CHAPTER 7

Individual-based models

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1 Introduction

“Individuals” are regarded as an essential entity in illustrating the complex “organism–organism” and “organism–environment” relationships in biological systems. Properties in individuals have been conveniently accommodated in individual-based models (IBMs). IBMs are, in general, contrasted with the conventional mathematical models that deal with collective population properties as variables (e.g., differential equations for analyzing population density). Along with the development of computation sciences including computer techniques, mathematical biology, informatics, etc., local information on attributes of individuals has been effectively elucidated in IBMs to reveal collective or emergent properties in the individual–population framework of the system.

Research on IBMs has stemmed from the studies dealing with individual uniqueness and variability in ecology since the late 1970s, including resource partitioning [1], size-structure in population [2] and patrolling behaviors and cyclic changes in population dynamics [3]. The earlier researchers reported the problems caused by conventional mathematical methods based on the state variables in illustrating the issues on variation and uniqueness observed in individuals in ecological sciences [4]. Earlier reviews on IBMs could be referred to DeAngelis, Hogeweg, Lømnicki, and Van Winkle [5–10], while Grim [11] extensively discussed the trend of follow-up development of IBMs in the 1990s.

Since the 1990s, the IBMs have been greatly implemented in ecology widely across different scales: (1) individual structure (e.g., morphological growth and function [12]), (2) behavior (e.g.,
foraging and schooling of fish [13–15]), movement patterns [16, 17]), (3) structure and function within population (e.g., reproduction phase [18]), fragmentation of clones [19]), (4) population dynamics (e.g., fish population [10], dispersal in restoration and landscape modeling [20–22], exploitation of resources [23], spatial behavior [24], naturalization in farming [25], (5) inter-population relationships (e.g., predator–prey dynamics [26–30]), disease dispersal [31], mutualism and parasitism [32] and (6) community processes (e.g., forest dynamics [33], food web [34, 35]). Theoretical and computational aspects also have been discussed regarding system stability [7], chaos [36], complex adaptive systems [37] and spatially explicit techniques [38].

In addition to the ecological aspect, attention has been drawn to IBMs from the physical side regarding group motility (e.g., swarming, flocking) based on equations of motion [39–43], and simulation of group movements was carried out by using the Lagrangian (micro-aspect or individual based) model in contrast to the Eulerian (macro-aspect or continuum) model that deals with the total population as a variable [44, 45]. The mechanism causing complex behaviors of interacting individuals is embedded as interactive “force” terms with noise in equations of motion in IBMs, and the models have been efficiently used for revealing physical coherence residing in complex group movements [43, 46–49].

Extensive reviews on recent development of IBMs are available. Railsback [37] dealt with the concepts on complex adaptive systems. Grimm and Railsback [50] covered implementation of the IBMs in ecology widely, covering behaviors, population dynamics and ecosystems studies. Grimm et al. [51] proposed the protocols that can be standardized and generally adapted to the construction of IBMs in ecological sciences, whereas Breckling et al. [52] and Reuter [35] discussed overviews on emerging properties in the ecosystem along with theoretical implications on the hierarchical framework. The readers could refer to the standard protocol for describing IBMs and agent-based models available online through http://www.ufz.de/oesatools/odd according to Grimm et al. [51].

### 2 Properties of individuals

In the early days, IBMs were started with illustrating partition of populations (e.g., age structures). Metz and Diekmann [53] discussed the variability in population dynamics and proposed the “configuration model” with emphasis on individuality in population in contrast to the “distribution model” presenting conventional population partition. Grimm [11] additionally specified the IBMs as “pragmatic” or “paradigmatic” models based on the motives of model development. The pragmatic model was used to address ecological processes to which methods of the state variables could not be directly applied as the model was presented by DeAngelis et al. [2] in revealing the switch of cannibalism in fish population. In contrast, the paradigmatic approach was motivated to overcome the limit of usage in the state variables in dealing with individual variability and was demonstrated by Łomnicki [54] in elucidating unequal resource partitioning among individuals. Uchmanski and Grimm [55] more specifically discussed the IBMs by accommodating the properties such as “individual variability in population,” “complexity of the individual’s life cycle,” “changes in numbers of individuals (rather than in population density),” “explicit presentation of resource dynamics used by the individuals,” etc.

Based on previous studies on IBMs, complex individual properties can be incorporated into the hierarchy of biological systems. First at the individual level, attributes in life processes could be addressed such as general identification (e.g., name, position), physiology (e.g., age, health state), morphology (e.g., growth, structure) and ecology (e.g., movement, resource utilization). Individual uniqueness and variability can be feasibly illustrated in the framework of IBMs.
A notable biological characteristic that can be additionally incorporated into the IBMs is reproduction, ensuring continuity of individual properties through generations in the model. Complex processes of reproduction (e.g., mating, fission) could be efficiently elucidated in IBMs, as IBMs are suitable for fabricating the complex inter-individual relationships and for assigning new attributes to progenies in simulation. Subsequently, the individual properties could be projected upwards to the population at higher levels by integrating individual attributes through competition, predation, parasitism, etc. The inter-individual relationships in populations can be further extrapolated to larger scales, such as communities and ecosystems in a hierarchical manner in biological systems [35, 50, 52].

By integrating information from lower levels, IBM is feasible in addressing collective and emerging properties at higher systems. The collective and emergent properties, in turn, influence changes in attributes of individuals. This type of the complex individual–population relationships would further lead to adaptation of individuals and eventually to the long-term evolution in the system. Important topics for future direction in biological sciences, such as stability, complexity and continuity in ecological systems, could be efficiently elucidated with the IBMs.

3 Model construction

Various properties of individuals can be identified across different scales and regimes in biological sciences, as stated before. In this section, we focus on the provision of the step-wise processes in construction of IBMs. To provide a comprehensive view for modeling processes, we illustrate the scope of the key components needed for IBMs, covering program outline, system environment, variables selected for modeling, model structure and interaction, parameters, and output data.

3.1 Program outline and system environment

Individual based models are feasible in accommodating complexity in life processes, including individual uniqueness and variability, the inter-individual and individual–population relationships, resource utilization, etc. In the program outline, the overall procedure of modeling can be sketched in accordance with the aim of the study. The selected attributes of the individuals can be outlined with regard to interactions with other individuals and environmental factors. Information required for operation of the model such as input data, parameters and initial conditions could be also described in this section. Subsequently, output data and the model results could be further outlined in this section in revealing how the given local processes could contribute to produce collective and emergent properties in the system.

System environment is the overall framework in which the programs of IBMs are explicitly executed (e.g., simulation space, computer languages). In the specified system environment, the model results are projected onto spatial and temporal domains defined in the program. Whole life processes simulated in the proposed IBMs are operated in relation to the time progress either directly or indirectly, while the time is, in general, controlled by the clock residing in the computer. Some individual attributes could be specifically expressed in time domain, such as age, life stage, development, etc. Changes in population growth and succession are additional examples that could be explicitly addressed in large scales in time domain.

Along with the time domain, spatial domain is also frequently presented to elucidate dynamic states of life processes in simulation. Structural growth of individuals can be an important issue in spatial and time domain in a small scale, while population dispersal, invasion of species, and
community establishment can be illustrated in IBMs in larger scales. Dimension (e.g., 2D) and number of units and size (e.g., 800 × 800; 10 m²/unit) can be accordingly specified in system environment.

In addition to spatial and temporal domain, boundary conditions (e.g., periodic, reflecting, absorbing) and the conditions for termination of simulation can be specified in this section. Finally, information on the computer language (e.g., C, Basic) and related software in construction of models can be described.

3.2 Variables

Various attributes of individuals can be expressed as variables in IBMs, covering different aspects of life processes such as morphological (e.g., growth), behavioral (e.g., movement) and physiological (e.g., development) properties. If progenies are generated through reproduction, new attributes can also be assigned to progenies, ensuring continuity of biological systems. Attributes of the individuals can be further integrated to illustrate population characteristics at higher levels, producing collective or emergent properties in the system [56, 57]. Collective properties can be defined as information provided at higher levels in the system (e.g., population density, birth rate) without losing component properties observed at a low level, while emergent properties are expressed with new properties [e.g., water (made from hydrogen and oxygen) or coral formation (produced from coelenterates and algae)] that are not observed at lower levels [57].

Environmental factors can be additionally considered as variables in IBMs. Resources such as nutrients can be provided to the individuals as environment factors and will be accordingly varied in interaction with the individuals (e.g., resource utilization).

3.3 Model structure and interaction

In this section, the overall logical processes in IBMs are outlined. The whole processes can be logically decomposed to key components (or submodels) and the components are addressed with regard to the system to ensure emergent or collective properties residing in the model. Consequently, computational interactions of the variables within and between the components are further described in this section to achieve the aim of the study. Mathematical formulas or appropriate algorithms can also be included for the key processes, if necessary.

3.4 Parameters and input data

After provision of the model structure, parameters and input data can be incorporated to the model. The parameters are defined as coefficients in the mathematical representation in the proposed model and can be provided to IBMs in a way similar to that used in conventional methods for ecological modeling [58]. For operation of the model, input data and initial conditions are given to the model in this section, for instance, the number and location of individuals in the system, environmental conditions, etc.

3.5 Output and model results

Along with operation of the model, output data can be accordingly produced. The scope of the output variables can be specified in time/spatial domains with regard to changes in other variables and parameters for provision of suitable answers to the objectives of modeling. The model could be further refined to increase reliability of output data (e.g., population dispersal computationally...
integrated by movement distances of individuals). The procedures used classically in ecological modeling such as calibration, verification or validation [58], can be considered in this section. Also, the data processes analogous to sensitivity analysis [59] can be additionally discussed in revealing the influence of the parameters in determining the variability of the output variables. As a higher degree of complexity resides in the individual–population relationships, however, the traditional post-model analyses cannot be readily illustrated in the IBMs by considering the fact that IBMs contain a highly fabricated model structure compared with the conventional models usually consisting mathematical formulae (e.g., differential equations) in simple forms. We will not cover the details in the topics of evaluating the input–output relationships in IBMs due to constraints of space. We illustrate life processes in IBMs with two case studies in this chapter.

4 Case study 1: flocking behavior

We selected two topics that could be efficiently investigated with IBMs, group behavior and population dispersal. An additional IBM dealing with the gene–individual–population relationships is provided in Chapter 15 that covers ecotoxicology.

4.1 Program outline and system environment

Self-organization of individuals has been a key issue in demonstrating group behaviors. In this case, equations of motion were incorporated to simulation of aggregation behavior of prey individuals and the predator’s attack. The purpose of the model is to obtain a suitable range of parameters in alignment of prey flock and to find computational coherence existing between chasing and escaping behaviors executed by the predator and prey flock. Local rules regarding activities of individuals (e.g., attraction, repulsion, alignment) were applied as interaction forces between individuals for achieving self-organization in movement of prey population. After alignment of the individuals in the flock, a predator was introduced to the system to elucidate the chasing processes shown by the predator. Velocities of prey and predator were regarded as variables at the individual level, whereas degree of alignment and flock size were expressed as variables at the population level. Some parameters such as angle of the predator’s attack and radius of predation risk were given to the system to check flock responses to the predator’s attack. Overall description on modeling for the case study is listed in Table 1. Simulation was carried out without boundary in 2D, while units for the spatial and time domain were imaginary. MATLAB was used to simulate the system. The demonstration program is listed in FLOCKI (“Flocking thorough IBM”) in a CD in this volume.

4.2 Variables

At individual levels, the attributes are velocities of individual preys and a predator. A prey-flock, consisting of \( N \) prey with mass \( m_i \) at position \( x_i \) with velocity \( v_i \) for each individual \( i \), is arrayed in an open field. Each prey is subject to various types of forces that control the movement of individuals. At population (higher) levels, the degree of ordering in prey flock is expressed as:

\[
\phi = \frac{\sum_{i=1}^{N} v_i}{N},
\]
Table 1: Description of IBM implemented to flocking behavior in response to a predator’s attack.

<table>
<thead>
<tr>
<th>Component</th>
<th>Sub-component</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>System environment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domain</td>
<td>Space</td>
<td>2D (imaginary unit)</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>Time step in simulation, discrete</td>
</tr>
<tr>
<td>Constraint</td>
<td>Boundary</td>
<td>Boundaryless</td>
</tr>
<tr>
<td></td>
<td>Termination of simulation</td>
<td>Predator’s arrival to the center of flock</td>
</tr>
<tr>
<td><strong>Tool</strong></td>
<td>Simulation language</td>
<td>MATLAB</td>
</tr>
<tr>
<td><strong>Attributes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual level</td>
<td>Velocity of prey individuals</td>
<td>$x$, $y$ coordinates (eqn (3))</td>
</tr>
<tr>
<td></td>
<td>Velocity of predator</td>
<td>$x$, $y$ coordinates (eqn (8))</td>
</tr>
<tr>
<td>Population level</td>
<td>Degree of alignment ($\phi$)</td>
<td>Absolute value of the unit velocity (eqn (1))</td>
</tr>
<tr>
<td></td>
<td>Flock size ($\sigma$)</td>
<td>Distance: center of flock - each individual (eqn (2))</td>
</tr>
<tr>
<td></td>
<td>Flock expansion speed</td>
<td>Slope of the curves for $\sigma$ (Fig. 3)</td>
</tr>
<tr>
<td><strong>Model structure and interaction</strong></td>
<td></td>
<td></td>
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<tr>
<td>Prey individuals</td>
<td>Alignment</td>
<td>Inverse of square of the distance between individuals (eqn (4))</td>
</tr>
<tr>
<td></td>
<td>Attraction</td>
<td>Exponential function (eqn (5))</td>
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<tr>
<td></td>
<td>Repulsion</td>
<td>Exponential function (eqn (6))</td>
</tr>
<tr>
<td></td>
<td>Friction force</td>
<td>Proportional to speed of individuals (eqn (7))</td>
</tr>
<tr>
<td></td>
<td>Avoiding predator</td>
<td>Depending upon $D$, $r$ and $\omega$ (eqn (9))</td>
</tr>
<tr>
<td>Predator</td>
<td>Attacking</td>
<td>Unit vector heading to the center of prey-flock (eqn (8))</td>
</tr>
<tr>
<td><strong>Parameters and data</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial conditions</td>
<td>Number of preys</td>
<td>200 individuals</td>
</tr>
<tr>
<td></td>
<td>Velocity of prey individuals</td>
<td>0 (unit per time step)</td>
</tr>
<tr>
<td></td>
<td>Flock size ($\sigma$)</td>
<td>$\sigma$=2.0</td>
</tr>
<tr>
<td></td>
<td>Distance between predator and flock</td>
<td>$D$=860</td>
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<tr>
<td>Parameters</td>
<td>Mass of prey individuals</td>
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<tr>
<td></td>
<td>Stochastic strength for prey movement</td>
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<td></td>
<td>Strength of aligning force</td>
<td>$g$ =0.5 (eqn (4))</td>
</tr>
<tr>
<td></td>
<td>Constant for attraction</td>
<td>$c_{at}$=7 (eqn (5))</td>
</tr>
<tr>
<td></td>
<td>Attraction range</td>
<td>$l_{at}$=100 units (eqn (5))</td>
</tr>
<tr>
<td></td>
<td>Constant for repulsion</td>
<td>$C_{rep}$=10 (eqn (6))</td>
</tr>
<tr>
<td></td>
<td>Range for repulsive force</td>
<td>$l_{rep}$=150 units (eqn (6))</td>
</tr>
<tr>
<td></td>
<td>Friction force for movement of individuals</td>
<td>$\gamma$=0.05 (eqn (7))</td>
</tr>
</tbody>
</table>
where \( N \) is the number of prey individuals in the flock, and \( \hat{v}_j \) is the unit velocity vector the direction of which is the same as the moving direction of the individuals in prey population. The ordering parameter would be approximately zero when individual movements are distributed in random direction, while it would be close to one when all individuals were in the phase of aligned movement. We further investigated how collectively the prey population in the flock would respond to the predator’s attack. We defined the flock size as:

\[
\sigma = \sqrt{\frac{1}{N} \sum_{i=1}^{N} r_i^2},
\]

where \( r_i \) is the distance from the center of the flock to the \( i \)th prey.

### 4.3 Model structure and interaction

The system of flocking consisted of various components regarding individual movement and interaction with other individuals; alignment, attraction, repulsion and friction. The governing equations for controlling movement of each individual prey \( i \) are:

\[
m_i \frac{d\ddot{x}_i}{dt} = \ddot{\bar{f}}_i^{\text{align}} + \ddot{\bar{f}}_i^{\text{attr}} - \ddot{\bar{f}}_i^{\text{rep}} - \ddot{\bar{f}}_i^{\text{fric}} - \ddot{\bar{f}}_i^{\text{avoid}} + \zeta(t),
\]

\[
d_i \dddot{x}_i = \ddot{\bar{v}}_i,
\]

\[
\langle \zeta(t)\zeta(t') \rangle = 2s\delta(t-t'); \quad \langle \zeta(t) \rangle = 0,
\]

where \( \ddot{x}_i \) is the position vector of prey individual \( i \) with mass \( m_i \), \( \ddot{\bar{f}}_i^{q} \) \((q = \text{align, att, rep, fric and avoid})\) represents various forces to address interactive behaviors among prey individuals (align: alignment, att: attraction, rep: repulsion, fric: friction and avoid: avoidance from a predator), and \( \zeta(t) \) is a Gaussian noise force with strength \( s \) and \( \delta \)-correlated time dependence.
The force of alignment is proportional to the inverse of square of distances between individuals:

\[
\vec{f}_{\text{align}}^i = \sum_{j \neq i} \frac{g}{|\vec{x}_i - \vec{x}_j|^2},
\]

where \(\vec{v}_j = \frac{\vec{x}_j}{|\vec{x}_j|}\), \(\vec{v}_j\) is the velocity of the \(j\)th prey individual, \(x_i\) (and \(x_j\)) indicate the \(i\)th (and the \(j\)th) prey position. The symbol \(g\) is the strength of the aligning force and contributes to making each member of the population move in the same direction. The attractive force is the sum of such forces for all individuals with the exception of the following:

\[
\vec{f}_{\text{at}}^i = c_{\text{at}} \sum_{j \neq i} \exp \left(-\frac{1}{l_{\text{at}}^2} |\vec{x}_i - \vec{x}_j|^2 \right) \hat{\vec{e}}_{i,j},
\]

where \(\vec{f}_{\text{at}}^i = (\vec{x}_j - \vec{x}_i)/|\vec{x}_j - \vec{x}_i|\) and \(c_{\text{at}}\) is a constant. The strength of the attractive force is characterized by an attraction range \(l_{\text{at}}\) in the decreasing exponential function.

The repulsive force between the individuals is expressed additionally by using the exponential function:

\[
\vec{f}_{\text{rep}}^i = c_{\text{rep}} \sum_{j \neq i} \exp \left(-\frac{1}{l_{\text{rep}}^2} |\vec{x}_i - \vec{x}_j|^2 \right) \hat{\vec{e}}_{i,j},
\]

where \(\vec{f}_{\text{rep}}^i = (\vec{x}_j - \vec{x}_i)/|\vec{x}_j - \vec{x}_i|\) and \(c_{\text{rep}}\) is a constant. Similar to the case of attraction, \(l_{\text{rep}}\) is used for characterizing repulsive forces.

To prevent preys from moving too quickly, the friction force with coefficient \(\gamma\) is set to be proportional to the current speed of a prey individual:

\[
\vec{f}_{\text{fric}}^i = \gamma \vec{v}_i.
\]

After establishment of the ordered prey population in a flock, a single predator is additionally generated outside the prey-flock at a distance \(D (= 860)\). Velocity of the predator, \(\vec{v}_{\text{p},t}\), is expressed as:

\[
\vec{v}_{\text{p},t} = \frac{\kappa}{\Delta t} \hat{\vec{x}}_{\text{p},t} + \zeta(t),
\]

\[
\langle \zeta(t)\zeta(t') \rangle = 2\beta \delta(t-t'); \quad \langle \zeta(t) \rangle = 0,
\]

where \(\kappa\) is the strength of bias (i.e., speed of predator) towards the center of prey-flock, and \(\hat{\vec{x}}_{\text{p},t}\) is the unit vector heading to the center of prey-flock. The stochastic force \(\zeta(t)\) with strength \(\beta\) and \(\delta\)-correlated time dependence is also introduced to the attacking course of the predator. The predator is designed to move towards the center of the prey-flock in the biased random walk in this study. The predator’s attack to the center of the prey flock has been observed as improving the success of hunting in nature, for instance, a bird predator attacking a crab flock [60] or whales capturing a small-sized fish school [61]. Simulation was terminated after the predator’s arrival at the center of prey flock for simplicity of calculation.

Prey individuals respond to the size of the predator’s attacking zone. When the \(i\)th prey is in the region of predation risk \(r\) in radius, prey individuals move away from the predator. Given that the predator is located at a distance \(|\vec{x}_p - \vec{x}_i|\) from prey \(i\), the force executed on the \(i\)th prey’s
avoiding movement is:

\[
\vec{f}_{t, \text{avoid}} \equiv C_{\text{avoid}} \frac{1}{1 + \exp \left[ \omega \left( |\vec{x}_{p, i} - \vec{x}| - r \right) \right]} \vec{x}_{p, i},
\]

(9)

where \( \vec{x}_{p, i} \) is the unit vector directing from the predator to the \( i \)th individual and \( \omega \) is an exponent term controlling the degree of decay in avoiding forces [62].

### 4.4 Parameters and input data

In the proposed model, the parameters for operation of the model are given in Table 1 to provide information on interaction forces (e.g., alignment, attraction, repulsion) based on previous results [63, 64]. The attributes for individuals (i.e., velocities of individuals) were calculated at each time step and were fed back to the system. Radius of risk, \( r \), and attacking speed, \( \kappa \), of the predator were varied to check flock responses. Variables such as flock expansion speed and degree of ordering in flock in response to the predator’s attack at population level were used to characterize dynamics in flock responses.

Initially, two hundred prey individuals were randomly distributed with no speed in an open space without a predator. Individuals started to move according to eqn (3) with \( \vec{f}_{t, \text{avoid}} = 0 \). Simulation was started from a disordered configuration with \( \phi (t = 0) \sim 0 \). After alignment, a predator was introduced with a distance \( D \) from the center of prey flock. Subsequently, chasing and escaping behaviors were elucidated between the predator and prey individuals. Simulation was terminated when the predator reached the center of prey flock.

### 4.5 Output and results

Location of all the preys and the predator was determined at each time step. Along with the progress of time, movements of individuals were gradually aligned with an increase in the order parameter, \( \phi \) (Fig. 1a). Initially, the individuals showed random movement (Fig. 1b). The order parameter was saturated at a long time domain (\( t > 750 \)) when all individuals in the prey population eventually showed aligned movements (Fig. 1c). During the course of alignment, however, sharp downward peaks were observed intermittently as shown in Fig. 1a. The sudden decrease in alignment usually occurred when the prey-flock changes its movement direction sharply [62].

After alignment of prey flock, escaping behaviors of prey-flock could be elucidated after a single predator was introduced to the system (Fig. 2). The degree of deformation increased with the increase in the size of predation risk \( r \). With the large size in the radius of risk (\( r = 400 \)), for instance, prey flock was greatly affected to produce a crescent form in the flock. We further investigated how collectively the prey population in the flock would respond to the predator’s attack. Compression and expansion of flock size were consistently observed with different radii of \( r \) as time progressed (Fig. 3), showing three phases until the predator reached the center of the prey-flock: decreasing (Regime I), increasing (Regime II) and decreasing again (Regime III). The attack angle was important in determining prey response in some ranges of the speed of the predator. When the speed was sufficiently high (e.g., \( \kappa = 4 \)) (Fig. 4), the flock expansion speed was in the highest range at the attack angle of 180°, while the flock expansion speed tended to be minimized around 0°. This illustrated a possibility of optimal range in the attacking angles shown by the predator.
Figure 1: Increase in alignment of prey flock. Time evolving of order parameter $\phi$ (a). Snapshots showing alignment of prey individuals in the flock at $t = 1$ (b) and $t = 1000$ (c). Circles show the positions of prey individuals in the flock while arrows attached to the circles indicate velocity in (b) and (c) (modified from Lee et al. [62]).

The influence of parameters can be outlined in the variability of the output variables. The degree of alignment of individuals ($\phi$) in the population was accordingly dependent upon different levels of $r$ and $\kappa$ values during the procedure of escaping in response to the predator (Fig. 5). When the attack speed of the predator, $\kappa$, was low, the prey-flock lost alignment more frequently with the stronger fluctuation in $\phi$ (Fig. 5a). The values of $\phi$ appeared to decrease at lower values of $\kappa$ and at higher values of $r$ (Fig. 5b and c). At the highest speed with $\kappa = 8$, prey-flock mostly maintained alignment except for a few drops in $\phi$ with the highest value of $r = 400$ (Fig. 5d). When the biased strength $\kappa$ was small and the radius of predation risk $r$ was large, the order parameter $\phi$ was decreased. This demonstrated that the model was feasible in revealing two species’ relationships through behavioral parameters. The predator’s speed and predation risk accordingly controlled ordering of prey population [62].
While group behavior of individuals was illustrated previously, a case study on dispersal of pest population is provided in a larger scale in this section. Pine wilt disease (PWD) is caused by pine nematodes (*Bursaphelenchus xylophilus*) in pine trees, and pine nematodes are, in turn, transmitted by the insect vector, the pine sawyer beetle (*Monochamus alternatus*). PWD severely affected pine forests in North Eastern Asia, and dispersal of PWD has been reported in numerous accounts [65–71]. Due to the problem of complexity residing in population dispersal, however, not many computational studies have been carried out regarding spatial dynamics of insect pests. Recently, studies on population models were carried out on the spread of PWD [72, 73]. However, the spatially explicit models based on IBMs have not been proposed for predicting dispersal.

Figure 2: Simulation of escaping behavior of prey-flock in 2D (artificial units on x and y coordinates) with different radii of predation risk ($r = 100, 200, 300$, and $400$) where $\beta = 0.5$ and $\kappa = 2$. The predator is shown with the dark arrow with a surrounding circle representing the area of predation risk ($r$) (from Lee et al. [62]).

5 Case study 2: population dispersal

5.1 Program outline and system environment

While group behavior of individuals was illustrated previously, a case study on dispersal of pest population is provided in a larger scale in this section. Pine wilt disease (PWD) is caused by pine nematodes (*Bursaphelenchus xylophilus*) in pine trees, and pine nematodes are, in turn, transmitted by the insect vector, the pine sawyer beetle (*Monochamus alternatus*). PWD severely affected pine forests in North Eastern Asia, and dispersal of PWD has been reported in numerous accounts [65–71]. Due to the problem of complexity residing in population dispersal, however, not many computational studies have been carried out regarding spatial dynamics of insect pests. Recently, studies on population models were carried out on the spread of PWD [72, 73]. However, the spatially explicit models based on IBMs have not been proposed for predicting dispersal.
of the pest population. In this study, invasion processes of the insect vectors were illustrated on a lattice space by incorporating movement, reproduction and control rates.

Local rules regarding movement and reproduction were applied to the individuals in the model. In addition, movement of the individuals with jumps was described by Lévy flight [74, 75].

Figure 3: Changes in the flock size of prey population in escaping from the predator’s attack with \( \beta = 0.5 \) and \( \kappa = 2.0 \) across different levels of predation risk \( (r) \) (from Lee et al. [62]).

Figure 4: Flock expansion speed across different levels of attack angles by the predator (i.e., \( \kappa = 4 \)).
Control of the insect vectors was provided as an additional constraint in determining population growth. Parameters in the Lévy flight and control rates were adjusted to predict location of the infested lattices.

Simulation was implemented on 2D (1000 × 1000) lattice space. To match the model results to the field data, the size of the lattices was fixed to 10 × 10 m\(^2\) while one time step was assigned as a half month. Absorbing boundary conditions were assumed. As the study area was surrounded by ocean or natural boundaries, the emigrants who crossed over the boundary could not return to the original areas. For simplicity of modeling, the period for the active phase for the sawyer beetle was considered from 1 May to 30 September for simulation. Simulation was carried out for 3 years (2002–2004). The outline of the model is presented in Table 2. The program for demonstrating population dispersal POPDIS is available in a CD in this volume. (The updated programs can be obtained by correspondence with the first author.)

5.2 Variables

The variables were positions (x and y coordinates) of the different individuals of the pine sawyer beetle in the lattice space. Stage, gender and age were also regarded as attributes of the individuals.
Table 2: Description of IBM implemented to dispersal of pest population.

<table>
<thead>
<tr>
<th>Component</th>
<th>Subcomponent</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>System environment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Domain</td>
<td>Space</td>
<td>2D, Lattice; 1000 × 1000 (unit: 10 × 10 m²)</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>2 days per time step, discrete, from May to September each year</td>
</tr>
<tr>
<td>Constraint</td>
<td>Boundary</td>
<td>Absorbing</td>
</tr>
<tr>
<td></td>
<td>Termination of simulation year</td>
<td></td>
</tr>
<tr>
<td><strong>Variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual level</td>
<td>Position of individuals</td>
<td>x, y coordinates</td>
</tr>
<tr>
<td></td>
<td>Age</td>
<td>Time step multiplied by 2</td>
</tr>
<tr>
<td></td>
<td>Life stage</td>
<td>Immature or adult</td>
</tr>
<tr>
<td></td>
<td>Gender</td>
<td>Female or male</td>
</tr>
<tr>
<td>Population level</td>
<td>Population density</td>
<td>Summation: number of individuals in infested lattices</td>
</tr>
<tr>
<td></td>
<td>Infested area</td>
<td>Summation: number of infested lattices</td>
</tr>
<tr>
<td>Environment</td>
<td>State of lattice</td>
<td>Vegetation, Infested vegetation, Without vegetation, or Outside boundary</td>
</tr>
<tr>
<td></td>
<td>Local carrying capacity</td>
<td>100 individuals minus the number of entering individuals</td>
</tr>
<tr>
<td><strong>Model structure and interaction</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Life processes</td>
<td>Movement</td>
<td>Lévy flight (eqn (10))</td>
</tr>
<tr>
<td></td>
<td>Search</td>
<td>Finding the most closely located infested lattices</td>
</tr>
<tr>
<td></td>
<td>Emergence</td>
<td>Stochastic (May 10%, June 80%, July 10%)</td>
</tr>
<tr>
<td></td>
<td>Reproduction</td>
<td>Production of progenies by adult females</td>
</tr>
<tr>
<td>Mortality</td>
<td>Control</td>
<td>Death due to control practices in the limited range</td>
</tr>
<tr>
<td></td>
<td>Natural death</td>
<td>Adult: last day of simulation in each year</td>
</tr>
<tr>
<td><strong>Parameter and data</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial conditions</td>
<td>Infested lattices</td>
<td>21 locations randomly selected</td>
</tr>
<tr>
<td></td>
<td>Individuals</td>
<td>2 individuals per lattice</td>
</tr>
<tr>
<td></td>
<td>Local carrying capacity</td>
<td>100 individuals</td>
</tr>
<tr>
<td>Parameters</td>
<td>Number of progenies</td>
<td>10 individuals per female</td>
</tr>
<tr>
<td></td>
<td>Movement patterns</td>
<td>Scale parameter (µ; 1.1–2.0) in Levy flight (eqn (10))</td>
</tr>
<tr>
<td>Output</td>
<td>Number of infested lattices</td>
<td>In relation with control rates and the Lévy parameter</td>
</tr>
<tr>
<td></td>
<td>Coincidence rate</td>
<td>In relation with the Lévy parameter, control rates and size of evaluation lattices</td>
</tr>
</tbody>
</table>
Stage is expressed in two states: the period from egg to emergency as immature stage, and the period from emergency to death as adult stage. Gender was determined equally by coin tossing. Age increased accordingly with the time step in simulation. When the progenies were produced from females, all the individual attributes were newly assigned to the progenies. At the population level, the number of lattices infested by PWD was expressed as a variable.

Environmental factors were also provided to the system. The four states of vegetation were given in each lattice as environment: healthy pine forest, infested pine forest, without pine forest (within boundary) and outside the boundary. The maximum number of insects allowed per lattice (i.e., local carrying capacity) was assumed to be 100 individuals. It was further supposed that the maximum number of insects per lattice would cumulatively decrease in accordance with the entering number of the sawyer beetles. If different numbers of insects invaded into a lattice separately in two times, for instance, 2 individuals at the 10th time step and 8 individuals at the 20th time step, the local carrying capacity for the lattice at the next time step would be 90 (= 100 – 2 – 8) individuals.

All the insects in simulation were assumed to be infested with nematodes and the lattice (with pine forest) could be turned to the infested state if at least one infested individual invaded the lattice. After control by human effort (i.e., cutting down the infested vegetation), however, the state of the infested lattice returned to healthy state, while the carrying capacity remained at the same value. For instance, if the control practice was carried out at the lattice stated above, the local carrying capacity would be still 90, not 100.

5.3 Model structure and interaction

Models could be composed of key life processes: life stage (i.e., immature stage and adult), movement, reproduction and death. In addition, a high level of mortality was caused by human control practices. The individuals were designed to emerge from May to July after overwintering according to the reports on life stage of the pine sawyer beetle [76–78]. The random numbers were generated for determining the emergence of immature insects in 10% in May, 80% in June and 10% in July.

Individuals were designed to move according to Lévy flight [74, 75, 79, 80]. The probability of the length, \( l \), in Lévy flight is determined as:

\[
P(l) = l^{-\alpha},
\]

where \( 1 < \alpha < 3 \).

For simplicity of modeling, we assumed that 10 surviving individuals for the next generation are produced from an adult female at the same time on the 60th iteration time after initiation of simulation. The females die after production of progenies. In the field condition, control practices were carried out (i.e., cutting down infested trees). We employed control of the sawyer beetles in the model: a certain proportion of the individuals were killed due to control practices on the probability basis. Although control was conducted mainly in November in winter, the control efforts were assumed to be practiced on the last day of September in simulation for simplicity of modeling, as the states of the individuals do not change greatly in winter. Based on information from the field data, control rates were applied differently in different years.

5.4 Parameters and input data

The states of the lattice (i.e., pine forest, infested pine forest, no pine forest or outside boundary) were used as input data for simulation. The maximum allowable density of the insects was
additionally provided to the system as a constraint. The carrying capacity accordingly decreased as new individuals entered the lattice as stated before. The parameters such as the control rate and the number of progenies produced from a female were incorporated into the system (Table 2). Additionally, the parameter controlling the degree of jump in the Lévy flight, $\mu$, was given as 1.1–2.0.

On the basis of information from the field, we checked different ranges of control: 70–95% for 2002–2003, and 30–60% for 2003–2004. After the best fit for the control was obtained in 2002–2003, simulation was conducted again from the best fit to predict the level of infestation for the next stage (i.e., 2003–2004) on the yearly basis. According to field data available from the Division of Forest Inventory, Korea Forest Research Institute, Korea, the infested 21 lattices in May 2002 were given as the initial data for simulation. Considering that control practices (November 2001) had been already carried out before start of simulation (May 2002), simulation for checking control levels in 2001–2002 was not included.

5.5 Output and results

Through simulation, dispersal of the infested lattices was observed on the map (Fig. 6). Different combinations of the control rates (in per cent) and the parameter, $\mu$, in the Lévy flight were applied to the system. Averages in 10 simulations were used for obtaining output data. Overall,
the trend of population dispersal appeared to be similar between the field and calculated data. Although individual locations of the infested lattices (x, y coordinates) did not precisely match between the field and calculated data lattice by lattice, the densely infested area appeared to be in the similar range between the two data sets (Fig. 6).

The number of infested lattices greatly increased from 2002 to 2004. Figure 7 shows the number of infested lattices calculated by the proposed model in different years (control rate: 90% in 2002–2003 and 45% in 2003–2004) across different values of $\mu$. Although variation in the number of infected lattices was not great in response to different values of $\mu$, the most suitable match to field data appeared to lie on the range of 1.4–1.6 in $\mu$. When the parameter was <1.4 in 2004, the calculated data notably underestimated the number of infested lattices compared with the field data. This may be due to geomorphology of the study area. As shown in Fig. 6, the bottom part of the map mostly consisted of small areas without pine trees. Consequently, the areas vegetated with the pine trees appeared to be numerous small islands; a large proportion of the lower map was left outside the boundaries. In 2004, the majority of infested areas advanced down to the end of the southern area (Fig. 6). Figure 8 shows changes in the number of infested lattices across different levels of control rates when $\mu$ was fixed with 1.5. In 2003, control rate with 90% presented the suitable fit, while control rate with 35–40% produced reasonably the closest approximation to the field data in 2004 (Fig. 8a and b). Figure 9 illustrates variability observed in the number of the infested lattices according to changes in the control rates and $\mu$. Increase in the number of the infested lattices in averages was accordingly observed in 2002–2003 (Fig. 9a) and in 2003–2004 after control effort (Fig. 9c). Coefficients of variation (CV; standard deviation divided by mean) in infested lattices across different levels of the parameter were similar showing 0.30 and 0.32 in 2002–2003 and 2003–2004 respectively. This indirectly indicated that changes in the parameter in the Lèvy flight ranging 1.1–2.0 caused approximately 30% of variation in the number of the infested lattices at the given control rates in the model.

Figure 7: The number of infested lattices calculated from the model across different levels of the scale parameter in the Lèvy flight ($1.1 \leq \mu \leq 2.0$) [control rates: not considered (2002), 90% (2003) and 45% (2004)].
Figure 8: The number of infested lattices calculated from the model across different levels of control rates (%) ($\mu = 1.5$). (a) 2003 and (b) 2004.

Figure 9: Range in the number of infested lattices in accordance with different combinations of the parameter in the Lévy flight ($\mu$) and control rates. $\mu$ in 2002–2003 (a), control rates in 2002–2003 ($\mu = 1.5$) (b), $\mu$ in 2003–2004 (c), and control rates in 2003–2004 (d) [control rate = 95% for (a), control rate = 45% for (c), and $\mu = 1.5$ for (b) and (d)].
The variability in the infested lattices was also presented according to changes in control rates when the parameter in the Lévy flight was fixed with $\mu = 1.5$ (Fig. 9b, d). When the control rates varied in the range of 70–95% for 2002–2003, CV in the infested lattices was 0.40, while CV was 0.37 for 2003–2004 with control rates varying between 30% and 60%. The results indicate that the range of variability in output data (i.e., the number of the infested lattices) can be obtained in response to the changes in the selected ranges of parameters for control rates and movement patterns in IBMs. This type of simulation would be useful for providing information for planning pest management policies.

The “lattice by lattice” correspondence between the field and calculated data was also checked by using coincidence rate. In this study, coincidence rate was defined as the number of coincident lattices (observed in both field and calculated data) divided by the sum of infested lattices in the field and calculated data minus the number of coincident lattices. For instance, if 22 points were the coincident lattices observed in both field and calculated data when 65 lattices and 57 lattices were the total number of the lattices for the field and calculated data respectively, the obtained coincidence rate would be $0.22 = 22/(65 + 57 - 22)$. As stated before, individual locations of lattices in the field and calculated data did not match precisely lattice by lattice. We checked the trend of increase in the coincidence rate, as the size of the lattices for checking the field and calculated data correspondingly increased (Fig. 10). In case the size of the lattice for checking the coincidence rate was 1 $\times$ 1 unit (i.e., “one-lattice by one-lattice” matching), a majority of

Figure 10: Coincidence rates (%) obtained from the calculated and field data across different levels of control rates and the size of lattice for comparing the field and calculated data: (a) 2002, (b) 2003 and (c) 2004.
coincidence rates were <20%. When the size was increased to 3 × 3 units, the coincident rates were in the range of 20–60%. The coincident rate accordingly increased to 40–80% if the size of unit was enlarged to 5 × 5 units (i.e., 110 × 110 square meter in field condition).

The coincidence rate also tended to increase at the areas of the infested lattices in higher densities. The overall densities of the infested lattices substantially increased from 2002 (approximately 1000 lattices) to 2004 (approximately 5000 lattices). The higher coincidence rates were correspondingly observed when the number of infested lattices increased. The results from the coincidence rates indicated that the size of evaluation lattice ≤5 × 5 units (110 × 110 m²) could be the practical criteria for predicting occurrence of the infested lattices in this case (Fig. 10). However, it is too early to draw conclusions on the appropriate size of the evaluation lattice, as the model has been based on numerous simple assumptions in this study, and this type of the “position by position” coincidence study in IBMs is in the beginning stage. In future, detailed studies are required regarding the relationships of the size of evaluation lattice and predictability of the model for improvement of precision for forecasting (e.g., decrease in the size of evaluation).

Other factors such as environmental effects (e.g., wind, human carry) and spatial heterogeneity (e.g., landscape) can also be further related to the model to improve forecasting in real situation in the infested area. About three quarters of the adults of vector insects are found within 100–200 m distance of the place of emergence while the rest of individuals disperse up to 3300 m (field observation by YJC). In this study, we used the unit in a short distance (10 m) for simulation and assumed continuous movement in small scale with the occasional jumps within the 100 m distance in simulation. However, small scale movement has not been clearly disclosed and a majority of the adult insects appeared to stay near the area of emergence in some longer scale (100–200m) as stated above, Study on further simulation may be needed to check different rates and scales in movement (i.e., early and long movement in a short period) in the lattice space in future.

The results from the model indicate that IBMs would be feasible in predicting population dispersal in the context of individual–population relationships. At the lower level, the model employed reproduction and local movement of individuals. Subsequently the model efficiently projected local processes upwards to the higher level at population, covering increase in the infested area and spatial conformation of infestation. Individual properties were efficiently elucidated in the processes of population dispersal in IBMs. Different spatial conformations of infestation could be specifically formed in different localities on the lattice space: some places were more densely located with the infested lattices whereas some other places were more sparsely located with the infested lattices as shown in Fig. 6. This spatially explicit information can provide an extra dimension in revealing dispersal processes in real situations. While the mean field models based on diffusion equations usually provide global patterns of population dispersal in average values [38, 81], spatially explicit information may be more suitable for specifically providing answers to some key issues in pest control in spatial and time domains in IBMs, covering formation of the front lines of dispersal, determination of threshold levels for control, prediction of local eruption of pests, effects of environmental heterogeneity, continuity of genetic information, etc. The feasibility of the model in handling the “close-to-real” life processes stems from IBM’s capacity in inter-linking the lower and higher levels in the hierarchy of biological systems.

In summary, by integrating the local processes in individual life process (e.g., movement, reproduction) in the total framework of IBMs, the proposed model was suitable for forecasting the number and positions of the infested lattices in a spatially explicit manner and for estimating the degree of influence of the selected parameters such as control rates in determining the levels of dispersal of the pest population. Further development of IBMs is envisioned along with development of computation techniques and progresses in biological and ecological sciences on population dynamics.
Acknowledgements

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