Influence of post-harvest silviculture on understory vegetation: Implications for forage in a multi-ungulate system

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ABSTRACT

Natural disturbance emulation has emerged as a key management approach to maintaining biodiversity in logged boreal forests. Forest managers' success in emulating understory forest ecosystem functions, e.g., for the provision of habitat even for large mammals, has not been tested due, in many cases, to incomplete records of silviculture. We examined regenerating areas of previously conifer-dominated forests in northwestern Ontario, Canada, 10 and 30 years after logging and 10 and 30 years after fire to test if understory development and moose (*Alces alces*) forage abundance differed between the two disturbance types and artificial or natural regeneration approaches. In addition, we counted moose pellet groups as a measure of moose use of the region. Specific treatments included: (1) naturally regenerating, fire-origin forests, (2) post-harvest, regenerating forests with natural establishment of trees, and (3) post-harvest, regenerating forests with mechanical or chemical site preparation and planting and/or herbicide spraying. We hypothesized that the understory in post-harvest stands would support higher forage availability for moose compared to similarly-aged, fire-origin stands. Abundance of hardwoods, shrubs, and herbaceous plants was greater in naturally-regenerated post-harvest stands than in fire-origin and artificially regenerated post-harvest stands at both 10 and 30 years post-disturbance. However, post-harvest, naturally regenerating stands were not significantly associated with higher moose use, rather evidence of moose use increased as a function of the amount of naturally regenerating logged forest in the surrounding landscape. This study suggests that, relative to fire, the intensity of post-harvest silviculture influences habitat suitability for moose. The effect likely cascades to other ungulates, such as woodland caribou (*Rangifer tarandus caribou*), and vegetation management needs to be considered at scales greater than the stand level in order to achieve habitat management for large mammals.

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1. Introduction

The concept of emulating natural disturbance has emerged in forestry as a management strategy that seeks to maintain economic benefits from clearcutting while sustaining the structure and composition of boreal forests (Bergeron et al., 2002). Two observations provide the rationale; (1) boreal forests experience frequent disturbances and possess inherent resilience to recover from them, and (2) boreal fauna have adapted in such a way that they can persist in this disturbance driven forest ecosystem. The emulation approach speculates, for example, that whereby wildlife species are adapted to wildfire, the predominant disturbance in unmanaged boreal forests, they should likewise adapt to timber harvesting, if practices are applied whose outcomes resemble the effects of wildfire. This study was motivated by the considerable

range recession of woodland caribou (*Rangifer tarandus* L. *caribou*) in Ontario over the past century (Schaefer, 2003). A proposed contributing cause is logging-associated increases in the extent of early successional forests that offer forage to moose (*Alces alces* L.) and white-tailed deer (*Odocoileus virginianus* Zimm.), but, except during migration (Ferguson and Elkie, 2004) and in the spring (Hins et al., 2009) are avoided by caribou (Wittmer et al., 2007). This avoidance is likely due to an altered predator–prey dynamic created by a larger prey base (Rettie and Messier, 1998; McLoughlin et al., 2005; Briand et al., 2009) that equates functional habitat loss for caribou.

In boreal forests, significant conversion from conifer to hardwood and mixedwood stands has been documented where logging has replaced fire as the main forest disturbance (Carleton and MacLellan, 1994). Relative to fire, disturbance from logging tends to lower dominance by conifer trees (Whittle et al., 1997). Deciduous trees can regenerate from stump sprouts and root suckers and dominate post-harvest sites. Wildfire, on the other hand, depending on its intensity, can kill or impede developing

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hardwood understory (Flinn and Wein, 1977) and facilitate seed dispersal in conifers (Arsenault, 2001). Condition of the seed bed also affects forest regeneration, and intense fires can expose mineral soil to improve the establishment of conifers.

Most silvicultural studies on understory species in boreal forests have focused on competition with crop trees (e.g., McDonald and Abbott, 1997). While there are claims that effects of herbicide application on moose forage quality and quantity are negligible (Cumming et al., 1995; Raymond et al., 1996), they come from studies on short-term effects (i.e., <5 years) at a small scale (i.e., the stand level). Tree planting, which has the potential to offer control over future stand density and structure, is often undertaken in productive stands where competition with shrub and hardwood species is expected, and is frequently used in combination with herbicides to control competing vegetation (Perera and Euler, 2000). Post-harvest silviculture may be able to reverse conversion from conifer to hardwood and mixedwood stands, as diversity and abundance of understory plants are strongly related to the intensity of site preparation (Newmaster et al., 2007) and to overstory composition (Hart and Chen, 2008). However, intensive silviculture is often avoided in favour of natural regeneration for ecological and economic reasons. Moreover, good records of silviculture to test long-term and larger-scale effects on maintenance of functions like moose or caribou habitat supply have only been recently assembled in a way to field-test changes over time.

We used the long-term records of silviculture on the English River and Caribou Forest Management Units (FMU) maintained by AbitibiBowater, Inc. to track forest successional pathways to different degrees of investment in forest management. Our objectives were to compare the abundance of common trees, shrubs and herbaceous plants that comprise moose forage, and to compare moose use among 10- and 30-year-old: (1) naturally regenerating,

fire-origin forests, (2) post-harvest, regenerating forests with natural establishment of trees, and (3) post-harvest, regenerating forests with mechanical or chemical site preparation and planting and/or herbicide sprayed. Relative to the other treatment types, we expected that natural regeneration would result in stands with higher deciduous tree and shrub counts, and a greater percentage of herbaceous groundcover. We expected differences among fire-origin, naturally regenerating and more intensively-treated forests to be greater for younger than for older stands, as increasing shade under a developing overstory will eventually limit the shrub and herb layers regardless of treatment type. We expected moose forage availability and moose pellet group counts to be highest in logged areas with natural regeneration, both at the stand and home range scale.

2. Methods

2.1. Study area

The study took place in the English River Forest Management Unit (FMU) and in southern portions of the Caribou FMU, approximately 200 km northwest of Thunder Bay, Ontario, and in Wabakimi Provincial Park, a large (892,000 ha) park east and northeast of the management units where logging is not permitted (49°47′N, 91°02′W; Fig. 1). Forest cover in the area consists mainly of black spruce (*Picea mariana* [Mill.] B.S.P.) and jack pine (*Pinus banksiana* Lamb.) growing in relatively pure stands or in mixed stands in association with white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* L. Mill), trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.). Jack pine stands are extensive on dry sand plains and rocky uplands,
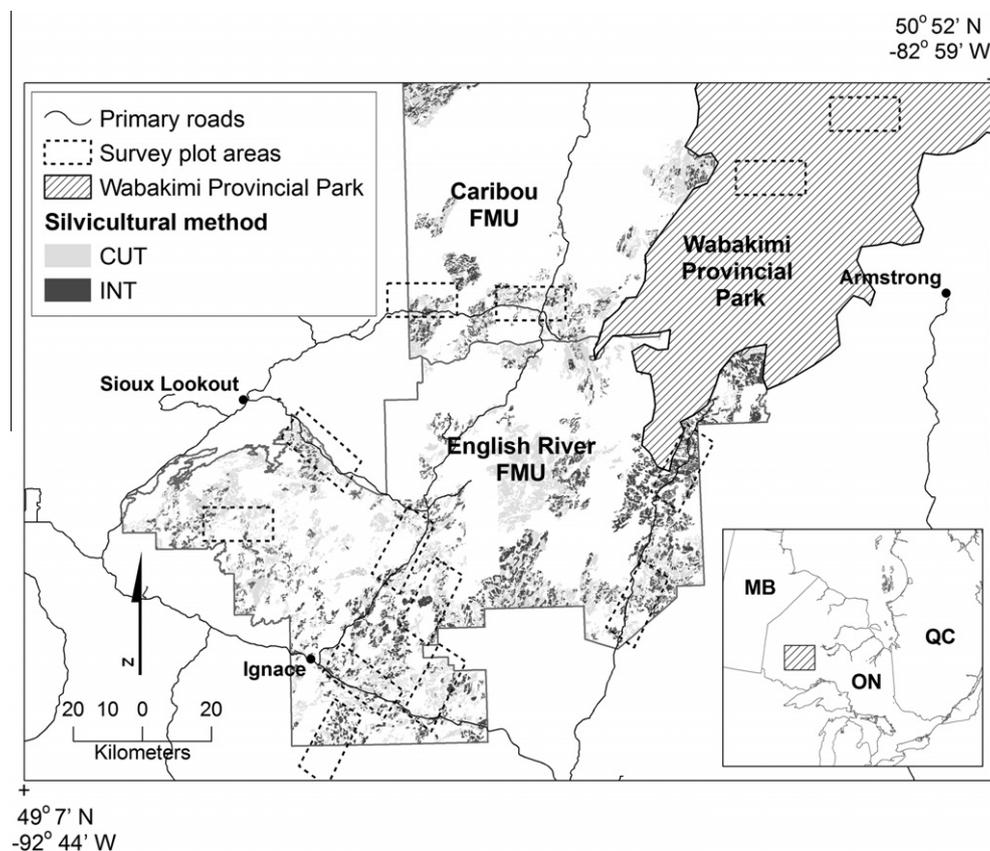
Fig. 1. Location of study area in northwestern Ontario, Canada, showing the survey plot areas, major roads and towns, and the distributions of two treatment types (CUT = clear-cut, natural regeneration; INT = clear-cut, planted and/or sprayed) in the Caribou and English River Forest Management Units.

whereas black spruce dominates in peat-filled depressions. Monthly mean temperatures are −19 °C in January and 19 °C in July, with 204 cm average annual snowfall and 517 mm average annual rainfall (Environment Canada: Sioux Lookout 50°7′N, 91°54′W, 1971–2000).

The study area supports 0.23–0.26 moose/km^2 (McKenney et al., 1998), the dominant ungulate in the region. Moose occur in a range of forest types, especially when pre-sapling or sapling seral stages dominate (Rempel et al., 1997). Moose population growth rate is positively related to the abundance of mixed deciduous habitat (Brown, 2011). Prior to the late 1950s, woodland caribou populated the entire study area. At present, about one-half of the English River FMU and the entire Caribou FMU are north of the line of continuous caribou occupancy defined by Ontario's Ministry of Natural Resources (OMNR, 2009), and are consequently managed under provincial guidelines aimed at maintaining long-term caribou habitat. The OMNR defines caribou habitat as nearly contiguous stands ⩾60 years old comprising 100% black spruce, eastern white cedar (*Thuja occidentalis* L.) and American larch (*Larix laricina* [Du Roi] Koch) on sites considered to have low productive capacity due to drainage and soil types, as well as stands with ⩾70% black spruce and ⩽20% trembling aspen and white birch (Racey et al., 1999; Ferguson and Elkie, 2004; Brown et al., 2007). Jack pine stands are eligible if they comprise ⩾70% jack pine and ⩽20% trembling aspen and white birch, or the trembling aspen and white birch component of the stand is ⩽20% and the jack pine component is larger than the combined black spruce and white spruce components. In the 1940s, white-tailed deer, with similar general habitat requirements as moose, extended over the entire English River (and former Brightsand) FMU, but was considered absent from the Caribou Forest (Great Lakes Forest Products Ltd., 1975). During the 1950s and 1960s, white-tailed deer range contracted south of the FMUs as a result of severe winters, at which time moose populations began to rise (OMNR, unpublished data). Currently, white-tailed deer appear to be expanding northward again, with some recent sightings in the Caribou Forest, the northern extent of our study area. White-tailed deer and woodland caribou are distributed more sporadically in the study area and density estimates are not available for these species.

2.2. Data collection

We used 1976 and 1996 Forest Resource Inventory (FRI) maps (OMNR, unpublished) to select jack pine and black spruce stands that were conifer-dominated prior to disturbance. We sampled stands in three post-disturbance regeneration types: fire (FIRE), clearcutting followed by natural regeneration (CUT), and clearcutting followed by intensive silviculture (INT). CUT stands typically incorporated seed trees (i.e., a small number of seed bearing trees left on site following logging), and were generally not mechanically or chemically treated after the harvest. Stand density and composition after the harvest were not controlled. The INT treatment always had mechanical site preparation followed by manual planting or spraying with herbicide, or a combination of planting and spraying with herbicide. We amalgamated planting and herbicide combinations into one treatment based on a pilot study in 2008 that showed no significant effects on shrub and tree composition between the two treatments. For this study, INT did not include any pre-commercially thinned stands.

We randomly selected twenty FRI-defined stands in each of the three treatment types that were approximately 10 years post-disturbance (i.e., logging/fire occurred in 1996–1999) and twenty at approximately 30 years post-disturbance (i.e., logging/fire occurred in 1976–1979). The equipment used for mechanical site preparation differed between the two age classes. In general, skidder-pulled passive trenchers were used on 10-year-old stands and

tractor-pulled drags (barrels and chains) were used on the 30-year-old stands. The primary herbicide used on 30-year-old INT stands was 2,4-D (2,4-Dichlorophenoxyacetic acid), whereas glyphosate herbicides (Round Up® and Vision®) were introduced in the mid-1980s and applied aerially using helicopters in many of the 10-year-old INT stands. To ensure that soil types did not systematically vary among the treatments, we sampled soils with an auger to a depth of 1 m and classified each sample into a "soil moisture regime" based on Ontario's Forest Ecosystem Classification protocol (Sims et al., 1997).

We conducted field plot measurements between July and early September in 2008 and 2009. Using ArcView (v. 9.1), we selected a random point in each stand 100–500 m from the nearest truck-accessible secondary road to serve as the starting point of a 60-m long transect. The mean distance between stands of the same treatment was 3.2 km. Circular plots of 5.65-m radius (100 m^2) were centered at the ends and middle of the transect (i.e., three plots per stand). Within a plot, all individual stems >2 m in height were counted by species. These included the woody species that are considered the most important moose forage: mountain maple (*Acer spicatum* Lam.), white birch, beaked hazel (*Corylus cornuta* Marsh.), balsam fir, trembling aspen, cherry (*Prunus* spp.), willow (*Salix* spp.), and ash (*Sorbus* spp.) (Peek et al., 1976; Crête and Bedard, 1975; Irwin, 1985; Cumming, 1987). We counted stems <2 m in height using a 1-m wide bar held at 1 m in height along two 10-m long belt transects running N–S and E–W across each plot (20 m^2 in total) (adapted from Rodgers et al., 2008). Percent of ground covered by vascular plants, moss, lichen, exposed soil, coniferous litter, deciduous litter and coarse woody debris (CWD) was visually estimated in four 1-m^2 subplots per plot.

We counted moose fecal pellet groups in a random subset of five stands per treatment, by use of five 5.65 m (100 m^2) radius circles in each stand (Neff, 1968); i.e., an additional two plots were located 30 m perpendicular to the original 60 m vegetation transect. A pellet group was defined as a group of at least five pellets within one pellet distance from one another, with at least half of the pellet group falling within the plot; this definition corresponds to estimated moose density (Harkonen and Heikkila, 1999). Plots were located at a maximum distance of 500 m from the nearest secondary road, a requirement due to our interest in silviculture.

2.3. Data analyses

Analyses were undertaken separately for 10- and 30-year-old stands. Composition and abundance of woody stems in tree and shrub layers and groundcover estimates were examined by use of non-metric multidimensional scaling (NMDS). A Sorensen (Bray-Curtis) distance was used for the ordination, as it assigns less weight to outliers, which are common in ecological data (Sørensen, 1948). Ordinations were developed based on plotting a measure of fit ("stress") to the number of solutions. We calculated Kendall's tau rank correlation coefficients to test the strength of the association between species and ordination axes.

To test the hypothesis that no floristic differences existed among the treatments, we used a Multiple Response Permutation Procedure (MRPP), set at the Sorensen distance measure (in order to be consistent with our ordination). MRPP is a non-parametric analog to Discriminant Function Analysis and determines whether variation between treatments exceeds that expected based on the variance within treatments.

We applied Dufrêne and Legendre (1997) indicator species analysis (ISA) to tree and shrub data and groundcover estimates to describe differences in individual species abundances among treatments and to identify target species that were more abundant in one or another of the treatments. Relative abundance, RA, and

relative frequency, RF, were multiplied to calculate an indicator value, IV, for each species j in each treatment k:

$$IV_{kj} = 100 \ (RA_{kj} \times RF_{kj}) \tag{1}$$

In addition, we applied a Monte Carlo test of significance of observed maximum indicator value, based on 1000 randomizations (McCune and Grace, 2002). Only species with alpha levels less than 0.05 and with an indicator value greater than 25 were considered indicator species for a treatment (Dufrêne and Legendre, 1997). We applied a Bonferroni correction to account for multiple comparisons in pairwise comparisons among treatments. All multivariate tests were carried out using PC-ORD ver. 5 (McCune and Mefford, 2006).

Analysis of variance (ANOVA) was used to determine the relationship between moose pellet counts and treatment at the stand-level. Examination of residuals indicated that the assumptions of homogeneity and normality were satisfied. In addition, we were interested in the degree to which variation among moose pellet counts could be attributed to the degree of regeneration in the surrounding landscape. Home ranges for North American moose can vary, on average, from 10–40 km^2 (Crête, 1988). Accordingly, we measured the area of INT, CUT and FIRE in circular regions surrounding the plot centers at three scales: 10 km^2 (1.75 km radius), 20 km^2 (2.5 km radius), and 40 km^2 (3.55 km radius). Since we found that the random selection of stands expanded to larger scales resulted in some spatial overlap in two home ranges of both the CUT and INT treatments, we compared moose pellet counts, silvicultural treatments and between-site distances using Focus 2.1 (Holland et al., 2004) to evaluate potential lack of spatial independence associated with multi-scale analysis.

3. Results

3.1. Tree, understory and ground-layer vegetation composition

3.1.1. 10-year-old stands
Soil moisture regimes did not differ significantly among treatments (Table 1). Differences in species composition between the treatments occurred for 10-year-old stands, especially for jack pine and trembling aspen growth in tree and shrub layers (Table 2). The NMDS ordination for shrubs and trees resulted in a three-dimensional solution that explained 85% of the variation in the data (final stress = 13.8), a reliable solution for ecological data (McCune and Grace, 2002). Examination of the third axis showed little evidence of variation related to the treatments, so only Axes 1 and 2 are presented (Fig. 2A). Axis 1, which explained 39% of the variation in the data, was most positively correlated with shrubs considered preferred moose forage, including, serviceberry ($\tau = 0.456$), mountain maple ($\tau = 0.419$), trembling aspen ($\tau = 0.387$), and beaked hazel ($\tau = 0.277$). This axis was most negatively correlated with jack pine

($\tau = -0.660$), which is more associated with caribou habitat. Axis 2, which explained 29% of the variation in the data, was most positively correlated with beaked hazel ($\tau = 0.379$) and mountain maple ($\tau = 0.331$) and most negatively correlated with black spruce ($\tau = -0.431$). There was strong differentiation between CUT stands and the other two stand types (FIRE and INT) due to relatively high densities of deciduous shrubs in the former (upper right quadrant); differentiation between the latter two stand types was not as evident.

The MRPP permutation procedure ($p < 0.01$, $T = -12.09$) led to a small A value ($A = 0.087$) indicating differences among the FIRE, CUT and INT groups. The greatest difference in community composition and abundance, based on pairwise comparisons, was between CUT and FIRE ($p = 0.001$, $T = -11.22$, $A = 0.09$) followed by CUT and INT ($p = 0.001$, $T = -9.97$, $A = 0.08$) and FIRE and INT ($p = 0.01$, $T = -4.94$, $A = 0.04$). Several species were significantly more frequent and abundant in the FIRE and CUT treatments in the 10-year-old stands, based on the ISA (Table 3). Jack pine, white birch, black spruce and jack pine and white birch shrubs were significantly associated with FIRE stands. In contrast, trembling aspen, serviceberry, beaked hazel, willow and mountain maple were significantly associated with CUT stands.

The NMDS ordination on ground cover in the 10-year-old stands yielded an optimum solution in three dimensions with a final stress of 10.813 (Fig. 3A). Axis 1, which explained 52% of the variation in the data, was most positively correlated with vascular plants ($\tau = 0.462$), and most negatively correlated with CWD ($\tau = -0.702$). Axis 2, which explained 26% of the variation in the data, was most positively correlated with litter/exposed soil ($\tau = 0.696$) and most negatively correlated with moss ($\tau = -0.277$). FIRE stands were strongly distinguished from INT and CUT stands due to their high relatively high CWD, although several of the CUT sites in the top right of the figure grouped separately from the other two stand types due to high percent cover of soil/litter.

In the MRPP permutation procedure ($p < 0.001$, $T = -11.64$, $A = 0.135$), the greatest difference in community composition and tree and shrub abundance, based on pairwise comparisons, was between CUT and FIRE ($p < 0.001$, $T = -12.01$, $A = 0.16$), followed by INT and FIRE ($p < 0.001$, $T = -7.10$, $A = 0.09$) and INT and CUT ($p = 0.002$, $T = -4.47$, $A = 0.05$). CWD was an indicator of FIRE stands ($p < 0.001$), whereas lichen ($p < 0.001$) and moss ($p = 0.02$) were indicators of INT stands, and herbaceous plants ($p = 0.01$) were an indicator of CUT stands.

3.1.2. 30-year-old stands
Again, soil moisture regimes did not differ significantly among treatments (Table 1). The NMDS ordination resulted in a three-dimensional solution that explained 82% of the variation in the data (final stress = 12.2). Axis 1, which explained 35% of the

Table 1
Soil moisture regime frequencies based on soil auger sampling of 360 field plots in northwestern, Ontario according to treatment type (FIRE = fire-origin, CUT = clear-cut, natural regeneration and INT = clear-cut, planted and/or sprayed). Pearson's chi-square comparing treatment types for 10-year-old stands = 7.8, $p = 0.10$; for 30-year-old stands = 8.4, $p = 0.08$.

Treatment		10-year-old stands ($n = 180$)				30-year-old stands ($n = 180$)			
		Dry-fresh	Moist	Wet	Total	Dry-fresh	Moist	Wet	Total
FIRE	Count	47	11	2	60	46	5	9	60
	Expected	42.3	13.0	4.7		45.3	9.3	5.3	
CUT	Count	37	14	9	60	47	9	4	60
	Expected	42.3	13.0	4.7		45.3	9.3	5.3	
INT	Count	43	14	3	60	43	14	3	60
	Expected	42.3	13	4.7		45.3	9.3	5.3	
Total		127	39	14	180	136	28	16	180

Table 2
Stand characteristics of 120 stands (360 field plots) sampled in northwestern Ontario, Canada (FIRE = fire origin, CUT = clear-cut harvested, naturally regenerated, INT = clear-cut harvested with planting, herbicide-spraying or both). Values are mean percentage tree composition by stand (with SE in parentheses).

Origin and age class	n	Post-disturbance stand composition (%)					Other
		Jack pine	Black spruce	Balsam fir	Aspen	White birch	
FIRE							
10 years	20	79 (5)	2 (2)	0	3 (2)	16 (4)	<1
30 years	20	44 (8)	35 (7)	6 (3)	9 (5)	6 (1)	<1
CUT							
10 years	20	27 (8)	3 (5)	3 (1)	48 (9)	11 (2)	8
30 years	20	30 (8)	28 (7)	24 (7)	10 (4)	8 (3)	<1
INT							
10 years	20	73 (7)	8 (5)	3 (1)	11 (4)	4 (3)	<2
30 years	20	29 (6)	44 (6)	6 (3)	9 (3)	11 (3)	<1
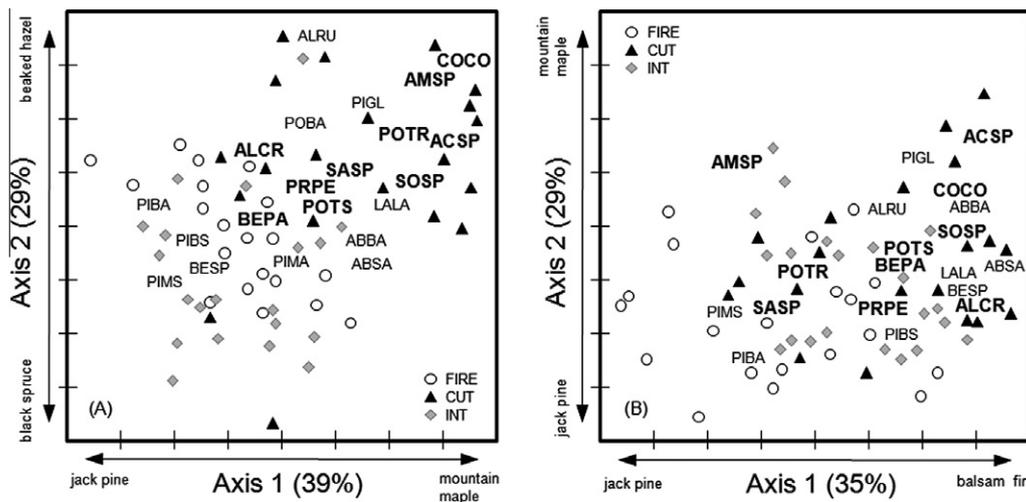
Fig. 2. Non-metric multidimensional scaling ordination for tree (taller than 2 m) and shrub species (including trees shorter than 2 m) composition on (A) 10-year-old stands ($n = 60$), and (B) 30-year-old stands ($n = 60$) in northwestern Ontario, Canada. Axes 1–3 had an R^2 of 0.845 cumulatively (0.388, 0.291, and 0.167, respectively) for 10-year-old stands, and corresponding values of 0.816 (0.351, 0.287, and 0.180) for 30-year-old stands. Acronyms are: ABBA (*Abies balsamea*), ABSA (*Abies balsamea* shrub), ACSP (*Acer spicatum*), ALRU (*Alnus rugosa*), ALCR (*Alnus crispa*), AMSP (*Amelanchier* spp.), BEPA (*Betula papyrifera*), BESA (*Betula papyrifera* shrub), COCO (*Corylus cornuta*), LALA (*Larix laricina*), PIGL (*Picea glauca*), PIMA (*Picea mariana*), PIMS (*Picea mariana* shrub), PIBA (*Pinus banksiana*), PIBS (*Pinus banksiana* shrub), POTR (*Populus tremuloides*), POTS (*Populus tremuloides* shrub), PRPE (*Prunus pensylvanica*), SASP (*Salix* spp.), and SOSP (*Sorbus* spp.). Important species for moose forage shown in bold type.

Table 3
Significant indicator species based on age class and treatment in northwestern Ontario, Canada (FIRE = fire-origin stands and CUT = clear-cut harvested, naturally regenerated). See text for details.

Species	Treatment	Observed indicator value	IV from randomized groups		
			Mean	S. dev.	p
10-year-old sites (n = 60)					
Pinus banksiana	FIRE	58.1	38.9	4.54	<0.01
Betula papyrifera	FIRE	50.4	30.7	5.20	<0.01
Pinus banksiana shrub	FIRE	60.1	31.2	5.60	<0.01
Picea mariana shrub	FIRE	57.9	31.4	4.91	<0.01
Betula papyrifera shrub	FIRE	38.4	38.4	7.79	0.02
Populus tremuloides	CUT	44.8	31.7	6.48	0.05
Amelanchier spp.	CUT	37.5	19.3	6.93	0.01
Corylus cornuta	CUT	44.8	14.4	5.27	<0.01
Salix spp.	CUT	49.9	36.3	6.43	0.04
Acer spicatum	CUT	49.9	14.0	5.83	<0.01
30-year-old sites (n = 60)					
Alnus crispa	CUT	44.9	26.3	6.34	0.01
Corylus cornuta	CUT	45.0	11.6	4.56	<0.01
Acer spicatum	CUT	35.0	10.1	4.41	<0.01
Abies balsamea	CUT	39.2	10.3	4.61	0.04

variation in the data, was similar to the case for 10-year-old stands: most positively correlated with shrubs considered preferred moose forage, this time including mountain maple ($\tau = 0.421$), balsam fir ($\tau = 0.420$) and green alder ($\tau = 0.419$), and most negatively correlated with jack pine ($\tau = -0.466$, Fig. 2B). Axis 2, which explained 29% of the variation in the data,
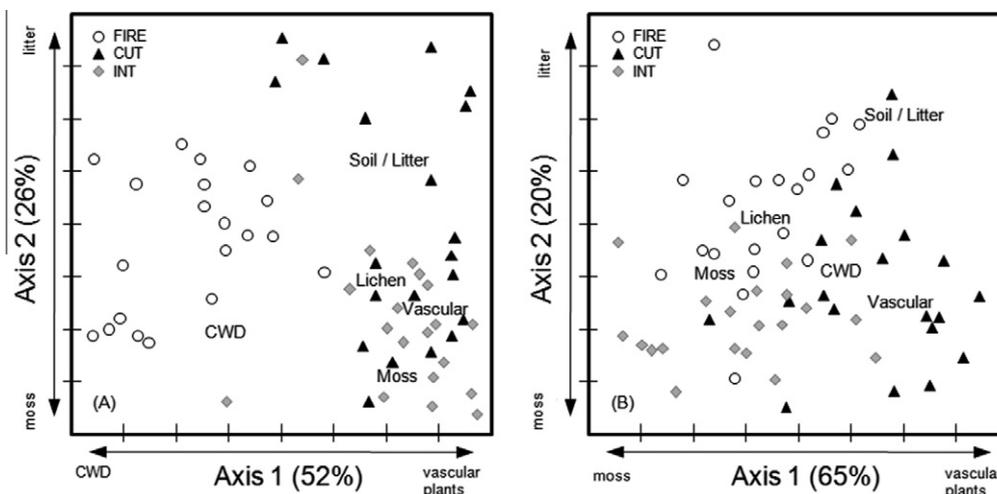
Fig. 3. As Fig. 2 except that ordination is for percent groundcover composition on (A) 10-year-old stands (n = 60), and (B) 30-year-old stands (n = 60) in northwestern Ontario, Canada. Groundcover classes were: vascular plants, moss, lichen, rock, exposed soil/litter, and coarse woody debris (CWD). Axes 1–3 (NMS 3-dimensional solution) had an R^2 of 0.931 cumulatively (0.504, 0.220 and 0.207, respectively) for 10-year-old stands and Axes 1 and 2 (NMS 2-dimensional solution) had an R^2 of 0.857 cumulatively (0.265 and 0.591, respectively) for 30-year-old stands.

was most positively correlated with mountain maple (τ = 0.372) and beaked hazel (τ = 0.347) and most negatively correlated with jack pine (τ = −0.532). Strongest differentiation among the treatments was shown along the first axis, with CUT tending to have high values, INT having intermediate values, and FIRE the lowest values.

The MRPP had a T value of 6.16 ($p < 0.01$), indicating weaker separation among treatments compared to the 10-year-old stands. In pairwise comparisons, the greatest difference was between CUT and INT ($p = 0.01$, $T = −4.90$, $A = 0.04$), followed by CUT and FIRE ($p = 0.01$, $T = −4.21$, $A = 0.03$) and FIRE and INT ($p = 0.01$, $T = −4.02$, $A = 0.03$). Three shrub species were significantly associated with CUT stands by ISA: green alder, beaked hazel and mountain maple (Table 3).

Groundcover differed between treatments in 30-year-old stands (Fig. 3B), although there was weaker separation evident among the treatments relative to 10-year-old stands (stress = 13.18, 2-dimensional solution). Axis 1, which explained 65% of the variation in the data, was most positively correlated with vascular plants (τ = 0.542), and most negatively correlated with moss (τ = −0.662). Axis 2, which explained 20% of the variation in the data, was most positively correlated with litter/exposed soil (τ = 0.743) and most negatively correlated with moss (τ = −0.401). Groundcover also differed among the FIRE, CUT and INT stands based on the MRPP permutation procedure ($p < 0.001$, $T = −6.14$, $A = 0.072$). The greatest difference, based on pairwise comparisons, was between CUT and INT ($p > 0.001$, $T = 7.40$, $A = 0.11$), followed by CUT and FIRE ($p = 0.006$, $T = −3.63$, $A = 0.042$) and INT and FIRE ($p = 0.05$, $T = −1.94$, $A = 0.023$). As with 10-year-old stands, CWD ($p = 0.02$) and lichen ($p = 0.02$) were indicator species for FIRE stands, moss ($p = 0.02$) was an indicator species for INT stands (Fig. 3).

3.2. Moose pellet counts

Moose pellet counts were variable and low in both 10-year-old (mean [±standard error of the mean (SEM)] 0.17 [0.07] pellet groups per 100 m^2) and 30-year-old stands (mean [±SEM] 0.09 [0.05] pellet groups per 100 m^2). Differences in pellet counts among the silvicultural treatments in both age classes were not significant at the stand level ($F_{1,9} = 1.23$, $p = 0.30$). The percentage of the landscape around the plots that was harvested and naturally regenerated (CUT) at a scale of 10 km^2 was significantly correlated

with moose pellet counts in 10-year-old stands ($F_{(1,7)} = 20.7$, $p = 0.004$, $R^2 = 0.74$). The same was true for areas of 20 km^2 ($F_{1,7} = 13.2$, $p = 0.011$, $R^2 = 0.63$) and 40 km^2 ($F_{1,7} = 9.6$, $p = 0.021$, $R^2 = 0.55$). The percentage area of INT and FIRE were not correlated with moose pellet counts at these scales (10 km^2, $p = 0.18$, $p = 0.47$; 20 km^2, $p = 0.17$, $p = 0.32$; 40 km^2, $p = 0.45$, $p = 0.42$). Moose pellet counts and the percentage of the landscape harvested were not significant for 30-year-old stands for FIRE (10 km^2, $p = 0.28$, 20 km^2, $p = 0.43$; 40 km^2, $p = 0.61$), CUT (10 km^2, $p = 0.29$, 20 km^2, $p = 0.26$; 40 km^2, $p = 0.24$) or INT (10 km^2, $p = 0.36$, 20 km^2, $p = 0.42$; 40 km^2, $p = 0.51$).

4. Discussion

Silvicultural investment was important in determining understory, a critical component of habitat for ungulates. Planting and herbicide-spraying accelerate succession toward conifer-dominance by establishing conifer stock and killing competing vegetation (Bell et al., 1997). Stands where the overstory had a higher abundance of deciduous trees also had higher deciduous and total shrub abundance, consistent with other studies (e.g., Legare et al., 2002). Age and post-harvest treatment both influenced ground-layer vegetation, but differences relating to disturbance type and post-harvest treatment may have been more a result of the influence of silviculture on overstory composition. Stands with low non-vascular plant abundance in the composition were likely due to higher leaf litter associated with higher deciduous tree and shrub composition (Beatty and Scholes, 1988). Previous research has shown that deciduous trees (e.g., aspen and birch) are associated with high transmission of light filtering to the understory, high foliar nutrient content, and high pH and base cations, which support greater understory richness and diversity (Paré and Bergeron, 1996; Messier et al., 1998). Pre-established rhizomatous species are more likely to persist after harvesting compared to fire, as logging mainly results in removal of the overstory (Hart and Chen, 2008). In addition to competition for light and moisture, allelopathic effects likely contribute to lower vascular plant cover as a result of conifer-dominance associated with more intensive silviculture. We propose that two mechanisms are driving differences among the two age classes. For 10-year-old stands, a higher legacy of the pre-disturbance vegetation remains and can explain why the groundcover of harvested treatments differed from groundcover in

fire-origin stands. For 30-year-old stands, allelopathic suppression due to the acidity of conifer litter (Mallik, 2008) can explain why post-harvest, naturally regenerating stands were most different from fire-origin and intensive silviculture. Lichen was not abundant and rarely present in young fire-origin stands, consistent with other understory studies in boreal forests (Hart and Chen, 2008).

During the stand initiation phase, i.e., for the young forests we assessed, treated areas were closer to emulating natural disturbance in terms of understory composition than the older forests we assessed. This result suggests two possibilities: (1) the difference in the silvicultural treatment, primarily the type of herbicide sprayed, between the 30- and 10-year-old stands was less effective for the 30-year-old stands or (2) the advantage of using intensive silviculture to emulate vegetation composition post- disturbance is largely lost by 30 years. Both possibilities are supported by previous research. For example, Kennedy and Jordan (1986) found gyphosate-treated areas support half as much moose forage as 2,4-D-treated stands. Likewise, some convergence in forest successional pathways in burned and treated stands is expected, as previously reported for Alaska (Rees and Juday, 2002) and Quebec (Bergeron and Dubuc, 1989). Over time, the influence of herbicide applications on forest understory can be diminished due to persistence of seeds in the seed bank, seed sources adjacent to the harvested area and the sprouting capacity of competing vegetation (Freedman et al., 1994). Lower abundance of most woody forage species by 30 years in our study is likely explained by the lower light transmission occurring during competitive stem exclusion processes (Ross et al., 1986), which we expect to occur regardless of the disturbance origin and regeneration method.

The potential impact of understory vegetation on ungulates is direct. For the same region, moose, white-tailed deer and wolf populations were largest, and woodland caribou populations smallest, in forests with a higher deciduous component (Bowman et al., 2010), suggesting a link between the increased prevalence of deciduous cover and increased predator abundances. Woodland caribou have been found to use less young, shrub-rich habitat than what is available to them (Hillis et al., 1998), they also avoid mixed and deciduous stands (Courtois et al., 2008). Conversely, both moose and white-tailed preferentially occupy deciduous forests (Krefting and Phillips, 1970), where higher food availability of forage results in earlier sexual maturity and more frequent multiple births (McNicol and Timmermann, 1981). Briand et al. (2009) showed that woodland caribou avoided forest with a dense shrub layer and consequently separated themselves from areas attractive to moose. For moose, trembling aspen, white birch, willow, mountain maple, mountain ash, beaked hazel, green alder, serviceberry and pin cherry are used for forage throughout the year (Peek et al., 1976; Irwin, 1985) with the addition of balsam fir and balsam poplar in the winter (Thompson and Vukelich, 1981; Cumming, 1987). We found stands left for natural regeneration after clear-cut harvesting supported higher abundance of all of these species compared to planted, herbicide-sprayed and post-fire stands.

Thompson et al. (2003) developed aspatial models based on estimated probabilities of habitat use for a range of boreal wildlife species: in 5–10-year-old conifer-dominated stands, they predicted that moose were three times as likely to use stands harvested and left for natural regeneration than stands with more intensive silviculture; for mixedwoods of the same age, moose use was six times as likely. For stands 10–30-years-old, the same prediction was reduced to twice as likely for both conifer-dominated and mixedwoods stands. Although we found that post-disturbance treatments influence moose forage availability, our estimates of moose use were not correlated to silvicultural treatments at the stand level. As suggested by other studies (e.g., Dussault et al., 2006), moose habitat suitability may be more accurately assessed at scales larger than the forest stand. When we investigated post-disturbance treatments at scales of 10–40 km^2, we found support for the relationship we were expecting (i.e., increased moose use as the amount of CUT forest increased), consistent with forage studies at the moose home range scales (e.g., van Beest et al., 2010). Other factors also may affect habitat use, including cover, human impacts, time lags, and proximity of nearby populations (Gasaway et al., 1989; Rempel et al., 1997; Herfindal et al., 1999; Nikula et al., 2004), factors that we did not investigate in our study. In addition, Laurian et al. (2000) found less moose use <=500 m from roads which may explain relatively low pellet counts on all of our treatment stands.

4.1. Management implications

Our study supports the conclusion that post-harvest, vegetation management influences moose forage, and that vegetation changes associated with silviculture during stand initiation can impact moose use. Stands left to regenerate naturally after harvest were most likely to support increases in moose densities, as a result of associated increases in mixed deciduous habitat abundant in forage (Brown, 2011). Predetermined financial allocations for silviculture have been a factor limiting past application of intensive silviculture, although other factors include ease of access to a site for planting and availability of natural seed on-site. Regeneration is usually the highest cost in stand management and has the longest return time on investment (Brace and Bella, 1988). While there are economic advantages in support of higher quality and quantity of merchantable wood associated with higher silvicultural investment, these investments are significant, ranging from $10/ha for natural regeneration to upwards of $1300/ha for intensive renewal (Arlidge, 1995). Pre-commercial thinning, which we did not include in our investigation, can also result in diverse understory and overstory vegetation conditions, as moose forage and moose use may be higher following this additional investment (Sullivan et al., 2007; McLaren et al., 2000).

Forest regeneration has important implications for both woodland caribou, which is protected under the Endangered Species Act, and moose, an economically important species that can also reach levels that eliminate benefits of silvicultural investments (Thompson and Curran, 1993; McLaren et al., 2000). However, research linking woodland caribou recovery to silvicultural strategies has concentrated on improving lichen biomass in mature forests (e.g., Stone et al., 2008), and current management practices potentially underestimate the importance of forest composition, particularly understory composition, in the short to medium terms. Across Canada, guidelines have been implemented to ensure that harvesting in caribou range is aggregated to minimize habitat fragmentation due to harvesting blocks and road building. However, even where the amount and configuration of harvesting achieve patterns similar to fire, the potential for shrub-rich regeneration can create conditions less suitable for woodland caribou. Thus, we recommend forest managers consider moose forage abundance in younger forests as an important monitoring criterion in evaluating silviculture effectiveness in multiple-ungulate systems where caribou occur or may recover.

Geographic Information Systems (GIS), satellite imagery and computer modeling capabilities allow for rigorous evaluation of landscape scale forest dynamics over time and space. There is now opportunity to improve integration of information between the landscape and stand scales, including historical silviculture. The influence of silvicultural treatments on wildlife habitat needs to be better understood within a larger landscape disturbance and regeneration pattern. To improve natural disturbance emulation, an important next step is to integrate the effect of forest regeneration resulting from stand-level silviculture and

aggregations of silvicultural treatments over the landscape with population densities of moose, woodland caribou, and their predators.

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