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A REVIEW ON THE DEVELOPMENT OF INDIVIDUAL-BASED MODEL IN ECOLOGY

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Abstract. Unlike traditional population models which are defined in terms of top-down parameters, individual-based models are bottom-up models in which population level behaviors are emerging from the interactions among individuals. Ecologists can use individual-based models to tackle new kinds of problems that are not easily solved by population models, so individual-based modeling has been fueled the desire of ecologists to understand natural complexity and how it emerges from the variability and adaptability of individual organisms. In this paper, we investigate the improvements that ecology has made from the individual-based models during the last five decades, and talk about the two primary challenges to individual-based modeling.

Keywords: ccological modeling; individual-based models; theoretical ecology; review.

2010 AMS Subject Classification: 62P10, 92B05.

1. Introduction

The aims of modeling are to capture the essence of a system and to address some specific questions related to the system. Although the systems that we deal with are always in the form of communities and populations, the models of the systems sometimes may prefer to adopt individual-based models (hereafter we refer to them as IBMs). Comparing with traditional

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TABLE 1. Time series of the number of papers which use IBMs in ecology

year	# of papers	year	# of papers	year	# of papers	year	# of papers
1970	3	1980	13	1990	21	2000	105
1971	11	1981	20	1991	28	2001	133
1972	6	1982	12	1992	26	2002	135
1973	9	1983	26	1993	27	2003	115
1974	19	1984	27	1994	45	2004	121
1975	14	1985	21	1995	53	2005	185
1976	17	1986	22	1996	67	2006	203
1977	15	1987	19	1997	77	2007	243
1978	14	1988	23	1998	78	2008	280
1979	13	1989	23	1999	92	2009	329
2010	338	2011	384	2012	451	2013	464
2014	547	2015	632	//	//	//	//

population models, one obvious advantage of IBMs is that they can accommodate any number of elements in their individual-level, and then the population-level behaviors can be concluded from the interactions among independent individuals with each other. The population models are described by imposed top-down population parameters (such as birth and death rates) [1] whose accurate value does not get easily and IBMs are usually used when some aspects of the systems are almost impossible or hard to be depicted by population-level models. Especially in ecology, The simulation and analyzation of populations or communities which are modeled by individual-based modeling method have become an important methodology for the study of complex phenomena [2].

A conceptual model [3] has been created for the growth of individual tree seedlings from rates of photosynthesis and the distribution of photosynthates, but no one has successfully reproduced the major characteristics of a mixed-species and mixed-aged forest from a conceptual basis before JABOWA [4] is proposed. JABOWA is the first major use of individual-based model [1], and from then on, many researchers start to put emphasis on the study of IBMs. In [5], the authors predicted that ‘Within the next decade we expect to see a rapid development of this

TABLE 2. Time series of the total # and average # of papers which use IBMs in ecology

Serial #	Years	Total # of papers	Average # of papers
1	70-74	48	10
2	75-79	60	12
3	80-84	98	20
4	81-84	108	22
5	90-94	147	29
6	95-99	367	73
7	00-44	609	122
8	05-09	1240	248
9	10-14	2184	437

approach', and the exponential increase in the number of publications per year which use IBMs from 1970 to 1998 [6] proved that their prediction is right. And the number and the average number of papers from 1970 to 2015 which we get from Google scholar databases further proved that the IBMs are attracting more and more attention since from 2005, for more details, please say Table 1,Table 2, Figure 1 and Figure 2.

In this paper, we intend to provide a summary and introduce some applications both in applied issues and theoretical questions of existing individual models. The rest of this paper is organized as follows. In the next section, we explain why IBMs are important in ecology. In section 3, we will give a min-review of IBMs published in the last five decades, and we will discuss the relationship of more traditional analytical modeling approaches with IBMs in this section as well. Section 4 will give a conclusion and outlook for IBMs.

2. Why do we need IBMs?

There are two motivations that encourage modelers to use the individual-based approach: one is that each individual is as a unique entity in respect to establishment, growth and death, while its important features are not considered in traditional population-level models (such as the law of individual variability), and the other motivation is that the existing theory from population-level models has some degree of deficiencies.

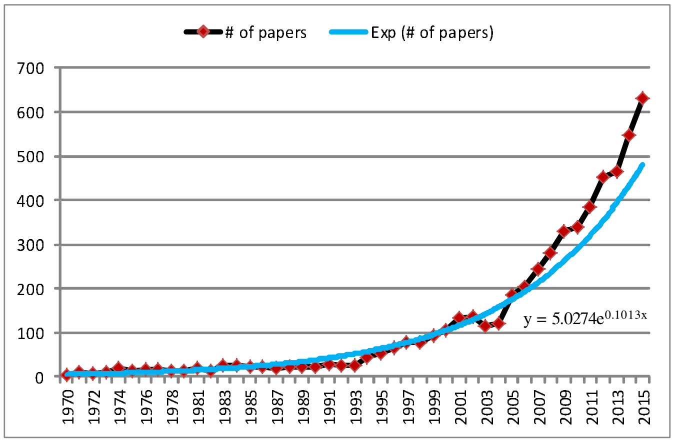

FIGURE 1. Time series of the number of papers which use IBMs in ecology of table 1

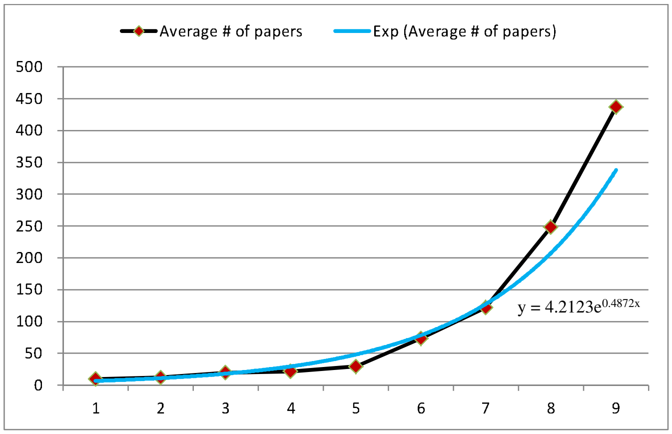

FIGURE 2. Time series of the total num. and average num. of papers which use IBMs in ecology of Table 2

The above two motivations are both pragmatic. The first emphasizes that the individual-level modeling can be a new complementary tool to the modeling realm of population and community. In fact, IBMs are a necessary supplement for ecology modeling. Each community is composed by a wide variety of individuals. The individuals are essentially different from each other in size, life span and behavior such as response to environmental stress, growth and reproduction patterns [7]. Ecology is a complex system, and it's not enough to just model it from the population level, thus, the complete features should be modeled both from population level and individual level. The second motivation is a direct consequence of the first. It points out when a community is modeled from both population and individual level, the existing analytical methods used on population-level models are not sufficient, because most of the basic corresponding features of populations such as life spans, reproduce style and variability of individuals would have to be revised.

3. A mini-review of IBMs published in the last five decades

In the last five decades, individual based modeling has broadened its application field from the forest succession modeling to the modeling of animal populations. The early papers used IBMs to simulate some specific population (such as deciduous forest, tropical rainforest and salmon) or ecosystems. While following with the mutuality of the IBMs, researchers found that a paradigm shift is needed from traditional modeling which is based on differential equations to models, theories and concepts that are based on the emerging new individual-based methods [1,8-9]. But unfortunately the use of IBMs in dealing with paradigmatic problems has not developed significantly, thus, comparing with available mathematical models such as Markov chain and ordinary differential equation, Lacking formal structure and unified methods of analysis are the shortages of IBMs, thus from 2005, researchers put their emphasis on the standardization, formalization and systematization of IBMs. Based on the previous progress, and coupled with increased computing power, researchers such as [10] has made big progress in addressing key problems in mixed ecosystems and epidemiology by IBMs. In the following of this section, we will introduce the progress of the IBMs in ecology in detail.

3.1. IBMs in forest succession modeling and animal dynamic modeling

The gap-phase replacement model JABOWA [4] is the first effective model centering on the individual-based modeling idea. By with a view to the different effects causing by shading on trees of different species, and their different heights in relation to their neighbors as well, JABOWA described the succession of the tree populations which are created in forests because of the demise of a canopy tree [4]. Following with its success in describing altitudinal change and ecological succession, a couple of new forest models such as FORET [11], FORTNITE [12], FORMIND [13] and a spatial and mechanistic model [14] are proposed. These later models are also “gap models” that a tree is characterized by only its stem diameter, that is, it has only one state variable, and all other variables are deduced from stem diameter via allometric growth relationships.

Different from early models which restrict space within $1000m^2$, the forest model [14] extended modeled space beyond $1000m^2$, and further revealed a wide variety of causal relationships based on more than one parameter. From 2004 to now, sophisticated visualization and detail in physiological aspects of forest have been steadily increased. [15] presents a new approach called as 'field of neighbour-hood'(FON) that enables the influence of neighborhood effects on the dynamics of forests and plant communities to be analyzed and proposes a model KiWi to model the dynamics of the mangrove forests. In [16], the authors use FORMIND [13] which is an individual-based forest model to analyze the carbon balances of a tropical forest. In the FORMIND model, most of the parameters of the forest, such as tree growth rate, mortality, competition and regeneration are all considered. This study offers an example to explain how forest individual based models can be used to investigate forest structure and local carbon balances in combination with forest inventory data.

Available mangrove forest models such as KiWi and FORMAN are not ideal for tropical mangrove systems, because these models have a built-in assumption that regard environmental conditions are more applicable for subtropical mangrove systems [17]. The MANGRO model [18] is more applicable to the tropical mangrove systems because it considers the effect of tidal flooding on tree growth. But it does not offer a complete mechanism for seedling or sapling dispersal [17]. An individual-based model of forest growth and carbon sequestration in mangroves under salinity and inundation stresses is proposed in [19]. It is used to assess the success of mangrove restoration programs in the tropical mangrove systems [20]. Following with the increased computing power of computers, the forest IBMs simulating tools also have achieved quite remarkable progress. A forest growth simulator TRAGIC++ (tree response to acidification in groundwater in C++) is developed in [21] for ecologists and forestry practitioners, and it can be used as a combination of decision support system and a visualization tool. [22] propose a series of methods based on IBMs which allow the detailed prediction, observation, and testing of forest ecosystem changes at very large scales and under novel environmental conditions.

In the 1980s, much attention is paid to the forest modeling using IBMs, while in the 1990s, extension of IBMs to the other areas of ecology began to increase rapidly. A review paper [23] introduced the IBMs used in animal-aspect modeling. To our knowledge, fish species are the earliest and have the highest proportion among the models about animal populations, because in order to assess the impact of humans having on the mortality of young fish, abundance in fish population number and distribution, you need to understand the complex interactions of the parameters such as foraging ability, growing rate and survival rate to predation in younger age classes, and coincidentally these parameters can best be solved by modeling interactions of individual fish but not the fish population. [24-31] whose approaches are reviewed in [32] all focused on the growth and survival of young fish. A good yet simple IBM is proposed in [33], the IBM incorporates a two stage growth response for squid hatchlings in continual exposure to seasonal fluctuations of temperature considers. Different from the above models which are used to modeling single populations, [34] proposes an individual-based model to describe and analyze the population dynamics of sympatric rainbow trout. Sometimes, it may be much efficient to combine IBMs with population-level models, and [35-38] are four representatives.

Most of the fish models described above are based on freshwater species, however, IBMs can also be used to modeling marine ecosystems. The effects of variability such as turbulence, flow, temperature, and predication in the environment are detailed considered in these studies. In combination with the ecological formalization of hydrodynamic models of varying degrees, the IBMs are used to model the movement of planktonic life of the marine ecosystems (such as [39-41]). Ecologists also have tried to model the marine ecosystems in three-dimensional [42-43] and to find a combination with optimal algorithms [22] for a high-resolution, free-surface, terrain-following coordinate oceanic model(such as [44]).

From [6], we know that fish species have the highest proportion among the models reviewed, but IBMs were also applied to many other animal populations. IBMs are ideal for those species which are economic species or endangered species. IBMs of this type include ungulate grazes [45], birds([46-51]), brown bears([52-53]), insects([54-58]), microtine rodents([59-62]) and beetles([63]). For example, in [55], the authors point out that to capture the pattern of variability within a system relies on correct assumptions about the temporal scale of the processes involved is not easy. To address this concern, they constructed ANN (multistate and artificial neural network models) to provide forecast and hind-cast vegetation communities considered critical foraging habitat for an endangered bird, the Florida Snail Kite.

3.2. pragmatic and paradigmatic models

Unlike differential equations which can model and analyze populations, communities, or ecosystems by a series of generalize theories. IBMs lack such generalization tools and theories in modeling and analyzing as well. In sections 3.1, the pragmatic IBMs are in preponderance over those aimed at more general ecological phenomenon, thus, it is urgent to make a paradigmatic shift for IBMs.

Early applications of IBMs in solving paradigmatic problems focused on addressing the effect of space, temporal dynamics and animal movement on population stability [64-66]. The individual is the fundamental block in these models, and the dynamics are governed by rules in individual scale for movement, feeding, ingestion, growth, reproduction, and death. Through simulation, they also reveal that although average densities and vital rates are virtually unaffected, limited individual mobility greatly reduces fluctuations in total density. These models are the early results of solving paradigmatic questions, and they are highly abstract, just as [6] have pointed out, these models do not fully exploit the potential of IBMs.

In order to investigate the theoretical relationships between size asymmetry, spatial distribution, and plant density in crowded plant populations, [67] and [68] both proposed a individual-based plant competition model which emphasize the influence of zones based on overlapping zones of influence. Their methods have been extended to include more spatial interactions geometries [15,69], rainfall [70], below-ground interactions [71], IBMs based on metabolic scaling theory [72]. Animal interactions are also described by the zones-of-influence approach in [73-74].

3.3. Standardization, formalization and systematization of IBMs

IBMs are an important tool for understanding complex systems, but scientists still needs a general strategy for designing, testing and learning form such bottom-up models [75]. Researchers also have put their emphasis on the standardization, formalization, and systematization of IBMs.

Many contributions have been made. An individual-based modeling analysis procedure is introduced in [76] by Railsback and Harvey. A "pattern-oriented" process is developed to test theories of individual behaviors by producing a series of behavior patterns to exam the individual's ability. Most of the models assume that population or communities make decisions just for maximizing their growth rate, and this is an ideal assumption and too simple. An overall conceptual framework-Complex Adaptive Systems for IBMs is proposed in [77]. It provides a list of issues considered in the designing process of IBMs. [78] reviews the most popular software platforms for IBMs: NetLogo [79], MASON [80], Repast [81], the Objective-c and Java versions of Swarm [82]. In [83] and [84], Grimm proposes a standard format for describing IMBs, and in its appendices, Grimm offers descriptions of about twenty IMBs in this standard format. The standard format is organized around the three main components (ODD) to be documented: Overview, Design concepts, and Details. These components include seven sub-elements that must be documented in sufficient depth for the models purpose. The inSTREAM [85] is an IBM of trout in a stream environment, and it is originally designed as an instream flow assessment tool, it can also be used for assessing the effects of environmental processes other than instream flow and temperature.

3.4. The use of IBMs in epidemiology

The mathematical modelling of infectious diseases is a large research area with a wide literature [86], but now most of the papers are focusing on population models. On the other hand, the development of individual models that consider the disease transmission and evolution at a fine-grained level [86] is pushed toward by the increasing computing power.

In [75,87-89], the spread of rabies is modeled by combining an individual-based model which is used to describe the dispersal of rabies with a grid-based model describing local interactions. In epidemic theory, it is undoubtably that R(0) (the basic reproductive ratio) is the most widely used quantity. Many of the basic population-level models for R(0) were out of operation when we consider the transmission of infection to be a stochastic process which involves discrete individuals. [90] clarifies why and when this difference arises and forecasts the circumstance under which IBMs are likely to be more important in modelling infection dynamics than population-level models.

Other researchers concentrated on the public health perspective, are using IBMs to research what the physical contact patterns will be when the movements of individuals between specific locations affect disease outbreaks [91-94]. In order to understand the dynamics of infection outbreaks, [95] developed an IBM to study the stochastic characteristics of the corresponding state transitions, the impact of different network structure choices and the heterogeneity of the individual interactions on the poliovirus transmission process.

An essential part of the plant pathology study is the plant disease epidemiology, and IBMs are also used in the research of plant disease epidemiology, In [96-98], the authors studied the effects of brown rot infections in potatoes to some possible risk factors. A compartmental state-variable model and a spatial IBM is evaluated where the a realistic yet more detailed representation of the spread of infected seed lots is given by the above spatial IBM.

4. Challenges of IBMs

Deangelis has said that “Nothing makes sense in ecology in the light of the individual” [1]. In ecology IBMs are playing a special role in dealing with highly complex systems, especially when the decision making process of the complex systems are emerging from the interactions of individuals. Thus, it’s urgent to perfect individual-based modeling subject. In general, there are two challenges for specialists.

Firstly, it is urgent to promote the standardization of IBMs. Unlike population-level models whose profiling tools are accurate and rigid ordinary differential equations that can be analyzed using mature dynamical system theory, IBMs lacks efficient general tools to describe and analyze the effect caused by the inherently random nature of interactions between individuals or the finite population quantity. Thus, it is urgent to propose a standard model to express the interactions among individuals regardless of the species.

Secondly, the primary aim of IBMs is to predict the behaviors of the corresponding system. The most appropriate approach to modeling prediction depends on what variables are being predicted and how certain that variables are. The Bayesian framework offers a comprehensive approach to this, but its corresponding standard Monte Carlo methods are always computationally intractable for all models unless the models are carefully structured [99]. On the other hand, the Approximate Bayesian Computation (ABC) method enables approximate Bayesian inference for models of almost arbitrary complexity [100]. Within ecology there have been relatively few applications of ABC methods, this may become a fertile area of application for ABC [100].

Conflict of Interests

The authors declare that there is no conflict of interests.

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