Chapter 2
What Are the General Conditions Under Which Ecological Models Can be Applied?

Felix Müller, Broder Breckling, Fred Jopp, and Hauke Reuter

Abstract The purpose of this chapter is to discuss the conditions under which models can be applied. Modelling can help to solve specific problems, but not all questions in ecology require or benefit from the application of a model. It is therefore necessary to have an idea about the criteria under which the development of a model can provide useful information or help to solve questions in ecological analysis and which conceptual and technical approaches are the most appropriate ones. Technical knowledge about the particular modelling techniques is presented in the subsequent chapter of this book. Here, we intend to give an overview of the basic criteria of model application.

2.1 Models as Instruments of System Analysis

Models are abstractions of reality and instruments for the survey and analysis of complex systems (Wainwright and Mulligan 2004; Dale 2003). They are used to reduce the complexity of systems with reference to the specific problem that the observer wants to solve. Ecological models can depict the interactions and changes of environmental elements and simulate the dynamics of spatial and temporal patterns in ecosystems. Thus, they are instruments of environmental systems analysis (Bossel 1992; Gnauck 2000; Hannon and Ruth 2001).

A fundamental system comprehension should be considered as an initial conceptual condition for successful modelling. Ecological systems are complexes of biotic and abiotic elements, which are interrelated by flows of energy, matter and information (Breckling and Müller 1997). These interactions build up a comprehensive and complicated network of heterogeneous direct and indirect effects (Fath and Patten 2000). This network has an extraordinary high connectivity and its complexity rises drastically with the number of elements, relations and nonlinear interactions (Salthe 1993; Grant and Swannack 2007). This has the implication that

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F. Jopp et al. (eds.), *Modelling Complex Ecological Dynamics*,
DOI 10.1007/978-3-642-05029-9_2, © Springer-Verlag Berlin Heidelberg 2011

we might never be able to fully understand these ecological systems structures and functions and the resulting dynamics. On the other hand, there are many good reasons why we should attempt to do so, e.g., the need to search for solutions of our urgent environmental problems. Systems analysis (see Chap. 4) and modelling provides steps and theories to cope with complexity in ecological systems.

Ecological modelling provides a large set of different approaches to analyse drivers of systems dynamics and extrapolate developments. However, it also has to be applied critically. The modeller should be conscious of the following:

- Models are observer-defined abstractions that can reflect reality only in the framework of the observer's viewpoint, the amount and quality of input information and the basic assumptions of the modeller
- There is an optimal degree of model complexity. This is not the highest complexity because large and complicated models tend to be difficult to handle and can increase uncertainty (Joergensen and Bendoricchio 2001)
- In any case the model *outputs* comprise specific uncertainties. To optimize the results, modelling needs extensive information about the investigated system and about the modelled object or process, as well as a precise question or hypothesis and data for both model development and model testing

2.2 Model Creation Should Be Carried Out in a Systems-Analytical Procedure

To make the general modelling procedure more illustrative, Fig. 2.1 sketches the single steps of a system analysis leading to an applicable ecological model. More technical details are elaborated in Chaps. 4 and 23) on model development, while the conceptual fundament is discussed here. The steps of model preparation begin with basic questions like:

- What is the focal object of the model?
- What is the specific aim of the model and what is its role in solving the focal problem?
- What are the spatial and temporal extents of the model and in what dimensions should the outputs be provided?
- What are the spatial and temporal resolutions of the model and how detailed should the processes be that are represented in the model (*model complexity*)?
- What are the most important issues to be represented and what are the relations between them?
- What data are necessary to (a) develop and (b) test the model?
- What are the forcing functions of the modelled systems and how do these constraints affect the elements?
- How can the interrelations be depicted in a clear and understandable graphical scheme?
- What are the basic assumptions made in model development?

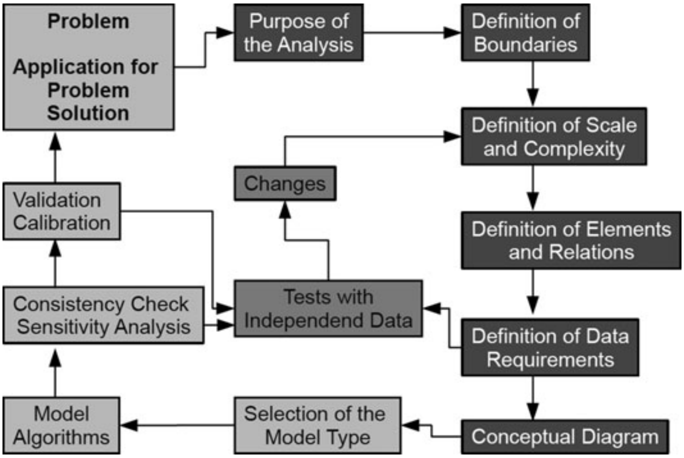


Fig. 2.1 Basic steps of environmental systems analysis and modelling (adapted from Müller 1999)

Although these questions seem to be trivial, they are often not dealt with in a satisfactory manner in practical modelling applications. However, answering these questions and documenting the derived conception needs to be done before technical steps of model development are taken. There are two main reasons for this requirement: On the one hand, this allows one to find the optimal conception for the model without forgetting or neglecting basic preconditions, and on the other hand, the documentation of the respective answers will enable the modeller to return to his original objectives when he has been lost in the complexity of model improvement. Figure 2.1 further illustrates that model development follows a cyclic process: Already with the definition of the data requirements, limitations might become obvious that make it necessary to change the general outline. The results of calibration and validation (see below) usually support this *experience*, and sometimes demand the modeller to go back to the very first steps because some basic requirements could not be met.

Taking into account these working procedures, two focal strategic items should be highlighted to avoid an exaggerated application of the cyclic principle:

Models Require a Clear and Precise Specification of the Focus of Investigation

A clear distinction needs to be made between what is part of the problem and what is left out of the considerations. This may sound fairly straightforward; however, in almost any practical situation this decision poses a serious challenge. The web of ecological interactions is complex. However large the resources for research might be – there will always be additional influences that have to be ignored and cannot be integrated in a given context. A *complete* model of ecological interactions in any field is impossible. Therefore, delimitations (where to end the list of relevant influences) require good reasoning and judicious decisions of the modeller. Regardless of how well the rest of the work is done, unreasonable decisions about what to consider and what not, can determine the usefulness of the entire work. Therefore, this issue should be taken very seriously. Decisions require a balance and linkage of the general nature of the problem under consideration, as well as the specific working conditions and available technical, logistical and intellectual means.

Models Need Intelligently Chosen Criteria for the Distinction of Important and Unimportant Aspects

There has to be a consideration of relevance concerning elements and relations that could make an important part of a model. The decision about which subjects and interactions are considered to be relevant depends on the available background information. During the work, it may turn out that the background information was not sufficient. A careful analysis of what is already known in the field is crucial. The modeller needs a clear view of which influences contribute (sometimes, always or only under specific conditions) in an important way to the given problem. Therefore, a literature survey to attain an overview that goes well beyond the current focus is required. Often the necessary decisions should be prepared in a discussion with co-operators or other experts in the field and experts in related topics.

Furthermore, a consideration of the working conditions for the modelling process is required: What is the available time span, what are the resources, manpower, data bases, etc., and what are the temporal constraints of model development? The answers can be integrated into a synopsis of the requirements to solve a given problem and the compromises that derive from the limitations (and preferences) of the specific situation. This background knowledge will allow the modeller to develop a reasonable work plan. Experience tells us that the duration (time requirement) of model elaboration is difficult to anticipate. Certain steps may be achieved much more easily and faster than expected; however, in most cases unexpected obstacles occur and things usually take longer than expected.

2.3 The Modelling Potential: What Can Models Help to Do?

Models are used for a wide range of purposes. Wainwright and Mulligan (2004) list different application fields for environmental models. They can, for example, be applied as an aid in research, as tools for understanding, tools for simulation and prediction, as virtual laboratories, and integrators between disciplines, and in addition, they are research products and means for communication. In the following, some of these model purposes and potentials are elucidated.

Models Can Help to Analyse the Results of Empirical Investigations or a Theoretical Problem that Is Not Accessible Through Statistical Data Interpretation Alone

Models can generally work within two types of situations – helping to solve empirical problems where a model needs to meet certain requirements resulting from field or laboratory measurements (data), and for theoretical purposes that investigate conditions and possibilities based on assumptions. Models usually go beyond situations and questions that require only data interpretation and statistical analysis. A good example for such a modelling approach is the complex competition situation between hardwood hammocks and mangroves (see Fig. 2.2). In the marshlands of South Florida Everglades (U.S.) hardwood hammocks and mangroves occur with distinct boundaries between their respective areas. Teh et al. (2008) applied a spatially-explicit simulation model to examine the effects of the salinity of the aerated zone of soil overlying a saline body of water, known as the vadose layer, as a function of precipitation, evaporation and plant water uptake (Fig. 2.2 right) on the vegetation. The model predicted that mixtures of saline and freshwater vegetative species represent unstable states, which are highly dependent on initial conditions of the system. The model conceptually explains the mechanism

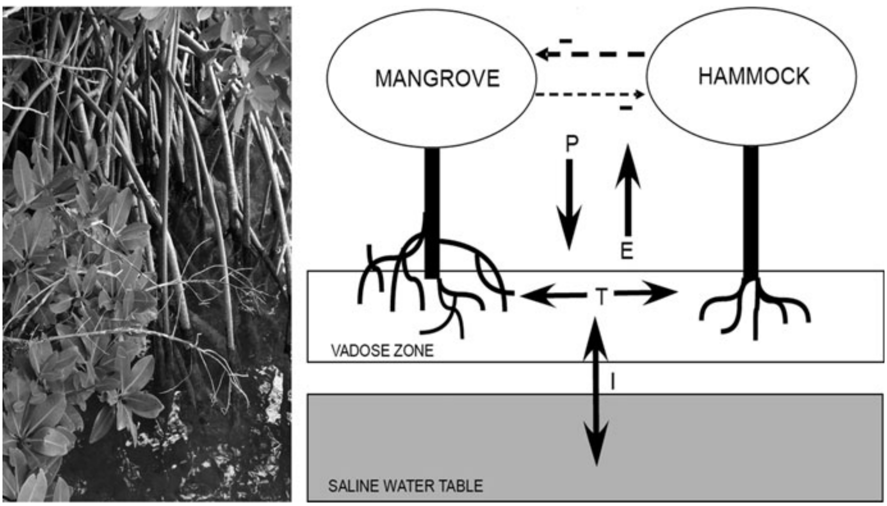
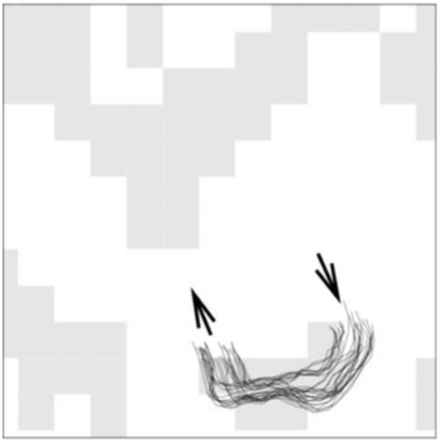


Fig. 2.2 Model on separation of mangroves (*left*) and hardwood hammocks in the marshlands of South Florida Everglades (U.S.). The model focuses on water transport and effects of the salinity on the vegetation (*P* precipitation, *E* evaporation, *T* transpiration, *I* infiltration, Teh et al. 2008)

that allows both vegetation forms to coexist – and why disturbance pattern can have long lasting influences.

Statistics are applied to data, while models are used to interpret systems states and processes, representing the dynamic developed and often applying an iterative procedure. However, models and statistical applications cannot be strictly and consistently delimited, though specific domains of application can be defined – with a minor overlap.

Furthermore, modelling allows to test the coherence and degree of completeness of the understanding of distinct ecological processes. For instance, for a long period it was not clear what kind of behavioural modes would be sufficient to lead to highly aligned fish schools. With an individual-based modelling approach to represent different behavioural patterns of individual fish it was possible to test the existing assumptions (Fig 2.3). Results revealed that, depending on distances between neighbouring fish, attraction, adjustment of direction and swimming speed and repulsion were sufficient to produce schools. Modelling also revealed, that it was only necessary to consider a limited number of nearest neighbours to keep a school together (Huth and Wissel 1994). For aggregation of a school, weighting of neighbours according to distance turned out to be a more efficient model assumption (Reuter and Breckling 1994). Thus models may help to check if knowledge on partial processes is sufficient to represent observed system behaviour.



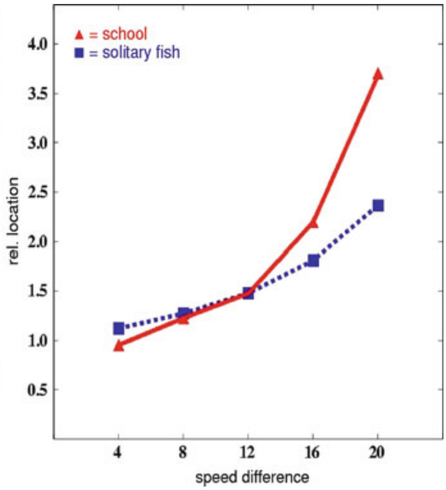


Fig. 2.3 Schooling in fish. *Left*: Traces of a fish school in a heterogeneous environment: the gray shaded area is a part of the environment with higher food density where individuals move more slowly. Coming from the upper right some individuals are outside the food patch and accelerate. To stay within the school these individuals change direction (turn right). As a result the whole school stays on the food patch. *Right*: This phenomenon occurs as an emergent property if the speed difference between preferred and non-preferred parts of the habitat is sufficiently large. Simulated schooling fish stay considerably longer on food patches than do solitary fish. (rel. location indicates how much longer a fish stays on food patches in relation to their coverages; speed difference to normal cruising speed of 25 units/timestep)

Models Can Help to Understand Emergent Properties (Emergent Phenomena)

Usually the modeller works in a situation where he has gathered various information about specific interactions of partial processes but is interested in the overall result to demonstrate how single processes overlay and produce new (emergent) phenomena. Nielsen and Müller (2000) have defined such emergent properties as self-organized features of a system that are not properties of the subsystems. Rather, these properties emerge as a consequence of the interactions within the system. They appear at one organizational level of a system and are not immediately deducible from observation of the single units in isolation, which compose the system. Many examples of emergence can be found in the regulation mechanisms of physiological processes, ranging between the levels of biochemical compounds, organelles, cells, tissues, organisms or populations. On all of these levels certain features emerge, which cannot be provided by the parts: For instance, an isolated chlorophyll molecule cannot use the energy of solar radiation for living processes. Only if it is embedded in a complex system of biochemical compounds, can it help to transform energy to become beneficial for the organism. Or – to consider a larger ecological context – cyclic processes in an ecosystem are only possible due to the interaction of the different subsystems. The storage of nutrients in the system can be comprehended as an important emergent property.

Many interpretations of emergence are based on the information flows between the systems' components. O'Neill et al. (1986) and also Allen and Starr (1992) have founded their ideas on the frequency distribution of ecosystem processes (Fig. 2.4). Following their hypotheses in hierarchy theory, the interactions between a single high frequency process produces the potential for processes of lower frequencies to provide constraints on the higher frequency units due to selected signal filtering procedures.

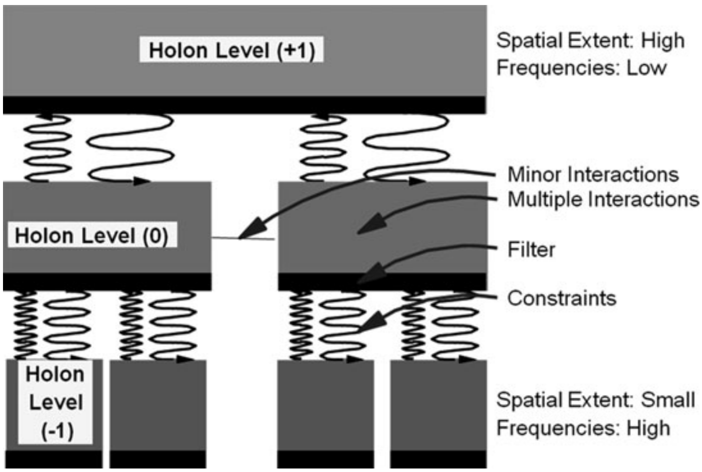


Fig. 2.4 Characteristics of hierarchical structures. Signal transfer between different levels of a hierarchy construct (modified after Müller 1992)

These temporal distinctions are linked with spatial differences: fast processes mostly operate on small spatial units while slow processes tend to have broader spatial extents.

A very practical consequence of hierarchical views on environmental systems is used to make the distinction of working scales for models: The modeller should focus on a certain part of the spatio-temporal continuum of ecological processes: by the selection of the *natural* frequencies and typical spatial extents of the core model variables, the modeller can define the focal level in the hierarchy of ecological relations. To depict the system's organization with minimum information, it is recommended that one works on three scales (with three typical frequencies), that are (a) the focal scale of the main variables (highlighting the interactions between subsystems at the same level of integration) and the two adjacent scales to consider, (b) the fast variables related with the sub-systems as well as (c) the slow variables that act as constraints. The latter frequently can be treated as forcing functions. Often, in model applications, the slow variables are set constant. This represents an approximation that can be reasonable for a limited time horizon but usually limits the long-term applicability of the model: The only constant phenomenon in living systems is change, and the way changes occur.

Models Can Clarify Interaction Implications Between Different Levels of Organization and Can Help to Understand Level-Crossing Phenomena

In the context of hierarchy theory, an organization level is considered as a result of the interactions of a number of elements that bring up specific properties on a broad scale coming into existence due to small scale interactions. For example, interactions among different individuals can result in a specific age distribution on the population level. The level of the individual and the emergent properties on the level of the population (age distribution, pattern of spatial distribution, or distribution of other properties) can be analysed.

The same conditions can be found concerning the overall properties of an ecosystem, based on the interactions of individuals, populations, and abiotic conditions of a particular location (see Fig. 2.5).

Models often use inputs from a lower level of organization and provide results on a higher level. Thus the modeller has to deal with the question, whether the knowledge on lower level processes (used as model input) is in accordance with the overall results on a higher level. In this sense, models deal with level-crossing phenomena. The model of beetle dispersal (Jopp and Reuter 2005) may be used as an illustrative example. It represents movements of carabid beetles in heterogeneous landscapes, depending on the species properties and landscape characteristics. The rules for the step length and angular deviation of single movement steps are derived from empirical data (Fig. 2.6 *left*). It can then be investigated what

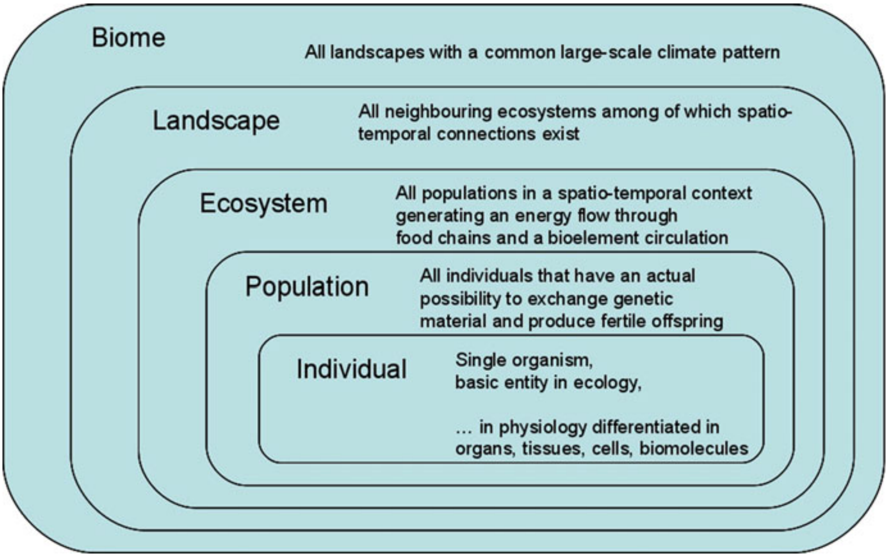


Fig. 2.5 Hierarchichal levels, which are distinguished as organization levels. Ecological modelling deals with individuals, populations, ecosystems, landscapes, and biomes. Still lower levels, from the biomolecule up to the individual, are the domain of physiology; however, sometimes these are also included in models along with ecological levels of interactions

effects these properties have on dispersal in differently structured landscapes (Fig. 2.6 *right*). Depending on the distribution of suitable and less suitable habitats, the model can provide results of how individual behaviour and landscape dispersal patterns relate over the long run.

This field of ecological analysis should not be dealt with by *expert's intuition* alone. In this regard, models allow an extension of conclusions beyond what is accessible in direct empirical investigations. With appropriate model approaches it can be studied how components of a level-crossing interaction network influence each other. For instance, Chap. 18 illustrates how trophic pyramids and trophic cascades of a wetland ecosystem (Everglades) are affected by hydrological changes.

Models Can Illustrate Iterative and Feedback Processes

In ecological models interactions between elements are in most cases specified in a computer programme and executed on a computer. The rationale behind this is that the number of repeated executions of all steps can be several orders of magnitude higher than what can be done by manual calculation. Modelling has special merits when feedback or iterative processes are involved: If we know the elementary interactions – what will be the result if they re-occur 10, 1,000 or 100,000 times? In linear cases, sometimes mathematical calculations can directly lead to a precise

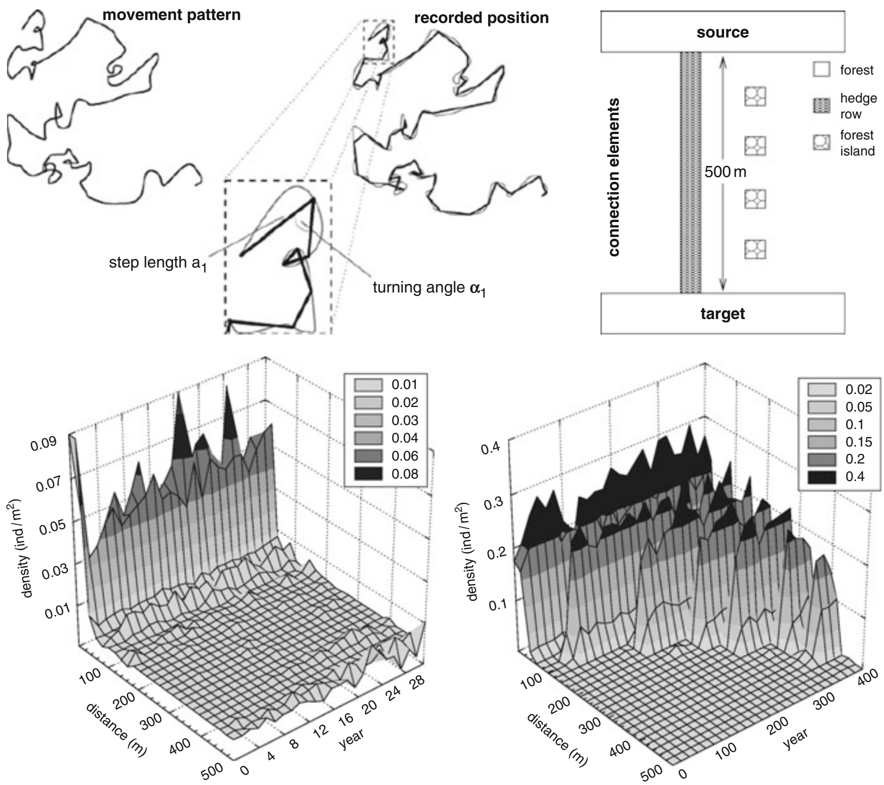


Fig. 2.6 The construction of Move Steps distributions and Model output from a model on beetle dispersal (Jopp and Reuter 2005). *Upper Left and Middle*: Derivation of movement rules from empirical data. *Upper Right*: Simulation set-up for the analysis of connectivity effects of hedgerows and stepping stones. The width of the hedgerows and the number of stepping stones are varied in the scenarios. *Lower Left and Right*: Resulting long term pattern of dispersal for a model population from a source habitat (*top*) to a sink habitat (*bottom*) which are connected by six habitats functioning as stepping stones. Dispersal success and densities result from a combination of movement speed, mortality on hostile lands and probability to cross habitat boundaries. *Abax parallelepipedus*, a slow disperser with high habitat fidelity, has to colonize all stepping stone habitats before reaching the sink habitat (lower right). In contrast, *Carabus hortensis*, which easily crosses borders between habitats, does not colonize the stepping stones, but reaches the sink habitat in a fraction of time (lower left)

result. Nonlinearities frequently are not so easy to extrapolate. Here models are often the only promising way to expand ecological knowledge. For instance, this is frequently the case on grid-based processes (see Chap. 8 on Cellular Automata).

A pattern studied on the basis of grid-based processes are forest fires. The final pattern can be well observed on the regional scale. The overall transition-rules on the small-scale, however, can only be estimated. Model assumptions can be tested to determine whether they lead to patterns that are in line with the observed findings (e.g. Ratz 1995).

New approaches additionally facilitate the potential to work with flexible interaction networks, where the number of elements and the way they are connected can change (see Chap. 11 on L-Systems, and Chap. 12 on Individual-based models). This poses high challenges to the conceptual development of simulation frameworks, especially if not only the involved quantities change in a nonlinear way, but also the structure changes in the course of interactions. This can be the case in modelling the structure and physiological processes in plants (see e.g. Figs. 4.3 and 4.4).

Models Can Facilitate an Understanding of Multi-Scale Problems in Ecology

Phenomena that involve several orders of magnitude in scales are usually difficult to handle. There are examples where model approaches can help to deal with large-scale issues that depend on very small scale interactions.

Nutrient budgets on the landscape level are an example (see Fig 2.7). Here initially the soil physicochemical potentials of different sites are used to calculate local nutrient flows, representing e.g. a patch scale. If the modelling question is

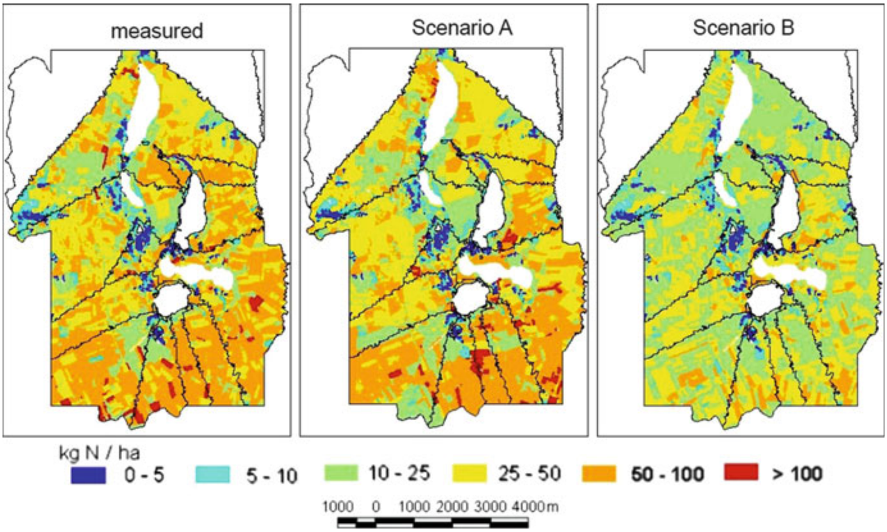


Fig. 2.7 Nitrogen leaching in the Bornhöved Lakes landscape simulated with the WASMOD modelling system (Reiche 1996). *Left*: The measured nutrient retention capacity of different soil types has been taken to calculate a business-as-usual scenario with a dominant small-farm structure. *Right*: Simulation of different scenarios: (**a**) Industrial agriculture – a structure with big farms and efficient land use practice leads to a change in land cover and land-use, providing an overall reduction of nitrogen leaching amounts. (**b**) Green agriculture – due to the reduced use of fertilizers and due to reduced pressures, i.e., on poor soils the nitrogen flows into the groundwater are heavily reduced

related to the budgets of landscapes or catchments, these small items have to be integrated to build up a landscape picture. But as the spatial scale increases, new processes arise, which were not evident at the smaller scale; for instance erosion, groundwater flow or airborne transports connect patches in a horizontal manner. Thus for the respective model analysis, a multi-scale approach has to be used with emergent processes at each level (see Chap. 22 for more examples).

Models Can Support Decision Making Processes

Besides their potential in basic research, ecological models can also be very helpful tools in decision making processes (also see Chap. 22 on Integrated Environmental Models). Often the environmental manager can hardly foresee the effects of certain measures for the states of environmental or social-ecological systems. To reduce this uncertainty, models can illustrate assessment components. In this context scenario modelling is playing a very important role. In that case the model constraints are defined due to the representation of different assumptions on environmental situations, management options or political strategies. From the model application the potential effects can be illustrated and an optimal strategy can be selected. On the other hand, model applications are usual parts of our everyday life; think of the weather forecasts, the characterisations of economic developments or the multiple economic applications of programmes to show what might happen if certain constraints of a system are changed. A most influential example can be taken from global climate models (Fig. 2.8). The predictions of future trends of global temperature rise, depending on different mitigation strategies, are basic elements of global political decisions.

2.4 The Limitations: What Models Cannot Do

Now that we have seen the potential of ecological models, it is also necessary to mention some limitations of models as well.

Limits in Predictability

Ecological models are not a new form of alchemy. You cannot put in cognitive lead, tin, and other low value materials, expect the computer to do magic and hope for intellectual gold as a result. The potential of modelling has limitations, and the “garbage in – garbage out” principle holds. Enthusiasm about modelling sometimes tends to obscure that. Modelling can expand knowledge; however, it cannot replace it. It can derive implications of given knowledge and it can be used to test interactive hypotheses. Because of the complex interactions that take place in ecological

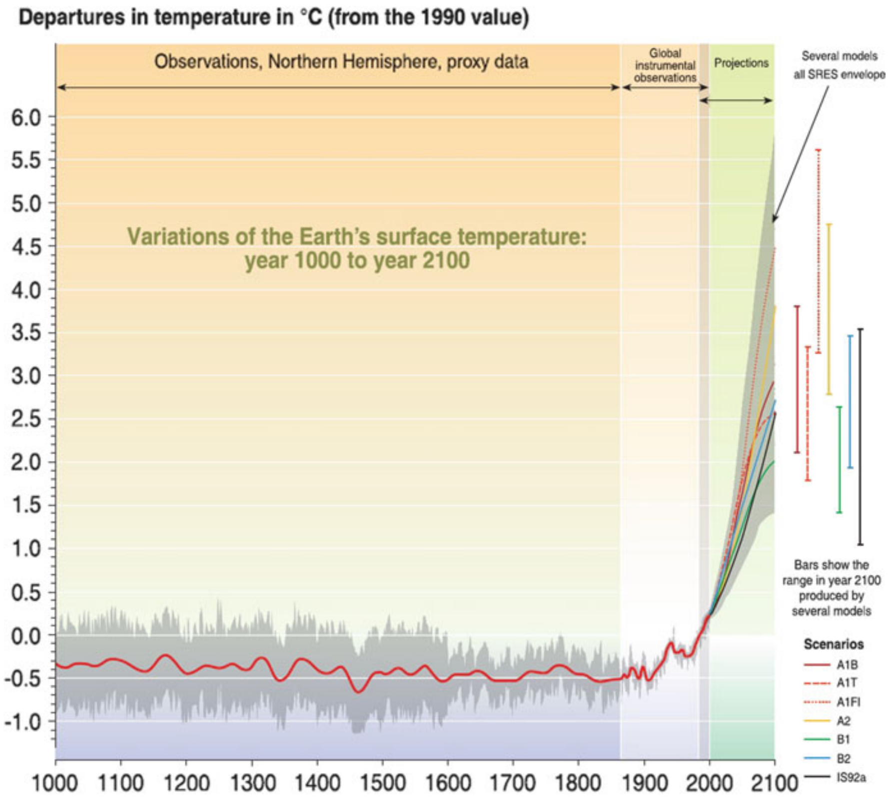


Fig. 2.8 Temperature trends and projections of global average surface temperature
source: UNEP/GRID-Arendal Maps and Graphics Library (2005), Philippe Rekacewicz, http://maps.grida.no/theme/climatechange

systems, the predictive power of models is usually limited. This is especially true for processes with a pronounced singularity, where local specific events largely influence the subsequent dynamics in a way that cannot be precisely forecast. However, probability estimations can often be derived through ecological modelling. To have an idea about this limitation is a precondition to reasonably applying ecological modelling.

Models Cannot Function Without a Precise Question or Hypothesis and an Appropriate Underlying Theoretical Framework

Although this demand seems to be trivial, it has to be stated that a very detailed task specification in connection with explicit knowledge about the purpose is a basic condition for successful modelling. It is essential to know the purpose and the modelling objective before one can decide how far the complexity of reality should be reduced in the modelling approach. The underlying theory is crucial for the interpretation and validation of the results.

Models Cannot Function Without a Data Base for Model Development and Testing

The correctness of a model has to be re-evaluated again and again during the model developmental procedure. The outputs have to be compared with the target system, usually the ecological reality. Thus, the modeller needs data from the reference system during several steps of model development.

The improvement of model quality proceeds in different steps. For these procedures, a deep understanding of the modelled subject is necessary, as well data for different types of model testing. The procedural steps generally are the following (Nielsen 2009):

1. *Consistency check and sensitivity analysis*. The model is checked versus logical predictions of what is likely to be the result of any change in the parameters and forcing functions of the model. Furthermore the question of parameter sensitivity should be assessed.
2. *Calibration*. One major issue to be addressed here is that the chosen parameter values need to be justified. This means that several aspects (e.g. uncertainty of the parameters, their accuracy, their significance for the model) have to be considered. Also, the results of the calibration can be observed by comparing the outputs with data sets.
3. *Validation*. This phase is the highest level of model quality assessment. It is a test of how well, model predictions (prognoses) are matched with actual observations. The higher the potential effect of the modelling results is, the higher should be the emphasis in testing model results against independent data. For validation, one or more datasets are required that describe the modelled situation *independent* of the data used during model development.

Different possibilities to apply data sets for model validation, for quality assessment of models and to secure correctness of model results are described in Chap. 23.

Models Have to Be Treated Skeptically When They Are Applied Outside the Validation Regimes

A consequence of the validation strategy is information on the range of validity of the model. If it is applied within the validation range, the results usually are of

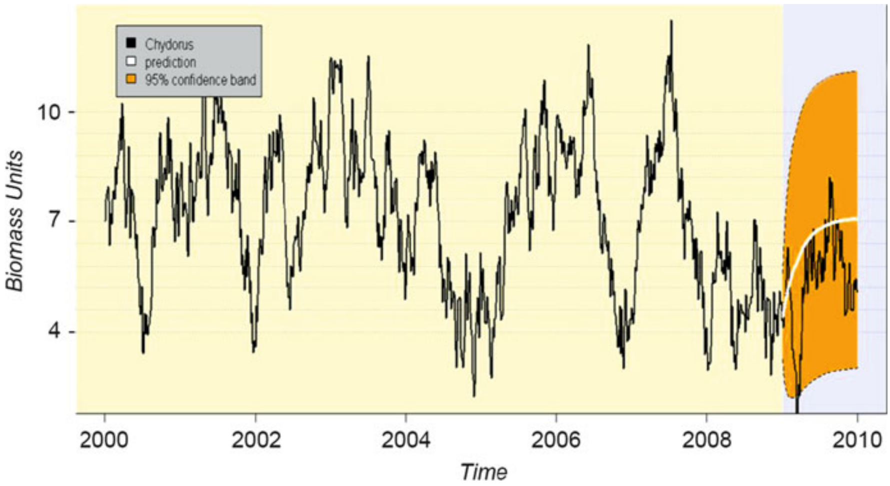


Fig. 2.9 Biomass dynamics of specific Northern-German zooplankton groups from Berlin lakes; *left part* of the figure: real measurements until 2009; *right part*: the projection for a further year on the basis of an autoregressive moving average model (Jopp, unpublished)

a high quality. But regrettably this is usually the most uninteresting case. Most models are developed to show potential future developments, and these dynamics of interest cannot be used for validation, because they are the application cases (However, later, the model quality can be improved on the basis of wrong predictions of the formerly future dynamics). We can never fully know how forcing functions and other input variables for our future model projections will develop through time; we can only know them later, retrospectively . Therefore model results will remain uncertain to a high extent (see e.g. Fig 2.9). If the ranges of the validation data sets are exceeded, the typical nonlinear relations or hysteresis effects can be responsible for extreme modifications of the system's behaviour (see Fig. 6.12). Also, if we apply models to other places than the area or system for which they were developed, there may be new parameter constellations that could not be taken into account during the development phase. Summarizing, a model will never be free of uncertainty and it is essential to respect the range of validity for each part of the model when discussing its results.

Models Rarely Produce Reliable Prognoses, but Can Be Used in Scenarios

Taking this point into account, models should not be used for specific prognoses. But as we still want to benefit from the modelling power, scenarios are a good level for applied modelling. When defining scenario conditions the user has to be aware that his model output may never be realized; i.e.; because it is likely that he will choose extreme initial conditions to show the potential difference of the outputs against 'business as usual' conditions.

If we summarize these limitations, we can list that:

- Successful models should be based on the awareness that they are abstractions. Therefore reality can only be reflected in the frame of the abstract input information.
- Models can provide results only within the limits of the basic assumptions.
- Models cannot mimic the complexity of nature. High model complexity does not mean high modelling efficiency.
- Models produce uncertainty.

As a consequence of these points, the modeller should try to assess the uncertainty of his predictions and – this may be the most important point – document all model assumptions and report the uncertainties to the user and the scientific community. By doing so, modelling as a scientific method does not exclusively follow the golden scientific rules of comprehensibility and reproducibility. It also enables the great opportunities that uncertainties provide: when prior conditions are not fully met and the output allows different interpretations, there is always the chance to follow sidelines of current scientific knowledge. Then, aside from the well-trodden trails, some of the most interesting findings and thrilling discoveries can be made http://www.springer.com/978-3-642-05028-2

Modelling Complex Ecological Dynamics
An Introduction into Ecological Modelling for Students, Teachers & Scientists
Jopp, F.; Reuter, H.; Breckling, B. (Eds.)
2011, XVII, 397 p. 131 illus., Softcover
ISBN: 978-3-642-05028-2