



# Fire history, fuels, and overstory effects on the regeneration-layer dynamics of mixed-pine forest ecosystems of eastern Upper Michigan, USA



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## ABSTRACT

Mixed-pine forest ecosystems of the northern Lake States were historically dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.). The late 18th and early 19th century logging activities, followed by significant changes in the characteristics of the fire regime altered the structure and composition of these forests. Prior to making decisions about restoration treatments aimed at promoting natural regeneration of red pine and eastern white pine, there is a need to develop a better understanding of the influence of fire history and current stand conditions on the regeneration-layer. To this end, we quantified the seedling and sapling densities of tree species in altered second-growth and reference old-growth stands at Seney National Wildlife Refuge in eastern Upper Michigan. We then related these densities to descriptors of fire history, fuel loadings, and overstory characteristics. Our results indicate lower densities of red pine and eastern white pine seedlings compared to saplings in second-growth stands. Red pine and eastern white pine seedling densities were positively associated with number of fires in the last 142 years, and negatively associated with time since last fire. Time since last fire also influenced red pine and eastern white pine regeneration indirectly through positive correlations with organic matter depth and negative correlations with importance values for these species in the overstory. Jack pine (*Pinus banksiana* Lamb.) seedling density was also positively associated with the number of fires in the last 142 years. Red pine and eastern white pine seedling and sapling densities exhibited negative relationships with most of the descriptors of fuel loadings. Compared to the second-growth stands, the overstory was found to be a stronger driver of regeneration-layer dynamics in the old-growth stands. Our findings suggest that regeneration of red pine and eastern white pine in the second-growth stands is limited due to unfavorable seedbed conditions, abundance of competing species, and an insufficient seed source. The long-term management objective should be to reintroduce fire with characteristics that resemble those of the historical fire regime. In the short-term, however, managers need to explore management options focused on creating favorable conditions for regeneration of red pine and eastern white pine, and on reducing jack pine. Our findings indicate that opportunities exist for restoration treatments that can manipulate successional dynamics to favor red pine and eastern white pine dominance in these stands.

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## 1. Introduction

Fire has shaped the structure and composition of many forest ecosystems across North America. Pine-dominated ecosystem

types, including longleaf pine (*Pinus palustris* Mill.) ecosystems of the Southeast, ponderosa pine (*P. ponderosa* C. Lawson) ecosystems of the Southwest, and mixed-pine ecosystems of the northern Lake States were historically maintained by a fire regime generally characterized by low- to mixed-severity surface fires (Covington et al., 1994; Drobyshev et al., 2008a; Ware et al., 1993). In these forest types, fire created conditions necessary for germination, seedling establishment, and dominance of the pine species (Ahlgren,

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1976; Bergeron and Gagnon, 1987; Romme et al., 2009), and played a major role in regulating stand density and functional processes (Fulé et al., 2009; Naficy et al., 2010). Fires occurring within the natural range of severity and return intervals also provided the dominant pine species with a competitive advantage during establishment by reducing competition from other vegetation (Kershaw, 1993). Fire history studies in many of these ecosystem types have, however, revealed significant changes in the historical fire regimes (Covington and Moore, 1994; Drobyshev et al., 2008a; Frost, 1993). As a result, many of these ecosystems face a variety of similar management issues associated with these changes in fire regime (Corace et al., 2009; Fulé et al., 2009; Palik et al., 2005; Wilson et al., 2009).

Within the northern Lakes States region, extensive logging during EuroAmerican settlement, followed by a period of catastrophic slash fires, extended periods of fire-suppression, and even-aged harvesting practices such as clear-cutting have resulted in significant changes in many forest ecosystems (Cleland et al., 2004; Rist, 2008; Stephens and Ruth, 2005). Among these changes are shifts in species composition, inadequate regeneration of historically dominant pine species, structurally simplified stands, and accumulation of fuels outside of the natural range of variation (Corace et al., 2012; Drobyshev et al., 2008b; Frelich, 1995). While extended periods of fire suppression likely favored increases in deciduous species such as red maple (*Acer rubrum* L.), the high intensity slash fires following logging activities in many areas likely destroyed most of the remaining pine seed trees (Barrett, 1998; Whitney, 1987). In eastern Upper Michigan, mixed-pine forests historically dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.) have declined from about 39% of the land area prior to EuroAmerican settlement to only about 13% of the land area (Zhang et al., 2000). Further, many of the current stands have a significant component of jack pine, a species whose regeneration was favored by clearcutting (Rist, 2008), and is of concern for fire management in these stands (Corace et al., 2009).

While changes in fire history have been documented (Cleland et al., 2004; Drobyshev et al., 2008a), the legacy effects of these changes and their interaction with stand characteristics on regeneration have not been studied comprehensively in mixed-pine forests of the northern Lake States. Compared with other pine-dominated ecosystems in the southern and western regions of the United States, relatively little information exist on the effects of fire on stand development processes and ecosystem components for pine-dominated ecosystems of the northern Lake States (Miesel et al., 2012). Recent efforts to improve access to (and exchange of) information about fire and fuel issues (Kocher et al., 2012; Miesel et al., 2012), coupled with increasing public support for ecologically based management activities (Shindler et al., 2009; Wilson et al., 2009), indicate increasing interest in restoring these altered forest ecosystems. If land managers are going to take advantage of these opportunities to develop restoration strategies, especially where management goals include restoring historically dominant species, a better understanding of the important factors that drive regeneration-layer dynamics in current stands is needed.

This study focused on exploring the following question: how do fire history, fuels, and overstory characteristics influence the regeneration-layer dynamics of mixed-pine forest ecosystems of eastern Upper Michigan? We addressed this question by examining seedling and sapling densities (with emphasis on red pine and eastern white pine as restoration target species) in both second-growth (representing altered conditions) and old-growth (representing reference conditions in forest composition and structure) stands. We then related these data to three primary factor groups: (1) fire history; (2) current down fuel loadings; and (3) current overstory characteristics (composition and structure) (Fig. 1). While fire plays a key role on the regeneration and

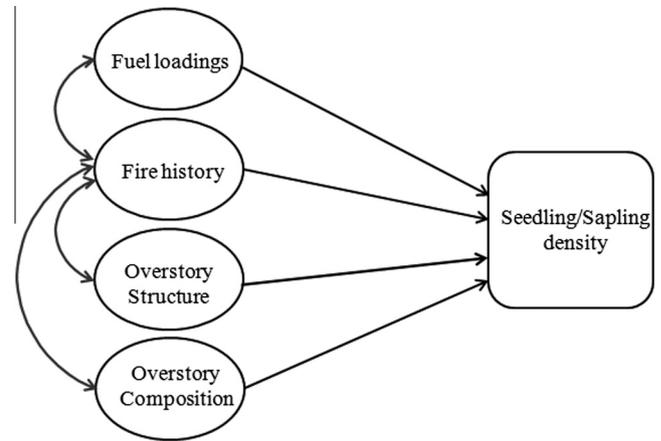


Fig. 1. Conceptual diagram illustrating the factor groups (inferred from measured variables) that likely influence seedling and sapling densities in mixed-pine forest ecosystems of eastern Upper Michigan, USA.

dominance of red pine and eastern white pine (Ahlgren, 1976; Carey, 1993a), we know that there have been changes in the historical fire regime in our study area (Drobyshev et al., 2008a), that might be expected to influence the structure and composition of current stands. We, therefore, focused on fire history, fuels, and overstory characteristics because these are the primary factor groups that we anticipate are important drivers of regeneration dynamics in current stands, and that can be manipulated by management. This important baseline information on the effects of fire history and current stand characteristics on regeneration dynamics will contribute to restoration efforts by facilitating decision-making when selecting and implementing restoration alternatives in this and other similar ecosystem types.

## 2. Materials and methods

### 2.1. Study area

The study was conducted within the 38,542-ha Seney National Wildlife Refuge (SNWR), Schoolcraft County, eastern Upper Michigan (N46.271594° W86.057078°) (Fig. 2). SNWR lies within the Seney Lake Plain ecoregion and is characterized by soils and physiographic features that resulted from postglacial erosion and soil formation processes (Albert, 1995). Two major landform types dominate the landscape: glacial outwash channels and a

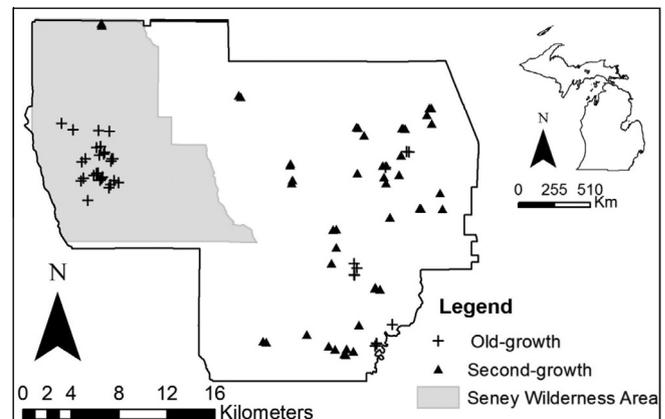


Fig. 2. Study area at Seney National Wildlife Refuge showing study plot locations in old-growth and second-growth stands.

patterned-fen matrix interspersed by wind-induced sand ridges (Heinselman, 1965). Soils range from poorly drained peats to excessively drained coarse sandy soils, on which mixed-pine stands are found. The climate is influenced by its close proximity to the Great Lakes. Temperatures vary between a minimum of  $-9^{\circ}\text{C}$  in the coldest month (January) to  $30^{\circ}\text{C}$  in the warmest month (July), and the average annual precipitation is 78 cm, with most of the precipitation falling in the form of snow (MRCC, 2013). The length of the growing season averages 119 days, and the average daily humidity during spring and fall varies between 50% and 60%.

The Seney Wilderness Area comprises 26% (10,583 ha) of the total SNWR area (USFWS, 2009). Because extensive areas of the Seney Wilderness Area are wetland ecosystems (Heinselman, 1965), difficulty in accessing these areas precluded logging and other anthropogenic disturbances that were common in the surrounding areas throughout the 19th and 20th century (Losey, 2003). As a result, mixed-pine stands found on sand ridges in the Seney Wilderness Area represent perhaps the best remaining examples of reference, old-growth mixed-pine conditions in terms of species composition and stand structure. The remaining SNWR landscape is composed of a mosaic of upland and lowland forests, and wetland vegetation (USFWS, 2009). The mixed-pine forests were historically dominated by red pine and eastern white pine, but altered stands are currently characterized by a substantial component of jack pine that originated following the harvesting and subsequent stand-replacing fires associated with settlement of the area between 1860 and 1935 (Drobyshev et al., 2008b; Rist, 2008). Thus, the study area provides a model landscape for our analyses because of the availability of altered, naturally regenerated second-growth stands that reflect the changes in conditions characteristic of the ecosystem type, as well as adjacent old-growth stands that represent reference conditions.

## 2.2. Vegetation sampling

Vegetation data were collected across a network of 50 mixed-pine stands that had been selected for a previous fire history study (Drobyshev et al., 2008a). The stands used in the fire history study had been selected based on the availability of fire-scarred trees, snags, and stumps to enable fire history reconstruction using dendrochronology. In 2006 and 2007, a total of 85,500- $\text{m}^2$  (50 m  $\times$  10 m) sample plots were randomly established within these stands, with each stand containing between one and three plots, depending on the size and configuration of the stand. In stands where more than one plot was established, the plots were randomly established 100–200 m from each other. Within each sample plot, seedlings (stems  $<2.5$  cm dbh) were counted by species in four 2- $\text{m}^2$  quadrats located at the 10, 20, 30 and 40 m along the long axis of the sample plot, while saplings (stems 2.5–10.0 cm dbh) were counted by species in a nested 300- $\text{m}^2$  (30 m  $\times$  10 m) subplot located along the long axis of the sample plot. To characterize the overstory composition associated with each sample location, the species and diameter at breast height (1.37 m above the ground) of all living trees (stems  $>10.0$  cm dbh) within the sample plot were recorded. The overstory consisted of trees of all crown classes (dominant, codominant, intermediate and overtopped) as long as they met the 10.0 cm dbh criteria. Taxonomic authorities followed the PLANTS database (USDA, NRCS, 2013).

At the center of each sample plot, we collected digital hemispherical photographs at 1 m above the ground using a fisheye lens mounted on a Nikon 8400 digital camera. We then used the WinSCANOPY digital image processing software (Regent Instruments Inc., Chemin Saint-Foy, Quebec) to estimate the proportion of the canopy that was open (percent canopy openness). Fuel data were

collected by following the standard Forest Inventory and Analysis (FIA) fuel sampling protocols (Woodall and Monleon, 2008). Specifically, we recorded estimates of coarse (1000-h fuels) and fine (1-h, 10-h and 100-h fuels) down woody material, fuelbed depth (duff and litter) as well as live and dead shrubs and herbs using a line intercept method along three 7.3-m transects aligned at  $30^{\circ}$ ,  $150^{\circ}$ , and  $270^{\circ}$  from the center of each sample plot. We then used standard calculations from Woodall and Monleon (2008) to obtain fuel biomass. Due to the landscape matrix of the Seney Wilderness Area, availability of candidate stands representing the reference (old-growth) conditions was limited compared with the altered second-growth areas of SNWR. We, therefore, had fewer sample plots established in the old-growth stands ( $n = 38$ ) compared to the second-growth stands ( $n = 47$ ).

## 2.3. Fire history data collection and processing

The fire history data used in this study had been collected as part of the dendrochronological study described in Drobyshev et al. (2008a). Here we provide a brief outline of the fire history data sampling and processing procedures only to provide context for the current study. In each of the 50 stands, live trees, stumps, and deadwood that had fire scars on them were identified. From all the identified potential samples, those that were considered to be most informative for fire history reconstruction were selected and marked for sampling. The search for all potential sample trees in each stand covered an estimated area of up to 1 ha (or less in cases where sand ridges were  $<1$  ha), and was limited to a 2.5-h maximum search time. From each marked sample tree, a wedge was extracted from the bole using the method of “wedge sampling” (Arno and Sneek, 1977). A total of 97 wedge samples were collected in the old-growth stands and 151 samples in the second-growth stands. Trees that represent the oldest cohort were typically sampled to recover scars not visible from outside of the tree (overheated scars). The majority of the samples were from red pine, with only a few samples from eastern white pine and jack pine.

Once collected, the samples were processed in the lab to determine age and fire scars. Specifically, the samples were mounted on wooden plates, and progressively polished with up to 400-grit sandpaper to enable clear recognition of annual rings and fire scars under a binocular microscope (with up to  $40\times$  magnification). The visual crossdating approach (Stokes and Smiley, 1968) was used to date fire scars and annual rings in all samples. Local and master 300-year-long pointer-year chronologies (Schweingruber et al., 1990) were developed for red pine using ring widths, early and latewood widths, and visible differences in early and latewood densities. The developed pointer-year chronologies were verified using existing red pine chronologies for the region, available on the International Tree-Ring Data Bank (<http://www.ncdc.noaa.gov/paleo/treering.html>). Dates of known fires, such as the Seney Fire of 1976 (Anderson, 1982), were also used to verify the cross-dating accuracy.

Once the crossdating was complete, calendar dates for all fire occurrences were recorded. We used these data to develop the following descriptors of fire history: (1) number of fires in the last 142-years, 1864–2006 (NF142), (2) number of fires in the last 50 years, 1956–2006 (NF50), and (c) time since last fire (TLF). The 50-year time frame was selected because it represents recent fire activity in the study area. The 142-year time frame was selected because (1) captures changes in fire occurrences during and post-settlement, (2) all stands had samples dating back to 1864, which allowed for comparisons among stands, and (3) 1864 was also a major fire year in the study area with many of the cohorts dating back to this year.

## 2.4. Statistical analyses

We used a multi-response permutation procedure (MRPP) with a Sorensen (Bray–Curtis) distance measure and  $n/\text{sum}(n)$  weighting function in PC-ORD version 5.0 (MJM Software, Glendon Beach, OR) to examine if there were differences in the overall species composition of the seedling and sapling layers between the second-growth and old-growth stands. We used the Mann–Whitney test to examine the differences in mean densities of seedling and sapling-size woody stems between the second-growth and old-growth stands. The Mann–Whitney test is a non-parametric test used to test for differences between two non-paired groups, and is robust in cases where the data comprise independent observations, but do not need to meet the normal distribution and homogeneity of variance assumptions required in parametric analyses (Zar, 2010).

To examine the relationships between the target species and metrics representing each factor groups (fire history, fuels, and overstory), we used Structural Equation Modeling (SEM) in AMOS version 21 (SPSS Inc., Chicago, IL). SEM is an extension of the Generalized Linear Models approach and is useful due to its capability to solve path equations simultaneously using Maximum Likelihood estimation (Grace and Bollen, 2005). Compared to multiple regression, SEM is robust in examining interactions among both measured and latent variables through direct and indirect pathways, thus allowing for a more comprehensive examination of complex relationships among variables and underlying processes within the system of study (Grace and Bollen, 2005). While we mainly focused on red pine and eastern white pine as restoration target species, we also included analysis for jack pine because it is a species of concern for fire management in these ecosystems.

The SEM process begins with the development of a conceptual model based on the theoretical understanding of potential underlying mechanisms and interactions (Fig. 1), followed by comparing how well different models describe the data and hypothesized relationships (Grace and Bollen, 2005). SEM uses a chi-square ( $\chi^2$ ) test statistic, which tests the magnitude of discrepancy between the sample covariance matrix and the covariance matrix of the fitted model (model fit) (Barrett, 2007). The null hypothesis is that there is no difference between the sample covariance matrix and that implied by the fitted model ( $\chi^2 = 0$ ). The probability ( $P$ ) value represents a test against this null hypothesis, hence the model that best represents the data (a good fit) will provide an insignificant result at the 0.05 threshold (Barrett, 2007). We used SEM to examine the relationships between the pine seedling and sapling densities and measured predictor variables in each of the two stand types separately. Where more than one good-fit model was generated, the final model (best-fit) we selected was the one with the least chi-square value, and a nonsignificant  $P$  value that indicates the absence of significant deviations between data and model (Grace and Bollen, 2005). We also used standardized path coefficients to allow for comparison of strengths among paths in the model, and therefore, the relative influence of the predictor variable associated with each path (Grace and Bollen, 2005). All our final selected models did not include latent variables, which are unobserved variables that are inferred based on a group of measured variables (Grace and Bollen, 2005).

## 3. Results

### 3.1. Seedling and sapling densities

MRPP suggested that there were significant differences between second-growth and old-growth stands in the overall species composition of the seedling layer ( $T = -3.53$ ,  $A = 0.02$ ,  $P < 0.001$ ),

largely due to significantly higher densities of eastern white pine seedlings in the old-growth stands ( $379 \pm 469$  seedlings  $\text{ha}^{-1}$ ) compared to the second-growth stands ( $136 \pm 254$  seedlings  $\text{ha}^{-1}$ ) (Table 1; Mann–Whitney test,  $W = 670$ ,  $P = 0.03$ ). We found low densities of red pine seedlings in both the second-growth ( $64 \pm 138$  seedlings  $\text{ha}^{-1}$ ) and old-growth ( $79 \pm 269$  seedlings  $\text{ha}^{-1}$ ) stands, and the difference between the two stand types was not significant (Table 1; Mann–Whitney test,  $W = 916$ ,  $P = 0.77$ ). We observed relatively low densities of jack pine in the seedling layer ( $60 \pm 181$  seedlings  $\text{ha}^{-1}$ ) compared to the sapling layer, with all the jack pine seedlings only found in the second-growth stands (Table 1). High densities of deciduous species were observed in the seedling layer, with red maple and downy serviceberry (*Amelanchier arborea* (Michx. f.) Fernald) as the most common species in the seedling layer of both second-growth and old-growth stands (Table 1).

There were also significant differences between second-growth and old-growth stands in the overall species composition of the sapling layer ( $T = -3.26$ ,  $A = 0.02$ ,  $P = 0.01$ ). Unlike in the seedling layer, red pine was the most common species in both the second-growth ( $3051 \pm 3748$  saplings  $\text{ha}^{-1}$ ) and old-growth ( $1805 \pm 2633$  saplings  $\text{ha}^{-1}$ ) stands, with no significant differences between the two stand types (Table 1; Mann–Whitney test,  $W = 779$ ,  $P = 0.31$ ). Further, we observed higher densities of eastern white pine saplings in the second-growth stands ( $766 \pm 1739$  saplings  $\text{ha}^{-1}$ ) compared to the old-growth stands ( $158 \pm 335$  saplings  $\text{ha}^{-1}$ ), although these values were not significantly different (Table 1; Mann–Whitney test,  $W = 952$ ,  $P = 0.54$ ). We also observed significantly greater densities of jack pine saplings in second-growth stands ( $1404 \pm 3680$  saplings  $\text{ha}^{-1}$ ) compared to old-growth stands ( $21 \pm 101$  saplings  $\text{ha}^{-1}$ ) (Table 1; Mann–Whitney test,  $w = 1159$ ,  $P < 0.001$ ). Overall, the three pine species (in decreasing densities: red pine, jack pine, eastern white pine) were the most common species in the sapling layer of the second-growth stands.

### 3.2. Summary of fire history, fuels, and overstory characteristics

While the average fire occurrence was relatively similar between the second-growth and old-growth stands, we found that there were longer fire-free periods in the second-growth stands (time since last fires =  $55.3 \pm 31.7$ ) compared to the old-growth stands (time since last fires =  $39.3 \pm 24.3$ ) (Table 2). We also found generally higher fuel biomass in the second-growth stands (mean biomass =  $30.7 \pm 57.0$ ) compared to old-growth stands (mean biomass =  $26.1 \pm 48.0$ ), largely due to greater fine fuel (1-h and 10-h fuels) biomass in the second-growth stands (Table 2). With regards to overstory composition, red pine was less dominant in the overstory of second-growth stands (importance values =  $54.3 \pm 37.8$ ) compared to the old-growth stands (importance values =  $75.7 \pm 30.7$ ), while jack pine was more dominant in the overstory of the second-growth stands (Table 2).

### 3.3. Structural equation modeling of seedlings

#### 3.3.1. Red pine seedlings

In second-growth stands, red pine seedling density was influenced by fire history (number of fires in the last 142 years, time since last fire) and fuel (coarse and fine woody materials) variables, with the model explaining 20% of the variation in seedling density ( $\chi^2 = 0.64$ ,  $P = 0.73$ ,  $df = 2$ ) (Fig. 3A). Based on the path coefficient estimates, red pine seedling density exhibited a strong positive association with number of fires in the last 142 years (0.33), but a weak positive association with time since last fire (0.06) (Fig. 3A). Red pine seedling density was negatively associated with coarse ( $-0.28$ ) and fine ( $-0.34$ ) woody materials (Fig. 3A).

**Table 1**

Mean ( $\pm$ 1SD) seedling and sapling densities (stems ha<sup>-1</sup>) in second-growth and old-growth stands in mixed-pine forest ecosystems of eastern Upper Michigan, USA. Mann-Whitney tests were used to test for differences in mean densities between stand types.

Species	Seedlings			Saplings		
	Second-growth	Old-growth	<i>P</i> value	Second-growth	Old-growth	<i>P</i> value
Red pine	64 $\pm$ 138	79 $\pm$ 269	0.98	3051 $\pm$ 3748	1805 $\pm$ 2633	0.52
Eastern white pine	136 $\pm$ 254	379 $\pm$ 469	0.03	766 $\pm$ 1739	158 $\pm$ 335	0.42
Jack pine	60 $\pm$ 181	0 $\pm$ 0	0.02	1404 $\pm$ 3680	21 $\pm$ 101	0.0008
Red maple	1344 $\pm$ 2944	1678 $\pm$ 2433	0.02	328 $\pm$ 2100	442 $\pm$ 1131	0.007
Downy serviceberry	757 $\pm$ 1122	547 $\pm$ 752	0.17	17 $\pm$ 70	310 $\pm$ 643	0.001
Northern red oak	166 $\pm$ 409	142 $\pm$ 502	0.77	0 $\pm$ 0	0 $\pm$ 0	0.38
Paper birch	4 $\pm$ 29	37 $\pm$ 112	0.02	34 $\pm$ 113	195 $\pm$ 508	0.05
Black spruce	64 $\pm$ 325	47 $\pm$ 188	0.84	140 $\pm$ 341	78 $\pm$ 200	0.92
Bigtooth aspen	9 $\pm$ 41	11 $\pm$ 45	0.93	102 $\pm$ 273	95 $\pm$ 311	0.46
Quaking aspen	0 $\pm$ 0	63 $\pm$ 390	0.08	89 $\pm$ 395	100 $\pm$ 254	0.09

**Table 2**

Summary (means  $\pm$  1SD) of measured metrics representing fire history, fuels and overstory characteristics in second-growth and old-growth stands in mixed-pine forest ecosystems of eastern Upper Michigan, USA.

Metrics	Second-growth	Old-growth
<i>Fire history</i>		
Number of fires in the last 142 years	6.1 $\pm$ 3.4	5.9 $\pm$ 2.3
Number of fires in the last 50 years	0.9 $\pm$ 1.2	0.9 $\pm$ 0.6
Time since last fire (years)	55.3 $\pm$ 31.7	39.3 $\pm$ 24.3
<i>Fuels</i>		
Coarse woody material (1000-h fuels; tonnes/ha)	2.3 $\pm$ 7.6	2.1 $\pm$ 3.1
1-h fine woody material (tonnes/ha)	5.3 $\pm$ 6.8	3.0 $\pm$ 1.8
10-h fine woody material (tonnes/ha)	6.7 $\pm$ 5.3	5.4 $\pm$ 3.2
100-h fine woody material (tonnes/ha)	10.3 $\pm$ 10.5	10.0 $\pm$ 11.1
Fuelbed depth (litter + duff; cm)	14.7 $\pm$ 4.9	16.0 $\pm$ 6.6
Live shrubs and herbs (tonnes/ha)	146.9 $\pm$ 77.0	123.8 $\pm$ 60.8
Dead shrubs and herbs (tonnes/ha)	12.7 $\pm$ 11.9	12.5 $\pm$ 9.0
Mean fuel biomass (tonnes/ha)	30.7 $\pm$ 57.0	26.1 $\pm$ 48.0
<i>Overstory</i>		
Canopy openness (%)	28.7 $\pm$ 4.9	24.4 $\pm$ 10.8
Red pine (IV)	54.3 $\pm$ 37.8	75.7 $\pm$ 30.7
Eastern white pine (IV)	7.8 $\pm$ 22.9	6.5 $\pm$ 10.3
Jack pine (IV)	8.3 $\pm$ 17.5	0.3 $\pm$ 2.0
Northern red oak (IV)	0.4 $\pm$ 3.1	0.4 $\pm$ 2.2
Bigtooth aspen (IV)	1.5 $\pm$ 7.7	1.3 $\pm$ 8.1
Quaking aspen (IV)	0.2 $\pm$ 1.2	0 $\pm$ 0

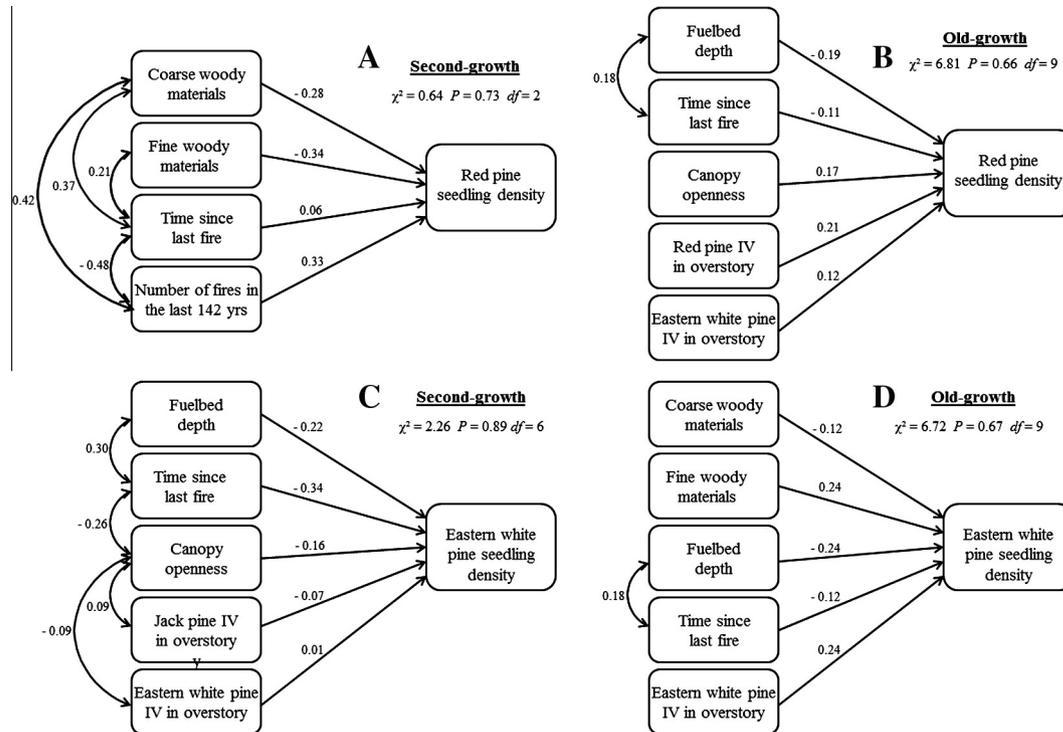
Correlations identified between predictor variables in the model suggested their indirect influence on red pine seedling density. For example, the number of fires in the last 142 years influenced red pine seedling density indirectly through a positive correlation with coarse woody materials (0.42), and a negative correlation with time since last fire ( $-0.48$ ) (Fig. 3A). While the direct influence of time since last fire on red pine seedling density was relatively weak (0.06), the positive correlations with both coarse (0.37) and fine (0.21) woody materials resulted in an overall strong negative influence of time since last fire on red pine seedling density (Fig. 3A).

In old-growth stands, red pine seedling density was influenced by fire history (time since last fire), fuels (fuelbed depth), and overstory characteristics (canopy openness, importance values for red pine and eastern white pine in the overstory), with the model explaining 16% of the variation in seedling density ( $\chi^2 = 6.81$ ,  $P = 0.66$ ,  $df = 9$ ) (Fig. 3B). Red pine seedling density was positively associated with canopy openness (0.17), but negatively associated with both time since last fire ( $-0.11$ ) and fuelbed depth ( $-0.19$ ) (Fig. 3B). Compared to observations in the second-growth stands, overstory composition exhibited a stronger influence on seedling density in the old-growth stands. For example, red pine seedling density was positively associated with importance values for both red pine (0.21) and eastern white pine (0.12) (Fig. 3B). Although we observed little correlation between predictor variables compared

to that observed in the second-growth stands, we identified a positive correlation between time since last fire and fuelbed depth (0.18) (Fig. 3B). Time since fire, therefore, also influenced red pine seedling density indirectly through its correlation with fuelbed depth.

### 3.3.2. Eastern white pine seedlings

In second-growth stands, eastern white pine seedling density was influenced by fire history (time since last fire), fuels (fuelbed depth), and overstory characteristics (canopy openness, importance values for jack pine and eastern white pine in the overstory), with the model explaining 21% of the variation in seedling density ( $\chi^2 = 2.26$ ,  $P = 0.89$ ,  $df = 6$ ) (Fig. 3C). Eastern white pine seedling density was negatively associated with time since last fire ( $-0.34$ ), and fuelbed depth ( $-0.22$ ) (Fig. 3C). Contrary to our expectation, eastern white pine seedling density was also negatively associated with canopy openness ( $-0.16$ ), and showed a relatively weak positive association with importance values for eastern white pine (0.01) (Fig. 3C). Correlations identified between predictor variables in the model suggested their indirect influence on eastern white pine seedling density. Time since last fire influenced eastern white pine seedling density indirectly through its positive correlation with fuelbed depth (0.30) and negative correlation with canopy openness ( $-0.26$ ). Canopy openness was also positively correlated with importance values for jack pine (0.09) and



**Fig. 3.** Structural equation models of red pine (models A and B) and eastern white pine (models C and D) seedling densities with predictor variables in second-growth and old-growth stands. Pathway coefficient estimates (associated with each single-headed arrow) are standardized and when compared across each model, represents the relative strength of influence of the predictor variable on the response variable (Grace and Bollen, 2005). The models also include correlation estimates (associated with each double-headed arrow) between predictor variables.

negatively correlated with importance values for eastern white pine ( $-0.09$ ) (Fig. 3C).

In old-growth stands, eastern white pine seedling density was influenced by fire history (time since last fire), fuels (coarse and fine woody materials), and overstory characteristics (importance values for eastern white pine in the overstory), with the model explaining 21% of the variation in seedling density ( $\chi^2 = 6.72$ ,  $P = 0.67$ ,  $df = 9$ ) (Fig. 3D). Eastern white pine seedling density was negatively associated with time since last fire ( $-0.12$ ), coarse woody materials ( $-0.12$ ), and fuelbed depth ( $-0.24$ ), but positively associated with fine woody material ( $0.24$ ) (Fig. 3D). Compared to observations in the second-growth stands, eastern white pine seedling density showed a stronger positive association with importance values for eastern white pine ( $0.24$ ) (Fig. 3D). Similar to the model for red pine seedlings in old-growth stands, little correlation was observed between predictor variables in the old-growth stands. We only identified a positive correlation between time since last fire and fuelbed ( $0.18$ ), meaning that time since last fire also influenced eastern white pine seedling density indirectly through its correlation with fuelbed depth (Fig. 3D).

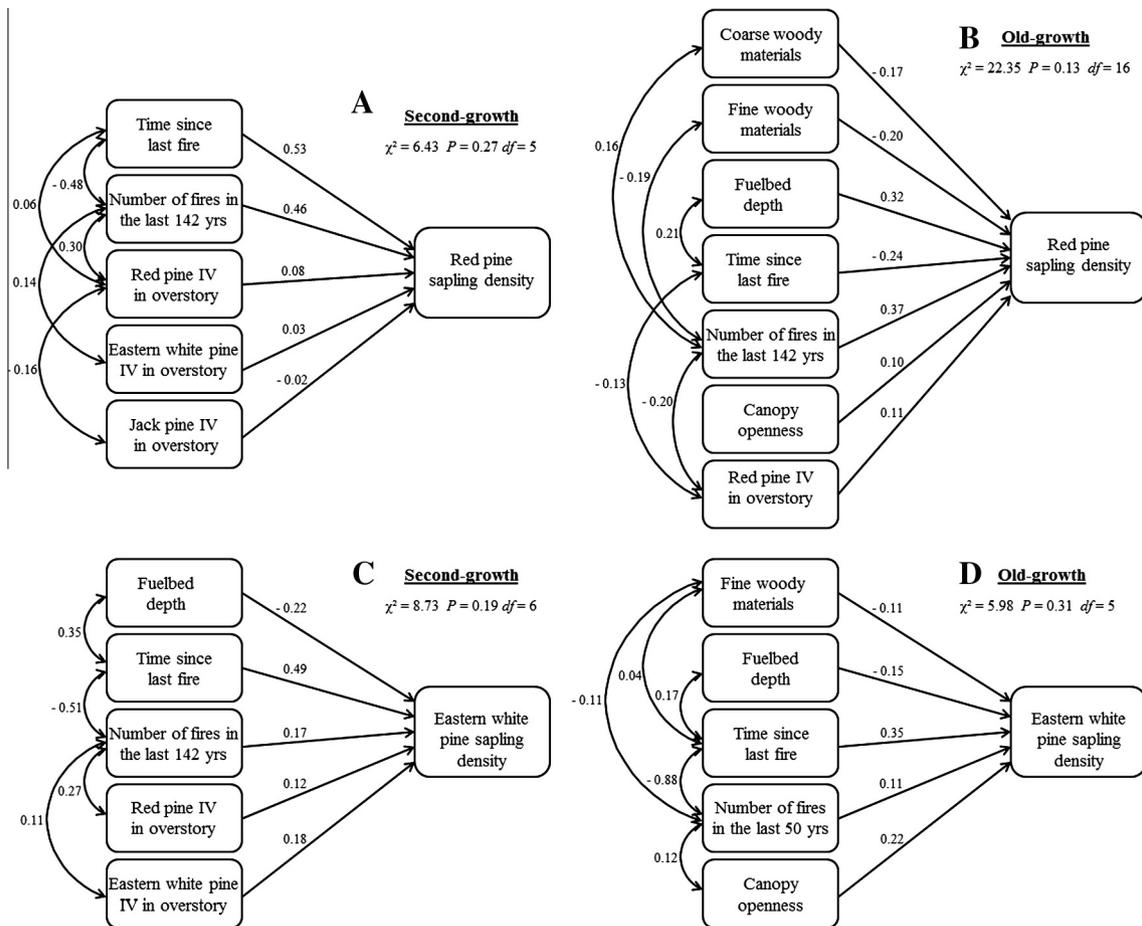
### 3.4. Structural equation modeling of saplings

#### 3.4.1. Red pine saplings

In second-growth stands, red pine sapling density was influenced by fire history (number of fires in the last 142 years, time since last fire) and overstory characteristics (importance values for red pine, eastern white pine, and jack pine in the overstory), with the model explaining 30% of the variation in sapling density ( $\chi^2 = 6.43$ ,  $P = 0.27$ ,  $df = 5$ ) (Fig. 4A). Red pine sapling density was positively associated with time since last fire ( $0.53$ ) and number of fires in the last 142 years ( $0.46$ ) (Fig. 4A). Relative to the associations with metrics of fire history, we observed weaker associations between red pine sapling density and descriptors of

overstory characteristics. For example, red pine sapling density was positively associated with importance values for red pine ( $0.08$ ), eastern white pine ( $0.03$ ), and negatively associated with importance values for jack pine ( $-0.02$ ) (Fig. 4A). Correlations identified between predictor variables in the model suggested their indirect influence on red pine sapling density. For example, number of fires in the last 142 years influenced red pine sapling density indirectly through its positive correlations with importance values for red pine ( $0.30$ ) and eastern white pine ( $0.14$ ), and through a negative correlation with time since last fire ( $-0.48$ ) (Fig. 4A).

In old-growth stands, red pine sapling density was influenced by fire history (number of fires in the last 142 years, time since last fire), fuels (coarse and fine woody materials, fuelbed depth), and overstory characteristics (canopy openness, importance values for red pine in the overstory), with the model explaining 35% of the variation in sapling density ( $\chi^2 = 22.35$ ,  $P = 0.13$ ,  $df = 16$ ) (Fig. 4B). Compared to overstory characteristics, fire history and fuels exhibited a stronger influence on red pine sapling density in these stands. Red pine sapling density was positively associated with number of fires in the last 142 years ( $0.37$ ) and negatively associated with time since last fire ( $-0.24$ ) (Fig. 4B). Red pine sapling density was also positively associated with fuelbed depth ( $0.32$ ), but negatively associated with both coarse ( $-0.17$ ) and fine ( $-0.20$ ) woody materials (Fig. 4B). In comparison to the second-growth stands, overstory characteristics showed a stronger influence on red pine sapling density, exhibiting positive associations with canopy openness ( $0.10$ ) and importance values for red pine ( $0.11$ ) (Fig. 4B). Correlations identified between predictor variables in the model suggested their indirect influence on red pine sapling density. Time since last fire influenced red pine sapling density indirectly through a positive correlation with fuelbed ( $0.21$ ) and a negative correlation with importance values for red pine ( $-0.13$ ). Similarly, number of fires in the last 142 years influenced red pine sapling density indirectly through a positive correlation



**Fig. 4.** Structural equation models of red pine (models A and B) and eastern white pine (models C and D) sapling densities with predictor variables in second-growth and old-growth stands. Pathway coefficient estimates (associated with each single-headed arrow) are standardized and when compared across each model, represents the relative strength of influence of the predictor variable on the response variable (Grace and Bollen, 2005). The models also include correlation estimates (associated with each double-headed arrow) between predictor variables.

with coarse woody materials (0.16), a negative correlation with fine woody materials ( $-0.20$ ), and through a negative correlation with importance values for red pine ( $-0.13$ ) (Fig. 4B).

### 3.4.2. Eastern white pine saplings

In the second-growth stands, eastern white pine sapling density was influenced by fire history (number of fires in the last 142 years, time since last fire), fuels (fuelbed depth), and overstory characteristics (importance values for red pine and eastern white pine in the overstory), with the model explaining 22% of the variation in sapling density ( $\chi^2 = 8.73$ ,  $P = 0.19$ ,  $df = 6$ ) (Fig. 4C). Eastern white pine sapling density was positively associated with time since last fire (0.49) and number of fires in the last 142 years (0.17) (Fig. 4C), but negatively associated with fuelbed depth ( $-0.22$ ). Compared to its influence on red pine sapling density, overstory characteristics exhibited a stronger influence on eastern white pine sapling density in the second-growth stands (Fig. 4C). Eastern white pine sapling density was positively associated with importance values for both red pine (0.12) and eastern white pine (0.18). Correlations identified between predictor variables in the model suggested their indirect influence on eastern white pine sapling density. Number of fires in the last 142 years influenced eastern white pine sapling density indirectly through positive correlations with importance values for red pine (0.27) and eastern white pine (0.11), and through a negative correlation with time since last fire ( $-0.51$ ) (Fig. 4C). Time since last fire also influenced eastern white pine sapling density indirectly through a positive correlation with fuelbed depth (0.35).

In the old-growth stands, eastern white pine sapling density was influenced by fire history (number of fires in the last 142 years, time since last fire), fuels (fine woody materials, fuelbed depth), and overstory characteristics (canopy openness), with the model explaining 14% of the variation in sapling density ( $\chi^2 = 5.98$ ,  $P = 0.31$ ,  $df = 5$ ) (Fig. 4D). Eastern white pine sapling density was positively associated with time since last fire (0.35) and number of fires in the last 142 years (0.11) (Fig. 4D). Eastern white pine sapling density was, however, negatively associated with fine woody material ( $-0.11$ ) and fuelbed depth ( $-0.15$ ) (Fig. 4D). Unlike in the previous models, canopy openness exhibited a strong influence in this model, showing a positive association with eastern white pine sapling density (0.22) (Fig. 4D). Correlations identified between predictor variables in the model suggested their indirect influence on eastern white pine sapling density. Number of fires in the last 142 years influenced eastern white pine sapling density indirectly through a negative correlation with fine woody materials ( $-0.11$ ), a positive correlation with canopy openness (0.12), and through a negative correlation with time since last fire ( $-0.88$ ) (Fig. 4D). Time since last fire also influenced eastern white pine sapling density indirectly through positive correlations with fine woody materials (0.04) and fuelbed depth (0.17) (Fig. 4D).

### 3.5. Structural equation modeling of jack pine seedlings and saplings

Jack pine seedling density was positively associated with number of fires in the last 142 years (0.40) and negatively associated

with time since last fire ( $-0.15$ ) in the second-growth stands. We also observed positive associations between jack pine seedling density and importance values for jack pine in the overstory ( $0.15$ ) and canopy openness ( $0.08$ ). There were no jack pine seedlings observed in the old-growth stands (Table 1). In the sapling layer, we observed a positive association between jack pine sapling density and both number of fires in the last 142 years ( $0.10$ ) and canopy openness ( $0.21$ ), and a negative association with time since last fire ( $-0.45$ ) in the second-growth stands. Similar to the seedling layer of old-growth stands, we observed low densities of jack pine in the sapling layer of the old-growth stands (Table 1).

#### 4. Discussion

Increased focus on ecological benefits and the need to promote use of fire in the management of pine-dominated ecosystems have spurred restoration efforts focused on improving conditions for regeneration of historically dominant pine species, enhancing stand structural complexity, and reducing fuel accumulations (Corace et al., 2009; Palik et al., 2005; Palik and Zasada, 2003). These efforts can benefit from a better understanding of not only the changes in the fire regime, but also the effects of their interactions with stand characteristics on stand development processes such as regeneration. Where red pine and eastern white pine are restoration target species, among the important aspects to consider with regards to regeneration are seedbed conditions, availability of seed source, competition, and penetration of light to the understorey (Ahlgren, 1976; Palik and Pregitzer, 1994; Peck and Zenner, 2009). We hypothesize that in mixed-pine ecosystems of eastern Upper Michigan, these key aspects are influenced by fire history, fuels, and overstorey characteristics.

##### 4.1. Regeneration in the seedling and sapling layers

Our results indicate inadequate regeneration of the historically dominant red pine and eastern white pine, especially in the seedling layer of second-growth stands. For example, we observed only an average of 64 seedlings  $\text{ha}^{-1}$  of red pine and 136 seedlings  $\text{ha}^{-1}$  of eastern white pine in the these stands. Although little information is available on specific seedling densities for naturally regenerated mixed-pine stands, these densities are relatively low compared to 647 trees  $\text{ha}^{-1}$  densities of mature trees that have been suggested for old-growth, unmanaged red pine stands with similar site quality as our study area (Rudolf, 1990). The high densities of other species such as red maple observed in the seedling layer suggest that these species may be competitors for resources in the regeneration-layer. We suggest that by limiting resources such as nutrients, these competing species may be negatively affecting the regeneration of red pine and eastern white pine (Ahlgren, 1976; Carleton et al., 1996). Our results also suggest a shift in species composition with deciduous species becoming common in the seedling layer and jack pine in the sapling layer of second-growth stands, findings that compare with those of other studies within the region (Zhang et al., 2000).

Despite low densities of seedlings, we found high densities of red pine and eastern white pine saplings in the second-growth stands. We propose two hypotheses that may account for the higher abundance of the two species in the sapling-layer compared to the seedling layer. First, sapling-sized stems may have been able to survive increased fire frequencies or prolonged fire suppression periods characteristic of an altered fire regime, down fuel accumulations, and changes in overstorey characteristics than the seedling-sized stems. For example, it may be that the sapling-size stems had developed thicker barks and taller crowns to enable them better survive repeated fires. Second, stand conditions at the time of

germination and early establishment of stems in the sapling layer may have been more favorable than they are currently. For example, the deeper litter layer or increases in tree density and shading associated with altered stands that have experienced a longer fire-free period may inhibit recruitment. For land managers, the high sapling densities, and ability of saplings to have significant growth response following canopy disturbances (Rist, 2008) suggest opportunities exist for restoration strategies that could facilitate stand development by enabling recruitment into both the sapling stratum and canopy layer.

##### 4.2. Influence of fire history on regeneration

Fire history seems to influence the target species (red pine and eastern white pine) through the effects of both fire occurrence and absence of fire (longer fire-free periods). The overall patterns indicate positive relationships between the number of fires in the last 142 years and the densities of the target species in these ecosystems, especially in the second-growth stands. The influences of these fires on regeneration may be attributed to the effects of fire on reducing competing vegetation and exposing mineral soil seedbeds for germination and establishment of red pine and eastern white pine. Red pine and eastern white pine are species that have been thought to regenerate better following frequent, low-severity surface fires that reduce competing vegetation and expose mineral soils (Ahlgren, 1976; Carey, 1993a; Heinselman, 1981). Drobyshev et al. (2008a) reported pre-settlement period (1707–1859) fire return interval of  $32.7 \pm 19.2$  years for the reference stands. The positive effects of fire occurrence on red pine and eastern white pine regeneration may, however, be limited if a competing species such as jack pine benefits more from these fires (Carey, 1993b) (see below for discussion of jack pine). Compared to the last 142 years, our results suggest that fire occurrence in the last 50 years has had relatively little impact on the target species.

Our results also suggest a negative influence of longer fire free periods on seedling densities. We hypothesize that the negative relationship between the target species and time since last fire is driven by the effects of longer fire-free periods, periods likely outside of the historical range of return intervals (Drobyshev et al., 2008a). If so, then these extended fire-free periods limit regeneration of the target pine species by creating opportunities for fire-intolerant species (Corace et al., 2012). Further, we hypothesize that the positive correlations among time since last fire and metrics of fuel loadings and fuelbed depth also suggests that longer fire-free periods contributed to unfavorable seedbed conditions through increases in the litter layer and organic matter depth (Ahlgren, 1976). We, however, observed positive relationships between time since last fire and sapling densities of target species, which may indicate that longer fire-free period has had greater detrimental effects in the seedling layer compared to the sapling layer. Unfortunately, we are not able to make inferences about the variability in occurrence of these fires in our study area as our fire history information only included the number of fires occurring on each site and not fire return interval as a predictor variable.

Jack pine has become a species of management concern for resource managers across the Lake States region, both as a competitor to red pine and eastern white pine, and as a species of concern for fire management (Corace et al., 2009; Scheller et al., 2005). The strong positive correlations observed between fire occurrence and jack pine seedling densities suggest that jack pine might have significantly benefitted from the fires in these ecosystems. Further, based on the positive correlations between fire occurrence and coarse woody materials, we suggest that some of the fires that have occurred in these ecosystems over the last 142 years may have been of relatively higher severities than the low-severity surface fires characteristic of the historical regime in this ecosystem

type (Drobyshev et al., 2008a). Although jack pine might not require multiple fires to dominate stands, severe fires characterized by high intensities are likely to benefit jack pine as the high temperatures associated with these fires promote the opening of serotinous cones to release seeds (Carey, 1993b). In addition to its efficient regeneration following crown fires, jack pine is a poor self-pruner with ladder-fuels that provide vertical fuel continuity between the surface and tree crowns, creating a positive feedback for occurrence of crown fires (Carey, 1993b; Rudolph and Laidly, 1990).

Overall, our findings suggest that fire history influences regeneration-layer dynamics in these forest ecosystems by: (1) promoting regeneration of the target species in areas with greater fire occurrence; (2) limiting regeneration in areas that have had longer fire-free periods; and (3) favoring regeneration of the competitor species jack pine, especially in cases of high-severity fires.

#### 4.3. Influence of fuels on regeneration

Our results suggest an overall negative influence of down woody materials (coarse and fine materials) and fuelbed depth on the regeneration of the target species. Observed relationships indicate decreasing red pine and eastern white pine seedling and saplings densities with high values for coarse and fine woody materials and fuelbed depth, although saplings appear to survive better in areas with higher organic matter depth. While the direct influence of fuels on regeneration was not investigated in this study, the potential impacts of fuels on seedbed conditions, and the feedback mechanism between available fuels and fire characteristics means that fuel accumulations may adversely affect regeneration of red pine and eastern white pine. First, accumulations of down woody materials contributes to increases in the depth of the duff and litter layers, causing unfavorable seedbed conditions that may limit the germination and early establishment of red pine and eastern white pine (Ahlgren, 1976; Rudolf, 1990; Wendel and Smith, 1990). Second, high fuel loadings can lead to severe fires characterized by high intensities that could: (1) kill younger stems, and potentially destroy seed trees through crown scorching (Rouse, 1988; Van Wagner, 1971); (2) consume the organic layer and cause tree mortality through root damage (Zeleznik and Dickmann, 2004); (3) limit regeneration by altering soil chemistry (Barrett, 1998); and (4) promote regeneration of a competitor species such as jack pine as discussed above.

In second-growth mixed-pine forests where land managers face fuel management issues, it is critical to monitor the dynamics of jack pine particularly due to its ability to contribute ladder fuels that could influence fire behavior and complicate the use fire as a management tool (Corace et al., 2009). In addition to being a relatively short-lived species, jack pine snags exhibit a high snapping rate, with most falling within the first year (Corace et al., 2010). Such high snapping rates suggest that in addition to live fuels, jack pine will contribute significant amounts of down fuels, increasing the potential to influence fire behavior.

#### 4.4. Influence of overstory characteristics on regeneration

Overstory characteristics, as represented by canopy openness and importance values for species in the overstory were found to be important factors in the regeneration of red pine and eastern white pine. Compared to the second-growth stands, overall relationships indicate the overstory as being a stronger driver of regeneration-layer dynamics in the old-growth stands, with stronger positive associations between the target pine species in the regeneration-layer and the overstory. We suggest that these differences may be due to limitations on the seed source in second-growth stands stemming from the interactions between past harvesting

activities and current overstory composition of second-growth stands compared to the unharvested old-growth stands. The positive relationships between red pine and eastern white pine seedling and sapling densities with canopy openness suggest that the regeneration of these species may benefit from restoration treatments that increase canopy openness. Shade tolerance of the pine species decreases in the order of eastern white pine, red pine, and jack pine (Rudolf, 1990), meaning that red pine will require a more open canopy compared to eastern white pine. A recent study in these mixed-pine ecosystems indicates that both species will respond to release following partial opening of the canopy (Rist, 2008). The positive association between jack pine seedling density and canopy openness in the second-growth stands may be an indication to managers that there is potential for competing species such as jack pine to take advantage of natural gaps or those created by treatments (Powers et al., 2008).

We also found relatively weak relationships between the seedling and sapling densities of red pine and eastern white pine and their importance values in the overstory in second-growth stands. High importance values for these species in the overstory would be expected to translate to availability of a seed source, which is critical to the natural regeneration of red pine and eastern white pine, and the successional development of the stand (Ahlgren, 1976; Palik and Pregitzer, 1994). We suggest two potential reasons for the observed weak relationships. First, we know that the second-growth stands are a result of historical harvesting activities that specifically targeted red pine and eastern white pine, and thereby contributing to a poor seed source and potentially low seed production in residual trees (Rist, 2008; Whitney, 1987). As such, the interactions between current overstory composition and past harvesting activities likely contribute to greater variability in overstory effects on the regeneration-layer of the second-growth stands compared to old-growth stands where the seed source may be greater. Second, the direct contribution of the seed trees as seed sources may be masked by potentially poor seedbed conditions as discussed earlier. Weyenberg et al. (2004) suggests that the patterns of seedling spatial distribution in relation to seed trees are likely to be influenced by the interaction between seed supply and the characteristics of the sites to be occupied. Overall, we suggest that the influence of the overstory on target species, especially in second-growth stands, is primarily through the interaction between potentially insufficient seed source, and unfavorable seedbed conditions.

#### 4.5. Additional factors specific to red pine and eastern white pine requirements

While the measured metrics associated with each of the three factor groups (fire history, fuels, overstory) may directly influence regeneration dynamics, their effects are further compounded by other factors related to past harvesting activities (Drobyshev et al., 2008b; Rist, 2008; Whitney, 1987) and regeneration requirements of red pine and eastern white pine. Red pine is characterized by low seed-setting ability, narrower seedbed requirements, and a high sensitivity to competition, all of which make its natural regeneration greatly restricted relative to other pine species in the region (Ahlgren, 1976). Inconsistent seed production may be another confounding factor in the regeneration of both red pine and eastern white pine. Good crop years will generally occur every 3–7 years in red pine (Rudolf, 1990) and 3–5 years in eastern white pine (Wendel and Smith, 1990). As a result, restoration treatments would be expected to have the most impact in improving regeneration of the two species when they coincide or follow immediately after good crop years, although determining these good crop years may be a challenge.

## 5. Restoration and management implications

Our findings suggest that regeneration-layer dynamics in mixed-pine forest ecosystems of eastern Upper Michigan are influenced by fire history, fuel loadings, and overstory characteristics, as well as by interactions among these factor groups. We found that regeneration of the historically dominant red pine and eastern white pine in second-growth stands is limited due to unfavorable seedbed conditions, abundance of competing species, and an insufficient seed source. Being fire-dependent ecosystems, the long-term objective of restoration efforts should be to reintroduce surface fire with characteristics similar to those that occurred historically in these forests (Scheller et al., 2005). Due to high fuel accumulations in many of the current stands, however, there is need to explore new treatment options that will improve stand conditions so that not only is use of fire feasible, but that red pine and eastern white pine can benefit from such fires.

In current old-growth stands, prescribed fire within the historical range of variation (e.g., FRIs of  $32.7 \pm 19.2$  years) should suffice in maintaining the reference conditions. In second-growth stands where jack pine dominance is low, prescribed fires could be used to create the required seedbed conditions and reduce densities of competing fire intolerant species. In stands with greater jack pine dominance where immediate use of fire may be limited, mechanical treatments (e.g., thinning) should be explored. Thinning treatments could be followed by mechanical scarification of the soil surface to break up the slash and expose mineral soil. Where fire or mechanical treatments are not adequate to control species such as red maple, chemical treatments may be explored to set them back or control sprouts. Although it may be costly overall, underplanting the pines may be an option in cases where the seed supply is significantly inadequate.

Overall, proposed restoration strategies should allow for increased canopy openness, provide for retention of adequate seed trees, and target reductions of jack pine, red maple and other species that may have gained a competitive advantage over red pine and eastern white pine. The interaction between fuel loadings and fire occurrence observed in this study suggests that fuel reduction objectives will also need to be a priority for land managers in the efforts to restore these ecosystems. Specifically, managers should target jack pine to minimize ladder-fuels, and reduce accumulations of fine and coarse woody materials in ways that are compatible with the potential role of these materials as wildlife habitats (Corace et al., 2014).

A variety of alternative silvicultural strategies have been suggested for management of pine-dominated ecosystems within the region (Franklin et al., 2007). We recommend that these silvicultural strategies should be explored with the objective of creating conditions that provide a competitive advantage to red pine and eastern white pine, as well as addressing fuel loading concerns in these ecosystems. Future studies that evaluate the response of red pine and eastern white pine regeneration to restoration and fuel reduction treatments will be useful in taking the information from this study further in the efforts to restore this forest ecosystem type across the landscape.

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