Landscape Ecology 19: 235–253, 2004.

Research article

Human influence on the abundance and connectivity of high-risk fuels in mixed forests of northern Wisconsin, USA★

Brian R. Sturtevant*, Patrick A. Zollner, Eric J. Gustafson and David T. Cleland
USDA Forest Service, North Central Research Station, 5985 Highway K, Rhinelander, WI 54501 USA;
**Author for correspondence (e-mail: bsturtevant@fs.fed.us)*

Received 20 September 2002; accepted in revised form 19 May 2003

Key words: Fire risk, Fire suppression, Fuel distribution, LANDIS, Landscape pattern, Simulation model, Succession, Timber harvest

Abstract

Though fire is considered a "natural" disturbance, humans heavily influence modern wildfire regimes. Humans influence fires both directly, by igniting and suppressing fires, and indirectly, by either altering vegetation, climate, or both. We used the LANDIS disturbance and succession model to compare the relative importance of a direct human influence (suppression of low intensity surface fires) with an indirect human influence (timber harvest) on the long-term abundance and connectivity of high-risk fuel in a 2791 km^2 landscape characterized by a mixture of northern hardwood and boreal tree species in northern Wisconsin. High risk fuels were defined as a combination of sites recently disturbed by wind and sites containing conifer species/cohorts that might serve as "ladder fuel" to carry a surface fire into the canopy. Two levels of surface fire suppression (high/current and low) and three harvest alternatives (no harvest, hardwood emphasis, and pine emphasis) were compared in a 2×3 factorial design using 5 replicated simulations per treatment combination over a 250-year period. Multivariate analysis of variance indicated that the landscape pattern of high-risk fuel (proportion of landscape, mean patch size, nearest neighbor distance, and juxtaposition with non fuel sites) was significantly influenced by both surface fire suppression and by forest harvest ($p > 0.0001$). However, the two human influences also interacted with each other ($p < 0.001$), because fire suppression was less likely to influence fuel connectivity when harvest disturbance was simultaneously applied. Temporal patterns observed for each of seven conifer species indicated that disturbances by either fire or harvest encouraged the establishment of moderately shade-tolerant conifer species by disturbing the dominant shade tolerant competitor, sugar maple. Our results conflict with commonly reported relationships between fire suppression and fire risk observed within the interior west of the United States, and illustrate the importance of understanding key interactions between natural disturbance, human disturbance, and successional responses to these disturbance types that will eventually dictate future fire risk.

Introduction

Understanding the role of human influence on fire regimes is vital to both the successful management of fire-affected forest ecosystems and for projecting future fire risk. Ecologists have devoted considerable effort toward understanding natural disturbance regimes in general (Bormann and Likens 1979; Frelich and Lorimer 1991) and fire disturbance in particular (Heinselman 1973; Romme 1982; He and Mladenoff 1999). We now know that disturbance is often a fundamental component of ecosystem function (Aber and Melillo 1991). During the past century, historic disturbance regimes have been either strongly modified by humans or replaced by human disturbances

★The U.S. Government's right to retain a non-exclusive, royalty-free licence in and to any copyright is acknowledged.

such as forest harvest and land development, sometimes producing unexpected results as ecosystems shift from one state to another (Holling and Meffe 1996). Fire suppression during the last century resulted in large accumulations of surface fuels and increased tree densities throughout most inland forests of the western United States, escalating the risk of catastrophic fires throughout the region (Mutch 1995). Similarly, intense fires raged across the upper Midwest following widespread logging in the late 19th century (Stearns 1997). These two examples represent two very different human activities that led to the same result – a landscape condition characterized by highly contiguous fuels capable of sustaining intense wildfires. Understanding how human activities influence the landscape connectivity of fuels within different ecosystems is therefore paramount to assessing future fire risk.

Human influence on fire regimes may be classified into two different categories: direct and indirect. Humans directly influence fire regimes both by igniting fires and by suppressing the spread of those fires. For example, humans were responsible for over 97% of all fire ignitions in the northern forests of the upper Midwest during the 1980's and 1990's (Cardille et al. 2001). However, an efficient fire suppression policy practiced throughout the region has simultaneously reduced fire size, resulting in fire rotations (i.e., the number of years required to burn a given area) an order of magnitude longer than the presettlement fire regime (Cleland et al. this issue). Humans also indirectly influence fire regimes by either changing climate, which we will not consider further here, or by manipulating vegetation types that differ in their relative flammability. For example, volatile chemicals present in coniferous foliage allow coniferous canopies to burn, whereas deciduous foliage lacks volatile chemicals, making deciduous stands resistant to high-intensity crown fires. Tree species also differ in the relative flammability of their litter (Frelich and Reich 1995). Hence, both direct and indirect human influence can have long-term consequences for fire disturbance regimes by altering successional pathways that influence the likelihood of successful fire ignitions (Frelich and Reich 1999), the ability of fires to spread (Miller and Urban 2000; Cumming 2001), and the transition from low intensity surface fires to high intensity crown fires (Kafka et al. 2001).

The influence of disturbance and succession on fire regimes depends on the mix of tree species present and the constraints imposed by the abiotic environment. Pines (*Pinus* spp.) within temperate deciduous forests often compete best on drier sites (Burns and Honkala 1990). Many pines are initially vulnerable to fires, but become more fire resistant as they age due to self-pruning and development of thick bark (McCune 1988; Burns and Honkala 1990). Yet some species, such as jack pine (*P. banksiana*), require stand-replacing fire to reproduce, and readily burn at almost all growth stages. As a very shade intolerant species, jack pine competes best on xeric sites where dry understories are more likely to burn. In contrast, most fir species (*Abies* spp.) are sensitive to fire, but are also shade tolerant and can become established in the understory of sites that do not often burn. Firs are often known as "ladder fuels" in the western United States because their low branch architecture easily transmits surface fires into the canopy (Moore et al. 1999; Miller and Urban 2000). Fire suppression often leads to increased fire risk in western coniferous forests because firs can invade previously fire resistant systems if fire disturbance is removed (e.g., Stephensen 1999). In contrast, fire suppression often decreases fire risk in temperate mixed coniferous – deciduous forests by allowing the establishment of deciduous species that inhibit fire spread (Frelich and Reich 1995).

Neighborhood effects, such as seed dispersal, can create strong spatial feedbacks to fire that can either increase or decrease system flammability, and other natural disturbances, such as severe wind events, can create new opportunity for intense fires (Frelich and Reich 1995). Forestry practices often interrupt spatial relationships between natural disturbance and forested ecosystems by planting specific tree species (e.g., pines), and by imposing a new pattern and scale of disturbance "patches" on the landscape (Spies et al. 1994; Hessburg et al. 1999). The large temporal and spatial scales associated with these agents of forest change hinder our understanding of human influence on fire risk.

Our objective in this study was to evaluate how direct and indirect human influences on fire regimes affects the abundance and landscape configuration of volatile fuels capable of producing catastrophic fires in northern mixed forests of the upper Midwest, using the ecological disturbance and succession model LANDIS (He et al. 1999a). Specifically, we wished to understand how fire suppression (a direct human influence) and forest harvest practices (an indirect human influence) might affect high-risk fuel sources: (1) conifer species and age cohorts that can serve as

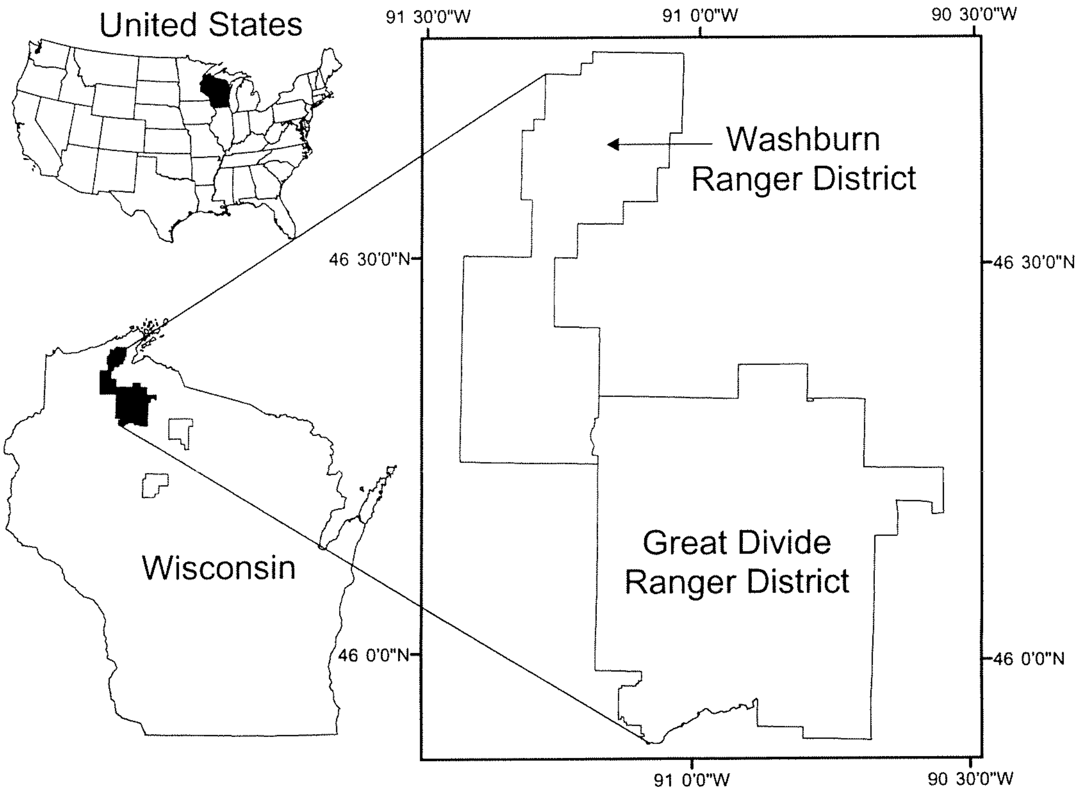

Figure 1. Study area: Washburn and Great Divide Ranger Districts of the Chequamegon-Nicolet National Forest.

ladder fuels, and (2) recent wind damage that can provide flammable coarse woody debris. We simulated two alternative surface fire regimes and three alternative forest harvest strategies in a national forest in northern Wisconsin.

Based on the literature, we hypothesized that (a) fire suppression would decrease high-risk fuel sources over successional (i.e., century) time scales by encouraging the establishment of nonflammable deciduous species (e.g., Frelich and Reich 1995), and that (b) forestry practices that encouraged the establishment of deciduous species would similarly reduce high-risk fuel sources. To test these hypotheses, we evaluated the interactions between direct and indirect human influence factors, as well as spatial interactions between forest management, the abiotic environment, and fire risk in the mixed conifer-deciduous forests of the upper Midwest.

Methods

Study area

Simulations were applied to the Washburn and Great Divide Ranger Districts (RD) of the Chequamegon-Nicolet National Forest (CNNF), located in northern Wisconsin, USA (Figure 1). The CNNF is located within a transition zone between the boreal forests of Canada and the cool temperate deciduous forests to the south, known as the northern hardwoods (Pastor and Mladenoff 1992). Quaternary geology and mesoclimatic gradients are the primary determinants of environmental variation in the region. The northern portion of the Washburn RD falls on the Bayfield Sand Plains Subsection (Keys et al. 1995) and is characterized by coarse sandy soils and xeric growing conditions. This area was historically occupied primarily by jack pine (*P. banksiana*), red pine (*P. resinosa*), and scattered oaks (*Quercus* spp.), but is

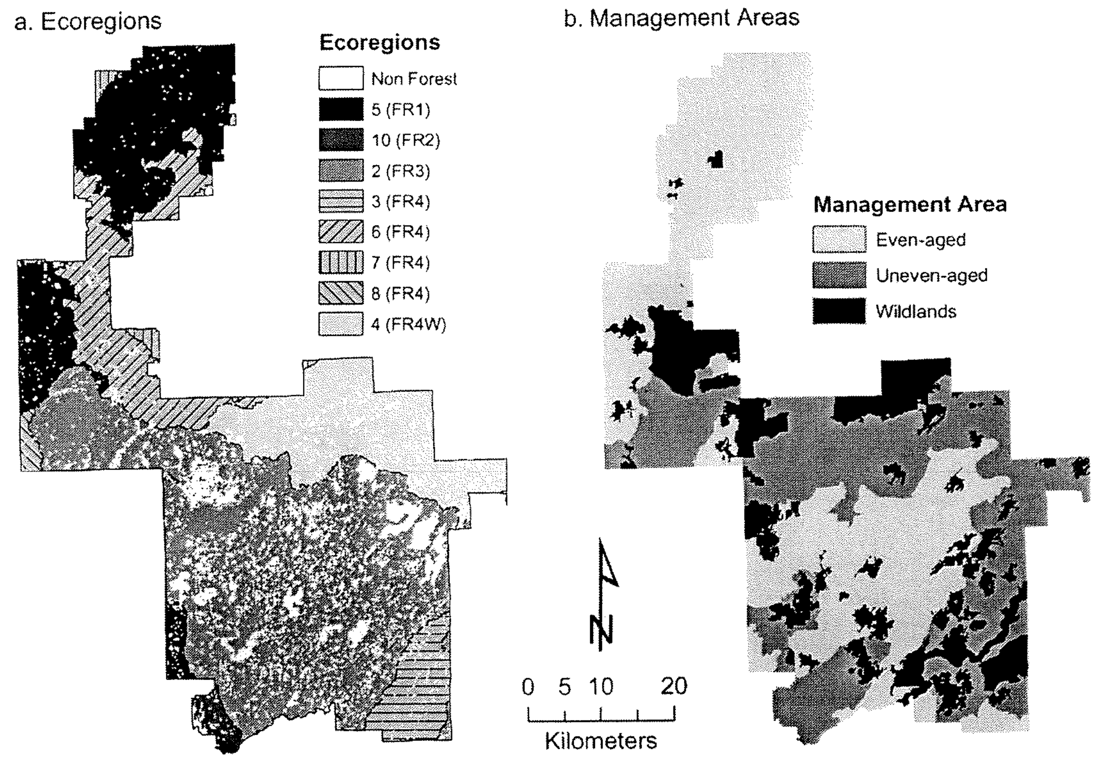

Figure 2. (a). Ecoregions (Host et al. 1996) used to represent coarse-scale environmental heterogeneity in the simulations. Non-forest land cover types (water, lowland, and residential) are not modeled. Fire rotation (FR) classes correspond with classes listed in Table 1. (b). Simplistic management areas used to control silvicultural treatments in the study area.

now dominated by oak and aspen (*Populus* spp.) forests where pines are less common (Radeloff et al. 1999a). The southern portion of the Washburn RD and the Great Divide RD are located mostly within the Winegar Moraine and Central Wisconsin Loess Plain Subsections, characterized by well-drained to rich loamy soils, and historically occupied by white pine (*P. strobus*) and eastern hemlock (*Tsuga canadensis*) on well drained sites and northern hardwood systems (e.g. *Acer saccharum*, *Betula alleghaniensis*) on the richer soils. Spruce- fir (*Picea glauca – Abies balsamea*), aspen and paper birch (*B. papyrifera*) were historically most common along the south shore of Lake Superior (Curtis 1959). Current vegetation in this section of the study area is characterized by second-growth forests with a mixture of northern hardwood and boreal species, following widespread destructive logging and fires in the late 19th century (Mladenoff and Pastor 1993; Stearns 1997).

Host et al. (1996) captured environmental heterogeneity of the study area and adjacent lands into spatial zones known as ecoregions that are relatively homogeneous with respect to climate, landforms, and soils (Figure 2a). These ecoregions are similar in scale to the Land Type Associations (LTA) in the hierarchical land classification system used by the Forest Service (Cleland et al. 1997), and we used characteristics of each system to parameterize our simulations (see Simulation Section). Fires are routinely suppressed in the study area, but disturbance by high winds is a regular occurrence (Canham and Loucks 1984).

Study overview

Our application of LANDIS (described below) was novel in that we evaluated the risk of high-intensity fire indirectly, using the landscape abundance and pattern of "high-risk fuel" as a surrogate for the risk of stand-replacing fires. Local fire ecologists believe that high-intensity fires in northern Wisconsin are only possible under a limited set of conditions, i.e., requiring the presence of either wind-thrown trees or coniferous tree species in growth stages conducive to fire spread (L. Kempf, G. Knight, US Forest Service, personal communication). Without these high-risk fuels, successful fire ignitions will generally remain as low-intensity surface fires. The current version of LANDIS (3.6) does not recognize conifer species as a source of standing fuel, limiting its ability to simulate crown fire dynamics in these mixed forest systems. Nonetheless, LANDIS is well equipped to simulate essential interactions between multiple disturbance regimes and tree species composition across large forested landscapes. We therefore used LANDIS to investigate the relative influence of *surface fire* rotation and forest harvest patterns on the abundance, connectivity, and spatio-temporal pattern of high-risk fuels capable of producing *stand-replacing fires*.

We simulated two surface fire regimes (high/current suppression and low suppression) and three simplistic harvesting strategies (no harvest, hardwood emphasis, pine emphasis), and analyzed the effect on high-risk fuels using a 2×3 factorial design. A simulation period of 250 years was used to allow the effects of surface fires and forest management on forest succession to be fully manifested. Decadal output from the simulations documented the presence/absence of high-risk fuel on each cell. High-risk fuel included sites affected by recent wind disturbance, defined as wind events occurring within the last 30 years, and/or the presence of any conifer that might transfer a low intensity surface fire into the canopy. However, the susceptibility of conifers to crowning varied by species based on their characteristic branching structure. Jack pine, balsam fir, white spruce, and northern white cedar (*Thuja occidentalis*) all have low branching structures that make them susceptible to crowning during a fire. However, red and white pine self-prune and can therefore "escape" fire damage if trees are of a sufficient age, which we assumed was 80 years. Eastern hemlock (*Tsuga canadensis*) can also escape fire damage (Burns and Honkala 1990), but only if trees are much older (i.e., ≥ 200 years). We also assumed that the youngest cohort of any conifer (i.e., < 10 years) would not create enough heat to transfer a fire into the canopy. Landscape metrics of high-risk fuel abundance (i.e., proportion of landscape), patch size, and nearest-neighbor distances were calculated from the mapped simulation output, and five replicate simulations of each scenario allowed statistical comparisons of fuel patterns among the different factors.

LANDIS model

The LANDIS model simulates spatial forest dynamics including forest succession, seed dispersal, species establishment, disturbance, and their interactions (Mladenoff and He 1999; Gustafson et al. 2000). The purpose of LANDIS is to simulate the reciprocal effects of disturbance processes (fire, wind, vegetation management) and patterns of forest vegetation on each other across large (10^4 to 10^7 ha) landscapes and long time scales (50 to 1000 years). The model operates on a raster (grid) map, where each cell contains information on the presence/absence of tree species and their 10-year age-cohorts (species – age list), but not information about the density or size of individual stems. The model requires mapped land types/ecoregions, initial conditions, mapped stands and management areas as spatial input, as well as parameters for species establishment, fire characteristics, and fuel accumulation regimes for each ecoregion.

The model simulates differential reproduction, dispersal, and succession patterns using the vital attributes of species, and incorporates effects of disturbance and environmental heterogeneity interacting spatially across the landscape (Mladenoff and He 1999). Wind disturbance affects species' cohorts from the top-down, i.e., killing the oldest cohorts first, followed by younger cohorts depending on the severity of the disturbance. In contrast, fire disturbance affects species cohorts from the bottom up, killing the youngest cohorts first, followed by older cohorts depending on both the severity of the disturbance (controlled by a landtype-specific fuel accumulation curve) and species-specific tolerance to fire. Vital attributes influencing forest succession include shade tolerance, fire tolerance, seed dispersal, ability to sprout vegetatively, and longevity (Burns and Honkala 1990). The design and behavior of the succession components of the model, and model test results, are described in detail elsewhere (He et al.

1999a; 1999b; He and Mladenoff 1999; Mladenoff and He 1999).

The forest harvest module of LANDIS allows simulation of disturbance by vegetation management activity (Gustafson et al. 2000). Harvest activity is specified independently for each management area, a spatial zone with specific management objectives. The LANDIS data structure is rich in site information, allowing the heterogeneity of stands to be expressed as heterogeneity both within cells and among the cells that comprise a stand. This structure allows flexible simulation of a wide range of management activities. The user specifies the details about how timber management activities selectively remove age-cohorts of each species on harvested cells. The order in which stands are selected for harvest is based on ranking algorithms that can be related to specific management goals. Succession on harvested cells is simulated based on the residual species and age classes both on the cell and by dispersal from other cells.

The LANDIS model simulates wind and fire disturbance regimes based on user-specified parameters for wind and fire events on each ecoregion. These parameters are spatially implemented on the landscape using a stochastic algorithm to approximate a desired return interval across the ecoregion over a long-temporal scale (e.g., ≥ 100 years) (He and Mladenoff 1999). LANDIS sequentially simulates windthrow, fire, harvesting, and forest succession at each 10-yr time step.

The fire simulation algorithm in LANDIS is based on the observation that fire appears to be stochastic for a single site, but has repeated patterns in terms of ignition rates, location, size, and shape at landscape scales. Simulation of fire ignition in LANDIS involves selection of random locations and stochastic ignition attempts at those sites. Successful ignition depends on the probability of fire (P) computed using the mean fire return interval (MI) for the ecoregion, and the time since last fire (lf) on the cell:

$$P = B \cdot lf \cdot MI^{-(e+2)}$$

B is the *fire probability coefficient*, and it is used for model calibration to ensure that stochastically simulated fire events follow a known historical or empirical distribution (He and Mladenoff 1999). Ignitions are more likely to occur on cells with shorter MI and as lf increases. Once an ignition is successful, the probability of having second or more ignitions decreases exponentially (He and Mladenoff 1999). However, we modified the ignition algorithm to decrease the exponential rate of decline in ignition probabilities to properly model the frequent and small fires that typify the modern fire regime described below. Once a fire is successfully ignited, fire size is randomly selected from a lognormal distribution that is controlled by a mean fire size parameter (MS). Fire spread is a function of a randomly selected wind direction, fire size, fire probability, the susceptibility of tree species, and spatial configuration (He and Mladenoff 1999). In our simulations, fire shapes were roughly circular or elliptical with irregular edges, particularly when fires occurred adjacent to nonactive land types (e.g., lakes). Fire severity is determined by relating an ecoregion-specific fuel accumulation curve with the time since last fire (lf) recorded for the site. Wind disturbance follows a similar approach to fire, except that sites disturbed by a wind event do not need to be contiguous.

Simulations

Input data

Input maps for LANDIS were derived from existing spatial databases, and were gridded to a 60 m cell size. We used GIS coverages provided by the CNNF to generate input maps of stand and management area (MA) boundaries. Initial forest composition maps (spatially explicit species and age-cohort data) and ecoregion maps were based upon those used by He et al. (1999b). The spatial location of dominant species was derived from a classified TM image (Wolter et al. 1995), and then randomly assigned age classes and associated species (by ecoregion) to match the statistical distributions found in Forest Service Forest Inventory and Analysis data (Hansen 1992) as described by He et al. (1999b). However, rather than assigning initial conditions on a cell by cell basis, we initialized each stand in the map with a homogenous condition. The demographic parameters (e.g. longevity, dispersal range, age of first reproduction) of the 23 tree species modeled were developed from the literature for a previous study (He et al. 1999a). One important exception was the shade tolerance for balsam fir, which we set at 4 rather than the maximum value of 5. Balsam fir reaches the southern limits of its range in the study area, and observations from the region indicate that it cannot compete well with sugar maple, another important shade tolerant species in the

Table 1. Description of fire rotation classification of land type associations. Modern fire rotations were calculated for this study using a fire database for northern Wisconsin dating from 1985 – 2000. The modern fire rotations were used to parameterize the mean fire return intervals (*MI*) in the "High Suppression" surface fire regime. *MI* for the "Low Suppression" surface fire regime was estimated as an order of magnitude lower than the current modern fire rotations. Ecoregions (Host et al. 1996) used in the study (see Figure 2a) were assigned to a fire rotation class based on spatial overlap with the land type associations.

Fire Rotation Classification	Soil Moisture	Dominant Presettlement Vegetation	Fire Rotation (yrs)			Ecoregions
			Presettlement[a]	Modern ~ High Suppression	Low Suppression	
FR1	xeric	jack pine and barrens	135	2900	290	5
FR2	less xeric	red & white pine, oak	320	6700	670	10
FR2W	hydric	wetlands adjacent xeric LTAs	490	not simulated	not simulated	None
FR3	dry mesic	white pine – hemlock	467	9800	980	2
FR4	mesic	northern hardwoods	1820	14200	1420	3, 6, 7, 8
FR4W	hydric	wetlands adjacent mesic LTAs	2925	18000	1800	4

[a]Cleland et al., this issue

study area (T. Crow, USDA Forest Service, personal observation). Lowering the shade tolerance of balsam fir allowed us to capture this relationship by blocking the establishment of fir under an established sugar maple canopy.

Ecoregion-specific species establishment coefficients are an estimate of the probability that a species will successfully establish from seed within a given ecoregion, given adequate sun exposure for the species. Past studies have used the ecosystem model LINKAGES (Pastor and Post 1986) to estimate the probability of species establishment based on the relative biomass accumulation of the species given the climate and soil conditions characteristic of the ecoregion (He et al. 1999b). However, total biomass is not necessarily an indicator of long-term survival. Further, LINKAGES assumes uniform soils because the intended scale of the model is less than a hectare. Since LANDIS requires species establishment coefficients for broad-scale (10^4 ha) ecoregions, the assumption of soil uniformity is no longer valid. R. Scheller (unpublished manuscript) modified LINKAGES to input the range of variability in soil carbon and soil nitrogen within an ecoregion, based on information from the STATSGO database (USDA 1994), to stochastically evaluate whether a monoculture of a given species will maintain a positive net gain in biomass over a 10 year period, given the range of variability in both soils and climate within the ecoregion. Species establishment coefficients were calculated as the number of successful establishments divided by the total number of replications. The results were consistent with the known distributions of each species in the study area, however the values of the establishment coefficients increased substantially over the values calculated by He et al. (1999b). As a result, sites in our simulations tended to be more diverse than comparable simulations using the establishment coefficients estimated by He et al. (1999b), as more species successfully established on individual sites. The implications of this difference are addressed later in the *Discussion*.

Surface fire disturbance

Cleland et al. (this issue) classified LTAs into six fire rotation (FR) categories based on common soil characteristics, current and presettlement vegetation. For example, FR1 LTAs were historically dominated by jack pine systems underlain by coarse-textured sandy soils and experienced frequent, large catastrophic stand-replacing fires (Table 1). In contrast, FR4 LTAs were historically dominated by northern hardwood systems, underlain by fine-textured sandy loam to heavy clay and silt loams soils, and experienced very infrequent stand-replacing or surface fires (Table 1). While fire suppression by humans has increased fire rotations by roughly an order of magnitude, the rank order of the FR classification has remained consistent (Cleland et al. this issue).

We parameterized the modern fire regime for our simulations using a 16-year fire database compiled by the Wisconsin Department of Natural Resources and the U.S. Forest Service for northern Wisconsin (see Cardille and Ventura 2001 for detailed description of the fire database) in conjunction with the FR classification developed by Cleland et al. (this issue). Modern forest fire rotations were estimated by calculating the reciprocal of the annual proportion of forest land

Table 2. Description of harvest alternatives. Even-aged, uneven-aged, and wildland prescriptions represent a simplification of actual harvest prescriptions currently applied to the CNNF. Each prescription was applied to its corresponding management area (MA), shown in Figure 2b.

Harvest Alternative	Even-aged Prescriptions	Uneven-aged Prescriptions	Wildland Prescriptions
No Harvest	none	none	none
Hardwood Emphasis	clearcut harvest ~ 8% / decade shelterwood harvest, red oak planted ~ 2% / decade	selection harvest, old pines removed ~ 20% / decade	none
Pine Emphasis	clearcut harvest ~ 8% / decade shelterwood harvest, white pine planted ~ 2% / decade	selection harvest, old pines retained ~ 20% / decade	none

burned within each FR class in northern Wisconsin. Forest land area in each FR class was calculated by using classified TM imagery (Lillesand et al. 1998). Only those fires greater than the resolution of the simulation (i.e., 0.36 ha) and recorded as having occurred in a forest cover type were used to parameterize the fire regime. While the ecoregion boundaries developed by Host et al. (1996) did not match the new LTAs exactly, we assigned an FR class to each ecoregion using the dominant corresponding LTA based on land area (Table 1, Figure 2a).

Since LANDIS does not currently allow mean fire size (MS) to vary by ecoregion/landtype we parameterized the modern fire regime to match the *MS* for the entire study area, and substituted the estimated fire rotations of each FR class for their mean fire return intervals (*MI*; Table 1). The time since last fire (*lf*) in each ecoregion was set equal to 130 years because virtually the entire study area was logged and burned in the late 19th century (Stearns 1997). Finally, the fire probability coefficient (*B*) values were adjusted iteratively for each ecoregion to produce a simulated mean return interval that matched the modern fire rotations using the procedures of He and Mladenoff (1999). The resulting fire regime represented the "high suppression" regime intended to simulate current fire policies. The second fire regime ("low suppression") was simulated by decreasing the fire rotation an order of magnitude for each FR class to approximate the presettlement fire rotation. In the low suppression scenarios, we maintained a similar frequency of fire ignitions, but increased the mean fire size until the estimated presettlement fire rotation was reached. The low suppression scenario was intended to simulate the expected surface fire regime if fire suppression was relaxed to allow low intensity surface fires to burn.

Fire intensity was controlled by holding fuel constant for the entire simulation, limiting fire effects to those expected by surface fires alone. However, surface fires should still be more intense on the most xeric sites. With fuel levels ranging from 1 (low) to 5 (high), we assigned fuel levels 3, 2, and 1 to FR classes FR1, FR2, and FR3-FR4W, respectively. Wind disturbance regimes remained constant for all simulations, using windfall return intervals derived from a regional historical and empirical study (Canham and Loucks 1984).

Harvest scenarios

We created two alternative but simplistic harvest scenarios that were each based on management prescriptions currently practiced in the CNNF (USDA Forest Service 1999). The first alternative was parameterized to discourage establishment of pines on the landscape (Hardwood Alternative), while the second encourages establishment by pines on the landscape (Pine Alternative); these two scenarios were also compared with a No Harvest Alternative (Table 2). The study area was divided into three generic management areas (MAs) indicating the dominant silvicultural options practiced there: 1) even-aged management, 2) uneven-aged management, and 3) wildlands (Figure 3). One of the goals of the CNNF is to increase the proportion of longer-lived species in certain management areas, which is achieved by planting species such as white pine and red oak (*Q. rubra*) using a shelterwood system that discourages the reestablishment of short-lived species such as aspen and birch (M. Thiesson, USDA Forest Service, personal communication). We used the harvest module to simulate this

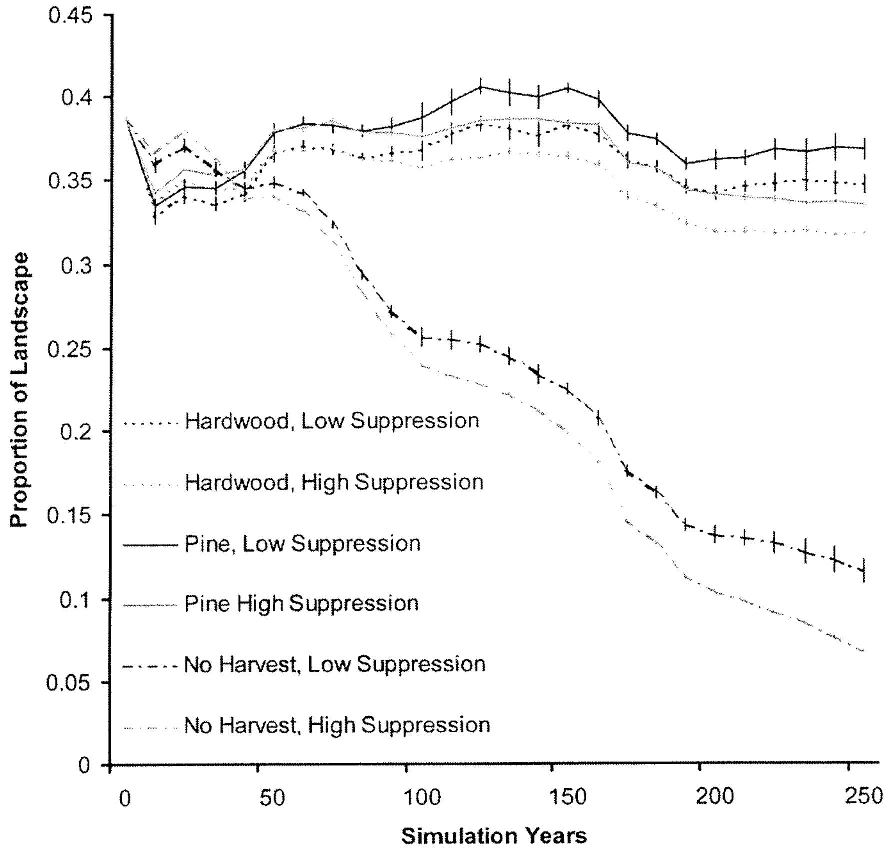

Figure 3. Proportion of the sites in the study landscape occupied by "susceptible conifers" during each decade of the simulation for each of two suppression and three harvest treatments. Lines represent mean values from five replicate simulations, and error bars reflect one standard error of the mean to illustrate system variability.

shelterwood prescription, where we "planted" red oak in the Hardwood Alternative, and planted white pine in the Pine Alternative. Shelterwood prescriptions were applied to two percent of the even-aged MA during each decade of the simulation. Another eight percent of the even-aged MA was disturbed using a basic clear-cut prescription, yielding a total of 10% of the MA disturbed in each decade.

Within the uneven-aged MA, a selection cut harvest prescription was applied to 20% of the MA each decade to mimic a typical silvicultural strategy designed to promote northern hardwood species. While the oldest cohorts of most species (see comments regarding eastern hemlock below) are typically removed in a selection cut, CNNF will at times leave old pines on site to encourage structural diversity (M. Thiesson, USDA Forest Service, personal communication). To simulate the influence of this policy on fire risk, we removed the oldest cohorts of pine for the Hardwood Alternative, and retained the oldest cohorts of pines in the Pine Alternative. All harvest disturbances were placed randomly using the periodic stand-filling harvest algorithm in LANDIS to harvest stands (Gustafson et al. 2000). No harvests were applied to the wildland MA in either harvest scenario, or to any MA in the No Harvest scenario. Finally, eastern hemlock is considered a rare species in the CNNF that was historically common throughout the region. The CNNF therefore does not harvest hemlock, and we therefore did not harvest hemlock in any of the harvest alternatives.

Statistical analysis

Cumulative area damaged by windthrow during each 250-year simulation was analyzed using PROC GLM in SAS (SAS version 8.0) using a randomized block, 2×3 factorial design. The random number seed, held constant among scenarios for each of five replicates, was treated as a block, whereas fire suppression (low and high) and harvest alternative (No Harvest, Hardwood Emphasis, Pine Emphasis) were treated as factors. Four landscape metrics [proportion of total area (p), mean patch size (MPS), Euclidean nearest neighbor distance (ENND), and interspersion juxtaposition (IJI: McGarigal and Marks 1995)] were calculated for mapped output of (a) susceptible conifers and (b) susceptible conifers and recent windthrow combined at the final decade of the simulation. Proportion (p) describes the relative landscape abundance of high-risk fuels, MPS indicates the average size of fuel patches present on the landscape, ENND measures the average distance between patches (used as an indicator of fire breaks), and IJI serves as an indicator of the interspersion of fuel and nonfuel patch types. All indices were calculated in Fragstats (Version 3.3, see McGarigal and Marks 1995), using an eight-neighbor rule (i.e., cells sharing a common edge or corner are considered members of the same patch). However, most landscape metrics are highly related to the proportion of the landscape occupied by the class of interest (Gustafson 1998), suggesting that the various indicators of fuel connectivity will be correlated with p. We therefore analyzed the four response variables together in a multivariate analysis of variance (MANOVA) to test the global hypothesis that direct and indirect human influence factors affect the landscape pattern of high-risk fuels. The design of the MANOVA was otherwise identical to the design of the ANOVA for wind disturbance described above. We used the Pillai's Trace statistic to test our hypotheses because it is the least sensitive of the four multivariate tests provided by SAS to the heterogeneity of variance assumption of MANOVA (Zar 1999).

We also calculated the landscape metrics for each time step in the simulations to qualitatively evaluate temporal trends in the data. This analysis was conducted for the entire study area, separately for each of the major ecoregions (lumped by FR class) to search for patterns created by fire disturbance, and for each of the three management areas to search for patterns created by forest management. Each of these temporal analyses was exploratory, and the reader should note that the ecoregions and MAs are not spatially independent (Figure 2a,b). Nonetheless, the temporal analysis helped with the interpretation of the MANOVA results.

Table 3. Analysis of variance results for wind damage as a function of suppression and harvest alternative. Model $R^2 = 0.79$.

Source of variation	df	Type III SS	F	Prob > F
Replicate (r)	4	133328607	7.01	0.0011
Suppression (s)	1	96110112	20.20	0.0002
Harvest Alternative (h)	2	107822857	11.33	0.0005
s*h	2	28375228	2.98	0.0736
Error (e)	20	95156685		
Total	29	406793489		

Results

The cumulative area damaged by wind throw during the 250-year simulation was significantly influenced by both fire suppression and by forest management, as indicated by ANOVA (Table 3). The highest amounts of wind damage were observed in the *No Harvest* management alternative under *High Fire Suppression* (mean cumulative area damaged ≈ 24000 ha), whereas the same management alternative under low suppression averaged about 20300 ha after 250 simulation years. Tukey's comparison indicated that the two other harvest scenarios (*Hardwood* and *Pine*) had similar area damaged by winds, approximately 20400 and 19100 ha under *High* and *Low Fire Suppression*, respectively. Results indicate that the protection of forests from both harvest and fire disturbance creates a landscape more susceptible to windthrow, probably because the resulting older forests are more likely to be damaged by wind.

MANOVA results indicated that both fire suppression and harvest disturbance also significantly affected the landscape pattern of susceptible conifers across the study landscape, however the direction of the response was opposite that observed for wind damage. Interestingly, adding sites that experienced recent wind disturbance to those occupied by susceptible conifers had little influence on the results of the MANOVA; both treatments and their interaction had a significant influence on the overall pattern of combined fuels (Table 4), and the direction of influence by each treatment was identical to that observed for susceptible conifers alone. The number of sites dis-

Table 4. MANOVA and individual ANOVA results for four landscape pattern metrics of combined fuel sources (susceptible conifers + recent wind disturbance) as a function of suppression and harvest alternative.

Effect	df (n,d)	Pillai's Trace/Type III SS	F	Prob > F
MANOVA global test of hypotheses				
Suppression (s)	4,17	0.91	45.63	< 0.0001
Harvest Alternative (h)	8,36	1.86	63.74	< 0.0001
s*h	8,36	1.01	4.70	0.0005
Individual ANOVA tests of hypotheses				
Total Area of Susceptible Conifers – Model R^2 ~ 1.0				
Replicate (r)	4	0.0007	2.07	0.1223
Suppression (s)	1	0.0086	108.43	< 0.0001
Harvest Alternative (h)	2	0.4115	2601.36	< 0.0001
s*h	2	0.0003	1.70	0.2077
Error (e)	20	0.0016		
Total	29	0.4226		
Mean Patch Area – Model R^2 = 0.98				
Replicate (r)	4	1.47	0.93	0.4675
Suppression (s)	1	13.55	34.24	< 0.0001
Harvest Alternative (h)	2	391.31	494.44	< 0.0001
s*h	2	1.51	1.91	0.1741
Error (e)	20	7.91		
Total	29	415.76		
Euclidean Nearest Neighbor – Model R^2 = 0.99				
Replicate (r)	4	1.37	0.19	0.9422
Suppression (s)	1	242.65	132.68	< 0.0001
Harvest Alternative (h)	2	2846.93	778.37	< 0.0001
s*h	2	169.96	46.47	< 0.0001
Error (e)	20	36.58		
Total	29	3297.49		
Interspersion Juxtaposition – Model R^2 ~ 1.0				
Replicate (r)	4	2.51	1.68	0.1937
Suppression (s)	1	1.87	5.02	0.0366
Harvest Alternative (h)	2	2201.38	2949.52	< 0.0001
s*h	2	1.15	1.55	0.2374
Error (e)	20	7.46		
Total	29	2214.38		

turbed by wind in any given 30-year time period averaged about 3000 ha, approximately an order of magnitude less than the number of sites occupied by susceptible conifers. Hence, the pattern of susceptible conifers in the landscape overwhelmed any influence of wind disturbance on the pattern of fuel on the landscape.

Harvest activity had a strong positive influence on the proportion of the landscape occupied by susceptible conifers (p) relative to the *No Harvest* alternatives (Figure 3). As expected, the *Hardwood* alternative had lower p than the *Pine* alternative, but the differences were much more subtle compared to *No Harvest*. Fire suppression also had a subtle negative influence on p, but the response was consistent across harvest alternatives (Figure 3). These results indicate that disturbance by either fire or harvest had a positive influence on the abundance of susceptible conifers in the landscape. By increasing the proportion of sites occupied by susceptible conifers, each disturbance type also increased the connectivity of high-risk fuel in the landscape, reflected by the significance of each treatment on MPS, ENND, and IJI (Table 4). MANOVA also showed a significant interaction between fire suppression and forest harvesting, because fire suppression did not have a significant influence on either ENND or IJI when the landscapes were subjected to harvest disturbance (Table 4).

The temporal pattern of different conifer species suggests that both fire and harvest disturbance positively influence the landscape abundance of high-risk fuel by encouraging establishment of moderately shade-tolerant conifer species (Figure 4). Under the *No Harvest* alternatives (Figure 4e,f), most conifer species declined over time. Two exceptions were white pine and eastern hemlock, both of which are very long-lived species that essentially maintained their initial distributions, and both were assumed to be less susceptible to fire as older trees. Jack pine declined to near extinction in all 6 scenarios (Figure 4), suggesting that the levels of disturbance simulated in this study were insufficient to maintain this species in the landscape. Jack pine is a very shade intolerant species that requires either stand-replacing fires or specialized management to regenerate. Since only surface fires were simulated and jack pine was not planted in any harvest scenario, it is not surprising that this species disappeared. However, both of the harvest alternatives increased the distributions of white and red pine, balsam fir, and white spruce (Figure 4a-d). These species range from moderately shade intolerant (red pine) to moderately shade tolerant (balsam fir).

Disturbances kept the most shade tolerant competitor, sugar maple, held in check. This response is illustrated by the age distribution of sugar maple at simulation year 250 (Figure 5). The youngest age classes of sugar maple were most common in the even-aged MA, with increasingly older maples found in uneven and wildland MAs (Figure 2b) in both the *Hardwood* and *Pine* harvest alternatives, whereas the *No Harvest* alternative was almost entirely dominated by old growth sugar maple (Figure 5). An important exception was the most xeric LTA at the northwestern part of the study area, where sugar maple had poor establishment. Surface fires simulated in the *No Harvest, Low Suppression* scenario disturbed relatively large patches of sugar maple, creating further opportunity for establishment by less shade tolerant conifers. Age distributions of sugar maples were very similar for all harvested scenarios. Comparing the landscape distribution of susceptible conifers at simulation year 250 (Figure 6) with the age distribution of sugar maples at the same time step illustrates the strong constraining influence of sugar maple on landscape abundance and connectivity of live coniferous fuel.

At the scale of the entire study landscape, each of the landscape metrics were closely related to the landscape abundance of high-risk fuel, but closer inspection of individual management areas (MAs) shows some interesting effects of harvest patterns on fuel connectivity. For example, p calculated for combined fuel maps (susceptible conifers + recent windthrow) in the even-aged MA show that fuel abundance was similar between the two harvest alternatives relative to the *No Harvest* alternative (Figure 7a). Yet the mean patch size is much smaller for the *Hardwood* alternative than for the *Pine* alternative (Figure 7c). In the uneven-aged MA, mean patch size for either harvest alternative was similar to that observed for *No Harvest*, despite large differences in p (Figure 7b,d).

Varying surface fire regimes among ecoregions also influenced the connectivity of high-risk fuel within the study landscape. For example, ecoregions with the longest simulated fire rotations (i.e., FR4 and FR4W) showed a sharp increase in ENND near the end of the 250-year *No Harvest* simulation (results not shown). This result indicates that fuel connectivity may be sensitive to fire disturbance – fewer fire disturbances created less opportunity for conifers to establish new sites, resulting in fewer and widely-separated fuel patches (Figure 6). However, harvest disturbance created ample opportunity for conifers to establish, resulting in little change in ENND over the course of the simulation.

Discussion

Moderate disturbance such as surface fire and harvest activity increase the abundance and connectivity of conifers capable of transmitting a surface fire into the canopy within a mixed deciduous-conifer landscape of the upper Midwest. This result stems from the negative influence of disturbances on sugar maple, which eventually excludes most conifers in the absence of disturbance. Wind disturbance was more common in old forest undisturbed by humans, but the area of fuel created by wind disturbance was not sufficient to alter the observed relationship between disturbance and the abundance of high-risk conifer fuels. While our results are contrary to the commonly reported pattern of increased fire risk following fire suppression, they are consistent with empirical studies of fire and succession in northern mixed forests of the upper Midwest.

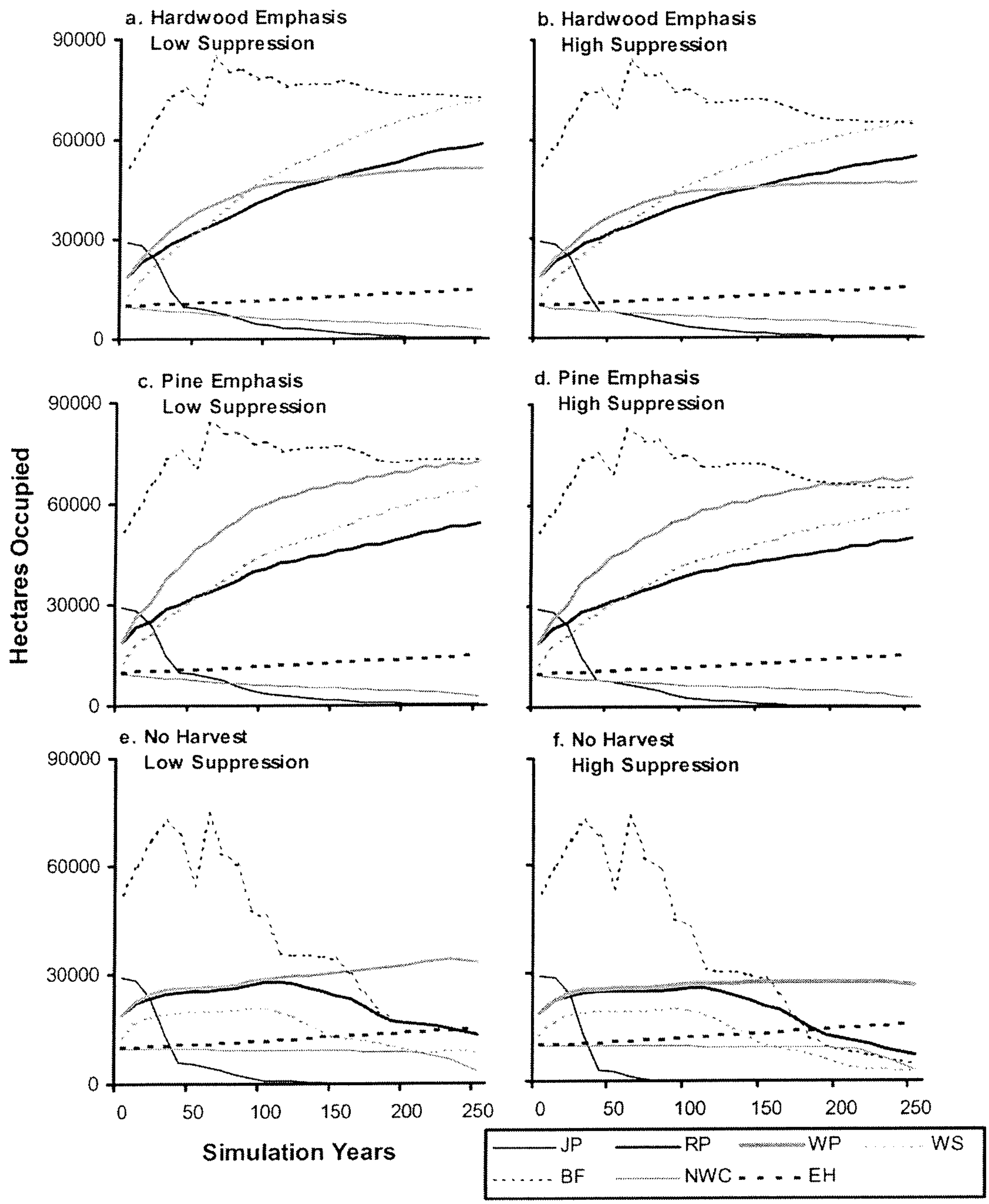

Figure 4. Total hectares occupied by each of the conifer species during the 250-year simulation. JP = jack pine, RP = red pine, WP = white pine, WS = white spruce, BF = balsam fir, NWC = northern white cedar, and EH = eastern hemlock.

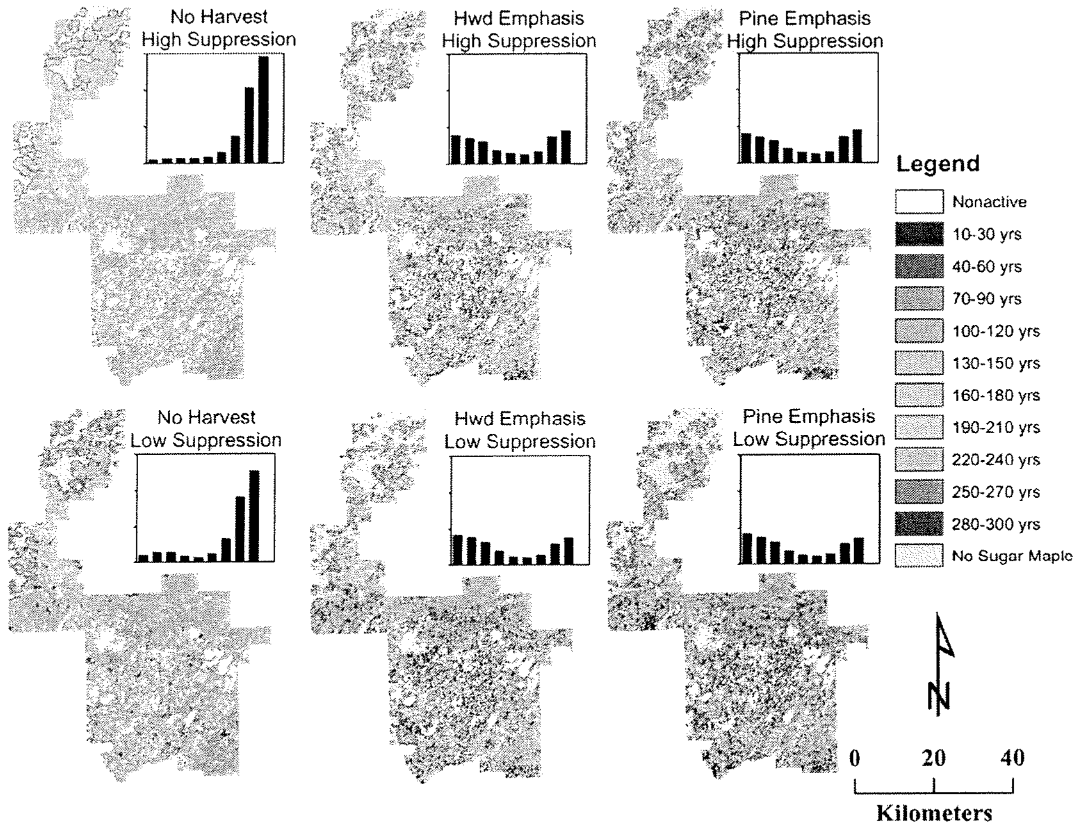

Figure 5. Age structure and distribution of sugar maples at simulation year 250. Compare maps with Figure 2 to evaluate spatial influence of ecoregions and management areas. Histograms show the frequency of age classes, with 30-year age classes on the x-axis (range = 0–300) and the area occupied by each age class on the y-axis (range = 0–1200 km^2).

Fire suppression is the most cited direct human influence on fire disturbance regimes (e.g., Johnson et al. 2001), but our study demonstrates that not all systems respond to fire suppression in the same way. The stereotypical pattern observed in many coniferous forest systems of western temperate North America is that fire suppression leads to an increase in shade-tolerant but fire sensitive conifer species, resulting in an increased risk of high intensity wildfires (Mutch 1995). However, the dominant shade tolerant species in northern Wisconsin is sugar maple, a deciduous species that, while sensitive to fire, also inhibits fire spread once established (Frelich and Reich 1995). Sugar maple historically dominated the richest soils in the region, but has also become established on less productive sites in recent decades following fire suppression (Almendinger and Hanson 1998). Results from our study indicate that an increase in the area burned by fires will negatively impact sugar maple and therefore encourage the establishment of moderately tolerant conifer species. These results are consistent with the work of Frelich and Reich (1995), who observed that fire-prone systems in the region may "switch" to a new system state that inhibits fire if fire disturbance is removed for a period of time. Had our simulated fires been more severe, the fire-adapted jack pine may have shown a similar response. Indeed, even the xeric systems of the pine barrens in northwestern Wisconsin can convert to oak if fire rotations are not sufficient to retain jack pine (Radeloff et al. 1999b). The most shade tolerant conifer in the region, hemlock, is currently restricted to a few rem-

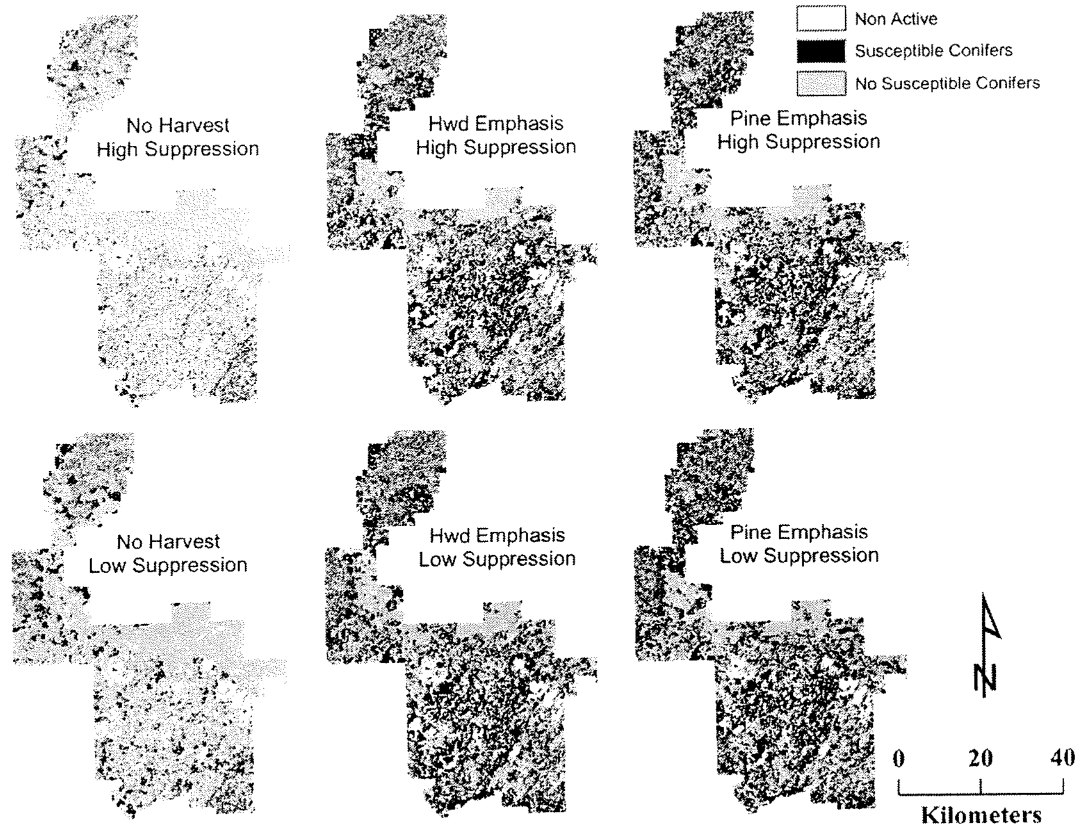

Figure 6. Spatial distribution of sites occupied by susceptible conifers at simulation year 250. Note the negative correlation with the age distribution of sugar maples (Figure 5).

nant populations, and our simulations indicate that it will not likely recover its presettlement distribution even if protected from harvest (Mladenoff and Stearns 1993). Since deciduous species rarely carry a crown fire, deciduous stands often act as fire breaks (Burns and Honkala 1990, Cumming 2001), further inhibiting future disturbance by fire by reducing fuel connectivity. Hence a critical difference between northern mixed forests of the upper Midwest and the coniferous forests of western North America is that the "endpoint" of succession in the absence of fire is typically deciduous, creating a negative feedback between fire suppression and fire disturbance.

Our study also shows that harvest activity will likely influence fire behavior by manipulating composition, structure, and landscape pattern of forest vegetation and fuel characteristics. In fact, harvest activity overwhelmed high-risk fuel responses to surface fire suppression by providing greater opportunity for moderately tolerant conifers to become established. However, since LANDIS could not account for the effect of live fuel on fire intensity, we could not simultaneously investigate the interaction between surface fire suppression, crown fire suppression, and harvest activity on the distribution of high-risk fuels. Had we modeled crown fires explicitly, fire suppression may have had larger influence on the distribution and abundance of high-risk fuels, particularly in the fire-prone land types that supported jack pine communities.

Different harvest methods simulated within different management areas in our study had qualitatively different impacts on both the abundance and connectivity of high-risk fuels. Even-aged management gen-

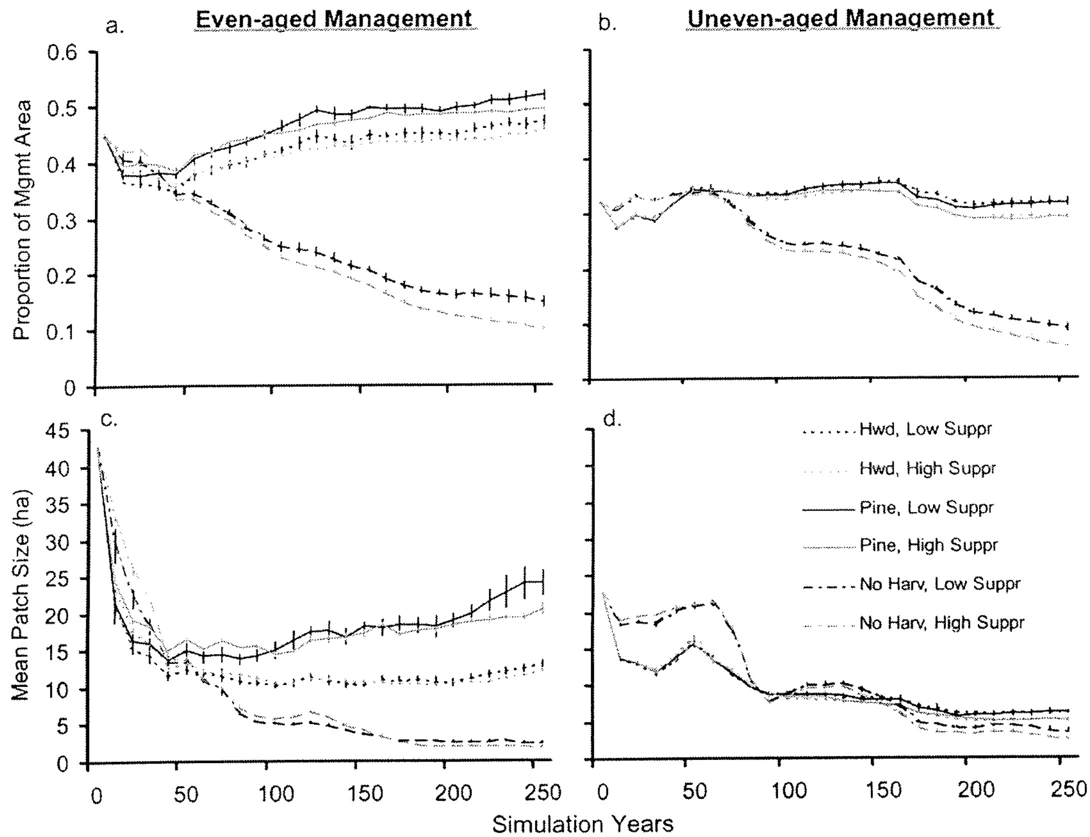

Figure 7. Temporal pattern of the proportion of sites occupied by high-risk fuel (susceptible conifers + recent windthrow) within (a). the even-aged management area, and (b). the uneven-aged management area, compared with the temporal pattern of mean patch size for the same areas (c,d). Lines reflect mean values from five replicate simulations, and error bars reflect standard errors of the means.

erally created more homogeneous fuel conditions within a stand than uneven-aged management because there were no residual hardwood cohorts to interfere with site establishment by conifers. However planting pine insured that entire stands had established conifers, whereas planting oak required establishment of conifers entirely by seed dispersal, resulting in a more fine-scale distribution of conifers at the stand scale. One caveat that deserves mention is that each of the landscape metrics likely has a nonlinear relationship with p dependent on the "rule" used to define patches (i.e., eight-neighbor). The critical proportion p_c, a threshold above which patches in random maps coalesce into a large patch spanning the entire map, is estimated at 0.41 when using an eight-neighbor rule to define patches (Stauffer 1985). For example, the larger differences in MPS observed between harvest alternatives in the even-aged management areas in comparison with the uneven-aged management areas is probably due in part because even-aged harvesting allowed the proportion of sites occupied by high risk fuel to exceed p_c, whereas uneven aged management did not (Figure 7). Nonlinear relationships between fuel abundance and connectivity likely affect the spread of fires (Turner et al. 1989). However, the scale at which sites are connected in terms of fuel, and therefore the appropriate neighborhood rule defining fire spread, is not well understood.

Empirical studies of forest succession in the Lake States are consistent with our findings that disturbance in the northern hardwoods encourages establishment of moderately shade tolerant conifers. Frelich and Reich (1995) use the hemlock/hardwood system as a case study to describe their punctuated stability concept of succession, where disturbance disrupts successional pathways of an otherwise stable forest community. They review a recurrent pattern where a catastrophic fire, such as one occurring within a recent blowdown, will convert a hemlock – hardwood site to aspen – birch, followed by colonization of white pine. Heinselman (1954) also recognized the tendency of aspen – birch sites originating from previous disturbance to convert to a mixed conifer-deciduous community. Mladenoff et al. (1993) demonstrated that a managed forest landscape in the Upper Peninsula of Michigan had a much higher proportion of boreal species, including balsam fir and white spruce, than a comparable old-growth forest. Since catastrophic disturbance is much more common in boreal systems in comparison with the northern hardwoods, boreal species are better able to colonize new sites, and become more common within harvested landscapes (Mladenoff et al. 1993). Since both balsam fir and white spruce have characteristically low branching architecture, they may increase the risk of crown fire in mixed stands (Kafka et al. 2001), and harvesting in our simulations encouraged their landscape abundance. Notably, planting pine seemed to have a relatively minor influence on the overall abundance of fire susceptible conifers (Figure 3). This was due in part because planted white pine simply replaced some of the area occupied by white spruce (e.g., Figure 4a,c), and partly because white pine has a shorter window of susceptibility than most other conifers in the study.

While our results indicate that the periodic pulses of fuel created by wind events are generally overwhelmed by the distribution of conifers across the landscape, we caution that the relative importance of blowdowns and conifers as "high-risk fuels" is not well understood. In fact, large presettlement fires recorded by surveyors of the General Land Office located within the largely fire-resistant northern hardwoods systems were very often associated with recent blowdown (Maclean and Cleland, in press). One limitation of our approach is that, due to the design of LANDIS, we relied on the presence/absence of conifer species as the sole indicator of live fuel present on a cell. Conifer density within a site could not be assessed.

The species establishment coefficients used in this study were relatively high compared with previous LANDIS studies in the region (He et al. 1999; Gustafson et al. this issue). Higher establishment coefficients increased the overall abundance of all species, including conifers, and likely influenced the relative importance of windthrow events as a fuel source. However, we did apply the same species establishments as specified in He et al. (1999) in a test case and observed the same relative result (unpublished data). We therefore believe that our results are robust with respect to conifer establishment.

Two other key assumptions likely affected our conclusions. The first is that balsam fir is less shade tolerant than sugar maple. If, alternatively, balsam fir were simulated as having the highest possible shade tolerance (i.e., equal to sugar maple), our results would have been reversed, because balsam fir would thrive best in sites that were undisturbed. Balsam fir is a well-known shade tolerant species, but it reaches the southern limit of its range just south of our study area. In contrast, sugar maple seems to grow exceptionally well in the upper Great Lakes region (Burns and Honkala 1990), and is thought to be a superior competitor in the vicinity of the study area (Mladenoff et al. 1993). Since balsam fir appears much more common in the study area where sugar maple is lacking, we feel comfortable with our assumption. Nonetheless, given its impact on our results, the successional dynamics of fir in the transition zone between boreal and northern hardwood systems warrants further study. A second assumption is that the species establishment coefficients do not vary at the scale of ecoregions. In reality, fine scale heterogeneity in soil moisture and nutrient availability may influence the establishment of a nutrient-demanding species such as sugar maple (Smith and Huston 1989). In fact, less productive sites are often colonized by red maple (*A. rubrum*) rather than sugar maple. Since red maple has a lower shade tolerance than sugar maple, balsam fir can grow beneath a red maple overstory. Hence, the overwhelming influence of sugar maple observed in our study may have been overestimated. Using finer-scale land units to parameterize our simulations would have alleviated this problem, but there are no data currently available to estimate species establishment coefficients at a finer spatial scale.

In summary, we found that both direct and indirect human influences over fire regimes have important effects on the abundance and connectivity of live fuel susceptible to crown fire in northern Wisconsin. We conclude that fire suppression decreases the risk of catastrophic fire over successional time scales (i.e., centuries) and at landscape scales, by encouraging sugar maple establishment that will eventually displace conifers capable of sustaining a crown fire. Harvest disturbance has a similar influence on the distribution of conifers, indicating that disturbance in general is important for retaining fire as a disturbance agent in the system. These results have important implications for both land managers who wish to alleviate fire risk, and for ecosystem restoration initiatives designed to restore fire prone ecosystems to the region.

Acknowledgments

Conversations with Greg Knight, Lenny Kempf, and Jeff Cardille helped us parameterize the surface fire regimes simulated in this study. Discussions with Mark Theisen helped us construct the harvest rules for the even and uneven-aged management prescriptions. Bob Cummings provided valuable programming and technical assistance. Hong He provided some of the initial input data from his previous research. Rob Scheller provided the species establishment coefficients based on his unpublished work. We also thank two anonymous reviewers for helpful reviews on earlier reviews of the manuscript. The National Fire Plan funded this research.

References

Aber J.D. and Melillo J.M. 1991. Terrestrial Ecosystems. Saunders College Publishing, Philadelphia, Pennsylvania, USA, 429 pp.

Almendinger J.C. and Hanson D.S. 1998. Ecological land classification handbook for the northern Minnesota Drift and Lake Plain and the Chippewa National Forest. Minnesota Department of Natural Resources.

Borman F.H. and Likens G.E. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist 67: 660–669.

Burns R.M. and Honkala B.H. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC, USA, 877 pp.

Canham C.D., and Loucks O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65: 803–809.

Cardille J.A. and Ventura S.J. 2001. Occurrence of Wildfire in the Northern Great Lakes Region: Effects of Land Cover and Land Ownership Assessed at Multiple Scales. International Journal of Wildland Fire 10: 145–154.

Cardille J.A., Ventura S.J., and Turner M.G. 2001. Environmental and Social Factors Influencing Wildfires in the Upper Midwest, United States. Ecological Applications 11: 111–127.

Cleland D.T., Crow T.R., Saunders S.C., Dickmann D.I., Maclean A.L. and Brosofske K.D. 2004. Characterizing historical and modern fire regimes in the Lakes States: A landscape ecosystem approach. Landscape Ecology 19: this issue.

Cleland D.T., Avers P.E., McNab W.H., Jensen M.E., Bailey R.G., King T., and Russell W.E. 1997. National Hierarchical Framework of Ecological Units. In: Boyce M.S. and Haney A. (eds), Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources. Yale University Press, New Haven, Connecticut, USA, pp. 181–200.

Cumming S.G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: What do fires burn? Ecological Applications 11: 97–110.

Curtis J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

Frelich L.E. and Reich P.B. 1995. Neighborhood effects, disturbance, and succession in forests of the western Great Lakes region. Ecoscience 2: 148–158.

Frelich L.E. and Reich P.B. 1999. Neighborhood effects, disturbance severity, and community stability in forests. Ecosystems 2: 151–166.

Frelich L.E. and Lorimer C.G. 1991. Natural Disturbance Regimes of the Upper Great Lakes Region. Ecological Monographs 61: 145–164.

Gustafson E.J., Shifley S.R., Mladenoff D.J., Nimerfro K.K., and He H.S. 2000. Spatial Simulation of Forest Succession and Timber Harvesting Using LANDIS. Canadian Journal of Forest Research 30: 32–43.

Gustafson E.J. 1998. Quantifying landscape spatial pattern: What is the state of the art? Ecosystems 1: 143–156.

Gustafson E. J., Zollner P.A., He H.S., Sturtevant B.R., and Mladenoff D. J. 2004. Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. Landscape Ecology 19: this issue.

Hansen M.H. 1992. The Eastwide forest inventory data base: user's manual. USDA Forest Service, General Technical Report NC-151.

He H.S. and Mladenoff D.J. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80: 81–99.

He H.S., Mladenoff D.J., and Boeder J. 1999a. An object-oriented forest landscape model and its representation of tree species. Ecological Modelling 119: 1–19.

He H.S., Mladenoff D.J., and Crow T.R. 1999b. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecological Modelling 114 : 213-233.

Heinselman M.L. 1954. The extent of natural conversion to other species in the Lake States aspen-birch type. Journal of Forestry 52: 737–738.

Heinselman M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3: 329–382.

Hessburg P.F., Smith B.G., and Salter R.B. 1999. Detecting change in forest spatial patterns from reference conditions. Ecological Applications 9: 1232–1252.

Holling C.S. and Meffe G.K. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10: 328–337

Host G.E., Polzer P.L., Mladenoff D.J., and Crow T.R. 1996. A quantitative approach to developing regional ecosystem classifications. Ecological Applications 6: 608–618.

Johnson E.A., Miyanishi K., Bridge S.R.J. 2001. Wildfire Regime in the boreal forest and the idea of suppression and fuel buildup. Conservation Biology 15: 1554–1557

Kafka V., Gauthier S., and Bergeron Y. 2001. Fire impacts and crowning in the boreal forest: Study of a large wildfire in western Quebec. International Journal of Wildland Fire 10: 119–127.

Keys J. Jr., Carpenter C., Hooks S., Koenig F., McNab W.H., Russell W., and Smith M.L. 1995. Ecological units of the eastern United States: first approximation. USDA Forest Service Southern Region, Atlanta, Georgia, USA, 83 pp.

Lillesand T., Chipman J., Nagel D., Reese H., Bobo M., and Goldman R. 1998. Upper Midwest Gap Analysis Program image processing protocol. U.S. Geological Survey, Onalanska, Wisconsin, USA.

Maclean Ann L. and Cleland David T. 2003. Determining the spatial extent of historical fires with geostatistics in northern lower Michigan. In: Fire, fuel treatments, and ecological restoration. Conference proceedings; 2002 April 16-18. Omi, Philip N.; Joyce, Linda A., tech. eds. Fort Collins, CO. Proc. RMRS-P-29. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA, pages 289–300.

McGarigal K., and Marks B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

McCune B. 1988. Ecological diversity in North American pines. American Journal of Botany 75: 353–368.

Miller C. and Urban D.L. 2000. Modeling the effects of fire management alternatives on Sierra Nevada mixed-conifer forests. Ecological Applications 10: 85–94.

Mladenoff D.J. and Baker W.L. (eds), 1999. Spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge, UK, pp. 125–162.

Mladenoff D.J. and He H.S. 1999. Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff D.J. and Baker W.L. (eds), Spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge, UK, pp. 125–162.

Mladenoff D.J. and Pastor J. 1993. Sustainable forest ecosystems in the northern hardwood and conifer forest region: concepts and management. In: Aplet G.H., Johnson N., Olson J.T., and Sample V.A. (eds), Defining sustainable forestry. Island Press, Washington D.C., USA, pp. 145–180.

Mladenoff D.J. and Stearns F. 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: A re-examination and model simulation. Conservation Biology 7: 889–900.

Mladenoff D.J., White M.A., Pastor J., and Crow T.R. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3: 294–306.

Moore M.M., Covington W.W., and Fulé P.Z. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications 9: 1266–1277.

Mutch R.W. 1995. Restoring forest health: Do we have the will to apply science findings? In: Proceedings on the conference Forest Health and Fire Danger in Inland Western Forests. American Forests, Washington D.C., USA, pp. 18–22.

Pastor J. and Post W.M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. Biogeochemistry 2: 3–27.

Pastor J. and Mladenoff D.J. 1992. The southern boreal – northern hardwood forest border. Pages 216-240 In: Shugart H.H., Leemans R., and Bonan G.B. (eds), A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, UK.

Radeloff V.C., Mladenoff D.J., He H.S., and Boyce M.S. 1999a. Forest landscape change in the northwestern Wisconsin Pine Barrens from pre-European settlement to the present. Canadian Journal of Forest Research 29: 1649–1659.

Radeloff V.C., Mladenoff D.J. Manies K.L., and Boyce M.S. 1999b. Analyzing forest landscape restoration potential: Presettlement and current distribution of oak in the northwest Wisconsin Pine Barrens. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86: 189–205.

Romme W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199–221.

Smith T. and Huston M. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83: 49–69.

Spies T.A., Ripple W.J. and Bradshaw G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4: 555–568

Stauffer D. 1985. Introduction to percolation theory. Taylor and Francis, London, UK.

Stearns F.W. 1997. History of the Lake States Forests: Natural and human impacts. In: Webster H.H., Vasievich J.M. (eds), Lake States Regional Forest Resources Assessment: Technical Papers. General Technical Report NC-189. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA, pp. 8–29.

Stephenson N.L. 1999. Reference conditions for giant sequoia forest restoration: Structure, process, and precision. Ecological Applications 9: 1253–1265.

Turner M.G., Gardner R.H., Dale V.H., and O'Neill R.V. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55: 121–129.

Wolter P.T., Mladenoff D.J., Host G.E., and Crow T.R. 1995. Improved forest classification in the northern lake states using multi-temporal Landsat imagery. Photogrammetric Engineering and Remote Sensing 61: 1129–1143.

U.S. Department of Agriculture. 1994. State Soil Geographic (STATSGO) data base: data use information. USDA Natural Resources Conservation Service, National Soil Survey Ctr. Misc. Pub. 1492. 74 p

Zar J.H. 1999. Biostatistical Analysis. Prentice-Hall Inc. Upper Saddle River, USA.