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CHANGEMENTS TEMPORELS DE L'ABONDANCE DU LIÈVRE D'AMÉRIQUE ET DE L'ÉCUREUIL ROUX LE LONG DE SUCCESSIONS FORESTIÈRES APRÈS FEU ET APRÈS COUPE

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Résumé

Ce mémoire évalue l'influence des perturbations naturelles et anthropiques sur l'utilisation de l'habitat par deux espèces animales. Nous avons comparé l'intensité d'utilisation de l'habitat par le lièvre d'Amérique (*Lepus americanus*) et par l'écureuil roux (*Tamiasciurus hudsonicus*) le long de deux chronoséquences de succession, l'une après feu (20-200 ans) et l'autre après coupe (20-80 ans), dans la forêt boréale du Nord-Est québécois. Nous avons également caractérisé les changements temporels de la végétation le long des chronoséquences. Nos résultats révèlent que le lièvre d'Amérique utilise préférentiellement les coupes et que le maximum d'utilisation de l'habitat par l'écureuil roux a lieu environ 20 ans plus tôt après coupe qu'après feu. Le développement plus rapide de la régénération du sapin baumier (*Abies balsamea*) après coupe qu'après feu pourrait partiellement expliquer ces différences. Ces résultats indiquent que la coupe à blanc ne reproduit pas parfaitement les effets du feu.

Abstract

This study aims to assess the potential influence of natural and anthropogenic disturbances on habitat use by two animal species. We compared the intensity of habitat use by snowshoe hare (*Lepus americanus*) and red squirrel (*Tamiasciurus hudsonicus*) along chronosequences of succession after fire (20 to 200 years) and after cutting (20 to 80 years) in the boreal forest of eastern Canada. We also characterized the temporal changes of vegetation along both chronosequences. Our results show that the snowshoe hare preferentially uses cutting-origin stands, and that the peak of habitat use by red squirrels occurs about 20 years earlier after cut than after fire. The earlier balsam fir (*Abies balsamea*) regeneration observed after clear-cut than after fire could partly explain why each animal species responded differently to anthropogenic than natural disturbances. These results indicate that forest fires cannot be simply reproduced by clear-cutting.

Avant-propos

Ce mémoire inclut une introduction générale, un article scientifique et une conclusion générale. En tant qu'auteur principal de l'article, j'ai élaboré les objectifs de recherche, planifié et réalisé l'échantillonnage sur le terrain, réalisé les analyses statistiques et rédigé ce mémoire. Mon directeur de recherche, David Pothier, et mon co-directeur, Daniel Fortin, ont amplement contribué aux étapes de l'élaboration des objectifs et des protocoles d'échantillonnage, ainsi qu'à l'analyse statistique et à la rédaction de l'article scientifique. L'article scientifique inséré dans ce mémoire a été soumis au Canadian Journal of Forest Research pour publication. Nous sommes cependant encore dans l'attente de son acceptation.

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Enfin, j'utiliserais ces dernières lignes pour remercier du fond du cœur mes parents, mon frère et mon conjoint pour leur patience, leur confiance et leur soutien moral.

À mes parents, mon frère et Séb ...

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Introduction générale

Refonte du régime forestier québécois et aménagement écosystèmique

L'année 2010 a été marquée par une prise de conscience sur l'importance de la biodiversité et par la refonte du régime forestier québécois. Ces deux changements illustrent la volonté et la nécessité d'associer les espaces naturels, dont les forêts, à notre avenir. Afin d'assurer la pérennité des ressources forestières et de protéger leur diversité, les techniques d'exploitation sont actuellement redéfinies à la lumière de l'aménagement écosystèmique. Ce concept vise à respecter les capacités de résilience d'un écosystème en s'appuyant sur nos connaissances du régime de perturbations qu'il subit et de sa variabilité spatiale et temporelle (Gauthier *et al*. 2008). Mieux connaître les différences entre l'impact d'une perturbation naturelle et celui d'une coupe sur la végétation forestière, notamment sur sa structure, sa composition et ses fonctions, apparaît alors comme une étape essentielle vers l'aménagement écosystèmique.

Forêt boréale irrégulière et perturbations naturelles

La dynamique de la forêt boréale est naturellement orchestrée par des perturbations causées par les invasions d'insectes, le vent et les feux de forêt. Ces perturbations, en créant des ouvertures dans le couvert forestier, représentent le point de départ de la succession végétale. Les feux constituent la perturbation naturelle majeure de la forêt boréale et sont indispensables à son renouvellement. Ils consument en partie ou en totalité la litière forestière qui a tendance à s'accumuler au fil des ans à cause des températures froides du climat boréal. En effet, ces dernières ralentissent la décomposition de la matière organique par les micro-organismes du sol. Au Québec, la forêt boréale de l'ouest se distingue de celle de l'est par une différence dans le gradient de précipitations. À l'est, le climat maritime engendre des précipitations suffisamment fréquentes pour limiter l'éclosion et la dispersion des feux (Foster 1983 ; Wein et Moore 1977 ; Lorimer 1977), contrairement au climat plus continental de l'Ouest. Le temps de retour moyen d'un feu est d'environ 100 à 150 ans dans la forêt boréale de l'ouest du Québec (Heinselman 1981 ; Johnson 1992 ; Larsen 1997 ; Bergeron 2000), alors qu'il atteint 270 à 500 ans dans la région de la Côte-Nord (Bouchard *et al.* 2008). Cet intervalle de temps est assez long pour que les peuplements développent une structure irrégulière, due à la chute des arbres morts.

Perturbations naturelles ou anthropiques: similitudes et différences

Au cours des 50 dernières années, l'exploitation forestière est devenue une perturbation de plus en plus répandue au Québec (Boucher *et al.* 2009). Une coupe à blanc et un incendie peuvent présenter des caractéristiques similaires, telles que la suppression de l'étage dominant sur une vaste étendue et donc une augmentation de la température du sol et de la décomposition du bois, stimulant ainsi la libération des éléments nutritifs (Hart et Chen 2006). Cependant, la réduction de l'épaisseur de matière organique est beaucoup moins importante après une coupe qu'après un feu (Rees et Juday 2002), ce qui tend à limiter la disponibilité des nutriments. De plus, après une coupe, les strates arbustives, herbacées et muscinales sont maintenues sur place ainsi qu'une partie de la régénération préétablie, c'est-à-dire les jeunes pousses issues du peuplement précédent (Webber *et al.* 1969 ; Frisque *et al.* 1978 ; Ruel 1989 ; Ruel 1992 ; Pominville 1993 ; Ruel et Huot 1993). La quantité des ressources disponibles après une coupe forestière est donc moins importante qu'après un feu. Or, c'est cette augmentation des ressources en début de succession qui détermine en grande partie la composition de la végétation des premiers stades (Brumelis et Carleton 1988). De plus, après un feu, l'ensemble de la régénération est recruté au même moment, engendrant des peuplements de structure équienne, mais la présence de la régénération préétablie après une coupe conduit plus rapidement à des peuplements de structure inéquienne. Après un feu, on observe également plus de chicots et de débris ligneux grossiers.

La composition et la structure des peuplements sont importantes pour la biodiversité, puisqu'elles déterminent la capacité d'un environnement à apporter de la nourriture et fournir un abri pour la faune. Nous avons orienté cette étude vers l'impact des modifications des peuplements forestiers sur les populations d'écureuils roux (*Tamiasciurus hudsonicus*) et de lièvres d'Amérique (*Lepus americanus*) car ces espèces sont considérées comme des espèces 'clés' de la chaîne alimentaire. Leur abondance peut influencer la présence et l'abondance de leurs prédateurs, tels que le lynx (*Felis lynx*), le renard (*Vulpes vulpes*) ou encore les oiseaux (Keith 1963 ; Vaughan et Keith 1981 ; Finerty 1980). De plus, le comportement de ces animaux peut être observé à des échelles relativement fines.

Initialement, nous souhaitions aussi évaluer la réaction des petits mammifères, tels que le campagnol à dos roux (*Myodes gapperi*) et la souris sylvestre (*Peromyscus maniculatus*). Ces derniers constituent les principales proies de certains prédateurs tels que la Nyctale de Tengmalm (*Aegolius funereus*), mais peuvent également servir d'alimentation de substitution pour d'autres prédateurs, moins spécialistes, lorsque la population d'autres espèces de proie diminue. Ils sont également consommateurs de graines, de champignons, de lichens, de plantes et de vertébrés (Martell 1981 ; Martell et Macaulay 1981 ; McCay et Storm 1997 ; Ure et Maser 1982). Comme pour le lièvre d'Amérique et l'écureuil roux, nous avons évalué l'utilisation de l'habitat par les petits mammifères grâce à une méthode dite indirecte, c'est-à-dire sans capture, marquage et recapture. Nous avions disposé systématiquement vingt tubes de plastique de 30 cm de long et 5 cm de diamètre, munis d'une feuille de papier et d'encre, dans chacune de nos stations d'étude. Cependant, les empreintes laissées par les petits mammifères sur les feuilles de papier n'étaient généralement pas assez distinctes pour nous permettre de déterminer s'il s'agissait d'empreintes de campagnol à dos roux ou de souris sylvestre, les deux espèces les plus abondantes sur la Côte-Nord du Québec (Banfield 1977 ; Crête *et al.* 1995 ; Sims et Buckner 1973 ; Le Blanc *et al.* 2010 ; Lemaître *et al.* 2010). Or, la souris sylvestre est définie comme une espèce de milieu ouvert (Parker 1989) contrairement au campagnol à dos roux (Martell 1981 ; Pearce et Venier 2005 ; Darveau *et al.* 2001). Les données recueillies ne nous ont donc pas permis de mettre en évidence les changements temporels de l'utilisation de l'habitat après coupe et après feu pour les différentes espèces de petits mammifères. Nous avons alors choisi de nous concentrer plus spécifiquement sur le lièvre d'Amérique et l'écureuil roux.

Objectif général

Le premier objectif de cette étude était de déterminer les changements temporels de la structure et de la composition des différentes strates de végétation forestière le long de deux chronoséquences, l'une après coupe et l'autre après feu. Une chronoséquence vise à positionner une série de placettes d'observation couvrant une gamme étendue de temps écoulé depuis la dernière perturbation. Dans un deuxième temps, nous avons évalué les réactions des populations d'écureuil roux et de lièvre d'Amérique aux changements de structure et composition végétales prenant place au fil des ans, après chacune de ces deux perturbations.

Chapitre principal. Temporal changes in abundance of snowshoe hares and red squirrels along post-fire and post-logging forest succession

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Résumé

Ce mémoire évalue l'influence des perturbations naturelles et anthropiques sur l'utilisation de l'habitat par deux espèces animales. Nous avons comparé l'intensité d'utilisation de l'habitat par le lièvre d'Amérique (*Lepus americanus*) et par l'écureuil roux (*Tamiasciurus hudsonicus*) le long de deux chronoséquences de succession, l'une après feu (20-200 ans) et l'autre après coupe (20-80 ans), dans la forêt boréale du Nord-Est québécois. Nous avons également caractérisé les changements temporels de la végétation le long des chronoséquences. Nos résultats révèlent que le lièvre d'Amérique utilise préférentiellement les coupes et que le maximum d'utilisation de l'habitat par l'écureuil roux a lieu environ 20 ans plus tôt après coupe qu'après feu. Le développement plus rapide de la régénération du sapin baumier (*Abies balsamea*) après coupe qu'après feu pourrait partiellement expliquer ces différences. Ces résultats indiquent que la coupe à blanc ne reproduit pas parfaitement les effets du feu.

Abstract

This study aims to assess the potential influence of natural and anthropogenic disturbances on habitat use by two animal species. We compared the intensity of habitat use by snowshoe hare (*Lepus americanus*) and red squirrel (*Tamiasciurus hudsonicus*) along chronosequences of succession after fire (20 to 200 years) and after cutting (20 to 80 years) in the boreal forest of eastern Canada. We also characterized the temporal changes of vegetation along both chronosequences. Our results show that the snowshoe hare preferentially uses cutting-origin stands, and that the peak of habitat use by red squirrels occurs about 20 years earlier after cut than after fire. The earlier balsam fir (*Abies balsamea*) regeneration observed after clear-cut than after fire could partly explain why each animal species responded differently to anthropogenic than natural disturbances. These results indicate that forest fires cannot be simply reproduced by clear-cutting.

Introduction

Human disturbances, such as logging and road construction, can cause profound changes to the structure and function of forest ecosystems. Ecosystem-based management has emerged as a promising avenue for alleviating human impacts on ecosystem properties by preserving key forest attributes, such as soil productivity, tree age structure, vegetation composition, and spatial configuration of forest units at the stand- and landscape-levels (Gauthier *et al.* 2008). These attributes are closely linked to the resilience and resistance of forest ecosystems (Gauthier *et al.* 2008). Ecosystem-based management strategies generally involve harvesting techniques that emulate natural disturbances (Attiwill 1994; Bergeron and Harvey 1997; Angelstam 1998; Vaillancourt *et al.* 2008) because the forest biota should be adapted to the periodic occurrence of these disturbances. The strategy should therefore be adjusted to the characteristics of the given ecosystem under management.

In the northeastern Canadian boreal forest, stand-replacing disturbances are mainly caused by fires with return intervals varying from 270 to 500 years (Bouchard *et al.* 2008), whereas return intervals of windthrows are nearly 4000 years (Bouchard *et al.* 2009) and spruce budworm outbreaks are more than 9000 years (Bouchard and Pothier 2011). The effects of forest fires are generally emulated by clear-cutting because this treatment produces a similar degree of overstory removal over wide areas, thereby increasing soil temperature, decomposition rates of organic matter, and nutrient availability (Hart and Chen 2006). However, short-term differences are apparent between fire and clear-cutting. On the one hand, clear-cutting tends to preserve a thicker humus layer (Rees and Juday 2002), while a large part of the understory vegetation, including shrubs, herbaceous species, mosses and advance regeneration, remains intact (Webber *et al.* 1969; Frisque *et al.* 1978; Ruel 1989; 1992; Pominville 1993; Ruel and Huot 1993). On the other hand, stand-replacing fires often destroy the advance tree regeneration and the tree seedbank present in the upper organic layer (Archibold 1979, 1980; Johnson and Fryer 1996). Relative to logging, fire should increase the local availability of many plant resources (water, nutrients), with significant consequences on post-disturbance vegetation (Brumelis and Carleton 1988).

The differences in plant composition and development between post-fire and post-logging stands may create differences in the availability of food and shelter for some animal species, thereby affecting local wildlife communities (Morrison *et al.* 1992; Jonsell *et al.* 1998; Franklin *et al.* 2002). Our study focuses on the effects of post-disturbance succession on snowshoe hare (*Lepus americanus* Erxleben) and red squirrel (*Tamiasciurus hudsonicus* Linnaeus) populations, two species that are typical of the boreal forest. Hares consume herbs and woody vegetation (Keith 1983). Squirrels eat fungi, plants and small vertebrates (De Graaf and Rudis 1986), but they are mainly conifer seed specialists (Kemp and Keith 1970; Rusch and Reeder 1978). The abundance of these two species may influence the abundance and distribution of many predators, such as lynx (*Felis lynx* Kerr), red fox (*Vulpes vulpes* Say), marten (*Martes Americana* Turton), and predatory birds (Keith 1963; Finerty 1980; Vaughan and Keith 1981; Flyger and Gates 1982; Thompson *et al.* 1989).

Several studies have compared the abundance of animal species following fire and logging, but most of these have covered only short periods of time following disturbance (from 0 to 25 years) (Crête *et al.* 1995; Imbeau *et al.* 1999; Fisher and Wilkinson 2005; Thompson *et al.* 2003). Collecting long-term information is essential, however, to gain an overall understanding of disturbance effects because differences observed soon after disturbance may disappear with time (Barber *et al.* 2001). Long-term information is particularly lacking in the case of logging impacts on red squirrel, as previous studies have emphasized short-term comparisons between recently cut stands and old-growth forests (Fisher and Wilkinson 2005; Thompson et al. 2003). To our knowledge, no long-term chronosequence studies have focused on red squirrel in boreal forest. In contrast, Hodson (2011) used chronosequences to determine habitat preferences of snowshoe hare in boreal forest on a yearly rather than a seasonal basis. Because hares have limited access to food and cover in winter, assessing their response to disturbance during this season becomes important in understanding the role of factors limiting the species' distribution and abundance (Ferron *et al.* 1996). Accordingly, we estimated hare abundance along chronosequences using browsing intensity on hardwood saplings, a measurement that is related to habitat use by snowshoe hare during winter (Pease *et al.* 1979). We chose to study red squirrel and snowshoe hare because the former is considered a late-seral stage species (Fisher and Wilkinson 2005), whereas the latter is an early- to mid-successional species (Thompson *et al.* 1989; Koehler 1990; Paragi *et al.* 1997; Newbury and Simon 2005; Hodson *et al.* 2011). Studying these species should thus provide general insights regarding the effects of plant succession after fire and logging on wildlife habitats.

Our objectives are: 1) to characterize successional changes in forest structure and composition after fire and clear-cutting in northeastern Canadian boreal forest, and 2) to determine the intensity of habitat use by snowshoe hare and red squirrel during forest succession.

Methods

Study area

The study area was located north of Baie Comeau (49°07'N, 68°10'W), Québec, Canada, in the spruce – moss bioclimatic subdomains (Robitaille and Saucier 1998). According to the closest meteorological station (Baie Comeau), the mean annual temperature (1971-2000) is 1.5 °C, with mean annual precipitation of 1014 mm (Environment Canada 2011). Snow represents 35 % of annual precipitation and air temperature is above 6 °C during approximately 155 days per year.

The long fire cycle in this region (270 years, Bouchard *et al.* 2008) has led to a forest landscape composed of 60-65 % irregularly structured late-successional stands that are dominated mainly by black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.) (Boucher *et al.* 2003; Côté et al. 2010). White spruce (*Picea glauca* (Moench) Voss), white or paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), tamarack or eastern larch (*Larix laricina* (Du Roi) K. Koch), and trembling aspen (P*opulus tremuloides* Michx.) are also common in the study area.

The study area is composed of a mosaic of forest stands originating from fires and clear-cuts of different ages (Bouchard *et al.* 2008; Bouchard and Pothier 2011). We established post-fire and post-logging chronosequences; arranging forest stands into a chronosequence represents a powerful approach to studying post-disturbance succession (Glenn-Lewin and van der Maarel 1992; Bergeron 2000; Foster and Tilman 2000). A drawback of this approach, however, relates to the possibility that the observed differences among stands composing the chronosequence may not be entirely explained by the time elapsed since the last disturbance. Environmental and physical factors specific to each site may confound temporal changes in forest structure and composition. Such problems can be alleviated by having replicates of each stand age, and by selecting them over a broad spatial domain. Arranging forest stands into a chronosequence has provided significant insights into the patterns and mechanisms of plant succession (Cowles 1899; Cooper 1926; Olson 1958; van der Maarel and Werger 1978; Inouye *et al.* 1987; Pickett 1989; Olff *et al.* 1997).

We identified 25 stands for the post-fire chronosequence, based on a map of all fires larger than 10 km^2 that had occurred since 1800 in our study area (Bouchard et al. 2008) (Figure 1). Twenty-nine clear-cut stands were identified from the archives of forest product companies. Increment cores taken from dominant trees were used to validate the age of each stand. In addition, the stand origin (fire or clear-cut) was confirmed from field observations of the presence of stumps or fire-derived charcoal. Pedons were also used to establish sample plots on mesic sites.

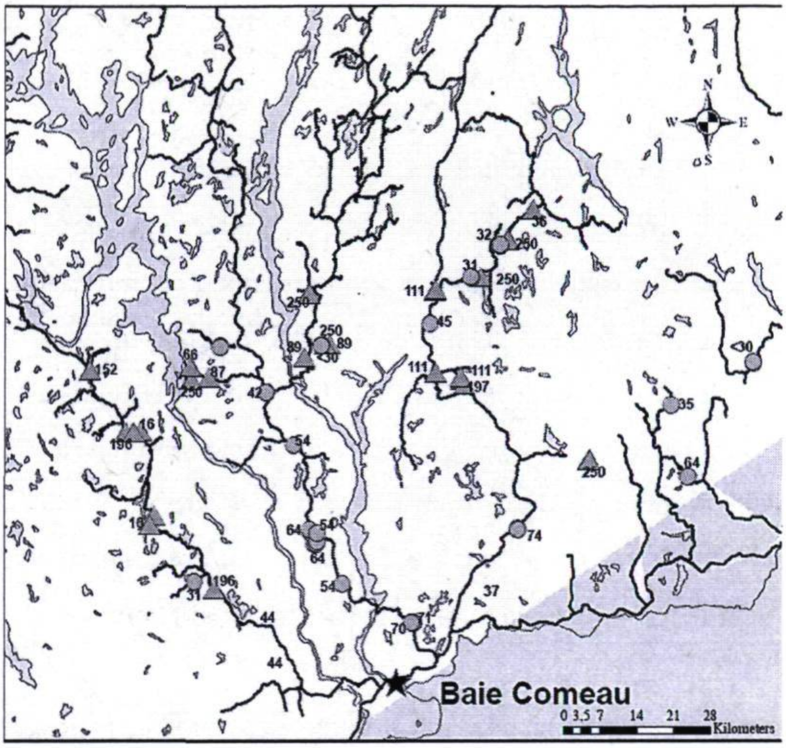

Figure 1. Location of the sampled black spruce stand. Triangles indicate fire-origin stands and circle harvest-origin ones.

Vegetation inventory

Vegetation was characterized in each stand of each chronosequence, within a 400-m^2 circular plot (11.28 m radius) (Figure 2). We recorded the species and diameter at breast height (DBH, 1.3 m) of all merchantable trees (> 9.0 cm DBH) located in the plot. We also determined the species and DBH of each tree sapling (1.0 cm < DBH < 9.1 cm) located in two perpendicular belt transects of 2 × 20 m, crossing the centre of the plot (Figure 2). We estimated the percent cover of each shrub species in four 1-m^2 sub-subplots located 5 m from the centre, in opposite directions (Figure 2). These measurements were used to assess changes in vegetation structure and composition along the chronosequences.

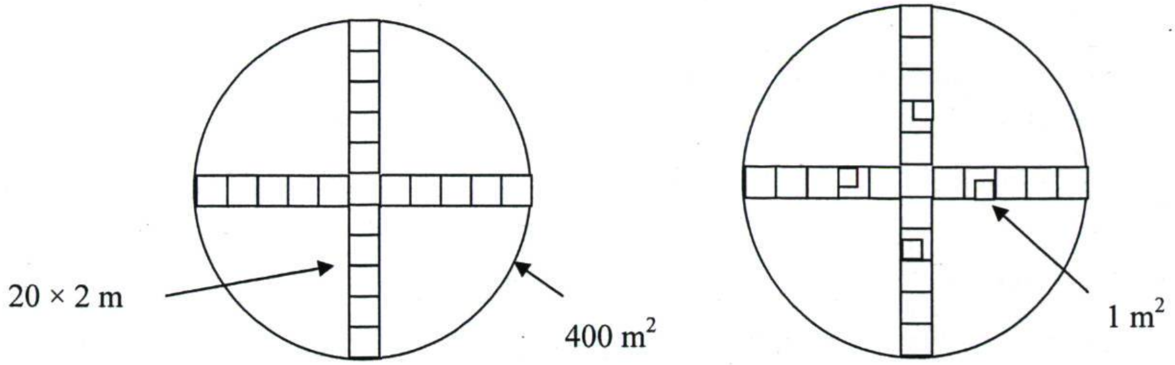

Figure 2. Design of the observation plots used for the data measurements.

Habitat use by snowshoe hare and red squirrel

The intensity of local habitat use by snowshoe hare and red squirrel was assessed by resource use indices (i.e., browse scars and cone shell piles) in the same two transects of 2 × 20 m sub-plots used for saplings (Figure 2). These indices should faithfully reflect the abundance of the two species using each habitat while minimizing their disturbances (Gurnell *et al.* 2009; Keigley and Frisina 1998).

As in many previous studies (Keigley *et al.* 1998, 2003; Hodson 2011), we estimated snowshoe hare abundance by counting all browsed shoots of the following woody species: white or paper birch, alder (*Alnus* spp.), willow (*Salix* spp.), serviceberry (*Amelanchier* spp.), mountain maple (*Acer spicatum* Lamb.), American mountain-ash (*Sorbus americana* Marsh.), and pin cherry (*Prunus pensylvanica* L.f.). These species were chosen because they are the main food source for snowshoe hare in winter (Pease *et al.* 1979). Twigs browsed by hares are easily distinguished from those browsed by other herbivores because only hares clip twigs at a clean 45° angle (Hodson 2011).

To estimate the abundance of squirrels, we counted the number of cone shell piles on the ground or logs within the two 2 × 20 m subplots. In conifer forests, a systematic assessment of feeding signs, such as residual cones eaten by squirrels, provides information on squirrel numbers and habitat use (Gurnell *et al.* 2009). To verify whether or not the number of cone shell piles adequately represented the abundance of red squirrel, and not only local cone production, we also used squirrel capture data that originated from the same study area. Capture sessions had been carried out during summer 2007 in 35 clear-cut-origin stands: eight from 5 to 10 years, 10 from 20 to 30 years, eight from 40 to 50 years, and nine from 60 to 70 years. A grid of 7 × 7 (49 in total) aluminum collapsible live traps (7.7 × 8.8 × 23.0 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) was centered on each focal point, with a distance of 10 m between traps. To increase overnight survival, each live trap was baited with peanut butter, an apple slice and a cotton ball in equal quantities inside each trap. Trapping at focal points lasted three days (three capture occasions), and traps were set, inspected, and eventually restocked each morning. Small mammals that were captured were identified to species, sexed, and weighted to the nearest 1 g using a 300 g spring balance (Pesola, Baar, Switzerland). For subsequent identification, live animals were ear-tagged with a unique tag number (style 1005-1 from National Band & Tag Company, Newport, KY), and released following measurements.

Data analysis

We modelled temporal changes in vegetation along the chronosequences using negative binomial regression, which allows for valid inferences despite overdispersion in the data. The "chronosequence model" tested for differences between anthropogenic and natural disturbances by including a dichotomous variable (Disturbance) for disturbance origin. To account for possible non-linear successional changes in the vegetation, the chronosequence model included stand age (Age) and stand age-squared (Age^2) to capture potential quadratic effects. To avoid multicollinearity, age was standardized (Age_{std}) by subtracting each observed value from the overall mean (Neter *et al.* 1985). In the end, the variance inflation factor (VIF) for every model parameter was < 3.5, indicating the absence of multicollinearity issue.

Temporal changes in the intensity of habitat use by snowshoe hare were modelled based on $\mathrm{Age}_{\mathrm{std}}$, $\mathrm{Age}_{\mathrm{std}}^2$, and Disturbance (i.e., the baseline "chronosequence model"), together with winter browse density and basal area of balsam fir. Live branches of balsam fir are often observed close to the ground and, thus, may provide better winter shelter for hare than do spruce. The total number of shoots was used as the offset of the model. To determine which plant species snowshoe hares preferentially consumed, we used mixed-effects logistic regression with subplot identity as a random effect (Annexe 1).

To assess variation in red squirrel along the chronosequences, the negative binomial regression included $\mathrm{Age}_{\mathrm{std}}$, $\mathrm{Age}_{\mathrm{std}}^2$, Disturbance, and basal area of softwoods. We also accounted for the basal areas of spruce and fir because they should be related to cone production, an important food source for red squirrel (Kemp and Keith 1970; Rusch and Reeder 1978). We tested for an effect of the quadratic mean diameter of conifers within stands because cone production in conifers is correlated with their diameter (Smith and Greenwood 1995) and the calculation of the quadratic mean diameter gives greater weight to trees with larger diameters.

To determine whether or not different habitat variables improved our baseline "chronosequence model" (i.e., $\mathrm{Age}_{\mathrm{std}}$, $\mathrm{Age}_{\mathrm{std}}^2$, and Disturbance) of both animal species, snowshoe hare and red squirrel, we used a log-likelihood ratio test for a nested model (Hilborn and Mangel 1997), which is based on differences in deviance (-2LL) between the baseline model and more complex models including additional terms. We used a 10 % significance level to determine whether or not the additional variables significantly improved the model, thereby reducing the risk of type II error.

Results

Changes in vegetation along post-disturbance chronosequences

Tree density

Merchantable tree density increased with time-since-disturbance, reached a maximum after 120 years (Figure 3), and then decreased thereafter with stand age. Post-logging changes in tree density did not display such non-monotonic temporal changes in tree density, presumably because the 80-year chronosequence was too short to observe the same bell-shaped curve. Overall, merchantable trees remained at higher density after cutting than after fire (Figure 3, Table 1).

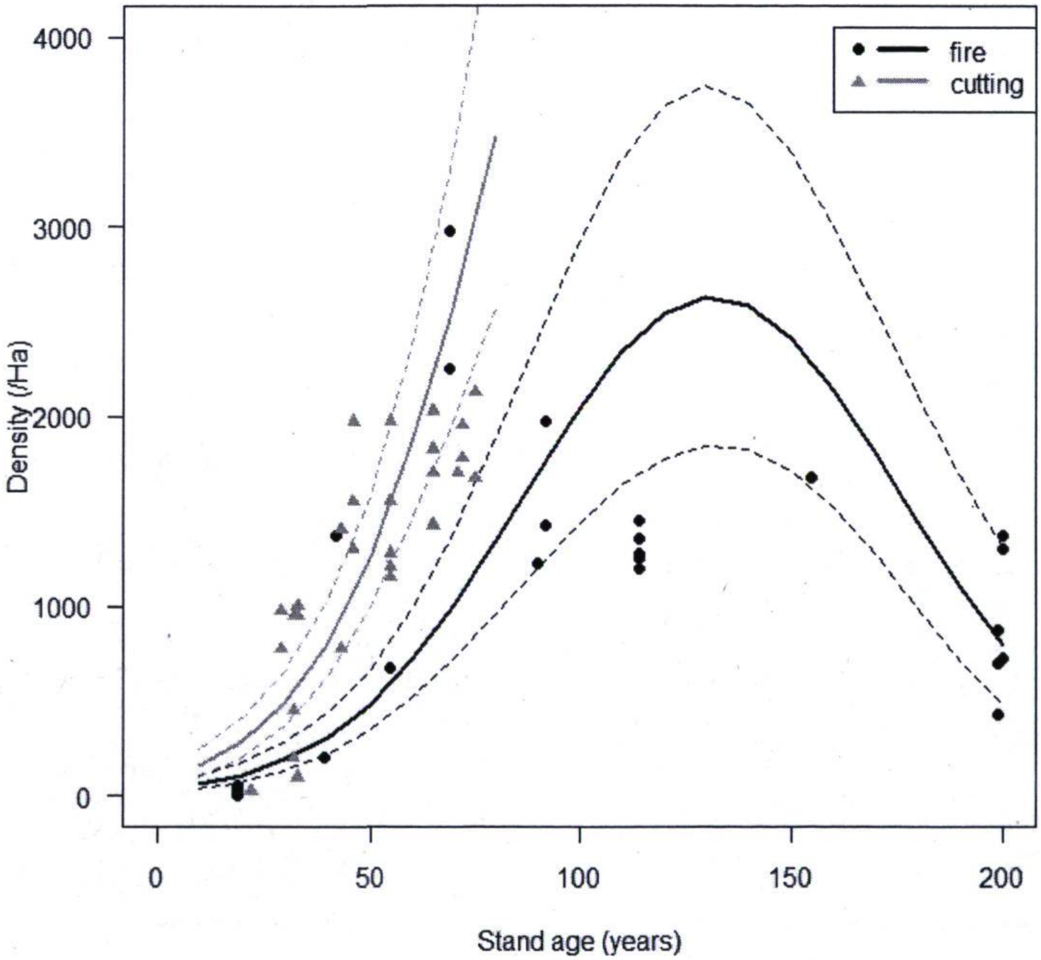

Figure 3. Statistical model (solid lines) ± approximate 90 % confidence intervals (dotted lines) describing changes in merchantable tree density along post-disturbance chronosequences ($n = 54$ stands).

Table 1. Parameter estimates and *P*-values from the model predicting merchantable tree density as a function of standardized stand age (Age_{std}) and type of disturbance. Disturbance is a binary variable discriminating between post-logging and post-fire stands, with post-logging stands being the reference category ($n = 54$).

Parameter	**Estimate ± SE**	***P***
Intercept	8.00 ± 0.18	<0.001
Age_{std}	0.03 ± 0.003	<0.001
Age_{std}^2	-2.6e-04 ± 3.7e-05	<0.001
Disturbance	-0.95 ± 0.24	<0.001

Pseudo-$R^2 = 0.45$

Balsam fir basal area

Stand age and type of disturbance explained 57 % of temporal variability in merchantable balsam fir basal area (Table 2), whereas stand age-squared did not improve model fit ($P = 0.7$) and, therefore, was excluded from the final model (Table 2). Basal area of balsam fir increased with stand age following both types of disturbance, but did so at a much faster rate after logging than after fire (Figure 4). A period of about 100 years was necessary for balsam fir to occupy a significant portion of the post-fire overstory, whereas it was relatively abundant soon after clear-cutting (Figure 4).

Table 2. Parameter estimates and *P*-values from the model predicting merchantable balsam fir basal area as a function of standardized stand age (Age_{std}) and type of disturbance. Disturbance is a binary variable discriminating between post-logging and post-fire stands, with post-logging stands being the reference category ($n = 54$).

Parameter	**Estimate ± SE**	***P***
Intercept	2.76 ± 0.19	<0.001
Age_{std}	0.03 ± 0.004	<0.001
Disturbance	-3.88 ± 0.56	<0.001

Pseudo-$R^2 = 0.57$

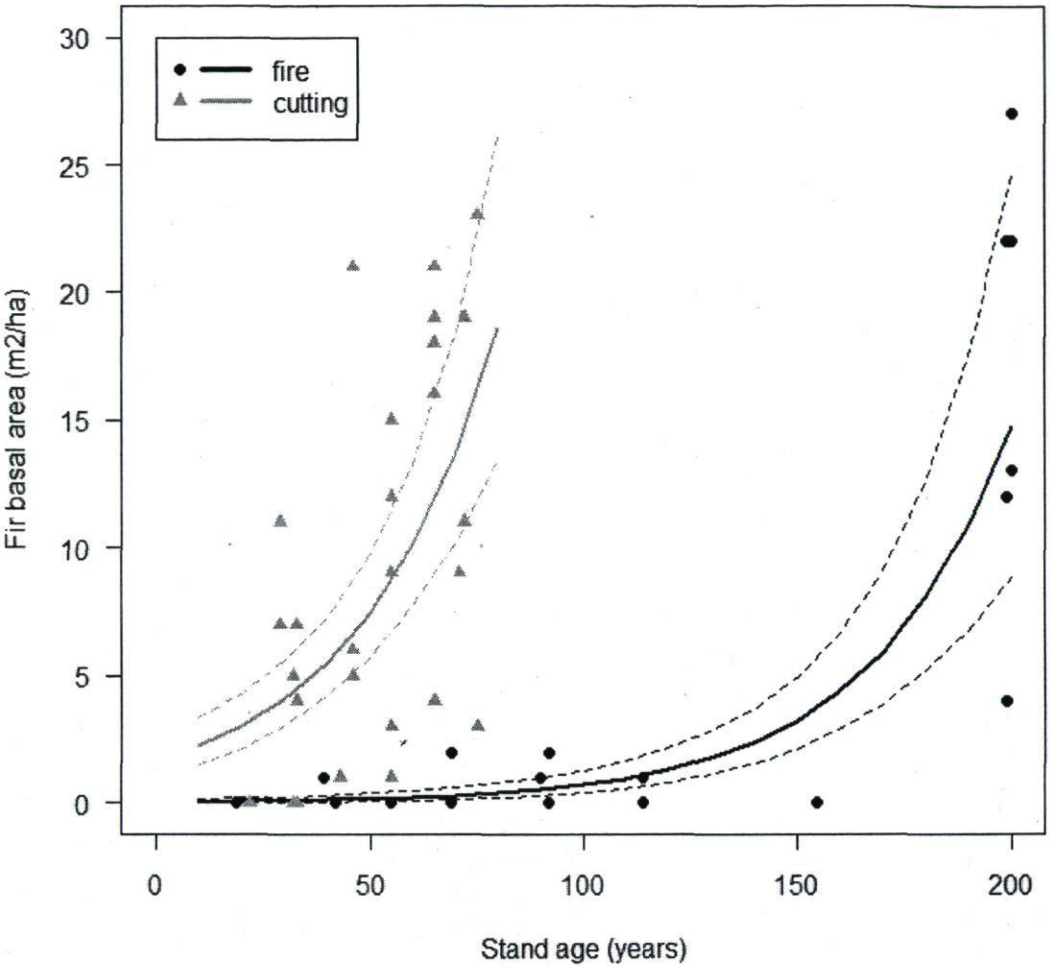

Figure 4. Statistical model (solid lines) ± approximate 90 % confidence intervals (dotted lines) describing changes in balsam fir basal area along post-disturbance chronosequences (*n* = 54 stands).

Changes in habitat use by snowshoe hare along post-disturbance chronosequences

According to a mixed-effects logistic regression, snowshoe hare preferentially browsed young shoots of white birch, mountain maple and mountain-ash ($P < 0.001$), but not alder, willow, serviceberry, and pin cherry ($P > 0.10$). To evaluate the browse intensity of snowshoe hare, the densities of these three plant species were included in the set of candidate independent variables, together with those of the "chronosequence model." None of these variables improved the model, and browse intensity of snowshoe hare was best explained by the chronosequence model – Age_{std}, Age_{std}^2, and Disturbance – with a pseudo-R^2 of 0.47 (Table 3). Consequently, habitat use intensity by snowshoe hare was higher after cutting than after fire, which also presumably reflected higher hare abundance after logging. The peak of abundance occurred 50-60 years after disturbance for both fire- and clear-cut-origin stands (Figure 5), as the age × disturbance interaction was not significant ($P = 0.2$).

Table 3. Parameter estimates and *P*-values from the model predicting browse intensity by snowshoe hare as a function of standardized stand age (Age_{std}) and type of disturbance. Disturbance is a binary variable discriminating between post-logging and post-fire stands, with post-logging stands being the reference category ($n = 42$).

Parameter	**Estimate ± SE**	***P***
Intercept	-0.60 ± 0.13	<0.001
Age_{std}	0.007 ± 0.004	0.14
Age_{std}^2	-0.0005 ± 0.0003	0.07
Disturbance	-0.57 ± 0.26	0.04

Pseudo-$R^2 = 0.47$

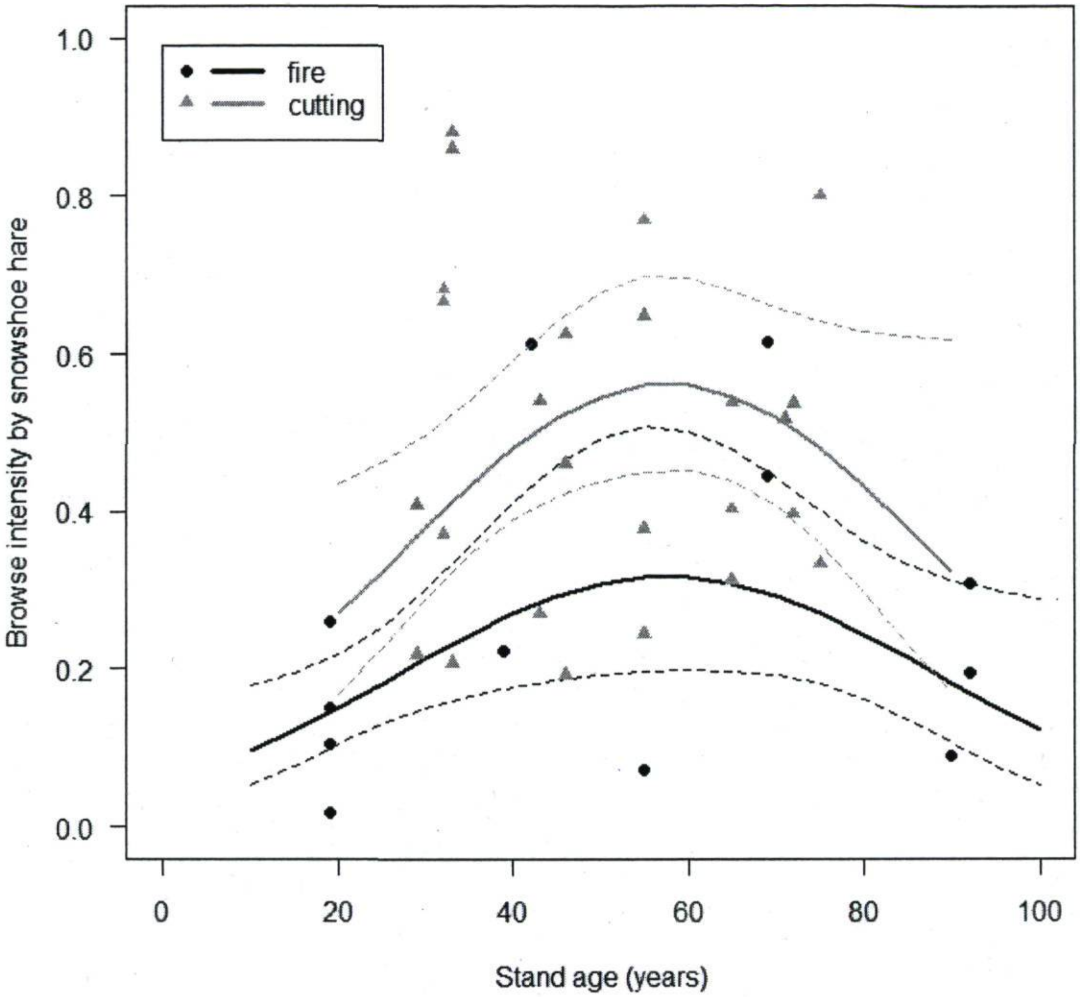

Figure 5. Statistical model (solid lines) ± 90 % confidence intervals (dotted lines) describing changes in habitat use by snowshoe hare during winter along post-disturbance chronosequences ($n = 42$ stands).

Changes in habitat use by red squirrel along post-disturbance chronosequences

In addition to the explanatory variables of the "chronosequence model," spruce basal area and the age-disturbance interaction explained significant variability in the number of cone shell piles (Table 4). The changes in the number of cone shell piles were bell-shaped along both chronosequences, with maximum abundance being reached 20 years earlier in stands originating from clear-cuts than from those of fire-origin (Figure 6). The number of squirrels captured per 100 trap nights in clear-cut stands of different age classes agreed with the curves corresponding to the number of cone shell piles (Figure 6).

Table 4. Parameter estimates and *P*-values for the relationship between the number of cone shell piles as a function of standardized stand age (Age_{std}), type of disturbance and spruce basal area. Disturbance is a binary variable discriminating between post-logging and post-fire stands, with post-logging stands being the reference category ($n = 35$).

Parameter	**Estimate ± SE**	***P***
Intercept	3.64 ± 0.34	<0.001
Age_{std}	-0.04 ± 0.01	0.005
Age_{std}^2	-0.002 ± 0.0005	<0.001
Disturbance	-1.03 ± 0.41	0.02
Spruce basal area (m^2/ha)	0.08 ± 0.02	0.001
Age_{std} × Disturbance	0.07 ± 0.02	<0.001

Pseudo-$R^2 = 0.20$

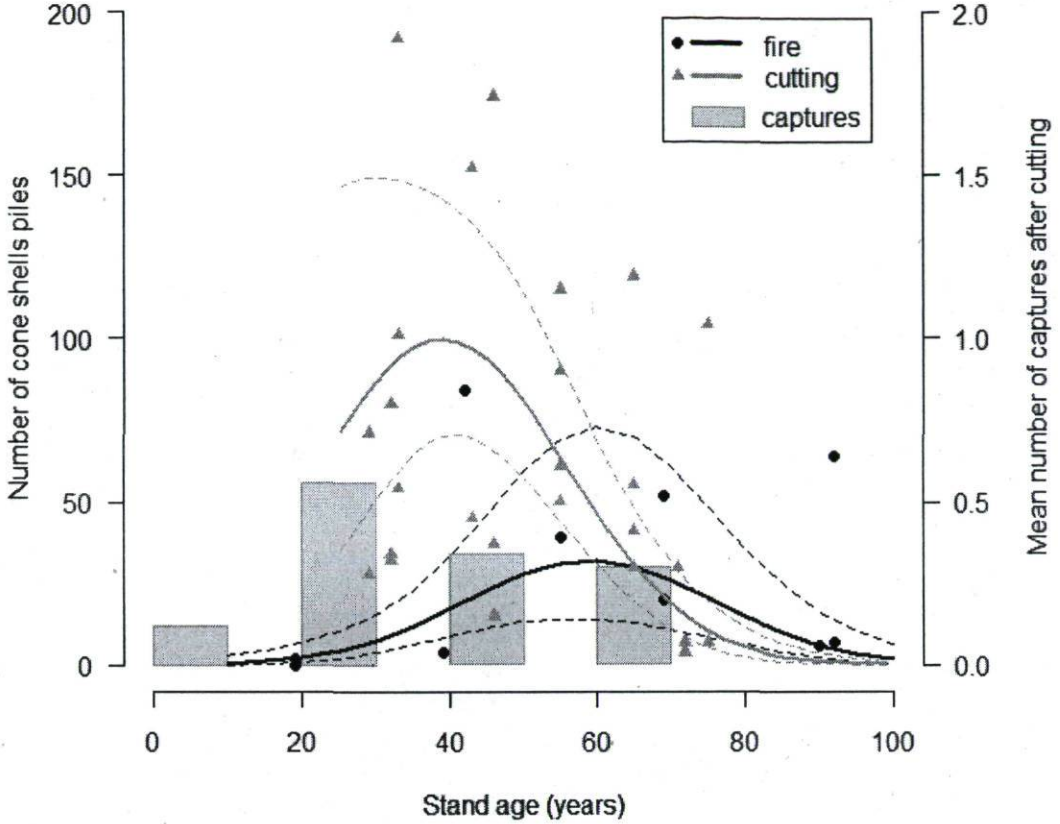

Figure 6. Expected changes (solid lines) ± 90 % confidence intervals (dotted lines) in habitat use by red squirrel along post-disturbance chronosequences ($n = 42$ stands). The bar diagram represents the mean number of squirrels captured per 150 trap nights in post-harvest stands ($n = 35$).

Discussion

Post-disturbance plant succession

Disparities in post-fire and post-logging forest succession were sufficient to produce substantial differences in vegetation and habitat use by wildlife. The number of cone shell piles left by red squirrels and the browse intensity by snowshoe hare revealed that these two species used similar-aged stands differently, depending on whether they originated from fire or from clear-cutting. These findings have implications for ecosystem-based management which should mitigate the effects of timber harvest on wildlife by creating disturbances that are similar to natural ones. Our study shows important differences, which highlights some of the changes to the ecosystem that can be expected.

One of the main changes in wildlife habitat noted between stands originating from clear-cuts and from fires relates to the rapid establishment and development of balsam fir. These differences in vegetation structure and composition are related to the protection of advance regeneration during harvest activities. The regeneration strategy of balsam fir consists of creating a bank of shade-tolerant seedlings that are able to survive and develop under cover (Carleton and Maycock 1978; Foster 1983; Kneeshaw and Bergeron 1996; Bergeron 2000; De Grandpré *et al.* 2000). This advance regeneration can develop into saplings as tall as 6 m (Pothier *et al.* 1995), thereby quickly creating a closed canopy (Ruel 1989, 1992; Pominville 1993). Conversely, advance regeneration is generally destroyed by fires (Archibold 1979, 1980; Johnson and Fryer 1996; Greene *et al*. 1999) and post-fire stands are usually colonized by pioneer species such as trembling aspen, white birch, jack pine or black spruce (Dix and Swan 1971; Pothier 2001; Lesieur *et al.* 2002). Depending on the availability and proximity of seed sources, it may take more than 100 years for balsam fir to become established in post-fire stands, a period that corresponds to the longevity of the first tree cohort (Bouchard *et al.* 2008).

To better emulate the effects of forest fires, logging methods should be adjusted to reduce the dominance of balsam fir, which is generally observed after cutting. Indeed, the dominance of post-harvest stands by balsam fir leads to a successional pathway different from that generally expected during post-fire succession. This compositional difference may alter canopy architecture and structure, the next generation of understory vegetation through differences in light transmittance, and susceptibility to certain forest pests (Freedman *et al.* 1994). For example, balsam fir is more vulnerable to decay (Basham 1991) and to spruce budworm attack relative to black spruce (MacKinnon and MacLean 2004; Pothier *et al.* 2012). Scarification or prescribed burning that is followed by the planting of black spruce or jack pine seedlings, two species naturally present after fire, could be used to reduce the dominance in balsam fir regeneration.

Higher abundance of snowshoe hare after cutting than after fire

Browsing intensity by snowshoe hare peaked 50–60 years after both fire and logging, which presumably also indicates when hares occur at highest density. This finding agrees with other North American studies reporting that peak hare densities occurred in early- to mid-successional stands (Thompson *et al.* 1989; Koehler 1990; Paragi *et al.* 1997; Newbury and Simon 2005; Hodson *et al.* 2011). Mid-succession stands are suitable habitat for snowshoe hares because the amount of understory development provides both high food availability and protective cover (Fisher and Wilkinson 2005). The highest density of snowshoe hares that had been observed in mid-successional stands might be attributable to high availability of woody browse, and vertical and lateral covers (Hodson *et al.* 2011). The quality of forest cover is crucial against both terrestrial and aerial predators.

Even if the long-term temporal pattern was similar, snowshoe hare tended to be more abundant after cutting than after fire. The difference could be the result of the greater density of balsam fir in harvest-origin stands, as this species provides more protective cover relative to black spruce or early-seral deciduous trees. Indeed, black spruce has a straight trunk with little taper and a narrow, pointed crown of short, compact, drooping branches with upturned tips, whereas branches of balsam fir tend to reach the ground. The abundance of protective cover would be closely related to the fitness of snowshoe hare (Hodson *et al.* 2010), which is to be expected given that more than 75 % of hares die annually from predation (Hodges *et al.* 1999; Etcheverry *et al.* 2005).

Hodson *et al.* (2011) found no differences in hare abundance during the first 80 years after both fire and logging. However, they conducted pellet surveys which reflect habitat use over a full year. During winter, snowshoe hare may preferentially use stands with abundant balsam fir because these trees provide adequate shelter when deciduous trees have shed their leaves (Ferron *et al.* 1996). We also found that saplings of white birch, mountain maple and mountain-ash were the preferred browse species eaten by snowshoe hare during winter, as previously reported (Ferron *et al.* 1996).

Earlier peak abundance of red squirrel after cutting than after fire

The differences in forest structure and composition observed between post-fire and post-logging stands influenced both the maximum number of cone shell piles and the timing of this peak along the chronosequence. Squirrel abundance peaked as soon as 40 years after cutting, much earlier than the peak abundance observed after fire.

This earlier and higher peak of squirrel abundance after cutting could be related to the presence of the advance regeneration. Indeed, the rapid development of advance regeneration, which is composed of balsam fir and spruces, reduces the period of time necessary to obtain mature trees. Red squirrel has a preference for mature cone-producing stands (Kemp and Keith 1970), where they can benefit from high availability of escape cover, food, and nesting sites (Vahle and Patton 1983; Smith and Mannan 1994; Fisher and Wilkinson 2005). Stand composition also influenced red squirrel. The basal area of black spruce was positively related to the intensity of habitat use by red squirrels, a species which is known for selecting mature spruce for nesting (Fancy 1980).

Balsam fir could also play an important role in habitat selection by red squirrel, but it is more likely related to feeding than nesting. Although red squirrels feed on seasonally produced berries and fungi, the species is recognized as a conifer seed specialist (Kemp and Keith 1970; Rusch and Reeder 1978), with the dynamics of its populations being closely associated with conifer cone crops (Koprowski 2005). Years of high cone production are usually followed by an increase in squirrel abundance (Smith 1968; Erlien and Tester 1984; Gurnell 1984, 1987). Red squirrel feeds heavily on the seeds of coniferous trees, including all pines (*Pinus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.) (Smith 1968; Gurnell 1987). However, seed production of balsam fir occurs earlier and is generally more abundant than that of black spruce (Bakuzis and Hansen 1965; Haavisto 1978; Johnston 1977; Black and Bliss 1980; Frank 1990). In addition, black spruce seeds are much smaller and lighter (890 000 seeds per kg) than those of balsam fir (66 000 to 208 000 seeds per kg) (Schopmeyer 1974; Viereck and Johnston 1990).

Red squirrel is generally considered as a late-successional species (Kemp and Keith 1970; Rusch and Reeder 1978; Thompson *et al.* 1989; Roy *et al.* 1995; Crête *et al.* 1995; Koprowski 2005; Patenaude *et al.* 2010), but this assertion was not supported by the observed decline in cone shell piles in late-succession. After cutting, this decline was confirmed by the temporal pattern in the number of captures. The decreasing abundance of red squirrel 50 years after harvest could be related to the increasing presence of predators such as the American marten, which is typically associated with mature conifer cover (Steventon and Major 1982; Buskirk 1984; Bateman 1986). Thompson *et al.* (1989) found that red squirrels may use regeneration stage forests more frequently when predator abundance is low. Squirrel abundance in post-fire stands generally followed the post-logging pattern but with lower overall values. These lower values could be explained by the lack of mature trees and escape cover. Whereas dead standing trees can be abundant after fire (Lowe *et al.* 2011), they provide little protective cover for red squirrels (Fisher and Wilkinson 2005).

Conclusion

Relative to the vegetation that remains after wildfires, the advance regeneration maintained after clear-cutting alters post-disturbance forest succession. Stands mature earlier and are richer in balsam fir, which provides better winter shelter for snowshoe hare and better escape cover and a food source for red squirrel. However, these differences in vegetation structure and composition, together with habitat use by the herbivores, highlight the need to better emulate natural disturbances such as wildfire if the long-term management objective is to maintain ecosystem integrity. Scarification or prescribed burning, followed by black spruce or jack pine planting, could be used to reduce the dominance in balsam fir regeneration.

Cutting with protection of advance regeneration and soils (CPRS) seems to have a positive effect on hare and squirrel populations, but it does not yield similar successional pathways and, therefore, should affect forest ecosystem functioning. Post-disturbance trends in herbivore abundance should differ between anthropogenic and natural disturbances during long periods of time, which implies that ecosystem processes, such as herbivory, seed dispersal, and predator-prey interactions, should also differ over extended periods of time. More hares and squirrels probably mean more predators. A more substantial presence of lynx, marten, or predatory birds could have a pronounced impact on populations of other prey, such as small mammals, grouse, and small forest birds. A greater abundance of hare and squirrel might also lead to a stronger impact on the vegetation, such as greater seedling and sapling browsing, thereby slowing down forest regeneration. Moreover, harvest rotations (<100 years) generally are shorter than fire return intervals in the eastern boreal forest of Canada (>250 years) (Bergeron *et al.* 2001; Harvey *et al.* 2002; Bouchard *et al.* 2008). The continued use of CPRS could therefore have important consequences for the spatiotemporal distribution and dynamics of snowshoe hare and red squirrel populations.

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Conclusion générale

Bien que les coupes avec protection de la régénération et des sols (CPRS) soient généralement considérées comme similaires aux feux de forêt, l'impact de ces deux perturbations sur la structure et la composition de la végétation présentent de nombreuses différences (Hart and Chen 2006). Notre étude a permis de mettre en évidence que l'écart observé entre les feux et les coupes est suffisant pour modifier les habitats fauniques que procurent les peuplements forestiers. Le lièvre d'Amérique et l'écureuil roux semblent utiliser préférentiellement les coupes car le maintien de la régénération préétablie semble accélérer la succession végétale. Cette régénération produit des peuplements plus denses qui atteignent leur maturité plus rapidement qu'après un feu. De plus, étant riche en sapin baumier, elle favorise la dominance de cette espèce au sein de chacune des strates de végétation (régénération, gaules, arbres marchands). Les peuplements issus d'une coupe fournissent alors un abri hivernal plus efficace pour le lièvre ainsi qu'un meilleur couvert de fuite et une source de nourriture plus abondante pour l'écureuil roux.

Cependant, les coupes ne permettent pas de maintenir l'intégrité écologique de l'écosystème. Elles pourraient alors avoir des répercussions non seulement sur la régénération des peuplements, mais également sur le reste de la faune, comprenant les prédateurs du lièvre d'Amérique et de l'écureuil roux et leurs autres proies. En effet, même si chaque prédateur peut présenter une préférence pour une certaine espèce de proie, il est généralement capable de se nourrir de proies de substitution lorsque nécessaire. À l'image de la relation de prédation observée entre l'orignal, le loup et le caribou, la forte utilisation des coupes par le lièvre d'Amérique et l'écureuil roux pourrait avoir des conséquences inattendues. Fortin *et al.* (2011) ont constaté que l'orignal utilise fortement les coupes et qu'il pourrait ainsi avoir tendance à remonter progressivement vers le nord au fur et à mesure que les coupes forestières sont effectuées. Le loup, qui est le prédateur principal de l'orignal, a alors lui aussi tendance à être davantage présent au nord. Or, cette remontée progressive a pour conséquence de rapprocher le loup du milieu occupé par les caribous, une proie alternative pour ce prédateur. Ainsi, en créant des habitats favorables à l'orignal, les coupes pourraient avoir des conséquences désastreuses pour les caribous.

L'objectif d'un aménagement écosystémique étant notamment de créer des perturbations anthropiques qui se rapprochent le plus possible des perturbations naturelles (Gauthier *et al.* 2008), les résultats de notre étude confirment l'existence d'écarts importants entre les CPRS et les feux de forêt. Ces écarts pourraient être réduits notamment en restreignant la dominance du sapin baumier au sein de la régénération préétablie. Nous avons vu que la forte abondance du sapin baumier a des répercussions sur la « valeur environnementale » de la forêt, puisqu'elle influence sa fonction d'habitat, mais également sa valeur économique. En effet, le bois du sapin baumier présente des propriétés mécaniques moins bonnes que le bois de l'épinette noire et est plus vulnérable à la carie. Il est donc généralement moins recherché par les industries forestières (Jessome 1977; Whitney 1995). De plus, les peuplements dominés par le sapin baumier sont plus vulnérables aux épidémies de tordeuse des bourgeons de l'épinette (MacKinnon and MacLean 2004). L'utilisation du scarifiage ou du brûlage dirigé lorsque les sols sont suffisamment profonds, suivis d'un reboisement en épinette noire et en pins gris, permettrait de réduire la dominance du sapin baumier dans les peuplements issus de coupe.

Sur la Côte-Nord du Québec, le long temps de retour des feux permet aux peuplements d'atteindre le stade de vieille forêt, caractérisé notamment par une structure irrégulière causée par la mortalité d'arbres individuels ou de petits groupes d'arbres. À l'échelle du territoire, l'utilisation des CPRS pourrait donc être amenée à diminuer en faveur des coupes partielles qui reflètent davantage ces perturbations secondaires formant des trouées. Cependant, même utilisées sur une plus petite proportion du territoire et en dépit des différences observées, les CPRS conservent leur place au sein d'un aménagement écosystémique puisque le feu reste la perturbation majeure de la région. Le défi actuel est alors de réussir à combiner, à l'échelle du territoire, les différentes techniques de coupe dans des proportions qui reflètent les différentes perturbations observées au sein du paysage.

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Annexe 1. Codes of the mixed-effects logistic regression with subplot identity as a random effect in R to determine which plant species snowshoe hares preferentially consumed.

```
BD <- read.table("C:/temp/brout_especes_feux_coupes.txt", header = TRUE)
LIEVRE$especes <- as.factor(LIEVRE$especes)
LIEVRE$agec <- LIEVRE$age - mean(LIEVRE$age)
LIEVRE$agec2 <- LIEVRE$agec^2
LIEVRE

# régression logistique avec effet aléatoire pour le site (les tiges des différentes espèces ne sont
pas indépendantes car elles proviennent du même site
library(lme4)
mod1<-glmer(brout/total ~ agec + agec2 + especes + (1|sites), weights=total, family=binomial,
data = LIEVRE)
summary(mod1)

LIEVRE$AULref <- relevel(LIEVRE$especes, ref="AUL")
mod1<-glmer(brout/total ~ age + agec2 + AULref + (1|sites), weights=total, family=binomial,
data = LIEVRE)
summary(mod1)

LIEVRE$BOPref <- relevel(LIEVRE$especes, ref="BOP")
mod1<-glmer(brout/total ~ age + agec2 + BOPref + (1|sites), weights=total, family=binomial,
data = LIEVRE)
summary(mod1)

LIEVRE$EREref <- relevel(LIEVRE$especes, ref="ERE")
mod1<-glmer(brout/total ~ age + agec2 + EREref + (1|sites), weights=total, family=binomial,
data = LIEVRE)
summary(mod1)
```

```
LIEVRE$PRPref <- relevel(LIEVRE$especes, ref="PRP")
mod1<-glmer(brout/total ~ age + agec2 + PRPref + (1|sites), weights=total, family=binomial, data = LIEVRE)
summary(mod1)

LIEVRE$SALref <- relevel(LIEVRE$especes, ref="SAL")
mod1<-glmer(brout/total ~ age + agec2 + SALref + (1|sites), weights=total, family=binomial, data = LIEVRE)
summary(mod1)

LIEVRE$SOAref <- relevel(LIEVRE$especes, ref="SOA")
mod1<-glmer(brout/total ~ age + agec2 + SOAref + (1|sites), weights=total, family=binomial, data = LIEVRE)
summary(mod1)

# créer une base de données par espèces pour pouvoir faire les prédictions dessus

newAME <- expand.grid(especes = as.factor(c("AME")), age = seq(15,100,5))
newAUL <- expand.grid(especes = as.factor(c("AUL")), age = seq(15,100,5))
newBOP <- expand.grid(especes = as.factor(c("BOP")), age = seq(15,100,5))
newERE <- expand.grid(especes = as.factor(c("ERE")), age = seq(15,100,5))
newPRP <- expand.grid(especes = as.factor(c("PRP")), age = seq(15,100,5))
newSAL <- expand.grid(especes = as.factor(c("SAL")), age = seq(15,100,5))
newSOA <- expand.grid(especes = as.factor(c("SOA")), age = seq(15,100,5))
newAME$agec <- newAME$age - mean(LIEVRE$age)
newAUL$agec <- newAUL$age - mean(LIEVRE$age)
newBOP$agec <- newBOP$age - mean(LIEVRE$age)
newERE$agec <- newERE$age - mean(LIEVRE$age)
newPRP$agec <- newPRP$age - mean(LIEVRE$age)
newSAL$agec <- newSAL$age - mean(LIEVRE$age)
newSOA$agec <- newSOA$age - mean(LIEVRE$age)
newAME$agec2 <- newAME$agec^2
newAUL$agec2 <- newAUL$agec^2
newBOP$agec2 <- newBOP$agec^2
```

```
newERE$agec2 <- newERE$agec^2
newPRP$agec2 <- newPRP$agec^2
newSAL$agec2 <- newSAL$agec^2
newSOA$agec2 <- newSOA$agec^2

# prédictions par espèces
library(AICcmodavg)
mod1<-glmer(brout/total ~ agec + agec2 + especes + (1|sites), weights=total, family=binomial,
data = LIEVRE)

predAME <- predictSE.mer(mod1, newdata=newAME, se.fit=TRUE, type="response") #voir
?predictSE.mer pour tous les détails ...
predAUL <- predictSE.mer(mod1, newdata=newAUL, se.fit=TRUE, type="response")
predBOP <- predictSE.mer(mod1, newdata=newBOP, se.fit=TRUE, type="response")
predERE <- predictSE.mer(mod1, newdata=newERE, se.fit=TRUE, type="response")
predPRP <- predictSE.mer(mod1, newdata=newPRP, se.fit=TRUE, type="response")
predSAL <- predictSE.mer(mod1, newdata=newSAL, se.fit=TRUE, type="response")
predSOA <- predictSE.mer(mod1, newdata=newSOA, se.fit=TRUE, type="response")
```