Boreal forests of eastern Canada revisited: Old growth, nonfire disturbances, forest succession, and biodiversity

2 authors:

Yves Bergeron
Université du Québec en Abitibi-Témiscamingue
912 PUBLICATIONS   **34,371** CITATIONS

SEE PROFILE

Nicole J Fenton
Université du Québec en Abitibi-Témiscamingue
183 PUBLICATIONS   **3,428** CITATIONS

SEE PROFILE

Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity

Yves Bergeron and Nicole J. Fenton

Abstract: Boreal forests have commonly been described as dominated by monospecific postfire stands that are reburnt well before other ecological process than those occurring immediately after fire can take place. Research undertaken over the last 30 years has given us a very different perspective of the complexity of Canadian boreal forests. Old-growth forests are common and their development is controlled by nonfire disturbances. Consequently, monospecific even-aged stands can develop towards more diversified uneven-aged stands with increasing time since fire. This complex disturbance regime, including both fire and nonfire disturbances, is partially responsible for a higher than expected biodiversity (e.g., understory) in these forests. The dominating forest management model in Canadian boreal forests, based on clear-cut harvesting and regeneration of short rotation even-aged stands, does not reflect the complexities of the disturbance–succession cycle observed in Canadian natural boreal forests.

Key words: Boreal forest, succession, old growth, understory biodiversity, fire, secondary disturbances.

Résumé : Les forêts boréales sont généralement considérées comme étant une large étendue de peuplements monospécifiques issus de feux qui vont rebrûler bien avant que des processus écologiques autres que ceux liés aux feux ne puissent avoir cours. Les recherches réalisées au cours des 30 dernières années révèlent une perspective très différente. Les vieilles forêts sont abondantes et elles sont souvent contrôlées par des régimes de perturbations autres que les feux. À mesure que le temps s'écoule après les feux, les peuplements équiennes et monospécifiques se transforment graduellement en peuplements plus diversifiés et à structure inéquienne. Ce régime de perturbations complexe qui inclut à la fois le feu et d'autres types de perturbations crée une biodiversité (ex., sous-bois) plus élevée que généralement attendue. Le modèle d'aménagement actuellement préconisé dans la forêt boréale canadienne basé sur la coupe totale, et la reconduction en rotation courte de peuplements monospécifiques équiennes, s'éloigne passablement de la complexité de la dynamique naturelle observée.

Mots-clés : Forêt boréale, succession, feu, biodiversité du sous-bois, forêts anciennes, perturbations secondaires.

Introduction

The circumboreal forest accounts for about one quarter of the world's closed-canopy forested area, almost 1 billion hectares (Burton et al. 2010). Although heavily exploited for a long time in its southern parts, the boreal zone still contains half of the world's unexploited frontier forests (Burton et al. 2010). This makes the boreal forest equal to tropical forests in terms of hosting the last large intact forest landscapes on earth (Potapov et al. 2008). In both regions, however, increased human pressure through logging and various kinds of resource extraction is rapidly changing the structure and dynamics of these forests. The uniqueness of the boreal forest has recently been emphasized from the perspectives of biodiversity conservation and the global carbon cycle (e.g., Bradshaw et al. 2009). For example, the circumpolar boreal forests and associated peatlands are estimated to contain more than five times the amount of carbon found in the world's temperate forests and almost double the carbon found in tropical forests (Kasischke 2000).

A significant proportion (12%) of the global boreal biome is found within Canada, with only the Russian Federation with a larger proportion (63%; Burton et al. 2010). Furthermore, over 53% of Canada is within the boreal zone, with many provinces with over 70% of their territory in the boreal zone (Burton et al. 2010). As a result, management decisions taken within Canada that affect the boreal forest impact the global boreal ecosystem. Situated along the northern edges

Y. Bergeron. CRSNG/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada; Centre for Forest Research, Université du Québec à Montréal, C.P. 8888, succ. Centre-Ville, Montréal, QC H3C 3P8, Canada.
N.J. Fenton. CRSNG/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada.

Corresponding author: Yves Bergeron (e-mail: Yves.bergeron@uqat.ca).

Professor Yves Bergeron, Université du Québec à Montréal and Université du Québec en Abitibi-Témiscamingue, was recognized as a Fellow of the Royal Society of Canada in 2010. A specialist in forest ecology, Dr. Bergeron has dedicated his career to studying the dynamics of the Canadian boreal forest. He has shown how Canada's boreal forest was controlled by fire and insect epidemics. He has helped develop new forest development approaches that are inspired by natural dynamics.

of densely populated regions, the boreal forests of Canada have historically been seen to be so vast as to be without limit (Burton et al. 2003). Fire has also been perceived as being so important on the boreal landscape (Payette 1992; Johnson 1992) that the only component of importance was believed to be monospecific even-aged stands that burned again before more complex stand structures could develop. (Dix and Swan 1971; Johnson et al. 1995). Compared with forests further south, boreal forests seemed structurally simple and species poor (De Grandpré et al. 2003).

This historic perception fit the management pattern of boreal forests in Canada that was developed following an agricultural model (Wagner 1993). Clearcut harvests were prioritized because it normalized the forest and allowed sustained yield planning (Seymour and Hunter 1999; Burton et al. 2003). The harvest cycle (determined by the maximum biomass accumulation in the forest) was frequently similar to the fire return interval (i.e., the average period at which a forest burned; Burton et al. 2010), allowing for an easy substitution of harvest for fire in public perception. However, it has now been clearly demonstrated that harvest is not equivalent to fire (Bergeron et al. 2002) and research over the last 30 years has indicated that boreal forests are far more complex than previously described (Puettmann et al. 2009), particularly in eastern Canada. This complexity emphasizes the importance of an integrated strategy for management of boreal forests that preserves the diversity of species dependent on it, but also its global ecosystem functions. However, the complexity of boreal forests makes the development of such a strategy more difficult.

The purpose of this mini-review is to illustrate some of the complexity within Canadian boreal forests, specifically the presence of old-growth forests and nonfire disturbances, and the compositional and structural successions that maintain them. Finally, some of the biodiversity maintained by these complex systems will be put in evidence, particularly in the understory. Although the discussion may apply to boreal forests of eastern Canada in general, specific examples come mainly from studies realised in the Clay Belt of western Québec and eastern Ontario (Fig. 1).

Old-growth forests: a major component of the boreal landscape

As the overall dynamics of Canadian boreal forests are mainly controlled by a few large stand replacing fires (Johnson 1992), fire cycles shorter than the life span of the dominant species were used to explain that old-growth forests make up only a small proportion of the landscape (Johnson et al. 1995). We define here old-growth forests as forests that are no longer dominated by individuals or species that dominated the canopy of the postfire cohort (Kneeshaw and Gauthier 2003, Wirth et al. 2009). Using available studies (Bergeron et al. 2004), we estimated the proportion of forests over 100, 200, and 300 years old in the different ecozones of the Canadian boreal forest (Table 1). In some cases these proportions can be directly estimated from data provided (Appendix A), but in many studies only mean age of the stands or fire cycle are available (Appendix A). In these later cases it is possible to estimate the theoretical amount of forests of different ages, including old growth, for a region

(Johnson et al. 1995) if one knows the fire frequency (or the fire cycle, i.e., the inverse). Assuming a constant fire frequency and a fire hazard independent of stand age (as is commonly reported for boreal ecosystems controlled by stand-replacing fires; Johnson 1992), the proportion of forests that can reach a defined age class follows a negative exponential distribution with a mean age equal to the fire cycle. This procedure assumes that fire cycle was constant through time, an assumption that is rarely completely met (Huggard and Arsenault 1999). To circumvent this limitation, recent studies (for example Senici et al. 2010) have used a more flexible Cox model to derive fire cycles. In most cases, however, when both empirical and modeled distributions are available, estimates of the proportion of stands older than 100, 200, and 300 years are comparable (Appendix A). Using the modeled rather than the observed distribution has also the advantage of taking into account the fact that in many cases observed age since fire is underestimated when trees initiated by an old fire have been replaced by a more recent cohort. Therefore, to standardize the available information, we used the modeled proportions to synthesize the information for each ecozone. Most of these studies used dendrochronology to estimate time since fire, and represent the mean fire frequency over the last 300 years. Current fire frequency (last 50 years) from a Canada-wide database (Stocks et al. 2002) was used for the Boreal Cordillera, Taiga Cordillera, Taiga Plains, and Hudson Plains ecozones (Ecological Stratification Working Group 1996), as no studies on historic fire frequency were available for these areas. Mean age of the forest (time since fire) before large clear-cutting activities began were used to estimate historic burn rates. These rates were averaged by ecozone and the proportion of stands of 100, 200, and 300 years was estimated using a negative exponential distribution (Appendix A).

Although the mean time since last fire for the different ecozones was highly variable, ranging from 78 years in the western Boreal Shield ecozone to 813 years in the Hudson Plains ecozone, a large proportion of the boreal landscape is estimated to be composed of forests over 100, 200, and 300 years old (Table 1). Assuming these studies are representative of the different ecozones, and taking into account the size of the ecozones, forests over 100, 200, and 300 years since fire should cover 49%, 27%, and 16%, respectively, of the boreal landscape in Canada. Important limitations to this estimate are present when ecozones are characterized by very few studies (Taiga Shield east for example) or by very high physiographic variability such as in the Cordillera regions. Although significant everywhere, proportions of forests over 100, 200, and 300 years since fire are distributed unevenly across Canada. As fires are less frequent in eastern Canada, old-growth forests are more abundant in this region. Although these estimates might be overestimated because of fire suppression activities this possible bias is minimal as effective fire suppression only began in the 1970s when the use of water bombers became common (Lefort et al. 2003). The presented results are rough estimates used here to raise the issue of the presence of boreal old-growth forests. Better estimates will emerge as new studies will be made available.

As stand break up occurs well before 150 years in eastern boreal forests (Harvey et al. 2002), we can conclude that a significant proportion of Canadian eastern boreal forests are

Fig. 1. Map of Canadian ecozones with the location of the Clay Belt. Dots represent the 18 fire frequency studies (cited in Bergeron et al. 2004, 2006, plus recent studies by Senici et al. 2010, and Bélisle et al. 2011) used to calculate the theoretical forest age distributions presented in Table 1.

Table 1. Estimated proportion (%) of forest over 100, 200, and 300 years after fire in hypothetical undisturbed (logged or cleared) landscapes according to historical mean forest age observed in the different ecoregions of Canada.

Region	>100 years	>200 years	>300 years
Boreal Cordillera	68	46	31
Taiga Cordillera	82	67	55
Taiga Plains	49	24	12
Boreal Plains	30	9	3
Hudson Plains	88	78	69
Taiga Shield west	43	18	8
Boreal Shield west	28	8	2
Boreal Shield east	48	23	11
Taiga Shield east	55	30	16
Total	49	27	16

Note: Current fire frequency (last 50 years) was used for ecozones where no long-term studies were available.

composed of stands dominated by individuals that reach the canopy a long time after fire disturbance: a gap dynamic that is typical of old-growth forests (Wirth et al. 2009). Natural boreal forests are thus not only composed of young postfire

stands but also include significant proportions of old-growth stands characterized by different structures and dynamics (Harper et al. 2005).

This significant proportion of old-growth forests on the boreal landscape is not a recent phenomena, as Cyr et al. (2009) were able to show that forests over 100 years old have constituted a significant portion of the forest mosaic throughout the Holocene (Fig. 2) in one boreal region. At no time during the Holocene was the forest mosaic composed of less than 30% of forests older than 100 years. While this study was undertaken on the Clay Belt of western Québec, this might also be true for most of the Canadian boreal forest where alternating periods of long and short fire intervals have commonly been observed (Flannigan et al. 2001; Hely et al. 2010).

Disturbance regimes: multiple agents and complex interactions

Although important, it has been suggested that the role of stand replacing fires may have been over-emphasized in some boreal ecosystems (Engelmark 1999; Kuuluvainen 2002). In Scandinavia, China, and Russia there has been a recognition

Fig. 2. (A) Fluctuations of the mean fire intervals during the Holocene and (B) the estimated proportion of forest over 100, 200, and 300 years after fire in northwestern Québec. Modified from data presented in Cyr et al. (2009).
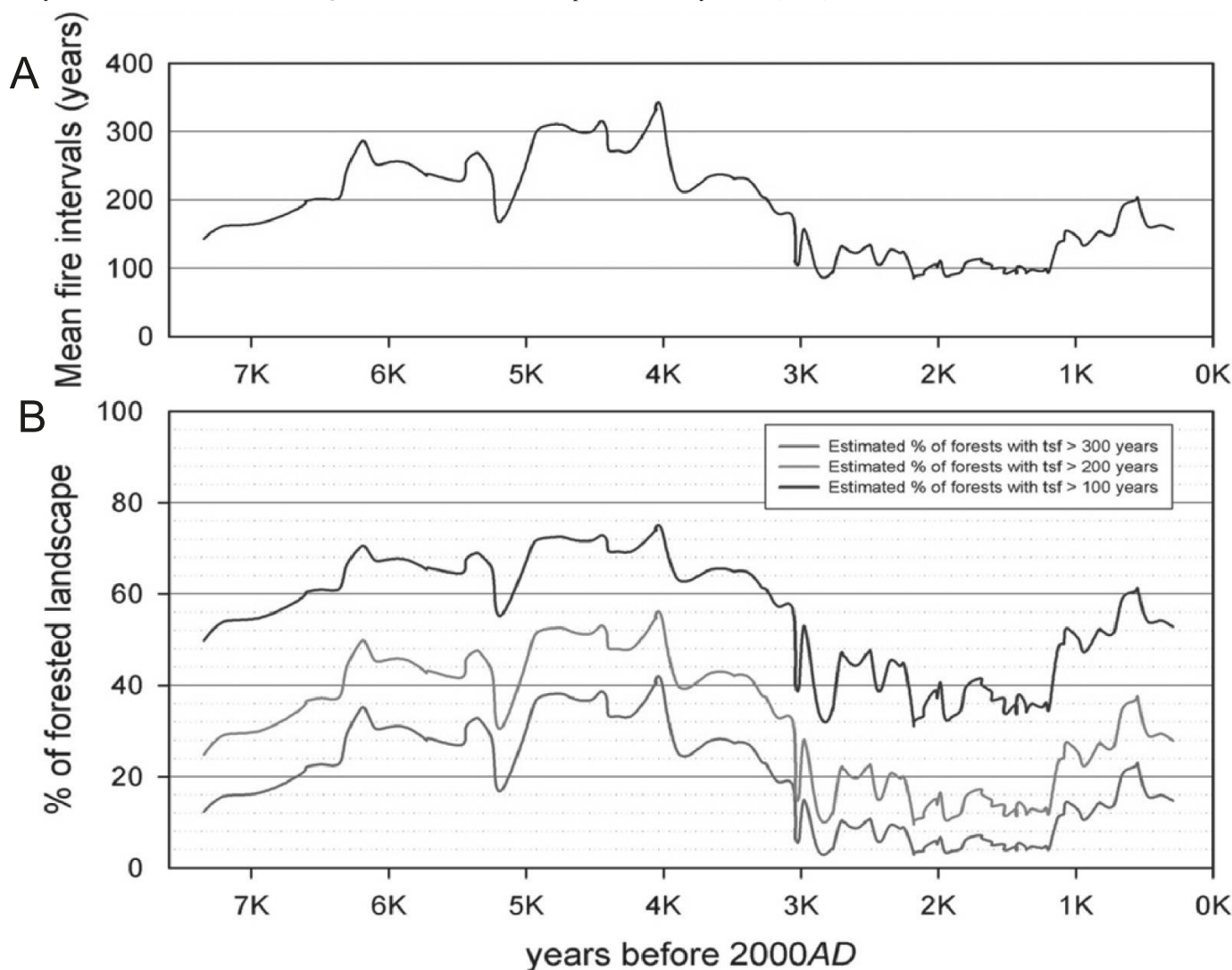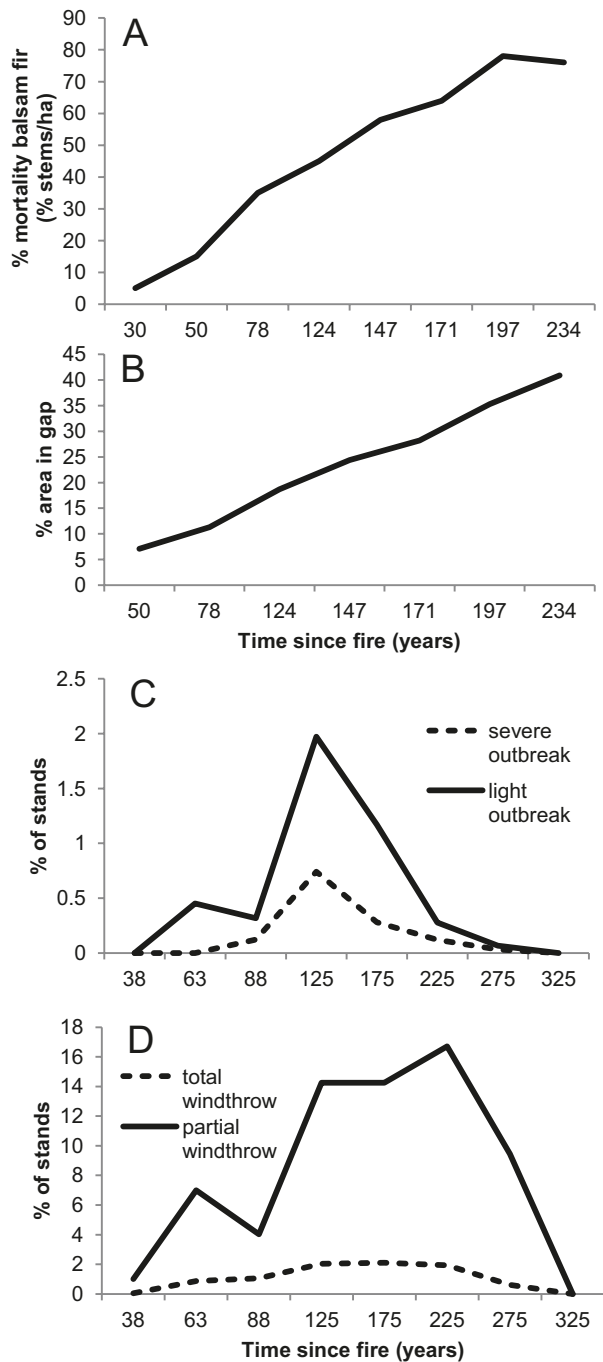

of the importance of gap dynamics in boreal forests that are little or rarely affected by fire (Ban et al. 1998; Drobyshev 1999; Kuuluvainen 1994; Liu and Hytteborn 1991) as well as in pine forests affected by nonstand replacing surface fires (Rouvinen et al. 2002). In North America this realisation has been longer in coming owing to the pervasive nature of stand-replacing fires, although nonlethal surface fires are also observed (Bergeron and Brisson 1990; Smirnova et al. 2008). The importance of secondary disturbance mediated dynamics in North America is, however, recognized more and more (e.g., Cumming et al. 2000; Kneeshaw and Bergeron 1998; McCarthy 2001; Pham et al. 2004).

In fact, in Canada, insects and other nonfire disturbances affect a larger area than fire each year (Kneeshaw 2001; Natural Resources Canada 2010). Among insects, spruce budworm (*Choristoneura fumiferana*) in the east and mountain pine beetle (*Dendroctonus ponderosae*) in the west have profound impacts on stand dynamics (Morin et al. 2009; Axelson et al. 2009). In both cases, outbreak severity (here defined as tree mortality) increases with long fire intervals that allow for the establishment or development of more vul-

nerable host trees in the stands. In the mixedwood and conifer dominated forests of the Clay Belt, increasing abundance of balsam fir (*Abies balsamea*) with time since fire is strongly correlated with an increase in spruce budworm outbreak severity (Fig. 3). The impacts of such disturbances on forest stands are, however, very different than the impact of fires. Fires create very heterogeneous patterns of mortality in forests, as within burnt areas fires kill most of the standing trees immediately (median estimates for live trees per hectare varied from 0 to 241, Perera et al. 2009). In contrast, disturbances such as insect outbreaks may take years to kill trees and some trees will always survive the outbreak (Rossi and Morin 2011). Furthermore, insects are often host specific, attacking only one species or a small group of species. For example, the eastern spruce budworm attacks only balsam fir and spruce (white *Picea glauca* and black *Picea mariana*), thus outbreaks do not directly kill broadleaf deciduous or *Thuja occidentalis* within stands (Bouchard et al. 2005). Following insect outbreaks, mortality and thus age-class distributions within stands across the landscape are consequently much patchier than following fires.

Fig. 3. Incidence of secondary disturbances in relation to time since fire in the mixedwood and coniferous forests of the Québec and Ontario Clay Belt. Percent of balsam fir (A) and area in gap (B) in mixedwoods (modified from Bergeron et al. 1995 and Kneeshaw and Bergeron 1998) and (C) severe and light spruce budworm impacts and (D) total and partial windthrow in black spruce feathermoss forests (modified from Harper et al. 2002). Note the different scales on the Y axes.

2005), but partial windthrow may be relatively frequent even in interior boreal forests (Fig. 3; Harper et al. 2002).

Finally, fine-scale local level disturbances such as root rot, partial windthrow, and insect mortality, as well as tree senescence, are also observed. In such circumstances, the canopy gaps created are small, corresponding to the growing space of single to multiple canopy trees. Some studies have suggested that insects and wind are responsible for a large proportion of the mortality observed in areas characterized by a continuous canopy interspersed with gaps (de Römer et al. 2007; Kneeshaw and Bergeron 1998). However, such individual tree mortality often has multiple underlying causes (Rouvinen et al. 2002; Reyes and Kneeshaw 2008).

Complex forest succession and dynamics

Where stand replacing fires are frequent, the effects of other disturbances will be minor and the boreal landscape will be controlled by the recurrence of large fire events. Under such cycles entire stands of trees are killed before trees attain their maximum longevity (Dix and Swan 1971), and the North American boreal landscape is often thought of as large patches of trees recovering from burns. The longterm cumulative effect of short fire cycles has been to limit not only successional processes but also the presence of tree species with late successional characteristics such as shade tolerance and recruitment from seedling banks (Kenkel et al. 1997). However, as discussed earlier, long fire cycles observed in many parts of the Canadian boreal forest allow for species replacement and, consequently, the presence and even dominance of late successional species. To illustrate this, we will separately discuss postfire succession in the eastern mixedwood and black spruce forest zones. We used here the term succession in its broad sense defined as a change in species dominance or structure in the canopy (Drury and Nisbet 1973). The mixedwood boreal forest is a zone of transition from the Great Lakes – Acadian forest in the south and the black spruce forest in the north. Typically, stands are a mix of deciduous and coniferous species (Bergeron 2000). In contrast, the black spruce forest zone lies between the mixedwood zone to the south and the Taiga to the north (Bergeron et al. 2004).

Mixedwood boreal forest

It has long been claimed that there was no real species succession in boreal forests as most species were present immediately after fire, and that it was only different growth rates that explained their successive dominance in the canopy (Viereck 1983; Johnson 1992). Although most species are commonly present after fire, there is, however, a significant inseeding of late successional species with time since fire (Galipeau et al. 1997; Bergeron 2000). Consequently, mixedwood boreal forests in central and eastern Canada show a clear change in composition of the forest cover in relation to time since fire (see Chen and Popadiouk 2002 for a review). This is clearly illustrated (Fig. 4) by a reconstructed 300 year forest succession from the Lake Duparquet area in Québec (Bergeron 2000). Over 300 years, stands were successively dominated by broadleaf deciduous trees (aspen (*Populus tremuloides*) and birch (*Betula papyrifera*), a mixture of deciduous trees with some conifers (fir and spruces), and finally

Wind is another important nonfire disturbance, mainly found in boreal coastal areas where hurricanes generate very strong winds and in continental areas where large water bodies generate strong stormcells (Frelich 2002). Return intervals are, however, quite long from 450 to 10 500 years for stand-replacing windthrow events (Schulte and Mladenoff

Fig. 4. Natural forest succession in the Lake Duparquet mixedwood boreal forest. The top panel illustrates succession from a broadleaf deciduous, to a mixedwood, and finally coniferous stand along with the dominant disturbance agents. The bottom panel illustrates the changes in tree species with time since fire. Modified from data presented in Bergeron (2000).
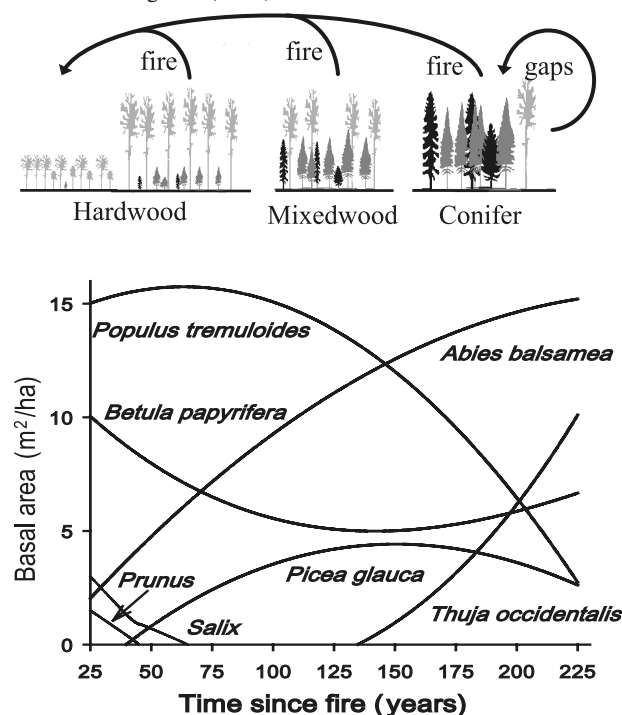
dominated by conifers. Although invading late in succession, *T. occidentalis* gradually increases in abundance and appears to be dominant in old-growth stands. A similar pattern of canopy replacement was also found in Minnesota, USA (Frelich and Reich 1995). Although transition from broadleaf species to conifers is mainly explained by different growth rates and shade tolerance, it has been suggested that the decrease in abundance of deciduous litter and the increase in available coarse woody debris facilitates conifer establishment under the decaying deciduous canopy (Simard et al. 2003). This seems particularly important for *T. occidentalis*, which shows a long delay in establishment before becoming abundant in late successional stands (Fig. 4). The duration of this process varies depending on late successional species seed availability. For example, multiple cohorts of aspen have been observed (Namroud et al. 2005), and in extreme cases where no late successional species seed is present, uneven-aged stands of aspen have also been observed (Cumming et al. 2000).

In mixedwood boreal forests, windthrow or insect outbreaks do not generally return shade intolerant species to dominance as it does after fires. Shade tolerant species that have formed a seedling bank are generally recruited into the canopy. Balsam fir has been shown to follow cyclical patterns, with pre-established seedlings replacing canopy dominants following windthrow or insect outbreak (Morin et al. 2009; Thompson et al. 2003). However, a return to deciduous dominance (Bouchard et al. 2005), or a succession to shrub dominated stands (Kneeshaw and Bergeron 1998), has also been observed after severe defoliation. Understory plants

also show a similar successional pattern from light demanding species under deciduous trees to shade tolerant shrubs under coniferous trees (De Grandpré et al. 1993; Hart and Chen 2008). The gaps created by secondary disturbances allow for the persistence of light demanding herbs on the landscape (De Grandpré and Bergeron 1997).

Black spruce forests

Black spruce forests make a large belt at the interface between closed-canopy boreal forest and open-canopy (taiga) boreal forest. While generally dominated by very few species (black or white spruce, jack pine, and trembling aspen) forest succession is an important factor in these forests, as in the boreal mixedwood. While species replacement from jack pine or aspen to spruce has been observed (Lecomte and Bergeron 2005; Harper et al. 2005), black spruce is present as both a postfire dominant and a late successional species. Consequently, successional changes in these forests relates less to tree species succession and more to structural changes (Harper et al. 2005) and to changes in the understory composition, which we will examine in detail below (Fenton and Bergeron 2006) (Fig. 5).

The understory of coniferous boreal forests is characterized by a dominant bryophyte layer (LaRoi and Stringer 1976), with a few species of vascular plants (Taylor et al. 1987). While many vascular plant species tend to regenerate immediately after fire from surviving buried buds (Rowe 1983), succession via species replacement is observed in the bryophyte layer (Black and Bliss 1978; Fenton and Bergeron 2006). Immediately after fire and before canopy closure, lichens and herbs dominate the forest floor (Shafi and Yarranton 1973; Taylor et al. 1987); however, with black spruce canopy closure, a continuous cover of feather mosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*) is established, which can persist for many years. However, in the prolonged absence of fire, facilitative succession takes place in mesic to moist sites (Fenton and Bergeron 2006; Fig. 5). Shade and drought tolerant (Hayward and Clymo 1983) hummock sphagna (mostly *Sphagnum capillifolium*, *Sphagnum girgensohnii*, and *Sphagnum subtile*) establish colonies in, or in some cases expand colonies over, the feathermosses (Fenton et al. 2007; Taylor et al. 1987; Foster 1983). As these sphagna increase the thickness of the organic layer and consequently decrease fluctuations in water saturation of the organic layer, species associated with peatlands dependant on constant hydration subsequently establish in the bryophyte carpet (*Sphagnum magellanicum*, *Sphagnum rubellum*, and *Sphagnum fallax*). As the canopy opens up, these heliotrophic species (Hayward and Clymo 1983) increase their growth rates and overtop the slower growing shade tolerant species (Rochefort et al. 1990; Schipperges and Rydin 1998). As a consequence, three distinct phases are distinguishable in the successional sequence: mature black spruce forests, open paludified black spruce forests, and forested peatland (Fenton and Bergeron 2011).

These changes in the bryophyte layer have significant effects on the tree layer. The fast growth rate of sphagna compared with that of feathermosses (Bisbee et al. 2001) results in the overtopping of most seedlings in the understory. Tree regeneration is then almost solely dependent on layering (Doucet 1988); as the organic layer is generally 40–60 cm

Fig. 5. Natural forest succession in black spruce forest of the Québec Clay Belt. The top panel illustrates stand structural changes with time since fire, including the influence of paludification (organic layer thickness). The bottom panel describes changes in the bryophyte layer and suggests three forest stages that integrates tree and bryophyte layer characteristics. Modified from data presented in Lecomte et al. (2006), Fenton and Bergeron (2006), and Fenton and Bergeron (2011).
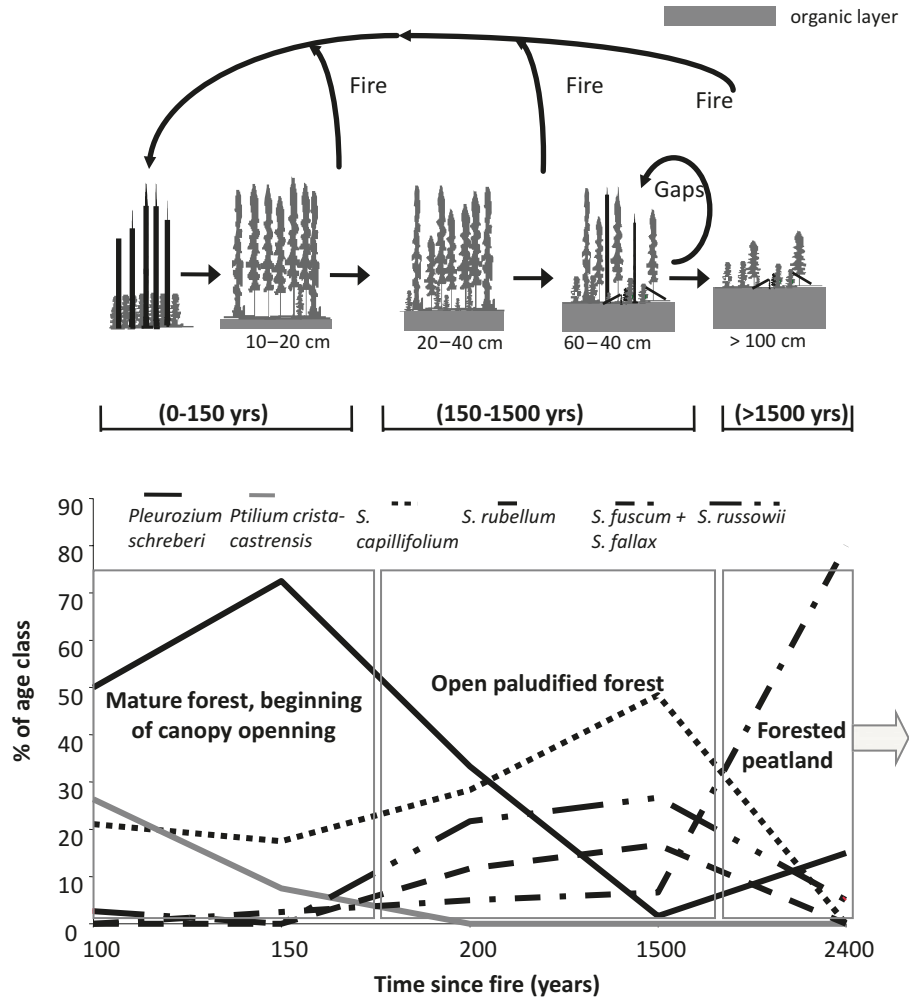
thick in older stands (>150 years; Lecomte et al. 2006), the roots are unable to reach the mineral soil (Simard et al. 2007). Black spruce rooted in the organic layer grow in a colder, less nutrient rich environment than black spruce rooted in the mineral soil, resulting in a significant drop in site productivity over time (Simard et al. 2007). Consequently, the structure of the forest is affected with a gradual decline in stand height and an opening up of the stand, which reaches an extreme in the oldest stands that are dominated by gaps (St-Denis et al. 2010).

## Species richness: a vital attribute of boreal forests

Boreal forests are generally considered to have low species richness, as they are located towards the polar ends of the latitudinal species richness gradient (De Grandpré et al. 2003). Furthermore, species richness of vascular plants at the stand scale (alpha richness) is frequently quite low. However, the complex patterns that create and maintain old-growth boreal forests in both the mixedwood and black spruce forest regions support a diverse understory community not present in the younger stands (Figs. 6 and 7). Within the mixedwoods (Fig. 6), richness at the stand level is not higher in old-growth stands than in young stands (50–100 years since fire); however, beta diversity (Whittaker 1972) of epiphytic mosses and liverworts increases in the older stands, indicating that there is more variation in composition among stands in these older age classes. Finally, when looking at the cumulative species curve it is clear that the vascular plant community is largely present in young stands (nearly 90% of vascular species), while only 70% of mosses were present in young stands.

The important role of old-growth forests in maintaining understory diversity is even more evident in the black spruce forests (Fig. 7). Stand level richness of all groups (vascular plants, terrestrial mosses, liverworts, and lichens) increased significantly after 150 years since fire. The increase in liverwort richness is particularly significant, as the beta diversity of this group also increases with time, indicating that there is significant turnover among stands of a same age group in the old-growth forests. Within a stand type, species composition is highly stochastic in the nonvascular plant layer (Fenton and Bergeron 2006, 2008; Carleton 1990; LaRoi and Stringer 1976), driven by antecedent events in the stand itself and in

Fig. 6. Species richness of the understory in mixedwood stands over time since fire. (A) Mean stand richness for vascular plants, epiphytic mosses, liverworts, and lichens in age classes representing an age gradient from 50 to over 200 years. Mean total understory richness (the sum of the four groups) is represented on the left Y axis. (B) Beta diversity illustrating turnover within age groups. (C) Cumulative species curves (percent) illustrating gamma diversity among age classes. Note the difference in scale between the panels. Based on data published in De Grandpré et al. 1993 (vascular plants) and Boudreault et al. 2000 (mosses, liverworts, and lichens).
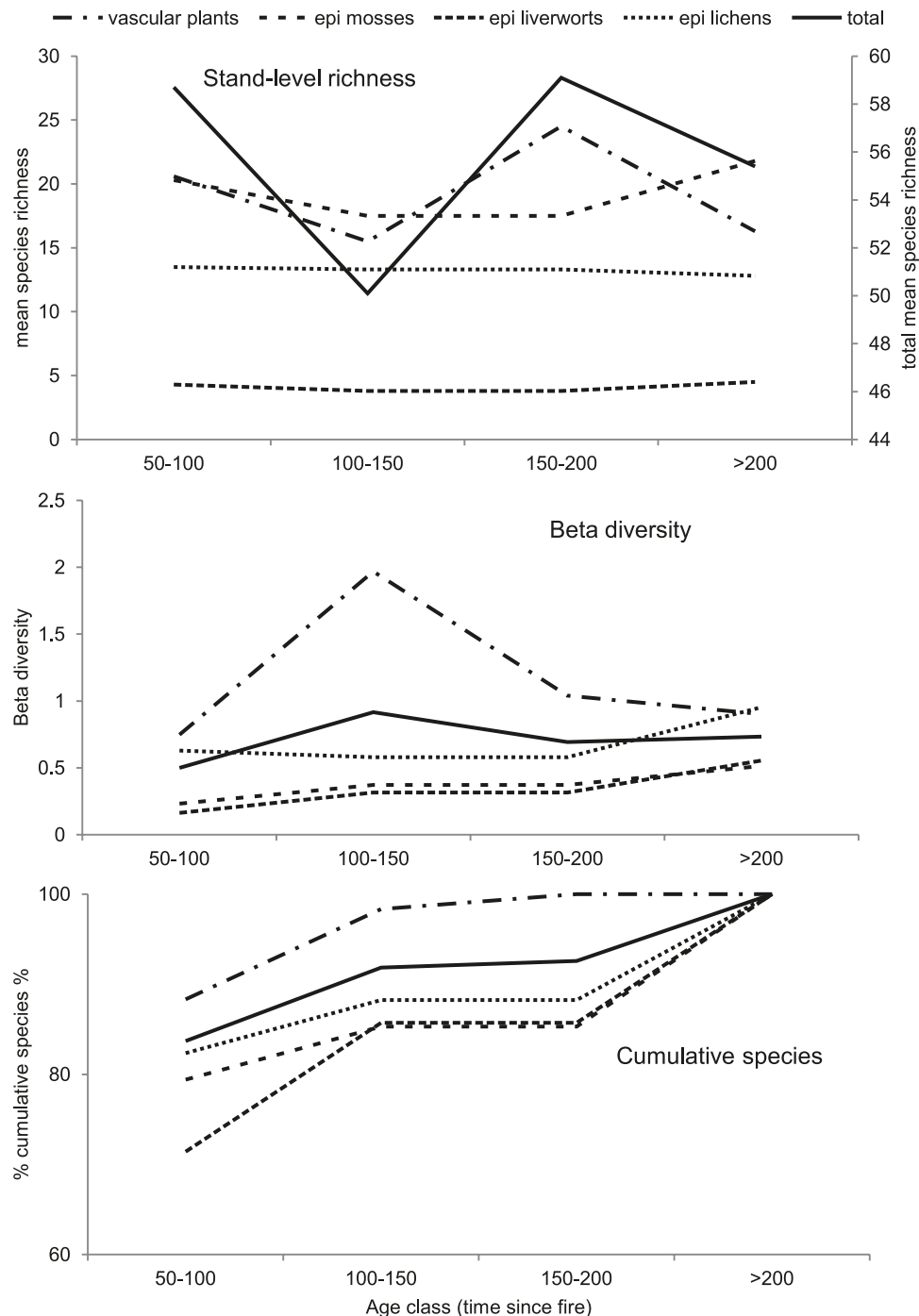

surrounding populations (McCune and Allen 1985; Kimmerer and Driscoll 2000; Økland et al. 2003; Hurtt and Pacala 1995). Finally, the cumulative species curve indicates that 20% of all species are found in older stands (over 150 years since fire) and not in younger stands. For liverworts fully 50% of species are not found in younger stands.

Boreal forests of all types and across all scales are less species rich than similar elements closer to the equator. How-

ever, the stereotypical view of a "depauperate" boreal landscape is clearly not true of all forests. Old-growth boreal forests clearly maintain a diverse understory community that is not present in younger stands. The loss of these stands across the landscape would result in significant species loss, as has been observed in Fennoscandinavia (Esseen et al. 1997; Siitonen 2001). However, just as significant to biodiversity conservation are early and intermediate stages of for-

Fig. 7. Species richness of the understory in black spruce stands over time since fire. (A) Mean stand richness for vascular plants, terrestrial mosses, liverworts, and lichens in age classes representing an age gradient from 50 to over 200 years. Mean total understory richness (the sum of the four groups) is represented on the left Y axis. (B) Beta diversity illustrating turnover within age groups. (C) Cumulative species curves (percent) illustrating gamma diversity among age classes. Note the difference in scale between the panels. Based on data published in Harper et al. 2003 (vascular plants), Fenton and Bergeron 2008 (mosses, and liverworts), and Boudreault et al. 2002 and Zouaoui 2011 (lichens).
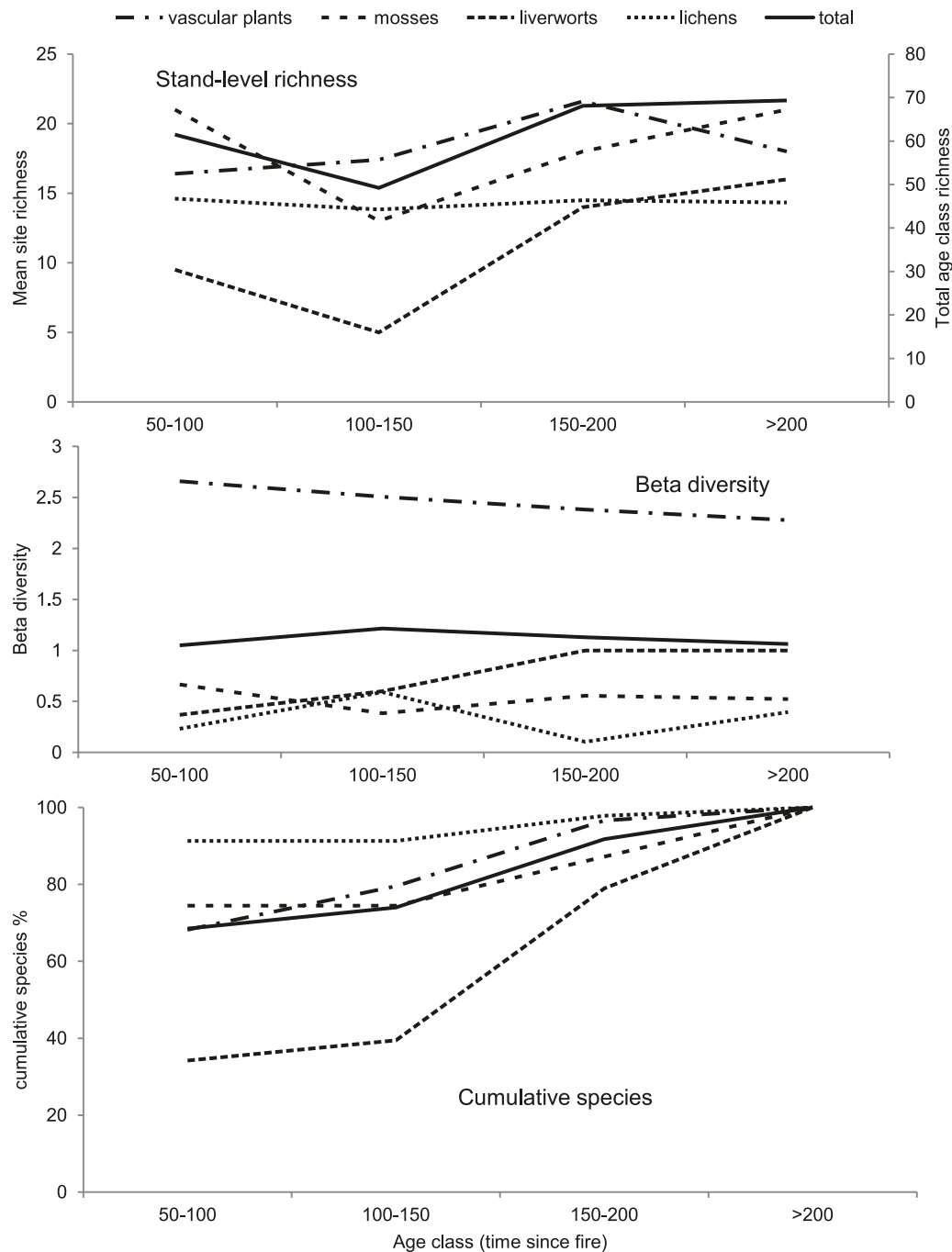
est development. Consequently, conservation of all successional stages, including old growth, needs to be taken into account during any proposed management.

Conclusion

The preceding arguments demonstrate that the Canadian boreal forest is complex and one should be careful to generalize its characteristics over all Canadian landscapes. In its eastern part and to a lesser degree but still significantly in its western part, old-growth forests are common and controlled by nonfire disturbances. A complex disturbance regime including both fire and nonfire disturbances and structural succession are responsible for a diversity of habitats that in turn are responsible for an important understory diversity. These observations are important elements that should influence our understanding and management of this important ecosystem.

The dominant forest management model in Canadian boreal forests, based on clear-cut harvesting and growing even-aged stands with short rotations, does not reflect the complexities of the disturbance–succession cycle observed in our natural boreal forests. We believe the widespread application of even-aged, single species management at all scales of boreal forest management interferes with fundamental ecological processes that maintain ecosystem integrity in boreal forests. Boreal forest management should no longer be solely based on a paradigm of repeating catastrophic disturbances. This being said, emulating fire as an important process of boreal forest dynamics as discussed above in paludifying forests remains an important issue, as do other unusual regeneration patterns. Consequently, completely replacing even-aged management by high retention systems would be another mistake. As usual, one solution does not fit all and maintaining the complexity of natural systems through a diversity of silvicultural approaches is our best strategy (Fenton et al. 2009; Puettmann et al. 2009).

Global change, especially the projected climate change in northern latitudes, presents a further daunting challenge for boreal forest management. The potential for major climate-mediated ecosystem change, as well as uncertainties about the degree and rate of climate change, necessitates a significant shift in thinking about forest management. Sustainability goals must operate in an environment of constant change with uncertain future conditions. Boreal ecosystems may be more resilient than other systems, as they mainly include generalist species that evolved under highly variable disturbance and climatic stresses (Bergeron et al. 2010; Carcaillet et al. 2010) allowing us some room to manoeuvre. However, further north where a harsher climate and a lower diversity prevail, Jasinski and Payette (2005) and Girard et al. (2008) documented that open forest woodlands, associated with regeneration failure, are frequent and are expanding into the closed-crown boreal forest zone. Forest and land managers must consider how their practices must change to minimize the risk of undesirable future outcomes that could arise from boreal forests being ill-adapted to future conditions (Millar et al. 2007). Future management in boreal forests must involve deliberate, on-the-ground forest practices that maintain ecosystem complexity across multiple scales of time and space, and facilitate or mitigate ecosystem change in response to climate change.

Acknowledgements

References

Axelson, J.N., Alfaro, R.I., and Hawkes, B.C. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. For. Ecol. Manage. **257**(9): 1874–1882. doi:10.1016/j.foreco.2009.01.047.

Ban, Y., Xu, H., Bergeron, Y., and Kneeshaw, D.D. 1998. Gap regeneration of shade-intolerant *Larix gmelini* in old-growth boreal forests of northeastern China. J. Veg. Sci. **9**(4): 529–536. doi:10.2307/3237268.

Bélisle, A.C., Gauthier, S., Cyr, D., Bergeron, Y., and Morin, H. 2011. Fire regime and old-growth boreal forests in central Québec, Canada: an ecosystem management perspective. Silva Fenn. **45**(5): 889–908 http://www.metla.fi/silvafennica/full/sf45/sf455889.pdf.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Québec's southern boreal forest. Ecology, **81**(6): 1500–1516. doi:10.1890/0012-9658(2000)081[1500:SASDIT]2.0.CO;2.

Bergeron, Y., and Brisson, J. 1990. Fire regime in red pine stands at the northern limit of the species' range. Ecology, **71**(4): 1352–1364. doi:10.2307/1938272.

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Québec. Can. J. For. Res. **25**(8): 1375–1384. doi:10.1139/x95-150.

Bergeron, Y., Denneler, B., Charron, D., and Girardin, M.P. 2002. Using dendrochronology to reconstruct disturbance and forest dynamics around Lake Duparquet, northwestern Québec. Dendrochronologia, **20**(1–2): 175–189. doi:10.1078/1125-7865-00015.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., and Lefort, P. 2004. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio, **33**(6): 356–360. PMID:15387074.

Bergeron, Y., Cyr, D., Drever, R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, E., Leduc, A., Le Goff, H., Lesieur, D., and Logan, K. 2006. Past, current, and future fire frequencies in Québec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can. J. For. Res. **36**(11): 2737–2744. doi:10.1139/x06-177.

Bergeron, Y., Cyr, D., Girardin, M.P., and Carcaillet, C. 2010. Will climate change drive 21st century burn rates in Canadian boreal forests outside of natural variability: collating global climate model experiments with sedimentary charcoal data. Int. J. Wildland Fire, **19**(8): 1127–1139. doi:10.1071/WF09092.

Bisbee, K.E., Gower, S.T., Norman, J.M., and Nordheim, E.V. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia (Berl.), **129**(2): 261–270. doi:10.1007/s004420100719.

Black, R.A., and Bliss, L.C. 1978. Recovery sequence of *Picea mariana – Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. Can. J. Bot. **56**(17): 2020–2030. doi:10.1139/b78-243.

Bouchard, M., Kneeshaw, D.D., and Bergeron, Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in western Québec. For. Ecol. Manage. **204**(2–3): 297–313. doi:10.1016/j.foreco.2004.09.017.

Boudreault, C., Gauthier, S., and Bergeron, Y. 2000. Epiphytic lichens and bryophytes on *Populus tremuloides* along a chronosequence in the southwestern boreal forest of Québec, Canada. Bryologist, **103**(4): 725–738. doi:10.1639/0007-2745(2000)103[0725:ELABOP]2.0.CO;2.

Boudreault, C., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Can. J. For. Res. **32**(6): 1080–1093. doi:10.1139/x02-027.

Bradshaw, C.J.A., Warkentin, I.G., and Sodhi, N.S. 2009. Urgent preservation of boreal carbon stocks and biodiversity. Trends Ecol. Evol. **24**(10): 541–548. doi:10.1016/j.tree.2009.03.019. PMID:19679372.

Burton, P.J., Messier, C., Weetman, G.F., and Prepas, E.E. Adamowicz, and Tittler, R. 2003. The current state of boreal

forestry and the drive for change. *In* Towards sustainable management of the boreal forest. *Edited by* P.J. Burton, C. Messier, D.W. Smith, and W.L. Adamowicz. National Research Council of Canada, Ottawa, Canada. pp. 1–40.

Burton, P.J., Bergeron, Y., Bogdanski, B.E.C., Juday, G.P., Kuuluvainen, T., McAfee, B.J., and Ogden, A. Teplyakov, Alfaro, R.I., Francis, D.A., Gauthier, S., and Hantula, J. 2010. Sustainability of boreal forests and forestry in a changing environment. *In* Forests and society — responding to global drivers of change. *Edited by* G. Mery, P. Katila, G. Galloway, R.I. Alfaro, M. Kanninen, M. Lobovikov, and J. Varjo. IUFRO World Series Vol. 25. Vienna. pp. 247–282.

Carcaillet, C., Richard, P.J.H., Bergeron, Y., Fréchette, B., and Ali, A.A. 2010. Resilience of the boreal forest in response to Holocene fire-frequency changes assessed by pollen diversity and population dynamics. Int. J. Wildland Fire, **19**(8): 1026–1039. doi:10.1071/WF09097.

Carleton, T.J. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. J. Veg. Sci. **1**(5): 585–594. doi:10.2307/3235563.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. **10**(3): 137–166. doi:10.1139/a02-007.

Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J. 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol. Appl. **10**(3): 744–759.

Cyr, D., Gauthier, S., Bergeron, Y., and Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ, **7**(10): 519–524. doi:10.1890/080088.

De Grandpré, L., and Bergeron, Y. 1997. Diversity and stability of understorey communities following disturbance in the southern boreal forest. J. Ecol. **85**(6): 777–784. Available from http://www.jstor.org/stable/2960601.

De Grandpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. **4**(6): 803–810. doi:10.2307/3235618.

De Grandpré, L., Bergeron, Y., Nguyen-Xuan, T., Boudreault, C., and Grondin, P. 2003. Composition and dynamics of the understory vegetation in the boreal forests of Québec. *In* The herbaceous layer of forests of eastern North America. *Edited by* F.S. Gilliam and M. R. Roberts. Oxford University Press. pp. 238–261.

de Römer, A.H., Kneeshaw, D.D., and Bergeron, Y. 2007. Small gap dynamics in the southern boreal forest of eastern Canada: do canopy gaps influence stand development? J. Veg. Sci. **18**(6): 815–826. doi:10.1658/1100-9233(2007)18[815:SGDITS]2.0.CO;2.

Dix, R.L., and Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. J. Bot. **49**(5): 657–676. doi:10.1139/b71-103.

Doucet, R. 1988. La régénération préétablie dans les peuplements forestiers au Québec. For. Chron. **64**(2): 116–120.

Drobyshev, I.V. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum–Myrtillus* old-growth forests. For. Ecol. Manage. **115**(1): 71–83. doi:10.1016/S0378-1127(98)00437-X.

Drury, W.H., and Nisbet, I.C.T. 1973. Succession. J. Arnold Arbor. Harv. Univ. **54**: 331–368.

Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Agriculture and Agri-Food Canada and Environment Canada, Ottawa.

Engelmark, O. 1999. Boreal forest disturbances *In* Ecosystems of disturbed ground. Ecosystems of the World. *Edited by* L.R. Walker. Elsevier, New York. pp. 161–186.

Esseen, P.A., Ehnström, B., Ericson, L., and Sjöberg, K. 1997. Boreal forests. Ecol. Bull. **46**: 16–47.

Fenton, N.J., and Bergeron, Y. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. J. Veg. Sci. **17**(1): 65–76. doi:10.1111/j.1654-1103.2006.tb02424.x.

Fenton, N., and Bergeron, Y. 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal *Picea mariana* forests. Biol. Conserv. **141**(5): 1389–1399. doi:10.1016/j.biocon.2008.03.019.

Fenton, N.J., and Bergeron, Y. 2011. Dynamic old-growth forests? A case study of boreal black spruce forest bryophytes. Silva Fenn. **45**(5): 083–994. Available from http://www.metla.fi/silvafennica/full/sf45/sf455983.pdf.

Fenton, N.J., Beland, C., DeBlois, S., and Bergeron, Y. 2007. *Sphagnum* establishment and expansion in black spruce (*Picea mariana*) boreal forests. Can. J. Bot. **85**(1): 43–50. doi:10.1139/b06-148.

Fenton, N.J., Simard, M., and Bergeron, Y. 2009. Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America. J. For. Res. **14**(5): 258–267. doi:10.1007/s10310-009-0134-8.

Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., and Bergeron, Y. 2001. Future fire in Canada's boreal forest: paleoecology results and general circulation model – regional climate model simulations. Can. J. For. Res. **31**(5): 854–864. doi:10.1139/x01-010.

Foster, D.R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. **61**(9): 2459–2471. doi:10.1139/b83-269.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen–deciduous forests. Cambridge University Press, New York.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**(3): 325–346. doi:10.2307/2937063.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**(2): 139–147. doi:10.1139/x96-148.

Girard, F., Payette, S., and Gagnon, R. 2008. Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J. Biogeogr. **35**(3): 529–537. doi:10.1111/j.1365-2699.2007.01816.x.

Harper, K.A., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: a landscape scale study. Silva Fenn. **36**(1): 249–263.

Harper, K., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., and Bergeron, Y. 2003. Structure, composition and diversity of old-growth black spruce boreal forest of the Clay Belt region in Québec and Ontario. Environ. Rev. **11**(Suppl. S1): S79–S98. doi:10.1139/a03-013.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., and DeGrandpré, L. 2005. Structural development following fire in black spruce boreal forest. For. Ecol. Manage. **206**(1–3): 293–306. doi:10.1016/j.foreco.2004.11.008.

Hart, S.A., and Chen, H.Y.H. 2008. Fire, Logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol. Monogr. **78**(1): 123–140. doi:10.1890/06-2140.1.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. **155**(1–3): 369–385. doi:10.1016/S0378-1127(01)00573-4.

Hayward, P.M., and Clymo, R.S. 1983. The growth of *Sphagnum*:

Experiments on, and simulation of, some effects of light flux and water-table depth. J. Ecol. **71**(3): 845–863. Available from http://www.jstor.org/stable/2259597.

Hély, C., Girardin, M.P., Ali, A.A., Carcaillet, C., Brewer, S., and Bergeron, Y. 2010. Eastern boreal North American wildfire risk of the past 7000 years: a model-data comparison. Geophys. Res. Lett. **37**(14): L14709. doi:10.1029/2010GL043706.

Huggard, D.J., and Arsenault, A. 1999. Comment–Reverse cumulative standing age distribution in fire frequency analysis. Can. J. For. Res. **29**(9): 1449–1456. doi:10.1139/x99-114.

Hurtt, G.C., and Pacala, S.W. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. J. Theor. Biol. **176**(1): 1–12. doi:10.1006/jtbi.1995.0170.

Jasinski, J.P.P., and Payette, S. 2005. The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol. Monogr. **75**(4): 561–583. doi:10.1890/04-1621.

Johnson, E.A. 1992. Fire and vegetation dynamics-studies from the North American boreal forest. Cambridge Studies in Ecology, Cambridge University Press, Cambridge.

Johnson, E.A., Miyanishi, K., and Weir, J.M.H. 1995. Old-growth, disturbance, and ecosystem management. Can. J. Bot. **73**(6): 918–926. doi:10.1139/b95-100.

Kasischke, E. 2000. Boreal ecosystems in the global carbon cycle. *In* Fire, climate change and carbon cycling in the boreal forest. *Edited by* E. Kasischke and B. Stocks. Spring, New York. pp. 19–30.

Kenkel, N.C., Walker, D.J., Watson, P.R., Caners, R.T., and Lastra, R.A. 1997. Vegetation dynamics in boreal forest ecosystems. Coenoses, **12**(2–3): 97–108. Available from http://www.umanitoba.ca/science/biological_sciences/botany_lab/pubs/1997a.pdf.

Kimmerer, R.W., and Driscoll, M.J.L. 2000. Bryophyte species richness on insular boulder habitats: the effect of areas, isolation, and microsite diversity. Bryologist, **103**(4): 748–756. doi:10.1639/0007-2745(2000)103[0748:BSROIB]2.0.CO;2.

Kneeshaw, D. 2001. Are non-fire gap disturbances important for boreal forest dynamics? Recent Devel. Ecol. **1**: 43–58.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southern boreal forest. Ecology, **79**(3): 783–794. doi:10.1890/0012-9658(1998)079[0783:CGCATR]2.0.CO;2.

Kneeshaw, D.D., and Gauthier, S. 2003. Old-growth in the boreal forest: a dynamic perspective at the stand and landscape level. Environ. Rev. **11**(S1): S99–S114. doi:10.1139/a03-010.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann. Zool. Fenn. **31**(1): 35–51.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn. **36**(1): 97–125.

LaRoi, G.H., and Stringer, M.H.L. 1976. Ecological studies in the boreal spruce–fir forests of the North American taiga. II. Analysis of the bryophyte flora. Can. J. Bot. **54**(7): 619–643. doi:10.1139/b76-065.

Lecomte, N., and Bergeron, Y. 2005. Successional pathways on different surficial deposits in the coniferous boreal forest of the Québec Clay Belt. Can. J. For. Res. **35**(8): 1984–1995. doi:10.1139/x05-114.

Lecomte, N., Simard, M., Fenton, N., and Bergeron, Y. 2006. Fire severity and long-term biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems, **9**(8): 1215–1230. doi:10.1007/s10021-004-0168-x.

Lefort, P., Gauthier, S., and Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the lake Abitibi area, Eastern Canada. For. Sci. **49**(4): 509–521.

Liu, Q.H., and Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J. Veg. Sci. **2**(3): 391–402. doi:10.2307/3235932.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. **9**(1): 1–59. doi:10.1139/a00-012.

McCune, B., and Allen, T.F.H. 1985. Will similar forests develop on similar sites? Can. J. Bot. **63**(3): 367–376. doi:10.1139/b85-043.

Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. **17**(8): 2145–2151. doi:10.1890/06-1715.1.

Morin, H., Laprise, D., Simard, A.A., and Amouch, S. 2009. Spruce budworm outbreak regimes in in eastern North America. *In* Ecosystem management in the boreal forest. *Edited by* S. Gauthier, M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron. Les Presses de l'Université du Québec, Québec. pp. 156–182.

Namroud, M.-C., Tremblay, F., and Bergeron, Y. 2005. Temporal variation in quaking aspen (*Populus tremuloides*) genetic and clonal structures in the mixedwood boreal forest of eastern Canada. Ecoscience, **12**(1): 82–91. doi:10.2980/i1195-6860-12-1-82.1.

Natural Resources Canada. 2010. The State of Canada's Forests — Annual Report 2010. Forest Canadian Service, Ottawa.

Økland, R.H., Rydgren, K., and Økland, T. 2003. Plant species composition of boreal spruce swamp forests: closed doors and windows of opportunity. Ecology, **84**(7): 1909–1919. doi:10.1890/0012-9658(2003)084[1909:PSCOBS]2.0.CO;2.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, New York. pp. 144-169.

Perera, A.H., Dalziel, B.D., Buse, L.J., and Routledge, R.G. 2009. Spatial variability of stand-scale residuals in Ontario's boreal forest fires. Can. J. For. Res. **39**(5): 945–961. doi:10.1139/X09-024.

Pham, A.T., DeGrandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Québec. Can. J. For. Res. **34**(2): 353–364. doi:10.1139/x03-265.

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D., Aleksey, E., Yesipova, Y., Glushkov, I., Karpachevskiy, M., Kostikova, A., Manish, A., Tsyikova, E., and Zhuraleva, I. 2008. Mapping the world's intact forest landscapes by remote sensing. Ecology and Society, **13**(2): 51. Available from http://www.ecologyandsociety.org/vol13/iss2/art51/.

Puettmann, K.J., Coates, K.D., and Messier, C. 2009. A critique of silviculture: managing for complexity. Island Press, Washington, D.C.

Reyes, G.P., and Kneeshaw, D.D. 2008. Moderate-severity disturbance dynamics in *Abies balsamea–Betula* spp. forests: the relative importance of disturbance type and local stand and site characteristics on woody vegetation response. Ecoscience, **15**(2): 241–249. doi:10.2980/15-2-3082.

Rochefort, L., Vitt, D.H., and Bayley, S.E. 1990. Growth production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology, **71**(5): 1986–2000. doi:10.2307/1937607.

Rossi, S., and Morin, H. 2011. Demography and spatial dynamics in balsam fir stands after a spruce budworm outbreak. Can. J. For. Res. **41**(5): 1112–1120. doi:10.1139/x11-037.

Rouvinen, S., Kuuluvainen, T., and Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. Silva Fenn. **36**(1): 127–145.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley and Sons, Chichester, UK.

Schipperges, B., and Rydin, H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated dessication. New Phytol. **140**(4): 677–684. doi:10.1046/j.1469-8137.1998.00311.x.

Schulte, L.A., and Mladenoff, D.J. 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. Ecology, **86**(2): 431–445. doi:10.1890/03-4065.

Senici, D., Chen, H.Y.H., Bergeron, Y., and Cyr, D. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems, **13**(8): 1227–1238. doi:10.1007/s10021-010-9383-9.

Seymour, R., and Hunter, M.L.J. 1999. Principles of ecological forestry. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Port Chester, New York. pp. 22–61.

Shafi, M.I., and Yarranton, G.A. 1973. Vegetational heterogeneity during a secondary (postfire) succession. Can. J. Bot. **51**(1): 73–90. doi:10.1139/b73-012.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. **49**: 11–41. Available from http://www.jstor.org/stable/20113262.

Simard, M.-J., Bergeron, Y., and Sirois, L. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can. J. For. Res. **33**(4): 672–681. doi:10.1139/x02-204.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1. PMID:17913128.

Smirnova, E., Bergeron, Y., and Brais, S. 2008. Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Québec: live trees, understory vegetation and dead wood dynamics. For. Ecol. Manage. **255**(7): 2916–2927. doi:10.1016/j.foreco.2008.01.071.

St-Denis, A., Kneeshaw, D., and Bergeron, Y. 2010. The role of gaps and tree regeneration in the transition from dense to open black spruce stands. For. Ecol. Manage. **259**(3): 469–476. doi:10.1016/j.foreco.2009.11.002.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., and Skinner, W.R. 2002. Large forest fires in Canada, 1959–1997. J. Geophys. Res. **107**: 8149. [printed 108 (D1), 2003.] doi:10.1029/2001JD000484.

Taylor, S.J., Carleton, T.J., and Adams, P. 1987. Understory vegetation change in a *Picea mariana* chronosequence. Vegetatio, **73**(2): 63–72. doi:10.1007/BF00031853.

Thompson, I., Larson, D., and Montevecchi, W. 2003. Characterization of old "wet boreal" forests, with an example from balsam fir forests of western Newfoundland. Environ. Rev. **11**(S1): S23–S46. doi:10.1139/a03-012.

Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W Wein and D.A. MacLean. John Wiley and Sons, New York.

Wagner, R.G. 1993. Research directions to advance forest vegetation management in North America. Can. J. For. Res. **23**(10): 2317–2327. doi:10.1139/x93-286.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, **21**(2): 213–251. Available from http://www.jstor.org/stable/1218190.

Wirth, C., Messier, C., Bergeron, Y., Frank, D., and Fankhänel, A. 2009. Old-growth forest definitions: a pragmatic view. Ecol. Stud. **207**(1): 11–33. doi:10.1007/978-3-540-92706-8_2.

Zouaoui, S. 2011. Dynamique des lichens terricoles du genre *Cladina* après les feux et les coupes dans le domaine de la pessière à mousses. Ph.D. thesis, Biological Sciences, Université du Québec à Montréal, Montréal, Québec, Canada.

Appendix A
Table A1 appears on the following page.

Table A1. Fire frequency and stand age distribution for the Canadian ecozones.

Location						Observed %			Modeled %		
Ecozone	Study	Period	Source	% burnt·yr^{-1}	Mean age	>100-years	>200-years	>300-years	>100-years	>200-years	>300-years
Boreal Cordillera		1959–1997	Stocks et al. 2002	0.392	255	—	—	—	68	46	31
Taiga Cordillera		1959–1997	Stocks et al. 2002	0.495	495	—	—	—	82	67	55
Taiga Plains		1959–1997	Stocks et al. 2002	0.702	142	—	—	—	49	24	12
Boreal Plains				1.22	82	—	—	—	30	9	3
	Wood Buffalo Park	<1750–1989	Larsen 1997	1.41	71	—	—	—	24	6	1
	Prince Albert	<1890	Weir et al. 2000	1.03	97	—	—	—	36	13	5
Hudson Plains		1959–1997	Stocks et al. 2002	0.123	813	—	—	—	88	78	69
Taiga Shield west				0.85	118	—	—	—	43	18	8
	Rutledge Park	<1760–1980	Johnson 1979, 1992	0.85	118	—	—	—	43	18	8
Boreal Shield west				1.29	78	—	—	—	28	8	2
	Northern Ontario	<1870–1974	Suffling et al. 1982	1.92	52	—	—	—	15	2	1
	Lake Nipigon	<1820–2008	Senici et al. 2010	0.66	150	—	—	—	51	26	14
Taiga Shield east				0.6	166	—	—	—	55	30	16
	Northern Québec	<1920–1984	Payette et al. 1989	1.0	100	—	—	—	37	14	5
	Labrador	<1870–1975	Foster 1983	0.2	500	—	—	—	82	67	55
Boreal Shield east				0.74	135	—	—	—	48	23	11
	Lake Abitibi Model Forest	<1740–1998	Lefort et al. 2003	0.58	172	78	32	0	56	31	17
	Abitibi West	<1750–1998	Bergeron et al. 2004	0.72	139	61	23	1	49	34	12
	Algonquin Park	<1696–1920	Cwynar 1977	1.4	71	—	—	—	24	6	1
	Abitibi East	<1770–1995	Bergeron et al. 2001	0.9	11	61	23	1	40	16	7
	Central Québec	<1720–1998	Lesieur et al. 2002	0.79	127	53	15	0	44	19	8
	Waswanipi	<1720–2003	Le Goff et al. 2009	0.78	128	38	10	0	38	14	5
	Lac-St-Jean	<1734–2009	Belisle et al. 2011	0.4	250	79	31	7	53	28	15
	Côte-Nord	<1640–2003	Cyr et al. 2007	0.36	281	69	19	1	48	23	11
TOTAL	% according to area of each ecozone								49	27	16

References

Bélisle, A.C., Gauthier, S., Cyr, D., Bergeron, Y., and Morin, H. 2011. Fire regime and old-growth boreal forests in central Québec, Canada: an ecosystem management perspective. Silva Fenn. **45**(5): 889–908. Available from http://www.metla.fi/silvafennica/full/sf45/sf455889.pdf.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**(3): 384–391. doi:10.1139/x00-178.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., and Lefort, P. 2004. Past, current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio, **33**(6): 356–360. PMID:15387074.

Cwynar, L.C. 1977. The recent fire history of Barron Township, Algonquin Park. Can. J. Bot. **55**(11): 1524–1538. doi:10.1139/b77-180.

Cyr, D., Gauthier, S., and Bergeron, Y. 2007. Scale-dependant determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. Landsc. Ecol. **22**(9): 1325–1339. doi:10.1007/s10980-007-9109-3.

Foster, D.R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. **61**(9): 2459–2471. doi:10.1139/b83-269.

Johnson, E.A. 1979. Fire recurrence in the subarctic and its implications for vegetation composition. Can. J. Bot. **57**(12): 1374–1379. doi:10.1139/b79-171.

Johnson, E.A. 1992. Fire and vegetation dynamics-studies from the North American boreal forest. Cambridge Studies in Ecology, Cambridge University Press, Cambridge, UK.

Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr. **24**(5): 663–673. doi:10.1111/j.1365-2699.1997.tb00076.x.

Le Goff, H., Flannigan, M.D., and Bergeron, Y. 2009. Potential changes in monthly fire risk in the eastern Canadian boreal forest under future climate change. Can. J. For. Res. **39**(12): 2369–2380. doi:10.1139/X09-153.

Lefort, P., Gauthier, S., and Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the Lake Abitibi area, eastern Canada. For. Sci. **49**(4): 509–521.

Lesieur, D., Gauthier, S., and Bergeron, Y. 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Québec, Canada. Can. J. For. Res. **32**(11): 1996–2009. doi:10.1139/x02-113.

Payette, S., Morneau, C., Sirois, L., and Desponts, M. 1989. Recent fire history of the northern Québec biomes. Ecology, **70**(3): 656–673. doi:10.2307/1940217.

Senici, D., Chen, H.Y.H., Bergeron, Y., and Cyr, D. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems, **13**(8): 1227–1238. doi:10.1007/s10021-010-9383-9.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., and Skinner, W.R. 2002. Large forest fires in Canada, 1959–1997. J. Geophys. Res. **107**: 8149. [printed 108 (D1), 2003.] doi:10.1029/2001JD000484.

Suffling, R., Smith, B., and Dal Molin, J. 1982. Estimating past forest age distributions and disturbance rates in North-western Ontario: a demographic approach. J. Environ. Manage. **14**: 45–56.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecol. Appl. **10**(4): 1162–1177. doi:10.1890/1051-0761(2000)010[1162:FFATSA]2.0.CO;2.