

Introduction: An Overview

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1.1 APPLICATION OF ECOLOGICAL MODELING

The field of ecological modeling has developed rapidly during the last four decades due to essentially three factors:

1. The development of computer technology, which has enabled us to handle very complex mathematical systems.
2. A general increased knowledge about environmental problems, including that a complete elimination of pollution is not feasible (denoted zero discharge), but that a proper pollution control with limited economical resources available requires serious considerations of the influence of pollution impacts on ecosystems. Models are indispensable tools in this context.
3. Our knowledge about environmental and ecological problems has increased significantly. We have particularly gained more knowledge of the quantitative relations in the ecosystems and between the ecological properties and the environmental factors.

Good models are syntheses of our knowledge about ecosystems and their environmental problems, in contrast to a statistical analysis, which only will reveal the relationships

between the data. A model is able to include our entire knowledge about the system, if required for a proper solution of the environmental problem:

- which components interact with which other components, for instance that zooplankton grazes on phytoplankton,
- our knowledge about the processes often formulated as mathematical equations which have been proved valid generally,
- the importance of the processes with reference to the problem;

These are a few examples of knowledge which may often be incorporated in an ecological model. This implies that a model can offer a deeper understanding of the system than a statistical analysis. It is therefore a stronger tool in research and can result in better management plans, on how to solve environmental problems. This does of course not mean that statistical analytical results are not applied in the development of models. On the contrary, models are build on all available knowledge, including knowledge gained by statistical analyses of data, physical-chemical-ecological knowledge, the laws of nature, common sense, and so on. That is in short the advantage of modeling.

The idea behind the use of ecological management models is demonstrated in Fig. 1.1. Urbanization and technological development has had an increasing impact on the environment. Energy and pollutants are released into ecosystems, where they may cause more rapid growth of algae or bacteria, damage species, or alter the entire ecological structure. An ecosystem is extremely complex, and it is therefore an overwhelming task to predict the environmental effects that such emissions may have. It is here that the model comes into the picture. With sound ecological knowledge, it is possible to extract the components and processes of the ecosystem that are particularly involved in a specific pollution problem to form the basis of the ecological model (see also the discussion in Chapter 2). As indicated in Fig. 1.1, the

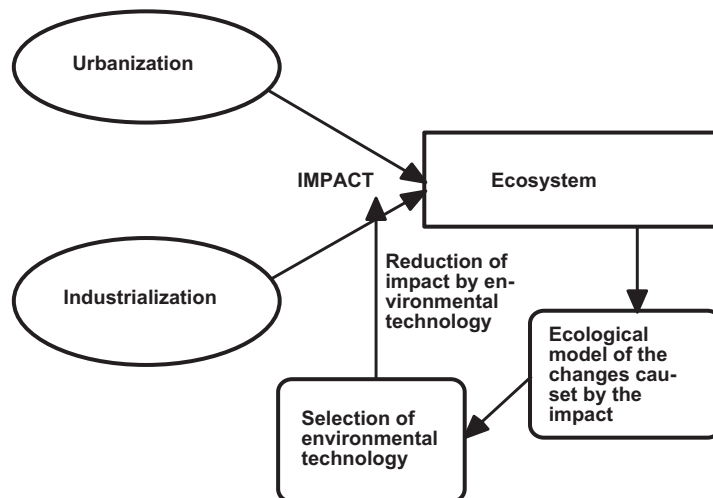


FIGURE 1.1 The environmental problems are rooted in the emissions resulting from industrialization and urbanization. Sound ecological knowledge is used to extract the components and processes of the ecosystem that are particularly involved in a specific pollution problem to form the ecological model applied in environmental management to select good solutions to the focal problem.

resulting model can be used to select the environmental technology eliminating the emission most effectively.

Fig. 1.1 represents the idea behind the introduction of ecological modeling as a management tool around years 1970–1975. The environmental management of today is more complex and applies therefore a wider spectrum of tools.

Today, we have as alternative and supplement to environmental technology, cleaner technology, ecotechnology, environmental legislation, international agreements, and sustainable management plans. Ecotechnology is mainly applied to solve the problems of nonpoint or diffuse pollution, often originating from agriculture. The significance of nonpoint pollution was hardly acknowledged before around 1980. The global environmental problems play furthermore a more important role today than 20 or 30 years ago, for instance the reduction of the ozone layer and the climatic changes due to the greenhouse effect. The global problems can hardly be solved without international agreements and plans. Fig. 1.2 attempts to illustrate the more complex picture of environmental management today.

Mathematical models are not only applied in environmental management but are widely applied in science, too. Newton's laws are for instance relatively simple mathematical models of the influence of gravity on bodies, but they do not account for frictional forces, influence of wind, etc. Ecological models do not differ essentially from other scientific models not even by their complexity, as many models used in nuclear physics today may be even more complex than ecological models. The application of models in ecology is almost compulsory, if we want to understand the function of such a complex system as an ecosystem. It is simply not possible to survey the many components and their reactions in an ecosystem without the use of a model as a holistic tool. The reactions of the system might not necessarily

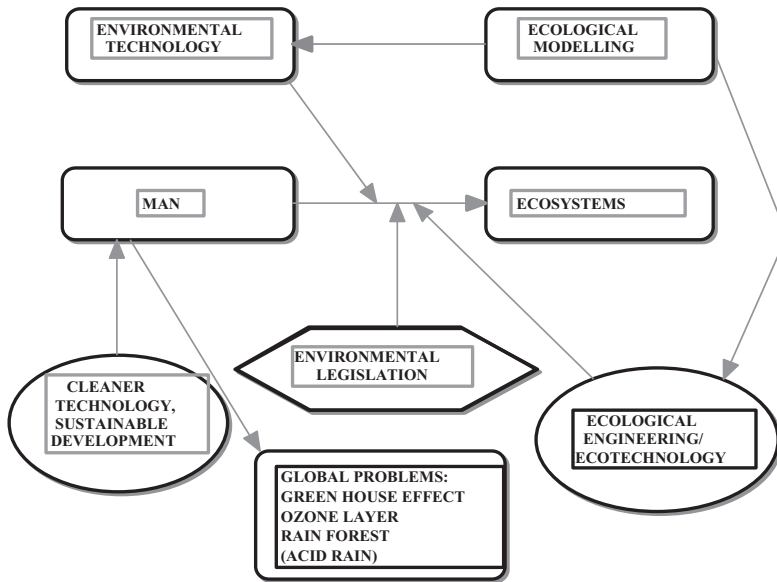


FIGURE 1.2 The idea behind the use of environmental models in environmental management. The environmental management of today is very complex and must apply environmental technology, alternative technology, and ecological engineering or ecotechnology. In addition the global environmental problems play an increasing role. Environmental models are used to select environmental technology, environmental legislation, and ecological engineering.

be the sum of all the individual reactions, which implies that the properties of the ecosystem as a system cannot be revealed without the use of a model of the entire system.

It is therefore not surprising that ecological models have been used increasingly in ecology as an instrument to understand the properties of ecosystems as systems. This application has clearly revealed the advantages of models as a useful tool in ecology, which may be summarized in the following points (Jørgensen and Fath (2011)):

1. Models are useful instruments in **survey** of complex systems.
2. Models can be used to reveal **system properties**.
3. Models reveal the weakness in our knowledge and can therefore be used to set up **research priorities**.
4. Models are useful in tests of **scientific hypotheses**, as the model can simulate ecosystem reactions, which can be compared with observations.

And we would add here:

5. Models are useful **experimental tools**. If a model is developed and it is working reasonably meaning that the calibration and validation are acceptable, it is possible to ask the model several questions. A few examples are given here, while a couple of more detailed illustrations are presented in Chapter 11, as models have been used as experimental tools frequently in the development of toxic substance models. The model can be used as an experimental tool by answering for instance the following illustrative questions that are easily answered by the model:
 - a. an alternative equation has been proposed for a certain specific process and therefore it is natural to ask: would it be beneficial to use this alternative equation or is the previously used equation giving more acceptable results?
 - b. the model is working fully acceptable for a number of cases (for instance for several compounds in ecotoxicological modeling) but not for other cases (or other compounds in ecotoxicological modeling). Would it be possible to explain this discrepancy by the lack of some processes in the nonworking cases? Let us try and see how the model reacts to addition of one or more processes in the nonworking cases.
 - c. if the model is not working in a minor number of cases, could it be explained by the influence of a factor which has another value in the nonworking cases or maybe another equation is valid in these cases.

Hence, be open to ask the model questions and to test the model and its components. A model is a very useful experimental tool in this context. It is easy to test additions or changes, and performances of these tests imply that we use the model as an experimental tool.

1.2 MODEL CLASSIFICATION AND MODEL TYPES

Table 1.1 shows a general perception of ecological model classification 40 years ago. The differences among the three model types are the choice of the ecological components that are used as state variables. If the model aims for a description of a number of individuals, species, or classes of species, then the model will be called **biodemographic**. A model that describes the energy flows is named **bioenergetic** and the state variables will typically be

TABLE 1.1 Model Identification

Model Types	Organization	Pattern	Measurements
Biodemographic	Conservation of genetic information	Life cycles of species	Number of species or individuals
Bioenergetic	Conservation energy	Energy flow	Energy
Biogeochemical	Conservation of mass	Element cycles	Mass or concentrations

expressed in kW or kW per unit of volume or area. **Biogeochemical models** consider the flow of material, and the state variables are indicated as kg or kg per unit of volume or area. These model classes were extensively used in ecological modeling 40 years ago and are still widely applied today, because ecological models have, indeed, focus on the mass flows, energy flows, and the changes of populations, as they describe the dynamics of ecosystems.

The title of this book is ecological model types, because the development in ecological modeling has to a high extent been: How can we consider the many other additional factors in our model? For instance:

- How can we include the spatial distribution which is often significant for the ecological reactions and dynamics? or
- How can we consider the differences among individuals in a population? or
- How to account for adaptations and shifts in species compositions?
- Can we build models if we have heterogeneous databases? Or only qualitative data?
- How do we tackle the problem of ecological changes caused by the expected climatic changes?

These kinds of problems that were emerging in ecological modeling as the field developed called for solutions, and the problems have been solved during the last 30–40 years. We have today 14 model types meaning that it is possible to distinguish between 14 different modeling approaches that are able to solve the model problems that emerged during the development of ecological modeling during the last 40 years. Models of today are, however, often using two or more of these approaches simultaneously because two or more of the factors mentioned above have impact on the ecosystem dynamics at the same time. Therefore, we should maybe rather distinguish between 14 different tool boxes that are available to develop ecological models today, considering *all* the possible factors, influencing the ecological processes in ecosystems. Throughout the book we will use the expression model type, but it will be understood that the 14 types represent 14 solutions to processes and factors that are important to consider if we want to cover almost all possible ecosystem dynamic cases.

The 14 different model approaches are denoted model types, but it is acknowledged that they are 14 different tool boxes that can be applied to solve the modeling problem that confronts us, when we want to develop a model that is able to solve a specific environmental or scientific problem. We do acknowledge that in a practical and specific model situation, we need to apply two or more—sometimes several—of the modeling tool boxes.

The 14 tool boxes or model types can be described as follows:

1. Biogeochemical models are models that describe the flows of mass and/or energy in ecosystems by using the mass and energy conservation principles. The models are often based on differential equations, expressing accumulation per unit of time = inputs – outputs. As flows of energy and matter are important dynamic processes in ecosystems, it is not surprising that this model type is the most applied of the 15 types.
2. Population dynamic models describe the changes of the number of individuals in populations. This model type applies differential equations. Increasing numbers are explained by growth and decreasing numbers by mortality. Interactions between populations are often considered in this type and the age structure of the population is often considered in the model, as the properties of a population are dependent on the age class.
3. Steady state models are as the name indicates not able to consider the dynamics of ecosystems, but often are these simpler models very useful to apply, because the models are simpler than type 1 and 2, and often is a steady state sufficient information for environmental management or for understanding of ecological reactions?
4. Spatial models give, in addition to the flows of matter and energy and the changes of populations, information about the spatial distribution of matter, energy, or populations. The spatial distribution in ecosystems is often crucial for the ecological reactions to ecosystem impacts. We distinguish between surface models that describe the spatial distribution and
5. Spatial models, geo process models, that not only describe the spatial distribution but also the spatial movements. It is a further development of surface models. Generally, advanced software has been developed to cope with the spatial distribution of both forcing functions and state variables, as for instance a geographical information system, GIS.
6. Structural dynamic models that include a description of the changes of the species' properties due to adaptation and the shifts in the species composition due to changes of the prevailing conditions. These models attempt therefore to describe the changes in the ecological structure due to changes in the impacts (described by the forcing functions) on the ecosystems. The abbreviation SDM is often applied. SDM can be developed either by use of a goal function and use of knowledge about which species are best fitted under which circumstances. The latter approach is sometimes denoted artificial intelligence.
7. Individual-based models (IBM) consider that individuals in a population may be different and have different properties. Obviously, differences are often crucial for the ecological processes and reactions to changed impacts and may be used to cover the selection of the best fitted properties—it means that the adaptation can be described by IBM.
8. Artificial Neural Network (ANN), is mathematical modeling tool that is able to extract model information from a large database even if it is heterogeneous. A direct use of ANN leads to a black box model, but it is possible to include algorithms that can account for causality and thereby develop at least grey models.
9. Self-organizing maps (SOM), is another mathematical tool that like ANN is able to develop a model from large databases. Like for ANN, it is possible by use of suitable algorithms to include causality into the model.

10. Ecotoxicological models are focusing on ecotoxicological problems. All the other tool boxes can in principle be used to develop ecotoxicological models. The biogeochemical tool box is very frequently applied to develop ecotoxicological models. When it is beneficial to distinguish ecotoxicological models from other model types, it is due to the special properties of ecotoxicological models. They are often simple, because they have often a high uncertainty, which is acceptable because they are applied with a high safety margin. The parameters of the models are often very dependent on the properties of the toxic substance. And as there are a high number of different chemical compounds with different properties, only a relatively limited number of the parameters have been determined by measurements in the laboratory. It has therefore been necessary to introduce estimation methods, which can be used to find approximate values of the parameters.
11. Fugacity models are focusing on the distribution of chemicals (mainly toxic chemicals) in the environment. They are therefore a special type of ecotoxicological models. They have often a high standard deviation, which is, however, acceptable, as they are mainly used to compare the total environmental impacts of the use of two or more chemicals. The comparison makes it possible to select the chemical that should be preferred from an environmental point of view among the possible ones.
12. Fuzzy models are used when the data are fuzzy, meaning only qualitative or semiquantitative. Obviously the model results cannot be presented more accurately than the underlying data and the model results are therefore presented qualitatively or semiquantitatively, for instance a few numbers of levels. Fuzzy models are anyhow important to use in ecology, because a level is important not necessarily the exact number, for instance when the distribution of species is in focus.
13. Stochastic models are considering that many forcing functions are stochastic, which implies that they should be described by using a probability distribution. It is for instance the case with the meteorological variables that often play a significant role for the model results.
14. Climate change models (CCM) encompass models that attempt to predict the climate changes due to increased emissions of greenhouse gases (mainly carbon dioxide and methane) and models that cover the ecological consequences of the climate changes. The latter group models belong to SDM, but it is preferred in this overview to include them in CCM, because the problems associated with the increased emission of greenhouse gases and with the climate changes in general are very central in the environmental debate. There has therefore been an increased number of CCMs and it is therefore beneficial to try to understand the characteristics of these models to learn from previous experience gained by development of CCMs.

1.3 APPLICATION OF THE 14 MODEL TYPES

It is difficult to make a statistical study of the use of different types of models due to the overlap in the application of the types (tool boxes) in practice both when environmental management problems and when scientific ecosystem problems are in focus. It has, however,

been attempted to consider 10 different model types as the following types in the overview in [Section 1.2](#) are considered as one type 4+5, 6+14, 8+9, and 11+12. From the statistics of the 10 types, we will be able to see the development in the application of models from the mid-1970s, when the journal *Ecological Modelling* started, and up to the past 3 years 2012–2014. To make the statistics more informative, the number of papers of the 11 types in *Ecological Modelling* the first 5 years (1975–1979) and the past 3 years (2012–2014) has been supplemented by the number of theoretical papers covering modeling theory and covering systems ecology. The results of the statistics are summarized in [Table 1.2](#).

The development of *Ecological Modelling* reflects the development of the field ecological modeling, as *Ecological Modelling* is publishing 40–50% of all ecological modeling papers published in international peer-reviewed scientific journals. First of all the field has grown enormously as we today published in *Ecological Modelling* 16 times as many pages per year. The number of pages has been calculated as pages using the format of 1975–1979.

TABLE 1.2 Ecological Model Types, Statistics

Model Type	Number of Papers 2012–2014	Number of Papers 1975–1979
Biogeochemical models	309	62
Population dynamic models	176	13
Spatial distribution models	110	4
Structural dynamic models	50	4
Steady state models	2	0
Ecotoxicological models	16	8
Individual-based models	31	0
ANN and SOM	5	0
Stochastic models	3	0
Fuzzy and fugacity models	6	0
Modeling theory	58	15
Systems ecology	62	14
Socio-economic-ecological models	3	3
Total	830	123
Pages	9690	2323
Pages, format 1975–1979	22,287	2323
Pages/paper format 1975–1979	26.8	18.9
Pages/year format 1975–1979	7429	465
Ratio pages/year	16	1

The number of words per page is 2.3 times as much today as in the years 1975–1979. The number of papers published per year has increased by a factor 12. The papers are therefore about 33% longer today, which is probably due to an increased complexity of the published models. It is also characteristic for the development that the six model types that today cover 7% of the papers were not identified in 1975–1979. The field ecological modeling has therefore increased not only in the number of publications but also in the number of model types applied for model development. Spatial models and IBMs have increased in number more than the number of papers in general, indicating that these model types are clearly more significant than in the 1970s. Biogeochemical models have only increased by a factor about 7–8, but this type is still the most applied model type in ecological modeling. One-third of all models published are biogeochemical models today, while it was about two-thirds in the 1970s.

The theoretical papers—modeling theory and systems ecology—have increased less than the other types of papers. It is understandable as these theoretical questions—How to develop a good model? and How does an ecosystem function?—were core problems in the 1970s. Still, significantly more papers are published today to cover these two important theoretical fields.

1.4 THE ECOSYSTEM AS AN OBJECT FOR MODELING

Ecological models attempt to capture the properties and characteristics of ecosystems. Ecologists generally recognize ecosystems as a specific level of organization, but the open question is the appropriate selection of time and space scales. Any size area could be selected, but in the context of ecological modeling, the following definition presented by [Morowitz \(1968\)](#) will be used: “An ecosystem sustains life under present-day conditions, which is considered a property of ecosystems rather than a single organism or species.” This means that a few square meters may seem adequate for microbiologists, while 100 square kilometers may be insufficient if large carnivores are considered ([Hutchinson, 1970, 1978](#)). Population–community ecologists tend to view ecosystems as networks of interacting organisms and populations. [Tansley \(1935\)](#) claimed that an ecosystem includes both organisms and chemical–physical components, which of course has to be reflected in the ecological models. It inspired [Lindeman \(1942\)](#) to use the following definition: “An ecosystem composes of physical-chemical-biological processes active within a space-time unit.” [E.P. Odum \(1953, 1959, 1969, 1971\)](#) followed these lines and is largely responsible for developing the process–functional approach, which has dominated the last few decades.

This does not mean that different views cannot be a point of entry. [Hutchinson \(1970, 1978\)](#) used a cyclic causal approach, which is often invisible in population–community problems. Measurement of inputs and outputs of total landscape units has been the emphasis in the functional approaches by [Likens \(1985\)](#). [O’Neill \(1976\)](#) has emphasized energy capture, nutrient retention, and rate regulations. [H.T. Odum \(1957\)](#) has underlined the importance of energy transfer rates. [Quinlin \(1975\)](#) has argued that cybernetic views of ecosystems are appropriate and [Prigogine \(1947\)](#), [Mauersberger \(1983\)](#), and [Jørgensen \(1981, 1982, 1986\)](#) have all emphasized the need for a thermodynamic approach for a proper holistic description of ecosystems and to include the important energetic aspects of ecosystems.

For some ecologists, ecosystems are either biotic assemblages or functional systems. The two views are separated. It is, however, important in the context of ecosystem theory to adopt both views and to integrate them. Because an ecosystem cannot be described in detail, it cannot be defined according to Morowitz's definition, before the objectives of our study are presented. Therefore the definition of an ecosystem used in the context of system ecology and ecological modeling, becomes:

An ecosystem is a biotic and functional system or unit, which is able to sustain life and includes all biological and nonbiological variables in that unit. Spatial and temporal scales are not specified a priori but are entirely based upon the objectives of the ecosystem study.

Currently there are several approaches ([Likens, 1985](#)) to the study ecosystems:

1. Empirical studies where bits of information are collected, and an attempt is made to integrate and assemble these into a complete picture.
2. Comparative studies where a few structural and a few functional components are compared for a range of ecosystem types.
3. Experimental studies where manipulation of a whole ecosystem is used to identify and elucidate mechanisms.
4. Modeling or computer simulation studies.

The motivation ([Likens, 1985](#)) in all of these approaches is to achieve an understanding of the entire ecosystem, giving more insight than the sum of knowledge about its parts relative to the structure, metabolism, and biogeochemistry of the landscape. [Likens \(1985\)](#) has presented an excellent ecosystem approach to Mirror Lake and its environment. The study contains all the above-mentioned studies, although the modeling part is rather weak. The study demonstrates clearly that it is necessary to use all four approaches simultaneously to achieve a good picture of the system properties of an ecosystem. An ecosystem is so complex that you cannot capture all the system properties by one approach!

Ecosystem studies are widely using the notions of order, complexity, randomness, and organization. They are used interchangeably in the literature, which causes much confusion. As the terms are used in relation to ecosystems throughout the volume, it is necessary to give a clear definition of these concepts in this introductory chapter. According to the Third Law of Thermodynamics about entropy at 0 K, see [Jørgensen \(2008\)](#), randomness and order are each other's antithesis and may be considered as relative terms. Randomness measures the amount of information required to describe a system. The more information required to describe the system, the more random it is.

Organized systems are to be carefully distinguished from ordered systems. Neither kind of systems is random, but whereas ordered systems are generated according to simple algorithms and may therefore lack complexity, organized systems must be assembled element by element according to an external wiring diagram with a high level of information. Organization is functional complexity and carries functional information. It is nonrandom by design or by selection, rather than by a priori necessity. Complexity ([Jørgensen and Svirezhev, 2005](#)) is a relative concept dependent on the observer. We may distinguish between structural complexity, defined as the number of interconnections between components in the system, and functional complexity, defined as the number of distinct functions carried out by the system.

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