Partial harvests in the boreal forest: Response of the understory vegetation five years after harvest

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ABSTRACT

In the eastern boreal forest of Canada long fire cycles allow for a significant portion of stands to become old growth. These old-growth boreal forest stands are subjected to secondary disturbances that create uneven structure, which supports a variety of types of organisms. In order to maintain the proportion of stands with uneven structure on the landscape, partial cuts have been suggested as a management technique that could create or maintain these uneven structures. This study compares the effects of partial and low-retention harvests and un-harvested control on understory plants in four sites five years after harvest. The relative abundance of species was examined by a habitat group. While richness did not vary among treatments, increasing severity of harvest favoured pioneer species that prefer disturbed mineral soil and high light levels. Sites with thicker organic layers that were harvested in the winter were significantly less impacted by both partial and low-retention harvest. Canopy opening alone had little impact in the three most northern sites. As old-growth black spruce forests are open by nature, this suggests that soil perturbation is a bigger driver of community change after harvest than proportion of canopy removed for this forest type.

Key words: Quebec, *Picea mariana*, harvest, variable retention, sustainable forest management, understory, structural retention, vegetation

RÉSUMÉ

Dans la forêt boréale de l'Est du Canada, les longs cycles de feu permettent à une portion importante des peuplements d'évoluer en vieille forêt. Ces peuplements sont soumis à des perturbations secondaires qui entraînent la création de structures inéquiennes servant de support à une diversité d'organisme. Afin de maintenir, dans le paysage, une proportion de peuplement ayant une structure inéquienne, il est envisagé d'utiliser les coupes partielles en tant qu'outil sylvicole dans l'aménagement forestier pour créer ou maintenir des peuplements ayant des structures proches de celles que l'on retrouve dans les vielles forêts. Cette étude compare l'effet des coupes partielles et des coupes à faible rétention sur les plantes de sous-bois dans quatre dispositifs cinq ans après la récolte. L'abondance relative des espèces a été examinée par groupe d'habitat. Alors que la richesse ne variait pas parmi les traitements, l'augmentation de la sévérité de la récolte a favorisé les espèces pionnières qui préfèrent les sols perturbés et la lumière. Les sites, où la couche de matière organique est la plus épaisse et dans lesquels la récolte a été réalisée en hiver, ont été moins affectés par les coupes partielles et de faible rétention. L'ouverture de la canopée a eu peu d'impact dans les trois sites les plus nordiques. Les vieilles forêts d'épinette noire étant ouvertes naturellement, ceci suggère que les perturbations du sol ont un rôle plus important sur les changements dans les communautés suite à la récolte que la proportion de la canopée récoltée dans ce type de forêt.

Mots-clés : Québec, *Picea mariana*, récolte, rétention variable, aménagement forestier durable, sous-bois, rétention structurale, végétation

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Introduction

The natural forest dynamic in the boreal zone is thought to be predominantly driven by forest fires (Johnson 1992), resulting in even-aged stands that are frequently burned before secondary disturbances can significantly influence the forest structure (Dix and Swan 1971). However, in some regions of the boreal zone, for example parts of Alaska, eastern North America and Siberia, the fire cycle is longer (over 100 years), resulting in an increased role for successional changes in stand structure driven by secondary disturbances (individual stem or group death due to senescence, insects, fungus or windthrow (Lecomte *et al.* 2006)). These stands develop an uneven structure with new stems establishing in the gaps created by stem death (Foster 1985, Taylor *et al.* 1987). In the eastern boreal forest of North America long (i.e., 200 years) to very long (over 400 years) fire cycles are created by the proximity to coasts (both the Atlantic and Arctic oceans) and these uneven stands can dominate the landscape (Bergeron *et al.* 2006).

Current forest management techniques in eastern North America depend almost exclusively on clearcutting, regenerating predominately even-aged stands (Ruel *et al.* 1998, Bergeron *et al.* 1999) This significantly reduces the importance of uneven-aged stands on the landscape, decreasing both stand and landscape level heterogeneity (Harper *et al.* 2002, Fenton *et al.* 2009). Many species, particularly vascular plants, bryophytes, lichens and birds are associated with these stands with uneven structure (Boudreault *et al.* 2002, Drapeau *et al.* 2003, Fenton and Bergeron 2006), and their continued existence depends on the availability of habitat at appropriate spatial scales across the landscape.

Recently, partial cuts have been suggested as a technique to maintain or create uneven stands and therefore maintain stand and landscape level heterogeneity, and hopefully the species dependant on this variation (Rosenvald and Lohmus 2008). However, the degree to which partial cuts succeed in maintaining the appropriate structure and habitat conditions for species associated with uneven structure is still unclear, as is whether the stands created via partial cuts are actually used by the targeted species in the boreal forest. Retention levels over 15% seem efficient for some groups in the Pacific Northwest (Aubry *et al.* 2009) but to our knowledge no information is available for North American boreal systems.

Plants in the forest understory experience two types of disturbance (modified from White and Pickett 1985); direct disturbance on the machinery trails where they are physically crushed or removed and indirect disturbance where they experience a changed microclimate (increased solar radiation and greater variations in temperature and humidity regimes due to canopy removal [Renhorn *et al.* 1997]). Similarly, Roberts (2007) classified forest management disturbance along three axes: soil removal (direct disturbance), understory removal (direct disturbance) and canopy removal (indirect disturbance). Combining these classifications, communities that experience partial harvest would experience a variable level of indirect disturbance due to the removal of part of the canopy (except for the machinery trails), while those that experience low-retention harvest would experience a higher severity of indirect disturbance and a greater proportion of the community would experience direct disturbance, due to soil removal and removal or damage to the plants themselves. Overall partial cuts could be classified as less severe disturbances than low-retention cuts and would have lower levels on Robert's axes than low-retention cuts.

A large project that aims to address this question in the boreal forest over the long term for a variety of indicator groups was initiated in 1998. In this specific study the understory community five years after low-retention harvest (clearcut with protection of regeneration and soils—required by law in Québec), partial harvest (harvest with variable retention), and unharvested control are compared to see whether composition and diversity after partial harvest is more similar to unharvested stands or stands that were subjected to low-retention harvest.

In this context, while it is impossible to specifically test Robert's model with a large-scale operational trial, we address several hypotheses related to his model. We suggest that clearcuts, compared to partial cuts, present higher levels of severity of direct disturbance (soil disturbance) and indirect disturbance (overstory removal). This in turn causes (1) community attributes (species guild richness and cover) and (2) community composition in partial cuts to be more similar to unharvested control than to low-retention cuts.

Methods

Study site

The Claybelt of eastern North America is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent and Hardy 1977). In its northern portion, it is dominated by black spruce (*Picea mariana* [Mill.] BSP) – feather moss (e.g., *Pleurozium schreberi* [Brid.] Mitt.) forests (Grondin 1996), and is particularly prone to paludification between fires due to its poorly drained clay-dominated soil. Across the landscape, the clay is interrupted by sand and till deposits. The landscape is dominated by low topographic relief, and a moderately humid and cold climate (889.9 mm of precipitation annually; annual mean temperature 0.7°C [Environment Canada 2004]). The dominant disturbance type is large fires that kill most of the aboveground vegetation. Between 1850 and 1920 the fire cycle (i.e., fire return interval) was about 135 years, and it has since increased to around 398 years (Bergeron *et al.* 2004); as a result the average age of the forests is in excess of 100 years.

Of the 10 sites established between 1998 and 2007 the first four sites for which data five years post-harvest was available are included in this study. These sites are described in Table 1 and shown in Fig. 1. Three sites were located in the north and were dominated by black spruce, had an irregular structure and were at least 120 years old, and established after a stand-replacing fire. One site was located in the south and was also dominated by black spruce but was mixed, with trembling aspen (*Populus tremuloides* Michx.) and balsam fir (*Abies balsamea* [L.] Mill.) as co-dominants. At each site there is a low-retention cut block, a partial cut block and an unharvested control block, and each block is over 50 ha in size. The sites were harvested using a single-grip harvester and forwarder. Two of the four sites (Muskuchii and Dufay) were harvested with cut with protection of small merchantable stems, which was designed to retain small-diameter trees on the cutover and to promote their growth following canopy removal. The other two sites (Gaudet and Maïcasagi) were harvested with "cut with conservation of canopy cover" (variable retention), where stems are harvested from all diameter classes in order to maintain a similar proportion as was present before harvest. This second technique is more dependent on the abilities of the operator; however, it generally results in a more even cover

Table 1. Environmental variables for each site and treatment type. Plot level values are means (SE). Values followed by different letters are statistically different ($p < 0.05$).

	Muskuchii			Maïcasagi			Gaudet			Dufay		
	Control	Partial cut	CPRS	Control	Partial cut	CPRS	Control	Partial cut	CPRS	Control	Partial cut	CPRS
Site level variables												
Latitude/longitude		50°12′5″N, 78°42′54″ W			49°56′N, 76°20′31″W			49°53′46″N, 78°48′W			48°04′N79°24′W	
Deposit type/drainage		sand/dry–mesic			till/mesic			clay/sub-hydric			till/mesic	
Forest stand before harvest		black spruce, jack pine			black spruce, jack pine			black spruce			black spruce, white pine, white birch	
Last stand-replacing fire (approx.)		1850			1725			1775			1775	
Harvest season		summer			fall			winter			summer	
Machinery		Single-grip harvester on tracks Forwarder on wheels			Single-grip harvester on tracks Forwarder on wheels			Single-grip harvester on wheels Forwarder on wheels			Single-grip harvester on wheels Forwarder on wheels	
Before harvest basal area (m^2/ha)		20.3			~ 14 [a]			12			17	
% harvested		66			~ 45			83			67	
Plot (400m^2) level variables												
% Trail	0.03 a (0.014)	0.17 b (0.025)	0.23 b (0.03)	0 –	9.19 (3.27)	7.29 (3.64)	0 a –	19.12 b (4.48)	31.25 b (5.27)	0 a –	20.31 b (5.80)	25.19 b (5.76)
O.M. depth (cm)	12.92 (0.84)	11.38 (0.57)	11.77 (0.47)	34.44 b (1.11)	30.44 ab (1.68)	24.37 a (1.42)	52.79 c (2.65)	43.90 b (1.89)	31.47 a (1.14)	20.48 b (1.71)	11.88 a (2.01)	16.15 a (1.30)
% Canopy	12.68 c (0.29)	7.22 b (0.59)	3.30 a (0.48)	15.83 c (0.64)	6.92 b (0.65)	0.75 a (0.42)	15.89 b (0.76)	4.20 a (0.60)	2.90 a (0.84)	83.69 b (2.24)	39.02 a (4.09)	27.14 a (5.26)
Quadrat (1 m^2) level variables												
% Rock	0 –	0.10 (0.01)	0.08 (0.06)	0 –	0 –	0 –	0 –	0 –	0 –	0.12 (0.12)	0.08 (0.058)	0 –
% Litter	3.90 (0.63)	2.60 (0.38)	4.91 (0.578)	0.42 a (0.16)	1.72 b (0.42)	2.44 b (0.68)	0.27 a (0.11)	1.65 b (0.41)	2.62 b (0.55)	14.98 (1.26)	13.65 (1.23)	11.19 (1.22)
% Branch	1.65 a (0.33)	3.12 a (0.40)	5.51 b (0.60)	1.96 (0.40)	2.69 (0.42)	1.73 (0.47)	1.08 a (0.29)	5.32 b (7.0)	5.25 b (0.68)	0.42 a (0.33)	2.96 ab (0.79)	4.17 b (0.91)
% Water	0 –	0 –	0.01 (0.005)	0 –	0.01 (0.015)	0 –	0.08 (0.077)	0.24 (0.15)	0.22 (0.11)	0 –	0.38 (0.20)	0.87 (0.51)
% Soil	0.01 (0.007)	0.19 (0.09)	1.13 (0.363)	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –	0 –
% Tree	0.21 b (0.09)	0.04 a (0.023)	0 a –	0.19 b (0.058)	0.03 a (0.021)	0 a –	0.10 b (0.041)	0.07 ab (0.032)	0 a –	0.12 (0.07)	0.08 (0.065)	0.04 (0.3)
% CWD 1	0 –	0 –	0 –	0 –	0 –	0 –	0.08 (0.077)	0.06 (0.059)	0 –	0 a –	0.13 ab (0.11)	0.38 b (0.17)
% CWD 2	0.17 (0.086)	0.41 (0.096)	0.09 (0.05)	0.22 (0.12)	0.53 (0.18)	0.46 (0.17)	0.69 (0.23)	0.78 (0.20)	0.65 (0.17)	0.23 (0.11)	0.15 (0.10)	0.85 (0.28)
% CWD 3	0.29 (0.097)	0.33 (0.078)	0.15 (0.056)	0.62 (0.19)	0.56 (0.18)	0.63 (0.22)	0.35 (0.14)	0.68 (0.18)	0.81 (0.18)	0.06 a (0.06)	0.04 a (0.03)	0.62 b (0.32)
% CWD 4	0.28 a (0.09)	0.60 ab (0.13)	0.98 b (0.17)	0.43 (0.13)	0.43 (0.16)	0.08 (0.05)	0.15 (0.09)	0.21 (0.10)	0.25 (0.097)	0.56 (0.24)	0.60 (0.22)	0.23 (0.23)
% CWD 5	0.06 a (0.029)	0.18 ab (0.11)	0.76 b (0.17)	0.18 (0.096)	0.21 (0.11)	0.02 (0.02)	0.10 (0.050)	0.41 (0.19)	0.44 (0.19)	0.44 (0.20)	0.54 (0.17)	0.12 (0.07)

[a]Precise before harvest data unavailable, value based on after harvest value and % harvested.

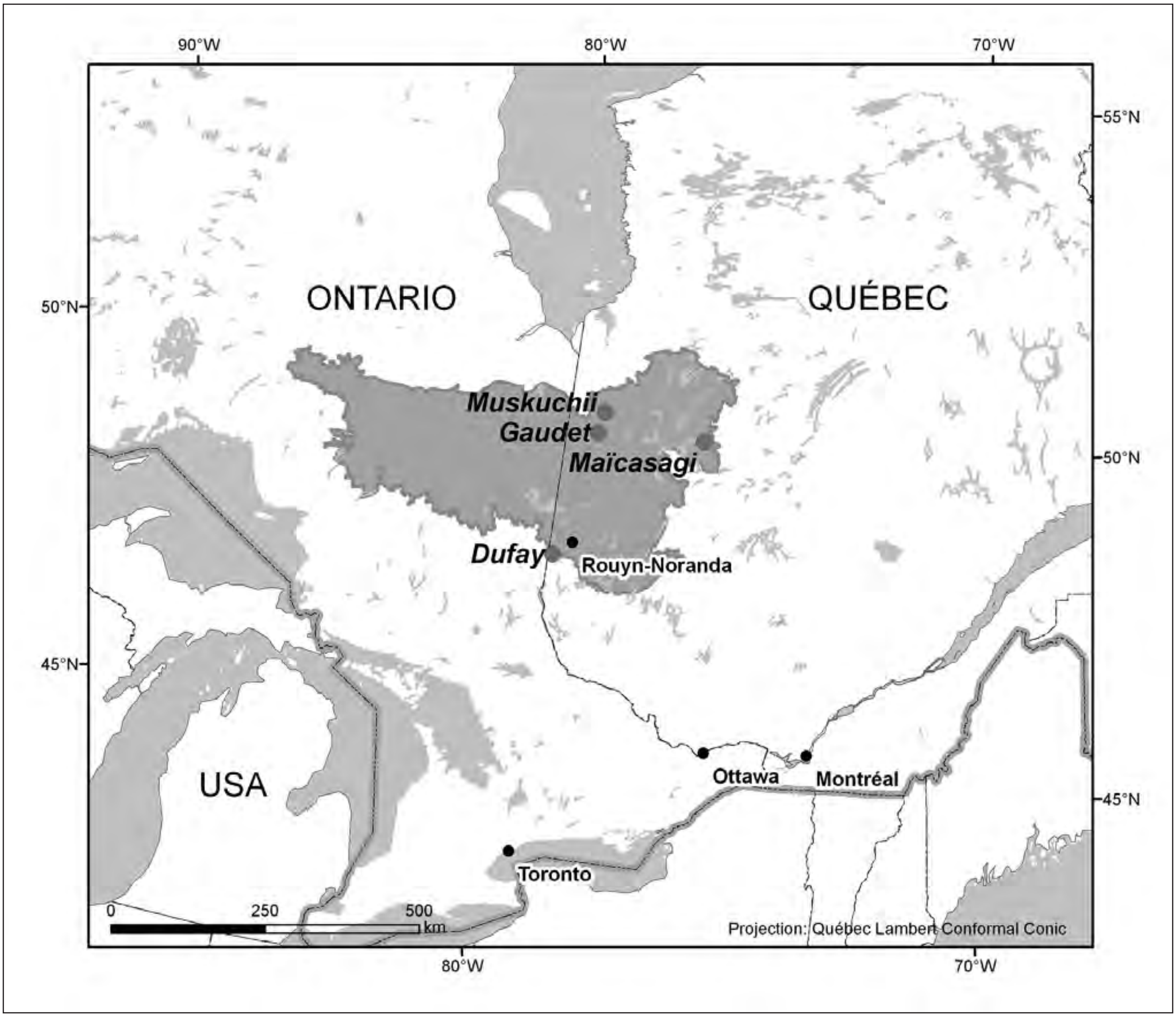

Fig. 1. Location of the Claybelt (grey) of eastern Canada (Ontario and Québec) in relation to the Great Lakes and major Canadian cities. The extent of the Claybelt reflects the extent of glacial Lake Barlow–Ojibway. Study sites are indicated by dark grey circles.

and the retention of larger stems than cutting with protection of small merchantable stems. As a result of both the use of two methods, and the different operators associated with each site the harvest level varied considerably among sites (Table 1) from 45% to 83% (i.e., retention level from 17% to 55%).

Within each silvicultural treatment (partial cut, low-retention) and in the unharvested control, 17 plots were established at randomly selected points in the stands before harvest. Within the largest 11.28-m-radius plots all dead and living trees (>9 cm DBH) were measured (diameter at breast height, height, vigour) and enumerated before and immediately after harvest. The portion of the plot covered by machinery trails was also estimated. Canopy openness and organic layer thickness were also evaluated for each plot. Four 1-m^2 nested quadrats were established inside the 11.28-m plots in which the cover of understory vegetation (vascular plants, and some non-vascular plants) was measured five years post-harvest. The cover of non-plant material (mineral soil, humus, rock, coarse woody debris [by decay class]; see Table 1 for a full list) was also determined in these plots. Species nomenclature follows Marie-Victorin *et al*. (2002) for the vascular plants and Crum and Anderson (1981) for the bryophytes.

Analyses

Initially all sites were included in the analyses. However, as floristic differences among sites masked the effect of treatment, sites were subsequently analysed separately, as has been done in other large-scale analyses of forestry operations (Dovčiak *et al*. 2006). This decision is further supported by the result of Multi-Response Permutation Procedures (MRPP; McCune and Mefford 1999) that showed a 10-fold greater difference among sites then among treatments (Appendix A). Subsequently, analyses were completed on each site individually as they differed in pre-harvest composition, soil characteristics, and partial harvest method.

The use of species habitat groups integrates changes in individual species presence or abundance in order to track community-level changes. In order to determine the impact of partial harvest on the understory community compared to the impact of low-retention harvest and of unharvested control, five species habitat groups were created. These groups are: forest species, bog species, tree seedlings, light pioneers (shrubs that establish and/or expand when the canopy opens), and soil pioneers (species that establish from the soil propagule bank or freshly deposited seeds on newly exposed mineral soil). Species were classified based on information in the *Flore laurentienne* (Marie-Victorin *et al*. 2002), or the experience of the authors (bryophytes). Appendix B lists all species, their occurrence by site and their classification.

Quadrat-level richness (number of species of a species habitat group present within a given quadrat), evenness and Shannon's diversity were calculated. Percent cover of the different species habitat groups was also calculated. For each plot, a mean of the four quadrats was calculated, and the means were then compared among treatments with analysis of variance tests (ANOVA; SPSS v.12.0), followed by Bonferroni's post-hoc test. Only richness and cover were retained as the results for all three indices were similar. β diversity, the number of species per treatment/site, was also calculated using Whittaker's measure $\beta w = (y/a)-1$ where y is total species richness for treatment type, and a is mean species richness per plot (MacDonald and Fenniak 2007).

Similar analyses were completed for the non-plant cover of the 1-m^2 quadrats, i.e., the mean cover of a given material for a plot was calculated and compared among treatments with ANOVA followed by Bonferroni's post-hoc test.

The cover of species that were found in at least 10% of quadrats (i.e., 104 quadrats) was compared among treatment types, all sites mixed together. As these species were by definition common, they were found in all sites thus eliminating the need to look at sites individually. Mixed models were initially tested; however, none of the species fit the requirements of the data (homogeneity of the variances), and non-parametric Kruskal-Wallis tests were used in their place.

In order to balance the merits of detrended correspondence analysis (DCA; Hill 1979, Hill and Gauch 1980) and non-metric multidimensional scaling (NMS; Kruskal 1964), the data were analyzed with both techniques, in order to summarize community response to forest harvest. A series of analyses was carried out on each site independently, using quadrat data. Both techniques gave the same pattern, so only the DCA is presented for ease of interpretation. Only species occurring in a total of five or more quadrats, and only quadrats in which five or more such species were present, were included in the ordination. Habitat variables were passively fitted to the ordination axes as vectors in the ordination diagram (indirect gradient analysis). CANOCO ver. 4 (ter Braak and Šmilauer 1998) was used for DCA ordination, and PC-Ord v. 3.4 (McCune and Mefford 1999) was used for the NMS.

Results

In order to document the impact of the two types of forest harvest on the sites, the cover of the machinery tracks and non-plant material was analyzed. Generally, differences in environmental variables (Table 1) were as would be expected, with increases in trail cover and decreases in canopy cover from unharvested control, to partial cut, to low-retention cut in all sites. In terms of the non-plant composition of the forest floor, partial cuts and low-retention cuts had similar values at Gaudet, with higher covers of litter and branches. However, in Muskuchii and Dufay partial cut values were generally intermediate to unharvested control and low-retention cut values, particularly for branch cover and CWD cover. Few forest floor components differed significantly among treatments at Maïcasagi.

Relationship between community attributes and disturbance severity

Eighty-six species were found in total (Appendix B). While no species were restricted to any one treatment type in the three northern sites, there were 23 species that were found in only one treatment type at Dufay. In Dufay, six species were only found in the unharvested control plots: four forest species, one tree seedling, two light pioneers, and one soil pioneer. Fifteen species were only found in the partial cut plots: eight forest species, two bog species, four tree seedlings, and one soil pioneer. Two light pioneers were only found in low-retention cut plots.

Total richness did not vary significantly among treatment types at any of the sites (Table 2). However, soil and light pioneer richness increased with disturbance at three of the four sites. The only other significant trend in richness was a reduction in tree seedling diversity after either partial cut or low-retention cut in Maïcasagi. β diversity increased in either the partial cut or low-retention cut in three of the four sites.

Relationship between community composition and disturbance severity

At all four sites there was a consistent pattern of increased range in values of quadrats with increasing disturbance severity, generally on the second axis (Fig. 2 to Fig. 5). Soil and light pioneer species were clustered in association with the partial cut and low-retention cut plots in all four ordinations, specifically with the low-retention plots, except for Dufay where they were clustered with the partial cut plots. Tree seedlings were generally found associated with the partial cut and low-retention cut plots, while bog and forest species were found throughout the diagrams.

Individual species varied little in their percent cover among harvest types (Table 3). Only seven of 17 species that were frequent enough to be analyzed had significant differences in their percent cover among the treatments. Of these *Cladina rangifera* Nyl.*, Kalmia angustifolia* L. and *Vaccinium myrtilloides* Michx. all had higher percent cover in the partial cut plots than in the unharvested control or low-retention cut plots. *Picea mariana* and the non-vascular species (*Pleurozium schreberi, Ptilium crista-castrensis* De Notaris) decreased in harvested plots. Finally, *Cornus canadensis* L. cover increased with increasing disturbance severity.

Environmental variables associated with harvest (litter, branch, trail, CWD1) were all correlated with community patterns in the four sites (Fig. 2 to Fig. 5). These variables were associated with the spread of partial cut and low-retention cut plots, while percent cover was correlated with the control plots. Variables that were not related to harvest were also important—particularly organic layer thickness—in all sites.

Table 2. Treatment level β diversity, and plot level mean species richness (SE) by species guild for the four sites and three treatments. Significant differences among treatments within a site are indicated by letters (b > a).

Site	β div	Total richness	Forest	Bog	Tree	Soil	Light
Gaudet							
control	2.38	10.06 (0.36)	4.48 (0.21)	2.33 (0.23)	0.94 (0.06)	0.15 (0.06)	1.83 (0.06)
partial cut	3.62	10.18 (0.41)	4.96 (0.24)	1.84 (0.21)	0.94 (0.08)	0.19 (0.05)	1.79 (0.08)
low-ret cut[a]	3.70	10.00 (0.35)	5.19 (0.25)	1.43 (0.15)	0.85 (0.08)	0.41 (0.08)	1.94 (0.69)
Muskuchii							
control	8.33	7.03 (0.22)	4.91 (0.20)	0.10 (0.02)	0.64 (0.05)	0.21 (0.04)a	0.49 (0.06)a
partial cut	8.70	7.36 (0.17)	4.52 (0.14)	0.08 (0.02)	0.63 (0.04)	0.38 (0.53)ab	0.85 (0.05)b
low-ret cut[a]	8.91	7.41 (0.20)	4.79 (0.16)	0.08 (0.02)	0.68 (0.05)	0.91 (0.07)b	0.80 (0.06)b
Maïcasagi							
control	4.04	8.67 (0.25)	4.74 (0.21)	1.03 (0.12)	1.00 (0.08)b	0.13 (0.04)a	1.57 (0.08)ab
partial cut	4.09	9.03 (0.23)	4.66 (0.18)	1.22 (0.20)	0.54 (0.06)a	0.24 (0.06)a	1.75 (0.07)b
low-ret cut [a]	5.36	8.02 (0.33)	4.27 (0.24)	0.58 (1.36)	0.50 (0.07)a	0.63 (0.13)b	1.31 (0.12)a
Dufay							
control	6.50	6.69 (0.42)	4.42 (0.30)	0.23 (0.08)	0.87 (0.11)	0.21 (0.05)	0.25 (0.06)
partial cut	7.48	7.62 (0.40)	4.48 (0.29)	0.33 (0.12)	1.08 (0.12)	0.71 (0.12)	0.10 (0.05)
low-ret cut [a]	5.95	6.21 (0.33)	3.28 (2.69)	0.29 (0.08)	1.04 (0.12)	0.31 (0.07)	0.10 (0.06)

[a]low-retention cut

Table 3. Abundance (mean ± SE of plots of all sites) of common species in three treatment types. P-values for Kruskal-Wallis H test are given. Species in bold have significant differences at the p = 0.05 level.

Species	Control	Partial cut	Low-retention cut	*P*
Abies balsamea	3.20 ± 0.81	2.29 ± 0.81	3.58 ± 0.92	0.063
Cladonia rangifera	**13.67 ± 2.88**	**17.99 ± 2.88**	**7.14 ± 1.38**	**0.033**
Clintonia borealis	1.04 ± 0.19	1.02 ± 0.16	1.33 ± 0.21	0.916
Coptis groenlandicum	3.51 ± 0.90	3.51 ± 1.05	4.53 ± 0.93	0.487
Cornus canadensis	**11.90 ± 1.97**	**14.10 ± 1.76**	**23.51 ± 2.57**	**0.009**
Dicranum polysetum	7.16 ± 1.16	7.66 ± 1.16	6.93 ± 0.85	0.929
Kalmia angustifolia	**19.29 ± 2.44**	**25.36 ± 2.95**	**11.93 ± 1.86**	**0.003**
Linnaea borealis	2.71 ± 0.79	2.63 ± 0.58	3.97 ± 0.95	0.413
Maianthemum canadensis	8.92 ± 1.49	6.35 ± 1.26	6.58 ± 1.42	0.421
Picea mariana	**18.19 ± 1.86**	**13.88 ± 1.44**	**12.49 ± 1.92**	**0.009**
Pleurozium schreberi	**57.72 ± 3.16**	**53.83 ± 3.18**	**43.49 ± 2.74**	**0.006**
Ptilium crista-castrensis	**7.29 ± 1.55**	**1.85 ± 0.57**	**2.34 ± 0.57**	**0.001**
Ptillidium ciliare	9.06 ± 1.66	11.60 ± 1.90	8.26 ± 1.48	0.578
Rhododendron groenlandicum	28.58 ± 4.02	29.10 ± 4.02	23.45 ± 3.46	0.734
Sphagnum capillifolium	5.92 ± 1.17	8.80 ± 1.78	7.72 ± 1.66	0.878
Vaccinium angustifolium	18.56 ± 2.26	28.32 ± 3.11	23.89 ± 2.51	0.227
Vaccinium myrtilloides	**11.20 ± 2.54**	**18.58 ± 2.61**	**12.92 ± 1.63**	**0.003**

However, these relationships were relatively weak with the amount of the species variation explained by the environmental variables ranging from 5% and 8% in Gaudet and Muskuchii to 13% and 20% in Maïcasagi and Dufay.

Discussion

Overall species richness and forest species plot-level richness did not vary among treatments in any site. Several other studies have documented the neutral effect of forest harvest on plot level richness (Deal 2001, Kern *et al.* 2006, MacDonald and Fenniak 2007, Kembel *et al.* 2008) and the influence of time since disturbance on the evolution of species richness (Tellier *et al.* 1995). In contrast, β diversity increased from unharvested control, partial cut, to low-retention cut plots in three of the four sites. While forest harvest has previously been shown to have a homogenizing effect on the understory (MacDonald and Fenniak 2007), the inherently uneven nature of the harvests in our sites, (the low-retention cut is carried out in strips), result in a greater heterogeneity in the community at the treatment level as was found by Scheller and Mladenoff (2002).

In contrast to richness, composition did vary among the treatments. While the details of the response of the understory vegetation vary among the sites, some overall trends can be found in all sites, particularly in terms of species richness and community composition. These trends follow the model proposed by Roberts (2007), where the response in the herbaceous layer is dependant in part on the severity of the disturbance as defined along three axes: % forest canopy removed, % understory vegetation removed, and % forest floor soil dis-

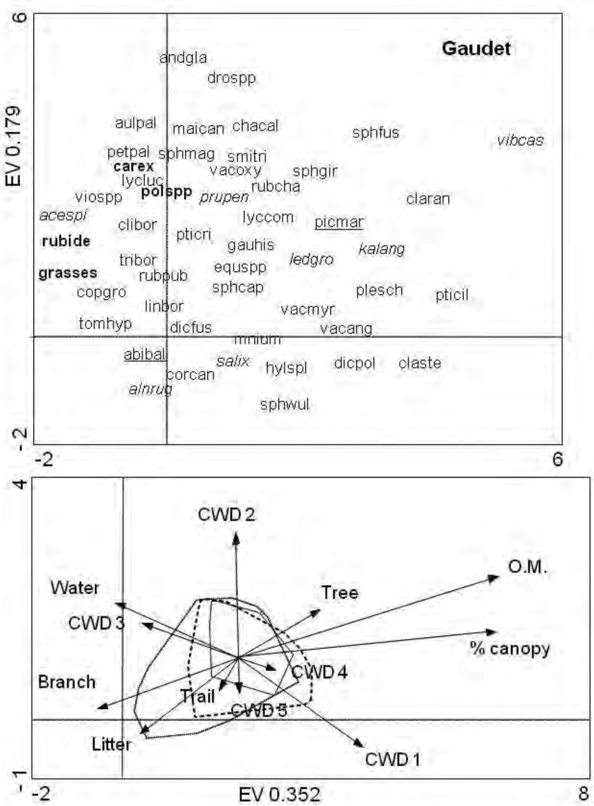

Fig. 2. Detrended Correspondence Analysis (DCA) plots of the first two axes for Gaudet, represented by two plots. In the upper plot, species plot with the species habitat groups indicated by font (forest and bog species, normal font; tree seedlings, underlined; light pioneers, italics; soil pioneers, bold). Refer to Appendix B for species abbreviations. In the lower plot, the spread of the plots of each treatment type is indicated by the polygons (control, solid line; partial cut, dashed line; low-retention cut, dotted line). Vectors indicate the strength and the direction of correlation between the spread of the plots and habitat variables. Eigenvalues are indicated for each axis on the left hand plot. Total inertia for Gaudet is 3.01. The amount of variation in the species plot explained by the environmental variables for each site is 8%.

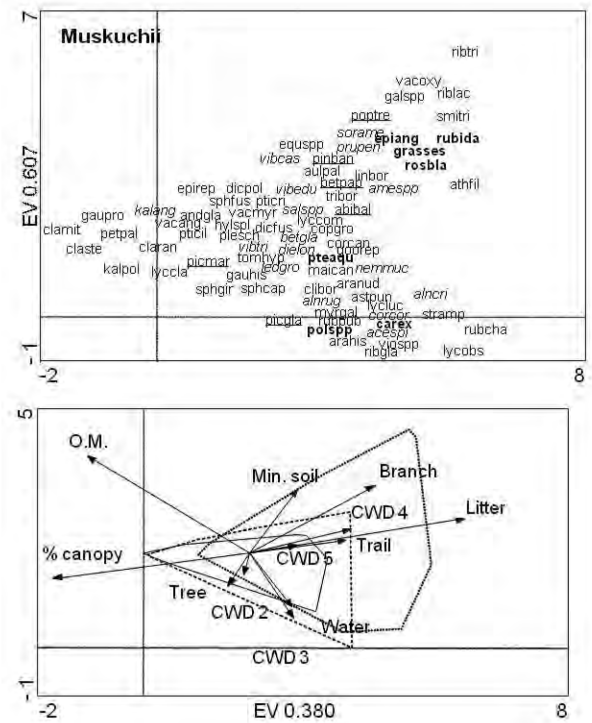

Fig. 3. Detrended Correspondence Analysis (DCA) plots of the first two axes for Muskuchii, represented by two plots. For a detailed description of legends see Fig. 2. Total inertia for Muskuchii is 8.95. The amount of variation in the species plot explained by the environmental variables for each site is 5%.

turbed and removed. At all four sites disturbance severity increased along these axes from control to partial cut to low-retention cut, with less canopy cover, more litter and branches covering the soil, and more exposed mineral soil in low-retention cut plots than in partial cut plots. The impact of these factors will be examined in further detail.

Response of the community to forest soil disturbance and removal of the understory

Differences in community composition among the three treatments at the four sites reflect the dominant role of soil disturbance in determining community response to forest harvest disturbance. The richness and cover of soil pioneer species increased in partial cut and low-retention plots in nearly all sites, and soil pioneer species were associated with low-retention cut plots in the ordinations. This is consistent with both Robert's (2007) model and previous studies that have linked soil disturbance to increased richness and cover of "invader" species (Beese and Bryant 1999, Haeussler *et al.* 2002, Berger *et al.* 2004, Zenner and Berger 2008). At Dufay, soil pioneer species richness and cover were higher in the partial cut plots than in the low-retention plots. This may have been due to the slightly thinner organic layer present in the partial cut plots than in the low-retention cut plots at this site five years after the harvest.

Despite the shift in community composition to include pioneer species in low-retention cut plots, overall their cover was very low in all sites. This is in contrast to other studies examining the impact of forest harvest on the understory vegetation that noted a dramatic increase in invader species cover (disturbance species reached nearly 20% cover in clearcut and site-prepared stands in southern New Brunswick [Roberts and Zhu 2002]). The relatively small invasion or expansion of these species in our study is probably due to three factors that reduced the level of soil disturbance during and after forest harvest. Firstly, all sites have relatively thick forest floors (11–52 cm) that would attenuate the impact of forest harvest equipment. This is particularly true of the paludified sites, Gaudet and Maïcasagi, where forest floor thickness exceeded 30 cm and harvests were thus carried out during late fall and winter when the soil was frozen and/or covered in snow, offering additional protection (Berger *et al.* 2004, Kembel *et al.* 2008, Zenner and Berger 2008). The variation in the understory community was lower overall in these two sites (smaller total inertia) compared to Muskuchii and Dufay

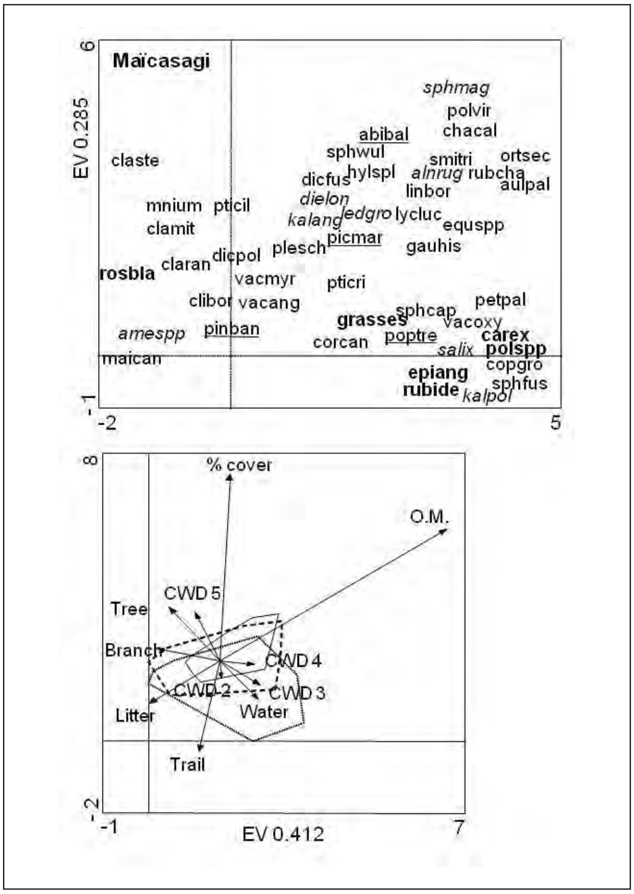

Fig. 4. Detrended Correspondence Analysis (DCA) plots of the first two axes for Maïcasagi, represented by two plots. For a detailed description of legends see Fig. 2. Total inertia for Maïcasagi is 3.94. The amount of variation in the species plot explained by the environmental variables for each site is 13%.

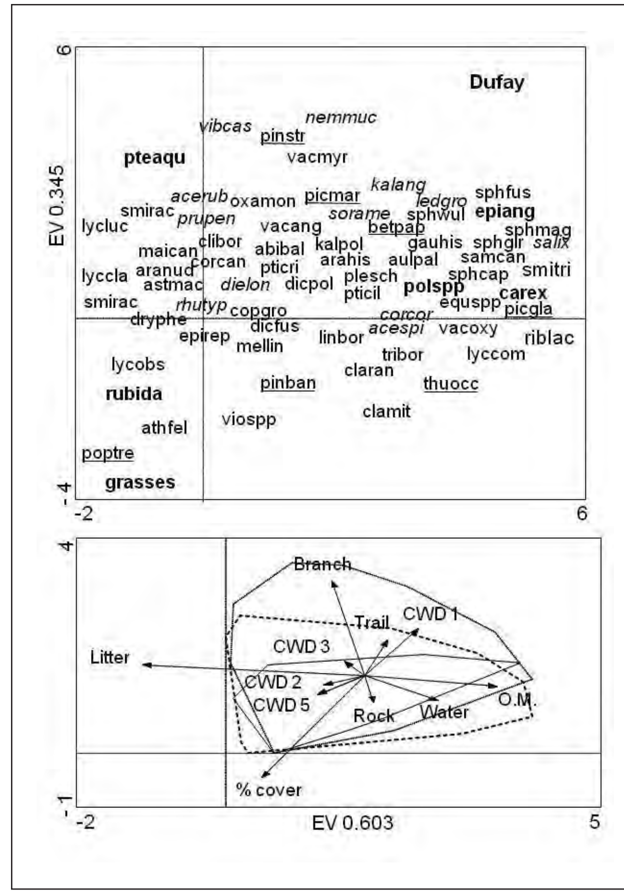

Fig. 5. Detrended Correspondence Analysis (DCA) plots of the first two axes for Dufay, represented by two plots. For a detailed description of legends see Fig. 2. Total inertia for Dufay is 5.46. The amount of variation in the species plot explained by the environmental variables for each site is 20.8%.

where the soils are thinner and harvests were carried out in the summer. Secondly, the type of low-retention cut practised in Quebec reduces soil disturbance, by its nature. The norms for CPRS, ("cut with protection of regeneration and soils") require that machinery trails be widely spaced and that "soft-spots" are avoided. Consequently, less soil is disturbed and pioneer species have less space for establishment, reducing their diversity and cover. Finally, landscape scale factors may have limited the establishment of pioneer and invasive species (Halpern *et al.* 2005, Kern *et al.* 2006), as our study sites are found within a forest matrix that has only recently been subjected to industrial forestry (<50 years), and therefore the presence of pioneer or invasive species is minimal.

Response of the community to removal of the canopy cover

The response of the understory community to canopy cover removal varied among sites and treatments. Generally, richness and cover of light pioneer species increased in partial cut and low-retention cut plots, although only significantly in Muskuchii and Maïcasagi. Interestingly, contrary to what would be predicted by Robert's (2007) disturbance model, cover and richness of forest floor species varied little among treatments, even the low-retention cut, and only in Dufay were several typical forest species absent from low-retention plots. Bryophytes may be particularly sensitive to this factor, as indicated by the drop in cover in two dominant bryophytes: *Pleurozium schreberi* (moss) and *Ptillidium ciliare* (L.) Hampe (liverwort). The relatively higher sensitivity of bryophytes to changes in micro-climate has been well documented in the literature (Fenton and Frego 2005, Hylander *et al.* 2005, Dovčiak *et al.* 2006) and these species may be the best indicator of microclimatic change after forest harvest.

Previous studies have documented the apparently large tolerance window of many boreal species to incident light intensity and ambient air temperature (Brumelis and Carleton 1989, Bergstedt and Milberg 2001, Kembel *et al.* 2008). This is in contrast to studies in other forest ecosystems where removing significant amounts of the canopy cover results in significant changes in the understory (Deal 2001, Halpern *et al.* 2005, Dovčiak *et al.* 2006, Macdonald and Fenniak 2007, Smith *et al.* 2008). While growth form (typically facultative stress tolerators [Brumelis and Carleton 1989] or generalist endurers [Kembel *et al.* 2008] in the boreal zone) is frequently evoked to explain the ability of many of these boreal species to withstand microclimatic changes associated with forest harvest, the character of the forest before harvest may ultimately explain the sensitivity of the understory community to overstory removal. Boreal forests are dominated by stand-replacing disturbances, but also experience gap disturbances in regions that have long fire cycles. As a result, they alter between very open (establishment and over-mature) and very dense (stem-exclusion stage) canopies. Consequently, the vast majority of the perennial species were exposed to a wide variety of light conditions. De Grandpré and Bergeron (1997) found similar results in mixed forest stands in the southern boreal forest. In contrast, hardwood forests (for example, northern hardwoods or west coast conifer or mixedwood) tend to be dominated by small gap disturbances and therefore tend to have a relatively constant microclimate. Consequently, the species present are not required to tolerate a wide variety of microclimatic conditions, and they are more vulnerable to large fluctuations in canopy cover.

Implications for management

In this study, partial cuts compared to low-retention cuts disturbed the soil less, removed less of the overstory and consequently had less impact on the understory community, suggesting that the partial cuts were successful in retaining characteristics of old-growth forests. While partial cuts always resulted in a community composition different from unharvested control, sites harvested in the summer months, with thinner organic layers (Muskuchii and Dufay) saw the greatest shifts. Partial cuts carried out in the winter would then be expected to result in the least disturbance to the community. Furthermore, the very minimal response of the understory community to microclimatic change suggests that in these naturally relatively open forests, protection of the soil is more important than limiting overstory removal. However, caution should be used in applying these results to forests that are not open black spruce stands, as is suggested by the results from Dufay. This most southern site had the most mixed composition before harvest, and was also where the pre- and post-harvest communities differed the most, including several species that were extirpated from the site.

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Appendix A

Analyses of the composition of all four sites simultaneously by detrended correspondence analysis (DCA) and nonmetric multidimensional scaling (NMS; only DCA is illustrated for simplicity) indicated that the variation among sites was such that all impacts of the harvest was lost. Fig. A1 the sites Gaudet and Maïcasagi are clustered on the left of the diagram while the spread of the sites Dufay and Muskuchii includes the spread of Gaudet and Maïcasagi and the rest of the ordination space.

When the same DCA is plotted with silvicultural treatments illustrated instead of sites, it is obvious that any differences in individual sites among treatments was completely masked by the differences among sites (Fig. A2)

Multi-Response Permutation Procedures (MRPP; McCune and Mefford 1999) indicated the same pattern with an A value ten times higher among sites than among treatments (A = 0.08 vs. 0.008, $p < 0.001$ in both cases).

Both of these results indicated that community level response could not be measured by analysing all sites together.

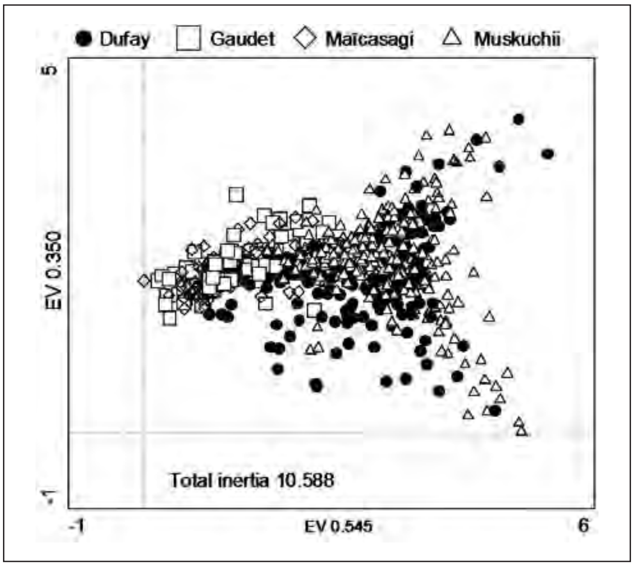

Fig. A1. DCA of all four sites. Plots of individual sites are indicated by different symbols.

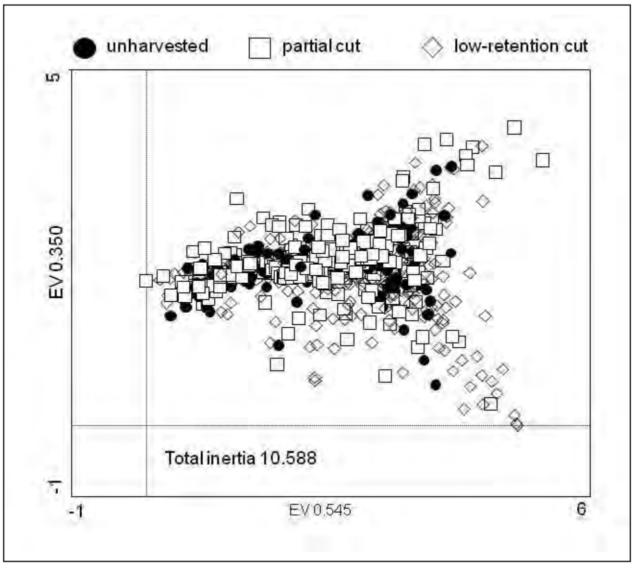

Fig. A2. DCA plot of all four sites. Different silvicultural treatments are illustrated with different symbols.

Appendix B

List of species found in the five year post harvest surveys. The code used in the DCA figure, habitat group and frequency in the four sites is listed.

Species	Code	Species habitat group	Gaudet	Muskuchii	Maïcasagi	Dufay
Andromeda glaucophylla	andgla	bog	1	8	–	–
Aster puniceus	astpun	bog	–	1	–	–
Aulacomnium palustre	aulpal	bog	8	3	5	–
Chamaedaphne calyculata	chacal	bog	36	1	16	–
Drosera spp.	drospp	bog	4	–	–	–
Kalmia polifolia	kalpol	bog	1	2	18	1
Myrica gale	myrgal	bog	–	3	–	–
Rubus chammaemorus	rubcha	bog	36	6	17	–
Smilacina trifolia	smitri	bog	22	3	28	3
Sphagnum fuscum	sphfus	bog	33	2	5	6
Sphagnum magellanicum	sphmag	bog	28	–	11	6
Sphagnum wulfianum	sphwul	bog	8	–	4	1
Tomenthypnum nitens	tomnit	bog	3	7	–	–
Vaccinium oxycoccos	vacoxy	bog	70	2	15	1
Aralia hispida	arahis	forest	–	3	–	5
Aralia nudicaulis	aranud	forest	–	34	–	5
Aster macrophyllus	astmac	forest	–	–	–	2
Athyrium filix-femina	athfil	forest	1	4	–	4
Clintonia borealis	clibor	forest	11	115	3	48
Coptis groenlandica	copgro	forest	15	67	2	27
Cornus canadensis	corcan	forest	45	318	52	35
Dicranum fuscescens	dicfus	forest	14	75	18	60
Dicranum polysetum	dicpol	forest	27	185	66	85
Dryopteris disjuncta	drydis	forest	1	–	–	–
Dryopteris phegopteris	dryphe	forest	–	–	–	1
Epigaea repens	epirep	forest	–	15	–	1
Equisetum spp.	equspp	forest	102	6	62	2
Galium spp.	galspp	forest	–	1	–	–
Gaultheria hispidula	gauhis	forest	138	21	95	27
Gaultheria procumbens	gaupro	forest	–	1	–	–
Goodyera repens	goorep	forest	–	2	–	1
Hylocomium splendens	hylspl	forest	13	10	27	1
Linnaea borealis	linbor	forest	12	89	4	10
Lycopodium complanatum	lyccom	forest	1	1	–	1
Lycopodium lucidulum	lycluc	forest	17	33	15	2
Lycopodium obscurum	lycobs	forest	–	11	–	7
Lycopodium clavatum	lyccla	forest	–	8	–	1
Maianthemum canadensis	maican	forest	25	183	5	39
Melampyrum lineare	mellin	forest	–	1	–	2
Mnium spp.	mnium	forest	2	–	1	–
Orthilia secunda	ortsec	forest	–	–	1	–
Oxalis Montana	oxamon	forest	–	–	–	3
Petasites palmatus	petpal	forest	1	4	4	–
Pleurozium schreberi	plesch	forest	154	430	168	77
Polygonatum pubescens	polpub	forest	–	–	–	2
Polypodium virginianum	polvir	forest	–	–	1	–
Ptilium castrensis	pticri	forest	4	81	33	2
Ptillidium cilare	pticil	forest	68	120	65	21
Ribes glandulosum	ribgla	forest	–	7	–	–
Ribes lacustre	riblac	forest	–	13	–	1
Ribes triste	ribtri	forest	–	1	–	–
Rubus pubescens	rubpub	forest	6	8	–	–
Smilacina racemosa	smirac	forest	–	–	–	1
Sphagnum capillifolium	sphcap	forest	116	5	58	25
Sphagnum girgensohnii	sphgir	forest	91	5	66	24
Streptopus amplexifolius	stramp	forest	–	7	–	–
Trientalis borealis	tribor	forest	6	80	–	2
Vaccinium angustifolium	vacang	forest	54	326	108	76
Vaccinium myrtilloides	vacmyr	forest	84	189	74	39
Viola spp.	viospp	forest	6	8	–	4

Species	Code	Species habitat group	Gaudet	Muskuchii	Maïcasagi	Dufay
Cladina mitis	clamit	forest	–	57	17	2
Cladina rangiferina	claran	forest	53	175	64	21
Cladina stellaris	claste	forest	7	66	11	–
Acer spicatum	acespi	light	1	9	–	8
Acer rubrum	acerub	light	–	–	–	7
Alnus crispa	alncri	light	–	9	–	–
Alnus rugosa	alnrug	light	31	8	15	–
Amelanchier spp.	amespp	light	–	21	2	1
Betula glandulosa	betgla	light	–	1	–	–
Corylus cornuta	corcor	light	–	3	–	6
Diervilla lonicera	dielon	light	–	17	2	4
Kalmia angustifolia	kalang	light	135	117	122	54
Rhododendron groenlandicum	ledgro	light	177	51	147	25
Nemopanthus mucronatus	nemmuc	light	–	1	–	11
Prunus pensylvanica	prupen	light	1	35	–	2
Rhus typhina	rhutyp	light	–	–	–	2
Salix spp.	salix	light	3	40	6	3
Sambucus racemosa	samrac	light	–	–	–	2
Sorbus americana	sorame	light	–	4	–	5
Viburnum cassinoides	vibcas	light	1	19	–	11
Viburnum edule	vibedu	light	–	1	–	–
Viburnum trilobum	vibtri	light	–	1	–	–
Carex spp.	carex	soil	24	23	23	20
Epilobium angustifolium	epiang	soil	–	88	4	3
Grasses	grasses	soil	4	60	3	1
Polytrichum spp.	polspp	soil	17	44	22	11
Pteridium aquilinum	pteaqu	soil	–	10	–	22
Rosa blanda	rosbla	soil	–	29	1	–
Rubus idaeus	rubida	soil	4	18	2	4
Abies balsamea	abibal	tree	39	35	27	49
Betula papyrifera	betpap	tree	–	69	–	37
Picea glauca	picgla	tree	–	1	–	4
Picea mariana	picmar	tree	132	204	105	51
Pinus banksiana	pinban	tree	–	44	1	2
Pinus strobus	pinstr	tree	–	–	–	6
Populus tremuloides	poptre	tree	–	30	1	1
Thuja occidentalis	thuocc	tree	–	–	–	1