

Fifty-seven years of composition change in the eastern boreal forest of Canada

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Abstract

Question: In the boreal forest of eastern Canada, how does forest vegetation change in the sustained absence of fire?

Location: Eastern boreal forest in Quebec's North Shore region, Canada (49°30'–50°00'N; 67°30'–68°35'W).

Methods: Aerial photos from three different periods (1930, 1965 and 1987) were used to characterize changes in vegetation composition in 23 scenes of 200 ha. Time since fire, presence of secondary disturbances and data on soil and topographic variables were obtained. Ordination and clustering techniques were used to define compositional trajectories of change over the 57-yr period. These trajectories were further grouped into pathways based on compositional changes, time since fire and preferential deposit-drainage types.

Results: Among the 26 compositional trajectories, three successional pathways were distinguished. Two start post-fire succession with a dominance of intolerant hardwood. In one of these, this is followed by an increase in *Abies balsamea*, while in the second the importance of *Picea mariana* increases with time. In the third pathway *P. mariana* is an important component from the outset. In this pathway, we observed modest fluctuation in the relative dominance of *P. mariana* and *A. balsamea* and variation in stand structure.

Conclusion: The boreal forest vegetation of Eastern Canada is diverse and dynamic even in the absence of fire, notably under the influence of partial disturbances. Such disturbances can be associated with changes in composition or stand structure. The development of management strategies aimed at maintaining stand diversity by emulating a broader variety of partial and secondary disturbances should be encouraged.

Keywords: *Abies balsamea*; Aerial photography; Chronosequence; Disturbance; Intolerant hardwood; Long-term study; *Picea mariana*; Succession pathways; Time since fire.

Nomenclature: Hosie (1979).

Abbreviations: TSF = Time since fire; DCA = Detrended Correspondence Analysis.

Introduction

Vegetation dynamics in the boreal forest have often been described as relatively simple. Wildfire was thought to be the main form of disturbance, recurring at short intervals relative to the longevity of forest species. It has been claimed that canopy succession was rare if not absent from the system (Cogbill 1985; Johnson 1992). It is now more and more recognized that fire recurrence time is variable across Canada (Gauthier et al. 2009), and that some regions experience fire regimes in which a majority of the stands will be exempted from fire for a time period longer than the lifespan of the major post-fire species. The North Shore of Quebec is one such region, with mean interval between successive fires estimated to be greater than 270 yr (Foster 1983; Cyr et al. 2007; Bouchard et al. 2008). In the absence of fire for a long interval, vegetation dynamics can be controlled by other types of disturbance such as insect outbreaks, windthrow that occurs at variable spatial scales (McCarthy 2001), or simply by individual tree senescence.

Canopy succession may involve changes in composition, or sometimes in forest structure (Chen & Popadiouk 2002; Brassard & Chen 2006). In our study area, chronosequence studies used to describe vegetation changes suggest that *Abies balsamea* stands tend to replace deciduous pioneer species when the interval between successive fires is long enough to allow the pioneer species to die (De Grandpré et al. 2000). In places where *Picea mariana* (Mill.) B.S.P. is dominant, stands can be invaded by *A. balsamea* (L.) Mill., which may become the dominant species, or *P. mariana* may maintain its dominance over time with a change in the forest structure (Carleton & Maycock 1978; Bergeron & Dubuc 1989; Groot & Horton

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1994; De Grandpré et al. 2000; Boucher et al. 2003, 2006). However, gap dynamics, which are important in those forests, may contribute to creating a dynamic equilibrium in old stands (Pham et al. 2004). *Abies balsamea* stands could be maintained by gap dynamics in the absence of fire (Kneeshaw & Bergeron 1998; Bergeron 2000) or reinitiated after a spruce budworm outbreak (*Choristoneura fumiferana* Clem.) (Baskerville 1975; MacLean 1984; Morin 1994).

Chronosequence studies have been used to suggest successional pathways after major disturbances, although it is difficult to confirm that the conditions and processes involved in the observed changes were really the same between sites (see Johnson & Miyanishi 2008 for a critical assessment of the chronosequence approach). Moreover, where partial disturbances are important, this method may be difficult to use as successional trajectories may depend on the intensity and timing of the secondary disturbance. The use of aerial photographs allows us to observe changes in vegetation for the same location over a long period of time (Frelich & Reich 1995; Rhemtulla et al. 2002).

In the North Shore region, thanks to the availability of aerial photos since 1930 at a scale that allows species identification, it is possible to study vegetation changes over a long time period. The objectives of this work were to (1) define the successional pathways for regional forest vegetation, (2) relate the observed changes to site factors and secondary disturbances, and (3) evaluate the age of stand break-up in deciduous stands and assess their future composition. We also wanted to compare the results of a chronosequence study (De Grandpré et al. 2000) to the observed changes and to assess whether the increase in balsam fir suggested by chronosequence analysis had occurred. We hypothesized that in the absence of fire over a long period of time, changes in canopy composition and structure would occur. A good knowledge of vegetation dynamics is a pre-requisite for developing sustainable forest management strategies. In order to maintain forest biodiversity and productivity, it is essential to maintain not only the diversity of habitat types but also the important processes involved in vegetation changes (Bergeron et al. 2002).

Study Area

The study was conducted in the boreal forest of Quebec's North Shore (49°30'–50°00'N; 67°30'–68°35'W) (Fig. 1), in an area of 4340 km² encompassing the two forest regions of Rowe (1972). The

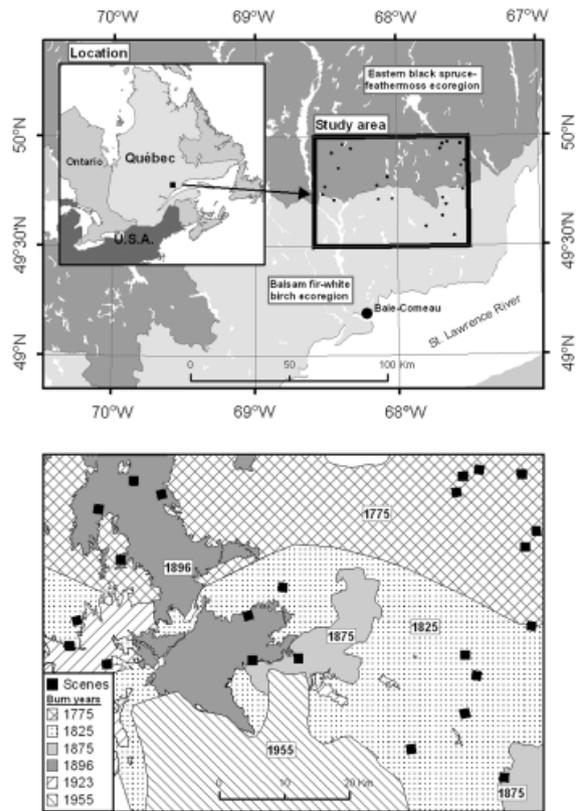


Fig. 1. Location of the study area and of the scenes within the study area.

southern part of the study area belongs to the Laurentide-Onatchiway region and is characterized by a predominance of *A. balsamea* on hill slopes and moist, well-drained sites, while *P. mariana* is more important on thin soil and poorly drained sites. The northern section touches the Chibougamau-Natasquan region, where black spruce becomes the main dominant species and balsam fir becomes rare. The study area has a slightly rugged topography, where high hills are present with rock outcrops at high altitudes. Altitude varies from 36 m to 681 m, with an average of 360 m. Surficial deposits are of glacial origin, and the soils are mostly ferro-humic or humo-feric podzols (Rowe 1972). Till is the major surficial deposit throughout the region. Mean annual temperature is between -2.5°C and 0.0°C , and mean annual precipitation varies from 900 mm to 1300 mm, with 40% falling as snow (Robitaille & Saucier 1998).

The fire regime of this region has recently been characterized (Cyr et al. 2007; Bouchard et al. 2008). Cyr et al. (2007) estimated the fire cycle to be almost 300 yr. Even though fires are relatively rare, they usually cover large areas. Insect outbreaks are also frequent in the region: over the last century, three spruce budworm outbreaks have affected the study

area, resulting in relatively low mortality except for the last outbreak (Blais 1983; De Grandpré et al. 2009). Part of the area may also suffer from hemlock looper outbreaks. Many stands are susceptible to small windthrows, larger ones being rare events that can however affect large areas. The main species' longevity (*A. balsamea*, *Betula papyrifera* Marsh., *Populus tremuloides* Michx, *P. mariana*) is generally below 150 yr, i.e. shorter than the average fire interval.

Material and Methods

Scene Choice and Location

A satellite image (Landsat 1993) was used to exclude areas recently affected by logging or fire as our objectives were to study the vegetation dynamics in the absence of fire for a long time period. Fire history was reconstructed using archival data from the *Direction de la protection et de l'environnement forestier du ministère des Ressources naturelles et de la Faune du Québec* (MRNFQ) for the period between 1941 and 1987. Moreover, analysis of the 1930s aerial photo series allowed us to map three major fires that occurred prior to 1930. Field sampling into the fire perimeter allowed us to determine the fire dates: 1875, 1896, 1923. For the portion of the study area where no fire dates were available, we used data gathered by the MRNFQ on the age of trees to establish two approximate dates corresponding to the minimum fire age (1775 and 1825; Fig. 1).

Aerial photo series from three different periods were available. The first, in black and white, dates from 1930 to 1932, with an average scale of 1:13 613. This aerial photo series covers 91% of the study area. The second series dates from 1965, is also in black and white, and the average scale is 1:15 778. Finally, the third series of infrared photos was taken in 1987, also by the MRNFQ; the mean scale of this series is 1:16 011. We define a scene as an area of 200 ha for which the photos from each time period were interpreted.

In order to be able to compare the scene in 1930, 1965 and 1987, the exact scale of each photo was computed by comparing the distance between two visible features (roads, lake shore, island, etc.) with the same distance on a forest inventory map at a 1:20 000 scale. At least three distances were used per photo. From the scale thus obtained, a grid of 100 2-ha cells (141 m × 141 m) was produced and placed at the same location for each date. Each photo of each scene was then digitized and georeferenced together with its grid, using a second-order polynomial cor-

rection. Overall, after the correction, the average area of each cell was 2.0027 ± 0.0636 ha.

Aerial Photo-Interpretation

Stereo pairs of photos were interpreted for a total of 23 scenes of 200 ha. Table 1 shows the distribution of the scenes in the different times since fire classes. The use of successive aerial photos taken around 1930, 1965 and 1987 allowed us to follow stand evolution *in situ* over a 57-yr period. Each scene was located near a study plot visited by the MRNFQ in 1988. The data gathered in those ground plots were used by the photo-interpreters to ascertain their evaluation of species composition, density and height.

The photo-interpretation was based on the forest inventory norms used by the *ministère de l'Énergie et des Ressources du Québec* (MERQ) in the second inventory programme (MERQ 1984). The variables recorded and the classes used are presented in Appendix S1. For each 2-ha cell, total cell canopy cover, height and stand age were recorded in classes. Note that the age classes do not correspond to the time since fire; they represent an interpretation of the estimated age of trees based on stand structure and height. When the total canopy cover was below 25%, the cell was not considered forested and therefore it was not included in further analysis. For the main species (*P. mariana*, *Pinus banksiana* Lamb., *P. tremuloides*, *B. papyrifera* and *A. balsamea*), the relative canopy cover occupied was measured in six classes (Appendix S1). The type of disturbance (fire, insect or windthrow) that had occurred in the cell and whether it was a partial cell disturbance was also recorded.

Data from Other Sources

Altitude (m), slope (%), cell position on slope and slope aspect (degrees) were derived from a digi-

Table 1. Number of scenes and cells photo-interpreted or observed in the study area as a function of time since fire classes. *Estimated time since fire.

TSF in 1930	Photo-interpreted			Study area	
	Number of scenes	Number of cells	% of cells	(km ²)	%
7	2	117	5.1	198	5.6
34	6	515	22.4	548	15.6
55	3	205	8.9	222	6.3
105*	12	874	38.0	1350	38.5
155*	7	589	25.6	1189	33.9
	Total	2300	100.0	3507	100.0

tal elevation model (DEM) of 3 arc second ($\sim 75 \text{ m} \times 75 \text{ m}$) resolution using Arc/GisTM 8.3 (ESRI[®]). Data for surficial deposit and drainage were obtained from the eco-forestry maps of the MRNFQ using a spatial joint on the centroids of each cell and the map (Appendix S1). Combinations of surficial deposit \times drainage were created based on their potential for vegetation growth. A method developed by Zimmermann (Zimmermann, N. E. 1999, *Toposcale AML ArcInfo program*; http://www.wsl.ch/staff/niklaus.zimmermann/programs/aml4_1.html) was used to compute cell position on slope. This method uses successive neighbourhood analysis, computing the difference between mean elevation of the mobile window and the cell value. The mobile window varies from 2 DEM pixels (75 m) to 19 (which is the scene width). A hierarchical comparison of each of the 18 layers allows the definition of slope position, which was then validated by photo-interpretation. Solar radiation (MJ m^{-2}) was computed using the method described by Thornton et al. (2000), and the number of degree-days above five was computed using BIOSIM (Régnière 1996).

Data Analyses

Several steps were used to synthesize our information (Fig. 2). An ordination was used to assess the changes in species composition over the 57 yr. For each cell, the value used for this analysis was the percent cover of the species (the median of overall canopy cover class multiplied by the median of the relative canopy cover of the species; Appendix S1). This value was used as it allows us to better describe the overall variation in forest composition and structure. We excluded 303 cells: those located on rare surficial material or containing rare species (*P. banksiana*), those where species were difficult to identify during one period, and those where land use had changed over time. In total, we used 1997 cells belonging to 23 scenes. In a detrended correspondence analysis (DCA), only the data from the 1930 period were used to obtain the position of each cell on the ordination space, whereas the position for the same cells in 1965 and 1987 was attributed passively. To control the geographic gradient, longitude and latitude data were used as co-variables. Correlations between ordination axes and environmental variables, time since fire, and observed disturbances were computed and represented in the ordination space to assess their potential influence on composition.

In order to synthesize the information on vegetation change and define the main compositional

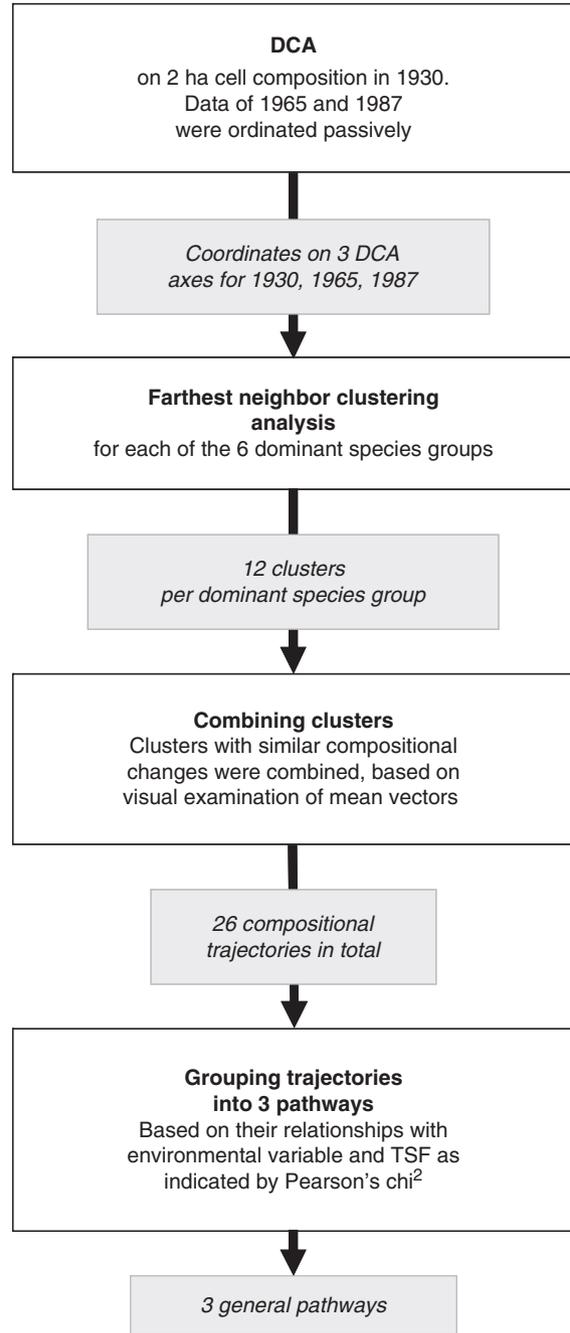


Fig. 2. Diagram of the main data analysis steps.

trajectories, we used the farthest neighbour clustering technique (also called “complete linkage clustering”; Legendre & Legendre 1998) using PC-ORD (version 4, MJM Software Design, Gleneden Beach, OR, US). As we were interested in grouping cells that underwent similar changes over the entire period, the clustering analyses were conducted using the coordinates of each cell on the first three ordination axes (which correspond to 80% of the

variation in species composition) for the three time periods (Fig. 2). Clustering analyses were performed separately based on the dominant species group in 1930: *Betula* (cells with more than 25% of relative cover of *B. papyrifera*), *Populus* (cells with more than 25% of relative cover of *P. tremuloides*), intolerant hardwood (cells with more than 25% of relative cover of both *P. tremuloides* and *B. papyrifera*), *Picea mariana* (cells with more than 75% of relative cover of *P. mariana*) and *Picea–Abies* (cells with more than 75% of relative cover of *P. mariana* and *A. balsamea* combined). The pure *Abies* cells (cells with more than 75% of relative cover *A. balsamea*) were too few to be submitted to such analysis ($n = 20$). Only cells for which data were complete for the three periods were used (over all groups: 1776 cells within 22 scenes). Twelve clusters per dominant species group were identified, for a total of 60 (Fig. 2).

For each identified cluster, we then computed mean vectors to represent compositional changes on the ordination, and those that were similar were combined based on visual examination of their vectors on the first three DCA axes. Finally, 26 compositional trajectories were identified, including that for *Abies* (Fig. 2). In order to describe vegetation changes over time, the average composition of each trajectory at each period was computed. We then summarized this information by giving a stand type name to each composition type using the MERQ forest stand classification scheme (Appendix S2), which reflects the dominant species observed in the canopy.

The relationship between environmental variables or time since fire (TSF) classes and each compositional trajectory was assessed using frequency distribution (Fig. 2). The Pearson χ^2 component was computed as $\chi_p^2 = (O - E)/\sqrt{E}$, where O = frequency of cells occupied by a trajectory in a particular environmental class, and E = frequency of cells within this environmental class in all trajectories (Legendre & Legendre 1998). Values above a threshold ($(\chi_{(df,\alpha)}^2/\text{number of possible combinations})^{1/2}$) at $\alpha = 0.001$ indicate that the observed frequency of a trajectory differed from that expected under a null hypothesis of no association between the environmental variable and the trajectory (Legendre & Legendre 1998).

To estimate the TSF required for stand break-up (i.e. when the post-fire cohort is replaced by new individuals in the canopy), we used the TSF observed in the period when the cell had more than 75% of relative cover of coniferous species (our threshold for completion of stand break-up). This

approach does not allow estimation of time to stand break-up for cells that were initially coniferous or cells where the deciduous component remains important even when the post-fire cohort is replaced.

In order to define the long-term successional pathways, the compositional trajectories were connected sequentially (with increasing TSF), based on their composition and their preferential deposit–drainage type (according to Pearson's χ^2 tests; Fig. 2). Some trajectories were harder to attribute to a pathway than others. For instance, some trajectories with long TSF in 1930 and dominated by conifers could have started succession with pioneer species that are now rare or absent from the stand. These trajectories were placed within the pathway we judged the most probable.

Results

Composition and Environmental Factors

Ordination of the initial – 1930 – vegetation data (Fig. 3c) yielded a first axis expressing 48% of the total variance and distinguishing stands with a high component of *A. balsamea* and *P. mariana* from those with a high component of intolerant hardwood. The second axis (21% of the variance) discriminated stands with *Abies* from those with *Picea*, and those with *B. papyrifera* from those with *P. tremuloides*.

The first axis is strongly and negatively correlated with TSF and, to a lesser extent, with solar radiation, number of degree-days and slope aspect, while it is positively correlated with cell slope (Fig. 3a). TSF is also negatively correlated with axis 2 even more strongly. Even though the centroids of nominal variables are quite close to each other on the ordination space, a few trends emerge. For instance, sites with poor drainage tend to be located on the left side of the first axis, along with coniferous stands (Fig. 3b). The depth of the surficial deposit and slope position (from toe to crest) both tend to increase with the position on axis 1, along with the importance of deciduous species (Fig. 3b). Finally, partial windthrow is associated with stands with a high content of *A. balsamea*, whereas fire is associated with high contents of *P. mariana* (Fig. 3b).

Among the 1776 cells analysed, we defined eight types of compositional trajectories in the *Betula* group, four in the intolerant hardwood group, three in the *Populus* group, six in the *P. mariana* group, four in the *P. mariana–A. balsamea* group and one in the *Abies* group (Appendix S3). All identified

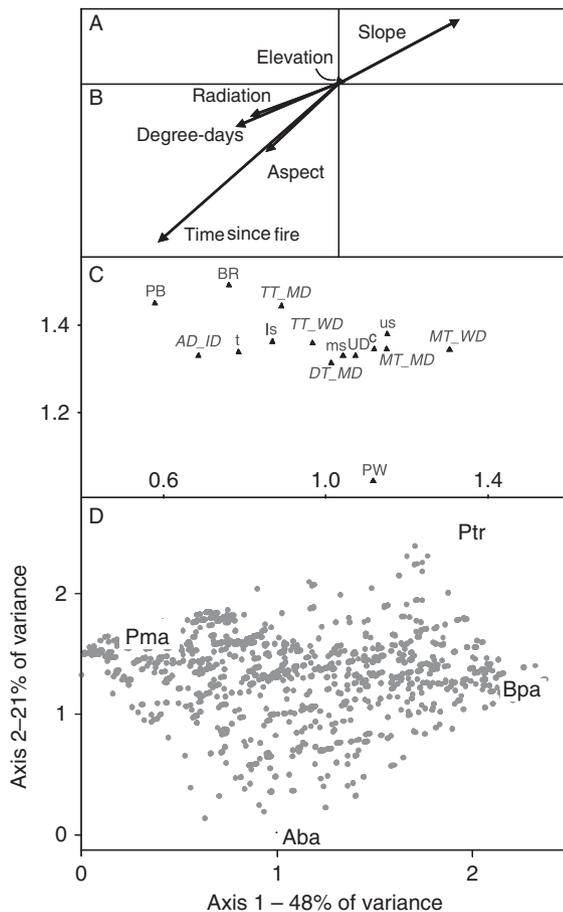


Fig. 3. DCA ordination diagram based on cell composition in 1930 showing (a) quantitative environmental variables; (b) nominal environmental variables (Site position on slope: c = crest, us = upper slope, ms = middle slope, ls = lower slope, t = toe; Combination of surficial deposit and drainage: TT_WD = thin till – well drained, MT_WD = moderately deep till – well drained, TT_MD = thin till – moderately well drained, MT_MD = moderately deep till – moderately well drained, DT_MD = deep till – moderately well drained, AD_ID = any deposit – imperfectly drained; Disturbances: BR = burn, PB = partial burn, PW = partial windfall, UD = undisturbed); and c) species and cell (grey points) positions on axes 1 and 2 (Species: Pma = *Picea mariana*, Ptr = *Populus tremuloides*, Bpa = *Betula papyrifera*, Aba = *Abies balsamea*). Note the change in axis scale for each panel.

trajectories but one (Ptr3) are represented in more than four scenes (Appendix S3).

Successional Pathways

Three general successional pathways were distinguished (Figs 4 and 5 and Table 2). The rationale for grouping the trajectories into a particular path-

way is presented in Appendix S3. Here we describe the compositional changes and the observed preferred surficial deposits of the three pathways.

Pathway 1: Intolerant Hardwood – *Abies balsamea*

The first pathway is composed of stands with initial dominance of intolerant hardwood and where *A. balsamea* increases with time, while *P. mariana* is unimportant or absent (Fig. 4). It tends to be over-represented on well-drained till with a moderate depth and on moderately well-drained thin tills, although it is present in all site types (Fig. 4 and Appendix S3.2). The youngest trajectory of this pathway had a mean TSF of 74 years in 1930, and four of the five intolerant hardwood-dominated trajectories reached dominance of *Abies* during the study period (Fig. 4). Aba1 was also included in this pathway based on its initial composition, which was similar to the end composition of other trajectories (Fig. 3 and Appendix S3). Stand break-up completion ranged between 109 to 133 yr (Table 2). Only one trajectory, Bpa1, did not reach a coniferous dominance: *Abies* slightly dominated the stand in 1965, but decreased in 1987 (Appendix S3.3) and stand break-up remained incomplete 156 yr after fire (Table 2). Disturbances were common in this pathway: 66% of the cells showed signs of disturbance in 1965 or 1987, mainly light insect outbreaks in 1987, but also partial windthrows in 1965 (Table 2).

Pathway 2: Intolerant Hardwood – *Picea mariana*

The second pathway is composed of stands that also start succession after fire with dominance by intolerant hardwood (mainly *B. papyrifera*, potentially with an understorey of *P. mariana*) but where *P. mariana* increases in canopy dominance (Fig. 4). In these stands, importance of *A. balsamea* may also increase in the canopy (Fig. 4), and relative dominance of *A. balsamea* and *P. mariana* can fluctuate. The PmaAba4 trajectory was also included in this pathway as its deposit–drainage preferences were similar, even though no deciduous component was observed over the period (Fig. 4 and Appendix S3). These trajectories are observed on all site conditions but are over-represented on moderately well-drained tills with moderate to high depth (Fig. 4 and Appendix S3.2). They are under-represented at both ends of the drainage gradient (Fig. 4 and Appendix S3.2). Six trajectories with an initially large deciduous component reached coniferous dominance during the study period (Fig. 4 and Appendix S3.3), with estimated age of break-up completion from 101

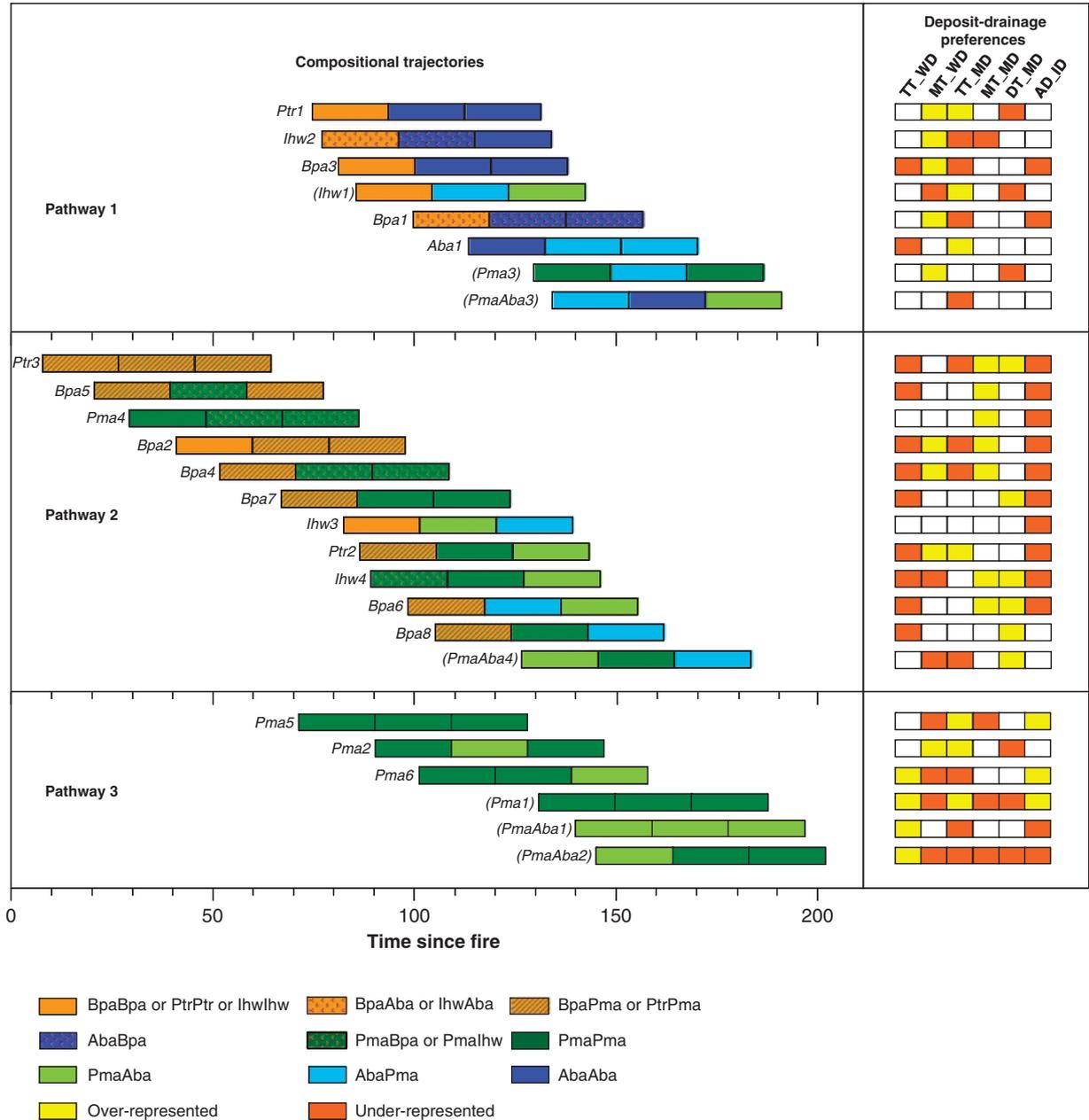


Fig. 4. Representation of the compositional trajectories classified into successional pathways along the time since fire (TSF) gradient and their surficial deposit–drainage class preferences (see Appendix S3 for complete results). For each trajectory, the three boxes in the left part of the figure represent, successively, the 1930, 1965 and 1987 forest types. Trajectories in parentheses were attributed to the most probable pathway. The name of the forest type is composed of a couplet of species acronym where the first species is the most abundant (see Appendix S2 for more details). See Fig. 2 for species and deposit–drainage codes.

to 140 yr (Table 2). Other deciduous stands were too young (<51 yr old in 1930) to have completed stand break-up (Table 2). All deciduous trajectories, even the youngest, showed high abundance of *P. mariana*, whereas low abundance of *Abies* was observed in stands <80 yr old (Fig. 4 and Appendix

S3.3). Compared with intolerant hardwood stands of the same age in pathway 1, stands of pathway 2 showed less disturbance: nearly 60% of the stands <100 yr old showed no signs of disturbance in 1965 and 1987 compared with only 27% in pathway 1 (Table 2).

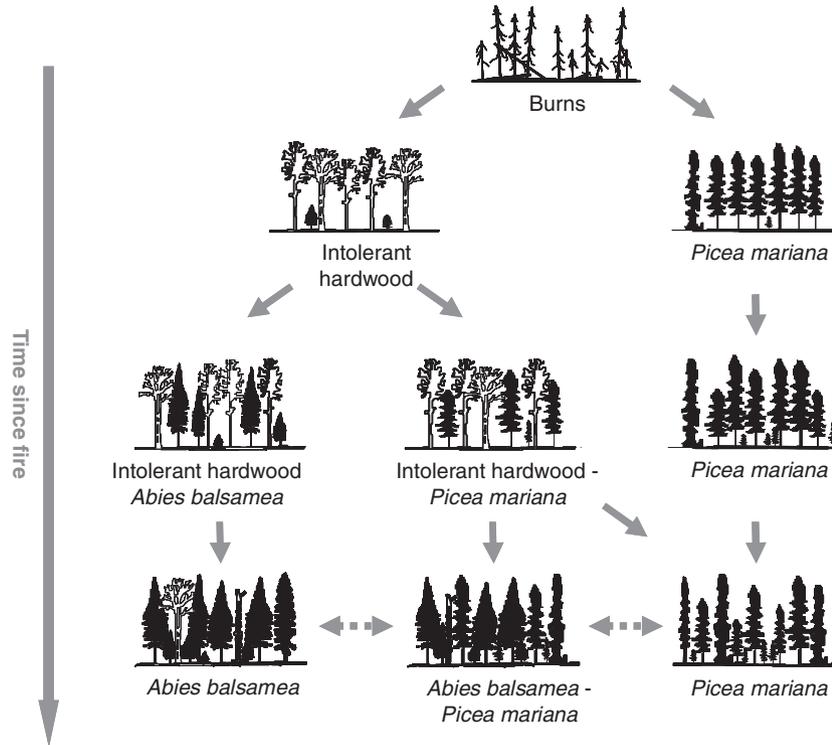


Fig. 5. Main successional pathways observed in the study area. Dashed arrows represent potential fluctuation between these forest types.

Pathway 3: *Picea mariana* – *Picea mariana*

The third pathway is defined by an initially large component of *P. mariana*. This species remains important throughout succession, with some fluctuations in the relative dominance of *P. mariana* and *A. balsamea* (Fig. 4 and Appendix S3.3). Almost half of the cells studied belong to this pathway (Table 2). These stands are present on all site types but are over-represented on sites at each end of the drainage gradient (well-drained thin till or imperfectly drained soils) (Fig. 4 and Appendix S3.2). Secondary disturbances were less involved in this pathway than in the first: 57% of the cells showed no sign of disturbance in 1965 and 1987 (Table 2).

Change in Stand Structure

The analysis of variation of canopy cover, height and age classes suggested that in many of the conifer-dominated trajectories, there was a change in stand structure (Table 3). For instance, in pathway 1, the three composition trajectories dominated by *Abies* or *Picea* in 1930 (Aba1, Pma3 and PmaAba3) showed a decrease either in canopy cover or age class between 1930 and 1965, and an increase be-

tween 1965 and 1987. In pathway 2, this type of variation was also observed in Idw3, Bpa8 and PmaAba4. Finally in pathway 3, structural variation was observed in all trajectories, except Pma5 (either in the cover density or in the age class). Canopy structure changes can therefore occur in the absence of compositional change.

Discussion

This long-term study allowed us to assess successional trends derived from previous chronosequence studies. Some trends from chronosequence studies were confirmed whereas others were rejected. For instance, using the chronosequence approach with our data on species composition in 1930 (ordination results), we could link stand composition and TSF in 1930, as is often reported in the literature (Bergeron 2000; De Grandpré et al. 2000; Gauthier et al. 2000). Initial patterns also suggested that vegetation changes gradually as a function of site characteristics, even though none of the major species is restricted to any site condition or stand age. These trends were also confirmed by our long-term data: all three successional pathways were observed in all types of site

Table 2. Time since fire, stand break-up age and disturbances for each compositional trajectory classified into successional pathways. Trajectories in parentheses were classified into the most probable pathway. The name of the forest type is composed of a couplet of species acronym where the first species is the most abundant (see Appendix S2 for more details). Mean percentages of cells without disturbance within each pathway are indicated in bold. Pma = *Picea mariana*, Ptr = *Populus tremuloides*, Bpa = *Betula papyrifera*, Aba = *Abies balsamea*, Ihw = Intolerant hardwood, BR = Burn, LIO = Light insect outbreak, PB = Partial burn, PC = Partial cutting, PW = Partial windthrow.

Pathways	Compositional trajectories			n	Time since fire in 1930 (years ± sd)	Age at stand break-up completion (years)	Cells without disturbance (%) / Main disturbances				
	Name	Forest type sequences	Scenes				Cells	1930	1965	1987	1965 & 1987
1	Ptr1	PtrPtr -> AbaAba -> AbaAba	4	13	74.2 ± 25.3	109	100.0	92.3	30.8/LIO	23.1	
	Ihw2	IhwAba -> AbaBpa -> AbaAba	4	14	76.4 ± 25.7	133	100.0	85.7/PW	42.9/LIO	28.6	
	Bpa3	BpaBpa -> AbaAba -> AbaAba	7	67	80.4 ± 28.0	115	100.0	88.0/PW, LIO	17.9/LIO	10.4	
	(Ihw1)	IhwAba -> AbaPma -> PmaAba	4	10	85.0 ± 25.8	120	100.0	100.0	50.0/LIO	50.0	
	Bpa1	BpaAba -> AbaBpa -> AbaBpa	7	30	99.3 ± 34.3	> 156	100.0	93.3/PW, LIO	26.7/LIO	23.3	
	Aba1	AbaAba -> AbaPma -> AbaPma	7	20	112.6 ± 33.2	100	75.0/LIO, PC	60.0/LIO, PW, PC	40.0	57.1	
	(Pma3)	PmaPma -> AbaPma -> PmaPma	9	63	128.9 ± 31.5	-	100.0	82.5/LIO, PC	66.7/LIO	36.2	
	(PmaAba3)	AbaPma -> AbaAba -> PmaAba	11	105	133.6 ± 27.5	-	100.0	73.3/PW, LIO	54.3/LIO	33.6	
	2	Ptr3	PtrPma -> PtrPma -> PtrPma	1	18	7.0 ± 0.0	> 64	0.0/BR	100.0	94.4/LIO	94.4
	Bpa5	BpaPma -> PmaBpa -> BpaPma	5	18	19.9 ± 24.5	> 77	33.3/BR	100.0	72.2/LIO	72.2	
	Pma4	PmaPma -> PmaBpa -> PmaBpa	5	28	28.8 ± 19.4	-	35.7/BR	96.4/PW	89.3/LIO	89.3	
Bpa2	BpaBpa -> BpaPma -> BpaPma	8	98	40.2 ± 19.7	> 97	96.9/BR	87.8/PC	83.7/LIO	71.4		
Bpa4	BpaPma -> PmaBpa -> PmaBpa	8	91	51.1 ± 25.0	> 108	93.4/BR	96.7	50.5/LIO	48.4		
Bpa7	BpaPma -> PmaPma -> PmaPma	13	89	66.3 ± 38.6	101	94.4/BR	87.6/PC	71.9/LIO	62.9		
Ihw3	IhwIhw -> PmaAba -> AbaPma	6	15	81.7 ± 25.8	117	100.0	100.0	33.3/LIO	33.3		
Ptr2	PtrPma -> PmaPma -> PmaAba	6	31	86.0 ± 37.3	121	83.9/BR	87.1/PC, LIO	51.6/LIO, PW	48.4		
Ihw4	PmaIhw -> PmaPma -> PmaAba	7	40	88.7 ± 29.6	124	92.5/BR	87.5/PC, LIO	42.5/LIO, PW	42.5		
Bpa6	BpaPma -> AbaPma -> PmaAba	11	47	97.9 ± 36.2	133	97.9	85.1/PW, LIO	29.8/LIO	29.8		
Bpa8	BpaPma -> PmaPma -> AbaPma	9	58	104.6 ± 23.9	140	98.3	84.5/LIO	19.0/LIO	15.5		
(PmaAba4)	PmaAba -> PmaPma -> AbaPma	11	89	125.9 ± 31.3	-	100.0	88.7/PC, LIO	40.4/LIO	31.5		
3	Pma5	PmaPma -> PmaPma -> PmaPma	16	260	70.8 ± 38.7	-	66.2/BR	90.0/PW	82.3/LIO	77.7	
Pma2	PmaPma -> PmaAba -> PmaPma	10	65	89.6 ± 29.9	-	83.1/BR	73.8/PW, LIO	73.8/LIO	55.4		
Pma6	PmaPma -> PmaPma -> PmaAba	17	62	100.4 ± 51.6	-	83.9/BR	88.7/PB, LIO	53.2/LIO, PW	43.5		
(Pma1)	PmaPma -> PmaPma -> PmaPma	15	272	130.3 ± 39.3	-	97.8	82.7/BR, PC, LIO	86.4/LIO	71.0		
(PmaAba1)	PmaAba -> PmaAba -> PmaAba	11	58	139.5 ± 28.2	-	100.0	72.4/LIO, PC	65.5/LIO, PC	44.8		
(PmaAba2)	PmaAba -> PmaPma -> PmaPma	8	115	144.6 ± 20.4	-	100.0	83.5/LIO, PW, PC	65.2/LIO	51.3		
								71.1	57.3		

Table 3. Modes of photo-interpreted stand canopy cover, height and age classes of each compositional trajectory in 1930, 1965 and 1987. Trajectories in parentheses were classified into the most probable pathway. Note that trajectories are placed in increasing order of average time since fire within each successional pathway. Canopy cover classes: A = 81–100%, B = 61–80%, C = 41–60%, D = 24–40%; Height classes: 2 = 17–22 m, 3 = 12–17 m, 4 = 7–12 m, 5 = 4–7 m, 6 = 1.5–4 m; Age classes: 10 = 0–20 yr, 30 = 21–40 yr, 50 = 41–60 yr, 70 = 61–80 yr, 90 = 81–100 yr, 120 = > 100 yr, Oua = Old uneven-aged.

Successional pathway	Canopy cover class			Height class			Age class		
	30	65	87	30	65	87	30	65	87
<i>Pathway 1</i>									
Ptr1	B	C	D	3	3	3	90	90	120/Oua
Ihw2	A	C	B	3	3	3	70	70	90
Bpa3	A	B	C	3	3	3	70	90	90
(Ihw1)	A	B	C	3	3	3	90	120	120/Oua
Bpa1	A	B	C	3	3	3	70	70	90
Aba1	B	C	C/A	4	3	3	50	70	120
(Pma3)	B	B	B	3	3	3	120	90	120
(PmaAba3)	B	B	B	3	3	3	120	70	120
<i>Pathway 2</i>									
Ptr3	A	B	B	6	3	2	10	50	70
Bpa5	A	B	B	6	3	3	10	50	70
Pma4	B	B	B	5	3	3	30	50	90
Bpa2	B	B	B	4	4	3	30	50	90
Bpa4	B	B	B	3	3	3	70	50	90
Bpa7	B	B	B	3	3	3	30	50	90
Ihw3	A	B	B	3	3	3	70	120	90
Ptr2	A	C	C	3	3	3	90	120	120
Ihw4	B	B	C	3	3	3	90	120	120
Bpa6	B	C	C	4	3	3	90	90	120
Bpa8	A	B	C	3	3	3	70	120	90
(PmaAba4)	B	C	C	3	3	3	120	90	Oua
<i>Pathway 3</i>									
Pma5	C	C	C	3	4	3	30	50	120
Pma2	B	C	C	3	3	3	90	90	120
Pma6	B	B	B	4	3	3	70/120	50	90
(Pma1)	B	C	C	4	3	3	120	50	120
(PmaAba1)	B	C	C	3	3	3	120	90	120
(PmaAba2)	B	C	C	4	3	3	90	90	90

even though their frequency is correlated with site type. The relationship between stand composition and the type of surficial deposit–drainage is seen in relative dominance of species, not in their presence or absence. Using the chronosequence approach alone (i.e. the 1930 DCA only), we could also establish that stands where intolerant hardwoods dominate are generally those that were disturbed within the last 60 yr. On the other hand, stands older than 120 yr tend to be dominated by coniferous species, although we have observed young stands dominated by *P. mariana* in the early phase of succession. This was further confirmed by our long-term data.

The long-term data allowed us to identify three main succession pathways followed in the long-term absence of fire (Fig. 5), confirming changes in composition or in stand structure already suggested in the literature (Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; De Grandpré et al. 2000; Gauthier et al. 2000; Harper et al. 2002). In two pathways, succession begins with the establishment of *Betula*

and *Populus* followed by an increase in coniferous species dominance (*Abies* in one case and *Picea* in the other). The third pathway, dominated by *P. mariana*, included almost half of the stands in this study. These stands do not show major changes in composition, although *Abies* is a recurrent component of this path. Based on the chronosequence approach, it is very difficult to predict the change that will occur in stands that present a mixture of *P. mariana* and *A. balsamea* and that were already over 120 yr old in 1930. De Grandpré et al. (2000) and others have predicted that in the prolonged absence of fire, stands would tend to be dominated by *A. balsamea*. Our results using long-term observation of particular stands clearly indicate that this is not the case. This suggests that partial disturbances play an important role in long-term successional dynamics. Such disturbances could also be associated with the great variability observed within each successional pathway. In the following section, we will discuss in more detail some of the changes that our study revealed.

Evolution of Intolerant Hardwood Stands and Stand Break-Up

In both pathways, the canopy of intolerant hardwood stands showed an increase in coniferous dominance with increasing TSF. This varied according to the TSF in 1930 and the site conditions, among other things. Young, intolerant hardwood trajectories (7-51 yr in 1930) did not complete the transition from deciduous to coniferous dominance over the course of the study period. On the other hand, trajectories that had an average TSF > 60 yr in 1930, with one exception (Bpa1), were conifer-dominated by TSF between 101 and 140 yr, indicating near-complete mortality of the post-fire cohort of intolerant hardwoods.

Stands that start succession with intolerant hardwoods seem to be more prone to a future dominance of *A. balsamea* than those starting with *P. mariana*. In fact, after 57 yr of change, the only trajectories where *A. balsamea* has become dominant (over 75% relative cover) are those that started with hardwood dominance. These composition changes can also be related to spatial context; the presence of *A. balsamea* close to a fire could explain the rapidity of reinvasion by this species. The stands are also very dynamic, with a high frequency of secondary disturbances such as spruce budworm outbreaks or windthrow.

Our results also suggest that when secondary disturbances are severe, *Betula* can maintain itself for a very long time after fire. In one trajectory with a mean TSF of 156 yr, *Betula* still represented 45% of the stand cover in 1987, probably because of the high occurrence of secondary disturbances favouring intolerant recruitment. These results corroborate suggestions that *Betula* can be maintained through sufficiently large secondary disturbances (Kneeshaw & Bergeron 1999; Chen & Popadiouk 2002; Lesieur et al. 2002).

Evolution of Picea mariana Stands

Our results confirm that post-fire succession can start with dominance of *P. mariana* (e.g. Carleton & Maycock 1978; Foster 1985). In trajectories that had a mean TSF < 80 yr in 1930, the change in species composition was generally small, suggesting that the first cohort of trees established after the fire was not yet declining, even though average TSF was over 120 yr by 1987. In older stands dominated by *P. mariana* in 1930, subsequent changes in composition were slight, but changes in stand structure over the 57 yr of the study were revealed by de-

creases in the photo-interpreted age or canopy cover. This suggests that there was some *P. mariana* mortality resulting in a change in vertical structure of the stands, even though we did not identify causes of mortality with our interpretation methodology. These types of structural changes have been suggested by many authors but have so far been difficult to observe directly (Bergeron et al. 1999; De Grandpré et al. 2000; Harper et al. 2002; Boucher et al. 2006).

Fluctuations in Relative Abundance of Picea mariana and Abies balsamea

All trajectories with mixed composition of *Picea* and *Abies* in 1930 were, on average, older than 125 yr, suggesting that a high importance of *A. balsamea* in the canopy can only be reached late in succession (Bergeron & Charron 1994). For the majority of the cells of these trajectories, there were signs of secondary disturbances in 1965 or 1987, or in both periods. Those disturbances are probably linked to the observed fluctuations in relative abundance of *P. mariana* and *A. balsamea* over time. However, the probability of *P. mariana* being totally replaced by *A. balsamea* with increasing TSF appears to be very low. This concurs with the results of Pham et al. (2004), which showed a reciprocal replacement of the two species in gaps, but contrasts with what has been suggested using chronosequence approaches in the same region (De Grandpré et al. 2000).

Our approach does not directly indicate processes involved in these fluctuations, but we can propose some mechanisms. In old stands of *P. mariana*, it is plausible that individual, senescent *P. mariana* trees can be replaced by *A. balsamea* in the canopy (Baskerville 1975; Morin 1994; Kneeshaw & Bergeron 1999; Lesieur et al. 2002). On the other hand, it appears that larger disturbances, such as windthrow and spruce budworm outbreaks, to which *A. balsamea* trees are more vulnerable than *P. mariana*, are very important for maintaining a mixed composition of *Picea* and *Abies* (Pham et al. 2004; Morin et al. 2009). Our results suggest that a combination of disturbances prevents either species from becoming completely dominant.

Conclusion

Our results clearly indicate that in the absence of fire for a long period of time, changes in composition and/or structure in a stand canopy continues even in older stands. Stand break-up in intolerant

hardwoods, with increasing coniferous dominance, appears to be completed on average when TSF is around 120 yr. Stands of this age in the Quebec North Shore landscape are frequently of mixed dominance. Even stands with subtle changes in composition are dynamic due to secondary disturbances such as windthrow or spruce budworm outbreaks. Stand cover or photo-interpreted age can decrease or increase over 30 yr, indicating mortality-driven changes in structure and composition. These results confirm that, as suggested by De Grandpré et al. (2000), Harper et al. (2002) and Lesieur et al. (2002), stand structure can change even when there is no fire over a long time period. Observed variations in stand structure or composition are asynchronous over the landscape, perhaps partly because susceptibility to secondary disturbances depends on stand age or composition, which also vary across the landscape. This contributes to diversity in compositional trajectories.

Even with only a few tree species present in the North Shore region, we find significant variation in stand composition and structure. Moreover, this diversity is only partly explained by the site characteristics and is related to the occurrence of partial and secondary disturbances affecting the forest at many spatial scales. It therefore appears important to develop management strategies aimed at maintaining this diversity of stand types by emulating a broader variety of partial and secondary disturbances if we want to maintain forest attributes in the landscape, along with their associated biodiversity, and succeed in sustainable management of the forest.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table SA1. Description of the observed variables and species codes.

Table SA2. Description of forest types, including conifer proportion in the stand (% basal area) and composition of the conifer and deciduous com-

ponents (% basal area), according to the *ministère de l'Énergie et des Ressources du Québec* (1984). Briefly, the name of the forest type is composed of a couplet of species acronym (Appendix S1). If the relative cover of coniferous trees is higher than 75%, the couplet will be composed of two conifer species, with the most important one coming first. If the relative cover of coniferous species is lower than 25%, then the couplet will be composed of two deciduous species, with the most important one coming first. Finally, when the relative cover of coniferous species is between 25% and 75%, the couplet will be composed of one deciduous and one coniferous species; in that case, we have mixed stands and the species coming first is the most important species in the dominating component (deciduous or coniferous).

Appendix S3. Method and rationale for grouping compositional trajectories into successional pathways.

Fig. SA3.1. Average compositional trajectories (1930–1965–1987) in the DCA ordination space for each initial composition group. Arrow thickness of a trajectory reflects its cell proportion relative to other trajectories within the same composition groups. Trajectories in blue belong to pathway 1, those in red to pathway 2, and those in green to pathway 3. See Appendix S1 for species codes.

Table S3.2. Frequency distribution (% of cells) of compositional trajectories, classified into successional pathways, for time since fire, surficial deposit–drainage and site position on slope. Values in bold indicate a significant over-representation

within the class as compared with the overall distribution, whereas underlined values in bold indicate an under-representation (Pearson χ^2 component, $\alpha < = 0.001$). Trajectories in parentheses were classified into the most probable pathway. Note that trajectories are placed in increasing order of average time since fire within each successional pathway.

Table SA3.3. Mean cover (%) and mean relative cover (%) of tree species and average composition type of each compositional trajectory in 1930, 1965 and 1987. Trajectories in parentheses were classified into the most probable pathway. Note that trajectories are placed in increasing order of average time since fire within each successional pathway. See Appendix S1 for species codes, and Appendix S2 for forest type codes.

Photo S1. In the background, an old *Picea mariana* (Black spruce) and *Abies balsamea* (Balsam fir) forest in the Quebec North Shore Canada.

Photo S2. Close view of an *Abies balsamea* (balsam fir) forest.

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