





Forest Ecology and Management 236 (2006) 113-126

Forest Ecology and Management

www.elsevier.com/locate/foreco

Modeling forest harvesting effects on landscape pattern in the Northwest Wisconsin Pine Barrens

Volker C. Radeloff ^{a,*}, David J. Mladenoff ^a, Eric J. Gustafson ^b, Robert M. Scheller ^a, Patrick A. Zollner ^b, Hong S. He ^c, H. Resit Akçakaya ^d

Department of Forest Ecology and Management, 1630 Linden Drive, University of Wisconsin-Madison, Madison, WI 53706, USA
 USDA Forest Service, North Central Research Station, 5985 Highway K, Rhinelander, WI 54501, USA
 The School of Natural Resources, University of Missouri-Columbia, Columbia, MO 65211, USA
 Applied Biomathematics, 100 North Country Road, Setauket, NY 11733, USA

Received 13 June 2006; received in revised form 2 September 2006; accepted 3 September 2006

Abstract

Forest management shapes landscape patterns, and these patterns often differ significantly from those typical for natural disturbance regimes. This may affect wildlife habitat and other aspects of ecosystem function. Our objective was to examine the effects of different forest management decisions on landscape pattern in a fire adapted ecosystem. We used a factorial design experiment in LANDIS (a forest landscape simulation model) to test the effects of: (a) cut unit size, (b) minimum harvest age and (c) target species for management. Our study area was the Pine Barrens of northwest Wisconsin, an area where fire suppression has caused a lack of large open areas important for wildlife. Our results show that all three management choices under investigation (cut unit size, minimum harvest age and target species for management) have strong effects on forest composition and landscape patterns. Cut unit size is the most important factor influencing landscape pattern, followed by target species for management (either jack pine or red pine) and then minimum harvest age. Open areas are more abundant, and their average size is larger, when cut units are larger, target species is jack pine, and minimum harvest age is lower. Such information can assist forest managers to relate stand level management decision to landscape patterns.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Landscape ecology; Simulation modeling; LANDIS; Pine Barrens; Wisconsin; Forest harvesting; Spatial pattern

1. Introduction

Landscape ecology aims to link disturbance processes to landscape pattern (Turner, 1987; Turner et al., 2001) and has demonstrated that landscape pattern strongly affects ecosystem processes. For example, the probability of wind disturbance increases as forest edges become more abundant (Franklin and Forman, 1987), and tree species that are poor dispersers cannot establish themselves in the center of large fire patches (He and Mladenoff, 1999a). The importance of landscape pattern on processes makes it essential to examine how human land management changes disturbance processes and the resulting landscape pattern (Foster et al., 1997). For example, fire suppression may alter natural disturbance regimes, thereby indirectly changing landscape pattern (Baker, 1994), however

climate variability may often be a more important factor for changing fire regimes than human activities (Johnson et al., 1990). Forest harvesting affects landscape pattern directly (Franklin and Forman, 1987; Gustafson and Crow, 1998), resulting in landscape patterns that may be quite different from those observed in the absence of forest harvesting (Mladenoff et al., 1993; Wallin et al., 1996).

Some landscape ecologists have suggested using natural disturbance regimes as a guideline for forest management by trying to mimic their effects on landscape pattern when allocating silvicultural treatments and harvests (Hunter, 1993; Cissel et al., 1994, 1999; Wallin et al., 1994; Radeloff et al., 1999). For example, clear-cuts may be appropriate in areas where extensive crown fires were common, such as the boreal forest (Hunter, 1993), whereas selective cutting may be more appropriate in areas where single-tree gap dynamics are prevalent, such as the northern hardwood region (Lorimer, 1977).

This suggestion has intuitive appeal, but it has rarely been implemented in forest planning. One reason is that the effects of

^{*} Corresponding author. Tel.: +1 608 263 4349; fax: +1 608 262 9922. E-mail address: radeloff@wisc.edu (V.C. Radeloff).

forest management decisions on landscape pattern are not well understood. The spatial patterns of managed forests depend on the size of harvest units, the spatial allocation of harvest units, the tree species-specific minimum harvest age, and the tree species selected for forest regeneration. Quantitative information on the relative importance of each of these management choices, and their cumulative effects, on forest landscape pattern is largely lacking.

Our goal was to estimate the effects of different forest management decisions on long-term landscape patterns in the Northwest Wisconsin Pine Barrens. We used a factorial design experiment to test the effects of three different forest management decisions on landscape patterns: (a) cut unit size, (b) minimum harvest age, and (c) target species for management. We did not examine spatial allocation of harvest units as an additional variable. The model that we used operated in 10 year time steps, and that made it more straightforward to simulate neighboring harvests via the cut unit size variable. Cut unit size was hypothesized to have a strong effect on the size of

open habitat areas. Minimum harvest age was hypothesized to affect the total area of open habitat. The same was hypothesized for the effect of target species, because the minimum harvest ages commonly employed for jack pine and red pine are very different.

2. Methods

2.1. Forest management challenge in the Northwest Wisconsin Pine Barrens study area

The role of the spatial patterns of forest management in the northwest Wisconsin Pine Barrens is debated by foresters and wildlife biologists (Borgerding et al., 1995; Moss, 2000, Fig. 1a). The northwest Wisconsin Pine Barrens is located on a 450,000 ha outwash plain with predominantly coarse, sandy soils (Murphy, 1931; Radeloff et al., 1998, 1999). These soils are prone to drought and lead to conditions that are conducive to fires. This area experienced significant fire disturbance before

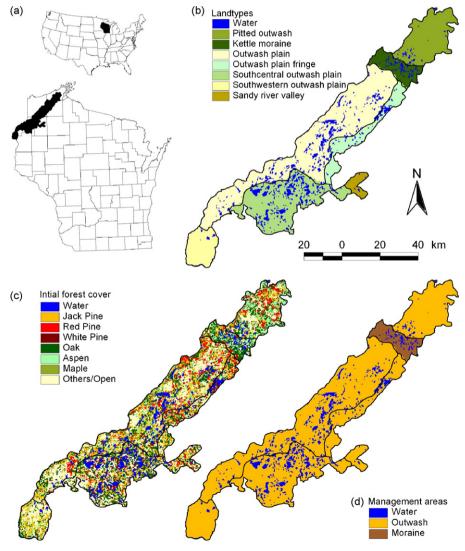


Fig. 1. (a) The location of the Pine Barrens study area in Wisconsin (U.S.), (b) landtypes of the Pine Barrens, (c) initial forest conditions derived from a satellite classification and (d) forest management areas. The southwestern corner of the study area is located at $45^{\circ}34''N$ and $92^{\circ}53''W$; the northeastern corner of the study area is located at $46^{\circ}47''N$ and $91^{\circ}04''W$.

European settlement, but European settlement over the last 150 years has significantly altered disturbance processes and landscape pattern (Radeloff et al., 1999). Local management agencies are particularly interested in the effects of forest harvests on landscape pattern in this area because of the decline of open habitat wildlife species that persisted in fire generated openings at pre-settlement times (Borgerding et al., 1995; Moss, 2000).

Pre-settlement fire regimes were not uniform across this region. In the northern part of the Pine Barrens (Fig. 1b, landtype 'Pitted outwash'), fire return intervals were longest (300-500 years), forests were comparatively old and dense, and white, red, and jack pine (Pinus strobus, resinosa, and banksiana) occurred together (Radeloff et al., 1999). In the central part of the Pine Barrens (Fig. 1b, landtype 'Outwash plain'), frequent crown fires (30-70 years return interval) were common and jack pine dominated the forests, creating a shifting mosaic of large openings intermixed with dense, regenerating jack pine stands. In the southern Pine Barrens (Fig. 1b, landtypes 'Southcentral outwash plain' and 'Southwestern outwash plain'), fire return intervals were as low as 5 years, but fire intensity was much lower, permitting the establishment of pin and burr oak (Ouercus ellipsoidalis and macrocarpa) and red pine savannas (Radeloff et al., 1998).

Since the 1850s, European settlers logged, farmed and ultimately reforested the Pine Barrens region. The overall result of the last 150 years of land management is a much lower total area of open habitat in the current landscape, as well as smaller areas of individual open-habitat patches (Radeloff et al., 1999), which is detrimental to area-sensitive open habitat species, such as sharp-tailed grouse (*Tympanuchus phasianellus*), bobolink (*Dolichonyx oryzivorus*), and upland sandpiper (*Bartramia longicauda*, Niemuth, 1995; Gregg and Niemuth, 2000) which require large openings for breeding. The decline of these species prompted the Wisconsin Department of Natural Resources (DNR), local county forests, and the Chequamegon-Nicolet National Forest to initiate an adaptive landscape management project for the Pine Barrens (Borgerding et al., 1995; Moss, 2000).

2.2. Landscape modeling of forest management scenarios

Spatially explicit landscape models are in most cases the only feasible scientific approach to study the effects of different disturbance regimes on landscape pattern and to experiment with different harvesting scenarios (Mladenoff and Baker, 1999). The scientific literature on landscape models has rapidly grown in recent years, and we will review here only a few of the models that focus on forest management (for a complete review, see Mladenoff, 2004). Initial modeling attempts focused on a single process, i.e., forest harvesting, sometimes even ignoring forest regeneration (Franklin and Forman, 1987; Li et al., 1993). A number of these models focused on the spatial allocation of harvesting units and their size, a question that arose in the Pacific Northwest during the controversy about the harvest of old-growth forests and the population status of the spotted owl. Model results suggested that aggregated clear-cuts

could preserve larger patches of interior forests (i.e., spotted owl habitat) than the common management practice of dispersed clear-cuts (Franklin and Forman, 1987). In order to examine the effects of other spatial factors on forest harvesting patterns, later models included data on road and stream networks (Li et al., 1993) and digital elevation data (Tang et al., 1997). Different spatial allocations of harvesting units (clustered versus dispersed) exhibited strong effects on forest interior and edge habitat (Gustafson and Crow, 1994, 1996; Gustafson, 1998; Borges and Hoganson, 1999). Landscape models of forest management developed further by including rotation length in addition to harvest unit size and spatial allocation (Wallin et al., 1994, 1996). Ultimately, these management models became modules in more complex forest landscape models which simulate numerous natural processes and management actions plus their interactions (Mladenoff and Baker, 1999; Gustafson et al., 2000; Klenner et al., 2000).

The inclusion of management modules into forest landscape models allowed the examination of the effects of different management scenarios on forest economics and wildlife population dynamics (Liu et al., 1994, 1995; Liu and Ashton, 1995) making model results more relevant for management decisions (Fall et al., 2004). Several Canadian companies are now offering forest planning software based on forest landscape models that include harvesting (e.g., Spatial Woodstock by Remsoft, 2005, ALCES by Forem Technologies, 2005, and Patchworks by Spatial Planning Systems, 2005). This trend parallels a general increase of spatial components in the forest planning process in recent years (Bettinger and Chung, 2004; Bettinger et al., 2005). In forest science, wildlife habitat consideration has been a particularly active area of research using forest landscape models because area sensitive species may not occur in a given landscape if their habitat occurs only in small, disjunct patches (Andrén, 1994; Fahrig, 1997; Akcakaya et al., 2004), and it appears that brood parasitism by brownheaded cowbirds is elevated in fragmented forests (Brittingham and Temple, 1983; Gustafson et al., 2002).

Despite all of these efforts to model forest management spatially, much is still unknown about the effects of different forest management decisions on landscape pattern. Only recent developments in landscape simulation modelling, permit simultaneous modeling of numerous ecosystems as well as a wide range of silvicultural treatments (Liu and Ashton, 1998; Gustafson et al., 2000, 2001, 2004; Shifley et al., 2000; Gustafson and Rasmussen, 2002; He et al., 2002; Fall et al., 2004; Fan et al., 2004; Garman, 2004; Mehta et al., 2004; Seely et al., 2004; Scheller et al., 2005).

2.3. Landscape simulation model used

We chose the landscape model LANDIS for this study (Mladenoff et al., 1996). LANDIS incorporates natural processes (fire, windthrow, succession, and seed dispersal, He and Mladenoff, 1999a), and forest harvesting, allowing many different silvicultural treatments to be simulated (Gustafson et al., 2000). The model has been tested in northern hardwood (He and Mladenoff, 1999b), and central hardwood

forests (Shifley et al., 2000; Fan et al., 2004), chaparral in California (Franklin et al., 2001), and boreal forests in Finland (Pennanen and Kuuluvainen, 2002) and Quebec (Pennanen et al., 2004). For a more detailed discussion of model design and implementation see Mladenoff and He (1999) and Mladenoff (2004).

2.4. Input data preparation

Landscape simulations in LANDIS require several input maps and parameter files for model initialization (Mladenoff and He, 1999). All input raster maps were generated with 100 m spatial resolution and total landscape extent of 450,000 ha.

2.4.1. Landtype map

Differences in environmental conditions, such as soil types and climate, are incorporated into LANDIS via the landtype map. Landtype determines the likelihood that a tree species will grow (species establishment coefficient) at a given location and is characterized by return intervals for fire and wind disturbance. We divided the Pine Barrens into seven landtypes (Fig. 1b) based on climate data, soil information (Radeloff et al., 1998), tree species distribution at pre-settlement times (Radeloff et al., 1999), and differences in fire frequency observed between 1930 and 1990 (see below). We chose seven landtypes to ensure relative homogeneity in terms of the environmental factors mentioned above, while keeping the number low enough so that parameterization for each landtype was still feasible.

2.4.2. Stand boundaries map

The harvest module in LANDIS requires a stand boundary map (Gustafson et al., 2000). Digital forest maps exist only for a small portion of the study area, which is in public ownership. This necessitated deriving stand boundaries from other data. Our approach to stand boundary mapping incorporated both forest conditions and size constraints. Based on available digital stand boundary maps for national and state forests, the minimum stand size is 2 ha and maximum size is 250 ha in our study area. We conducted an unsupervised satellite classification of a Landsat TM satellite image (28.5 m resolution, recorded on May 19, 1995) to identify spectrally homogeneous areas. The image was clustered into 30 spectral classes based on spectral reflectance values in TM band 1-5 and 7. Areas that were spatially contiguous and classified into one land cover class were considered stands. Areas that were too small in size to be considered separate stands were merged with neighboring larger stands. All stands larger than 250 ha were subdivided using a digital road data set derived from U.S. Census Bureau TIGER data (Fig. 2).

2.4.3. Management areas map

The harvest module also requires a management area map to implement, for instance, management strategies specific to soil types (Gustafson et al., 2000). We used two management areas in our simulations (Fig. 1c). The majority of the study area is located on sandy soils where forest management focuses on

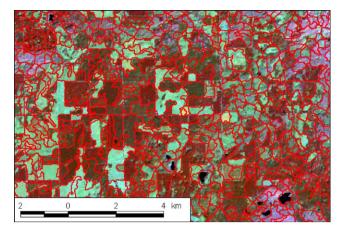


Fig. 2. Forest stand boundaries superimposed on a Landsat TM satellite image (channels 4, 5, and 3 shown in red, green, and blue) for a selected area in the central portion of the Pine Barrens. Water bodies are depicted in black, deciduous stands in pink and purple, red pine stands in dark red, jack pine stands in dark blue/gray, and clear-cuts in light blue/turquoise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

clear-cuts of jack and red pine. The glacial moraine in the north is dominated by hardwood stands managed by selective cutting or group selection. No harvesting was simulated on the moraine because these harvests have little effect on open habitat.

2.4.4. Forest cover map

The stand boundary map derived from satellite data was also used to derive an initial forest cover map (Fig. 1d). The unsupervised classification assigned each stand polygon a class value between 1 and 30. Each of these 30 classes was visually assigned the major forest type it represented. Areas devoid of forests were assigned to a class 'open'. This class represented 121,000 ha, partly due to recent salvage cuts in response to a jack pine budworm outbreak (Radeloff et al., 2000b). Forest cover classes included jack pine, red pine, oak spp., aspen, and sugar maple. Classes representing multiple tree species were labeled accordingly (e.g., red pine/hardwood mix). In a second step, summary forest inventory statistics for the entire Pine Barrens region were obtained from the Forest Inventory Analysis (FIA) database, providing an estimate of the area of each of the five major forest types (aspen, oak, red pine, jack pine, and maple-birch) in the study area. The FIA database contains data for permanent sampling plots that are measured on average every 10 years by the U.S. Forest Service, and represents the most comprehensive forest inventory data available across the United States (Chojnacky, 2001; Miles et al., 2001; Vissage et al., 2004). However, we could not use the FIA data as ground truth for our classification, or to identify forest types for given stands and perform an accuracy assessment, because we did not have access to the actual plot locations but only to perturbed plot locations which are up to 1 mile offset. We ensured that the relative proportions of these five forest cover types were maintained in the forest cover map, by assigning spectrally ambiguous clusters to underrepresented forest cover types.

Table 1 FIA data on tree regeneration in the five major forest types in the Pine Barrens study area

Forest type	Number of plots	Hectares	Most common species	Second most common species	Third most common species	Fourth most common species
Aspen Number of trees <	102 ≤4 in.	84,150	Quaking aspen 223 (40%)	Bigtooth aspen 187 (34%)	Red maple 99 (18%)	Red oak 48 (9%)
Oak Hickory Number of trees <	95 ≤4 in.	98,269	Red maple 45 (50%)	Red oak 19 (21%)	Bigtooth aspen 13 (14%)	Quaking aspen 13 (14%)
Red Pine Number of trees \le	63 ≤4 in.	48,876	Red pine 68 (58%)	Jack pine 19 (16%)	Quaking aspen 16 (14%)	Pin oak 14 (12%)
Jack Pine Number of trees \(\leq \)	41 ≤4 in.	49,610	Jack pine 125 (60%)	Burr oak 40 (19%)	Red pine 30 (14%)	Quaking aspen 13 (6%)
Maple-Birch Number of trees <	32 ≤4 in.	26,607	Red maple 104 (50%)	Sugar maple 53 (27%)	Red oak 27 (13%)	Bigtooth aspen 23 (11%)

These five major types represent 333 out of a total of 371 plots in the timberland category of FIA.

LANDIS simulates presence—absence of tree species in different age cohorts and uses input data of both primary and secondary species. The FIA data were also used to provide aggregate information on forest composition and age for the five major forest types. We extracted data on secondary tree species by examining the percentage of the four most common tree species in the ≤ 4 in. size class. Important secondary species were identified by computing the percentage of the five most important species in terms of tree volume (Table 1). Based on the FIA data we also assigned the presence and absence of age cohorts for both primary and secondary tree species in each of the 30 classes.

2.4.5. Tree species data

LANDIS simulates seedling establishment under different environmental conditions (landtypes) by a likelihood factor (establishment coefficient) that a seed of a given tree species will successfully establish (Mladenoff and He, 1999). In terms of seed availability, we assumed that the two main commercial species (jack pine and red pine) would either regenerate naturally or be planted, and thus simulated no limits on seed availability in clear-cuts. Tree species coefficients were derived from pre-settlement vegetation data (Radeloff et al., 1999), soil maps (Radeloff et al., 1998), and natural history information

about the growing requirements of each tree species (Curtis, 1959; Burns and Honkala, 1990). Tree species coefficients vary by landtype, whereas longevity and sexual maturity are constant among landtypes in LANDIS (Table 2). Tree species that occur only as subdominants, such as yellow birch, were not simulated. Additional tree species data required to parameterize LANDIS, such as seed dispersal distances, were obtained from He and Mladenoff (1999b).

2.4.6. Fire frequency and fire size distribution

Fire was a frequent disturbance in the pre-settlement landscape but is much less common now due to fire suppression, which started in the 1930s (Radeloff et al., 1999). We decided to simulate current fire cycles, rather than pre-settlement conditions for two reasons. The first is that human habitation in the study area makes it highly likely that fire suppression will continue in the future (Radeloff et al., 2001). The second reason is that our main objective was to compare the effects of different forest management decisions on landscape pattern. The simulation of pre-settlement fire cycles would have confounded those results due to the effects of fires on landscape pattern. The fire module in LANDIS was parameterized using a Wisconsin Department of Natural Resources (DNR) map recording all fires since 1930 for the

Table 2 Natural history attributes of the tree species that were simulated

Species	Longevity	Sexual maturity	Shade tolerance	Establishment coefficients for each landtype						
				Bayfield	Moraine	Outwash	Fringe	Savanna	Polk	Hayward
Red maple	150	10	3	1	1	0	0	0	0	0
Sugar maple	400	40	5	0.5	1	0	0.5	0.2	0.2	0
Jack pine	90	15	1	1	1	1	1	1	1	1
Red pine	250	35	3	1	1	1	1	1	1	1
White pine	450	15	3	1	1	0.3	0.5	1	1	1
Aspen	120	15	1	1	1	0.3	1	1	1	0.8
Pin oak	300	35	2	1	1	0.5	0.5	1	1	1
Red oak	250	25	3	1	1	0	0	0.1	0.5	0.5
Herbaceous spp.	50	10	-1	1	1	1	1	1	1	1

Longevity and sexual maturity are reported in years, shade tolerance is a class value with 5 representing the highest shade tolerance. Species establishment coefficients are scaled between 0 and 1, with 1 representing the highest likelihood that a seed will establish on a site if the light regime is favorable.

Table 3
Fire return intervals in the different landtypes; observed fire return intervals were derived from a map of fire boundaries from 1930 to 1960 (courtesy of the Wisconsin DNR)

Landtype	Observed fire return interval (in years) 1930–1990	Fire return interval (in years) after 500 model years
Pitted outwash	∞	784
Kettle moraine	∞	∞
Outwash plain	355	399
Outwash plain fringe	387	424
Southcentral outwash plain	697	513
Southwestern outwash plain	306	341
Sandy river valley	1078	1940

southern 2/3 of the study area. Fire return intervals were computed for each landtype (Table 3) and average and maximum fire size was calculated for the entire study area (334 and 7685 ha, respectively).

2.4.7. Forest management information

We obtained information of common forest management practices in our study area from management guidelines published by the U.S. Forest Service (Benzie, 1977), and the Wisconsin DNR (Wisconsin DNR, 2005), as well as in conversations with resource managers familiar with local conditions (e.g., D. Zastrow, Wisconsin DNR State Silviculturist; J. Halverson, Washburn County Forester).

Jack pine in our study area is solely grown for pulp wood production not for saw timber. Jack pine stands are single-species and even aged. Harvesting activities are limited to clearcuts, no selective harvesting or thinning occurs. Harvests are scheduled at a stand age between 40 and 60 years. Both natural regeneration and plantations are common, often accompanied by soil scarification and herbicide treatments to limit competition from hazel and oaks.

Red pine in our study is managed largely for maximum yield of sawtimber (Wisconsin DNR, 2005). Red pine is grown in even aged plantations, as natural regeneration is in most cases too sparse. Red pine plantations require on average at least 100 years to reach harvestable age, at which point plantations are clear-cut. Two to three thinnings within this period are common.

2.5. LANDIS simulations

The approach to our modeling experiment was a factorial design in which three variables (minimum age for harvest, cut unit size, species of management interest) varied (Table 4) resulting in 16 scenarios that were simulated over 500 years in 10 year time steps. We chose 16 scenarios that captured the entire range of management options that are commonly practiced and that influence landscape pattern. The minimum age limit for clear-cuts in jack pine was either 40 or 60 years, cut unit sizes were set at a mean of 4, 16, 65, or 259 ha, and the standard deviation of the cut unit size was set to 1/4 of the mean to mimic variability in cut unit size. The full range in cut unit sizes can be observed in the current landscape; large cuts are especially common after jack pine budworm defoliation when

Table 4
The 16 different forest management scenarios that were explored in the LANDIS simulations

Scenario number	Minimum age for jack pine before harvesting	Mean cut unit size (ha)	Percent of the landscape managed for red pine
1	40	4	0
2	40	16	0
3	40	65	0
4	40	259	0
5	40	4	50
6	40	16	50
7	40	65	50
8	40	259	50
9	60	4	0
10	60	16	0
11	60	65	0
12	60	259	0
13	60	4	50
14	60	16	50
15	60	65	50
16	60	259	50

salvage logging occurs (Radeloff et al., 2000b). Forest managers are not restricted in terms of adjacency rules; new cuts can be placed next to existing cuts. However, LANDIS will not place a new cut next to an existing cut in the same time step in the simulation if the result is that the total area of both cuts exceeds the cut unit size limit.

Because the minimum harvest age for red pine is about twice that for jack pine, this may significantly decrease the amount of open area. One half of our management scenarios did not include management for red pine, and all stands were eligible for harvest when they reached the minimum stand age (see above). The other half of our management scenarios included red pine management on 50% of the landscape (Table 4). In the red pine management scenarios, jack pine harvests left all red pine >50 years old. This means that a jack pine harvest would create a clear-cut if no red pine 50 years or older was present; otherwise a red pine stand would remain. Red pine harvests required a minimum age of 100 years and removed all species when a harvest occurred. We did not simulate thinnings in red pine because LANDIS does not track tree density, but rather the presence of each tree species in each cell. Because thinnings would not remove all red pine from a 100 m cell thinnings could not be simulated. This was of relatively little concern for our research question though, because thinnings do not affect the amount and pattern of open areas.

Harvests were applied to entire stands. We parameterized the harvesting algorithm in LANDIS to cut all stands meeting the criteria in a given scenario at each decade. The harvested area was not held constant among management scenarios. The reason for this decision was that one of the response variables we were interested in was the total area of open habitat created under each management scenario. All else being equal, a minimum harvest age of 40 will result in more frequent harvests, and thus create more open area compared with a minimum harvest age of 60. We would have not been able to assess such differences had the harvest area been held constant.

2.6. Statistical analysis

We calculated the total area where tree species were: (a) dominant and (b) present as well as the area harvested for each time step. The dominant tree species is defined in LANDIS as the oldest species present in a given cell; LANDIS does not estimate tree density. In addition to the overall abundance of different cover classes, we were interested in the spatial patterns of open habitat areas. Landscape patterns were quantified by computing average, minimum, maximum, and standard deviation of patch size for each tree species and for open habitat using APACK (DeZonia and Mladenoff, 2002).

We conducted two separate statistical tests to examine which management options are most strongly correlated with land-scape pattern, and to determine which management scenarios result in significantly different landscape pattern. Our statistical analysis followed the approach established by Scheller and Mladenoff (2005). Mixed linear regression models were used to

test the significance of the different management decisions (cut unit size, minimum harvest age, and target species for management). Due to the limited range of management options explored, each management option was treated as a categorical variable. However, such an analysis precludes the use of either coefficients or their signs for model interpretation. Separate regression models were developed for each response variable: the total area harvested, the average area of harvests, the total area in open habitat (age 0-10), and the average size of openings. Data from years 100, 110, 120, ..., 500 was used as the sample (n = 41). Time series data can be temporally autocorrelated. Therefore, we compared both autoregressive (order one) models and models with an unstructured covariance structure using decadal data (within scenario) as a repeated measure within our mixed models (Littell et al., 1999). Because of the small sample size, a robust standard error estimator (Huber-White) was used (Maas and Hox, 2004). The autoregressive and the unstructured models were not significantly

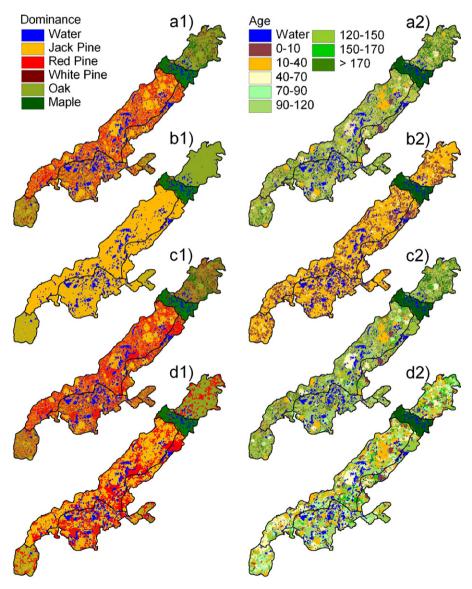


Fig. 3. Dominant forest type after 500 model years for management scenario (a1) 1, (b1) 4, (c1) 13 and (d1) 16, and the age of the oldest age cohort present after 500 model years for management scenario (a2) 1, (b2) 4, (c2) 13 and (d2) 16.

different indicating that temporal autocorrelation did not affect our analysis, and we used an unstructured model for our final results.

A second set of statistical tests was conducted to test for significant differences among the 16 management scenarios for the four response variables (the total area harvested, the average area of the harvests, the total area in open habitat (age 0–10), and the average size of openings). We used ANOVA for these tests, examining least square differences at $\alpha = 0.05$ (Littell et al., 1999).

Finally, we used hierarchical partitioning (Mac Nally, 2000) to estimate the amount of variance explained by each of six independent variables (minimum age of jack pine harvest, clearcut size, percentage of red pine management, plus three two-term

interactions). Within hierarchical partitioning, all possible multiple regression models, including sub-sets, are considered for identifying the probable causal factors (Mac Nally, 2000).

3. Results

All three management choices under investigation (clear-cut size, minimum harvest age, and target species for management) affect forest composition (Fig. 3) and resulting landscape pattern (Fig. 4). Legacies of the initial conditions persisted for up to 100 years, but the remaining 400 model years exhibited relatively constant landscape pattern (Fig. 6). Jack pine and red pine dominated at least two-thirds of the landscape during the last 400 model years (Fig. 5), and results will therefore focus on

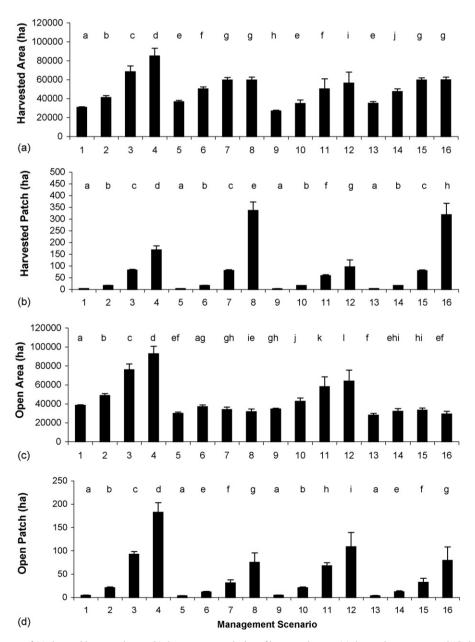


Fig. 4. Differences in the mean of (a) the total harvested area, (b) the average patch size of harvested areas, (c) the total open area, and (d) the average size of openings for the 16 different management scenarios. Management scenarios with the same letter indicated above the bar are not significantly different. Means and ANOVA results are based on model years 100–500; error bars represent one standard deviation.

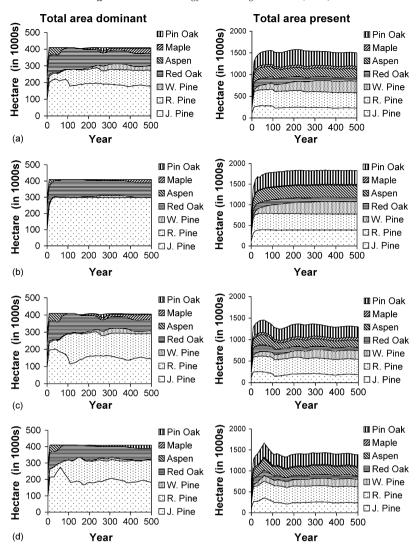


Fig. 5. Total area dominant and total area present of different tree species over time for management scenario: (a) 1, (b) 4, (c) 13, and (d) 16.

those two species. However, pin oak, aspen, and white pine (in this order) were also present on substantial portions of the landscape, albeit without reaching dominance (Fig. 5).

The ANOVA showed significant differences among all pairs of management scenarios with only two exceptions: scenarios 5 and 13 were statistically identical in terms of the total area and the average area of harvests and openings, as were scenarios 7

and 15 (Fig. 4). The only independent variable differing within these two pairs of management scenarios was the minimum age for jack pine before harvesting.

The hierarchical partitioning regression analysis also highlighted the minimum age for jack pine before harvesting as having on average the least effect among the three management variables that were investigated (Table 5). Overall, the total area

Table 5

The percentage of variance explained by different management decisions on the total area and the average patch size of harvests and openings

Predictor variable	Response variable in each of the four regression models					
	Average patch size of harvests	Total area of harvests	Average patch size of openings	Total area of openings		
Minimum age for jack pine before harvesting	1.1	10.8	2.6	5.6		
Mean cut unit size	29.4	44.2	45.6	19.3		
Percent area managed for red pine	2.7	2.9	6.5	22.2		
Interaction: minimum jack pine age and cut unit size	21.2	28.0	29.8	11.3		
Interaction: minimum jack pine age and percent red pine	2.3	4.1	5.2	18.6		
Interaction: cut unit size and percent red pine	43.3	9.9	10.3	22.9		

The results are from separate hierarchical partitioning models for each of the four response variables of interest; the sample consisted of data for 41 decades and 16 management scenarios.

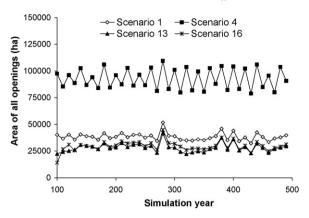


Fig. 6. Fluctuations in the total area of openings over time for management scenarios 1, 4, 13, and 16.

and the average area of harvests and average open area size were most strongly related with the mean cut size. The second most important variable was the percentage of the landscape area managed for red pine, which also explained the second largest amount of variance in the model of the total area of openings. Minimum age for jack pine before harvesting ranked third for the model of the total area of harvest, otherwise it explained less than 10% of variance and ranked lower than the interaction term for cut unit size and percent red pine. In the following, more detailed results for the three management choices are presented in the order of their importance in terms of impacting landscape pattern.

3.1. Clear-cut size

Clear-cut size had the most direct effect on landscape pattern (Fig. 6). An increase in target clear-cut size from an average of 4–259 ha (64.75-fold) under constant minimum harvest age (40 years) and no red pine management resulted in a 45-fold increase of the average harvest area and a 39-fold increase in the average open patch size (scenarios 1 and 4, Fig. 4d). Red pine management increased the area of harvests but decreased the size of openings (scenario 4 versus scenario 8, Fig. 4b and d). Harvests in red pine stands 50 years or older effectively functioned as thinnings, because they removed only jack pine, and left a canopy of mature red pine until these reached the minimum harvest age of 100 years.

Increasing clear-cut size also affected the patch size of dominant forest types. A 4-fold increase in clear-cut size resulted in a doubling of the average jack pine patch size (Fig. 7). However, further increasing clear-cut size to 259 ha resulted in only slightly larger forest patches. Red pine patch size and total area decreased in those scenarios that did not include active red pine management (scenarios 1–4 and 9–12), but increased otherwise (Fig. 7). However, red pine patches reached on average only 50% of the size of jack pine patches. Changes were again most pronounced when clear-cut size increased from 4 to 16 and then to 65 ha, but leveled off thereafter. The reason for this trend is that average harvest size did not reach the goal of 259 ha because the patch size of jack

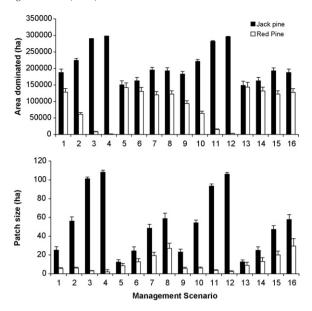


Fig. 7. Average area dominated by jack pine or red pine in each management scenario, and the average patch size throughout model years 100–500.

pine peaked at around 110 ha and was smaller than the clear-cut size goal.

One surprising result was that scenarios with larger sized cut units resulted in 2–3 times larger total areas being harvested (Fig. 4a). The reason for this pattern is that when clear-cuts were small and dispersed, there were simply less stands available for harvesting. Once a cut is placed in a management scenario with small cuts, then all stands in the direct vicinity of this cut are effectively temporary 'no-harvest' zones because their harvesting would result in an opening larger than the size limit.

3.2. Red pine versus jack pine management

Setting the target for red pine to 50% of the landscape had strong effects on landscape pattern. At smaller clear-cut sizes, red pine management decreased the amount of openings and their mean size roughly by a third. At larger clear-cut sizes, the effect was more pronounced and decreases in the amount of open areas and their mean size reached up to two-thirds (Fig. 4). As expected, the abundance and the mean patch size of red pine increased strongly under red pine management (Fig. 7). However, red pine patches were on average only about half as large as jack pine patches and jack pine remained more abundant.

3.3. Minimum harvest age

Increasing the minimum harvest age for jack pine from 40 to 60 years had only minor effects (maximum of $\pm 15\%$ of all response variables) when clear-cut sizes where limited to 4 or 16 ha (scenarios 1–4 versus scenarios 9–12, Fig. 4). However, at the larger clear-cut sizes, the 60 year minimum harvest age resulted in a reduction in the total area being harvested by about a third and similar reductions in average size of openings (e.g., scenario 4 versus scenario 12, Fig. 4). The increase in minimum harvest age for jack pine had practically no effect in those

scenarios that incorporated red pine management in 50% of the landscape (scenarios 5–8 versus scenarios 13–16, Fig. 4). Similarly, there were few changes in the landscape pattern of the dominant forest types present when minimum harvest age increased (Fig. 7).

4. Discussion

Forest management has become the dominant process affecting landscape pattern in many forests throughout North America. Our results demonstrate that substantial differences in landscape pattern were generated by the different forest management scenarios that we simulated. Among three different forest management decisions (cut unit size, minimum harvest age, and target species for management), cut unit size clearly had a strong effect on landscape pattern, especially the amount and the size of openings, which provide important wildlife habitat. This finding is not surprising, and many forest policies include cut unit size restrictions for aesthetic and/or environmental reasons. Any attempt to create certain desired landscape patterns via forest management will have to include a careful choice of the cut unit size.

However, our results also indicate that focusing on cut unit size alone does not suffice. For example, increases in the minimum harvest age may prohibit the creation of large openings, independent of the target cut unit size, simply because there are no stands present that are large enough. In our scenarios, a minimum harvest age of 40 with clear-cut size limited to 65 ha created more open areas and openings that were almost as large, as a 60 year minimum harvest age with 259 ha clear-cuts.

The most surprising result may be the strong effects of a partial switch in management target species from jack pine to red pine. Even though this change was only applied to 50% of the landscape, and red pine was actively harvested, the amount and the size of openings decreased by one to two-thirds. This decrease was strongest for larger clear-cut sizes; red pine management in half of the landscape decreased the average patch size from a maximum of 182 ha (scenario 4) to 80 ha (scenario 16).

Changes in the target species for forest management have received comparatively little attention in the discussion on forest management effects on landscape pattern. Target species for management are commonly selected based on economics. It is comparatively easy and common to limit clear-cut size via regulation, compared to mandating management for certain tree species. However, our results suggest that more research is needed to fully understand the effects of changes in target species on landscape pattern.

What do our results suggest for the management of ecosystems such as the Pine Barrens? In the Pine Barrens, there is a fairly unique situation where a lack of openings constitutes the major environmental challenge (Borgerding et al., 1995; Moss, 2000). Clear-cuts have been suggested as an alternative disturbance process to replace the fires that created large openings in the pre-settlement landscape (Borgerding et al., 1995; Radeloff et al., 2000a). Our results

provide indication that the size of clear-cuts, the rotation length, and the target species for management will all affect the amount of the size of openings. However, clear-cuts only partially mimic fires; they do provide canopy openings, but they differ considerably in other aspects such as the abundance of coarse woody debris (Niemuth and Boyce, 1998). Further research is needed on long-term changes in soil fertility, herbaceous species diversity, and wildlife communities, to identify to what extent clear-cuts, and possibly prescribed burning of the slash after harvesting, can mimic natural fire disturbance. However, initial monitoring results for sharp-tailed grouse, one indicator species of open habitat, suggest that large openings created by salvage cutting after insect defoliation do indeed provide a landscape pattern conducive for this species (Radeloff et al., 2000b; Akcakaya et al., 2004).

Increasing the size of clear-cuts is the most important management choice foresters can make if increasing the size and abundance of large openings is intended. Minimum harvest age for jack pine should be 40-45 years, which is also economically most beneficial for pulp wood production (Rose, 1973; Benzie, 1977). However, such a low harvest age would require much more active management on private nonindustrial holdings, which at present exhibit the lowest cutting rates (Radeloff et al., 2000b). An increase in red pine management via plantations would have strong impacts on landscape pattern, and may not be prudent when open habitat is one goal of forest management. Some timber industry companies are managing for red pine on about half of the holdings, partly to increase tree species diversity and thereby decrease the likelihood of future jack pine budworm outbreaks (Radeloff et al., 2000b). However, this will also have a very strong effect on the abundance and the size of openings and these ecological detriments may outweigh other considerations. Ultimately, there will be tradeoffs between different management goals. For example, the production of red pine sawlogs conflicts with the goal to increase the size and abundance of openings in the landscape. Our simulation approach does not permit optimizing multiple management goals (Hof and Joyce, 1992; Nevo and Garcia, 1996), but results indicate how different management decision affect landscape pattern.

One management suggestion was to use forest management to mimic natural disturbance patterns (Radeloff et al., 2000a). The assumption underlying this suggestion is that human activities, most notably fire suppression, caused the decrease in open habitat. We recognize that this may not necessarily be the case, and that climate trends may be the actual cause for changes in fire frequency. Forest fire behavior is determined primarily by weather rather than fuels (Johnson et al., 1990; Johnson and Larsen, 1991; Bessie and Johnson, 1995), and fire suppression is by no means always successful as wildfires of 5300 and 4500 ha in 1977 and 1980 indicate (Radeloff et al., 2000a). However, in general, fire suppression has been effective in reducing fire return intervals in this region, and is one of the major factors for the decrease in open habitat (Radeloff et al., 1999).

4.1. Model assumptions and possible effects on results

There were a number of modeling assumptions that affected our results and have to be taken into account when interpreting them. Management differences among landowners were not simulated, even though clear-cut size and minimum harvest age differs markedly between public and private holdings (Radeloff et al., 2000b). We do not expect that a single management scheme will be applied across all ownerships in the Pine Barrens in the future. We did not model management differences among landowners, to avoid confounding our experimental design. We also assumed that stands available for harvesting will be harvested, and did not hold harvest area constant. This assumption is realistic for industrial forests, but may not always apply to public lands. We also did not assess the effects of errors in our input data (e.g., forest cover types, stand boundaries) on final model results. We suggest that effects of the initial conditions will not persist over 500 years, because our results show that species composition and landscape pattern are fairly constant throughout years 100-500, and an equilibrium appears to have been reached (Figs. 5 and 6). Last but not least, we did not conduct a sensitivity analysis, i.e., we did not alter model input parameters, such as the species establishment coefficients to test the robustness of our model results. A full sensitivity analysis would be interesting, but was beyond the scope of our study given the number of input parameters involved.

The current implementation of forest harvesting in LANDIS is somewhat limited in that the removal of a given tree species is not dependent on the forest structure present in a given cell (Gustafson et al., 2000). However, this limitation had little impact on our simulations, given that pine management in our study area does not involve complex silvicultural treatments. It may highlight though that a forest landscape model such as LANDIS cannot, and should not, be used to identify stands for harvesting over the next one or two decades. What landscape models provide is a framework to experiment with different management decisions and evaluate their long-term effects. This is the modeling philosophy on which our simulation scenarios were based, and this must be kept in mind when interpreting and potentially implementing our findings.

Any simulation model represents a compromise between model realism and generality (Levins, 1966), and our use of LANDIS is no exception. More general results could have been obtained by simulating idealized landscapes, rather than the Pine Barrens landscape, but that would have diminished the applicability of our results in the real world. Conversely, our decision to report results after the first 100 years made results less sensitive to initial conditions, and thus more applicable to other areas, but it decreased model realism since more management decisions are made on much shorter time horizons. Again we stress that any interpretation of our results must take the underlying model philosophy into consideration.

5. Conclusions

Forest management has become the dominant disturbance process across a major portion of today's landscapes. Forest management decisions have strong effects on landscape pattern, and thereby on ecosystem processes, but a thorough understanding of these relationships is lacking. Our research suggests that cut unit size is the most important factor influencing landscape pattern, target species for management the second most important, and minimum harvest age least important. These findings are landscape specific and result from the importance of large openings to the Pine Barrens ecosystem, which is fire adapted.

Acknowledgements

We thank K. Nimerfro, S. Shifley, B. DeZonia and J. McKeefry for their significant contribution in implementing the harvest module into LANDIS and providing an ARC/VIEW interface for rapid output visualization. Four anonymous reviewers greatly improved the manuscript and we appreciate their comments. This project was supported by a Research Joint Venture Agreement between the University of Wisconsin-Madison and the North-Central Research Station of the U.S. Forest Service and by the Integrated Science Services Bureau of the Wisconsin Department of Natural Resources.

References

- Akcakaya, H.R., Radeloff, V.C., Mladenoff, D.J., He, H.S., 2004. Integrating landscape and metapopulation modeling approaches: viability of the sharptailed grouse in a dynamic landscape. Conserv. Biol. 18, 526–537.
- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355–366.
- Baker, W.L., 1994. Restoration of landscape structure altered by fire suppression. Conserv. Biol. 8, 763–769.
- Benzie, J.W., 1977. Manager's Handbook for Jack Pine in the North-central States. General Technical Report NC-32. North Central Research Station, USDA Forest Service, St. Paul, MN.
- Bessie, W.C., Johnson, E.A., 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. Ecology 76, 747–762.
- Bettinger, P., Chung, W., 2004. The key literature of, and trends in, forest-level management planning in North America, 1950–2001. Int. For. Rev. 6, 40–50.
- Bettinger, P., Lennette, M., Johnson, K.N., Spies, T.A., 2005. A hierarchical spatial framework for forest landscape planning. Ecol. Modell. 182, 25–48.
- Borgerding, E.A., Bartellt, G.A., McCowen, W.M., 1995. The Future of the Northwest Wisconsin Pine Barrens: A Workshop Summary. 21–23 September 1993, Solon Springs, WI. Wisconsin Department of Natural Resources. Madison, WI.
- Borges, J.G., Hoganson, H.M., 1999. Assessing the impact of management unit design and adjacency constraints on forestwide spatial conditions and timber revenues. Can. J. For. Res. 29, 1764–1774.
- Brittingham, M.C., Temple, S.A., 1983. Have cowbirds caused forest songbirds to decline? Bio. Sci. 33, 31–35.
- Burns, R.M., Honkala, B.H., 1990. Silvics of North America, Vol. 1 and 2. USDA Forest Service Agriculture Handbook 654. USDA Forest Service, Washington, DC, USA.
- Cissel, J.H., Swanson, F.J., McKee, W.A., Burditt, A.L., 1994. Using the past to plan the future in the Pacific Northwest. J. For. 92, 30–46.
- Cissel, J.H., Swanson, F.J., Weisberg, P.J., 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecol. Appl. 9, 1217–1231.
- Chojnacky, D.C., 2001. On FIA variables for ecological use. In: Reams, G.A., McRoberts, R.E., Van Deusen, P.C., (Eds.). Proceedings of the second annual Forest Inventory and Analysis symposium; 2000 October 17–18; Salt Lake City, UT. Gen. Tech. Rep. SRS-47. U.S. Department of Agri-

- culture, Forest Service, Southern Research Station, Asheville, NC, pp. 102–105
- Curtis, J.T., 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison. Wisconsin. USA.
- DeZonia, B., Mladenoff, D.J., 2002. APACK 2.22 User's Guide Version 5-6-02. University of Wisconsin-Madison, Department of Forest Ecology and Management, Wisconsin, USA.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. J. Wildlife Manage. 61, 603–610.
- Fall, A., Fortin, M.J., Kneeshaw, D.D., Yamasaki, S.H., Messier, C., Bouthillier, L., Smyth, C., 2004. Consequences of various landscape-scale ecosystem management strategies and fire cycles on age-class structure and harvest in boreal forests. Can. J. For. Res. 34, 310–322.
- Fan, Z.F., Shifley, S.R., Thompson, F.R., Larsen, D.R., 2004. Simulated cavity tree dynamics under alternative timber harvest regimes. For. Ecol. Manage. 193, 399–412.
- Forem Technologies, 2005. ALCES-An Integrated Landscape Management Tool. http://www.foremtech.com/, last accessed June 13th 2006.
- Foster, D.R., Aber, J.D., Melillo, J.M., Bowden, R.D., Bazzaz, F.A., 1997.
 Forest response to disturbance and anthropogenic stress. Bio. Sci. 47, 437–445
- Franklin, J.F., Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landsc. Ecol. 1, 5–18.
- Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P., Deutschman, D., 2001. Simulating the effects of different fire regimes on plant functional groups in Southern California. Ecol. Modell. 142, 261–283
- Garman, S.L., 2004. Design and evaluation of a forest landscape change model for western Oregon. Ecol. Modell. 175, 319–337.
- Gregg, L., Niemuth, N.D., 2000. The history, status, and future of sharp-tailed grouse in Wisconsin. Passenger Pigeon 62, 159–173.
- Gustafson, E.J., 1998. Clustering timber harvests and the effect of dynamic forest management policy on forest fragmentation. Ecosystems 1, 484–492.
- Gustafson, E.J., Crow, T.R., 1998. Simulating spatial and temporal context of forest management using hypothetical landscapes. Environ. Manage. 22, 777–787
- Gustafson, E.J., Crow, T.R., 1994. Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird brood population. Landsc. Ecol. 9, 237–248.
- Gustafson, E.J., Crow, T.R., 1996. Simulating the effects of alternative forest management strategies on landscape structure. J. Environ. Manage. 46, 77–
- Gustafson, E.J., Rasmussen, L.V., 2002. Assessing the spatial implications of interactions among strategic forest management options using a windowsbased harvest simulator. Comput. Electr. Agric. 33, 179–196.
- 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.
- Gustafson, E.J., Murphy, N.L., Crow, T.R., 2001. Using a GIS model to assess terrestrial salamander response to alternative forest management plans. J. Environ. Manage. 63, 281–292.
- Gustafson, E.J., Knutson, M.G., Niemi, G.J., Friberg, M.H., 2002. Evaluation of spatial models to predict vulnerability of forest birds to brood parasitism by brown-headed cowbirds. Ecol. Appl. 12, 412–426.
- Gustafson, E.J., Zollner, P.A., Sturtevant, B.R., He, H.S., Mladenoff, D.J., 2004. Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. Landsc. Ecol. 19, 327–341.
- He, H.S., Mladenoff, D.J., 1999a. The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems 2, 308–319.
- He, H.S., Mladenoff, D.J., 1999b. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. Ecology 80, 81–99.
- He, H.S., Mladenoff, D.J., Gustafson, E.J., 2002. Study of landscape change under forest harvesting and climate warming-induced fire disturbance. For. Ecol. Manage. 155, 257–270.
- Hof, J.G., Joyce, L.A., 1992. Spatial optimization for wildlife and timber in managed forest ecosystems. For. Sci. 38, 489–508.
- Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. 65, 115–120.

- Johnson, E.A., Fryer, G.I., Heathcott, M.J., 1990. The influence of man and climate on frequency of fire in the interior wet belt forest, British-Columbia. J. Ecol. 78, 403–412.
- Johnson, E.A., Larsen, C.P.S., 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. Ecology 72, 194–201.
- Klenner, W., Kurz, W., Beukema, S., 2000. Habitat patterns in forested landscapes: management practices and the uncertainty associated with natural disturbances. Comput. Electr. Agric. 27, 243–262.
- Levins, R., 1966. The strategy of model building in population biology. Am. Sci. 54, 421–431.
- Li, H., Franklin, J.F., Swanson, F.J., Spies, T.A., 1993. Developing alternative forest cutting patterns: a simulation approach. Landsc. Ecol. 8, 63–75.
- Littell, R.C., Milliken, G.A., Stroup, W.W., et al., 1999. SAS System for Mixed Models. SAS Institute, Cary, North Carolina, USA.
- Liu, J.G., Ashton, P.S., 1995. Individual-based simulation-models for forest succession and management. For. Ecol. Manage. 73, 157–175.
- Liu, J.G., Ashton, P.S., 1998. Formosaic: an individual-based spatially explicit model for simulating forest dynamics in landscape mosaics. Ecol. Modell. 106, 177–200.
- Liu, J.G., Cubbage, F.W., Pulliam, H.R., 1994. Ecological and economic effects of forest landscape structure and rotation length: simulation studies using ECOLECON. Ecol. Econ. 10, 249–263.
- Liu, J.G., Dunning Jr., J.B., Pulliam, H.R., 1995. Potential effects of a forest management plan on Bachman's Sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. Conserv. Biol. 9, 62–75.
- Lorimer, C.G., 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology 58, 139–148.
- Maas, C.J.M., Hox, J.J., 2004. Robustness issues in multilevel regression analysis. Statistica Neerlandica 58, 127–137.
- Mac Nally, R., 2000. Regression and model-building in conservation biology, biogeography, and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodivers. Conserv. 9, 655– 671.
- Mehta, S., Frelich, L.E., Jones, M.T., Manolis, J., 2004. Examining the effects of alternative management strategies on landscape-scale forest patterns in northeastern Minnesota using LANDIS. Ecol. Modell. 180, 73–87.
- Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.F., Woudenberg, S.W., Glover, J.F., Ezell, E.N., 2001. The Forest Inventory and Analysis Database Description and Users Manual Version 1.0. Technical Report NC-218. U.S. Dept. of Agriculture, Forest Service, North Central Research Station, St. Paul, MN.
- Mladenoff, D.J., Baker, W.L., 1999. Advances in Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, UK.
- Mladenoff, D.J., He, H.S., 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Advances in Spatial Modeling of Forest Landscape Change: Approaches and Applications, Cambridge University Press, Cambridge, UK, pp.125–162.
- Mladenoff, D.J., White, M.A., Pastor, J., Crow, T.R., 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecol. Appl. 3, 294–306.
- Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: a spatial model of forest landscape disturbance, succession and management. In: Goodchild, M.F., Steyaert, L.T., Parks, B.O. (Eds.), GIS and Environmental Modeling: Progress and Research Issues. GIS World Books, Fort Collins, Colorado, pp. 175–179.
- Mladenoff, D.J., 2004. LANDIS and forest landscape models. Ecol. Modell. 180, 7–19
- Moss, B.A., 2000. Northwest Sands Landscape Level Management Plan. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.
- Murphy, R.E., 1931. Geography of northwestern pine barrens of Wisconsin. Trans. Wisc. Acad. Sci. Arts Lett. 26, 96–120.
- Nevo, A., Garcia, L.A., 1996. Spatial optimization of wildlife habitat. Ecol. Modell. 91, 271–281.
- Niemuth, N.D., 1995. Avian Ecology in Wisconsin Pine Barrens. University of Wyoming, Laramie.

- Niemuth, N.D., Boyce, M.S., 1998. Disturbance in the Wisconsin Pine barrens: implications for management. Trans. Wisc. Acad. Sci. Arts Lett. 86, 167–176.
- Pennanen, J., Kuuluvainen, T., 2002. A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. For. Ecol. Manage. 164, 157–175.
- Pennanen, J., Greene, D.F., Fortin, M.J., Messier, C., 2004. Spatially explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes. Ecol. Modell. 180, 195–209.
- Radeloff, V.C., Mladenoff, D.J., Manies, K.L., Boyce, M.S., 1998. Analyzing forest landscape restoration potential: pre-settlement and current distribution of oak in the northwest Wisconsin Pine Barrens. Trans. Wisc. Acad. Sci. Arts Lett. 86, 189–205.
- Radeloff, V.C., Mladenoff, D.J., He, H.S., Boyce, M.S., 1999. Forest landscape change: the northwest Wisconsin Pine Barrens before European settlement and today. Can. J. For. Res. 29, 1649–1659.
- Radeloff, V.C., Mladenoff, D.J., Boyce, M.S., 2000a. History and perspectives on landscape scale restoration in the northwest Wisconsin Pine Barrens. Restorat. Ecol. 8, 119–126.
- Radeloff, V.C., Mladenoff, D.J., Boyce, M.S., 2000b. Effects of interacting disturbances on landscape patterns: budworm defoliation and salvage logging. Ecol. Appl. 10, 233–247.
- Radeloff, V.C., Hammer, R.B., Voss, P.R., Hagen, A.E., Field, D.R., Mladenoff, D.J., 2001. Human demographic trends and landscape level forest management in the Northwest Wisconsin Pine Barrens. For. Sci. 47, 229–241.
- Remsoft, 2005. Spatial Woodstock. http://www.remsoft.com/, last accessed June 13th 2006.
- Rose, D.W., 1973. Simulation of jack-pine budworm attacks. J. Environ. Manage. 1, 259–276.
- Scheller, R.M., Mladenoff, D.J., 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biol. 11, 307–321.

- Scheller, R.M., Mladenoff, D.J., Thomas, R.C., Sickley, T.A., 2005. Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the Boundary Waters Canoe Areas, northern Minnesota, USA. Ecosystems 8, 396–411.
- Seely, B., Nelson, J., Wells, R., Peter, B., Meitner, M., Anderson, A., Harshaw, H., Sheppard, S., Bunnell, F.L., Kimmins, H., Harrison, D., 2004. The application of a hierarchical, decision-support system to evaluate multi-objective forest management strategies: a case study in northeastern British Columbia, Canada. For. Ecol. Manage. 199, 283–305.
- Shifley, S.R., Thompson, F.R., Larsen, D.R., Dijak, W.D., 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Comput. Electr. Agric. 27, 7–24.
- Spatial Planning Systems, 2005. Spatial modeling using Patchworks. http://www.spatial.ca/products/spatial.html, last accessed June 13th 2006.
- Tang, S.M., Franklin, J.F., Montgomery, D.R., 1997. Forest harvest patterns and landscape disturbance processes. Landsc. Ecol. 12, 349–363.
- Turner, M.G., 1987. Landscape Heterogeneity and Disturbance. Springer Verlag, New York.
- Turner, M.G., O'Neill, R.V., Gardner, R.H., 2001. Landsc. Ecol. in Theory and Practice: Pattern and Process. Springer Verlag, New York.
- Vissage, J.S., Brand, G.J., Mielke, M.E., 2004. Wisconsin's forest resources in 2002. Resour. Bull. NC-237. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN, p. 31.
- Wallin, D.O., Swanson, F.J., Marks, B., 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecol. Appl. 4, 569–580.
- Wallin, D.O., Swanson, F.J., Marks, B., Cissel, J.H., Kertis, J., 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. For. Ecol. Manage. 85, 291–309.
- Wisconsin Department of Natural Resources (DNR), 2005. Silviculture and Forest Aesthetics Handbook 2431.5. Madison, Wisconsin, DNR. Accessible at http://dnr.wi.gov/org/land/forestry/Publications/Handbooks/24315/, last access June 13th 2006.