# How well does Kirtland's warbler management emulate the effects of natural disturbance on stand structure in Michigan jack pine forests?

Susan E. Spaulding, David E. Rothstein *

Department of Forestry, Michigan State University, East Lansing, MI 48824-1222, United States

A B S T R A C T

Jack pine (*Pinus banksiana*) forests in parts of northern Lower Michigan have been managed with 30 years of extensive clearcut harvesting followed by planted stand establishment in order to maintain habitat for the endangered Kirtland's warbler (*Dendroica kirtlandii*). We used two, parallel chronosequences to study how this management has affected the structural development of jack pine stands relative to the historically dominant disturbance regime of stand-replacing wildfire. Each chronosequence consisted of three young stands (age range 3–6 years), three intermediate-aged stands (age range of 12–17 years) and three mature stands (age range of 39–69 years). Average stem density in young plantations (2300 stems/ha) was lower than the average for young, fire-origin stands (11,000) and varied over a much narrower range among stands (1403–2667 for plantations and 1552–24,192 in fire stands). In addition, within-stand patchiness of stem density was also much higher in the wildfire sites for young and intermediate ages. Plantation sites possessed very little dead wood at young ages (averaging 3 snags/ha and 12 m³/ha CWD) compared to young fire-origin stands (averaging 252 snags/ha and 49 m³/ha CWD). In contrast, mature plantations had similar levels of dead wood (averaging 269 snags/ha and 22 m³/ha CWD) as mature fire-origin stands (averaging 557 snags/ha and 12 m³/ha CWD). Differences between the plantation and fire-origin chronosequences were driven mainly by young- and intermediate-aged stands, whereas mature stands were typically quite similar in all structural features. Our results show clearly that forest management aimed at preserving and enhancing the population of a single endangered species results in greatly simplified habitat structure at the stand level, and suggest that this simplification is perpetuated across the landscape as well. Of particular concern are the effects of extensive harvesting and planting on the availability of snags and CWD.

© 2009 Elsevier B.V. All rights reserved.

## 1. Introduction

There is a dichotomy in modern conservation biology between managing for preservation of a single species (for example, an endangered species or an indicator species) and managing for broader ecosystem characteristics (Simberloff, 1998). Single-species management makes the assumption that management that preserves a sensitive species will automatically preserve additional desirable characteristics and components of the ecosystem. This approach has been criticized on the grounds that single-species-focused approaches often fail to account for the needs of other species (Simberloff, 1998; Lindenmayer et al., 2002). Certainly, aggressive plans to preserve endangered species are sometimes necessary for the short-term goal of preventing imminent extinction; however, the additional ecosystem effects of such a plan often go unmeasured.

Prior to European settlement, jack pine (*Pinus banksiana*) forests of northern Lower Michigan were regenerated by stand-replacing fires with an average return interval estimated at 59 years (Cleland et al., 2004). This historic disturbance regime has been largely replaced by one of intensive harvesting and planting. An unusual aspect of this plan is that the driving goal behind this intensive management is the conservation of biodiversity—not maximization of timber production. These forests provide the only significant breeding habitat for the federally endangered songbird, the Kirtland's warbler (*Dendroica kirtlandii*). The Kirtland's warbler has very narrow habitat requirements, requiring large dense stands of young (6–22 years) jack pine (Probst and Weinrich, 1993) for breeding and nesting. Aggressive fire suppression, primarily in the middle of the last century, resulted in a landscape-level decline of suitable early-successional jack pine habitat, pushing the Kirtland's warbler to the brink of extinction by the early 1980s

* Corresponding author at: Department of Forestry, Michigan State University, 126 Natural Resource, East Lansing, MI 48824-1222, United States.
Tel.: +1 517 432 3353; fax: +1 517 432 1143.
*E-mail address:* rothste2@msu.edu (D.E. Rothstein).

(Donner et al., 2008). In response to this decline, and because of the risks of prescribed fire to human safety and infrastructure demonstrated by the Mack Lake Fire of 1980 (Simard et al., 1983), in 1981 state and federal forest managers began an extensive program of harvesting and planting jack pine to restore this early-successional habitat.

This intensification of plantation management has been a great success in terms of promoting warbler populations (Solomon, 1998; Donner et al., 2008); however, it raises the possibility that extensive management, narrowly focused on maximizing suitable habitat for a single endangered species, could have the unintended consequence of driving stand structure towards conditions that differ significantly from what natural disturbance would produce. According to Lindenmayer and Recher's (1998) definition of sustainable forest management, structure is one of the three important components that need to be maintained within the bounds of normal disturbance regimes, along with species composition and the rate of ecological processes and functions. Of particular interest is whether management that emulates natural disturbance regimes will allow sustainable forest management without long-term degradation or disruption of the system (Attiwill, 1994). Forest structure is highly affected by disturbance and is critical because it, in turn, affects many ecosystem elements, including herbaceous plants (Houseman and Anderson, 2002; Abrams and Dickman, 1982), insects (Heliola et al., 2001), birds and mammals (Converse et al., 2006), and nutrient cycling (Brais et al., 2005; Laiho and Prescott, 2004).

Stand structure is the vertical (volume, mass and density) and horizontal (spatial distribution) pattern of all the dead and living components of the stand. Together, these components form the internal shape of a stand, comprised of patterns of size, density and distribution of live and standing dead trees (snags) and amounts and patterns of coarse woody debris (CWD) and forest floor detritus. These elements of forest structure undergo dramatic changes in composition and volume as a result of a major disturbance (Brassard and Chen, 2006; Harper et al., 2006; Kashian et al., 2004; Wright et al., 2002; Tinker and Knight, 2001).

Development of silvicultural systems that mimic natural disturbance, under the assumption that the biota of a forest are adapted to a natural disturbance regime, is particularly challenging in areas where even-aged stands of shade intolerant trees were historically maintained by stand-replacing wildfires (Franklin

et al., 2002). Clearcut harvesting has been the traditional approach to managing forests characterized by a severe fire regime, and should aim to replicate natural systems by emulating disturbance frequency, size and distribution, and residual organic matter (Hunter, 1993; Bergeron et al., 1999). While a good surrogate for fire in many ways, harvesting also has some notable differences. Fire is a stochastic process, often resulting in spatially irregular patterns of regeneration in the new stand (Kashian et al., 2004). Post-wildfire stand composition can vary as a function of these irregularities, creating pockets of very dense trees adjacent to large areas with no trees at all (Charron and Greene, 2002). In contrast, clearcutting followed by planting creates a uniform stand, with evenly spaced recruits in regular rows. Furthermore, while wildfire and harvesting both kill trees, only a small fraction of aboveground biomass is actually consumed by fire (primarily foliage and small branches; Stocks, 1989). Fire leaves behind large amounts of legacy structure in the form of CWD and snags (Franklin et al., 2002), and such components are critical to many fire-dependent species. In contrast, whole-tree harvesting removes virtually the entire overstory, leaving little legacy structure in young stands.

Because some structural changes due to disturbance are immediate (e.g. reduction of live biomass), while other effects occur over time (e.g. reallocation of dead wood from snags to CWD), it is important to examine structural changes throughout stand development to fully understand the effects of a shift in disturbance regime. We used the chronosequence approach – comparing extant stands varying in age – to investigate the consequences of different disturbance regimes over time in northern Lower Michigan jack pine forests; we did this by examining structural features of stands of three distinct age classes regenerated by either wildfire or harvesting and planting.

## 2. Materials and methods

### 2.1. Study system and experimental design

In order to investigate dynamics of forest structure as stands develop following harvesting vs. wildfire, we developed two parallel chronosequences, one of wildfire-origin stands and one of plantations. The stands were located within four counties in northern Lower Michigan (Crawford, Oscoda, Roscommon and Ogemaw) across an area of approximately 130 km$^2$ (Fig. 1). Jack
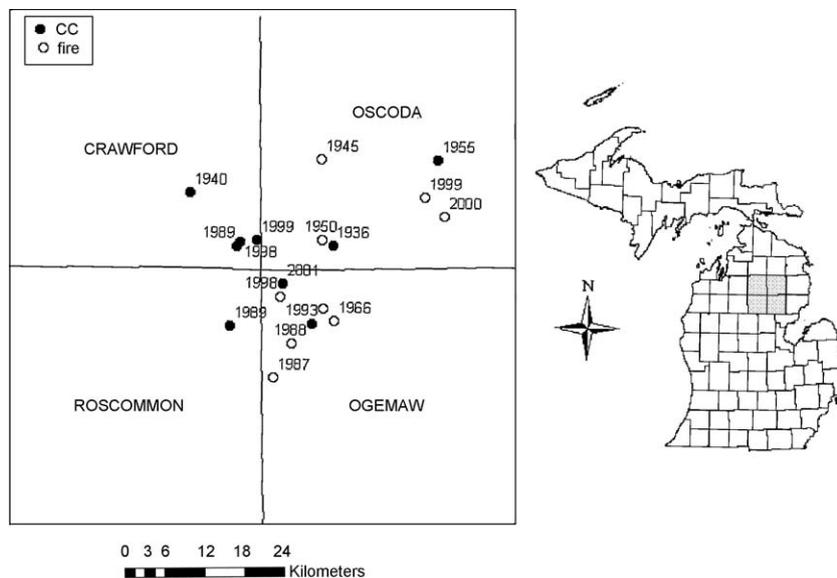


Fig. 1. Locations and year of stand origin of study sites in northern Lower Michigan. Closed circles indicate clearcut-origin plantations and open circles indicate wildfire-origin stands.

pine is the dominant forest type in this region on outwash landforms with acidic, excessively drained, poorly developed sands of the Grayling soil series (Werlein, 1998). Potential stands were identified using information on fire and harvest history of public lands through the United States Department of Agriculture Forest Service (USDA-FS) and Michigan Department of Natural Resources (MDNR). Potential stands were then visited and eliminated if any of the following were discovered: (1) stand had been partially harvested, (2) preceding stand was not jack pine, (3) stand had been salvage-logged after fire, (4) fire had not been completely stand-replacing (for example, strips of unburned original stand remained), (5) soil samples taken to 2-m depth revealed soil type other than sand (for example, clay bands or gravel layer), (6) predominance of species indicating higher water or nutrient availability, such as trembling aspen (Populus tremuloides), (7) stand had significant topographical variation, or (8) stand was less than 10 ha in size. Planting as the mode of stand origin was confirmed by the presence of furrows and trees growing in rows. Fire as the stand origin was confirmed by the lack of furrows or tree rows, and also by the presence of charred snags and coarse woody debris. If there was any ambiguity about the origin of a stand, the stand was excluded.

Stands ages for this comparative chronosequence study were selected with the goal of achieving replication ($n$ = 3) within three age classes representing distinct periods of stand development post-disturbance determined from a previous study (Rothstein et al., 2004): establishment (3–6 years), exponential growth (12–17 years) and maturity (39–69 years). Our original goal was to include a self-thinning phase as well (25–35 years); however, we were unable to locate plantations in this age class that met our other criteria. An important, potentially confounding factor that could not be controlled is that the harvest and planting regime employed during the years of origin of the mature plantations (1936–1955) is different than that of the more recent stands. The current management strategy put into place in the 1980s to promote Kirtland's warbler calls for dense stands (approximately 3700 trees/ha) with regular openings (1/4 acre opening for every acre planted); this differs from less dense stands planted previously for timber that have no planned openings (Phil Huber, USDA Forest Service Wildlife Biologist for the Mio Ranger District). Exact planting densities for stands planted prior to warbler management are unavailable, but are estimated between 1700 and 3000 trees/ha. We included these older stands because they were the only option to provide insight into structural features of mature plantations in this system. We address the implications of this change in density for our results in Section 4.

## 2.2. Plot layout and field measurements

Once a stand was accepted, an approximately 10-ha square site was located within the boundary, at least 50 m from any edge and on a north/south axis. The shape of three of the stands required fitting the site along a northwest/southeast axis with a slightly rectangular shape (1950 fire, 1936 plantation and 1999 fire; Fig. 1). Stratified random sampling was used for plot selection within each site to assign 20 locations for sampling plots. Each 10-ha site was divided into four quadrats of equal size. Within each quadrat we randomly selected five plot locations using a random number table for selection of $X$ and $Y$ coordinates on a UTM grid. Each plot was circular and 8 m in diameter. In the event that two plot boundaries overlapped, a new plot center was randomly chosen for the second plot. Some plots in the plantation sites fell within openings, some fell within planted rows, and some overlapped both; all sites were included in analysis.

Within each plot, we measured the diameter at breast height (DBH, 1.37 m) and total tree height (using a laser hypsometer) for

all standing trees, live and dead greater than 2 m high, and counted and measured the heights of all tree seedlings and saplings less than 2 m in a 1/4 section of each plot. We measured the length and diameter at each end of all pieces of CWD larger than 5 cm in diameter. We only included the volume of CWD that fell within the plot border. We assigned each piece of CWD to one of four decay classes: (I) newly downed wood with most or all bark still present, (II) wood with sloughing bark that held its original shape and was structurally sound (could not be crushed), (III) wood that still held its shape but could be crushed, or (IV) wood that had lost its structure and was variously flattened. For decay classes I–III one diameter measurement was made with calipers at each end, whereas for decay class IV, two orthogonal measurements were taken at each end, a height and width. These two measurements were averaged to estimate diameters for volume calculations. To calculate volume, we used the formula for the frustrum of a cone (Eq. (1)):

$$\text{volume} = \frac{1}{3}\pi l(r^2 + rR + R^2) \tag{1}$$

where $l$ is the total length of the piece, $r$ is the radius of the small end, and $R$ is the radius of the large end (Robertson and Bowser, 1999). To quantify forest floor mass, we placed a square metal frame (37 cm × 37 cm) on the south edge of each plot, and collected all recognizable plant litter (Oi + Oe horizons) within the frame. Samples were initially air-dried in a warm greenhouse until they could be oven-dried at 65 °C for at least 48 h and weighed.

Aboveground biomass of jack pine trees from the intermediate and mature stands were calculated using the allometric biomass equation based on DBH and height reported by Perala and Alban (1994) for upper Great Lakes jack pine. Aboveground biomass of jack pine seedlings from the young sites were calculated using an allometric biomass equation reported by Rothstein et al. (2004) predicting biomass from seedling height. Snag volume was determined by first calculating the amount of taper in dead wood (using the CWD measurements of decay classes 1 and 2 from all plots in all sites combined; Eq. (2)),

$$y = 0.0122x \tag{2}$$

where $y$ is the difference in diameter between the two ends of a piece of CWD (cm) and $x$ is the length of the piece in centimeters. This taper calculation was used to estimate the diameters at the base and apex of each snag from the measured DBH and total height. The same equation was used for snags in all sites. The volume of each snag was calculated using the formula for volume of the frustrum of a cone (see Eq. (1)).

## 2.3. Data analysis

For each structural parameter examined (standing biomass (Mg/ha), stem density (#/ha), snag density (#/ha), snag volume (m$^3$/ha), CWD volume (m$^3$/ha), total dead wood volume (m$^3$/ha) and forest floor mass (Mg/ha)), we examined differences in vertical and horizontal structure as a function of mode of stand origin and stand age. We calculated stand-level means based on measurements from all 20 plots within each site as metrics of vertical structure. In order to assess within-stand stand patchiness, or horizontal structure, we used the coefficient of variation (CV) of each structural parameter calculated from the 20 plots within each stand. We used general linear models to analyze effects of stand origin (wildfire vs. plantation; fixed effect), age (years, fixed effect) and site (random effect) on vertical and horizontal structure using R (R Development Core Team, 2008). Data were square-root transformed after adding 0.5 to each value (Zar, 1999) to improve normality and homogeneity of variances. In the analyses of coefficient of variation of snag density and snag volume, one young

plantation was excluded because there were no snags present at any of the plots. Statistical significance for all analyses was accepted at $\alpha = 0.05$.

## 3. Results

Aboveground biomass of jack pine increased consistently with time since disturbance ($P < 0.001$), from a low of 0.25 Mg/ha at age 4 to a high of 105 Mg/ha by age 69 (Fig. 2a). There was no difference in aboveground biomass between wildfire-origin and plantation stands ($P = 0.408$), nor was there any interaction between stand origin and age ($P = 0.634$). Within-stand patchiness of aboveground biomass declined significantly with stand age ($P = 0.011$) with CVs of young stands ranging from 122 to 197% and CVs of mature stands ranging from 43 to 95% (Fig. 2b). There was no difference between wildfire and plantation chronosequences in the pattern of within-stand patchiness over time ($P = 0.740$), nor was there any interaction between stand origin and age ($P = 0.154$).

Despite the extremely high live stem density of some of the young fire-origin stands, and the apparent decline in density with stand age (Fig. 2c), neither age ($P = 0.165$), mode of stand origin ($P = 0.715$) nor age × origin interaction ($P = 0.971$) was statistically significant in our mixed-effects model. This is likely due to the fact that the range of variation in live stem density of young, fire-origin stands (1552–24,192) far exceeded that among any of the other stands (Fig. 2c). Density in plantation stands averaged approximately 2300 stems/ha in the young and intermediate-aged sites and approximately 550 stems/ha in the mature stands. However, it is important to note that the three oldest plantation stands were likely planted at lower density than the others, potentially exaggerating density declines with age. In contrast, density in fire-origin stands ranged from an average of approximately 11,000 stems/ha in the young stands, 2100 stems/ha in intermediate-aged sites, and an average of approximately 1500 stems/ha in the mature stands. In contrast to stand-level means of stem

density, changes in within-stand patchiness over time followed very different patterns for wildfire-origin vs. plantation stands (origin × age interaction $P < 0.001$) (Fig. 2d). Patchiness of stem density within fire-origin stands was very high in establishing stands, intermediate in the exponential growth phase and low in mature stands. In contrast, patchiness within plantation stands was uniformly low and similar to that of mature fire-origin stands across all stand ages.

Snag density was significantly affected by both stand age ($P < 0.001$) and stand origin ($P = 0.002$) with no significant interaction between origin and age ($P = 0.777$) (Fig. 3a). In plantation stands, snag densities increased from an average of 3 ha$^{-1}$ in young stands to 83 ha$^{-1}$ in intermediate stands to 268 ha$^{-1}$ in mature stands. Snag densities were nearly always higher in fire-origin stands, with a less pronounced temporal trend, with densities averaging 252, 156 and 557 snags/ha in the young, intermediate and mature stands, respectively. Of particular note was the difference in snag density in the youngest age class, where all the three of the youngest wildfire stands had greater than 150 snags/ha, reflecting the legacy structure inherited from the preceding stand. Within-stand patchiness of snag density (Fig. 3b) declined with stand age in both plantation and fire-origin stands ($P < 0.001$). There was a significant interaction between stand age and stand origin ($P = 0.043$) reflecting the extremely high CVs of two young and one intermediate-aged plantation stand. This interaction should be interpreted with caution, however, because these two high CV values are driven by the near-zero means, rather than by true patchiness. For these three sites, we encountered only a single snag among the 20 plots. Furthermore, the third young plantation stand was not included in estimates of patchiness because we encountered no snags in any of our plots.

Snag volume increased with time since disturbance ($P < 0.001$) with significantly greater volume in wildfire stands ($P = 0.014$) (Fig. 3c). The difference in snag volume between wildfire-origin and plantation sites appeared greater in young stands (2.5 m$^3$/ha
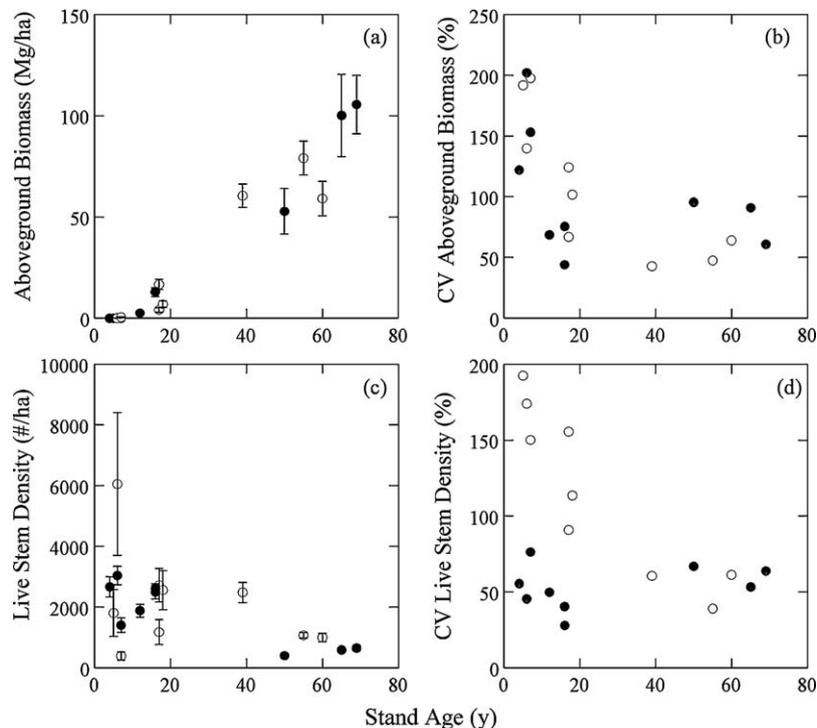


**Fig. 2.** Aboveground biomass (a) and stem density (c) of jack pine and patchiness of aboveground biomass (b) and stem density (d) along chronosequences of both plantation and fire-origin. Values in (a) and (c) represent means (±1 SEM) of 20 plots per site and values in (b) and (d) represent coefficients of variation across all 20 plots per site. Closed circles indicate plantation stands and open circles indicate wildfire-origin stands.
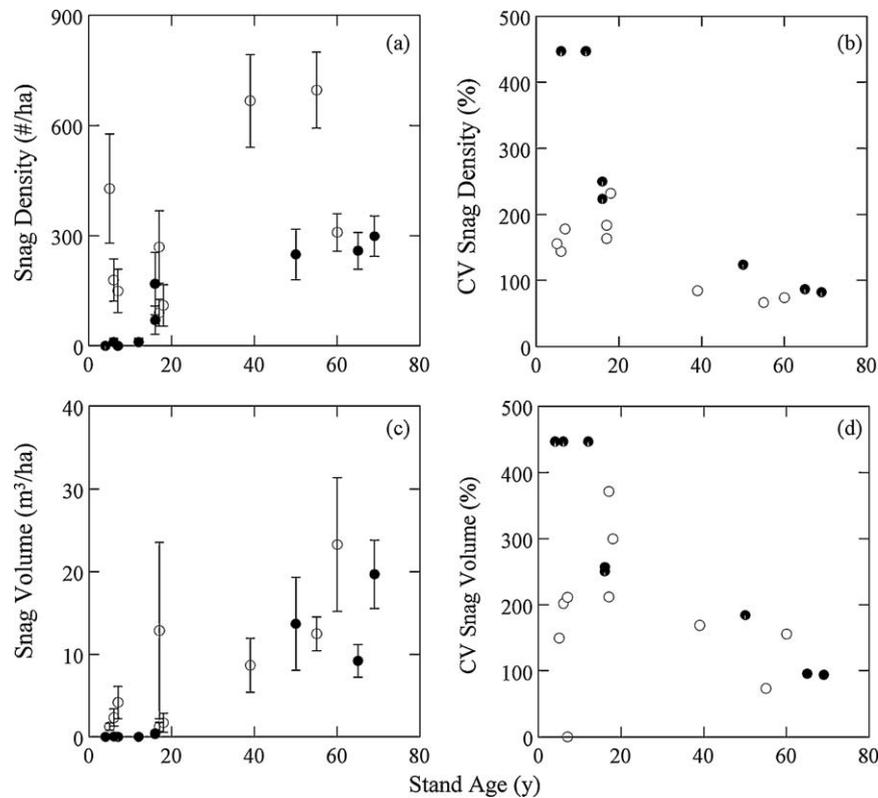
**Fig. 3.** Snag density (a) and volume (b) of jack pine, and patchiness of snag density (b) and volume (d) along chronosequences of both plantation and fire-origin. Values and symbols are as described for Fig. 2.

vs. 0.02 m³/ha) than old stands (14.8 m³/ha vs. 14.2 m³/ha); however, the interaction term was not statistically significant ($P = 0.992$). Within-stand variation in snag volume followed patterns nearly identical to variation of snag density with significant declines with stand age in both wildfire-origin and plantation chronosequences ($P = 0.001$), and significant differences between wildfire-origin and plantation stands ($P = 0.009$) (Fig. 3d). In this case, however, the age × origin term was not statistically significant ($P = 0.080$). As for snag density, within-stand patchiness of snag volume was inflated in young plantation stands due to the near-zero means ($P = 0.001$).

There was a significant effect of stand origin on CWD volume ($P = 0.002$), as well as a significant age × origin interaction ($P < 0.001$) whereby CWD followed distinctly different temporal patterns with stand development in wildfire-origin vs. plantation chronosequences (Fig. 4a). Coarse woody debris volume was highest in jack pine sites of wildfire-origin during early stand development (as high as 62 m³/ha at 6-year post-fire, with a mean of 49 m³/ha in sites aged 5, 6 and 7 years) and then declined with stand age until about 40 years of age in an inverse J-shaped curve (Fig. 4a). Plantation sites, on the other hand, initially contained a much lower volume of CWD (mean of 12 m³/ha in sites aged 4, 6 and 7 years) than the wildfire sites at those ages and then increased in volume in old stands to a mean of 22 m³/ha. Within-stand patchiness of CWD volume was higher in plantation stands ($P = 0.025$), but displayed no significant pattern with stand age ($P = 0.918$) (Fig. 4b).

We also separated CWD by decay classes to compare trends across stand age and between modes of stand origin (Fig. 5). Wood of decay class 1 made an insignificant contribution to CWD pools across all stand ages for both plantation and wildfire-origin sites. Young wildfire sites were dominated by CWD of decay class 2 (82% of total volume), with dominance shifting to decay classes 3 (69%)

and 4 (27%) at intermediate-aged sites. In contrast, CWD of mature, fire-origin stands was evenly distributed among decay classes 2 (32%), 3 (40%) and 4 (26%). Distribution of CWD among decay classes was similar between fire-origin and plantation stands of similar ages.

Total dead wood volume (snag + CWD volume) was calculated to understand dead wood structure in the stands without the confounding effects of the timing of snag transfer to CWD in each individual site (Fig. 4c). While most snags generally fall a few years after a fire, some snags fall earlier or later, or in different stages of decay, or only break away partially, leaving part of the snag behind (Passovoy and Fule, 2006). By examining all dead wood together, we can see a snapshot of each site at one time for a total volume measurement. The difference between plantation and wildfire-origin stands was significant ($P = 0.001$), as was the interaction between mode of origin and stand age ($P < 0.001$). The patterns observed were similar to that of CWD volume, but with the addition of snag volume, the difference between young wildfire and young plantation stands was exacerbated. Across fire-origin stands total dead wood volume showed a U-shaped curve with decreasing volume from young to intermediate ages, followed by increasing volumes in the oldest stands. Because plantation stands start with such low levels of dead wood, the pattern over stand development is dominated by the increase from intermediate-aged to older stands. Patchiness of total dead wood volume did not vary significantly with stand age ($P = 0.166$), was not significantly different between plantation and wildfire-origins ($P = 0.222$), and there was no significant interaction between origin and age ($P = 0.139$) (Fig. 4d).

Forest floor mass differed significantly between wildfire-origin and plantation chronosequences ($P = 0.002$) and there was a significant interaction between effects of age and origin on forest floor mass ($P = 0.002$) (Fig. 6a). In the three youngest stands, forest floor mass was lower following fire (mean = 6.4 Mg/ha) than
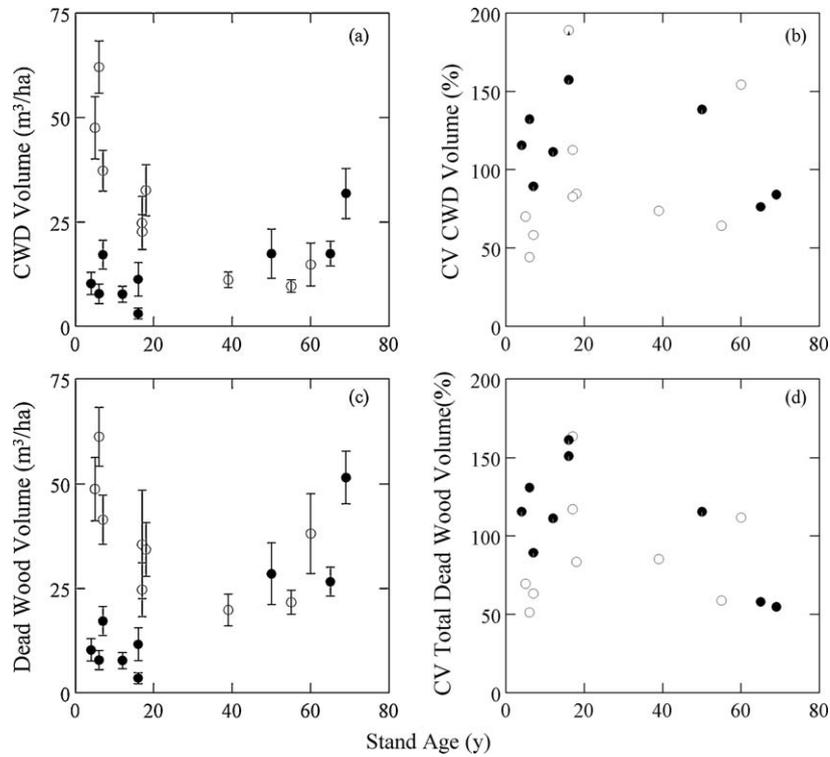
**Fig. 4.** Coarse woody debris volume (a), patchiness of coarse woody debris volume (b), total dead wood volume (c) and patchiness of total dead wood volume (d) along chronosequences of both plantation and fire-origin. Values and symbols are as described for Fig. 2.

planting (mean = 12.6 Mg/ha). For the rest of the chronosequence, forest floor mass was similar between wildfire-origin and plantation stands averaging 8.6 and 10.6 Mg/ha across intermediate and old stands, respectively. Forest floor patchiness declined

with increasing stand age ($P$ = 0.001), with no difference between plantation and wildfire-origin stands in forest floor patchiness ($P$ = 0.797), nor any interaction between origin and age ($P$ = 0.266) (Fig. 6b).
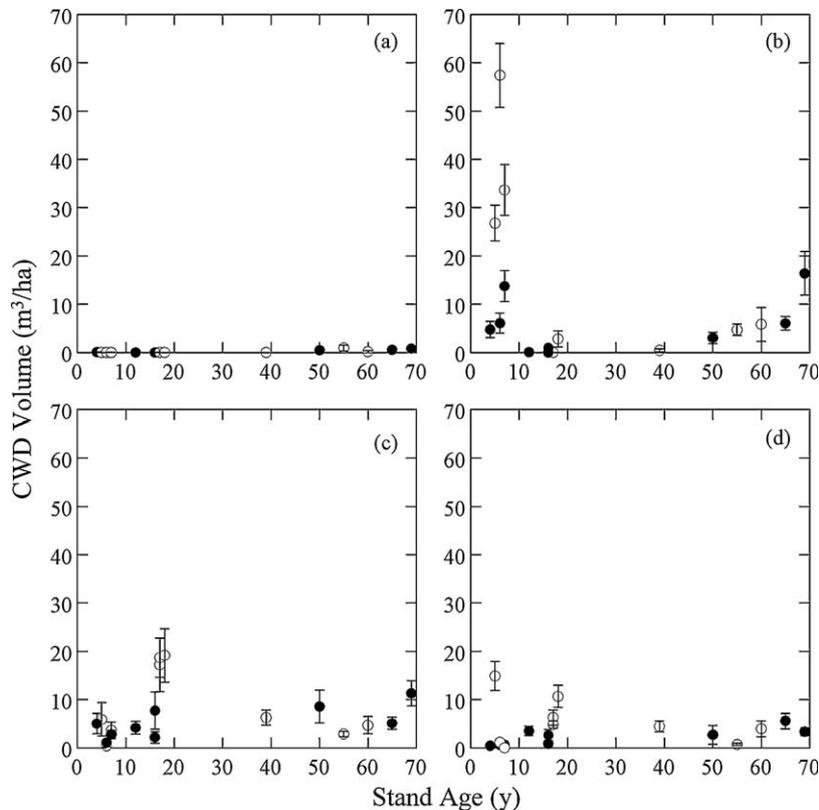


**Fig. 5.** Volume of coarse woody debris along chronosequences of both plantation and fire-origin for decay classes 1 (a), 2 (b), 3 (c) and 4 (d). Values are means (±1 SEM) of 20 plots per site and symbols are as described for Fig. 2.
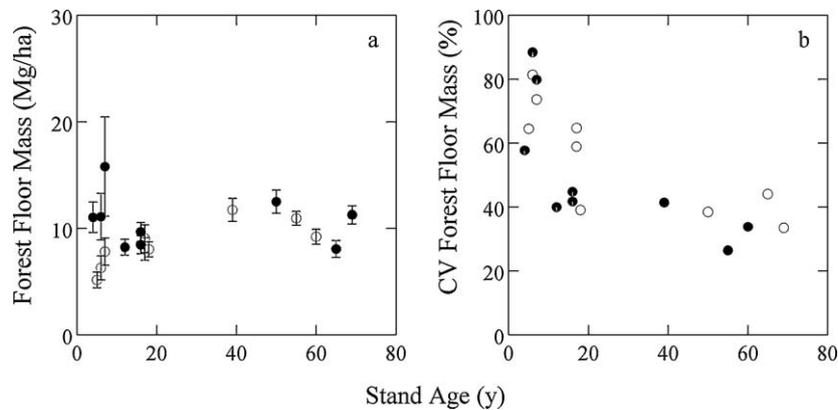
**Fig. 6.** Forest floor mass (a) and patchiness of forest floor mass (b) along chronosequences of both plantation and fire-origin. Values and symbols are as described for Fig. 2.

## 4. Discussion

We found that plantations produced jack pine stands that were largely indistinguishable from wildfire-origin stands in the later stages of stand development, but that differed markedly in structure early in stand development. Key structural features of young and intermediate-aged stands not replicated well in plantations included stem density, internal patchiness, snags, CWD and forest floor mass. Widespread harvesting and planting of jack pine for Kirtland's warbler habitat has largely replaced wildfire as the dominant mode of stand initiation in this area. For example, Donner et al. (2008) found that warbler plantations made up over 80% of the 5–23-year old jack pine stands on public lands in 2004. Harvesting and planting has clearly been demonstrated as an effective method of creating habitat for this single endangered species (Probst and Weinrich, 1993; Donner et al., 2008), but our results demonstrate that this management has resulted in marked differences in other ecosystem components at the stand level. This, in turn, may affect the landscape-scale distribution of habitat over the larger areas managed predominantly for Kirtland's warbler.

Stem density has been identified as a factor that is strongly related to stand function (Turner et al., 2004) and has been shown to be highly variable among stands of trees that regenerate following stand-replacing wildfire (Kashian et al., 2004). As expected, we observed a high degree of variability of stem density in young and intermediate-aged wildfire stands (both within and among stands) that far exceeded that of similar-aged plantations. Within stands, we observed much greater patchiness in stem density of wildfire-regenerated stands through the first ∼20 years of stand development, which declined to levels comparable to those of plantations in stands aged 40 years+ (Fig. 2d). Our results are in good agreement with those of Kashian et al. (2005) who found that CVs of stand density for a chronosequence of lodgepole pine decreased from 231% in 12-year old stands to 91% in stands aged 50–100 years and to 37% for stands aged 200–250 years. This patchiness in density creates increased horizontal complexity in a stand, such that sparse areas have greater light availability, while dense areas likely experience canopy closure sooner. Declines in patchiness with stand age likely result from a combination of increased mortality in initially dense patches and infill recruitment in initially sparse patches (Kashian et al., 2005). Despite the planting pattern of these plantations, which involves regularly spaced openings designed to emulate variable patterns associated with fire, patchiness of stem density was found to be much lower in the plantations early in stand development.

Jack pine regeneration following wildfire also appears highly variable among stands, with young stands in this study ranging in seedling density from 1500 to 24,000 stems/ha (Fig. 2c). Kashian et al. (2004) also found great variability in stem densities among four, 12-year old lodgepole pine forests in Wyoming, USA. Regeneration density following fire is dependent on both deterministic factors such as density, age, serotiny and cone crop of the preceding stand, as well as stochastic factors such as weather conditions that affect seedling establishment and survival following fire. Interestingly, the young stand in our study with the lowest seedling density regenerated following a summer fire (July 23, 1998) (Table 1) where germinating seedlings would be expected to experience much greater drought stress compared to the other two sites which regenerated following fires in the early spring (May 1, 1999 and April 30, 2000). Stem densities of plantations were much less variable among stands and were centered at the lowest end of the range of stem densities observed in young fire-origin stands. This suggests two important landscape-level consequences of the transition from wildfire to harvesting/planting as the dominant disturbance regime. First, our data point to an overall homogenization of young stand density with reduced variation among patches across the landscape. Second, our data suggest an overall loss of extremely dense young stands across the landscape—the planned openings in current plantations are designed to preserve habitat associated with low-density jack pine barrens, but there are no analogous management features designed to mimic the structural features of extremely dense young stands.

Snags are crucial in forested ecosystems for many organisms, especially cavity-nesting birds. Early in stand development in

**Table 1**
Stand attributes. Age refers to the age of the stand in 2005. Percent jack pine refers to jack pine basal area/total stand basal area. NA = not applicable, ND = no data.

| Name | Origin | Age | Ownership | Fire date | Mean snag dbh (cm) | % jack pine |
|------|--------|-----|-----------|-----------|--------------------|-------------|
| cc01 | Clearcut | 4 | DNR | NA | ND | ND |
| pbr | Clearcut | 6 | USFS | NA | ND | ND |
| cc98 | Clearcut | 7 | USFS | NA | ND | ND |
| tow | Clearcut | 12 | DNR | NA | ND | 99 |
| kw | Clearcut | 16 | USFS | NA | ND | 94 |
| pin | Clearcut | 16 | DNR | NA | ND | 83 |
| par | Clearcut | 50 | USFS | NA | ND | 96 |
| can | Clearcut | 65 | USFS | NA | ND | 67 |
| val | Clearcut | 69 | USFS | NA | ND | 76 |
| np | Wildfire | 5 | USFS | April 30 | 3.8 | ND |
| atv | Wildfire | 6 | USFS | May 1 | 9.1 | ND |
| mech | Wildfire | 7 | DNR | July 23 | 13.4 | ND |
| per | Wildfire | 17 | DNR | June 13 | 8.6 | 100 |
| rfg | Wildfire | 17 | DNR | July 9 | 7.4 | 90 |
| hel | Wildfire | 18 | DNR | July 18 | 5.1 | 100 |
| dam | Wildfire | 39 | DNR | ND | ND | 95 |
| brg | Wildfire | 55 | USFS | ND | ND | 90 |
| club | Wildfire | 60 | USFS | ND | ND | 98 |

wildfire sites, large numbers of fire-killed trees provide potential habitat for birds and small mammals, as well as for wood-eating organisms (Nappi et al., 2003; Hutto, 2006; Lonsdale et al., 2008). As predicted, snag density in young plantations is very low due to recent removal for harvest and low snag density in the preceding stands (Fig. 3a). Greater numbers of snags in these wildfire sites at early ages are consistent with previous studies (Clark et al., 1998); however, we also observed greater numbers of snags in two of the wildfire stands at the older ages. It is important to note that comparisons with mature plantations are potentially confounded by the lower density of planting at the time those plantations were established—the current generation of plantations is likely to produce higher numbers of snags as they age due to their higher planting density.

Many studies measuring the effects of reduced snag densities in conifer stands due to post-fire salvage logging have shown strong effects on woodpecker populations; these studies reinforce the importance of post-fire snags in fire systems. Nappi et al. (2003) showed direct correlations between the larger, less deteriorated snags found immediately after a fire, and wood-boring beetle larvae holes. The holes strongly predicted foraging activity by black-backed woodpeckers. Hutto (2006) stresses that the current management guidelines for 6–10 snags/ha in most conifer harvest systems are inadequate, due to much higher snag requirements of fire specialist bird species. Clearly, this density of snags is far lower than the 150–430 snags/ha we observed in young wildfire-origin stands. Not only are the recommended densities initially too low for these birds, but the lower densities may leave the existing snags more vulnerable to wind throw, so the lifespan of the snags is likely shorter (Mast and Chambers, 2006).

Examination of CWD dynamics between wildfire-origin and plantation chronosequences further enhances the importance of the stands less than 20 years old in assessing differences between the two modes of stand origin (Fig. 4a and c). While mature plantations and mature fire-origin stands are indistinguishable in terms of CWD volumes, the young fire stands contain approximately five times the CWD volume of young plantations. The data for total dead wood in fire-origin stands match well with the U-shaped model of dead wood dynamics after stand-destroying disturbance (Sturtevant et al., 1997) composed of two stages: (1) an initial stage in which legacy dead wood from the preceding stand decays and declines, followed by (2) an accumulation stage in which new dead wood is added from mortality in the regenerated stand. In this case, wildfire stands initially have much higher dead wood levels than plantations due to legacy wood; however, both treatments show a nearly identical pattern of de novo dead wood accumulation after age 40 (Fig. 4c). The pattern of decay of legacy CWD and addition of new CWD wood through self-thinning processes is clear in examining the distribution of CWD among decay classes in fire-origin stands. CWD pools are dominated by sound, undecomposed material shortly after the fire, followed by decomposition and deterioration over the next ~10 years which shifts dominance to decay classes 3 and 4 by the exponential growth phase, then finally mature stands receive a pulse of relatively sound CWD through self-thinning (Fig. 5). These patterns suggest that habitat quality for organisms requiring relatively sound dead wood will be high early and late in stand development, but poor in the middle years.

Reductions in snags and CWD across the landscape due to replacement of wildfire by extensive harvesting and planting are likely to be even greater than those indicated by simple stand-level comparisons (Figs. 3 and 4). Because wildfire disturbance is highly stochastic and harvesting is highly regular, these two disturbance regimes lead to very different stand age distributions across the landscape. In an unmanaged forest, approximately one-third of the landscape would be older than the average fire return interval (Van Wagner, 1978), whereas no stands in a fully regulated forest would be older than the harvest rotation length. Therefore extensive plantation management should result in major reductions in dead wood pools across the landscape due to the combination of the elimination of legacy wood in young stands, as well as the harvesting of older stands before they are able to accumulate significant quantities of new snags and CWD.

Forest floor detritus holds moisture and nutrients (Simard et al., 2001), provides sites for mineralization of nitrogen (Hazlett et al., 2007; Westbrook et al., 2006; Yermakov and Rothstein, 2006), regulates temperature (Matsushima and Chang, 2006), and provides habitat for small mammals, insects and other invertebrates (Hannam et al., 2006). Furthermore, depth of forest floor detritus can have an important selective effect on plant seedling establishment as some species may be able to establish with thick duff layers, whereas others may require a mineral seedbed. As has been reported elsewhere (Greene et al., 2007), wildfire reduced mass of the forest floor relative to mature stands. In contrast, forest floor mass of young plantations was elevated relative to mature stands, presumably due to additions of fine litter associated with harvesting. Harvesting and planting in jack pine forests of this area often results in reduced vascular plant diversity relative to fire-regenerated stands (Abrams and Dickman, 1982; Houseman and Anderson, 2002); the absence of a mineral seedbed in recently harvested stands may contribute to this phenomenon by restricting establishment of small-seeded species.

Interestingly, fire-regenerated stands and plantations are indistinguishable in terms of forest floor mass at intermediate and mature age classes. Differences in dead wood loads between the two modes of stand origin may explain the different trajectories of forest floor mass early in stand development. Presumably, decomposition and fragmentation of large volumes of snags and CWD contributes to the forest floor in the 10–20 years following wildfire. In contrast, slash from logging leaves behind large amounts of fine litter in the young plantations, but while that litter decays there is no major pool of snags and CWD to contribute to further development of the forest floor, so levels drop rapidly, until the developing stand begins to add significant amounts of fine litter.

## 5. Conclusions

In this study, we show that forest management aimed at preserving and enhancing the population of a single endangered species results in greatly simplified habitat structure in young and intermediate-aged stands. Because the period of suitable Kirtland's warbler habitat is short (ca. 10 years) relative to the standard 50-year rotation length for jack pine in this area, continual harvesting of older stands is necessary just to maintain existing levels of breeding habitat. Thus it is logical to expect that the trend in simplification evident at the stand level is perpetuated across the landscape as well. Of particular concern are the effects of extensive harvesting and planting on the landscape-level availability of snags and CWD. We have shown that these structural features are most prevalent in young, fire-origin stands and in older stands—the two stand types most threatened by extensive plantation management.

Our finding that Kirtland's warbler plantations fail to mimic the structural features associated with a natural disturbance regime, are supported in a recent review by Hutto et al. (2008), where they argue that utilizing artificial means to mimic post-fire conditions will never suffice to mimic the structural and functional properties of fire-origin stands. Hutto et al. (2008) argue instead that we should work to accommodate natural fire events and embrace natural processes wherever possible. Unfortunately, public lands in northern Lower Michigan are highly fragmented and dotted with inholdings and small communities, making large wildfires in

this area socially and politically unacceptable. Given these constraints, state and federal land managers interested in emulating natural disturbance dynamics will need to work creatively with limited opportunities. We argue that their highest priority should be to protect areas burned by the occasional large fires that do still occur in this area—in other words no salvage logging and no infill planting. This will ensure that the unique habitat structures associated with young, fire-origin stands are maintained to some degree. Furthermore, managers should also consider increasing their goals for snags and CWD in Kirtland's warbler plantations, perhaps even leaving some patches of snags by girdling groups of trees, recognizing that girdled-tree snags are not ecologically equivalent to fire-killed snags (Hutto, 2006). Leaving more snags in the system will also help to increase the CWD levels as the snags fall. Lastly, management should address these issues at the landscape scale. Large-scale harvest management skews stand age toward younger stands (Lindenmayer and McCarthy, 2002; Hansen et al., 1991); over time there are fewer really old stands and more evenly distributed numbers of cohorts in all other ages. Management that allows a more natural distribution of stand ages by leaving some old stands would more closely reproduce wildfire-generated landscape conditions.

## Acknowledgements

## References

Abrams, M.D., Dickman, D.I., 1982. Early revegetation of clear-cut and burned jack pine sites in northern Lower Michigan. Canadian Journal of Botany 60, 946–954.

Attiwill, P.M., 1994. The disturbance of forest ecosystems—the ecological basis for conservative management. Forest Ecology and Management 63, 247–300.

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. Forestry Chronicle 75, 49–54.

Brais, S., Sadi, F., Bergeron, Y., Grenier, Y., 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. Forest Ecology and Management 220, 216–226.

Brassard, B.W., Chen, H.Y.H., 2006. Stand structural dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25, 115–137.

Charron, I., Greene, D.F., 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Canadian Journal of Forest Research 32, 1607–1615.

Clark, D.F., Kneeshaw, D.D., Burton, P.J., Antos, J.A., 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Canadian Journal of Forest Research 28, 284–290.

Cleland, D.T., Crow, T.R., Saunders, S.C., Dickman, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M., Brosofske, K.D., 2004. Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. Landscape Ecology 19, 311–325.

Converse, S.J., White, G.C., Farris, K.L., Zack, S., 2006. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. Ecological Applications 16, 1717–1729.

Donner, D.M., Probst, J.R., Ribic, C.A., 2008. Influence of habitat amount, arrangement, and use on population trend estimates of male Kirtland's warblers. Landscape Ecology 23, 467–480.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155, 399–423.

Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noel, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., Swift, L., 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research 37, 1012–1023.

Hannam, K.D., Quideau, S.A., Kishchuk, B.E., 2006. Forest floor microbial communities in relation to stand composition and timber harvesting in northern Alberta. Soil Biology & Biochemistry 38, 2565–2575.

Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests. Bioscience 41 (6), 382–392.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., De Grandpre, L., 2006. Changes in spatial pattern of trees and snags during structural development in Picea mariana boreal forests. Journal of Vegetation Science 17, 625–636.

Hazlett, P.W., Gordon, A.M., Voroney, R.P., Sibley, P.K., 2007. Impact of harvesting and logging slash on nitrogen and carbon dynamics in soils from upland spruce forests in northeastern Ontario. Soil Biology & Biochemistry 39, 43–57.

Heliola, J., Koivula, M., Niemela, J., 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology 15, 370–377.

Houseman, G.R., Anderson, R.C., 2002. Effects of jack pine plantation management on barrens flora and potential Kirtland's warbler nest habitat. Restoration Ecology 10, 27–36.

Hunter, M.L., 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65, 115–120.

Hutto, R.L., 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology 20, 984–993.

Hutto, R.L., Conway, C.J., Saab, V.A., Walters, J.R., 2008. What constitutes a natural fire regime? Insight from the ecology and distribution of coniferous forest birds in North America. Fire Ecology 4, 115–132.

Kashian, D.M., Tinker, D.B., Turner, M.G., Scarpace, F.L., 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. Canadian Journal of Forest Research 34, 2263–2276.

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86, 643–654.

Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Canadian Journal of Forest Research 34, 763–777.

Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I., McCarthy, M.A., 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology 16, 338–345.

Lindenmayer, D.B., McCarthy, M.A., 2002. Congruence between natural and human forest disturbance: a case study from Australian montane ash forests. Forest Ecology and Management 155, 319–335.

Lindenmayer, D.B., Recher, H.F., 1998. Aspects of ecologically sustainable forestry in temperate eucalypt forests—beyond an expanded reserve system. Pacific Conservation Biology 4, 4–10.

Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. European Journal of Forest Research 127, 1–22.

Mast, J.N., Chambers, C.L., 2006. Integrated approaches, multiple scales: snag dynamics in burned versus unburned landscapes. Professional Geographer 58, 397–405.

Matsushima, M., Chang, S.X., 2006. Vector analysis of understory competition, N fertilization, and litter layer removal effects on white spruce growth and nutrition in a 13-year-old plantation. Forest Ecology and Management 236, 332–341.

Nappi, A., Drapeau, P., Giroux, J.F., Savard, J.P.L., 2003. Snag use by foraging black-backed woodpeckers (Picoides arcticus) in a recently burned eastern boreal forest. Auk 120, 505–511.

Passovoy, A.D., Fule, P.Z., 2006. Snag and woody debris dynamics following severe wildfires in northern Arizona ponderosa pine forests. Forest Ecology and Management 223, 237–246.

Perala, D.A., Alban, D.H., 1994. Allometric biomass estimators for aspen-dominated ecosystems in the upper Great Lakes. In: Research Paper NC-314, Forest Service, U.S. Department of Agriculture, North Central Forest Experiment Station, St. Paul, MN.

Probst, J.R., Weinrich, J., 1993. Relating Kirtland's warbler population to changing landscape composition and structure. Landscape Ecology 8, 257–271.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria ISBN 3-900051-07-0, URL http://www.R-project.org.

Robertson, P.A., Bowser, Y.H., 1999. Coarse woody debris in mature Pinus ponderosa stands in Colorado. Journal of the Torrey Botanical Society 126, 255–267.

Rothstein, D.E., Yermakov, Z.Y., Buell, A.L., 2004. Loss and recovery of ecosystem carbon pools following stand-replacing wildfire in Michigan jack pine forests. Canadian Journal of Forest Research 34, 1908–1918.

Simard, A.J., Haines, D.A., Blank, R.W., Frost, J.S., 1983. The Mack Lake fire. In: USDA For. Serv. Gen. Tech. Rep. NC-83, .

Simard, D.G., Fyles, J.W., Pare, D., Nguyen, T., 2001. Impacts of clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal forest. Canadian Journal of Soil Science 81, 229–237.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation 83, 247–257.

Solomon, B.D., 1998. Impending recovery of Kirtland's warbler: case study in the effectiveness of the Endangered Species Act. Environmental Management 22, 9–17.

Stocks, B.J., 1989. Fire behavior in mature jack pine. Canadian Journal of Forest Research 19, 783–790.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecological Applications 7, 702–712.

Tinker, D.B., Knight, D.H., 2001. Temporal and spatial dynamics of coarse woody debris in harvested and unharvested lodgepole pine forests. Ecological Modeling 141, 125–149.

Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7, 751–775.

Van Wagner, C.E., 1978. Age-class distribution and forest fire cycle. Canadian Journal of Forest Research 8, 220–227.

Werlein, J.O., 1998. Soil Survey of Crawford County, Michigan. U.S. Department of Agriculture. Natural Resources Conservation Service and U.S. Forest Service, 277 pp., 96 sheets.

Westbrook, C.J., Devito, K.J., Allan, C.J., 2006. Soil N cycling in harvested and pristine Boreal forests and peatlands. Forest Ecology and Management 234, 227–237.

Wright, P., Harmon, M., Swanson, F., 2002. Assessing the effect of fire regime on coarse woody debris. In: General Technical Report, PSW-GTR-181, US Department of Agriculture Forest Service.

Yermakov, Z., Rothstein, D.E., 2006. Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. Oecologia 149, 690–700.

Zar, J.H., 1999. Biostatistical Analysis. Prentice Hall, New Jersey, 663 pp.