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ARTICLE

Pines and porcupines: a tree-ring analysis of browsing and dynamics of an overmature pine forest

Amélie Rivet, Serge Payette, Dominique Berteaux, and François Girard

Abstract: Past feeding activities of the North American porcupine (*Erethizon dorsatum* L.) in an overmature forest were reconstructed using tree-ring dated feeding scars on jack pine (*Pinus banksiana* Lamb.) trees in Parc national du Bic (Quebec). Following a long fire-free period, most pines that regenerated after the 1847 fire are currently senescent, moribund, or dead, and the youngest trees are nearly 100 years old. Balsam fir (*Abies balsamea* (L.) Mill.), the most abundant species in the regeneration layer, is predicted to replace jack pine given the absence of recent fire and present fire protection practices in the park. According to the age structure of feeding scars, porcupine activity has been particularly high during the 1980s, which is coincident with the creation of the park. Porcupine activity was lower before this decade and in the late 20th century and absent in this century (2000–2015). The recent decrease in the number of feeding scars is consistent with the decline of the porcupine population, as shown by censuses of active dens and inventories of individuals. Observed tree death is linked with tree senescence rather than excessive feeding. In the absence of fire, it is probable that the shift from the overmature pine stand to a balsam fir stand will profoundly affect porcupine activity. This research shows how the study of tree rings can unravel some of the ecological relationships structuring a forest ecosystem through fire, succession, and animal browsing.

Key words: Erethizon dorsatum, feeding scars, jack pine, *Pinus banksiana*, porcupine, postfire succession, tree ring.

Résumé : Les patrons d'alimentation du porc-épic d'Amérique (*Erethizon dorsatum* L.) dans une forêt âgée ont été reconstitués par l'analyse dendrochonologique des cicatrices d'alimentation du pin gris (*Pinus banksiana* Lamb.) dans un parc côtier situé au Bic (Québec). Après une longue période sans feu, la plupart des pins régénérés après le feu de 1847 sont devenus sénescents, moribonds ou sont morts, et les plus jeunes arbres ont au moins 100 ans. Le sapin baumier (*Abies balsamea* (L.) Mill.), l'essence la plus abondante dans la strate de régénération, devrait remplacer le pin gris étant donné l'absence de feu récent et les pratiques de protection contre le feu dans le parc. Selon la structure d'âge des cicatrices d'alimentation, l'activité du porc-épic a été particulièrement élevée durant les années 1980, ce qui coïncide avec la création du parc. Le niveau d'activité du porc-épic était plus bas avant cette décennie et à la fin du 20^{e} siècle, puis nul par la suite (2000–2015). La diminution récente du nombre de cicatrices d'alimentation correspond au déclin de la population de porc-épic documenté par des recensements de terriers actifs et des inventaires des individus. La mortalité observée chez les arbres est liée à la sénescence des arbres plutôt qu'à une alimentation excessive. En l'absence de feu, on s'attend à ce que le remplacement du pin gris par le sapin baumier affecte gravement l'activité du porc-épic dans le peuplement. Cette étude montre comment l'analyse dendrochronologique peut mettre en lumière certaines des relations écologiques structurant un écosystème forestier via le feu, la succession et le broutement par les animaux. [Traduit par la Rédaction]

Mots-clés : Erethizon dorsatum, cicatrices d'alimentation, pin gris, *Pinus banksiana*, porc-épic, succession après feu, cernes de croissance.

Introduction

The North American porcupine (*Erethizon dorsatum* L.) is found naturally in coniferous and mixed forests of North America, from Alaska to Labrador and the Atlantic provinces, except Newfoundland. The distribution of the species also extends to shrubland, tundra, and desert habitats as far south as northern Mexico (Roze and Ilse 2003). In eastern North America, porcupines have been located even in the northernmost forest and tree line sites along the Labrador coast (Payette 2007).

The porcupine spines offer protection against predators such as fishers (*Martes pennanti* Erxleben), Canada lynx (*Lynx canadensis* Kerr), coyotes (*Canis latrans* Say), wolves (*Canis lupus* L.), wolverines (*Gulo gulo* L.), black bears (*Ursus americanus* L.), and cougars (*Puma concolor* L.) (Roze 1989; Roze and Ilse 2003). Nevertheless, predation can sometimes result in significant population decreases (Dodge 1982; Roze 1989; Powell 1993; Sweitzer et al. 1997; Roze and Ilse 2003).

The porcupine is strictly herbivorous, and its diet changes throughout the year according to food preference and accessibility (Roze 1989). Leaves, buds, and fruits from deciduous trees and herbaceous plants are consumed during the summer, whereas the inner bark of trees and conifer foliage are eaten in the winter (Harder 1979; Dodge 1982; Roze 1984, 1989). The winter diet is rich in fiber but poor in nitrogen (Roze 1989), forcing the animal to rely

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A. Rivet and S. Payette. NSERC Northern Research Chair and Département de biologie, Université Laval, Québec, QC G1V 0A6, Canada.
D. Berteaux. Canada Chair on Northern Biodiversity, Université du Québec à Rimouski, 300, allée des Ursulines, C.P. 3300. Rimouski, QC G5L 3A1, Canada.
F. Girard. Département de géographie, Université de Montréal, 520 Chemin de la Cote Sainte-Catherine, C.P. 6128 succursale Centre-Ville, Montréal, QC H3C 3J7, Canada.
Corresponding author: Serge Payette (email: serge.payette@bio.ulaval.ca).

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on its fat-stored reserves and to reduce nitrogen loss in the feces (Fournier and Thomas 1997). For example, the average weight of an adult porcupine in southern Quebec (in the Parc national du Bic, hereafter PNB) increases from 6 to 9.4 kg between May and October (Berteaux et al. 2005) and then decreases in winter because of a low-quality diet (Sweitzer and Berger 1993).

During winter, porcupines often eat the phloem and cambium (inner part of the bark) of trees. For example, in the state of New York and in central Massachusetts, porcupines feed on eastern hemlock (*Tsuga canadensis* L.) (Shapiro 1949; Griesemer et al. 1998), American beech (*Fagus grandifolia* Ehrh.), and sugar maple (*Acer saccharum* Marsh.) (Roze 1984). In New Brunswick, porcupines prefer spruce (*Picea* spp.) and eastern white pine (*Pinus strobus* L.) bark (Speer and Dilworth 1978). In boreal and mixed forests of Quebec, porcupines feed on the bark of paper birch (*Betula papyrifera* Marsh.), eastern larch (*Larix laricina* (Du Roi) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill.) B.S.P.), jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), and eastern white pine (Payette 1987; Klvana et al. 2004).

Given the food preference of porcupines for inner bark, the radial growth of the consumed trees ceases because cambial cells are destroyed, resulting in the production of a characteristic feeding scar showing the exposed xylem. Porcupine feeding scars are easily distinguished from other scars produced by fire, blowdown, or rubbing because of their oval, elliptic, or circular shape. Their position and dimension along the tree also are characteristic, and incisor marks can sometimes be found on the exposed xylem (Payette 1987). The age of a feeding scar is determined by tree-ring counts. When a large number of scars are dated, it gives information on porcupine activity in a given area (Spencer 1964; Payette 1987; Klvana et al. 2004). The number of feeding scars per year may be used to evaluate the activity of the animal at a given site but not the size of the porcupine population.

Tree-ring analysis was used several times to study animal populations. The traces left in the annual rings by herbivores differ across species. For species feeding on tree leaves, for example, a radial growth decrease generally follows defoliation, as observed for moose (*Alces alces* L.) (McLaren and Peterson 1994), Sitka deer (*Odocoileus hemionus sitkensis* Merriam) (Vila et al. 2005), and phytophagous insects (Jardon et al. 1994; Simard and Payette 2001; Filion et al. 2010). Feeding scar dating was used to reconstruct field vole (*Microtus agrestis* L.) (Danell et al. 1981), brown lemming (*Lemmus sibiricus* Kerr) (Erlinge et al. 1999), and northern collared lemming (*Dicrostonyx groenlandicus* Traill) (Predavec et al. 2001) activities. The long-term activities of migratory caribou (*Rangifer tarandus* L.) (Morneau and Payette 1998, 2000; Boudreau et al. 2003) and white-tailed deer (*Odocoilus virginianus* Zimm.) (Querrec and Filion 2008) were assessed by dating trampling scars produced by the animal's hoofs on roots, basal branches, and stems. Rubbing scars left by the antlers of red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) indicate when a site was occupied by these species (Motta and Nola 1996). In addition, tree-ring growth of conifers in open areas and stump dating in riverine sites allow the determination of periods occupied by the North American beaver (*Castor canadensis* Kuhl) (Bordage and Filion 1988; Lafond-Desrosiers 2005).

In this study, tree-ring dating was used to evaluate past porcupine activity in the PNB. This area was selected because of the high density of porcupines observed in the late 1990s to early 2000s (40 individuals·km^{-2}; D. Berteaux, unpublished data) compared with lower densities (1.9–10.7 individuals·km^{-2}) in other regions (Shapiro 1949; Roze 1984; Ilse and Hellgren 2001). Because porcupines feed heavily on jack pine trees of the PNB and because feeding scars found on the trees are well preserved by resin (Klvana et al. 2004), a large jack pine stand was selected for this study.

The analysis of porcupine activity also provides an opportunity to evaluate the dynamics of the jack pine stand, which is currently a lengthy process of demographic and ecological changes likely caused by the advanced age of all of the pines. Jack pine is found in pure, even-aged stands or as a dominant species of the boreal forest over large areas of eastern Canada. In continental areas, jack pine is also an important component of black spruce, paper birch, and trembling aspen (*Populus tremuloides* Michx.) stands. In maritime areas such as the PNB area, jack pine is most likely a component of red pine and northern red oak (*Quercus rubra* L.) stands (Farrar 1996). In eastern Canada, jack pine trees reach sexual maturity at 35 years and can live for over 150 years. Because it bears serotinous cones, the regeneration of jack pine is assured mostly by wildfire (Rudolph and Laidly 1990). In maritime areas where fires are infrequent because of abundant humidity, regeneration of jack pine stands is most likely at risk. Archeological evidence of agriculture and land use in PNB was dated to 8000 years, suggesting that fires may have been used for pasture purposes (Forest and Dionne 2006). Small, controlled fires may have occurred in the recent past to maintain pine stands of the PNB area. However, with the creation of the park in 1984, jack pine dynamics have changed dramatically as the forest is now protected from fire.

In this study, our objectives were to characterize the recent dynamics of a senescent jack pine stand in eastern Canada, to reconstruct past activities of porcupines from feeding scars, to assess the influence of tree size and age on porcupine feeding activity, and to evaluate the impact of porcupine feeding activity on jack pine growth and mortality.

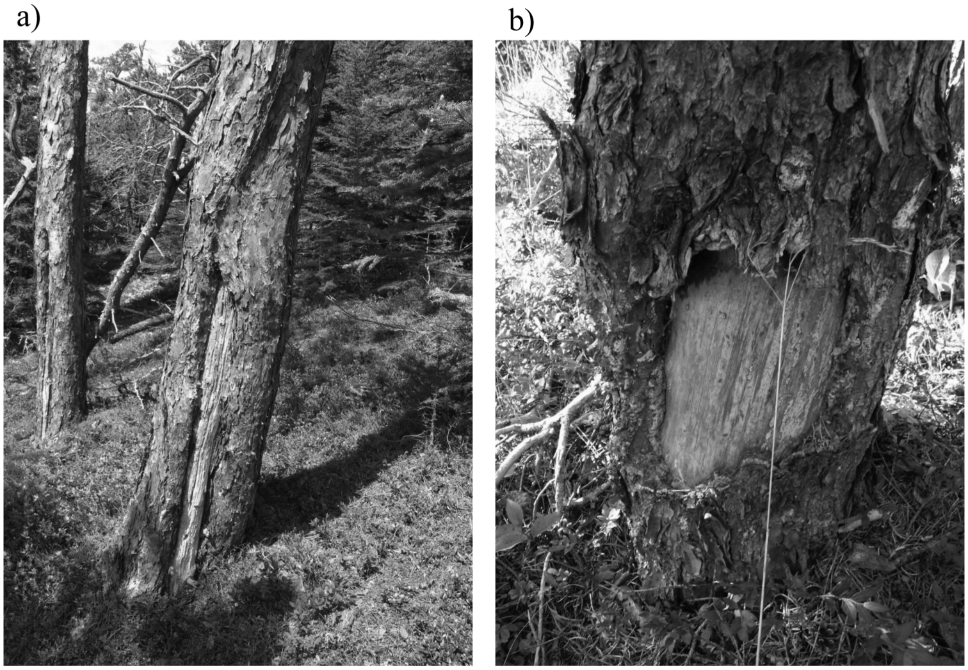
Study site

The studied jack pine stand (14 ha) is located at 48°21′28″N and 68°48′39″W in the PNB area (150 m above sea level, 30 km²), along the St. Lawrence estuary (Pomerleau 1987). The jack pine stand has unique features that make it an ideal study site: (*i*) jack pine bark is highly used by porcupines; (*ii*) feeding scars remain visible and well preserved for more than a century; (*iii*) jack pine growth rings are clearly visible, allowing accurate dating; (*iv*) the old age of this specific stand permits the construction of long time series of past porcupine activity; and (*v*) the stand is easy to access. In addition, porcupines are abundant in the region, but old jack pine stands are rare. The selected stand is close to a study area where capture–mark–recapture of porcupines is ongoing (Berteaux et al. 2005). The protected status of the study area ensured lack of disturbance and long-term access to the pine site.

The tree canopy is mainly occupied by jack pine, but scattered red pine, white pine, white birch, and eastern white cedar (*Thuja occidentalis* L.) trees are also distributed across the stand. Balsam fir and white spruce are the dominant tree species in the understory. The shrub stratum is composed of *Vaccinium angustifolium* Ait., *Arctostaphylos uva-ursi* (L.) Sprengel, *Vaccinium vitis-idaea* L., and other taller shrubs such as *Amelanchier bartramiana* (Tausch) M. Roemer and *Alnus viridis* ssp. *crispa* (Ait.) Turrill. The soil surface is covered by lichens of the genus *Cladonia*, including *Cladonia rangiferina* (L.) Weber ex F.H.Wigg. and *Cladonia stellaris* (Opiz) Pouzar & Vězda, and mosses such as *Pleurozium schreberi* (Brid.) Mitt. Jack pine trees are growing on a well-drained podzol soil composed of more or less decomposed schist material. The pH of the thin organic horizon (3–5 cm) and the B and C horizons is relatively acid, varying from 4.2 to 4.6–4.7, respectively.

The climatic data (1952–1998 period) from the Trois-Pistoles weather station (48°09′N, 69°07′W), located 35 km southwest of the study site, indicate a mean annual temperature of 3.6 °C. The climate is tempered by the large water body of the St. Lawrence River, with a mean January temperature of –11.7 °C and a mean July temperature of 17.6 °C. Precipitation is relatively well distributed throughout the year and totals >1000 mm, 30% of which falls as snow. One of the most important climatic influences of the

Fig. 1. (*a*) Fire scar on a Jack pine and (*b*) porcupine feeding scar on a red pine. (Photo credit: Serge Payette, 20 May 2015.)



proximity of the St. Lawrence River is the extension of the growth season to 140 days (Pomerleau 1987).

Methods

Stand sampling

Size and age structures of the jack pine stand were evaluated using a rectangular plot (20 m × 120 m) positioned at random along the main slope of the site. All the trees, seedlings, and saplings were numbered. The diameter at the base of each tree was measured and the state of each tree was noted (dead or alive; standing or lying on the ground, in the case of dead trees). Scars along the trunk were numbered and their origin was noted (fire, porcupine, or rubbing). The length of lying trees and height of seedlings and saplings were measured.

Tree age distribution was determined by sampling systematically one tree out of two. Only jack pines, red pines, balsam firs, and white spruces with a diameter over 5 cm were sampled. The selected trees were cored as near as possible to the stem base with a Pressler borer. Two cores were taken on each sampled tree. Wood section (samples cut at the base of the stem with a chainsaw) samples were also recovered on about 10 living trees and most dead trees, including a small number of living stems bearing fire scars. Fire scar sampling also was executed on several dead trees to determine the date of establishment of the stand.

Vegetation sampling

The vegetation cover was sampled using the point relevé method (Mueller-Dombois and Ellenberg 1974). Along a 50 m line, all of the plants touched by a fine metal knitting needle at every 25 cm were recorded and identified ($n = 200$ relevés). Because the growing season begins in late May and ends in late August, all of the relevés were conducted in early August when the plants were fully developed. All woody and herbaceous plant species were recorded in each relevé, allowing the calculation of the relative frequency of each species. Also, each plant species common on the site but absent from the relevés was noted.

Feeding scar sampling

All feeding scars found on jack pine trees were sampled for dating in 2006, and a second survey was executed in 2015 (see Fig. 1). Because there were not enough scars in the initial transect to allow robust analyses, scar sampling was done on two other contiguous plots 15 m × 20 m on the eastern and western sides of the main plot, respectively. The expanded transect was then 55 m × and 120 m long (6600 m^2). Feeding scars were cored over the entire diameter of the tree (Spencer 1964). Only one core was taken on each tree, because cross-dating was possible from the growth curve of jack pine constructed from wood sections. Scar height, which corresponds to the distance between the ground and the lower part of the scar, was determined using a measuring tape. Once dated, the standardization of feeding scar abundance was used to measure the effect of tree size on feeding activity. Feeding scar data were also combined using empirical data deduced from porcupine surveys and predation to validate the frequency of feeding scars as a reliable index of porcupine activity.

Tree-ring analysis

All sampled cores were glued on a wooden frame. The cores, the feeding scars, the fire scars, and the sampled wood disks were finely sanded to make the xylem cells visible under a binocular microscope (at 40×). Each sample was visually dated using a master chronology established during preliminary analyses (Klvana et al. 2004). Fire and feeding scar (Fig. 1) dates were calculated by counting the number of tree rings from the bark to the center of the disk and from the scar to the center of the disk. Scars that could not be dated with accuracy ($n = 62$, 14%) were discarded. It is not possible to determine the exact year of a scar's formation, because most feeding scars analyzed were produced during the dormant period, from the fall of a given year to the spring of the following year. Thus, the accuracy of age determination of feeding scars is ±1 year. The year of the growth season preceding scar formation was used as the year of each dated scar.

The ring widths (±0.002 mm) of each core were measured using a Velmex micrometer (Velmex Inc., Bloomfield, NY). Ring-width series were first cross-dated visually and a second check was made using the program COFECHA (Holmes et al. 1986). All of the tree-ring series correlated > 0.65 were included in the master chronology. Each ring-width series was standardized using a 32-year cubic spline with the software package ARSTAN (Cook 1985; Cook and Kairiukstis 1990). The program was used with a double detrending technique: (*i*) a negative exponential or a straight line and (*ii*) a cubic spline function with a 50% cutoff wavelength. The standardization process allows age-related tendencies to be removed from the growth curve to obtain a homogenized variance. The resulting data consist of a dimensionless, standardized index with variations representing the effect of stress factors (climate, insect herbivory, etc.) on tree growth. Once the ring-width series were accurately cross-dated and standardized, elementary series were averaged for each tree and a master chronology was constructed by averaging the residual indexed tree series.

The relationships between the residual jack pine master chronology and climate were investigated using partial least square (PLS) regression (Wold 1995; Amato and Vinzi 2003). PLS regression was chosen because it handles many variables with relatively few observations (Cramer et al. 1988) and deals with correlated variables (Wold 1995). Residual tree-ring chronologies were used to control tree-ring temporal autocorrelation. Residual tree-ring chronology is the difference between predicted and estimated values obtained following standardization processes. The number of components was chosen using a permutation test (Good 1994) with a 5% threshold for the explained variance. Variables were tested with a 50 000-step cross-validation test (Amato and Vinzi 2003). Variables were retained only when the 95% confidence interval for their partial correlation coefficient excluded zero. Monthly climatic variables tested for the regression were precipitation and mean temperature from June of the previous year ($n-1$) to September of the current year (n), and this was performed for the 1950–2005 period. Climatic data were provided by the weather station located in Trois-Pistoles. Grouping of significant variables in the PLS algorithm allowed evaluation of the importance of each variable in the model. The measure of importance of a variable is given by its modeling power. A variable with a modeling power equal to one is completely relevant for building the PLS model. Variables with modeling power close to “number of components” divided by “number of variables” are considered less significant.

Minimum tree diameter for feeding

Stem diameter at the time of scar formation was estimated as twice the distance between the center of the core and the scar. These data were used to estimate the minimum diameter of a stem to be fed on by porcupines. This threshold value corresponds to the average of the minimum diameter distribution of scar formation on trees. Then, two standard errors were removed to the threshold value, allowing 95% of the dataset to be included in the analysis. The proportion of trees with a diameter larger than the threshold value was calculated. An approximation of porcupine feeding period (±1 year) on a tree was determined for each sampled scar. Also, tree diameter at the moment of feeding was assessed based on tree-ring dating. The addition of all tree-ring widths is used to determine the year when the minimum diameter threshold is reached. A cumulative curve showing the proportion of jack pine trees with a diameter (measured at the stem base) larger than the threshold value was constructed, allowing us to evaluate the number of trees available for yearly porcupine feeding. This proportion of trees was then standardized to avoid overestimation of porcupine activity. Furthermore, feeding scar circumference was measured to calculate the percentage of the tree circumference impacted by porcupine feeding on the trunk. A nonparametric paired *t* test was used to evaluate if foraging had a significant impact on radial growth. To do so, a 5-year average of annual growth before the event was compared with a 5-year average of annual growth following the event.

Additional statistical analysis

Frequency of feeding scars

The chronology of feeding scars was standardized using the number of trees available for porcupine feeding. The standardized annual frequency corresponds to the ratio between the number of dated scars and the number of trees with a diameter over the minimum diameter threshold value. The logarithmic distribution of scar age was used in a linear regression to simulate a constant loss of scars with time (Morneau and Payette 2000). The residuals of the linear regression were calculated to evaluate the number of feeding scars with time.

Predators and porcupine population

Since 1984, the sales of fisher furs have been listed in a database of the Ministère des Forêts, de la Faune et des Parcs (MFFP, Quebec), the “Système Fourrure”. These transactions are used to estimate the annual catch of fishers in different regions of Quebec where the species is trapped. According to Fortin et al. (2004), the yield (or the number of captures per 100 km^2) is considered the best indicator to monitor fisher populations. These data have been used to document the dynamics of the fisher population in the Bas-Saint-Laurent region. The yield is calculated as the ratio between the number of fishers caught in a year (1 September to 31 August of the following year) and the size of the area, which is 21 873 km^2 for Bas-Saint-Laurent (Poulin et al. 2006). The relationship between the number of porcupine feeding scars and the fisher yield was then evaluated.

Results

Vegetation

With a relative frequency of 12%, jack pine is the dominant tree species in the forest. Jack pine frequency is almost six times higher than that of paper birch (2%), the second most encountered species in the canopy. The understory is mainly composed of *V. angustifolium* (12%) and *A. uva-ursi* (11%). *Amelanchier bartramiana* (3%) is also found but remains marginal. The forest floor is covered by mosses such as *P. schreberi* (11%) and *Dicranum polysetum* Sw. (4.5%) and the lichens *C. rangiferina* (2%) and *C. stellaris* (1%) (Table 1).

Size and age structures

Two forest fires have occurred on the site in the second half of the 19th century, in 1847 and 1867. These disturbances have greatly influenced the age structure of jack pine, because the species regenerates mainly after fire. The size structure (in the 1867 fire area) of the two dominant tree species, jack pine and balsam fir, differs greatly (Fig. 2*a*). Balsam fir distribution follows a reversed J-shaped distribution. The 0.1–2 cm size class is the most represented size class in the stand, with 41% (n = 211) of all of the measured individuals. The next class (2.1–4 cm) is nearly half the first class, with 21% (n = 109) of all balsam firs. The stem diameter of balsam fir varies between 0.1 and 19.4 cm, but less than 1% of the trees are found in the two highest size classes (16.1–18 and 18.1–20 cm). The median size distribution is 2.7 cm and corresponds to a large number of small balsam firs in the stand. The size distribution of jack pine, which follows a normal distribution (Shapiro–Wilk (hereafter SW), $p > 0.05$), was determined based on data of living trees (n = 202), i.e., 47% of the pines measured in the initial transect. Jack pine diameter varies between 6.7 and 34.4 cm. No jack pine stem is found in the size classes < 6 cm. The 18.9 cm median size distribution for jack pine is seven times higher than that of balsam fir.

The age structure of balsam fir and jack pine are different (Fig. 2*b*). Balsam fir (n = 66) occupies the youngest age classes, with minimum age values varying between 13 and 76 years. The mean age of balsam fir is 31 years (σ = 18.1). The minimum age of jack pine trees varies between 97 and 155 years, with a mean age of 131 years, i.e., nearly four times the mean age of balsam fir. The relationship between the diameter and the age of all jack pines measured is not significant (R^2 = 0.001, $p > 0.05$). Data on the minimum age of jack pine show that the stand is composed of two postfire cohorts. The average age of the 1867 postfire cohort is 144 years ± 5.5 and includes jack pines older than 136 years. The

Table 1. Frequencies of trees, shrubs, mosses, lichens, and herbaceous species sampled every 25 cm along a 50 m line in the overmature jack pine forest of the Parc National du Bic, Quebec.

Species	*n*	Frequency (%)
Trees		
Pinus banksiana Lamb.	68	11.58
Betula papyrifera Marsh.	11	1.87
Pinus resinosa Ait.	10	1.70
Abies balsamea (L.) Mill.	4	0.68
Thuja occidentalis L.	2	0.34
Shrubs		
Vaccinium angustifolium Ait.	68	11.58
Arctostaphylos uva-ursi (L.) Sprengel	63	10.73
Amelanchier bartramiana (Tausch) M. Roemer	19	3.24
Vaccinium vitis-idaea L.	11	1.87
Alnus viridis ssp. *crispa* (Ait.) Turrill	7	1.19
Diervilla lonicera Mill.	7	1.19
Prunus pensylvanica L.f.	6	1.02
Sorbus americana Marsh.	1	0.17
Mosses		
Pleurozium schreberi (Brid.) Mitt.	64	10.90
Dicranum polysetum Sw.	25	4.26
Lichens		
Cladonia rangiferina (L.) Weber ex F.H. Wigg.	13	2.21
Cladonia stellaris (Opiz) Pouzar & Vězda	6	1.02
Herbaceous species		
Deschampsia cespitosa (L.) Beauv.	27	4.60
Aster macrophyllus L.	21	3.58
Linnaea borealis L.	17	2.90
Maïanthemum canadense Desf.	13	2.21
Deschampsia flexuosa (L.) Trin.	8	1.36
Melampyrum lineare Desr.	4	0.68
Carex sp.	2	0.34
Diphasiastrum complanatum (L.) Holub	2	0.34
Chimaphila umbellata (L.) Barton	1	0.17

size and age distributions of red pine and white spruce were not determined because of the small number of trees in the stand.

Tree-ring growth of jack pine

The growth curve of jack pine follows a postdisturbance pattern common to pioneer trees, with an initial rapid radial growth in the first decades after fire followed by sustained growth reduction for the rest of the lifespan of the trees (Fig. 3*a*). The two growth peaks on the curve correspond to the initial growth of trees of the two postfire cohorts of 1847 and 1867. The standardized index curve (Fig. 3*b*) shows the yearly variations of ring width irrespective of tree age. The curve varies around a mean index of 1.0 ± 0.2. About 70% of the indexed values vary between 0.8 and 1.2, whereas the remaining values (30%) are beyond one standard deviation. Less than 5% of the indexed values are beyond two standard deviations relative to the mean.

The response functions of the jack pine indexed residual chronology to climatic parameters show tree growth to be associated with less precipitation during winter or early spring (January to April) and abundant precipitation during summer and fall (June to September) (Fig. 4*a*). Mild temperature during spring (March to May) was correlated with growth. On the other hand, low mean temperature during the current and previous summers was positively correlated with growth. This model explained 64% of the variance and was highly significant ($p < 0.01$). The annual radial growth of jack pine has been estimated with this model and compared with the measured values. Grouping of significant variables showed that precipitation and mean temperature of current summer (June to September) were the most important variables (power > 0.5) for jack pine (Fig. 4*b*). The standardized mean curve of jack pine was significantly correlated with the estimated curve ($R^2 = 0.60$, $p < 0.001$) (Fig. 4*c*).

Feeding scars

A total of 528 porcupine scars were surveyed on jack pine trees (Fig. 5*a*). A large proportion of the scars, i.e., 457 scars, were located at less than 4 m above the ground. Among the <4 m high scars, 395 scars (86%) were dated accurately, and scar height was measured for 392 of them. The 528 feeding scars were distributed among 238 jack pines. The number of scars per tree ranged between 1 and 13 and averaged 2.2 scars per tree. However, almost half of the trees ($n = 118$) had only one scar. Among the trees ($n = 92$) having several dated scars, almost half of them had at least two scars produced during the same year ($n = 42$). Tree diameter at the time of scar formation follows a normal distribution (SW, $p > 0.05$) centered on an average value of 14.5 ± 4.7 cm. Porcupines fed on 33.7% ± 18.4% of the stem circumference (feeding scars occupy maximum and minimum proportions of the stem circumference of 77.5% and 9.3%, respectively). No significant radial growth decrease in each tree-ring series was observed following foraging ($p > 0.05$ for each series).

The age distribution of porcupine scars indicates that the pine stand has been visited sporadically at least since 1873 (Fig. 5*b*). Scar frequency was particularly high between 1980 and 1997 (68% of all the scars dated). During this period, the maximum frequencies occurred in 1987, 1988, and 1989, with 25, 23, and 20 scars dated, respectively, i.e., 21% of the total number of scars. Before 1980, the highest scar frequencies were registered in 1965 ($n = 7$) and in 1973 ($n = 6$). Before 1955, the number of scars dated per year was small, and in most years, no scar was apparently formed, as, for example, from 1914 to 1928. No feeding scar was formed between 2000 and 2015.

To evaluate the influence of tree size on the age distribution of porcupine scars, a minimum stem diameter was fixed at 5 cm. The formation of a porcupine scar on stems < 5 cm diameter is exceptional. Moreover, the origin of scars formed on small stems is difficult to identify because peripheral bulges often completely cover the scars. The number of stems > 5 cm diameter has been used to evaluate the potential number of scar-bearing stems. Every year, this number corresponds to the cumulative proportion of jack pine trees with a diameter > 5 cm. For example, about 50% of the pine stems found today in the stand had the minimum diameter threshold in 1900. Thirty years later, this proportion has reached 90%. The scar age distribution weighted according to the number of potential scar-bearing stems (Fig. 5*b*) differs from the unweighted age distribution (Kolmogorov–Smirnov test (KS hereafter), $p < 0.05$). The main difference between these two distributions is related to the frequency of scars formed before 1900. This difference is due to the small number of trees available for porcupines at this time. According to the weighted age distribution, scar frequencies for the years 1879, 1888, and 1896 were comparable with those calculated for the mid-1980s. Also, scar frequencies for the years 1884, 1885, and 1897 were similar to that of the year 1965.

The spatial variability of the scar age distribution was analyzed according to scar height along the tree stems (Fig. 6). Scars were classified into four groups according to height along the stem: 0–1 m (group 1, $n = 205$), 1–2 m (group 2, $n = 76$), 2–3 m (group 3, $n = 62$), and 3–4 m (group 4, $n = 49$). All four scar age distributions coming from different sections of the tree show a maximum of scars formed in the second half of the 1980s. In addition, a peak in the formation of scars from groups 1, 3, and 4 occurred during the 1990s. Group 2 was characterized by a high percentage of scars formed before the 1980s. The scar distribution of group 2 is indeed significantly different from those of groups 1 and 4 (KS, $p < 0.05$), but similar to that of group 3 (KS, $p > 0.05$). The distributions of scars of groups 1, 3, and 4 were similar (KS, $p > 0.05$).

Fig. 2. (*a*) Size structure (diameter at breast height (dbh), 2 cm classes) of balsam fir (black bars) and jack pine (gray bars). (*b*) Age structure (5-year classes) of balsam fir (black bars) and jack pine (gray bars).

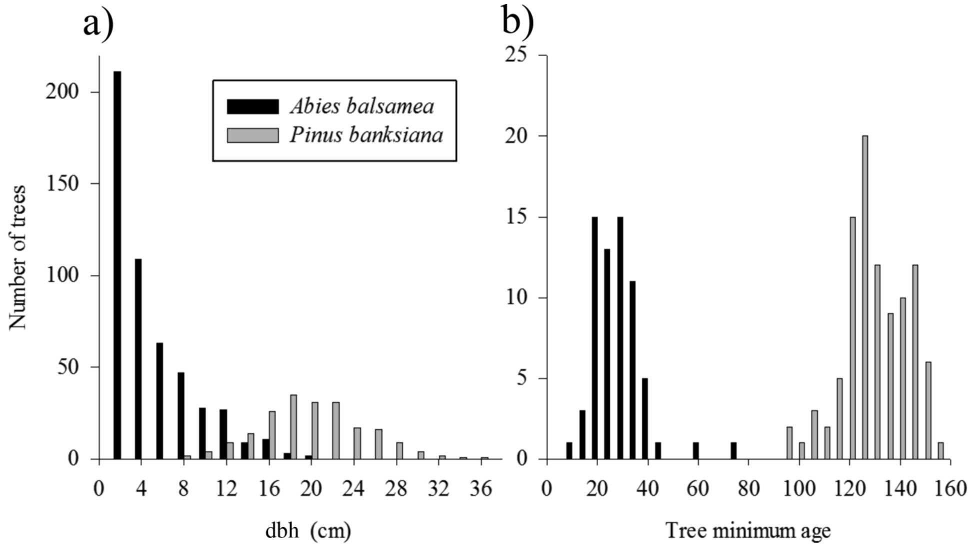
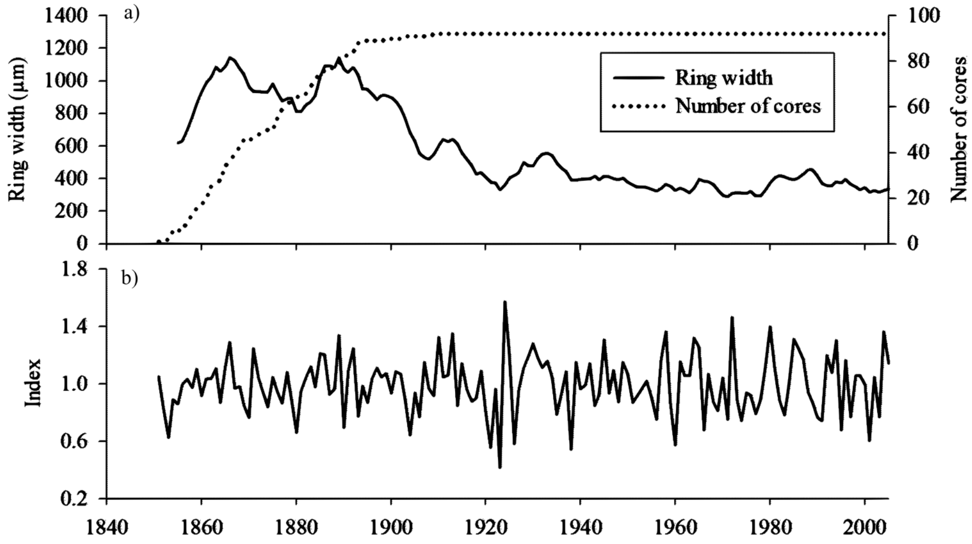


Fig. 3. (*a*) Averaged ring width of jack pine cores (solid line) and number of cores used to average the master chronology (dotted line). (*b*) Indexed master chronology of jack pine used for further calculations.



A slight but significant increase ($p < 0.05$) in the number of feeding scars was observed through time. The use of residuals instead of true values allows one to remove the long-term positive trend through time and shorter-term fluctuations of porcupine activity (Fig. 7). Residuals were positive for a period of 18 years, between 1979 and 1997, particularly in the late-1980s. Before this period, residuals close to the 1980s values only occurred in 1896 and 1897. Residuals suggest moderate peaks of activity in 1888, 1935, 1945, and 1965.

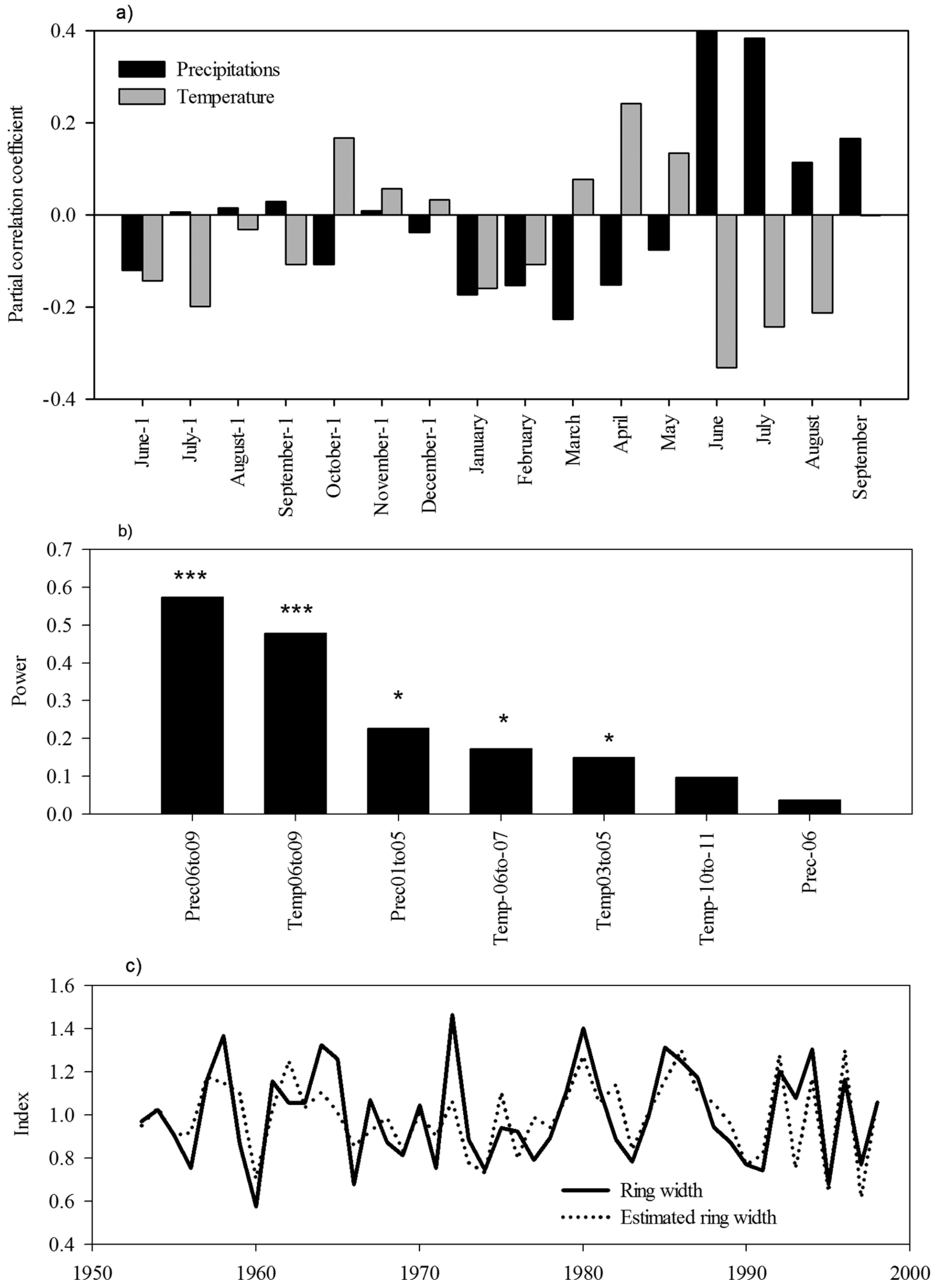
Predation and porcupine population

Over the period 1985–2005 preceding field sampling, the number of fisher captures significantly increased in the Bas-Saint-Laurent region ($R^2 = 0.74$, $p < 0.001$) (Fig. 8). Between 1984–1985 and 1991–1992, it stayed under 2 captures per 100 km², with an average of 1.48 captures per 100 km². During the 1997–1998 season, the yield exceeded 3 captures per 100 km² and has remained above this value since 1999–2000. Between 1997–1998 and 2005–2006, the average yield was 3.84 captures per 100 km², which is 2.6 times higher than in the 1980s. The relationship between the number of porcupine feeding scars and the fisher captures is negative and highly significant ($R^2 = 0.54$, $p < 0.001$).

Discussion

At the southeastern limit of the jack pine range, on the Atlantic coast of Maine, Conkey et al. (1995) observed a high mortality and a low recruitment of jack pine in a forest that has not burned since the 19th century. This is a situation similar to that described in our study site, where the absence of fire for nearly 150 years has prevented pine regeneration. The youngest jack pines at our site are 100 years old. In general, jack pine becomes senescent after 80 years, or even after 60 years in nutrient-poor sites (Rudolph and Laidly 1990). Most jack pine trees 130–150 years old are senescent, moribund, or dying (Desponts and Payette 1992; Le Goff and Sirois 2004). This explains why nearly two-thirds of the trees are currently moribund or dead, and radial growth of living trees is declining rapidly.

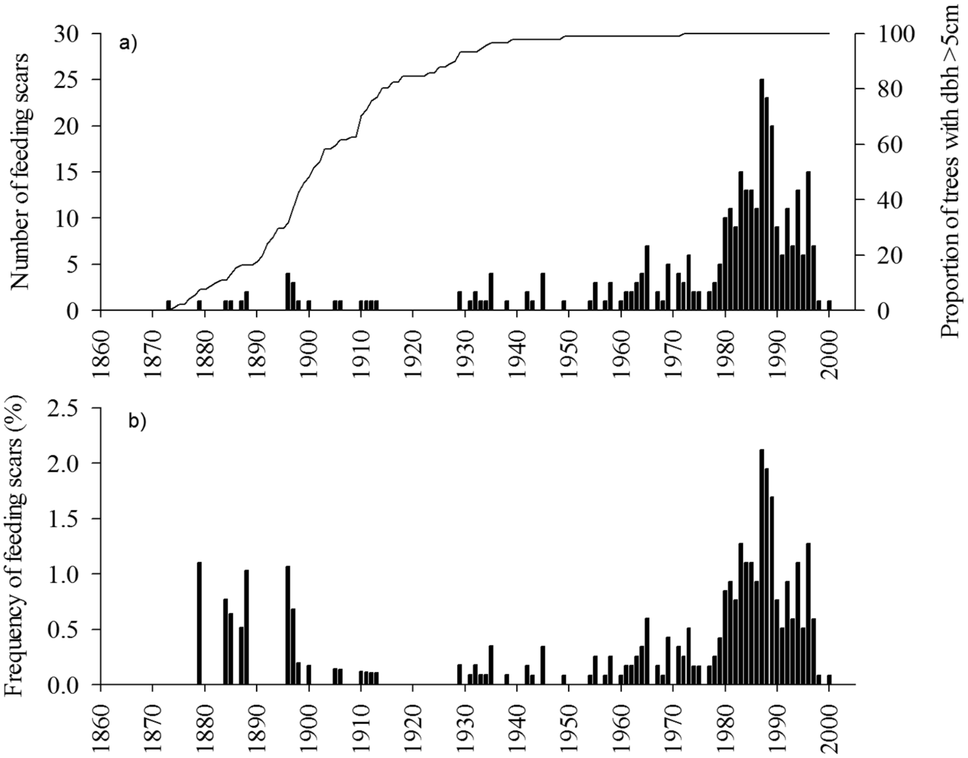
Fig. 4. (*a*) Response function results for jack pine for June of the previous year to September of the current year. Black bars represent mean monthly precipitation; gray bars represent mean monthly temperatures. (*b*) Statistical power of each variable in the response function PLS model. Asterisks indicate the significance of each variable in the model (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$). (*c*) Master indexed chronology (bold line) and modelled ring width (dotted line) using response functions results from 1950 to 2000.



Unlike jack pine, balsam fir is susceptible to forest fires. The majority of individuals are decimated after a forest fire of moderate intensity (Heinselman 1981). When fire is absent for several years, shade-tolerant species and species susceptible to fire grow in height in gaps created by the death of dominant trees. In a jack pine forest, this situation occurs after a period of about 75 to 105 years following a fire (Cayford and McRae 1983). In the jack pine forest, the abundance of balsam fir saplings and small trees in the shrub and tree layers suggests that this species is taking advantage of gaps created by dead pines. This can already be seen in some areas where balsam fir has reached heights comparable with those of jack pine in the 1867 and 1847 fire areas (Fig. 9).

The age and size distributions of balsam fir would probably have a similar form if sampling had not been restricted to individuals with a diameter greater than 5 cm. The youngest age classes are occupied by balsam fir, which confirms that this species contributes largely to the regeneration of the forest. However, these observations have not been validated by the vegetation survey where balsam fir is less abundant. The vegetation survey was conducted in the central area of the 1867 fire area, which was selected at random. This area had a less dense understory than the rest of the pine stand. In the absence of fire, the jack pine stand is in a process of major demographic and ecological changes and transformation toward a balsam fir stand.

Fig. 5. (*a*) Age structure of porcupine feeding scars (black bars) and the proportion of trees having a diameter at breast height (dbh) > 5 cm (gray line). (*b*) Weighted frequency of porcupine feeding scars.



It has been suggested that jack pine growth is influenced by climatic conditions of both previous and current years (Hofgaard et al. 1999; Meinzer et al. 2011; Genries et al. 2012). As for many other tree species, the current annual growth is mostly predetermined in annual buds (Pallardy 2010). The response functions for jack pine in the PNB were similar to those observed for this species and black spruce elsewhere in the southern boreal forest (Hofgaard et al. 1999; Genries et al. 2012). Jack pine growth was strongly related to summer rainfall and temperature of the current year. On the other hand, a rather minor influence of climate of the previous year on radial growth has been observed in the PNB. This suggests that climate was not a limiting growth factor in this site during the studied period. Along the St. Lawrence estuary, the climate is humid and chilly throughout the year, which is favorable for jack pine and balsam fir growth. The deformed shape of jack pine trees in the PNB site was not caused by exposed climatic conditions; this is the consequence of asymmetric growth and senescence of several trees that are facilitating blowdown and gap expansion (Fig. 9).

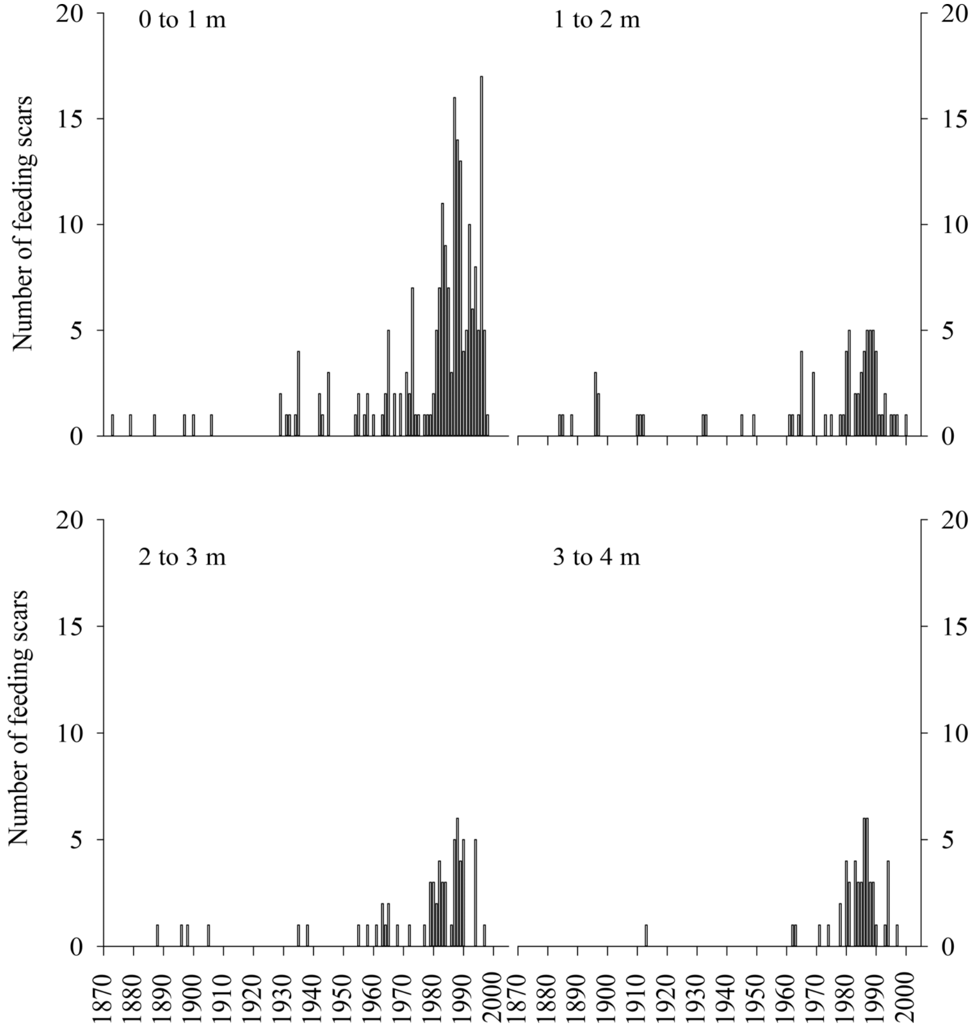
Feeding scars and porcupine activity

Past porcupine activity over the last centuries has been reconstructed from tree rings in contrasted environments from the arctic tree line (Payette 1987) to the mixed forests and semi-deserts of southwestern and northeastern North America (Spencer 1964; Payette 1987; Klvana et al. 2004). Our data cover 150 years of porcupine activity in an overmature pine forest where the animal population fluctuated largely with repetitive lows and highs. The protected status of the study area ensured reduced stand disturbances. Stand development and senescence similar to what was observed in PNB is rare in the eastern boreal forest, because the fire interval is shorter than the time to achieve senescence. The long-term absence of fire and other disturbances in PNB allowed porcupines to occupy the pine stand for nearly 150 years. The distinctiveness of this stand is due to its disturbance history, climate, and location, all factors that render comparisons with other sites occupied by porcupines difficult. The oldest scars found on the trees date back to the early 1870s. The time elapsed between the first fire event and the age of the first scars formed on the young, rapid-growing pines was long enough to provide a large number of food-stored stems able to sustain a growing porcupine population.

Many porcupine scars were produced from the early 1980s to the mid-1990s. Compared with previous years, the increase in the number of scars fits well with the early stages toward the creation of the PNB in 1984. Indeed, land expropriation within the park's boundaries began in the late 1970s (Pomerleau 1987). PNB has become a suitable habitat for porcupines for three reasons: (*i*) the conservation status of the park has led to protection of the animal; (*ii*) numerous rock and tree cavities provide porcupines with natural refugia against harsh winter conditions (Roze 1987; Griesemer et al. 1996) and potentially biting insects (Comtois and Berteaux 2005); and (*iii*) the diversified vegetation cover offers abundant food of high quality to porcupines, especially trembling aspen leaves (Morin et al. 2005). Even though the status of PNB provides protection, shelter, and food for porcupines, our data show a decreasing number of scars since the mid-1990s and even the absence of scars during this century, from 2000 to 2015. The decline in the activity of porcupines is probably caused by a decrease in the population itself.

Few predators specialize enough on porcupines to affect their population dynamics (Roze 1989). The cougar would have caused the near extinction of porcupines in the Great Basin Desert (Sweitzer et al. 1997), but this predator is rare in most of the porcupine's range. In Quebec, the cougar population has probably never been abundant (Tardif 1997). Of all known porcupine predators, fishers may have the morphology and behavior best suited to attack and kill porcupines, and porcupines are an important component of their diet (Mabille and Berteaux 2014). In some areas, porcupines can constitute up to 35% of the fisher's diet (Powell 1993), and fisher re-introduction can significantly reduce

Fig. 6. Age structure of porcupine feeding scars according to height of scars on trees: (top left) group 1, 0–1 m (*n* = 205); (top left) group 2, 1–2 m (*n* = 76); (bottom left) group 3, 2–3 m (*n* = 62); and (bottom right) group 4, 3–4 m (*n* = 49).



the population (Earle and Kramm 1982; Powell 1993). Since 1984, the number of captures of fishers in the Bas-Saint-Laurent region has followed an upward trend. According to Poulin et al. (2006), increased catches of fishers in Quebec are not due to a greater trapping effort but to an increasing fisher population. In the PNB, fishers were rare before the late 1990s but are regularly seen since then (Berteaux 2009). This fits both the observed decline of the porcupine population and the decreasing number of feeding scars since the mid-1990s. Mabille et al. (2010) have identified the causes of porcupine mortality by examining several carcasses distributed in the PNB area. Predation was responsible for the death of 61% of the porcupine carcasses found. In the cases where predators could be identified, the death of 86% of all of the specimens examined where predators could be identified was caused by the fisher. The proportion of porcupines killed by predation increased from 40% to 92% between 2000 and 2004. The protected status of the PNB helped to maintain quality habitats for porcupines, but also for predators.

Jack pine stand as an habitat for porcupine and impact on tree growth

Porcupines are generalists found in all kinds of habitats. However, they prefer somewhere near food sources. For example, during summer, deciduous forests may be selected, whereas in winter, pine and hemlock stands can be favored (Morin et al. 2005). In eastern Canada, the porcupine has a preference for birch (*Betula alleghaniensis* Britton and *B. papyrifera*) in temperate forests, for pines (*P. banksiana*, *P. strobus*, and *P. resinosa*) in the boreal forest, and for black spruce (*P. mariana*) in the forest–tundra (Roze 1984, 2009; Tenneson and Oring 1985; Payette 1987). It has been demonstrated earlier that jack pine is among the major winter foods for porcupines in North America (Roze 2009). Porcupines have a strong preference for young and vigorous pines (Griesemer et al. 1998). This is linked with porcupine habitat as young stands provide food, shelter, and insulation during winter months. On the other hand, vigorous trees with large open crowns produce thick annual increments in phloem and provide more foliage and greater volume of inner bark than trees growing in denser stands. In our study, porcupines fed on trees of all diameter classes, following a normal tendency in which the average selected trees are in the 15 cm class (results not shown). Porcupines usually feed on inner bark that is accessible from positions that can be maintained without excessive effort (Harder 1979). For example, open-crowned trees tend to produce larger branches, allowing the porcupine greater access to food. Porcupines will produce proportionally larger feeding scars on small trees than on big ones. On large trees, porcupines tend to feed higher on the trunk, producing scars that are small but numerous (Klvana et al. 2004). Whether this is a general rule could not be tested in our study as scars were sampled under a 2 m stem height due to logistic constraints.

Fig. 7. (*a*) Semi-logarithmic regression between the number of porcupine feeding scars (5-year classes) and time. (*b*) Residuals of the semi-logarithmic regression.

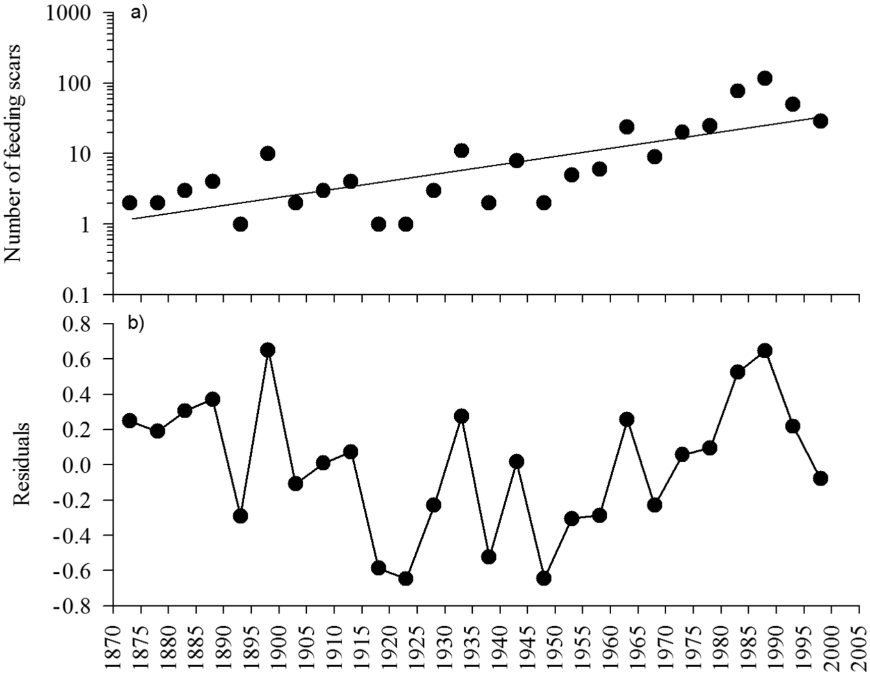


Fig. 8. (*a*) Number of fishers captured per 100 km² in the Bas-Saint-Laurent region between 1984 and 2006. Linear regression of capture success versus time (black line). (*b*) Relationship between number of fishers captured per 100 km² in the Bas-Saint-Laurent region and number of feeding scars.

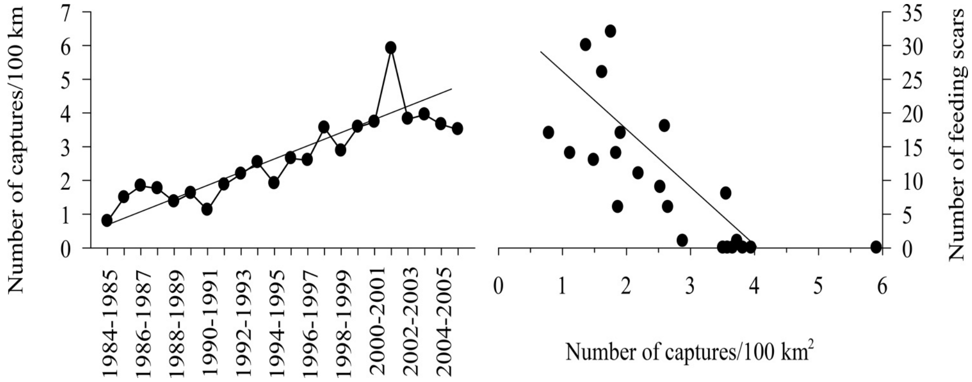


Fig. 9. Jack pine decline and rise of balsam fir during postfire succession in (*a*) the 1847 fire area and (*b*) the 1867 fire area. (*c*) Tree falls and soil disturbance in the 1867 fire area. (Photo credit: Serge Payette, 20 May 2015.)

Phloem of conifers can contain high concentrations of nonstructural carbohydrate reserves such as sugars and starch (Puri et al. 2015). Porcupines feed on the cambium and phloem of trunks and branches (Roze 2009) and may feed preferentially on large trees with extensive crowns (Harder 1979; Tenneson and Oring 1985). Thus we can propose the hypothesis that porcupines choose a tree by its physical features. Porcupines are known to feed on those structures in the crown where growth is rapid (Fournier and Thomas 1997). If verified, this hypothesis may explain why PNB has such a high occurrence of feeding scars. Therefore, PNB would be a highly favoured porcupine habitat because the jack pine stand is unique in the area. The recent decline in the number of feeding scars could also be attributed to the deteriorating condition of the jack pine forest. Several trees are dead or senescent, and the radial growth of living trees is greatly reduced. However, the sharp decrease in the number of feeding scars, which occurred during the decade preceding field sampling, could hardly be attributed solely to this cause as jack pine's growth has slowed since at least the 1960s. Other causes linked to predation and various climatic factors were possibly involved in the decline process (Klvana et al. 2004; Mabille et al. 2010). It is possible for a porcupine to cause the death of jack pine trees. To do so, the porcupine must feed around the trunk to stop water uptake. Young trees may have lost the apical tip in several cases due to porcupine feeding. Jack pine has the ability to produce reiterations (through the process of polycyclism) throughout the growing season (Plourde 2007). This ability is greater in young and vigorous trees. To cause death of larger trees, the porcupine must stop water uptake at the base of the trunk. The scar must cover 90%–100% of the total stem circumference. Thus, it is very unlikely that porcupines kill vigourous trees. Given that feeding scars occupy between 9% and 77% (33% on average) of the trunk circumference, authors found it doubtful that the animals are responsible for the growth decline and senescence of jack pine in the PNB area.

Conclusion

We showed that several jack pine trees in the studied stand are senescent, moribund, or dead. The cause of senescence is not attributed to porcupine feeding but to other forcing factors such as climate and tree aging in absence of fire. Because balsam fir is currently the most abundant tree species in the shrub layer, the overmature pine stand will be gradually replaced by a balsam fir – white spruce forest in the absence of fire disturbance. Porcupine activity in this forest has fluctuated over 140 years, being particularly important during the 1980s. The high number of scars produced in the 1980s is consistent with the creation of the PNB, which provided protection, food, and shelter to porcupines. The recent decline of the porcupine population is also mirrored in the overall age distribution of porcupine scars. The decline was caused in part by increased predation from fishers. Long-term studies should monitor the relationship between the porcupine and its main predator, the fisher. The observed and relatively rapid shift of the overmature jack pine stand to a balsam fir stand provides a rare opportunity to monitor the process of successional change of a dominant forest type of the boreal forest at risk because of reduced frequency of fire events. The PNB area is a favourable winter habitat for porcupines because of the jack pine stand. The decline in tree growth and feeding scars suggests that porcupines may leave the site in case of jack pine death. The number of trees available for feeding decreased along with porcupine population. Jack pine population renewal is critical for porcupine habitat in this area. In maritime areas, such a jack pine stand is unique. Our study provides an example of the complex interplay between fire, forest succession, and animal behaviour.

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