

PRESENTATION

MATHEMATICAL MODELS IN ECOLOGICAL THEORY: A REVIEW BY BRAZILIAN RESEARCHERS ON ITS CURRENT STATUS AND PERSPECTIVES

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When Darwin chose the term “Economy of Nature” (credited to Carl Linnaeus in the 18th century) (Egerton 2010), he was intentionally pointing to a similarity between biological and economical sciences, the latter more commonly applied in our daily activities. Maybe the intention was to familiarize readers with the arguments he was presenting. The comparison is still used, and it was indeed well succeeded as it made clear the relationship between ecological and economical phenomena, frequently expressed in the form of mathematical models. Trade-offs, limiting resources, cost-benefit analyses, optimization are examples of common concepts. However, the incorporation of mathematical models in Ecology did not happen when it crystallized as a distinct discipline in the turn of the 20th century, but only in the decades of 1950-1960.

In the beginning of the 20th century the scientific community was in great effervescence, when Hilbert was announcing the 23 mathematical problems that influenced the development of science in the remaining of the century, Einstein was publishing his first version of the Relativity Theory, which would influence Physics decisively, Russell was publishing *Principia Mathematica*, changing not only Mathematics, but the epistemology of science, Poincare was presenting the first ideas about dynamic systems, Freud “discovered” the subconscious, and the fundamentals of genetics were being established. The first building concepts of Ecology as science were also being laid, such as niche, food webs, and population regulation, but most Ecologists kept a natural history and empirical

approach, using exploratory and inductive methods.

In 1950-60 the approach used by ecologists changed greatly after the work of ecologists such as George Evelyn Hutchinson (1958), Howard and Eugene Odum (1963, 1967), Ramon Margalef, Robert May (1976), Robert MacArthur (1966, 1972), crystallizing Theoretical Ecology as a subdiscipline. Also in this period Ecology begins to appear as a distinct discipline in the Austral region, outside Europe and North America.

At the moment a variety of mathematical models are used in all ecological approaches, from individuals to populations, communities, and ecosystems. The use and development of mathematical models is now part of the discipline, but a gap remains between the formation ecologists receive and their knowledge of the mathematical models used in Ecology (Turchin 1998). There are signs that this gap is reducing, judging by the increasing number of specialized journals, such as *Ecological Modelling*, *Journal of Theoretical Biology*, *Theoretical Ecology*, and also the increasing number of submissions (Hastings 2010).

Biological and ecological problems are also exceptionally interesting to Mathematics, and differ epistemologically from Physics problems, which have always received mathematical treatment. Important mathematical developments were based on biological problems, such as the discovery of the Golden Ratio, one of the first models of population ecology, also known as Fibonacci’s rabbits. The Fibonacci problem (Odifreddi 2011) is a curious and interesting example of the use of models, but also represents an example

of an interdisciplinary approach to solve the problem. It is not sufficient to have a perfect logic-deductive development of a model (the mathematical aspect), and is not sufficient either to have only proximate realistic assumptions (the biological aspect): it is necessary to combine both aspects.

The interdisciplinary effort required to develop mathematical models in ecology is not easily achieved. For example, compare the papers published in the journals *Mathematical Biology* and *Ecological Modelling*. The first is mainly for mathematically driven researchers, whereas the second receives submissions mostly from researchers of the biological sciences. Both journals cover subjects that can be identified within the domains of population, community, and ecosystem ecology, yet differ in profile and target audience. In general, an average researcher of the biological sciences will not have the background to fully understand a paper based on dynamic systems published in *Mathematical Biology*, and a researcher in mathematical sciences will not have the necessary background in ecology and evolution to understand the important parameter set and state variables used in models published in *Ecological Modelling*.

In this volume researchers from Brazil review the use of mathematical models in their area of study in the ecological theory. These reviews represent the areas emphasized by researchers in a country in the Austral region where the ecological science has had a large development in recent decades. The point of view of these researchers and professionals on the use of mathematical models is particularly interesting for the development of ecological theory in the Austral region. Of course the reviews assembled do not cover the full diversity of mathematical models used in the ecological theory, but the intention was to present the views of these researchers, and foster new interest and interdisciplinary initiatives. General models were emphasized, which serve as a basic structure to add specific variables of each system. These models also provide valuable tools to formulate hypothesis objectively, generating quantitative predictions and more powerful hypothesis tests.

The reviews can be grouped in demography and population dynamics (1-3), dynamic systems and species interactions, particularly applied to disease control and management (4-9), consequences

of heterogeneity in space or variation between individuals to population dynamics (10), game theory and evolutionary stable strategies (11), an agent/individual based models (12). In the opening paper, Maja Kajin, Paulo José Almeida, Marcus Vieira and Rui Cerqueira (Kajin *et al.* 2012) review matrix models starting from first principle: the Leslie matrix (Leslie 1945) and how eigenvalues, sensibility and elasticity analyses, can be used in the management of populations. Following, Pedro Vieira Esteves and Michel Iskin da Costa reviewed the occurrence of multiple stable states in populations structured in stage classes (Esteves & Costa 2012). Also discussed are the possible consequences of management and conservation actions, considering that different stages of the life cycle of organisms may present distinct behavioral, physiological, and morphological characteristics. Using this demographic and population dynamics approach, Wesley Godoy reviews the use of population trajectories and critical population sizes as probes to determine time trends (Godoy 2012).

Interaction between species and the dynamics systems they form are reviewed in the next papers. Ana Paula Battel, Rafael Mora and Wesley Godoy review the history of predator-prey models based on Lotka-Volterra equations (Lotka 1925, Volterra 1926), host-parasite models, and their applications in biological control (Battel *et al.* 2012). Dynamic systems is a field of study in mathematics where the interactions between populations are naturally inserted. An introduction to the theory of dynamic systems is then presented by Baaba Ghansa, Paulo José Almeida, Carlos Frederico Palmeira and Lucas Faria, presenting four different models of populations under different functional responses, analyzing the stability of these systems to understand the possibilities of a sustainable use under these scenarios (Ghansa *et al.* 2012). Amit Bhaya and Magno Enrique Mendoza Meza review two classes of mechanisms that allow stability in predator-prey dynamic systems, named “threshold policy” or “threshold policy with hysteresis” (Bhaya & Meza 2012). The applications of these mechanisms (or policies) of renewable natural resource management is discussed.

Predator behavior can have important consequences to the dynamics of the system. Lucas Faria and Michel Skin review studies that classify the

preference of predators for prey in two forms, non-switching and switching (Faria & Costa 2012). The analysis of the structure of preference by predators is may affect trophic structure, diversity, species coexistence, and ecosystem stability.

The dynamics of transmissible diseases is also a dynamic system, particularly important to the control of diseases in human and economically exploited populations. Cláudia Codeço and Flávio Coelho describe the emergence of mathematical modelling in the study of the dynamics of transmissible diseases and its characteristics, as well as the current challenges inherent in the application of these models to face public health issues (Codeço & Coelho 2012).

The first papers approached population dynamics under various aspects, but considering mostly temporal dynamics. Sabrina Borges Lino Araujo and Marcus Aloizio Martinez de Aguiar review the consequences of heterogeneity within a population in foraging strategies using spatially explicit modeling (Araújo & Aguiar 2012). The predictions of these models are distinct from predictions based on more traditional models.

Another distinct and particularly appropriate approach to evolutionary phenomena is ESS, Evolutionary Stable Strategies. Paulo José Almeida, Maja Kajin and Marcus Vinícius Vieira, review the concept of ESS starting from the economic theory of its origin, game theory (Almeida et al. 2012). The authors review discrete and continuous approaches to model ESS. Both can be used as a starting point to study and model biological traits subject to natural selection.

Individual based models (IBM), also known agent or algorithm based models, are the subject of the last paper, by Arthur da Silva Lima (Lima 2012). These models allow extreme versatility, necessary to the application of mathematical models to more complex – hence more realistic - situations. They provide a flexible structure to incorporate specific aspects to more strategic models, generally based on so the called mean-field assumption, that individual variation can be ignored, such as those reviewed in most papers of this volume.

Mathematical models are fundamental to the development of a solid body of theory necessary to Ecology as a science. Predictions of consequences of disturbances in ecological systems, particularly

those caused by human activity, are only possible with the improvement of ecological theory. Ecology goes on a steady pace towards the consolidation of fundamental concepts and models through this development (Scheiner & Willig 2011). In this sense, the comprehension of the mathematical models that are part this theory and its applications are essential. The contents and mathematical models of this volume are only a part of the variety of mathematical models already developed in Ecology, but we believe that basic and fundamental models of this variety were included, including frequent applications to the management of species and biological control of diseases. Possibly equally important, the selection presented allows a visualization of the action of Brazilian researchers in the field of Theoretical Ecology. We hope that the papers in this volume stimulate further development of ecological theory, and serve as entrance into the mathematical models used in the ecological theory by researchers and graduate students.

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