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Forest Succession Models

Guy R. Larocque, Herman H. Shugart, Weimin Xi, and Jennifer A. Holm

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7.1 Introduction

Forest succession models occupy a special niche among models that simulate the dynamics of forest ecosystems. While empirical models (see Chapter 6) focus on the prediction of tree and forest productivity to optimize forest management from an economic point of view, succession models predict the changes in species composition over long-term periods to examine different forest successional pathways. A fundamental difference between

empirical and succession models resides in their theoretical foundation. Empirical models are generally derived from statistical relationships using data that can be obtained from forest inventories. On the other hand, succession models are based on relationships that represent the essential underlying mechanisms of seedling establishment and individual-tree growth and mortality. However, the modeling of abiotic and biotic processes is simpler than process-based models (see Chapter 8).

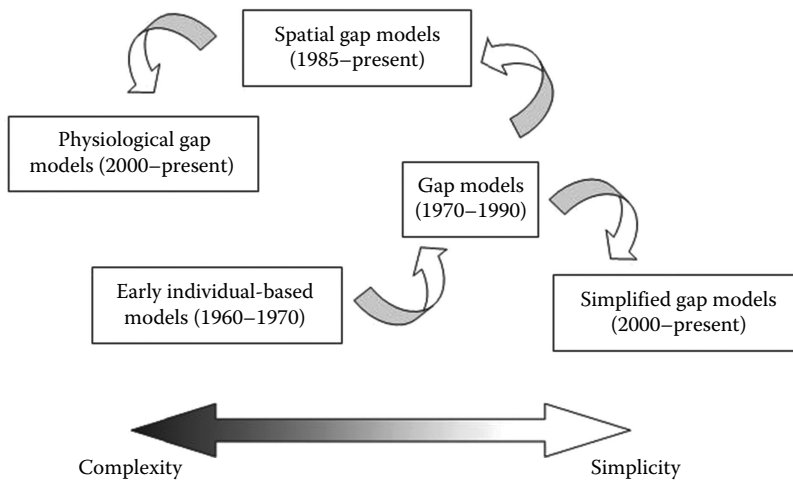
There are two broad categories of succession models: gap and forest landscape models (FLMs). In this chapter, the basic concepts and characteristics of both types of succession models are reviewed, along with some of their strengths and limitations. Their development history is discussed, and the applicability of models commonly used is described and compared. Several key characteristics, including modeled processes, forest types, main drivers, spatial scaling, and contributions, are summarized. Last, the use of succession models in relation to ecological indicators and their application in ecological forest management, the modeling of regeneration dynamics, and the application of remote sensing (RS) are presented.

7.2 Types and Structure of Succession Models

7.2.1 Individual-Based Models (Gap Models)

7.2.1.1 Initial Developments in Individual-Based Models

In the mid-1960s, foresters developed individual-based dynamic models of forests (mostly for commercial forests). They did not realize at the time that their computational innovation was being paralleled in other fields, notably in astronomy, physics, and several engineering sciences (Huston et al. 1988). Despite their independent origin in multiple disciplines, these are strongly ecological models. Of the thousands of such models developed across all sciences, about half of them originated in ecology (Grimm et al. 2005). In forest ecology, these models originated in forestry applications as early as 1964 (see Shugart and Woodward 2011 for a review) and have been characterized as an innovation uniting ecological theory (Huston et al. 1988). The individual-based models (IBMs) have been nurtured by the increase in computation infrastructure over the past decades, and the issues in model development have transitioned from computational issues to the richer theoretical problem of attaining the sweet spot (the “Medawar zone”) between the utility of a model to solve a problem and its degree of realism (Grimm et al. 2005). Perhaps it is this search for the Medawar zone that has led to the development of forest IBMs to cycle from high complexity in their early development to simplifications and then back to complexity (Figure 7.1). Starting in the 1960s, remarkably complex 3D dynamic models were developed primarily by forestry researchers to investigate problems in stand spacing and timber dimensions in novel forestry practices. Gap models, which were simpler models simulating change in diameters for individual trees competing for light on a sample plot, were developed for ecological applications on the dynamics of mixed-species, mixed-aged forests. These gap models were simplified for landscape-scale simulation of forest change. With the steadily increasing computer capability, gap models became relatively more complex with a return to 3D simulations and the addition of more mechanistic plant physiology along with the biogeochemical and hydrological features. These eventually closed

**FIGURE 7.1**

A cycle of development for individual-based models. (From Shugart, H.H. and Woodward, F.I., *Global Change and the Terrestrial Biosphere: Achievements and Challenges*, John Wiley & Sons Ltd., Oxford, UK, 2011.)

back to models with the complexity of the original forest IBMs. The continued increase in computational muscle has allowed continental-scale simulations with relatively complex simulators.

Forest IBMs have much to offer for assessing the potential effects of climate change over large regions through their ability to project standard state variables such as leaf area, biomass, and productivity and also to simulate changes in forest vertical, horizontal, and 3D structures and in species composition over time and space. One advantage of IBMs is that two implicit assumptions associated with the more traditional state-variable approach used in ecological modeling of populations are not necessary. The unique features of individuals are not assumed to be identical, nor is the population assumed to be “perfectly mixed” with no important spatial interactions. These assumptions seem particularly inappropriate for trees, which are sessile and vary greatly in size over their life span. For this reason, tree-based forest models are among the earliest and most widely elaborated models of this genre. Botkin et al. (1972), with the JABOWA model, introduced an important simplification of early forestry work to ecologists, but earlier forestry work still remains unknown to most ecologists.

The first IBMs developed in forestry were closely associated with prediction needs for stand growth and involved stand yield tables. Models were either distance independent or distance dependent. For distance-dependent models, the location of trees was used to compute competition indices. The first model of this type was developed by Newnham (1964). These models are based on the derivation of empirical statistical relationships and are used for traditional forestry applications.

7.2.1.2 Concepts of Gap Models

Gap models, a term coined in Shugart and West (1980), are a category of individual-tree models that have been widely used in ecological studies. In addition to predicting individual-tree growth, they predict tree mortality and regeneration, which allow them to predict forest succession. First developed in the early 1970s and seemingly a simplification

of earlier IBMs, they have been further developed ever since. The JABOWA model (Botkin et al. 1972) was developed for forest types in New England. Since then, other models were developed with different types of modifications and ecosystems (Table 7.1), but their basic formulation, at least initially, was close to that of the JABOWA model. The models listed in Table 7.1 consist of examples of development and/or application for the three main forest types of the world: boreal, temperate, and tropical. The gap models that have been derived using JABOWA as a framework are sometimes called *JABOWA-type* models.

For many JABOWA-type models, the basic form of the annual dbh growth rate equation of individual trees is

$$\frac{\Delta D_{\text{real}}}{\Delta t} = \frac{\Delta D_{\text{pot}}}{\Delta t} \times f(\text{Limiting site factors}) \quad (7.1)$$

The left-hand term is the realized annual dbh growth rate computed from the species-specific potential growth rate reduced by the effect of site factors, which may include the effects of temperature, intra- and interspecific competition, precipitation, and basic soil properties. The species-specific potential dbh growth rate, which represents the maximum dbh growth rate that a species can achieve under the optimal conditions within its area of distribution, is computed as

$$\frac{\Delta D_{\text{pot}}}{\Delta t} = G D \left(1.0 - \frac{DH}{D_{\text{max}} H_{\text{max}}} \right) \times \frac{1}{f(D)} \quad (7.2)$$

where

D is the dbh

H is the stem height

G is the growth rate parameter

D_{max} and H_{max} are the maximum dbh and height that a species can reach under optimal conditions

$f(D)$ is the relationship between dbh and height

The effect of limiting site factors varies among models. For instance, in the original version of JABOWA, the effect of light interception on growth is modeled as an annual insolation factor adjusted by a shading leaf area factor obtained from the sum of the leaf areas from all the trees within the plot. ZELIG (Urban 1990), a derivative of JABOWA, computes the effect of light interception on individual-tree dbh growth rate by calculating the available light growing factor as a function of the summation of the leaf areas of all trees within a plot divided by canopy length.

Individual-tree mortality is usually modeled as a random process. Typical JABOWA-type gap models include model components to represent the effects of both natural mortality related to age and stress originating from site factors or suppression (Shugart 1998). For natural mortality, it is assumed that 1% of individual trees within a plot will reach the species-specific maximum age, but the death probability remains constant with age:

$$P_m = 1 - e^{\frac{-4.605}{\text{AGEMX}}} \quad (7.3)$$

where

P_m is the probability of mortality, -4.605 is the natural logarithm of 0.01 (1%)

AGEMX is the maximum age that a species can live

TABLE 7.1**Main Characteristics of Individual-Based Gap Models**

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
JABOWA	Botkin et al. (1972)	Growth, mortality, effects of temperature and precipitation, mortality, and regeneration. Semiempirical equations.	Northern hardwood forest/North America	Tree dbh ^a , species-specific ecological parameters (min and max dbh, degree-days, min and max values for evapotranspiration index).	Individual-based model with individual trees on a 0.01 ha plot updated annually using a Monte Carlo simulation of many plots	First gap model; simulation of the succession and altitudinal transition between hardwood and conifer forests for Hubbard Brook Watershed (New Hampshire, United States).
FOREST	Ek and Monserud (1974)	Individual-tree growth equations with competition driven by 3D canopy encroachment between trees; seed rain computed for each tree based on tree height and seed aerodynamics; “windowing” used to increase computational efficiencies. Empirical equations.	Northern hardwood forests in Wisconsin/ North America	Tree coordinates, tree diameter and height, clear bole length, and reproduction options.	3D map of individual trees on a plot of arbitrary size	Uncensored in model detail, even though FOREST was an early 3D vegetation model
FORET	Shugart and West (1977)	Derived from JABOWA model; species-specific regeneration conditions control germination; sprouting included; change in computations involving vertical light competition to increase computational efficiency. Semiempirical equations.	Appalachian deciduous forest/ North America	Tree dbh, species-specific ecological parameters (min and max dbh, degree-days, min and max values for evapotranspiration index); growth altered by degree-days and water availability; shading and approach to plot biomass maximum also reduce tree growth.	Individual trees on a 0.083 ha plot with Monte Carlo simulation	Simulations of elimination of American Chestnut by blight; reconstructions of forests over the past 18,000 years; simulation of song bird habitat dynamics; theoretical investigations of long-term dynamics of forests; simulations of pollution effects on forests.

(Continued)

TABLE 7.1 (Continued)

Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
KIAMBRAM	Shugart et al. (1980)	Derived from the FORET model with options to harvest trees by dbh and species; mortality increase with felling trees included as a source of mortality; stochastic variation in seed rain. Semiempirical equations.	Australian subtropical rain forest/Australia	Selective harvest by species and size with increase in harvest mortality from empirical experiments; competition for light and crowding according to stand basal area.	Individual trees on a 0.05 ha plot with Monte Carlo simulation of hundreds of plots	Very diverse forest (125 species in the model); inclusion of strangler life form; simulation of selective harvest in rain forests; application with new species parameters to southern African montane rain forests.
FORTNITE	Aber and Melillo (1982)	Derived from JABOWA, Inclusion of nitrogen dynamics. Semiempirical equations.	Northern hardwood forest/North America	Same as JABOWA, with the addition of nitrogen cycling and nitrogen uptake; used to evaluate the effects of different harvest rotations.	Individual trees on a 0.01 ha plot with Monte Carlo simulation of multiple plots	Inclusion of detailed nitrogen cycle in individual-based models
LINKAGES	Pastor and Post (1985)	Based on the development of soil processes merged with components from JABOWA and FORET. Semiempirical equations.	Northern hardwood forest/eastern North America	Tree dbh, species-specific ecological parameters (min and max dbh, degree-days, min and max values for evapotranspiration index); soil moisture capacity, litter content, initial soil organic matter and nitrogen contents.	Individual trees on a 0.083 ha plot with Monte Carlo simulation	Demonstration of multiple stable states in simulated northern forests mediated by high or low nitrogen availability
FORSKA	Leemans and Prentice (1987)	Derived with considerable alteration from the FORET model; Mitscherlich curve for maximum tree height and tree growth; explicit consideration of canopy foliage distributed for each tree's crown depth; two-year time step. Semiempirical equations	Swedish <i>Pinus-Picea</i> forest/Europe	Similar to FORET but initial model was simplified and used no stochasticity in the driving variable, which provided clear results (no stochastic variation) but limits simulations to the calibration site.	Individual trees on a 0.5 ha plot with Monte Carlo simulation	Reproduction of composition for an ancient uncut forest in Sweden; model was adapted to different locations in Europe and elsewhere for climate-related simulations.

(Continued)

TABLE 7.1 (Continued)
Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
SORTIE	Pacala et al. (1993)	Individual-based gap model with empirical parameterizations for birth, growth, dispersal, and mortality. Empirical equations	Northern Hardwood Forest/United States	Tree coordinates, more complex light extinction calculations, basic site characteristics, individual-tree data.	Spatially explicit in 2D (spatial locations of trees).	Demonstration of statistical/empirical methodologies for gap model parameterization.
ZELIG	Urban (1990)	FORET model applied to a map of trees on a forest plot of arbitrary size using windowing. Resolution can be adjusted for greater computational speed or spatial detail; canopy structure simulated and light computed with a ray tracing approach through a 3D canopy; growth altered by degree-days and water availability; shading and approach to plot biomass maximum also reduce tree growth. Semiempirical equations.	Appalachian deciduous forest and other forests, notably Douglas fir forests/ North America	Tree dbh, species-specific ecological parameters (min and max dbh, degree-days, min and max values for evapotranspiration index); nutrient tolerance factor, species-specific regeneration probabilities.	Can be implemented in 3D as a gap model, as a transect model, or over a multiple ha plot.	Used to simulate expected spatial patterns in remote sensing for high-resolution panchromatic optical as well as radar (microwave) instruments.

(Continued)

TABLE 7.1 (Continued)
Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
ZELIG-CFS	Larocque et al. (2011)	Adapted from ZELIG; modifications include new algorithms for crown interaction, mortality, and regeneration. Semiempirical equations.	South Canadian boreal mixed hardwood forest/Southern Canada.	Same as ZELIG.	Implementation at the plot level.	Used to test new competition algorithms at the canopy level; integration of the Stand Visualization System and the geographic information system Quantum GIS.
ZELIG-TROP	Holm et al. (2012, 2014)	Adapted from ZELIG and ZELIG-CFS; modifications include a new exogenous disturbance routine, optional basal-sprouting routine, adjustment to natural mortality equation for tropical trees. Semiempirical equations.	Tropical forests; both subtropical dry and Amazonian wet rain forests/South America	Same as ZELIG.	Can be implemented in 3D as a gap model, as a transect model, or over a multiple ha plot.	Used to simulate diverse and complicated tropical forests and evaluate changes due to multiple disturbance types.
FORCLIM I and FORCLIM II	Bugmann (1994), Fischlin et al. (1995)	Derived from the FORECE model (Kienast and Kuhn 1989), which is derived from FORET; considerable development of functional responses to environmental variables. Semiempirical equations.	Swiss alpine forest/ Central European forests	Heat sums, minimum mean monthly temperature, carrying capacity constrained by NPP equation, nutrient constraints on growth, water balance and dry days.	Individual trees on a 0.083 ha plot with Monte Carlo simulation.	Capable of simulating forests in multiple locations with different locations in Switzerland; produces alpine patterns and regional patterns on forest change; sensitivity analyses using equilibrium as starting point.

(Continued)

TABLE 7.1 (Continued)

Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
FORMIX, FORMIX 2, FORMIX 3	Bossel and Krieger (1994)	Functional type-based mortality, seed banking, and growth equations with shading through canopy geometry (Beer's law). Tree increment uses a photosynthesis equation decremented by tissue-specific respiration and growth respiration; forest harvest and cutting included. Process-based equations.	Tropical rain forest on several continents and islands/South America	Driven primarily by the light environment interacting with physiologically based tree performance equations.	Spatial: a hectare or larger plot tiled with 0.04 ha gaps, details of canopy, form factors, etc.; use of a functional type approach to allow implementation in a number of rain forests.	Many good applications in diverse tropical ecosystems with a number of independent model tests.
FORMOSAIC	Liu and Ashton (1998)	Growth function calculated for 502 species based on tree growth rate in diameter, basal area of neighbors for inter-tree competition, slope, distance from water and an error term; four levels of recruitment distributed among species by "guilds." Mortality by size and longevity classes. Semiempirical equations.	Malaysian rain forest/ Southeastern Asia	Tree coordinates. Parameters were fit to half the data using an empirical approach; environmental couplings through site conditions (basal area, slope, etc.).	Tree locations in grid scales (0.01 ha) with internal and external seed dispersal; scaled up to a 50 ha spatial plot.	Initially implemented for the Pasoh forest of Malaysia with some landscape complexity; parameterized on half the 50 ha plot and tested on the other half.

(Continued)

TABLE 7.1 (Continued)

Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
DRYADES	Mailly et al. (2000)	JABOWA/FORET growth equations, but using a Chapman–Richards equation for height. Use of a cross section of sapwood to determine the leaf area. More detailed crown geometry. Semiempirical equations.	Conifer forests of the North American Pacific Coast/ Northwestern America	Probability of wildfire; stochastic variation in seed rain; light competition, moisture and dry days computation; includes harvesting simulation.	3D spatial model.	Comparison with measured stand data after fire and clearcut
PICUS	Lexer and Hönninger (1998)	Tree growth, reproduction, and death. Semiempirical equations.	Austrian forests/ Europe	Growing degree-days, winter minimum temperatures; drought and site conditions (pH, C/N ratio of upper soil layer, soil texture).	0.01 ha plots tiled onto 1 ha grid elements.	Climate change assessment for Austrian forests from 2000 to 2065; change in forest composition, biomass and zonation with altitude.
FAREAST	Xiaodong and Shugart (2005), UVAFME model (Shuman et al. 2014)	Fusion of the FORET model modified through several Chinese forest models and then merged with the FORSKA model with several modifications, notably dynamics of soil organic carbon and nitrogen cycling. Semiempirical equations.	Forest of northern China subsequently expanded to simulate forests of northern Eurasia/East Asia	Tree data; monthly temperature and precipitation and derived heat and water balance indices; nitrogen cycling data.	0.083 ha plots; largest simulation is 20 km on a side lattice over Russia (31,000+ grid points with 200 replications at each point)	Applications in climate change projections over continental-scale regions.

(Continued)

TABLE 7.1 (Continued)

Main Characteristics of Individual-Based Gap Models

Model Name	References	Main Processes Modeled and Equation Types	Forest Type(s)/ Region(s) of the World	Main Drivers and Response Variables	Spatial Scaling	Main Contributions
TreeMig	Lischke et al. (2006)	Local tree dynamics from the FORCLIM model to produce ingrowth and outgrowth from height classes. Semiempirical equations.	Central European forests/Europe	Same environmental drivers as in FORCLIM.	0.083 ha grid elements on a larger landscape, typically 1 km ² ; grids interact through seed dispersal.	Local pattern formation in forests, tree species migration rates in the alpine region of central Europe.
FORSITE-BPM	Caplat and Anand (2009)	Growth uses a Gompertz function. Mortality with two components: one actuarial, one from disturbances. Seed dispersal function, also sprouting regeneration. Semiempirical equations.	Birch–Pine–Maple forest of Minnesota/ North America	Tree data and habitat cells; disturbance regime.	Cell diameter of 20 m simulated over 400 cells.	Investigation of the resprouting tendency of trees to alter the rate and patterns of ecological succession.
ForestMAS	Kolmanič et al. (2014)	Light, temperature with indicators for soil moisture, acidity, nutrients/nutrient requirements; regeneration uses a seed rain approach; approximation of Yoda's law ($-3/2$ thinning law for mortality). Semiempirical equations.	Forests of Slovenia/ Europe	Tree data; ray tracing for light as a function of topography; site quality indicators: moisture, incoming solar radiation, soil pH, and nutrient availability.	3D IBM ^b with topographically mapped fields of underlying driving variables.	Reforestation and ecological succession in Slovenia; use of classic Ellenberg indicator values from European phytosociological studies.

^a Diameter at breast height.^b Individual based model.

Stress-related mortality occurs when trees fail to reach a threshold minimum dbh growth rate. The implementation of stress mortality algorithms varies among models. Some models set a specific value, such as 1 mm year⁻¹ in dbh growth rate; other models specify a minimum value, such as a percentage of optimum growth rate for a given tree size. Trees that do not meet these conditions see their death probability increased for a given number of years.

As these equations are based on the application of basic ecological principles, they may be considered as semiempirical because they are a compromise between empirical models and process-based models. Some of their components are based on empirical knowledge, while other components have an ecological foundation. For instance, the species-specific dbh growth rate equation is similar in concept to the Gause's model for competition (Gause and Witt 1935), the classic competition model in population dynamics, as it is computed by estimating potential growth rate (absence of competition) reduced by the intensity of competitive interactions. Also, the potential growth rate component of the dbh growth model includes species-specific ecological parameters, such as the minimum and maximum growing degree-days within the area of distribution. The models that are considered as semiempirical in Table 7.1 are generally based on the approach of computation of potential growth rate reduced by a competitive interaction factor.

The more recent gap models feature relatively simple protocols for estimating the model's parameters (Shugart 1998). For instance, Moore (1989) developed a relatively simple model formulation after noting that the JABOWA model implied that the rate of carbon loss in large trees increased proportionally more than their rate of increase in stem volume. The new diameter increment equation, also used in FORCLIM (Bugmann 1994), was formulated as

$$\frac{\Delta D}{\Delta t} = GD \left(\frac{1 - \frac{H}{H_{\max}}}{274 + 3b_2 - 4b_3} \right) \quad (7.4)$$

Pacala et al. (1993) identified the need to relate the parameters of gap models directly to empirical field observations because they believed that the high degree of complexity of JABOWA-type models required information difficult to obtain from the scientific literature. Their model, SORTIE, is based on the development of statistical relationships using field data. The growth rate equation for diameter increment was developed as follows:

$$\Delta r = r \left(\frac{\frac{P_1 GLI}{P_1 + GLI}}{\frac{P_2}{P_2 + GLI}} \right) + \alpha \quad (7.5)$$

where

r is the radius of a tree

Δr is the annual increment rate (ring width)

GLI is the "general light index" that is computed from changing sun angles, ratios of diffuse and direct radiation, and canopy openness to represent an integrated measure of annual local light availability

P_1 and P_2 are the regression parameters

α is the random variable normally distributed with a mean = 0. The variance of α is computed as $C(\text{predicted ring width})^D$, where C and D are estimated parameters.

7.2.1.3 Applications

For many of the more common temperate and boreal forest species, there is a considerable body of information on the performance of individual trees (growth rates, establishment requirements, and height/diameter relations) that can be used directly to estimate the parameters for such models. The models have simple rules for interactions among individuals (e.g., shading and competition for limiting resources) and equally simple rules for the birth, death, and growth of individuals. The simplicity of the functional relationships in the models has positive and negative consequences. The positive aspects are largely involved in the ease of estimating model parameters for a large number of species; the negative aspects highlight a desire for more physiologically or empirically “correct” functions (Shugart 1984, 1998; Shugart and Woodward 2011). The representation of interactions among trees may also be influenced by the location factor. Similarly to distance-dependent models, some gap models require tree coordinates to compute the intensity of competition, but the majority of them do not require location data (Table 7.1). Trees may be positioned in a random pattern within a delimited zone or along a transect.

In many cases, the recent gap models have functional relationships that are different from those used in earlier gap models (Table 7.1). These models differ in their inclusion of processes that may be important for the dynamics of the particular forests being simulated (e.g., hurricane disturbance, flooding, and formation of permafrost). However, the models share a common set of characteristics. Each individual tree is simulated as an independent entity with respect to the processes of establishment, growth, and death. This unifies individual tree-based forest models and allows the computation of species- and size-specific tree demography. Also, gap models emphasize two features that are important for a dynamic description of the vegetation pattern: the response of an individual plant to the prevailing environmental conditions and the modification of those environmental conditions by the individual tree. Gap models are hierarchical in that the higher-level patterns observed (i.e., population, community, and ecosystem) represent the integration of plant responses to the environmental constraints defined at the level of the individual. Recent increases in the capability of RS instruments allow the detection of some of the structural patterns in forests generated by individual-tree processes (Shugart et al. 2010). The possibility of testing and implementing IBMs over very large areas has increased the potential to apply these biologically rich models over continental-scale areas.

Due to the remarkable drop in the cost of computation and the development of object-oriented computer languages, the computational environment of today's gap models is much more conducive to IBM applications than in the past. Initial individual-based forest models were extremely complex and implemented with 3D spatially explicit models. We have seen a complexity to simplicity and back to complexity cycle over the past 4 decades with the developers intending to improve the models at each step of the process. With a cycle from complexity-to-simplicity and back again in gap models (Figure 7.1), there has also been a significant push to expand the application of gap models to subcontinental representations of landscapes. These involve the understanding of global and regional carbon cycles and representing the dynamics of vegetation responding to climate change. Initial simplified versions of gap models ranged from automatic programs that converted gap model output into Markov models to computationally fast models that assessed the probability of transition of the vegetation from one type to another (Moore and Noble 1993).

Alternate approaches to developing computationally fast representations of gap models involve reducing the species in a gap model to a collective of species called functional types or roles. Both Acevedo et al. (1996) and Shao et al. (1996) treated the problem of deriving a

computationally fast role-based model based on four abstract tree-species roles. Acevedo et al. (1996) developed a Markovian model directly from a gap model and then inspected the behavior of the resultant model against dynamic simulations of forest succession from a gap model. Shao et al. (1996) used a somewhat more simulation-based approach and developed regional applications for the four northern provinces of China.

Another important application to tropical rain forests is that of Moorcroft et al. (2001), who parameterized a gap model for an Amazonian rain forest using a postulated relationship between growth rate, photosynthesis, and wood density. The resultant model was used to parameterize a statistical model of the size distribution of trees across the Amazon Basin using an approach pioneered by Kohyama (1993) to represent forest structural dynamics as a partial differential equation in time, numbers of trees, and tree size. The partial differential equation model provides canopy structure to constrain the results produced by a photosynthesis model. This model, called the Ecosystem Demography (ED) model, was used to summarize the demography of forest mosaics over large areas (Amazonia). The ED model represented Amazonian forests as a Kohyama-type partial differential equation of numbers versus tree size and used a gap model to estimate the growth (the forward vector with respect to the size axis) and mortality (the downward vector) under the constraint of cohort size-specific photosynthesis rates.

7.2.1.4 Future Developments

There are several promising directions for gap model development. These involve the following:

1. Continued development of the models for novel ecosystems and inclusion of new environmental phenomena in the models as well updating internal model functions
2. Application of the models to a diverse array of topics, including paleo-reconstruction, climate change applications, and simulations of forest under altered management regimes
3. Theoretical developments derived from the models, including a better understanding of landscape and regional dynamics

In [Figure 7.1](#), these are illustrated as branches into topics, such as ecological theory and spatial ecology. There are also several branches of application and development of the models as simulators for non-forest ecosystems. The hope is for a synthesis that seamlessly moves among model development, ecological theory, and ecological applications. Too frequently, the latter two (theory and application) are viewed as antithetical by young scientists—a misconception for which gap models are a prominent counterexample.

7.2.2 Forest Landscape Models

Since the 1980s, new developments in landscape ecology, quantitative ecology, computer sciences, geographic information systems (GIS), RS technologies, decision support systems, and geospatial statistics have provided opportunities for developing FLMs that are increasingly valuable for forest ecological management and long-term research in macroecology, such as studying the equilibrium between landscape-scale biodiversity and human activities under global climate change.

7.2.2.1 Concepts

FLMs have been developed approximately over the past 30 years. Compared with IBMs (gap models), FLMs (the term *raster* model is also used) simulate forest change through time across a broad spatial scale (i.e., landscape scale) generally larger than a single forest stand and focus more on disturbances. Spatial interactions among forest components are keys for such models since spatially referenced data are often used. Thus, they consider that ecological processes occur at different scales, among forest ecosystems within a forest region or a landscape. FLMs can incorporate spatiotemporal processes such as succession, seed dispersal, natural disturbances (e.g., wildfires, hurricanes, outbreaks of native and exotic invasive pests and diseases), and human influences (e.g., harvesting and commercial thinning, planting, fire suppression, global climate change). Thus, these models are increasingly used as tools for studying different scenarios of forest management, ecological assessment, restoration planning, and climate change. LANDIS is a good example of this type of model, originally designed to simulate forest landscapes varying from hundreds of ha to thousands of km² (Mladenoff 2004). Its structure is based on a raster GIS format that contains information and data on ecological attributes, species composition, and disturbances (Figure 7.2).

FLMs are founded on concepts and theories of ecological succession, disturbance, and ecological equilibrium and nonequilibrium. They also incorporate forest landscape changes, biological characteristics of tree species within forest ecosystems, competition process among species, and synergistic effects with environmental disturbances. They can quantitatively describe the spatial distribution of trees and illustrate the relationship between dynamic variations in tree species composition and forest communities as well as other influences. These models have been broadly applied in various fields, including

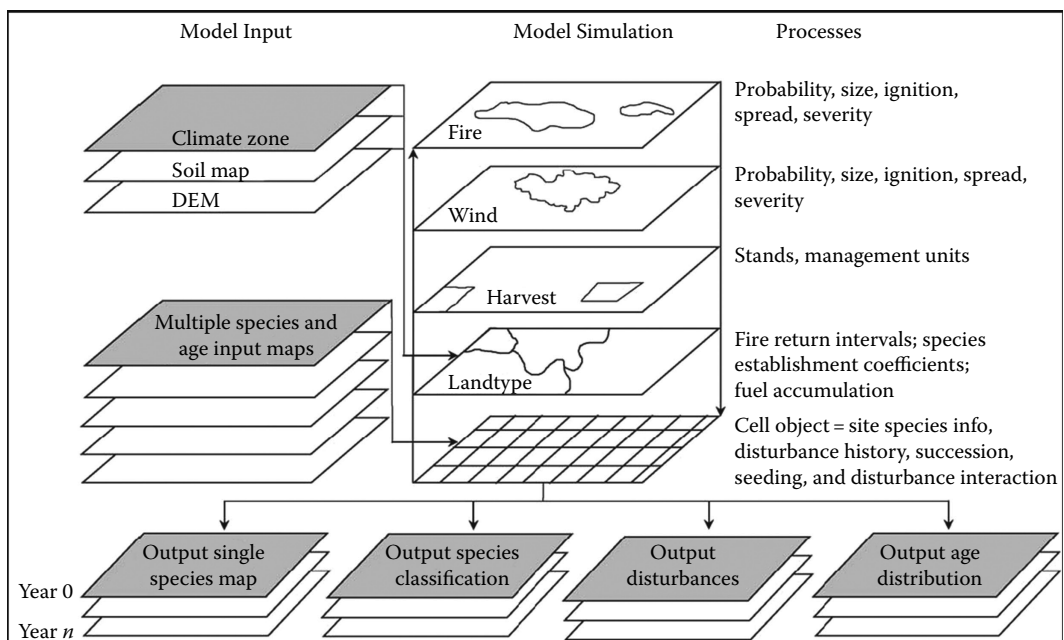


FIGURE 7.2

Basic schematic diagram that illustrates the integrated structure of LANDIS to simulate forest succession and disturbance over landscapes. (Reprinted from *Ecol. Modell.*, LANDIS and forest landscape models, 180, Mladenoff, D.J., p. 7, Copyright 2004, with permission from Elsevier.)

forest sciences, ecology, resource management, and wildlife habitat evaluation. Even though they share common functions, FLMs differ in several aspects, including representation of processes, methods of landscape change, and required data inputs and outputs (Table 7.2). The FLMs listed in Table 7.2 are good examples that highlight the main forest types that were used in model development and application and their main contributions.

It is essential to understand the concept and scope of FLMs. According to the literature, there are diverse definitions of FLMs. For example, Mladenoff and Baker (1999) define FLMs as computer models that simulate the change in forest landscapes across broad spatiotemporal scales. Scheller and Mladenoff (2007) broadly define FLMs as computer programs or software packages for projecting landscape change over time. He (2008) provided both general and specific definitions and key terminology commonly used in classifying FLMs. These models can be used to predict variations in spatial characteristics (i.e., distribution, shape, abundance) for simulated objects. More specifically, an FLM is one that simulates the spatiotemporal characteristics of at least one recurrent spatial process in a spatially interactive manner. According to the aforementioned definitions, He (2008) indicates that an FLM under this specific definition should have the following characteristics: (1) it is a simulation model, (2) it is able to run simulations of spatial processes repeatedly, and (3) it operates at a large spatial and temporal scale that is adequate to simulate the spatial process.

Xi et al. (2009a,b) considered that FLMs are computing models that simulate and predict the spatiotemporal trends of forest changes at the landscape level based on mechanisms of forest dynamics and the interaction of disturbances. Common research questions include the interaction between diverse ecological processes and their implications for spatial patterns of forest landscapes, disturbance mechanisms (i.e., forest growth and succession, carbon, nitrogen and water cycles, forest wildfire, insect and disease dispersal, climate change and other factors), as well as the effects on animal and plant habitats. A typical FLM usually has the following characteristics: (1) projection of landscape-level spatiotemporal changes; (2) simulation of spatially interactive processes; and (3) prediction of long-term interactions among multiple factors. FLMs are used increasingly often in studies of forest planning, forest management, resource conservation, ecological restoration, and global climate change.

The processes of forest succession and disturbance may take place over long time frames and broad spatial extents. Thus, there is a limitation to solving problems using traditional fine-scale ecological methods. FLMs provide a solution to overcome these issues. Hence, FLMs can be useful tools to assist in long-term forest landscape planning and decision-making in resource management. Scale is important for FLM theory and applications. The object that is simulated using FLMs is the forest landscape. In general, the temporal scale of forest landscape simulations ranges approximately from decades to hundreds of years (i.e., ~50–500 years), while the spatial scale (e.g., spatial extent) is generally of about 100–10,000 km².

In landscape ecology, extent and resolution are used to define scale. Extent, especially temporal extent, plays a key role in understanding forest ecosystem dynamics (e.g., physicochemical reactions of wildfires) or long-term succession processes (e.g., soil development, organism decomposition, nutrient loss, or tree species competition). Landscape resolution, also known as grain, indicates the finest unit that can be identified in landscape spatial and temporal extents. Generally, considering the constraints of computational power and interpretation of the results, studying broader landscapes will necessarily increase the grain of a study while small-extent landscapes allow the simulation and integration of more detailed information.

TABLE 7.2

Main Characteristics of Forest Landscape Models (FLMs)

Model Name	References	Main Processes and Model Type	Type of Landscape Change	Forest Type(s)/Region(s) of the World	Main Drivers and Outputs	Spatial Scaling	Main Contributions
LANDIS	Mladenoff et al. (1996); He et al. (1999); Mladenoff (2004); Wang et al. 2013	Succession, seed dispersal, disturbances (windthrow, fire, insect), harvest management: a grid model derived from JABOWA–FORET gap models and LANDSIM model. Process-based simulation model.	A spatially explicit and stochastic model.	Second-growth forests in the Northern Lake States region; temperate, southern, and boreal forests of eastern North America; montane and boreal western forests; coastal California forests and shrub types; boreal Finnish forests. Montane forests in Switzerland and northeastern China/ North America, Europe, and East Asia.	Species life history parameters (shade tolerance, seed dispersal, longevity); map layers of ecological land and soil types, and climate zone. Outputs: maps based on landscape composition.	Allow operations at different scales of resolution by modifying cell size.	Analysis of spatial dynamics and succession. Analysis of the impacts of fire, windthrows and forest harvesting on landscape structure; analysis of management consequences.
FIRESCAPE	Cary (1997, 1998); Cary and Banks (1999)	Vegetation development/ dynamics; spatial pattern and variation in fire regime (fire ignition, location of ignition sites, fire line intensity, head fire rate of spread, drought factors, fuel load) and spatial extent of ignition neighborhoods. Process-based simulation model.	Spatial landscape.	Eucalyptus-dominated forest landscapes/ Southeastern Australia.	Digital elevation maps; weather data, fire danger, litter accumulation, fire regime parameters. Outputs: digital or GIS maps that represent the spatial variation of fire regime components (predicted frequency, predicted stand variation).	Variable complex landscape areas.	Includes terrain-induced effects; identifies the spatial extent of fire ignition neighbourhoods as important process in topographically complex landscapes.

(Continued)

TABLE 7.2 (Continued)

Main Characteristics of Forest Landscape Models (FLMs)

Model Name	References	Main Processes and Model Type	Type of Landscape Change	Forest Type(s)/Region(s) of the World	Main Drivers and Outputs	Spatial Scaling	Main Contributions
LANDIS-II	Scheller et al. (2007)	Same as LANDIS.	Same as LANDIS.	Boreal forests, mixed hardwood forests, pine forests, and Mediterranean woodlands/North America and Europe.	Mostly the same as LANDIS, additional biomass and carbon succession.	Same as LANDIS, but allows spatial and temporal flexibility for ecological processes that differ in their temporal resolution.	Same as LANDIS.
Fire-BGC	Keane et al. (1996a,b)	Simulation of biogeochemically driven forest succession (carbon, nitrogen, and water cycles); seed dispersal and fire modeled in a spatial domain using raster data layers; individual-tree succession model with stochastic properties implemented in a spatial domain; use of FOREST-BGC routines. Process-based simulation model.	Landscape level using raster data layers (greater than 10,000 ha).	Glacier National Park, Montana. The McDonald and St. Mary drainages of Glacier National Park/ North America.	Ecophysiological properties of species; carbon and nitrogen contents in ecosystem pools. Outputs: Carbon and nitrogen contents, tree data, fire occurrence, seed dispersal.	Tree to landscape levels.	Analysis of the impacts of climate change and the role of fire on long-term (~200 years) landscape dynamics.

(Continued)

TABLE 7.2 (Continued)

Main Characteristics of Forest Landscape Models (FLMs)

Model Name	References	Main Processes and Model Type	Type of Landscape Change	Forest Type(s)/Region(s) of the World	Main Drivers and Outputs	Spatial Scaling	Main Contributions
Fire-BGCv2	Keane et al. (2011)	Second version of the original FIRE-BGC model; mechanistic, individual-tree, gap model that is implemented in a spatial domain; vegetation development/ dynamics; integration of the latest ecophysiological simulations of BIOME-BGC; complex, spatially explicit landscape fire and vegetation model; simulation of the initiation, spread, and effects of mountain pine beetle and white pine blister rust epidemics. Process-based simulation model.	Same as Fire-BGC.	Same as Fire-BGC.	Same as Fire-BGC, plus a wildlife suitability model.	Same as Fire-BGC.	Simulation of wildland fire ignition and spread, along with cone crops and seed dispersal; species phenology are simulated at the site level at a daily time step; better cross scale integration of processes.

(Continued)

TABLE 7.2 (Continued)
Main Characteristics of Forest Landscape Models (FLMs)

Model Name	References	Main Processes and Model Type	Type of Landscape Change	Forest Type(s)/Region(s) of the World	Main Drivers and Outputs	Spatial Scaling	Main Contributions
ALFRESCO	Rupp et al. (2000, 2007)	Transient landscape-level model of vegetation dynamics, changing climate and disturbance regime; changes in vegetation flammability; stochastic simulation of fire regime driven by climate, vegetation type, and time since last fire; simulation of fire spread across the landscape using a cellular automation approach. Process-based simulation model.	Landscape scale using a cellular automation approach. Pixel resolution: 1 km × 1 km.	Upland tundra, black spruce forest, white spruce forest, deciduous vegetation, and coastal forest/Cold regions of North America.	Inputs: Maps of climate, initial vegetation type, and topography. Ouptuts: Maps of vegetation dynamics, generation of growing season climate.	Frame-based spatially explicit model; use of remote sensing data.	Representation of spatial processes of disturbance propagation and seed dispersal; effect of moose browse pressure on the rate of succession.

(Continued)

TABLE 7.2 (*Continued*)

Main Characteristics of Forest Landscape Models (FLMs)

Model Name	References	Main Processes and Model Type	Type of Landscape Change	Forest Type(s)/Region(s) of the World	Main Drivers and Outputs	Spatial Scaling	Main Contributions
LANDSUM	Keane et al. (2002, 2006)	Simulation model, including the effects of disturbances (e.g., fire, insects and disease). Process-based simulation model.	Spatially explicit, vegetation dynamics; potential vegetation type (PVT), cover type, and structural stage; landscapes were defined by watershed boundaries.	Lodgepole pine and Douglas fir forests/ Northwestern United States.	Inputs: Data on vegetation and disturbance, management plan. Outputs: Vegetation and disturbance maps.	Square landscapes of 100,000 ha; derivation of potential vegetation type over landscapes.	Use of a stochastic approach to model disturbances; U.S. mapping development project based on the integration of remote sensing biophysical modelling and landscape simulation to produce maps of historical fire regimes.
LandClim	Schumacher et al. (2004, 2006)	Same as LANDIS, but the following model components were added: (1) succession submodel that models the effects of competition, climatic conditions and soil characteristics on the dynamics of tree populations and (2) disturbance submodel of forest fire dynamics.	Spatially explicit and stochastic.	Montane forests, subalpine forests/ United States.	Species' life history parameters (shade tolerance, seed dispersal, longevity); map layers of ecological land and soil types, and climate zone; fire parameters (e.g., ignition coefficient). Outputs: Maps based on landscape composition.	Same as LANDIS.	Improvement of the representation of fire dynamics, quantitative forest structures (tree cohorts) and ecological processes.

The scale of FLMs refers to the suitable spatiotemporal scale for the study area. It includes the spatial (i.e., spatial extent, grain size) and temporal scales, which are defined by the temporal resolution (i.e., length of a time step) and the duration of the simulation. Temporal resolution for the FLMs, which is not as obvious as spatial resolution, is usually specified as a model parameter. An FLM can have multiple spatial and temporal resolutions when multiple processes are considered. The spatiotemporal scale is an indicator of the degree of complexity of a model. “The challenge of FLMs is to find the equilibrium between resolution level, amount of details and practical considerations” (Mladenoff et al. 1996).

A key issue for the development and application of FLMs is choosing a suitable scale. Due to the complexity and variability of spatial extents, no individual model can ever predict all of the forest ecological information and attributes precisely. On the one hand, landscape ecologists may wish to understand fine-scale ecosystem processes; on the other hand, forest landowners and forest managers need to determine their management plans across broad scales. Forest landscape modelers need to consider both these factors and make compromises based on specific study areas, research interests, computer hardware, and software capabilities. How to define the “best” or the most reasonable scales for FLMs is an important and outstanding research question for theoretical and practical landscape ecologists (e.g., scaling and across-scale landscape modeling).

7.2.2.2 Development History

FLMs have a younger history than gap models. Major developments in FLMs took place in the late 1980s and coincided with the development of landscape ecology (Mladenoff 2004). The need was identified to address large-scale environmental concerns and land management issues, which were becoming more complex. The development of FLMs represents the advance and integration of the disciplines of forest ecology and landscape ecology.

Landscape ecologists, particularly those who work in North America, have made significant contributions to the advancement and evolution of FLMs. With the goal of finding “the best” policy for both forest management and ecological sustainability, North American forest ecologists and forest industry managers have a long history of developing forest models and applying them to important ecological problems. Early in this development, North American forest ecologist focused on forest management problems occurring within forest stands (i.e., forest areas with similar environmental conditions, tree species compositions, and disturbance history) or at the scale of small watersheds.

In the 1980s, driven by the wider use of satellite images (30 m resolution Landsat Thematic Mapper data) and GIS software, larger-scale spatial analysis became easier. Computational speed and storage capacity achieved significant breakthroughs. At the same time, various new programming language and software made model coding and data input and output more efficient. Those advances in computer science greatly improved the capabilities for developing multiscale simulation models. Forest ecologists then began to focus on increasingly important, large-scale landscape management issues, and the development of spatially explicit FLMs became a rapidly developing research area. These new spatially explicit models began to be used to simulate several decades or even hundreds of years of landscape change.

Since the late 1980s, more diverse spatial data are available to forest ecologists and managers. Besides the continuous use of stand-scale, *in situ* data, other data sources include land cover RS images, large-scale spatial database of soil types, vegetation plots (e.g., Forest Inventory and Analysis National Program), land use survey data, and historical landscape information.

In the 1990s, initial data collection, parameter design, and data validation techniques for FLMs were greatly improved. During this era, parameter design of FLMs mainly used two methods: the physical method and the empirical method. The physical method uses mathematical equations to link physical variables to the resulting phenomena deterministically, while the empirical method synthesizes the modeled processes using aggregated parameters generated from physical variables.

During the 1990s, many FLMs that can simulate many processes at multiple scales were developed rapidly, including LANDIS, LANDSIM, FORMOSAIC, and DELTA. He (2008) considers that FLMs developed during this period have similar characteristics to ecosystem process simulation models; not only they can track the spatial variation of individual trees, but they can also use integrated physical simulation methods to model key ecological processes, material cycles, and energy flow. FLMs of this period have adapted stochastic methods and can simulate the long-term effects of ecosystem processes, such as forest harvesting, wind, pests, and diseases. They were no longer limited to a single stand and can be used to represent larger areas including entire forests or ecosystems. Moreover, some smaller-scale FLMs became the integrated components for these large-scale models.

7.2.2.3 Methods

Early forest spatial dynamic models combined cellular automata methods with principles of forest dynamics. Cellular automata are grid-based, space-time discrete models. It is a classic method for the study of the complexity of a system and particularly well suited to simulate multiscale spatial and temporal dynamics. The cellular automata approach has become increasingly complex and has been widely used in ecological research. Cellular automata were also incorporated into certain rule-based methods for studying relationships between fire disturbance and forest changes.

The continuous development of forest succession theories and the knowledge on ecosystem disturbance and nonequilibrium hypothesis have established the foundation of ecological landscape models. Ecological theories have experienced a paradigm transition from the classic concepts of equilibrium, ecological succession, and climax community to dynamic structure representing nonequilibrium dynamics and the spatial heterogeneity of ecosystems. This transition of core ecological concept and theory is one of the fundamental motivations for the expansion of forest landscape modeling. The advance of FLMs in the past 2 or 3 decades can be viewed as an integrated and quantitative process linking knowledge of forest landscape succession, influencing factors and the nonequilibrium nature of ecosystems.

Hierarchy theory is a theory of the complexity of the system structure, function, and dynamics that forms the theoretical basis for building a coherent modeling approach across multiple-scale and complex systems. From a scaling perspective, hierarchy theory acts as a tool to partition complex systems in order to minimize model error. It can help ecologists to understand landscape patterns and scale-dependent properties of ecosystems and to simplify their complexity and analytical features. Hierarchy theory provides a theoretical basis for scaling and examining the cross-correlation between spatial and temporal scale functions. Together with other theories (including systems theory, information theory, modern philosophy and mathematics, and cross-scaling research), it provides a systematic and scientific foundation for FLMs.

The development of scaling methodologies allows multiscale more realistic modeling. Scaling refers to the translation of information between or across spatial and temporal scales or organizational levels, and two general scaling approaches can be

distinguished: similarity-based and dynamic model-based methods. In the context of scaling, landscape ecologists are able to seek the spatial process in the vertical integration of scales. For spatially explicit FLMs, the scaling process is also the key to integrating social and spatial data. For example, Geoghegan et al. (1998) suggested that spatial scaling is a useful tool for the integration of spatial data for the society using social data.

At the dawn of the 21st century, with advances in RS technology, landscape ecologists are able to quickly obtain time-series RS images. Also, RS imagery and other related GIS data can be directly used as the initial input data for FLMs, allowing pixel-based simulations for the entire target area. The emergence of supercomputers and the progress of computer graphics technology enhanced hardware capabilities to perform large-scale and more complicated imagery or quantitative analyses. Hence, more and more researchers around the world have begun using RS imagery and spatial analysis software to conduct landscape change modeling and prediction.

7.2.2.4 Classification

Unlike gap models and many ecological models, FLMs include a spatial dimension, that is, they can simultaneously examine the dynamics of landscape change and interactions in both time and space. Generally, FLMs can be divided into two categories: stochastic landscape models and process-based landscape models.

Stochastic models evolved from the Markov process theory and are based on the transition probability, which combines probability distribution and spatial information. This type of model has been widely used in studies of forest ecology and forest management planning. Process-based landscape models simulate spatiotemporal interactions through the establishment of more realistic computer models. Because this type of model focuses on the study of landscape composition and ecosystem spatial structure, it is also known as the true structural model. For example, Costanza and Voinov (2001) developed a spatial dynamic model for predicting the transitions of coastal landscapes through the use of integrated water cycle nutrient dynamics and the response of biological factors.

More recently, rule-based landscape models have been developed that have adopted artificial intelligence technology. Although these types of models are still in the developmental stage, the wide application of the artificial intelligence theory in other scientific fields suggests that they will soon become an effective tool to address regional resources, ecosystem management, and complex landscape questions.

Horn et al. (1989) classified ecological models that simulate landscape changes into two categories: analytical models and simulation models. Analytical models derive equations using mathematical analysis, analyze the mechanism of forest dynamics, and focus on long-term integrated ecosystem dynamics, which is also known as a strategic model or a generic model, and is usually used for long-term landscape planning. Simulation models are usually based around more intuitive ecological principles and nonlinear equations and often incorporate more details about the simulation system. Simulation models are often known as tactical models that can be used to develop specific and short-term management plans.

Perry and Enright (2006) classified simulation models into spatially explicit models and forest gap dynamic models based on whether or not a model simulates forest vegetation dynamics. Spatially explicit models are a tool for simulating and studying landscape dynamics mechanisms. They are also considered as “the essence of landscape ecological methods.” This type of model assumes that landscape spatial composition and structure change over time and these dynamic changes can be expressed by mathematical

relationships. Such models are generally applicable to larger spatial and temporal scale landscape questions. Among them, the LANDIS model is a successful example. Grid-based spatially explicit models can be used to simulate landscape-scale forest changes and natural (e.g., wildfires and hurricanes) and anthropogenic (e.g., logging) disturbance impacts. Compared with the earlier spatially explicit models, LANDIS is much closer to the basic principles of landscape processes.

Baker (1989) suggested that landscape models could be categorized as “whole,” “distributional,” or “spatial” landscape models based on the details emphasized by the model. Gardner et al. (1999) developed a FLM for simulating the landscape-scale patterns of fire effects. They also classified landscape models into six categories: theoretical, exploratory, spatially explicit, physical, probabilistic, shape and statistical models. Although they did not provide specific criteria for each subcategory of the classification, this classification scheme did offer a useful summary of the relationship between forest succession and fire disturbance and also provided a technical framework for further development of forest fire models. Perry and Millington (2008) divided FLMs into predictive and exploratory models based on the motivations for their development and their use. The first category (i.e., predictive models) includes empirical–statistical models, transition models, and forest gap models, which are mainly used to predict future changes in an ecosystem; the second category of models (i.e., exploratory models, also known as heuristic models) are mainly used to explore the relationship between spatial and temporal ecological process.

Scheller and Mladenoff (2005) classified FLMs into eight types from the perspective of ecological function. They mainly considered three ecological processes: reciprocal spatial interaction, tree species community dynamics, and ecosystem process. This classification emphasized the ecosystem process for the subset of FLMs. Based on Scheller and Mladenoff (2005) classification, He (2008) further developed quantitative criteria for FLM classification; he also applied similar criteria as those proposed by Scheller and Mladenoff (i.e., whether an FLM simulates a spatial process) to make the first distinction, and then used temporal resolution and the forest succession simulation method as secondary criteria to separate physical fire growth models (e.g., FARSITE) from the rest of FLMs. The criteria He (2008) used emphasize the choice of model resolution, the amount of spatial process, the methods of simulating forest succession in the model design, the modeling approaches, and the scope of model applications.

7.2.2.5 Applications

The application of FLMs refers not only to the synthesis of practical issues in forestry and ecology but also to the specific interpretation of model results, including refinement of the models and the exchange of knowledge with experts and practitioners in the field. Although FLMs are often viewed as a research tool, they do provide new ideas and an effective way to examine the relationship among environmental factors, forest landscape spatial distribution, and forest landscape response to climate change.

FLMs have been increasingly applied to study and solve practical management issues in forestry. He (2008) suggested that the application of FLMs generally falls into one of three categories: (1) spatiotemporal patterns of model outputs, (2) sensitivity of model outputs to input parameters, and (3) comparison of different simulation scenarios. Currently, FLMs are used in forestry management, watershed planning and management, postdamage forest landscape restoration, and forestland use development and planning. The application of these models to different forestry disciplines continues to expand ([Table 7.2](#)).

In North America, FLMs have most often been designed for forest landscape management and resource assessment. A typical example is the landscape model DISPATCH (Baker et al. 1991). The model uses GIS-based spatial data to simulate the environmental impacts of climate change on the landscape in the Minnesota Boundary Waters Canoe Area. The LANDMAN model represents another good example of a landscape management model. The model suggests that initial landscape structure and harvesting patterns are the major factors affecting the future landscape patterns and that forest managers need to develop planning strategies around the existing landscape structure and harvesting patterns. The LANDMAN model uses quantitative methods to measure spatial structure and includes logging disturbance patterns and a management efficiency evaluation index to develop optimal solutions for landscape management. The LANDFIRE project started in 2004. Between 2004 and 2009, the project developed over 1200 unique state and transition models to predict the pre-European settlement conditions for all of the major ecosystems of the United States and served as a solid foundation for model development efforts related to land management and planning (Kerns et al. 2012).

7.2.2.6 Interactions between Gap and Landscape Models

Forest resource monitoring and operational planning are other major fields for which FLMs have been developed and used. For example, LANDIS has been widely used for the simulation of broad-scale ($>10^5$ ha) landscape dynamics, including succession, disturbance, seed dispersal, forest management, carbon dynamics, and climate change effects. At the landscape scale, LANDIS uses age-defined cohorts to represent the age structure of tree species and a 10-year time step to determine changes in these age classes driven by key ecological processes such as establishment, competition, and dispersal. In addition, it allows the user to quantitatively define disturbances such as forest fires and wind damage. He et al. (1999) provided a method for linking the forest gap model LINKAGES with LANDIS to study species' responses to large spatial scale climate warming in northern Wisconsin, United States.

Xi et al. (2008) recently applied LANDIS and provided a more integrated and automatic methods for integrating LINKAGES with LANDIS. The LANDIS modeling environment has been used to examine forest landscape restoration strategies and forest management following southern pine beetle (*Dendroctonus frontalis*) outbreaks in the southern Appalachian Mountains of the United States, including pine-oak forest succession, the reciprocal interaction of forest landscape structure and southern pine beetle herbivory, the relationship between natural disturbances, such as wildfires and changes in forest composition and spatial patterns.

Other applications of FLMs include forest fire management and forestry practice policies. For example, LANDIS has been used to investigate the effects of climate change and forest fire dynamics on the California coastal shrub landscape in the United States. He et al. (2004) and Yang et al. (2007) used LANDIS to simulate the effects of different forest harvesting methods and fire disturbances caused by human activities on forest composition and productivity. Scheller et al. (2007) used LANDIS-II to simulate the effects of various disturbances, including forest fires, harvesting strategies, and wind damage on northern broad-leaved forests of the United States. They also investigated the effects of spatial relationships of disturbance and reintroduction of natural forest fire on long-term forest landscape changes under various climate change scenarios. LANDIS-II is a new generation of LANDIS and is distinguished by the inclusion of variable time steps for different ecological processes. The model builds upon and preserves the functionality of

previous LANDIS forest landscape simulation models. Recent LANDIS-II developments have expanded the cohort definition to include other relevant data, including above-ground biomass and density, and tree diameter data. These additions expand the range of ecosystem processes that can be represented in the model and provide additional quantitative output. FARSITE, a fire behavior and growth model, uses grid-cell input data but models the spread of fire using a vector format and has exogenous climate drivers that control fire spread. FARSITE incorporates existing models of surface fire, crown fire, point-source fire acceleration, spotting, and fuel moisture to provide a comprehensive fire prediction model. This is particularly useful to forest managers for exploring the connections between different fire behavior models, for revealing the implications of their assumptions to fire growth, and for identifying missing components among the various models. SAFE FORESTS has been used to simulate and analyze the effects of fire dynamics and timber harvesting in the forests of Sierra Nevada, California, and to support forest management decisions on wildfire and harvesting. LINKNZ, an extended version of the LINKAGES model, was used to simulate the effects of disturbance on forest succession in native evergreen New Zealand forests.

The application of existing models to investigate Chinese forest dynamics and management practices is underway. In the past few years especially, these applications have grown considerably. For example, Chinese ecologists have used LANDIS to examine forest succession and management in northeastern China. Hu et al. (2004) used LANDIS to assess the long-term forest landscape changes under various harvesting and logging scenarios in the Daxinganling region and also quantitatively evaluated the effects of harvesting on forest landscape changes. He et al. (2005) used LANDIS to simulate the long-term forest landscape dynamics in the Changbai Mountain National Nature Reserve. In general, current applications of FLMs in China are mainly limited to the northeastern region and the current focus of applied studies is to simulate forest succession, landscape-scale disturbance effects and mechanisms, and resource management strategies in various forest ecosystems of China.

7.2.2.7 *Advantages and Limitations of FLMs*

Currently, the increasing availability of FLMs provides forest ecologists and managers with opportunities to conduct spatial simulation research. However, all computer models have limitations. The customized, user-friendly interfaces still cannot overcome the inherent limitations in each model. Current FLMs mainly focus on the simulations of certain species or communities within a relatively small spatial area. Therefore, simulating overall species diversity on larger-scale landscapes may be more difficult. The development of landscape models requires certain trade-offs among landscape extent, data resolution, prediction accuracy, parameterization, and validation. Costanza and Maxwell (1994) indicate that the conflicts between model resolution and model predictability exist in spatially explicit landscape models. Although increasing resolution provides more descriptive information about the patterns in the data, it also increases the difficulty of accurately simulating those patterns. In addition, Wennergren et al. (1995) indicated that there is uncertainty in processing spatial data (e.g., the phenomenon of seed mortality during seedling dispersal). Hence, landscape spatial models are more appropriate to use as a management planning tool rather than as a tool to predict variations in species composition.

The existing limitations of FLMs are largely the result of the incomplete understanding of forest ecological processes and patterns. Simulating landscape dynamics is essential to understand not only evolution patterns and processes of landscapes from their current

status to the future but also the causes of landscape change. One of the key factors for the current limitation of the FLMs is the lack of understanding of landscape changes and development. While interest in the development of FLMs grows over time, these models are still difficult to apply on a greater range of time and space. Running these models requires a lot of parameter settings and advanced computing power. In addition, if current model users ignore inherent model limitations, the risk of model misuse increases.

The development of forest landscape modeling still faces critical issues in model result verifications. First, independent temporal or spatial series data, which may be necessary for model validation, are not always available. According to the conventional method, the results require specific time and spatial datasets to verify model prediction results. Normally, if the results confirm the effective phase, the following simulations will be considered valid. However, it is often impossible to perform overall time series verification on the FLMs using traditional methods; doing so would make the FLM no longer significant. Each landscape is unique in nature and cannot be replicated. In fact, the data used to conduct validation exercises are often difficult to obtain or cannot be easily collected. Second, when the effects of biological or nonbiological factors on model simulations are discussed, these factors are actually included in the model parameters and have already been expected to show in simulation results.

Inadequate postsimulation data analysis techniques may also limit the capability of FLMs. In order to effectively analyze complex spatial patterns, the postsimulation analysis tool, data management methods, output visualization technique, and model validation still need to be further improved. LANDISVIEW partly contributed to solving this problem (Birt et al. 2009).

FLMs have become a useful and, to some extent, indispensable tool in modern forest ecosystem studies and ecological forest management. Improving the design and performance of the models has become the focus of forest landscape ecologists in this research field. FLMs can simulate landscape processes and patterns in time and space. The models are able to store information on past and existing vegetation and on the status of disturbance and management, and, more importantly, they can also be used to predict changing trends and contribute to a more effective study of forest responses to various disturbances and forest landscape management. Because landscape models can simulate the complicated process of spatial patterns and reflect the spatial and temporal characteristics of information, FLMs will be further developed and have good prospects for use in both theoretical and practical application research. In the coming decades, ecologists and foresters will have a better understanding of forest landscape patterns and processes. The technologies and methods used for the development of FLMs will become more comprehensive, and the types of FLMs will be more diversified in accordance with different research questions.

7.3 Application of Forest Succession Models and Linkages with Ecological Indicators

7.3.1 Introduction to Ecological Indicators and Definitions

Ecological indicators, defined here as an index of measures that characterizes an ecosystem or one of its critical components, are typically used to assess the state of a specific environment and to evaluate the trajectory of that system under current and future conditions.

The future trajectories of an ecosystem are contingent on its ecological memory (Padisák 1992; Sun et al. 2013), that is, the state of the environment, which has been influenced by historical events. Ecological memory is fundamental in influencing future ecosystem response, spatial resilience, and the direction of ecosystem change. Ecological indicators should represent key information about the composition, structure, function, and vigor of an ecosystem. Ideally, there should be a wide range of indicators that represent a suite of ecosystem processes and that can be measured repeatedly. Examples of critical ecological indicators are species composition or diversity (i.e., “composition”), vegetation structure, related light environments and spatial heterogeneity (i.e., “structure”), and ecosystem productivity, nutrient cycling, and life history strategies (i.e., “function”) (Noss 1990; Dale and Beyeler 2001). Within these three main categories are many processes that occur at different scales, such as (but not limited to) species distribution, abundance and richness, soil conditions, canopy openness, fragmentation, growth rates, phenology, regeneration metrics, response to abiotic stress, resilience, and resistance (Table 7.3). While conducting this review of forest succession models and linkages with ecological indicators, we found that the definition of ecological indicators may vary between studies or that an indicator might fall into one or several of the broad categories used here (i.e., composition, structure, function). Therefore, we are keeping each author’s definition and rationale for categorizing an indicator. Ecological indicators are explained in more details in Chapters 11 through 17.

TABLE 7.3
Examples of Ecological Indicators Separated into Three Main Indicator Categories (i.e., Composition, Structure, and Function) and Repeated into Two Ecosystem Scales (i.e., Community and Landscape)

Ecosystem Hierarchy	Indicator Category	Indicator Example	Examples of Gap Models and FLMs (Not Exhaustive)
Community	Composition ^a	Abundance, distribution, diversity	FORCLIM (Bugmann 1996), FORMIX3 (Huth and Ditzer 2001), PICUS (Lexer et al. 2002), FAREAST (Shuman et al. 2011, Lutz et al. 2013)
	Structure	Age, size, canopy structure, canopy openness, light conditions, spatially explicit	SORTIE (Pacala et al. 1993, 1996), ZELIG (Urban 1990), FORSKA (Linder et al. 1996, 1997), Mountain (Cordonnier et al. 2008), ZELIG-CTF (Larocque et al. 2011)
	Function	Productivity, growth and mortality rates, phenology, regeneration metrics, nutrient cycling, and nutrient limitations	LINKAGES (Pastor and Post 1985), PICUS (Lexer and Hönninger 1998), ZELIG-TROP (Holm et al. 2012, 2014), ForestMAS (Kolmanič et al. 2014)
Landscape	Composition	Richness, diversity	LANDSUM (Keane et al. 2008), 4C (Kint et al. 2009), SELES (Hope et al. 2006)
	Structure	Spatial heterogeneity, soil conditions, fragmentation	LandClim (Schumacher et al. (2004, 2006), LANDSUM (Keane et al. 2006)
	Function	Response to abiotic stress, nutrient cycling resilience, resistance, disturbance	FIRESCAPE (Cary and Banks 1999), TreeMIG (Lischke et al. 2006), FireBGCv2 (Keane et al. 2011), LANDIS-II (Kretchun et al. 2014, Loudermilk et al. 2013)

Source: Derived from Dale, V.H. and Beyeler, S.C., *Ecol. Indic.* 1, 3, 2001.
^a By default, all species-specific gap models simulate community composition behavior. A limited list of gap models that focus mainly on community distribution, diversity, or compositional changes is listed here.

Forest gap and landscape models can simulate the state and trajectory of many of the ecological indicators mentioned earlier and in Table 7.3, thus allowing managers and scientists to alleviate some of the challenges pertaining to on-the-ground diagnosis and indicators monitoring programs. Ecological systems are complex and measuring only a few indicators can fail to capture this complexity. Long-term monitoring programs are costly, and they usually do not cover a large spatial extent. However, they are needed to evaluate sensitivity to stress and climate change. Gap and landscape models are able to overcome many of these barriers. Gap models take into account environmental constraints and, as a result, predict resource competition among trees (Shugart and West 1980), thus achieving the capability to quantify many key ecological indicators over time. For example, a timber harvest forest simulator was able to link ecosystem indicators at the landscape scale to measure forest sustainability and evaluate the impacts of multiple forest management strategies (Gustafson et al. 2007). It has also been demonstrated that multiple indicators, for example, structural complexity and indicators of stand- and landscape-level heterogeneity, are more successful at assessing biodiversity and sustainable forest management (Lindenmayer et al. 2000). Fortunately, these ecosystem characteristics can be described in forest succession models, and it can be done at fine resolutions when using gap models. While these results help to evaluate the cumulative effects of management and landowner decision making, models need to be improved to be able to predict a wider range of indicators, and more modeling efforts are needed (Mäkelä et al. 2012).

7.3.2 Review of Forest Succession Models Linked to Ecological Indicators

7.3.2.1 Composition: Biodiversity and Species Composition

Biodiversity can be an important ecosystem service (Mace et al. 2012) and an indicator of forest health. For example, increased diversity in species composition leads to increased genetic diversity and resistance to disease, invading species, and to the ecological impacts of climate change (Duffy 2009; Thompson et al. 2009), and thus to potentially more stable ecosystems. However, it might have limited validity in increasing forest function (Nadrowski et al. 2010; Grossiord et al. 2014). The relationship between species diversity and ecosystem functioning is more complex and at times could be uncorrelated. For example, functional diversity may play a stronger role than species diversity in ecosystem functioning (Naeem et al. 2000). However, species composition does play a major role as an indicator of forest health and resistance to disturbances (Montréal Process Working Group 2009; Thompson et al. 2009). Representing species diversity in models can be a challenge. However, forest succession models, in particular gap models, have the capability of predicting change in species composition over time and simulating the trajectories of species as influenced by site conditions, seasonal shifts, disturbances, or meteorological changes.

While the majority of individual-based, forest gap models represent separate species and their attributes, the following models are useful for investigating ecological indicator species composition. FORCLIM (Bugmann 1996) is a simplified forest gap model that uses a minimum number of ecological assumptions in order to assess the effect of climate on plant population dynamics. The model is robust when it comes to matching tree species composition to empirical records, as well as aboveground biomass patterns and dominating tree species niches across climate gradients. The FORMIX family of models (Bossel and Krieger 1994), specifically FORMIX3 (Huth and Ditzer 2001), investigates the change in four variables: total yield, yield per cut, species composition, and canopy opening as indicators of long-term impacts caused by logging in rain forests. They found that longer

logging cycles using low impact methods were needed to conserve species composition and minimize the erosion risk. The shorter logging cycles (<40 years) resulted in low yields and highly disturbed species composition. Shuman et al. (2011) utilized the gap model FAREAST to evaluate species composition shifts in response to a changing climate (i.e., shifts in temperature and precipitation) in boreal forests and found that low diversity sites exhibited an abrupt vegetation shift from deciduous larch forest to evergreen conifer forest in response to increased temperatures. Due to albedo changes, the shift in species composition enhanced the climate–vegetation feedback process and created a positive radiative forcing effect. Using the same model, Lutz et al. (2013) looked further into interactions and feedback between species composition shifts, vegetation cover changes, and a changing climate.

FLMs have also been successful tools for predicting changes in species composition, which is an indicator of diversity. Using the landscape fire succession model LANDSUM, Keane et al. (2008) assessed landscape composition over time in response to different scenarios of climate and fire regimes. Keane et al. (2008) used the area occupied by the dominant vegetation class and the Sorenson index for measuring similarity as indicators of change in landscape composition. The landscape model 4C has been used as a tool to describe forest biodiversity after a dozen forest conversion regimes (Kint et al. 2009), a useful practical application. The goal of conversion management was to convert Scots pine stands into a mixed oak-birch stand, promoting biodiversity and stand productivity. As another example, the FLM SELES evaluated forest–woodland recovery and woodland expansion in Scotland as a means to offset habitat loss and fragmentation and promote biodiversity conservation (Hope et al. 2006).

7.3.2.2 *Structure: Vegetation and Canopy Structure*

Canopy and stand structure parameters, such as canopy coverage, range in age of canopy trees, and canopy stratification, can be used as ecological indicators of forest vitality and tools for forest management (Gao et al. 2014). For examples of vegetation structure used as a modeling tool, we first look at the FORSKA-based family of models (Leemans and Prentice 1989; Desanker 1996; Lindner et al. 1996, 1997), which have adopted a cylindrical crown model as opposed to the original disk crown geometry to represent more realistic vertical canopy structures. FORSKA-based models take into account the length of the crown and the amount of leaf area determined from the pipe model theory (Shinozaki et al. 1964). Lindner et al. (1997) improved the capabilities to model stand structure by improving the height growth functions, which included accounting for indicators such as the competition status and shade tolerance of the tree. They argued that the updated height growth function was flexible, simple, and could be applied to forest management simulations. Improvements to vertical canopy structure can increase the accuracy of light competition estimates, thereby influencing growth and survival. The SORTIE model (Pacala et al. 1993, 1996) then added width of tree crowns to canopy depth and varying crown transmissivity, dropping the horizontal homogeneity assumption. Urban (1990) developed a spatially explicit model (i.e., ZELIG) that computes 3D canopy interactions among trees, which was then further developed into later versions by Weishampel and Urban (1996) and Larocque et al. (2011). ZELIG-CFS (Larocque et al. 2011) updated the application of the ZELIG family of gap models by developing algorithms to improve the realism of the representation of crown interactive effects between relative light availability, crown recession rate, foliage distribution, and shade tolerance, and thus predicted crown structure characteristics that were consistent with species' life history. Cordonnier et al. (2008) used the individually

based, spatially explicit model called “Mountain” as a management tool and modeled structural indicators (i.e., diversity of diameter distribution, sapling cover, and basal area) to evaluate stand resilience and forest stability.

7.3.2.3 Functions: Competition, Forest Resistance, and Resilience

Competition can influence the composition, structure, and function of all forest types around the globe. In gap models, competition is modeled as the performance of trees under varying environmental conditions (Shugart 1998). Individual trees can influence environmental conditions (e.g., by modifying light conditions and soil characteristics), which can influence each tree (e.g., temperature, disturbance). Accounting for resource competition among species and for the related forest resilience and resistance within gap models and FLMs makes it possible to track different aspects of forest function, which is a critical ecological indicator.

For example, further modifications to ZELIG (i.e., ZELIG-TROP, Holm et al. 2012) led to successful simulations of tropical forest dynamics and evaluated the response of tropical forests to disturbance. ZELIG-TROP was applied to look at the resilience of secondary forest succession and found that forest recovery on abandoned agricultural farmland with degraded soils had a delayed response prior to full recovery. Ecological indicators related to early resource acquisition, such as canopy height, canopy coverage, and high stem density, were the fastest to recover, but structural indicators, such as biomass acquisition and basal area, took longer to recover and were less resilient. Holm et al. (2014) used ZELIG-TROP to investigate the impacts of increased natural disturbance in the Central Amazon and evaluated the extent to which variations in disturbance regimes in the Amazon contributed to existing forest gradients across the Amazon Basin. Application of the gap model found that aboveground biomass stocks in the Central Amazon forest significantly decreased but were otherwise resistant to continual, elevated disturbance. Additionally, after controlling for disturbance effects, the forest structure and functional variability across the Amazon Basin was not entirely explained by the variability in disturbance regimes, suggesting that forests have the capacity to adapt to varying degrees of disturbance or other intrinsic environmental factors that contribute to the regional gradients.

The “mountain” model (Cordonnier et al. 2008) was used as a management tool in Norway spruce stands using structural indicators to evaluate stand resilience. This study determined that forest resilience decreased with thinning intensity and that applying different management scenarios led to the best protection against different natural disturbance events, suggesting that a compromise strategy was found to achieve the best results for all natural disturbance events. The succession gap model ForestMAS (Kolmanič et al. 2014) utilizes Ellenberg indicator values (also used in ForClim) to look at secondary forest succession on abandoned cropland in Slovenia and to forecast regeneration processes after clearcutting or natural disasters. The spatially explicit FLM TreeMig, which is based on a forest gap model (Lischke et al. 1998), incorporates spatial interactions and competition to address tree migration from the stand to the continental scale (Lischke et al. 2006).

As stated in the Montréal Process: Criteria and Indicators (The Montréal Process Working Group 2009), two of the indicators used to quantify “maintenance of ecosystem health and vitality” are (1) the area and percentage of forest affected by disturbance, processes, or agents beyond the range of historic variations and (2) the area and percentage of forestland with diminished biological components. Multiple FLMs have evaluated the effect on forest functioning resulting from multiple disturbances, with a strong emphasis on modeling fires (Baker 1995 using DISPATCH; Cary and Banks 1999 using FIRESCAPE;

Keane et al. 2011 using Fire-BGCv2), but also a changing climate (Loudermilk et al. 2013 using LANDIS-II), or land use change (Voinov et al. 1999 using PLM), as well as biotic processes and agents such as insects (Kretchun et al. 2014 using LANDIS-II), and exotic species invasions (Waldron et al. 2010 using LANDIS). Up to 44 landscape-fire succession models have been listed and classified based on the approach of modeling fire-vegetation interactions (Keane et al. 2004).

7.3.2.4 Global Geographic Coverage of Forest Succession Models

The application of gap and landscape models to address ecological indicators has covered a wide range of ecosystem types and many regions of the world (Tables 7.1 and 7.2). However, there are still some ecosystems that are lacking representation. For instance, the evaluation of compositional, structural, and functional changes in all tropical regions could benefit from future model development. Current gap models that simulate tropical forest dynamics are KIAMBRAM (Shugart et al. 1980), FORICO (Doyle 1981), OUTENQUA (Van Daalen and Shugart 1989), FORMOSAIC (Liu and Ashton 1998), FORMIND (Köhler and Huth 1998), FORMIX3 (Huth and Ditzer 2001), SORTIE (Uriarte et al. 2009), and ZELIG-TROP (Holm et al. 2012, 2014). Tropical forests cycle more water and carbon than any other biome on the planet and are high priority ecosystems for predictive modeling. The overwhelming majority of successional models have been developed for temperate deciduous and mixedwood forests of North America and Europe (Shugart and Smith 1996). A growing group of gap models and FLMS have been developed for boreal forests. In addition to tropical forests, boreal forests exhibit strong feedback in response to climatic change and are critical regions to study. These models include BOFORS (Shugart et al. 1992), EXE (Martin 1992), ALFRESCO (Rupp et al. 2000), SORTIE-ND (Coates et al. 2009), FAREAST (Zhao et al. 2009), ZELIG-CFS (Larocque et al. 2011), LANDIS and LANDIS II (Scheller et al. 2007), and UVAFME (Shuman et al. 2014). While some successional models only cover a specific geographical location and ecosystem type, these models have a strong potential to be adapted and transferred to other regions. For example, models such as SORTIE, ZELIG, and LANDIS have been used in multiple ecosystems.

7.4 Dynamics of Regeneration and Succession Models

Regeneration dynamics is a very complex process that remains poorly understood. For most species, many regeneration surveys have been conducted at least in European and North American forests. However, regeneration surveys consist merely in estimating the number and distribution of seedlings or saplings. Even though regeneration surveys provide basic information that can be used in the decision-making process in forest management, they have limited usefulness for the study of forest succession since they only consist of a picture at one point in time. Regeneration dynamics includes several processes, including seed production, dispersal and germination, and seedling survival and development (Price et al. 2001). When established, the survival and growth of seedlings can be affected by competition from neighboring species or other random factors such as wildlife browsing. All these processes vary considerably among species and from years to years and they all have an impact on the long-term development of forest ecosystems (Bugman 2001; Price et al. 2001). Several studies have been conducted to better understand

regeneration dynamics, including the growth response of different species to the availability of light and soil resources (e.g., Dai 1996; Finzi and Canham 2000; Kincaid 2012; Salazar et al. 2012; Major et al. 2013). However, most of them took place within short periods of time. They provide rich information on the relationships between site factors and seedling growth, but the duration of these experiments was too short to answer questions on long-term dynamics to better understand interactions between changes in site conditions, seedling development and survival over time. Being able to answer these questions would be important to improve the modeling of regeneration dynamics in succession models (Larocque et al. 2006; Pabst et al. 2008).

Despite the lack of empirical information, regeneration dynamics in most succession models has been modeled using biologically consistent algorithms based on species-specific seedling ecological characteristics, including shade, water, and nutrient tolerance factors. For instance, JABOWA, FORET, and ZELIG account for the effect of understory light conditions, degree-days, water availability, and fertility level. For model initialization, users provide species-specific potential seedling numbers that may appear during each year of the simulation. Then, this potential number is modified by understory light conditions, water, and nutrient factors and a random number to account for annual variability. As a consequence, when there are gaps in forest ecosystems due to tree mortality, gap models are sensitive enough to model the change in regeneration dynamics.

Most of the studies on the simulation of regeneration dynamics with succession models were conducted using gap models. There are studies that focused on the simulation of the impacts of different regeneration scenarios or disturbances on potential successional pathways. Using the model ZELIG, Pabst et al. (2008) modified the regeneration probabilities for different ecoregions and forest types. Historical datasets were used to compare predictions and observations. Kolmanič et al. (2014) used the single-tree succession model ForestMAS to predict regeneration dynamics over landscapes of farmland regions abandoned in the 1940s in Slovenia. In other studies, the prediction of regeneration dynamics between models was compared. Garman (2004) compared the predictions of regeneration dynamics between the landscape model LandMod and the gap model PNWGap in three forest types of western Oregon Cascades, United States. Papaik et al. (2010) performed a similar exercise with the landscape model LANDIS and the gap model SORTIE-ND in an eastern boreal mixedwood forest type in north-western Québec, Canada. Simulations of the modifications of site factors were also performed. Beaudet et al. (2011) compared predicted and observed light levels using the SORTIE-ND gap model in boreal mixedwood forests and discussed the effects on regeneration dynamics. Working with the original version of ZELIG, Larocque et al. (2006) simulated the effect of the variation in “plot size,” which represents the zone within which trees use site resources, on regeneration dynamics in two southeastern Canadian mixedwood forest types.

These studies contributed to evaluating the performance of gap models on regeneration dynamics, since they provided biologically consistent results. In a way, these efforts may be considered as a form of model validation (see Rykiel 1996). However, there is still a need to determine how well existing regeneration model components in succession models represent reality with a reasonable level of accuracy or realism. There are some studies that compared simulated results with long-term historical observations (e.g., Larocque et al. 2006, 2011; Pabst et al. 2008), but they were limited to mature trees. The comparison of simulated regeneration dynamics with observations still remains to be performed. One study that would come close to this type of comparison was conducted by Chen and Twilley (1998). They simulated the dynamics of mangrove forests along gradients

of soil salinity and nutrient availability using the model FORMAN. The number of saplings added in each year of a simulation is a function of available light below the canopy, random effect, and effect of flooding and seed consumption. Their equation was based on Botkin (1993). Using different sapling recruitment scenarios, they compared the predicted patterns of mangrove development with observations made 34 years after a hurricane. This exercise allowed them to estimate initial values of sapling density in their model that would match the observed mangrove pattern 34 years after the hurricane. This procedure is an indirect way to compare predictions and observations, because the adjustment of initial sapling density to approximate observations made 34 years later does not guarantee that the new initial values were even close to reality. In addition to these issues, additional research in the modeling of regeneration dynamics is needed to improve the capacity of succession models to predict how forests may respond to climate change (Price et al. 2001).

7.5 Application of Remote Sensing

The use of RS technology with succession models is relatively new. It can be used to obtain information at the individual-tree or landscape levels to initialize or validate models. Using remotely sensed aerial images or digitized aerial photographs at high spatial resolution, it is possible to depict the crowns of individual trees and identify species using semiautomated recognition software (Gougeon et al. 1998; Gougeon 2010). It is even possible to obtain estimates of stand height (Mora et al. 2013). There are not many study cases on the use of this methodology jointly with succession models, particularly gap models. However, this method has a lot of potential for the use of gap models at the landscape level. The delineation of individual-tree crowns over large areas offers the potential to provide individual-tree information in the input file of a gap model to run simulations at the landscape level. Thus, it is possible to run simulations at the single-tree level over a landscape.

However, for large-scale models, including landscape or global vegetation models, it is generally difficult to initialize or validate these models. Large-scale datasets are rarely available. Zhao et al. (2009) mentioned that the examination of land cover change over large areas is difficult to estimate using conventional forest inventory and, thus, RS facilities are very useful. RS also facilitates data integration with ecological models (Xu and Chen 2013). For Song and Woodcock (2002) and Song et al. (2002, 2007), RS is the only realistic way to examine succession over large areas in an efficient manner. Their project consisted in linking the GORT canopy reflectance model with ZELIG, and they acknowledged the necessity for further developments.

However, relatively few studies on linkages between RS and ecological models have been conducted. Among good examples, there is the study by Wallentin et al. (2008), which included RS analysis based on aerial photos and LiDAR data. Photos were good enough to recognize individual trees. Their individual-tree model is based on the prediction of seedling germination, tree height growth, and mortality. Zhao et al. (2009) combined the use of RS data with the gap model FAREAST to model spatial variation and uncertainties of East Siberian boreal forest biomass change over time. RS was also used in conjunction with simple models. Both Chuang et al. (2011) and Petit et al. (2001) use Markov chains to simulate succession in forests using data from SPOT images.

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