



Effects of small canopy gaps on boreal mixedwood understory vegetation dynamics

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Abstract: Boreal mixedwood understory communities are highly dynamic because they are simultaneously influenced by canopy succession, small-scale environmental variation and disturbances. In such a system, fire initiates succession but canopy gaps, resulting from spruce budworm outbreaks or other disturbances, also affect forest dynamics during succession. In this study, we assessed the short-term response of understory communities along a canopy gap severity gradient in mature and old-growth forest stands. The objective was to determine if resource heterogeneity is driving understory community composition and diversity. We created artificial gaps of varying severities in stands of two late successional forest stages. Four treatments, i.e., total cut, conifer cut, girdling of conifers and a control treatment, were each applied over an area of 100 m² and replicated three times in both types of forest stands. The cover of each understory species was measured before treatment application and 1, 2 and 11 years following it, in seven 1 m² plots per replicate. Percent transmission of photosynthetic photon flux density and soil temperature were also measured on different occasions after the beginning of the experiment. Species richness, alpha diversity and total cover all increased following gap creation, and this increase was sustained up to 11 years. Increases were more pronounced in total cut than in other treatments. The increase in species richness and diversity was also more pronounced in old-growth stands, while total cover increase was greater in mature stands. Gap creation resulted in significant changes in abundance patterns that were associated with the resident species assemblages. The magnitude of changes in community composition did not significantly differ between mature and old-growth forests and differences in species composition among stands were maintained following gap creation. This study supports the evidence that resource heterogeneity resulting from small-scale disturbances will contribute to maintaining diversity among understory communities by allowing species more typical of early-successional communities to coexist with species from late-successional ones. Such a process may be essential for maintaining the species pool likely to re-invade the stands following major disturbances.

Nomenclature: Marie-Victorin (1995). ~~NOT NEEDED IF AUCTORS ARE GIVEN~~

Introduction

The boreal forest is highly dynamic and canopy change, although being predictable by tree life history strategies (Noble and Slatyer 1980), is greatly influenced by disturbances that occur throughout the course of succession (Bergeron and Charron 1994, Kneeshaw and Bergeron 1998). Such disturbances can either accelerate successional changes or allow early successional species to increase their abundance in the stand. As in the case of the canopy, boreal understory communities are dynamic and vary with overstory successional changes (Gilliam and Roberts 2003, Hart and Chen 2008), fine scale differences in environmental conditions (Økland and Eilertsen 1996, Rydgren et al. 1998, Økland 2000) and time since last disturbance (De Grandpré et al. 1993). These processes affect understory composition and diversity along different spatial and temporal scales. In a recent review,

Bartels and Chen (2010) argued that both resource heterogeneity and quantity were structuring understory species diversity but at different stages of forest development and in the presence of intermediate disturbances. They hypothesized that resource heterogeneity, resulting from intermediate disturbances, would be the main driver of understory diversity in older successional communities.

In the mixedwood boreal forest, although fire is the main disturbance initiating succession (Bergeron 1991), gap creation resulting from spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreaks or other small-scale disturbances is an important process driving understory community changes (Kneeshaw and Bergeron 1998, Kneeshaw et al. 1998, De Grandpré et al. 1993). Canopy gaps, depending on their size, affect resource availability in the understory environment by locally increasing light transmission, soil temperature, and nitrogen mineralization rates (Hart and Chen

2006), thus increasing resource heterogeneity at the stand level. Response of understory vegetation communities to small-scale disturbances will depend on the stand successional status (De Grandpré and Bergeron 1997), the severity of the disturbance, site conditions, and initial understory composition (Roberts 2004).

Commonly, these changes result in increased abundance of the resident assemblages present in the site (Halpern 1989, De Grandpré and Bergeron 1997, Kembell et al. 2005), while some early successional species could colonize some large gaps (Hughes and Fahey 1991). It has been suggested that large gap creation throughout the course of succession could be a determining factor in ensuring the maintenance of many understory boreal species, allowing some species to persist longer in the understory and some others to invade the openings (Jonsson and Esseen 1990, De Grandpré and Bergeron 1997). However, only the short-term response (1 or 2 years) of understory vegetation following small-scale disturbances has been assessed, and little is known on the longer term effects of such disturbances on understory community dynamics.

The objective of this study was to assess understory community response (1, 2 and 11 years), in terms of change in diversity and composition, following the creation of artificial canopy openings of different severities. The openings aim to emulate the gap creation resulting from spruce budworm outbreaks occurring in such forests. Our hypotheses are that: 1) the majority of changes in understory community will occur in the first 2 years and we should observe a return towards original conditions 11 years after gap creation; 2) the disturbance severity (canopy removal) effect will differ according to the variable measured (richness, alpha diversity, total cover) and the extent of compositional changes should increase along the severity gradient while beta diversity should be highest in the less severe disturbance; 3) the successional status of the forest will be an important predictor of changes in composition and diversity patterns: the understory of mature forests will experience less changes following gap creation than that of older forests. As forests develop in the absence of disturbances, understory community composition converges towards the dominance of late successional species, which have weak resilience to sudden changes in environmental conditions. Changes in understory light conditions and soil temperature are assessed in parallel as drivers of community changes.

Methods

Study area

The study was conducted in the mixedwood boreal forest of Quebec, along the shores of Lake Duparquet, in the Abitibi region, in the white birch-balsam fir ecoregion (Saucier et al. 1998). The closest meteorological station is located 35 km north of Lake Duparquet. Mean annual temperature is 0.7°C (highest is July with 16.9°C and lowest is January with -18.2°C), mean annual precipitation is around 890 mm with 70% as rainfall, and the number of frost-free days is 64 per

year (Environment Canada 2005). The sampling sites belong to a vast physiographic region, created from lacustrine deposits of the proglacial lakes Barlow and Ojibway between 10,000 and 8,000 yrs BP (Veillette 1994).

In the Lake Duparquet area, fire has played a major role in structuring successional plant communities. Fire cycle length has been reported to be >100 years (Bergeron 1991). After fire, tree communities are mostly dominated by shade intolerant and deciduous species such as *Populus tremuloides* Michx., *Betula papyrifera* Marsh. and the conifer *Picea glauca* Moench. (Bergeron and Dubuc 1989), although conifers *Abies balsamea* L. and *Thuja occidentalis* L. also invade those sites successfully. After 100 to 150 years, *Abies balsamea* (dominant) and *Thuja occidentalis* (co-dominant) are the main components of the tree layer. These *Abies* communities are susceptible to attacks by the spruce budworm, resulting in tree death and the creation of canopy gaps. From the beginning of the 20th century, three major outbreaks have been reported in the study region (Morin et al. 1993); the last one occurred between 1970 and 1987.

Understory succession is closely associated with overstory changes. Species such as *Acer spicatum* Lamb., *Aster macrophyllus* L. and *Aralia nudicaulis* L. usually dominate in the understory of *Populus* stands. As conifers increase in the canopy, shade tolerant understory species become more frequent and diversity increases. *Clintonia borealis* (Ait.) Raf., *Streptopus roseus* Michx., *Linnaea borealis* L. and *Ribes* spp. are typical of these communities. Finally, when *Abies balsamea* eventually dominates the canopy, light penetration in the understory decreases and species such as *Taxus canadensis* (Marsh.) dominate in the understory. Species diversity in these forests is low and can only increase when canopy openings are created through disturbance.

Sampling

From the communities resulting from the eight most important fire dates identified in the area (1760, 1816, 1823, 1847, 1870, 1916, 1944, 1964; Bergeron 1991, Dansereau and Bergeron 1993), we selected two: one originating after the fire of 1870 (stand age of 122 yrs in 1992) and one originating after the fire of 1760 (stand age of 232 yrs in 1992). The forest that burned in 1870 was, in 1992, in transition from a deciduous to a coniferous composition and will be named "mature forest" hereafter. The canopy was dominated in 1992 by *Populus tremuloides*, *Picea glauca* and *Abies balsamea* (Table 1). The 1760 forest is one of the oldest successional communities of this area and is dominated by *Abies balsamea* and *Thuja occidentalis*. Because it possesses many of the characteristics of an old-growth forest (dominance of shade tolerant trees, presence of snags and coarse woody debris, uneven-sized tree distribution), it will be called "old-growth forest" hereafter.

In each of the two stand ages, four treatments were replicated within three blocks (of >625 m²) in a stratified random design, where a minimum of 5 m (usually > than 10 m) separated the different treatments. In total, we had 24 plots of

Table 1. Initial overstory composition and basal area removed or girdled in each treatment for the two stand types. Standard deviations are in parentheses.

Stands	Initial composition (%)					Basal area removed or girdled (m ² /ha)		
	<i>Abies balsamea</i>	<i>Betula papyrifera</i>	<i>Picea glauca</i>	<i>Populus tremuloides</i>	<i>Thuja occidentalis</i>	Girdling	Conifer cut	Total cut
Old-growth	52.5 (26.3)	3.1 (10.8)	9.7 (19.5)	2.7 (6.6)	32.0 (29.9)	21.2 (13.4)	17.6 (6.1)	38.5 (9.3)
Mature	9.2 (6.8)	7.6 (6.8)	25.6 (21.2)	57.5 (18.7)	0.2 (0.7)	8.0 (2.9)	14.7 (7.8)	41.0 (11.5)

100 m² corresponding to 2 stand ages × 4 treatments × 3 blocks. The treatments were designed to emulate different severities of canopy disturbance. From the most severe to the least, the treatments were: 1) total cutting, where all trees were cut and removed from an area of 100 m², 2) cutting and removal of all coniferous trees, with the exception of *Thuja occidentalis* (not a host of the spruce budworm), 3) “girdling” (> 1-cm-deep cut around the trunk circumference using a chain saw) of all coniferous trees, also with the exception of *Thuja occidentalis* (the purpose was to simulate the effect of a spruce budworm outbreak where trees died but remain standing for a certain period of time (Bergeron et al. 1995)), and 4) a control where no intervention was done. The treatments were applied in late spring of 1992, before the beginning of the growing season. Table 1 shows initial composition and removed basal area for each stand age and each treatment.

Within each 100-m² plot, seven 1-m² permanent subplots were selected randomly within two intersecting transects, one running N-S and the other E-W. In order to cover a maximum of environmental condition variability, each transect extended a few meters outside the actual size of each plot (from 3 to 5 m). In northern latitudes, the light environment outside the actual gap projection will be affected by gap creation. Subplots were separated from each other by 1 to 3 m. In each subplot, the cover (%) of each herbaceous and shrub species was estimated according to the following classes: 1) 0-1%; 2) 1-5%; 3) 5-25%; 4) 25-50%; 5) 50-75%; 6) 75-99% and 7) 100%. Species were assigned to four different categories following Rowe (1983): endurers, avoiders, evaders and invaders (see Appendix S1 in Supporting Information). Briefly, “invaders” (pioneers with high seed production and highly dispersed) and “evaders” (species evading fire by storing propagules in the soil or in the canopy) are present in early succession. “Evaders” were separated into two groups whether they were present before gap creation (shade tolerant) or most probably germinated from buried seeds afterwards, as they were not present in the stands before treatment application (shade intolerant). “Endurers” can be present at early or intermediate stages of the succession as they take advantage of the new resources by resprouting from stems or any belowground organs. They usually survive fire and resprout vigorously afterwards. “Avoiders” are shade tolerant species that would be more likely found in cool and moist environments, characteristic of the later stages of succession. Although Rowe’s reproductive strategy was described according to fire, we wanted to assess how gap creation could influence the persistence of species within each group along the successional sequence, and thus eventually

contribute to post-fire regeneration. Sampling was conducted during the summers of 1992, 1993, 1994 and 2003. Most plants were identified to the species, although some species were grouped to the genus as they were rarely encountered (e.g., *Amelanchier*, *Viola* and *Prunus*).

Soil temperature at 15 cm depth was measured three times in summer 1993 (mid-June, early July and late August) and one time in mid-September 2003, at three different locations in the 100-m² plot. The transmission of photosynthetic photon flux density (%PPFD) was measured following the method described in Parent and Messier (1996) under completely overcast sky conditions. The measurements were taken in five 1-m² subplots per 100 m² plots during the growing season in 1992 and in 12 1-m² subplots in 2003. Percent of PPFD was determined at 1 m above the ground using a light sensor (LI-190SA point quantum sensor, LICOR, Lincoln, Nebraska, USA) linked to a data logger (LI-1000, LICOR, Lincoln, Nebraska, USA) and was compared with measurements in an open area nearby. Percent PPFD of subplots was calculated as a percentage of open area PPFD. Soil humidity and ammonium were also measured during the first two years of the experiment, but since these variables did not differ between treatments, the results were not shown.

Data analysis

Response in species richness, diversity and total cover. Species richness (S = total number of species), Shannon-Wiener diversity index ($H = -\sum c_i \ln c_i$, where c_i is the proportional cover of the i th species in the subplot or plot) and total cover (% - sum of all species’ cover class median) were calculated for each 1-m² subplot and each 100-m² plot for each sampling year (1992, 1993, 1994 and 2003). Beta diversity was calculated by converting the diversity index’s gamma and alpha components to number equivalents and dividing, as suggested by Jost (2007): $H_\alpha = \exp(H_\alpha) / \exp(H_\alpha)$, where $\exp(H_\alpha)$ is the exponential of the Shannon-Weiner diversity index for the subplot, and $\exp(H_\alpha)$ is the average of the exponential of the Shannon-Weiner diversity index of subplots of the same plot.

Changes in richness, diversity and total cover among treatments and stand ages were tested based on a mixed model for repeated nested designs (MIXED procedure; SAS Institute Inc. 2002). The model included fixed effects for treatments, stand age, years and their interactions, and random effects for blocks within stand age, for subplot within treatment, block and stand age, for treatment × block within stand age and for the interaction between year and subplot within treatment, block and stand age. The latter was the re-

Table 2. Mixed model for repeated measures analyses on understory species richness, Shannon-Wiener diversity index, total cover and beta diversity. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. WHAT IS DEN Df??

Effect	Num. df	Species richness		Diversity		Total cover (%)		Beta diversity	
		Den. Df	F	Den. Df	F	Den. Df	F	Den. Df	F
Stand age	1	4	2.46	4	2.70	16	4.19	16	7.33 *
Year	3	54.6	40.47 ***	50.1	40.83 ***	57	35.02 ***	57	8.64 ***
Treatment	3	12	0.67	171	2.12	16	0.08	16	0.10
Stand age X Year	3	54.6	0.67	50.1	1.02	57	5.09 **	57	1.05
Stand age X Treatment	3	12	0.69	170	2.84 *	16	0.27	16	0.03
Year X Treatment	9	55.4	4.57 ***	50.2	2.20 *	57	2.16 *	57	0.53

sidual error. The variance-covariance matrix of the residual errors was assumed to be block-diagonal. Several covariance structures for the error term within treatment, block and stand age were evaluated and the structure with the smallest Akaike Information Criterion (AIC) was selected for the final model. Comparison of means was done using Tukey tests. Beta diversity was tested using mixed model analysis as described above, after removing the subplot related terms.

Response in species composition and environmental variables. Compositional changes were first estimated using mean character difference, a metric distance coefficient, calculated between 1992 and 1993, 1992 and 1994, and 1992 and 2003 for each 1-m² plot as:

$$D(x_1, x_2) = \frac{1}{p} \sum_{j=1}^p |y_{1j} - y_{2j}|$$

where $D(x_1, x_2)$ is the mean character difference between period 1 and 2 of the same subplot, y_{1j} and y_{2j} are the covers of species j at periods 1 and 2, respectively, and p is the number of species present in the site at least one time (excluding double zeros). This coefficient is minimal when a subplot had similar composition between two years, and is maximal when the composition is completely different. According to Legendre and Legendre (1998), this distance coefficient gives the same importance to abundant and rare species and may be more appropriate in mature communities. In order to test the effect of treatment and stand age on understory compositional change, mixed model analyses were done on mean character difference, including block (stand_age) and treatment \times block (stand_age) as random factors. Mean character differences were log transformed to achieve normality and homogeneity of the residuals.

Whereas the previous analysis allowed us to test treatment and stand age effects on the extent of understory compositional change, the use of an ordination analysis helps to illustrate and better interpret the compositional change of plots with time. A Detrended Correspondence Analysis (DCA) was performed on the mean cover of the species present in the seven subplots for a given year within each 100-m² plot using R and Vegan package, ver 1.17-4 (Oksanen et al. 2010). The same plots were connected at the different periods on the ordination space to illustrate their compositional trajectories. In order to help interpret the nature of compositional changes, species richness, Shannon-Wiener diversity

index and total cover, although not explicative, were correlated with DCA axes using Kendall's correlation coefficients.

Light in 1992 and 2003, and soil temperature in 2003 were analyzed using mixed models. Mixed models included treatments and stand age as fixed factors and block (stand_age) and treatment \times block (stand_age) as random factors. Because only one value per plot was available for 1993, soil temperature was analyzed using ANOVA (GLM procedure; SAS Institute Inc. 2002), including treatments and stand age as fixed factors.

Results

Response in species richness, diversity and total cover

Species richness, Shannon-Wiener diversity and total species cover all increased significantly with time since treatment application (Table 2; Fig. 1). The significant increase was observed two years after the treatment application and was still present 11 years after. There was also a significant interaction effect between treatment and year for the three variables, indicating that the increase was more pronounced in the total cut treatment, followed by conifer cut and girdling treatments, and then by the control (Table 2; Fig. 1). For instance, the probabilities associated with differences between 1992 and 2003 total cover for control, girdling, conifer cut and total cut are, respectively: $p=1.0$, $p=0.0123$, $p=0.0034$, $p<0.0001$; differences between 1992 and 2003 diversity: $p=0.1126$, $p=0.001$, $p=0.0253$, $p<0.0001$; differences between 1992 and 2003 richness: $p=0.9801$, $p=0.0082$, $p=0.0003$, $p<0.0001$ (Tukey multiple comparison adjustments). The increase in species richness and diversity after total cut tends to be more pronounced in old-growth stands than in mature ones, although the interaction between stand age and year was not significant (Table 2; Fig. 1A-D). On the contrary, the increase in total species cover was significantly more pronounced in mature than old-growth stands (Table 2; Fig. 1E-F).

Beta diversity increased significantly in 1994 ($p=0.0027$) and in 2003 ($p<0.0001$) compared with the level of 1992, but there were no significant treatment or interaction effects (Table 2; Fig. 2). However, mature stands showed significantly higher beta diversity than old-growth stands (Table 2).

Table 3. Mixed model analyses of character mean distance in understory composition between 1992 and 1993, 1992 and 1994, and 1992 and 2003. * $p < 0.05$; *** $p < 0.001$.

Effect	Num. df	1992-1993		1992-1994		1992-2003	
		Den. Df	F	Den. Df	F	Den. Df	F
Stand age	1	4	0.06	4	0.01	4	0.37
Treatment	3	156	2.03	156	2.07	156	8.07 ***
Stand age X Treatment	3	156	0.80	156	2.77 *	156	0.17

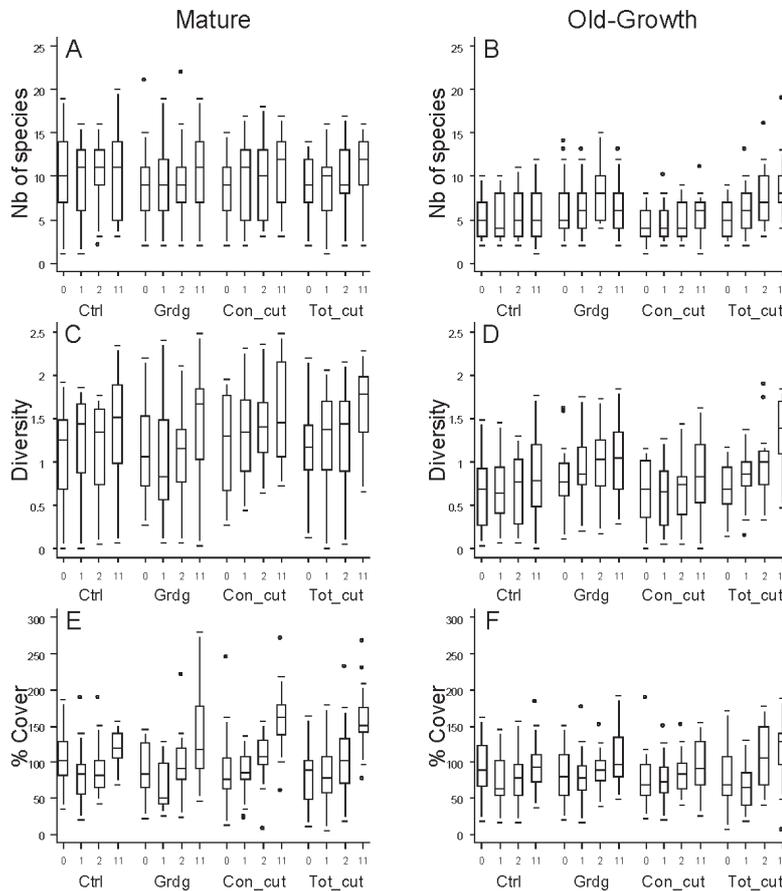


Figure 1. The effect of treatment severity over an 11-year period on changes in understory species richness (A, B), Shannon-Wiener diversity (C, D) and total cover (E, F) over in mature and old-growth stands. Ctrl = Control, Grdg = Girdling, Con cut = Conifer cut, Tot cut = Total cut. The box includes 50% of all values, with the median inside the box. The whiskers denote the minimum and maximum values within 1.5 interquartile distances. Outliers are represented by circles.

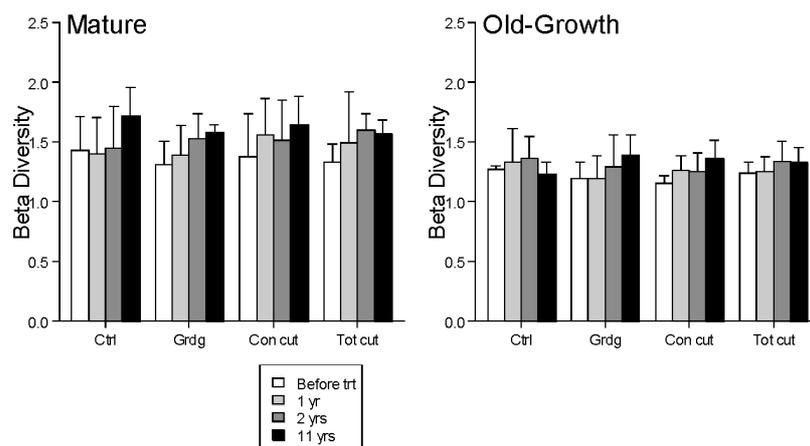


Figure 2. The effect of treatment severity over an 11-year period on changes in understory community beta diversity. Beta diversity expresses the heterogeneity observed between subplots of each stand (see formula in methods).

Table 4. Mixed model analyses of understory light in 1992 and in 2003. *** $p < 0.001$; * $p < 0.05$.

Effect	1992			2003	
	Num. df	Den. Df	F	Den. df	F
Stand age	1	4	0.36	4	0.00
Treatment	3	84	16.12 ***	276	3.75 *
Stand age X Treatment	3	84	2.43	276	0.97

Table 5. Mean (standard error) understory light and soil temperature among treatments and stand types. Means with the same letter were not significantly different at $P < 0.05$ (Tukey’s test).

	Treatments				Stand age	
	Control	Girdling	Conifer cut	Total cut	Mature	Old-growth
Understory light (%PPFD)						
1992	1.54 (1.40) c	2.00 (1.40) bc	4.27 (1.40) b	11.58 (1.40) a	2.99 (1.47) a	4.14 (1.47) a
2003	7.72 (1.31) b	12.14 (1.31) a	8.88 (1.31) b	11.01 (1.31) ab	9.87 (1.42) a	9.70 (1.42) a
Soil temperature (degrees Celsius)						
14-06-1993	7.37 (0.24) b	6.95 (0.24) b	7.78 (0.24) b	9.01 (0.24) a	9.35 (0.17) a	6.21 (0.17) b
02-07-1993	13.14 (0.17) c	13.48 (0.17) bc	13.90 (0.17) ab	14.58 (0.17) a	13.99 (0.12) a	13.55 (0.12) b
24-08-1993	14.21 (0.22) a	14.27 (0.22) a	14.55 (0.22) a	14.86 (0.22) a	14.21 (0.15) a	14.74 (0.15) a
16-09-2003	13.53 (0.10) a	13.66 (0.10) a	13.72 (0.10) a	13.75 (0.10) a	14.05 (0.12) a	13.28 (0.12) b

Table 6. Analysis of variance of soil temperature conducted three times during the summer of 1993 and mixed model analysis of soil temperature in 2003. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Effect	14-06-1993		02-07-1993		24-08-1993		16-09-2003		
	df	F	df	F	df	F	Num. df	Den. df	F
Stand age	1	166.29 ***	1	6.48 *	1	5.98	1	4	22.01 **
Treatment	3	13.32 ***	3	12.93 ***	3	1.85	3	60	1.78
Stand age X Treatment	3	0.95	3	1.40	3	0.67	3	60	1.67

femina (L.) Roth.) are associated with the lower portion of the axis (Fig. 3).

Even without treatment application, mature stands were relatively dynamic during the 11-year period (Fig. 4A). On the contrary, old-growth control stands showed much inertia in species composition (Fig. 4A). The girdling treatment resulted in a highly variable response, but was overall characterized by more changes in the mature stands (Fig. 4B). The conifer cut treatment did not result in an understory response greater than the girdling treatment, and again it was highly variable between stands (Fig. 4C). As could be expected, the total cut treatment led to the greatest changes in understory composition and abundance (Fig. 4D). Mainly, the three mature stands moved toward the right and slightly up in the ordination space, with changes mainly characterized by an increase of endurers such as *Aster macrophyllus* and *Aralia nudicaulis*, and in some cases of tolerant evaders, such as *Viburnum edule* (Michx.) Raf. It must be noted that even the mature stand that showed an initial composition similar to an old-growth stand was displaced towards the other mature stands following treatment application. Understory community changes in old-growth stands were associated with an increase in avoider cover and in some cases by the invasion

of species such as *Rubus idaeus* L. Overall, there was a distinction between old-growth and mature stands in terms of species invasion strategies. Intolerant evaders were more frequently encountered in old-growth stands, while invaders were more characteristic of mature stands.

Light and soil temperature changes

In 1992, just after treatment application, there were strong and significant differences in the understory light environment (1 m above ground) between treatments: total cut had more light than the control, and than the girdling treatment (Tables 4 and 5). Conifer cut plots also showed higher light than the control. In 2003, differences in understory light environments were attenuated but still significant (Tables 4 and 5).

In 1993, soil temperature was higher in the total cut than in the other treatments in early summer, but there was no difference between treatments at the end of the summer (Tables 5 and 6). Soil temperature was also higher in mature than in old-growth stands in early summer. In September 2003, there were no longer significant differences in temperature between treatments, but differences remained with stand age.

Discussion

Community response along the temporal gradient

Although no major shifts in species composition occurred after gap creation, noticeable differences were observed in understory dynamics according to successional status and disturbance severity. In the boreal forest, most of the understory species are known to be able to grow under a wide range of forest conditions or successional stages (Carleton and Maycock 1980, 1981, Kembell et al. 2005). This study sheds some light on how understory communities respond along a disturbance severity gradient.

The creation of canopy openings induced a significant increase in species richness, diversity and total cover in both stand ages. Differences were perceptible 2 years after gap creation and, contrary to our first hypothesis; they persisted even after 11 years. The 2-year delay response likely represents the time lapse necessary for species to adjust to the new environmental conditions. Other studies found various responses, going from a maximum richness after 2-5 years (Rees and Juday 2002, Rydgren et al. 2004), to ones where richness or cover were still increasing more than 12 years following disturbances (Thomas et al. 1999, Takafumi and Hira 2009).

Disturbance severity and community responses

In accordance with our second hypothesis, increases in species richness, diversity and total cover vary with opening severities, the response to total cut being the strongest, but conifer cut and girdling treatments also induced significant responses. De Grandpré and Bergeron (1997) have already observed significant changes in understory species diversity and composition after the creation of much larger openings, of 400 m², in the same forest ecosystem. This study confirms that smaller gaps, one quarter of the area of the larger gaps, can also induce changes in the understory. According to Kneeshaw and Bergeron (1998), more than 70% of the openings resulting from the last spruce budworm outbreak in mature and old-growth forests were smaller than 100 m². Thus, the understory community response in this study reflects what would occur under natural disturbance.

These findings support the idea, as hypothesized by De Grandpré et al. (1993) that small gaps resulting from a spruce budworm outbreak will contribute to maintaining diversity in older successional communities, by providing a highly heterogeneous environment, allowing early and late successional species to coexist. This also supports the hypothesis that, in mature and old-growth environments, the heterogeneity of resources (mainly light) is driving understory plant diversity (Bartels and Chen 2010). Furthermore, because no significant differences in beta diversity were observed between treatments, as our second hypothesis supposed, we can suggest that the disturbance severities were not high enough to entail a homogenization of the understory composition.

In terms of species composition, as revealed by the mean character difference, only the total cuts were severe enough to result in significant changes. It has been mentioned that at boreal latitudes, most of the gaps are too small to allow direct sunlight to reach the forest floor (Bonan and Shugart 1989, Kneeshaw and Bergeron 1998). Furthermore, in the girdling treatment, conifer trees remained standing for several years, delaying increased light penetration to the forest floor for a period. Our light data confirm these hypotheses: in 1992, only the total cut treatment received higher light than the control, while the girdling treatment reached the total cut level of light only in 2003. The total cut also had a higher soil temperature in 1993. It must also be mentioned that the basal area removed or girdled varied among the conifer cut and the girdling treatments plots, as it was dependent on the initial composition and basal area of the stand. Such differences could explain part of the variability in the understory response observed among these treatments.

Stand age, community responses and beta diversity

Differences in response were observed between mature and old-growth stands. As expected in our third hypothesis, old-growth stands responded more strongly to gap creation than mature ones in terms of species richness and diversity. De Grandpré and Bergeron (1997) observed the same trend after the creation of a large 400 m² gap. Old-growth stands had initially lower species richness, diversity and total cover, compared with mature stands, and the sudden increase in light and soil temperature, particularly in the total cut treatment, produced greater environmental change in the understory environment when compared with mature stands. However, the increase in total cover after gap creation is greater in mature stands than in old-growth ones.

The difference in initial composition was marked between old-growth and mature stands. Abundance of avoider species was greater in old-growth forest, mainly *Taxus canadensis*, whereas endurers, such as *Acer spicatum*, and some tolerant evaders characterized the mature forest. Prior to experimental gap formation, understory community composition reflected time elapsed since the last fire, we were careful to choose stands with no signs of recent disturbances. Both at the successional community and the within stands scales (comparison of subplots) we observed greater compositional heterogeneity among sites and subplots in mature forests than among ones in old-growth forests. This corresponds to what other studies observed along chronosequence after fire, where beta diversity decreased with increasing time elapsed since fire (Taylor et al. 1987, De Grandpré et al. 1993). Canopy composition in mature stands was more variable both at the stand scale and among stands. The presence of deciduous species in the canopy has been associated with greater soil fertility and nutrient cycling rates than when the canopy is only dominated by coniferous species (Paré and Bergeron 1996, Côté et al. 2000). Community response following gap formation was thus tightly linked with the successional status of each site, as canopy composition exerts a

strong influence on understory composition (Légaré et al. 2002), and the presence of deciduous species (mainly *P. tremuloides*) in mature stands may certainly have contributed to the higher beta diversity observed in the understory. This contributed to increasing heterogeneity in the understory environment.

The understory of mature stands was more resilient to gap formation than that of old-growth stands, being characterized by a resident species assemblage that reacted quickly to the new conditions by increasing in cover. The different response in mature and old-growth stands highlights the fact that species, such as endurers, that are able to benefit from light increases to re-invade the available forest floor or increase their cover, were more abundant in mature forest stands. The understory species assemblage in old-growth stands was better suited to growing under uniform environmental conditions, including low light levels. Thus, there was much more inertia in old-growth communities, resulting in potentially more opportunities for new species to colonize these sites (either from buried viable propagules or by invasion). However, the low disturbance severity in this study, combined with the low species pool in this old-growth environment, probably contributed to limiting compositional change after gap formation.

Tree species composition in the mature stands was characterized by a high basal area of deciduous species (Table 1). Thus, treatment application in the mature stands (except for total cut) resulted in little basal area removal and the intensity of changes in species composition in the girdling and the conifer cut treatments was quite similar to that observed in the controls (for two of the stands). Moreover, even without a canopy opening, two mature stands showed considerable composition changes during the 11-year study, while the control old-growth stands showed very few changes. This is also revealed by the beta diversity patterns in the control plots of mature sites where we observed an increase in beta diversity with time, stressing the dynamic nature of understory communities at a small spatial scale. Yearly variations in the micro-environmental conditions have been shown to influence understory community dynamics in the boreal forest (Økland and Eilertsen 1996, Økland 2000). Furthermore, many of the understory species found in the mature stands, especially the herbaceous forms, have developed strategies enabling them to forage for resources such as light (Eriksson and Jerling 1990, Hutchings and Mogie 1990). A heterogeneous environment, such as the one found in mature stands, will allow clonal species to persist in the understory as they have the capabilities to exploit this spatial variability. This could probably explain the compositional variability observed in the control plots of the mature stands throughout the study. However, as forest cover becomes increasingly dominated by conifers, the understory environment becomes more uniform and understory composition moves toward a dominance of shade tolerant species and species with low nutrient requirements.

Following the total cut, composition changes in mature and old-growth stands took different directions in the ordination space. Mature forest showed a strong increase in endurer species such as *Aralia nudicaulis*, *Aster macrophyllus* and *Clintonia borealis*. Old-growth stands also showed an increase in endurer species, but the increase in avoiders was more pronounced. *Taxus canadensis*, which was initially very abundant, decreased one year after gap creation but recovered in treated blocks, as did *Mitella nuda* L. and *Linnaea borealis*. Some species appeared following canopy openings (*Rubus idaeus*, *Geranium bicknellii*) but most of the compositional changes in both stand types consisted of an increase in species already present in the stand. As mentioned above, it is possible that openings in this study were too small to allow an important reinvasion of early successional species, as has been observed in large canopy gaps (Hughes and Fahy 1991). It is interesting to note that even the mature stand dominated by coniferous trees, in which the understory composition was initially very similar to an old-growth forest, showed compositional change in the same direction as the other mature forest stands, with an increase in endurer species such as *Aralia nudicaulis* and *Aster macrophyllus*. It is probable that, although actual composition was old-growth in appearance, the larger species pool present within this forest and its surroundings was more similar to a typical mature forest than to an old-growth forest. The occurrence of a minor disturbance, such as our small gaps, likely allowed these species, mainly clonal species, to reoccupy the forest floor to the detriment of typically old-growth species. Maintenance of established clonal species and species composition in immediate surroundings have been recognized as important factors affecting post-disturbance composition (Frelich and Reich 1999, Økland et al. 2003, Schwarz et al. 2003, Tessier 2007).

Conclusion

This study confirms that even small-scale disturbances affect boreal understory vegetation composition by increasing species diversity, richness and total cover, and these effects are still noticeable a decade after treatment application. Community response was stronger in relation to increasing severity in the disturbance, and varied according to the successional status of the forest. Initial species composition had a large influence on future changes in community composition, and this was strongly linked to the successional status of each stand. In mature stands, understory vegetation responded more by the increase in cover of resident species through clonal spread. In old-growth stands, because these clonal species were less abundant, the slow reaction time of resident species to canopy opening led to invasion by some new species.

These results provide evidence that the heterogeneity created by disturbance, such as insect damage or wind throw, plays a major role in maintaining the species pool for a longer period along the successional gradient, by allowing some early-successional species to persist longer and coexist with

late-successional species. Overall, such small gaps contributed to maintaining understory community development under late successional conditions, similar to what has been found in other studies for tree regeneration or shrubs (Kneeshaw and Bergeron 1998, Rich et al. 2007, Reyes et al. 2010). This information could be useful in **ecosystemic** forest management, in order to more adequately develop management strategies that can maintain biodiversity and ecological integrity (Roberts 2004, Rydgren et al. 2004).

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Appendix S1. Classification of understory species observed in the study into reproductive strategy groups. Evaders species that were present in the site before treatment (shade tolerant); other evaders appeared following treatment (shade intolerant). The file may be downloaded from the web site of the publisher at www.akademai.com.