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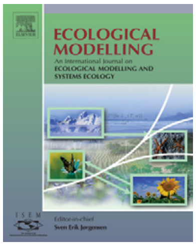

Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution

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ABSTRACT

We introduce LANDIS-II, a landscape model designed to simulate forest succession and disturbances. LANDIS-II builds upon and preserves the functionality of previous LANDIS forest landscape simulation models. LANDIS-II is distinguished by the inclusion of variable time steps for different ecological processes; our use of a rigorous development and testing process used by software engineers; and an emphasis on collaborative features including a flexible, open architecture. We detail the variable time step logic and provide an overview of the system architecture. Finally, we demonstrate model behavior and sensitivity to variable time steps through application to a large boreal forest landscape. We simulated pre-industrial forest fire regimes in order to establish base-line conditions for future management. Differing model time steps substantially altered our estimates of pre-industrial forest conditions. Where disturbance frequency is relatively high or successional processes long, the variable time steps may be a critical element for successful forest landscape modeling.

1. Introduction

Forested landscapes have been changing at an increasing rate, with novel perturbations becoming common and long-term changes to the climate and atmosphere prevalent (Pitelka et al., 1997; Paine et al., 1998; Aber et al., 2001). As a result, many forest communities are changing rapidly and disturbance regimes have been highly altered. Additionally, changes in carbon and nutrient cycling rates may modify successional, dispersal, and disturbance processes. All of these ecological processes have a distinctive spatial and temporal pattern. As our understanding of the complexity of ecological interactions and environmental stresses increases, models are needed that can rapidly evolve to accommodate both scientific inquiry and landscape management questions. Therefore, there is a growing need for simulation models that can represent dynamic communities, shifting species distributions, and diverse disturbance regimes (Scheller and Mladenoff, in press), with each process represented at the appropriate spatial and temporal scale.

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Scientific rigor within a simulation model is enforced through the process of peer-review, during which the model must meet certain requirements including conceptual validity, model verification, validation with empirical data, and testing with sensitivity analysis (Aber, 1997; Aber et al., 2003). Following peer-review of the model, users can focus on model output as it pertains to the question at hand. Therefore, a scientific model, particularly a complex spatial landscape model, requires substantial time investment before its output can be accepted by the broader scientific community.

Because of the overhead of scientific model building, few are able to invest the time required to create complex models from scratch. Instead, scientists often look to pre-existing, scientifically accepted models to apply to their own question. Often they are disappointed that the pre-existing model cannot directly address their particular question, or they find that the assumptions of the model do not transfer well to their system. At this stage they may choose to build a new model, adapt a pre-existing one, or adapt their question to fit the pre-existing model. Each choice represents a different balance between time, resources, and the scientific question at hand.

We have written, tested, and applied a new forest landscape simulation model, LANDIS-II. Our intention was to create an integrated model and modeling environment that can facilitate the creation of custom forest landscape disturbance and succession models, while maintaining and building upon the scientific rigor of previous LANDIS models, developed over the last decade (Mladenoff, 2004a). To that end, our design emphasizes spatial and temporal flexibility, ease-of-use, and collaboration among scientists. Our design shifts the scientific emphasis from model development to extension (module or 'plug-in') development, facilitating peer-review of new extensions in the context of the larger model. We combine this new architecture with open source code for extensions and an on-line extension repository, to facilitate rapid development of extensions, collaborative model development and wider application, and shared ownership of the model building process.

1.1. *Model purpose*

LANDIS-II is an elaboration of previous LANDIS (landscape disturbance and succession) models (Mladenoff et al., 1996; Mladenoff and He, 1999; Mladenoff, 2004a). Previous LANDIS models and LANDIS-II are intended for the simulation of broad-scale (>10^5 ha) landscape dynamics, including succession, disturbance, seed dispersal, forest management, carbon dynamics, and climate change affects (Scheller and Mladenoff, 2005; He and Mladenoff, 1999; Gustafson et al., 2000).

LANDIS-II is optimized for the simulation of spatial processes (Reiners and Driese, 2001) and the interactions between spatial processes and patterns (Turner, 1989; Mladenoff, 2004a,b; Scheller and Mladenoff, in press). Landscapes within LANDIS-II are represented as a grid of interacting cells with a user-defined spatial resolution (cell size) and extent. Practicable cell sizes can range from a few meters up to a kilometer. All LANDIS models assume that individual cells have homogeneous light environments. Cells are aggregated into ecoregions with homogeneous climate and soils and a user defined extent, thereby creating a hierarchy of spatial interactions.

LANDIS and LANDIS-II emphasize species life history attributes (including longevity, shade tolerance, fire tolerance, and others) to drive succession and disturbance, similar to Landsim (Roberts, 1996; Roberts and Betz, 1999). The simulation of broad spatial and long temporal scale dynamics was achieved by representing species of trees or shrubs not as individual stems (e.g., Pacala et al., 1993) but as age-defined cohorts. In comparison, other simulation models often use dynamic plant functional types (Neilson, 1995; Bachelet et al., 2001) or assume static communities with variable age (Li, 2000) to simulate broad scales.

Recent LANDIS developments have expanded the cohort definition to include other relevant data, including aboveground biomass (Scheller and Mladenoff, 2004) and density and diameter (Schumacher et al., 2004). These additions expand the range of ecosystem processes that can be represented in the model, and provide quantitative output. Nevertheless, a detailed representation of nutrient cycling (e.g., Parton et al., 1993; Aber et al., 1997) or other ecophysiological processes (Ollinger et al., 2002) has not been included in LANDIS-II developments to date.

Fall and Fall (2001) described current approaches to spatial landscape modeling as falling along a spectrum between two extremes: general purpose programming languages and complete models with few adjustable parameters. The LANDIS models fall closest to the latter in that they are preprogrammed models, though they have substantial flexibility in parameterization that increases their adaptability. LANDIS-II represents a significant shift toward domain-specific modeling environments such as the Spatially Explicit Landscape Event Simulator (SELES; Fall and Fall, 2001) and the Spatial Modeling Environment (Maxwell and Costanza, 1997), though its extensions are still programmed using compiled code. Strengths of LANDIS-II include the new flexibility introduced through multiple inter-woven time steps (see below), a library of ecological processes that have previously been published, and the optional integration of additional cohort data and biomass dynamics (Scheller and Mladenoff, 2004). LANDIS-II was also designed to maximize collaborative potential with easily modified extensions, code transparency and sharing, and substantial on-line support.

Rather than a predefined model *per se*, LANDIS-II is defined by its architecture, component interfaces, and its core assumptions. Scientific rigor within the model components is enforced by the software engineering best practices employed throughout the model development process (Scheller et al., in preparation). Ultimately the choice of whether to use LANDIS-II or a modeling framework such as SELES will depend on the degree to which the question at hand matches the core assumptions of LANDIS-II and time and resources available for model development and scientific review. We believe that the new capabilities, flexibility in architecture, rigorous development and model testing process (Scheller et al., in preparation), and collaborative capabilities of LANDIS-II will extend its applicability to a very broad range of questions pertaining to forest landscape change.

1.2. Objectives

A principle objective in our model design was to develop and implement a user-specified time step for each ecological process. A single time step for all ecological processes has not been adequate for addressing many scientific and management questions. Therefore, a method was needed to provide flexibility in temporal scales among ecological processes without creating overwhelming complexity. We then demonstrate how different time steps can be used for various ecological processes and how these choices affect model outputs. We demonstrate these model behaviors through application to the Manitoba Model Forest (MMF), a boreal forest located northeast of Winnipeg, Manitoba, Canada.

Additional goals when designing a next-generation forest landscape simulation model were numerous. The challenge was to meet our immediate needs and anticipate future developments in forest landscape modeling. Additional design goals included:

A. Preserve the existing multi-scale functionality of the original LANDIS model (Mladenoff et al., 1996; Mladenoff and He, 1999) whereby a landscape is divided into cells with unique combinations of species cohorts (as well as other site specific data), nested within ecoregions that define the climatic and edaphic character of multiple sites. Cell resolution and ecoregion extent may encompass a broad, variable range defined by the available computational capabilities and the level of biological realism desired.

B. Design a system architecture and interface that facilitates model development and refinement through the collaboration of multiple developers and users. Collaboration is often viewed as desirable, but the necessary logistical coordination is intimidating. If available, collaborative tools, such as a supporting web site, are often implemented *post hoc* and are not fully integrated into the model architecture. The model architecture and supporting services (web site, tools, utilities, and libraries) should be fully integrated and should enable a broad, geographically distributed community of ecologists and modelers to collaborate independently yet cohesively. In addition, collaborators should retain both ownership and responsibility for their contributions.

2. Variable time step

The science and algorithms for incorporating multiple variable time steps for ecological processes and output are a significant functional addition to previous LANDIS models. Each extension can have its own time step, Δt, for example, Δt_{fire} or Δt_{wind} or Δt_S (succession). Significantly, time steps may be synchronized or all different. Cohort age ranges are defined by Δt_S, i.e., the span for a cohort age class is equal to the succession time step. For example, if Δt_S is 10 years, then the age classes would be 1–10, 11–20, 21–30, and so on. Cohort age is referred to by the upper bound on its range. For example, the age class 11–20 would be referred to as age class 20 or simply, age 20.

The age of a cohort is updated as follows:

$$\text{age}(t) = \text{age}(t_{\text{LastAging}}) + (t - t_{\text{LastAging}})$$

Table 1 – Example of interactions between succession and disturbance (wind), operating at 10 and 3 years, respectively

Time step	Sequence of events	Site cohort ages (years)
Year 30	Start of time step	$C_1(100)$, $C_2(60)$
	After succession	$C_1(110)$; $C_2(70)$
Year 33	Start of time step	$C_1(110)$; $C_2(70)$
	After wind kills oldest cohort	$C_2(70)$
	After aging and mortality	$C_2(73)$
	After resprouting	$C_2(73)$; $C_{N1}(1)$
Year 36	Start of time step	$C_2(73)$; $C_{N1}(1)$
	After wind kills oldest cohort	$C_{N1}(1)$
	After aging and mortality	$C_{N1}(4)$
	After resprouting	$C_{N1}(4)$; $C_{N2}(1)$
Year 40	Before aging	$C_{N1}(4)$; $C_{N2}(1)$
	After aging	$C_3(10)$

where t is the absolute model time (in years), and $t_{\text{LastAging}}$ is the last time at which cohorts were aged for that site.

Without disturbance, cohorts are only aged when succession occurs and $t - t_{\text{LastAging}}$ equals Δt_S. However, if a disturbance happens at a time other than the successional time step, succession also occurs at the site or sub-set of sites. During succession, there are three stages: aging, age-related mortality, and reproduction. Therefore, reproduction and cohort aging may also occur at a disturbance time step. New cohorts ($\text{age} < \Delta t_S$) are created immediately after a disturbance event and initially belong to a single-year cohort age class.

In the case where the current time step is a disturbance time step and not a succession time step, the age of a new cohort is updated in the same manner as other cohorts:

$$\text{new cohort} \rightarrow \text{age}(t) = \begin{cases} \Delta t_S, \text{ if } t \text{ is a succession time step} \\ \text{age}(t_{\text{LastAging}}) + (t - t_{\text{LastAging}}) \end{cases}$$

It is possible for a species at a site to have two or more new cohorts with different ages depending upon the succession and disturbance time steps indicated. When a species at a site has two or more new cohorts during the aging stage of a succession time step, the new cohorts are combined into a single cohort with its age equal to the succession time step.

Table 1 illustrates this behavior: $\Delta t_S = 10$ years, $\Delta t_{\text{wind}} = 3$ years. At year 30, two cohorts exist on a site, aged 60 and 100. At year 33, a wind event kills the oldest cohort, causing the species to resprout and the addition of a new cohort (C_N). At year 36, a wind event kills the next oldest cohort, causing the species to resprout and the addition of another new cohort. At year 40, both new cohorts are combined into a single cohort, age 10.

3. LANDIS-II architecture

Our objectives required an architecture that could be rapidly extended and shared and that would maximize collaborative potential (He et al., 2002; Kerr, 2004; Michalakes et al., 2004).

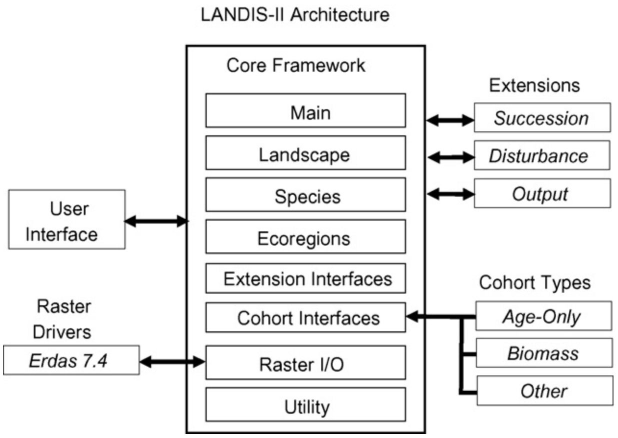

Fig. 1 – An overview of the LANDIS-II architecture, indicating the core modules and other external extensions ('plug-in' components representing ecological processes or generating outputs) and libraries.

Therefore, we designed the LANDIS-II architecture so that ecological processes are represented by separate components that attach to a core framework. These separate components are referred to as extensions (modules or 'plug-ins'). Extensions are not limited to ecological processes; they can also encapsulate algorithms for summarizing and/or mapping simulated data. The core serves primarily as an extension manager, and defines the data structure for representing the forested landscape. To sustain model reuse, stability, and longevity, these extensions must plug into LANDIS-II without any modification to the core framework. Because extensions are distributed separately, model users can select which extensions to install on their computers. In addition, this extensible architecture allows developers to create new extensions that represent new successional or disturbance processes or a new approach to an existing process (He et al., 2002).

The LANDIS-II architecture consists of the core framework, extensions that plug into the core, user interfaces (console and graphical), and raster drivers for handling various file formats for raster data (Fig. 1).

3.1. *Language choice*

We chose to program the core and extensions in the C# language, a part of the Microsoft .NET platform (Platt, 2003). Significantly, C# contains the necessary technologies to seamlessly implement the dynamic loading of extensions and new data types, i.e., C# was designed for the rapid loading of dynamic loadable libraries (dlls), which are separately compiled model components. The C# language is similar to Java in that object oriented design is strongly enforced and memory management is automated. Compilers and integrated development environments for C# are freely available over the internet. C# is also International Organization for Standardization (ISO) certified (ISO/IEC 23270).

3.2. *LANDIS-II core framework*

The core consists of eight modules (Fig. 1). Each module within the core is responsible for performing any necessary input validation. Input validation may include data type (integer versus floating point versus string), absolute ranges, and relative ranges (comparisons to other input data). For example, validation of species input data includes comparisons to absolute ranges (e.g., shade tolerance classes 1–5) and interdependencies among parameters (e.g., maturity age < life span). The eight modules are as follows:

3.2.1. *Main module*

The main module is responsible for reading and validating the scenario file. A scenario specifies the global landscape input (model duration, initial ecoregion data, initial community data) and the extensions (and their respective data files) that will be used to represent the ecology of the system (Scheller and Mladenoff, in press). This module co-ordinates the initialization of the other core modules and of selected extensions. The main module is also responsible for running the extensions in the order specified in the scenario. Disturbances can be executed in a pre-determined order or in random order.

3.2.2. *Landscape module*

The landscape module manages data for sites on the landscape. The module allows extensions to add new site variables, thereby providing considerable flexibility for the development of new succession and disturbance extensions. For example, the Base Fire extension adds the site variable *TimeOfLastFire* (years) that can be used by any other extension. The landscape module also records which sites are active versus inactive, and provides methods for iterating over all sites or only active forested sites.

3.2.3. *Extension interfaces module*

The extension interfaces module defines the interfaces related to extensions: the base interface that the core requires all extensions to implement; the more elaborate interface that the core requires of succession extensions; the interface that all extensions use to interact with the core; and the interface that the core uses to access the database with metadata about the extensions installed on the user's computer (Fig. 2).

3.2.4. *Raster input/output module*

The raster I/O module contains interfaces for input and output maps (raster data files). These interfaces allow the core framework and the extensions to access raster data and their associated metadata (e.g., projection, cell size) in a uniform manner which is independent of the data's actual file format. Raster drivers implement these interfaces for specific file formats. Currently, a driver for ERDAS 7.4 (8 or 16-bit) files has been implemented to support the raster format of earlier LANDIS versions.

3.2.5. *Utility module*

The utility module contains all the remaining functionality that the core framework provides for extensions. These services include generating random numbers, parsing text files, writing log files for simulation runs, and communicating with user interfaces (console and graphical).

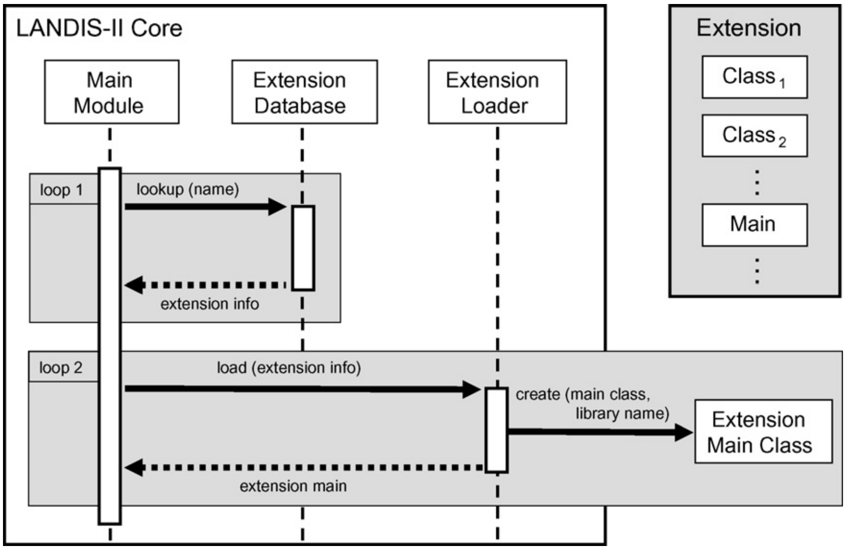

Fig. 2 – Interactions between LANDIS-II core and extensions. During initialization, the main module looks up an extension name in the Extension Database and retrieves the extension library and main class (loop 1). Next, the main module passes this information into an extension loader, which creates an instance of the extension main class (loop 2).

3.2.6. *Ecoregion module*

The ecoregion module has a dataset of ecoregion scale parameters, including the species establishment probabilities (He et al., 1998; Scheller et al., 2005), and interfaces to these data. Each ecoregion is designated as active (forested) or inactive (non-forested). This designation determines whether all the sites in an ecoregion are active or not. The ecoregions thus defined can be used by any extension. For example fire regimes (size and frequency) may vary by ecoregion.

3.2.7. *Species module*

The species module maintains a dataset of species parameters, including life history characteristics. The species and cohort interfaces modules are the most domain-centric modules. Whereas other modules could be used to simulate many different processes or systems (e.g., prairies, hydrological flow), the species module requires data specifically relevant to forest succession and disturbance: shade tolerance, longevity, maturity age, seed dispersal distances, fire tolerance, etc. The list of life history parameters can be readily extended from within any extension.

3.2.8. *Cohort interfaces module*

The cohort interfaces module provides templates for defining a set of interfaces for each specific cohort type (e.g., age-only, biomass, density and diameter). A developer uses these templates to create a new cohort type. Each cohort type has its own separate library outside of the core; the library contains the interfaces for the type along with their implementation.

The cohort interfaces module also provides a type-independent set of interfaces for accessing the attributes of any cohort type. These interfaces are used by extensions that need to work with different cohort types, such as the output cohorts extension.

3.3. *LANDIS-II extensions*

The three primary types of extensions are succession, disturbance, and output. The succession and disturbance extensions encapsulate the ecological knowledge represented within LANDIS-II. Succession is the primary ecological process in forested landscapes. The succession extension must implement methods for cohort reproduction, cohort growth (not including aging), and cohort mortality. For example, the biomass succession extension includes appropriate methods for increasing or decreasing cohort biomass, dependent upon maximum growth rate, age, and competition; and decomposition of dead biomass (Scheller and Mladenoff, 2004). Only one succession extension can be used within a model scenario.

Disturbance extensions have individual time steps, specified by the user, and these can be different from the succession time step. There can be zero or more disturbance extensions for each scenario. If two or more disturbances are executed at a time step during a scenario run, they may be done in an order pre-determined by the user, or in random order. In addition to implementing the scientific algorithms, each disturbance extension also reads, parses, and validates input files specific to the extension, and creates relevant output maps (e.g., fire severity) and a log file of individual disturbance events.

Output extensions read and aggregate landscape data and create output text files and/or raster maps. These extensions range from simple (writing shade maps) to complex (reclassifying forest types).

The LANDIS-II architecture allows extension developers to define additional types of extensions. For example, a developer may define a ‘meta-population’ extension type for use by both a bird extension and an invasive-species extension.

Extensions can define site data variables on the landscape. Examples of site variables for succession and disturbance extensions include time-since-last-fire (He and Mladenoff, 1999), coarse woody debris (Scheller and Mladenoff, 2004), fuel loads (Shang et al., 2004), etc.

4. Web site

In order to facilitate collaboration, a significant component of the LANDIS-II model is the supporting web site (http://landis.forest.wisc.edu). The web site serves as an interface and repository for LANDIS-II extensions and an arena for model user and model developer interactions. New extensions are posted and shared via the web site. All model developers have access to extension source code although the original extension developers retain ownership and responsibility. Allowing open access to existing extensions allows for new ideas to be rapidly developed and increases code verification for all existing extensions. Other web site features include a community forum for exchanging information and standardized User's Guides for the LANDIS-II core and all extensions. The extensible architecture and the web site with its library and communication forums allows the modeling community to build an ever-expanding library of extensions.

5. Model application in the Manitoba Model Forest

To demonstrate model behavior and outputs, particularly in regards to the novel variable time steps, we applied LANDIS-II to scenarios of pre-industrial conditions in the Manitoba Model Forest (MMF). Although MMF is a new application, LANDIS has previously been applied successfully in boreal forests (Scheller et al., 2005). Boreal forests have relatively low tree species diversity and complex fire regimes that span a broad temporal scale (Johnson, 1992). Because of the low diversity and relatively high fire frequency, we expected that tree species dominance across the landscape would be sensitive to the variable time steps, and would therefore offer an ideal opportunity to observe model response to the variable time step.

The current management paradigm of much of Canada's boreal forest considers natural forest dynamics and the natural or "pre-industrial condition" of the forest when identifying objectives for future forest conditions. The pre-industrial condition is defined as the state of the forest prior to broad-scale human intervention and management. The pre-industrial condition of the boreal forest does not refer to a single "condition" or state of the forest, as there is no unique state of the forest which is "natural" (Landres et al., 1999). There are numerous difficulties in using historic or present day inventories to estimate pre-industrial conditions (Swetnam et al., 1999; Suffling and Perera, 2004) and therefore a modeling approach (e.g., Nonaka and Spies, 2005) was chosen.

The Manitoba Model Forest (MMF) is a 1 million ha boreal forest northeast of Winnipeg, Manitoba, Canada (Fig. 3). The forest is dominated by balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*), and includes additional species such as black ash (*Fraxinum nigra*), tamarack (*Larix laricina*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*) as sub-dominant stand components. The climate is sub-polar with a mean January temperature of −14 °C, mean July temperature of 25 °C, and mean annual precipitation of 52.1 cm, 80% of which is rainfall. MMF is managed as a non-profit partnership-based agency dedicated to sustainable forest management and community-based decision making. The forest area is licensed by the Manitoba government to Tembec Inc., which are both MMF partners (http://www.manitobamodelforest.net/).

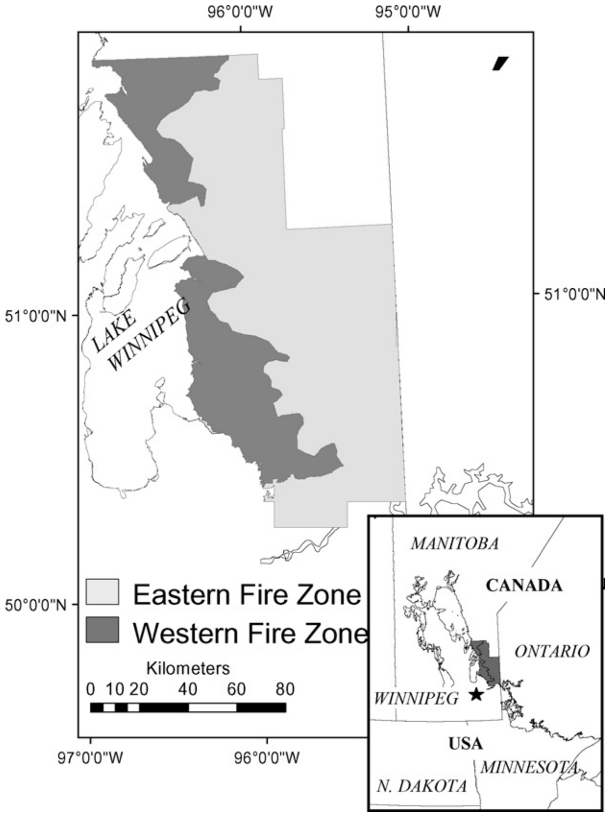

Fig. 3 – Study area of the Manitoba Model Forest (MMF).

The major disturbances in boreal forests are wildfire, insect defoliation and windthrow (Johnson, 1992; Pastor et al., 1994; Thompson, 2000; Li, 2000; Pennanen et al., 2004). Although spruce and jack pine budworm can be locally very important (MacLean, 1985; Bergeron and Dansereau, 1993; Fleming et al., 2000), in more arid parts of the boreal forest such as eastern Manitoba, fire is generally the largest cause of mortality (Fig. 4). Therefore, our estimates of pre-industrial conditions initially considered only the effect of fire on mortality, succession, and the MMF forest age-distribution.

To assess the effects of fire and the variable temporal resolution of fire and succession, we examined the output from three combinations of succession and fire time steps: 1 year succession with 1 year fire time steps; 5 years succession with 5 years fire time steps; and 10 years succession with 10 years fire time steps. The effects of the variable time step were evaluated by examining landscape dominance of 10 tree species over 750 simulation years. The decision as to which combination of time steps produced the most realistic results was determined by an expert panel composed of the ecologists and foresters guiding MMF planning.

Table 2 – Species life history data

Name	Longevity (years)	Sexual maturity (years)	Shade tolerance[a]	Fire tolerance[b]	Seed dispersal distances (m)		Post-fire regeneration
					Effective	Maximum	
Abies balsamea	80	30	5	1	25	160	None
Betula papyrifera	80	15	1	2	100	5000	None
Fraxinus nigra	200	30	2	3	50	50	None
Larix laricina	130	45	1	3	25	40	None
Picea glauca	200	30	4	3	100	200	None
Picea mariana (lowland)	250	30	4	3	50	150	None
Picea mariana (upland)	130	30	4	3	50	150	None
Pinus banksiana	120	10	1	3	20	100	Serotiny
Populus balsamifera	120	20	1	2	1000	5000	None
Populus tremuloides	120	20	1	2	1000	5000	None

[a] Shade tolerance is an index of the species ability to germinate under varying light levels; 1 = open conditions required; 5 = very shade tolerant.
[b] Fire tolerance is an index of the species susceptibility to fire mortality; 1 = very susceptible; 5 = very fire tolerant.

5.1. *LANDIS-II parameterization for MMF*

The core LANDIS-II model requires species life history attributes, initial forest conditions, and ecoregions as input data. Simulations were run at a resolution of 50 m × 50 m with a total simulation time of 750 years. The LANDIS-II Age-Only Succession and Base Fire extensions were used to simulate the pre-industrial conditions of the MMF.

Species life history attributes (Table 2) were based on a review of existing literature and supplemented by input from the Project Steering Committee composed of 10 foresters and ecologists with extensive experience with the MMF and similar forests. Black spruce was divided into upland and lowland black spruce with differential maximum life spans.

We used a classification of the MMF provided by Manitoba Conservation (http://www.gov.mb.ca/conservation/) that indicates standard provincial sub-type groups and 5-year age classes. The classification was derived from Forest Resources Inventory (FRI) data, which in turn was created from color infrared 1:15,480 scale aerial photographs taken in 1997 and 2003 and stand crusie data. For each sub-type group and age class, species presence summary statistics were generated from FRI data; species found within <10% of a group were not included. For example, statistics from 100 stands classified as aspen-jack pine (sub-type 81) within the 80–85 age class group showed the following species present: balsam fir, white spruce, upland black spruce, jack pine, aspen and balsam poplar. Balsam poplar only occurred in 5% of the stands and was excluded. All other species were included and assigned an age of 80 years.

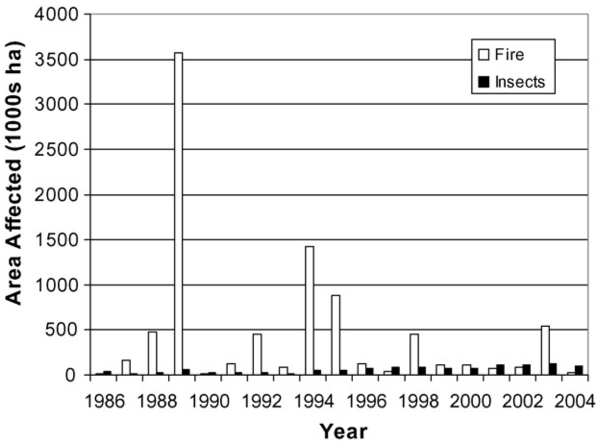

Fig. 4 – Area burned and affected by moderate to severe insect defoliation and fire in Manitoba 1986–2004. Data from the National Forestry Database: http://nfdp.ccfm.org/compendium/data.

The landscape was divided into two principle fire zones (Fig. 3) that reflect variations in soil moisture with observed effects on fire rotation periods (sensu Frelich, 2002). In addition, moisture classes and landform types were interpreted from the aerial photographs used in the classification above. Four moisture classes, ranging from wet to arid, were identified, and eight landform types were distinguished. The combined classification resulted in over 20 possible ecoregions per fire zone. However, the majority of the area (98% of the eastern fire zone, 91% of the western) fell within seven dominant moisture–landform classes. To simplify the ecoregion classification, many classes that represented less than 1% of the landscape were combined with similar, more extensive ecoregions. Treed muskeg and treed rock (non-productive areas) were retained as active ecoregions to help ensure proper fire spread.

The Age-Only Succession extension implements successional processes as defined in previous LANDIS models (Mladenoff et al., 1996; Mladenoff and He, 1999) and uses cohorts containing only species and age information (Scheller and Domingo, 2005a). Establishment probabilities were estimated by determining the percentage of each ecoregion occupied by each species.

The Base Fire extension was derived from previous LANDIS research (He and Mladenoff, 1999; Scheller and Mladenoff, 2004, Jian Yang, University of Missouri, personal communication, 2004) with significant modifications (Scheller and Domingo, 2005b). The Base Fire extension requires only cohort species and age data and is therefore compatible with all cohort data types (Scheller and Domingo, 2005b).

The Base Fire extension requires fire spread age and fire size distributions as input data (Table 3). The probability of fire initiation and spreading ($P_{\text{init-spread}}$) is a log function of the

Table 3 – LANDIS-II ecoregion fire parameters

Vegetation zone	Ecoregion description	Minimum fire size (ha)	Mean fire size (ha)	Fire spread age	Age of stand replacing fire
East	Treed muskeg	15,000	1000	50	20
East	Treed rock	15,000	1000	80	20
East	Arid igneous outcrops	15,000	1000	80	10
East	Dry igneous outcrops	15,000	1000	80	10
East	Dry sand gravel flats, outwash plain	15,000	1000	80	10
East	Moist igneous outcrops	15,000	1000	80	15
East	Moist lower slopes	15,000	1000	80	20
East	Moist sand gravel flats, outwash plain	15,000	1000	80	20
East	Wet depressions, poorly drained	15,000	1000	150	20
West	Treed muskeg	6,000	500	300	20
West	Treed rock	6,000	500	300	20
West	Arid igneous outcrops	6,000	500	300	10
West	Dry igneous outcrops	6,000	500	300	10
West	Dry sand gravel flats, outwash plain	6,000	500	200	10
West	Moist igneous outcrops	6,000	500	200	15
West	Moist lower slopes	6,000	500	200	20
West	Moist sand gravel flats, outwash plain	6,000	500	200	20
West	Wet depressions, poorly drained	6,000	500	200	20

time-since-last-fire (years) for each cell and the fire spread age parameter (years), which is indicated by ecoregion. The fire spread age parameter determines how rapidly $P_{\text{init-spread}}$ increases over time, such that $P_{\text{init-spread}}$ equals 0.62 when time-since-last-fire equals the fire spread age (Jian Yang, University of Missouri, personal communication, 2004). A value of 80 years was used for the fire spread age within the eastern vegetation zone except on the wet sites, and values ranging from 150 to 300 years in the western vegetation zone. The minimum and mean fire size (in hectares) was differentiated between the east and west vegetation zones. The eastern vegetation zone has a more intense fire regime than the west, and the minimum and mean fire sizes were set to 1000 and 15,000 ha, respectively, versus 500 and 6000 ha in the west, respectively. In both vegetation zones, the maximum fire size was set to 133,000 ha, which is the size of the largest fire recorded within the MMF.

5.2. *Results from MMF*

The duration of each simulation varied with spatial resolution (cell size). At a resolution of 50 m (4,138,876 active cells) and including annual succession and fires with species outputs every 10 years, processing time was approximately 2 h per 100 years simulated. At a resolution of 200 m (258,568 active cells) and identical time steps, processing time was approximately 5 min per 100 years simulated. All simulations were performed on a personal computer with 3.25 Gb RAM running at 3.2 GHz.

LANDIS-II with the Age-Only Succession and Base Fire extensions reasonably reproduces the expected fire sizes and fire rotation periods. Simulated fire sizes were generally close to the expected historical sizes (Fig. 5a). Likewise, the simulated fire return intervals were generally very similar to expected historic return intervals (Fig. 5b).

Changes in estimated overstory species composition have some general characteristics regardless of time step length (Fig. 6). All species showed an initial decline in abundance because the mean forest age declined due to increased disturbance (Fig. 7) associated with the modeled removal of the fire suppression program, which has been effective in reducing fire incidence and severity. The abundance of most species reached equilibrium after 100 years (Fig. 6). Of the species with high initial overstory abundance, tamarack was eventually eliminated. Tamarack is poorly adapted to fire (Table 2) and the ability of tamarack to persist in bogs and re-colonize neighboring wet ecoregions was not modeled. Trembling aspen also

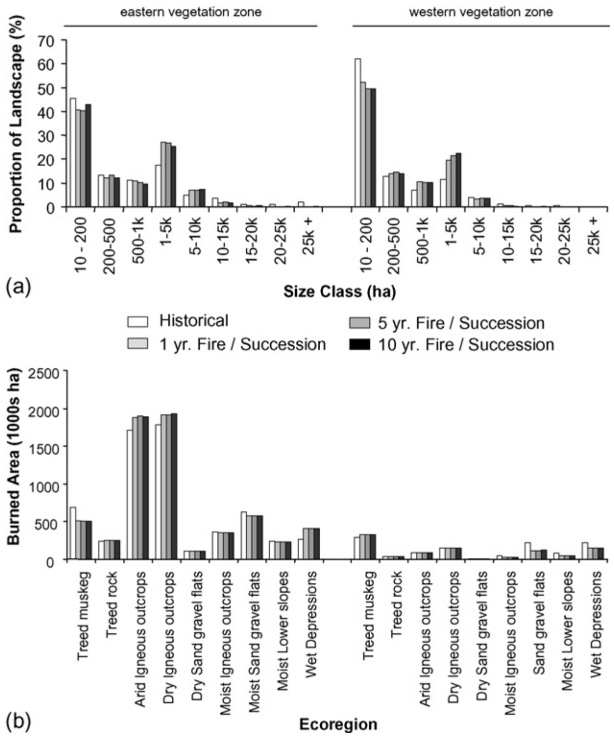

Fig. 5 – (a) Historic and simulated fire size class frequencies for the eastern and western fire zones of the MMF. (b) Expected and simulated burned areas for the MMF. Burned area is calculated as ecoregion area (ha) × simulation length (years)/fire rotation period (years).

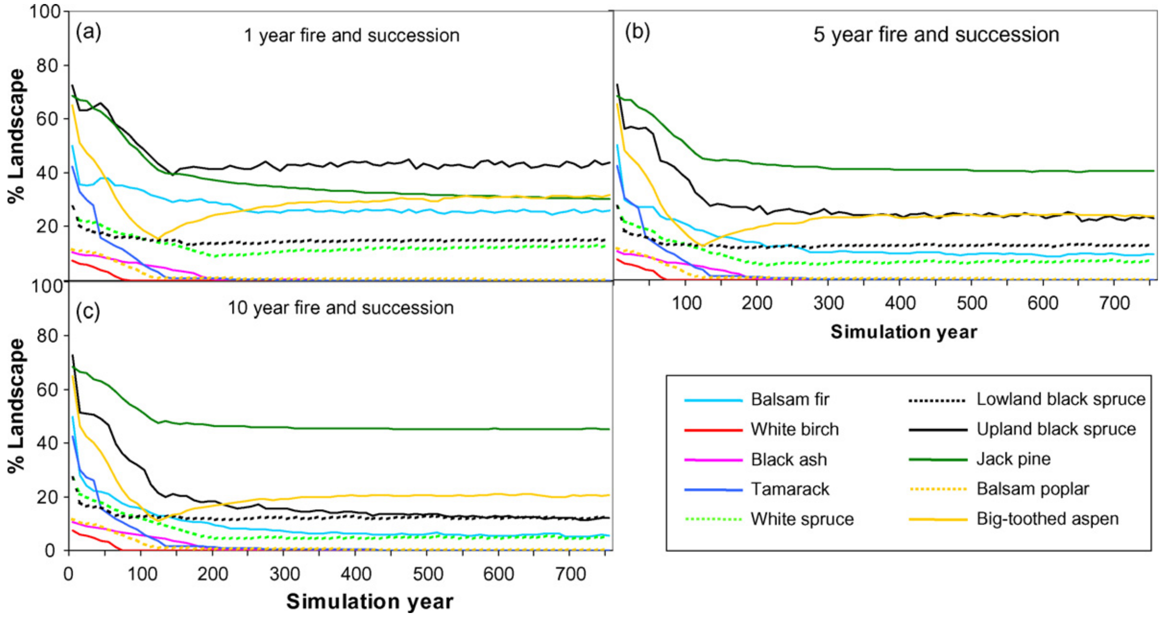

Fig. 6 – Simulated species overstory proportions in MMF over 750 years. Species cohorts were considered to be in the overstory when the ratio of the cohort age to site age (the age of the oldest species) was greater than 0.66. (a) Simulated using 1 year fire and 1 year succession time steps; (b) simulated using 5 years fire and 5 years succession time steps; (c) simulated using 10 years fire and 10 years succession time steps.

declined significantly although this effect was highly sensitive to the time step length. Species that were initially not widely distributed, such as white birch, balsam poplar, and black ash were reduced to a very minor presence after 100 years. Both white birch and balsam poplar have life history attributes very similar to trembling aspen and may have been out-competed for available early-successional habitat because of their low initial abundance.

There was significant variation in species overstory dominance (Fig. 6) and mean forest age (Fig. 7) among the three scenarios. One-year succession and fire time steps produced the smaller declines in overstory presence for all tree species except black ash and white birch. With 1-year time steps there was greater evenness among species and upland black spruce was found in the overstory of a greater proportion of the landscape than jack pine. One-year time steps also produced the youngest simulated forest age (Fig. 7). The MMF steering committee regarded this scenario as most realistic because it simulated the smallest decline in species overstory abundances and mean forest age.

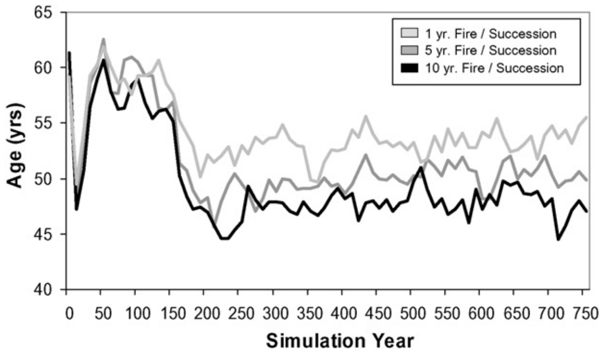

Fig. 7 – Simulated mean landscape age (cell age is defined as the maximum cohort within the cell) for the MMF under three scenarios with varying time steps, not including non-forested cells.

Clearly the model presents an approximation of the pre-industrial forest based on the input data, and there are inaccuracies. For example, our simulations created significantly different age structures and species composition in the west and east vegetation zones, although we would expect a more intermediate state in the transition area between the eastern and western zones. Some of the changes in species composition suggested by the model do not appear to be reasonable (e.g. the complete loss of tamarack).

Nevertheless, LANDIS-II provides valuable insights into the character of the pre-industrial forest. First, pre-industrial forest stands likely had less varied overstory species composition than current day forests. Assuming that the 1-year time steps best represent reality, there may have been proportionally less jack pine than previously thought, and more black spruce. Model results also indicate that balsam fir was more dominant in the western than the eastern vegetative zone (data not shown), due to variations in fire frequency.

The results provide information that would not otherwise be available, although the model results remain an untestable hypothesis about past conditions. Model output could be analyzed and compared to the ecological structure found in parks, but due to the impact of fire suppression in parks, such a comparison may be of questionable value. Another alternative may be to compare model results to areas unexploited for timber harvesting, such as the Yukon or parts of Russia, and assume that the results are transferable to other locations within the boreal forest. But these assumptions may not be valid, and in the absence of other methods to estimate pre-industrial conditions, then the use of models such as LANDIS-II is required to obtain the desired information.

In summary, this application demonstrates how additional time step choices can significantly affect the ability of the model to adequately capture forest dynamics. In this example, the ability of LANDIS-II to simulate succession and disturbance at a finer temporal resolution (<10 years) was deemed critical to adequately capturing forest dynamics because these forests are typified by relatively frequent disturbances. Forests characterized by less frequent disturbances may be less sensitive to the time step chosen. Long-lived forests, such as are found in the Pacific Northwest, could likely be simulated at much longer time steps. This flexibility can provide modelers with additional options for optimizing model performance.

6. Summary

LANDIS-II fills a strong need for a modeling environment that is robust and rigorously tested; that has high potential for collaborative extension development; that preserves the cumulative ecological knowledge of previous LANDIS models; and that enables future growth and development of the LANDIS family of models. Collaboration is enhanced through the flexible model architecture and an integrated suite of on-line extensions and available source code.

LANDIS-II provides a computing environment that leverages many recent advances in software design, including object oriented design, automated memory management, and a rigorous development process patterned after current best practices in software engineering.

Finally, the variable time steps provide a demonstrated advantage over a fixed model time step. The differences among the three MMF scenarios highlight the advantages of the variable time steps. Without variable time steps, we may have reached very different and more limited conclusions about the pre-industrial conditions of the MMF. LANDIS-II extends the variable spatial resolution of the original LANDIS models by providing variable time steps which will allow ecologists to simulate processes at the appropriate temporal resolution. These features will significantly advance the next generation of landscape simulation modeling.

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