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REVIEW ARTICLE

The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models

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Abstract
Context Quantitative models of forest dynamics have followed a progression toward methods with increased detail, complexity, and spatial extent.
Objectives We highlight milestones in the development of forest dynamics models and identify future research and application opportunities.
Methods We reviewed milestones in the evolution of forest dynamics models from the 1930s to the present with emphasis on forest growth and yield models and forest landscape models We combined past trends with emerging issues to identify future needs.
Results Historically, capacity to model forest dynamics at tree, stand, and landscape scales was constrained by available data for model calibration

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and validation; computing capacity; model applicability to real-world problems; and ability to integrate biological, social, and economic drivers of change. As computing and data resources improved, a new class of spatially explicit forest landscape models emerged.
Conclusions We are at a point of great opportunity in development and application of forest dynamics models. Past limitations in computing capacity and in data suitable for model calibration or evaluation are becoming less restrictive. Forest landscape models, in particular, are ready to transition to a central role supporting forest management, planning, and policy decisions.
Recommendations Transitioning forest landscape models to a central role in applied decision making will require greater attention to evaluating performance; building application support staffs; expanding the included drivers of change, and incorporating metrics for social and economic inputs and outputs.

Keywords Process model · Individual-tree model · Gap model · Model validation · Ecosystem services · LANDIS · TreeMig · Forest Vegetation Simulator

Introduction

Forecasting forest change is essential to forest management, and over the past century the suite of quantitative modeling tools available to aid forest management decision-making has become increasingly sophisticated, quantitative, spatially explicit, and inclusive of multiple drivers of forest change (Moser 1980; Mladenoff and Baker 1999; Mladenoff 2005). The development and application of forest dynamics models has historically been constrained by the availability of computing capacity, observational data on forest change, and supporting software (e.g. for geographic information systems or GIS) (e.g. Moser 1980; Ek et al. 1988; Leary 1988; Mladenoff 2004; Risser and Iverson 2013). However, in recent decades model developers and users benefited from remarkable advances in modeling approaches, computing capacity, the body of observational data from which to calibrate and test predictive models, and knowledge about impacts of exogenous disturbances on forests. These advances removed some barriers to modeling forest dynamics, but they have also increased expectations for model access, performance, and relevance to emerging issues. Growing interest in issues other than timber production has demanded greater use of spatially explicit modelling methods that permit landscape-scale analyses in addition to tree- and stand-scale considerations that were emphasized in the early decades of forest dynamics modelling.

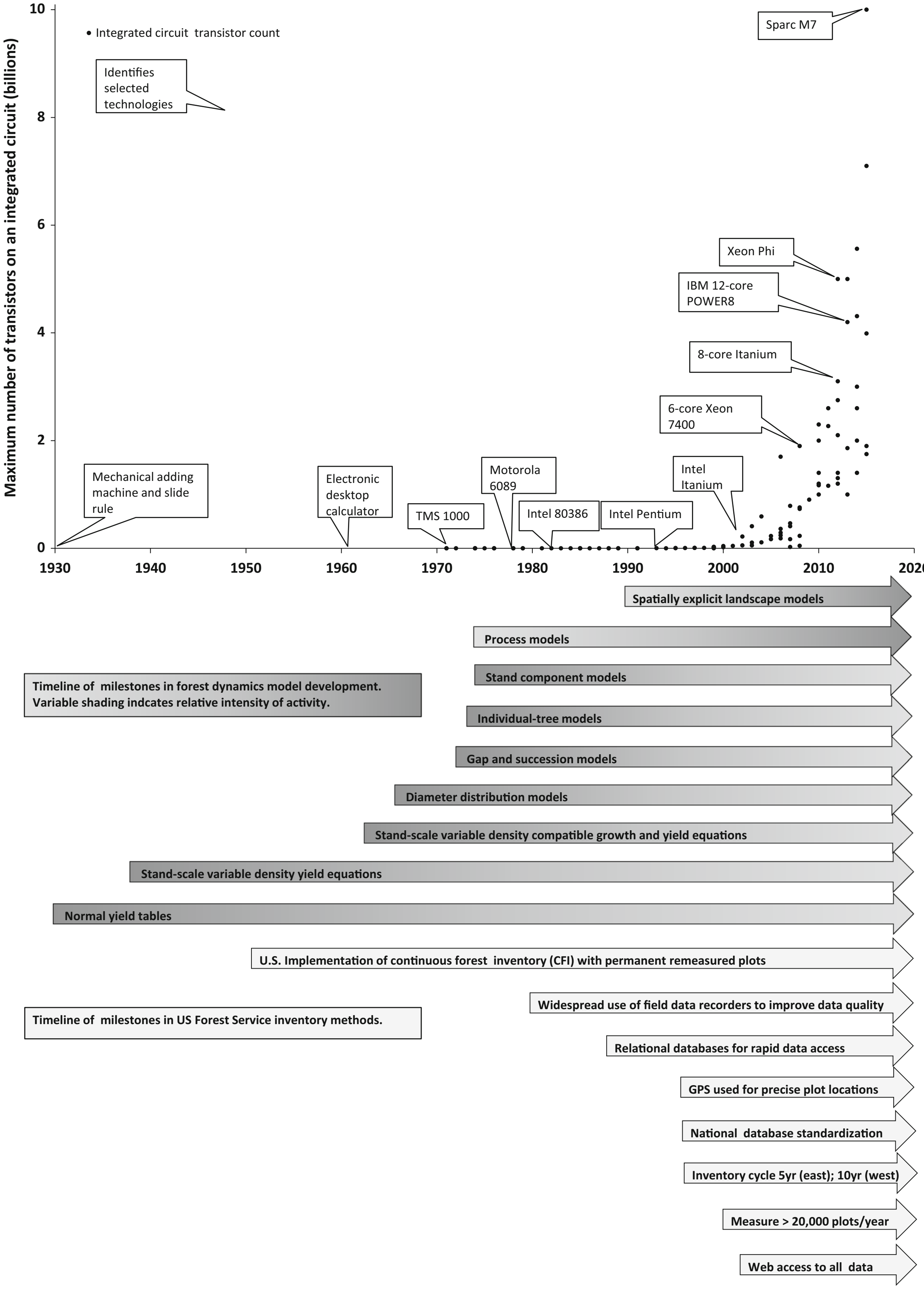
We briefly summarize progress and milestones in the evolution of forest growth and yield models and forest landscape models from the 1930s to the present, with emphasis on how progress has been linked to computing capacity and data availability. We subsequently identify specific actions needed to support future forest landscape model development and application.

Fig. 1 Time line of milestones in computing capacity, forest dynamics model development, and forest inventory data collection. "Moores' Law" (Moore 1965), backed by 40 years of empirical evidence, suggests the number of transistors on an integrated circuit (i.e. a computer chip) will double about every 2 years, leading to exponential increases in computing capacity *Sources* Wikipedia contributors (2016a, b) for transistor counts; personal communication with Dennis May, US Forest Service, for forest inventory milestones 18 Feb 2016 ►

Forest growth and yield models

The initial impetus for modeling forest dynamics was to estimate timber yields over time and thereby improve efficiency of timber production. The development of variable density yield equations (MacKinney et al. 1937) initiated the era of statistical (or empirical) growth and yield modeling. Regression models applicable to disturbed stands predicted future yield (or future periodic growth) as a function of current stand conditions and time. However, early regression models were limited to those that could be fit using a mechanical calculator and calibration data describing forest change over time were in short supply (Fig. 1).

Subsequent forest dynamics models incorporated systems of differential equations describing stand growth over time as the first derivative of yield over time for even-aged and uneven-aged stands (e.g. Clutter 1963; Moser and Hall 1969). Increased availability of detailed forest inventory data supported the development of complex systems of differential or difference equations that simultaneously modeled change in individual components of stand growth (Beers 1962; Moser 1974) including ingrowth, growth of surviving trees, mortality, and harvest. During the same period, diameter distribution models were developed that modeled change over time in the


Maximum number of transistors on an integrated circuit (billions)
• Integrated circuit transistor count
Identifies selected technologies
Mechanical adding machine and slide rule
Electronic desktop calculator
TMS 1000
Motorola 6089
Intel 80386
Intel Pentium
Intel Itanium
6-core Xeon 7400
8-core Itanium
IBM 12-core POWER8
Xeon Phi
Sparc M7
0
2
4
6
8
10
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Spatially explicit landscape models
Process models
Stand component models
Timeline of milestones in forest dynamics model development. Variable shading indcates relative intensity of activity.
Individual-tree models
Gap and succession models
Diameter distribution models
Stand-scale variable density compatible growth and yield equations
Stand-scale variable density yield equations
Normal yield tables
U.S. Implementation of continuous forest inventory (CFI) with permanent remeasured plots
Widespread use of field data recorders to improve data quality
Timeline of milestones in US Forest Service inventory methods.
Relational databases for rapid data access
GPS used for precise plot locations
National database standardization
Inventory cycle 5yr (east); 10yr (west)
Measure > 20,000 plots/year
Web access to all data

parameters of a diameter distribution (e.g. the Weibull distribution) and provided great flexibility in summarizing products by size class (Clutter and Bennett 1965; Burkhart 1971; Bailey and Dell 1973).

Empirical, individual-tree-based growth models flourished in the 1970s and 1980s with advent of the personal computer. They were intuitive in predicting growth and survival over time for individual trees on inventory plots, and cumulative change for the stands and landscapes represented by the inventory plots (e.g. Arney 1972; Stage 1973; Ek and Monserud 1974; Leary 1979), but they did not model spatially explicit landscape processes such as spread of fire or pathogens. Early development of empirical individual-tree-based growth models was constrained by limited data and computing capacity, but since the mid 1980s empirical individual-tree, distance-independent models exemplified by the forest vegetation simulator (FVS) have gradually become the dominant methodology for making operational, site-specific estimates of future forest change over time, with or without harvesting, fire, or climate effects (Crookston et al. 2010; US Forest Service 2016b). The notable exception is for planted conifers, where stand-scale models continue to dominate applications (e.g. Burkhart and Tomé 2012).

FVS model variants have been calibrated and validated for most regions of the U.S. and are readily linked to forest inventory databases to set initial forest conditions and to enable localized model calibration and validation. That process has been facilitated by a permanent U.S. Forest Service support staff serving private and public land managers. The outcome is a mature modeling technology that is documented, validated, integrated with forest inventory systems, and routinely applied to support on-the-ground forest planning and silvicultural decisions. Outputs of projected forest conditions include tabular and graphical summaries as well as three-dimensional visualizations.

There has been a propensity to increase the spatial extent of applications of growth and yield models and to integrate landscape-scale processes (e.g. seed dispersal, spread of wildfire, insects, diseases, climate change) and management for non-timber forest attributes (e.g. wildlife habitat over time) (Dixon 2002; Rebain 2010). Initially, such efforts were hampered by a lack of field inventory data or remotely sensed data describing initial forest conditions seamlessly across a landscape, lack of software suitable for manipulating geographically referenced data at the landscape scale, and lack of computing capacity to model landscape-scale, spatially explicit changes for landscapes thousands of hectares in extent. To some degree, those limitations have been overcome for modeling landscapes encompassing thousands of hectares (Crookston and Stage 1991), but not for applications spanning millions of hectares as is the case with some of the forest landscape models discussed in the following section.

Spatially interactive forest landscape models

Forest landscape models (FLMs) simulate forest stand dynamics in conjunction with interactive forest landscape processes in a spatially explicit (i.e., mapped) framework (Scheller and Mladenoff 2007; He 2008). Although many types of forest dynamic models can be spatially explicit, FLMs additionally model forest landscape processes—spatial and stochastic processes that include seed dispersal; natural disturbances such as fire spread, windstorms, avalanches, insect and disease propagation; and human influences such as forest harvesting, fuel treatment, and climate change. FLMs divide the simulated landscape into sites (or points or raster cells; the smallest unit of spatial resolution) with forest dynamics simulated for each site, and spatially interactive forest landscape processes simulated over all or a subset of sites. With current technology, sites typically range from 0.1 to 300 ha in size for landscapes ranging from 10^5 to 10^9 ha in extent. By simultaneously modelling site-scale forest dynamics and landscape processes across mapped forest landscapes, FLMs introduced a new paradigm for modeling forest dynamics.

Because the computation loads for FLMs increase nonlinearly with increasing landscape size and complexity, FLMs typically simplify site-scale processes (e.g. competition at the tree level) in order to make landscape scenario analyses possible within the confines of available computational capabilities (Mladenoff and Baker 1999; Mladenoff 2004). In contrast to forest growth and yield models that track the species, number, and size of each tree on site or stand, early FLMs did not explicitly simulate site-scale forest dynamics. Rather, variables from simulated forest landscape processes were used as a surrogate for those dynamics. The elapsed time since last fire, for example, was used to represent the age of trees on a site or the amount of accumulated fuel (Baker et al. 1991; Li et al. 1997; Cary 1998). The original LANDIS model (Mladenoff et al. 1996; Mladenoff and He 1999) used species age cohorts as a measure of forest structure and site occupancy. Recent FLMs incorporate more quantitative information at each site (e.g. seed number, total biomass, number of trees by age or height class, or in some cases individual trees with explicit positions), thus increasing the detail of site-scale forest dynamics. Alternative FLMs differ in how they balance the level of detail for each site and/or the complexity of modeled forest landscape processes given practical constraints on computing and the mechanisms needed to simulate robustly the processes of interest. The following are specific examples.

TreeMig tracks species-specific seed densities in the seedbank and tree population densities in height classes at each cell (Lischke et al. 2006). It captures dynamic within-stand heterogeneity in terms of species composition and vertical and horizontal stand structure. Besides modeling recruitment, growth, mortality and light competition as in gap-models, TreeMig includes processes and interactions essential for modeling landscape dynamics: seed production, seed density regulation, and seed dispersal. Thus, the model simulates patterns and shifts in species composition over time. Climate is a primary driver and basic model processes are formulated as temperature and precipitation dependent. Disturbances are simulated as generic, spatially-random mortality.

LANDIS II simulates biomass for each species age cohort (Scheller et al. 2007). The ratio of actual to potential biomass for a cell mimics resource availability (growing space), and assumes species-age cohort biomass implicitly incorporates density information. Potential biomass in LANDIS II is derived empirically (Smith et al. 2006) or derived from species-specific maximum aboveground net primary productivity estimated using the stand-level ecophysiological model PnET II (Aber et al. 1995). Recently, De Bruijn et al. (2014) developed a more mechanistic approach to simulating growth within LANDIS-II by embedding algorithms of PnET-II to simulate growth more mechanistically as a competition for light and water to support photosynthesis. As discussed in later sections, the practice of embedding stand-scale models to drive the site-scale forest dynamics within a FLM is a natural progression that is facilitated by advances in computing capacity.

LANDCLIM tracks the number of trees and biomass by species and age cohort (Schumacher et al. 2004). It is unique in introducing gap model dynamics into simulated site-scale dynamics by including the interactions of abiotic variables (soil water, and climate) and biotic variables (tree size). Stand-scale resource competition is modeled as shading and by a growth- and density-dependent mortality function based on site biomass relative to maximum potential biomass. Additionally, large-scale disturbances such as wind throw, wildfires, and bark-beetle infestations are modeled. Results are evaluated in terms of ecosystem services, e.g. protection against natural biohazards (Bugmann et al. 2014).

iLand represents a novel approach to integrate functional, structural, and spatial processes and their interactions through an individual-based model framework (Seidl et al. 2012). The model tracks the location and attributes of each individual tree within a cell. The approach is coupled with physiology-based resource use modeling, including competition for light via an upscaled shade-surface, and is embedded in a robust scaling framework to address landscape-level dynamics. iLand represents a FLM with exceptional detail at the individual cell level, but applications are therefore limited to relatively small areas.

LANDIS Pro models density and basal area for each species-by-age class cohort to track forest composition and structure for each cell (Wang et al. 2013). The model simulates population dynamics with competition intensity for each site quantified by the relative proportion of the total growing space that is occupied, with growing space estimates based on Reineke's (1933) stand density index. LANDIS PRO is designed to be compatible with standard U.S. Forest Service inventory data; consequently, detailed inventory data can be directly utilized for model initialization, calibration, and validation (Wang et al. 2014b). Unlike other FLMs, climate does not directly drive tree growth in LANDIS Pro. Rather LANDIS Pro can be coupled with an ecophysiological model, LINKAGES (Dijak et al. 2017), which uses daily weather data as a driver and simulates biogeochemical cycling and tree species growth and survival response to climate and soils variables. Relative growth and survival values by ecoregion and climate scenario are used to establish relative success rates for species establishment and maximum growing space (Wang et al. 2014a).

A note about process-based models of forest dynamics

We recognize that in addition to the growth and yield models and forest landscape models briefly summarized above, there are numerous other pioneering methodologies for modeling forest dynamics. Most notable are process-based models that focus on knowledge of plant demographic and biogeochemistry to model the underlying processes that drive forest change. This class of models has been actively developed since the 1970s (Botkin et al. 1972a, b; Shugart 1984; Landsberg et al. 1991; Tiktak and van Grinsven 1995; Landsberg 2003). The models often couple plant carbon budgets to environmental drivers—commonly climatic variables (e.g. temperature) and/or biogeochemical processes (e.g. nitrogen cycle) (Battaglia and Sands 1998). Such coupling not only enables process-based models to simulate forest responses to variations in environmental conditions (e.g. interannual precipitation variation) but also makes them valuable tools to study forest responses to novel conditions (e.g. future climate change) for which there can be no empirical observations of forest response (Bugmann 2001; Johnsen et al. 2001; Landsberg 2003; Medlyn et al. 2011).

Process-based models can be generally classified as simple demographic, simple physiological, complex physiological, and hybrid empirical-physiological models based on the complexity of ecological processes represented (Jin et al. 2016). As indicated in the previous section, process-based models such as simple physiological model PNET-II (Aber and Federer 1992; Aber et al. 1995) have been incorporated into the LANDIS-II FLM framework to model site-scale carbon budgets based on relationships between environmental and biological variables and the photosynthetic rate. And likewise the hybrid empirical-physiological model LINKAGES-II (Pastor and Post 1986; Wullschleger et al. 2003; Dijak et al. 2017) has been applied to estimate differential site-scale species dynamics in response to climate change in the process of calibrating LANDIS Pro to model forest response to alternative climate scenarios (Wang et al. 2016).

The following sections, while recognizing the contributions of process-based models individually and coupled with forest landscape models, principally focus on actions necessary to make forest landscape models better suited to supporting applied forest management decision-making with reference to the historical evolution of applied forest growth and yield models.

Progress and limitations in modeling forest dynamics

If we view developments in forest dynamics modeling over the past 80 years, we appear to be in a time of great abundance and opportunity. Data suitable for model calibration, validation, or implementation have never been more abundant and accessible from field inventories and remote sensing platforms. Computing capacity available for model development or application has expanded exponentially over the past three decades (Fig. 1). Software for model calibration, testing, and implementation is sophisticated and widely available. However, these assets come with the caveat of increased expectations for the capability and relevance of forest dynamics models, particularly forest landscape models, to address real and complex on-the-ground forest management and planning problems. Meeting those expectations requires effort to expand the reach of contemporary FLMs from tools used principally for scientific inquiry to tools essential for applied forest management and planning. FLMs have a potentially large role to play in assessing long-term, large-scale cumulative effects of forest management actions and inactions including information requirements for the National Environmental Policy Act (NEPA) (Council on Environmental Quality 1997) and the Endangered Species Act (US Fish and Wildlife Service 1973).

If we look at the current situation with regard to FLM development, testing and application, there are many parallels with the situation for individual-tree-based growth and yield models 30 years ago (e.g. Stage 1973; Leary 1979; Wykoff et al. 1982; Miner et al. 1988; Mladenoff and Baker 1999; US Forest Service 2016b). Specifically, the scientific basis of FLMs has been well described in the literature, and the models have been calibrated for several geographic regions. In a few specific situations, models have been validated using observed data, but comparisons among alternative models are rare. Data describing initial forest conditions necessary for FLM implementation are widely available, but those data often must be transformed with additional assumptions to match requirements of a given model. Computing resources required for single, simple model applications are sufficient, yet for a better model calibration (e.g. by Bayesian approaches) or optimization of management, computing time is still limiting. Most FLMs lack user-friendly interfaces and have a steep learning curve. Technical support for model applications is mainly ad hoc by model developers rather than offered by permanent support teams. The utility of the models to support practical forest management and policy decisions has been demonstrated (Leefers et al. 2003; Zollner et al. 2005; Rittenhouse et al. 2011; Brandt et al. 2014; Butler et al. 2015; Gustafson et al. 2016), but there is an ongoing push for the models to incorporate more site-scale detail about forest conditions and to accommodate larger geographic regions. Linkages to models that use modeled forest conditions to quantify forest-associated products and services such as wildlife habitat, biodiversity, or fire effects are straightforward in concept but not widely implemented (Millspaugh and Thompson 2009; LeBrun et al. 2017). And finally, there is need to incorporate socio-economic factors that drive forest change and those that respond to forest change.

In contrast to the similarities listed above, there are some notable ways that the FLMs differ from individual-tree-based growth and yield models of 30 years ago. More time and technical skill is needed to prepare mapped input data layers for FLM implementation and for analysis of results. It is more difficult to calibrate and validate FLMs that address large-scale forest change scenarios including tree species succession and exogenous disturbances such as climate change. FLM applications to address contemporary forest management and policy issues demand massive computing resources. Although the exponential rate at which computing capacity is increasing (Fig. 1) generally outstrips the rate at which FLM applications demand increased computing resources, this trend will reach a limit (Powell 2008), and even access to unlimited computing resources would not suddenly remove the barriers to new, creative FLM applications. Moreover, the expectation of expanding computing and data resources can be figured into plans for future FLM development (Mladenoff 2005).

As the science behind individual-tree-based growth and yield models matured in the 1970s and 1980s, permanent support staffs were established for model maintenance, improvement, and user training. That has been instrumental in widespread application of those models to support forest planning decisions and evaluation of silvicultural alternatives. Significant new developments by those research and development staffs focused on improving the user interface, training, automated calibration and validation, linkages to other forest-associated resources (e.g. fuels, carbon, wildlife), and modelling the effects of biological and anthropogenic disturbances including climate change (Dixon 2002; Crookston et al. 2010).

The future of forest landscape dynamics modeling

Given the historical context and current capabilities in forest dynamics modelling, several opportunities emerge, that if addressed, would result in significant progress in application of forest landscape models. The focus here is on forest landscape models because collectively that class of models appears poised to make the transition from research tools to applied tools suitable for addressing complex forest management and policy issues. The following sections provide additional detail on several such needs and opportunities.

Evaluate forest landscape model performance

Model evaluation is the process of determining if a model is suitable for its intended use and specifically if it is preferable to alternative forecasting methods that could be used instead (Johnsen et al. 2001). Thus, evaluation is context-specific and relative. Evaluation includes spatial and temporal validation of model forecasts, verification that computer code and embedded empirical or stochastic models are operating as intended, and assessment of the user interface (Buchman and Shifley 1983). Significant shortcomings in any of those three areas limit the utility of FLMs in applied decision-support.

Validate model forecasts

Validation or “demonstration that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with its intended application" (Rykiel 1996) has been especially problematic with FLMs. Rykiel (1996) suggests that data-intensive validation is not always a requirement for models used exclusively for research, but it is for operational models and in the latter context requires a comparison of modeled forest landscape change with observed changes for a comparable real forest system. Such comparisons are complicated by the large spatial scale (thousands to millions of hectares) and long temporal scales (a century or more) at which FLMs are typically applied. Practical validation methods for operational FLMs include quantitative comparisons with long-term field studies, cross-model validation comparing FLM estimates with estimates from other models, and evaluation by expert opinion panels.

Recent work has demonstrated that FLMs can be validated through quantitative comparisons of long-term FLM forecasts against independent series of spatiotemporal data (e.g. Wang et al. 2014a; Gustafson et al. 2015). However, the capacity to do so is limited by the availability of forest landscape monitoring data that are large-scale, long-term and spatially explicit, but such data are increasingly available. For example, in the last decade data from 250,000 remeasured U.S. forest inventory plots have been placed in public databases, and in the future data describing forest change will continue to accumulate at a comparable rate (US Forest Service 2016a). Experimental or observational data spanning two or three decades are increasingly available for short-term FLM validation (e.g. LANDCLIM, Schumacher et al. 2004; iLand, Seidl et al. 2012; LANDIS PRO, Wang et al. 2014b). Data sources include results from long-term, landscape-scale field experiments (Shifley and Brookshire 2000; Adams et al. 2008; Purdue University 2016); time series of repeated remote sensing measurements (e.g. LIDAR, Landsat) that capture the seasonal to interannual vegetation changes as well as detect contemporary disturbance events and trends (e.g. the UMD Global Forest Change product, Hansen et al. 2013, 2017; LandTrendr, Kennedy et al. 2017); and data from observatory networks (e.g. FLUXNET, Oak Ridge National Lab 2017; NEON, National Science Foundation 2017) that provide continuous measures of the hourly to yearly soil–plant–atmosphere CO_2, water, and energy exchanges for different vegetation types.

Validation of long-term FLM vegetation change forecasts (e.g. 5 decades or more) is constrained to established theories of forest dynamics (e.g. Reineke 1933; Yoda et al. 1963; Gingrich 1967; Oliver and Larson 1996; Leary 1997; Wang et al. 2014b) and limited empirical studies (e.g. TreeMig, Lischke et al. 2006; LANDIS II, Scheller et al. 2007). Old-growth forest monitoring studies provide references for forest composition and structure of late-successional forests (under a past climate and without anthropogenic disturbances).

When there are no suitable field data against which to validate FLM estimates of forest change (for example when modelling future forest dynamics under a changing climate) cross-model validation is desirable. For example, cross-model comparison is one of the approaches used to validate climate forecasting within the Intergovernmental Panel on Climate Change (IPCC) and has proven effective in building confidence in forecasts of future climate trends and variation for a given future greenhouse gas emissions scenario (Gates et al. 1992). In the same manner, results from FLMs can be compared to results from alternative modelling techniques. A recent example by Iverson et al. (2016) compares estimated future changes in the spatial distribution of trees under alternative climate scenarios for a species distribution model (Tree Atlas: Iverson et al. 1999), a hybrid empirical-physiological model (LINKAGES; Pastor and Post 1986; Wullschleger et al. 2003; Dijak et al. 2017), and a forest landscape model (LANDIS PRO; Wang et al. 2013; Wang et al. 2014a). Model comparisons such as this one do not indicate if model estimates are correct, but they can boost confidence in model forecasts when different modeling approaches produce similar results.

The focus of FLM validation is on comparisons of aggregate measures of landscape condition over time for future disturbance scenarios. For a given scenario, FLM forecasts are intended to be representative of future landscape conditions. Stochasticity in real and modeled disturbance processes (e.g. for wind, fire, harvest) renders meaningless any site-to-site comparisons of actual and modeled forest change. Reality is but one possible outcome of the inherently stochastic processes that shape landscapes, so it is most informative to compare the statistical distribution of landscape metrics between real and modeled landscapes. For example, Wang et al. (2014b) compared the predicted density and basal area by species group from LANDIS PRO outputs against data from Forest Inventory and Analysis plots (US Forest Service 2016a) at 1988, 1993, 2003, and 2008 for a landscape in Northern Arkansas (Fig. 2). The comparisons were stratified by land types to reduce the variation due to exogenous forces (e.g., soil, terrain, climate). Although only mean values are shown in Fig. 2, the distribution of values around each mean was used to statistically test differences between predicted and observed estimates.

Incorporation of expert panels in the model review process subjects the modeling process and predictions to scrutiny based on experiences outside those of the model developers. Even when data-intensive or cross-model validation methods are used, expert panels should be part of the continuous model validation process. Local experts act as a coarse filter to identify model behaviors and outputs that appear unreasonable in a given ecosystem. This is particularly important when the intent is for FLM applications to guide forest management decisions (e.g. Leefers et al. 2003; Zollner et al. 2005; Rittenhouse et al. 2011; Brandt et al. 2014; Butler et al. 2015; Gustafson et al. 2016). Model forecasts are unlikely to be accepted by managers if they cannot be reconciled with long-term observations of forest-change by local experts having decades of field experience.

Verify computer code

As software for model implementation becomes more sophisticated and complex, model verification—ensuring the computer code performs as intended—becomes increasingly important and difficult. Modern software engineering techniques that include iterative unit testing can almost completely eliminate coding errors in simulation models (e.g. Scheller et al. 2010). Modular programming with interchangeable program

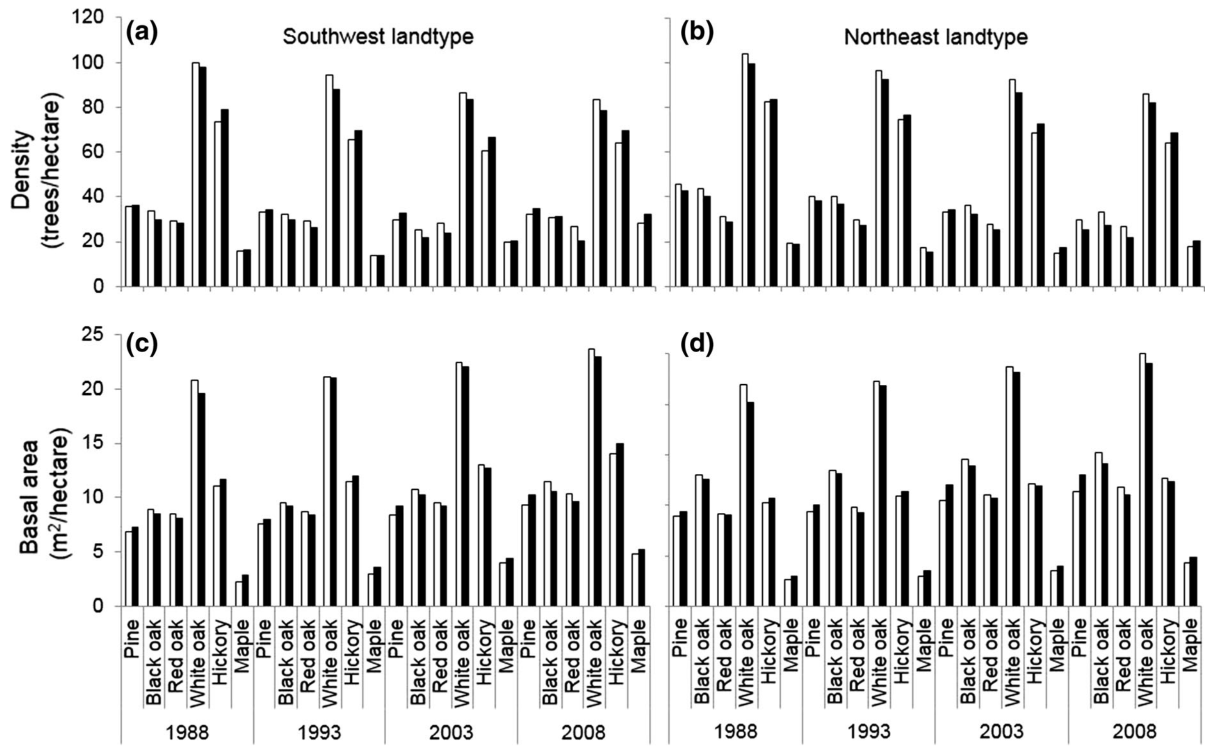


Fig. 2 Comparison of predicted mean density and basal area by species group from LANDIS PRO outputs against observed mean values from Forest Inventory and Analysis plots (US Forest Service 2016a) at 1988, 1993, 2003 and 2008 for a landscape in Northern Arkansas. From Wang et al. (2014b). *Open bars* are modeled estimates; *filled bars* are observed values from a field inventory

components can also help in this regard (Baker and Mladenoff 1999). Verification for FLMs requires establishing benchmark data suitable for identifying intended and unintended consequences of programming changes or of new components added to the model. Verification can also lead to an upscaling of the model (Lischke et al. 2007), e.g. by aggregating individuals to populations (Lischke et al. 1998), by converting random disturbances to survival probabilities (Scherstjanoi et al. 2013), or by simulating local processes only in representative cells in a landscape (Nabel 2015), which yields simpler and more efficient models.

Assess the application environment

The FLM application environment includes all the practical considerations that make a model easy or difficult for a user to apply. The situation for every user is different, but there are common questions and issues (Buchman and Shifley 1983). For example, is there formal or informal user support? What is the state of model documentation? What prerequisite skills are required by a user (e.g. programming or GIS skills)? How easy is the model to obtain, install and maintain? Are data requirements for model application compatible with the data the user has available? Does the user interface provide error checking for erroneous input data, and can the system estimate values for missing data? Is model output in a format that that makes spatial and non-spatial attributes of modeled scenarios easy to examine?

For practical applications, the FLM application environment is often the first consideration of a potential user. If the application environment is not compatible with technology, skills and data available to a potential user, the model will not be applied. The quality of user-support is an important part of the application environment and is discussed in the following section.

Provide technical support for model application

Increased application of FLMs for forest planning, management, and policy analysis will require attention to the user interface and other aspects of the application environment pertaining to ease of use. Developers of LANDIS II, for example, have put considerable effort into developing a user interface to visualize and evaluate model output (Gustafson et al. 2016), training materials, and networking among users. Although the complexity of FLMs may always require a high level of technical skill to initiate an analysis of future scenarios, the technical work could be simplified with permanent support staff dedicated to streamlined model implementation for contemporary forest management and policy problems. This approach—already proven successful for forest growth and yield model applications (US Forest Service 2016b)—can assist with distribution of software, improvement of a model's user interface, training, preparation of input data layers, summary and interpretation of results, model evaluation, and applications to inform forest planning, management, and policy decisions. At a larger spatial scale, a collaborative modelling approach has been applied with the Community Earth System Model (2016) to provide institutional-level support for an open-arm developer/user community to facilitate model verification in terms of coding and revision, and technical support for modeling applications. An expanded system of ongoing user support is required if FLMs are to make the transition from research tools to applied tools that can be routinely used for scenario analyses supporting long-term, large-scale forest landscape policy analysis, planning, and management.

Invest in shared efforts for model initialization

Developing the input files for FLM applications is time consuming. It requires preparing maps that describe site conditions (e.g. soils, landforms), land use, current vegetation, management areas, and disturbance probabilities (e.g. fire, harvest). In many situations, vegetation data are not available for initializing across a landscape the tree attributes required by a model, such as number of trees in height classes per cell and species (e.g. Lischke et al. 2006). In such cases, other observations and assumptions (e.g. remote sensing data, nearest neighbor imputation) must be applied to estimate initial landscape variables.

Our rule of thumb for FLMs is that about 60% of the effort goes into setup of the input files and disturbance scenarios, about 5% goes to actually running the modeled scenarios, another 15% goes to rerunning the models to rectify errors in the data or assumptions, and 20% goes to evaluating the results and deriving other forest-associated attributes (e.g. habitat quality for select wildlife species). There are economies of scale when using large standardized data sets such as public forest inventory data, remotely sensed imagery, topographic data, and soils data to describe initial conditions for each site on a large forest landscape (e.g. Dijak 2013; Duveneusck et al. 2015). New FLM applications would be facilitated if the required input data layers for large landscapes (e.g. countries, states, ecoregions, all National Forest holdings) were initialized in their entirety for use with one or more FLM and shared in the public domain.

Evaluate the utility of combining established stand-scale models with FLMs

The line is becoming blurred between FLMs with great site-scale detail and stand-scale models that can be applied to all forest stands on a given landscape. Exponential increases over time in computing capabilities (Fig. 1) have eased limitations on the level of detail that can be included and processed by a FLM for each site on a forest landscape. Likewise, for stand-scale process models or growth and yield models expanded computing resources have enabled development of techniques to estimate forest change over time simultaneously for multiple stands on a given landscape. Linking a FLM directly to a stand-scale growth and yield model or a process model for site-scale estimates of forest change is an intuitive next step. Already a variant of the LANDIS-II FLM uses the PnET-II ecophysiological model to estimate site-scale change in biomass for each time step (Gustafson et al. 2015). As computing capacity continues to increase, it is likely that developers will find it efficient to link detailed stand-scale process-based models (e.g. PnET (Aber and Federer 1992; Aber et al. 1995), LINKAGES (Pastor and Post 1986; Wullschleger et al. 2003), ED (Moorcroft et al. 2001; Medvigy et al. 2009)) or empirical models (e.g. FVS, US Forest Service 2016b) to FLMs to handle site-scale dynamics. This will increase site-scale detail carried in the FLM and it will inevitably force additional evaluations of model performance for FLMs as well as for the embedded stand-scale models. In the long run, such linkages will increase consistency in modeled dynamics across tree, stand and landscape spatial scales.

Develop FLMs as a framework for integrating knowledge of ecosystem services and human dimensions

As FLMs evolve to carry more detail about each site and as computing capacity becomes less restrictive, it becomes efficient to link other attributes to FLM scenarios over time. Linking forest products and services such as fuels, carbon, protection against rockfall and avalanches, and wildlife habitat suitability to FLMs has already been demonstrated (e.g. Gustafson et al. 2004; He et al. 2004; Larson et al. 2004; Zollner et al. 2005; Shifley et al. 2006; Elkin et al. 2013; Brandt et al. 2014; Zurbriggen et al. 2014; Butler et al. 2015). In most cases, ecosystem values and services are estimated after the fact from predicted changes to the forest landscape (loose coupling), and consequently opportunities for interactive coupling of multiple natural and human systems with integrated feedback loops (tight coupling) are not yet fully realized (but see, for example, Zurbriggen et al. 2014 and De Jager et al. 2016). The following sections discuss opportunities for integrating wildlife, hydrology and socio-economic models into FLMs.

Forest-associated wildlife

There is great interest in modeling forest-associated wildlife resources as a function of anticipated future forest attributes. Metrics of wildlife resources parallel those used for trees in forest models, including species habitat suitability, occurrence, abundance, population viability, and community-level attributes such as richness and diversity (Larson et al. 2009). Progress in wildlife modeling has followed a similar course to that of forest dynamics models and evolved from non-spatial models that utilize plot level forest measures to spatial models mapping abundance or viability at high resolutions over large areas based on remotely sensed data (Millspaugh and Thompson 2009).

Wildlife habitat suitability models were originally developed for use with field measurements of habitat attributes at the scale of a plot or management unit (US Fish and Wildlife Service 1981), but have since been adapted for application at landscape to regional scales through use of GIS (Donovan et al. 1987; Riitters et al. 1997; Dijak and Rittenhouse 2009) and applied with forecasts from forest dynamics models (Li et al. 2000; Marzluff et al. 2002; Larson et al. 2004). Wildlife habitat suitability models can be developed with knowledge from a variety of sources (empirical, expert opinion, or theoretical) and this flexibility has allowed researchers to match them with outputs from alternative forest dynamics models, including FLMs. Application of statistically derived empirical habitat models of occurrence or abundance to outputs from forest dynamics has been more limited, partially because there is often a mismatch in the variables and scale of inference of the two models. LeBrun et al. (2017) fit Bayesian hierarchical models to North American Breeding Bird Survey data from the Midwestern U.S. and used them to predict bird abundance under management and climate change scenarios simulated with the forest landscape model LANDIS PRO; they discuss some of the issues with matching empirical abundance models with a simulation model.

Forecasting wildlife species population trajectories and viability (rather than habitat suitability) as a function of forest dynamics is perhaps the most ambitious and complex goal for wildlife modeling; however, it is often the most useful way to assess future wildlife responses to alternative forest management scenarios. Population dynamics for wildlife species can be simulated using population matrix models in which demographic variables such as productivity, survival and carrying capacity are a function of modeled landscape attributes. Dynamic landscape metapopulation models are frameworks linking dynamic population models to dynamic landscape models (Akçakaya and Brook 2009; Bekessy et al. 2009). For example, ECOLECON (Liu 1993) links an individual-based wildlife population simulation with a forest growth and yield subroutine in a spatially explicit landscape (Liu et al. 1995). Akçakaya et al. (2004) linked a forest landscape model, LANDIS (He et al. 2005), with a wildlife metapopulation model, RAMAS GIS (Akçakaya 2006) to create RAMAS Landscape (Applied Biomathematics, Setauket, New York). Alternatively, wildlife population models can be loosely coupled with forest dynamic models by periodically updating model population parameters to reflect forest changes; Larson et al. (2004) modeled the viability of ovenbird (*Seiurus aurocapillus*) populations in Missouri using LANDIS and RAMAS GIS separately.

Ongoing research on hierarchical approaches to wildlife modeling is improving and accounting for uncertainties from different stages in a modeling framework, such as an animal abundance model and dynamic landscape model (LeBrun et al. 2017). Advancement in integrated wildlife population models and state-space models provide hierarchical approaches to simultaneously estimating demographic parameters from observation data and predicting responses to ecological processes (Schaub and Abadi 2011; Hostler and Chandler 2015). However, we are aware of no examples that link these models with a dynamic landscape model. We believe more realistically addressing uncertainties in dynamic population and landscape modes is important because of the increased use of structured decision making to formally address uncertainty in the decision process.

To date, outputs from FLMs have been used to estimate wildlife populations and wildlife habitat suitability, but estimates of wildlife abundance have not been applied reciprocally to model wildlife impacts on forest change. Wildlife herbivory is a case in point. In some regions of the eastern United States, browsing by white-tailed deer (*Odocoileus virginianus*) diminishes tree reproduction success differentially by species (Tilghman 1989). Tight coupling of FLMs and wildlife population models will be necessary to address that interaction by incorporating deer browsing pressure in modeled forest reproduction dynamics (De Jager et al. 2016). That particular interaction is further complicated by the socio-economic drivers of hunting regulations and deer harvests that also affect browsing pressure.

Water

The condition and proportion of forest cover on a landscape are tightly correlated with the quantity and quality of water produced from the landscape. Linking hydrology models to FLMs provides a mechanism to examine how natural forest changes, anthropogenic land use change, or alternative scenarios of forest management are likely to affect water yield, water quality, and avalanche risk.

In forested landscapes, changes in water yield are linked to changes in forest condition. Reductions in basal area or leaf area index at stand and landscape scales are known to increase water yield, but the amount and duration of increases depend on climatic conditions and the rate of forest regrowth (Hibbert 1967; Hornbeck et al. 1995; Brown et al. 2005). Paired catchment studies indicate that reductions of at least

15% of basal area are required for a detectable increase in water yield (Stednick 1996). Such changes commonly result from timber harvesting but may also be caused by other natural or anthropogenic disturbances. Prescribed fires for fuelwood reduction treatments have relatively little impact on water yield (Elliot 2010), and the impact of wildfires depends on their severity and extent. At the stand scale, increases in water yield due to timber harvest and other silvicultural procedures that reduce basal area are well documented (Troendle and Leaf 1980), but they are often short-lived. Increased water yield following basal area reductions rarely persist longer than 10 years without subsequent treatments (Hornbeck et al. 1995). Forest landscape model scenarios that track tree age, size, density, basal area, stocking or biomass can be linked to such hydrologic relationships and used to estimate the associated landscape-scale change in water yield over time. Such forest landscape/hydrology models should ideally include the full feedback (tight coupling) among soil, water, and forest dynamics, because not only does the forest structure influence hydrology, but also the water supply affects forest development and structure. This creates a feedback with the potential to dampen the effects of dry climates (Lischke and Zierl 2002).

In contrast to fluctuations in water yield associated with forest management practices, increases in water yield are permanent when forest land is converted to a non-forest land use category, and those increases are usually accompanied by a reduction in water quality. On the other hand, newly established forests due to land abandonment or afforestation can decrease water yield from these areas (Schattan et al. 2013). Thus, effective modeling of water yield and quality in association with an FLM must account for anticipated changes in land use. The proportion of forest cover is an important indicator of water quality in a given watershed; high water quality is associated with a high proportion of forest cover. Increases in agricultural, urban, or industrial land uses are associated with increased stream temperatures, sediments, nutrients, pesticides, and other pollutants (Tavernia et al. 2016). Thus, forest landscape models–particularly when linked to land use models that track area changes among land-use classes—provide a mechanism to tie future land management scenarios to water quality as well as water quantity. Forest landscape models that incorporate alternative climate scenarios, forest management scenarios, and land use scenarios are well suited to modeling water yield information in a manner that integrates socio-economic and biophysical changes at the landscape scale, e.g. by the Water Supply and Stress Index (Sun et al. 2008; Tavernia et al. 2013).

Water in another aggregate state, namely as snow-avalanches, can affect people living in mountainous areas. Avalanches are linked to forests because forests can impede avalanche release depending on their cover, grade, structure and density. Using forest landscapes in the Swiss Alps generated by the LANDCLIM FLM for different climate change scenarios as input to an avalanche release model showed decreased protection against avalanche release at nearly all elevations. Protection is expected to increase only above the current timberline, because with climate change new forest cover is expected to become established there (Elkin et al. 2013). Forests are destroyed by avalanches, which leads to a positive feedback (more avalanches—less forest—more avalanches), so Zurbriggen (2013) and Zurbriggen et al. (2014) coupled the FLM TreeMig with an improved avalanche release model and an avalanche flow model. Their simulations showed that closing the feedback loop produced more plausible results in terms of avalanche release probability and future landscape conditions than simulations without the full coupling.

Socio-economic drivers of forest change

Using output from FLMs to model the current and future economic forest landscape in terms of timing and location of future forest products, employment, and industrial output is intuitive, but using alternative economic forecasts to drive harvest scenarios within a FLM remains unrealized opportunity. Future challenges include a tighter coupling of FLMs with anticipated anthropogenic impacts such as land use change (Wear 2011; Sohl et al. 2014; Thompson et al. 2014, 2016), population dynamics, consumer preferences for forest products and ecosystem services, and other social dimensions. Those steps will likely create an opportunity (or necessity) to expand existing forest landscape models to a new generation of all-lands landscape models that encompass agricultural and urban lands in addition to rural forest land.

Conclusions

We are at a point of great opportunity in development and application of forest dynamics models. When viewed across 80 years of history, there were periods when forest modeling was limited by availability of computing resources, suitable data for calibration or implementation, or supporting statistical or GIS software. Now those limitations appear less daunting than the challenges of (a) utilizing the available data and technology for increased applications of forest dynamics models, and (b) routinely applying the best available forest modeling science to support decision-making.

Forest landscape models, in particular, are at a turning point. Supported by more than two decades of prior research and development, FLMs are ready to make the transition from use primarily for research studies to a central role in supporting forest management, planning, and policy decisions. Success in that transition will require greater attention to calibrating models for new conditions; validating model performance; building support staff for model applications; investing in data processing to support model applications; expanding the suite of included natural and anthropogenic drivers and feedbacks of change; and incorporating metrics for social and economic inputs and outputs. Greater attention to FLM applications does not diminish the need for ongoing research, but it may sharpen the focus of future research by highlighting important limitations and opportunities that require attention.

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