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Seven decades of change in forest structure and composition in *Pinus resinosa* forests in northern Minnesota, USA: Comparing managed and unmanaged conditions

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ABSTRACT

An understanding of long-term patterns of forest structural and compositional development is critical for anticipating management outcomes and developing appropriate silvicultural strategies for restoring complex forest conditions. In most cases, this information comes from stand-level assessments; however, the impacts and outcomes of management and other disturbances on forest development occur over multiple spatial scales across a landscape. We compared historical (1941) and contemporary (2012–2014) forest structure and composition on 301 plots distributed across managed and unmanaged, late seral red pine (*Pinus resinosa*)-dominated forests in a 1230 ha landscape in north-central Minnesota, USA. Discriminate factor analysis was used to determine which compositional and structural attributes best described the forest conditions between two sampling periods (1941, 2012–2014) and management histories (managed and unmanaged). Plot basal area, average diameter of live trees, richness of tree size classes, and the basal area of standing deadwood were the four most important variables in discriminating between the managed and unmanaged plots in 1941 and 2013. In some cases, structural conditions between managed and unmanaged plots converged, including contemporary BA, trees per hectare, size inequality, and structural complexity indices. In contrast, several attributes, including standing deadwood basal area and percent hardwood basal area, were significantly greater in unmanaged plots after 72 years and highlight the lasting influence of land use on these structural and compositional conditions. The broad ranges of structural and compositional conditions observed across the landscape highlight the importance of having spatially varying desired future conditions across managed stands to approximate this range in live and dead-tree attributes in unmanaged forests. In addition, the lower basal area of standing dead trees documented in this and other comparisons of unmanaged and managed *P. resinosa* systems argues for an increased emphasis on deliberate deadwood and live-tree retention to recruit these features if the restoration of late-successional forest conditions is included as a management objective.

1. Introduction

An understanding of the range of variability of forested ecosystems is recognized as a key element for guiding the development of sustainable forest management strategies (Landres et al., 1999; Franklin et al., 2002; Kuuluvainen, 2002; Haeussler et al., 2007; Keane et al., 2009). These strategies include emulating the natural disturbance processes that historically governed development of compositional and structural diversity across landscapes (Kuuluvainen, 2002; Fraver and Palik, 2012). Forest management within the range of natural variability has been argued as an effective strategy for maintaining diverse, productive, and resilient ecosystems (Swanson et al., 1994; Landres et al., 1999; Chapin et al., 2003). However, forests are slow growing, thus requiring years to appropriately assess the long-term impacts of any given management activity.

Landscape-scale, long-term data sets provide valuable insights into understanding ecological processes and dynamics (Luo et al., 2011), particularly in forested systems where the lifespan of dominant tree species commonly exceed several centuries. Numerous investigations have used long-term monitoring plots from a single

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site or experiment to provide insights on long-term forest dynamics in response to a given management or natural disturbance regime (O'Hara et al., 2007; Saunders and Wagner, 2008; D'Amato et al., 2010); however, high resolution, long-term datasets collected at broad spatial scales are rare thus limiting our understanding of the natural range of structural and compositional conditions at the landscape scale (Pontius et al., 2016). Moreover, patterns and processes within these conditions vary depending on the scale at which they are evaluated (Waring and Running, 2007). Although silvicultural practices have historically focused on the scale of a stand (5–50 ha) within a single time frame (e.g. rotation periods ranging from 30 to 100 years) (Nyland, 1996; Puettmann et al., 2009), their effects may extend beyond the stand level to impact landscape scale processes (Puettmann et al., 2009). In addition, large landscape altering events (i.e., fire, wind, insect outbreaks) affect stand-level dynamics (Tappeiner et al., 2007). Due to these multi-scale effects, the evaluation of forest structure and dynamics should be evaluated across a broad landscape scale (Puettmann et al., 2009).

Forests are typically evaluated based on various key attributes directly affected by management activities, including tree diameter distribution (Lin et al., 1998; Buongiorno and Gilless, 2003; Schwartz et al., 2005; Shao et al., 2005), species composition (Schwartz et al., 2005; Fu et al., 2007), diversity (Eriksson and Hammer, 2006), and the amount of deadwood present (Alban et al., 1994; Duvall and Grigal, 1999). Historically, management activities have typically affected these key forest attributes by creating more uniform sizes, less diversity, and less deadwood (Puettmann et al., 2009). Diversity is a key measure of forests, due to its importance in allowing species to evolve and adapt and to support their ecosystem function; it is measured often by species richness and abundance (Hubbell, 2001; Condit et al., 2006). Structural diversity, notably tree size diversity, is also a key component of forest diversity and is typically affected by forest management activities (McRoberts et al., 2008). While these traditional and non-spatial measures are important, they do not completely describe the overall complexity of a forest, particularly in relation to the spatial distribution of tree biomass (Gadow, 1993; Zenner, 2000).

Numerous studies have investigated the diversity of species and size classes in forests but fewer have combined these elements with tree spatial location as a marked point process (Pommerening, 2002; Kint et al., 2003). These nearest neighbor structural attributes are important in our understanding of forest development (Zenner and Hibbs, 2000; Pommerening, 2008). Management activities typically simplify spatial distributions of trees on the landscape (Puettmann et al., 2009). Given the importance of forest structure in affecting ecosystem processes, including tree growth and regeneration, biogeochemical cycles, and habitat provisioning (Spies, 1998; Young et al., 2011), an understanding of the long-term impacts of management on structural complexity, including spatial conditions, is critical.

Extended rotation forestry extends the period of stand development between harvests and is one approach recommended for enhancing stand structure and complexity in managed forests (Franklin et al., 2007). This approach has been shown to enhance ecological goals (e.g., diversity of age classes, variety of tree sizes, and large trees) thus restoring many old growth structural conditions while still maintaining high productivity (D'Amato et al., 2010; Silver et al., 2013). A comparison of this approach to previously unharvested stands as an assessment of structural and compositional developmental trajectories across a landscape; however, has received less attention.

This study takes advantage of a unique long-term dataset to document the structural and compositional development of a *P. resinosa*-dominated landscape in northern Minnesota, USA. Using stem mapping and modeling, the spatially-explicit structure of 301 inventory plots was reconstructed from historical records. Using this data we were able to quantify the structural and compositional development of managed and unmanaged plots over a 72-year time period. An emphasis was placed on interpreting how changes correspond to general theories of stand dynamics and exploring the implications this may have for future management and conservation efforts. Previous work using long-term, stand-scale re-measurements highlighted the potential for the use of extended rotation periods to restore late-successional, live-tree structural characteristics in managed *P. resinosa* forests (Silver et al. 2013); however, similar evaluations have not occurred at the broader spatial extents over which these systems are managed.

Our specific objectives were to (1) determine the range of variability in structural and compositional attributes that best described unmanaged and managed *P. resinosa* forests over broad spatial scales; and (2) compare these attributes through time within and between unmanaged and managed plots. Based on the findings of previous work conducted at the stand-level, we expect the following at the landscape scale: (1) the range of variability in the structural and compositional attributes will be greater in unmanaged plots (Silver et al., 2013), (2) the structural and compositional attributes will change more in the unmanaged plots (Silver et al., 2013a), (3) due to fire suppression in both the managed and unmanaged stands, we expect an increase in the abundance of fire-sensitive species, an increase in tree densities, and a reduction in small-diameter *Pinus* spp., (Hanberry et al., 2012) and, (4) more complex forest structure across the landscape will develop over time to a greater degree in unmanaged than managed plots (D'Amato et al., 2010; Silver et al., 2013). Through this approach, we address how structure and composition develop within both unmanaged and managed *P. resinosa*-dominated stands which in turn inform approaches for restoring complex structural and compositional conditions in managed landscapes.

2. Materials and methods

2.1. Study site

The Cutfoot Experimental Forest (CEF) located within the Chippewa National Forest in north-central Minnesota, USA, was established in 1932 and is approximately 1230 ha in size (47.549N, 94.092W, Fig. 1). The CEF has a continental climate with a mean annual temperature of 4 °C and a mean annual precipitation of 73 cm (MN State Climatologist, 2014). The soils are deep well-drained loamy sands derived from glacial outwash. The upland forests of this area are dominated by *Pinus resinosa* that largely established following logging and fire (Adams et al., 2004). These forests are classified as northern dry-mesic mixed forest, Red Pine-White Pine Woodland type (FDn33a), based on the Minnesota native plant community classification system (MN DNR, 2003). Historically, fire was the primary natural disturbance in this ecosystem with wind, insects, and diseases also playing an important role at localized scales. With mixed fire intensity and return intervals a landscape mosaic with varying patterns of structural dynamics, species composition, and regeneration were historically created and where *P. resinosa* could dominate in area with moderate severity and short return intervals (Scherer et al., 2016). In addition to *P. resinosa*, the other tree species found in relatively high abundance include: *P. strobus*, *P. banksiana*, *Acer rubrum*, *Populus tremuloides*, *P. grandidentata*, *Betula papyrifera*, *Abies balsamea*, *Picea glauca*, *Quercus rubra*, and *Thuja occidentalis*.

In the CEF's history, a range of forest management activities have occurred, including commercial timber harvests and numerous silvicultural experiments (e.g., Buckman, 1964; Adams et al.,

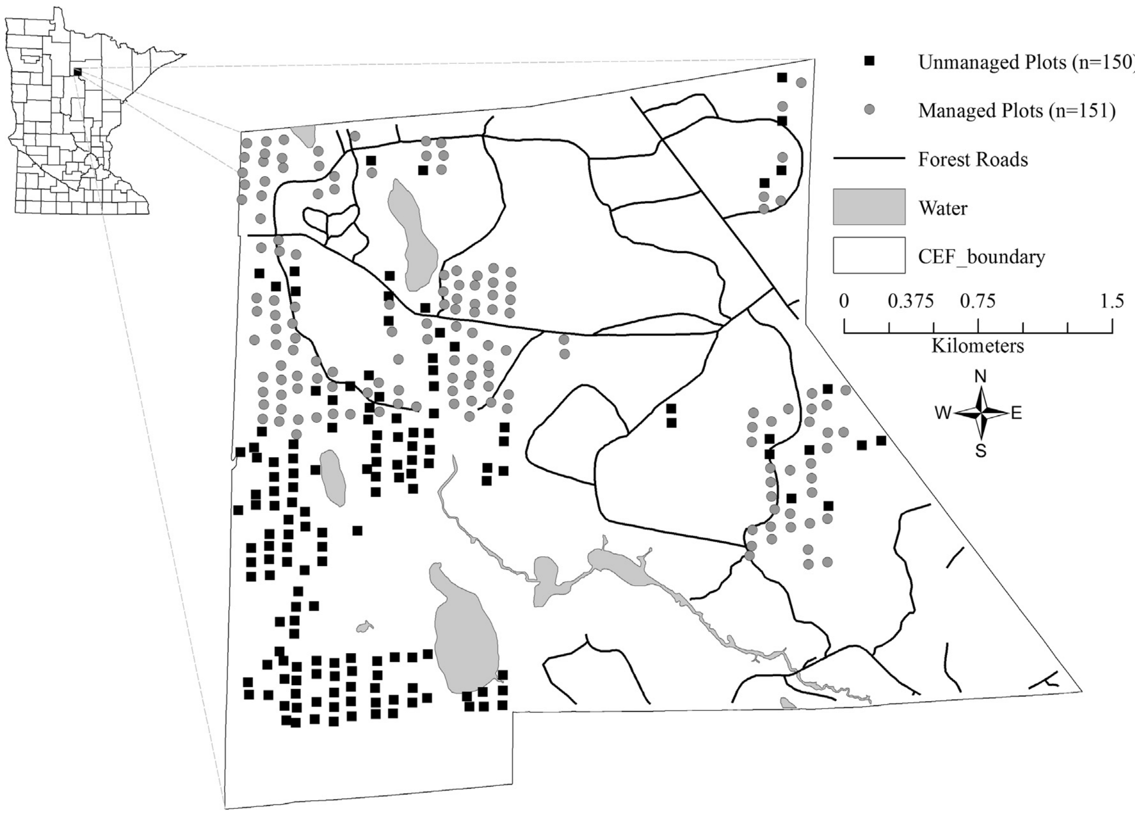

Fig. 1. Geographical distribution of the 301 sample plots within the Cutfoot Experimental Forest located within the Chippewa National Forest, Minnesota, USA.

2004; Bradford and Palik, 2009; D'Amato et al., 2010). The earliest recorded harvests within the study region occurred in the 1910s and have continued until present time (Cutfoot Experimental Forest Archive, Grand Rapids, MN). Within the CEF, the Sunken Lake Natural Area, comprised of approximately 234 ha, was never logged and contains many old-growth stands (Aakala et al., 2012; Fraver and Palik, 2012), providing a useful baseline for comparison with managed portions of the CEF.

2.2. Original plot establishment and design

Within the CEF, 1360 permanent forest inventory plots were established between 1931 and 1934 on a grid with an average spacing of 80.4 m between plots on a north-south transect and 100.5 m between transects. The CEF plots were comprised of a nested circular sampling plot design with an area of 814.3 m^2 and were used to identify species and measure the diameter at breast height (1.4 m; dbh), condition class (alive, dead, cut), and the spatial locations (stem-mapped) of all tree species $\geq$19.3 cm dbh. The central tier plot, with an area of 401.1 m^2, recorded the same attributes as the larger outer plot but included all trees greater than 8.9 cm dbh. The plots were first measured in 1941.

2.3. Plot reestablishment and measurement

From May 2012 through March 2014, 301 inventory plots were relocated, measured and mapped using original field notes and stem maps from 1941 (unpublished data). While each of the plot centers was originally marked with a wooden stake, approximately 65% of these posts were not found upright and intact but, due to the steel nail on the stakes we were able to find historical plot centers using a metal detector. We used the original stem maps to align the current trees with the historically plotted trees. After confirming alignment of all the trees on the plot, we then remeasured the plots in the same manner as was conducted in the original survey. A total of 32,792 trees (living and dead) were mapped in the resurvey. Using data from the 1941 and the 2012–2014 inventories (referred to as the 2013 inventory this point forward) we then grouped the plots into two categories (Fig. 1): (1) "managed plots" where plot data indicated some type of forest management activity based on the presence of stumps in either the 1941 or 2013 inventory (n = 151) or, (2) "unmanaged plots" where plot data indicated no evidence of cutting (i.e. the absence of stumps in 1941 or 2013; n = 150). All plots classified as either managed or unmanaged in either inventory year stayed in that grouping for our analysis. While the managed and unmanaged plots are clustered to one another (see Fig. 1), no significant difference in climate, topography, or soils exist between these groups of plots.

The overarching goal within the managed areas was to maintain or increase *P. resinosa* productivity (CEF Archive). Within the managed areas, 27% of the total basal area was harvested prior to the 1941 inventory and subsequently an additional 20% of the basal area was harvested sometime between the 1941 and the 2013 inventories. The targeted species in the harvested BA in 1941 were largely *P. banskiana* (59%) and *P. resinosa* (41%), whereas harvested BA between 1941 and 2013 included all the pine species (*P. resinosa* (49%), *P. banskiana* (47%), and *P. strobus* (4%)).

2.4. Estimating structural and compositional complexity

There are numerous approaches and indices for quantifying structural and compositional complexity of a forest (Spies and Franklin, 1991; Franklin et al., 2002; McElhinny et al., 2005). We chose to focus on a suite of non-spatial and spatial indices that have proven useful in previous investigations of long-term forest development and could readily be calculated over time from data collected in these inventories, namely tree species, tree diameter, and tree spatial location. Our initial dataset contained 28 variables (Appendix A), which included a range of traditional forest attributes (i.e. tree density, dbh, basal area) and both non-spatial and spatial diversity measures (see Table 2 for details). All variables were calculated at the plot level for each sampling period and area-based measures were standardized to hectares.

For the non-spatial diversity metrics of structural and compositional complexity, we used both richness and abundance measures of tree sizes and tree species. Tree diameter class richness (Nsc), using 2.54 cm dbh classes, and tree species richness (Nspp) were based on the total number of tree diameter classes and species present. Values for Nsc theoretically range from 0 to 33 while Nspp range from 0 to 27. In addition to richness, structural complexity was also assessed using the Gini coefficient (Gini; see Table 2 for details). This measure is calculated from a tree list that is ordered by ascending dbh and does not require arbitrarily delimited diameter classes. Values for this coefficient range from 0 to 1, with 0 values corresponding to plots with perfect size equality and values of 1 representing maximum size inequality (Weiner and Solbrig, 1984). To better understand compositional complexity, we used the Shannon's index (Shannon, 1948) for tree species diversity (Hspp; see Table 2 for details). This common index was chosen because it is sensitive to species richness and is not as influenced by dominant species as other diversity indices (Magurran, 1988; Barnes et al., 1997). With 27 possible species present within both inventories, the theoretical range of Hspp was between 0 and ln (27) = 3.29.

For the spatial diversity metrics, we wanted to include a range of metrics that would capture the variation in tree spacing, tree neighborhood associations, and the interaction between tree size and location of trees on each of the plots (See Table 2). For the variation in tree spacing, we used the Clark Evens index (CE: Clark and Evans, 1954). For this index, values <1 indicate clustering, while values >1 indicate regularity and, a value = 1 denotes a completely random pattern (Kint et al., 2003). To address tree neighborhood associations we evaluated the relative position of different tree sizes in relation to a reference tree using the Diameter Dominance index (DD; see Table 2 for details). For the construction of this neighborhood based index we used n = 4 neighbors, which has been previously shown to be ideal (Pommerening, 2002). This index has 5 possible values: 0.00, 0.25, 0.50, 0.75, and 1.00 that indicate a very suppressed, moderately suppressed, co-dominant, dominant, or strongly dominant condition of the reference tree, respectively (Gadow and Hui, 2002). The interaction between tree size and location was assessed using the stand complexity index (SC, refer to Table 2 for details; Zenner and Hibbs, 2000). This index equates increased structural complexity (higher index values) with increasing tree density and diameter variation. The SC does not appear to have an upper limit but the lower limit is 1 when all trees are the same size and distances between them is equal (Zenner and Hibbs, 2000; McElhinny et al., 2005; Saunders and Wagner, 2008).

2.5. Statistical analysis

To determine which structural attributes best represented the unmanaged and managed plots in 1941 and 2013, we employed a stepwise linear discriminant factor analysis (stepDFA) procedure on our original 28 variables using Wilks' lambda statistic within the klaR and MASS packages (Venables and Ripley, 2002; Weihs et al., 2005). For this analysis, a tolerance of 0.1 was set to eliminate the attributes that provided superfluous information at a 90% level. This analysis finds the best combination of predictor variables that best discriminate between groups while capitalizing on the covariation between the predictors (Legendre and Legendre, 1998). We then tested the significance and the relative importance of each structural attribute selected through stepDFA by using multivariate analysis of variance (MANOVA) based on Wilks' lambda statistic, and averaging the sequential sums of squares over orderings of regressors using the Shapley Value Regression metric within the relaimpo package (Grömping, 2006). To further evaluate the differences within each of the structural attributes between managed and unmanaged plots between 1941 and 2013, comparisons were made using Tukey-Kramer HSD (honestly significant difference) tests. This particular test was chosen because it can accommodate different sample sizes and is more conservative than similar tests (Venables and Ripley, 2002). Scatter diagrams of residuals and normal probability plots were inspected to verify the assumptions of parametric tests. Data were log transformed when necessary to meet parametric assumptions, but the means and standard deviations presented are based on untransformed data. All analyses were conducted using the R system (R Core Team, 2014).

The overall development of the unmanaged and managed plots from 1941 to 2013 was summarized using nonmetric multidimensional scaling (NMDS; Kruskal, 1964) using the structural and compositional attributes selected in stepDFA. Each attribute was standardized by the norm (Legendre and Legendre, 1998) and Bray-Curtis distances were used. The stress value (goodness-of-fit for NMDS) was calculated as described by Kruskal (1964). When stress values are $\leq$10%, the NMDS plot is considered to be a good representation of the structure in the original data (Clarke, 1993). Multiple response permutation procedures (MRPP) were used to determine if forest structural and compositional assemblages statistically differed, based on a $\alpha = 0.05$, between all management histories and sampling periods (1941 and 2012–2014) (McCune et al., 2002). The NMDS and the MRPP analyses were conducted using the vegan package in R (Oksanen et al., 2013).

3. Results

3.1. Structural conditions in managed and unmanaged plots in 1941 and 2013

The final classification resulted in 12 significant structural and compositional attributes that best described managed and unmanaged plots in 1941 and 2013 (Table 1), representing 79.3% of the variability in the final model (Table 3). Their relative importance ranged from 1.3% for percent cover of hardwood species (XHW) to 17.6% for DBH. Traditional plot level metrics explained a large portion (40.8%) of the variance in discriminating between the managed and unmanaged plots in 1941 and 2013 (Table 3). The accuracy of the traditional plot level metrics was largely attributed to plot basal area (BA) and DBH, the two variables with the highest relative importance. Non-spatial and spatial diversity metrics explained lesser amounts of variance. Tree class size diversity (Nsc) and Clark Evans (CE) represented the highest relative importance in non-spatial and spatial diversity metrics, respectively.

Of the factors identified by discriminant analysis, significant differences were observed for the majority of the structural attributes among and between management history and sampling periods (Table 4; Fig. 2). Some traditional metrics were important for distinguishing structural conditions of the management histories. For instance, DBH increased over time and remained greater in managed than unmanaged plots in both inventories (Fig. 2c). On the other hand, BA in unmanaged and managed plots were similar to one another in 2013, despite the managed plots having greater BA than the unmanaged plots in 1941 (Fig. 2a). While not found

Table 1
Mean and standard deviation (SD) of plot-level structural and compositional attributes of trees >8.9 cm dbh. The 12 variables were selected by stepwise discriminate analysis of 28 initial variables (see Appendix A).

Variable	Description	1941 Unmanaged		2013 Unmanaged		1941 Managed		2013 Managed	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Traditional plot metrics									
BA	Basal area of live stems ($m^2\ ha^{-1}$)	10.3	6.2	31.6	13.6	17.4	7.5	35.0	8.9
TPH	Density (100 stems ha^{-1})	6.0	3.5	5.2	2.3	5.5	2.5	4.5	1.8
DBH	Plot average Tree Diameter at 1.4 m (cm)	15.2	4.8	28.1	4.3	20.9	4.4	32.1	5.4
BASn	Basal area of standing deadwood (snags) ($m^2\ ha^{-1}$)	0.7	2.2	11.2	5.9	1.6	2.6	7.9	5.2
XHW	Percent cover of hardwood species	36.8	34.9	39.7	32.1	3.0	6.0	7.6	11.3
Non-spatial diversity metrics									
Nsc	Size class (2.5-cm dbh) richness	5.8	2.4	12.7	2.9	9.4	2.6	13.1	2.7
Nspp	Species richness	3.6	1.3	5.0	1.3	2.8	1.1	4.5	1.6
Hspp	Shannon's Index of species diversity (see Table 2)	0.9	0.4	1.1	0.4	0.7	0.3	0.6	0.4
Gini	Gini coefficient (see Table 2)	0.2	0.1	0.2	0.1	0.2	0.1	0.2	0.1
Spatial diversity metrics									
CE	Clark Evans (see Table 2)	0.7	0.2	0.9	0.2	0.9	0.2	1.0	0.1
DD	Diameter dominance (see Table 2)	0.5	0.2	0.3	0.1	0.5	0.1	0.3	0.1
SC	Stand Complexity Index (see Table 2)	2.5	1.1	4.6	1.2	3.3	1.0	5.0	1.4

Table 2
Spatial and non-spatial diversity indices used in the final analysis.

Index	Diversity of	Formula	Explanation	Source
Shannon's Diversity index for tree species (Hspp)	Tree species	$H_{spp} = -\sum_{i=1}^{Nspp} \frac{B_i}{B} \cdot \ln\left(\frac{B_i}{B}\right)$	*B* - total plot basal area B_i - basal area of trees of species *i* *Nspp* - total number of tree species	Shannon (1948)
Gini coefficient for tree sizes (Gini)	Tree dimensions	$Gini = \frac{\sum_{i=1}^{n}(2_i - n - 1)x}{n^2\mu}$	*n* - total number of trees *x* - diameter of tree i μ – mean tree diameter	Weiner and Solbrig (1984)
Clark Evans index (CE)	Spatial patterns of tree locations	$CE = \frac{\frac{1}{N}\sum_{i=1}^{N} r_i}{0.5\cdot\left(\frac{A}{N}\right)^{1/2} + 0.0514\cdot\frac{P}{N} + 0.041\cdot\frac{P}{N^{3/2}}}$	r - distance b/w trees A - plot area (m^2) N - number of trees P – plot circumference	Clark and Evans (1954)
Diameter dominance index (DD)	Tree dimensions within a neighborhood group	$DD = \frac{1}{n}\sum_{j=4}^{n} U_j$	n – number of nearest neighbors $U_j \begin{cases} 1, dbh_j > dbh_i \\ 0, otherwise \end{cases}$	Hui et al. (1998), Aguirre et al. (2003)
Stand complexity index (SC)	Stand structural complexity	$SC = \frac{\text{surface area of TIN}}{\text{projected area of TIN}}$	TIN - triangulated irregular network	Zenner and Hibbs (2000)

Table 3
Combined accuracy (79.3%) of plot attributes selected by stepwise discriminant analyses (all variables are significant at $P < 0.001$) and their relative importance (RelImp, %). Definitions of variables can be found in Table 2.

Variable	RelImp (%)
Traditional plot metrics	
DBH	17.6
BA	11.4
BASn	8.1
TPH	2.4
XHW	1.3
Total	*40.8*
Non-spatial diversity metrics	
Nsc	10.0
Nspp	3.6
Hspp	2.3
Gini	1.7
Total	*17.6*
Spatial diversity metrics	
SC	9.3
DD	6.6
CE	5.0
Total	*20.9*

to be a significant factor in describing plot conditions, the traditional metric of stand density index (SDI, Appendix A), indicated a higher level of variability and a greater degree of change in the unmanaged plots compared to the managed, which in turn is driving the average structural conditions down over the sampling periods.

Snag basal area (BASn) development over the 72-year-period was quite distinct, increasing from 1941 to 2013 in managed and unmanaged plots (Table 1; Fig. 2D). In 1941, storm damage increased BASn more in managed than unmanaged plots. By 2013, however, standing deadwood abundance was greater in the unmanaged plots. The change in standing deadwood abundance is also notable in the distribution of standing deadwood size classes (Fig. 3). The relative frequency of standing deadwood shifted from smaller to larger size classes, especially in the managed plots.

Non-spatial diversity metrics changed more over time in the unmanaged than the managed plots (Tables 1 and 4; Fig. 2F–I). For instance, the unmanaged plots had the lowest number and distribution of DBH size classes in 1941 as measured by Nsc and Gini (Fig. 2F–I) and experienced significant increases over time to the levels found in 2013 managed plots (Fig. 2F). Species richness and diversity (Nspp and Hspp: Fig. 2G–H) increased between

Table 4
Tukey Kramer HSD comparisons and their level of significance for each plot attribute in the final model selected by stepwise discriminant analyses between Unmanaged (N) and Managed (M) plots in 1941 and 2013.

Management year interaction	Traditional plot metrics					Non-spatial diversity metrics				Spatial diversity metrics		
	BA	TPH	DBH	BASn	XHW	Nsc	Nspp	Hspp	Gini	CE	DD	SC
M:1941 × N:1941	***	n.s.	***	***	***	***	***	***	n.s.	***	**	***
M:2013 × N:2013	n.s.	n.s.	***	***	***	n.s.	*	***	n.s.	***	**	n.s.
N:1941 × N:2013	***	n.s.	***	**	n.s.	***	***	**	**	***	***	***
M:1941 × M:2013	***	*	***	n.s.	n.s.	***	***	n.s.	n.s.	*	***	***

n.s., not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

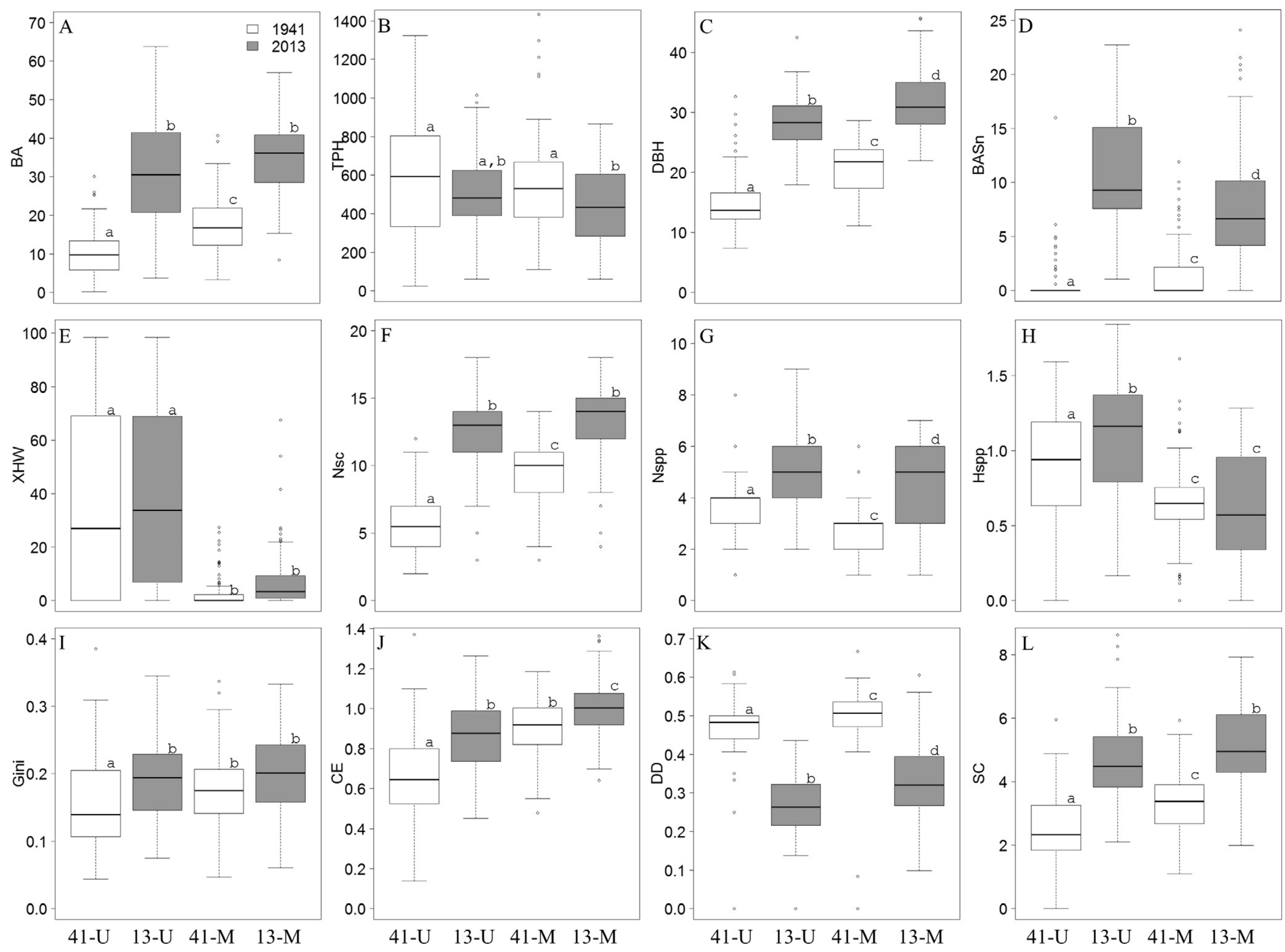

Fig. 2. Boxplots representing the selected forest attributes of managed (M) and unmanaged (N) plots in 1941 (41) and 2013 (13). The whiskers depict the upper and lower levels of the data, bars represent the upper and lower quartile of the data, and the solid line is the median value. Different letters above the bars indicate significant differences ($P < 0.05$) among year and management history according to Tukey-Kramer HSD tests.

sample periods and were significantly greater in unmanaged than managed plots in both inventories.

Spatial diversity metrics also showed significant changes across management history and time (Tables 1 and 4; Fig. 2J–L). For instance, the Structural Complexity Index (SC) was higher in unmanaged than managed plots in 1941 but the trend was not distinguishable in 2013 (Fig. 2L). In addition, between 1941 and 2013, Clark Evans (CE) indicated a change from an aggregated to random or regular spatial pattern of trees in unmanaged plots, while managed plots became more regular over time (Fig. 2J).

3.2. Changes in species composition and size classes over time in managed and unmanaged plots

Management history was associated with differing species composition and size class distribution over time. Within the managed plots, losses of basal area were greatest for *P. banksiana* in size classes <35 cm dbh and gains of basal area were greatest for *P. resinosa* in size classes >35 cm dbh and for non-pine species in size classes <35 cm dbh (Fig. 4). A large portion of non-pine species basal area gains were *A. balsamea* and *B. papyrifera* (Fig. 5). In the

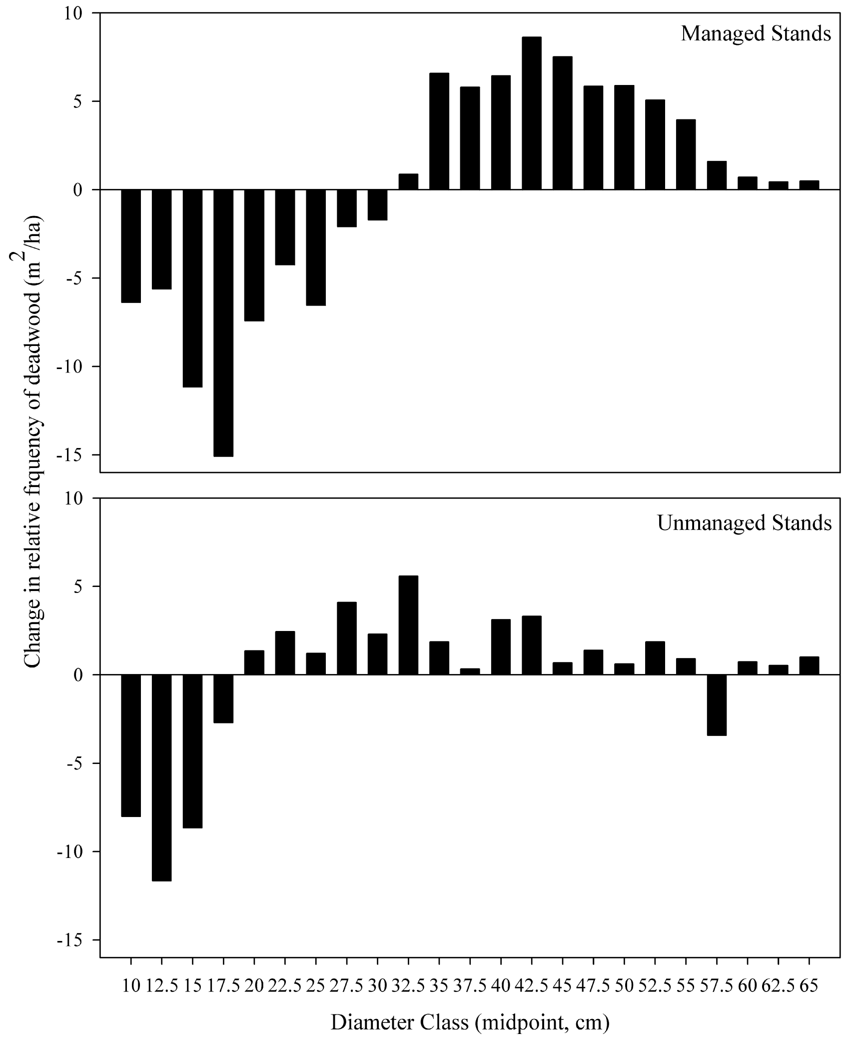

Fig. 3. Changes in relative frequency (expressed as percent change) of standing deadwood basal area (m^2/ha) by diameter classes between 1941 to 2013 in managed and unmanaged plots.

unmanaged plots, losses of basal area for non-pine species were in size classes <20 cm dbh (Fig. 4). In addition, basal area gains in unmanaged plots were composed largely of non-pine species and *P. resinosa* in size classes >25 cm dbh (Fig. 4). Losses of non-pine species basal area include *Q. rubra* and *B. papyrifera*, while basal area gains of non-pine species included *Populus* spp. and *A. rubrum* in unmanaged plots (Fig. 5).

3.3. Overall plot level structural attribute development from 1941–2013 by management history

Nonmetric multidimensional scaling (NMDS) ordination of the structural attributes describing the 1941 and 2013 conditions were significant for both unmanaged and managed plots ($P < 0.001$), converging on a two dimensional solution after 43 and 36 iterations, respectively (Fig. 6). The NMDS final stress met standards for a stable, robust configuration of points (9.3% and 10.8% in unmanaged and managed plots, respectively). In both management histories, negative values of Axis I were associated with diameter dominance (DD) which suggests moderate tree suppression for many of the trees and, on Axis II, negative values were associated with the percent cover of hardwood species (XHW) and Shannon's Index for tree species diversity (Hspp). Most notably, in both management history ordinations, Axis I represented time or change from 1941 (negative values) and 2013 (positive values) plot conditions. The separation of unmanaged and managed plots by measurement period within the ordination diagrams was confirmed using a multiple response permutation procedure (unmanaged plots, $A = 0.$ 0.287, $P < 0.001$; managed plots, $A = 0.104$, $P < 0.001$).

4. Discussion

Describing long-term forest developmental patterns and the relative influence of management and natural disturbance processes has long been a central focus of forest ecological research. In many cases, these works have relied on chronosequence approaches or repeated measurements of plots at a localized scale (e.g., Spies et al., 1988; Goodburn and Lorimer, 1999; Silver et al., 2013), but rarely have landscape-scale evaluations of forest development been conducted over the extended time periods afforded in this study. Harvesting has occurred sporadically in the managed areas examined in this study for over 72 years and the legacies of this land use on forest development was still apparent in contemporary forest conditions, particularly in relation to overstory species and in the abundance of standing deadwood. Overall, our results indicate both a convergence in some forest characteristics

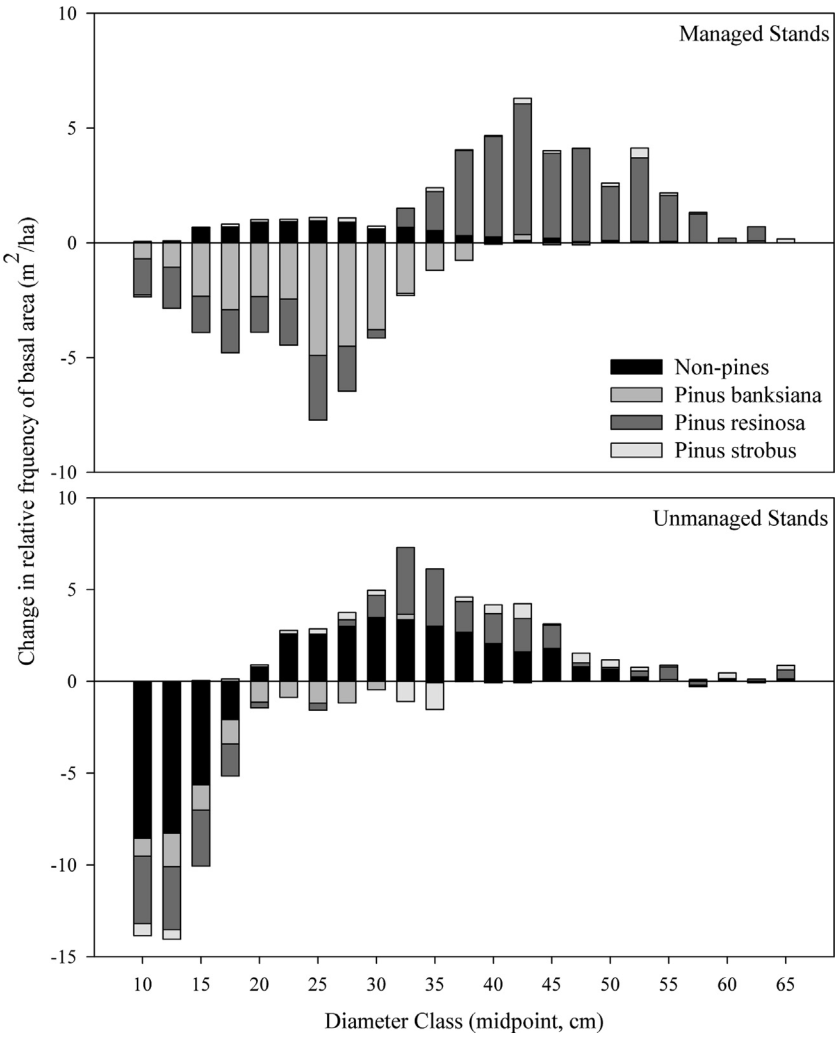

Fig. 4. Changes in relative frequency (expressed as percent change) of the basal area (m^2/ha) of trees grouped by the 3 different pine species and the non-pine species by diameter class between 1941 and 2013 in managed and unmanaged plots.

and divergence in others over time within the plots under different management histories.

The overall developmental patterns and structural conditions, as shown in the Nonmetric multidimensional scaling (NMDS) ordination (Fig. 6), in the unmanaged area and the managed forest, were overall quite similar at the landscape scale in 2013. Despite the tremendous variability in unmanaged stand conditions relative to managed areas in 1941, these areas converged over time in several structural conditions, particularly those related to stocking (BA and TPH) and size-class diversity (Nsc and Gini) and complexity (SC). This is likely related to the primary emphasis of management activities on removing *P. banksiana*, a relatively short-lived, early-successional species (Burns and Honkala, 1990) that naturally declined from the unmanaged plots between 1941 and 2013. Work examining long-term, stand-level structural development of extended rotation and old-growth *P. resinosa* forests near our study area also documented a similar dynamic with managed stands approximating live-tree conditions found in old-growth stands several decades sooner due to the early removal of *P. banksiana* and repeated thinnings (Silver et al., 2013).

Despite the numerous similarities in live-tree structural conditions highlighted here between the managed and unmanaged plots, there were important differences in other aspects of the structural and compositional conditions in these areas after 72 years of development. The greatest difference between these conditions was the amount and variation of hardwood and other non-pine species. These differences are mostly due to differences in the nature and mode of disturbance in these areas. Early management selectively discriminated against species other than *P. resinosa* and to a lesser extent, *P. strobus,* resulting in lower overall levels of hardwood basal area in managed plots (CEF Archive). Despite these efforts, ingrowth over the last 72 years within the managed plots has primarily been composed of non-pines species, particularly fire-sensitive species like *B. papyrifera* and *A. balsamea.* A similar long-term increase in fire-sensitive species (*A. rubrum* and *Populus* spp.) occurred in the unmanaged plots over this time period and reflects the elimination of surface fire regimes, which historically created suitable pine seedbed conditions and reduced the abundance of hardwoods and *A. balsamea* in these forests (Methven and Murray, 1974; Scherer et al., 2016).

Standing deadwood abundance (BASn) was generally low in 1941 (< 5 m^2/ha). By 2013, standing deadwood basal area had increased considerably across the landscape with the greatest change and amounts found in unmanaged plots (Fig. 2). The shift in landscape-scale conditions reflects general stand maturation processes with greater levels of standing deadwood recruitment associated with progression through a self-thinning process and the subsequent canopy transition associated with maturing stands

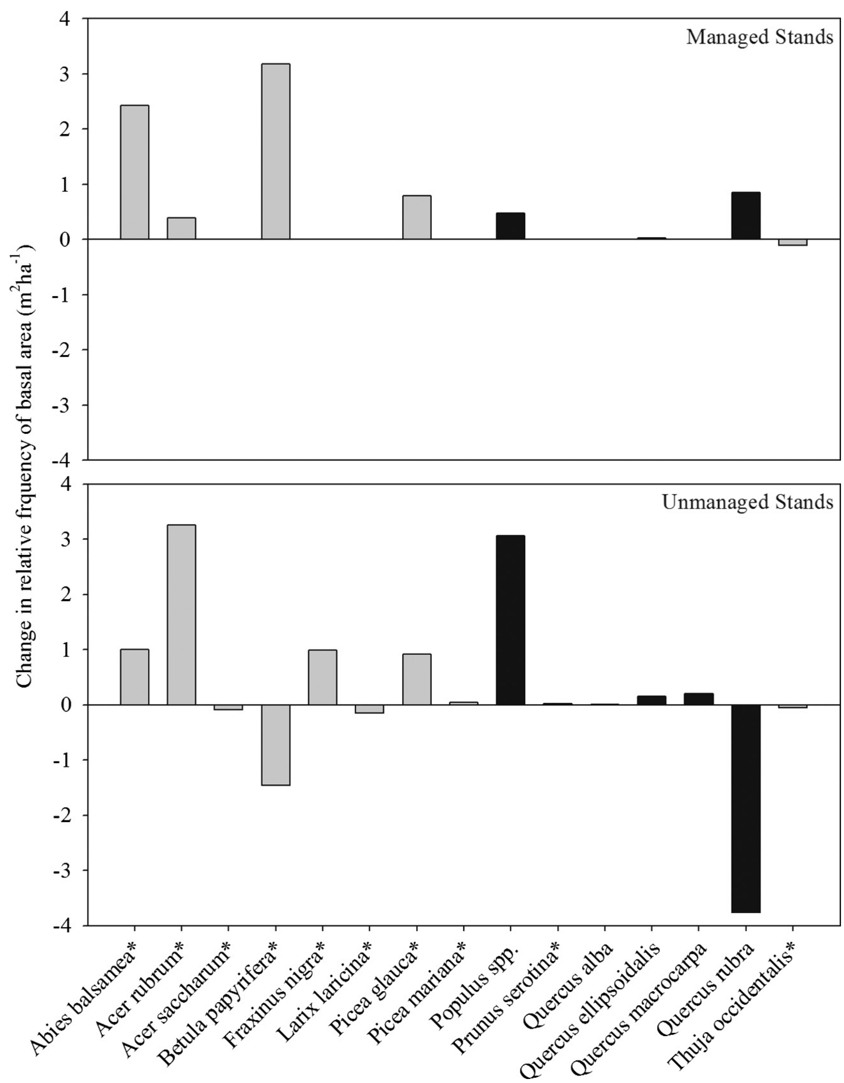

Fig. 5. Changes in relative frequency (expressed as percent change) of the non-pine tree species basal area (m^2/ha) between 1941 and 2013 in managed and unmanaged plots. Asterisk (*) and grey bars indicates a fire-sensitive species (USDA Forest Service, 2016).

(Oliver and Larson, 1990; Frelich and Reich, 1995). The higher standing deadwood basal area in unmanaged plots reflected both a greater number and diameter of standing deadwood and is consistent with other work comparing managed and old-growth red pine forest in which greater standing deadwood basal areas were documented in old-growth stands (Duvall and Grigal 1999; Silver et al. 2013). Also, these differences are likely a result of preferential harvest of trees likely to die before the next harvest entry in the managed plots.

The incorporation of the traditional, non-spatial diversity and, spatial diversity forest attributes lead to a more robust investigation of the managed and unmanaged plot types in the Cutfoot Experimental Forest. The four most influential measures on the final model respectively came from each of these three groupings. Basal area (BA) and diameter at breast height (DBH) represented the most common metrics of density and size with the greatest importance followed by size variation (Nsc) and the spatial patterns of size and density (SC). These results highly suggest that in order to gain a clear understanding of the dynamics within either managed or unmanaged plots one must use a variety of both spatial and non-spatial metrics in an analysis.

In summary, our hypotheses were supported in part. For example, we expected the range of variability in the structural and compositional attributes to be greater in unmanaged plots (hypothesis 1; Silver et al., 2013); however, this was only supported by the patterns in percent cover of hardwood species and to a much lesser degree from some of the other traditional plot attributes and not from either the spatial or non-spatial diversity measures. In contrast, we found strong support for our second hypothesis regarding greater change in structural and compositional conditions in unmanaged plots, particularly in relation to tree basal area (BA), standing deadwood (BASn), number of different size classes of trees (Nsc), the diversity of tree species (Hspp), the variation in tree sizes (Gini), variation in the patterns of tree locations (CE), and the variation of tress sizes in relation to their neighbors (DD). We only found partial support for our hypothesis regarding the temporal effect of fire suppression: the abundance of fire-sensitive species did increase and small-diameter *Pinus* spp. did decline over time, but the tree densities did not increase as anticipated. Our final hypothesis predicting more complex forest structure over time in unmanaged versus managed plots (D'Amato et al., 2010; Silver et al., 2013) was supported with greater change in spatial pattern

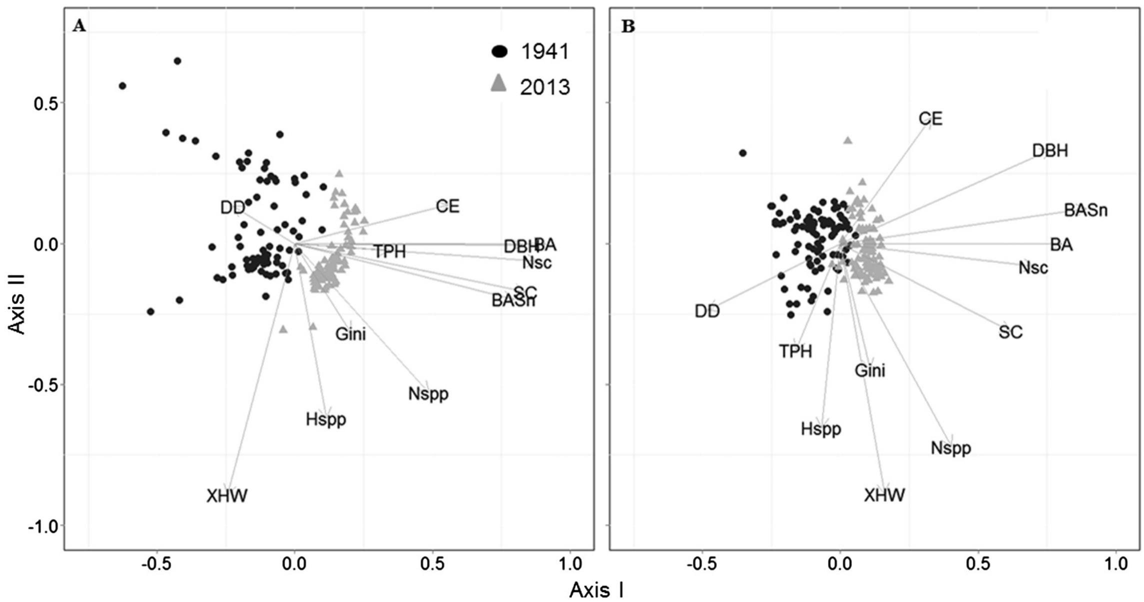

Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination of the composition and structural variables for the unmanaged (A) and managed (B) plots for plots measured in 1941 (circles) and 2013 (triangles). Variable scores are plotted from the centroid of the data and represent both the strength and direction of that variable in the ordination space. For definitions of the variables refer to Table 1.

of tree locations (aggregated to random, CE) and richness of tree size classes in unmanaged than managed plots over time.

5. Conclusions and management implications

The long-term, landscape-level patterns in structural and compositional development we documented for the Cutfoot Experimental Forest underscores both the persistent influence of past and current management on contemporary forest conditions, as well as the potential for long-term achievement of some aspects of old-growth live-tree conditions within the managed stands. These results support previous findings for the use of extended rotation forestry to restore live-tree structural and compositional conditions found in old-growth red pine forests to managed stands (D'Amato et al., 2010; Silver et al., 2013); however, the managed plots we examined still lack the standing deadwood conditions found in unmanaged plots. This finding is common to other work comparing managed and unmanaged stands in these and other ecosystems (Duvall and Grigal, 1999; Jönsson et al., 2009; Silver et al., 2013) and speaks to the need for explicit consideration of creation of deadwood structures through management activities if objectives include the restoration of natural stand conditions. Such objectives were not a consideration during the period of active management in the landscape we examined; however, the persistence of these management effects on contemporary standing deadwood abundance highlight the importance of including provisions for deliberate retention of large dead and living trees in contemporary managed landscapes. Most red pine stands within the Lake States of the United States are even aged having been established as plantations. Findings from this study can assist those interested in restoring red pine plantations to a more natural composition and structure where red pine was historically a natural component of the ecosystem.

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Appendix A. Definition of plot variables used in the analysis

Variable	Description	Unit/source
Traditional stand metrics		
BA	Basal area of live trees	$m^2\ ha^{-1}$
TPH	Live tree density	$100\ ha^{-1}$
DBH	Average DBH of live trees	cm
QMD	Quadratic mean diameter of live trees	cm
TPH_L25	Live tree density of stems <25 cm DBH	$100\ ha^{-1}$
TPH_25-50	Live tree density of stems 25–50 cm DBH	$100\ ha^{-1}$
TPH_G50	Live tree density of stems >50 cm DBH	$100\ ha^{-1}$
BASn	Basal area of standing deadwood (Snags)	$m^2\ ha^{-1}$
SnPH	Density of standing deadwood	$100\ ha^{-1}$
SnPH_L25	Density of standing deadwood <25 cm DBH	$100\ ha^{-1}$
SnPH_25-50	Density of standing deadwood 25–50 cm DBH	$100\ ha^{-1}$
SnPH_G50	Density of standing deadwood >50 cm DBH	$100\ ha^{-1}$

(continued on next page)

Appendix A (*continued*)

Variable	Description	Unit/source
BASt	Basal area of stumps	$m^2\ ha^{-1}$
StPH	Density of stumps	100 ha^{-1}
XHW	Percent cover of broad-leaf species	Percent
SDI	Stand Density Index	Reineke (1933)
Non-spatial diversity metrics		
Nsc	Tree size class richness	# ha^{-1}
Nspp	Tree species richness	# ha^{-1}
Hsc	Shannon's Index for DBH size classes	Shannon (1948)
Hspp	Shannon's Index for tree species	Shannon (1948)
Gini	Gini Index for DBH size classes	Weiner and Solbrig (1984)
Spatial diversity metrics		
CE	Clark Evans Index	Clark and Evans (1954)
SM	Species Mingling Index	Von Gadow and Hui (2002)
SD	Size Differentiation index	Füldner (1995)
DD	Diameter Dominance Index	Hui et al. (1998) and Aguirre et al. (2003)
MD	Mean Directional Index	Corral-Rivas (2006)
SC	Stand Complexity Index	Hui et al. (1998), Aguirre et al. (2003)
ESC	Enhanced Stand Complexity Index	Beckschäfer (2013)

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