Understory vascular plant responses to retention harvesting with and without prescribed fire

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Abstract

Wildfire is the predominant natural disturbance in the boreal forests of western Canada. Natural disturbance-based forest management involves the use of retention harvesting to retain stand structural diversity post-harvest; however, this partial harvesting technique does not cause combustion of the forest floor as does fire. Application of prescribed burning to areas treated with retention harvesting might emulate the influence of wildfires more effectively than harvesting alone. We compared understory vascular plant diversity, abundance, and composition between forest stands subjected to dispersed retention harvesting (10% retention) with and without prescribed burning one year, six years, and 11-12 years post-burn. Untreated forest was included as a reference. Research was conducted in conifer-dominated, mixedwood, and deciduous-dominated boreal forest stands in northwestern Alberta, Canada. In deciduous-dominated stands, burned areas of retention harvested stands had higher species richness and greater cover than did unburned areas. In all three forest cover types, effects of harvest with and without burn on species richness, cover, and composition were still evident a decade after disturbance. Fire-adapted species benefited most from the prescribed burn treatment. The combination of prescribed burning with retention harvesting can be considered a useful option in forest management that aims to emulate natural disturbance.

Keywords

Prescribed burning, retention harvesting, fire, understory vascular plants, boreal forest

Introduction

Wildfire is the predominant stand-replacing natural disturbance in the boreal forest and it drives the region's vegetation dynamics (Johnson 1992; Payette 1992). The understory vegetation layer hosts most of the plant diversity in the boreal forest and is important to many forest ecosystem functions (Nilsson and Wardle 2005; De Grandpré et al. 2014). This layer is strongly influenced by fire and many boreal species are adapted to a disturbance regime dominated by relatively frequent, severe, wildfires (Rowe and Scotter 1973; White 1979). Fire reduces organic layer depth (Greene et al. 2007) and exposes mineral soil, which is an important seedbed for plants (Charron and Greene 2002). Deposition of charcoal (Wardle et al. 1998), mobilization of nutrients in the form of ash (Noble et al. 1977), losses of nutrients due to combustion of organic material (Johnson et al. 2007), and post-fire increases in availability of resources (e.g., light, soil moisture) are important factors determining early post-fire vegetation dynamics. Adaptations of boreal plants to wildfire include the ability to survive and resprout after fire; deeply buried, long-lived seed banks; aerial seedbanks (with serotinous cones); and the ability to disperse into recently disturbed sites (Rowe 1983; Greene et al. 1999; Allen 2008; Donato et al. 2009). After wildfire, plant species richness and abundance tend to be high, reflecting rapid establishment of disturbance-adapted species combined with populations of residual species that survived the fire in situ (Liu et al. 2017). Over time following wildfire the understory vegetation re-develops as a function of prior fire history and severity, the pre-fire community, canopy cover, light, competing vegetation, and time-since-fire (Wang and Kemball 2005, DeGrandpré et al. 2014, Bergeron et al. 2017, Kumar et al. 2018).

Forest harvesting is an increasingly important large-scale disturbance in the boreal forest and its ecological impact differs from that of wildfire (McRae et al. 2001). Burned stands have lower decomposition rates (Wei et al. 1997), but thinner organic layers, higher pH levels, and greater short-term nutrient availability compared to harvested stands (Simard et al. 2001; Rees and Juday 2002; Thiffault et al. 2007). Further, wildfire leaves more coarse woody debris on site, particularly snags, than does harvesting (McRae et al. 2001; Pedlar et al. 2002). Post-disturbance forest regeneration patterns differ between wildfire and harvest with the latter supporting fewer pioneer species than post-fire sites where mineral soil is exposed (Nguyen-Xuan et al. 2000). The presence of fire-specialist species contributes to higher species richness in stands subjected to wildfire than in logged stands (Rees and Juday 2002).

Sustainable forest management incorporates, among other things, knowledge of natural disturbance patterns and processes as a basis for maintaining biodiversity following anthropogenic disturbance (Attiwill 1994). Retention harvesting is an approach that aims to emulate natural disturbance by retaining biological legacies and maintaining forest structural diversity (Franklin et al. 1997). Retention harvesting, which involves leaving patches of live, mature trees standing in patches (aggregated retention) or dispersed across the harvested area at time of harvest, has become an increasingly popular component of ecosystem-based forest management (Gustafsson et al. 2012) and is the main approach being used to address goals of sustainable forest management in Canada (Work et al. 2003*a*, 2003*b*).

A minimum of 10% retention is recommended for ameliorating disturbance effects on understory plant communities (Craig and Macdonald 2009). However, retention harvesting may not adequately emulate the effects of wildfire on understory vegetation, as there is no combustion of the forest floor and no heat to promote germination of fire-adapted species in the seed bank. Combining retention harvesting with prescribed burning could potentially attenuate the ecological differences between harvesting and wildfire.

Early post-fire plant communities are of conservation concern (Kurulok and Macdonald 2007) as stands affected by wildfires are often salvage logged (Nappi et al. 2004; Schmiegelow et al. 2006). Managed forests should contain early-successional forests, which are critical for habitat specialists and disturbance-adapted species (Swanson et al. 2011; Fedrowitz et al. 2014). Prescribed burning after harvest has been suggested as a tool for promoting the unique substrates and habitats critical for fire-specialized species (McRae et al. 2001; Hart and Chen 2006; Vanha-Majamaa et al. 2007; Brassard and Chen 2010; Halpern et al. 2012; Faivre et al. 2016). When combined with aggregated tree retention, prescribed fire promoted the recovery of some plant species that have wind-dispersed seeds (Johnson et al. 2014).

The objective of this study was to document the effects of prescribed burning after dispersed retention harvesting on understory vegetation. Specifically, we compared vascular understory plant diversity, abundance, and composition between forest stands subjected to 10% retention harvesting with and without prescribed burn post-harvest. We compared data from three different forest cover types pre-harvest and at three separate time periods up to 12 years post-burn. We predicted that total understory species richness and abundance would increase with disturbance and that these effects would be greater in stands burned after harvesting because of greater opportunities for establishment of fire-adapted species, such as those with deep rhizomes, buried seed banks, or those capable of wind dispersal. We also expected that differences between burned and unburned sites would be greatest immediately after disturbance and that these differences would diminish over time.

Methods

Study Site

Research was conducted at the large-scale Ecosystem Management Emulating Natural Disturbance (EMEND; emend.ualberta.ca) experiment located approximately 90 km northwest of Peace River, Alberta, Canada (56° 46’ 13” N, -118° 22’ 28” W). Climate data collected at nearby Eureka River (56° 29’ 00” N, -118° 44’ 00” W) from 1981 to 2010 indicated a mean annual precipitation of 436 mm and mean temperatures of -16.9 °C and 15.0 °C for January and July, respectively (Environment Canada 2017). The EMEND site is comprised of a total of ~1000 ha of experimental compartments in the boreal mixedwood forest. At the time of the experiment establishment in 1998, the majority of trees were approximately 103 or 161 years old having recruited from fires in the years 1895 and 1837 (Bergeron et al. 2017). The dominant tree species are *Picea glauca*, *Populus balsamifera*, and *Populus tremuloides* while the dominant understory shrub species include *Viburnum edule*, *Rosa acicularis*, and *Shepherdia canadensis*. The study included three different forest stand types based on canopy composition at the start of the study: 1) conifer-dominated (CD) (canopy > 70% coniferous trees); 2) mixed (MX) (conifer and deciduous (i.e., broadleaf) each 35%-65% of canopy); and 3) deciduous-dominated (DD) (canopy > 70% deciduous trees) (Spence et al. 1999) (Table A1). Soils, which are of glacial origin, are mainly Orthic and Dark Grey Luvisols and are largely homogenous across all three forest types (Kishchuk 2004). The DD, MX and CD forest types are located along a increasing gradient of site wetness, respectively, as quantified using a cartographic depth-to-water index based on discrete airborne laser scanning data (Nijland et al. 2015).

Compartments (~ 10 ha each) were harvested to 10% (basal area) tree retention in the fall of 2002. Harvesting was done by a standard feller-buncher that cut 5-m wide machine corridors with centres spaced 20 m apart. Partial harvest prescriptions were met by cutting seven out of every eight trees in the 15-m wide retention strips between the machine corridors to achieve a uniformly distributed 10% level of retention throughout the cutover area (Table A1). Logging slash was left on the ground to cure prior to burn treatments.

There were four replicate harvested compartments for each of the conifer-dominated and mixed forest types and three replicates for the deciduous-dominated forest type. Each harvested compartment was divided into two equal parts, one of which was randomly assigned to be burned and will hereafter be referred to as the ‘harvest + burn’ treatment while the other half of the compartment was left unburned and will hereafter be referred to as the ‘harvest’ treatment. All ‘harvest + burn’ compartments were burned in October 2003 except for those in the deciduous-dominated stands; the latter required additional drying time to provide appropriate conditions for the effective spread of ground fire and were, therefore, burned in May 2005. The prescribed burns were applied using aerial torches and hand-held drip torches, which resulted in low severity ground fires with low mortality of the retained trees (Table A1). Mean (standard deviation) depths of burn were 1.6 (± 1.2) cm, 0.68 (± 0.61) cm, and 0.58 (±0.6) cm for the conifer-, mixed, and deciduous-dominated forest types, respectively. Mean (standard deviation) proportional areas burned were 67.8 (± 9.4) %, 72.2 (± 25.5) %, and 49.8 (± 22.7) % for the conifer-, mixed, and deciduous-dominated forest types, respectively. The conditions for the prescribed burns differed somewhat among the forest types with the burns in the deciduous-dominated stands having a slightly lower Fire Weather Index (Table A2). We also included three replicate unharvested compartments (~10 ha each) for each forest type to serve as 'controls'. These were mature forest stands comparable to those to which the harvest and harvest + burn treatments had been applied. No comparable data from stands subjected to fire only were available for comparison.

Data Collection

Sampling occurred in the summers of 1998 (pre-harvest), 2004 (first growing season post-burn for conifer and mixed forest types only), 2009 (mixed and conifer-dominated stands; sixth growing season post-burn), 2010 (deciduous-dominated stands; sixth growing season post-burn), and 2015 (11^{th} growing season post-burn for deciduous-dominated stands; 12^{th} growing season post-burn for mixed and conifer-dominated stands). In 1998, six sampling points were established in each compartment; these were randomly located but at least 40 m from compartment edges. The sampling points in the control compartments remained the same during consecutive sampling years, but in the treated compartments 27 of the original 66 sampling points were re-established in a different location in 2004; these were randomly located with the constraint that each half (harvest and harvest + burn) of the treated compartments had three sampling points, which were sampled in consecutive sampling years. In 2015, three new sampling points were added to each replicate of the harvest and harvest + burn treatments to increase the number of sub-samples. Although sampling points were randomly distributed, sampling in the harvest + burn treatments may not reflect the complete spatial heterogeneity of the fire severity.

At each sampling point, there was a 2 m × 2 m quadrat nested in the southeast corner of a 5 m × 5 m plot. The presence of all vascular plant species (trees, shrubs, forbs, graminoids) was recorded in the 5 m × 5 m plot. In the embedded 2 m × 2 m quadrat, percent cover of tree saplings (< 150 cm in height), shrubs (< 150 cm in height), forbs, and graminoids was visually estimated for each species to the nearest 0.5% from 0% to 1%, to the nearest 1% from 1% to 10%, and to the nearest 5% from 10% to 100%. Specimens that could not be identified in the field were collected for identification in the laboratory. The proportion of specimens unidentifiable at the species level was 0.013; these specimens were identified to genus if possible and treated as species for the purpose of analysis.

Data Analysis

Species richness was expressed as the total number of species per 5 m × 5 m plot. Vascular plant diversity, at the scale of the 2 m × 2 m quadrat, was calculated using a Hill number to obtain the effective number of species (Hill 1973). Species diversity was considered Hill number of order 1, which is the exponential of Shannon's entropy and weights each species relative to their respective abundance (Jost 2006). Species diversity was therefore calculated as diversity = $\exp(-\sum_{i=1}^{S} p_i \ln p_i)$ where S is the number of species and p_i is the relative abundance of the i^{th} species. Response variables for the mixed-effects models of variance included vascular plant species richness, diversity, and percent cover (total and by vegetation type: shrubs [including saplings], forbs [including prostrate/trailing woody species], graminoids). Response variables were compared among treatments (harvest + burn, harvest, control) and among years (pre-harvest, 1st post-burn growing season [hereafter noted as '1 year post-burn'], 6th post-burn growing season [hereafter noted as '6 years post-burn], 11th or 12th post-burn growing season [hereafter noted as '11-12 years post-burn']). We chose to complete these analyses for each forest type separately because of differences in the conditions and outcomes of the prescribed burns (depth of burn mentioned above, Table A2), and in the time period between harvest and burn. Initial analyses with all forest types combined showed many instances of a significant three-way interaction (forest type by time by treatment). Data were analyzed using the R statistics programming environment version 3.2.3 (R Development Core Team 2015).

The mixed-effects models of variance (ANOVA) were developed using the *lme* function from the *nlme* package (Pinheiro et al. 2018) and included disturbance type (harvest + burn, harvest, control), time (pre-harvest [1998], one year post-burn [2004], six years post-burn [2009/2010], 11-12 years post-burn [2015]), and the interaction between disturbance type and time as categorical fixed effects. Sampling point nested within compartment was included as a random effect to account for the fact that the sampling points were sub-samples, for the split-plot design of the harvest and harvest + burn treatments, and for the fact that some points were sampled in multiple years. Random effects were fitted as random intercepts. Diagnostic plots were used to assess normality and homoscedasticity of the residuals for all of the mixed models. The *anova* function was used to extract F values, degrees of freedom, and *P* values for the mixed models. Assumptions of normality were not met for graminoid cover in conifer-dominated forest so those data were log-transformed. When only the treatment effect was significant ($\alpha = 0.05$), pairwise comparisons ($\alpha = 0.05$) of least-squares means were made between treatments, ignoring time. When the interaction between treatment and time terms was significant ($\alpha = 0.05$) or when both treatment and time terms were significant ($\alpha = 0.05$), pairwise comparisons ($\alpha = 0.05$, family-wise) of least-squares means were made between treatments for individual time periods separately. These analyses were completed using the *lsmeans* package (Lenth 2017).

We assessed the effect of treatment and time on understory species composition using distance-based redundancy analyses (db-RDA) with the *capscale* function and the Bray-Curtis distance measure (Legendre and Anderson 1999) in the *vegan* package (Oksanen et al. 2018) with Hellinger-transformed (Legendre and Gallagher 2001) percent cover data for each species. The analysis was performed separately for the conifer-dominated, mixed, and deciduous-dominated forest types. The primary matrix of the db-RDA was the species data for each 4-m^2 sampling quadrat while the secondary matrix consisted of treatment (harvest + burn, harvest, control) and time (pre-harvest, one year post-burn, six years post-burn, 11-12 years post-burn) as categorical variables. Compartment was included as a conditional variable. Statistical significance of the distance-based redundancy analysis model terms was determined using 999 permutations. We subsequently performed additional db-RDAs that examined the differences in species composition between treatments for each post-burn sample year and each forest type, separately. The *ordiellipse* function was used to add dispersion ellipses (95% confidence regions) based on standard errors of the weighted average of scores around the centroids (Oksanen et al. 2018).

Indicator species analyses were performed with the *indicspecies* package (De Cáceres and Jensen 2016) for the three different forest types to identify species associated with specific treatments (harvest + burn, harvest, control) or combinations of treatments. The point biserial correlation coefficient analysis, which uses abundance values (in this case, percent cover) to determine the associations between species and disturbance types, was conducted with unlimited grouping variables (De Cáceres 2013). Significant indicator species ($\alpha = 0.05$) were identified after 999 permutations.

Results

Although there were differences among the forest types in the conditions during, and outcomes of, the prescribed burns (greater depth of burn in the conifer stands, lower Fire Weather Index and percent area burn for the deciduous stands) all prescribed burns were relatively low-severity ground fires with low mortality of retained trees (Tables A1, A2). Post-treatment regeneration was fairly similar in the harvest *versus* the harvest+burn treatments for each forest type (Table A1). Densities increased over time due to survival of the retained trees combined with growth of surviving trees (mainly aspen) that grew into the size class to be counted as a tree (> 5 cm diameter at 1.3 m height) (Table A1).

Species richness and abundance

In total, eight tree sapling, 34 shrub, 115 forb, and 36 graminoid species were found (Table A3). The interactive effects of treatment and time influenced overall species richness (except for deciduous forest), total cover, shrub cover (except for mixed forest), and graminoid cover (Table 1). Forb cover was affected by the interaction between treatment and time only in mixed forest, while time had a significant influence on overall species diversity (except for deciduous forest) (Table 1; Table A4).

Species richness was significantly higher in the harvest + burn compartments than in controls for conifer-dominated forest six years and 12 years post-burn, while the harvest compartments were intermediate (Fig. 1A). In contrast, species richness in mixed forest was significantly lower in the harvest + burn treatment compared to the control one year post-burn while the harvest treatment was intermediate (Fig. 1B). By six years and 12 years post-burn, however, species richness was significantly higher in both harvest + burn and harvest stands compared to the controls (Fig. 1B). In deciduous-dominated forest, the harvest + burn compartments had higher species richness than either harvested compartments or the controls six and 11 years post-burn; the harvest and control treatments did not differ from one another (Fig. 1C).

Total understory plant cover in conifer-dominated forest changed little from pre-harvest to one year post-burn, but had more than doubled by six years after disturbance in both harvest + burn and harvest stands, which had significantly higher cover compared to the control (Fig. 1D). In mixed forest, total cover in both disturbance treatments increased dramatically from pre-harvest to 12 years post-burn, when cover in both disturbance treatments was significantly higher than in the control (Fig. 1E). Total cover in deciduous-dominated forest six years post-burn was similar in the two disturbance treatments and both were significantly higher than in control compartments (Fig. 1F). By 11 years post-burn, however, the harvest + burn treatment in deciduous forest had significantly higher cover than both the control and harvested forest, which did not differ from one another (Fig. 1F).

In conifer forest, graminoid cover was significantly higher in the harvest treatment than in the harvest + burn treatment and control one year post-burn (Fig. 1G). However, by six and 12 years post-burn graminoid cover did not differ between the two disturbance treatments, but was significantly higher in both disturbance treatments than in the controls (Fig. 1G). In mixed stands, graminoid cover in both disturbance treatments was higher than in the controls six and 12 years post-burn; by 12 years post-burn graminoid cover in the harvest + burn treatment was also significantly higher compared to the harvest treatment (Fig. 1H). In deciduous-dominated stands, graminoid cover was significantly higher in both disturbance treatments compared to the control six years post-burn and was significantly higher in the harvest + burn compartments than in either the harvest or control compartments 11 years post-burn (Fig. 1I).

Shrub cover in conifer-dominated forest one year post-burn was significantly lower in the harvest + burn treatment compared to the control ($P = 0.027$) but was not significantly different from the harvest treatment and there were no significant differences among treatments for the other time periods (not shown, see Table A5). In deciduous-dominated stands, there were no significant differences in shrub cover between treatments despite a significant treatment by time interaction (Table 1).

Forb cover in mixed forest 12 years post-burn was significantly higher in the harvest treatment compared to the control ($P = 0.014$) but was not significantly different from the harvest + burn treatment; the harvest + burn treatment and control did not differ from one another and there were no significant differences among treatments for the other time periods (not shown, see Table A5). In deciduous-dominated stands, treatment had a significant effect on forb cover (Table 1). Although forb cover was highest in the harvest + burn treatment (lsmean = 32.6 ± 3.2% over all sample times), there were no significant differences in forb cover between the harvest treatment (lsmean = 25.3 ± 3.2%) and the control (lsmean = 26.4 ± 3.%).

Community composition and indicator species

There was a significant interactive effect between treatment (harvest + burn, harvest, control) and time on understory plant composition in conifer-dominated and mixed stands, but not in deciduous-dominated forest (Table 1; Fig. 2). For conifer-dominated and mixed compartments, the first axis of the distance-based redundancy analyses separated communities in the control and pre-harvest sampling periods on the left from communities in the two disturbance treatments on the right (Fig. 2). The second axis revealed changes in communities over time as pre-harvest communities were in the middle, one year post-burn communities were towards the upper end of the axis, while six and 12 years post-burn communities were towards the lower end of the axis (Fig. 2).

Vascular plant community composition differed between treatments (harvest + burn, harvest, control) at all post-burn time periods in all forest cover types (based on non-overlapping 95% confidence interval ellipses; Fig. 3). For all years and forest types, the first axis of the distance-based redundancy analyses separated plant communities between the three treatments (harvest, harvest + burn, control), while the second axis separated plant communities between the two disturbance treatments (harvest, harvest + burn) (Fig. 3).

There were more indicator species for the control (22 species) than the harvest + burn treatment (15 species), and harvest treatment (seven species) (Table 2). Seven species were significant indicators of both the harvest and the harvest + burn treatment (Table 2).

Discussion

Application of prescribed fire after retention harvesting significantly affected understory vascular plant communities immediately post-treatment with these effects still being evident 12 years post-burn. While there was a time lag in responses of species richness and abundance to disturbance, differences in species composition between burned and unburned forest stands were apparent within one year post-burn. The harvest + burn treatment promoted species commonly associated with early post-wildfire sites (see below), supporting the idea that prescribed fire combined with retention harvesting can be a useful option for natural disturbance-based management in forests historically influenced by wildfire.

Both species richness and abundance of understory vascular plants were higher in compartments treated with disturbance than in unharvested controls, which was expected due to increased availability of above- and below-ground resources for understory vegetation that accompanied removal of the canopy (Hart and Chen 2006). Graminoid cover increases post-treatment were an important component of the response in overall cover, corroborating results of prior studies of disturbance effects on boreal understory vegetation (Macdonald and Fenniak 2007; Craig and Macdonald 2009; Økland et al. 2016). In mixed and deciduous forests, greater increases in graminoid cover in the harvest

+ burn treatment than in the harvesting alone treatment could be attributed to reduced organic layer depths in burned sites that supported the growth of fire-specialist species (Rees and Juday 2002).

High graminoid cover dominated by *Calamagrostis canadensis*, as revealed in the indicator species analysis, in the harvest + burn treatment for mixed and deciduous forest types 11-12 years post-burn could be problematic for forest managers. *Calamagrostis canadensis* is a shade-intolerant species (Lieffers and Stadt 1994) that can reduce the number and growth of *Populus tremuloides* suckers (Landhäusser and Lieffers 1998; Landhäusser et al. 2007). The growth of conifer seedlings could also be hindered by decreased soil temperatures caused by the presence of *Calamagrostis canadensis* (Hogg and Lieffers 1991). Sprouting *Calamagrostis canadensis* can increase in abundance after light burns (Smith and James 1978; Dyrness and Norum 1983). However, severe fire typically kills its belowground rhizomes and *Calamagrostis canadensis* is unlikely to be associated with more intense burns that would better mimic wildfire (Lieffers et al. 1993). Fire severity is known to have an important influence on re-development of understory vegetation (Wang and Kemball 2005) and thus the severity of prescribed burns is an important consideration in their application as part of natural disturbance-based management. The differences among the forest types in conditions during, and outcomes of, the prescribed burns likely underlie some differences in understory vegetation response among them. For example, the deeper burn in the conifer-dominated stands might have better controlled *Calamagrostis canadensis*, although abundance of that species was lower in all three treatments in conifer-dominated stands.

Substantial differences in understory community composition between the two disturbance treatments in all three forest cover types could be attributable to the presence of fire-tolerant/fire-adapted species, which have also been documented to be more abundant in stands disturbed by wildfire than those disturbed by logging (Rees and Juday 2002). Indicator species of the harvest + burn treatment included *Geranium bicknellii*, a fire-specialist that regenerates from buried seed banks (Rowe 1983; Haeussler and Bergeron 2004; Reeves 2007), and *Petasites frigidus*, which has been associated with forests that were burned after clearcut (Ton and Krawchuk 2016). Other indicator species for burned sites were fire-adapted rhizomatous forbs, such as *Achillea millefolium* (Merrill et al. 1980; Aleksoff 1999), *Vicia americana* (McLean 1969; Coladonato 1993), and *Aquilegia brevistyla* (Ladyman 2006). Graminoids characteristic of burned sites, including *Agrostis scabra* and *Calamagrostis canadensis*, were shade-intolerant species with wind-disseminated seeds (Rowe 1983). Similar to our study, Pidgen and Mallik (2013) found indicator plants for prescribed burns post-clearcut to be early successional ruderals with wind-dispersed seeds and/or seedbanks. Indicator plants for prescribed burned sites in our study were characteristic of those that persist after wildfire (Donato et al. 2009).

Meanwhile, indicator species exclusive to the harvest treatment, such as *Actea rubra* and *Delphinium glaucum*, prosper in moist, open areas (Moss 1983). *Chamerion angustifolium*, an indicator species of both disturbance treatments, was previously found to be associated with aggregated retention harvesting followed by prescribed burn (Johnson et al. 2014). Other indicator species of both disturbance treatments were also disturbance-adapted/early successional species, such as *Populus tremuloides* and *Leymus innovatus* (Moss 1983).

We expected, but did not find, an initial increase in species richness and abundance one year post-burn; however, the effects of disturbance on species composition were immediate. This held for all forest types, despite the fact that the prescribed burn depth was slightly greater in the conifer-dominated stands. During the first year post-burn, replacement of shade-tolerant species by shade-intolerant species could have masked the differences in species richness and cover compared to those pre-harvest. Lindholm and Vasander (1987) found species richness to be lowest immediately after prescribed burning and to increase post-burn for 15 years. Another study found no differences in species richness between clearcut with prescribed burn, clearcut, and wildfire more than 15 years after disturbance (Pidgen and Mallik 2013).

Responses of vascular plants to disturbance varied with time, which was expected since recovery over time is an important factor influencing plant communities affected by wildfire or other disturbances (Liu et al. 2017). The fate of the retained trees, and subsequent vegetation regeneration and growth, no doubt drove changes in understory vegetation (Kumar et al. 2018). Survival of retained trees was high in both the harvest and harvest+burn treatments, and previous studies on understory vegetation at the EMEND experiment indicated that 10% retention differs little from clearcutting (Macdonald and Fenniak 2007; Craig and Macdonald 2009). Thus, the most important influence of the prescribed burn treatment (*versus* just partial harvesting) was likely through effects on immediate post-disturbance conditions and competitive interactions as the vegetation redeveloped (Kumar et al. 2018). In our study, species richness following both disturbance treatments had started to decline 11-12 years post-burn, yet understory cover was still increasing in mixed and deciduous forest; this was despite substantial regrowth of deciduous tree species (i.e., aspen suckering; Table A1). Indicator species changed over time from a fire-specialist that regenerates from buried seed banks (*Geranium bicknellii*) immediately after the burn to fire-adapted rhizomatous forbs and graminoids with wind-dispersed seeds (e.g., *Achillea millefolium*, *Calamagrostis canadensis*). Beyond the time period of our study, we expect that the cover of shade-intolerant forbs and graminoids will eventually decrease, similar to the typical progression of forest succession after wildfire (Rees and Juday 2002; Liu et al. 2017).

The fact that deciduous forest was the only forest type with notable differences in richness and total understory cover between the harvest and the harvest + burn treatments could be due to differences in the time of prescribed fire application among forest cover types. The conifer-dominated and mixed stands were subjected to prescribed fire one year post-harvest, while prescribed fire was applied to the deciduous-dominated stands three years post-harvest. Thus, the longer elapsed time between the application of the two disturbance treatments in the deciduous-dominated stands might explain their greater differences in species richness and cover between the harvest and harvest + burn treatments, as compared to the other forest cover types. Future studies should apply prescribed fire the same year in all forest cover types to gain a better understanding of comparisons between harvesting treatments with and without prescribed burns in different forest cover types, although this can be logistically challenging.

The prescribed burns under investigation were low severity ground fires applied to areas that had been harvested to a relatively low retention level. We would expect greater differences in understory vegetation between the harvested sites with and without prescribed burns if the fires were more severe, since vegetation dynamics are known to be strongly affected by burn severity (Schimmel and Granström 1996; Whittle et al. 1997; Ryan 2002; Lecomte et al. 2005; Wang and Kemball 2005). If the prescribed burns had been more severe, and consequently consumed more of the forest floor, plants with buried viable seeds may have been less abundant post-fire. Future studies should measure fire severity at sampling plot locations to gain a better understanding of the relationship between fine-scale spatial heterogeneity of burn severity and plant communities. When combined with retention harvests, effects of prescribed fire on vegetation dynamics also depend on retention level (Johnson et al. 2014). At higher retention levels, we would expect greater abundance of shade-tolerant species characteristic of intact forest (Johnson et al. 2014).

In conclusion, our findings suggest that the application of prescribed burns after retention harvests create conditions that are favourable for fire-adapted species and thus can be an important additional treatment to retention harvesting as part of natural disturbance-based management of boreal forests. Our results corroborate studies that demonstrated the benefits of combined prescribed fire and retention harvest treatments to berry production (Granath et al. 2018), structural diversity (Heikkala et al. 2014), and pyrophilous insects (Hyvärinen et al. 2006; Hyvärinen et al. 2009; Heikkala et al. 2016; Heikkala et al. 2017). Stronger effects of the harvest + burn treatment than retention harvesting alone on understory plant species richness (deciduous forest), total understory cover (deciduous forest), and graminoid cover (mixed and deciduous forest) suggests there were synergistic effects resulting from compounding disturbances (Paine et al.

1998; Pidgen and Mallik 2013). Plant species that have traits adapted to thrive after wildfire were indicators of the harvest + burn treatment, reflecting their adaptations to the major natural disturbance in boreal forest. Retention harvesting could therefore better emulate the effects of wildfire on understory vascular plant communities when combined with prescribed burns. Prescribed fire does not entirely emulate wildfire (Pastro et al. 2011) and future research should directly compare the effects of wildfire and prescribed burns on understory plants. Early-successional plant communities play important ecological roles and thus should be maintained (Swanson et al. 2011; Fedrowitz et al. 2014); the application of prescribed fire post-retention harvest could be a beneficial option for sustainable forest management.

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Table 1. ANOVA **r**esults of mixed models [F values (*F*), degrees of freedom (*df*), and *P* values (*P*)] examining the influence of treatment (harvest + burn, harvest, control), time (pre-harvest, one year post-burn, six years post-burn, 11-12 years post-burn), and treatment × time interaction on understory vegetation. The *P* values in bold were considered significant (α = 0.05).

	Forest type[a]	Treatment			Time			Treatment × Time		
		F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Richness	CD	1.41	2	0.252	**59.89**	**3**	**< 0.001**	**6.97**	**6**	**< 0.001**
	MX	1.40	2	0.254	**83.92**	**3**	**< 0.001**	**11.80**	**6**	**< 0.001**
	DD	**8.79**	**2**	**< 0.001**	**11.88**	**2**	**< 0.001**	2.35	4	0.065
Diversity	CD	1.09	2	0.344	**18.88**	**3**	**< 0.001**	1.96	6	0.078
	MX	0.26	2	0.770	**19.68**	**3**	**< 0.001**	0.84	6	0.545
	DD	0.69	2	0.508	0.72	2	0.491	1.12	4	0.355
Total cover	CD	0.94	2	0.396	**47.86**	**3**	**< 0.001**	**2.80**	**6**	**0.014**
	MX	1.98	2	0.146	**81.44**	**3**	**< 0.001**	**9.79**	**6**	**< 0.001**
	DD	**12.65**	**2**	**< 0.001**	**54.85**	**2**	**< 0.001**	**6.65**	**4**	**< 0.001**
Shrub cover	CD	0.06	2	0.942	**19.51**	**3**	**< 0.001**	**2.51**	**6**	**0.026**
	MX	0.58	2	0.565	**27.60**	**3**	**< 0.001**	1.84	6	0.099
	DD	0.99	2	0.377	**34.60**	**2**	**< 0.001**	**2.78**	**4**	**0.035**
Forb cover	CD	0.20	2	0.816	**25.83**	**3**	**< 0.001**	0.11	6	0.995
	MX	0.92	2	0.404	**35.07**	**3**	**< 0.001**	**4.60**	**6**	**< 0.001**
	DD	**3.34**	**2**	**0.043**	3.00	2	0.057	0.39	4	0.815
Graminoid cover	CD[b]	**7.81**	**2**	**< 0.001**	**37.45**	**3**	**< 0.001**	**7.03**	**6**	**< 0.001**
([b]log-transformed)	MX	**9.46**	**2**	**< 0.001**	**25.45**	**3**	**< 0.001**	**6.96**	**6**	**< 0.001**
	DD	**5.64**	**2**	**0.006**	**12.23**	**2**	**< 0.001**	**3.83**	**4**	**0.008**
Composition	CD	**12.61**	**2**	**0.001**	**4.48**	**3**	**0.001**	**1.44**	**6**	**0.012**
	MX	**7.90**	**2**	**0.001**	**4.71**	**3**	**0.001**	**1.79**	**6**	**0.001**
	DD	**4.53**	**2**	**0.001**	**4.13**	**2**	**0.001**	1.02	4	0.407

[a]Forest type based on canopy composition prior to disturbance: CD = conifer-dominated (canopy > 70% coniferous trees); MX = mixed (conifer and deciduous (i.e., broadleaf) each 35%-65% of canopy); and DD = deciduous-dominated (canopy > 70% deciduous trees)

Table 2. Results of indicator species analysis (correlation coefficients of indicator species) for different forest types (conifer-dominated, mixed, deciduous-dominated) and number of years post-burn (one year, six years, 11-12 years). Only species with $P < 0.05$ in at least one forest type and time period are listed ('-' = not significant).

	Conifer			Mixed			Deciduous	
	1	6	12	1	6	12	6	11
Harvest + Burn								
Achillea millefolium	-	0.44	0.45	-	-	-	-	-
Agrostis scabra	-	0.28	-	-	-	-	-	-
Aquilegia brevistyla	-	-	-	-	-	-	-	0.39
Arnica cordifolia	-	-	-	-	0.34	-	-	-
Calamagrostis canadensis	-	-	-	-	-	0.41	-	0.49
Chamerion angustifolium	-	-	-	-	-	-	-	0.34
Eurybia conspicua	-	-	-	-	-	-	0.38	-
Geranium bicknellii	0.40	-	-	-	-	-	-	-
Petasites frigidus	0.42	-	-	-	-	-	-	-
Ribes oxyacanthoides	-	-	-	-	0.32	0.28	-	-
Rubus idaeus	-	-	-	-	0.37	-	-	-
Symphyotrichum ciliolatum	-	-	0.31	-	-	0.33	-	-
Taraxacum officinale	-	0.51	0.54	-	-	-	-	-
Trifolium hybridum	-	-	-	-	-	0.34	-	-
Vicia americana	-	0.54	0.58	-	-	0.47	-	-
Harvest								
Actaea rubra	-	0.26	-	0.35	0.35	-	-	-
Delphinium glaucum	-	-	0.33	0.37	-	-	-	-
Epilobium ciliatum	0.45	-	-	-	-	-	-	-
Heracleum maximum	-	-	-	-	-	-	0.43	-
Linnaea borealis	-	-	-	-	-	0.34	-	-
Petasites frigidus	-	0.38	-	-	-	-	-	-
Populus tremuloides	-	-	-	0.42	-	-	-	-
Harvest + Burn/Harvest								
Chamerion angustifolium	-	0.51	0.47	-	0.42	0.47	-	-
Fragaria virginiana	-	-	-	-	-	0.32	-	-
Lathyrus ochroleucus	-	-	-	-	-	0.32	-	-
Leymus innovatus	-	-	-	-	-	0.36	-	-
Petasites frigidus	-	-	-	-	-	0.38	-	-
Populus tremuloides	-	-	-	-	0.39	-	-	-
Symphyotrichum ciliolatum	-	-	-	-	0.38	-	-	-
Control								
Alnus viridis	-	-	-	-	0.39	0.38	-	0.30
Aralia nudicaulis	-	-	-	0.39	0.40	0.42	-	-
Arnica cordifolia	-	-	-	-	-	-	-	0.32
Circaea alpina	-	-	0.34	-	-	-	-	-
Cornus canadensis	0.51	0.54	0.51	0.56	0.48	0.46	-	-
Equisetum arvense	0.37	0.36	-	-	-	-	-	-

Equisetum pratense	-	-	0.31	-	-	-	-	-
Goodyera repens	-	-	0.45	0.45	0.40	0.45	-	-
Ledum groenlandicum	-	0.33	0.29	-	-	-	-	-
Linnaea borealis	0.51	0.33	-	0.46	-	-	-	-
Lycopodium annotinum	-	-	-	0.37	0.33	0.34	-	-
Mertensia paniculata	-	0.35	0.30	-	-	-	0.49	-
Mitella nuda	-	-	0.35	-	-	-	-	-
Moneses uniflora	-	-	0.33	-	-	-	-	-
Orthilia secunda	-	-	-	0.55	-	-	-	-
Osmorhiza depauperata	-	-	-	-	-	-	0.44	-
Pyrola asarifolia	-	-	-	0.36	-	-	-	0.38
Rosa acicularis	0.49	-	-	0.39	-	-	-	-
Vaccinium cespitosum	-	-	-	0.40	-	-	-	-
Vaccinium vitis-idaea	-	0.31	0.38	-	-	-	-	-
Viburnum edule	-	-	-	0.42	-	-	-	-
Viola renifolia	-	-	-	0.43	0.40	-	-	-

Figure 1. Least-square means ± SE of: species richness (A-C), total cover (D-F), and graminoid cover (H-I) in conifer-dominated (A, D; n = 4), mixed (B, E, H; n = 4), and deciduous-dominated (C, F, I; n = 3) forest types, and median, 25th, and 75th percentiles of graminoid cover in conifer-dominated forest (G) for different treatments (harvest + burn, harvest, control) pre-harvest, one year, six years, and 11-12 years post-burn. Means with different letters are significantly different within a given time period (pairwise comparison of least-squares means; $P < 0.05$). G) Box-plot was used because data were log-transformed for analysis. Dots outside the box-whiskers represent outlier values.

Figure 2. Results of distance-based redundancy analysis for the influence of the interaction between disturbance type [harvest + burn (black filled symbols), harvest (grey symbols), control (open symbols)] and time [pre-harvest (●), 1 year = one year post-burn (▲), 6 years = six years post-burn (▼), 12 years = 12 years post-burn (■)] on understory vascular plant species composition for (A) conifer-dominated and (B) mixed forests. Ellipses represent 95% confidence intervals of time periods and treatments; the arrows link the label to the ellipse.

Figure 3. Results of distance-based redundancy analysis testing the influence of disturbance type [harvest + burn (black filled symbols), harvest (grey symbols), control (open symbols)] on understory vascular plant species composition one year (A-B), six years (C-E), and 11 or 12 years (F-H) post-burn in conifer-dominated (A, D, G), mixed (B, E, H), and deciduous-dominated (C, F) forest types. Ellipses represent 95% confidence intervals for the different treatments.

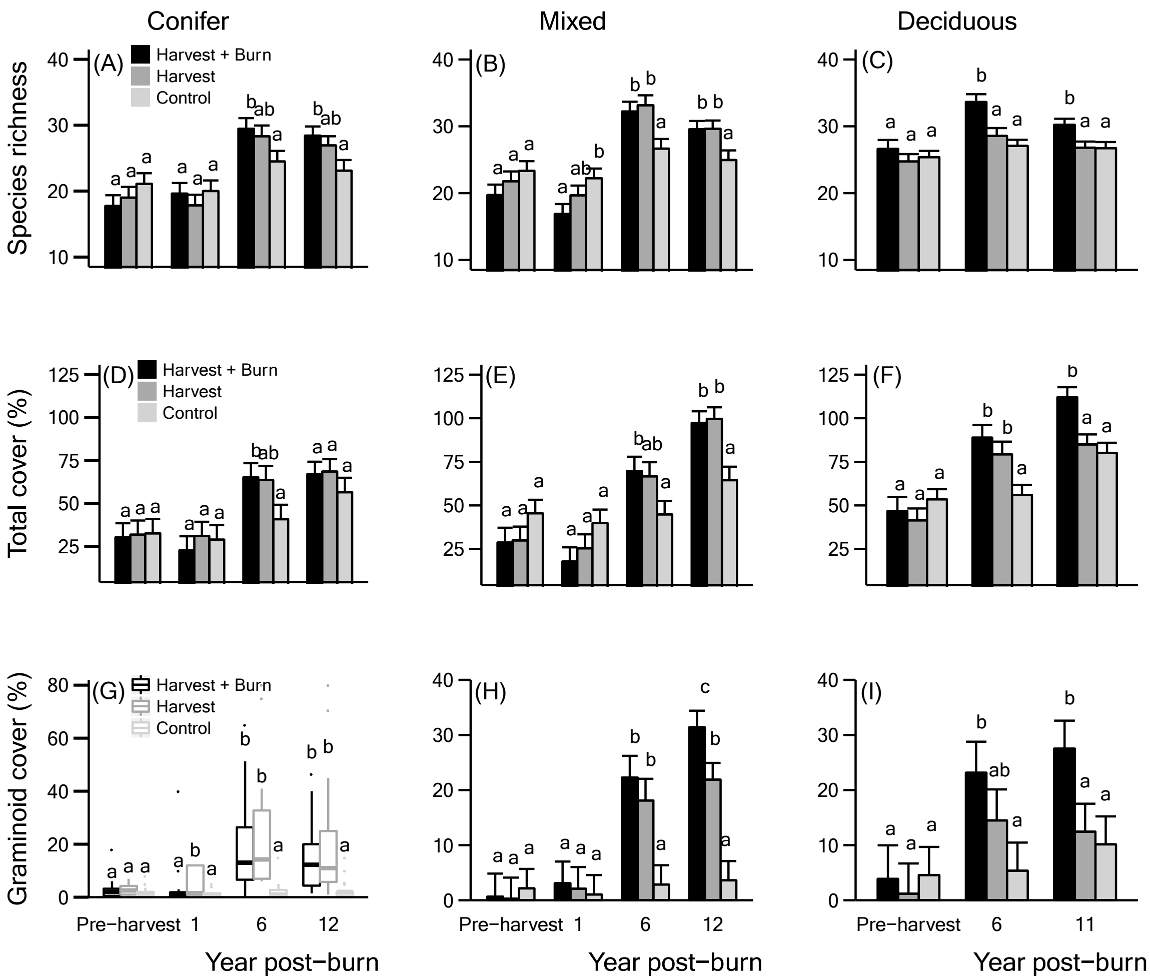

Figure 1. Least-square means ± SE of: species richness (A-C), total cover (D-F), and graminoid cover (H-I) in conifer-dominated (A, D; n = 4), mixed (B, E, H; n = 4), and deciduous-dominated (C, F, I; n = 3) forest types, and median, 25th, and 75th percentiles of graminoid cover in conifer-dominated forest (G) for different treatments (harvest + burn, harvest, control) pre-harvest, one year, six years, and 11-12 years post-burn. Means with different letters are significantly different within a given time period (pairwise comparison of least-squares means; $P < 0.05$). G) Box-plot was used because data were log-transformed for analysis. Dots outside the box-whiskers represent outlier values.

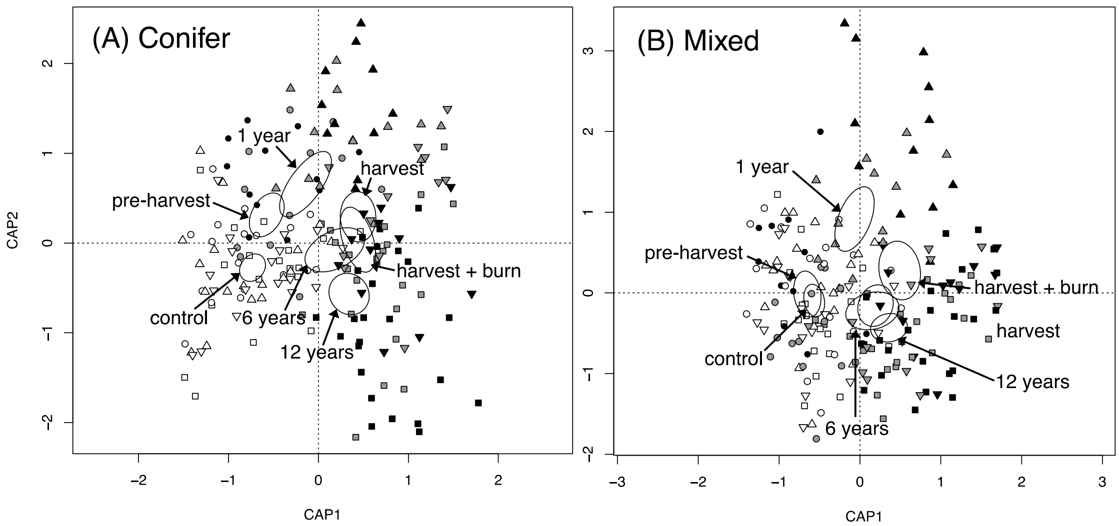

Figure 2. Results of distance-based redundancy analysis for the influence of the interaction between disturbance type [harvest + burn (black filled symbols), harvest (grey symbols), control (open symbols)] and time [pre-harvest (●), 1 year = one year post-burn (▲), 6 years = six years post-burn (▼), 12 years = 12 years post-burn (■)] on understory vascular plant species composition for (A) conifer-dominated and (B) mixed forests. Ellipses represent 95% confidence intervals of time periods and treatments; the arrows link the label to the ellipse.

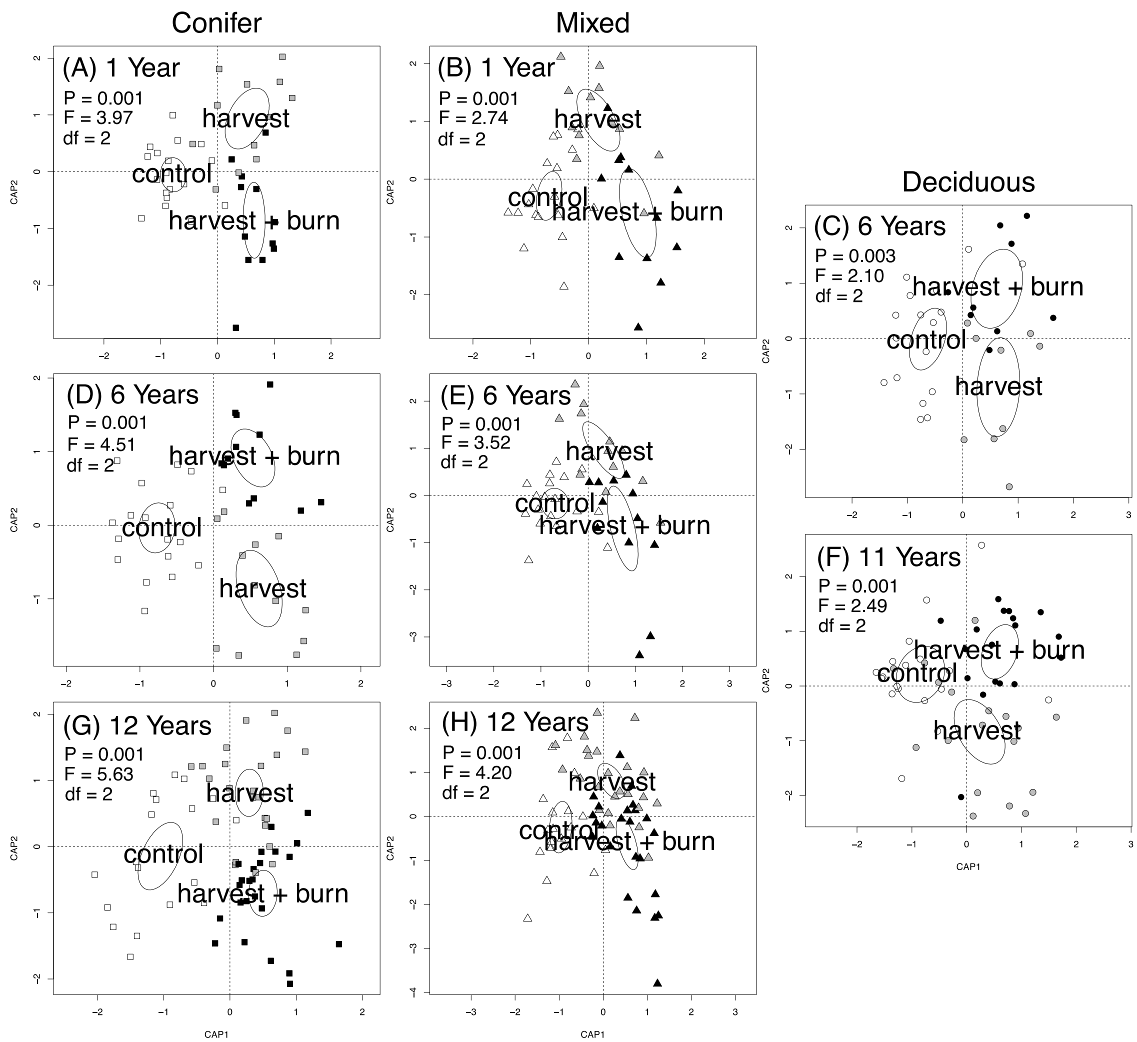

Figure 3. Results of distance-based redundancy analysis testing the influence of disturbance type [harvest + burn (black filled symbols), harvest (grey symbols), control (open symbols)] on understory vascular plant species composition one year (A-B), six years (C-E), and 11 or 12 years (F-H) post-burn in conifer-dominated (A, D, G), mixed (B, E, H), and deciduous-dominated (C, F) forest types. Ellipses represent 95% confidence intervals for the different treatments.

Table A1. Stand density (trees ha^{-1}) and composition (% density that was coniferous trees) prior to partial harvest and density after the harvest or harvest + burn treatments for conifer-dominated (CD), mixed (MX) and deciduous-dominated (DD) forest stands. Given is the mean (standard deviation) of all tree species (stems > 5 cm diameter at 1.3m height) based on three 80 m^2 plots per compartment with four (three for DD) compartments per forest type by treatment combination. The initial post-treatment data were collected in 2007 (4th post-burn growing season for CD and MX, 3rd for DD) and the longer-term post-treatment data were collected in 2015 (12th growing season post-burn for CD and MX, 11th for DD). The increase in density between the two post-treatment periods was largely due to broadleaf trees (aspen and balsam poplar) growing into the size class to be counted as trees.

		Pre-harvest Density (ha^{-1})	Pre-harvest % Conifer	Initial Post-treatment Density (ha^{-1})	Longer-term Post-treatment Density (ha^{-1})
CD	burn	1541.8 (208.4)	86.5 (2.34)	291.7 (125.0)	736.2 (378.1)
	No burn	1055.6 (502.3)	87.8 (7.7)	222.2 (213.8)	889.0 (433.7)
MX	burn	833.4 (290.7)	53.6 (3.9)	270.9 (175.1)	635.5 (419.9)
	No burn	1052.2 (299.3)	60.4 (16.2)	354.2 (53.8)	895.9 (277.5)
DD	burn	1111.2 (354.4)	2.5 (4.3)	263.9 (63.7)	1041.8 (578.9)
	No burn	1013.9 (347.0)	6.8 (6.5)	305.6 (168.4)	652.8 (229.5)

Table A2. Conditions during the prescribed burns of partially-harvested stands of the three forest types. Given is the range of values (across three compartments per forest type for deciduous-dominated (DD) and four for mixed (MX) and conifer-dominated (CD) forests) for the length of the burn, air temperature, relative humidity, wind speed, Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), Drought Code (DC), Initial Spread Index (ISI), Buildup Index (BUI), and Fire Weather Index (FWI) (Natural Resources Canada 2019). (data from Solarik et al., unpublished)

	CD	**DD**	**MX**
Burn Length (Hours)	2h50-3h30	3h05 – 3h45	3h00 – 5h00
Temperature (°C)	20.3 – 26.0	17.9 – 19.7	19.9 – 26.0
Relative Humidity (%)	24 - 26	18-25	19.9 - 25
Wind Speed (Km/h)	3.1 - 8	6.4-9.5	4.3 - 8.6
FFMC	90.1 – 91.7	89.7 -90.6	91.2 – 91.7
DMC	30 - 37	10 -12.8	32 – 37
DC	448 - 471	120 -124.8	453 – 481
ISI	5.4 – 7.3	7 – 7.5	5.8 – 7.3
BUI	51 - 62	16.6 -20.4	55 – 62
FWI	14 - 20	10.2 -10.7	16 - 20

Table A3. List of vascular plant species identified in sampling plots. Nomenclature follows USDA, NRCS (2017). Tree saplings and shrubs were combined and referred to as 'shrubs' for analyses of cover, richness, and diversity.

Tree saplings		
Abies balsamea	*Betula papyrifera*	*Larix laricina*
Picea glauca	*Picea mariana*	*Pinus contorta*
Populus balsamifera	*Populus tremuloides*	
Shrubs		
Alnus incana	*Alnus viridis*	*Amelanchier alnifolia*
Betula occidentalis	*Betula pumila*	*Betula sp.*
Cornus sericea	*Ledum groenlandicum*	*Lonicera dioica*
Ribes glandulosum	*Ribes hudsonianum*	*Ribes lacustre*
Ribes oxyacanthoides	*Ribes triste*	*Ribes sp.*
Rosa acicularis	*Rubus idaeus*	*Salix arbusculoides*
Salix bebbiana	*Salix discolor*	*Salix maccalliana*
Salix myrtillifolia	*Salix petiolaris*	*Salix planifolia*
Salix pseudomonticola	*Salix pyrifolia*	*Salix scouleriana*
Salix sp.	*Shepherdia canadensis*	*Shrub unknown*
Sorbus scopulina	*Symphoricarpos albus*	*Vaccinium cespitosum*
Viburnum edule		
Forbs		
Achillea alpina	*Achillea millefolium*	*Actaea rubra*
Adoxa moschatellina	*Aquilegia brevistyla*	*Aralia nudicaulis*
Arctostaphylos uva-ursi	*Arnica chamissonis*	*Arnica cordifolia*
Aster unknown	*Astragalus alpinus*	*Astragalus americanus*
Botrychium virginianum	*Botrychium sp.*	*Calypso bulbosa*
Cardamine pensylvanica	*Carum carvi*	*Chamerion angustifolium*
Chrysosplenium alternifolium	*Circaea alpina*	*Cirsium arvense*
Coptis trifolia	*Corallorhiza maculata*	*Corallorhiza trifida*
Cornus canadensis	*Corydalis aurea*	*Crepis tectorum*
Cystopteris fragilis	*Dactylorhiza viridis*	*Delphinium glaucum*
Dracocephalum parviflorum	*Dryopteris carthusiana*	*Epilobium ciliatum*
Epilobium palustre	*Epilobium sp.*	*Equisetum arvense*
Equisetum pratense	*Equisetum scirpoides*	*Equisetum sylvaticum*
Eurybia conspicua	*Forb unknown*	*Fragaria vesca*
Fragaria virginiana	*Galium boreale*	*Galium trifidum*
Galium triflorum	*Gentianella amarella*	*Geocaulon lividum*
Geranium bicknellii	*Geum aleppicum*	*Geum macrophyllum*
Goodyera repens	*Gymnocarpium dryopteris*	*Halenia deflexa*
Heracleum maximum	*Hieracium umbellatum*	*Impatiens noli-tangere*
Lathyrus ochroleucus	*Lathyrus venosus*	*Linnaea borealis*
Lycopodium annotinum	*Lycopodium complanatum*	*Maianthemum canadense*
Maianthemum trifolium	*Mentha arvensis*	*Mertensia paniculata*
Mitella nuda	*Moehringia lateriflora*	*Moneses uniflora*

Orthilia secunda	*Osmorhiza depauperata*	*Packera indecora*
Packera paupercula	*Parnassia palustris*	*Pedicularis labradorica*
Petasites frigidus	*Phacelia franklinii*	*Plantago major*
Platanthera huronensis	*Platanthera obtusata*	*Platanthera orbiculata*
Polemonium acutiflorum	*Polygonum arenastrum*	*Potentilla norvegica*
Prosartes trachycarpa	*Pyrola asarifolia*	*Pyrola chlorantha*
Ranunculus abortivus	*Ranunculus sceleratus*	*Rhinanthus minor*
Rubus arcticus	*Rubus pubescens*	*Rumex aquaticus*
Senecio vulgaris	*Solidago canadensis*	*Spiranthes romanzoffiana*
Stellaria calycantha	*Stellaria crassifolia*	*Stellaria longifolia*
Symphyotrichum ciliolatum	*Symphyotrichum puniceum*	*Taraxacum officinale*
Thalictrum sparsiflorum	*Thalictrum venulosum*	*Trientalis borealis*
Trientalis europaea	*Trifolium hybridum*	*Trifolium pratense*
Urtica dioica	*Vaccinium vitis-idaea*	*Vicia americana*
Viola adunca	*Viola canadensis*	*Viola palustris*
Viola renifolia		
Graminoids		
Agrostis scabra	*Alopecurus pratensis*	*Beckmannia syzigachne*
Bromus ciliatus	*Bromus inermis*	*Calamagrostis canadensis*
Carex aquatilis	*Carex aurea*	*Carex brunnescens*
Carex canescens	*Carex concinna*	*Carex deweyana*
Carex disperma	*Carex interior*	*Carex norvegica*
Carex peckii	*Carex praticola*	*Carex raymondii*
Carex sect. Montanae	*Carex siccata*	*Carex sp.*
Carex vaginata	*Cinna latifolia*	*Elymus sp.*
Elymus trachycaulus	*Grass unknown*	*Hordeum jubatum*
Juncus bufonius	*Leymus innovatus*	*Luzula multiflora*
Phleum pratense	*Poa palustris*	*Poa pratensis*
Poa sp.	*Schizachne purpurascens*	*Trisetum spicatum*

Table A4. LME results of mixed models [coefficients (β), standard errors (SE), and *P* values (*P*) for fixed effects; standard deviation for random effects] examining the influence of treatment (harvest + burn, harvest, control) and time (pre-harvest, one year post-burn, six years post-burn, 11-12 years post-burn), and treatment × time interaction on understory vegetation. Reference categories were the control for treatment and pre-harvest for time. YPB = year(s) post-burn.

	Richness		Diversity		Total cover		Shrub cover		Forb cover		Graminoid cover	
Conifer-dominated												
Fixed effects	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Harvest + burn	-3.37 (2.30)	0.147	0.27 (1.33)	0.838	-2.39 (11.75)	0.839	-2.68 (3.60)	0.459	-2.29 (7.71)	0.767	0.11 (0.24)	0.633
Harvest	-2.10 (2.30)	0.364	1.19 (1.33)	0.372	-0.78 (11.75)	0.947	2.75 (3.60)	0.447	-3.13 (7.71)	0.686	0.23 (0.24)	0.345
1 YPB	-1.11 (1.12)	0.325	-0.61 (0.69)	0.380	-3.62 (5.67)	0.524	0.28 (2.41)	0.908	-3.10 (3.96)	0.435	-0.22 (0.12)	0.068
6 YPB	3.39 (1.12)	0.003	1.04 (0.69)	0.136	8.21 (5.67)	0.151	1.49 (2.41)	0.536	6.37 (3.96)	0.110	-0.02 (0.12)	0.852
12 YPB	2.00 (1.12)	0.078	1.82 (0.69)	0.010	23.96 (5.67)	< 0.001	7.76 (2.41)	0.002	15.17 (3.96)	< 0.001	0.19 (0.12)	0.107
Harvest + burn: 1 YPB	2.99 (1.82)	0.104	-0.27 (1.13)	0.808	-3.93 (9.09)	0.666	-5.46 (3.88)	0.162	-0.40 (6.35)	0.950	0.05 (0.19)	0.791
Harvest: 1 YPB	-0.06 (1.91)	0.973	-0.28 (1.18)	0.816	2.88 (9.26)	0.757	-8.41 (4.01)	0.038	-3.08 (6.51)	0.637	0.38 (0.20)	0.059
Harvest + burn: 6 YPB	8.34 (1.84)	< 0.001	-0.79 (1.14)	0.487	26.77 (9.13)	0.004	6.70 (3.91)	0.076	2.43 (6.39)	0.705	0.86 (0.19)	< 0.001
Harvest: 6 YPB	5.94 (1.91)	0.002	-1.94 (1.18)	0.103	23.59 (9.26)	0.012	-0.67 (4.01)	0.868	-0.14 (6.51)	0.982	0.95 (0.20)	< 0.001
Harvest + burn: 12 YPB	8.68 (1.75)	< 0.001	1.98 (1.09)	0.070	12.90 (8.53)	0.133	2.99 (3.69)	0.419	0.96 (5.99)	0.873	0.63 (0.18)	0.001
Harvest: 12 YPB	5.93 (1.82)	0.002	-0.37 (1.13)	0.744	12.78 (8.64)	0.142	-4.59 (3.78)	0.228	0.79 (6.09)	0.897	0.61 (0.19)	0.002
Random effects	Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation	
Compartment		1.81		0.78		12.08		1.27		7.37		0.20
Plot in Compartment		4.01		2.69		9.90		6.38		8.07		0.35
Residual		3.37		2.08		17.01		7.23		11.87		0.35
Mixed												
Fixed effects	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Harvest + burn	-3.62 (2.13)	0.093	-0.82 (1.11)	0.461	-16.72 (11.44)	0.148	-6.18 (7.30)	0.400	-8.24 (6.01)	0.175	-1.50 (5.44)	0.784
Harvest	-1.55 (2.05)	0.452	-1.11 (1.05)	0.294	-15.53 (11.07)	0.165	-2.86 (7.06)	0.686	-10.71 (5.74)	0.067	-1.89 (5.19)	0.717
1 YPB	-1.11 (1.13)	0.326	-0.92 (0.64)	0.155	-5.58 (6.74)	0.410	0.06 (3.75)	0.987	-4.52 (3.58)	0.209	-1.12 (3.62)	0.759
6 YPB	3.33 (1.13)	0.004	-0.09 (0.64)	0.894	-0.64 (6.74)	0.924	-1.89 (3.75)	0.615	0.57 (3.58)	0.873	0.68 (3.62)	0.852
12 YPB	1.61 (1.13)	0.155	1.34 (0.64)	0.040	19.06 (6.74)	0.006	12.34 (3.75)	0.001	5.29 (3.58)	0.143	1.43 (3.62)	0.693
Harvest + burn: 1 YPB	-1.74 (2.02)	0.392	-1.41 (1.19)	0.239	-5.34 (11.44)	0.642	-6.27 (6.68)	0.350	-2.35 (6.38)	0.714	3.53 (6.30)	0.576
Harvest: 1 YPB	-1.02 (1.84)	0.580	-0.04 (1.06)	0.972	1.00 (10.79)	0.926	-4.91 (6.11)	0.424	2.79 (5.83)	0.634	2.94 (5.85)	0.617
Harvest + burn: 6 YPB	9.15 (2.02)	< 0.001	0.22 (1.19)	0.853	41.75 (11.44)	< 0.001	10.67 (6.68)	0.113	10.43 (6.38)	0.105	20.91 (6.30)	0.001

Harvest: 6 YPB	8.03 (1.84)	< 0.001	0.14 (1.06)	0.897	37.41 (10.79)	0.001	6.99 (6.11)	0.256	13.09 (5.83)	0.027	17.14 (5.85)	0.004
Harvest + burn: 12 YPB	8.23 (1.89)	< 0.001	0.17 (1.12)	0.880	49.55 (10.60)	< 0.001	5.95 (6.23)	0.342	13.42 (5.96)	0.026	29.28 (5.85)	< 0.001
Harvest: 12 YPB	6.24 (1.73)	< 0.001	1.08 (1.01)	0.286	50.67 (10.04)	< 0.001	6.50 (5.75)	0.261	23.88 (5.49)	< 0.001	20.17 (5.48)	< 0.001
Random effects	Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation	
Compartment		1.69		0.47		9.55		6.26		3.75		2.77
Plot in Compartment		2.99		2.10		11.11		9.36		9.10		7.58
Residual		3.38		1.93		20.21		11.26		10.74		10.87
Deciduous-dominated												
Fixed effects	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Harvest + burn	1.22 (1.63)	0.458	1.35 (1.36)	0.326	-6.70 (9.93)	0.502	-7.11 (7.56)	0.352	2.00 (6.30)	0.753	-0.70 (7.94)	0.930
Harvest	-0.65 (1.43)	0.654	-0.63 (1.24)	0.616	-12.05 (8.93)	0.183	-6.70 (6.83)	0.331	-1.88 (5.59)	0.738	-3.37 (7.47)	0.654
6 YPB	1.67 (0.91)	0.072	0.52 (0.66)	0.429	2.48 (5.54)	0.656	-0.46 (3.92)	0.907	2.16 (3.52)	0.543	0.78 (2.90)	0.788
11 YPB	1.33 (0.91)	0.148	-0.14 (0.66)	0.828	26.64 (5.54)	< 0.001	16.16 (3.92)	< 0.001	4.93 (3.52)	0.167	5.56 (2.90)	0.060
Harvest + burn: 6 YPB	5.35 (1.82)	0.005	-2.15 (1.32)	0.108	39.64 (10.70)	0.001	16.52 (7.76)	0.038	6.00 (6.96)	0.392	18.48 (6.05)	0.003
Harvest: 6 YPB	2.14 (1.57)	0.178	-1.26 (1.13)	0.271	35.42 (9.47)	< 0.001	20.11 (6.73)	0.004	2.70 (6.05)	0.657	12.48 (5.04)	0.016
Harvest + burn: 11 YPB	2.28 (1.71)	0.187	-1.99 (1.24)	0.113	38.60 (9.95)	< 0.001	13.06 (7.26)	0.077	6.41 (6.50)	0.329	18.10 (5.74)	0.003
Harvest: 11 YPB	0.73 (1.47)	0.623	-0.12 (1.06)	0.913	16.88 (8.76)	0.059	11.66 (6.29)	0.069	-0.60 (5.64)	0.916	5.70 (4.79)	0.239
Random effects	Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation		Standard deviation	
Compartment		0.60		0.93		6.09		4.73		3.03		6.92
Plot in Compartment		2.36		1.75		10.30		9.36		8.16		10.20
Residual		2.73		1.97		16.63		11.74		10.57		8.69

Table A5. Least-square means (SE) of species diversity, shrub cover, and forb cover pre-harvest, one year post-burn, six years post-burn, and 11-12 years post-burn for conifer-dominated (n = 4), mixed (n = 4), and deciduous-dominated (n = 3) forest cover types in three different treatments (H + B = harvest + burn; H = harvest; C = control).

	Conifer-dominated			Mixed			Deciduous-dominated		
	Species diversity	Shrub cover (%)	Forb cover (%)	Species diversity	Shrub cover (%)	Forb cover (%)	Species diversity	Shrub cover (%)	Forb cover (%)
Pre-harvest									
H + B	7.3 (1.0)	8.7 (2.7)	17.0 (5.5)	7.9 (0.8)	10.7 (5.3)	18.1 (4.5)	10.9 (1.1)	17.7 (6.1)	26.1 (5.2)
H	8.2 (1.0)	14.1 (2.7)	16.2 (5.5)	7.6 (0.8)	14.0 (5.0)	15.7 (4.2)	8.9 (0.9)	18.1 (5.2)	22.2 (4.3)
C	7.0 (0.9)	11.4 (2.4)	19.3 (5.4)	8.7 (0.7)	16.9 (5.0)	26.4 (4.0)	9.5 (0.8)	24.8 (4.5)	24.1 (3.6)
1 year post-burn									
H + B	6.4 (1.0)	3.5 (2.7)	13.5 (5.4)	5.6 (0.8)	4.5 (5.1)	11.3 (4.3)	-	-	-
H	7.3 (0.9)	6.0 (2.7)	10.0 (5.4)	6.6 (0.8)	9.2 (5.1)	13.9 (4.3)	-	-	-
C	6.4 (0.9)	11.7 (2.4)	16.2 (5.4)	7.8 (0.7)	16.9 (5.0)	21.9 (4.0)	-	-	-
6 years post-burn									
H + B	7.5 (1.0)	17.2 (2.7)	25.8 (5.4)	8.0 (0.8)	19.5 (5.1)	29.1 (4.3)	9.3 (1.0)	33.8 (5.5)	34.2 (4.6)
H	7.3 (0.9)	15.0 (2.7)	22.4 (5.4)	7.7 (0.8)	19.1 (5.1)	29.3 (4.3)	8.2 (1.0)	37.8 (5.5)	27.1 (4.6)
C	8.0 (0.9)	12.9 (2.4)	25.7 (5.4)	8.6 (0.7)	15.0 (5.0)	27.0 (4.0)	10.1 (0.8)	24.4 (4.5)	26.2 (3.6)
11 (deciduous-dominated) or 12 (conifer-dominated, mixed) years post-burn									
H + B	11.1 (0.8)	19.5 (2.1)	33.1 (4.7)	9.4 (0.6)	29.0 (4.3)	36.9 (3.4)	8.8 (0.8)	47.0 (4.5)	37.4 (3.6)
H	9.6 (0.8)	17.3 (2.0)	32.1 (4.7)	10.0 (0.6)	32.9 (4.3)	44.8 (3.4)	8.7 (0.8)	46.0 (4.5)	26.5 (3.6)
C	8.8 (0.9)	19.1 (2.4)	34.5 (5.4)	10.1 (0.7)	29.2 (5.0)	31.7 (4.0)	9.4 (0.8)	41.0 (4.5)	29.0 (3.6)