal of pest population and control effects (Chon *et al.*, Chapter 7).

The models for CA are presented in Chapter 16 (Chen). As stated above, the models in CA are defined as systems of cells interacting in a simple way with application of local rules in spatial domain, but could display complex overall behaviour after integrating local information. Spatially lumped models, for instance, the Lotka–Volterra model may not be able to take into account the effects of individual difference, spatial heterogeneity and local interactions. The individual variations are sometimes crucial to the dynamics and evolutions of ecosystems. The states are updated in discrete time steps according to local evolution rules, which are functions of the states of cell itself and its neighbours. Cellular automata often exhibit 'self-organization' behaviour. Even starting from complete disorder, the simple components act together to produce complicated patterns of behaviour (Chen, Chapter 16).

In Chapter 16, EcoCA was introduced as an example to illustrate application of CA. EcoCA is a two-dimensional CA model for simulating predator–prey system. The states of the model (i.e. empty, prey and predator) are determined by the previous state of the neighbour cells and provide the spatially explicit progresses in the predator–prey relationships. The models in IBM and CA were not represented in Ecological Modelling in the period 1975–1982, whereas 5% of the model papers were published on IBMs from 2000 to 2006.

Advantages of IBM and CA are:

- capable of accounting for local information (IBM: individuality; CA: site (or cell));
- could reveal the local–global relationships;
- capable of accounting for adaptation within the spectrum of properties;
- software available, although the choice is more limited than by conventional dynamic models;
- spatially explicit information available.

The disadvantages are:

- complex models as many properties are considered in the system;
- can be used to cover the individuality of populations, but they can hardly cover mass and energy transfer based on the conservation principle;
- require many data to calibrate and validate the models.

3.8 Spatial models: Chapters 6 and 20

The individual differences may be crucial for the model results and are expressed uniquely in ecological processes. In addition, variability resides in spatial differences in ecological processes and is illustrated in many important theoretical (e.g. distribution–abundance relationships) and practical (e.g. spatial invasion of species) issues. Spatial presentation has been one of the main directions in model development as discussed above. Models that give the spatial presentation must also consider the spatial differences produced from forcing functions and state variables. Spatial information on the forcing function and the state variables (non-biological and biological) may be decisive in presenting the model results in various situations: practical use, understanding the ecological reactions, providing proper policies of ecosystem management, etc.

There are a number of possibilities to cover the spatial differences in the development of ecological models. It is not possible to cover them all in this volume. The chapters on surface modelling (Chapter 6) and flow pattern and mass distribution (Chapter 20) are directly related to presentation of spatial information. IBM (Chapter 7) and CA (Chapter 16) can also present ecological processes in spatial domain.

Chapter 6 (Yue *et al.*) on surface modelling directly demonstrates the spatial presentation of ecological processes and shows how the obtained data through interfacing are processed to produce meaningful geographical and ecological information. The model output provides a comprehensive view on spatial conformation of the variables at issue in the system. Chapter 6 computationally presents surface modelling of population distribution on the earth surface systems with known spatial coordinates. In analogy to the physical gravity model, the concept of potential population distribution was developed: the influence of a city upon a grid cell is assumed to be proportional to the city's size, weighted inversely by the distance of separation between the grid cell and the city. Within a given threshold distance, the potential population distribution is formulated according to size of city and distance between grid cell and city. The procedures in surface modelling include creation of a surface for weighting factors covering the study area, derivation of weights adjusted with auxiliary data sources and illustration of population distribution corresponding to the weights (Yu *et al.*, Chapter 6). The major auxiliary tools such as ArcInfo GIS and Delphi computer were also used for modelling.

As an example, population distribution in national scale in China was provided in Chapter 6. The models in Surface Modelling of Population Distribution (SMPD) were applied to various spatial data (e.g. net primary productivity, elevation, water system, city distribution and urbanization) and produced map for population distribution on the national scale.

While Chapter 6 provides the spatial distribution on the large-scale geographical information, Chapter 20 (Miranda and Neves) illustrates the specific fluid processes under hydrodynamic conditions based on the Navier–Stokes and continuity equations. The chapter discusses how water properties change due to the flow pattern and spatially redistribute at each time step in 2D or 3D by utilizing the Mohid system. The Mohid includes the three-tier system, such as the bottom tier for the hydrodynamic model, the middle tier for the transport models and the top tier for water quality models. The hydrodynamic model provides the transport models with a velocity

field: evolution of water properties is calculated with Eulerian and Lagrangian transport models to compute how water properties change due to the flow pattern (Miranda and Neves, Chapter 20).

Examples for the fluid patterns were provided with the program of Tagus Operational Model. The operational model illustrates historical and real-time observations and predicts daily changes in atmospheric and water conditions in the Tagus estuary. In addition, the program for sediment transport was provided to reveal sediment transport at Nazaré Canyon (off Portugal) by using Lagrangian tracers. The models simulated bottom sediments, highlighted erosion and deposition areas and tracked the particles in transport (Miranda and Neves, Chapter 20).

It is not surprising that Ecological Modelling has published almost 250 papers about spatial modelling from 2000 to 2006. This model type was not represented in *Ecological Modelling* in the period 1975–82, while as much as 19% of the model papers were published on the topics of spatial distribution in the period 2000–2006.

Spatial models that are represented in Chapter 6 and Chapter 20 and other related chapters offer the following advantages:

- covering spatial distribution specifically;
- presenting many informative ways, for instance, GIS;
- available for interlinking with other information system.

The disadvantages are:

- require usually a huge database to provide a sufficient amount of information for calculating spatial distribution of variables;
- difficult in calibration/validation and time-consuming;
- complex model is usually needed to give a proper description of the spatial patterns.

3.9 Ecotoxicological models: Chapters 14 and 15

As stated before, ecotoxicology has been an important topic in the development of ecological sciences. Toxic agents are human-originated and produce toxic effects in complex and integrative manner across different levels of biological systems (Chon *et al.*, Chapter 15). Toxic effects are critical in maintaining safety of ecosystems without provision of energy subsidy, whereas other sources of disturbance (e.g. organic pollution) may produce some positive side (e.g. increase in productivity at low levels, intermediate disturbance hypothesis) in the system. Along with rapid industrial development, numerous toxic chemicals have been either discovered or synthesized and the chemicals affect biological systems in various ways. Appropriate policies on risk assessment could be established from proper model development in estimation of toxic affects and provision of suitable management strategies.

Two chapters, 14 (Jørgensen) and 15 (Chon *et al.*), are provided to cover toxic effects in an integrative way in this volume. Chapter 14 on ecotoxicological models deals with estimation of toxic agents in environment, providing information on presence of toxic materials and safety criteria in ecosystems. The procedures of ecotoxicolgical model covers: (1) obtaining the best possible knowledge about the possible processes and roles of toxic substances, (2) measuring parameters from the literature and/or from survey and experiments, (3) estimating the parameters through modelling, (4) comparison of the actual and calculated data and estimating feasible processes, (5) estimating feasible processes and state variables and (6) carrying out sensitivity analysis to evaluate the significance of the individual processes and state variables (Jørgensen, Chapter 14).

Example of ecotoxicological model is given with estimation of tylosine in Chapter 14. The model is explained in Section 3.1. Regarding that the criticality of toxic materials, the model needs to be calibrated and validated for every toxic substance that may be applied on the model. A general estimation is possible with the software EEP (estimation of ecotoxicological parameters).

While ecotoxicological models in Chapter 14 regard toxic substances as environmental factors, Chapter 15 (Chon *et al.*) focuses on the side of biological organisms and introduces a new aspect in dealing with modelling toxic effects across different levels in biological systems. The chapter presents (1) monitoring response behaviours and (2) modelling integrative effects of toxic substances in the gene–individual–population relationships based on IBM.

Behavioural measurements have notable advantages in environmental assessment: (1) to close the gaps existing between large (e.g. community surveys) and small (e.g. molecular analyses) scales in measurements, (2) to provide continuous information on environmental changes (e.g. water quality) in an appropriate time scale and (3) to be economical in terms of continuous measurement (Chon *et al.*, Chapter 15).

Behavioural monitoring itself may not be directly related to conventional concept of ecological modelling. However behavioural methods are included in this volume as detection of data of response behaviours provides a broad scope in characterization of toxic effects in a comprehensive manner. Behavioural data, however, are complex to analyse as a high degree of variability resides in the observed data. The chapter introduces computational methods for detecting data for response behaviour observed after the chemical treatments to the indicator specimens. ANNs including multi-layer perceptron and self-organizing map (SOM) and Fourier transform were used for data analysis.

Examples for detecting behaviour are introduced as the program named as ANNBED. ANNBED is used for monitoring the changes in the movement patterns after the treatments with the trained SOM as time progresses. New input data entering the network as a time series was accordingly recognized on the map. If the entering data are placed in the marked zone of abnormal behaviour, the recognition system of the SOM can accordingly issue a warning signal.

Chapter 14 also introduces the models covering toxic effects in an integrative manner at different levels (i.e. gene, individual and population) of biological systems based on IBMs. Various phenotypic and genotypic traits were assigned as attributes of the individuals and were inter-linked through the individual–individual interactions.

An example of modelling on integrative toxic effects is provided in the program of Integrative Gene–Individual–Population (IGIP) relationships. The models were presented to elucidate both genetic and demographic processes through simulation of genetic and behavioural interactions among individuals.

As stated above, ecotoxicological models are, in principle, not representing a ubiquitous model type, as biogeochemical models or population dynamic models are applied widely in ecotoxicology and in other ecological processes. It is, however, preferable to treat ecotoxicological models as a separate model type, because they are characterized by:

1. Our knowledge to the parameters is limited and estimation methods are therefore needed and have been correspondingly developed recently.
2. Due to the use of safety factors and the limited knowledge, the parameters of the ecotoxciological models often need to be conservative and straightforward in determining the degree of toxicity in the system; in particular, the so-called fugacity models illustrate this feature.
3. The models include often an effect component.

Chapter 14 illustrates points (1) and (2), while Chapter 15 illustrates the effect in this case on the behaviour and on the gene–individual–population relationships as well. The area of application is, in this case, obvious: to solve ecotoxicological research and management problems and perform environmental risk assessment for the application of chemicals.

The advantages of this model type are:

- tailored to ecotoxicological problems;
- simple to use in most cases;
- often includes an effect component or easily interpreted to quantify the effect.

The disadvantages are:

- requires a large number of parameters for toxic substances needed for model development due to complex factors residing in ecotoxicological systems (e.g. toxins, organisms, environmental factors) (we know only at the most 1% of these parameters);
- implies that we need estimation methods that inevitably have a high uncertainty; therefore, the model results also have a high uncertainty;
- inclusion of an effect component requiring a high level of knowledge to the effect, which is also limited.

3.10 Stochastic models: Chapter 12

Uncertainty is one of the critical issues residing in ecological data. In contrast to conventional deterministic models, stochastic models are characterized by using randomness in the system and deal with variability in addressing ecological processes. The randomness could be applied to various components in ecological models, in the forcing functions (e.g. factor) or in the model variables (e.g. population densities).

The randomness is generated to deal with limitation in our knowledge in revealing natural phenomena. We cannot, for instance, have accurate and decisive information on the temperature on the 5th of May next year at a given location, but can have information on the patterns of measured temperatures based on previous measurements. Changes in temperatures have been recorded to follow the normal distribution in the last hundred years. Consequently, this normal distribution could be used as a probability density function to represent a probable temperature in the future. Similarly, many of the parameters in the ecological models are dependent on random forcing functions or on the factors that we hardly can include in our model without presenting them too complex. A normal distribution of these parameters is known and by using Monte Carlo simulations based on this knowledge, it is possible to consider the randomness. By running the model several times, it becomes possible to obtain information on the uncertainty of the model results due to the uncertainty in our knowledge – in this case, about the parameters. It is recommended to apply stochastic models, whenever the randomness of forcing functions or processes covered by the parameters are significant.

Stochastic processes could be expressed in various models. The processes could be presented in a biogeochemical model, a spatial model, a structural dynamic model, an IBM or a population dynamic model as in Chapter 12. Chapter 12 deals with population density as a principal parameter with variability. Densities were randomized along with changes in the survival and maturation rates. Probability was used for generating variability in the variables observed in dynamic processes in populations. Changes in population status such as extinct or losing significant genetic resources could be dealt with in stochastic processes. Especially, the probabilities of catastrophic outcomes or population explosions can be efficiently considered using stochastic models through simulation of temporal or spatial variation (Borsuk and Lee, Chapter 12).

Chapter 12 illustrates both aspects of the advantages of the stochastic models: characterizing the central tendencies of a population and addressing variable sources of variability and uncertainty. Probability networks were used to generate probabilistic inferences and predictions in this chapter. Once all relationships in a network are quantitatively defined, probabilistic predictions

of model endpoints can be generated conditional on values (or distributions) of any 'up-arrow' causal variables. These predicted endpoint probabilities and provided information on various aspects of population changes: the relative change in probabilities between alternative scenarios, the magnitude of expected population response to historical changes or management policies, while accounting for uncertainties and stochasticity (Borsuk and Lee, Chapter 12).

Examples are provided to estimate population dynamics of fish. BayVAM [12] was used to estimate population changes in Westslope Cutthroat Trout in the Upper Missouri River Basin, USA. BayVAM is a stochastic, stage-structured demographic model that has been recast as a probability network by incorporating results from many Monte Carlo simulations over all possible combinations of model parameters.

Next example was shown in CATCH-Net in elucidating population dynamics in Brown Trout in the Rhine River Basin, Switzerland. CATCH-Net is a probability network model developed to assess the relative importance of different local stress factors in limiting brown trout density in Swiss rivers (Borsuk and Lee, Chapter 12). In contrast to BayVAM, CATCH-Net does not rely on an external simulation model, but rather includes a dynamic representation of the fish life cycle within the network itself. This is accomplished by creating dynamic nodes for which the values at one time step depend on the values of other nodes at a previous time step. Chapter 12 also provides information on the stochastic life-cycle model underlying BayVAM.

The model of stochastic dynamics has the following advantages:

- randomness in forcing functions or processes considered;
- the uncertainty in the model results obtainable.

This model type has the following disadvantages:

- information on the distribution of randomness in the model necessary;
- highly complex and requires longer computer time and resources.

3.11 Rule-based models: Chapter 17

Numerous types of data are obtained in ecological studies according to heterogeneous environmental conditions and different sampling practices. It has been widely recognized that various mechanisms in ecosystem dynamics are still unclear owing to high complexity and non-linearity. In addition, the majority of the understandings are qualitative rather than quantitative. It is therefore necessary to develop methods that combine semi-knowledge with semi-data (Chen, Chapter 17). The application focuses on the development of models based on a dataset limited in quality and/or in quantity, but the method can, in principle, also be applied in cases where the model would be improved by formulation of rules that are incorporated from available knowledge.

Chapter 17 (Chen) focuses on the rule-based technique, which derives the rules from the often limited data available from *in situ* measurements, while taking expert knowledge as reference. This model type makes it possible to develop a model in spite of a limited dataset, provided that some general knowledge about the system reactions is available. The rule-based techniques (i.e. feature reasoning, case reasoning, decision trees, physically based empirical rules) that are applicable to qualitative data are introduced in Chapter 17. As an example, an integrated numerical and rule-based model was provided to forecast the algal blooms in the Dutch coastal waters. The model used the integrated numerical and rule-based techniques to forecast the algal blooms in Dutch coastal waters.

Fuzzy approaches are also partly dealt with in Chapter 17, covering the knowledge-based Mamdani-inference method [18]. In addition, qualitative reasoning is introduced in Chapter 19

(Bredeweg and Salles). The models on rules for elucidating transition of states of the variables are covered in this chapter and the chapter will be outlined later in Section 3.13

This type of the rule-based model has the following advantages:

- applicable to the situations where the data sets are limited in quality and quantity;
- reveals the causality relationships (if causal 'rules' are applied).

The disadvantages are:

- knowledge of rules (e.g. causality relationships) necessary for modelling;
- constrained by calibration and validation in application of the limited dataset.

3.12 Hybrid models: Chapter 10

Flexibility of model execution has been one of the key issues in contemporary development of the models to cope with more complex phenomena observed in various ecological processes. In principle, the hybrid models can be designed by any combination of the 11 previously listed models; but only very few hybrid models have been developed up to now. It is expected that numerous additional models will be developed in the future to combine the advantages of some selected models, while eliminating some of the disadvantages of the other models.

In this volume, Chapter 10 (Cao and Recknagel) introduces hybrid models combining evolutionary algorithm and the object oriented model. The methods presented in biologically inspired algorithms were flexible to be combined with other models to present validity of highly complex processes in ecological sciences. The proposed hybrid model has demonstrated significant improvements of the model feasibility in presenting the lake categories 'warm-monomictic hypertrophy' and 'dimictic mesotrophic' after the optimization of either process or parameter representations. As an example, a model was provided in parameter optimization in phytoplankton population dynamics 'SALMO'.

The hybrid models have the following advantages:

- flexible and being able to squeeze as much information out of the database;
- applicable to complex systems;
- reveal the causality relationships (if the causal 'rules' are applied in the model).

The disadvantages are:

- complicated in model implications; precise knowledge of rules needed (if information on the causality-relationships is required);
- constrained by calibration and validation (in case the limited dataset is used for modelling).

3.13 Mediated/institutionalized models: Chapters 4 and 19

In addition to computational algorithm, institutionalization is important for realization of successful construction of the designed models. This volume also presents the processes of model building to ensure that the models could be appropriately constructed in accordance with the purpose of model building. With the roots of the modelled problems, the procedure implies that all relevant partners participate or are represented in the model development. Consequently all participants can accept the models as the problems included their roots and all possible factors that are decisive for solving the problems.

Chapter 4 (Jørgensen) on model making discusses the overall procedure for designing model development in practice. The procedure could be applied to construction of all different model types. The chapter focuses on institutionalized or mediating modelling. When the problem is complex with many different interests, interactions, and various aspects on model development, it is recommended to use institutionalized modelling. There are many examples of non-institutionalized models that have failed, because, without the workshop of institutionalization, it is difficult to collect all knowledge about the system and the very roots of the problems. It may even be difficult sometimes to understand what the real core problem is. It is here the procedure proposed for the development of institutionalized models showing how possibly to zoom down to the key issues in model building. Complex problems are like icebergs; it may be only 10% that is visible. We have to know the form and shape of the entire iceberg – also what is under the water surrounding the iceberg.

Chapter 19 (Bredeweg and Salles) introduces qualitative reasoning and provides guidelines for the procedure of institutionalized modelling procedure based on this method: (1) identification of a common reference for all the participating group, (2) definition of the problem and of the scale in modelling, (3) construction of qualitative model as a preliminary prototype, (4) construction of quantitative model, (5) testing various selected scenarios and the conclusions and (6) follow-up evaluation.

Chapter 19 presents implementation of qualitative reasoning for modelling [19]. The chapter introduces an approach to knowledge capture from the data, especially when theoretical background on the target system is weak, when the problems are ill-defined and when data are incomplete, uncertain or simply not available. Conceptual models based on qualitative reasoning are valuable tools for both pre-mathematical modelling and standalone artefacts for understanding, predicting, and explaining the system's behaviour (Bredeweg and Salles, Chapter 19). The procedure proposed in Chapter 4 for model building could be also elucidated by following the guidelines proposed in qualitative reasoning.

A typical qualitative reasoning engine takes a scenario as input and subsequently produces output, a state graph capturing the qualitatively distinct states in which a system may manifest. A scenario is an initial description of the system subject to the reasoning. The models provided in the chapter are implemented as Garp3, a modelling workbench with a graphical user interface that integrates facilities for model building and for running qualitative simulations. The software, Qualitative Reasoning and Modelling, was used to run the model (Bredeweg and Salles, Chapter 19). The model type represented in Chapter 19 is particularly fitted to be used whenever a mediated / institutionalized model has to be developed. After considering the application of the presented model types, institutionalized models could be recommended as possible answer to solve the complex problems.

The model type has the advantages:

- characteristic for institutionalized modelling, namely that a holistic view and inclusion of the roots of the problems are ensured;
- highly probable to workable solution in a comprehensive manner, being opposite to the experience from the selected use of models that may focus partially on the core problems not necessarily covering detailed issues from all the participants.

The disadvantage of institutionalized modelling is:

- cumbersome and time consuming for application (because the model requires all the relevant aspects from partners discussed in the workshops for model building).

3.14 Network analyses and calculations: Chapter 18

Ecosystem data mostly consists of numerous components (e.g. nutrients in environmental factors, species in communities) and the components are inter-connected in a complex manner in the system. Considering numerous components and all possible connections among the components, there is a need for analysing the data from the aspect of ecological networks. The network calculations in general can be interpreted ecologically. A network model can be considered a special type of biogeochemical/bioenergetic models that focuses particularly on the transfer of mass or energy in the food web. Ecological networks have been extensively studied in this regard. The properties of ecological networks are one of the basic columns in theoretical perceptions in all ecosystems. It is therefore under all circumstances very useful to perform network analyses and calculations. It has been considered useful to include in this model overview network models or network analyses.

Chapter 18 (Kazanci) presents a useful tool to perform network analyses and to develop an ecological model of a network with the idea to understand the properties and characteristics in the ecological systems. Software called EcoNet is presented and the possible calculations that can be made with the software are illustrated. EcoNet includes definition of flows among component storage of information and compartment flow types (i.e. donor or donor–recipient controlled flows, Michaelis–Menten flow). In principle, the network models are, as already mentioned, stock-flow models that are comparable with the biogeochemical and bioenergetic dynamic models. The essential difference from these models, however, is that the holistic properties of networks can be calculated.

As an example, an eight-compartment model based on John M. Teal's work is provided to carry out the classic study of energy flow in a Georgia salt marsh. The EcoNet model provides model description, results and evaluation.

The network models have the following advantages:

- flexible and efficient in deducing connectivity among components based on flow analysis;
- reveal information on interactions among variables in complex ecological processes in a comprehensive manner (e.g. food web dynamics, flow of nutrients in ecosystems).

The disadvantages are:

- sufficient datasets required;
- numerous parameters to be checked in models.

4 Applicability of the model types

As mentioned in the introduction, new model types were provoked by the model problems that became clear in the early–mid-1970s when ecological modelling started to be applied more extensively as a tool for environmental management, as stated above. The conventional models, biogeochemical/bioenergetic dynamic models and population dynamic models had some shortcomings to cope with the difficulties. The ecological modellers tried to solve the problems since 1970s. Today, the shortcomings have been at least partially eliminated by development of contemporary modelling types.

It is possible to indicate which model type would be the most optimal choice in a given modelling situation based on data types and the problems the model is dealing with. Overall scope has been presented in Table 1 as stated above, covering objectives, computational techniques and examples for the different types of models. For more practical purpose, to answer on 'Which

Table 2: Model types applicable to different data sets.

Description of data sets	Model types recommended
High quality, homogenous	Biogeochemical/bioenergetic dynamic models; population dynamic models; other models based on mass balance or structural dynamics
High quality, heterogeneous	Ecological informatics; fuzzy models; hybrid models
Only typical or average values	Static models
Uncertainty in data	Fuzzy models
No quantitative data, only rules	Fuzzy models; rule-based models; conceptual knowledge
Important to utilize data sets	Ecological informatics
Individuality in data	IBMs
Stochastic property in data	Stochastic models
Spatial information	Surface models; CA; models for mass distribution
Connectivity among components	Network models

Table 3: Model types applicable to different problems/systems.

Problem/system	Model types for recommendation
Distribution of matter or energy*	Biogeochemical/bioenergetic dynamic models; other models based on mass balance or structural dynamics
Development of populations*	Population dynamic models; stochastic models
Toxic compounds: distribution/effect	Ecotoxicological models
Individuality important	IBMs
Structural changes emphasized	Structurally dynamic models
Forcing functions and/or processes stochastic	Stochastic models; IBMS
Spatial distribution important	Spatial models; CA; IBMs; models based on mass distribution
Connectivity of components emphasized	Network models
Holistic view important to solve problems	Mediated/institutionalized models
Causality relationships in complex situations	Rule-based models; conceptual knowledge

*ANNs and other techniques in ecological informatics could also be applied if causality is less important and optimum data utilization is important. Hybrid models may be applied to combine causality with good data utilization.

model type should be applied in which context?', some suitable models for consideration at initial stage are suggested in Tables 2 and 3 in simpler forms. Table 2 sketches optimal models according to different types of data available for modelling.

In addition to data types, the optimal models could be outlined according to different problems and/or systems for which the models are designed (Table 3). The typical problems in ecosystems such as distribution of matter or energy could be conveniently dealt with the biogeochemical/bioenergetic dynamic models including other conventional models based on mass balance (e.g. Ecopath). Similarly, population dynamics, another key problem in ecology,

can be specifically handled by population dynamic models or stochastic population dynamics models if probabilistic property resides in the data sets.

In addition to fundamental issues such as material distribution and population dynamics, various biological and environmental properties are observed in ecological processes. Individual variability residing in the ecological systems has drawn a strong attention from the modellers. IBMs could be specifically used for this purpose. Adaptation in biological properties is an additional issue that has been significantly noted for model development. Structurally dynamic models could be efficiently used in this case and could be efficiently incorporated into the conventional models on material distribution and energy dynamics along with the concept of adaptive changes in ecological structure.

Stochastic properties are also frequently observed in either biological or abiological factors in biological/ecological systems. Stochastic nature could be elucidated in a stochastic population dynamics model as stated above. Stochastic dynamics models would be also suitable for dealing with all the probability-related problems in forcing functions and ecological processes observed in biological and abiological components in the system in model building. The probabilistic features could be additionally presented in other types of models. In IBMs, for instance, movement of each individual could be determined by probability density functions, or other dynamic and spatial models could be linked to stochastic processes.

Spatial conformation and connectivity among the components are other key properties observed frequently in ecological processes. Spatial models and CA could be useful for the former case to convey information on spatial and temporal dynamics of the variables in the system. Network models are efficient in handling the latter case and would provide useful information for various aspects on the network-related ecological processes (e.g. food web dynamics, nutrient cycles). Due to unique properties in toxic effects, toxicological models could be specifically developed under the framework of ecotoxicology and integrated risk assessment. In complex situations generally shown in ecological systems, rule-based models and methods in conceptual knowledge could be used to reveal the causality relationships. Finally, flexible models such as mediated/instutionalized models would be suitable for solving the problems or designing plans under the holistic view with qualitative information (Table 3). The list of optimal models in the table, however, is not exclusive. The other models could be certainly modified or can be combined with other models to be inclusively used for solving different problems in a flexible manner.

References

[1] Jørgensen, S.E. & Bendoricchio, G., *Fundamentals of Ecological Modelling*, 3rd edn, Elsevier: Amsterdam, 2001.

[2] Jørgensen S.E., *Integration of Ecosystem Theories: A Pattern*, 3rd edn, Kluwer Academic Publishers: Dordrecht, 2002.

[3] Ermentrout, G. & Edelstein-Keshet, K., Cellular automata approach of biological modelling. *Journal of Theoretical Biology*, **160**, pp. 97–133, 1993.

[4] Wolfram, S., *Collected Papers in Cellular Automata and Complexity*, Addison-Wesley: Reading, MA, 1994.

[5] Walters, C., Pauly, D. & Christensen, V., Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*, **2**, pp. 539–554, 1999.

[6] Lek, S. & Guégan, J.F., *Artificial Neuronal Networks: Application to Ecology and Evolution*, Springer: Berlin, 2000.

[7] Recknagel, F. (ed.), *Ecological Informatics: Scope, Techniques and Applications*, Springer-Verlag: Berlin, 2006.
[8] Grimm, V. & Railsback, S.F., *Individual-Based Modeling and Ecology*, Princeton University Press: Princeton, 2005.
[9] Jørgensen, S.E. (ed.) Modelling concepts. *Modelling in Ecotoxicology*, Elsevier: Amsterdam, pp. 15–35, 1990.
[10] Bornholdt, S. & Schuster, H.G. (eds), *Handbook of Graphs and Networks: From the Genome to the Internet*, Wiley-VCH: Weinheim, 2003.
[11] Bredeweg, B. & Struss, P. Current topics in qualitative reasoning. *AI Magazine*, **24**, pp. 13–130 (Special issue), 2003.
[12] Lee, D.C. & Rieman, B.E., Population viability assessment of salmonids by using probabilistic networks. *North American Journal of Fisheries Management*, **17**, pp. 1144–1157, 1997.
[13] Jørgensen, S.E. & Fath, B., *A New Ecology: A Systems Approach*, Elsevier: Amsterdam, 2007.
[14] Peters, R.H., *The Ecological Implications of Body Size*, Cambridge University Press: Cambridge, 1983.
[15] Lett, C., Silber, C. & Barret, N., Comparison of a cellular automata network and an individual-based model for the simulation of forest dynamics. *Ecological Modelling*, **121**, pp. 277–293, 1999.
[16] Breckling, B., Müller, F., Reuter, H., Hölker, F. & Fränzle, O., Emergent properties in individual-based ecological models – introducing case studies in an ecosystem research context. *Ecological Modelling*, **186**, pp. 376–388, 2005.
[17] Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Muller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U. & DeAngelis, D.L., A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, **198**, pp. 115–126, 2006.
[18] Mamdani, E.H. & Assilian, S., An experiment in linguistic synthesis with a fuzzy logic controller. *International Journal of Man-Machine Studies*, **7**, pp. 1–13, 1975.
[19] Weld, D. & de Kleer, J. (eds), *Readings in Qualitative Reasoning about Physical Systems*, Morgan Kaufmann Publishers: Palo Alto, CA, 1990.