Landscape Ecol (2007) 22:491–505
DOI 10.1007/s10980-006-9048-4

REVIEW

An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems

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Received: 3 November 2004 / Accepted: 19 September 2006 / Published online: 19 October 2006

Abstract Computer models are increasingly being used by forest ecologists and managers to simulate long-term forest landscape change. We review models of forest landscape change from an ecological rather than methodological perspective. We developed a classification based on the representation of three ecological criteria: spatial interactions, tree species community dynamics, and ecosystem processes. Spatial interactions are processes that spread across a landscape and depend upon spatial context and landscape configuration. Communities of tree species may change over time or can be defined a priori. Ecosystem process representation may range from no representation to a highly mechanistic, detailed representation. Our classification highlights the implicit assumptions of each model group and helps define the problem set for which each model group is most appropriate. We also provide a brief history of forest landscape simulation models, summarize the current trends in methods, and consider how forest landscape models may evolve and continue to contribute to forest ecology and management. Our classification and review can provide novice modelers with the ecological context for understanding or choosing an appropriate model for their specific hypotheses. In addition, our review clarifies the challenges and opportunities that confront practicing model users and model developers.

Keywords Landscape ecology · Forest models · Simulation models · Gap models · Ecosystem process models

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Introduction

Broadly defined, forest landscape simulation models (FLSMs) are computer programs for projecting landscape change over time. FLSMs can also be used to test hypotheses about the interactions among processes and patterns across forested landscapes. Processes are the endogenous and exogenous forces that drive forest change. Patterns are the spatial configuration, composition, and heterogeneity of landscape elements, such as community types, tree species age classes, ecosystem process rates, or aboveground biomass.

In this review, we will provide an introduction to FLSMs and outline the 'hypothesis space' for which they are suitable, as well as provide an update and synthesis for practicing modelers. We first explain the theory, concepts, and technology that have preceded and produced the current ''landscape'' of FLSMs. We place FLSMs into the broader context of ecological modeling and examine what is unique about FLSMs. Next, we review FLSMs using a classification that ties together distinct groups of FLSMs and provides an ecological perspective on landscape models. We discuss strategies for deploying FLSMs, particularly for users who are not model developers. Last, we speculate about the future challenges and opportunities for FLSMs.

History and development of forest models

The history of FLSMs mirrors the history of both forest and landscape ecologies. Within forest ecology, there has been a long history of model development and application, driven by management imperatives and evolving ecological paradigms (Shugart 1998; Mladenoff and Baker 1999a). Forest ecology in the United States initially focused on the forest stand (typically $<10^2$ ha with relatively homogeneous site conditions, composition, and disturbance history) or small watersheds (Likens et al. 1970; Botkin et al. 1973; Whittaker et al. 1974). Concurrently, forest models were developed to estimate forest change at this scale (Botkin et al. 1973; Ek and Monserud 1979). Empirical data collected at the stand scale continue to serve as inputs to broader-scale models. In addition, stand-scale models are often used as components within broader-scale models (Urban et al. 1991).

During the late 1980s, landscape ecology emerged as a new perspective for understanding ecological dynamics and addressing broad-scale management concerns (Levin 1992). A focus on large landscapes ($>10^3$ ha) developed as forest managers and ecologists confronted natural disturbances (e.g., fire, hurricanes) and human induced stresses (e.g., land use change, climate change) that required the context of the larger landscape to be sufficiently understood. The effects of management practices, logging in particular, also motivated the shift in perspective towards broader spatial and temporal scales (Franklin and Forman 1987). Over time, this emphasis on broader scales evolved into forest ecosystem management (Levin 1999), management of disturbance regimes (Engstrom et al. 1999), and forest landscape planning (Barrett 2001).

In the past two decades, forest models have benefited from ongoing improvements in technology and data availability (Mladenoff 2004). Computer speed and memory have increased dramatically, following Moore's prediction of a doubling of transistors per integrated circuit every 18 months (Moore 1965). Simultaneously, software has eased model development and the manipulation of input and output data. Hardware and software improvements have increased our ability to simulate many processes at multiple scales. The availability of data to parameterize, initialize, and validate forest models has also increased significantly. Spatially extensive data are now readily available from either satellite classifications (Wolter et al. 1995; Defries et al. 2000), national surveys (Hansen et al. 1992; STATSGO 1994), and historical data sources (Schulte et al. 2002).

Forest landscape simulation models

Within this broader context, FLSMs were designed specifically to address management or research questions about spatially extensive landscapes. All FLSMs are spatially explicit: landscape elements have map coordinates and are placed within their geographic context. Landscape elements must be assigned values before simulating a landscape, i.e., the landscape must have an initial configuration. A geographic information system (GIS) is typically used to input, store, and display data. FLSMs may also be spatially interactive, i.e., simulate lateral (horizontal) fluxes or processes that spread across the landscape (Reiners and Driese 2001; Mladenoff 2004; Peters et al. 2004).

Another distinctive feature of FLSMs is their emphasis on large-scale forcing, including disturbance (Baker 1989; Mladenoff and Baker 1999b). The types of disturbances that have been modeled are extensive, although wild fire has been the largest focus of previous modeling (Keane and Long 1998; Keane et al. 2004). Human effects on landscape change have also become a significant focus, including harvesting (Wallin et al. 1994; Gustafson and Crow 1998; Gustafson et al. 2000), land use change (Dale and Pearson 1999; Soares-Filho et al. 2002), and climate change (Baker et al. 1991; Scheller and Mladenoff 2005). Because of the emphasis on broad-scale change, FLSMs are typically used to simulate landscape change for multiple decades (50–500 years). Therefore, FLSMs are better described as strategic (long-term landscape planning), versus tactical (intended for immediate application), tools for assisting management decision-making (Barrett 2001).

FLSMs vary widely in their algorithms, complexity, and input requirements. Computer languages now allow tremendous flexibility for joining diverse numerical or computational methods within a single model or modeling system (Woodbury et al. 2002). In particular, object oriented design (OOD) has permeated the field and simulation models are evolving towards multi-purpose and multi-scale applications built from modular components (Scheller et al. in press; Maxwell and Costanza 1997; Sequeira et al. 1997). As a result, a single model may represent different processes using a combination of rules, continuous mathematics, probability theory, and both deterministic and stochastic algorithms. Spatial and temporal resolution have also become flexible model parameters. Finally, models vary significantly in the breadth of the intended model user community, often dependent upon the existence and quality of the user–model interface.

FLSMs are typically used to compare alternative ecological assumptions or management options. The suite of conditions simulated are typically referred to as scenarios. Scenarios define the assumptions and parameters necessary to estimate potential future conditions, identify key processes, or reveal important interactions among simulated processes. Multiple scenarios form a suite of hypothetical circumstances, the results of which are compared against each other. Scenarios enable an experimental approach to landscape change by allowing alternative hypotheses that would otherwise not be possible (Mladenoff and Baker 1999a; Mladenoff 2004). Operationally, a scenario may begin either with empirical landscape data as input or with an artificially generated initial state, such as a random or fractal arrangement of spatial locations (Gardner et al. 1987).

Given the history and ongoing dynamic development of FLSMs, a coherent picture of current modeling paradigms and trends can be difficult to discern. Therefore, we offer the following classification to highlight similarities and clarify critical differences among models. Our classification can aid the novice modeler in understanding the models available, their respective qualities and weaknesses, and their ability to address diverse hypotheses. For the experienced practitioner, our classification can help to identify areas of uncertainty and potential improvement and highlight current and future trends.

Model classification

Our goal was to develop a classification valuable to both novice modelers and current practitioners. Therefore, rather than focus in detail on model implementation, we approached FLSMs from an ecological perspective and developed a classification to capture the breadth of ecological approaches to forest landscape simulation modeling. We chose three ecological criteria for our classification: spatial interactions, ecosystem processes, and community dynamics (Fig. 1). Within each criterion there is a broad gradient of representation, ranging from none to a detailed, mechanistic representation. After defining these criteria and explaining how they are represented within FLSMs, we introduce eight model groups derived from the three criteria. We explain how choices within each of the three criteria defines the questions each model can address and their inherent limitations.

Criteria for landscape models

Spatial interactions

Spatially interactive (also 'landscape' or 'contagious') processes transfer energy, matter, or information across the landscape (Reiners and Driese 2001). Spatial interactions across landscapes produce emergent behavior and spatial

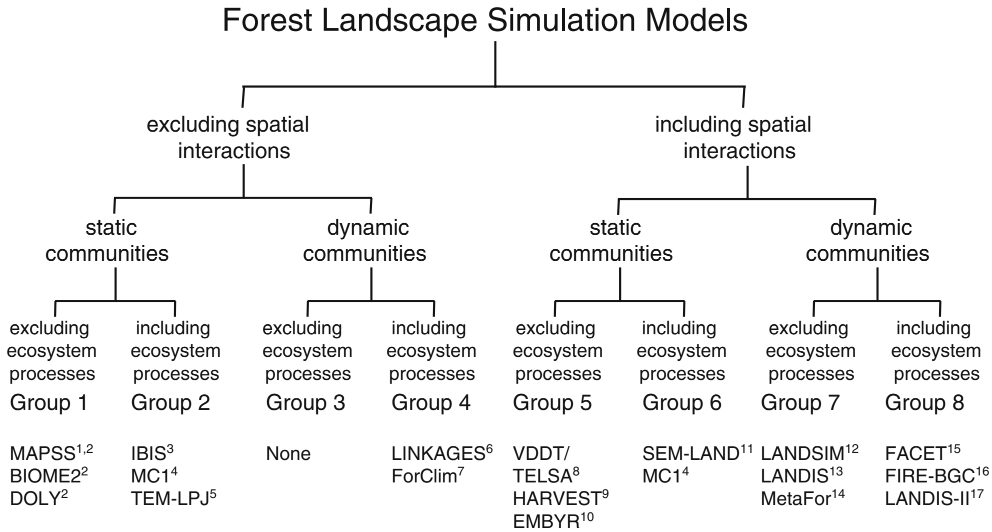


Fig. 1 An example decision tree based on three ecological criteria: inclusion of spatial interactions, static or dynamic communities, and inclusion of ecosystem processes. The order of the decision tree can be reconfigured, dependent upon the individual's ranking of the three criteria. Group numbers correspond to the group labels in the text. Two or three exemplar models are provided for each group. *Subscripts*. [1]Neilson (1995); [2]VEMAP Members (1995); [3]Foley et al. (1996); [4]Bachelet et al. (2001a, b); [5]Pan et al. (2002); [6]Pastor and Post (1986a); [7]Bugmann (1996); [8]Klenner et al. (2000); [9]Gustafson and Crow (1998); [10]Hargrove et al. (2000); [11]Li (2000); [12]Roberts (1996b); [13]Mladenoff et al. (1996); [14]Urban et al. (1999); [15]Urban and Shugart (1992); [16]Keane et al. (1996); [17]Scheller et al. (in review)

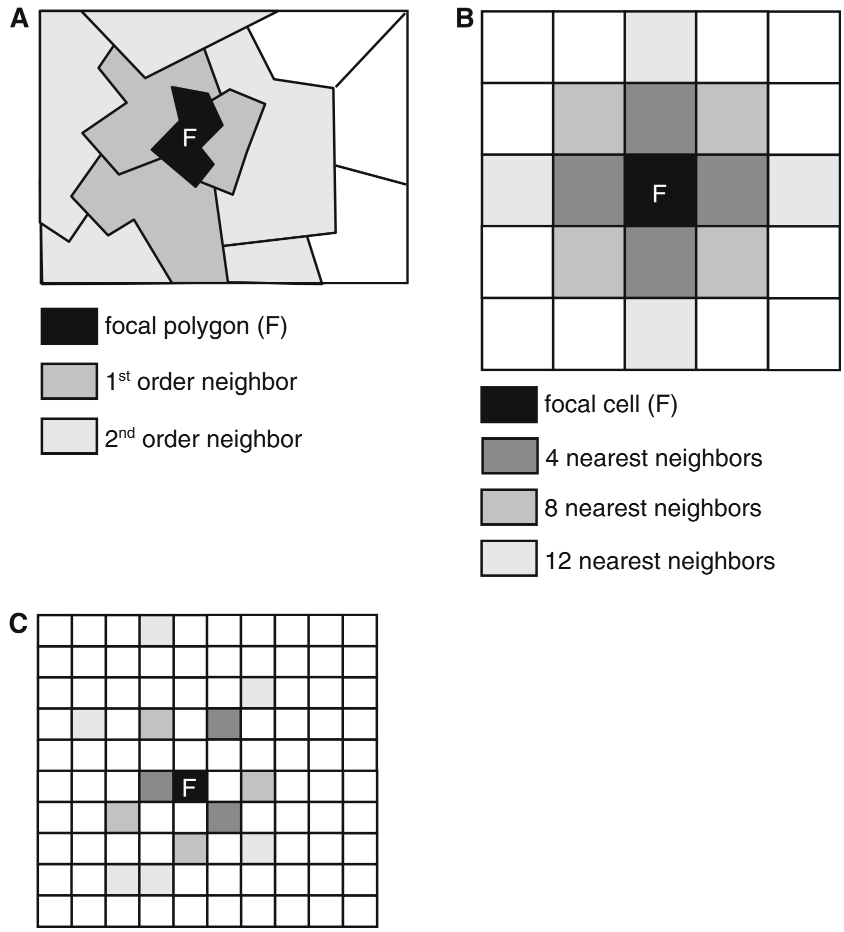
patterning at multiple scales and therefore contribute to the evolution of landscape pattern and changes in spatial heterogeneity. Examples of spatial interactions include the dispersal of seeds, a fire spreading, the movement of herbivores, and neighboring trees competing for light.

Essential to the simulation of spatial interactions is the representation of spatial information and the neighborhood structure. Vector polygons are contiguous areas that can have any size or shape within the maximum extent of the landscape (Fig. 2A). Vector polygons assume within-polygon homogeneity. Spatial interactions among vector polygons are often limited to first-order neighbors, defined by a shared edge between polygons (Fig. 2A). A landscape can also be broken into a grid of equal sized, typically square or hexagonal, cells. Spatial interactions among cells can be defined by either neighborhoods (e.g., the 4, 8, or 12 nearest neighbors; Fig. 2B) and/or can be a function of the distance between cell center points (Fig. 2C), thereby allowing more flexibility in spatial interactions than vector polygons (Mladenoff and He 1999; Mladenoff and Baker 1999b).

Every representation of spatial interactions incurs a computational penalty. Finer resolution spatial interactions (e.g., neighborhood shading) will incur a larger computational penalty than coarse-scale interactions (e.g., the dispersion of large clear-cut patches). The computational cost of a spatial interaction is sensitive to landscape resolution and increases non-linearly with decreasing cell size.

Finally, the simulation of a particular spatial interaction may not be appropriate for a given hypothesis or scale (Peters et al. 2004). For example, at continental scales, most landscape variation will be explained by patterns of temperature and precipitation. Conversely, short-term projections may not require estimates of continental tree species migrations. If spatial interactions provide only a marginal increase in predictive power, the additional complexity, computational overhead, and parameterization required may not warrant their inclusion (Peters et al. 2004).

Fig. 2 Sample neighborhood structures: (**A**) polygons with first and second order neighborhoods; (**B**) a grid with 4, 8, and 12 cell neighborhoods. Larger neighborhoods include all cells from smaller neighborhoods; (**C**) an unstructured neighborhood where spatial interaction is a function of distance from the focal cell. Resolution and extent are arbitrary and are not indicative of neighborhood structure or interactions



Static or dynamic communities

All FLSMs include spatial and temporal change of tree species composition—forests change over time. How a community of tree species is represented varies widely and will be explored below. The principle difference among FLSMs is whether the community itself is static or dynamic. For a static community, tree species composition and associated characters are defined a priori and do not evolve during a simulation, although the spatial distribution of the community will change over time. This property has been termed the 'invariance hypothesis' (Logofet and Lesnaya 2000). A dynamic community is not fixed and the composition and character of simulated communities will evolve over time.

Forest communities can be represented as successional stages or 'seral community types' (Cattelino et al. 1979; Keane and Long 1998). The terms 'community state', 'vegetation classification', and 'land cover type' also apply (Yemshanov and Perera 2002). A successional stage is associated with species, age, and/or biogeochemical information. Successional pathways are typical, likely, or potential transitions among successional stages. Without disturbance, these pathways will converge on a single ''climax'' community or potential vegetation type (Keane and Long 1998; Logofet and Lesnaya 2000). Transitions occur after a certain time passes or disturbance occurs (Klenner et al. 2000; Keane et al. 2002). Alternatively, time dependent transitions probabilities (Markov chain) can be used (Balzter et al. 1998; Logofet and Lesnaya 2000; Yemshanov and Perera 2002). Successional stages, pathways, and transition probabilities are often estimated from stand-scale models

(Acevedo et al. 2001), multi-temporal data (Turner et al. 1996), field measurements (Logofet and Lesnaya 2000; Yemshanov and Perera 2002), or subjectively defined by managers and forest ecologists.

Since successional stage models have static communities, their application is limited to stable ecosystems or short time horizons. For example, climate change or species invasion will likely alter successional processes and cannot be modeled with static communities. Another critical assumption is that all successional pathways are known and that novel combinations of species will not occur. Finally, the use of static communities typically assumes that all species propagules are universally available.

Alternatively, other FLSMs explicitly include discrete tree species and their life history traits (Mladenoff et al. 1996; Roberts 1996a). Species can be recorded as present or absent, stratified into classes (diameter and age classes being the most common), or recorded as individual trees. The inclusion of discrete species implicitly assumes that forest change can only be adequately predicted by considering individual species life history attributes, physiology, behavior, and/or biochemistry. Communities represented by multiple species, each individually responding to changing environmental drivers, are dynamic and will evolve over time. Although apparently more flexible, dynamic communities require that a greater number of demographic processes be parameterized and simulated, including at least birth, ageing, and death. The duration of the model simulation and the estimated stability of community types will determine whether simulating a dynamic community is justified, given the additional parameterization required.

Ecosystem processes

Ecosystem processes encompass a broad range of biophysical and biological processes that mediate the exchange of energy and matter between biotic pools and the abiotic environment. Within forests, ecosystem ecology has traditionally focused on nutrient cycling, productivity, and decomposition (Whittaker et al. 1974; Pastor and Post 1986b; Rastetter et al. 1991; Saxe et al. 2001). FLSMs that explicitly include ecosystem processes typically simulate the net growth of trees (photosynthetic carbon fixation minus autotrophic respiration) at a minimum. Complexity and detail increase as biotic pools are added or further divided, more processes are included (e.g., heterotrophic respiration), and time scales are shortened.

Inclusion of ecosystem processes may be particularly relevant when abiotic constraints are not expected to remain constant, as may be the case with climate change, changes in atmospheric chemistry, or nutrient deposition (Pitelka et al. 2001; Saxe et al. 2001). Ecosystem processes are also important when there are feedbacks between biological processes (e.g., succession) and ecosystem function (e.g., water retention, nitrogen cycling) (Pastor and Post 1986b; Hooper and Vitousek 1997).

Functional classification of forest landscape simulation models

For each of the three ecological criteria, we classified FLSMs on the basis of the inclusion or exclusion of these processes (spatial interactions excluded or included; static or dynamic communities; ecosystem processes excluded or included), providing a total of eight model groups. These three ecological criteria were used to form a binary decision tree (Fig. 1). Since our classification was intended to highlight assumptions and perspectives, we provide only examples and many excellent models have not been listed here. There are many other reviews that together can provide a more comprehensive list of available models (Baker 1989; Mladenoff and Baker 1999a; Gratzer et al. 2004; Keane et al. 2004; Perry and Enright 2006).

Group 1. Excluding spatial interactions; static communities; excluding ecosystem processes

Many of the models in this group and the next were designed to project broad-scale (continental to global) change. Species are amalgamated into plant functional types (PFTs, e.g., 'temperate conifer') with homogeneous physiological attributes (growth rates, structure, disturbance tolerance, etc.). PFTs are not limited to forest types but also include tundra, grasslands, savannas, shrub lands, and arid lands (Neilson 1995; Neilson and Drapek 1998; Bachelet et al. 2001a, b, 2003). Transitions between PFTs are dependent upon climate change, soils, disturbance, and the physiological constraints for each PFT.

Specific to Group 1 are Dynamic Global Vegetation Models (DGVMs). DGVMs project shifts in the location of vegetation types as a function of climate. Disturbances are generally not simulated. For example, the Mapped Atmosphere-Plant-Soil System (MAPSS) projects where different forest types are likely to persist using current or projected climate and broad estimates of fundamental niches (VEMAP Members 1995; Neilson 1995; Neilson and Drapek 1998).

DGVMs have been criticized because of their assumption that PFTs can migrate rapidly and remain in equilibrium with climate (Pearson and Dawson 2003). The validity of this assumption will depend on the functional diversity of the PFTs. Since these and similar models do not incorporate dispersal, disturbance, or human fragmentation of the landscape, the results should not be regarded as either predictions or projections. Instead, the results define a baseline estimate of where various forests types could exist, given the projected climate change. These models provide valuable broad scale data and serve as an important contrast to more regional, strictly forest models.

Group 2. Excluding spatial interactions; static communities; including ecosystem processes

This group of models simulate changes in vegetation and various carbon pools at continental to global scales (Foley et al. 1996; Lenihan et al. 1998; Mcguire et al. 2001; Cramer et al. 2001; Aber et al. 2001; Bachelet et al. 2003). Similar to the first group, communities are not limited to forest tree species and seed dispersal is not limiting. Disturbances are simulated to occur at or below the resolution of the grid cell (Thonicke et al. 2001) and therefore there are no explicit spatial interactions. Within a PFT, there is no variation in disturbance effects. For example, all species within the conifer plant functional type (Bachelet et al. 2001a, b) will react identically, with no variation due to serotiny, bark thickness, epicormic branching, etc. Finally, these models do not yet incorporate human influences, particularly logging or fragmentation.

Nevertheless, because of the very large spatial extents that can be simulated, such models are valuable for evaluating broad-scale changes in carbon stocks or nutrient cycling due to interactions between the terrestrial biome and the atmosphere. Similar to the first group, these models can also define potential vegetation at broad (continental) scales.

Group 3. Excluding spatial interactions; dynamic communities; excluding ecosystem processes

When simulating dynamic communities, model developers have usually made an implicit choice between including ecosystem processes or including spatial interactions, both of which are computationally expensive. Consequently, currently there are no FLSMs with dynamic communities and neither spatial interactions nor ecosystem processes.

Group 4. Excluding spatial interactions; dynamic communities; including ecosystem processes

Many of the first models that included dynamic species composition and ecosystem processes were gap models (Urban and Shugart 1992). Gap models operate at the scale of individual trees or small forest gaps, typically an area less than 0.1 ha (Urban and Shugart 1992; Shugart 1998). Gap models simulate individual tree growth and mortality and may include decomposition. Therefore gap models represent at least one ecosystem process and simulate dynamic species composition. Although individual trees are modeled, they are not given explicit spatial coordinates. Nor is the larger landscape context represented. Seeds are assumed to be universally distributed and disturbances are not modeled as spatially dynamic processes.

Although gap models have been linked together to model larger landscapes (Urban et al. 1991; Busing 1991; Easterling et al. 2001), the application of linked gap models at scales >10^2 ha has been limited due to high computational demands and the intensive input data required (Mladenoff 2004). The calculation of disturbance effects on individual trees is inherently complex (Hely et al. 2003) and spatial interactions within linked-gap models are typically limited to fine-scale processes, including fire, seed dispersal, and competition (Miller and Urban 1999; Easterling et al. 2001).

Nevertheless, gap models have played a critical role forming the links between ecosystem process rates and dynamic communities. In addition, gap models have become an important source of input data for broader-scale FLSMs (He et al. 1998; Urban et al. 1999; Acevedo et al. 2001; Scheller et al. 2005).

Group 5. Including spatial interactions; static communities; excluding ecosystem processes

Within this model group, community types are sometimes extraordinarily broad with the landscape divided only into forested (with forest age) and non-forested types. Such models commonly serve as 'null' models for exploring interactions among landscape processes and a small number of state variables. Such null models have been used extensively to simulate fires, including the effects of landscape connectivity on fire spread (Turner et al. 1989), fires and fuel moisture (Turner et al. 1995; Finney 1998), or time since last fire (Baker et al. 1991; Baker 1992, 1993; Peterson 2002). Null models have also been used to simulate species dispersal and rate of spread (Hart and Gardner 1997) and the effects of harvesting on landscape pattern (Wallin et al. 1994; Gustafson and Crow 1998).

Other models within this group focus on the transitions between community types due to disturbances (generally fire and logging) (Klenner et al. 2000). Successional stages (and any associated ecosystem properties) and transition probabilities among stages are calculated a priori. Using relatively simple community types and likely transitions has enabled rapid model deployment based on surveys of expert knowledge (Klenner et al. 2000).

Models in Group 5 benefit from the emphasis on spatial interactions. Limiting the array of possible interactions (with species, with ecosystem processes) has yielded important insights on the interactions between disturbances and landscape pattern or between disturbances and the distribution of different community types.

Group 6. Including spatial interactions; static communities; including ecosystem processes

Several spatially interactive models simulate ecosystem processes and have static communities. Again, static communities dictate certain assumptions. For example, MC1, which operates without spatial interactions at continental scales, has been applied to a smaller landscape (1250 ha) through the inclusion of a fire spread module (Bachelet et al. 2000). The application of MC1 to a grassland-forest ecotone assumed that all propagules were available throughout the landscape (Bachelet et al. 2000). Similarly, SEM-LAND simulates forest growth and fire spread (Li 2000). Notably, SEM-LAND assumes that the climate is stable and forest type never changes, although age and biomass accumulation are dynamic (Li 2000).

These models can address local or regional scale questions (<10^4 ha) that require consideration of the effects of ecosystem process rates and spatially interactive fire regimes (Li et al. 2000; Bachelet et al. 2000). In forested landscapes with relatively low species diversity and over relatively short time horizons, the assumption of community invariance may not limit the value of the results. Particularly where topography is significant, the diversity of species associations may be limited by steep climatic or edaphic gradients.

Group 7. Including spatial interactions; dynamic communities; excluding ecosystem processes

This model group includes many closely related FLSMs, all of which include discrete tree species binned into age categories that allow for dynamic communities. One of the first such models, LANDSIM, uses vector polygons to simulate seed dispersal and disturbance spread to explore the relationships between species' vital attributes, disturbance, and landscape patterns (Roberts 1996a). Later models extended species age categories to grids that allowed spatial interactions beyond the first-order neighborhood (Mladenoff et al. 1996; Urban et al. 1999). For example, LANDIS includes many types of spatially interactive processes, each with its own neighborhood structure (He and Mladenoff 1999; Gustafson et al. 2000; Sturtevant et al. 2004).

However, the emphasis on individual species behavior can introduce significant uncertainty. For example, mean and maximum seed dispersal distances for many tree species remains unresolved (Clark 1998; Higgins et al. 2003). Assembling the necessary species data can be time consuming and may require significant estimation.

All of these models generate estimates of species age distributions across a forested landscape. Species age distribution data provide an opportunity to link to many other processes correlated with age, including reproduction and mortality, harvesting, and the development of uneven-aged stand characteristics (Scheller et al. 2005). Significantly, they provide estimates of landscape-scale demographics that are necessary for identifying local extinction risk (Syphard et al. 2006; Scheller et al. 2005).

Group 8. Including spatial interactions; dynamic communities; including ecosystem processes

FLSMs that include spatial interactions, dynamic communities, and ecosystem processes are a more recent development. At a relatively small extent (typically $<10^2$ ha), forest models may simulate individual trees using Cartesian coordinates (Gratzer et al. 2004). The first such model, FOREST, was restricted to small (0.08 ha) plots and the only spatially contingent process was an estimate of competition from neighboring trees (Ek and Monserud 1979). More recently, simulation of individual trees has been extended to larger landscapes with more spatial interactions, including dispersal and disturbance (Pacala et al. 1993; Liu and Ashton 1999; Lett et al. 1999; Keane and Finney 2003). These models contain multiple biotic and abiotic pools and offer opportunities for answering fine-scale questions that are significantly dependent upon short-distance spatial interactions. Similar to gap models, these models have had limited application at broader scales due to the computational overhead and intensive parameterization required.

FLSMs designed to simulate broader extents ($>10^4$ ha) often represent ecosystem processes using relatively simple growth, mortality, and decay functions (Keane et al. 1996; Scheller and Mladenoff 2004). By necessity, such models exclude many finer-scale interactions, such as shading caused by neighboring cells. These models benefit from direct and indirect links to relatively simple ecosystem process models, such as PnET-II (Aber and Federer 1992; Scheller and Mladenoff 2004) or FOREST-BGC (Running and Gower 1991; Keane et al. 1996) and simultaneously include broad-scale spatial interactions and dynamic communities.

Discussion

Strategies for deploying FLSMs

Increases in model availability and usability provide an opportunity to open up the modeling process to more forest ecologists and managers. However, a friendly interface cannot overcome the inherent limitations found in every model. Modeling requires many choices between extent and resolution, precision and generality, accuracy and meaningful prediction, parameterization and validation (Levins 1966; Baker and Mladenoff 1999; Mladenoff 2004).

Our classification can serve as a guide insofar as it can help elucidate what kind of model will be appropriate for a researcher or manager. Each research question will require that different weights be applied to our three criteria and the classification system can be customized into a unique decision tree based on an individual ranking of the three criteria. Although each model group is diverse, there are common assumptions within each group that will limit hypothesis testing or the scope of the projections generated. Often, the scale or resolution of potential hypotheses is implicitly limited within a group. Whether a particular FLSM will be appropriate is dependent upon the model's generality, availability, and the quality of documentation. If the creation of a new FLSM is required, our classification can serve as a guide to making assumptions and balancing comprehensiveness and tractability.

An equally important decision is the choice of scenarios. Scenarios can produce projections of landscape change or can be used to test hypotheses (Aber 1998; Dale and Winkle 1998). Dependent upon the confidence in the simulated process formulation, one approach or the other may be appropriate, but rarely both. Comparisons among scenarios can provide meaningful indicators of trends and likely changes in system behavior. Management decisions can immediately benefit from these general indicators of the consequences of management choices (Carpenter 2000; Clark et al. 2001). Alternatively, scenarios can be used to test hypotheses at temporal and spatial extents for which no other route to hypothesis testing exists (Pielke 2003). In this sense, FLSMs are similar to any tool in that deciding how to use the tool is as important as choosing the proper tool.

Although the scope and application of FLSMs continues to expand, FLSMs are never appropriate for making predictions about the timing and location of events. The causes that precipitate sudden landscape change (including disturbance and land use change) are driven by stochastic or idiosyncratic events that prevent site and time specific prediction. Furthermore, the inherent complexity of FLSMs limits their predictive power (Oreskes 2003) and no FLSM can represent all relevant processes. Model results should therefore always be presented as qualified 'projections' (Dale and Winkle 1998). These projections are limited by our ability to formulate meaningful questions and describe plausible futures through scenarios.

Remaining challenges

Validation remains a challenge at broad spatial and temporal scales (Rastetter 1996), particularly under unexpected environmental conditions, as may be produced by climate change or species invasions (Rykiel 1996; Rastetter 1996). We define validation as the 'quantitative comparison of model results against observations' (Prisley and Mortimer 2004). Although tools for validating known landscape patterns exist (Gardner and Urban 2003), validation of many landscape-scale phenomena remains difficult. For example, U.S. Forest Inventory and Analysis (FIA) data are spatially extensive but the resolution of the data is relatively coarse (Hansen et al. 1992). At best, FIA data can only provide bounds for model output. Similarly, analyses of existing empirical data for corroboration can suffer from uneven spatial and temporal resolution, differing units, and varying motivations for data collection. Nevertheless, validation is not insurmountable. As more FLSMs generate increasingly quantitative projections and more empirical data become available, greater validation of individual ecological processes (represented as model components) is possible. After achieving such reductionist validation, the validation of the interactions between processes will be the next significant challenge.

Another large contribution of FLSMs can be to our understanding of uncertainty. Uncertainty can be divided into three components: model uncertainty (internal representation of an ecological process), inherent uncertainty (stochastic variation), and parameter uncertainty (the measured and natural variation of model inputs) (Higgins et al. 2003; Peters et al. 2004). FLSMs with a flexible architecture can help quantify model uncertainty by allowing different algorithms to be tested within the same modeling framework, thereby isolating the effects of process representation. Model uncertainty can also be assessed through cross-model comparisons (e.g., VEMAP Members 1995; Badeck et al. 2001; Burke et al. 2003). Inherent uncertainty can be assessed within FLSMs by incorporating stochastic variation when simulating many processes. Scenarios can address parameter uncertainty by encompassing significant sources of uncertainty. For example, if future disturbance rates are highly uncertain, scenarios could be designed to represent the highest and lowest expected disturbance rates. New computational methods have also been developed to separate the relative contribution of sources of uncertainty and increase inferential and predictive power (Clark 2005).

Finally, many existing models risk becoming 'black boxes' to model users and many implicit assumptions are often overlooked. Consequently, the risk of mis-application and misunderstanding of model results will increase. Therefore greater transparency in model intentions, assumptions, and limitations will be required for further acceptance by managers and policy makers (Aber et al. 2003). In this regard, advances in model architecture (Scheller et al. in press) and implementation of the emerging open-source paradigm can increase model rigor while simultaneously enhancing comprehension.

Conclusions

FLSMs reflect the changing focus of ecology and society (Mladenoff 2004). Placing FLSMs into this broader context highlights the implicit and explicit assumptions and the ecological choices that ultimately dictated their design and behavior. Model designers and users must acknowledge these compromises, assumptions, and weaknesses if their results are to be used by policy or decision makers.

FLSMs have made tremendous contributions to understanding forest landscape change and have been particularly valuable to forest management. Nevertheless, many management challenges remain to be substantially addressed at broad scales. Examples include the effects of nutrient deposition, changes in atmospheric chemistry, exotic or invasive species, and landscape change caused by rural development and fragmentation. These and other issues confronting managers and policy makers can be expected to increase the need for FLSMs and will likely determine the future scope and application of FLSMs.

Acknowledgements Dean Urban and two anonymous reviewers provided an excellent review and contributed significantly to the final product. Numerous other people have provided critical review, including Monica Turner, Stephen Carpenter, and Volker Radeloff.

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