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Review of forest landscape models: Types, methods, development and applications

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ABSTRACT

Forest landscape models simulate forest change through time using spatially referenced data across a broad spatial scale (i.e. landscape scale) generally larger than a single forest stand. Spatial interactions between forest stands are a key component of such models. These models can incorporate other spatio-temporal processes such as 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). The models are increasingly used as tools for studying forest management, ecological assessment, restoration planning, and climate change. In this paper, we define forest landscape models and discuss development, components, and types of the models. We also review commonly used methods and approaches of modeling forest landscapes, their application, and their strengths and weaknesses. New developments in computer sciences, geographic information systems (GIS), remote sensing technologies, decision-support systems, and geo-spatial statistics have provided opportunities for developing a new generation of forest landscape models that are increasingly valuable for ecological research, restoration planning and resource management.

1. Introduction

Landscape modeling, which has developed over approximately the past 30 years, is a useful approach for exploring landscape dynamics and spatial patterns. Landscape modeling is not only important for quantitative studies in landscape ecology, but is also a principal research topic at the forefront of modern ecology [2,23,37,56,84,106]. Landscape modeling, which integrates the fields of landscape ecology, quantitative ecology, computer simulation and geographic information systems (GIS) technology, is essential for long-term research in macroecology, such as studying the equilibrium between landscape-scale biodiversity and human activities under global climate change [17,37,38,77,85,88,91].

Forest landscape models are an important component of landscape modeling. These models are founded on concepts and theories of ecological succession, disturbance, ecological equilibrium and non-equilibrium. They also incorporate forest landscape changes, biological characteristics of tree species within forest ecosystems, competition process among species, and synergistic effects with environmental disturbances. Forest landscape models can quantitatively describe the spatial distributions of trees, illustrate the relationship between dynamic variations of tree species composition and forest communities as well as other influences. Forest landscape models have been broadly applied in various fields, including forest sciences, ecology, resource management and wildlife habitat evaluation [20,22,26,28–30,46,51,60,70].

In this article, we review the history, recent developments, and main types of forest landscape models, as well as their applications in forest ecology research and forest management. We also compare the characteristics and applicability of different forest landscape models. Based on our recent forest landscape modeling work, we provide key research questions and future perspectives, to help the development of this field and promote the effective application of such models.

2. Concepts of forest landscape models

It is essential to understand the concept and scope of forest landscape models before presenting our own review. According to the literature, there are diverse definitions of forest landscape models. For example, Mladenoff and Baker [57] define forest landscape models as computer models which simulate the change in forest landscapes across broad spatio-temporal scales. Scheller and Mladenoff [79] broadly define forest landscape simulation models as computer programs or software packages for projecting landscape change over time.

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He [41] provides both general and specific definitions and key terminologies commonly used in classifying forest landscape models. Forest landscape models can be used to predict the variations of spatial characteristics (i.e. distribution, shape, abundance) for simulated objects. More specifically, a forest landscape model is one that simulates spatiotemporal characteristics of at least one recurrent spatial process in a spatially interactive manner. According to the definitions above, He indicates that a forest landscape model under this specific definition should have the following characteristics: (1) it is a simulation model, (2) it is able to run the simulations of spatial processes repeatedly, and (3) it operates at a large spatial and temporal extent that is adequate to simulate the spatial process [41].

We consider that forest landscape models are computing models which simulate and predict the spatio-temporal 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 and nitrogen cycles, 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 forest landscape model usually has following characteristics: (1) projection of landscape-level spatio-temporal changes, (2) the simulation of spatial interactive processes, and (3) the prediction of long-term interactions among multiple factors. Forest landscape models 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 [67]. Forest landscape models provide a solution to overcome these issues. Hence, forest landscape models can be useful tools to assist long-term forest landscape planning and decision-making of resources management [20,46,51,68,100,109].

3. Scale

Scale, a key concept in landscape ecology, is also important for forest landscape modeling theory and applications. The object that is simulated using forest landscape models is the forest landscape. In general, the temporal scale of forest landscape simulations ranges from decades to hundreds of years approximately (i.e. $\sim$50–500 years), while the spatial scale (e.g. spatial extent) is generally about 100–10,000 km^2.

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. physic-chemical reactions of the wildfire) or long-term succession process (e.g. soil development, organism decomposition, nutrient loss or tree species competition) [57,68]. 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 computing power and interpretation of 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 [93].

The scale of forest landscape models refers to the suitable spatio-temporal scale for the study area. It includes the spatial scales (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 forest landscape models, which is not as obvious as spatial resolution, usually is specified as a model parameter. A forest landscape model can have multiple spatial and temporal resolutions when multiple processes are considered. The spatio-temporal scale is an indicator of the degree of complexity of a model [17,18].

A key issue for the development and application of forest landscape models is choosing a suitable scale [109]. Due to the complexity and variability of spatial extents, no individual model can ever predict all of the forest ecological information and attributes precisely [19]. 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 [55,57,71]. 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 reasonable scales for forest landscape models is an important and outstanding research question for theoretical and practical landscape ecologists (e.g. scaling and across-scale landscape modeling) [57,93].

4. Development of forest landscape models

The development of forest landscape models represents the advance and integration of the disciplines of forest ecology and landscape ecology [57,68]. Forest landscape models descend from ecological concepts developed over approximately the past 30 years [57]. Such models are driven by fundamental concepts such as ecological succession, disturbance, ecological equilibrium and non-equilibrium, and may be centered around populations, communities and/or landscapes. Within the past three decades, such models have flourished thanks to advances in computation and simulation speed and the low costs of spatial data [56]. At the same time, more and more forest landscape models have been developed to support the increasingly important processes of forest planning, management and decision-making.

Landscape ecologists, particularly those who work in North America, have made significant contributions to the advance and evolution of forest landscape models. 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 the forest models and applying them to important ecological problems [57]. Early in their development, North American forest ecology focused on the forest management problems occurring within the forest stands (i.e. forest areas with similar environmental conditions, tree species compositions and disturbance history) or at the scale of small watersheds [7].

During the 1970s, several approaches were developed to apply non-spatial succession concepts to predictive models; mainly Markov chain models and vital-attribute models. Markov models are a mathematical approach utilizing a matrix of empirical transition probabilities to predict future tree-species replacement and composition over time [57]. In the 1970s, forest gap models based on individual tree growth and forest growth and yield models were also developed. For example, Botkin et al. [7] developed an early forest gap model called JABOWA. Gap models simulate the survival, growth and mortality of all individual trees at forest gap scale (ca. 1000 m^2) non-spatially [57,68]. Shugart [87] developed the FORET model based on the JABOWA model. These two forest gap models established the fundamentals for the development of later gap models. Another notable pioneering gap model was LINKAGES [69]. These models provide a vital contribution to understanding the stand-level dynamics of forest ecosystems [87,95]. However, due to the computational limitations, they are difficult to scale up to the landscape scale and are usually applied to assess the forest changes within stands [57,68].

In the 1980s, driven by the wider use of satellite images (30-m resolution Landsat Thematic Mapper [TM] data) and GIS software, larger-scale spatial analysis became easier [22,60]. Computing speed and storage capacity achieved significant breakthroughs. At the same time, various new programming languages and software made model coding, data input and output more efficient. Those advances in Computer Science have greatly improved the capabilities for developing multi-scale simulation models. Forest ecologists then began to focus on increasingly important, large-scale landscape management issues, and spatially explicit forest landscape models development 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 1980s, more diverse spatial data were available to forest ecologists and managers. Besides the continuous use of the stand-scale *in situ* data, other data sources include land cover remote sensing images [33,98], large-scale spatial database of soil types, vegetation plots (e.g. Forest Inventory and Analysis National Program), land-use survey data as well as historical landscape information.

In the 1990s, initial data collecting, parameter design, and data validation techniques for forest landscape models were greatly improved. During this era, parameter design of forest landscape models mainly used two methods: the physical method and empirical method. The physical method uses mathematical equations to link the physical variables to the resulting phenomena deterministically, while the empirical method synthesizes the modeled processes using aggregated parameters generated from physical variables [41].

During the 1990s many forest landscape models that can simulate multi-scale, multi-process developed rapidly, including LANDIS [39,82,83], LANDSIM [57], FORMOSAIC [53] and DELTA [57]. He [41] considered that forest landscape models during this period have characteristics of ecosystem process simulating models; they can not only track the spatial variation of individual trees, but they can also use integrated physical simulation methods to model the key ecological processes, material cycles, and energy flow. The forest landscape models 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. These models 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 forest landscape models become the integrated components for these large-scale models [94].

Now in the dawn of the 21st Century, with advances in Remote Sensing (RS) technology, landscape ecologists are able to quickly obtain time-series remote sensing images. Also, remote sensing imagery and other related GIS data can be directly used as the initial input data for forest landscape model, allowing pixel-based simulations for the entire target area. The emergence of super-computing machines and the progress of computer graphics technology enhanced the hardware capabilities to perform large-scale and more complicated imagery or quantitative analyses. Hence, more and more researchers around the world have begun the use of remote sensing imagery and spatial analysis software to conduct landscape change modeling and prediction.

5. Types of forest landscape models

Unlike many ecological models, forest landscape models include a spatial dimension, that is, they can simultaneously examine the dynamics of landscape change and interactions in both time and space. Generally, forest landscape models can be divided into two categories: stochastic landscape models and process-based landscape models. Stochastic models evolved from Markov process theory and are based on the transition probability which combines probability distribution and spatial information. This type of model currently has been widely used in studies of forest ecology and forest management planning.

Process-based landscape models simulate spatio-temporal 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 [17] developed a spatial dynamic model for predicting the transitions of coastal landscapes through the use of integrated water cycle nutrients 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 development 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 and Shugart [42] classified ecological models which simulate landscape changes into two categories: analytical models and simulation models. Analytical models derive equations of mathematical analysis, analyze the mechanism of forest dynamics, and focus on long-term integrated ecosystem dynamics [67], which is also known as the strategic model or a generic model [6], and is usually used for long-term landscape planning [77]. Simulation models are usually based around more intuitive ecological principles and non-linear equations, and often incorporate more of details about the simulation system [42]. Simulation models are often known as tactical models that can be used to develop specific and short term management plans [77].

Perry and Enright [67] classified simulation models into spatial explicit models and forest gap dynamic models based on whether 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" [2]. This type of model assumes that the landscape spatial composition and structure changes 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, LANDIS model is a successful example [38,56,57]. Grid-based spatially explicit models can be used to simulate landscape-scale forest changes and natural (e.g. wildfires and hurricanes) and anthropogenic disturbance (e.g. logging) impacts. Compared with the earlier spatially explicit models, LANDIS is much closer to the basic principles of landscape processes.

Forest gap models, which are mainly based on individual tree growth, can assess the changes of forests within a small patch of forest (i.e. a forest gap, ca. 1000 m^2 in size) [106,107]. At present, forest gap models have been widely used in both ecological and forestry applications to study the impacts of natural disturbances on forest structure and composition [50,55]. More recent developments in forest gap models (such as SORTIE) allow the simulation of spatial processes (e.g. seed dispersal, tree regeneration) through spatial scaling [9,61]. Latter versions of the early forest gap models, such as LINKAGES v2.2 and ZELIG [55,81], still generate wide interest among foresters, population biologists, modelers, and ecosystem ecologists.

Baker [2] suggested that landscape models can be categorized as 'whole landscape models', 'distributional landscape models', and 'spatial landscape models', based on the details emphasized by the model. Gardner et al. [122] developed a forest landscape model for simulating landscape-scale patterns of fire effects; at the same time, they classified landscape models into six categories: theoretical models, exploratory models, spatially explicit models, physical models, probabilistic models, shape models, and statistical models. Although they did not provide specific criteria for each sub-category of the classification, this classification scheme did offer a useful summary of the relationship between forest succession and fire disturbance, hence also provided a technical framework for further development of forest fire models [41,57].

Perry and Millington [68] divided forest landscape models into predictive models and exploratory models based on the motivations for their development and use of the models. 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 (i.e. exploratory models), also known as heuristic models, are mainly used to explore the relationship between spatial and temporal ecological process and forest change changes.

Scheller and Mladenoff [93] classified forest landscape models into eight types (Fig. 1) 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 forest landscape models. Based on Scheller and Mladenoff's classification, He [41] further developed quantitative criteria for forest landscape model classification. He applied similar criteria proposed by Scheller and Mladenoff (i.e. whether forest landscape model simulates a spatial process), to make the first distinction, then used temporal resolution and the forest succession simulation method as a second criteria to separate physical fire growth models (e.g. FARSITE) from the rest of forest landscape models. The criteria He used emphasizes the choices of model resolution, the amount of spatial process, and the methods of simulating forest succession in the model design, modeling approaches and the scope of model applications.

6. Theories and methods of forest landscape models

Early forest spatial dynamic models combined cellular automata methods with principles of forest dynamics [45]. Cellular automaton 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 multi-scale spatial and temporal dynamics. The cellular automata approach has become increasingly complicated, and has been widely used in ecological research. Cellular automata are also incorporated with certain rule-based methods for studying relationships between fire disturbance and forest changes [36,66].

The continuous development of forest succession theories, disturbance and non-equilibrium hypothesis of ecosystems establish 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 non-equilibrium dynamics and the spatial heterogeneity of ecosystems [66,91]. This transition of core ecological concept and theory is one of the fundamental motivations for the expansion of forest landscape modeling [67]. The advance of forest landscape models in the past two or three decades can been viewed as an integrated and quantitative process of linking knowledge of forest landscape succession, influencing factors and the non-equilibrium nature of ecosystems.

Hierarchy theory is a theory of the complexity of the system structure, function and dynamics and forms the theoretical basis for building a coherent modeling approach across multiple-scale and complex systems [18]. 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-dependant properties of the ecosystems [18]; simplify the complexity and analytical features of an ecosystem. Hierarchy theory provides a theoretical basis for scaling and for 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 forest landscape models.

The development of scaling methodologies allows multiple-scale 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 [105]. In the context of scaling, landscape ecologists are able to seek the spatial process in the vertical integration of scales [18]. For spatial explicit forest landscape models, the scaling process is also the key of integrating social and spatial data. For example, Geoghegan et al. [119] suggested that the spatial scaling is a useful tool of spatial data using for the society and using social data for spatial data integration.

7. The application of forest landscape models

The application of forest landscape models 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 forest landscape models 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.

Forest landscape models have been increasingly applied to study and solve practical management issues in forestry [56]. He [41] suggested that the application of forest landscape models generally falls into one of three categories: (1) spatiotemporal patterns of model outputs, (2) sensitivities of model outputs to input parameters, and (3) comparisons of different simulation scenarios. Currently, forest landscape models have been used in forestry management [70], watershed planning and management, post-damage forest landscape restoration [89,108,109], as well as forest land use development and planning [57,103]. The application of these models to different forestry disciplines continues to expand (Table 1).

In North America, forest landscape models have most often been designed for forest landscape management and resource assessment. A typical example is the landscape model DISPATCH [2–4]. The model uses GIS-based spatial data to simulate the environmental impacts by climate change on the landscapes in the Minnesota Boundary Waters Canoe Area. The LANDMAN model [57] represents another good example of a landscape management model. The model suggests that initial landscape structure and

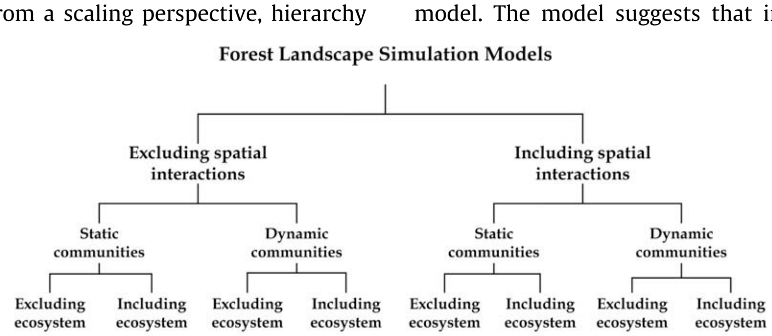

Fig. 1. A classification of forest landscape simulation models based on three ecological criteria: inclusion of spatial interactions, static or dynamic communities, and inclusion of ecosystem processes. The order of the decision tree can be reconfigured, dependent upon the individual's ranking of the three criteria (Scheller and Mladenoff [79]).

harvesting patterns are the major factors to affect the future landscape patterns and that forest managers need to develop planning strategies around 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 the landscape management.

Forest resource monitoring and operational planning are another major field in which forest landscape models 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 affects [32,38,86]. At the landscape scale, LANDIS uses age-defined cohorts to represent the age structure of tree species and uses 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. [38] provided a method linking the forest gap model LINKAGES [69] and LANDIS to study species' responses to large spatial scale climate warming in northern Wisconsin, USA. We have recently developed a software tool LANDISLINK which provides a more integrated and automatic methods for integrating LINKAGES [38] and LANDIS. The LANDISLINK modeling environment has been used to examine forest landscape restoration strategies and forest management following Southern Pine Beetle (*Dendroctonus frontalis*) outbreaks in 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 the changes of forest composition and spatial patterns [10,11,50,98,109,110].

Other applications of forest landscape models include forest fire management and forestry practice policies [78,83]. For example, LANDIS has been used to investigate the effects of climate change and forest fire dynamics on California coastal shrub landscape of the United States [25,90]. He et al. [39] and Yang et al. [113,114] used LANDIS to simulate the effects of different forest harvesting and fire disturbances caused by human activities on forest composition and productivity. Scheller et al. [78] used LANDIS-II model to simulate the effects of various disturbances, including forest fires, harvest strategies, and wind damage on northern broad-leaved forests of the United States. They also investigated the spatial relationships of disturbance and re-introduction of natural forest fire on long-term forest landscape changes under various climate change scenarios [76,78]. 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 aboveground biomass and density and diameter. These additions expand the range of ecosystem processes that can be represented in the model, and provide additional quantitative output [78]. 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, revealing the implications of their assumptions to fire growth, and identifying missing components among the various models [23]. SAFE FORESTS [57] has been used to simulate and analyze the effects of fire dynamics and timber harvesting in the forests of Sierra Nevada, California, USA, and provide forest management decisions on wildfire and harvesting. LINKNZ, an extended version of LINKAGES model, was used to simulate the effects of disturbance on forest succession in native evergreen New Zealand forests [34] (Table 1).

In contrast to work in North America, the developments and application of forest succession models in China began relatively late. However, since the late 1980s, research and development of forest gap models became increasingly important for Chinese vegetation ecologists. A number of forest gap models that were developed by western ecologists have been tested and applied to China's forests. In addition, a group of forest gap models have been independently developed by Chinese scholars based on long-term forest dynamic research in China. Up to date, three forest gap models have been generally recognized in China: (1) The KOPIDE (growth and succession) model [85] developed by Shao in broad-leaved Korean pine forests of northeast China; (2) The NEWCOP model [112] by Yan et al. for simulating the development and dynamics of forest species composition, and (3) The FOROAK model by Sang et al. to model Korean pine-oak (*Quercus mongolica*) forest succession [71]. All in all, these three forest gap models have demonstrated good predictive results in northeast China's forest areas. However, currently, the regions to which these models have been applied are limited to the temperate northeastern mixed broad-leaved and conifer forests, their application to other forest areas is as yet unexplored. It should also be noted that the validity of these models still needs further work and their recognition by international ecologists remains limited. In addition, these three forest gap models, like other forest gap models in general, cannot simulate forest management practices due to their assumptions of small patch sizes (ca. 1000 m^2) and therefore have limited use for practical forestry applications.

Although no forest landscape models exist that have been independently developed by Chinese scholars, the application of existing models to investigate Chinese forest dynamics and management practices, is already underway. In the past few years especially, the applications have grown considerably. For example, Chinese ecologists used LANDIS to examine forest succession and management in the northeast China [41,99,111]. Hu et al. [43] used LANDIS to assess the long-term forest landscape changes under various harvesting and logging plans within the Daxinganling region, and also quantitatively evaluated the effects of harvesting on forest landscape changes. He et al. [40] used LANDIS model for simulating long-term forest landscape dynamics in the Changbai Mountain National Nature Reserve. In general, current application of forest landscape models in China are mainly limited to northeast region; the current focus of the applied studies is to simulate forest succession, landscape-scale disturbance effects and mechanisms, and resource management strategies in various forest ecosystems of China.

8. Limitations of forest landscape models

Currently, the increasing availability of forest landscape models provides forest ecologists and managers opportunities to conduct spatial simulation research. However, all computer models have limitations. The customized, user-friendly interfaces still cannot overcome the inherent limitations of each model. Current forest landscape models mainly focus on the simulations of certain species or communities within a relative small spatial area. Therefore, simulating overall species diversity on larger-scale landscapes may become more difficult. The development of landscape model requires certain trade-offs among landscape extent, data resolution, prediction accuracy, parameterization, and validation [56,57,73,90]. Costanza and Maxwell [16] 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 data, it also increases the difficulty of accurately simulating those

Table 1
A list of forest landscape models: features, key research questions and applications.

Model type	Reference	Model name	Methods and features	Key research question and application	Spatial extent and resolution	Spatially explicit?	Dynamic?
Gap models	Botkin et al. [7]	JABOWA	Projects the dynamics of forest composition based on simulating the optimum growth of trees	Simulate the interaction between environment factors and forest growth for the Hubbard Brook Forest, New Hampshire, USA	100–830 m^2	No	Yes
	Shugart [87]	FORET	A gap model which studies the relationship between soil attributes and tree growth. Uses a Markov matrix approach to simulate dynamics	Simulates forest distribution and development for the western Great Lake area, USA	100–830 m^2	No	Yes
	Shao [84]	KOPIDE	Forest gap dynamic model	Used to assess the dynamic responses of a mixed broadleaved-Korean pine forest stand to climate change in northeastern China	$\sim$800 m^2	No	Yes
	Post and Pastor [69]	LINKAGES	Individual tree gap model based on ecosystem cycling	Developed to simulate the long-term effects of climate change and nutrient cycling for the structure and composition of the northeast hardwood forests	830 m^2	No	Yes
	Pacala et al. [124]	SORTIE	An individual-based, stand-level, spatial and mechanistic model. Driven by parameters representing competition among tree species, tree dispersal, establishment, growth, mortality and fecundity	Predicts the long-term dynamics (i.e. $\sim$2000 years) of transition in northern oak hardwoods forests, USA	1 km^2; 10 $\times$ 10 m^2 grid cell	Yes	Yes
	Chen and Twilley [15]	FORMAN	Individual-based gap dynamic model; derived from JABOWA and FORET	Used to study the long-term dynamics of mangrove forest development at southern Florida, USA	500 m^2	No	Yes
	Sang et al. [74]	FOROAK	An individual-based forest dynamic model	Simulate forest succession dynamics and species composition for temperate Mongolian oak-Korean pine forests in the northeast China	$\sim$500 m^2	No	Yes
	Miller and Urban [55]	ZELIG	Spatial explicit gap model that integrates climate, fire, soil nutrient storage to simulate forest patterns	Used to investigate the interactions between fire, climate and the dynamics of forest system at Sequoia and Kings Canyon National Park in the Sierra Nevada of California, USA	9 $\times$ 10^4 m^2; 15 $\times$ 15 m^2 grid cell	Yes	Yes
	Hall and Hollinger [34]	LINKNZ	Gap model derived from LINKAGES; Integrates ecological processes such as soil moisture balance, decomposition rates and nutrient cycling	Used to simulate the effects of disturbance on forest succession in native evergreen New Zealand forests	830 m^2	No	Yes
	Seagle and Liang [81]	N/A	Modified from ZELIG but also includes factors such as small seedling demography, soil saturation effects, shade adaption and browsing	Used to investigate the impacts of white-tailed deer browsing in the Patuxent River watershed in Maryland, USA	800 m^2; 11 $\times$ 11 m^2 study plot; 2 $\times$ 2 m^2 stub-plot	No	Yes
	Yan et al. [113]	NEWCOP	An individual-based, gap model	Simulates the effects of climate changes for forest succession in temperate Korean pine forests in the northeast China	$\sim$800 m^2	No	Yes
	Lafon [49]	LINKADIR	Modified form LINKAGES model that includes ice-storm disturbance	Investigates the effect of ice storms on long-term forest structure of northern hardwoods forests in the Adirondack Mountains, New York, USA	3000 m^2; 830 m^2	No	Yes
Landscape models	Andrews [1]	BEHAVE	Forest model that includes fire behavior prediction and fuel modeling	Used to estimate forest fuels and predict fire dispersal patterns, wildfire behavior and provide effective fire management decisions	N/A	No	No
	Green [27]	N/A	A grid model incorporating fire, seed dispersal to project the distribution of resources, species and forest dynamics	Used to study the interaction between seed dispersal and fire and how these drive spatial patterns of vegetation	0.25 km^2–25 km^2; 50 $\times$ 50 m^2 grid cell	Yes	Yes
	Hall et al. [33]	N/A	Used remote sensing (LANDSAT) to determine transition rates of forest patches	Used to study key forest landscape changes in northern Minnesota, USA. Also investigates the influence of human activities such as harvesting	9.4 $\times$ $10^2$$km^2$; 3600 km^2	Yes	Yes
	Baker [3]	DISPATCH	Application and integration of a Geographic Information System (GIS) database	Used to examine how climate change influences landscape structure in Minnesota, USA	4000 km^2; 200 $\times$ 200 m^2 grid cell	Yes	No
	Bugmann [8]	ForClim	A model of plant population dynamics driven by soil C/N turnover	Used to simulate the long-term ($\sim$1200 years) dynamics of forest structure in the Swiss part of the European Alps.	N/A	No	Yes
	Keane et al. [123]	FIRE-BGC	A simulation of biogeochemical driven forest succession	Used to investigate the role of fire on long-term ($\sim$200 years) landscape dynamics in the coniferous forests of Glacier National Park, Montana, USA	500 km^2; 500 m^2	Yes	Yes
	Li et al. [116]	ONFIRE	A grid model incorporating fire	Used to simulate the long-term response of forest landscape structure in northwestern Ontario, Canada, under different fire regimes	10 $\times$ 10 km^2; 0.01 km^2 grid cell	Yes	No
	Baskent [118]	LANDMAN	GIS-based landscape management model	Used to explore the structural effects of initial landscapes and different harvest patterns for landscape fragmentation in New Brunswick, Canada	43 km^2	Yes	Yes
	Liu and Ashton [53]	FORMOSAIC	A spatially explicit, multi-scale, stochastic and individual-based model integrating tree location, regeneration, growth, death, spatial interaction and environmental factors	Used to study the interaction between fine-scale changes in tropical forest landscapes	5 $\times$ 10^6 m^2; 10 $\times$ 10 m grid cell	Yes	Yes
	Mladenoff and He [37]	LANDIS	A grid model derived from JABOWA-FORET gap models and LANDSIM model	A spatially explicit and stochastic model that not simulates forest succession and explores the interaction between disturbances (e.g. fire) and landscape pattern	10–10^4 km^2	Yes	Yes

	Sessions et al. [120]	SAFE FORESTS	Non-linear regression and grid-based model	Used to simulate and analyze the effects of fire dynamics and timber harvesting in the forests of Sierra Nevada, Califolina, USA, and provide forest management decisions on wildfire and harvesting	120 km^2; 10–25 km^2	Yes	No
	Dale and Pearson [125]	DELTA	A simulation model that integrates land use GIS data and ecological processes	Used to investigate the effects of alternative forms of land management in the Brazilian Amazon and to estimate patterns and rates of deforestation under different immigration policies	296+ km^2; 0.53–12 km^2	Yes	Yes
	Roberts and Betz [117]	LANDISIM	A mechanistic, spatially explicit model incorporating a fuzzy systems approach	Used to simulate forest species age-class distributions and calculate a range of community and landscape statistics from basic site-specific species age-class dynamics in Bryce Canyon National Park, Utah, USA	142.5 km^2	Yes	Yes
	Wimberley et al. [104]	LADS	Landscape scale forest species demography model	Used to model the historical variability of old-growth and late-successional forests in the Oregon Coastal Range (USA) over the past 3000 years and to evaluate the influence of fire regimes on forest structure and species composition	400–22,500 km^2; 1 km^2 grid cell	Yes	Yes
	Klenner et al. [48]	VDDT/TELSA	A spatially explicit model emphasizing the interactions among vegetation succession, disturbances and forest management	Investigate how forest management policies and natural disturbances affect the habitats development in British Columbia, Canada	62,966 km^2	Yea	No
	Li [52]	SEM-LAND	A spatially expect model focusing on simulating pre-fire and post-fire forest vegetation distributions and landscape changes	Used to simulate the effects of various fire regimes on forest landscape structure in west-central Alberta, Canada	74.32 km^2; 0.01 km^2	Yes	No
	Hargrove et al. [36]	EMBYR	A broad-scale, GIS-based, probabilistic model	The application of probabilistic models to simulate large scale fire spread and effects of the burning through heterogeneous landscapes	625 km^2; 50 $\times$ 50 m grid cell	Yes	Yes
	Gustafson et al. [31]	HARVEST	HARVEST module of LANDIS model	Used to simulate forest succession under forest management scenarios (i.e. harvesting) and other disturbances in the Ozark Mountains, USA	8.36 km^2; 30 $\times$ 30 m grid cell	Yes	No
	Carmel et al. [13]	N/A	An empirical linear/logistic regression model	Used to investigate the potential of empirical modeling for understanding, planning and managing Mediterranean vegetation dynamics in the Galilee mountains, northern Israel	4 km^2; 15 $\times$ 15 m^2 grid cell	No	No
	Yemshanov and Perera [115]	BFOLDS	Time-dependent Markov model	Used to study long-term dynamics in North American boreal forest (Canada), and investigate the role of disturbances	3.7 $\times$ 10^4 km^2; 0.01 km^2 grid cell	Yes	Yes
	Perry and Enright [66]	N/A	GIS grid-based model	Examine how fire and human activity interacted to shape present-day landscape pattern	$\sim$1.21 km^2; 10 $\times$ 10 m^2	Yes	Yes
	Pennanen and Kuuluvainen [65]	FIN-LANDIS	A stochastic, grid-based model modified from LANDIS	Used to predict landscape-scale effects of historical or potential fire regimes for conifer forest landscapes in the Ulvinsalo area, eastern Finland	25.16 km^2; 20 $\times$ 20 m^2 grid cell	Yes	Yes
	Keane et al. [47]	LANDSUM	Spatially explicit, vegetation dynamics simulation model	Quantify the range and variability of temporal vegetation distribution for four landscapes in the northwestern United States	25–5,160 km^2	Yes	Yes
	McGarigal et al. [121]	RMLANDS	Spatially explicit disturbance-succession model linked to landscape pattern and wildlife habitat	Simulate the interactions between natural disturbances (fire), human activities (harvesting) and forest succession and their effects on landscape patterns and wildlife habitats in the Rocky Mountains, USA	100–1000 km^2; 25 $\times$ 25 m^2 grid cell	Yes	Yes
	Schoenberg et al. [75]	N/A	Non-linear regression model	Used to study the frequency-area distribution of fires in Los Angeles County (USA). Includes a statistical evaluation of the most effective model	0.4046 + km^2	No	No
	Roy et al. [72]	N/A	Cellular Automata model of succession and disturbance	Used to investigate how landscape dynamics affect competitive coexistence in a disturbance-structured system	N/A	Yes	Yes
	Pennanen et al. [64]	Q-LAND	A spatially explicit model derived from LANDIS to simulate stand-level landscape process	Incorporates stand-level prediction of tree volume and seed dispersal to simulate landscape dynamics and the long-term ($\sim$1500 years) development of mixed boreal forests in Quebec, Canada	$\sim$1 km^2; 0.01–0.1 km^2 grid cell	Yes	Yes
	Pausas [63]	FATELAND	A grid-based model integrating landscape characteristics, disturbance and vegetation dynamics	Used to study the implications of fire regime and landscape pattern for community structure	10^6 + m^2; 10 $\times$ 10 m^2	Yes	Yes
	Scheller et al. [78]	LANDIS-II	Upgraded model derived from LANDIS, which includes biomass	Used to simulate the reciprocal interaction of succession and disturbances in the Manitoba Model Forest (Canada)	10^4 km^2; 50 $\times$ 50 m grid cell	Yes	Yes
Regional models	Daly et al. [21]	PRISM	Regional, geographic, and statistical climate model	Used to predict the variation in precipitation for watersheds in the north Oregon mountain areas, USA	5-min grid cell	No	Yes
	Neilson [59]	MAPSS	Regional bio-geographic model to simulate potential climax vegetation	Used to investigate biosphere-atmosphere feedbacks from climate change	$\sim$8,080,464 km^2; 10 $\times$ 10 km^2 grid cell	No	No

(*continued on next page*)

Table 1 (*continued*)

Model type	Reference	Model name	Methods and features	Key research question and application	Spatial extent and resolution	Spatially explicit?	Dynamic?
	VEMAP members [96]	BIOME	Multi-biome generalization of FOREST-BGC to simulate biosphere cycling processes and balance	Uses climate, vegetation and environmental factors to simulate carbon, nitrogen and water cycling and their effects on vegetation distribution in the United States	~8,080,464 km^2; 0.5° × 0.5° grid cell	No	No
	VEMAP members [96]	DOLY	Regional biogeochemical process circulations model	Used to investigate daily photosynthesis and potential vegetation distribution in USA	~8,080,464 km^2; 0.5° × 0.5° grid cell	No	No
	Foley et al. [24]	IBIS	Global terrestrial biosphere model	Used to simulate the relationship between terrestrial ecosystem phenomena and atmospheric circulation	Global; 2° × 2° grid cell	No	No
	Moritz [58]	N/A	External event statistics model	Used to study how fire management and climate have affected fire regimes in Los Padres National Forest, California, USA	7×10^4 km^2	No	No
	Bachelet et al. [126]	MC1	Regional bio-geographic model	Uses historical data to simulate changes in potential equilibrium vegetation distribution across a gradient of temperature changes	~8,080,464 km^2; 10 × 10 km^2 grid cell	No	No
	Cardille et al. [12]	N/A	General linear regression model (GLM)	Used to investigate the role of biotic, abiotic and human factors and the origin of fires in forested landscapes of the upper Midwest, USA	2.5×10^5 km; 5–10 km^2 grid cell	Yes	No
	Hardy et al. [35]	FRCC	Regional wild fire predicting and forest fuel classification models	Integrates historical fire data and vegetation data to establish classification criteria for forest fuels, simulate fire regimes, evaluate fire risk and aid the management decision-making process	~8,080,464 $km^2$1 km^2 grid cell	No	No
	Cawsey et al. [14]	N/A	Generalized regression analysis and spatial prediction	Simulate and predict the pre-European conditions and distribution of various vegetation types in Central NSW, Australia	10^5 + km^2; 50 × 20 m grid cell	Yes	No
	Iverson et al. [44]	N/A	Coupled regression tree and Cellular Automata model	Used to study the abundance of Virginia pine (*Pinus virgiana*) and landscape fragmentation under various climate change scenarios in the southeastern USA	10^5 + km^2; 3 km^2 grid cell	Yes	Yes
	Pan et al. [62]	TEM-LPJ	A large-scale dynamic vegetation model driven by interactions between water, light and nitrogen	Used to simulate C, N and water interactions during stand development or following a fire disturbance in temperate deciduous forests, coniferous forest and a C3 grassland	12 km^2 – 780 km^2; 0.5° × 0.5° grid cell	No	No
	Malamud et al. [54]	N/A	Non-linear regression model	Used to examine how fire regimes vary across broad-scale patterns. Applied to 18 eco-regions spanning the conterminous USA	~8,080,464 km^2; 10 × 10 km^2 grid cell	Yes	No

patterns. In addition, Wennergren et al. [101] indicated that there is uncertainty in processing spatial data (e.g. the phenomenon of death seeds during seedling dispersal), hence landscape spatial models are more appropriate to use as a management planning tool, rather than to predict the variations of species composition.

The existing limitations of forest landscape models are largely the result of the incomplete understanding of forest ecological processes and patterns. Simulating landscape dynamics is essential not only to understand the evolution patterns and process of landscapes through the current status to the future, but also to understand the causes of landscape change [80,92,97]. One of the key factors for the current limitation of the forest landscape models is a lack of understanding of landscape changes and development. While interest in the development of forest landscape models grows over time, these models are still difficult to apply a greater range of time and space. Running these models requires lots of parameter settings and advanced computing power. In addition, if current model users ignore inherent model limitations, the risk of model misuse increases [100,102].

The development of forest landscape modeling still faces critical issues in model result verifications [41]. 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 the overall time series verification on the forest landscape modes using traditional methods; doing so will make the forest landscape model no longer significant. Each landscape is unique in nature, and cannot be replicated. In fact, the data used to do validation is often hard to obtain or are not be easily collected [71]. Second, when the effects of biological or non-biological factors on model simulations are discussed, these factors are actually included in modeling parameters and already have been expected shown in simulation results.

Inadequate post-simulation data analysis techniques may also limit the capability of forest landscape models [37]. In order to effectively analyze complex spatial patterns, the post-simulation analysis tool, data management methods, output visualization technique and model validation still need to be further improved. LANDISVIEW, which we have developed, provides some contribution to solving this problem [5].

9. Conclusions

In modern terrestrial forest ecosystem studies, forest landscape models have become a useful, and to some extent, indispensable tool. Improving the design and performance of the models has become the focus of forest landscape ecologists in this research field. Forest landscape models can simulate landscape process and pattern in time and space revealing the landscape-scale change. The models are not only able to store information of past and existing vegetation and the status of disturbance and management, more importantly the models can also be used to predict change trends, and contribute to more effective study of forest response to various disturbances and forest landscape management. Because landscape models can simulate the complicated process of spatial pattern and reflect the spatial and temporal characteristics of information, forest landscape models will be further developed and have are good prospects both in theory and practical application research. In the coming decades, ecologists and foresters will have more understanding of forest landscape pattern and process. The technologies and methods for the development of forest landscape models will become more comprehensive, and the types of forest landscape models will be more diversified in according to different research questions.

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