

INDIVIDUAL-BASED MODELING OF ECOLOGICAL AND EVOLUTIONARY PROCESSES¹

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■ **Abstract** Individual-based models (IBMs) allow the explicit inclusion of individual variation in greater detail than do classical differential-equation and difference-equation models. Inclusion of such variation is important for continued progress in ecological and evolutionary theory. We provide a conceptual basis for IBMs by describing five major types of individual variation in IBMs: spatial, ontogenetic, phenotypic, cognitive, and genetic. IBMs are now used in almost all subfields of ecology and evolutionary biology. We map those subfields and look more closely at selected key papers on fish recruitment, forest dynamics, sympatric speciation, metapopulation dynamics, maintenance of diversity, and species conservation. Theorists are currently divided on whether IBMs represent only a practical tool for extending classical theory to more complex situations, or whether individual-based theory represents a radically new research program. We feel that the tension between these two poles of thinking can be a source of creativity in ecology and evolutionary theory.

INTRODUCTION

The past decade and a half has been a period of enormous growth of individual-based modeling (IBM) in ecology and evolutionary biology. A survey of articles with “individual-based” (or “individual-oriented”) and “model” in the title, abstract, or keywords showed a linear increase from 1 in 1990 to approximately 150 in 2004. Not all papers about IBM use these keywords, and papers on the IBM approach go back at least to the 1960s, so the actual number of studies that employ IBM is considerably higher. An objective of our review is to assess whether this numerical increase corresponds to real scientific progress.

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IBM has expanded across a wide swath of ecology and evolutionary biology; it parallels the growth of related “agent-based” models of economics, social science, and artificial intelligence and of particle-based models in physics (Hockney & Eastwood 1989). An early review of IBM in ecology (Huston et al. 1988) pointed to the promise of IBM to provide a unified approach to applied and theoretical questions in ecology. However, a minireview by Grimm (1999) of IBMs in ecology ($N = 50$) showed that “most of the IBMs of the period 1990–1999 did not directly address general questions, but were narrower in their scope” or “pragmatic.”

The field has also been reviewed in Hogeweg & Hesper (1990), DeAngelis & Gross (1992), Uchmanski & Grimm (1996), and Lomnicki (1999). In a recent book, Grimm & Railsback (2005) provide a set of guidelines for building, testing, and analyzing individual-based models. Our objective is more investigative. We ask ourselves, on the basis of the database of approximately 900 references found in our literature survey, among other sources, how has the field of IBM developed over the past decades? We classify IBMs according to their purposes and the way they take into account variation at the individual level. From this perspective, we explore and assess the current state of IBM.

What is an individual-based model? We agree with Grimm & Railsback (2005) that no absolute definition exists. In principle, IBMs simulate populations or systems of populations as being composed of discrete agents that represent individual organisms or groups of similar individual organisms, with sets of traits that vary among the agents. Each agent has a unique history of interactions with its environment and other agents. IBMs attempt to capture the variation among individuals that is relevant to the questions being addressed. Our interpretation of what constitutes an IBM is deliberately broad and inclusive. However, this interpretation is compared with a stricter definition in the Conclusions and Perspectives section below.

We provide a solid conceptual basis for our review by describing five major types of individual variation in IBMs: spatial, ontogenetic, phenotypic, cognitive, and genetic. To survey the breadth of applications of IBM, we next formulate seven groups of biological processes for which IBMs have been developed, and we highlight within each group a number of research foci. To measure the depth of the contributions of IBMs to important questions, we illustrate several areas of high concentrations of IBMs by describing papers that have been particularly influential in those areas. We offer suggestions for design and analysis of IBMs. We conclude that the explicit accounting for individual variation plays a crucial role in the development of ecological and evolutionary theory.

THE NATURE OF INDIVIDUAL VARIATION

Although a balance between parsimony and detail is essential in modeling, the growth in IBM reflects a perception that inclusion of variation among individuals is often indispensable for understanding and prediction at the population,

community, and ecosystem levels. The trend toward inclusion of variation at finer resolution is already apparent in extensions of differential-equation and difference-equation models (which, for convenience, we refer to as classical models) to structure within populations, such as age or size classes, and to subpopulations within metapopulations. However, better understanding of some population and community phenomena requires zooming down to even lower levels. The level of resolution of IBMs is the individual organism, so IBMs allow accounting for differences among individuals. We suggest that it is convenient to categorize this resolution as an increasing level of mechanistic detail along each of five directions or axes. The structural characteristics along these axes are (a) spatial variability, local interactions, and movement; (b) life cycles and ontogenetic development; (c) phenotypic variability, plasticity, and behavior; (d) differences in experience and learning; and (e) genetic variability and evolution. Demographic stochasticity could be considered a sixth category, but we see it as an intrinsic property of any IBM and thus part of each of the above categories.

Variability in Space

Classical predator-prey models, in their functional responses, contain at least an implicit concept of the space in which interactions occur; some metapopulation models incorporate distances between patches; and reaction-diffusion models can simulate the spread of population density explicitly in space. However, classical models cannot take into account discrete individuals, which create local population nonuniformity that can affect population dynamics and ecosystem function (Durrett & Levin 1994). Myers (1976) was one of the first to show, in a spatially explicit IBM of herbivorous insects feeding on plants, that local inhomogeneity, in the form of herbivore outbreaks and extinctions that arise stochastically, could affect total-population dynamics.

Life Cycle Detail

The inclusion of age-structure or stage-structure detail has been dominated by difference-equation (matrix) models, such as Leslie models (Caswell 2000, Leslie 1945), which have proved effective at incorporating important key dynamic features that result from life cycles of organisms. However, a number of practical and theoretical questions require examination of the life cycle in finer detail, such as demographic variability, spatial structure, and short-term temporal variability. Such situations can, in principle, be handled by matrix models but then require partitioning of the population into such a large number of subclasses that IBMs become advantageous.

Phenotypic Variation and Behavior

In addition to the variation within populations caused by ontogenetic changes through the life cycle, variation also results from the unique experiences of each

individual. This observation is true for plants, each of which exists on a site with its own characteristics of soil, light, water, and nutrients, as well as for animals, each of which has its own trajectory through the environment and history of feeding, disease, and exposure to other stresses. Lomnicki (1978) recognized the importance of individual phenotypic variation to populations. The earliest genre of IBMs to gain prominence, the forest gap-phase replacement models (Botkin et al. 1972, Shugart 1984), accounted for the phenotypic variations among individual trees caused by effects of shading on growth. Phenotypic variability, even within a cohort of genetically identical organisms born at roughly the same time, poses a fundamental theoretical question of how it affects population dynamics. Classical size-structure models, such as the McKendrick-von Foerster model, have been used to study variable size in populations (e.g., De Roos et al. 1992, Sinko & Streifer 1967) but have the same difficulty as matrix models in dealing with more than one or two phenotypic features, with stochasticity, or temporal autocorrelations, in changes in condition of individuals (i.e., cases in which individuals with a higher than average feeding rate one day have a higher probability of a higher than average feeding rate the next day). An additional difficult task for classical models is in dealing with complex behavioral sequences, which can occur in foraging, mating, and other activities.

Experience and Learning

Implicit learning at the population level is built into some classical models of interacting populations; for example, a predator population could increase its preference for certain prey relative to other prey types when the first type increases its proportional representation in the prey community (Steele 1974). However, learning, like phenotypic change, is a product of individual experiences. All learning involves memory, so memory of past experiences must be considered an internal state of organisms. Two general types of learning can be distinguished: learning from the environment and learning from other organisms. The latter type of learning, which results from encounters with other individuals that affect fitness, requires a game-theory approach, which can be difficult to include in classical models.

Genetics and Evolution

Genetic and evolutionary biologists have always tended to focus on the individual organism. Many of the concepts of evolutionary genetics, such as mutations, genetic drift, and founder effects, inherently involve small numbers of individuals, so that stochasticity is important. Although analytic models of dynamics are well understood for many single-locus populations, computational models are usually needed for more complex situations. IBMs are more flexible than are classical models of genetic change and can mimic real populations. IBMs have long been applied to human populations, for example, in studying the maintenance of balanced polymorphisms such as the sickle cell trait (Schull & Levin 1964).

Mechanistic detail is assumed to increase along all of these five axes. Classical structural models are usually close to the origin. IBMs, however, tend to depart substantially from the origin along more than one axis at the same time.

ECOLOGICAL AND EVOLUTIONARY PROCESSES ADDRESSED WITH IBMS

A categorization of more than 900 IBM papers with respect to the main type of biological process they deal with showed seven major groups of studies.

Movement Through Space

Models of animal local movement encompass the detailed active movement behaviors of animals and include their interactions with complex landscapes and other animals (Johnson et al. 1992) as well as the development of home ranges (South 1999). These models have been used to design and evaluate empirical studies of movement. Animal migration models take into account detection of sensory cues and the following of older, experienced members of a school, herd, or flock. Fish-migration models have revealed that the proportion of experienced members of schools is important for accurate migration to the previous year's site (Huse et al. 2002). Models of migrating birds have raised questions regarding traditional concepts of carrying capacity when applied to overwinter survival (Goss-Custard et al. 2002, Pettifor et al. 2000). Models of active animal dispersal from natal sites take into account effects of conspecifics and avoidance as well as attraction behaviors in patchy environments (McCarthy 1997). Such models can be used to determine the nature of dispersal patterns (Schwarzkopf & Alford 2002). A considerable number of studies focus on movement by water or air. Marine biologists use ocean-current models to study passive movement of ichthyo- and other plankton (Miller et al. 1998), and analogous models are used to simulate wind dispersal of seeds, especially important for grassland vegetation (Jongejans & Schippers 1999).

Formation of Patterns Among Individuals

Models of swarm/aggregation formation are used to study environmental and social forces and individual decision rules that lead to formation of swarms, flocks, schools, herds, and other groups (Flierl et al. 1999, Gueron et al. 1996, Hemelrijk & Kunz 2005, Huth & Wissel 1992, Young et al. 2001). A limited set of rules can give rise to highly organized group aggregation and movements. Settlement, territory-formation, and home-range models predict propagule settlement rates as well as the spatial patterns of territories that arise from the settling organisms (Murai et al. 1979, Tanemura & Hasegawa 1980). Learning behavior can be a factor in territory formation (Stamps & Krishnan 1999). Models of the dynamics of social networks simulate the ontogeny of caste structure in insect societies

(Hogeweg & Hesper 1983) as well as of foraging paths. Some models describe effects of sociality in vertebrates, such as development of cooperative behavior (Schank & Alberts 2000) and its effect on fitness (Vucetich et al. 1997). How animals should act in encounters with conspecifics (hawkish or dovish, selfishly or altruistically) depends on the expectation of the behavior of the other animal in the encounter. Study of this behavior is the field of game-theoretic interactions. IBM simulations that incorporate game theory are used to simulate the outcome of competing strategies (Broom & Ruxton 1998).

From Foraging and Bioenergetics to Population Dynamics

Foraging models examine the effects of variation of prey preferences among predators on frequency-dependent selection (Sherratt & Macdougall 1995) and variance in growth (Breck 1993). Complex models use artificial-life approaches to show that foraging in large flocks versus solitary foraging for birds, for example, can arise out of resource distribution (Toquenaga et al. 1995) and that spatial memory is important to optimal foraging in a complex environment (Folse et al. 1989, Nolet & Mooij 2002). A related set of models deals with spatial heterogeneity and habitat choice. The mechanisms for formation of an ideal free distribution (IFD) have been simulated by use of exploratory movements combined with memory (Regelmann 1984). Deviations from the IFD occur in spatial systems in which individuals have less than perfect knowledge (Hugie & Grand 2003, Humphries et al. 2001) or when temporal variation occurs in mortality and food availability (Railsback & Harvey 2002).

Bioenergetics models of individuals, including physiological abilities and constraints, combined with foraging models, take account of time and energy budgets and make finer-scale predictions about foraging decisions of individuals (Hölker & Breckling 2002, Kooijman 2000). Some practical and theoretical questions require attaching bioenergetics models to life-history models, as well as demographic variability, spatial structure, and environmental change (Dunham & Overall 1994, Grimm & Uchmanski, Poethke & Hovestadt 2002, Reuter & Breckling 1999, Tyre et al. 2001). An important subset of life-history models are those on fish early-life history, which focus on determination of growth and survival of young-of-year fish. These models have been useful for understanding stock-recruitment dynamics (DeAngelis et al. 1993b, Madenjian & Carpenter 1991, Rose et al. 1999, Scheffer et al. 1995). Classical life-cycle models often leave out important phenotypic variation and have special difficulty in capturing the large variances in size and other traits that can develop through positive-feedback effects in the life cycle when growth rates or other phenotypic traits are autocorrelated from one time step to the next (DeAngelis et al. 1993a, Pfister & Stevens 2002). Phenotypic variation generated by positive feedback can lead to population-level consequences.

Kaiser (1979) was among the earliest investigators to recognize the importance of properties of individuals in population dynamics, particularly their

interactions with space, in which population inhomogeneities that can have profound effects arise. Logistic growth simulated on a spatial arena produces dynamics far different from those of the classic logistic model (Berec et al. 2001, Bolker & Pacala 1997, Kaitala et al. 2001, Law et al. 2003, Molofsky 1994, Rodd & Reznick 1997), and mate-search strategies in space affect the occurrence of the Allee effect (Berec et al. 2001). Inclusion of spatially explicit landscapes and discrete individuals has greatly extended the power and realism of metapopulation models. IBMs allow accounting for differences in individuals (e.g., age, energy levels, and dispersal ability), variation in site quality (e.g., overgrazing), population levels, and demographic stochasticity (Gustafson & Gardner 1996, Keeling 2002, Kostova et al. 2004, Ovaskainen & Hanski 2004, Rushton et al. 2000). Deviations from the classical Levins metapopulation model are observed in multispecies IBMs that result from correlations between patch occupancy and population levels (Keeling et al. 2002).

Exploitative Species Interactions

Intense interest focuses on the effects of diffusion and mixing of populations on stability and spatial pattern formation in predator-prey and host-parasitoid interactions (Cuddington & Yodzis 2002; De Roos et al. 1991; Donalson & Nisbet 1999; McCauley et al. 1993; Myers 1976; Pascual & Levin 1999; Petersen & DeAngelis 2000; Wilson et al. 1993, 1999). Smith (1991) showed that detailed movement patterns of predators and prey, such as pursuit or avoidance, can drastically affect the stability of the interaction. Microbial systems often allow model comparisons with data (Kooi & Kooijman 1994). Models of host-pathogen interactions demonstrate how the spread of parasites and disease is related to variations in individual characteristics (Jeltsch et al. 1997, Rand et al. 1995). The possible amplification of small initial size differences within a fish cohort has been shown (DeAngelis et al. 1979) in models of size-dependent predator-prey interactions. Because of the complex interactions between numbers, size distribution, and resource pool, the IBM approach has become a popular modeling tool for projecting the dynamics of fish populations in particular (Claessen et al. 2000, De Roos & Persson 2002).

Local Competition and Community Dynamics

Models of local competition of sessile organisms keep track of individual organisms either within grid cells or on a continuum. This class includes benthic or intertidal organisms (Robles & Desharnais 2003) and terrestrial plants (Law & Dieckmann 2000, Pacala 1986, Pacala & Silander 1990, Weiner et al. 2001). Models of this type show a variety of emergent phenomena, such as the development of bimodal distributions of plants from even-aged stands (Ford & Diggle 1981). A subset of these models focuses on bacterial colony growth (Kreft et al. 1998). Forest models are a particular class of local-competition models, and the earliest genre of IBMs to gain prominence were the forest gap-phase replacement models

(Botkin et al. 1972, Shugart 1984). Interactions were averaged over tree gaps (approximately 0.1 ha). Another class of forest models (e.g., Pacala et al. 1996) includes spatial locations of each tree. In recent models, physiological detail and sophisticated visualization have been increased (Parrott & Lange 2004).

Many models of community dynamics are aimed at explicating the factors that control species richness and diversity (Chave et al. 2002). In particular, the mechanisms of competition-colonization trade-offs, conspecific density-dependence effects, and niche differences all interact in a spatial context. Models also study the factors that affect community patterns and transitions between types of community (Higgins et al. 2000, Van Nes & Scheffer 2003). Food webs can be influenced by individual behaviors, such as prey behavioral responses to predator presence, the complexities of changing size distributions of populations in food webs, and the size of available habitat (Schmitz & Booth 1997).

Evolutionary Processes

The modeling of fitness and trait evolution does not always attempt to replicate the mechanisms of evolution, but instead uses computing approaches that range from simple comparisons of trait values to genetic algorithms to find optimal traits for foraging and predator avoidance, dispersal, and reproduction (Rees et al. 1999, Travis & Dytham 1998, Vos et al. 2002, Warren & Topping 2001). Other models, such as those describing coevolution of parasite or pathogen virulence and host resistance, attempt to simulate evolutionary processes (Fellowes & Travis 2000). Competition models, coupled with the capacity to evolve, have shown that the details of local interaction determine whether character displacement of competitive exclusion result (Kawata 1996). Various mechanisms of sympatric and parapatric speciation have been investigated (Dieckmann & Doebeli 1999, Gavrillets et al. 1998, Rice 1984, Savill & Hogeweg 1998, Van Doorn et al. 2004). Hybrid spatial zones can develop where speciation occurs (Sayama et al. 2003). An important evolutionary process addressed by IBMs is the maintenance of genetic diversity. Models have been used to show when balanced polymorphisms could be maintained in populations (Heuch 1978, Schull & Levin 1964). Factors affecting the threat of hybridization to diversity have been investigated (Wolf et al. 2001). The advantages of different mating systems and sexual reproduction are compared under various environmental conditions. This comparison includes dioecy versus hermaphroditism (Wilson & Harder 2003) and polygyny versus monogamy (Gronstol et al. 2003).

Management-Related Processes

IBMs have been applied in population-viability analysis for a large variety of taxa, including birds (Letcher et al. 1998), mammals (Li et al. 2003), and insects (Griebeler & Seitz 2002). Conservation models describe conservation of communities, food webs, or other groups of species at the landscape scale (Macdonald & Rushton 2003, Turner et al. 1994, Wiegand et al. 2004, Wiegand et al. 1999). Fate,

effects, and risks of contaminants have been modeled for PCBs (polychlorinated biphenyls), organic toxicants, oil spills, and radiation, among other pollutants (Baveco & De Roos 1996). Invasive species such as weeds have been modeled, including the effects of plant life-history characteristics and properties of the environment (Higgins et al. 1996). Models are used to study the efficiency and sustainability of harvesting and effects of regulations, as well as to predict recruitment to stock and to analyze harvest data (Lammens et al. 2002, Whitman et al. 2004). Effects of increased landscape fragmentation, global warming, and other aspects of disturbance and environmental change on species populations and ecological systems have been modeled (Keane et al. 2001, McDonald et al. 1996, Shugart et al. 1992).

CONTRIBUTIONS OF INDIVIDUAL-BASED MODELS

The above overview illustrates the breadth of subject areas that IBMs now cover in ecology. Has the impact been deep as well?

The significance of IBM to ecology has been obvious in certain applied areas. Forest gap-phase models have been used for more than three decades and are a routine tool in forest ecology (e.g., Shugart 1984). These models are effective at projecting the influence of environmental factors on forest productivity and species composition. The commercial importance of trees and the availability of species-level data are factors in their success. The use of IBMs in fish early-life history beginning in the early 1990s and continuing today resembles the growth of forest models. Understanding the factors that affect recruitment is crucial for the fisheries industry, and IBMs are indispensable for simulating complex interactions between size, growth rate, and survival (e.g., Rose et al. 1999). A third applied area is population-viability analysis, applied to the conservation of endangered species (e.g., Letcher et al. 1998) or to the reintroduction of extinct species (Figure 1). IBMs are efficient at modeling populations in which the factors of spatial heterogeneity, behavioral complexity, and small population-size effects (e.g., stochasticity, the Allee effect) are important.

Usage of IBM in several areas of theory has also gained prominence. One of these areas involves spatial heterogeneity and scale aspects of space to populations (e.g., Levin 1994, Levin & Durrett 1996). Spatially explicit IBMs are used to investigate how local interactions and movements of organisms manifest themselves in population-level consequences, such as stability, persistence, and coexistence. Models of local competition of sessile organisms allow investigation of the emergence of size distributions and spatial patterns (Robles & Desharnais 2003). Modeling of fish schooling and other animal-swarmling behaviors is a sub-field that has grown dramatically (Huse et al. 2002). Researchers can use IBMs to examine how intricate patterns of swarm-scale movement emerge from the movements of individual fish, which know the positions and orientations of only a few neighbors. Understanding the connections between rules of individuals and

large-scale patterns is an underlying theme of ecological theory. The study of how speciation occurs is another subfield in which IBMs have been used with success (e.g., Gavrillets et al. 1998). Discreteness and local interactions (mating) are fundamental aspects of real populations that are captured naturally by IBMs. Speciation is an emergent property of such models.

IBMs have also played a role in interpretation of empirical data from field studies. These studies include the analysis of data on movements of animals, where radio-tagging has produced enormous amounts of information on locations or organisms through time. Models can be used to infer the rules governing the movement, although the development of statistical connections is a challenge (Mooij & DeAngelis 2003). A related subfield is the simulation of passive movements of organisms in oceanic currents. Data on settlement densities of benthic-organism propagules are often known. When linked with hydrologic circulation models, IBMs can be used to trace the paths of dispersal of propagules from sources (Miller et al. 1998).

A SAMPLE OF INDIVIDUAL-BASED MODELS

We have selected for in-depth consideration six papers as representative of areas of high concentration of IBMs. They include the most-cited papers on fish and forest IBMs by Rice et al. (1993) and Ribbens et al. (1994), respectively. More recent papers are a unifying community paper by Chave et al. (2002), a highly cited paper by Dieckmann & Doebeli (1999) on speciation, a paper by Wiegand et al. (1999) showing how landscape structure can effectively be linked to population dynamics, and a multimodel conservation study by Stephens et al. (2002).

The fish-recruitment model by Rice et al. (1993) demonstrated the importance of phenotypic variation, specifically the effects of growth-rate variation and size-dependent mortality on the size structure of a population through time. The authors modeled cohorts of initially even-sized individuals with a series of different growth-rate coefficients that stayed constant for individuals but varied among individuals. The mean growth rate of the cohort increased over a growing season because size-dependent mortality acted mostly on the smaller individuals. Both increased mean growth rate and increased growth-rate variance led to an increase in survivorship. This model was extended to allow random variation in growth rate between days, with some positive correlation between growth rates on successive days (i.e., successful foraging one day improved chances for success on the next day). With autocorrelated growth, the size-frequency distribution was substantially broader than when the growth rates were held constant over time, which demonstrates the importance of autocorrelations in addition to variation in growth rates.

The forest model by Ribbens et al. (1994) introduced a technique for calibrating a model of tree-seedling dispersal and demonstrated the effect of spatial variation in seedling recruitment on forest dynamics. The model, SORTIE, described growth,

probability of survival, recruit production, and resource density on a spatial domain. Earlier IBMs of forest dynamics made simple assumptions about seedling dependence on parent distribution. The authors used data on the spatial distribution of parent trees as well as transect data on seedlings through mixed stands. These data were used to calibrate and validate a seedling-dispersal submodel. Because this analysis showed that seedling establishment can be a limiting factor in forest dynamics, the authors next included their seedling submodel in SORTIE and demonstrated that seedling-recruitment limitation could significantly affect the dynamics of a forest.

Life-cycle variation in traits provides possible mechanisms for maintaining biodiversity of sessile organisms in a diversity model by Chave et al. (2002). Such mechanisms include (a) life-history niche differentiation mediated by competitive trade-offs, (b) frequency dependence caused by species-specific pests, (c) recruitment limitation caused by localized dispersal, and (d) a speciation-extinction dynamic equilibrium mediated by stochastic drift. The relative importance of these mechanisms was assessed using a spatially explicit IBM with individual-level processes of birth, death, speciation, dispersal, and immigration from outside on a 4096×4096 lattice. Community-level patterns, such as species-area curves, relative-abundance distributions, and spatial distributions (Figure 2) were extracted from the simulation output and compared with those in real communities. All contributed to species richness, but only life-history niche differentiation mediated by competitive trade-offs and frequency dependence caused by species-specific pests produced robust coexistence. The scale of dispersal was the most important factor affecting species area curves (steep at small scales, then more shallow, and finally steep across large scales). The model is successful because of its unifying nature in explaining many spatial patterns.

Incorporation of genetic variation in a speciation model by Dieckmann & Doebeli (1999) showed that sympatric speciation can emerge much more easily than previously expected from competition for resources. Analytic models had already been used to describe the evolution of traits in asexual species with trait value x , associated with a carrying capacity $K(x)$, which is unimodal with a maximum at the trait value x_0 . Analysis predicts that in the absence of competition a species with trait x , associated with a carrying capacity $K(x)$ unimodal around x_0 , will evolve toward x_0 . This outcome could be evolutionarily stable, but given a sufficient level of competition at x_0 , a branching occurs and two phenotypes split from the original. The authors extended this result to a sexual species. Many additive diploid loci represented the feeding preferences of individuals. The simulated population first evolved toward x_0 . Under the assumption of assortative mating, on the basis of either the similarity of an ecologically important character or an ecologically neutral "marker" trait, branching occurred (Figure 3). A great advantage of this model is its simplicity and matching to the analytic result for the asexual species.

Wiegand et al. (1999) demonstrated the importance of a spatially explicit representation in examining the effects of landscape heterogeneity on populations.

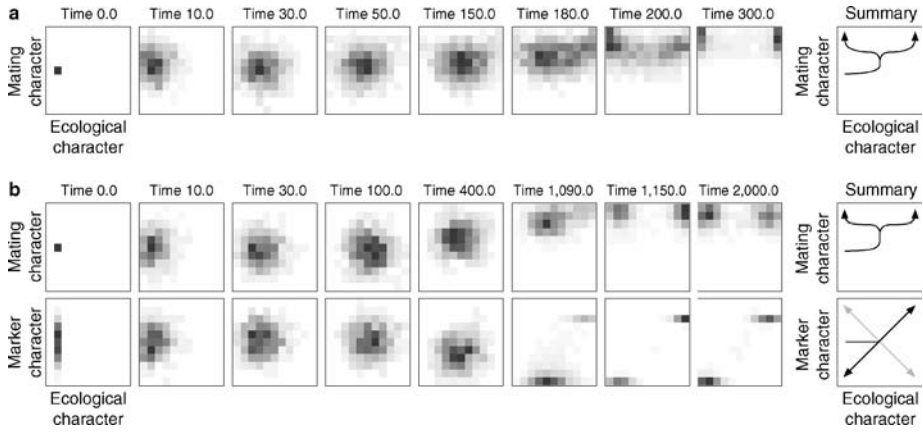


Figure 3 Evolutionary branching in sexual populations was simulated by Dieckmann & Doebeli (1999). In panel *a* the mating probabilities of individuals depend on an ecological character. In panel *b* the mating probabilities depend on a “marker” trait that is neutral with respect to ecological factors such as competition for resources. This result shows that sympatric speciation can occur, even if assortative mating is associated with an ecologically neutral marker trait. (Reprinted with permission of *Nature*.)

In a general-modeling framework, they used an algorithm to produce realistic patterns of good ($\lambda > 1$) and poor ($\lambda < 1$) habitat and matrix (avoided) cells on a 50-by-50 cell-model grid. This grid allowed them to produce various landscape types and examine effects of different levels of fragmentation. Using the European brown bear as their focus, the authors formulated rules on dispersal, habitat-selection strategies, home-range selection, mortality during dispersal, reproduction, and mortality within home ranges. One application of the model was to test earlier results on population viability based on nonspatially explicit models. An implication of earlier models was that increases in poor, or sink, habitat, while the amount of good habitat is held fixed, would result in population declines, because the models assumed that individuals would have more trouble finding the good habitat (needle in haystack effect). The results of IBM simulation by Wiegand et al. (1999) showed, however, that increases in poor habitat help the population by increasing connectivity of good habitat and that increases in poor habitat did not hinder the modeled individuals in finding good habitat.

The conservation model by Stephens et al. (2002) showed the importance of individual optimization by comparing four different approaches to a metapopulation of alpine marmots on the basis of 13 years of field data: model 1, a population-level matrix model; model 2, a matrix model based on the social group level; model 3, a spatially explicit IBM model with empirically based behavioral rules; model 4, a spatially explicit IBM with behavioral rules based on fitness optimization. In model

4, at each time step, the estimated optimal action by a given individual was calculated, and the individual was allowed to behave according to fitness optimization. Models 1, 2, and 4 were used to predict equilibrium population sizes well. However, only with model 4 were researchers able to predict an important contribution to an Allee effect. This Allee effect emerged from stochastic skewing of the sex ratio at low-population sizes, less efficient thermoregulation during winter hibernation, and difficulty finding mates during dispersal, even at relatively high population levels. The model is successful in elucidating important population-level effects that arise from social interactions.

DEVELOPING INDIVIDUAL-BASED MODELS

The way in which IBMs are constructed generally requires more careful consideration than is typical for classical models. The state variables of an IBM can be visualized as a table in which the rows represent the individuals and the columns represent their traits. A typical IBM keeps track of between 100 and 10,000 organisms. The table of individuals can easily be created using standard spreadsheet or database software. To add dynamics to the model, we must iterate over the individuals (see example in Figure 4). This iteration is easily done using mathematical programs. When the model reaches application stage, performance often becomes an issue. At this stage, dedicated programs written in a standard computer language such as C++ come into play. They can be optimized for the particular computational bottlenecks of a given program and are also very flexible in their input and output. A clear drawback of dedicated programs is the effort required to develop, maintain, and document them.

To get both good performance and standardization, researchers have made a number of efforts to develop flexible but high-performance frameworks for IBMs (e.g., Baveco & Lingeman 1992, Mooij & Boersma 1996). Despite the promise of these frameworks, their use tends to be limited to the developer and coworkers. We know of no framework that has been so well developed, documented, and maintained as to attain widespread use. Typically, they are built around databases that contain tables with some of the basic concepts of ecological theory, such as the individuals, the spatial units they live in, and the environmental conditions and available resources in those spatial units. To maintain a considerable flexibility in the way the actual dynamics are implemented, they often have a built-in "event handler," comparable with the ones that drive a multitasking operating system.

The focus of a developer of an individual-based model is usually on the short-term task of getting it to work, rather than on the long-term task of thorough analysis of the model. This approach runs the risk of generating a model for which a systematic analysis of its dynamics is a tedious or virtually impossible task. In this sense, the culture of IBM development is quite different from that of the culture of classical model development in theoretical ecology. In the latter, almost all the focus is either on getting analytical solutions for various aspects of the model

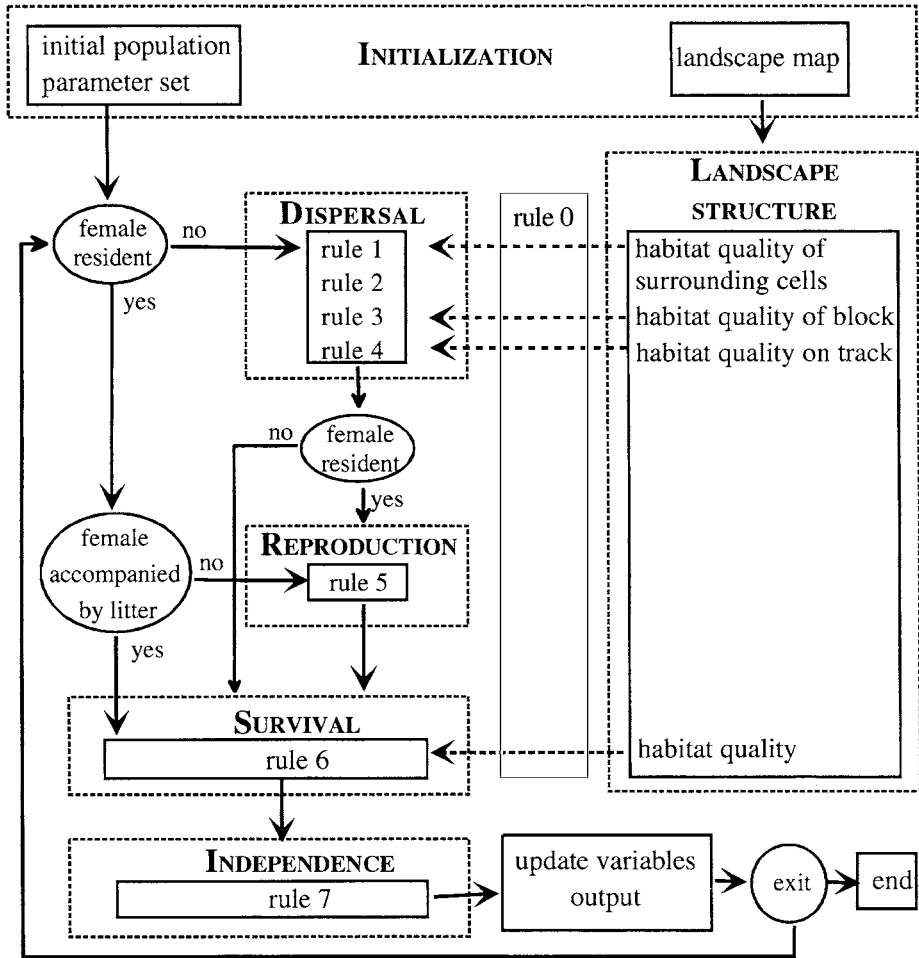


Figure 4 Flow chart for the individual-based simulation model of a bear population (Wiegand et al. 1999). The flow chart shows each of the events that can happen to a female bear during the yearly time step of the model: dispersal, reproduction, survival, and independence (from the mother). Each of these events is governed by one or more rules not shown here. This hierarchical presentation of the model results in a good overview of the general model structure and the general flow of logic. (Reprinted with permission of the University of Chicago Press.)

behavior or on a formal numerical analysis of the model, including sensitivity and bifurcation analysis. Given that an individual-based model is kept simple enough that it runs within a couple of minutes, many of the techniques applied in the analysis of classical models can also be applied to individual-based models. This aspect of the field of IBMs in ecology could use more attention.

CONCLUSIONS AND PERSPECTIVES

We can safely predict that the proportion of papers in the literature that feature IBMs will continue to increase and that, with time, new uses and aspects of IBMs in ecology and evolutionary biology will develop. We are less certain about what philosophical role IBMs will play in the future of these fields. Two general views have emerged.

One perspective is that IBMs are an extension of classical approaches (Bolker et al. 1997). From this viewpoint, use of IBMs in modeling spatial systems, life cycles, and evolution is an elaboration of the types of structures already found in some classical models. However, IBMs are more appropriate for exploring dynamic behaviors that are currently too complex for analysis, because of difficulties caused by local interactions in space, demographic stochasticity, and other types of complexity. The types of IBMs used in such explorations are as simple as possible; individuals have a minimum number of attributes and are often just points in space. Theoretical ecologists examine IBMs for indications of general relationships that can act as a starting point for the development of analytic models. They emphasize the continued building of classic mathematical theory to cover more and more complex types of ecological systems. This approach is well suited to the expansion of the understanding given by analytic models into borderlands," where analytic models cannot be formulated but where the processes are still simple enough that results of simulations can be related back to analytic results. These models at the more analytic end of the spectrum of IBMs will probably continue to have great appeal, as parsimony is a cardinal trait in science.

Nonetheless, other ecologists see in IBMs a new research program that differs radically from the classic mathematical approach to ecological theory and constitutes a new philosophical paradigm (Uchmanski & Grimm 1996). These researchers explicitly restrict the term IBM to describe models that include some threshold level of individual detail. In this view, individuals by nature have highly complex responses to their environment. Such responses include phenotypical change and learning and are thus better described by rule-based simulations than by mathematical models. Behaviors at the population and community levels should emerge from individuals behaving in an adaptive way. Future development of such models can allow individuals to have more sophisticated internal states and as much individual autonomy (an expression of variability) within the model as possible to behave and make decisions and, through mating, such models can provide the basis for evolution. Although this simulation approach generally precludes mathematical analysis, approaches such as pattern-oriented modeling (Grimm et al. 1996) provide ways of designing models and comparing model behavior with natural systems. For proponents of this strong role of IBM (e.g., Grimm & Railsback 2005), mathematical notation is not essential for rigor, as long as a model is formally documented. Grimm (1999) expressed the view that IBMs should play a much more direct role in "paradigmatic" science, that is, in making new scientific breakthroughs.

The difference in the two approaches outlined is a special case of the contrasting top-down and bottom-up views of system models. The top-down objective is to extend classic equation models into more complex domains with the assistance of IBMs. The bottom-up objective is to find the appropriate individual-level bases for the emergence of patterns at larger scales. These two viewpoints, the classical and the IBM approach, form opposite poles of thinking. We can expect that in due time a synthesis of both views will develop (e.g., Fahse et al. 1998, Wilson 1998). As we move in that direction, the stress lines between these poles can be the source of a creative tension for the fields of ecology and evolution.

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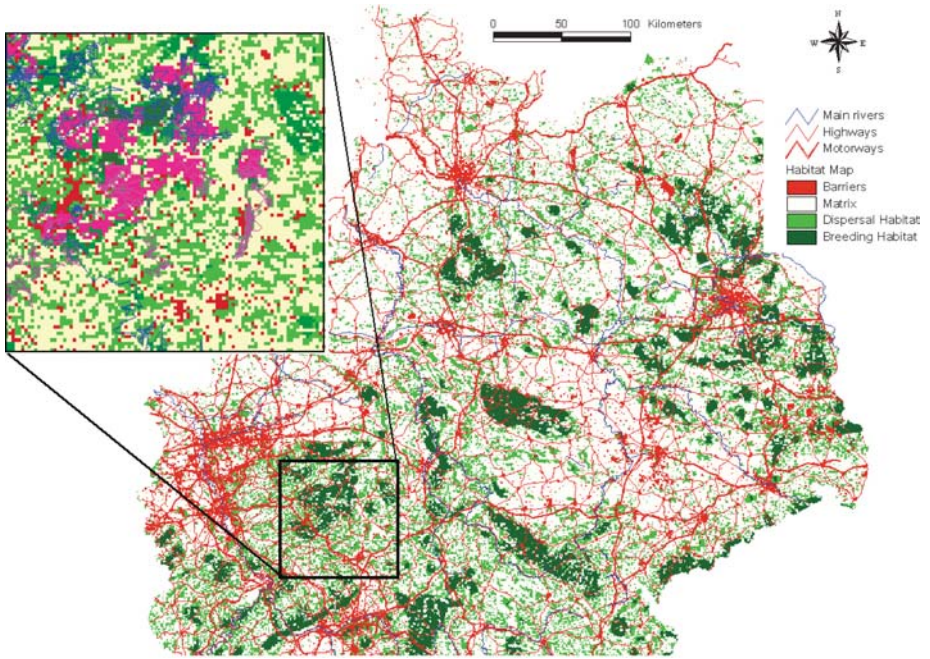


Figure 1 Detailed map of the northern half of Germany that classifies the landscape as barriers, matrix, dispersal, and breeding habitat of the Eurasian lynx. This map is used as basis for a study of the reintroduction of this species (Kramer-Schadt et al. 2004). The small inset figure shows the output of an individual-based simulation running on the landscape map: Pink areas represent home ranges occupied by adult female lynx, pink lines show dispersing subadult females, and blue lines show dispersing subadult males.

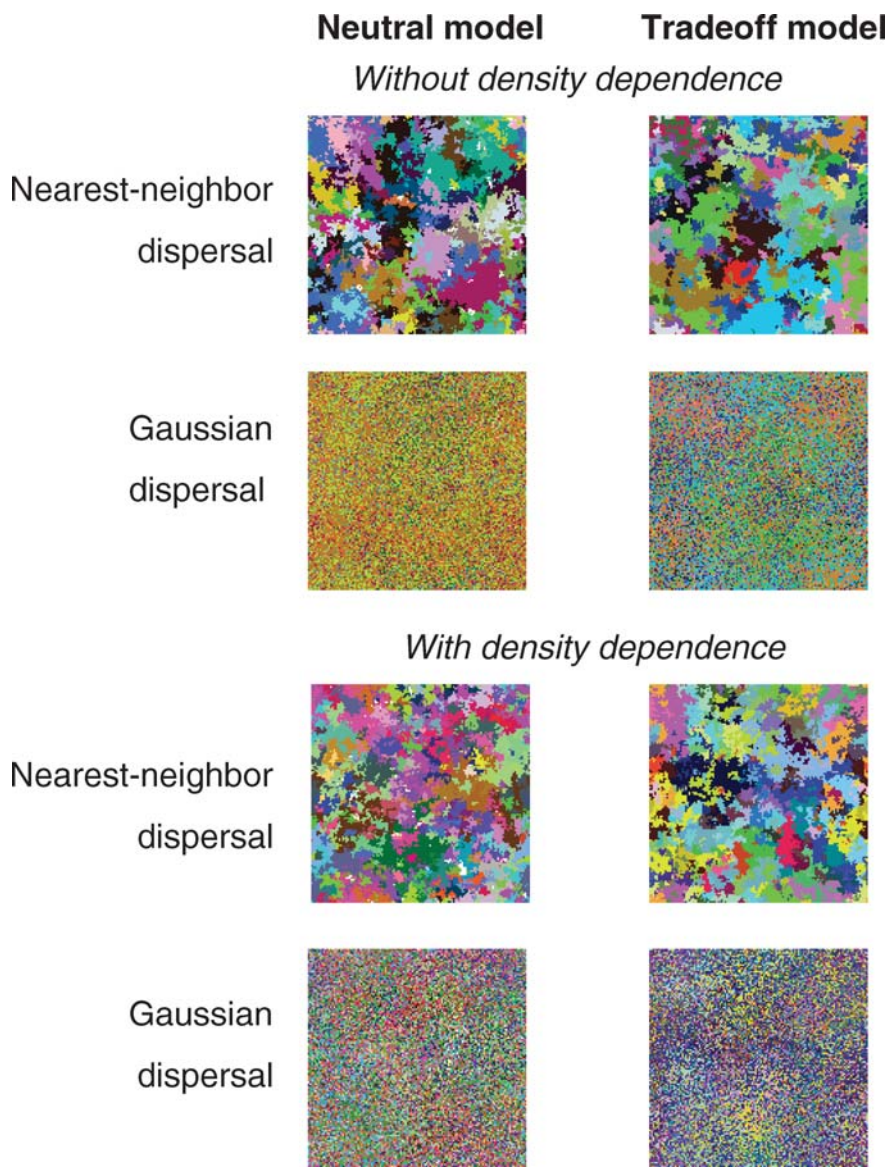


Figure 2 Spatial mosaics of individual species were created by different forms of the multispecies model (Chave et al. 2002). The grain of the patterns depends on (a) whether trade-offs are made between species traits or the traits are neutral, (b) whether conspecific density dependence (negative effects on individual if conspecific density is high) is included, and (c) whether the dispersal of propagules in space is only local or is larger in scale and described by a Gaussian distribution. (Reprinted with permission of the University of Chicago Press.)