Individual-based models in ecology after four decades

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Abstract

Individual-based models simulate populations and communities by following individuals and their properties. They have been used in ecology for more than four decades, with their use and ubiquity in ecology growing rapidly in the last two decades. Individual-based models have been used for many applied or "pragmatic" issues, such as informing the protection and management of particular populations in specific locations, but their use in addressing theoretical questions has also grown rapidly, recently helping us to understand how the sets of traits of individual organisms influence the assembly of communities and food webs. Individual-based models will play an increasingly important role in questions posed by complex ecological systems.

What are individual-based models?

Individual-based models, also called agent-based models, are a population and community modeling approach that allows for a high degree of complexity of individuals and of interactions among individuals. Individual-based models simulate populations or systems of populations as being composed of discrete individual organisms. Each individual has a set of state variables or attributes and behaviors. State variables can include spatial location, physiological traits and behavioral traits. These attributes vary among the individuals and can change through time. Behaviors can include growth, reproduction, habitat selection, foraging, and dispersal. Unlike traditional differential equation population models, which are described in terms of imposed top-down population parameters (such as birth and death rates), individual-based models are bottom-up models in which population-level behaviors emerge from the interactions among autonomous individuals with each other and their abiotic environment. An advantage of individual-based models over traditional models is that they can incorporate any number of individual-level mechanisms. They are thus used whenever one or more of the following aspects, which are hard or impossible to represent in population-level differential equations, are considered essential for answering a research question or solving an applied problem: variation among individuals and of individuals during their life cycle; local interactions among individuals; and adaptive behavior, which includes physiology and energy budgets.

Beginnings of individual-based models in forest succession modeling

The first major use of an individual-based model was that of JABOWA [1], a "gap-phase replacement" model, which described a succession of tree communities in gaps created in forests due to the death of a canopy tree (typically 1000 m^2) by taking into account the differential effects of shading on trees of different species and different heights in relation to their neighbors. The success of JABOWA in describing succession and altitudinal change in tree communities inspired many variations of forest gap models, for example, FORET [2], FORTNITE [3], and FORMIND [4], as reviewed by Bugmann [5]. An important feature of JABOWA and all later "gap models" is that a tree is characterized by only one state variable, its stem diameter. All other variables, such as height, vertical

leaf profile and so on, are deduced from stem diameter via allometric relationships. Different species are represented via different growth and allometric parameters, not via different model structures. Later forest models [6], extended modeled space beyond the 1000 m^2 range of local interactions by including spatial locations of each tree. Physiological detail and sophisticated visualization have been steadily increased (e.g. Parrott and Lange [7]).

Spread of individual-based models to modeling of animal populations

Extension of individual-based models beyond the forest modeling to other areas of ecology was initially slow, but began to increase rapidly in the 1990s, especially following a 1990 workshop that reviewed these models [8]. One area of early use of individual-based models was modeling the recruitment in fish populations, largely because assessing the impact humans have on the mortality of young-of-the-year fish required understanding of the complex interactions of size, foraging ability, growth rate, and vulnerability to predation of fish in younger age classes, which could best be approached by modeling interactions of individual fish. As a result, an important subset of models combining an individual-based model and bioenergetics was devoted to fish early life history, focused on determining growth and survival of young-of-the-year fish [9,10,11,12]. This approach was reviewed by Van Winkle *et al.* [13] and subsequently by Sibly *et al.* [14]. DeAngelis and Mooij [15] counted over 100 fish-oriented individual-based models in a review of the literature. These models were generally limited to modeling single populations, although Clark and Rose [16] modeled interspecific competition between native and non-native salmonids in a stream.

While many of the above fish models are for freshwater species, similar needs motivated the application of individual-based models to marine ecosystems, in this case often in order to follow the fate of the planktonic life stages, where the organism movement is largely controlled by the currents [17-19]. Individual-based models focused on explicitly coupling the biological and ecological formulations to hydrodynamic models of varying degrees of three-dimensional and temporal complexity (e.g. [20,21]). The effects of variability in the physical environment (flow, temperature, salinity, turbulence, and light) are explicitly considered in the study of dispersal, growth and mortality of the target, analogously to the above terrestrial models.

It is not surprising that individual-based models were applied to many other animal populations. They are well suited to incorporating spatial landscapes in a realistic manner and simulating complex behaviors in populations.

This is ideal for species that are of particular interest (e.g. for economic reasons or because they are endangered), for which there is often detailed empirical information. Spatially explicit models of this type include ungulate grazers [22], wood storks [23], brown bears [24], Cape Sable seaside sparrows [25], European robins [26], snail kites in Florida [27], and Alpine marmots [28,29]. For example, the Cape Sable seaside sparrow model (SIMSPAR) has the goal of predicting the effects of particular water management operations in the Everglades, which can affect nesting success. A high degree of detail on topography, daily water depths (information provided by hydrologic models), and sparrow behavior is essential in making predictions.

Pragmatic and paradigmatic models

The motivation to develop individual-based and other simulation models in ecology can be divided into two main categories by their goals [30]. One type of model is used in the simulation of specific populations, communities, or ecosystems, usually with a management goal in mind; these are termed "pragmatic" because representing individuals explicitly is essential for the problem addressed and because simple mathematical models are too limited for this. Several such models were mentioned above. The other type aims to help us to gain a better general understanding of the underlying causes of ecological phenomena and is termed "paradigmatic" because it is assumed that a paradigm shift is needed from physics-style modeling, based on differential equations, to models, theories, and concepts that are based on emergence and evolutionary principles [31,32]. Grimm [30] noted the preponderance of pragmatic individual-based models over those aimed at more general ecological questions.

The use of individual-based models in addressing paradigmatic questions has gradually increased. Early applications addressed the effect of space and animal movement on population stability [33-35]. These investigated spatially structured predator-prey systems through simulation modeling, showing stabilization due to limitations in mobility, leading to local asynchrony of spatially separated predator-prey populations. Somewhat related simulation modeling was done by Cuddington and Yodzis [36]. They also found similar results of limited mobility on predator-prey stability but interpreted the stabilization as a "diffusion-limiting" effect rather than asynchrony; that is, the rate of the predator-prey interactions was slowed due to slow diffusion across space. These models have influenced theory, but they are highly abstract, with individuals effectively simulated as particles. As Grimm [30] noted, such abstract models do not fully exploit the potential of individual-based models.

More realistic but still paradigmatic individual-based models of plants have widely been used to address generic questions regarding the emergence of size distributions in plant populations and density-biomass relationships in even-aged self-thinning stands. A generic approach representing plant-plant interactions are "zones-of-influence", which represent the circular areas on which plants acquire resources [37-39]. As plants grow, their zones-of-influence grow and start overlapping. Competition in these overlapping areas can be size-asymmetric (i.e. the bigger of the two interacting plants obtains an over-proportional share of the resources), or size symmetric. The zones-of-influence approach has been extended to include more realistic geometries of spatial interactions [40], above- and below-ground interactions [41], growth models based on metabolic theory [42], and facilitation [43]. The zones-of-influence approach has also been used to represent animal interactions [44].

Bringing systematic approaches to the development and analysis of individual-based models

A criticism of individual-based models has been that they lack the formal structure and methods of analysis that are available to mathematical models, such as differential equation and Markov chain models. Three decisive contributions made over the last ten years are helping to address this criticism. One of these was the publication of the first monograph on individual-based modeling and ecology [45], which provided a standardized approach to developing individual-based models and emphasized the role of these models in simulating how complex adaptations of individuals shape populations and communities. The second and third contributions were the publication of a standardized format for describing individual-based models in publications (the "ODD [overview, design concepts, and details] protocol" [46,47]), and a general modeling methodology, "pattern-oriented modeling" [48], defined as the "multi-criteria design, selection and calibration of models of complex systems" [49]. In pattern-oriented modeling, multiple patterns, both specific and generic ones, observed at different scales and levels of information, are used to optimize model complexity, to select among alternative submodels representing key behaviors of individuals, and to inversely determine entire sets of unknown parameters.

Advancing community ecology, food web ecology, and epidemiology with individual-based models

Sound modeling methodologies, coupled with increased computing power, are allowing individual-based models to live up to the promise [50] of exploring basic concepts across a wide swath of ecology and evolutionary biology.

Individual-based models are making big inroads in addressing key questions concerning the assembly and structure of communities. This was stimulated by a statement of McGill *et al.* [51]: "There is considerable debate about whether community ecology will ever produce general principles…We suggest that a focus on four research themes can clean up the mess, bringing general patterns to community ecology: traits, environmental gradients, the interaction milieu, and performance currencies". Inspired by this challenge, Giacomini *et al.* [52] noted that, unlike analytic models that are limited in the diversity of species traits that can be considered simultaneously, individual-based models are ideal for addressing that challenge. For example, individual-based models can simulate the assembly of animal communities characterized by life history and trophic interactions with multiple physiological tradeoffs as constraints on species performance. Giacomini *et al.* [52] carried out simulation experiments to evaluate the distribution of six life history and four feeding traits of fish along gradients of resource productivity and prey accessibility. These simulations revealed that traits differ greatly in importance for species sorting along the gradients.

In a similar approach, Weiss *et al.* [53] used a trait- and individual-based model of community assembly in grasslands. Their model represented above- and below-ground competition, and included more than 90 hypothetical plant functional types, defined by certain trait combinations and trade-offs. Traits were parameterized from trait databases, and the response of the emerging model communities to changes in soil resource levels and to different grazing intensities were explored. Even without calibration, model output matched observations regarding species richness, diversity, and productivity. The model was also local, representing 2 m², without external seed input, which shows that it is not always true (as assumed in metacommunity theory) that regional processes are required to explain local diversity patterns.

Food webs also pose many fundamental questions. Is the herbivore level regulated by autotroph resources or carnivores? What causes population cycles in some food chains? These questions have been addressed for many years by traditional differential equation population models, but there is increasing opinion that individual-based models are needed to provide better answers by allowing heterotrophs to behave realistically. This view was expressed by Schmitz and Booth [54], who used the modeling code "Gecko" to incorporate perception based on zones-of-influence and intentional choices of action by individuals on a landscape. Unlike differential equation models, in which the outcomes are predestined by the assumptions made in the equations, Gecko produced

unexpected emergent results when applied to terrestrial food chains, such as nutrient-plant-grasshopper-spider. For example, simulations showed that high densities of vegetation did not support high densities of herbivores, a result traced back to the fact that the individual plants had low nutrient:biomass ratios.

An interesting convergence of epidemic modeling from the point of view of ecologists as well as social and public health scientists is occurring through the common use of individual-based models. Individual-based modeling of epidemics in the ecological context is represented by such models as simulations of the spread of rabies [55,56]. In these models, the spread of rabies by foxes is modeled by simulating their spatially explicit dispersal and interactions. Individual-based models are also helping to better understand how the discrete nature of populations alters the traditional criterion for epidemic outbreaks in deterministic epidemic models: the basic reproductive ratio, R_0. In some situations where stochasticity is important, this index loses accuracy as a criterion for epidemic outbreak [57]. Other specialists on epidemics, oriented around the public health perspective, are using individual-based models (usually referred to as agent-based models in that literature) to study how behaviors and social networks affect disease outbreaks [58,59]. This convergence is a road towards a useful synthesis of ecological and public health science.

Future trends and challenges in individual-based modeling

The future of individual-based models will be based on further standardization of submodels, so that not every individual-based model has to be fully developed from scratch, and on merging the pragmatic and paradigmatic perspective. Standard submodels representing interactions were the key to the success of JABOWA and related fish individual-based models. Interaction models can, similar to zones-of-influence, be based on perception radii [54,44]. Buchmann *et al.* [60] based a community model of mammals on allometric relationships between body mass, home range size, and habitat quality. Dynamic Energy Budget theory [61] is a generic approach with species-specific applications only differing in model parameters, not model structure. This theory has been widely used to describe individual organisms but has recently been shown to correctly predict population dynamics (e.g. cycles) and response to toxicant for laboratory populations of the waterflea, *Daphnia magna* [62,63].

The trait-based approach allows us to assemble functional types from a limited number of traits. Future individual-based models might thus be assembled from a tool-kit of tested and ready-to-use building blocks representing, for example, energy budget, habitat selection, and trait composition. Implementing such models is already facilitated by software platforms specifically designed to implement individual-based models [64,65].

A merger of the pragmatic and paradigmatic perspective will also be needed. A merger is possible because of the existence of more and more well-tested submodels for representing certain behaviors and interactions. Pattern-oriented modelling allows for the testing of how well these submodels, embedded in a full individual-based model, reproduce multiple observations; standardized designs (communicated in standardized formats like the ODD protocol), and implementations allow the systematic comparison of model structure and scope. Still, model analysis of future individual-based models needs to go beyond the "construction" phase, where elements are added to a model until it reproduces observations and include a "deconstruction" phase, where the model is systematically simplified to understand which processes and features of the model were essential to capture the internal organization of the real system.

Ecology is dealing with highly complex systems, so that a wide range of modeling approaches, including individual-based models, is needed to understand the emergence and functioning of ecosystems. However, individual-based models play a special role as, essentially, ecology emerges from what decision-making individuals, which are different and interact locally, are doing. Paraphrasing Dobzhansky [66], it can be said that: "Nothing makes sense in ecology except in the light of the individual".

Abbreviations
ODD, overview, design concepts, and details.

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