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Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec

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Abstract. In this study we compared the effects of fire on understorey vegetation in the Québec southern boreal forest with effects of salvage-logging (clear-cutting after fire). All 61 400-m^2 sampling sites were controlled for overstorey composition (Deciduous, Mixed and Coniferous) and disturbance type, which consisted of three fire impact severity (FIS) classes (Light, Moderate and Extreme) and two harvesting techniques (Stem-only and Whole-tree Harvesting). Percent-cover data of vegetation and post-disturbance environmental characteristics were recorded in the field during the first two years after fire as well as soil texture. Ordination of fire alone demonstrated that, on Coniferous sites, fire initiates a succession whereby the understorey Coniferous sites approaches that of Deciduous-Mixed sites, due to the release of the understorey from *Sphagnum* spp. dominance, this pattern being a function of FIS. On Deciduous-Mixed stands, increased FIS resulted in a transition from herb to shrub dominance. Ordination of all five disturbance types showed that the impact of salvage-logging on understorey composition was within the range of fire, but marginalized to the extreme end of the FIS spectrum. Variance partitioning demonstrated that overstorey and soil texture were the most important explanatory variables of fire alone, while disturbance type explained the largest independent fraction of understorey variation when salvage-logging was introduced. Salvage-logging also results in significant reductions in understorey abundance, richness and diversity, while indicator species analysis suggests that it favours meso-xerophytic to xeric species. Results are interpreted in light of shade-tolerance dynamics, forest floor disturbance and soil moisture regimes. Implications for sustainable forest management are discussed.

Keywords: Disturbance; Ecosystem management; Shade tolerance.

Nomenclature: Marie-Victorin (1995).

Abbreviations: CON = Coniferous site; DEC = Deciduous site: FIS = Fire impact severity; FIS-1 = Light FIS; FIS-2 = Moderate FIS; FIS-3; Extreme FIS; MIX = Mixed site; STEM = stem-harvesting; WTH = whole-tree harvesting.

Introduction

In the boreal forest, fire maintains the heterogeneity of the forest landscape via variation in its frequency (Dansereau & Bergeron 1993) and severity (Kafka et al. 2001). By establishing a frame of reference, this historical disturbance-dependent heterogeneity aids in assessing the ecological impact of management and is the basis for ecosystem management (Bergeron & Harvey 1997; Bergeron et al. 2002). Secondary succession after fire should thus serve as a benchmark by which we evaluate the biological integrity (*sensu* Angermeier & Karr 1994) of salvage-logging. This is important given that salvage-logging (clear-cut logging after fire) has increased over recent years in Québec, from 3 m^3 timber harvested per ha burned in 1991 to 10 m^3 in 1996 (Québec Ministry of Natural Resources, pers. comm. 1999).

As separate disturbances, both fire and harvesting contribute to patterns in vegetative re-establishment. Fire re-initiates succession by razing the understorey vegetation and burning the forest floor, increasing soil pH and rendering nutrients available in a highly concentrated mineral form, ash (MacLean et al. 1983). The intensity of a fire will depend on fuel loadings (Raison et al. 1985) and stand composition (Hély et al. 2000; Hély et al. in press). Fire and variations in its severity are important in determining the early stages of secondary succession through its effects on the amount of mineral soil exposed (Nguyen-Xuan et al. 2000), influencing the depth of burn which determines the success of vegetation reproductive strategies (Rowe 1983; Schimmel & Granström 1996), and on the microclimate, particularly the reduction of soil moisture content (Pietikäinen & Fritze 1993). Direct impacts to the forest floor resulting from harvesting alone (no burning) are more localized, being due mostly to compaction and rutting resulting from harvest machinery (Brais & Camiré 1998; Harvey & Brais 2002). However, there are important indirect effects resulting from logging: reduced evapotranspiration, accelerated soil drying (Childs & Flint 1987), and reduced nutrient assimilation (Prescott 1997).

Few comparative studies (i.e. Che & Woen 1997) of understorey vegetation response to fire and salvage-logging exist. Furthermore, most studies comparing disturbances have been restricted to one overstorey composition type. Regarding the relationship of understorey vegetation to overstorey composition and fire, Carleton & Maycock (1980, 1981) concluded that among distinct overstorey boreal communities, understorey communities are more or less uniform. They attribute this phenomenon to the predominant reproductive strategies that permit species to survive fire – vegetative suckering and underground seed banks. Where relationships do occur, this is explained by a common substrate rather than affinities between overstorey canopy and the understorey. Substrate qualities such as soil texture have been found to be important in explaining vegetation associations and regeneration (Harvey & Bergeron 1989; Harvey et al. 1995; Gerhardt & Foster 2002). However, other boreal forest studies have shown that forest stand composition is important in mediating understorey composition after disturbance (De Grandpré & Bergeron 1997).

Our main objective was to determine if clear-cutting after fire (salvage-logging) has an impact on early understorey vegetation composition, abundance and diversity additional to the impact of fire.

Material and Methods

Study area

The study area is located just east of Val-Paradis, Québec (49°10' N, 79°17' W) within the northern Clay Belt forest region at the transition area from mixed wood to coniferous boreal forest (Gauthier et al. 2000). Climatic information comes from the closest meteorological station at La Sarre (48°47' N, 79°06' W). Total precipitation is 857 mm and mean annual temperature is 0.8 °C, while the average frost-free period extends from June to August for a total of 64 days (Anon. 1998). Lacustrine clay soils left after the postglacial retreat of lakes Barlow and Ojibway are the primary surface deposits, along with coarse-textured tills and fluvio-glacial soils (see Gauthier et al. 2000 for references).

The Val-Paradis fire burned 12 540 ha of mixed-wood boreal forest from June 9 to 11, 1997 (Bordeleau unpubl.) and is thus considered to have been a spring fire, occurring when the soil was still partially frozen. Duff removal was minimal and mineral soil rarely exposed (Noël 2000). Under the Quebec Forest Act of the time (L.R.Q., c. F-4.1), forest tenure holders are required to harvest forest that has been burned, blowndown or infested by insects. In this case, the salvaged area was under license to two companies who started salvage-logging in the summer of 1997, resulting in a total harvest of approximately 64% of the burnt area (8015 ha) (M. Jerome (Norbord) & G. Laprise (Tembec), pers. comm. 2000). The vast majority of the forests in the study area had not been harvested before and most of our burned unlogged sites did not show signs of recent human intervention. However, two deciduous lightly burned sites located along the primary access road, bore evidence of selective-logging for fuelwood in the past. However, this impact was modest (one or two stumps) and we do not believe it compromises the integrity of our data. Finally, we did not find unburned logged sites for use as a control.

Site description

Site selection process

In total 61 sampling sites of 400 m^2 were chosen in order to be representative of three overstorey stand composition classes: Deciduous (DEC), Mixed (MIX) and Coniferous (CON) and five disturbance types: Light (FIS-1), Moderate (FIS-2), Extreme (FIS-3), Stem-harvesting (STEM), Whole-tree harvesting (WTH). The 36 burned unlogged sites were selected in the fall of 1997 and the species, mortality status and DBH were recorded for each individual tree. In the summer of 1998, 25 salvage-logged sites were selected and their composition verified by species identification and diameter measurements of all stumps. These stump measurements were then converted to DBH using established regression equations (P. Sutherland & D. Greene, pers. comm.). DBH data from both fire and salvage-logged sites were then used to calculate species' basal area for each site (App. 1). Sites were classified as DEC if they were > 75 % deciduous, MIX were 15% - 75%, while CON were < 15%.

Three FIS classes based on tree mortality were used to categorize the 36 burned unlogged sites: FIS-3 > 75% mortality; FIS-2 25 - 75%; FIS-1 < 25 %. Though not as precise as measures of fire intensity, such a classification scheme is a useful tool for forest managers because it can be deployed rapidly using aerial photographs to assess crown scorching, a good indicator of tree mortality (Ryan & Reinhardt 1988). Using our same sites, Hély et al. (2003) estimated fire intensity for the FIS classes (App. 1). Their results indicate that DEC stands burn at lower intensities than MIX and CON stands – maximum char height (and thus fire intensity) was significantly lower for *Populus tremuloides* than for *Pinus banksiana* and *Picea mariana*. Salvage-logging was thus divided between the two logging methods: STEM:

delimbing on the site; WTH: delimbing at the roadside. The FIS classification system was not available for salvage-logged plots because only stumps were remaining when these sites were selected. Based on infrared aerial photos taken after the fire and before harvesting however, canopy mortality prior to salvage-logging was assessed. From these, 15 sites were determined to have been of the extreme FIS class burned, seven moderately burned, and one lightly burned. Two remaining salvage-logged sites could not be assigned a FIS class with certainty. In the subsection Statistical analysis below we address how we treated the tendency towards an over-representation of salvage-logging sites of FIS-3 origin.

Site characterization

Basal area: Basal area of *Populus tremuloides* was similar between fires and salvage-logged sites (App. 1). *Betula papyrifera* was found in abundance at only one DEC burned site. For CON sites, *Picea mariana* was dominant in the burned sites, and *Pinus banksiana* in the salvage-logged sites. This is likely due to the economic preference for *P. banksiana*.

Soil texture: Four soil samples were taken at 25-30 cm at the perimeter of each 400-m^2 site; soil texture was analysed using a modified Bouyoucos hydrometer method (Sheldrick & Wang 1993). While CON sites (both fire and salvage-logged) were confined to coarse-textured soils (sandy loam to sand), the soil texture of DEC and MIX sites demonstrated a broader distribution (clay to sandy loam) (App. 1). Burned unlogged DEC and MIX sites were found over the range of surface deposits. However, DEC and MIX salvage-logged sites were more restricted: whole-tree harvested sites were confined to coarse-texture sites (sandy loam), located in the southern section of the study area, while stem-harvested sites were found on finer soils (clay to loam) dominant in the northern part.

Sampling procedures

Each site was sampled for vegetation in the summers of 1998 and 1999; 15 1-m^2 microquadrats were systematically placed within each site – the placement of which was changed between years in order to be more representative. Cover estimates were made for both vegetation and environmental characteristics in each microquadrat using a percent cover scale corresponding to median area values (m^2). Thus, Class 0 = 0 m^2; 1 = 0.018 m^2; 2 = 0.038 m^2; 3 = 0.076 m^2; 4 = 0.18 m^2; 5 = 0.38 m^2; 6 = 0.63 m^2; 7 = 0.88 m^2. Vegetation estimates were taken for two strata : 0-1 m and 1-3 m. Sampling took place between early July and late August in both years.

In total 17 post-disturbance environmental variables were considered. By 'post-disturbance' we mean that it was expected that the type of disturbance would have a distinguishing effect on these variables. The first seven of these are the surface variables (0 m) of each microquadrat: mineral soil exposure, rock exposure, litter exposure, % cover of downed CWD, exposed duff, water, and dead moss. While estimating the percent cover of CWD, their decay class was also noted using a five-level scale (Daniels et al. 1997). The presence or absence of the following was also noted for each microquadrat: uprooted tree, skidder road, stump, coniferous snag, deciduous snag, live coniferous tree, and live deciduous tree. Finally, mean and standard deviation of site humus depth were obtained along a single 30-m transect of each site (Noël 2000). Summary tables of the entire vegetation and post-disturbance environmental data sets are found in Apps. 3 and 4, respectively.

Statistical analysis

We used a combination of multivariate ordination and grouping methods, as well as ANOVA with orthogonal contrasts to examine different levels of organization of the vegetative data: composition (correspondence analysis ordination, parametric ANOVA and non-parametric multivariate ANOVA, and variance partitioning), indices of abundance and diversity (parametric ANOVA), and species level (indicator species grouping). The main objective was to determine if overstorey composition, disturbance type and their interaction significantly characterize variation in understorey and their associated post-disturbance environmental variables. However, it was also necessary to assess the importance of soil texture. Because results were similar between the two study years, mainly 1999 results are reported here.

Except for non-parametric multivariate ANOVA (NPMANOVA), all statistical analyses were conducted first on fire sites alone and then on fire and salvage-logged sites together. Because of the possibility of a bias towards an over-representation of salvage-logged sites of extreme FIS origin in our experimental design, we also report results of ANOVA (for axis scores and vegetation indices) strictly comparing salvage-logging with extremely burned unlogged sites. If differences between salvage-logging and extreme FIS were found, this would indicate that salvage-logging had an effect in addition to that found in the FIS range.

Ordination analysis

Correspondence analysis with passive regression analysis (CA-PRA) was used to visualize variation in the understorey and to show relations between its composition and environmental variables, both the post-disturbance and soil texture data. The method used proceeded by calculating a CA onto which significant environmental variables were overlayed using the passive regression feature of CANOCO v. 3.12 (ter Braak 1991). Only those environmental variables determined as significant through the forward selection procedure of CCA ($p < 0.05$, 999 permutations) were used.

We chose CA because it assumes a unimodal model of species distribution across environmental gradients (ter Braak 1985). Under this model the occurrence of a species at two different sites is meaningful, but the absence of species is not because it may indicate different situations: both sites are below optimum conditions, both are above, or one is above and the other below (Legendre & Legendre 1998). Differing from linear ordination models such as PCA, the χ^2 distance used to calculate CA abstains from including zeros (absences) in the calculation of ecological resemblance. There were a large number of zeros in our data set: for the species matrix of the 36 fire sites, only 25% had occurrences (1177 cells of 4716 possible); for that of all 61 sites, only 21% of cells of the matrix had occurrences (1815 cells of 8418 possible).

Two additional CA-PRAs were conducted (App. 2). First, we controlled for soil texture in the CA-PRA ordinations by setting it as a covariable in CANOCO, separate analyses being conducted for fires only and then all 61 sites. Secondly, because of the discrepancy between stand compositions of coniferous sites (see Site characterization: basal area), we also conducted a CA-PRA on a subset of the species data from CON sites using tree species basal area as a discriminating factor.

Variance partitioning: We used variance partitioning (Borcard et al. 1992, Anderson & Gribble 1998) to determine the amount of variation in understorey composition that could be attributed to pre-disturbance conditions: overstorey composition class, disturbance type, and soil texture. Using different combinations of explanatory data sets placed in the CCA of the species matrix, this procedure determines the amount of variation in the understorey species data set as explained explicitly (orthogonally) by each set as well as their overlap (correlation). This allows for overstorey composition and soil texture to be ranked by their ability to explain patterns in understorey variation.

We applied variance partitioning twice, (1) to assess the relative importance of the three sets of explanatory variables towards variation in the 36 fire sites, with the three FIS classes in the disturbance matrix; (2) to all 61 sites, the disturbance type matrix was comprised of the three FIS classes and two salvage-logging methods.

Axis score ANOVA and non-parametric multivariate ANOVA: The above-mentioned ordination techniques are descriptive in character; we sought also to determine if our experimental model was able to account for the variation in observed understorey composition. To do so we conducted ANOVAs with orthogonal contrasts on the site scores for the first two axes of the CAs, testing for the significance of composition and disturbance as well as their interaction (Steel & Torrie 1980). Site scores were log-transformed to meet the requirements of homoscedasticity. The contrasts for disturbance type entailed a comparison (1) of all fire (three FIS classes) versus salvage-logging (two logging methods), (2) between FIS classes and (3) between the two salvage-logging methods.

Conclusions drawn from ANOVA of the first two axes of the CA site scores however cannot be interpreted to reflect the entire data set, but are meaningful because they represent the two largest sources of variation (gradients) in the species data set. To support such interpretations, we used NPMANOVA (using the χ^2 distance option) to conduct formal tests of hypotheses on entire species assemblage between treatments (Anderson 2000, 2001). Analogous to traditional ANOVA, results obtained in this manner apply to the entire species data set. A problem here is that this method is presently applicable only to balanced designs and could thus only be conducted on the 36 fire sites. Orthogonal contrasts as conducted above were also unavailable through the computer program.

ANOVA of vegetation indices: abundance, diversity, richness and heterogeneity: Species abundance was measured at each site as the sum of all species' cover from the 15 microquadrats. We investigated understorey diversity through species richness as well as diversity, measured as Shannon's diversity index H (Legendre & Legendre 1998). Steinhaus's similarity index (S_{17} in Legendre & Legendre 1998) was used to compare two microquadrats (mq_1 and mq_2) in terms of the minimum abundance of each species:

$$S_{17}(mq_1, mq_2) = 2W / (A + B) \qquad (1)$$

where W is the sum of the minimum species abundances while A and B are the sums of the abundances of all species at each of the two microquadrats. At each site, S_{17} was calculated for all 105 pairings of the 15 microquadrats. Site heterogeneity was then calculated as the standard deviation in S_{17} for each site, emphasizing the variability in the degree of microquadrat similarity between sites. In addition, differences in abundance, species richness and diversity, and heterogeneity between the 1998 and 1999 sampling years were tested by incorporating a univariate repeated-measures analysis into the ANOVA (Anon. 1986). All ANOVAs were conducted using orthogonal contrasts as described above for the CA axes ANOVAs.

Indicator species analysis

Indicator species analysis, available in PC-Ord software (McCune & Mefford 1997), was conducted on the vegetation cover data in order to determine if certain species were representative of specific treatment groupings (typologies) (Dufrêne & Legendre 1997). Our typologies were first divided into fire and salvage-logging (two typologies), then between the three fire impact severity classes and two logging methods (five typologies). The final analysis at the *composition* × *disturbance* level was composed of 15 typologies (three composition classes × five disturbance types). Only if species were found significant in either the composition classes or the disturbance types independently were they considered significant at this level. Though we conducted separate analyses on the 36 fire sites alone as well as all 61 sites, the analysis of fire alone did not identify a substantially different set of species and is not presented.

Results

Correspondence analysis: CA and CA-PRA

In the CA ordination of fire sites (Fig. 1a), DEC-MIX sites were found to the left of the origin, distributed along the length of the second axis. CON sites were placed to the right of the origin, extending along the first axis. Furthermore, light burns clustered at the margins of the ordination – DEC and MIX sites to the far left and CON sites to the far right. ANOVA of site scores along the first and second CA axes (Table 1) demonstrated a significant interaction on Axis 1, differentiating DEC-MIX and CON response to FIS. This result was supported by those from NPMANOVA which also demonstrated a significant interaction between composition and FIS ($p < 0.001$). Thus, axis 1 appears to represent both a composition and a disturbance gradient: the more severe the fire, the less pronounced were the differences between CON and DEC-MIX understorey communities. Axis 2 indicates a disturbance gradient, from the light burns to severe and moderate fires. An inspection of the CA species ordination (not shown) indicated the second axis to be a gradient of herbaceous to shrub dominance in the understorey. However, CA-PRA identified sandy soil texture as a significant environmental variable, increasing also along the second axis and with a tendency towards CON sites. Nonetheless, in support of our initial interpretation, the grouping of sites by disturbance type are clearer when soil texture was used as a covariable in the CA – particularly the ordination of extremely burned DEC sites – and the disturbance gradient along Axis 2 is more pronounced (App. 2a).

When the salvage-logged sites were introduced (Fig. 1b), they appeared clustered around the top-centre of the ordination space, near the extreme end of the FIS spectrum. A significant interaction was detected along the first axis between CON and DEC-MIX response to fire and salvage-logging (Table 1). This was the result of a constriction of salvage-logged sites around the origin, moved slightly to the right for DEC-MIX sites and to the left for CON sites. As for the disturbance gradient, salvage-logged sites were found placed significantly higher along Axis 2 when compared to fire, due mostly to whole-tree harvested sites. CA-PRA identified clay as significant here, increasing into DEC stands. However, when soil texture was used as a covariable in the CA, groupings of treatments along Axis 2 are again more apparent (App. 2b). For all compositions, the understoreys of light and moderate FIS are more clearly distinguishable from extreme FIS and salvage-logging. When comparing the ordination of salvage-logged sites strictly with the extreme fires (no covariables involved), no significant differences between the two were identified for either the first or second CA axis (Table 1).

Five post-disturbance environmental variables were significant for the CA-PRA of burned unlogged sites (Fig. 1a). The most important was the presence of coniferous snags, clearly increasing with decreasing FIS along Axis 1 into CON sites. When both burned unlogged sites and salvage-logged sites were included in the CA-PRA, six post-disturbance environmental variables were found significant (Fig. 1b). Of these, the most important was coniferous snags again increasing along Axis 1. We also note that in both CA-PRAs, exposed duff was found to increase with disturbance severity and was greater in the presence of salvage-logging.

The differences in tree species dominance between fire and salvage-logged CON sites explain in part the understorey composition of CON sites, *Picea mariana* and *Pinus banksiana* being found significant via CA-PRA (App. 2c). These figures demonstrate however that the effect of *P. banksiana* is balanced. Rather it is the increase in *P. mariana* basal area that explains the differences in understorey, distinguishing the FIS-1 and FIS-2 CON sites from the salvage-logged FIS-3 CON sites.

Variance partitioning

Overstorey composition class, disturbance type and soil texture altogether explained 33.39 % of the variance in the understorey data of the fire sites (Table 3). Though a low value, it is meaningful given the large number of zeros in the species data matrix. Results show that overstorey stand composition alone was able to explain 1.7 times more of the variation than the three FIS classes but was of similar significance to substrate. Of the sets

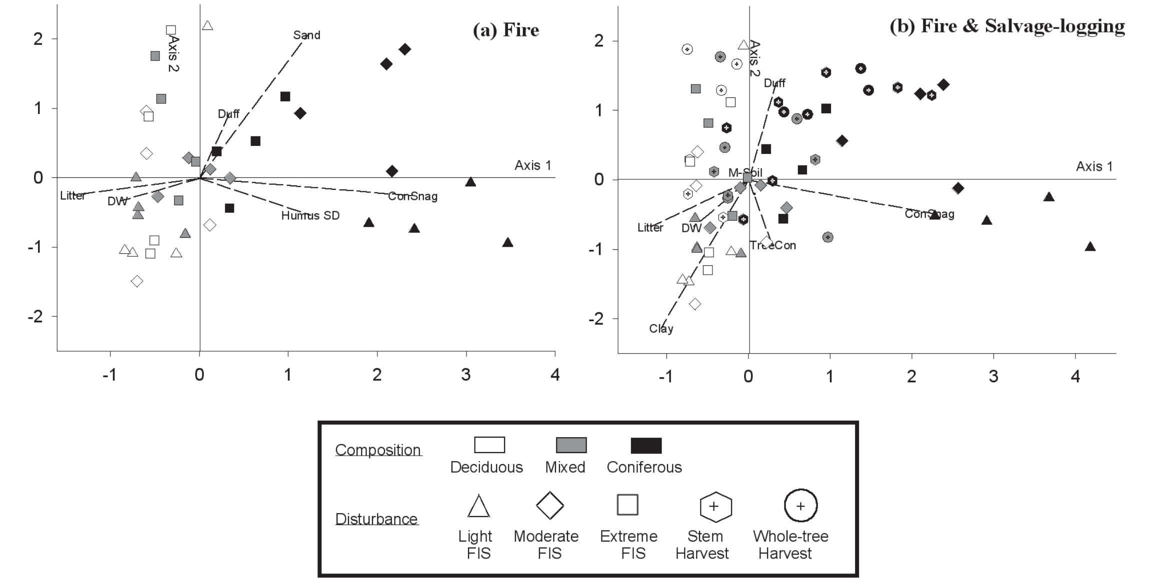

Fig. 1. a. Correspondence Analysis of 36 fire sites where sum unconstrained λ = 3.843 (Axis 1: λ = 0.551 (14.3%); Axis 2: λ = 0.388 (10.1%)); **b.** CA of fire and salvage-logging where sum unconstrained λ = 4.603 (Axis 1: λ = 0.517 (11.2%); Axis 2: λ = 0.416 (9.1%)). Environmental variables found significant via CA-PRA are overlaid onto their corresponding CA. **ConSnag** = frequency of coniferous snags, **Clay** = % clay; **Duff** = area of duff exposed; **DW** = % cover downed wood; **Humus SD** = humus depth standard deviation; **Litter** = area of litter cover, **M-Soil** = area of mineral soil exposed; **Sand** = % sand; **TreeCon** = frequency of live conifers.

of variables, overlap was greatest between soil texture and composition, but at only 1.69 %. The three sets of variables together had a negative effect, indicating that the three sets of variables have an opposite effect on one another—"one process hindering the contribution of the other" (Legendre & Legendre 1998, p. 534). However, this is hardly significant as it represents a very small fraction of the total variance (–0.39 %) Indeed, there was little interaction between the three sets of variables, indicating that they are highly orthogonal.

Variance partitioning of fire and salvage-logging sites (Table 3) resulted in a lower percentage of total variance being explained than after fire, 27.66 %. In contrast to fire sites only, disturbance type here accounts for a slightly greater proportion of the variation than stand composition alone (1.2 times) and soil texture alone (1.4 times). There was again little overlap between these two data sets, highest now for disturbance type and soil texture at 1.89 %.

ANOVA of selected community measures

In burned unlogged sites, abundance was reduced as the overstorey changed from DEC to CON composition and with greater FIS, the effects of fire severity being more pronounced on CON sites (Tables 1 and 2). The low abundance of lightly burned DEC sites is anomalous and may reflect that two of these sites showed indications of having been selectively harvested in the past (see Study area). The other two DEC sites of FIS-1 had higher, more representative abundance values (results not shown). From repeated measures analysis, a significant interaction between time and FIS ($p = 0.004$) was found indicating that abundance increased from 1998 to 1999 on extremely and moderately burned sites by 13% and 15%, respectively, while decreasing by 12.7% for light fires. Species richness and diversity (Tables 1 and 2) were found to decrease with FIS on DEC and MIX sites. On CON sites however, diversity decreased from light to moderate FIS, though increasing thereafter on extremely burned sites. Overall, species richness and diversity increased over the two year study period (both with $p < 0.001$) though an interaction between time and composition indicated that such increases were greater on CON sites (results not shown).

For site heterogeneity, an interaction indicated an inverse pattern from that for diversity: heterogeneity decreasing with FIS on DEC and MIX sites though increasing on CON sites (Tables 1 and 2). Time between study periods did not significantly affect this index.

Understorey abundance after salvage-logging was significantly reduced in comparison to fire, most significantly affecting MIX and CON sites (Tables 1 and 2). No difference between salvage-logging methods was identified. There was a significant interaction between time

Table 1. ANOVA results for site scores of the first two axes of CA and vegetation indices for (1) the 36 burned unlogged sites (Fire Only), (2) all three fire impact severity classes and two methods of salvage-logging (Fire vs Salvage-logging) as well as (3) the restricted ANOVA conducted for extreme fire impact severity and the two methods of salvage-logging (Extreme Fire vs Salvage-logging). Bold: $p < 0.05$.

	CA		Vegetation indices			
	Axis 1	Axis 2	Abundance	Diversity	Richness	Heterogeneity
Contrast	$p > F$	$p > F$	$p > F$	$p > F$	$p > F$	$p > F$
1.			Fire Only (n = 36)			
Composition						
CON vs DEC-MIX	***< 0.001***	0.270	***<0.001***	***<0.001***	***<0.001***	***<0.001***
DEC vs MIX	0.181	0.208	0.682	***0.030***	***0.033***	0.564
Disturbance (Fire)						
FIS-1 vs FIS-2,3	0.403	***0.019***	0.692	***0.097***	0.268	0.962
FIS-2 vs FIS-3	***0.010***	0.730	0.309	0.398	0.955	0.497
Interaction : CON vs DEC-MIX						
FIS-1 vs FIS-2,3	***< 0.001***	0.323	***0.014***	0.892	0.398	0.744
FIS-2 vs FIS-3	***0.023***	0.246	0.664	***0.006***	***0.049***	***0.009***
Interaction: DEC vs MIX						
FIS-1 vs FIS-2,3	0.119	0.644	***0.072***	0.180	0.171	0.856
FIS-2 vs FIS-3	0.464	0.987	0.572	0.321	0.917	0.466
2.			Fire vs Salvage-logging (n = 61)			
Composition						
CON vs DEC-MIX	***< 0.001***	0.310	***< 0.001***	***< 0.001***	***<0.001***	***<0.001***
DEC vs MIX	0.112	0.543	***0.040***	***0.004***	***0.014***	***0.045***
Disturbance						
Logging vs Fire	0.251	***0.006***	***0.002***	***0.025***	***0.003***	***0.003***
STEM vs WTH	0.500	***0.066***	0.324	***0.042***	***0.072***	0.159
FIS-1 vs FIS-2,3	***0.051***	***0.012***	0.700	0.111	0.244	0.985
FIS-2 vs FIS-3	***0.011***	0.706	0.312	0.423	0.952	0.589
Interaction: CON vs DEC-MIX						
Logging vs Fire	***< 0.001***	0.784	0.903	0.651	0.782	0.245
STEM vs WTH	0.724	0.288	0.319	0.303	0.397	0.916
FIS-1 vs FIS-2,3	***< 0.001***	0.225	***0.014***	0.897	0.375	0.793
FIS-2 vs FIS-3	***< 0.001***	0.104	0.672	***0.007***	***0.037***	***0.020***
Interaction: DEC vs MIX						
Logging vs Fire	0.410	0.160	***0.058***	0.691	0.663	***0.099***
STEM vs WTH	0.735	0.147	0.857	0.633	0.456	0.640
FIS-1 vs FIS-2,3	0.356	0.496	***0.076***	0.200	0.149	0.898
FIS-2 vs FIS-3	0.669	0.828	0.582	0.345	0.913	0.507
3.			Extreme Fire vs Salvage-logging (n = 37)			
Composition						
CON vs DEC-MIX	***< 0.001***	0.775	***< 0.001***	***< 0.001***	***< 0.001***	***0.007***
DEC vs MIX	0.141	0.416	***0.012***	***0.069***	0.153	***0.040***
Disturbance						
Logging vs Fire FIS-3	0.228	0.292	***0.083***	0.441	***0.047***	***0.025***
Stem vs WTH	0.529	***0.071***	0.314	***0.036***	***0.060***	0.219
Interaction: Con vs DEC-MIX						
Logging vs Fire FIS-3	0.695	0.729	0.596	***0.052***	0.432	***0.069***
STEM vs WTH	0.742	0.288	0.309	0.283	0.370	0.927
Interaction: DEC vs MIX						
Logging vs Fire FIS-3	0.594	0.163	0.224	0.197	0.832	0.386
STEM vs WTH	0.751	0.152	0.854	0.618	0.429	0.683

and the five disturbance types ($p = 0.013$), demonstrating a different response between salvage-logging and fire ($p = 0.086$). Compared to burned unlogged stands, abundance on salvage-logging sites increased more rapidly over the two year period, at 14% for stem-harvested sites and 28.7% for whole-tree harvested sites. It should be emphasized that 1999 abundance values were still less than those after fire. Species richness and diversity were significantly reduced by salvage-logging, due mostly to the lower diversity of whole-tree harvested sites (Tables 1 and 2). Heterogeneity was significantly greater after salvage-logging than after fire – no interaction being detected (Tables 1 and 2). No significant differences over the time of the two year study period are found for any of these four indices.

When salvage-logging sites were compared strictly with extreme fire, abundance and species richness (Tables 1 and 2) were both significantly reduced by salvage-logging. Species diversity (Tables 1 and 2) was reduced after salvage-logging on CON sites, though with a tendency to be increased on DEC and MIX sites, particularly after stem-harvesting. Heterogeneity was also increased after salvage-logging, but most significantly on CON sites.

Table 2. Average results of selected vegetation results per treatment for the 1999 sampling effort. Note that the SE reported for each index represents standard error (mean square error/$(n)^{1/2}$) as derived from ANOVA.

	Fire Impact Severity			Salvage-logging	
	FIS-1	FIS-2	FIS-3	STEM	WTH
Abundance (m^3)					
Deciduous	15.1	21.5	18.4	16.1	19.1
Mixed	18.4	17.8	16.9	10.8	13.1
Coniferous	10.9	5.8	5.2	4.0	3.5
SE = 0.238					
Richness (Total number of species)					
Deciduous	34.3	39.3	35.3	36.0	26.3
Mixed	46.5	43.3	38.5	37.7	33.6
Coniferous	25.3	15.3	23.5	17.3	15.3
SE = 0.87					
Diversity (Shannon's diversity index *H*)					
Deciduous	4.00	4.30	3.70	4.00	2.90
Mixed	5.30	5.00	3.80	4.70	4.00
Coniferous	2.90	1.90	2.90	2.10	1.80
SE = 0.102					
Heterogeneity (Standard deviation of Steinhaus's index S17)					
Deciduous	0.157	0.141	0.163	0.177	0.202
Mixed	0.148	0.145	0.149	0.144	0.154
Coniferous	0.179	0.206	0.158	0.209	0.229
SE = 0.0038					

Indicator species analysis

Only *Aralia hispida* and *Carex houghtonii* were identified for the salvage-logged sites, against 14 species for the fire grouping (Fig. 2). As to the five disturbance types, the majority of species attributed initially to the fire grouping belonged to class FIS-1. Of salvage-logged sites, only two indicator species were identified for tree-harvested sites: *Prunus pensylvanica* and *P. pensylvanica* (1-3 m). For the 15 categories of composition × disturbance, FIS-1 sites were again the most well characterized. For DEC salvage-logged sites, *Epilobium angustifolium* and *Calamagrostis canadensis* were indicative of stem-harvested DEC sites and *P. pensylvanica* for tree-harvested sites. Grasses were indicative of CON WTH sites: *Oryzopsis canadensis*, *A. scabra*, and *Carex brunnescens*/*C. trisperma* (two similar species difficult to distinguish in the field). Finally, *A. hispida* was indicative of CON WTH sites.

Table 3. Results of variance partitioning for the 36 burned sites and the 61 fire and salvage-logged sites.

Fraction of variance	Fire	Fire and Salvage-logging
Strictly Composition Class (%)	12.23	8.15
Strictly Disturbance Type (%)	7.36	9.41
Strictly Soil Texture (%)	11.29	6.84
Composition and Disturbance (%)	0.65	0.63
Composition and Soil Texture (%)	1.69	1.37
Disturbance and Soil Texture (%)	0.55	1.89
Comp and Dist and Soil (%)	-0.39	-0.63
Total Explained Variance (%)	33.39	27.66
Total Unexplained Variance (%)	66.61	72.34

Discussion

Early stages of secondary succession after fire

Our results indicate that in early stages after fire, secondary succession is driven primarily by overstorey composition rather than FIS. This is in agreement with initial floristics theory (e.g. McIntosh 1986). The importance of overstorey stand composition is most evident where FIS is low. This however may also be in part due to associations between the overstorey and soil texture. Recall that CON lightly burned stands were found on coarse-texture soils while the soils of lightly burned DEC and MIX stands were characterized by a finer soil texture. In undisturbed boreal forests, specificity between overstorey and understorey composition occurs where species from both layers make use of similar environmental conditions (Carleton & Maycock 1981; Bergeron & Bouchard 1983). We argue that under conditions of no disturbance or light FIS, this relation between substrate and overstorey composition holds. However, from variance partitioning, little correlation was found between overstorey and substrate in their capacity to explain variation in understorey composition. This is the result of a decoupling of the relationship between substrate and overstorey composition that proceeds with increasing FIS, which we describe below.

Fire severity is important in determining the extent to which species present prior to disturbance are able to re-establish themselves. What may have been identified as a homogenizing effect of fire by Carleton & Maycock (1981) is rather an interaction between overstorey stand composition and fire severity: differences between the

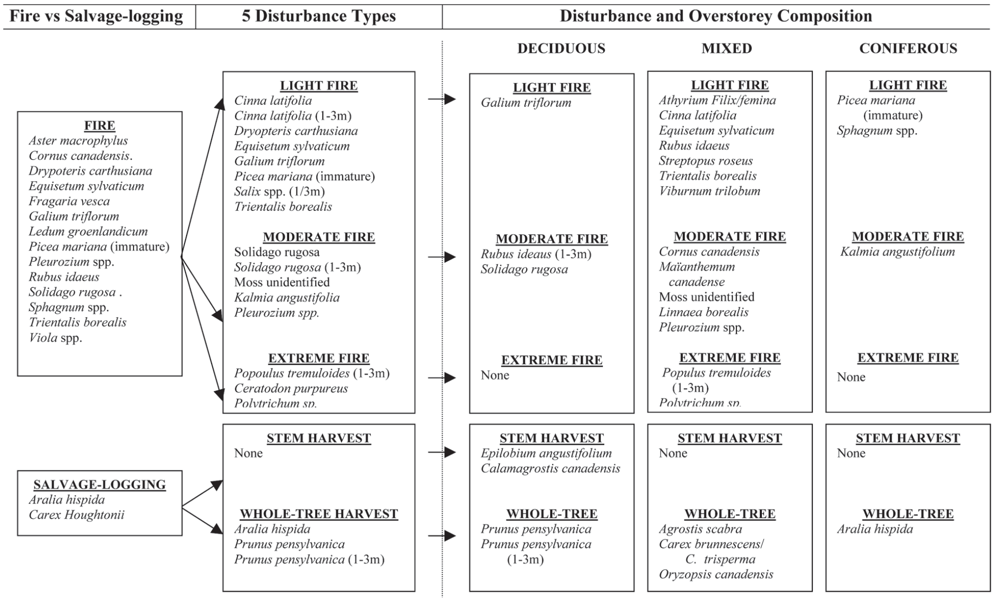

Fig. 2. Indicator species analysis for fire and salvage-logging (three Fire Impact Severity classes and two Salvage-logging methods).

understoreys of coniferous stands and those with an important DEC component are reduced as a function of FIS, primarily by the removal of *Sphagnum* dominance and the consumption of soil organic matter. This is indicated by a decrease in species richness and diversity from light to moderately burned CON sites but an increase after extreme fire.

Our results suggest that the interaction between fire severity and overstorey composition also affects the overstorey's interaction with substrate. Due to the diminished importance of the overstorey with increasing fire severity, there is less congruence between the overstorey and soil texture in terms of explaining understorey species composition. Our ordination analysis indicate that overstorey accounts for differences in understorey species composition (distinguishing CON and DEC-MIX understorey compositions) while soil texture accounts for a change from herb to shrub dominance as soils become more sandy. On sites with an important deciduous overstorey richer clayey soils are able to support a wider diversity of herbaceous plants (Harvey et al. 1995), while the more nutrient-poor, deciduous coarse-texture soils become dominated by a few shrub species such as *Diervilla lonicera*, *Prunus pensylvanica* and *Ribes* spp. (App. 3). For CON sites, patterns in understorey transition are less clear, but there is a trend towards a stronger presence of ericaceous species in moderately burned fires compared to light.

Overstorey - FIS interaction mechanism

The importance of overstorey composition can be attributed to its capacity to precondition understorey response to fire through (1) its influence on light regimes and (3) its ability to determine fire intensity directly. Stand succession after fire in the mixedwood boreal forest proceeds from intolerant tree species (mostly deciduous) to be outshaded by shade-tolerant coniferous species (Bergeron & Charron 1994). DEC stands may be more resilient to disturbance: De Grandpré & Bergeron (1997) concluded that the greater light transmittance to the understorey of deciduous stands prior to disturbance results in their understorey being able to benefit from the more open conditions resulting from gap formation and thus to maintain more resident species. In this manner, the understorey of DEC-MIX stands would be more resistant to fire than the CON stands.

The severity of the effects of fire to the forest floor is also mediated by stand composition. Hély et al. (2003) demonstrated that the fires on our CON sites were more intense than at the DEC and MIX sites (refer to values from their study presented in the table of App. 1). Though of the same FIS class, the actual severity of fire would thus also be greater on CON sites. Boreal understorey species are understood to have evolved different reproductive strategies to survive fire and variation in its severity (Rowe 1983; Schimmel & Granström 1996). We hypothesize that understorey species of stands with an important deciduous component are adapted to these less severe fire conditions. For example, the reproductive tissues of herbaceous plants of DEC-MIX sites such as *Trientalis borealis* and *Maianthemum canadense* are located in the upper litter layer, while the reproductive parts of *Vaccinium* spec. (found here on CON sites) are usually located in the mineral soil layers (Flinn & Wein 1977).

Effects of salvage-logging on understorey vegetation

Although the effects of salvage-logging on understorey vegetation were within the variability of fire, these effects did not include the entire range of this variability. Instead, salvage-logging tended to homogenize the understorey composition towards one most similar to extreme fires. In terms of abundance and diversity however, salvage-logging led to reductions even in explicit comparison with FIS-3. These results are particularly important as they indicate that reductions in abundance and diversity were not an artefact of the over-representation of salvage-logged sites of FIS-3 origin in our experimental design. Thus we can conclude that the overall composition of the understorey was not radically altered by non-native species after salvage-logging, rather it was more sparse and simplified in terms of native species, consistent with results of Che & Woen (1997).

In contrast to the 36 burned unlogged sites the most important group of factors in explaining understorey variation was not overstorey composition nor soil texture, but disturbance type. However, overstorey did appear to mitigate these effects: DEC and MIX sites were more resistant to logging, particularly in terms of species diversity. Between logging methods on these stands, it can be seen that the effect of stem harvesting on diversity is similar to that of extreme fire. CON stands however were distinguished by a decrease in diversity FROM FIS-1 TO 2, but an increase after FIS-3. Salvage-logging on CON stands is unable to mimic this: instead of increasing diversity it reduces it to levels below those of moderate burns. This suggests that salvage-logging is inhibiting the interaction between FIS and overstorey composition described above. In addition, results from CA-PRA showed that differences in post-disturbance variables between fire and salvage-logging followed differences in the overstorey: salvage-logging was characterized by lesser amounts of litter and downed-wood on DEC-MIX sites and the absence of coniferous snags on CON sites.

Mechanisms of salvage-logging impact

We offer two explanations for this greater impact which are not mutually exclusive: (1) greater forest floor disturbance and (2) accelerated soil drying due to snag removal. The use of heavy machinery during salvage-logging led to increased forest floor disturbance which accounted for differences in understorey composition. CA-PRA demonstrated that salvage-logging is associated with increased exposure of raw duff, while Noël 2000) reported that mineral soil exposure significantly increased after salvage-logging. Generally, differences in understorey composition between fire and harvesting increase with forest floor disturbance (Brumelis & Carleton 1989; Nguyen-Xuan et al. 2000), and logging favours the establishment of perennial grasses and other species (Harvey et al. 1995; Peltzer et al. 2000; Harvey & Brais 2002). Forest floor disturbance thus seems to explain why invader species such as *Epilobium angustifolium*, *Oryzopsis canadensis*, *Agrostis scabra*, *Carex* spp. and *Prunus pensylvanica* are found indicative of salvage-logged sites. *Prunus* has been demonstrated to be a buried seed strategist, its germination dependent on open conditions (Marks 1974).

Results from indicator species analysis also suggest that a mechanism for decreased abundance and diversity of the understorey layer after salvage-logging is accelerated soil drying. Rowe (1956) ascribed the following species, analogous to those identified as indicative for the cut sites, as being xero-mesophytic: *Oryzopsis pungens-asperifolia*, *P. pensylvanica*. Species indicative of salvage-logging (*Aralia hispida*, *Oryzopsis canadensis*, *Epilobium angustifolium*, and *P. pensylvanica*) were associated with xeric-oligotrophic sites by Bergeron et al. (1983). Moister conditions after fire are also supported by the concentration of *Picea mariana* and *Pinus banksiana* seedlings in severely burned sites – reductions in germination were in part due to reductions in *Sphagnum* as available seedbeds (Noël 2000). We note that though *P. mariana* sites are known to be more humid than other boreal stands (Bergeron & Bouchard 1983), coniferous basal area did not differentiate understorey composition between salvage-logged and extremely burned Coniferous sites. It is unclear however if such drying effects would be due (1) indirectly to reduced vegetation cover and resulting increases in light penetration to the forest floor as a result of the impact of logging (soil compaction and skidder trails) on the understorey or (2) directly due to alterations in the forest microclimate caused by the removal of snags. In support of the latter, a moister microclimate may be due to the physical effects of the dead tree boles, which can provide shade and function as wind breaks (Hawke & Wedderburn 1994). Our interpretation of the impact of salvage-logging may be confounded however by different soils conditions.

P. pensylvanica identified above has been demonstrated to be restricted to well-drained tills and rapidly drained organic sites after clearcutting

(Harvey & Bergeron 1989), conditions similar to our coarse-textured DEC whole-tree harvested sites. In support of our main conclusion however, reduced abundance and diversity were observed at the level of fire (which were found over the range of soil textures) vs salvage-logging, the combined of effect of both stem- and whole-tree harvesting (which were restricted to areas of more clayey and sandy soils, respectively). Furthermore, a disturbance gradient was preserved in our ordinations where soil texture was used as a covariable. We thus conclude that salvage-logging has had negative effects on the early stages understorey secondary succession despite differences in soil texture.

Conclusion: The sustainability of salvage-logging

The importance of our results in the assessment of the biological integrity of salvage-logging depends on the amount of extreme fire historically occurring in the region. In the Quebec boreal forest, extreme FIS has been found to account for only half of the area burned (Kafka et al. 2001) and is marked by an important variation in frequency, severity and size (Bergeron et al. 2002). At the landscape level, the extreme FIS class to which salvage-logging most resembles is not ubiquitous and indicates a reduction in the variability of fire at the landscape level.

However, our results suggest that differences in abundance between salvage-logging and fire were decreasing over time. Long-term studies are needed to validate this. To mitigate the effects of salvage-logging that we did observe we suggest (1) conducting salvage-logging operations in winter when the soil is frozen and the impact of logging machinery is reduced and (2) leaving more standing snags. However, such mitigation procedures must be conducted in a manner that also addresses the important social aspects of sustainable forest management (Purdon 2003).

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