Available online at www.sciencedirect.com

SCIENCE DIRECT®

Ecological Modelling 178 (2004) 329–334

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Classification of mathematical models in ecology

V.I. Gertsev [a,1], V.V. Gertseva [b,*]

[a] Department of Mathematics, Rybinsk State Academy of Technology, 57 Pushkin Street, Rybinsk 152934, Russia
[b] Mark O. Hatfield Marine Science Center, 2030 SE Marine Science Drive, Newport, OR 97365, USA

Received 5 August 2003; received in revised form 16 February 2004; accepted 12 March 2004

Abstract

This paper is devoted to the classification of mathematical models in ecology. It represents various classes of mathematical models distinguished on the base of both the characteristics of the object of investigation and research task. Each class of mathematical models is illustrated by references to particular studies. This classification aims to help ecologists, biologists and environmentalists navigate the diversity of methods and techniques in mathematical modeling and develop a standardized approach to the application of mathematics in ecological research.

Keywords: Classification; Mathematical model; Predicted parameter; Generalized argument

1. Introduction

During the last several decades mathematical modeling has become an essential part of ecological research (Edelstein-Keshet, 1988; Hoppensteadt, 1982; Jørgensen, 1994, 2002). Mathematical models make our assessments and predictions in ecology more objective and reliable. Among the definitions of a mathematical model let us accept the following. A mathematical model of a real object is a totality of logical connections, formalized dependences, and formulas, which enables the studying of a real object without its experimental analysis. The objects of ecological research are populations, communities, and ecosystems. Conducting experiments on such objects is not possible, because it can lead to changes or even destruction of the ecological objects. In this situation it is clear that mathematical modeling plays a key role in ecological research.

Although the history of using mathematics for description of ecological processes goes back to the twelfth century (Real and Levin, 1991), there is a definite gap between the mathematical approach and the application of this approach in ecology. This gap exists primarily because mathematicians and ecologists use different symbols, terms and definitions. To overcome this gap and to achieve, figuratively speaking, the point of convergence between mathematics and ecology, it is very important to clearly define mathematical terms and definitions applied in ecology. As a first step to accomplish this task, we should look at the diversity of mathematical models in ecology and try to classify this diversity.

There have been attempts to distinguish different types of models in ecology (Jørgensen, 1986; Jørgensen and Bendoricchio, 2001). These attempts, however, were primarily dedicated to philosophical and methodological aspects of the modeling. Our

* Corresponding author. Tel.: +1-541-8670382; fax: +1-541-8670389.
E-mail addresses: g137e@nekto.ru (V.I. Gertsev), vladlena.gertseva@noaa.gov (V.V. Gertseva).
[1] Tel.: +7-855-557624.

0304-3800/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2004.03.009

paper is devoted to the classification of strictly mathematical models in ecology with their specific features, terms and definitions.

2. Classification of mathematical models in ecology

2.1. Isomorphic and homomorphic models

All mathematical models in ecology can be divided into two groups: isomorphic and homomorphic models. A mathematical model is called isomorphic relative to the object of modeling if the following conditions have been met: (1) every element of the object is represented by the corresponding element of the model, and vice versa; (2) every function, defined by the elements of object, is represented by the corresponding function, defined by the corresponding elements of model, and vice versa; (3) every relationship of the object's elements is represented by a corresponding relationship of the model's elements. In other words, when all components of the object of modeling have analogous components in the model, the model is called isomorphic or symmetric relative to the object of modeling.

Ecological objects (populations, communities, ecosystems), however, are very complex, and it is impossible to reflect all the features of such objects in the model. The population model, for instance, cannot take into consideration linear-weight characteristics, productivity and ecological–physiological reactions of every organism in the population. Therefore, it is necessary to resort to definite assumptions and group characteristics. In this case, however, symmetry between the object of modeling and the model is lost: all components of the model have analogous components in the object, but not vice versa. As a result, isomorphic relationships between the object of modeling and the model transfer into so-called homomorphic relationships, and the mathematical model becomes homomorphic. It is clear that all mathematical models in ecology are homomorphic.

2.2. Time-dependent and stationary models

Let us designate all model components as $G_i (i = 1, \ldots, n)$. Depending on the objective of the research, during the process of modeling, some of these components will be considered as arguments and the others as functions which depend on the arguments. For example:

$$G_i = f(G_1, G_2, \ldots, G_{i-1}, G_{i+1}, \ldots, G_n) \quad (1)$$

where G_i is a parameter that we want to predict, and G_1, G_2, G_{i-1}, G_{i+1}, G_n, are arguments, defining the predicted parameter G_i.

If we combine all arguments under the function sign in the expression (1) into a generalized argument, mark it g, and get rid of the index at the predicted parameter G, then the expression (1) can be simplified and presented as:

$$G = f(g) \quad (2)$$

where G is the predicted parameter, and g is the generalized argument.

Since ecological objects are generally distributed in a definite way in the space with coordinates x, y and z and change over time t, expression (2) can be rewritten as:

$$G = f[g(x, y, z, t)] \quad (3)$$

where G is the predicted parameter, g the generalized argument, x, y, z the spatial coordinates, and t is the time.

When the predicted parameter G depends on both spatial coordinates and time, as it is shown in Eq. (3), the models are called time-dependent (Gertseva et al., 2003; Holtby and Scrivener, 1989; Jørgensen, 1990; Moss et al., 1994). There are situations, however, when the generalized argument g and, therefore, predicted parameter G, depend only on coordinates, but not on time. The models describing such situations are called stationary (Gertsev and Gertseva, 1999; Hall and Day, 1977; Jørgensen and Bendoricchio, 2001). They can be represented by the following expression:

$$G = f[g(x, y, z)]$$

where G is the predicted parameter, g the generalized argument, and x, y, z are the spatial coordinates.

It is possible to see that stationary models are a particular case of time-dependent models, and we can, therefore, write that:

stationary models $\subset$ time-dependent models

2.3. Models with distributed and lumped parameters

Very often in the literature, models with distributed and lumped parameters are mentioned. Models with distributed parameters, or in other words, models with heterogeneity along the coordinates, account for variations in the generalized argument g not only in time, but also in space. From this definition, it is clear that models with distributed parameters are the same as time-dependent models and, hence, can be represented by expression (3). We can write that:

models with distributed parameters

$\sim$ time-dependent models

Sometimes, however, the generalized argument g depends only on time, and not on spatial coordinates. These models are called models with lumped parameters, or punctual models, or models with homogeneity along the coordinates (Gersev et al., 1995; Volterra, 1926). They have the following form:

$$G = f[g(t)]$$

where G is the predicted parameter, g the generalized argument, and t is the time.

2.4. Models "Future time" and "Past time"

Most models in ecology are used for prediction of the future state of ecological objects. These models are called "Future-time" models (Bahr and Bekoff, 1999; Monte, 1998). In this case, we find the predicted parameter G from expression (3) at the time $t = 0$ (beginning of modeling) and then define it in a particular moment of time in the future t_k.

However, the investigation of ecological objects in the past relative to the beginning of modeling is also of significant interest. Since mathematical models in ecology are not invariant relative to time and its direction, we can perform the following procedure. We can consider the present moment in time t_k as the start of modeling, and define the predicted parameter G for this moment in time. Then, using Eq. (3), we can define the predicted parameter G for the time $t = 0$, which lies in the past relative to t_k. Thus, parameter G is interpreted as a result of the ecological modeling, directed to the past, with the time depth $\Delta t = (t_k - 0) = t_k$. Such models are called "Past time" models (Chadwick et al., 1999; Menshutkin et al., 1998).

The values of the predicted parameter G at time $t = 0$ and time$t = t_k$ are initial conditions for "Future time" and "Past time" models, respectively. We would like to emphasize again that time in "Future time" and "Past time" models goes in the same direction—from past to the future.

2.5. Continuous and discrete models

Relative to the temporal representation of the dynamics of the object of modeling, mathematical models can be divided into two groups. The first of them is continuous models, which represent continues changes of an object with time (Imboden and Gächter, 1978; Lotka, 1956). This type of models allows us to define the generalized argument g and the predicted parameter G in the expression (3) at every point in the time interval $[t_0, t_n]$, which is modeled.

The second group is discrete models (Behm and Boumans, 2001; Krivtsov et al., 2000; Liddel, 2001). These models use discrete time steps $t_0 < t_1 < \ldots < t_i < \ldots < t_n$ to describe changes in the object of modeling during the time interval $[t_0, t_n]$, which is modeled. In some cases, the time step $\Delta t = (t_i - t_{i-1})$ can be fixed, but in other cases it can be "floating".

2.6. Deterministic and stochastic models

If during the process of modeling, the generalized argument g in Eq. (3) is set as having a single meaning (with some error of calculation), but not estimated in terms of statistical distributions, we can define an exact value of the predicted parameter G. These models are called deterministic (Mauersberger, 1983; May, 1973).

However, measurements of nature have no precise relationships among variables, but include some statistical component (Hall and Day, 1977). When the generalized argument forms a distribution of the possible values, characterized by such statistical indexes as mean, dispersion and standard deviation, a model is called stochastic (Berg and Shuman, 1995; May, 1974). The predicted value in this case does not have a single meaning, but it is presented by spectrum of possible values.

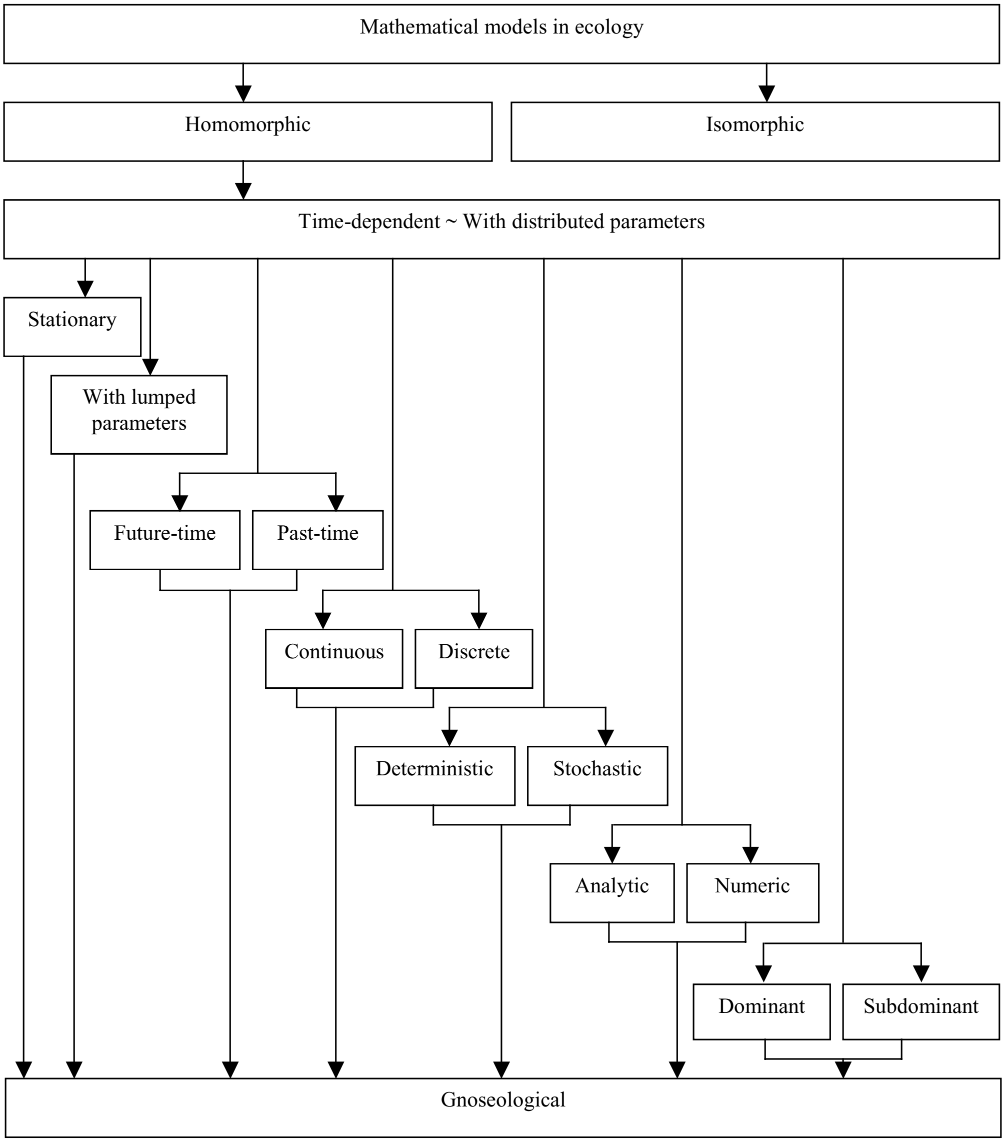

Fig. 1. Graphical representation of classification of mathematical models in ecology.

2.7. Analytic and numeric models

In some cases, the predicted parameter G from the expression (3) can be defined as the analytic function of generalized argument g. Such models are called analytic (Gertseva and Gertsev, 2002; Pearl, 1925). Since the behavior of some mathematical equations are well known, the analytic model describing a real object with one or several of such equations allows us to find the exact predicted value for every argument in every condition at every moment of time.

Sometimes, however, it is very difficult or even impossible to find an analytic expression for function (3). Therefore, we have to find the predicted parameter G from the set of expressions presented by dependencies between some components of the generalized argument, where the predicted parameter is not obvious. In this case, the time interval of modeling, initial conditions, and components of the generalized argument are set numerically. The obtained system of equations includes dozens to hundreds of equations that need to be solved simultaneously, which can be done with the help of a computer. Such models are called numeric (Krivtsov et al., 2003; Pate and Odell, 1981). Very often these models are also called simulation or imitating models. There is a deep meaning in these names. Numeric data for computer simulations should be based on the knowledge of how the real biological systems behave. Only in this case, can we trust the results of the modeling. The primary source of the knowledge about the real biological system is the observations. The numeric model, being based on the real data, aims to imitate an ecological object, its condition and development.

2.8. Dominant and subdominant models

To truly represent the real object of investigation and allow its quantitative interpretation, any mathematical model should be based on real data, obtained through the observation (monitoring) of the object of interest. There are two kinds of relationships of the model and the process of monitoring of the object of investigation. Following the first of them, we develop a mathematical model, and then monitor the object of investigation to validate the model. In this case, the model is primary relative to monitoring of the real system. Such models are called dominant (Edelstein-Keshet, 1988; Gertsev et al., 1996). Following the second alternative, we monitor the object of investigation and then, based on data obtained from the monitoring, develop a model. In this case, the model is secondary relative to monitoring. Such models are called subdominant (Krivtsov et al., 1999, 2003; Thomann, 1984).

2.9. Gnoseological models

As we pointed out before, mathematical models in ecology are based on our knowledge of the study system and reflect our understanding of how the system works. If the results of modeling go along with the general ecological theories, we can say that our understanding of the study system is correct (Loehle, 1989; Ulanowicz, 1980; Zeeman, 1978). Sometimes, however, modeling results may lie outside the limits of the general ecological knowledge and contradict common sense. For example, model output can show that a population's abundance has a negative value. In this case, our knowledge about factors affecting the population is incorrect and we should study the interactions within the modeled system further. That is to say that mathematical models force us to take a close look "inside" the study system and, therefore, play a gnoseological role.

Fig. 1 shows a graphical representation of the classification of mathematical models in ecology.

3. Conclusion

Classification of mathematical models in ecology serves a very important purpose. It helps to develop a general perspective on solving the ecological problems with the help of mathematics and enables ecologists, biologists and environmentalists to find their bearings in the diversity of various approaches and techniques in mathematical modeling.

Mathematical modeling now is at the threshold of a principal synthesis. Things have reached the point when it is necessary to unify mathematical models. Until now, every mathematical model in ecology has been an individual piece of art, which reflected the world-view, education, and scientific and personal characteristics of the modeler. Unification of the mathematical models will help to transfer the process of modeling from an individual art to a standardized and reliable method of ecological research, accessible by every scientist. Classification of the mathematical models in ecology plays an essential role on the way to such a unification.

References

Bahr, D.B., Bekoff, M., 1999. Predicting flock vigilance from simple passerine interactions: modelling with cellular automata. Anim. Behav. 58 (4), 831–839.

Behm, P.M., Boumans, R.M.J., 2001. Modeling herbivorous consumer consumption in the Great Bay Estuary. New Hampshire Ecol. Model 143 (1/2), 71–94.

Berg, M.T., Shuman, L.J., 1995. A three-dimensional stochastic model of the behavior of radionuclides in forests III. Cs-137 uptake and release by vegetation. Ecol. Model 83 (3), 387–404.

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., Hedin, L.O., 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397 (6719), 491–497.

Edelstein-Keshet, L., 1988. Mathematical Models in Biology. The Random House, New York.
Gersev, V.I., Safronov, A.M., Gerseva, V.V., 1995. Population as a freely oscillating system. Ecol. Model 80 (1), 41–45.
Gertsev, V.I., Safronov, A.M., Gertseva, V.V., 1996. Structure of the unified ichthyological prognosis. Ecol. Model 85 (2/3), 145–149.
Gertsev, V.V., Gertseva, V.V., 1999. A model of sturgeon distribution under a dam of hydro-electric power plant. Ecol. Model 119 (1), 21–28.
Gertseva, V.V., Gertsev, V.I., 2002. A model of fish population distribution in the space of inhabitation. Ecol. Model 147 (2), 161–170.
Gertseva, V.V., Gertsev, V.I., Ponomarev, N.Y., 2003. Tropho-ethological polymorphism of fish as a strategy of habitat development: a simulation model. Ecol. Model 167 (1/2), 159–164.
Hall, C.A.S., Day, J.W., 1977. Systems amd models: terms and basic principles. In: Hall, C.A.S., Day, J.W. (Eds.), Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories. John Wiley & Sons, New York.
Holtby, L.B., Scrivener, J.C., 1989. Observed and simulated effects of climate variability, clear-cut logging and fishing on the numbers of chum salmon (Oncorhynchus keta) and coho salmon (O. kisutch) returning to Carnation Creek, British Columbia. In: Leavings, C.D., Holtby, L.B., Henderson, M.A. (Eds.), Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci., vol. 105.
Hoppensteadt, F.C., 1982. Mathematical Methods of Population Biology. Cambridge University Press, Cambridge.
Imboden, D.M., Gächter, R., 1978. A dynamic lake model for trophic state prediction. Ecol. Model 4 (2/3), 77–98.
Jørgensen, S.E. 1986. Fundamentals of Ecological Modelling, Elsevier, Amsterdam
Jørgensen, S.E., 1990. Ecosystem theory, ecological buffer capacity, uncertainty and complexity. Ecol. Model 52, 125–133.
Jørgensen, S.E., 1994. Models as instruments for combination of ecological theory and environmental practice. Ecol. Model 75-76, 5–20.
Jørgensen, S.E., 2002. Integration of Ecosystem Theories: A Pattern, third ed. Kluwer Academic Publishers, Dordrecht.
Jørgensen, S.E., Bendoricchio, G. 2001. Fundamentals of Ecological Modeling, third ed. Elsevier, Amsterdam.
Krivtsov, V., Bellinger, E., Sigee, D., Corliss, J., 1999. Examination of the phytoplankton of Rostherne mere using a simulation mathematical model. Hydrobiologia 414, 71–76.
Krivtsov, V., Corliss, J., Bellinger, E., Sigee D., 2000. Indirect regulation rule for consecutive stages of ecological succession. Ecol. Model 133 (1/2), 73–81.
Krivtsov, V., Illian, J.B., Liddell, K., Garside, A., Bezginova, T., Salmond, R., Thompson, J., Griffiths, B., Staines, H.J., Watling, R., Brendler, A., Palfreyman, J.W., 2003. Some aspects of complex interactions involving soil mesofauna: analysis of the results from a Scottish woodland. Ecol. Model 170 (2/3), 441–452.
Krivtsov, V., Watling, R., Walker, S.J.J., Knott, D., Palfreyman, J.W., Staines, H.J., 2003. Analysis of fungal fruiting patterns at the Dawyck Botanic Garden. Ecol. Model 170 (2/3), 393–406.
Liddel, M., 2001. A simple space competition model using stochastic and episodic disturbance. Ecol. Model 143 (1/2), 33–41.
Loehle, C., 1989. Catastrophe theory in ecology: a critical review and an example of the butterfly catastrophe. Ecol. Model 49 (1/2), 125–152.
Lotka, A.I., 1956. Elements of Mathematical Biology, Dover, New York.
Mauersberger, P., 1983. General principles in deterministic water quality modeling. In: Orlob, G.T. (Ed.), Mathematical Modeling of Water Quality: Streams, Lakes and Reservoirs. Wiley, New York.
May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.
May, R.M., 1974. Ecosystem pattern in randomly fluctuating environments. Progr. Theor. Biol. 3, 1–50.
Menshutkin, V.V., Astrakhantsev, G.P., Yegorova, N.B., Rukhovets, L.A., Simo, T.L., Petrova, N.A., 1998. Mathematical modeling of the evolution and current conditions of the Ladoga Lake ecosystem. Ecol. Model 107 (1), 1–24.
Monte, L., 1998. Predicting the migration of dissolved toxic substances from catchments by a collective model. Ecol. Model. 110 (3), 269–280.
Moss, B., McGowan, S., Carvalho, L., 1994. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. Limnol. Oceanogr. 39, 1020–1029.
Pate, E.F., Odell, G.M., 1981. A computer simulation of chemical signaling during the aggregation phase of Dictyostelium discodeum. Theor. Biol. 88, 201–239.
Pearl, R., 1925. In: Knopf, A.A., The Biology of Population Growth, New York.
Real, L.A., Levin, S.A., 1991. The role of theory in the rise of modern ecology. In: Real, L.A., Brown, J.H. (Eds.), Foundations of Ecology. The University of Chicago Press, Chicago.
Thomann, R.V., 1984. Physio-chemical and ecological modeling the fate of toxic substances in natural water systems. Ecol. Model 22 (1/4), 145–170.
Ulanowicz, R.E., 1980. A hypothesis of the development of natural communities. Theor. Biol. 85, 223–245.
Volterra, V., 1926. Fluctuations in the abundance of species considered mathematically. Nature 118, 558–560.
Zeeman, E.C., 1978. Catastrophe Theory: Selected Papers 1972–1977. Addison, Wesley, London.