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RESEARCH ARTICLE

Snag Benchmarks and Treatment Options for Mixed-Pine Forest Restoration in Eastern Upper Michigan

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Abstract

Snags (dead-standing trees) are biological legacies that remain after disturbances in forests. We enhanced the ecological underpinnings of snag management within the context of mixed-pine forest restoration in the northern Lake States by quantifying characteristics of live trees and snags within eighty-five 500-m^2 plots at Seney National Wildlife Refuge (NWR) in eastern Upper Michigan. Study plots represented reference conditions (i.e. no past harvesting, relatively unaltered fire regime) and altered (i.e. harvested, altered fire regime) conditions. We also compared three treatments for creating snags from live trees. Snags were found in 87% of the reference plots and 85% of the altered plots. The only snag variables that differed between plot types were mean snag basal area, which was greater in altered plots (Student's t-test, $p = 0.04$), and mean percent total basal area of snags (greater in reference plots, $p = 0.06$). The composition of snags differed only in the 10- and 25-cm diameter classes (Multi-Response Permutation Procedure, $p < 0.10$). The percentage of snags that developed into the most advanced decay class (DC) differed among treatments after 4 years ($\chi^2 = 16.49$, $p < 0.01$), with 26% of girdled trees, 3% of prescribed fire trees, and zero topped trees reaching DC5. Logistic regression illustrated that the influence of predictor variables on DC development varied by species and treatment. The findings from this study, past studies, and ongoing projects at Seney NWR are directly applicable to innovative management of snags in mixed-pine forests.

Key words: biological legacy, ecological forestry, fire, red pine, Seney National Wildlife Refuge, snag transition rates.

Introduction

Snags (i.e. dead-standing trees) are biological legacies that remain after disturbances in forests. Snags play an important role in regulating ecological processes (e.g. nutrient cycling, carbon sequestration), providing refugia for propagules and microbes, and functioning as habitat for flora and fauna (Harmon et al. 1986). Snags, especially in mature forests, also play an important role as global carbon sinks (Luyssaert et al. 2008) and have important roles in fire ecology and management (Stephens 2004). Not surprisingly, snag management is a cornerstone of contemporary ecological forestry (Seymour & Hunter 1999; Franklin et al. 2007). However, substantial variation exists in snag abundance and development over time and among forest types (Harmon et al. 1986; Fridman & Walheim 2000) such that snag management guidelines must be geographically and forest type-specific.

Changes in land use have been implicated in the homogenization of forest composition and structure and the decline of fire-dependent ecosystems in the northern Lake States. Across many ownership types, fire-sensitive deciduous tree species have displaced fire-dependent coniferous species (Corace et al. 2012). One ecosystem type that has experienced a significant reduction in dominance is mixed-pine forests of red pine (*Pinus resinosa* Ait.) and eastern white pine (*P. strobus* L.). These forests were common during pre-EuroAmerican times, with 3.9 million ha dominated by mixed-pine or similar forest ecosystem types (Frelich 2002). Today many sites have been converted to monotypic, artificially regenerated pine plantations and turn-of-the-century logging, wildfires outside the natural range of variation, and fire suppression have altered the structure and composition of the remaining naturally regenerated, second-growth stands (Stearns & Likens 2002; Drobyshev et al. 2008*b*).

Efforts to restore mixed-pine forests have begun because of the multiple ecosystem services they provide and associated changes in some federal policy (Meretsky et al. 2006). Restoration at Seney National Wildlife Refuge (NWR; Corace

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et al. 2009) has been guided by studies of old-growth mixed-pine stands that serve as restoration benchmarks. The existence of these stands has allowed the reconstruction of fire regimes using dendrochronology (Drobyshev et al. 2008*a*) and the quantification of relationships among forest structure and composition variables along a disturbance gradient (Drobyshev et al. 2008*b*). Studies are also underway that examine recruitment of red pine and eastern white pine using variable-retention harvesting systems.

Learning more about the differences between snag populations in reference and altered (non-reference) stands is critical for a holistic approach to conserving or restoring forests. For example, Fridman and Walheim (2000) were able to provide a more complete picture of the natural range of variability in snag abundance among managed coniferous forest types in Sweden. However, much of the North American literature regarding the general concept of snag management in fire-dependent ecosystems consists of studies from the Intermountain West and Pacific Northwest (Morrison & Raphael 1993; Hutto 2006), ecosystems comprised of a different suite of species, growing on different landforms, and shaped by different disturbance regimes than are found in the northern Lake States. Throughout the northern Lake States, we know of only one study (Fraver & Palik 2012) that characterized snags from reference mixed-pine stands. A more complete understanding of the natural range of variation of the structure of, and the specific management practices for, snag populations in fire-dependent forest ecosystems of the northern Lake States is, therefore, needed.

The goal of this study is to enhance the ecological underpinnings of snag management for mixed-pine forest restoration and ecologically based management of second-growth pine stands (natural and artificial). We use data from two separate, but related, projects to: (1) improve our understanding of the natural range of variation of snag characteristics and (2) provide the most appropriate recommendations for snag management. The objectives of this study are to: (1) describe the natural range of variation in characteristics of live trees and snags sampled in reference mixed-pine plots and compare these findings to formerly mixed-pine plots that have been altered from their historic conditions, but are still pine-dominated and naturally regenerated; (2) examine relationships among these patterns and potential ecological drivers (e.g. density-dependence and fire); and (3) compare and contrast three treatments (girdling, prescribed fire, and topping) for creating snags from live trees. We hypothesize that the average abundance, density, and size of snags will all be greater within reference mixed-pine plots. We also hypothesize that snag decay class (DC) development will differ among treatments over time and among species, with shorter-lived tree species developing advanced DCs faster.

Study Area

This study was conducted at the 38,542-ha Seney NWR (N46.271594° W86.057078°), Schoolcraft County, Michigan, U.S.A. (Fig. 1). Due to their inaccessibility within a mosaic of shrub and open wetlands, refuge records and related research (Drobyshev et al. 2008*a*, 2008*b*) indicate that areas sampled within the Seney Wilderness Area have never been harvested and represent some of the best examples of reference, old-growth mixed-pine ecosystems in the northern Lake States. Most of the remaining plots were established on nearby glacial outwash channels that were altered from their pre-EuroAmerican condition, first by turn-of-the-century logging (Drobyshev et al. 2008*b*; Rist 2008).

Seney NWR lies within the Seney Sand Lake Plain (Albert 1995). This ecoregion is predominately forested and in mostly public ownership (Corace et al. 2012). Landforms of lacustrine origin characterize the area. The climate is influenced by its close proximity to the Great Lakes. The most common winds are from the southwest to northwest. Average daily humidity during spring and fall varies from 50 to 60%. Temperature extremes range from approximately −43 to 37°C. Average annual precipitation is 81 cm and average annual snowfall is 312 cm. According to the habitat typing system of Burger and Kotar (2003), 58% of the soil types would have mixed-pine forests as the dominant late-successional community type.

Methods

Snag Management Benchmarks

We used data from 85 50 m × 10 m (500 m^2) plots established as part of a fire-history study (Drobyshev et al. 2008*a*). The diameter at breast height (dbh; 1.37 m) of snags was measured as part of an inventory of all overstory trees (>10 cm dbh), and included 38 reference and 47 altered plots. The fire regime of reference plots are considered relatively unaltered based on the reconstructions of Drobyshev et al. (2008*a*). Specifically, the fire-return intervals (FRI) in the Seney Wilderness Area were found to not increase over time as would be expected in areas undergoing fire suppression: for the pre-European period (1707–1859), the FRI was 32.7 ± 19.2 years, the FRI was 14.5 ± 10.6 years for the settlement period (1860–1935), and the FRI was 18.5 ± 11.5 years for the post-refuge establishment period (1936–2006). All plots were established on deep, sandy soils with similar successional trajectories, and differences in the present structure and composition are a result of past management activities and disturbance regimes, and not site capability per se.

Plot data were tested for normality using the Shapiro–Wilk test; one altered plot was removed because of extreme outliers. Data with non-normal distributions were transformed (natural log transformation for live tree and snag dbh; square root transformation for live tree and snag basal area [m^2/ha], live tree density and snag density [stems/ha], percent snag basal area, and percent snag density) and then retested for normality. A two-sided Student's *t*-test for independent samples was used to compare data between reference and altered plots. All means shown are untransformed grand means for reference and altered plots. We used Multi-Response Permutation Procedure (MRPP) to test the hypothesis that snag composition (within diameter classes) was not different between reference and

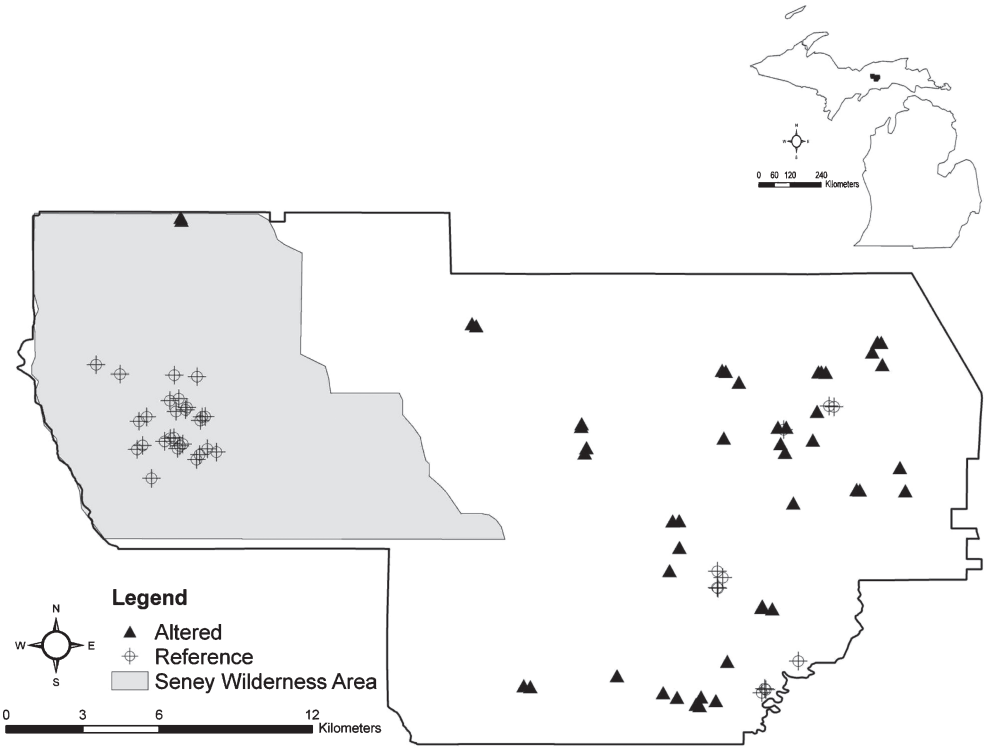

Figure 1. Distribution of reference (circles) and altered (triangles) plots at Seney National Wildlife Refuge, eastern Upper Michigan, U.S.A. Most reference plots were in the Seney Wilderness Area.

altered plots. MRPP is a nonparametric test and requires neither normally distributed data nor variance homogeneity (McCune & Grace 2002). We used Sorenson's distance and a weighting factor, and made pairwise comparisons.

Years since last fire (YLF) was determined by dendrochronological methods (Drobyshev et al. 2008*a*). Briefly, fire-scarred live trees, stumps, and snags were sampled by "wedge sampling." Samples were mounted on wood and polished to allow recognition of annual rings and fire scars under a binocular microscope. All samples were cross-dated using a visual approach, which included skeleton plots and local chronologies. Linear regression was used to examine the relationship between density of trees and snags and between YLF and snag density.

Snag Treatments

We determined 4-year patterns in snag DC development across a pool of tree species for three different treatments: girdled, prescribed fire, and topped. Girdling was done as part of a restoration treatment in July and August 2007. We used regionally common logging equipment (i.e. machines that fell and then cut trees to a pre-determined length) to girdle live trees. A single operator girdled 107 trees by attaching onto the main stem with a "clam head" and raising and lowering the arm of the machine, stripping bark off the tree. All girdled trees were >18 cm dbh, the approximate mean dbh of the pine-dominated stand before harvest. Snags were created from 15 red pine, 5 eastern white pine, 61 jack pine (*Pinus banksiana* Lamb.), and 26 aspen (*Populus* spp.). During the initial treatment, we recorded for each girdled tree: (1) species, (2) dbh, and (3) height (m). Because trees may protect one another from the influence of wind and thus reduce the breakage of snags, we also measured distance to the nearest tree (m) and number of trees in 10-m radius. During subsequent visits in May to August between 2008 and 2011, we revisited each girdled tree to collect data on DC development as adapted from Hunter (1990) (Table 1).

Table 1. Snag decay classes.

Decay class	*Characteristics*
DC1	Recently dead trees with intact tops and the majority of fine branching present
DC2	Trees with loose bark, intact tops, most of the fine branches
DC3	Trees with <50% of initial coarse branches and <50% bark
DC4	Trees with broken tops, with few or no coarse branches, >6 m in height
DC5	Blown down trees or trees with broken tops, no coarse branches, <6 m in height.

The 4-year patterns in DC development for girdled trees were compared with a retrospective analysis of snags resulting from two other treatments in 2004: prescribed fire and topped (i.e. cutting off a tree stem approximately 3 m above the ground

using the same mechanized logging equipment as above). Thirty prescribed fire trees were sampled (18 jack pine, 9 red pine, and 3 eastern white pine) and 31 topped trees (26 jack pine and 5 aspen) were sampled. A one-time assessment of DC development was measured for a random sample for both treatments in 2008. Because we only followed girdled trees during each of the 4 years and did not follow the trees in the other two treatments each year, we were only able to measure tree species-specific DC transition rates (proportion of snags that develop into different DCs over time) for girdled trees.

We used a chi-square test to ascertain whether there were differences in the percentage of snags reaching DC5 across the pool of treated trees in each treatment. We used ordinal logistic regression to examine the relationship of DC development after 4 years for girdled trees and for prescribed fire trees using tree dbh, height, distance to nearest tree, and number of trees in 10-m radius as predictor variables and DC1–5 as response variables. The same was done for the topped trees, but without height as a predictor variable.

Results

Snag Management Benchmarks

Reference and altered plots were dominated by live stems of red pine, with a lesser component of eastern white pine and other tree species: jack pine, aspen, paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), black spruce (*Picea mariana* Mill.), and balsam fir (*Abies balsamea* Mill.). Red pine had the greatest mean (±1 SD) basal area (33.8±13.1 m^2/ha), the greatest mean density (564.2 ± 266.0 stems/ha), and was the most frequently encountered live tree species in reference plots (100% of plots).

Live stems of red pine were also found in 96% of the altered plots, and red pine was the dominant tree species within them: mean basal area 24.9 ± 17.4 m^2/ha; mean density 482.6 ± 391.3 stems/ha. Although these same tree species were found in altered plots, live stems of jack pine were considerably more prevalent (67% of altered plots had jack pine), with a mean basal area and mean density of 6.1±7.7 m^2/ha and 223.5±361.2 stems/ha, respectively. The diameter class distributions of live trees in reference and altered plots were both "reverse-J" curves (Fig. 2). Unlike the reference plots, however, the number of live stems of the smallest size class in the altered plots was nearly twice the number of stems found in the next largest size class.

Snags were found in 72 (85%) of the sampled plots: 33 of the reference plots (87%) and 39 of the altered plots (85%). The compositions and structures of snags were similar to those for live trees, with jack pine being more prevalent in the altered plots. Surprisingly, altered plots had a lower percentage of snags (39%) in the smallest size class (≤10 cm) than reference plots (47%). The diameter class distributions for snags in reference and altered plots were similar (Fig. 3). However, MRPP suggested that differences existed between

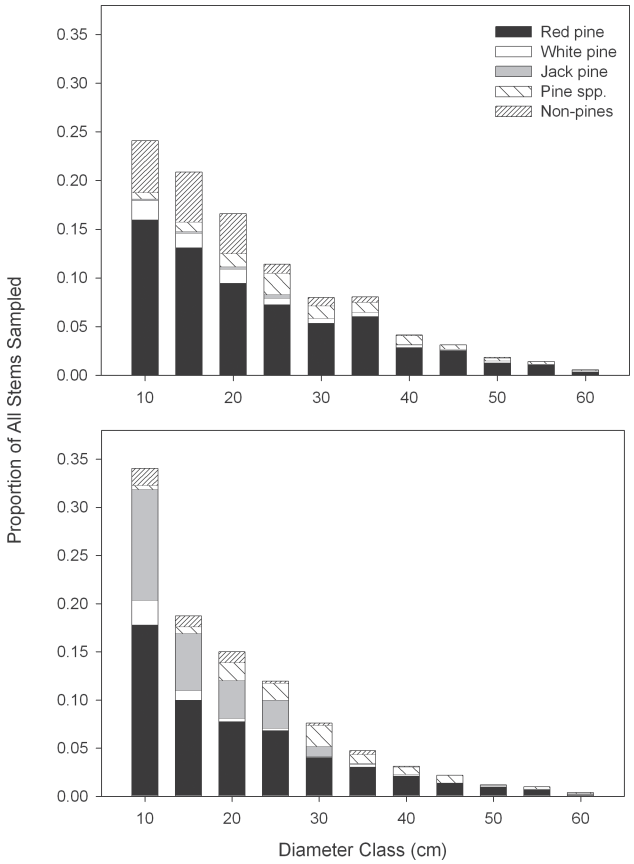

Figure 2. Diameter class distribution of live trees in reference (top) and altered (bottom) plots. "Non-pines" species are listed in the text.

snag composition of reference and altered plots in the 10-cm ($T = -1.58$, $A = 0.02$, $p = 0.08$) and 25-cm size classes ($T = -1.69$, $A = 0.53$, $p = 0.07$) only.

Reference plots were on average dominated by larger live trees, with both mean dbh ($p = 0.03$) and mean density of live trees >40 cm greater in these plots than altered plots ($p = 0.02$; Table 2). However, few differences in snag structure were observed between reference and altered plots, with only basal area of snags and percent overall basal area contributed by snags greater in altered plots ($p = 0.04$ and 0.06, respectively; Table 2). Regressions relating basal area and density of live trees and basal area and density of snags in reference and altered plots, respectively, explained little of the observed variability ($R^2 < 0.05$ in each), although greater variation was noted in each case for altered plots (Fig. 4). Similarly, the basal areas and densities of live trees and of snags were not closely related ($R^2 < 0.10$ in each) with YLF, with substantial variability within plots shown in the data corresponding with the most recent large (>10,000 ha) wildfire, the 1976 Seney Fire (Fig. 5).

Snag Treatments

Four years after treatment, the percentage of treated trees among snag DC1–5 differed by treatment group: none of

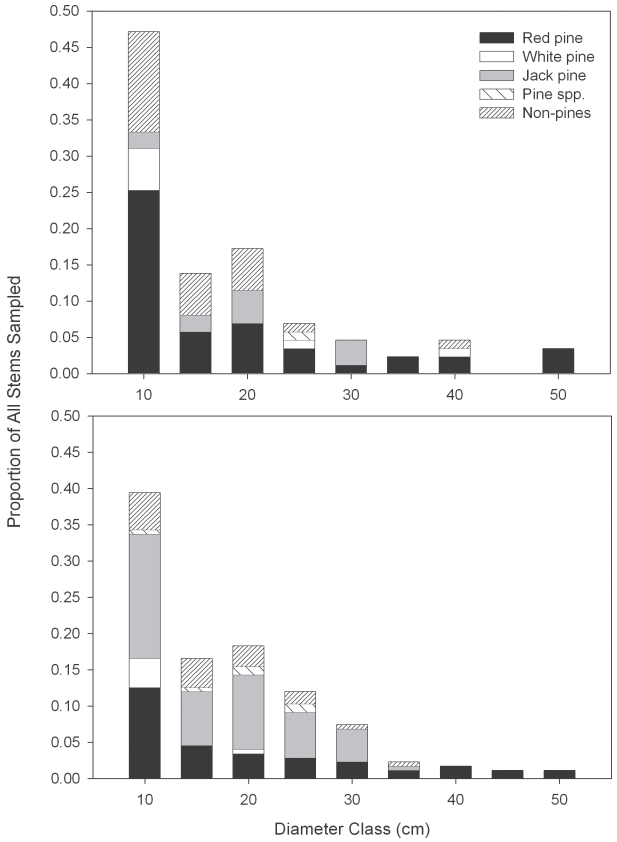

Figure 3. Diameter class distribution of snags in reference (top) and altered (bottom) plots. "Non-pines" species are listed in the text.

the topped snags were in DC1, while 3 and 5% were still in DC1 for the prescribed fire and girdled trees, respectively. The percentage of snags that developed to DC5 differed among treatments ($\chi^2 = 16.49$, $df = 2$, $p < 0.01$). None of the topped trees reached DC5, while 3% of the prescribed fire and 26% of the girdled trees did. Topped trees were found in DC2–4, while DC1–5 were represented in the prescribed fire and girdled trees; the modal DC for topped was DC2 and DC3 (tie, 45%), DC3 (43%) for prescribed fire, and DC4 (38%) for girdled.

For the 4 years over which we followed DC development in girdled trees, species-specific patterns of DC transition rates were observed (Table 3). Jack pine developed a greater range of DCs than did aspen or red pine in the first year after treatment, while all species illustrated some ability to move across DCs over 4 years. Unlike jack pine and aspen that had <5% of girdled snags in DC1 after 4 years, however, 31% or girdled red pine had not undergone further DC development. For all overall logistic regression models other than topped jack pine, at least one predictor variable influenced DC development (model likelihood ratio < 0.10), but the influence of predictor variables varied by species and treatment. For instance, DC development in girdled aspen was most influenced by height, whereas size (dbh) and distance to nearest tree influenced DC development in girdled jack pine, with more mixed effects of variables in girdled red pine (Table 4).

Discussion

Our data did not support the hypothesis that snag attributes would, on average, be greater within reference plots than altered plots. This contrasts with past studies in Sweden that showed the average abundance and size of coniferous deadwood (a proportion of which includes snags) was lower in managed stands across forest types (Fridman & Walheim 2000). Likewise, in red pine forests across the northern Lake States, Duvall and Grigal (1999) showed that timber harvesting had a negative impact on snag abundance. We suggest three possible explanations, supported by Rist (2008), for why our results differed and why we found seemingly less adverse impacts on snag populations from past forest harvesting:

Table 2. Characteristics of live trees and snags in reference and altered plots.

Variable	*Reference (n = 38)*	*Altered (n = 46)*	df	t (p)
Total no. of snags	87	175	—	—
Total no. of snags >40 cm dbh (cm)	7	8	—	—
Total no. of live trees	1640	2023	—	—
Total no. of live trees >40 cm dbh (cm)	181	159	—	—
Mean (±1 SD) dbh (cm)				
Snags	21.5 (9.8)	22.1 (9.6)	70	0.30 (0.77)
Live trees	25.2 (4.3)	23.1 (4.3)	82	2.16 (0.03)
Mean (±1 SD) density (stems/ha)				
Snags	45.8 (35.1)	76.1 (77.8)	82	1.49 (0.14)
Snags >40 cm dbh	3.7 (7.9)	3.5 (9.7)	82	0.11 (0.46)
Live trees	863.2 (279.6)	879.6 (363.4)	82	0.02 (0.98)
Live trees >40 cm dbh	95.3 (47.1)	69.1 (44.8)	82	2.48 (0.02)
% Snags of total live trees	6.1 (5.7)	10.6 (13.4)	82	1.41 (0.16)
Mean (±1 SD) basal area (m^2/ha)				
Snags	1.8 (1.7)	2.9 (2.8)	82	2.11 (0.04)
Live trees	48.8 (11.4)	41.7 (12.3)	82	2.72 (0.01)
% Total basal area = snag	4.0 (4.1)	8.1 (10.6)	82	1.93 (0.06)

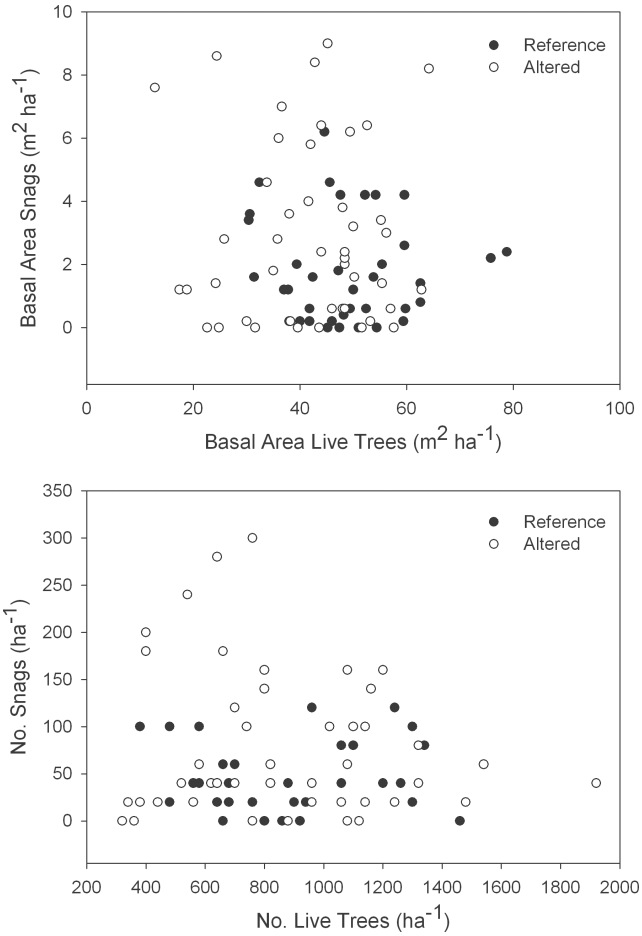

Figure 4. Relationship between basal area of live trees and the basal area of snags (top) and density of live trees and the density of snags (bottom) in reference and altered plots.

(1) inventories indicated that jack pine was a substantial component of altered plots at the time of refuge establishment in 1935 and jack pine was a focus of past harvesting, (2) that enough time has occurred between disturbances (harvesting and/or fire) for snag populations to converge to patterns similar to reference plots, and (3) that refuge management has differed from more commercially driven enterprises and snags and older trees were more likely retained. Moreover, unlike other fire-dependent pine ecosystems (Stephens 2004) in which high variability was observed in snag attributes of reference stands, we observed considerably more variability in snag characteristics in altered plots rather than reference plots. These findings extend our present knowledge of snag patterns across forest ecosystem types (Harmon et al. 1986; Fridman & Walheim 2000).

Unfortunately, we were not able to discern any clear relationships between snag abundance and density-dependent or disturbance-dependent mortality, leaving unanswered the difficult question of which factors are driving mortality in these forests. However, our findings of "reverse-J" diameter distributions of trees and snags does leave open the possibility that snags (especially jack pine snags) developed from competition and self-thinning, as suggested by studies in eastern boreal forests in Canada (Angers et al. 2010). Nonetheless, Franklin et al. (1987) indicated that a diverse array of potential abiotic and biotic contributors to tree death exists, including senescence and biotic stressors. Aakala et al. (2012) further suggest that although exogenous disturbances are often considered important factors in the dynamics of pine forests, background mortality may be just as important. More study is needed to understand the development of snags in both of our plot types over time.

Our data across three snag treatments support the hypothesis that DC development differs among treatments over time and among species, with shorter-lived tree species generally developing advanced DCs faster. Girdled trees did behave similarly to jack pines girdled by large equipment in Lower Michigan (Corace et al. 2010), and the variability observed in DC development among tree species has also been shown for snags developed under natural disturbances in unharvested forests of northwestern Quebec (Angers et al. 2010). However, whereas we show that jack pine had more variability in transition rates than most conspecifics, others have shown just the opposite, suggesting that DC development differs locally among tree species and forest type and supporting the general theory that species show individual responses to mortality (Angers et al. 2010). Whether or not DC patterns among our treatments emulates DC development under natural disturbances in mixed-pine forests requires more study.

Reference conditions are critical in that they can be used to quantify the natural range of variation that can guide forest conservation and restoration (Hansen et al. 1991). Our reference plots provide information that improves our understanding of snag patterns within the context of mixed-pine forest conservation and restoration in the northern Lake States by providing a contrast to the work of Fraver and Palik (2012). Our reference plots were similar to their reference sites in Minnesota in that the overstory was red pine-dominated, with eastern white pine and other species less dominant. Our reference plots differed in that they had, on average, slightly greater basal area of live trees (48.8 m^2/ha) and slightly less basal area of snags (1.8 m^2/ha) than covered by the range of values from Minnesota (trees: range, 25.6–43.1 m^2/ha; snags: range, 2.7–14.2 m^2/ha). The density of snags on our reference plots (45.8 stems/ha) was within the range from Minnesota (24–140 stems/ha). Conversely, relative to unharvested jack pine-dominated stands in Canada which had 275–525 snags/ha and 4.9–7.9 m^2/ha (Angers et al. 2010), our mixed-pine plots were significantly lower in both metrics.

Although reference plots had more large live trees for development into future snags, our findings indicate that both plot types may now provide habitat for cavity-dependent wildlife species, e.g. black-backed woodpecker (*Picoides arcticus* Swainson). Youngman and Gayk (2011) found that nesting woodpeckers were in snags similar to those found in our plots. Moreover, the heights of nests in snags they studied suggest that many snags reaching DC5 may still be used by this

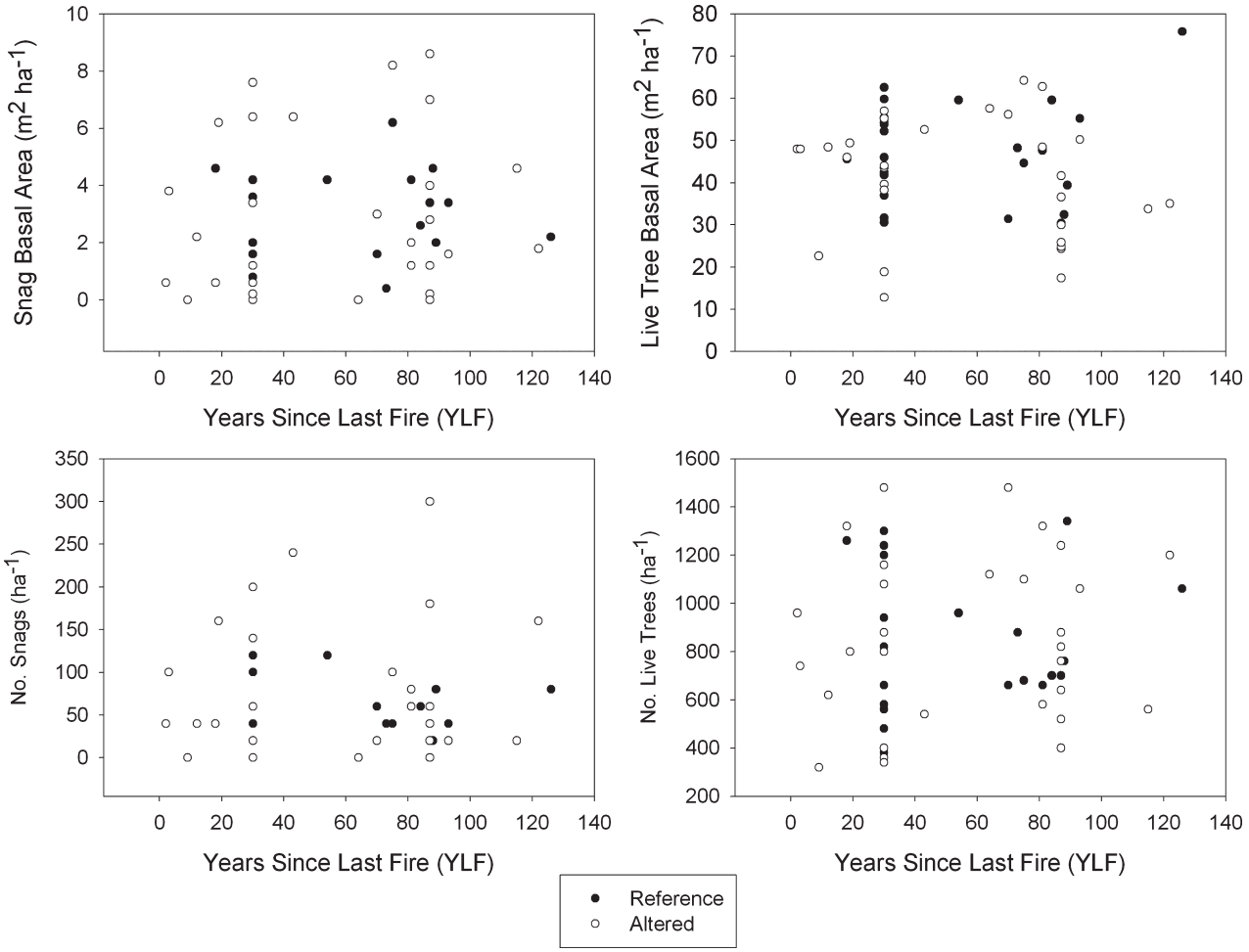

Figure 5. Relationship between years since last fire (YLF) and live tree and snag basal area and density in reference and altered plots.

Table 3. Snag transition rates for all girdled trees ($n = 103$) and for those girdled species with >10 individuals: aspen ($n = 25$), jack pine ($n = 59$), and red pine ($n = 14$).

		2008 Decay Class				
Species	*2011 Decay Class*	*1*	*2*	*3*	*4*	*5*
All	1	0.08				
	2	0.27	0.24			
	3	0.08	0.06	0		
	4	0.41	0.41	0	1.0	
	5	0.15	0.29	0	0	1.0
Aspen	1	0				
	2	0.16	0			
	3	0.11	0	0		
	4	0.58	0.50	0	0	
	5	0.16	0.50	0	0	0
Jack pine	1	0.04				
	2	0.39	0.23			
	3	0.09	0.08	0		
	4	0.26	0.42	0	1.0	
	5	0.22	0.27	0	0	1.0
Red pine	1	0.31				
	2	0.15	1.0			
	3	0	0	0		
	4	0.46	0	0	0	
	5	0.08	0	0	0	0

Decay classes are described in Table 1.

Table 4. Ordinal logistic regression analysis of decay class development (DC1 – 5) for three different treatments.

Treatment	*Tree species*	*Predictor*	n	*Coefficient*	*SE coefficient*	*Variable* p-*value*	*Odds ratio*	*Model likelihood ratio* p-*value*	*Pearson Goodness of Fit* p-*value (*df*)*
Girdled	Aspen	dbh	25	0.03	0.06	0.60	1.03	0.02	0.20 (68)
		Height		0.90	0.36	0.01	2.47	—	—
		Distance		−0.27	0.25	0.28	0.76	—	—
		No. of trees		−0.07	0.12	0.53	0.93	—	—
	Jack pine	dbh	59	0.10	0.04	0.02	1.11	0.04	0.00 (228)
		Height		−0.12	0.14	0.40	0.89	—	—
		Distance		−0.21	0.11	0.05	0.81	—	—
		No. of trees		−0.01	0.08	0.92	0.99	—	—
	Red pine	dbh	14	0.11	0.11	0.33	1.12	0.09	0.77 (35)
		Height		0.10	0.34	0.77	1.10	—	—
		Distance		−1.12	0.49	0.02	0.33	—	—
		No. of trees		−0.13	0.16	0.41	0.88	—	—
Fire	Jack pine	dbh	18	0.08	0.07	0.25	1.09	0.01	0.27 (64)
		Height		0.63	0.34	0.06	1.87	—	—
		Distance		0.36	0.26	0.16	1.43	—	—
		No. of trees		0.82	0.39	0.04	2.27	—	—
Topped	Jack pine	dbh	26	0.12	0.12	0.29	1.13	0.42	0.47 (47)
		Distance		−0.06	0.10	0.51	0.94	—	—
		No. of trees		−0.23	0.18	0.20	0.79	—	—

Predictor variables for girdled and prescribed fire trees were tree dbh (cm), height (m), distance to nearest tree (m), and number of trees in 10-m radius; height was not used as a predictor variable for topped trees. Analysis was only conducted for tree species with sample size >10.

species. Recently burned sites, whether reference or altered, may provide these birds habitat. The abundance of jack pine trees and snags we found in altered plots also suggests that fire would likely behave quite differently in altered plots relative to the reference plots. For instance, with the higher density of jack pine in stands similar to the altered plots managers may expect prescribed fires to be more severe as jack pine is a notoriously poor self-pruner and this characteristic helps promote severe crown fire.

Considerable research has documented the value of emulating forest patterns that arise from natural disturbances. To provide more structural heterogeneity in simplified pine plantations and other altered, formerly mixed-pine stands, we suggest land managers consider the range of treatments we described to produce more varied patterns of live and dead material, thereby providing conditions for a broader array of flora and fauna in naturally regenerated stands or in pine plantations (Palik & Zasada 2003).

Implications for Practice

- Given that the average snag density from our reference plots falls within the range from work in Minnesota, planners and managers should have considerable leeway in setting snag density objectives in mixed-pine forests of the Upper Midwest (i.e. 24–140 stems/ha).
- Snag composition should also be considered in management as snags of longer-lived species, such as red pine, may decay slower and thus be retained on site longer than snags of shorter-lived species (e.g. jack pine, aspen). Snag composition also is important as snags of some species (e.g. red pine) will often attain a greater size than snags of other species (e.g. jack pine).
- Variability in DC development among treatments and tree species suggests that forest managers should tailor snag prescriptions to provide a diversity of snag conditions over time.

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