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Design and evaluation of a forest landscape change model for western Oregon

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Abstract

This article describes the design and evaluation of a forest landscape model, called LandMod, developed by scaling a forest gap model to operate at a coarser resolution. LandMod is a spatially explicit, stochastic model designed to simulate forest dynamics in the west-central Oregon Cascades over long time frames (500+ years) and large spatial extents (>18,000 ha) at a relatively fine grain (0.04–1 ha). LandMod tracks diameter growth, death, and regeneration of individual tree species in 5-cm size classes at a 5-year time step. Demographics are modeled using simplified procedures from the PNWGap gap model and statistical abstractions of gap-model behavior. LandMod was parameterized for the three predominant forest types of the western Oregon Cascades. Performance of the underlying equations of LandMod was assessed by comparison of predictions with those of the PNWGap model over an elevation and thinning gradient, and with field observations. Landscape-scale performance was assessed by comparing LandMod predictions of potential natural vegetation with empirically based estimates for an 18,000-ha watershed. Results of performance assessments indicated reasonable predictions with LandMod. Compared to PNWGap predictions and observed stands, percent critical errors ($\alpha = 0.05$) of predictions for dominant tree species and stand-level measures with LandMod ranged from 1.4 to 29% with the majority of critical errors less than 15%. LandMod predictions of potential natural vegetation closely matched empirical estimates, with an average overall fit of 94% (S.E. = 0.01). Reasons for prediction error included under-prediction of canopy-stem size in old-growth stands and of mean size of sub-dominant species. Also, simplified light calculations in LandMod resulted in the under-prediction of stem growth under canopy structures induced by certain thinning strategies. Enhancements are recommended to improve model predictions. Intended applications with LandMod include ecological assessments of land-use strategies and research assessments of landscape pattern-process interactions that require explicit consideration of forest structure.

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1. Introduction

Modeling forest landscape change is of increasing importance in landscape management and research. Multiple-use goals for landscapes require management strategies that balance commodity production

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with a range of social and ecological values (Brown and MacLeod, 1996). Anticipating the ability of land-use prescriptions to achieve these goals is difficult given multiple responses of interest and the potential for long-term interactions to cause unintended changes (Armstrong, 1999). Observational studies of landscape dynamics are similarly constrained by the interactions among spatial and temporal scales of processes. Simulation models of forest change,

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however, offer a structured approach to forecast a range of responses and their interactions, and to evaluate assumptions related to complex pattern–process interactions (Mladenoff and He, 1999).

Modeling forest change in support of landscape management and research on public lands in the Pacific Northwest (PNW) region of the United States is especially challenging. Recent adoption of ecosystem-management goals requires development of strategies that promote ecological attributes while providing for timber extraction (FEMAT, 1993). Management alternatives under consideration include retention of structural components such as green trees and dead wood (Swanson and Franklin, 1992), variable patterns (aggregated, dispersed) and sizes (0.25-1 ha) of retention patches, variable harvest-rotation lengths (80-200+ years), and the development of late-successional (200+ years) forest reserves within managed watersheds (FEMAT, 1993). Inherent in these alternatives are specific objectives for stand structure (i.e. tree sizes and densities) and composition. Research efforts in support of ecosystem management seek to understand the role of stand structure on key processes operating at various scales, and the response of processes to disturbance-induced changes in landscape pattern (Swanson, 1997). Accommodating these multiple objectives requires a forest change simulator that: (1) explicitly simulates forest structure and composition over a broad range of forest ages, (2) simulates forest conditions at fine spatial scales, and (3) incorporates forest landscape processes (e.g. disturbance, seed dispersal) (Garman et al., 1995b).

Existing forest landscape simulators satisfy some but not all of these requirements. Simulators designed for forest-management planning provide detailed projections of species-level dynamics using growth and yield models (e.g. Crookston and Havis, 2002; Sessions et al., 1999). However, these simulators are limited to stand ages of commercial harvest rotations (<120 years), use relatively large (>5 ha) operational spatial units, and do not consider interactions among forest patches such as tree-seed dispersal. Ecological simulators model forest change over long time frames and in response to landscape processes, but use either large spatial grains or do not explicitly model forest structure. Simulators based on integrated tree and ecosystem models use large operational units as the spatial grain (e.g. Chertov et al., 2002), or simulate a small sample plot to represent the conditions of an entire stand (e.g. Keane et al., 1996b). Ecological simulators that explicitly model forest change at fine spatial scales tend to use simplified representations of forest conditions. Many simulators characterize forests as a set number of discrete states (e.g. successional classes, dominant forest-canopy species), and model transitions among states in response to disturbance frequency and intensity (e.g. Acevedo et al., 1995; Keane et al., 1996a, 2002; Yemshanov and Perera, 2002). Simulators that model complex interactions among individual tree species and large-scale, disturbance processes track species age or age classes instead of tree density and size (He and Mladenoff, 1999; Roberts and Betz, 1999; Li, 2002). These simulators indirectly estimate structure information from empirical age-class relationships (Li, 2000; Gustafson et al., 2000).

The ability to explicitly simulate fine-scale, forest structure over a landscape has been explored with meta-model variants of forest gap models (Urban et al., 1999). Gap models simulate species-level dynamics on small forest plots over long time periods, and are used to evaluate stand-level management alternatives in the PNW region (Hansen et al., 1995). Computational requirements of gap models limit their ability to simulate landscapes in a spatially explicit manner. Recent efforts by Urban et al. (1999), however, have shown how meta-model approaches can scale gap models to operate at the landscape level. In these approaches, scaling is primarily achieved by statistical representation of gap-model behavior and of input variables. The scaling of gap models to operate at a landscape scale has several advantages: (1) the landscape variant capitalizes on the detail provided by models designed and tested at the level of conventional knowledge (i.e. stand-level), (2) the finer-scale model can be scaled to variable resolutions based on application needs, and (3) a conceptual and empirical linkage is maintained between the landscape variant and the finer-scale model (Urban et al., 1999). Additionally, the simplified structure of meta-model variants of gap models facilitates the incorporation of key landscape processes, such as seed dispersal and disturbance.

This article describes the design and evaluation of a landscape model developed from a forest gap model using the meta-model scaling concepts initiated by Urban et al. (1999). The landscape model, called LandMod, is a spatially explicit, stochastic simulator designed to project forest dynamics in the west-central Oregon Cascades over long time frames (500+ years) and large spatial extents (\geq 18,000 ha) at relatively fine spatial scales (0.04–1.0 ha). The basis of Land-Mod is the PNWGap model (formerly ZELIG.PNW 3.0) that has been used to evaluate long-term, ecological implications of forest-management strategies in the PNW region (Garman et al., 2003). The ability of LandMod to reproduce gap-model dynamics and empirical observations was assessed through a series of comparisons between the two models and with empirical observations.

2. Methods

2.1. PNWGap overview

PNWGap is a variant of the ZELIG gap model (Urban, 1993). Models have the same demographic equations and algorithms, but PNWGap includes modules for simulating coarse-woody debris and forest-management strategies, and an option for simulating seed dispersal. Detailed descriptions of gap-model structure, model corroboration, and examples of applications with the PNW versions of ZELIG are reported in Urban (1993), Urban et al. (1993, 1999), Hansen et al. (1995), Goslin (2000), Busing and Garman (2002), and Garman et al. (1992, 2003). In short, PNWGap simulates the annual establishment, diameter growth, and mortality of individual trees on a small model plot (0.04 ha). Dynamics are based on species' maximum potential rates of demographic processes, which are subsequently reduced as plot-level light conditions, soil moisture or productivity, and ambient temperature deviate from optimal levels. Deviation from optimal levels for each environmental factor (i.e. available light, soil moisture and productivity, temperature) is derived from species-specific response curves as a scaled (0-1) reduction factor. The product of scaled reduction factors is used to constrain maximum tree growth and regeneration. Maximum diameter growth is a function of diameter and leaf area and is deterministic. Two types of mortality are modeled, both of which are implemented as stochastic processes. Ambient mortality is a low

baseline rate of tree death emulating processes unrelated to resource competition, and is estimated from species' maximum longevity. Stress-related mortality results from lack of vigor due to resource limitations (i.e. shading, drought), and is invoked when a tree fails to achieve a minimum growth threshold. Regeneration is keyed to seed source, available growing space, and environmental conditions. Species enter a plot as seedlings which are tracked separately from trees for 6 years and subjected to annual mortality. Seedlings surviving to the end of the sixth year are established as small trees. Annual weather conditions are generated as a stochastic process using empirical or estimated means and standard deviations of monthly values for precipitation, temperature, and mean daily solar radiation. Because PNWGap is a stochastic model, replicates of simulations are used to derive an average trajectory of forest dynamics.

Applications with PNWGap employ a grid of model plots to simulate spatial interactions and pattern within a forested stand. Spatial interaction primarily occurs through shading, where the stature of trees on neighboring plots influences light levels on a model plot. When the seed-dispersal option is selected, regeneration also is determined from spatial interactions. Inseeding composition is based on distance-weighted densities of sexually mature stems on the focal and surrounding plots. Diameter at breast height (DBH) serves as a surrogate for sexual maturity (Burns and Honkala, 1990). Additionally, seed recruitment levels from areas adjacent to the simulated stand can be specified. Soil conditions (i.e. total depth, water-retention capacity) can be varied among plots on a grid. Within-stand pattern develops in response to differences in soil properties, the dispersion of seed sources, and to random mortality events and subsequent regeneration and stem-growth opportunities.

2.2. LandMod structure and dynamics

2.2.1. Spatial structure

LandMod represents a landscape as a lattice of similarly-sized cells. Each cell represents either a forested plot or a non-forested landscape element (e.g. rock). Attributes of each cell are input as spatiallyregistered, raster data layers. Additionally, simulated attributes of forest structure and composition are stored in data structures associated with each cell. Because structures are dynamically allocated as needed, the spatial extent of a landscape is not limited by software design. Cell size cannot be smaller than the zone of influence of a large, canopy dominant stem (i.e. 0.04 ha minimum), but otherwise is not fixed.

2.2.2. Computational structure and dynamics

Book keeping and dynamics are simplified in LandMod to balance computational efficiency and prediction accuracy. LandMod is made up of a stage-structured framework, statistical representation of growth and mortality derived from data generated in gap-model simulations, and simplified regeneration and weather calculations. The stage-structured framework is the basis for tracking stems. The frequency of stems is tracked in 5-cm diameter growth stages (hereafter referred to as size classes) separately for each species. Associated with each size class is a single value for tree height and for crown ratio. Height is derived from the mid-point diameter of a size class using species-specific height-diameter equations (Garman et al., 1995a). Procedures for deriving leaf area, available light levels, and adjusting crown lengths are fundamentally similar to those of the gap model. Leaf area is derived from tree-diameter allometries and distributed in 1-m intervals along the crown in determining the vertical light profile on a stand; height-to-base of crown is then adjusted upward to the light compensation point of a species. In the gap model, these procedures are performed for each stem and involve the calculation of direct-beam (from the south) and diffuse-sky (other cardinal directions and vertical) light components as a function of sun angle. Calculations of leaf area and of the light profile account for about 80% of processing. In LandMod. leaf area is derived only once for each size class with stems and expanded to the stand-level by stem frequency, thus providing savings in processing time. To further simplify processing, LandMod does not incorporate shading by neighboring stands and assumes a light source directly above the canopy.

Methods for stem transfer among size classes are designed to accommodate a wide range of tree sizes over long time periods. Previous scaling efforts with the gap model successfully parameterized a transition-matrix model for Douglas-fir (*Pseudotsuga menziesii*) forests <160 years old (see ZelStage in Urban et al., 1999). However, to simulate older forests, the matrix-model required variable size-class intervals and time steps to adequately model the transition of large boles with limited diameter growth. Also, partial-stem transfer was problematic when simulating infrequent, large stems (Urban et al., 1999). Unlike analytical applications, spatially explicit modeling of landscape pattern requires whole trees. These problems were remedied in LandMod by using a calculated and an accrued diameter increment to model growth transition at a time step of 5 years. For each size class, diameter increment is derived from the mid-point of a size class, crown ratio, and overall growth reduction factor. If the diameter increment is less than the size-class interval, stems remain in the size class and the diameter increment is stored as the accrued increment. In successive time steps the sum of the accrued and the computed increment determines growth transfer among size classes. The accrued diameter increment is updated each time step stems fail to transfer out of a size class. When the sum of the accrued and computed diameter increment exceeds the size-class interval, the new size class is determined, all stems are transferred to the new size class, and the diameter increment in excess of the amount required to advance to the new size class is treated as the accrued increment of transferred stems. When stems enter a new size class, the crown ratio and accrued diameter increment of transferred stems are combined with values of the receiving size class by frequency-weighted averaging. The low end of size-class intervals is used to determine the receiving size class and the transferred accrued increment. When a size class is vacated, all stored information is cleared.

Mortality and regeneration calculations in Land-Mod are similar to those of the gap model, but simplified and scaled to a 5-year time step. A 5-year probability of stress-related mortality for each species is predicted from the mid-point of the size class, crown ratio, and overall growth reduction factor. Because ambient mortality is a totally random process, statistical representation of this mortality source is not possible. Similar to the gap model, LandMod derives the probability of ambient mortality from expected species' longevity, but scaled to a 5-year interval. Each time step, a uniform random variate is generated for each stem in a size class and compared to the maximum of the stress-related and ambient mortality probabilities to determine if the stem dies. This approach ensures removal of whole stems, but imposes a stochastic element on the model. Regeneration is deterministic and based on environmental conditions and available growing space on a cell, and a distance-weighted assessment of seed sources from neighboring cells. Available growing space is derived by determining the maximum tree density on a cell, assuming one stem per five square-meters, and subtracting the existing density of stems. Because of the longer time step in LandMod, seedlings are not tracked. To approximate seedling mortality, an elevated penalty for sub-optimal environmental conditions is assessed in the calculation of regeneration density. Stems entering a cell are placed in the smallest size class.

LandMod uses the same growth reduction factors as the gap model, but employs averages or statistical estimates of weather attributes in deriving factors. Mean annual growing degree-days is generated for each cell of a landscape in a pre-processing procedure and input to LandMod as a spatial data layer. The gap model determines the proportion of drought-days in a growing season from measures of solar radiation, elevation, soil conditions, stochastic estimates of precipitation and temperature, and calculated evapotranspiration. LandMod simplifies these calculations by using statistical functions to predict mean proportion of drought-days from elevation and leaf-area-index (LAI) for aspect classes. Because edaphic attributes influence evapotranspiration and thus the relationship between drought-days and LAI, separate equations are required for each soil type on a landscape. Equation coefficients are input to LandMod in an ASCII format, and are indexed by aspect class and soil type. During a simulation, aspect and soil-type data layers are accessed to determine the appropriate drought-day equation for a cell. Similar to the gap model, Land-Mod derives a soil-fertility growth reduction factor whenever biomass production exceeds a maximum amount. Species-specific response curves taken directly from the gap model determine growth reduction factors from input values of growing degree-days, and calculated values of drought-days, biomass production, and available light.

Forest-management events are specified with similar commands and options employed in the gap model, and are implemented during run time. Commands allow the user to specify an array of thinning and artificial regeneration strategies. Commands and options are numerically coded for each landscape cell in a pre-processing procedure and input to LandMod as spatially explicit data layers.

2.3. LandMod parameterization procedures

Gap-model predictions are used to parameterize the diameter growth, mortality, and drought-day statistical functions used in LandMod. Diameter growth and mortality data are derived with a modified version of the PNWGap model, called MetaGap, that records attributes of individual trees during a simulation. For each tree, MetaGap records the species, the diameter and crown ratio at the beginning of each 5-year period, 5-year diameter increment or cause of mortality (i.e. stress or ambient mortality) if the stem died, and averaged available light over a 5-year period. Additionally, stand-level averages for growing degree-days, proportion of drought-days, and biomass production are recorded for each 5-year period. In a post-processing procedure, averages of growth-reduction attributes (i.e. available light, growing degree-day, proportion of drought-days, and soil productivity) are converted to growth-reduction factors, then to an overall growth reduction factor for each 5-year period for each species. MetaGap simulations are performed on a representative sample of the environmental gradient of a landscape. For each sample location, initial stand configurations are generated by varying the density of a focal tree species from 25 to 100% of estimated maximum density for different stand ages, with all other species equally distributed among the remaining density. Simulations are extended over a 500-year period and replicated 30 times to sample the stochastic variation in gap-model predictions. Data from all simulations are combined and sub-sampled for further processing. For each species, 10 observations per combination of diameter interval (5-cm intervals up to expected maximum diameter), crown-ratio interval (20% intervals), and overall growth reduction factor interval (0.2 intervals) are randomly selected for use in deriving predictive functions.

Predictive functions of diameter growth and mortality are based on equation forms commonly used in forest-growth models (e.g. Hann and Wang, 1990; Hann and Larsen, 1991), but use measures simulated by the gap model as independent variables. Five-year diameter increment for each species is regressed on the mid-point diameter of a size-class, the crown ratio of a size class, and the product of the individual growth reduction factors (i.e. available light, growing degree-day, and the minimum of drought-days and soil-productivity reduction factors) by

Dinc = exp
$$[b_0 + b_1 \ln(\text{DBH} + 1) + b_2 \text{DBH}^2 + b_3 \ln(\text{CR} + 1) + b_4 \ln(\text{GRF} + 1)],$$
 (1)

where GRF is the overall growth reduction factor, CR is crown ratio, DBH is diameter at breast height (cm), b_0-b_4 are species-specific regression coefficients, and Dinc is the 5-year diameter increment (cm). Dinc is set to 0 if CR or GRF = 0.

For each species, the proportion of stems succumbing to stress-related mortality in a 5-year time step is derived for diameter, crown ratio, and growth reduction intervals noted above. The probability of stress-related mortality for each species is predicted by

$$S_{\text{mort}} = \frac{1}{1 + \exp[-1(b_0 + b_1 \text{DBH} + b_2 \text{CR} + b_3 \text{GRF})]},$$
(2)

where b_0-b_3 are species-specific regression coefficients and S_{mort} is the 5-year stress-mortality probability. S_{mort} is set to 1 if CR or GRF = 0.

Response surface functions are used to estimate the proportion of drought-days. Data used to generate these functions are derived from simulations with another variant of PNWGap, called MetaDry. MetaDry produces samples of drought-day proportions by exercising the stochastic weather calculations over a prescribed gradient of LAI values (e.g. 0–9). Similar to the procedures for generating growth and mortality data, MetaDry simulations are replicated over a representative sample of the environmental field of a study area. To minimize the number of equations, predictive functions are derived for aspect classes. A response surface for drought-day proportions for each aspect class by soil type is derived by

$$DrDays = b_0 + b_1 ELEV + b_2 LAI + b_3 ELEV^2 + b_4 LAI^2 + b_5 ELEV^3 + b_6 LAI^3, \qquad (3)$$

where LAI is stand-level leaf-area-index, ELEV is elevation (m), b_0-b_6 are regression coefficients for an aspect class and specific soil type, and DrDays is the 5-year average proportion of drought-days during a growing season.

2.4. Initial parameterization

The current version of LandMod was parameterized for the 18,000-ha Blue River Watershed located in the west-central Oregon Cascades, Willamette National Forest. The 500-1600 m elevation gradient of this watershed encompasses the three major vegetative zones of the western Oregon Cascades (Franklin and Dyrness, 1973). About 80% of the watershed falls within the western hemlock (Tsuga heterophylla) zone (<1100 m), which is characterized by the dominance of Douglas-fir 400-500 years after stand initiation. Western hemlock occurs as a sub-dominant species during this period after which it emerges as the canopy dominant species. Western redcedar (Thuja plicata), big-leaf maple (Acer macrophyllum), and red alder (Alnus rubra) occur sporadically throughout this zone at relatively low densities. Pacific silver fir (Abies amabilis) dominates the true-fir zone (1100–1500 m) with noble fir (Abies procera) and western hemlock occurring as co-dominants at lower elevations of this zone. Mountain hemlock (Tsuga mertensiana) is the dominant species above 1500-1550 m with Pacific silver fir occurring as a co-dominant. Environmental data for the watershed were derived at a 100-m resolution from a Digital Elevation Model, and from predictive models of temperature (Urban et al., 1993), precipitation (Daly et al., 1994), and solar radiation (Bonan, 1989). Due to limited information, a single soil type was assumed for the whole landscape. Cells of the watershed were characterized by combinations of slope, aspect, and elevation classes. Replicated MetaGap simulations were performed for a 10% random sample of cells in each combination using a 1-ha stand. Diameter growth and stress mortality functions were developed for the eight most common tree species (Tables 1 and 2). Drought-day estimates were derived from replicated MetaDry simulations conducted on a 5% sample of the landscape. Samples were equally distributed among combinations of eight aspect by six 200-m elevation classes. Because only one soil type was em-

Ta	ble	1

Regression coefficients for the diameter increment function in LandMod. Coefficients were derived from results of gap model (MetaGap) simulations in the Blue River Watershed, Oregon (see text). All regression models and coefficients were significant (P < 0.0001)

Species	Coefficients (Eq. (1))									
	b_0	b_1	b_2	<i>b</i> ₃	b_4	n				
Big-leaf maple (Acer macrophyllum)	-1.590210	0.267209	-0.000026784	2.007640	1.802077	10,000	0.93			
Douglas-fir (Pseudotsuga menziesii)	-0.710157	0.213618	-0.000042969	1.906055	1.331829	12,500	0.94			
Mountain hemlock (Tsuga mertensiana)	-0.389334	0.026130	-0.000015170	1.249021	1.334041	10,000	0.81			
Noble fir (Abies procera)	-0.391747	0.221986	-0.000059035	1.397007	0.825012	10,000	0.83			
Pacific silver fir (Abies amabilis)	-0.252922	0.158001	-0.000040061	1.100499	0.699160	10,000	0.72			
Red alder (Alnus rubra)	-1.359353	0.339679	-0.000161000	1.981622	1.714867	5,000	0.95			
Western hemlock (Tsuga heterophylla)	-0.925779	0.188380	-0.000038731	1.274983	2.070405	10,000	0.91			
Western redcedar (Thuja plicata)	-0.913087	0.177457	-0.000036407	1.205451	1.954673	12,500	0.89			

Table 2

Regression coefficients for the stress mortality function in LandMod. Coefficients were derived from results of gap model (MetaGap) simulations in the Blue River Watershed, Oregon (see text). All regression models and coefficients were significant (P < 0.0001)

Species	Coefficients (Eq.	Coefficients (Eq. (2))										
	b_0	b_1	b_2	<i>b</i> ₃	n							
Big-leaf maple	3.411904076	-0.136346649	-8.896625759	-4.955266536	10,000	0.94						
Douglas-fir	2.504101925	-0.108887048	-7.296973825	-2.041392553	12,500	0.98						
Mountain hemlock	1.487432766	-0.093757155	-7.239774890	-1.887944952	10,000	0.98						
Noble fir	2.087224896	-0.097609470	-7.142520430	-1.688087036	10,000	0.98						
Pacific silver fir	1.451741269	-0.099094357	-7.327145574	-1.559508276	10,000	0.98						
Red alder	3.823741754	-0.119934830	-7.721860300	-6.291407152	5,000	0.95						
Western hemlock	2.205636046	-0.092081963	-8.109368821	-1.967920536	10,000	0.98						
Western redcedar	2.365904514	-0.100754944	-7.643834319	-2.708449491	12,500	0.96						

ployed for the whole landscape (1-m deep silty-loam), only one set of drought-day functions was generated (Table 3). Mean growing degree-days was generated analytically for each cell of the landscape using monthly mean temperature values and a 5.5 °C daily minimum.

2.5. Performance assessments

Four assessments were conducted to evaluate the performance of LandMod (Table 4). The first two assessments evaluated the ability of LandMod to reproduce gap-model predictions of natural and

Regression coefficients for the drought-day function in LandMod. Coefficients were derived from results of gap model (MetaDry) simulations in the Blue River Watershed, Oregon (see text). All regression models and coefficients were significant (P < 0.0001)

Aspect	Coefficient	s (Eq. (3))							Adj. <i>R</i> ²
	b_0	b_1	b_2	<i>b</i> ₃	b_4	<i>b</i> ₅	b_6	n	
N	0.294273	-8.62E-4	0.018085	9.18000E-7	-0.001879	-3.15654E-10	5.4142E-5	6,288	0.65
NE	0.223535	-5.75E-4	0.020057	5.68000E-7	-0.001777	-1.88579E-10	2.9995E-5	6,780	0.69
Е	0.082038	-1.03E-4	0.025691	7.19783E-8	-0.002699	-2.65450E-11	7.7637E-5	8,404	0.62
SE	0.076554	-7.84E-5	0.029919	4.58417E-8	-0.003737	-1.78156E-11	1.4600E - 4	11,728	0.62
S	0.098794	-1.70E-4	0.031977	1.46000E-7	-0.004106	-5.23366E-11	1.6700E - 4	12,324	0.58
SW	0.157876	-3.46E-4	0.027567	3.10000E-7	-0.003449	-9.69923E-11	1.3500E-4	8,924	0.51
W	0.250829	-6.92E-4	0.024568	7.05000E-7	-0.002878	-2.35647E-10	1.0200E-4	9,740	0.62
NW	0.291185	-8.25E-4	0.018769	8.48000E-7	-0.002037	-2.83153E-10	6.3720E-5	10,080	0.63

Assessment	Basis of assessment	No., elevation, and location of simulated or observed stands	Initial conditions	Simulation duration (years)
Successional development	PNWGap vs. LandMod	23 ^a , 50-m intervals from 500 to 1600 m, Blue River Watershed, OR	Naturally regenerated 10-year-old stand for vegetation zone	500
Exp. thinning treatments (managed, uneven-aged stands) ^b	PNWGap vs. LandMod	8 thinning scenarios at locations listed above	40-, 450-year-old stands for vegetation zone	120
Douglas-fir time series	Observed ^c vs. LandMod Observed ^c vs. PNWGap	9,400–550 m, OR Cascades	Conditions at first observation	30–90
Landscape pattern of potential natural vegetation	Empirically based map (PNV) vs. LandMod	18,000, 500–1,600 m, Blue River Watershed, OR	10-year-old stand with all eight tree species	300

Table 4 Summary of the four comparative assessments with LandMod

^a Southern aspects.

^b Experimental thinning treatments consisted of the eight possible combinations of initial stand age (40 and 450 years), canopy-cover retention level (15 and 50%) and thinning method (thinning from above and thinning from below). Thinning was implemented at the initiation of a simulation, and at simulation years 60 and 120.

^c Unmanaged Douglas-fir stands first measured in 1910–1920s (Munger, 1946) at ca. age 54, and re-measured every 5–10 years for ca. 30 (n = 1), 60 (n = 3), 70 (n = 2), and 90 years (n = 3) (Acker et al., 1998).

managed forests over an environmental gradient. Simulations were performed on eight aspects. Because model performance tended to be invariant of aspect, only results for a southern aspect are presented. The third assessment involved comparisons of LandMod and PNWGap predictions with observed time series of Douglas-fir stand development. Observed stands were located in the same physiographic province as the Blue River watershed. This assessment afforded a direct comparison of LandMod predictions with empirical observations. It also provided a comparison of how well LandMod predicted observations relative to PNWGap. Environmental inputs to models were extracted from the data base created for the Blue River Watershed or generated using procedures noted above. Simulations used a 1-ha stand. The spatial data layers input to LandMod represented a one-cell landscape. A fixed level of background seed source (i.e. from neighboring stands) was employed for both models. Background levels corresponded to 'typical' forest conditions of the west-central Oregon Cascades and were held constant during a simulation. In the first two assessments, initial stand conditions representative of an elevation zone were generated with the gap model prior to comparisons. Simulations in the time-series assessment were initiated with stand conditions at the first observation period. All model simulations were replicated 30 times.

The landscape assessment (Table 4) evaluated the ability of LandMod to simulate the elevation-mediated pattern of forest communities in a large watershed. LandMod predictions of potential natural vegetation in the Blue River Watershed were compared to a map derived with the Potential Natural Vegetation (PNV) model (Henderson, 1998). The PNV model is a GIS-based, gradient model that uses empirical relationships to predict vegetative zones from moisture and temperature conditions. The PNV coverage for the Blue River watershed delineated the pattern of the three vegetation zones (see Section 2.4) at a 1-ha resolution. LandMod simulations used spatial data layers for the entire 18,000-ha watershed with a resolution of 1 ha. All cells were initialized with a young mixed-species forest. Forest development was simulated for 300 years to allow interactions between environmental conditions and modeled demographics to determine species composition and structure. Regeneration was determined dynamically using a maximum dispersal distance of 0.5 km. At the end of a simulation, species' relative importance (Mueller-Dombois and Ellenberg, 1974) on a cell was determined, and used to assign the cell to a natural vegetation zone. Cells were assigned to the western hemlock zone if Douglas-fir (the dominant species 400–500 years after stand initiation) had the highest relative importance, to the true-fir zone if Pacific silver fir had the highest importance value, to the mountain hemlock zone if mountain hemlock had the highest value, or to "other" if one of the other species dominated a stand. Ties were resolved

by assigning the zone according to the species with the largest quadratic mean diameter. Landscape-scale simulations were replicated 30 times.

2.6. Performance tests

A summary of performance tests is presented in Table 5. Simulated measures used in all except the

Table 5

Summary of the	tests used to evaluate	LandMod performance

Performance tests	Assessment	n ^a	Measures ^b	Simulation years examined
Elevation bias: regression of prediction residuals (PNWGap–LandMod) of individual measures on elevation	Successional development Experimental thinning treatments	23 23	T, S T, S (Wv)	50, 100, and every 100 years 55, 115 (60, 120)
Initial condition and stand-age bias: regression of prediction residuals (observed–modeled) of individual measures on initial basal area and density, and simulation duration.	Douglas-fir time series	9	T, S	Time of last observation
Accuracy: Freese's (1960) test of	Successional development	23	T, S	Every 10 years
accuracy, comparing PNWGap and LandMod predictions or	Experimental thinning treatments Douglas-fir time series	23 9	T, S (Wv) T, CHDI	55, 115 (60, 120) 20 years after initial
empirical observations and modeled predictions of individual measures				observation, and time of last observation
Similarity of diameter distributions: two-sample Kolmogorov–Smirnov	Successional development	23	Cfd	50, 100, and every 100 years
Goodness-of-fit test, comparing	Experimental thinning treatments	23	Cfd	55, 115
PNWGap and LandMod predictions or empirical observations and modeled predictions	Douglas-fir time series	9	Cfd	Same as accuracy test
Thinning treatment effects on prediction residuals (PNWGap–LandMod) of individual measures: three-way ANOVA of initial stand age, thinning treatment, thinning method, and all possible interactions	Experimental thinning treatments	184	T, S (Wv)	115 (120)
Spatial fit of PNV map and LandMod predictions of potential natural vegetation: multiple-resolution goodness-of-fit test (Turner et al., 1989)	Landscape pattern	18,000	Pv	300

^a Number of simulated or observed stands used in a performance test for each measure and for each simulation year examined.

^b Measures analyzed in performance tests. T: tree measures: basal area, density, quadratic mean diameter (QMD) by species and all species combined; S: stand-level measures: leaf-area-index (LAI) and canopy-height diversity index (CHDI) (a measure of multi-layer conditions; Spies and Cohen, 1992); Wv: wood volume extracted by thinning; Cfd: cumulative frequency distributions of 5-cm diameter classes by species and all species combined; Pv: potential natural vegetation (i.e. Douglas-fir, true fir, mountain hemlock).

landscape-scale tests were means of the 30 replications. Bias in LandMod predictions was evaluated with regression. In the assessments of natural and managed stand development, prediction residuals (PNWGap-LandMod) of individual measures were regressed on elevation to determine consistency in LandMod performance over an environmental gradient. A significant regression was interpreted to indicate bias, and would require subsequent examinations to reveal reasons for bias. Regressions also were performed for multiple time periods to examine for temporal trends in elevation bias. In the time series comparison, regressions of prediction residuals (observed-modeled) for individual measures evaluated bias due to initial stand conditions and observation length. Regressions were performed separately for PNWGap and LandMod predictions.

Agreement between PNWGap and LandMod predictions, and between observed and model predictions was tested with Freese's Chi-square test of accuracy (Freese, 1960) and Kolmogorov-Smirnov (K-S) goodness-of-fit test. Freese's accuracy test compares a level of desired accuracy (i.e. a critical error value) at a specified probability level with model-prediction error to determine model acceptability. In this study, critical errors and percent critical errors (critical error as a percentage of the true value) were used to indicate rather than test prediction accuracy. All critical errors were determined at the 5% probability level, and indicate a 5% chance of a model-prediction error equal to or greater than the critical value. Critical error values were based on differences between gap model and LandMod predictions, or observations and modeled predictions. Accuracy tests used data combined from all simulated or observed stands of a performance assessment. Predictions of structure (i.e. diameter distribution) were tested with a two-sample K-S test. Pair-wise comparisons were performed for each stand and year combination. In the natural succession and time-series assessments, accuracy and K-S tests were performed at multiple time intervals to evaluate temporal trends in LandMod performance. In the assessment of managed stands, tests with tree and stand measures were performed for simulation years just prior to thinning to evaluate maximal differences between PNWGap and LandMod predictions. Tests with extracted wood volume were performed for the last two thinning entries. All tests were performed separately for the eight experimental thinning scenarios.

Consistency in LandMod performance among management regimes was evaluated with a three-way ANOVA using prediction residuals (PNWGap– LandMod) for all eight treatment combinations at the 23 elevation sites. All experimental treatments (Table 4) and all possible interactions were included in the ANOVA. Differences between treatment means were tested for significance with the "least significant difference" test.

The goodness-of-fit between the PNV map and LandMod predictions was determined with the multiple-resolution method (Turner et al., 1989). This method uses a moving window of varying resolution (i.e. different window sizes) to compare cells of two maps. At the finest resolution, individual cells of the maps are compared. At coarser resolutions, the number of similar cells between maps without regard to spatial arrangement determines fit. Measures of fit are weighted by the corresponding resolution to generate a single overall measure of fit between maps. A mean overall goodness-of-fit was derived by averaging overall fit among the 30 replicates. To characterize prediction errors, topographic attributes and distance from vegetation-zone boundaries of incorrectly predicted cells were summarized.

3. Results and discussion

3.1. Successional development comparison

Elevation explained <14% of the variation in Land-Mod residuals, and was not significant (*Ps* > 0.05) in any regressions. Thus, performance tests of successional development used data combined from all elevations.

Percent critical errors of LandMod predictions of basal area, density, and size for canopy-dominant species and of stand-level measures were generally less than 15% (Fig. 1). An exception was the 15–22% error levels for density of mountain hemlock between ages 100–250. Prediction accuracy for sub-dominant species varied with frequency of occurrence. Western hemlock was the second most common species in stands <1250 m, accounting for 15–30% of total basal area in old-growth stands. Critical error values



Fig. 1. Critical error (CE) and percent critical error (PCE) for predictions of selected individual species and stand-levels measures with LandMod for the successional development assessment. Error values were derived at the 5% probability level using Freese's (1960) test of accuracy and indicate prediction accuracy of LandMod using the PNWGap model as the standard. All values were based on 23 simulations distributed over the 500–1600 m elevation gradient of the Blue River Watershed, Oregon. Noted in each graph is the tendency for LandMod to over-predict ("+") or under-predict ("-") relative to PNWGap predictions in the first and last half of the 500-year simulation period.

for western hemlock were lower but percent errors were much higher than those for dominant species (Fig. 1). For example, the maximum critical error for prediction of western hemlock basal area was only $4 \text{ m}^2/\text{ha}$, but this corresponded to a percent critical error of about 26%. Western redcedar, noble fir, and hardwood species were minor components in simulations with both models, collectively accounting for <2% of total basal area and <10% of total stem density. Trends in critical errors for these species were similar to those for western hemlock (Fig. 1). However, relative differences between model predictions for these sub-dominant species were much larger. For instance, the critical error for the prediction of big-leaf maple basal area at year 500 was $1.2 \text{ m}^2/\text{ha}$ which corresponded to a percent critical error of 122%.

Temporal trends in critical errors and prediction bias illustrated important differences between LandMod and the gap model. Relative to the gap model, Land-Mod prediction error for all measures except density tended to increase over the simulated 500-year period (Fig. 1). LandMod also tended to over-predict and under-predict these measures in the first and second half of the 500-year simulations, respectively. Differences in regeneration and growth rates between models accounted for the slight over-prediction. LandMod predicted higher levels of recruitment and diameter growth until stands acquired near maximum LAI at years 60–90 after which regeneration rates and growth rates of especially sub-canopy stems were slightly lower compared to the gap model. Under-prediction of basal area and tree size in the latter half of the simulation period largely reflected differences in underlying spatial processes between models. In the gap model, random mortality events create spatial variation in growing conditions within a stand. Stems adjacent to mortality-induced canopy gaps experience accelerated diameter growth due to increased light levels relative to similarly-sized stems located away from gaps. Over long time frames this leads to a noticeable differentiation in the sizes of canopy-dominant stems (e.g. Fig. 2B). Gaps also facilitate the establishment



Fig. 2. Comparison of LandMod and PNWGap predicted diameter distributions (all species combined) for (A) 100 and (B) 400-year-old Douglas-fir stands on a south slope at an elevation of 950 m, Blue River Watershed, Oregon.

and growth of species of intermediate to high shade tolerance. The distance-independent nature of Land-Mod, however, precludes the formation of gaps and thus limits the degree of horizontal variability within a stand. All stems within a size class in LandMod experience the same increase in available light whenever stems of similar or taller stature die. Also, all stems in a size class are advanced at the same rate, resulting in the lack of potential for stems of similar size to experience differential growth. For these reasons, LandMod predicted smaller stems and lower values of basal area in older stands compared to the gap model. Differences in predicted structure between models become more apparent with increasing gap formation in older stands. PNWGap and LandMod predicted diameter distributions for all stems combined and for dominant species were not significantly different (Ps > 0.06) up to age 300 (e.g. Fig. 2A), but were significantly different (Ps < 0.05) in simulation years examined thereafter at all 23 locations (e.g. Fig. 2B).

3.2. Experimental thinning treatments comparison

Elevation explained <20% of the variation in Land-Mod residuals and was not significant in any of the regressions (*Ps* > 0.08). Given the lack of an elevation bias, data for all 23 sites were used in the performance tests.

Trends in critical errors were similar for individual species and all species combined; only results for all species combined are presented (Table 6). For all experimental treatments, percent critical error values for predictions with LandMod ranged from 1.4 to 28.5% with most values being less than 15%. Percent critical errors for tree density and canopy-height diversity index tended to be higher compared to other measures. Error values for most measures did not exhibit obvious temporal trends. An exception was percent critical errors for basal area which tended to increase over time for treatments involving 50% canopy retention and to decrease over time for the 15% retention treatments.

Despite the relatively good agreement between models, there were significant thinning-treatment effects on LandMod predictions. Significant main treatment effects and interactions were indicated by the ANOVA of prediction residuals (PNWGap–LandMod) for each measure (Table 7). One or more of the main treatments tended to have substantially greater

Critical errors (CE) and percent critical errors (PCE) for predictions of stand measures (all species combined) with LandMod for experimental thinning treatments. Error values were derived at the 5% probability level using Freese's (1960) test of accuracy and indicate prediction accuracy of LandMod using the PNWGap model as the standard. All values were based on 23 simulations distributed over the 500–1600 m elevation gradient of the Blue River Watershed, Oregon. Year under each measure is simulation year

Thinning method/	Initial stand	Basal	area (m ² /	ha)		Density (no./ha)				Quadrat	Quadratic mean diameter (cm)				
retention level	age (years)	Year :	55	Year 1	15	Year 55		Year 1	15	Year 55		Year 1	15		
		CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE		
Below/15%	40	8.6	18.7	4.6	9.4	60.0	10.8	53.0	10.0	2.8	14.0	2.5	12.9		
	450	9.0	16.1	3.9	6.5	70.6	12.8	85.8	15.6	4.2	10.5	3.7	9.7		
50%	40	3.0	6.3	4.2	7.6	80.8	20.3	60.0	16.7	2.9	7.3	4.7	10.6		
	450	5.2	5.8	10.0	11.6	108.1	19.1	74.1	14.0	3.2	7.0	6.7	14.5		
Above/15%	40	4.5	8.2	3.8	7.9	27.6	4.4	34.9	6.0	0.9	2.9	0.7	2.2		
	450	5.1	11.7	3.0	6.3	61.5	9.8	45.2	7.5	3.0	10.3	1.1	3.6		
50%	40	3.9	8.2	5.7	10.5	73.7	12.5	66.3	10.4	3.1	9.2	0.5	1.4		
	450	4.0	10.7	10.4	18.9	50.5	8.2	52.5	8.7	1.4	4.8	3.3	9.9		
		Leaf-area-index			Canopy-height diversity index			Extracted volume (m ³ /ha)							
		Year	55	Year 1	15	Year 55		Year 115		Year 60		Year 120			
		CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE		
Below/15%	40	0.8	12.0	0.4	6.8	0.6	12.3	1.2	22.9	21.7	5.6	20.0	5.8		
	450	1.1	19.7	0.5	8.6	0.6	14.4	0.6	13.7	41.1	12.3	27.6	7.5		
50%	40	0.3	6.0	0.3	4.6	0.9	17.5	0.5	8.1	19.7	11.0	10.9	13.1		
	450	0.4	4.7	0.4	6.8	0.5	5.8	0.6	7.2	13.6	16.8	12.8	12.4		
Above/15%	40	0.3	4.0	1.1	14.5	1.0	22.9	0.9	19.2	44.4	8.0	64.6	16.7		
	450	0.5	7.4	0.6	8.1	1.0	22.9	0.9	20.1	103.1	19.5	48.4	8.1		
50%	40	0.5	8.1	0.7	9.4	0.8	13.6	0.6	11.5	49.8	9.4	49.6	10.2		
	450	0.6	9.3	0.5	6.4	1.7	28.5	0.8	14.0	93.6	18.3	57.6	9.6		

Table 7

Results of a three-factor ANOVA testing the effects of canopy retention level, initial stand age, and thinning method on the differences between PNWGap and LandMod predictions for stand measures (all species combined) at simulation year 115 (year 120 for extracted volume). Treatments included two levels of canopy retention (15 and 50%), two initial stand ages (40, 450 years), and two thinning methods (from below, from above). For all *F* tests, d.f. = 1183 (eight treatment combinations simulated at 23 elevations)

Source	Measure													
	Basal a (m ² /ha)		Density (no./ha)		Quadratic diameter		Leaf-ai index	rea	Canopy- diversity	•	Extracted volume			
	F	Р	F	Р	F	Р	F	Р	F	Р	F	Р		
Canopy retention (CR)	103.22	0.0001	0.58	0.4485	454.01	0.0001	1.51	0.2205	11.20	0.0010	3.69	0.0566		
Initial stand age (A)	75.75	0.0001	3.10	0.0825	2.29	0.1316	55.52	0.0001	12.34	0.0006	5.62	0.0190		
Thinning method (TM)	39.15	0.0001	118.00	0.0001	507.47	0.0001	60.82	0.0001	1.06	0.3055	2.31	0.1305		
$CR \times A$	34.97	0.0001	0.28	0.5982	75.67	0.0001	3.38	0.0694	9.79	0.0020	3.56	0.0610		
$CR \times TM$	0.71	0.4015	18.09	0.0001	263.57	0.0001	22.09	0.0001	11.13	0.0010	1.18	0.2795		
$A \times TM$	22.44	0.0020	17.10	0.0001	34.11	0.0001	1.76	0.1886	2.12	0.1485	10.28	0.0016		
$CR \times A \times TM$	0.03	0.8719	26.00	0.0001	284.60	0.0001	8.57	0.0038	9.77	0.0021	5.11	0.0250		

effect than interaction terms for most measures. For this reason, only main effect means were compared. Mean residuals of main treatment effects were mostly positive, indicating an overall tendency for Land-Mod to under-predict measures compared to the gap model (Table 8). Based on pair-wise comparisons of main-effect means, LandMod residuals tended to be significantly smaller (i.e. in terms of absolute value) for thinning treatments that promoted a sparse or compacted residual canopy (i.e. 15% canopy retention, 40-year-old stand, thinning from above) compared to treatments resulting in a dense or tall canopy (Table 8). The thinning method especially influenced agreement between models in predicted structure. Diameter distributions predicted by PNWGap and LandMod at simulation years 55 and 115 were not significantly different (Ps > 0.06) for treatments involving thinning from above but were significantly different (Ps < 0.04) for all treatment combinations that involved thinning from below.

Inspection of simulated stand conditions revealed increasing differences in regeneration and growth rates between models with increasing stature and density of the residual canopy. Contributing to these differences was the tendency for light-profile estimates to be less similar between models with increasing canopy complexity. This trend reflected underlying differences in how the two models calculate available light. Light penetration in gaps and under complex canopies is enhanced in the gap model due to its consideration of solar geometry (i.e. sun angle, diffuse and direct-beam sources) (Urban et al., 1991;

Mean (± 1 S.E.) of LandMod residuals (PNWGap–LandMod) for the main effects of the experimental thinning treatments (see Table 7). Measures are for all species combined. Pairs in boldface were significantly different (d.f. = 176, P < 0.05) based on the "least significant difference" test

Measure	Main effects										
	Canopy retention	on (%)	Initial stand ag	ge (years)	Thinning method						
	15	50	40	450	Below	Above					
Basal area (m ² /ha)	- 0.36 (0.39)	3.45 (0.62)	- 0.10 (0.46)	3.18 (0.60)	2.73 (0.62)	0.36 (0.50)					
Density (no./ha)	-9.41 (5.64)	-12.76 (7.21)	-6.39 (5.98)	-17.71 (6.95)	39.27 (5.66)	8.88 (4.91)					
Quadratic mean diameter (cm)	0.53 (0.20)	3.74 (0.50)	2.03 (0.58)	2.25 (0.26)	3.65 (0.53)	0.62 (0.15)					
Leaf-area-index	0.24 (0.06)	0.20 (0.04)	0.36 (0.05)	0.08 (0.05)	0.36 (0.05)	0.07 (0.04)					
Canopy-height diversity index	- 0.63 (0.13)	- 0.34 (0.04)	- 0.33 (0.07)	- 0.64 (0.12)	-0.53(0.13)	-0.44(0.06)					
Extracted volume (m ³ /ha)	3.74 (4.18)	0.20 (3.96)	- 3.88 (4.00)	7.66 (3.96)	-2.28 (2.03)	6.44 (5.52)					

Weishampel and Urban, 1996). Calculations are simplified in LandMod by assuming a vertical light source and no horizontal shading. For treatments promoting tall or dense canopies (e.g. thinning from below, thinning in old-growth stands, 50% canopy retention), gap model values of ground-level light levels were on average 11% (8–15%) greater than corresponding LandMod estimates. For the treatments promoting short or compacted canopies, predicted light levels generally were more similar between models, with gap-model values only about 5% (2–7%) greater than those estimated by LandMod.

3.3. Douglas-fir time series comparison

Both models predicted observed Douglas-fir and stand-level measures reasonably well, but LandMod was slightly less accurate than the gap model (Table 9). Critical error values for predictions with both models increased between the time periods examined. Overall, percent critical errors were <15% for predictions of basal area and quadratic mean diameter for all stems combined and for Douglas-fir, and for canopy-height diversity index. Model predictions were slightly less accurate for density of Douglas-fir and all stems combined, with percent critical error values ranging up to

16-22%. Densities of shade-tolerant tree species, primarily big-leaf maple and western hemlock, increased over time in the observed stands, but were only a minor component of total basal area. Both models predicted measures of these species with low accuracy (54–149%). The spatial variation simulated in the gap model, however, facilitated growth of shade-tolerant stems and resulted in slightly higher prediction accuracy for sub-dominant species compared to LandMod. Based on averages of prediction residuals, models over-predicted density of Douglas-fir by the last observation period and under-predicted all other measures in the two time periods examined. For both models, prediction residuals for measures at the end of simulations were not significantly correlated (Ps > 0.08) with initial stand attributes or length of observation. Also, modeled and observed diameter distributions for all stems combined and for Douglas-fir were not significantly different (Ps > 0.08) for the two time periods examined.

3.4. Landscape pattern comparison

LandMod predictions of potential natural vegetation closely matched the PNV map. Mean overall fit of LandMod predictions was 94% (S.E. = 0.01). On

Critical error (CE) and percent critical error (PCE) in the comparison of PNWGap and LandMod predictions with observed trends in nine, low-elevation (400–500 m) Douglas-fir stands. Error values were derived at the 5% probability level using Freese's (1960) test of accuracy and indicate the accuracy of models in predicting measures of actual stands. Comparisons were performed at 20 years after the initial observation and at the time of the last observation

Measure/stand age (years)	Total				Douglas-fir				All other species combined				
	LandMod		PNWGap		LandMod		PNWGap		LandMod		PNWGap		
	CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE	CE	PCE	
Basal area (m ² /ha)													
74	3.6	5.8	2.0	3.4	3.4	5.9	1.6	2.8	0.8	134.0	0.5	87.0	
84–144	9.9	12.1	7.1	8.6	7.5	9.7	5.7	7.5	4.9	147.3	4.5	125.2	
Density (no./ha)													
74	33.2	6.3	32.0	6.3	34.3	6.8	32.8	6.2	8.7	128.1	3.7	54.4	
84–144	47.9	18.4	45.8	15.7	48.4	22.2	41.3	16.8	79.3	148.9	73.4	136.7	
Quadratic mean diameter (c	m)												
74	1.8	4.8	1.7	4.5	1.9	5.0	1.7	4.6	26.9	67.8	24.2	61.8	
84–144	6.7	10.5	6.4	10.2	9.2	13.8	8.8	13.2	22.1	75.7	16.5	54.5	
Canopy-height diversity ind	ex												
74	03	6.1	0.3	6.1									
84–144	0.6	14.4	0.6	14.4									



Fig. 3. Potential natural vegetation of the Blue River Watershed estimated by the PNV model (Henderson, 1998) (A), and a representative example of incorrect predictions with LandMod (B).

average, LandMod incorrectly predicted 4.4% (S.E. = 0.32) of the cells in the western hemlock zone as true-fir, and 3.4% (S.E. = 0.21) of the cells in the true-fir zone as western hemlock (Fig. 3). About 85% (S.E. = 0.91) of these incorrect predictions occurred along the boundary (+3 cells) of the western hemlock and true-fir zones. Additionally, the majority of incorrectly predicted cells in these two zones occurred on aspect-elevation combinations characteristic of climatic conditions of the other zone. About 69% (S.E. = 1.81) of the incorrectly scored cells in the western hemlock zone were on northerly aspects between 1050 and 1200 m, with the remainder about equally distributed among the other aspects. Of the true-fir cells incorrectly predicted, about 47% (S.E. = 0.78) were on southerly exposures between 1100 and 1200 m, and 34% (S.E. = 0.31) were on north and northeast aspects at lower elevations (1000 and 1100 m). On average, LandMod incorrectly predicted 12% (S.E. = 0.43) of the mountain hemlock cells as true-fir, with 90% (S.E. = 0.10) of these cells occurring along the boundary with the true-fir zone on southerly aspects between 1400 and 1500 m.

The topographic position and boundary proximity of LandMod prediction errors suggest a deficiency in modeled environmental conditions. However, mean values of growing degree-days and of drought-day proportions of correctly and incorrectly predicted cells of similar topographic position were not significantly different (two-sample *t*-test; Ps > 0.29), and only a minority (7-15%) of cells along zone boundaries tended to be predicted incorrectly. Alternative explanations for the patterns of LandMod prediction errors include potential differences in the underlying climatic data layers between models, and error in the PNV map. Climatic information used in the two models were based on data from similar meteorological stations, but were expanded to the landscape scale with different interpolation methods. Slight differences in the two environmental fields could partly explain the aspect-elevation combinations of the LandMod prediction errors. The PNV map is derived from regression models that have inherent prediction error. Because of the overall difficulty in predicting discrete breaks between vegetation zones, error levels of the PNV model likely are higher at zone boundaries. This alone could explain the concentration of LandMod prediction errors along boundaries of vegetation zones. Despite these and other possible confounding factors, results of this comparison indicated a reasonable ability of Land-Mod to predict realistic forest-community patterns over an environmental gradient.

4. Summary and conclusions

An efficient model for simulating forest landscape change in western Oregon, called LandMod, was developed by scaling the PNWGap gap model to operate at a coarser resolution. Scaling was achieved with the statistical estimation of gap-model predictions of demographics for 5-cm size-classes and a 5-vear time step, and the use of mean approximations of environmental inputs. LandMod provided more rapid projections (about 58 times faster) of fine-scale, forest dynamics than the PNWGap model with only a nominal reduction in accuracy. In comparisons with the gap model, percent critical errors ($\alpha = 0.05$) for predictions of dominant tree species and stand-level measures with LandMod ranged from 1.4 to 29% with the majority of critical errors being less than 15%. Of the measures examined, predictions of stem density differed the most between models. Model comparisons with field observations indicated slightly lower prediction accuracy with LandMod compared to the gap model. Reduction in accuracy with LandMod was expected given the simplifications necessary for computational efficiency. Overall performance of Land-Mod, however, typifies achievements of other attempts to create simplified, diameter-class variants from existing tree models (e.g. Ek and Monserud, 1979; Haight and Getz, 1987), and to enhance gap-model efficiency by modeling stem aggregates (e.g. height classes) instead of individuals (Fulton, 1991).

Despite the relatively good performance of Land-Mod, tests revealed three notable deficiencies warranting further consideration. Uniform growth transfer of all stems in a size class led to under-prediction of stem-size variation and of large stems in older stands. A possible refinement is the use of multiple growth equations developed from the variance structure of the parameterization data. A range of equations for each species could be derived by varying the mean regression coefficients by one to two standard deviations in accordance with the underlying covariance structure. Diameter increment of individual stems in a size class could then be based on a randomly selected growth equation. Another deficiency was the under-prediction of available light and resulting stem growth in stands with complex canopies. Expanding the light-profile calculations to include effects of sun angle, topographic position, and horizontal shading should improve predictions, and additionally enhance the spatially explicit framework of the model. Efficient light-regime calculations could be developed as statistical abstractions of gap-model procedures. Lastly, LandMod consistently under-predicted mean size of infrequent, sub-dominant tree species. Refinements noted above are anticipated to enhance growth predictions for sub-dominant species. Further testing after model enhancements will be essential to ensure correction of deficiencies.

LandMod was parameterized and evaluated at a 1-ha spatial grain for the west-central Oregon Cascades. The applicability of the current parameterization to other ecoregions in the PNW region is unknown. A different parameterization likely will be required for landscapes of higher or lower site productivity and with substantially different environmental conditions. Also, the sensitivity of LandMod predictions to grain size remains to be determined. Before using LandMod outside of west-central Oregon or with spatial grains other than 1 ha, model behavior should be evaluated to determine parameterization adequacy or needs.

LandMod provides an alternative method for simulating forest change at landscape scales. Land-Mod simulates species-level dynamics similar to forest-management simulators (e.g. Sessions et al., 1999), but at a finer spatial scale and over much longer time periods. Similar to other species-based ecological simulators (e.g. Mladenoff and He, 1999; He et al., 1999a, 2002), LandMod incorporates environmental constraints to tree demographics and spatial processes in the form of seed dispersal, but explicitly models forest structure. Other spatial processes, such as natural disturbance and wood delivery to streams, and stand-level processes, such as dead-wood dynamics and carbon sequestration, are being incorporated in ongoing efforts.

LandMod was designed to address specific forest management and research questions in western Oregon. Topical issues pertaining to the effects of forest and landscape structure on a range of ecosystem properties warranted the explicit simulation of tree size and density at fine spatial scales. The computer memory and processing load required to accommodate this detail, however, imposes limits to the number of landscape cells and thus landscape area that LandMod can simulate. Most ecological simulators are capable of simulating landscapes 0.5–4-million hectares in size (e.g. He and Mladenoff, 1999; He et al., 1999b; Yemshanov and Perera, 2002). A reasonable upper limit for LandMod using a 1-ha cell size is about 500,000 ha. Thus, LandMod is best suited for studies at watershed to sub-regional levels rather than at regional levels.

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References

- Acevedo, M., Urban, D.L., Ablan, M., 1995. Transition and gap models of forest dynamics. Ecol. Appl. 5, 1040–1055.
- Acker, S.A., McKee, W.A., Harmon, M.E., Franklin, J.F., 1998. long-term research on forest dynamics in the Pacific Northwest: a network of permanent forest plots. In: Dallneier, F., Comiskey, J.A. (Eds.), Forest Biodiversity in North, Central and South America, and the Caribbean, Man and The Biosphere Series, vol. 21. The Parthenon Publishing Group, New York, pp. 93– 106.
- Armstrong, J.S., 1999. Forecasting for environmental decision making. In: Dale, V.H., English, M.R. (Eds.), Tools to Aid Environmental Decision Making. Springet-Verlag, New York, pp. 192–225.
- Bonan, G.B., 1989. A computer model for the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Model. 45, 275–306.

- Brown, J.R., MacLeod, N.D., 1996. Integrating ecology into natural resource management policy. Environ. Manage. 20, 289–296.
- Burns, R.M., Honkala, B.H. (Tech. Coords.), 1990. Silvics of North America: Volume 1. Conifers, Volume II. Hardwoods. Agriculture Handbook 654. US Department of Agriculture, Forest Service, Washington, DC, 675, 877 pp.
- Busing, R.T., Garman, S.L., 2002. Promoting old-growth characteristics and long-term wood production in Douglas-fir forests. For. Ecol. Manage. 160, 161–175.
- Chertov, O., Komarov, A., Andrienko, G., Andrienko, N., Gatalsky, P., 2002. Integrating forest simulation models and spatial–temporal interactive visulization for decision making at landscape level. Ecol. Model. 148, 47–65.
- Crookston, N.L., Havis, R.N., 2002. Second forest vegetation simulator conference. In: Conference Proceedings, RMRS-P-26. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 208 pp.
- Daly, C., Neilson, R.P., Phillips, D.L., 1994. A statisticaltopographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. 33, 140–158.
- Ek, A.R., Monserud, R.A., 1979. Performance and comparison of stand growth models based on individual tree and diameterclass growth. Can. J. For. Res. 9, 231–244.
- FEMAT (Forest Ecosystem Management Assessment Team), 1993. Forest Ecosystem Management: An Ecological, Economic, and Social Assessment. US Department of Agriculture, Portland, OR.
- Franklin, J.F., Dyrness, C.T., 1973. Natural vegetation of Oregon and Washington. General Technical Report PNW-GTR-8. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 417 pp.
- Freese, R., 1960. Testing accuracy. For. Sci. 6, 139-145.
- Fulton, M.A., 1991. Computationally efficient forest succession model: design and initial tests. For. Ecol. Manage. 42, 23–34.
- Garman, S.L., Acker, S.A., Ohmann, J.L., Spies, T.A., 1995a. Asymptotic height–diameter equations for twenty-four tree species in western Oregon. Research Contribution 10, Oregon State University, College of Forestry, Forest Research Laboratory. Corvallis, OR, 22 pp.
- Garman, S.L., Cissel, J.H., Mayo, J.H., 2003. Accelerating development of late-successional conditions in young managed Douglas-fir stands: a simulation study. General Technical Report PNW-GTR-557. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 57 pp.
- Garman, S.L., Hansen, A.J., Urban, D.L., Lee, P.F., 1992. Alternative silvicultural practices and diversity of animal habitat in western Oregon: a computer simulation approach. In: Luker, P. (Ed.), Proceedings of the 1992 Summer Simulation Conference. The Society for Computer Simulation, Reno, NV, pp. 777–781.
- Garman, S.L., Spies, T.A., Cohen, W.B., Means, J.E., Bradshaw, G.A., Dippon, D., 1995b. Modeling, monitoring, and displaying ecological change at watershed to landscape scales: tools for ecosystem management. Special Publication #2, Forest and Rangeland Ecosystem Science Center, USDI/NBS, Corvallis, OR, 179 pp.
- Goslin, M.N., 2000. Parameterization and assessment of the ZELIG simulation model for Coastal Oregon. Technical Report, Forest

Science Laboratory, Oregon State University, Corvallis, OR, 39 pp.

- Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. For. Res. 30, 32–43.
- Haight, R.G., Getz, W.M., 1987. A comparison of stage-structured and single-tree models for projecting forest stands. Natur. Resource Model. 2, 279–298.
- Hann, D.W., Larsen, D.R., 1991. Diameter growth equations for fourteen tree species in southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis, OR, Research Bulletin 69, 18 pp.
- Hann, D.W., Wang, C.-H., 1990. Mortality equations for individual trees in the mixed-conifer zone of southwest Oregon. Forest Research Laboratory, Oregon State University, Corvallis, OR. Research Bulletin 67, 17 pp.
- Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., Raphael, M.G., 1995. Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. Ecol. Appl. 5, 535–554.
- He, H.S., Mladenoff, D.J., 1999. Dynamics of fire disturbance and succession on a heterogeneous forest landscape: a spatially explicit and stochastic simulation approach. Ecology 80, 80–99.
- He, H.S., Mladenoff, D.J., Boeder, J., 1999a. An object-oriented forest landscape model and its representation of tree species. Ecol. Model. 119, 1–19.
- He, H.S., Mladenoff, D.J., Crow, T.C., 1999b. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol. Model. 114, 213–233.
- He, H.S., Mladenoff, D.J., Gustafson, E.J., 2002. Study of landscape change under forest harvesting and climate warminginduced fire disturbance. For. Ecol. Manage. 155, 257–270.
- Henderson, J.A., 1998. The USFS potential natural vegetation mapping model. PNV Model Documentation, USDA Forest Service, Pacific Northwest Research Station, Portland, OR, 22 pp.
- Keane, R.E., Long, D.G, Menakis, J.P., Hann, W.J., Bevins, C.D., 1996a. Simulating coarse scale vegetation dynamics using the Columbia River Basin Succession Model-CRBSUM. General Technical Report INT-GTR-340. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, 50 pp.
- Keane, R.E., Morgan, P., Running, S.W., 1996b. FIRE-BGC a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the Northern Rocky Mountains. Research Paper INT-RP-484. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, 122 pp.
- Keane, R.E., Parsons, R.A., Hessburg, P.F., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecol. Model. 151, 29– 49.
- Li, C., 2000. Reconstruction of natural fire regimes through ecological modelling. Ecol. Model. 134, 129–144.
- Li, C., 2002. Estimation of fire frequency and fire cycle: a computational perspective. Ecol. Model. 154, 103–120.

- Mladenoff, D.J., He, H.S., 1999. Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, pp. 125–162.
- Mueller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York, 547 pp.
- Munger, T.T., 1946. Watching a Douglas-fir forest for thirty-five years. J. For. 44, 705–708.
- Roberts, D.W., Betz, D.W., 1999. Simulating landscape vegetation dynamics of Bryce Canyon National Park with the vital attributes/fuzzy systems model VAFS/LANDSIM. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, pp. 99–124.
- Sessions, J., Johnson, K.N., Franklin, J.F., Gabriel, J.T., 1999. Achieving sustainable forest structures on fire-prone landscapes while pursuing multiple goals. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, pp. 210–255.
- Spies, T.A., Cohen, W.B., 1992. An index of canopy height diversity. Oregon State University, Coastal Oregon Productivity and Enhancement Report 5, pp. 5–7.
- Swanson, F.J., 1997. H.J. Andrews Experimental Forest. In: U.S. long-term Ecological Research Network Newsletter, pp. 6–7.
- Swanson, F.J., Franklin, J.F., 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecol. Appl. 2, 262–274.
- Turner, M.G., Costanza, R., Sklar, F.H., 1989. Methods to evaluate the performance of spatial simulation models. Ecol. Model. 48, 1–18.
- Urban, D.L., 1993. A user's Guide to ZELIG, version 2. Department of Forest Sciences, Colorado State University, Fort Collins, CO, 78 pp.
- Urban, D.L., Acevedo, M.F., Garman, S.L., 1999. Scaling fine-scale processes to large-scale patterns using models derived from models: meta-models. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, pp. 70– 98.
- Urban, D.L., Bonan, G.D., Smith, T.M., Shugart, H.H., 1991. Spatial application of gap models. For. Ecol. Manage. 42, 95– 110.
- Urban, D.L., Harmon, M.E., Halpern, C.B., 1993. Potential response of Pacific northwestern forests to climatic change; effects of stand age and initial composition. Clim. Change 23, 247–266.
- Weishampel, J.F., Urban, D.L., 1996. Coupling a spatially-explicit forest gap model with a 3-D solar routine to simulate latitudinal effects. Ecol. Model. 86, 101–111.
- Yemshanov, D., Perera, A.H., 2002. A spatially explicit stochastic model to simulate boreal forest cover transitions: general structure and properties. Ecol. Model. 150, 189– 209.