



REVIEW ARTICLE

## Use and limitations of ecological models

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### Abstract

- 1 - Modelling of ecological processes is not a recent area of scientific research but it is currently evolving fast due to the technological advances in computing power.
- 2 - Mathematical models can be readily used as tools for the efficient assessment of environmental quality, for studying the ecosystem functioning properties and for monitoring biodiversity.
- 3 - Conclusions based on ecological models are often used to reinforce policy design and environmental planning and management. A variety of different ecological models exists at the moment, each one with its advantages and disadvantages.
- 4 - The question that needs to be answered and the type of data available in each case, define the most suitable type of model. The limitations and malpractices occasionally observed during the use of ecological models are described.

### Introduction

Ecological models are been used in a variety of applications, such as the development of biodiversity conservation policies, the planning and management of natural reserve networks, and the impact assessment of global climate change, resources exploitation and expansion of alien species distributions. Policy makers and governmental organisations need fast, efficient and reliable management tools, such as the ones derived from the use of ecological models, in order to develop or update an environmental legislation framework. The predictive power of the modelling approaches makes them suitable for the investigation of hot spot scientific issues, such as the understanding of ecosystem functioning, the evaluation of

environmental health, and the monitoring of biodiversity. The ecological models can be used in both deep and shallow coastal systems to describe estuarine hydrodynamics, water quality, and ecosystem/food web dynamics. Some researchers have also used models which integrate socio-economic and ecological dynamics, in order to describe the environmental effects of future development scenarios (Langmead *et al.*, 2009; Lee *et al.*, 2009). The present viewpoint describes the different types of ecological models, their use in problem solving and management issues, as well as their limitations and potential for improvement.

*History and evolution of ecological modelling*  
Ecological modelling appeared for the first

time almost 90 years ago, but it was only during the last decades that the availability of high computing power allowed the development of significant advances and the more extensive use of ecological models. Lotka (1925) and Volterra (1926) made the first steps into presenting a simple ecological model, which constituted of simple equations for the description of prey-predator population dynamics. This simple model included parameters such as, the size of prey and predator populations, the intrinsic growth rate of prey, the grazing or attack rate of predator, the efficiency of consumed food incorporation into new offsprings, and the predator death rate. The first mechanistic, numerical ecosystem model was presented about two decades later by Riley (1946), who developed each biological rate as a function of environmental variables (e.g. temperature, irradiance, nutrient concentration). A few years later Riley *et al.* (1949) combined a phytoplankton and a zooplankton model with impressive consonance between predictions and observations. All these early approaches have formed the basis for the development of complex ecosystem models, which included parameters such as biogeochemical cycles, dissolved oxygen, suspended sediments and multiple biological components (phytoplankton, zooplankton, benthic producers and consumers, fish) (e.g. Wetzel and Wiegert, 1983; Hofmann, 2000; Giblin and Vallino, 2003). The use of models in coastal management exploded after the late 80s due to the widespread acceptance of modelling as a mainstream research tool and to the increasing availability of computing power capable of running simulation models (Brush and Harris, 2010). Several ecosystem models were developed for the management of coastal areas: e.g. for Chesapeake Bay (HydroQual, 1987), for the Baltic Sea (Stigebrandt and Wulff, 1987), and for the Ems Estuary (Baretta and Ruardij, 1988), which later became the basis for the European

Regional Seas Ecosystem Model (ERSEM).

#### *Types of ecological models, their use and limitations*

The types of ecological models available today can be categorised in the following types (based on Jørgensen, 2008):

1. *Bio-geo-chemical and bio-energetic dynamic models*: This type of models was dominantly used during the period 1975-1982 (62.5% of the publications in the *Ecological Modelling* journal), but their use was decreased during the 2000-2006 period (32% of model publications). They are easy to understand, interpret and use for predictions and they're supported by available software. These models are often based on causality and on mass or energy conservation principles. Some of the difficulties in the use of these models are that they require good and homogenous data, they are not easy to calibrate when they are complex and multi-parametric, and they cannot describe changes in species composition. The above-mentioned advantages and disadvantages define the area of application of these bio-geo-chemical and bio-energetic dynamic models, which is the description of the state of an ecosystem in terms of matter or energy distribution when a good dataset is available (Jørgensen, 2008). These models have been widely used as an environmental management tool for the prognosis of the reaction of ecosystems to pollutants.

2. *Static models*: These models can be considered as a special category of the bio-geo-chemical or bio-energetic dynamic models where all differential equations are set to zero in order to describe a static situation. They require smaller databases with typical or average values, their results are easily verified, and they are excellent for describing a worse or average case situation. However, they do not give any information about dynamics and changes over time.

3. *Population dynamics models*: These

models are widely used for keeping track on the development or recovery of a population and they have been extensively applied in the management of fisheries and national parks (25% of papers in *Ecological Modelling* over 2000-2006). They are easy to understand and interpret, they are often based on causality and they can include age structure and impact variables. The disadvantages of these models are that they require a homogenous and good database and that they might be difficult to calibrate.

4. *Structural dynamic models*: These models, which have recently gained more ground (8% of model papers over the period 2000-2006), can describe ecosystem adaptations and shifts in species composition. The structural dynamic models can include more than one species (even with slightly different properties), and they can be used to model biodiversity and ecological niches. The parameters of the models can be changed using literature or expert knowledge or even artificial intelligence. Their disadvantages include that they require information about structural changes, they need the determination of a goal function, and they are time consuming for programming development since currently no software is available.

5. *Fuzzy models*: These less frequently used models (only 1.8% of model papers during 2000-2006) can be applied when no data are available or when the data are uncertain (semi-quantitative information). They can be knowledge based (Mamdani type) or data based (Sugeno type). Bandelj *et al.* (2009) used a fuzzy clustering algorithm to identify three different benthic communities in a lagoon area based on their dominant taxa (macrophytobenthos and macrozoobenthos). A fuzzy model can also be used when fish habitat preference under natural conditions is investigated, since this model has improved prediction ability and is able to reduce

fluctuations in habitat preference evaluation (Fukuda, 2009). However, this type of models can hardly be used for complex formulations or when numeric indications are needed. These models are not based on causality but exclusively on statistics.

6. *Artificial neural networks*: These models are able to give relationships between state variables and forcing functions based on a heterogeneous database, e.g. discrete ecosystems of the same type. They are easy and fast to apply, they can be applied when other methods give up and they give a close to optimum use of the dataset. For example, the relationships between different benthic communities and a set of environmental parameters (water quality, hydrodynamics, sediment composition) can be modelled using an artificial neural network model with a back-propagation algorithm, which can be effectively applied when the communities' responses to environmental parameters are non-linear and complex (Bandelj *et al.*, 2009). These models need to be based on a sufficiently big database, which will allow determination of the relationships initially and testing of these relationships on an independent dataset afterwards. Their disadvantages are that they are not based on causality (unless algorithms are introduced, or a hybrid model is applied), they have limited accuracy of predictions and they cannot entirely replace the bio-geo-chemical models which are based on the conservation principles.

7. *Individual based models (IBM) and cellular automata*: The IBM models are able to derive the properties of a system from the properties of the components of this system. An IBM model incorporates the differences between individuals of the same species (e.g. differences in size), which might be very important for the ecological reactions and adaptations. The IBM models often use cellular automata models, which are systems

of cells interacting in a simple way, although they are displaying an overall complex behaviour. The cellular automata are spatio-dynamical models where space, time and states are discrete. The main disadvantage of this model type is that when many properties are considered the model gets very complex and a big dataset is required for its calibration and validation. In addition, the IBM models are not based on mass or energy conservation principles.

8. *Spatial models*: These models investigate the spatial distribution of the forcing functions and of the non-biological and biological state variables. Spatial system modeling can be effective in the investigation of spatial patterns of energy and material flows that occur for example during the process of land use change (Lee *et al.*, 2009). Such spatial differences can be crucial for the understanding of ecological reactions and then the application of a proper management plan. The results of these models can be presented using GIS. Spatial models have some disadvantages: since they are usually very complex, they require a very large database, and they can be time consuming regarding their calibration and validation. The *landscape models* are spatial models that can investigate the ecological, socio-economic and political pressures for land use changes, as well as their impacts. An example of a spatial system model is the Socio-Economic Metabolism and Land Use Change (SEMLUC) model, which was used for the simulation of the spatial-temporal dynamics of socio-economic metabolism and land use change in Taipei Metropolitan Region (Lee *et al.*, 2009).

9. *Ecotoxicological models*: This type of models includes simple to use bio-geo-chemical models or population dynamic models which additionally include an effect component. They can be used to solve management problems and to perform environmental risk assessments for the

application of chemicals (distribution and effect). However, these models are yet characterised by limited knowledge and high uncertainty. For example, the number of parameters needed for the development of models for all toxic substances is very high and our current knowledge covers only 1% of those required for their implementation (Jørgensen, 2008). Consequently, estimation methods have to be further developed.

10. *Stochastic models*: They can be a bio-geo-chemical, a population dynamic, a spatial, an IBM, or a structural dynamic model, which will be able to consider randomness of forcing functions or processes. Due to limitations to our knowledge on the exact values of the forcing functions or the parameters of the model we can use the normal distribution of a long-term dataset (*e.g.* climatic conditions). The uncertainty of the results of the model can be reduced by running the model several times. Stochastic models are complex and require much computer time, but they are recommended to use when randomness is significant. For example, a Bayesian Belief Network (BBN) is a stochastic modelling technique, which uses probabilistic dependencies as a common metric, allows the integration of quantitative and qualitative information in a conceptual model, and has been used to quantify impacts of socio-economic drivers on the marine ecosystem (Langmead *et al.*, 2009).

11. *Hybrid models*: The hybrid models can be created by the combination of any two of the previously mentioned model types, resulting in the synthesis of advantages and the elimination of disadvantages of the existing models (*e.g.* Bandelj *et al.*, 2009).

#### *Limitations and common malpractices in the use of ecological models*

In the early-mid seventies, when the first types of ecological models (bio-geo-chemical, bio-energetic and population dynamic models) were applied more extensively, some short-

comings appeared. The main problems were: 1) insufficient data for the development of models in order to get reliable prognoses, 2) weaknesses in parameter estimation, 3) not appropriate reflection of the real properties of ecosystems (i.e. ecosystem adaptability to changing forcing functions and the impact on species composition) (Jørgensen, 1999). Consequently, modellers developed new or hybrid types of ecological models during the last 30 years to solve these weaknesses and obtain reliable model results. These new types included the fuzzy models that can be used for poor datasets, the artificial neural networks which are applied for parameter estimation, and the structural dynamic models which are used for accounting ecosystem properties. The selection of the proper ecological model depends on the nature of the problem requiring to be solved and on the type of the available dataset. The evaluation criteria can be scientific (e.g. complexity, flexibility, treatment of uncertainty, easiness of parameter estimation, database size needed), or political and economical (regulatory acceptance, credibility, resources efficiency).

Modelling of ecological data is often based on competing scientific theories and simplifications of reality (Cressie *et al.*, 2009). This reality is not the data but what the data stand for. However, experimental observations still remain the only link between theory and reality (Solidoro *et al.*, 2009). For example, the bio-geo-chemical and bio-energetic models are based on the estimation of model parameters, either derived from field observations/measurements or from laboratory experiments, which can never be error free (Jørgensen, 1995). In other cases, it has been observed that growth and mortality models attempt to describe transfer of energy or matter along the trophic chain, but they fail to account for variations of growth during the different ontogenetic stages of an organism (Gamito, 1998). Population dynamic models

often use mean values of environmental factors, (e.g. mean temperature is used in the seasonal von Bertalanffy growth curve, see Pauly *et al.*, 1992), whereas values of extreme levels are the ones often defining the dynamics of a population (Bulling *et al.*, 2006). Such models can be rigid in comparison with the ecosystems natural flexibility, therefore their accuracy in predicting adaptation and structural dynamic changes can be limited (Jørgensen, 1995). The recently increasing use of the structural dynamic models can offer higher reliability in the quality of results because they are built in order to describe ecosystem adaptations and structural changes. Likewise, the spatial modelling systems are an emerging and synthesized simulation approach that combines system modelling, GIS and map algebra and they are used to explore the spatial-temporal dynamics of an ecosystem (Lee *et al.*, 2009). Of course, there is still potential ground for improvement since these models are quite complex and they require time and knowledge for programming.

The majority of ecological models have been based on experimental designs with model systems (microcosms or mesocosms) where the choice of species, the number of individuals and the starting physico-chemical conditions are under a high level of control (Bulling *et al.*, 2006). As an advantage these small-scaled controlled systems can be easily replicated, monitored and maintained and they are characterized by little or no spatial or temporal heterogeneity. Collection of data from field studies would not allow the level of control required to develop theories and test hypothesis (Bulling *et al.*, 2006). However, as a consequence, these models are very specific to the system, organisms and experimental configuration used, therefore excluding important characteristics of the natural communities and ecosystems. Sometimes the composition of species used in the model is not representative of the

natural assemblages in the ecosystem, but they may be selected because they survive well in microcosms (Lawton, 1995). Model systems that involve small organisms with short generation times are well suited to answer questions requiring many generations, but could be proved misleading if used to derive conclusions for long-lived species (Bulling *et al.*, 2006). Species-specific behavior trends fade out when the ecological biodiversity models aggregate parameter data on a great number of different species. Also, diversification of the available empirical information according to functional groups may increase the uncertainty of the model if based on a statistical segregation (Bruggeman and Kooijman, 2007).

Another issue that needs to be discussed is the frequently inappropriate and without consideration of any standard criteria use of the previously-mentioned models in ecological studies. For example, a hydrodynamic model that was initially constructed for an estuarine may not be readily appropriate for an open sea ecosystem, since energy flows, physical processes and environmental conditions are variable between the different ecosystems (Jørgensen, 1995). A more generic type of model, such as the functional group (trait based) models that can be applied in any ecosystem type would be more appropriate and give more reliable results. A trait-based model build on general concepts allows the description of the adaptive behaviour of many species or of community-aggregate properties to changing environmental conditions (Merico *et al.*, 2009). Several computer programs based on statistical models that were initially designed for fish populations are occasionally used for molluscs or crustacea without taking into account the differences in the life style and behaviour between these phyla which could result in erroneous conclusions. Jackson *et al.* (2000) indicated that size frequency analyses based on computer methods, which were

actually constructed for fisheries studies, are not appropriate for estimating growth curves of squid populations.

Several approaches have been proposed for handling uncertainty in ecological models, such as estimation of the unknown parameters (empirical-Bayesian analysis), expression of uncertainty via a prior probability distribution (Bayesian analysis) or hierarchical statistical modelling, which includes a data model (first level), a process model (second level) and a parameter model (optional third level) (Cressie *et al.*, 2009). An aquatic ecosystem model which includes a sophisticated representation of community diversity and interspecific differences and integrates theories on changes in species composition in both time and space was inspired by Bruggeman and Kooijman (2007). Most ecological processes evolve dynamically through space and time, therefore an efficient model design should take this issue into account. The structure of a biodiversity model should be subject to continuous modification as the dynamics of the ecosystem or communities are constantly changing due to species succession, physiological adaptation and genetic evolution (Bruggeman and Kooijman, 2007). Interactions between species and their relationship with their natural environment could be described using structural dynamic models or individual based models (IBM). The sampling design for biodiversity models should ideally be based on the principles of randomization, stratification and replication (Cressie *et al.*, 2009). Extra care should be taken when applying complicated statistical models to ecological data so that a scientifically meaningful and realistic explanation of the results can be finally derived. Complicated mathematical models which cannot be interpreted in the basis of species composition or their relationship with the natural environment may not of great use for an ecologist.

Although mathematical ecological models do not always delineate accurately the processes of the natural environment, they can still be very useful in ecosystem management especially when all the guiding principles and prerequisites are considered during their development and application. They can provide a wide overview of the environmental problem examined, they can give initial estimates on how ecosystem functioning is affected by anthropogenic or natural factors and finally they can indicate current knowledge gaps and guide future research. It cannot be argued that model systems provide us with a valuable starting point for studying ecosystems, but they should be used with care (Bulling *et al.*, 2006). Knowledge and careful consideration of the drawbacks of a model can help us to avoid or minimize many of these problems. The selection of the parameters that will be included in an ecological model is of great importance and depends on the specified area of study and on the questions that need to be answered. Therefore, a very simple ecological model may be easy and quick to run but removing too much detail may limit its prognostic use. The challenge is to define an optimum scope that minimises complexity, but which facilitates valid and robust predictions (Fulton *et al.*, 2003). The design of a set of evaluation techniques when building a model is also crucial. Application of a previously published model on a set of data should be performed only after thorough planning and consideration of its specific limitations and guidelines. Further investigation regarding the interpretation of results from ecological models, as well as their integration with results derived from other methodologies must be planned. The comparative and confirmatory use of multiple models is strongly recommended (Fulton *et al.*, 2003). The intelligent application of integrated ecological models in a global scale will provide sound and comparable results which

can contribute to the upcoming international policy planning and development.

In nowadays, ecological models are widely accepted by the scientific community and their importance in theoretical and applied studies is seldom questioned. However, according to Solidoro *et al.* (2009), ecological modelers currently face three challenges: 1) to meet the expectations of the scientific and the general society by providing reliable tools and critical interpretation of the results, and by clarifying the limits and approximations in any model, as well as the uncertainties in any prediction, 2) to avoid the generation of false expectations and 3) to keep modelling open to interbreeding with other scientific fields. The modelling approaches that currently exist are being continually developed depending on the question/field of interest, in order to allow for environmental simulations across a range of temporal and spatial scales. The creation of a toolbox based on the application of ecosystem models will complement the traditional methods, for the study of ecosystem structure and function, as well as for performing management evaluations.

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