9 Individual-Based Models

CHAPTER OUTLINE

A useful approach for modelling ecological systems of interacting organisms is through the use of individual-based models (IBMs). Individuals differ from each other in distinct ways and also from themselves during different stages of their life cycle. More important, they have self-directed motivation, can adapt to changing conditions, and can modify their environment through their actions. An IBM (also called agent-based models, ABM) allows the capture of this feedback within a modelling framework. Properties at higher levels — populations, communities, and ecosystems — emerge from these individual interactions and the interactions with their environment. Without self-direction and adaptation ecological systems would be much easier to model and understand. Such is the case with physical or chemical systems. Since individuals within ecological systems do have self-direction and the ability to adapt, IBMs are one way to capture this complexity.

9.1. History of Individual-Based Models

Early IBMs in ecology include a forest model (Botkin, Janak, & Wallis, 1972) and a fish cohort model (DeAngelis, Cox, & Coutant, 1980). The forest model, JABOWA, has successfully predicted species composition resulting from succession in a mixed-species forest, and has spawned

Fundamentals of Ecological Modelling. DOI: 10.1016/B978-0-444-53567-2.00009-0

a series of related models (Shugart, 1984; Liu & Ashton, 1995). The success of the fish cohort model was due to the inclusion of feedback processes such as cannibalism and competition, and it also precipitated a plethora of off-shoot models (Grimm & Railsback, 2005). Other early applications of ABMs originated in the artificial life literature, such as ECHO, Tierra, and Avida (Parrott, 2008).

The IBM approach was first formalized as a discipline in the article by Huston, DeAngelis, and Post (1988), and has developed considerably since then. What makes an IBM different from a population model? The first question to be addressed about this approach is what makes it different from the standard approaches already being employed in ecological modelling. For one thing, traditional population models were not able to answer specific questions central to ecology regarding mating, foraging, and dispersal because the models treated all individuals within the population as homogeneous; therefore, the entire population acted accordingly without any individual variation. Giving specific traits to each individual allowed for greater variation in the behavior of the population. Furthermore, in traditional models, the agents were unlikely to adapt their behavior throughout the length of the simulation. In IBMs, the heuristics that determine the individual behavior can be updated based on feedback from the success of previous interactions and encounters. Lastly, the environment can be altered by the actions of the individuals performing work on it to survive. In this manner, there is another level of feedback in which the organism influences the environment in which its future success is determined, exerting some degree of self-control on overall higher level system behavior. Such closed loop feedback is an important characteristic of systems ecology as expressed in network environ analysis (Patten 1978a, 1981) or niche construction (Odling-Smee, Laland, & Feldman, 2003).

Uchmanski and Grimm (1996) proposed four criteria that represent the core features of individuality, adaptability, and environmental feedback to consider what distinguishes an IBM from classical models:

1. The degree to which the complexity of the individual's life cycle is reflected in the model
2. Extent to which variability among individuals of the same age is considered

3. Whether real or integer numbers are used to represent the population size
4. Whether or not the dynamics of resources used by individuals are explicitly represented

The implementation of IBMs can affect the paradigm one has about ecology in general. This has led to a new approach called Individual-Based Ecology (IBE) in which the understanding of macroscopic organizational levels (populations, communities, ecosystems, and biosphere) arise from the interactions of microscopic components (agents and individuals). Characteristics of IBE have been proposed by Grimm and Railsback (2005):

- Systems are understood and modelled as collections of unique individuals.
- System properties and dynamics arise from the interactions of individuals with their environment and with each other.
- IBMs are a primary tool for IBE.
- IBE is based on theory.
- Observed patterns are a primary kind of information used to test theories and design models.
- Instead of being framed in the concepts of differential calculus, models are framed by complexity concepts such as emergence, adaptation, and fitness.
- Models are implemented and solved using computer simulations.
- Field and laboratory studies are crucial for developing IBE theory.

9.2. Designing Individual-Based Models

There are three primary aspects to consider when developing an IBM: (1) agent behavior, (2) agent-agent interactions, and (3) environment. The key to IBMs is developing them in a manner in which the adaptive traits can model behavior of real organisms. An adaptive trait is a rule or heuristic that allows the organism to make situation-specific decisions. The traits may be programmed or learned. They determine the choices that the organisms make during each encounter, and are often programmed using a series of IF-THEN statements and loops corresponding to the individual's specific conditions. Following the heuristics does not necessarily lead to an optimal behavior, since not all information is known to always make optimal decisions, but the behaviors are context-dependent and goal directed

(Grimm & Railsback, 2005). For example, rules describing foraging behavior describe how the agent responds to the local conditions (is food available or not) and the agent's internal goals (time since last feeding). The movement pattern may be programmed from a simple random walk function to a more complex environmental assessment and deliberate moves such as seeking a preferred food source, following subtle perceived differences in environmental gradients, or learning from previous encounters with the landscape. A conceptual model used in this instance is called beliefs-desires-intents (BDI), which models the hierarchical progression leading to certain actions. The beliefs contain the background information held by the agent (i.e., food is good, mating is necessary, run from predators, etc.), the desires are the goals, and the intents are the actions taken to achieve these ends (Parrott, 2008).

Agent-agent interactions may be direct such as mating, communication, predation, or resource competition, or indirect through modifications to the environment. An example of indirect interaction is the chemical or physical marking of an area as signals to ensuing agents upon that area. The end result is that group-level dynamics emerge from these agent-agent interactions.

The environment represents the local landscape on which the organisms move and interact. It is typical that the environment has variation but is regular enough for agent learning and adaptation. The environment is commonly modelled as a lattice or network. A lattice approach provides spatial variation such that each cell in the lattice may be heterogeneous and can include environmental variables as well as other agents. Network models forego some spatial capability to focus on the flows or interactions, such as trophic networks. An important, but not surprising, conclusion from IBM work is that the environment can have a substantial influence on the individual behavior and on the overall group dynamics (Parrott, 2008). This is consistent with the perspective of systems ecology, which also places high value on the role of environment, indirect interactions, and holism.

9.3. Emergent versus Imposed Behaviors

As stated previously, one of the important outcomes of IBMs is the unexpected macroscopic behavior that can be viewed from the results of the simulation. This occurs because the agent-agent interactions with adaptive traits and adaptive environmental variables allow for the emergence of novel system behavior. In addition to being unexpected, emergent behaviors can differ from the behavior of individuals and are holistic in the sense that the whole is more than the sum of the parts. Therefore, it is essential not to impose strict, unchanging attributes to the individual's choices. One way to view behavior is that if the attributes are derived from an understanding of process then there is more variability and freedom of option as the behavior unfolds. However, if the attributes are derived from strict empirical observations, that is, fixed parameters from field or laboratory experiments, then the outcome will be predictable since there can be no variation. For example, consider the case of egg production rate in fish in which temperature dependence has been documented (Secor & Houde, 1995). In one model, the rate is fixed based on empirically derived field studies and each individual has this trait. In the second model, the rate is a function of the temperature of the environment in which the individual inhabits at that time. In this manner, the results of the first model are imposed by the rigid constraint of the parameterization, whereas in the second model, variation and adaptability can lead to new patterns, such as clustering of high density populations around warmer pools. Another possibility in model development is to have intermediary outcomes so that the first stage might be imposed, such as egg production rate in each grid cell, but a second choice, based on movement across the environment, can allow for the same kind of clustering if there is a process preference for certain temperature ranges. Overall, the goal for IBMs is to develop rules that are process-based so that the organism can respond accordingly to different situations with flexibility. Therefore, it is important to know some factors that motivate, guide, and orient the behavior of the agents.

9.4. Orientors

A key question in formulating an IBM is determining the characteristics that comprise the individual's decision set. There are a primary set of survival and behavioral functions common to all agents (as modelled as complex adaptive systems). There have been proposals to holistically describe these tendencies in which these systems change over time. One approach worth mentioning identifies six fundamental orientors, which are meant to apply for all complex adaptive agents (Bossel, 1998, 1999). These include:

1. *Existence*: Attention to existential conditions is necessary to ensure the basic compatibility and immediate survival of the system in the normal environmental state.
2. *Effectiveness*: In its efforts to secure scarce resources (energy, matter, information) from, and to exert influence on, its environment, the system should on balance be effective.
3. *Freedom of action*: Ability to cope in various ways with the challenges posed by environmental variety.
4. *Security*: Ability to protect itself from the detrimental effects of variable, fluctuating, unpredictable, and unreliable environmental conditions.
5. *Adaptability*: Ability to change its parameters and/or structure in order to generate more appropriate responses to challenges posed by changing environmental conditions.
6. *Coexistence*: Ability to modify its behavior to account for behavior and interests (orientors) of other systems.

Orientors are defined as dimensions of concern, not specific goals, as they arise from the system interactions and are considered emergent system properties. They function as attractors of the system development and the six orientors are responsive to the six general properties of the environment.

1. *Normal environmental state*: The actual environmental state can vary around this state in a certain range.
2. *Scarce resources*: Resources (energy, matter, information) required for a system's survival are not immediately available when and where needed.
3. *Variety:* Many qualitatively different processes and patterns occur in the environment constantly or intermittently.
4. *Reliability*: Normal environmental state fluctuates in random ways, and the fluctuations may occasionally take it far from the normal state.
5. *Change*: In the course of time, the normal environmental state may gradually or abruptly change to a permanently different normal environmental state.

6. *Other systems*: Behavior of other systems changes the environment of a given system.

Bossel (1999) proposed a one-to-one relationship between the properties of the environment and the basic orientors of systems. Therefore, the system equipped to secure better overall orientor satisfaction will have better fitness, having a better chance for long-term survival and sustainability. The orientor approach provides some guidance for determining individual attributes that shape the choices according to a basic needs hierarchy.

9.5. Implementing Individual-Based Models

Many IBMs are created from scratch by the modelling team; however, it can be quite difficult and time-consuming to gather and analyze a large number of observations, equations, and parameters. Without a standard toolbox, such as from object-oriented programming, the developed software can be inefficient and not easily transparent. Alternatives for developing the model from scratch are using software libraries, such as Swarm and Repast, which are maintained by active user communities, or established modelling environments. These modelling environments, such as CORMAS and NetLogo, are more general programming platforms from which one can develop IBMs. They are also maintained by their developers and as teaching tools include tutorial support and examples, making them a good choice for beginners in the field. In any case, the field benefits from the extraordinary increase in computing power that every personal computer (PC) now has, which is sufficient to run most IBMs, although large models or sensitivity analyses may require PC clusters or other advanced computing power (Grimm, 2008).

One effort to add standardization to the IBM model development was the introduction of the ODD protocol by Grimm et al. (2006), which refers to three primary blocks: Overview, Design concepts, and Details. Within these three blocks there are seven elements. The overview block includes: (1) purpose, (2) state variables and scales, and (3) process overview and scheduling. This block lays out the model purpose and structure from which the model skeleton is apparent including the definition of the objects (state variables) and process scheduling. The second block, design concepts, with only one element – design concepts – links the study to the broader framework of complex adaptive systems. It should address issues of interaction types, adaptation, learning, emergence, and the role of stochasticity. The third block, details, includes three elements: (1) initialization, (2) input, and (3) submodels. This section includes all the model detail, such as initial conditions, equations, and parameters. The information should be sufficient for any reader to reconstruct the model and achieve the baseline simulations. In their paper, Grimm et al. (2006) referred to testing ODD on 19 different models (with specific examples therein), and, since then, the approach has been widely used in the IBM community.

An example following this protocol is given by Dur et al. (2009) to study the reproduction of egg-bearing copepods. The model was parameterized from laboratory and field experiments as well as data from the literature. It is a good application for IBM because the authors were able to model the detailed reproductive cycle of the organism (Figure 9.1). The IBM included attributes: location, number, age, longevity, embryonic development time,

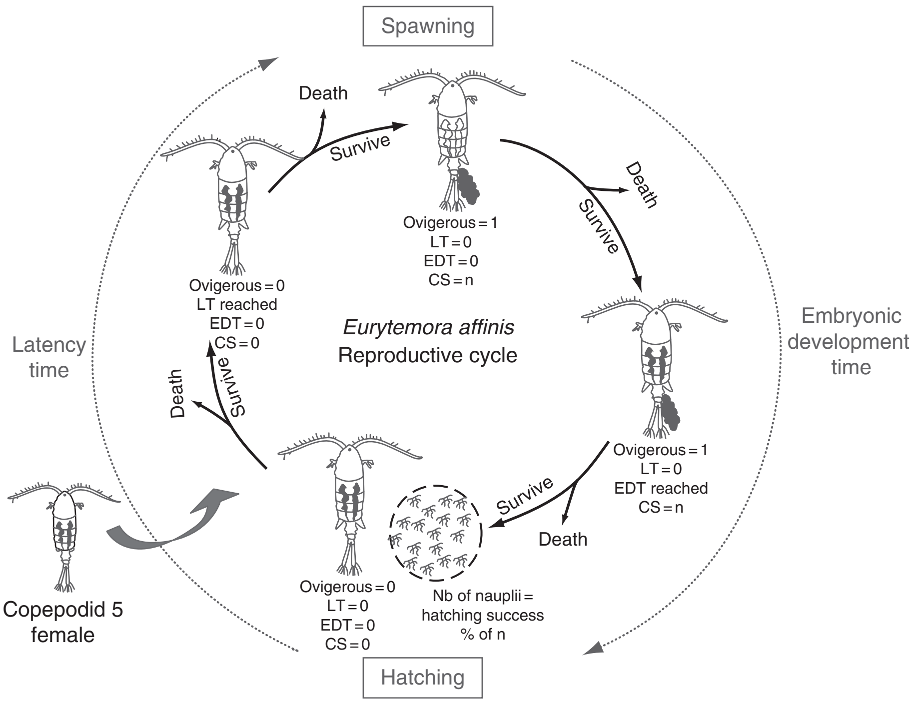

FIGURE 9.1 Complicated reproductive cycle of *Eurytemora affinis* permission statement.

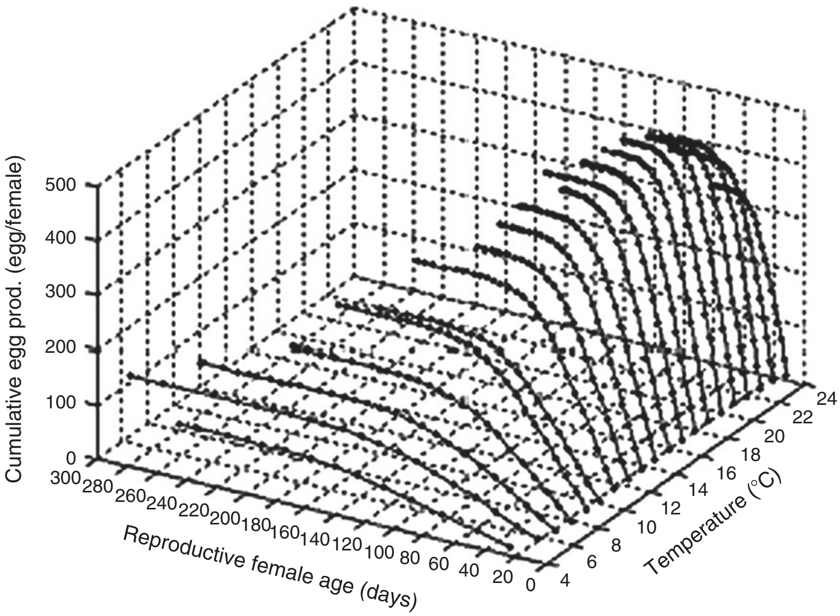

FIGURE 9.2 Results from an IBM developed using ODD shows that egg production is strongly affected by temperature with a maximum production at approximately 20°C.

latency time, spawning time, hatching time, ovigerous state of female, clutch size, and four intermediate parameters regarding the individual variability on longevity, latency, embryonic development time, and clutch size. The environment is represented by one attribute, temperature. Results showed that temperature effects are very important to daily egg production (Figure 9.2). For example, females at 4°C were able to produce only 16 clutches, whereas production reached a maximum of 30 clutches at 23°C. In this model, the emphasis of detail is on the life history of the reproducing individuals, not the environmental factors.

9.6. Pattern-Oriented Modelling

Due to the high complexity of IBMs, the results can be hard to understand. A new general strategy, pattern-oriented modelling (POM), has been developed to optimize model complexity and deal with uncertainty in model structure and parameters. A pattern is the macroscopic order that arises from the microscopic interactions from the system's internal organization and is an indicator that there is something more going on than simple random variation. Because of the emergence of higher order organization, it is necessary to develop approaches to recognize these patterns as different from the background. A pattern is a clearly identifiable structure in nature or data that is distinguishable from random variation indicating that underlying processes could be generating it (Grimm et al., 1996). In other words, the macroscopic pattern is generated by microscopic activity, such as the demographic interactions (dispersal, foraging, mating, etc.) and environmental constraints (topography, landscape, resources, climate, etc.). These patterns occur at a higher level than the processes that cause them. Comparing the observed processes with the model simulations that produced them, it is possible to restrict the parameter space available for uncertain or key features to detect the underlying processes. For example, Swannack et al. (2009) used POM to estimate life history characteristics of amphibian populations. Specifically, they compared simulation results to observations from four population-level patterns: population size, adult sex ratio, proportion of toads returning to their natal pond, and mean maximum distance moved. The models (11 of 16) that did not fit the observed patterns were rejected (Figure 9.3).

Table 3-summary of results from 650, 10-year, monte carlo simulations based on each of 16 versions of the model

Model version	Juvenile survival	Male survival	Population size	Sex ratio	Percentage at natal pond	Maximum distance moved
Field	?	0.15–0.27[a]	225[a]	5.5[b]	0.73[c]	900–1900[d]
1	0.005	0.15	0.02	0.00	0.73	1133
2	0.005	0.27	0.10	41.01	0.72	1184
3[e]	0.0075	0.15	3.32	5.76	0.66	1289
4	0.0075	0.27	7.69	15.81	0.65	1308
5[e]	0.009	0.15	45.35	6.67	0.62	1355
6	0.009	0.27	63.22	15.49	0.61	1399
7[e]	0.0095	0.15	86.52	7.33	0.60	1382
8	0.0095	0.27	123.05	15.81	0.60	1429
9[e]	0.01	0.15	164.88	7.65	0.59	1427
10	0.01	0.27	209.69	15.83	0.59	1460
11[e]	0.0105	0.15	290.00	7.85	0.58	1461
12	0.0105	0.27	365.29	16.31	0.57	1511
13	0.015	0.15	46814.61	4.48	0.70	1751
14	0.015	0.27	48967.53	5.98	0.71	1761
15	0.02	0.15	42581.38	1.92	0.84	1665
16	0.02	0.27	43335.67	2.72	0.84	1676

Results include mean (1) final population size, (2) final adult sex ratio, (3) percentage of toads at their natal pond at the time of their death or at the end of a simulation, and (4) maximum distance moved (m) by an individual toad during a simulation. Different versions of the model represent different combinations of annual survival estimates (probabilities) for juveniles and adult males. ? represents no field data available.

[a] Swannack (2007).
[b] Swannack, Grant, and Forstner (2007).
[c] Breden (1987).
[d] Price (2003).
[e] Versions of the model that generate reasonable patterns in all 4 system attributes.

FIGURE 9.3 Shows table from Swannack et al. (2009) in which the 16 model runs compare observations with simulation results.

The remaining models had a similar feature that population depends heavily on juvenile survival and provided a narrow range for the juvenile survival parameter. Values of juvenile survival below 0.01 had populations too small and those with values 0.015 and higher were too high. The model was very sensitive to this parameter. This is a very good application of using POM to identify key parameters and to provide a range for acceptable values.

9.7. Individual-Based Models for Parameterizing Models

Whereas the previous example used POM to test the uncertainty of certain parameters, a growing tendency is to supplement the paucity of certain field data with simulated data to parameterize and evaluate population models. One such approach is the use of a data set generated by IBMs. Two such examples are presented next.

Hilker, Hinsch, and Poethke (2006) used an IBM to parameterize a patch-matrix model (PMM) and a grid-based model (GBM). They first constructed an IBM (in this specific case, agents represent three different grasshopper species in varying landscapes with demographic and environmental stochasticity). From this model, they generated a long-term set of simulated data and extracted from this short-term "snapshot" data, which are used as estimators within the PMM and GBM (Figure 9.4). Specifically, they wanted parameter estimates for grasshopper movement regarding nest and mate radius as well as patch and matrix distance over a range of three mobility types. They used snapshot data from two or five years to correspond to typical field studies (amount of years ended up not having a big impact on the model performance). The best result was obtained with the inclusion independent migration data (such as from mark-recapture experiments). Overall, the authors were able to demonstrate the IBM as a general model that can be used to relate IBM-simulated parameters to emergent behavior at the metapopulation level.

In another example, Gilioli and Pasquali (2007) also used an IBM for estimating population parameters. In this case, the IBM is applied to egg production of a fruit fly. Specifically, an IBM simulates the number of eggs produced by the adults and a compartmental model simulates stage-structured population dynamics. The IBM allows for a precise description of the physiological age-structure (eggs, larvae, and pupae)

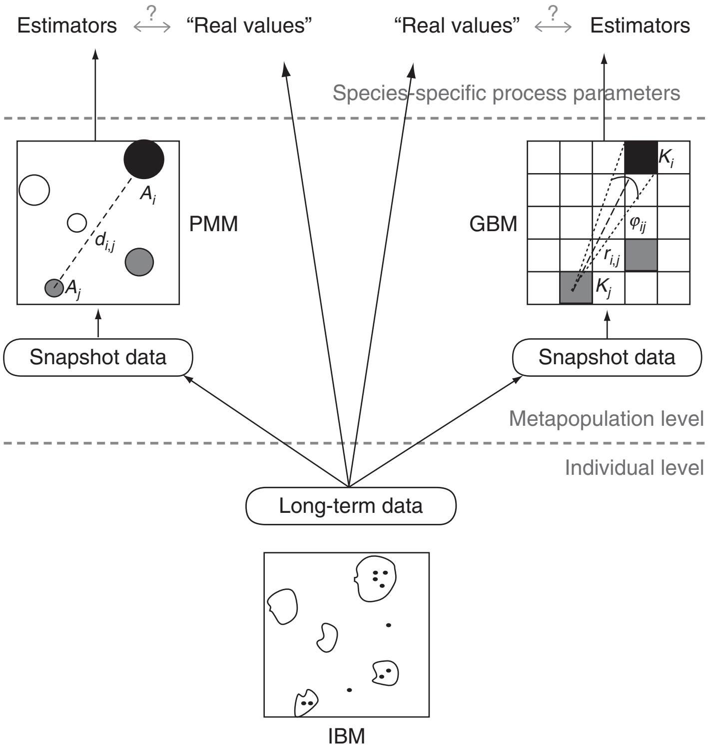

FIGURE 9.4 Conceptual diagram of using snapshot data taken from a long-term IBM simulation for estimating parameter values in a patch-matrix model (PMM) and the grid-based model (GBM). *(Reprinted from Hilker et al., 2006.)*

and time distribution such as recruitment and emergence profiles. The IBM also contributes to the estimation of age-structured mortality and fecundity parameter values. The combination of a microscopic (IBM) and macroscopic (compartmental) models provides a more detailed prediction of population dynamics and good agreement with the observed data. Overall, the use of IBMs for parameterizing models is becoming a more common approach.

9.8. Individual-Based Models and Spatial Models

While there are many different examples of IBM applications to address ecological questions, let us end this chapter with one further example that combines the IBM approach with a spatially explicit model (Chapter 11). Overall, we see there is a lot of synergy between the ability to model individual agents and the spatially explicit landscape on which they interact. Wallentin, Tappeiner, Strobla, and Tasserd (2008) constructed an IBM to understand alpine tree line dynamics. This model is used to test the effects of climate change on a forest community in the Austrian Central Alps. Due to a warming climate, the leading edge of the tree line from spontaneous forest regeneration is climbing to higher elevations. Forest regeneration is influenced by seed dispersal characteristics and land use changes (i.e., availability of migration into abandoned alpine pastures). The model construction involves six steps: (1) deriving landscape features from remote sensing data, (2) building the model, (3) parameterization based on ecological processes, (4) scenario runs, (5) validation, and (6) sensitivity analysis (Figure 9.5). The model includes as main processes recruitment, growth, and mortality. Recruitment is a function of distance to seed trees, land cover type, and elevation. Growth follows a standard sigmoid curve and mortality is impacted by age and density. The model iterates each year through the processes of recruitment, growth, and mortality. Establishment of new seedlings depends on distance to the nearest seed tree, ground vegetation, and elevation. A tree dies if the survival probability based

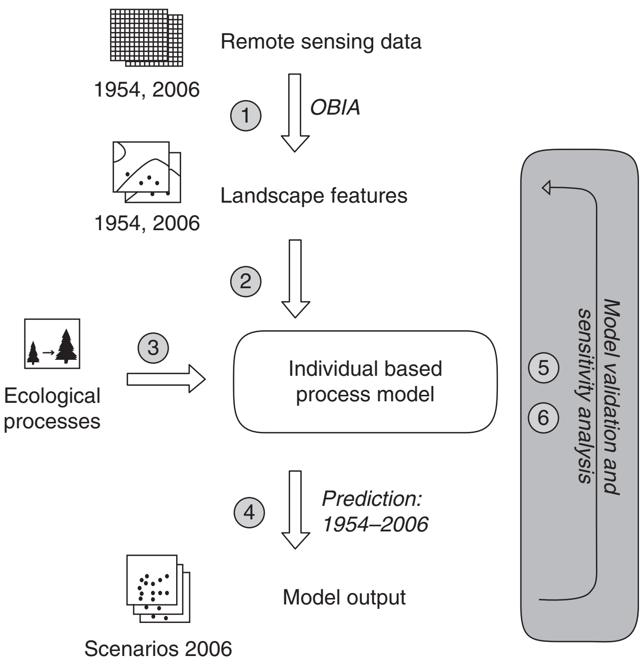

FIGURE 9.5 Model flow diagram of incorporating remote sensing data for studying the impact of climate on alpine tree line migration using an object based image analysis (OBIA) and individual-based model (IBM).

on tree age and tree density is smaller than random mortality values. Results from the model show the upward movement in elevation of the tree line, which is a good prediction of the observed forest regeneration trend during the study period from 1954 to 2006. Overall, the maximum elevation rose almost 150 m and the mean elevation about 90 m. This is a good example of how a spatially explicit IBM can be used to model population dynamics in response to changing environmental conditions, such as climate change.

9.9. Example

To give the reader a clearer idea of how to construct an IBM, in this section we present an IBM recently developed by Chon, Jørgensen, and Cho, (2010) for studying how individual survival is dependent on the dynamic relation between the gene-individual-population. At the lowest scale the genes are under different constraints regarding the metabolic efficiency and toxin susceptibility (Chon et al., 2010). In this model, the individuals move around in 2D space and compete for food, such that the entire population acquires the most adaptable genes (concerning combination of metabolic efficiency and toxin resistance) over the long run. The individual attributes are controlled by the gene information, which in turn determines the gene levels of the entire population.

Individual attributes include age, health score, and location (x and y coordinates). Food and toxins were present in the grid as environmental factors. Individuals on the same location as food or toxins would consume them and their health would be affected accordingly (positive for food and negative for toxin). Food and toxins were both resupplied regularly to the matrix. Variables in the model include total population densities and densities in different types of gene information in the population (Chon et al., 2010).

The model, programmed in Visual Basic, uses a lattice grid size of 800×800 units and was run for 7000 time steps. Each interior site (i, j) (where $i = 2, \ldots, n - 1$ and $j = 2, \ldots, n - 1$) has 8 immediate neighbor cells $(i - 1, j - 1)$, $(i - 1, j)$, $(i - 1, j + 1)$, $(i, j - 1)$, $(i, j + 1)$, $(i + 1, j - 1)$, $(i + 1, j)$, and $(i + 1, j + 1)$. Individuals move across this landscape according to a random walk (one unit per time step). If a nutrient is located at one of the neighbor lattices, then the individual moves to that lattice. In the case of multiple food items in the individual's nearest neighbors, the movement selection is made randomly. If there are no food items in the nearest neighbors, then the individuals move at random. Toxin exposure occurs randomly (Chon et al., 2010).

Two different genes carry information regarding the metabolic efficiency and toxin susceptibility, and both were determined at fixed rates with low, medium, or high levels (e.g., 0.1, 0.25, and 0.5 for metabolic efficiency). This information was converted to phenotypic properties through health scores. The maximum score of metabolic efficiency and toxin susceptibility was assumed to be 20 points. The health scores accumulate according to the food uptake and toxin exposure. If the health score drops below zero, then the individual dies. When the health score is greater than a fixed threshold and the age is older than three time steps, reproduction occurs. Reproduction can occur by asexual fission or conjugation if a neighboring cell is occupied. In each iteration, only gene type is randomly selected for exchange (see Chon et al., 2010).

The model was initialized with food occupying 20% of the total lattice and replenished at regular intervals in 10% of the empty spaces in each 100 time step. Toxin was also present initially in 20% of the total lattice but was resupplied at a rate of 1% of the remaining empty space (after resupply of nutrients) in each 100 time step. A range for the model parameters, metabolic efficiency (ME) and toxin susceptibility (TS), was determined to obtain balanced population densities, which occurred expectedly in the range of higher ME (i.e., efficiency in metabolism) and lower TS (i.e., higher resistance to toxins). Two similar sets of conditions (C1 and C2) for different genetic values were provided to ME and TS as follows.

The first condition (C1):

Type A: ME; 0.5; TS; 0.4
Type B: ME; 0.4; TS; 0.3
Type C: ME; 0.3; TS; 0.2

The second condition (C2):

Type A: ME; 0.5; TS; 0.4
Type B: ME; 0.3; TS; 0.25
Type C: ME; 0.1; TS; 0.1

Chon et al. (2010) found that the overall changes in population size showed common patterns through simulation. Population densities increased rapidly with consumption of initial nutrients, peaking at around 100 iterations. The population size decreased as nutrients were depleted, and reached the minimal size at around 200 iterations. Afterwards, population size periodically changed in the range of 400 to 800 individuals along with resupply of the nutrients at 100 iteration intervals (Figure 9.6). The Determination of dominant types of gene information appeared to be critical when the population size was minimized due to nutrient depletion.

The overall change in fitness due to reproduction was also modelled. The case without conjugation did not allow for gene recombination and is not discussed here. It is noted that the case with the best initial parameter values (type A-A) had the highest population and the one

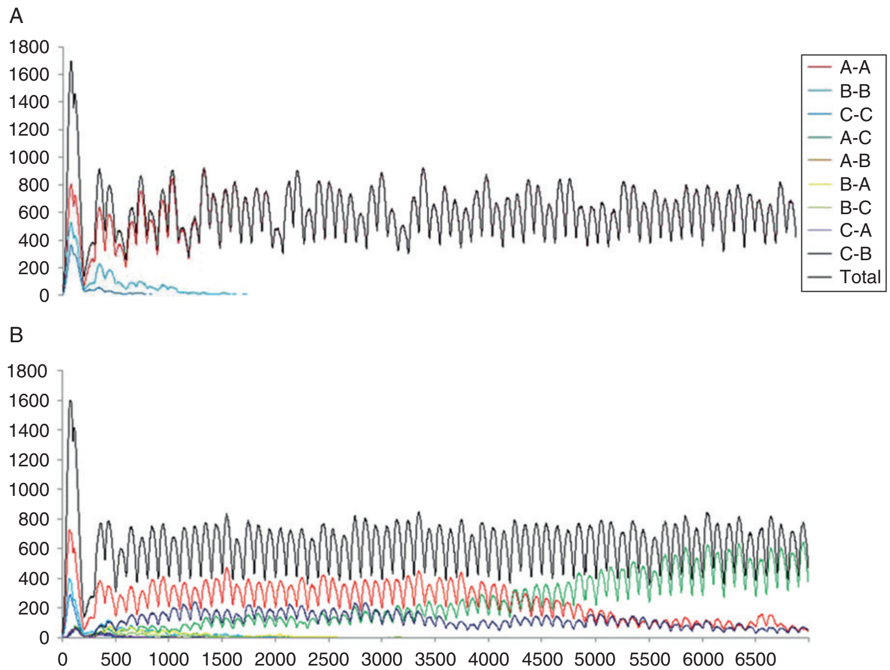

FIGURE 9.6 Changes in population size in different gene types in the gene-individual-population relationships: (a) without conjugation and (b) with conjugation = 25%.

with the worst values (type C-C) had the lowest or went extinct. Greater diversity was found in the species composition when conjugation was allowed for gene exchange between individuals. The amount of mixing depended on level of conjugation (which ranged from 0 to 100%). The dominant types changed depending on the different simulation conditions, C1 and C2. For condition C1, Type A-C, which is most suitable for both ME and TS, appeared as the first dominant type, followed by A-B and A-A at conjugation = 25%. For condition C2, however, type A-B was most dominant, followed by A-A and A-C. The overall diversity changed with increasing conjugation (Figure 9.7). In conclusion, the authors found by using an IBM that overall biomass and eco-exergy (see Chapter 10) increased with conjugation.

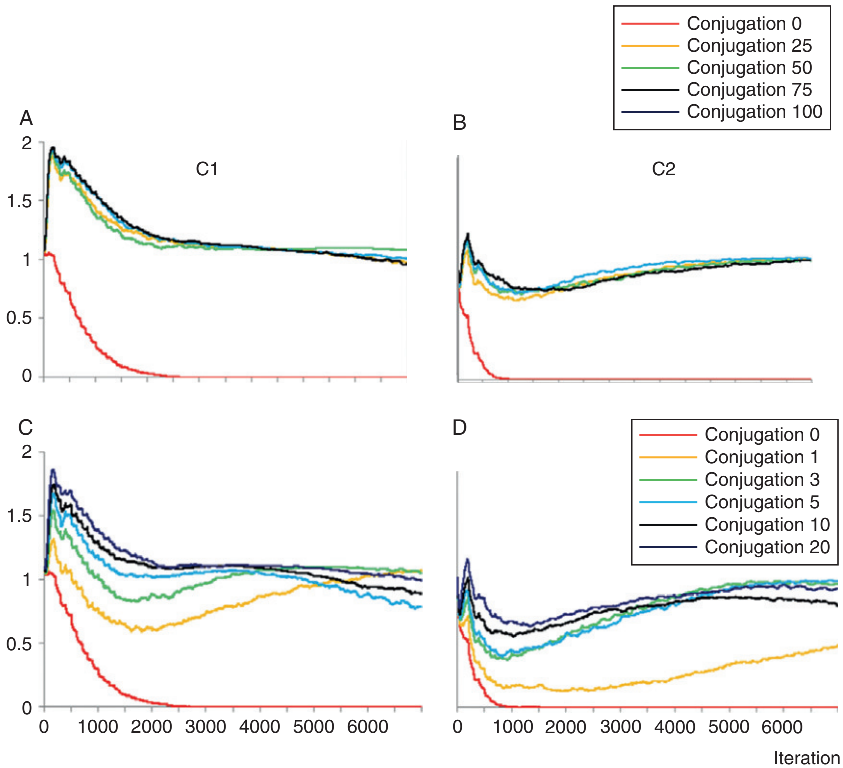

FIGURE 9.7 Changes in diversity indices in averages. C1 (a) and C2 (b) in different levels of conjugation = 0, 25, 75, and 100 %, and C1 (c) and C2 (d) in different levels of conjugation = 1, 3, 5, 10, and 20%.

9.10. Conclusions

Individual-based models have filled a natural gap in the ecological modelling toolbox. They allow more detail and flexibility for individual action than the traditional compartment modelling approach. The key factors in an IBM are: (1) the inclusion of individual variation including detail about the life history and age classes, (2) the possibility for agents to adapt and learn (i.e., update in real time the interaction rules) from experiences, and (3) the modification of the environment by the behavior of the individual. Libraries of data now exist for use in IBMs, development of a standard protocol for developing IBMs, and software platforms that are available for IBMs. Many applications of this new approach have been implemented and their use will continue to grow in the future.

Problems

1. What is an individual-based ecology? How does the interplay of microscopic and macroscopic levels influence ecological characteristics?
2. The three main features of an IBM are: (1) agent behavior, (2) agent-agent interactions, and (3) the environment. Explain how each of these could be modelled.
3. Explain the ODD protocol introduced to standardized IBM studies.
4. Develop a conceptual model for an IBM representing a forest ecosystem. Include a description of the spatial variation in the species distribution and how the different sized structures could be modelled. What are some important traits that should be considered in the model?
5. Adaptability is more likely to lead to emergent system properties. Explain why and how this could be modelled.
6. Results from IBMs are often most useful when analyzed at a higher scale of observation. Explain how POM is used to identify these structures. Give an example of how it could lead to estimation of model parameters.
7. What role do Geographical Information Systems (GISs) play in the development and implementation of IBMs?
8. Explain the difference between a metapopulation model and an IBM. Which circumstances would each one be best used?