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Interactions among forest composition, structure, fuel loadings and fire history: A case study of red pine-dominated forests of Seney National Wildlife Refuge, Upper Michigan

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ABSTRACT

Red pine (*Pinus resinosa* Ait.) has been a historically important species in the eastern United States and Canada. Prior to European settlement, fire played a major role in determining the composition and structure of red pine-dominated forests. However, fire suppression efforts have prevented natural regeneration of red pine and the development of structurally diverse red pine-dominated forests across its natural range. To better understand how past forest history affects the current state of red pine-dominated forests in Upper Michigan, we quantified the role of forest history on forest structure and fuel loadings on eighty 500 m^2 plots distributed across Seney National Wildlife Refuge (SNWR). The Seney Wilderness Area of SNWR has experienced few direct human effects, and has escaped the impact of fire suppression policies. Using principal components analysis, we quantified the variation in stand composition, structure, and diversity and related this variability to current fuel loadings, fire history, and harvesting history. The first principal component represented the structural and compositional variation across our dataset associated with the harvesting history of the 50 sampled stands. Stands with a history of cutting clearly differentiated themselves by high abundance of jack pine (*Pinus banksiana* Lam.) and lower structural diversity of the overstory and of the understory vegetation. The second principal component revealed a negative correlation between red pine overstory abundance and compositional diversity of the stands, as determined by the Shannon Diversity Index. The third principal component differentiated complex, multi-cohort stands with old (250–300 years) trees in the overstory, which we believe resulted from repeated fires, from younger, less structurally complex stands. Stands which experienced repeated fires showed reduced amounts of fine woody debris and shallower duff depth. No relationship was found between descriptors of fire history and the amount of coarse woody debris (CWD) or litter. CWD increased in multi-cohort stands with high variations in tree diameter, whereas litter depth was higher in both jack pine-dominated, harvested stands and structurally diverse red pine stands and lower in the middle of this gradient. We suggest that fire has a role in restoration programs and sustainable management of red pine-dominated forest ecosystems of this region.

1. Introduction

Across the northern Lake States of the United States, fire-maintained mixed-pine forests dominated by eastern white pine (*Pinus strobus* L.), red pine (*P. resinosa* Ait.), and jack pine (*P. banksiana* Lam.) were common features of the pre-European settlement landscape (Whitney, 1987; Noss and Scott, 1997). Although the distribution of these three pine species was variable depending on a variety of factors including glacial landform, soils, and frequency of fire (Whitney, 1986; Zhang et al., 1999), natural

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mixed-pine forests, and specifically jack pine (Burns and Honkala, 1990), are typically associated with relatively poor sandy soils (Entisols) on glacial outwash landforms. Among these three species, jack pine is considered the most shade-intolerant and least nutrient demanding species. However, the regeneration of red and jack pine, and probably to a lesser extent eastern white pine, was promoted by frequent low intensity fires. These forests were important natural and cultural resources, providing habitat for many plant and animal species (Benkman, 1993; Corace and Lundrigan, 2006; Harrington, 2006), areas for hunting and berry gathering that supported the Native American communities (Loope, 1991), and the timber needed for late 19th-century industrial and urban development.

Over the past century, logging (Karamanski, 1989), catastrophic wildfires (Zhang et al., 1999), and subsequent fire suppression (Cleland et al., 2004) have changed these forests dramatically, leading to increases in the abundances of jack pine and of fire-sensitive hardwoods, including aspens (*Populus* spp. L.) and oaks (*Quercus* spp. L.). While a variety of factors (e.g., climate, topography, soils, and fire) regulated the distributions of these species on the pre-European settlement landscape (Whitney, 1986), stem densities in many areas are now higher compared with the pre-European conditions (Zhang et al., 1999). Another result of changes in the disturbance regimes has been significant accumulations of fuels, which under the right climatic conditions may pose a serious threat to local communities. For example, extensive loadings of fine woody debris have been reported for Upper Michigan, with values ranging from 1.25 to 3.26 tons/ha (Woodall et al., 2005).

Currently, policy makers and resource managers from several organizations are looking for strategies to reduce fire hazards in fire-maintained mixed-pine forest ecosystems (Crow and Perera, 2004). Specifically, many resource managers are examining a variety of options, including the restoration of fire to these ecosystems, or alternatively designing silvicultural systems that emulate the effects of fire on ecosystem patterns and processes (Attiwill, 1994; Franklin et al., 1997; Bergeron et al., 2001; Palik and Zasada, 2003). Active fire suppression efforts over the past 80 years, however, have made the use of fire as a fuel reduction and restoration tool potentially dangerous and possibly ineffective. Consequently, focusing on adaptive management activities designed to emulate natural disturbances will likely be the most effective methods of reducing these dangerous fuel loads and restoring the composition and structure of these once extensive and culturally important forest ecosystems.

To support the development of new management systems, we need a better understanding of how the compositions of canopy and of sapling strata are linked to stand-level fuel loadings. Since fire disturbance provides a major control over canopy dynamics in red pine-dominated forests (Bergeron et al., 1997; Flannigan and Bergeron, 1998), it is also important to further quantify the influence of past fire regimes on the current structure and fuel loadings. Such investigations into past disturbances and the biological legacies resulting from specific disturbances can provide much-needed information on the successional pathways and potential success of management systems intended to help restore ecosystem processes (Engelmark et al., 1994; Bergeron et al., 2001; Harvey et al., 2002).

In this study, we evaluated the current compositions, structures and fuel loadings of natural mixed-pine dominated forests of Seney Wildlife Nature Refuge (SNWR) in eastern Upper Michigan, USA and related these characteristics to their fire and harvesting histories. The overstory of these mixed-pine forest ecosystems at SNWR tend to be dominated more by red pine than jack pine or eastern white pine, thus we focused our efforts specifically on the following questions:

(1) What are the main patterns of the structural variation among stands where red pine is or was the major species in the overstory?
(2) How does the variation in the overstory and in the sapling compositions relate to the fuel loadings at the stand scale?
(3) How does past fire history of mixed-pine stands relate to both their current compositions and fuel loadings?

To answer the first question we used stand and fuel data from eighty 500 m^2 plots, sampled in naturally regenerated red pine-dominated stands from across the SNWR landscape. For the second and third questions, we used the results of this study with the results of an on-going dendrochronological study of fire history of the SNWR landscape, which provides a 300-year reconstruction of the forest fires in this area (Drobyshev et al., in press).

2. Methods

2.1. Study area

SNWR is located within the Seney Sand Lake Plain Sub-subsection of eastern Upper Michigan, where poorly drained landforms of lacustrine origin (e.g., sand ridges) prevail (Albert, 1995; Fig. 1). The terrain is characterized by glacial outwash channels and a matrix of patterned fens interspersed with sand ridges (Silbernagel et al., 1997). This matrix was formed by the deposition of Valders glacial outwash, subsequent inundation by earlier stages of the Great Lakes, and drainage of the area during post-Algonquin period, i.e., 10 000 years BP (Heinselman, 1965).

The landscape of SNWR is currently dominated by both upland forest and wetland vegetation (Comer et al., 1995). Upland areas are dominated by several diverse mixed-forest types with varying proportions of deciduous species (e.g., American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britton), as well as several coniferous species (e.g., red pine, eastern white pine, jack pine, black spruce (*Picea mariana* (Mill.) B.S.P.), and balsam fir (*Abies balsamea* (L.) Mill.). The wetland vegetation is typically a sedge (*Carex* spp.) and shrub (*Salix* spp. and *Betula pumilla* L.) matrix. Both vegetation cover types were central elements of pre-European landscape (Zhang et al., 2000). Particularly, many areas of the SNWR were historically dominated by mixed red pine and eastern white pine forests (Vogl, 1970; Whitney, 1986). The current distribution of forest ecosystems across the landscape of SNWR is a product of the interactions among geological history, the natural fire regime, and human land-use practices, including logging and human-mediated fires (Tansy, 2003).

The climate of this ecoregion is continental, but also strongly influenced by both Lake Superior and Lake Michigan. The long-term (1971–2000) average annual temperature is 6.2 °C (MRCC, 2007), with considerable variation between the coldest (January, long-term average minimum temperature, −13.6 °C) and the warmest (July, long-term average maximum temperature, 26.7 °C) months. Total annual precipitation is 781 cm, with precipitation in the form of snow dominating over rain precipitation (248.7 cm snowfall on average). Precipitation tends to peak in July (93.7 mm) and be lowest in February (30.2 mm). The length of the growing season averages 119 days with evaporation of 64 cm. Average humidity, spring through fall, varies from 50 to 60% (Tansy, 2003).

2.2. Field data collection

Field sampling was designed to evaluate stands located on the two major landform types typical of the Seney Lake Plain Sub-subsection: (1) sand ridges interspersed within patterned fens and

(2) glacial outwash channels. The majority of the former type was located within the federally designated Seney Wilderness Area, a portion of SNWR where small remnant old-growth red pine forest ecosystems remain and where wildfires have been permitted to occur. This area is believed to be one of the best remaining tracts of old-growth red pine forest ecosystems in the region as the extensive, dense shrub matrix surrounding the sand ridges has possibly precluded extensive attempts at timber harvesting. The terrain of the other portions of the SNWR landscape did not constrain forest use to the same degree as in the wilderness area, and records of timber harvesting exist for this part of SNWR since 1935.

We sampled 50 red-pine stands across SNWR (Fig. 1). In identifying stand locations we stratified our sample to capture the variation in canopy composition, age structure, landform type and stand harvesting history. However, since fire history data was not available at the time of field sampling, only preliminary judgments could be made concerning fire history. Within these 50 stands, we randomly established a total of eighty 500 m^2 plots (50 m $\times$ 10 m), with one to three plots per stand depending on the variation in the stand structure and stand size. In instances where multiple plots were located within a stand, they were located 100–200 m from each other. Plot dimensions were chosen to fit the shape and size of stands on sand ridges, which were relatively narrow (20–40 m) and oblong.

On each plot, all overstory trees (>10.0 cm dbh) were mapped, and their dbh (diameter at 1.37 m above the ground), species, crown class (dominant, codominant, intermediate, or overtopped; *sensu* Barnes et al., 1998) and condition (dead or alive) were recorded. Also within each plot, the diameter, species, and condition (dead or alive) of saplings (2.5–10.0 cm dbh) were recorded on the central 30 m $\times$ 10 m portion of the plot. To describe the age structure of the stand, we cored up to 12 trees in each stand, with coring distributed among the observed cohorts and species. Increment coring was done at the height of 20–40 cm above the ground to more accurately determine tree ages (Lorimer, 1985).

Fuel loadings were assessed using standard protocols adopted by the Forest Inventory and Analysis (FIA) Program of the USDA Forest Service (Woodall and Williams, 2005). Estimates of coarse woody debris (CWD), fine woody debris (FWD), and fuel conditions (duff and litter) were recorded for each plot, and standard calculation routines were used to obtain total volumes of both CWD and FWD, and average fuel bed depth (sum of duff and litter depths).

To reconstruct the fire history of each stand, we searched for fire-scarred live trees, stumps, and deadwood, and used the method of wedge sampling to extract parts of the tree boles that contained scars (Swetnam, 1993). Trees representing the oldest cohorts within the stand were typically sampled to recover scars, including those not visible from outside of the trees (*overhealed* scars). Within each stand, we limited our maximum search time for potential samples to 2.5 h. In the majority of cases (97%), the samples were collected from red pine, while the remaining 3% were collected from eastern white pine and jack pine. In the field, we recorded dbh, species, type of sample (living tree, stump, or deadwood), and height at which wedge was taken. Further details about fire history sampling protocol are available elsewhere (Drobyshev et al., in press).

2.3. Reconstruction of the fire history

Fire-scarred wedge and cross-section samples were mounted on wood plates and progressively polished with up to 400-grit sand paper to allow clear recognition of annual rings and fire scars under a binocular microscope (using up to 40$\times$ magnification). We used a visual cross-dating method (Stokes and Smiley, 1968) to precisely date both fire scars and the youngest and the oldest annual rings on all samples collected. To aid in fire dating, we developed 300-year-long pointer-year chronology for red pine and used dates of major fires in the area as additional pointers.

In this paper, we utilize the available 300-year reconstruction of the fire history of SNWR (Drobyshev et al., in press) and relate this information to current stand composition, structure, and fuel loadings. Specifically, for each stand we determined these three fire history descriptors: (a) time since last fire (TLF), (b) number of fires over the last 50 years (NF50), and (c) number of fires recorded over the last 142-year period 1864–2006 (NF142). The last 50-year time frame was selected to represent the most recent fire history of SNWR; this period coincides with the approximate date when fire suppression policies were instituted. Although our fire history record extends for over 300 years, we selected the year 1864 as the beginning of our analysis because (1) all stands had samples dating back to 1864 which facilitated among-stand comparisons and (2) 1864 was a large fire year in the study area and many of the old red pine cohorts date back to this event. Since most of the fires reconstructed at SNWR were not stand-replacing fires (Drobyshev et al., in press), succession in many stands proceeded over a longer time period than the time since the last fire, indicating that a cumulative impact of repeated fires on the stand, together with time since the last fire, were likely important determinants of forest composition, structure, and fuel loadings. Harvest histories of the stands were reconstructed by sampling and dendrochronologically dating cut stumps and analyzing pattern of growth releases.

2.4. Statistical methods

Prior to analyses, we summarized a variety of stand composition and structure information. In terms of age for various cohorts, we used plot averages based upon tree-ring estimates obtained by visually separating different cohorts in the field and coring of 10–12 trees per plot. Importance values of each species were also calculated (sum of relative density and relative dominance as expressed by relative basal area divided by 2 and multiplied by 100). To characterize the presence of the coniferous and deciduous components in sapling stratum, we used only relative abundance of coniferous saplings to avoid redundancy in the data. To characterize species diversity, we used the Shannon Diversity Index (Magurran, 1988) which is expressed as:

$$H = \sum_{1}^{n} (p_i \ln(p_i))$$

where p_i is the relative importance of the ith species. Relative importance was calculated as the average of relative density and relative basal area. Relative basal area (also known as "relative dominance", *sensu* Curtis, 1959) was the proportion of the basal area of a species as compared to the total basal area in a plot. Finally, we summarized the within-plot variability of composition and structure of the overstory and sapling strata by calculating the coefficient of variation (ratio of the standard deviation and sample mean) of respective diameters. We also examined basic relationships among variables using Spearman correlation analyses.

We used Principal Components Analysis (PCA) to summarize the variation in both the overstory and sapling strata and to reduce the dimensionality of the dataset using the statistical software package Statistica (StatSoft, 2001). Prior to the PCA, all variables were normalized with their mean and standard deviation (S.D.) values, and the PCA was conducted using correlation matrices. The PCA utilized the plot values for the following structural variables: age of the dominant overstory cohort (AGEA), age of the youngest (AGEY) and the oldest (AGEO) cohorts, coefficient of variation of the overstory diameters (CVO), coefficient of variation of the sapling diameters (CVS), Shannon Diversity Index values for the overstory (SHAO) and the sapling strata (SHAS), sum of relative importance values for coniferous saplings (CORI), importance values of overstory red pine (ROVRP) and saplings (RSARP), and importance values of overstory jack pine (ROVJP). We interpreted all axes with eigenvalues > 1 to be significant following the Kaiser–Guttman criterion (McCune and Grace, 2002).

In order to examine the relationships among stand composition, structure, and diversity with fuel loadings, we used multiple non-linear regression to determine the association between the first three principal components (PCs) and variables representing the plot fuel loading, including volume of CWD, volume of FWD, and average depths of the duff, the litter, and the fuel bed. The rationale for this analysis was to identify which of the modes of variation in stand structure and composition are related to the stand fuels. We did not use PCA analysis to reduce number of fuel variables. We operated with only three fuel variables (CWD, FWD, and litter and duff layer thickness) which described essentially different components of stand fuel loadings. These fuel loadings were contrasted with each of the PCs in one-way ANOVA to identify which of the modes of variation (as expressed by the first three PCs) in stand structure and composition was related to fuel loadings on each plot. For this purpose we utilized the program PopTools (Hood, 2006). Because we did not reconstruct fire history for each sample plot, the number of degrees of freedom in the ANOVA was limited to the number of stands where we did determine the fire history ($n = 50$). To incorporate the full range of observed variability and to randomize the data prior to analyses, ANOVA was run on fully balanced datasets with the $n = 50$ (or $n = 51$, in case of three factor levels) produced by randomly re-sampling with replacement from the 50 stands in the software package PopTools (Hood, 2006). Each ANOVA was run 1000 times with bootstrapped means and S.D.s used to calculate the F and p values. This was a conservative approach for revealing differences among contrasts, acting towards decreasing Type I error and increasing Type II error. Due to the high variability observed in the data, we used a significance level of $\alpha = 0.1$ during interpretation of the results. Although many of the relationships were non-significant, we chose to present them all for the sake of consistency in the reporting of the results. Prior to the ANOVA analyses, TLF was divided into two groups: <40 years and >40 years. Actual mean values (±1S.D.) for the two groups were 25.4 ± 8.80 ($n = 28$) and 78.5 ± 8.80 ($n = 22$), respectively. Number of fires over the last 50 years (NF50) was coded as follows: no fires recorded ($n = 34$), one fire recorded ($n = 28$), and two and more fires recorded ($n = 18$). Number of fires over the last 142 years (NF142) was coded as follows: low fire frequency (up to 4 fires over this period, $n = 30$), moderate fire frequency (5–7 fires, $n = 28$) and high fire frequency (8–15 fires, $n = 22$). This corresponded to fire return intervals of 47–71 years, 20–28 years, and 10–18 years, respectively, for these three groups.

We also used one-way ANOVA to examine the relationships among the history of past harvesting and plot structural and fuel variables. We first ran this analysis by simply examining two groups of stands (a) with no signs of past harvest and (b) with signs of past harvest being present ($n = 40$). In a separate analysis, we examined these relationships further by using three contrasts including: no history of past harvest ($n = 37$), history of harvest and fire ($n = 30$), and harvest history only, with no fire recorded since the date of last cutting ($n = 13$). No contrasts were defined to differentiate between low-intensity surface fires and high-intensity stand-replacing fires. First, information on the latter was incorporated in the PCA through considering the age of the most abundant overstory cohort as one of the input variables. Second, another study (Drobyshev et al., in press) pointed to the dominance of intermediate and mostly non-stand replacing fires. Post-fire inventory of the most recent large fire of 1976 (Anderson, 1982) showed only partial removal of the overstory in most of the affected stands, which substantiates our observation.

3. Results

3.1. Overall stand composition, structure, diversity and fuel loadings

There was considerable variation among SNWR stands in terms of stand composition, structure and diversity (Table 1). The youngest cohorts were found in recently cut stands on glacial outwash channels, whereas the oldest cohorts were found on the sand ridges in the Seney Wilderness Area (Fig. 1). One plot had a single overstory tree, which resulted in the coefficient of variation (CV) of the overstory dbh distribution of zero. No saplings were present in several stands, which led to a CV of zero for sapling dbh. Of the 80 plots sampled, in only 29% was the sapling stratum composed exclusively of coniferous species.

Species diversity (as reflected by the Shannon Diversity Index) was directly related to the abundance of deciduous species; both in the overstory and understory strata the Spearman Correlation Coefficients between Shannon index and total relative importance of deciduous species were highly significant ($r = 0.76$, $p < 0.001$, and $r = 0.55$, $p < 0.001$, respectively). Overall, red pine saplings were not common, as we recorded red pine saplings in only 24% of the plots sampled. The majority of the plot overstories, however, were dominated by red pine; relative dominance of red pine exceeded 50% in 68% of the plots. Density of jack pine in the plots was generally low; in 54% of plots no jack pine was present in the overstory.

As with the stand composition and structure variables, fuel variables varied considerably across the plots, with the combined average CWD loading and average FWD loading being relatively

Table 1
Stand composition, structure, diversity, fuel variables and fire history descriptors used in the PCA (with the exception of LERI—relative importance of deciduous saplings)

Variable	Mean	S.D.	Mode/mode frequency	Minimum	Maximum
Structural variables					
AGEA	67	22.6	60/8	27	130
AGEY	55	18.1	55/6	23	112
AGEO	129	78.8	67/3	27	356
CVO	0.411	0.129	0.326/3	0	0.733
CVS	0.299	0.172	0/14	0	0.761
SHAO	0.508	0.419	0.001/16	0.001	1.473
SHAS	0.461	0.447	0.009/22	0.009	1.476
CORI	65.61	38.00	100/23	0	100
LERI	34.39	38.00	0/23	0	100
RSARP	5.35	17.08	0/61	0	100
ROVRP	67.60	33.17	100/13	0	100
ROVJP	17.63	31.82	0/43	0	100
Fuel variables					
CWD (m^3/ha)	28.39	38.68	0/13	0	165.73
FWD (m^3/ha)	17.48	100.23	Multiple	0	900.44
DUFF (cm)	1.49	0.70	Multiple	0.13	3.73
LITTER (cm)	2.44	1.88	1.88/3	0.74	1.03
Fire history descriptors					
NF 142	6.0	2.95	4/13	2	15
NF 50	0.8	0.90	0/21	0	4
TLF	48.1	29.6	30/30	2	88

See text for variable abbreviations.

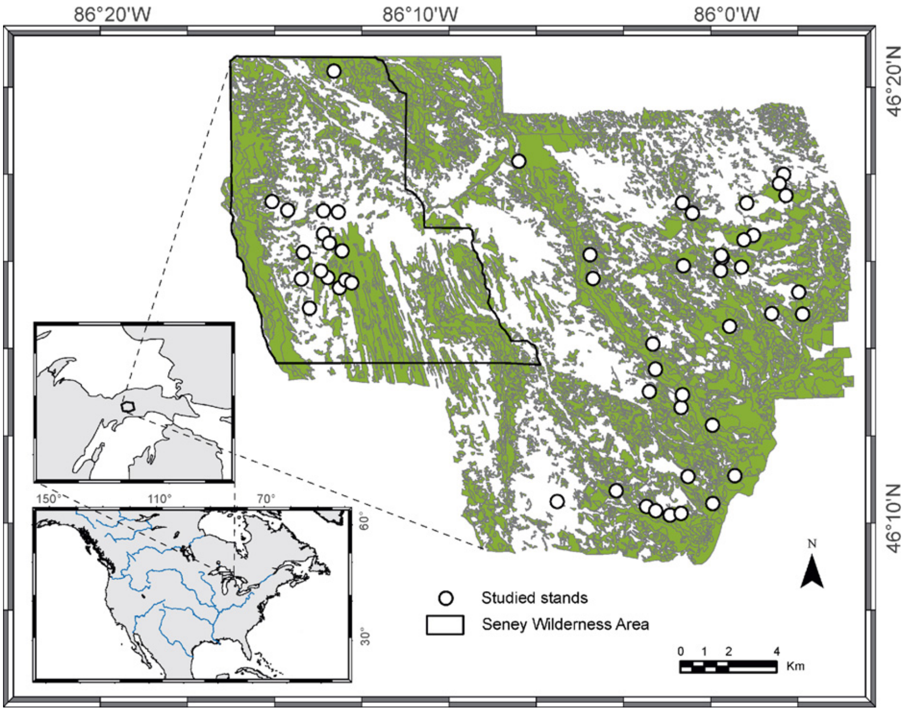

Fig. 1. Stand locations in the Seney National Wildlife Refuge, Upper Michigan. White areas on the refuge maps indicate treeless marshland areas and darker areas indicate forest vegetation.

moderate (46 m^3/ha). No CWD was recorded on 13 plots, encompassing different histories and structural properties. Three of these plots were old-growth mixed-pine stands on sand ridges located in the Seney Wilderness Area, and the remaining 10 were found on outwash channels, including pure jack pine stands (1 plot), pure red pine stands (1 plot), and mixed stands (8 plots). Average time since fire in these stands was 57.5 years with the range of 12–88 years. The three highest values of CWD (165.7–126.5 m^3/ha) were recorded in sand ridge stands that have likely experienced thinning-related mortality (one plot, 165.7 m^3/ha), beaver-caused disturbance (one plot, 137.5 m^3/ha) and windfall mortality (one plot, 126.5 m^3/ha). In these plots TLF were 43, 30, and 9 years, respectively. No pattern in minimum and maximum values of CWD was visible with respect to the cumulative number of fires.

Two plots with no FWD recorded were plots on sand ridges and outwash channels and both experienced a recent fire (TLF = 2 and 12 years, respectively). Three plots with the highest FWD volume were pure red or jack pine stands ((17.0 and 15.7 m^3/ha, respectively), and one mixed-pine stand (17.3 m^3/ha). All were located in glacial outwash channels and had times since last fire varying from 30 to 87 years. In the three plots where we observed the maximum amount of FWD, we found only one fire over the last 50 years, whereas each plot with no FWD had at least two fires recorded over the same period.

3.2. Principal components analysis

In total, the first four axes of the PCA explained 71.3% of the variation in stand composition, structure and diversity (Fig. 2). In the PCA, PC 1 extracted 28.5% of the variation in the dataset, PC 2 – 19.2%, and PC 3 – 15.7% (Fig. 2), and only these three PCs had eigenvalues greater than 1. While the first PC revealed a gradient from stands with high overstory dominance of jack pine to the older stands dominated by red pine overstories, the second PC captured structural stand variation associated with the gradient from red pine dominated stands to those stands with a structurally more diverse sapling stratum and more species-rich overstory and sapling strata (Fig. 2; Table 2). Finally, the third PC represented a gradient from structurally complex stands (in respect to both sapling and overstory strata) with higher variation in the age of tree cohorts (higher age of the oldest cohorts and lower of the youngest cohorts) towards structurally simple stands with more homogenous age structure and higher relative importance of red pine saplings.

3.3. Stand structural variation and fuel loadings

We found little correlation between stand structural characteristics and fuel loading variables (Fig. 3). CWD loadings were most strongly correlated to the third PC, suggesting that CWD loadings were highest with the most structurally complex stands. FWD loading showed little correlation to any of the PCs in the PCA (Fig. 3). Litter and duff depths showed a moderate (R^2 = 0.09 and 0.07, respectively) parabolic fit to PC 1 while duff depth showed a moderate decrease with increasing PC 1 axis and PC 3 axis scores (Fig. 3).

3.4. Fire histories of the stands

Historically, fires were frequent at SWNR as 80% of all stands experienced between four and eight fires over the last 142 years (1864–2006), with the maximum number of fires reaching 16 in one sand ridge red pine-dominated stand (Fig. 4). The mode of fire occurrence for the variable NF 142 was 5 fires, corresponding to the average fire return interval of 28.4 years. Distribution of TLF revealed two main fire events over the studied period: the Seney fire of 1976 and a fire in 1864. Together, these two fires were the last fires for 68% of all stands studied. NF 142 and TLF were negatively correlated (Spearman $r = -0.33$, $p = 0.019$), indicating that stands with more recent fires tend to have more frequent fires and, therefore, shorter fire return intervals.

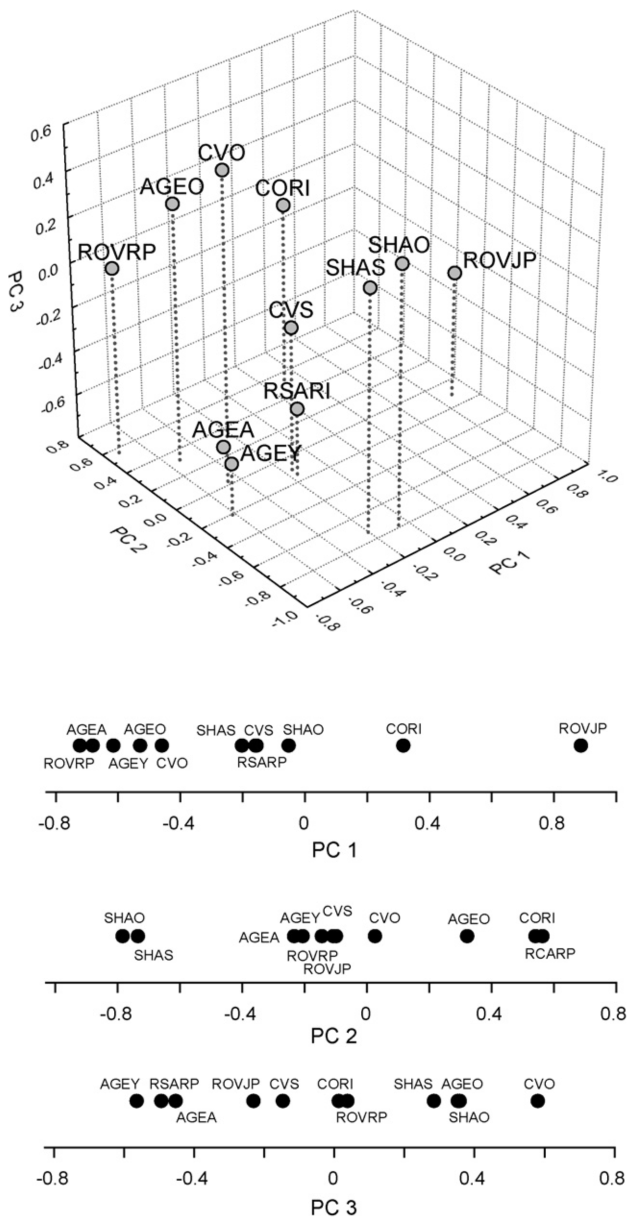

Fig. 2. First three principal components of variation in structure and composition of studied stands at Seney National Wildlife Refuge. To facilitate comparisons between axes, the factor loadings are also plotted along principal components. Numerical results are presented in Table 2. Factors' codes are as follows: age of the dominant overstory cohort (AGEA), age of the youngest (AGEY) and the oldest (AGEO) cohorts, coefficient of variation of the overstory diameters (CVO), coefficient of variation of the sapling diameters (CVS), Shannon Diversity Index values for the overstory (SHAO) and the sapling strata (SHAS), sum of relative importance values for coniferous saplings (CORI), importance values of overstory red pine (ROVRP) and saplings (RSARP), and importance value of overstory jack pine (ROVJP).

3.5. *Stand structural variation and fire history*

There were no significant correlations between the PCs summarizing the variation in stand composition, structure and diversity and fire history (p-values < 0.1, Table 3). NF50 was most strongly correlated with PC 3 (average p-value in ANOVA = 0.11), indicating that more frequent fire is associated with stands that have higher structural diversity of the overstory and understory strata, older trees in the oldest tree cohorts, but younger trees in the most abundant overstory and in the youngest cohorts (Fig. 2 and Table 2). NF142 was most highly correlated with PC 2 ($p = 0.13$), revealing a positive association between long-term frequency of fire occurrence and relative density of overstory red pine. TLF was most correlated with PC 3 ($p = 0.14$), suggesting that higher structural variation (as expressed through CV of dbh) in the stands with the most recent fires (Table 2). Harvest history showed highly significant correlation with PC 1 ($p \leq 0.001$) in both versions of the ANOVAs, reflecting an increase in the overstory importance of jack pine from fire-only to harvest-only stands (Tables 2 and 4).

Table 2
Factor-variable correlations from the PCA of stand composition and structure

Variable	PC 1	PC 2	PC 3
AGEA	**−0.671**	−0.056	**−0.507**
AGEY	**−0.589**	0.027	**−0.622**
AGEO	−0.543	0.203	0.421
CVO	−0.485	−0.124	**0.513**
CVS	−0.189	**−0.490**	**0.527**
SHAO	−0.097	**−0.822**	0.015
SHAS	−0.258	**−0.819**	0.062
CORI	0.315	**0.383**	0.402
RSARP	−0.130	−0.013	−0.364
ROVRP	**−0.703**	**0.550**	0.206
ROVJP	**0.890**	−0.101	−0.159

Largest absolute loadings on each axis are indicated by bold font. See text and caption for Fig. 2 for the explanation of the codes.

3.6. *Fire history and fuel loadings*

Of the three descriptors of fire history, NF50 showed the highest correlation with the fuel loading variables (Table 5). NF50 was negatively related to the amount of FWD ($p = 0.11$) and duff depth ($p = 0.01$). FWD and duff depth tend to increase with longer fire-free intervals ($p = 0.13$ and $p = 0.14$, respectively), and no associations with stand fuel loadings were found for NF142.

4. Discussion

4.1. *Stand structure and fuel loadings*

Our results suggest that at SNWR stand structural and compositional variation is associated with past harvesting activity (PC1), with successional trajectories (PC2 and PC3), and with history of fire disturbance (PC3). Even given the uncertainty associated with detecting low-intensity harvest events, stands with a history of harvesting clearly differentiated themselves in the PCA by possessing high importance values for jack pine overstory and for saplings, and lower levels of diversity of the overstory and of the understory vegetation. In the studied region, the most intensive timber harvesting took place at the end of 19th century, following the regional trend of expanding timber harvesting operations in Lake States at that time (Ahlgren and Ahlgren, 1983; Karamanski, 1989). The legacies of these activities at SNWR are stands dominated by jack pine, primarily on glacial outwash channels. A similar transition from mixed-pine to jack pine-dominated stands was also observed at other locations subject to intensive harvesting in Upper Michigan (Loope, 1991). In our study, the PCA suggests that overstory importance of jack pine was negatively associated with both stand age and overstory abundance of red pine, confirming the observation that red pine did not commonly regenerate on clearcut areas. Additionally, the first PC generally showed little association with fuel loadings, suggesting that the amount of fuel did not vary in a consistent pattern along a gradient from jack pine-dominated stands to mixed-pine and older stands. An exception to this pattern was litter depth, which was deeper in jack pine- and red pine-dominated stands and shallower in mixed-pine stands.

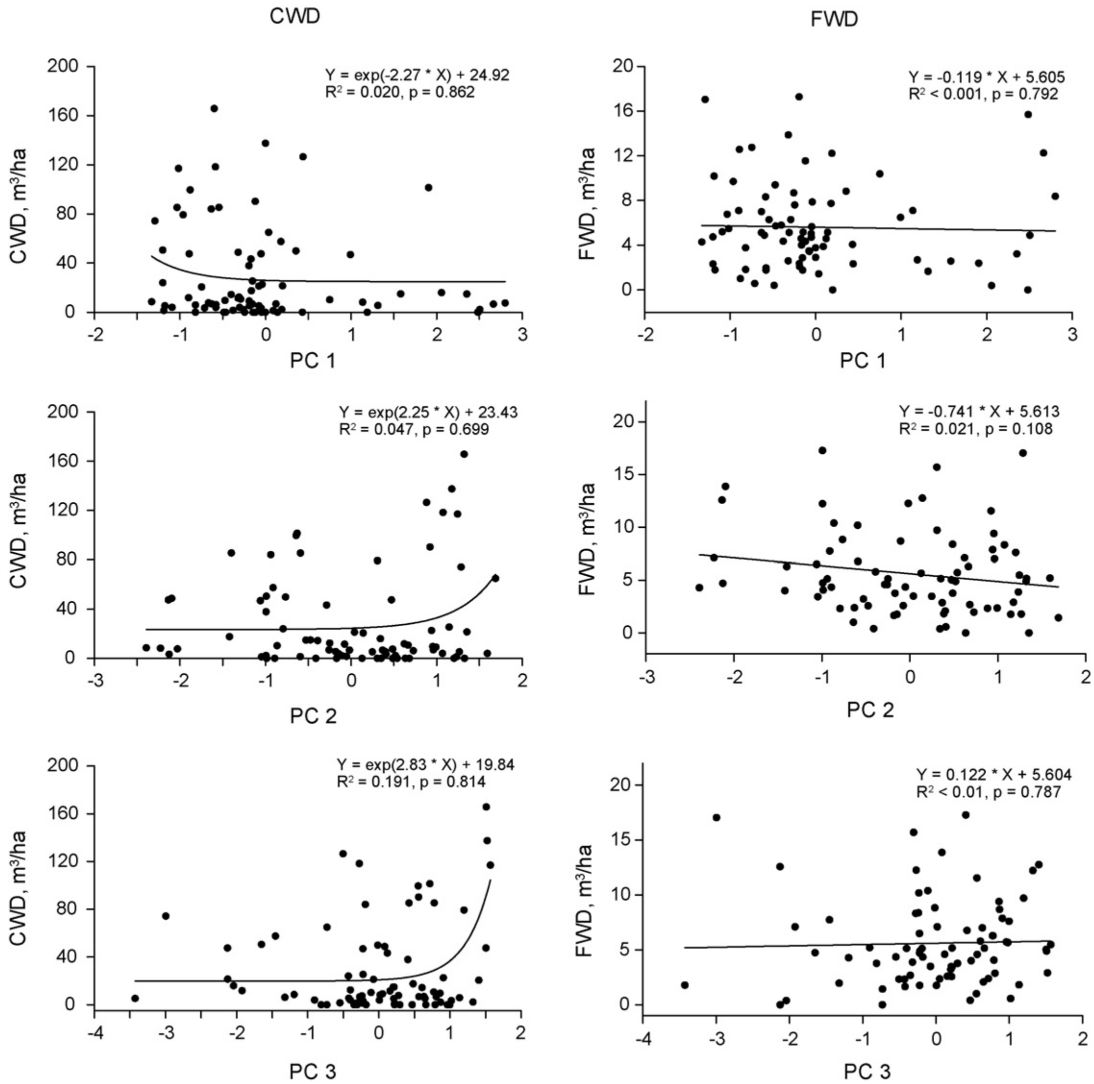

Fig. 3. Relationships between principal components of stand structural variation and fuel variables (CWD, FWD, litter, and duff depths).

In terms of species diversity, our study revealed several interesting patterns. The second PC revealed a negative correlation between overstory abundance of red pine and compositional diversity of the stands. Specifically, the diversity index values of our stands are regulated by the abundance of deciduous species, and this pattern is associated with a gradient from fire-adapted red pine-dominated communities to the stands with increasingly high proportions of fire-sensitive and shade-tolerant species. The transition from fire-adapted mixed-pine forests to hardwood-dominated communities has been commonly observed since the onset of fire-suppression policies in the region (Zhang et al., 2000) and over a large portion of northeastern hemi-boreal forest in North America (Drever et al., 2006). While we found no association between the second PC and the fuel loadings of these stands, this suggests a low predictive power of measures of structural and species diversity with respect to fuel loadings for these mixed-pine stands of SNWR.

Variation in tree diameters within the studied stands tended to increase with higher variation in tree cohort ages, and decrease in stands with abundant red pine saplings, as indicated by the factor loadings on the third PC. This pattern suggests that structurally diverse stands do not maintain red pine regeneration. Stands with high loadings on the third PC were typically multi-cohort stands, whereas low loadings on this PC were associated with mature, single-cohort communities. We propose that multi-cohort stands might result from successful regeneration of red pine after repeated non-stand-replacing disturbances. In comparison with structurally simple stands, such multi-cohort stands had higher amounts of (CWD), as indicated by an exponential increase in the CWD that coincided with highest values of PC3 loadings. To exemplify this pattern, we examined the properties of the three stands with maximum PC3 loadings. These were stands comprised of older individual trees (250–325 years old) and with dominant cohorts containing abundant young red pine stems (60–100 years old), suggesting that high CWD loadings might be a result of allogenic causes (e.g., natural density-dependent mortality).

4.2. Impact of fire history on stand structure and fuel loadings

History of past fire was related to two PCs of stand structural variation, highlighting the importance of fire in these mixed-pine ecosystems. Higher fire frequency tended to be associated with higher variation in tree diameters, suggesting that historic fire is important in maintaining multi-cohort stands. This observation agrees with the finding that most of the fires at SNWR were not

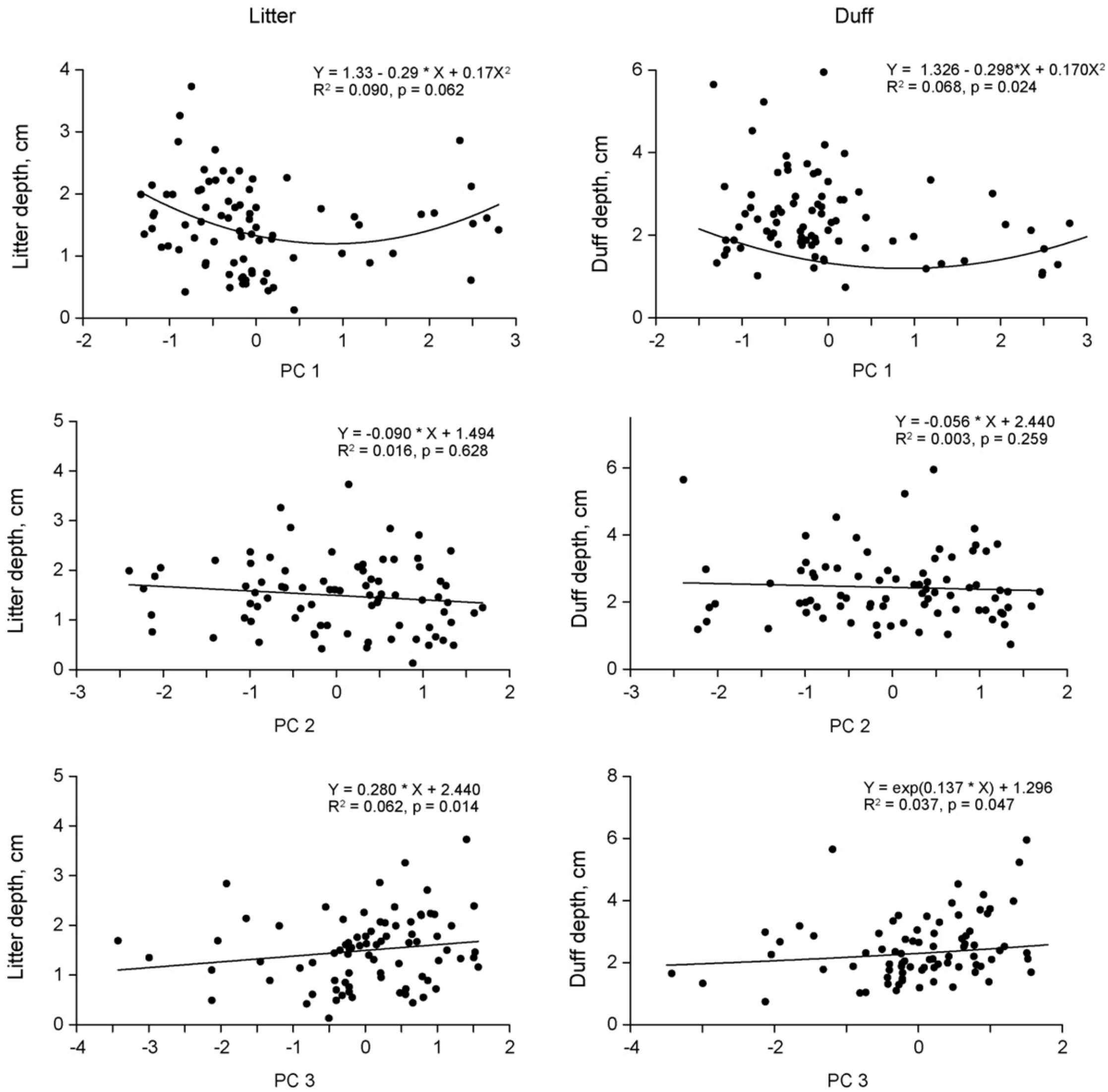

Fig. 3. (*Continued*).

stand-replacing (Drobyshev et al., in press), as well as other studies of red pine-dominated forest ecosystems (Engstrom and Mann, 1991; Cleland et al., 2004). Red pine is also reported to be more abundant on xeric sites across most of its range (Horton and Bedell, 1960), likely reflecting the lower fuel loadings on these sites which are not typically conducive of intense stand-replacing fires. In line with these findings, the abundance of red pine was higher on sites with more frequent fires, as exemplified by association between PC3 and NF142 (number of fires over the last 142 years).

Descriptors of fire history proved informative in relating the PCs to stand fuel loadings. Considered within the 50-year time frame, more frequent fires reduced fine woody debris and litter loadings. Surprisingly, no relationship was found between time since last fire and fuel loadings. High initial variability in pre-fire conditions and the generally moderate intensity of past fire events, preserving the legacy of pre-fire stand conditions, may explain these results. Although two different analytical designs were used to assess the impact of stand composition and stand history on fuel loadings, it appears that stand history may prove more informative than structural variables in explaining current fuel loadings.

4.3. Management implications for restoration of red pine forests

Our study shows that harvest history is the major determinant of stand structural variation across this landscape previously dominated by mixed-pine forests. Given the generally limited time of jack pine dominance under natural conditions (<100 years) and the presence of red pine regeneration, the long-term effects of this trend on forest cover appear limited. However, some forestry practices may cause an increase in the proportion of the jack pine at the expense of other pine species, resulting in dramatic changes in forest composition and structure across the landscape. Although in this study we do not explore the effects of different harvesting types on stand structure, our data may suggest that the clearcut stands exhibit the highest levels of departure from stands where some stand structure was retained following harvest. The reason for this is apparently the difference in regeneration conditions compared with those observed in natural mixed-pine stands. Regeneration of red pine, for example, is dependent on the presence of mineral soil (Ahlgren, 1976), and proximity to seed sources or presence of advanced regeneration (Van Wagner, 1971; Rudolf, 1990). The size of clearcuts was also shown to be an important determinant of successful red pine regeneration

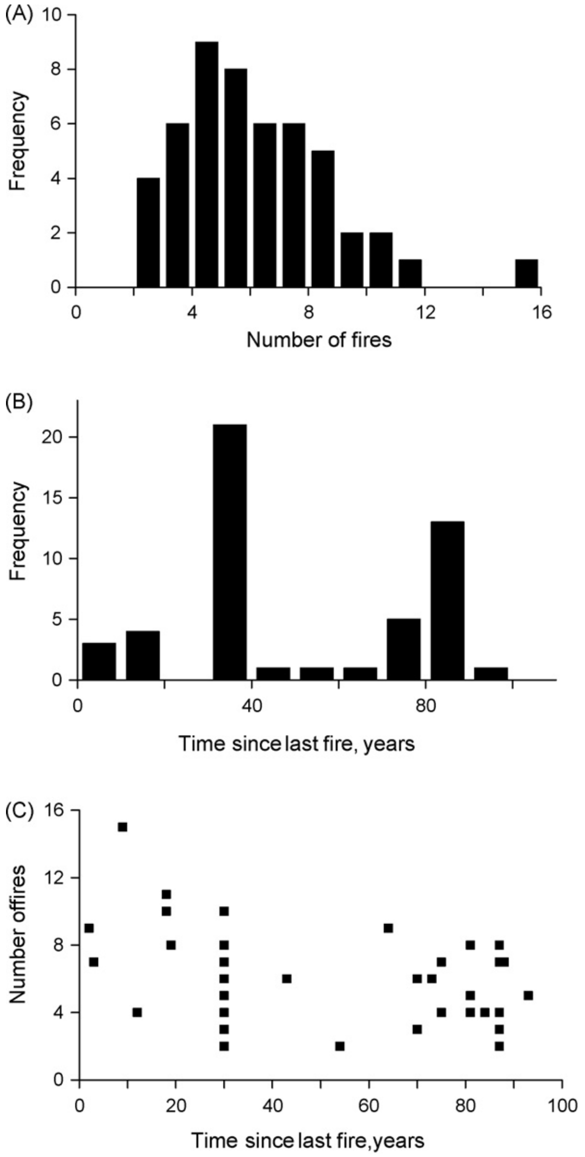

Fig. 4. Fire history descriptors for the studied stands: (A) Absolute frequency of the cumulative number of fires per site during the period 1864–2006, (B) Frequency of time-since-fire for studied stands, divided into 10-year intervals, (C) Relationship between cumulative number of fires per stand and time-since-fire during the period 1864–2006.

(Ahlgren, 1976). Apparently, regeneration conditions on formerly clearcut areas at SNWR were more favorable for jack pine, which might have benefited from fast early growth on relatively infertile sites (King, 1968).

Despite the dominant role of harvesting history in influencing the structural variation across SNWR, fuel loadings in mixed-pine stands are more closely related to the cumulative impact of past fires rather than to the stand composition and structure following harvesting. Specifically, FWD and duff depth were related to past fire frequency over decadal and centurial timescales. In contrast, CWD abundance increases in structurally complex, multi-cohort stands while both FWD and duff depth decrease. This highlights the importance of low-intensity fires in lowering the abundance of the most flammable fuels, resulting in more complex stand structures.

The moderate intensity of past fire events is a characteristic feature of SNWR mixed-pine forests (Drobyshev et al., in press), and our study further supports this observation by showing a positive association between fire frequency and importance of overstory red pine. Repeated fires create structurally complex and multi-cohort stands, with lower fine fuel loadings and shallower duff depths, but with higher amounts of CWD. Separate management actions may be required to address accumulation of different fuel types in mixed-pine forests. For example, mechanical removal of large fuels in conjunction with fire-mediated reduction of fine fuels may prove to be helpful.

In the context of restoration of mixed-pine forest ecosystems, our results suggest that higher species diversity of overstory and understory vegetation would be viewed as an undesirable trend in the successional development of the stands since it would reflect a decrease in the abundance of overstory red pine and an increase in non-fire adapted hardwood species such as red maple. Instead,

Table 3
Relationships between PCs and descriptors of fire history

Variables	d.f.	F[a]	p	Means of contrasts		
				I	II	III
Predictor: number of fires over the last 50 years (NF 50)						
PC 1	50	1.352 ± 1.496	0.462 ± 0.297	−0.018	−0.083	0.164
PC 2	50	3.325 ± 2.531	0.177 ± 0.228	−0.311	0.158	0.343
PC 3	50	4.385 ± 3.293	0.109 ± 0.158	0.252	0.001	−0.478
Predictor: number of fires over the last 142 years (NF 142)						
PC 1	50	3.224 ± 2.481	0.187 ± 0.224	0.319	−0.074	−0.341
PC 2	50	4.260 ± 3.289	0.127 ± 0.189	−0.405	0.335	0.126
PC 3	50	1.825 ± 1.670	0.330 ± 0.273	−0.214	0.237	−0.015

Variables	d.f.	F[a]	p	Means of contrasts	
				I	II
Predictor: time since last fire (TLF)					
PC 1	49	1.072 ± 1.548	0.486 ± 0.288	0.027	−0.035
PC 2	49	4.500 ± 4.572	0.190 ± 0.244	0.206	−0.265
PC 3	49	5.170 ± 4.311	0.137 ± 0.201	0.235	−0.303

For NF 50, means of contrasts were no fires (I), one fire (II), and two and more fires (III). For NF 142, means of contrasts were up to 4 fires (I), 5–7 fires (II), and 8–15 fires (III). For TLS, means of contrasts were time since last fire was less (I) or more (II) than 40 years.
[a] Results of one-way ANOVA, bootstrapped 1000 times. F- and p-values are means ± S.D.

Table 4
ANOVA of harvest and fire histories on first three PCs and fuel loadings

Variables	d.f.	F	p	Means of contrasts	
				I	II
Contrasts of harvesting history					
PC 1	80	11.06	0.001	−0.350	0.350
PC 2	80	0.38	0.538	0.069	−0.069
PC 3	80	1.91	0.167	−0.155	0.155
CWD	80	0.07	0.796	27.26	29.52
FWD	78	0.33	0.568	5.34	5.86
Duff	80	1.56	0.216	1.59	1.40
Litter	80	0.15	0.702	2.40	2.48

Variables	d.f.	F	p	Means of contrasts		
				I	II	III
Contrasts of harvesting and fire history						
PC 1	80	41.75	<0.001	−0.57	0.05	1.49
PC 2	80	0.18	0.837	0.04	0.01	−0.15
PC 3	80	1.14	0.326	−0.10	0.21	−0.21
CWD	80	0.27	0.766	29.00	30.71	21.36
FWD	78	0.61	0.549	5.20	5.64	6.61
Duff	80	1.09	0.343	1.58	1.35	1.60
Litter	80	0.69	0.503	2.45	2.55	2.15

See Section 2 for the details on coding of independent variable.

Table 5
Relationships between descriptors of fire history and stand fuel loadings

Variables	d.f.	F	p	Means of contrasts		
				I	II	III
Predictor: number of fires over the last 50 years (NF 50)						
CWD	50	2.201 ± 1.578	0.254 ± 0.237	17.76	37.61	34.13
FWD	50	4.334 ± 3.058	0.106 ± 0.170	6.95	5.23	3.59
Duff	50	8.620 ± 4.434	0.013 ± 0.043	1.69	1.60	0.95
Litter	50	2.457 ± 2.291	0.213 ± 0.245	2.72	2.24	2.23
Predictor: number of fires over the last 142 years (NF 142)						
CWD	50	1.171 ± 1.643	0.348 ± 0.283	21.13	29.67	36.66
FWD	50	2.395 ± 2.169	0.246 ± 0.268	6.62	5.45	4.44
Duff	50	1.634 ± 1.624	0.392 ± 0.299	1.56	1.54	1.33
Litter	50	1.634 ± 1.607	0.392 ± 0.301	2.35	2.34	2.68

Variables	d.f.	F	p	Means of contrasts	
				I	II
Predictor: time since last fire (TLF)					
CWD	49	2.265 ± 2.741	0.342 ± 0.297	33.37	21.99
FWD	49	5.838 ± 5.063	0.129 ± 0.204	4.61	6.89
Duff	49	5.472 ± 5.021	0.143 ± 0.217	1.32	1.71
Litter	49	4.069 ± 4.115	0.187 ± 0.242	2.23	2.71

Means of CWD and FWD are in m^3/ha; and for depth of the duff and litter are in cm. Results of one-way ANOVAs, bootstrapped 1000 times. *F*- and *p*-values are means ± 1S.D. See Table 3 for the explanation of the means of contrasts.

high structural variation and multi-cohort stands should be the targets of adaptive management (Palik and Zasada, 2003). However, the restoration of mixed-pine forests may not necessarily be conducive to fuel-reduction management, since multi-cohort stands may exhibit higher levels of CWD compared to more structurally simple communities. It is also important to realize that although resource management modifies vegetation structure and forest fuels, climate imposes a major control over forest dynamics and its variability may introduce another component of uncertainty into forest management (McKenzie et al., 2004). Finally, we stress that natural and semi-natural mixed-pine forests exhibit a wide range of structural and compositional variability, which complicates establishing significant links between stand structure and fuel loadings (Frelich and Reich, 1996). This variability and the uncertainty associated with a wide variation in the stand responses to natural and human disturbances should both be taken into account when designing forest restoration and management plans.

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