Logging-induced change (1930–2002) of a preindustrial landscape at the northern range limit of northern hardwoods, eastern Canada

Yan Boucher, Dominique Arseneault, and Luc Sirois

Abstract: Logging-induced changes from preindustrial (1930) to current conditions (2002) were studied in a landscape covering 13 550 ha in eastern Quebec. Age and types of forest cover were compared between 1930 and 2002 forest maps. In addition, we compared relative species abundance between living stems and coarse woody debris to study these changes at the stand scale. More than 90% of the 1930 preindustrial landscape was composed of forest stands older than 100 years. A balsam fir (*Abies balsamea* (L.) Mill.) – white spruce (*Picea glauca* (Moench) Voss) dominated conifer cover (77% of the landscape area) formed the landscape matrix across the lowlands and was intermingled with mixed stands of sugar maple (*Acer saccharum* Marsh.) and conifers on the highlands. As a result of recurrent logging, stands less than 70 years old accounted for 93% of the 2002 landscape. From 1930 to 2002, 37% of the landscape was converted from coniferous to mixed forest, and 19% evolved towards a deciduous cover. The total number of cover patches doubled to 193, whereas mean patch size decreased twofold to 65 ha. Sugar maple, red maple (*Acer rubrum* L.), striped maple (*Acer pennsylvanicum* L.), and white birch (*Betula papyrifera* Marsh.) probably experienced a greater increase in abundance, whereas balsam fir, white spruce, and eastern white-cedar (*Thuja occidentalis* L.) experienced a more pronounced decrease. Because it does not consider preindustrial landscape patterns, the system of ecological land classification currently in use in this area suggests that potential late-successional cover types should be more similar to present-day than to preindustrial conditions.

Résumé : Les changements causés par les coupes forestières ont été documentés dans un paysage de 13 550 ha de l'est du Québec. Les types et l'âge des couverts forestiers ont été comparés entre des cartes établies en 1930 et 2002. L'abondance relative des espèces a aussi été comparée entre les arbres vivants et les débris ligneux grossiers pour quantifier ces changements à l'échelle d'un site. Plus de 90 % du paysage de 1930 était âgé de plus de 100 ans alors qu'une matrice coniférienne de sapin baumier (*Abies balsamea* (L.) Mill.) et d'épinette blanche (*Picea glauca* (Moench) Voss) occupait 77 % de la surface totale du paysage dans les basses terres. Les hautes terres étaient plutôt colonisées par des peuplements mélangés d'érable à sucre (*Acer saccharum* Marsh.) et de conifères. À cause des coupes répétées qui ont suivi, le paysage de 2002 était composé à 93 % de forêts de moins de 70 ans. Entre 1930 et 2002, 37 % du paysage est passé d'un couvert coniférien à un couvert mélangé et 19 % est devenu feuillu. Le nombre total de plaques a doublé pour atteindre 193 alors que la superficie moyenne des plaques a été réduite de moitié à 65 ha. L'érable à sucre, l'érable rouge (*Acer rubrum* L.), l'érable de Pennsylvanie (*Acer pensylvanicum* L.) et le bouleau blanc (*Betula papyrifera* Marsh.) sont probablement les espèces qui ont affiché les plus fortes hausses d'abondance alors que le sapin baumier, l'épinette blanche et le thuya occidental (*Thuja occidentalis* L.) sont probablement celles qui ont subi les plus fortes baisses entre 1930 et l'actuel. Parce qu'il ne considère pas la végétation pré-coupe, le système de classification écologique utilisé dans notre région d'étude suggère que les types de couverts de fin de succession devraient être davantage similaires à la végétation actuelle qu'à celle de l'époque pré-industrielle.

Introduction

The northern hardwoods forest type, dominated by species of the genus *Acer*, *Betula*, and *Fagus*, along with various conifers, occurs in eastern North America at the transition between the deciduous and boreal vegetation zones (Rowe 1972; Bailey et al. 1994). In this area, historical records and studies of virgin stands generally suggest a presettlement disturbance regime dominated by small-scale tree-fall gaps with occasional large windthrows and rare fires (Lorimer

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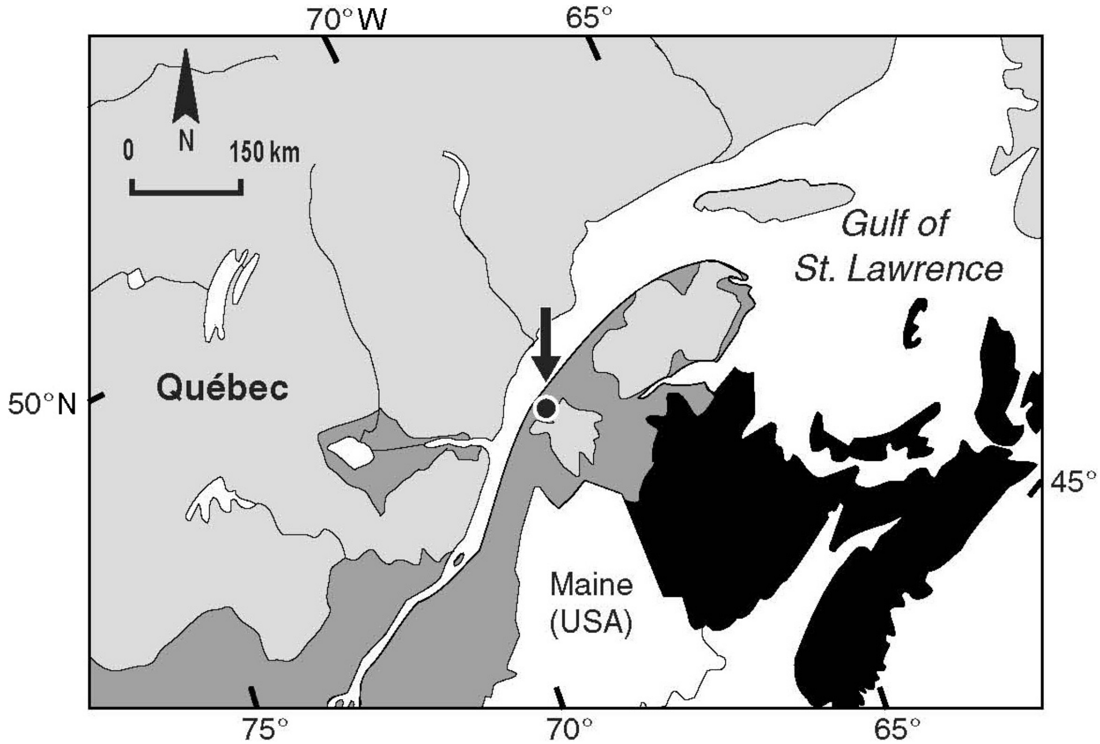
Fig. 1. Location of the Nicolas-Riou seignory in eastern Quebec (arrow) and vegetation zones according to Rowe (1972). The Acadian (black) and Great Lakes – St. Lawrence (dark grey) Forest Regions are mixed coniferous–deciduous. The Boreal Forest Region (light grey) is mostly coniferous.



1977, 2001; Runkle 1981; Payette et al. 1990). However, repeated logging and other land-use activities have disrupted the dynamics of ecosystems and landscapes (Foster et al. 1998; Abrams 2003). A very large proportion of studies comparing early land survey records and recent forest inventories show a marked increase in the abundance of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and birch (*Betula* spp.), whereas American beech (*Fagus grandifolia* Ehrh.) has declined sharply (Siccama 1971; Whitney 1994; Abrams 1998; Burgi et al. 2000; Hall et al. 2002; Leahy and Pregitzer 2003). Other common species (e.g., *Quercus* spp., *Pinus strobus* L., *Picea* spp., *Abies balsamea* (L.) Mill., *Tsuga canadensis* (L.) Carrière) have exhibited more localized behaviour, depending on presettlement abundance and postsettlement disturbance history. In addition, compared with preindustrial conditions, present-day forest landscapes tend to be more fragmented, to be composed of younger forest stands, and to demonstrate a modified influence of elevation on forest composition (Mladenoff et al. 1993; Östlund et al. 1997; Foster et al. 1998; Axelsson and Östlund 2001; Andersson and Östlund 2004).

There is increasing recognition that knowledge of presettlement species abundance and landscape structure helps establish baseline conditions and should therefore be considered when planning forest management (Landres et al. 1999; Axelsson and Östlund 2001; Harvey et al. 2002; Lindenmayer and Franklin 2002; Andersson and Östlund 2004). For example, for the northern hardwood zone of the northeastern United States and for similar vegetation zones of Fennoscandia, records of early land surveys have been extensively analysed to document preindustrial tree species abundance and disturbance regime (Whitney 1994; Linder and Östlund 1998; Östlund et al. 1997; Jackson et al. 2000; Axelsson and Östlund 2001; Ericsson et al. 2005; Schulte and Mladenoff 2005). In contrast, preindustrial forest vegetation and the impact of anthropogenic disturbances are less known for the northern hardwood zone of eastern Canada. This is especially true in Quebec because of the rarity of virgin forest remnants and scarcity of precolonial surveys based on precise, consistent methods. An exhaustive examination of wood sales reported in old notary deeds in an agroforested landscape of southern Quebec (Simard and Bouchard 1996; Brisson and Bouchard 2003) revealed anthropogenic impacts similar to those observed in the northeastern United States (i.e., decrease in beech abundance and increase in maple abundance). However, the nature of the data available in these studies did not allow a detailed examination of the spatial patterning of forest types across the preindustrial landscape, a frequent situation with presettlement forest surveys.

The Nicolas-Riou seignory (hereafter referred to as NRS) is a forest landscape located at the very northern range limit of northern hardwoods in eastern Quebec (Fig. 1). The NRS consists of about 13 550 ha of private land that had been owned by the Lord Nicolas-Riou family since 1751 and was sold to a sawmill company (The Price Brother's Co.) in 1911. Even though forests in the region have been harvested since the early 19th century (Fortin et al. 1993), no large-scale logging occurred in the NRS before detailed forest mapping by the Price Brother's Co. in 1930. The NRS landscape has subsequently experienced several logging and forest-mapping episodes, providing a unique opportunity to describe in a spatially explicit manner how forest cover types

Table 1. Scale and type of aerial photographs used to elaborate the forest maps employed in this study.

Map	Photo scale and type	Map scale	Smallest polygon (ha)	Source
1930	1 : 32 000; BW	1 : 32 000	1	Quebec's national archives at Chicoutimi, Price Fund, maps and plans
1948	1 : 35 000; BW	1 : 50 000	4	Université du Québec à Rimouski's archives
1973	1 : 15 000; BW	1 : 20 000	4	Ministère des Terres et Forêts, Gouvernement du Québec, 1er inventaire décennal, 1975
2002	1 : 15 000; IR	1 : 20 000	4	Ministère des Ressources Naturelles du Québec, 3^{e} inventaire décennal, 1993

Note: BW, black and white; IR, false-color infrared.

Table 2. Correspondence between the 1930 and 2002 age-classes and classification used in this study.

Age-class in present study (years)	Age-class for 1930 map (years)	Age-class for 2002 map (years)
10	Recently burned	10; clearcut, plantation
30	20–40	30, 30–50*, 30–70*; young; uneven aged
50	40–60	50, 50–90*
70	60–80	70, 70–30*, 70–50*
90	80–100	90, 90–30*, 90–50*
>110	>100	120; old, uneven aged

*Two-storied stands.

have evolved in response to recurrent logging. The objectives of the present study are thus (1) to compare forest maps elaborated in 1930, 1948, 1973, and 2002 in order to reconstruct the logging history and quantify landscape structure and composition prior to industrial logging (1930) and thus evaluate subsequent impacts of forest harvesting; (2) to describe the recruitment pattern of tree species and compare their abundance between living trees and coarse woody debris in a representative stand to help explain these landscape changes; (3) to evaluate the management implications of these new data.

Study area

The NRS is located 30 km southwest of Rimouski in eastern Quebec (Fig. 1). It is part of the Appalachian geological formation, characterized by sedimentary rocks capped with in situ weathering and glacial till (Robitaille and Saucier 1998). The topography consists of low hills in a southwest–northeast axis with elevations between 170 and 390 m a.s.l. Information from the nearest meteorological station (Mont-Joli; 50 km northeast of the SNR landscape) reveals a temperate climate influenced by the St. Lawrence Estuary (Environment Canada 2005). Mean annual temperature is 3.1 °C, and mean annual precipitation is 929 mm, of which 38% falls as snow. The growing season lasts for 160–170 days, with 1402 growing degree-days above 5 °C (Robitaille and Saucier 1998; Environment Canada 2005).

The NRS area is at the northern limit of the Great Lakes – St. Lawrence Forest Region (Rowe 1972). More specifically, it is part of the eastern balsam fir (*Abies balsamea* (L.) Mill.) – yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain (Robitaille and Saucier 1998). The landscape is currently dominated by deciduous stands of sugar maple on hilltops and upper slopes and by varying mixtures of red maple, paper birch (*Betula papyrifera* Marsh), balsam fir, and white spruce (*Picea glauca* (Moench) Voss) on mid and lower slopes (Savoie and Joncquas 1995). Eastern white-cedar (*Thuja occidentalis* L.) is frequent in the lowlands. Other less common species include yellow birch, red spruce (*Picea rubens* Sarg.), eastern white pine (*Pinus strobus* L.), and quaking aspen (*Populus tremuloides* Michx.). A study conducted in the southeastern quarter of the NRS indicated that small-scale tree-fall gap was the dominant disturbance during the 18th and 19th centuries (Sorel 2004), presumably in association with low-severity spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks, which recurrently affected the species' main hosts, balsam fir and white spruce (Boulanger and Arseneault 2004). No fire larger than 1 km^2 occurred in this part of the NRS landscape during at least the last 300 years (Sorel 2004), and to our knowledge, use of fire by Native Americans has not been documented as yet. In addition, effective fire suppression started around the 1970s (Grenier et al. 2005). The NRS has always been a for-

Fig. 2. Validation of the 1930 forest map using aerial photographs taken in 1941 over two contrasting areas of the Nicolas-Riou seignory. Similarity between the two maps is depicted by a black area, whereas dissimilarity is indicated by a white area. The 1941 maps were built using the same cover types definition as those used in 1930 mapping and the same smallest polygon threshold of 4 ha as used in the 2002 mapping.

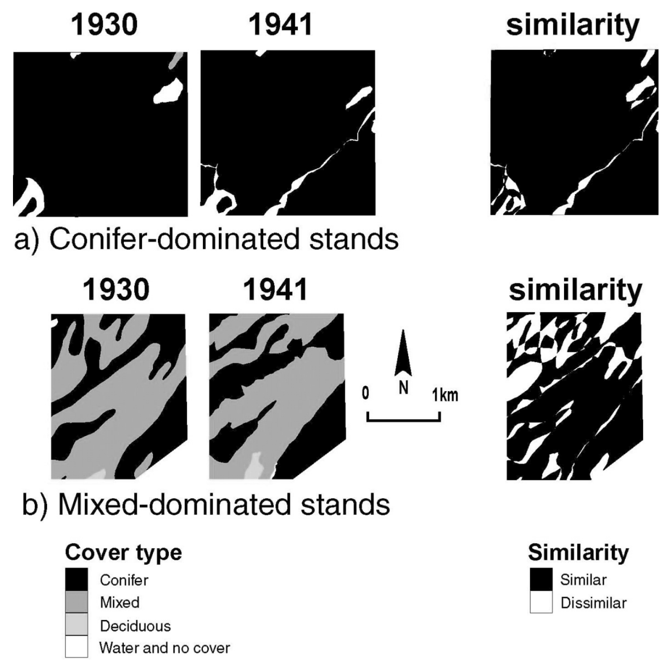
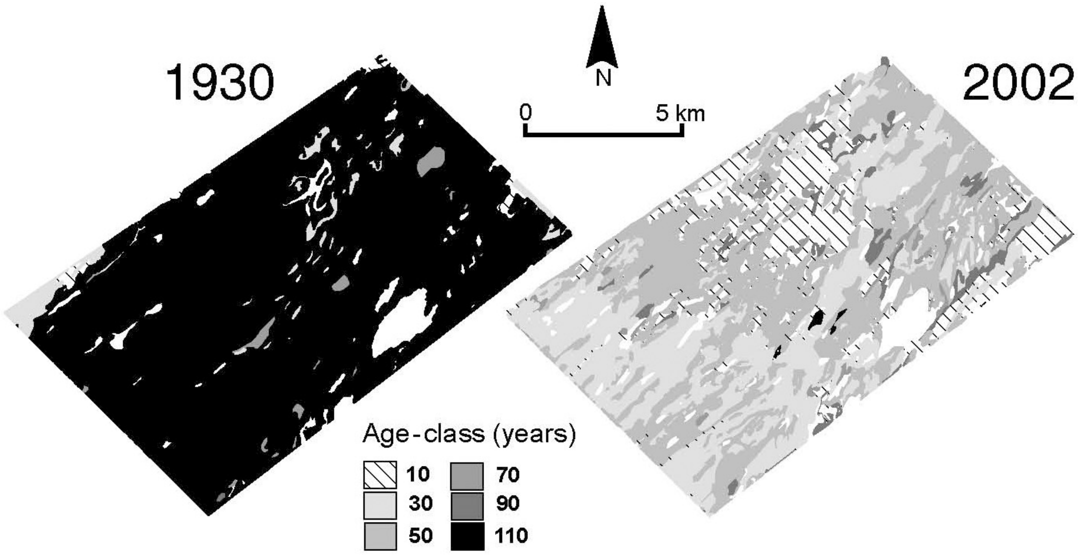


Fig. 3. Age-classes of the forest cover in 1930 and 2002 at the Nicolas-Riou seignory. Age-classes have been reclassified as described in Table 2.



ested landscape and has never been cleared for agriculture because of unsuitable soil conditions.

Methods

Logging history and landscape changes

Landscape changes were reconstructed by comparing age and type of forest cover, as well as logged areas, among forest maps elaborated using vertical aerial photographs taken in 1930, 1948, 1973, and 2002 (Table 1). Maps were digitalized in vector format using ARC/INFO (ESRI 1995), georeferenced using ARCGIS version 8.3 (ESRI 2003), and incorporated into a raster-based geographic information system using IDRISI32 I32.11 (Eastman 1999), with a pixel size of 100 m^2. A digital elevation model generated from a data layer of elevation produced by the ministère des Ressources naturelles du Québec (MRNQ 2002) in 2000 (scale 1 : 20 000; isoline 10 m) was used to evaluate relationships between forest types and elevation.

All four maps were used to reconstruct the logging history during the 20th century. Every polygon originally depicted as "cutover" (1930 map) or "partial cut" and "clearcut" (1948, 1973, and 2002 maps) was considered to have been logged during the time interval since the previous map. We believe that this procedure may slightly underestimate the area logged during each time interval because small-sized cutovers and partially logged areas may have been missed. In addition, areas logged at the beginning of an interval and not classified as such at the end of that interval are also more likely to exist than areas logged just before the end of an interval and classified as recently logged on both of the two following maps. Validation using successive aerial photographs indicated that most areas that apparently escaped logging between 1930 and 2002 were, in fact, logged; this was especially true for the 1930–1948 time interval.

Cumulative impacts of logging were evaluated by comparing forest age and cover types between the 1930 and 2002 maps. Water bodies were excluded from all computations. The 1930 map originally included five age-classes: 20–40, 40–60, 60–80, 80–100, and >100 years. We assigned the 0–20 age-class to four small patches covering 112 ha (0.9% of the NRS area) and labelled as "recently burned". Conifer-dominated cover types (>75% conifer, based on canopy coverage), which were labelled as "softwood", "swamp softwood", or "black spruce" on the 1930 map, were merged here into the "conifer" type. The 1930 map also included "deciduous" (>75% deciduous), "mixed" (>25% of both deciduous and conifers), and "no cover" (recently disturbed and naturally nonwooded areas) cover types. In addition to these four cover types, the 2002 forest map identified the dominant tree species in each mapped polygon. Field validation in a study area similar to the NRS landscape indicates that the tree species dominating each mapped polygon can be accurately identified from aerial photographs (false-color infrared photos; scale 1 : 15 000) for 80% of polygons (Groupe Optivert inc. 2004). Species identification is even more successful (>95%) when sugar maple is the dominant species. Accordingly, cover types and age from the 2002 map were reclassified to match the 1930 classification (Table 2), with the added modification that we separated each of the 2002 "mixed" and "deciduous" types into two subtypes based on the dominant hardwood species. We differentiated stands dominated by sugar maple (subtype A) from those dominated by other hardwoods (subtype B). The dominant hardwood species in this latter subtype were red maple (38% of polygons), white birch (15%), quaking aspen (11%), and unidentified as a result of recent logging (26%). Pixel-to-pixel changes between 1930 and 2002 cover types and subtypes were then cross-tabulated (Eastman 1999). In addition, total area, number of patches, and mean patch size were computed for the 1930 and 2002 maps according to cover types using the FRAGSTAT software (McGarigal and Marks 1995).

Although all forest maps used in this study were elaborated for forest inventory purposes, they were based on aerial photographs of varying quality, scale, and resolution. In addition, 1930 photographs have been badly preserved and only persist assembled as a useless, low-quality mosaic. To ensure that our 1930–2002 comparison of forest cover does

Fig. 4. Types of forest cover in 1930 and 2002 at the Nicolas-Riou seignory. Enclosed squares 1 and 2: areas depicted in Fig. 2; enclosed square 3: area depicted in Fig. 5; star: detailed study site; circle: sugar camp indicated on the 1930 map.

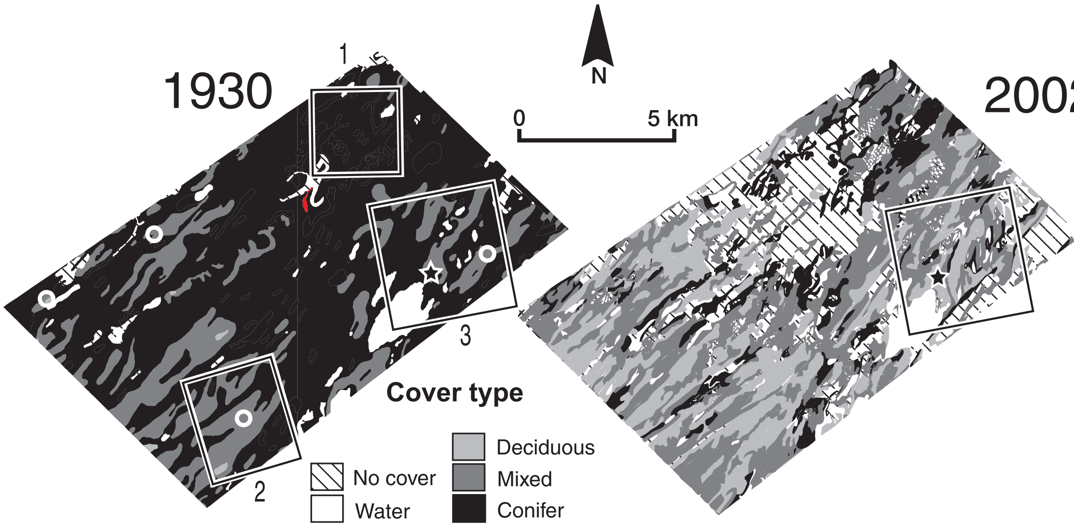
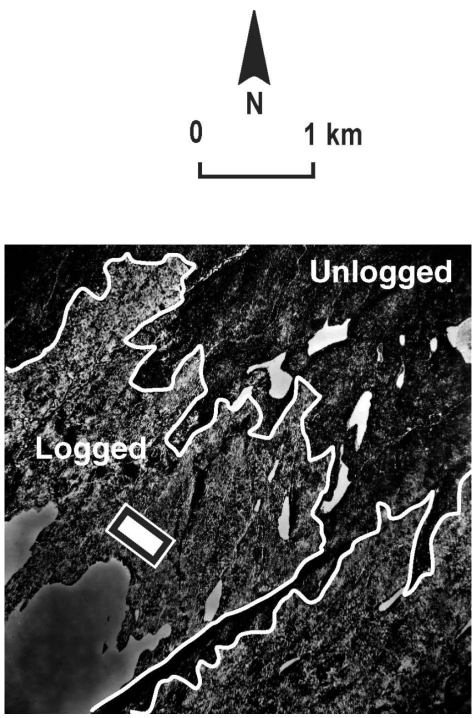


Fig. 5. Aerial photograph taken in the winter of 1941 (original scale 1 : 22 800) and showing the preindustrial conifer-dominated matrix, along with a recent cutover area surrounding the detailed study site (white square).



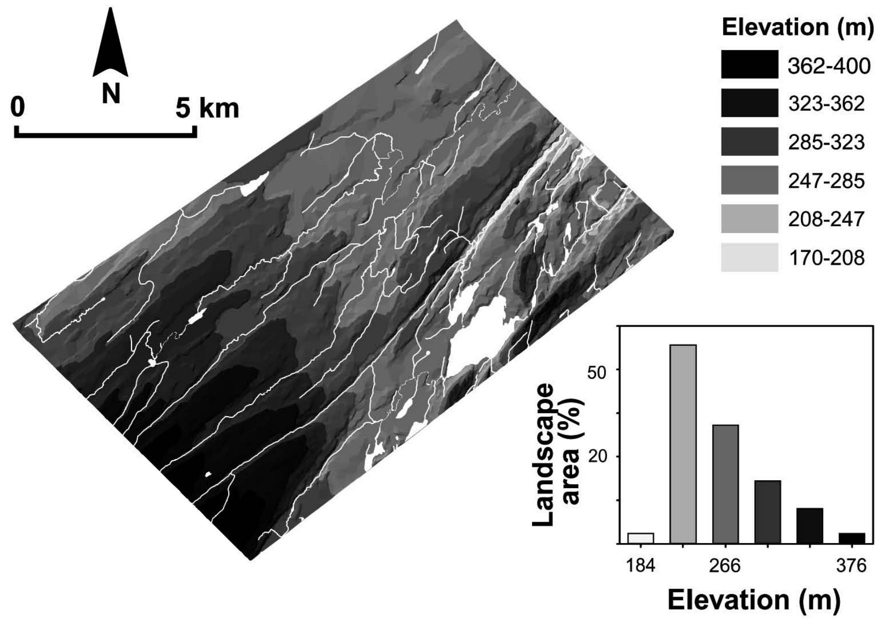
not reflect methodological differences in the construction of the respective maps, we validated the identification and spatial extent of the 1930 forest cover types using a forest cover map that we elaborated using a set of aerial photographs taken in 1941 (scale 1 : 22 800). Although 1941 photographs were taken in the winter (leafless deciduous trees), they constitute the only data source available to validate the 1930 map. Two sectors that were still unlogged in 1941 and collectively represent 10% of the NRS landscape were selected in areas dominated by conifers and mixed stands, respectively, on the 1930 map. Pixel-to-pixel comparison showed similarity of cover types (conifer, mixed, deciduous) of more than 95% and 77% between the 1930 and 1941 maps for the conifer- and mixed-stand-dominated areas, respectively (Fig. 2), which is a fairly good correspondence considering that the 1941 map represents the winter cover. In addition patch size and shape were fairly similar between the two maps (Fig. 2), indicating robust stand delineation in 1930. Accordingly, we have considered that differences of forest cover between 1930 and 2002 do not predominantly reflect methodological artefacts. We did not explicitly validate the 1930 age-classes because of the lack of appropriate data. However, more than 90% of the NRS was then classified as older than 100 years, a situation apparently in agreement with the old-growth structure of the unlogged forest cover remaining on the 1941 aerial photographs.

Stand-level logging impacts on species recruitment and composition

We evaluated the impact of logging on tree species composition at the stand scale by comparing taxon abundance between live stems and coarse woody debris within a homogeneous 20 ha forest stand located on an upperslope at 190–290 m a.s.l. Only one stand could be studied because of the time-consuming sample processing. However, this particular stand was selected because of its representativeness of the most widespread altitudinal band and soil conditions (Humo-Ferric Podzol on well-drained alterite) at the NRS. In addition, the stand's logging history was well known. Comparison of forest maps and successive aerial photographs indicated that the stand experienced severe logging in the 1930s and a few years after 1972. The forest tenant farmer who manages this area of the NRS also indicated that partial logging occurred in 1987 (C. Lemay, personal communication, 2000). Today, the stand is deciduous, whereas the 1930 map indicates that it was mixed.

In total, fifteen 400 m^2 circular plots were systematically located across the stand every 100 m along four transects running perpendicular to the slope. Transects were 100 m apart upslope but spacing increased downslope because of terrain configuration. Living stems were classified into three

Fig. 6. Elevation above sea level over the Nicolas-Riou seignory. Watercourses and lakes are in white. The histogram shows the area occupied by each elevation band.



categories: understorey (stem ≤1 m), subcanopy tree (>1 m and <50% crown exposition to direct sunlight), and canopy tree (≥50% exposition). Because of high stem density, understorey individuals were sampled within one 1 m^2 (genus *Acer*) or 20 m^2 (conifers and other deciduous species) subquadrat. A transversal stem section was taken at ground level in trees less than 15 cm DBH. Stems ≥15 cm DBH were sampled with a Pressler increment borer 30 cm above soil surface. Each wood sample was finely sanded to count tree rings under a binocular microscope. No correction was made to account for the time lag between stem establishment and growth to the sampled height. Growth releases (growth increases of more than 50% over a 5-year period compared with growth in the previous 5 years) were also dated to identify time periods of canopy openings and associated stem recruitment.

At each plot, all woody debris with maximum diameter ≥10 cm were grouped into two categories: (1) stump (remaining basal portions of a previously logged tree); (2) bole (standing, uprooted, or snapped trees). Each debris was identified to species or genus from wood anatomy (Hoadley 1990). Bearing in mind the regional species pool, we were able to identify eastern white pine, balsam fir, and eastern white-cedar to the species level. In contrast, spruce and birch specimens were identified to the genera level. Maples were classified into two groups: hard maple (consisting of only sugar maple) and soft maples (consisting of both red maple and striped maple).

Forest cover in 1930 and 2002 versus ecological land classification

We measured the pixel-to-pixel percent similarity between the potential old-growth cover that could develop from the 2002 stands and the cover in 1930 and 2002 maps. We examined the old-growth forest cover (conifer, mixed, deciduous) projected by the system of ecological land classification developed by the MRNQ (Grondin et al. 1999). This system is based on a detailed field description of soil conditions and relative abundance of late-successional herbaceous and woody species from 3031 plots in the bioclimatic domain encompassing our study area. It identifies eight coniferous, five mixed, and three deciduous old-growth forest types. Based on the geological setting, soil conditions, and species abundance, each present-day stand is associated with a potential old-growth forest type. For example, most successional stands with sugar maple individuals on well-drained soils are suggested to evolve toward old-growth sugar maple – yellow birch stands.

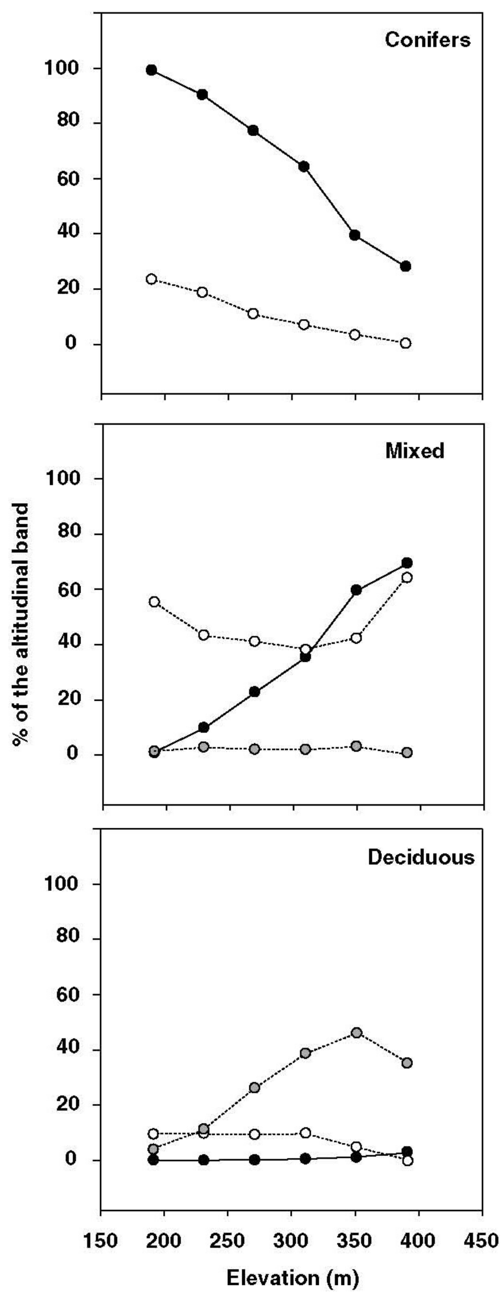
Results

Logging history and landscape change

In 1930, more than 90% of the NRS landscape was composed of forest stands older than 100 years (Fig. 3). Most of the younger stands were small (14.4 ± 3.5 ha; mean ± SE), were in the 30-year age-class, were labelled as cutover, and were located along a small river flowing through the NRS from southwest to northeast. The conifer cover type (77% of the NRS area) was much more extensive than the mixed (21%) or deciduous cover types (0.3%) and clearly formed the matrix of the 1930 landscape with a single patch covering 76% of the NRS area (Figs. 4 and 5). In contrast, the largest mixed and deciduous patches covered only 3% and less than 0.3% of the landscape, respectively. Elevation (and associated environmental conditions) was a strong determinant of cover type in 1930. Abundance of conifer stands progressively decreased from lowlands to uplands, whereas mixed stands displayed the reverse trend (Fig. 7). The few existing deciduous patches were restricted to the highest upper slopes and hilltops (Figs. 4–6).

The NRS landscape was frequently and extensively logged during the 1930–2002 time interval (Figs. 5 and 8). Whereas only 4.2% of the landscape was labelled as cutover in 1930, 57.8%, 56.3%, and 36.7% of this area was logged during the 1930–1948, 1949–1973, and 1976–2002 time periods, re-

Fig. 7. Relative abundance of cover types according to elevation bands depicted in Fig. 6. Solid circles: 1930 covers; grey circles: 2002 covers (subtype A; deciduous component dominated by sugar maple); open circles: 2002 covers (subtype B; deciduous component not dominated by sugar maple).



spectively. Consequently, the logging rotation period (i.e., the time needed to disturb an area equivalent to the NRS) averaged only 48 years during the 1930–2002 time interval. In addition, 43.7%, 39.8%, 17.4%, and 0.37% of the landscape was logged at least one, two, three, and four times during the 20th century, respectively, creating a complex mosaic of stands with differing logging histories.

The NRS landscape changed markedly between 1930 and 2002. Stands less than 70 years old and less than 50 years old composed 93.0% and 73.1% of the 2002 landscape, respectively (Fig. 3). The total number of cover patches doubled to 193, whereas mean patch size decreased twofold to 65 ha (Table 3). The coniferous forest disappeared from 63% of its former area, such that in 2002 it covered only 14% of this landscape (Fig. 4). Conversely, mixed and deciduous covers emerged over an additional 24% and 30% of the NRS landscape to occupy 45% and 31% of its 2002 surface area, respectively. Abundance of no-cover type increased from 1.6% to 10.7% of the NRS area. The size of the largest coniferous patch decreased from 9947 to 212 ha, while the size of the largest mixed and deciduous patches increased from 413 to 2331 ha and from 10 to 478 ha, respectively (Table 3).

Pixel-to-pixel comparison between the 1930 and 2002 maps (Table 4) indicated that 37% of the NRS landscape was converted from coniferous to mixed forest (1.3% subtype A; 35.3% subtype B), whereas 19% evolved towards a deciduous cover (11.2% subtype A; 7.4% subtype B). Accordingly, abundance of conifer stands strongly decreased over the entire altitude gradient (Fig. 7). Conversely, the mixed cover type tended to persist, mainly as subtype B, or to evolve towards a deciduous cover of subtype A. Relative to 1930 conditions, subtype B of the mixed cover increased progressively downslope, such that the mixed cover as a whole no longer displayed a clear relationship with altitude. Collectively, these results indicate that mixed stands of subtype B have tended to replace conifer stands on lower slopes, whereas deciduous stands of subtype A replaced conifer and mixed stands on upper slopes (Fig. 7). In 2002, sugar maple (i.e., cover subtype A) was the dominant species in only 5% of the mixed stands, but it dominated 70% of all deciduous stands (Table 4).

Detailed study site

Deciduous species, particularly sugar maple, largely dominated all canopy layers at the detailed study site. Excluding the understorey layer (stems less than 1 m high), the stand was clearly two storied with canopy and subcanopy stems averaging 933.3 ± 72.0 and 4046.7 ± 447.8 individuals/ha, respectively (Fig. 9). Sugar maple accounted for 60.1% of all individuals in the canopy layer and was followed in dominance by striped maple (12.9%), balsam fir (7.8%), red maple (7.5%), yellow birch (7.1%), paper birch (2.3%), and quaking aspen (1.4%). Similarly, the subcanopy layer consisted of sugar maple (66.0%), along with striped maple (16.0%), balsam fir (10.1%), yellow birch (5.1%), red maple (2.04%), and paper birch (0.6%). Conifer species were rare — apart from balsam fir only one eastern white-cedar and five white spruce individuals were present. The understorey layer ($8.7 \times 10^5 \pm 1.6 \times 10^5$ stems/ha) consisted of a dense seedling bank of sugar maple (89.5% of all individuals), in association with striped maple (7.0%), red maple (2.7%), and balsam fir (0.7%).

Tree recruitment and associated growth releases closely followed the three logging events (ca. 1930–1941, ca. 1973, and 1987) documented from maps, aerial photographs, and anecdotal reports from the forest manager. In fact, recruitment and release pulses help to precisely date the first two logging events (around 1936 and 1973) and to confirm the 1987 logging (Fig. 9). Although relative species abundance prior to logging is difficult to quantify, sugar maple, yellow birch, eastern white-cedar, and balsam fir were growing at

Fig. 8. Logging history at the Nicolas-Riou seignory as reconstructed from forest maps of 1930, 1948, 1973, and 2002. Enclosed square: area depicted in Fig. 5; star: detailed study site.

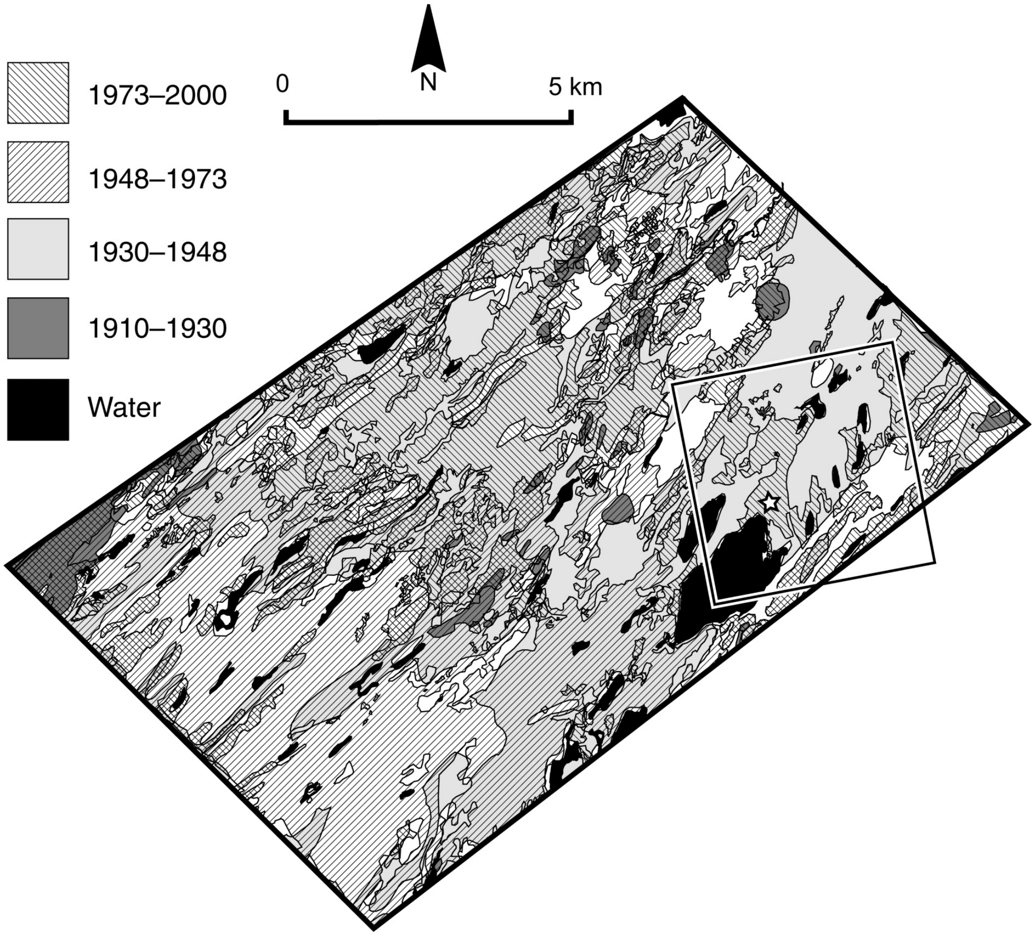


Table 3. Landscape metrics computed from the 1930 and 2002 forest maps.

Cover type	Total area (ha)	No. of patches	Patch size (ha) Mean ± SD	Range
1930				
Conifer	10 044	12	836±2869	1.7–9947
Mixed	2 698	54	50±89	1.5–413
Deciduous	38	6	6±3	2.2–10
No cover	231	19	12±16	1.0–54
All	13 011	91	143±1042	1.0–9947
2002				
Conifer	1 739	64	26±37	4.2–212
Mixed	5 771	40	143±384	4.7–2331
Deciduous	3 914	52	75±100	4.4–478
No cover	1 376	37	33±81	4.0–476
All	12 800	193	65±190	4.0–2231

this site before 1936 (Fig. 9, inset). Recruitment dates indicate that present-day canopy individuals of all species were recruited after the ca. 1936 and 1973 loggings, whereas subcapony trees were mostly recruited following the 1973 and 1987 loggings. The 1973 and 1987 logging events occurred a few years before or during the last spruce budworm outbreak (1975–1992) recorded in this area.

Relative abundance of live stems versus coarse woody debris differed between coniferous and deciduous taxa. All conifer taxa were more numerous among woody debris than live trees, whereas all deciduous taxa were more abundant among live trees than debris (Table 5). For example, 88% of total sugar maple specimens (live or debris) were living, whereas 96% of all eastern white-cedar specimens were woody debris. In addition, all conifer species had more logged stumps than live trees, whereas all deciduous species had more live trees than logged stumps. Balsam fir was by far the most abundant taxon among logged stumps (53%), followed by sugar maple (18%), *Betula* spp. (13%), eastern white-cedar (7%), *Picea* spp. (7%), the soft maples (red and striped maples; 2%), and eastern white pine (0.6%).

Forest covers in 1930 and 2002 versus ecological land classification

The potential vegetation map is similar to the 2002 landscape for 84% (conifer), 81% (mixed), and 62% (deciduous) of its pixels (75% overall). Conversely, the 1930 cover types differed from those suggested at the successional endpoint of the present-day vegetation for 70% of all pixels, a value similar to the 66.6% dissimilarity expected by randomly assigning the three potential cover types across the 1930 landscape.

Table 4. Spatially explicit correspondence (percentage of total landscape area) of cover types between the 1930 and 2002 forest maps.

	2002						
		Mixed		Deciduous			
1930	Conifer	Subtype A	Subtype B	Subtype A	Subtype B	No cover	Total
Conifer	12.2	1.3	35.3	11.2	7.4	9.5	76.9
Mixed	0.9	1.1	7.0	9.9	1.4	0.9	21.1
Deciduous	0.0	0.0	0.1	0.1	0.0	0.0	0.2
No cover	0.3	0.0	1.5	0.2	0.2	0.2	1.6
Total	13.5	2.4	42.8	21.5	9.1	10.7	100.0

Table 5. Abundance of taxa among living individuals and coarse woody debris summed over the 15 studied plots (total surface area of 0.6 ha) at the detailed study site.

	No. of individuals			
	Living	Debris	% living	No. of stumps
Eastern white pine	0	2	0.0	1
Eastern white-cedar	1	24	4.0	13
Picea spp.	5	14	26.3	12
Balsam fir	79	128	38.2	95
Betula spp.	42	38	52.5	23
Soft maples	110	38	74.3	4
Sugar maple	392	54	87.9	32
Quaking aspen	7	0	100.0	0

Note: Only individuals with maximum diameter equal or greater than 10 cm are considered.

The potential vegetation suggested by the ecological classification system underestimated the coniferous cover in the preindustrial forest, as 84% of the misclassified pixels were coniferous in 1930.

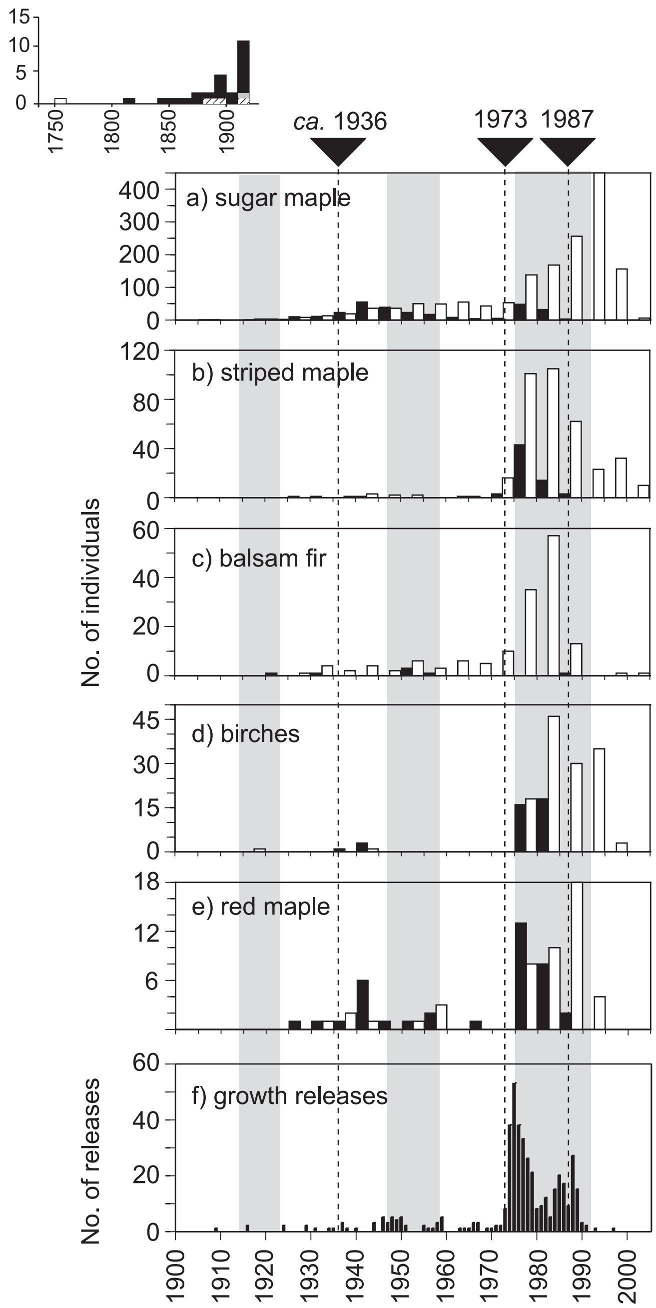
Discussion

This study provides the first evaluation of preindustrial landscape patterns at the northern range limit of northern hardwoods in eastern Canada. Before large-scale logging during the 20th century, a landscape matrix dominated by old-age conifer stands on the lowlands and lower slopes was intermingled with mixed stands on the upper slopes. This marked influence of elevation on cover types suggests that landform and associated drainage and soil conditions, as well as disturbances such as windthrow susceptibility (Foster and Boose 1992), were the primary factors influencing forest landscape structure and composition in the study area, as is the case in several documented presettlement forest landscapes (Siccama 1971; Mladenoff et al. 1993; White and Mladenoff 1994; Abrams and Ruffner 1995; Foster et al. 1998; Cogbill et al. 2002). Because large stand-replacing disturbance was uncommon, succession was of relatively low importance in structuring cover type and age at the landscape scale. In fact, a natural disturbance regime dominated by small-scale treefall gaps with occasional large windthrows and rare fires is a common finding throughout the northern hardwood zone (Runkle 1981; Payette et al. 1990; Brisson et al. 1994; Schulte and Mladenoff 2005). The widespread distribution of the >100 years age-class in 1930 (more than 90% of the NRS) indicates that such a disturbance regime prevailed in the NRS landscape, at least during the few centuries prior to logging. This is also supported by the widespread occurrence of eastern white-cedar, a late-sucessional species (Bergeron 2000; Park et al. 2005), which displayed a high number of contained tree rings and infrequent growth releases prior to logging in NRS (Sorel 2004). In northern Maine (about 100 km southwest of NRS), presettlement fire and large windthrow each recurred at intervals of more than 800 years, such that more than 80% of the landscape reached an advanced successional stage (Lorimer 1977).

Large-scale logging shifted the NRS disturbance regime from gap-phase dynamics to stand-replacing disturbance. Before 1930, logging had been restricted close to a river's course because of the prevalent use of waterways at that time for floating timber from inland forests to sawmills (Fortin et al. 1993). Extensive and repeated logging during the 20th century resulted in a fast rotation period of 48 years, a value that is markedly different from any natural stand-replacing disturbance regime that has occurred in forests of eastern Canada over the last 300 years (Bergeron et al. 2001; Grenier et al. 2005). Further, the spatially heterogeneous history of logging fragmented cover types and age-class distribution to generate patterns similar to those reported for several postlogging landscapes of eastern North America and Scandinavia. Relative to natural conditions, these altered landscapes frequently exhibit greater fragmentation, larger coverage by young and even-aged stands, more abundant and larger open habitats, an altered site–vegetation relationship, and a transitory nature due to dominance by younger successional stages (Mladenoff et al. 1993; White and Mladenoff 1994; Östlund et al. 1997; Fuller et al. 1998; Axelsson and Östlund 2001; Löfman and Kouki 2003). Contrary to 1930 conditions, postlogging succession is certainly a predominant cause of heterogeneity in the present-day NRS landscape.

Because logging is a relatively recent phenomenon in the NRS area, the exclusion and (or) introduction of tree species have probably not yet occurred at the landscape scale. First, although logging increased disturbance frequency and the size of the disturbed patches, all of the most long-lived, late-successional, and tolerant species historically present in eastern Quebec (eastern white-cedar, eastern white pine, white spruce, red spruce, black spruce, balsam fir, sugar maple), as indicated by paleoecological data (Richard et al. 1992; Richard and Larouche 1994) and a 1938 forest survey (Guay 1942), are still present in the NRS landscape. Second, the most intolerant, fast growing, and early-successional species

Fig. 9. Frequency distribution of the innermost tree ring according to species (*a–e*) and growth releases (*f*) summed over the entire studied surface (15 plots; 0.6 ha) at the detailed study site. Empty bar: subcanopy layer; solid bar: canopy layer. The majority of (70%) balsam fir individuals in the canopy layer could not be sampled because of wood decay. Marginal species (quaking aspen, white spruce, and eastern white-cedar) are not shown. Gray bars refer to spruce budworm outbreaks reconstructed from tree rings at a nearby site (2 km away; Boulanger and Arseneault 2004) and vertical broken lines indicate the logging events. The inset shows the frequency of innermost tree rings prior to 1920. Solid bar: sugar maple; hatched bar: yellow birch; grey bar: balsam fir; empty bar: eastern white-cedar.



(quaking aspen, white birch, red maple) that could have benefitted from the modified disturbance regime were also present in the primitive forests (Richard and Larouche 1994). Third, except for the marginal aspen and white pine, species composition is similar between coarse woody debris and live trees at the detailed study site. Thus, although some tree species may have been introduced or excluded at the stand level, the present-day species pool is probably very similar to primitive conditions, although relative species abundance has changed. Several comparisons of present-day forest inventory and presettlement land survey data suggested similar trends in the temperate zone of eastern North America (Zhang et al. 2000; Hall et al. 2002).

Dominant tree species in 1930 can be confidently identified from several sources of information. The 1938 forest survey for eastern Quebec (Guay 1942) indicates that balsam fir (32% by volume), white spruce (13%), eastern white-cedar (2%), white birch (37%), yellow birch (15%), sugar maple (0.8%), and other maple species (presumably red maple; 0.4%) were the only species to occur in measurable amounts in stands older than 100 years across the Rimouski River watershed (1635 km^2), which includes the NRS. Because balsam fir and white spruce are still widespread and locally abundant in the NRS landscape (Savoie and Joncquas 1995), they likely dominated the extensive prelogging conifer matrix. As indicated by their present-day abundance in several stands previously dominated by conifers, white birch and red maple were probably cooccurring species. Conversely, sugar maple most likely dominated the 1930 mixed stands on the uplands of the study area. This is indicated by the strong present-day dominance of this species in upper slope postlogging stands, its occurrence in the only two virgin stands known to persist in a similar topographic situation (D. Arseneault, unpublished data), its apparent dominance in the detailed study site prior to logging (Fig. 9, inset), and the occurrence of four sugar camps in mixed stands on the 1930 map (Fig. 4). A study conducted in unlogged areas of the northern hardwood – boreal forest transition in the Great Lakes area revealed similar landform influence on sugar maple versus conifer dominance and hypothesized that sugar maple is restricted to uplands because of cold-air drainage into the lowlands (Barras and Kellman 1998). Such a landform effect is also a likely explanation of the preindustrial landscape pattern in the NRS. The present-day occurrence of eastern white-cedar woody debris throughout the NRS (Sorel 2004) indicates that this species, although less abundant than fir and spruce, certainly grew in most conifer and mixed stands, a situation that is in contrast with its current almost complete restriction to swamps and cliffs (Savoie and Joncquas 1995; Robitaille and Saucier 1998). A similar presettlement fir–spruce–cedar forest, along with sugar maple – yellow birch stands, also occurred in northern New Brunswick (Etheridge et al. 2005), northern Maine (Lorimer 1977), and nearby regions of the northeastern United States (Siccama 1971; Cogbill et al. 2002).

Our landscape analysis revealed the demise of conifers over the entire altitudinal gradient during the 20th century. These results are parallelled by the contrasting abundance of conifers between live and dead stems at the detailed study site, even when considering that the decomposition rate varies among species (Chueng and Brown 1995; Harmon et al. 2000). For example, present-day abundance of the decay-resistant cedar is by far insufficient to explain its abundance among woody debris (1 vs. 24 individuals). Similarly, the difference between the number of living and dead fir individuals (79 versus 128) would imply that debris of this species persist for about two generations of live trees, an extreme value considering the fast decomposition rate of fir wood (Lambert et al. 1980; Foster and Lang 1982).

Such a decrease of conifers is not surprising given that historically, the regional sawmill industry used almost exclusively conifers rather than hardwoods (Fortin et al. 1993). For example, in 1938 spruce and fir (88%) and cedar (9%) composed the bulk of the trees used by the forest industry in the Rimouski region (Guay 1942). The last spruce budworm outbreak in 1976–1992 is certainly an additional factor explaining the decrease in the abundance of conifers. Based on intensity and duration of associated growth depressions in host species, this event is consistently reported as the most severe outbreak of the last 200 years in eastern Canada (Jardon 2001; Boulanger and Arseneault 2004). In addition, this outbreak triggered extensive salvage logging that may have further reduced conifer abundance. For example, 92 000 m^3 of softwood lumber were harvested in NRS during the 1984–1988 time interval, compared with less than 6000 m^3 of hardwood (Dallain 1989). The abundant balsam fir stumps at the detailed study site probably reflect the 1973 and 1987 logging events, which occurred in association with the last outbreak. However, if the effects of logging are not considered, the spruce budworm outbreak probably remains a insufficient explanation of the decreased conifer abundance, as demonstrated by the still strongly conifer-dominated landscape after a relatively severe outbreak in 1914–1923 (Jardon 2001; Boulanger and Arseneault 2004).

Sugar maple dominated deciduous stands (subtype A) have replaced mixed stands on the upper slopes. A large number of studies have reported that logging has greatly and consistently increased the abundance of sugar maple across the northern hardwood zone (Siccama 1971; Jackson et al. 2000; Hall et al. 2002; Brisson and Bouchard 2003; Whitney and DeCant 2003; Etheridge et al. 2005). Results from our detailed study site illustrate how sugar maple may have benefitted from logging near its northern range limit in the NRS area. Logging of fir, spruce, cedar, and pine individuals, in conjonction with outbreaks of the spruce budworm and postlogging windthrow (Sorel 2004), triggered massive recruitment of sugar maple. Many factors help explain the ecological success of sugar maple following conifer deletion, including a dense seedling bank (Houle and Payette 1991; Goldblum and Rigg 2002), a wide regeneration niche (Barras and Kellman 1998), high shade tolerance, and rapid growth rate in canopy openings (Canham 1985, 1988). Striped maple, a low-stature gap-phase specialist, also dominated at the detailed study site because of large recruitment peaks following logging (Hibbs et al. 1980; Hannah 1999).

Conversely, red maple, white birch, or aspen dominated mixed stands (subtype B) replaced conifers on the lower slopes. This result concurs with several studies showing that these three species are also among those that have exhibited the greatest abundance or frequency increase following logging across their respective geographical ranges (Siccama 1971; Whitney 1994; Abrams 1998; Weir and Johnson 1998; Whitney and DeCant 2003). High shade tolerance and wide ecological niche (maple), abundant seed production and rapid growth (all three species), long distance seed dispersal (aspen), a persistent seed bank (birch), opportunistic seed banking (maple), and abundant sprouting following disturbances (maple and aspen) are some of the characteristics that may have favoured these species (Burns and Honkala 1990; Abrams 1998; Lambers and Clark 2005).

Management implications

Although we have not documented the range of natural variability, our study revealed an unexpectedly high abundance of conifers in the NRS landscape prior to logging. The 1930 landscape, which represented one point within the natural range of variability, consisted of a matrix of late-successional, conifer-dominated forest stands in the lowlands and a greater proportion of conifers in the uplands as compared with present-day conditions. Because the system of ecological land classification currently used to identify late-successional forest stands is calibrated on the present-day landscape, along with the fact that this landscape no longer contains indications that conifers were much more important in the preindustrial forest, the system tends to reproduce the current landscape and thus underestimate conifer abundance in late-successional stands. Consequently, any management guidelines based on such ecological classification, without consideration of historical landscape patterns, will tend to maintain ecosystems and landscape away from prelogging conditions. If sustainable forest management based on natural ecosystem dynamics is to be a goal in the NRS and similar landscapes at the northern range limit of northern hardwoods, then the once extensive conifer-dominated landscape matrix should be restored to a suitable level. Further studies documenting variability of natural disturbance regime and associated tree species dynamics are much needed to refine such a management target.

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