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REVIEW

Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America

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Abstract Ecosystem-based forest management is based on the principle of emulating regional natural disturbance regimes with forest management. An interesting area for a case study of the potential of ecosystem-based forest management is the boreal forest of north-western Québec and north-eastern Ontario, where the disturbance regime creates a mosaic of stands with both complex and simple structures. Old-growth stands of this region have multi-storied, open structures, thick soil organic layers, and are unproductive, while young post-fire stands established following severe fires that consumed most of the organic soil show dense and even-sized/aged structures and are more productive. Current forest management emulates the effects of low severity fires, which only partially consume the organic layers, and could lead to unproductive even-aged stands. The natural disturbance and forest management regimes differ in such a way that both young productive and old-growth forests could ultimately be under-represented on the landscape under a fully regulated forest management regime. Two major challenges for ecosystem-based forest management of this region are thus to: (1) maintain complex structures associated with old-growth forests, and (2) promote the establishment of productive post-harvest stands, while at the same time maintaining harvested volume. We discuss different silvicultural approaches that offer solutions to these challenges, namely the use of (1) partial harvesting to create or maintain complex structures typical of old-growth stands, and (2) site preparation techniques to emulate severe soil burns and create productive post-harvest stands. A similar approach could be applied to any region where the natural disturbance regime creates a landscape where both even-aged stands established after stand-replacing disturbances and irregular old-growth stands created by smaller scale disturbances are significant.

Keywords Fire · Paludification · Partial cuts · Soil disturbance · Soil organic layer

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Introduction

Several concepts are at the basis of ecosystem-based management, but a relative consensus exists around the idea of a forest management approach that is based on natural disturbances and forest dynamics (Bergeron et al. 1999; Perera et al. 2004). This type of approach aims to reproduce the main attributes and processes of natural landscapes in order to maintain ecosystems within their natural range of variability and avoid creating an environment to which species are not adapted (Attiwill 1994). Natural disturbance-based forest management strategies should integrate at least two spatial scales. At the stand scale, forest operations should emulate the natural processes that occur in stands (e.g., succession, fire, insect outbreaks), whereas at the landscape scale, forest management should strive to maintain the proportions of, and transitions between, different stand types, ages, and structures across the landscape (Bergeron et al. 1999).

The challenge for managers in this type of framework is to correctly identify the natural forest dynamics of their region, and to design harvest interventions that emulate these dynamics at both stand and landscape scales. However, natural forest dynamics can vary widely among regions. For example, in the boreal forest, frequent and severe stand-replacing fires were considered to dominate all regions, with a return interval of less than a century. In such a context, a dominance of large-scale clear-cuts under relatively short rotations would be appropriate. However, research has shown that the fire cycle, and consequently mean forest age, varies widely across the boreal forest from about 70 years in western Canada to over 500 years on the Atlantic coast of Canada (Stocks et al. 2002; Bergeron et al. 2001, 2006). Within this long fire-free interval, secondary disturbance agents (e.g., small blow downs due to insect, pathogens, and tree death) are also active, resulting in species and/or structural succession in many boreal forest regions. These two types of disturbances need to be taken into account when developing a management plan based on the emulation of natural disturbances. In addition to the nature of the disturbance agents present, other unique elements of each region's natural disturbance regime (e.g., disturbance severity and size distribution, forest and soil dynamics) need to be taken into account in the development of distinct regional management plans.

In this article, we discuss the natural disturbance regime that dominates the Clay Belt of Québec and Ontario in eastern North America, and propose management strategies that effectively emulate the regional natural forest dynamics. As the natural disturbance regime and resulting forest dynamics of the Clay Belt of Québec and Ontario have been intensively studied over the last two decades, it is an ideal region in which to compare stand structures and landscape patterns created by these natural forest dynamics and those created by forest management (Fig. 1). The disturbance regime is dominated by large stand-replacing fires with a long fire-free interval during which very small-scale secondary disturbances (e.g., wind damage, pathogens) lead to species and structural succession. By comparing attributes created by the natural forest dynamics created by this disturbance regime and the forest management regime for this region, we show that a range of stand structures and conditions are not reproduced under the current forest management regime. We propose an approach to maintain these complex structures by diversifying forest management practices.

Natural forest dynamics

Ecosystem-based management is dependent on a thorough understanding of the natural disturbance regime and resulting forest dynamics of a regional landscape in order to both develop silvicultural practices and to measure the success of the management plan. Here, we discuss the key elements of the natural forest dynamics of the Clay Belt in order to highlight differences with anthropogenic disturbances and suggest strategies to better emulate the natural complexity on the landscape.

Stand succession and structural complexity

The small number of tree species on the Clay Belt results in a relatively simple post-fire species succession. After fire, regeneration is mainly established by black spruce

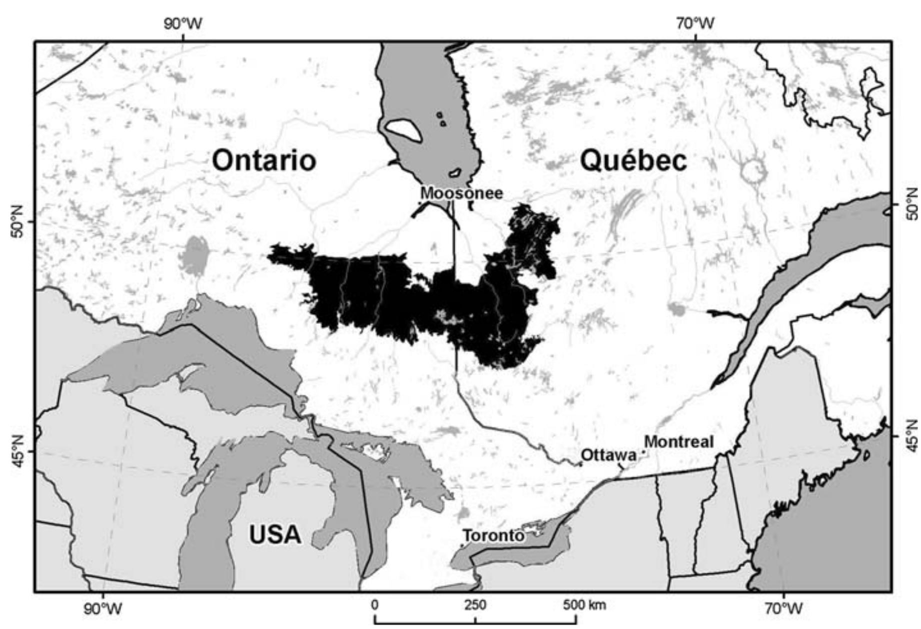


Fig. 1 Location of the Clay Belt of eastern Canada in relation to the Great Lakes, and major Canadian cities. The extent of the Clay Belt reflects the extent of glacial Lake Barlow-Ojibway

(*Picea mariana*), but jack pine (*Pinus banksiana*), and deciduous species [mainly trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*)], are also present in pure or mixed even-aged stands (Gauthier et al. 2000; Lecomte and Bergeron 2005). Succession in both jack pine and deciduous stands leads to a gradual replacement of the relatively short-lived pioneer stems by the shade-tolerant black spruce, and by about 200 years after fire, most stands are dominated by black spruce (Fig. 2a, Lecomte et al. 2006a).

In addition to this species succession, structural succession takes place in the majority of stands where black spruce is both a pioneer and a late-successional species. An initial even-aged structural cohort (trees of similar size and architecture) of black spruce establishes after fire, primarily by seed (Fig. 2b; Lecomte et al. 2005). Between approximately 100 and 200 years after fire, the gradual opening up of the canopy, due to localized secondary disturbances, leads to a second cohort being established mainly via layering (vegetative reproduction). In the prolonged absence of fire, a third cohort of uneven-aged stands develops by about 300 years after fire. Second and third cohort stands have a very heterogeneous structure, dominated by fewer and smaller trees (<10 m high) with abundant snags, and saplings filling the gaps (Fig. 2c; Lecomte et al. 2006a; Harper et al. 2002). Before large-scale logging began, the landscape was dominated by these old-growth stands, with over 50% of stands over 100 years old and more than 23% of forests older than 200 years (Bergeron et al. 2004). This dominance by old-growth is not recent, as paleoecological studies have shown that old-growth forests have been a major part of the forested landscape in this region throughout the Holocene (Carcaillet et al. 2001; Cyr et al. 2009).

Paludification

Paludification is a phenomenon that transforms a forested or non-forested soil into a peatland (Payette and Rochefort 2001) via the accumulation of peat and a rising water table (Fenton et al. 2006; Simard et al. 2007). Paludification is common in the boreal biome because low air temperatures reduce decomposition rates more than production rates (Swanson et al. 2000). The two main drivers of paludification are topography and succession, and consequently two types of paludification can be identified: edaphic paludification and successional paludification. Edaphic paludification (also called paludification of wet depressions; Payette and Rochefort 2001) dominates in natural depressions within the landscape, as high water tables promote the presence of hydrophilic plants (sedges, sphagna) and eventually the accumulation of peat. A second, less common type of paludification occurs when approximately 100 years after fire, *Sphagnum* spp. mosses establish and subsequently expand into the previously feather moss (*Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*)-dominated bryophyte layer (Foster 1985; Boudreault et al. 2002; Fenton and Bergeron 2006). The ecosystemic consequences of this change in bryophyte functional group can be dramatic because compared to feather mosses, sphagna have a greater carbon fixation rate (Bisbee et al. 2001; Swanson and Flanagan 2001), a greater buffering effect on soil temperature (Dioumaeva et al. 2002) and a slower decomposition rate (Swanson and Flanagan 2001). Together, these effects create conditions where an organic layer accumulates over the mineral soil (Van Cleve and Viereck 1981). Because this accumulation of a soil organic layer is primarily driven by forest succession, this type of paludification has been called successional paludification (Simard et al. 2007).

On the Clay Belt of Québec and Ontario, compacted clay soils, low topographic variation and a relatively cool and humid climate create an ideal environment for paludification (Fig. 2d). Black spruce stands become paludified over time, coinciding with the opening up of the canopy and establishment of the second cohort (see above; Fenton et al. 2005; Lecomte et al. 2006; Simard et al. 2007). The second and third cohorts have a lower mean height than the first cohort (Lecomte et al. 2006a), lower total tree biomass (Lecomte et al. 2006b) and lower productivity (Fig. 2e; Simard et al. 2007). Because of the accumulation of a thick organic layer over time, the second and third cohorts do not root in mineral soil but rather in the organic layer that overlays it (Simard et al. 2007). This shift in rooting zone probably explains the significant drop in productivity seen over time, as the organic layer is lower in exchangeable cations, and colder than the mineral soil (Fig. 1d, e; Simard et al. 2007).

Driven by these changes in the overstory and the soil are changes in the vascular and non-vascular components of the understory vegetation (Fig. 2f). Changes in the vascular community are essentially limited to an expansion of ericaceous species (e.g., *Rhododendron groenlandicum*). In contrast to the vascular plants, the non-vascular bryophyte community is diverse in these forests and changes significantly as the stand paludifies. As the stand becomes more open and humid, the typical boreal forest community is replaced by mosses more commonly found in peatlands (Fenton and Bergeron 2006, 2008). The sphagna go through a very specific successional sequence, from shade-tolerant hummock species, to carpet and hollow species, to shade-intolerant high hummock species (Fenton and Bergeron 2006). Overall, diversity of the bryophyte community peaks in second cohort stands (Fig. 2f; Fenton and Bergeron 2008).

Natural disturbances

Despite the relatively long fire cycle (Bergeron et al. 2004), fire is the dominant stand-replacing disturbance agent on the Clay Belt (Bergeron et al. 2006). However, between stand-replacing fires, individual tree death, sparked by secondary disturbances such as wind damage, insect infestations (mainly by the spruce budworm, *Choristoneura fumiferana*), or pathogens leads to structural succession within stands as illustrated in Fig. 2b. Large blow downs or insect outbreaks that lead to the replacement of an entire stand are exceedingly rare in this region, in contrast with the situation in the southern boreal forest (Harper et al. 2002). Severe summer fires, where not only the canopy is killed but also a significant proportion of the accumulated organic layer is burnt (thereafter called 'high severity fires'), restart the successional sequence, as even-aged jack pine, deciduous or black spruce stands establish post-fire, depending on seed availability (Lecomte and Bergeron 2005).

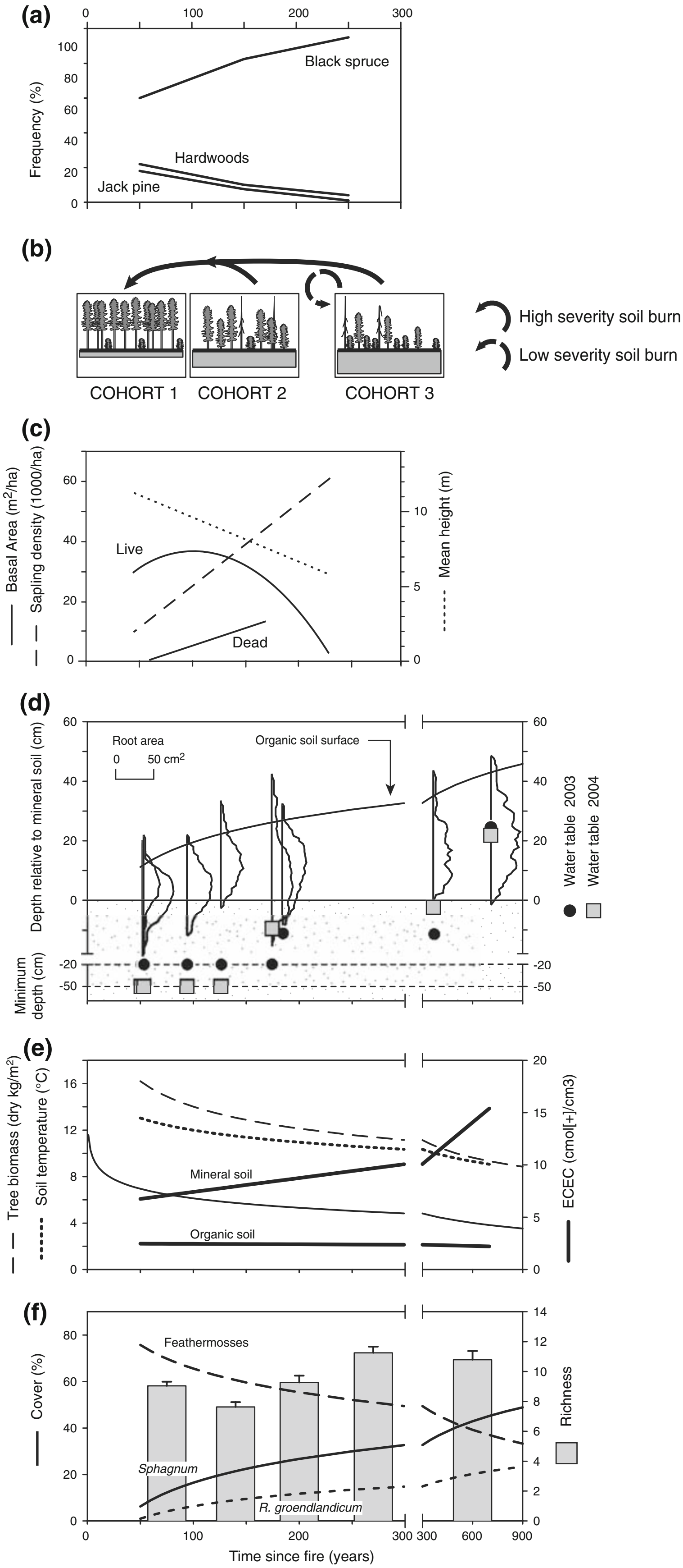
All fires are, however, not equal, as some do not consume enough of the accumulated organic layer for the regenerating stand to be rooted in mineral soil. These "low severity" fires (where severity is referring uniquely to the proportion of the organic layer consumed and not to tree mortality; Nguyen-Xuan et al. 2000, Simard et al. 2007) do not lead to the successional patterns discussed above (Fig. 2b). Instead, paludification rapidly restarts, as the remaining organic layer and open canopy favors *Sphagnum* spp. growth (Fenton et al. 2005; Simard et al. 2007), resulting in young stands that are already significantly paludified. Only black spruce establish on the organic soils remaining after a low severity fire (Lecomte and Bergeron 2005). These stands are both less dense and less productive (Lecomte et al. 2006a) because favorable microsites (very thin organic layers over mineral soil; Lavoie et al. 2007) are less abundant than after a severe fire, and the quality of these microsites is reduced. The reduced growth rate of trees after a low severity fire is probably caused by the same factors that result in lower growth rates in old paludified stands established after a high severity fire; i.e., reduced soil nutrient availability, and lower soil temperatures (Simard et al. 2007; Van Cleve and Viereck 1981).

While all stands within the boreal forest are equally likely to burn, they are not equally likely to burn with a high severity. The rise of the water table into the organic layer results in a permanently humid environment that dries out only during extreme drought conditions. As a result, paludified forests are probably less likely to experience a severe burn, and very paludified stands may never return to a dense even-aged stand under current climate conditions (Simard et al. 2007; Glebov and Korzukhin 1992).

Fig. 2 Synthesis of stand dynamics following high severity soil burns ▶ in the boreal forest of the Clay Belt of eastern Canada. **a** Canopy succession with time since fire. Proportions of the landscape dominated by the different tree species have been determined by different methods, including field surveys, interpretation of aerial photographs, and forest inventory databases. Modified from Simard et al. (2008) with original data from Gauthier et al. (2000), Harper et al. (2002, 2003), and Lecomte et al. (2005). **b** Stand dynamics can be synthesized using the cohort approach proposed by Bergeron et al. (1999) and Harvey et al. (2002), which simplifies the representation of forest succession by separating forest stands in three cohorts that differ by their age and structure, and that broadly correspond to early-, mid-, and late-successional stages of forest succession. Whereas high severity soil burns convert these stands to first cohort stands, low severity burns do not completely consume the organic layer (gray area under the stands) and create low-productivity forests that are structurally similar to third cohort stands. See text for further details. Modified from Lecomte et al. (2006a). **c** Changes in forest structure with time since fire. Basal area is shown for live and dead trees with a dbh > 10 cm only, whereas mean tree height includes all stems; saplings are trees smaller than 2 m. Source: Lecomte et al. (2006a). **d** Changes in soil organic layer thickness, water table depth (minimum depth is indicated when the water table was not reached), and black spruce rooting zone with time since fire. Each rooting profile (mean of 3 trees of the dominant height cohort) represents the cumulative area (*irregular lines* to the *right* of each profile) occupied by black spruce roots >1 cm in diameter at a distance of 30 cm from the center of the stump. Each profile is positioned vertically relative to the mineral (patterned area)–organic interface, and horizontally according to the postfire age of the stands (*vertical line* to the *left* of each profile). Modified from Simard et al. (2007). **e** Changes in tree productivity (site index and aboveground tree biomass), soil temperature at 10 cm below the soil surface, and exchangeable cationic capacity in the organic and mineral horizons of the soils. Effective cationic exchange capacity (ECEC) is expressed on a volume basis to account for soil density. Regressions are based on data from Simard et al. (2007). **f** Changes in total bryophyte richness and in the cover of major bryophyte taxa (*Sphagnum* spp. and feathermosses, *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*) and of an ericaceous shrub (*Rhododendron groenlandicum*) with time since fire. Modified from Lecomte et al. (2005), Simard et al. (2007), and Fenton and Bergeron (2008). All regressions are significant at alpha = 5%

Management challenges

The Clay Belt's natural forest succession and disturbance regime create a range of complex stand structures, from productive postfire stands to old, less productive, paludified forests. This landscape therefore offers two distinct challenges to forest managers, one at each end of the successional sequence: (1) old-growth forests represent a significant proportion of the landscape and it is therefore vital that they maintain a proportional presence on the managed landscape; and (2) paludification reduces the productivity of the landscape as a whole, and


(a)
Frequency (%)
Black spruce
Hardwoods
Jack pine
(b)
High severity soil burn
Low severity soil burn
COHORT 1
COHORT 2
COHORT 3
(c)
Basal Area (m2/ha)
Sapling density (1000/ha)
Mean height (m)
Live
Dead
(d)
Depth relative to mineral soil (cm)
Root area
0 50 cm2
Organic soil surface
Water table 2003
Water table 2004
Minimum depth (cm)
(e)
Site index (m)
Tree biomass (dry kg/m2)
Soil temperature (°C)
ECEC (cmol[+]/cm3)
Mineral soil
Organic soil
(f)
Cover (%)
Richness
Feathermosses
Sphagnum
R. groendlandicum
Time since fire (years)

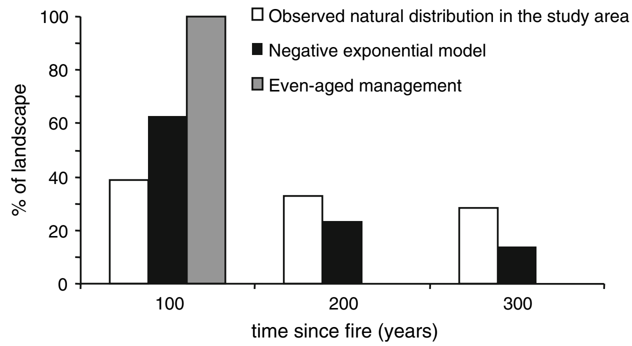


Fig. 3 Stand age-class distributions under fire-regulated and forest management regimes, for the Clay Belt of eastern Canada. Both natural distributions, those observed from Bergeron et al. (2004), and the theoretical negative exponential model, illustrate the importance of stands older than 100 years on the landscape. Under fully regulated even-aged management with a 100-year rotation period, no stands older than 100 years are found on the landscape

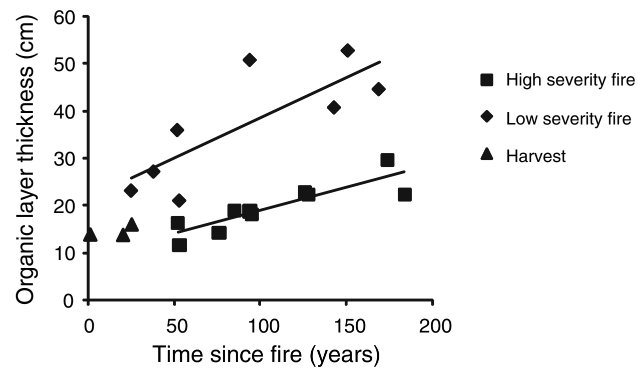


Fig. 4 Organic layer accumulation over time in stands established after high severity fires (where a maximum of 5 cm of residual organic matter remains after fire), low severity fires (where more than 5 cm of residual organic matter remains after fire) and harvest on the Clay Belt of eastern Canada. Data for organic matter accumulation after high and low severity fires is modified from Lecomte et al. (2006b) and Nguyen-Xuan et al. (2000), and data for accumulation after harvest is modified from Nguyen-Xuan et al. (2000)

young stands in particular, if they are not properly regenerated.

Challenge 1: maintaining a significant proportion of old-growth forests

At first glance, an even-aged management approach appears to resemble the natural disturbance regime if the timber harvest rotation age approaches that of the natural fire cycle. However, a full even-aged regulation does not produce an age-class distribution similar to that of a natural fire regime, even for forest rotations that are as long as the fire cycle, as illustrated in Fig. 3 (Bergeron et al. 2004). Indeed, in an even-aged management context, a forest is considered to be fully regulated when stand age classes are uniformly distributed within the rotation period. Thus, in theory, after one complete rotation in a region submitted to a 100-year rotation, no stands over the rotation age will exist. The same region submitted to forest fires intense enough to generate even-aged stands will, at equilibrium, present a completely different age-class distribution of stands composing the landscape. Assuming that the probability of burning is independent of stand age (Johnson 1992), the forest age structure will theoretically approach a negative exponential curve (Van Wagner 1978), with about 37% of the forest being older than the fire cycle as is illustrated in Fig. 3 by both observed data from the study area (Bergeron et al. 2004) and theoretical data generated with a negative exponential curve. This difference is fundamental because it implies that full regulation in an even-aged management regime will result in the loss of over-mature and old-growth forests, essential for the maintenance of biodiversity.

Our work (Bergeron et al. 2004) on the Clay Belt shows that the natural mosaic does follow the negative exponential model, with the exception of the last 50 years, during which there were almost no fires. This negative exponential distribution of stand ages, along with an observed mean stand age of 140 years, means that in the Clay Belt over 50% of the stands are older than 100 years and that more than 23% of the stands are older than 200 years (Bergeron et al. 2004). The loss of these stands on the landscape would result in a loss of diversity at two scales: at the landscape scale, this would significantly reduce the variation in stand structures, and perhaps more importantly, at the stand scale this would eliminate structurally complex stands that provide habitat for a wide variety of species. Many species (bryophytes, birds, lichens; Fenton and Bergeron 2008; Drapeau et al. 2003; Boudreault et al. 2002) are associated with these old-growth stands and would be lost from a landscape where the presence of old-growth stands is significantly diminished.

Over the long-term, in addition to the natural distribution in forest age structures, the natural spatial pattern of forests of different ages needs to be maintained in order to ensure both continued biodiversity and productivity (Belleau et al. 2007). The Clay Belt of Québec currently benefits from biodiversity associated with a relatively undisturbed landscape (Fenton and Bergeron 2008). However, if the spatial structure of the landscape is significantly altered, the ability of species to be maintained on the landscape could be jeopardised, as it has in other parts of the boreal forest like in Europe (Hansson 1997).

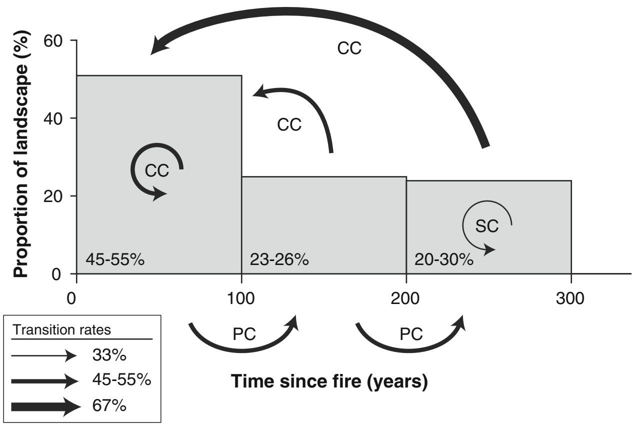


Fig. 5 Proposed forest management to recreate natural stand dynamics. The proportions (*numbers* at the *lower left* of each column) in the landscape of each cohort type follow the theoretical and observed distribution of stand ages under a 140-year fire cycle. Partial cuts (*PC*) are used to emulate succession of first to second cohorts and second to third cohorts, and selection cuts (*SC*) are used to maintain third cohort structures. Second and third cohort stands can be converted, and first cohort stands can be maintained, into first cohort stands by clear cutting (*CC*) with or without site preparation and planting. Thickness of the *arrows* is proportional to the proportion of each cohort type that must be converted to maintain a steady-state stand age distribution

Challenge 2: maintaining young productive stands

The process of paludification presents significant challenges for forest managers as it acts to reduce the productivity of stands and landscapes over the long-term. While high severity fires burn the accumulated organic layer and return stands to a higher productivity level with dense regeneration, low severity fires are also common across the landscape. These fires kill the existing stand without burning a significant amount of the organic layer (Fig. 4), and as a result, regeneration, growth, and forest productivity are reduced in these young paludified stands. Therefore, in order to maintain long-term productivity of stands across the landscape, management interventions in paludified stands should be inspired by high severity fires that not only consume the standing trees but also remove a significant portion of the accumulated organic layer. However, the current forest management regime on the Clay Belt requires harvesting practices that specifically protect the accumulated organic layer (cut with protection of regeneration and soils), suggesting that current forest management may promote paludification (Fig. 4) and reduce post-harvest productivity. Current work underway suggests that harvesting techniques used in the past that significantly disturbed the accumulated organic layer (clear-cuts with high soil disturbance by the machinery) resulted in higher post-harvest growth rates than techniques that left the organic layer intact.

Management solutions

To address the two distinct management challenges present on this landscape, two types of solutions are necessary (Fig. 5). First, our forest management must be able to emulate landscape level disturbance regimes, and therefore preserve uneven-aged stand structures on the landscape. Second, our management practices must be able to emulate high severity fires and regenerate productive even-aged stands.

Solution 1: accelerating succession and creating or maintaining uneven-aged stands

A fully regulated landscape under a given forest management rotation period contains no stands older than the rotation period, unlike a landscape regulated by a natural fire regime of the same rotation period (Fig. 3). To keep these old-growth stands in a managed landscape, one strategy would be to lengthen the rotation time on a proportion of the landscape (Hunter 1999). However, in forest systems such as the black spruce boreal forest, where individual trees do not have extended life spans (200 years compared with 1,000 years for tree species on the west coast of North America, for example), this results in a significant loss in wood available for harvest (Bergeron et al. 1999). In contrast, the use of silvicultural practices that either create or maintain an irregular structure, such as partial and selection cuts, allow some volume to be collected while maintaining an appropriate balance among structural cohorts across the landscape (Fig. 5). Furthermore, partial and selection cutting emulate the natural dynamics of old stands where structural development is caused by secondary disturbances that cause patch and individual stem mortality (Harvey et al. 2002).

On a landscape with a fire cycle of 140 years where the first, second and third structural cohorts represent 51, 25 and 24% of the landscape, respectively (based on a negative exponential curve and a rotation period of 140 years; Bergeron et al. 2004), partial and selective cutting should be used extensively to maintain this age structure (Fig. 5). Partial cutting should be applied to 45% of the first cohort stands to emulate succession and create second cohort stands. Similarly, 50% of the second cohort stands should be partially cut to emulate succession and create third cohort stands. Finally, selection cutting should be applied to 33% of the third cohort stands to emulate gap dynamics. The balance of each step (50% of cohorts 1 and 2 and 67% of cohort 3) could be treated by clear cutting to emulate a severe summer fire that recreates a young dense productive stand. By using these transition rates, the proportions of cohorts are stable over time at the landscape scale, even when considering the effect of fire (for more details, see Bergeron et al. 1999 and Harvey et al. 2002).

Natural variability in the fire cycle permits some flexibility in these proportions (Bergeron et al. 2006; Belleau et al. 2007). Specifically, the reduction in fire frequency in the last century (from approximately 140 years to 400 years) has resulted in a much greater proportion of the landscape that is occupied by old-growth forest than would have been the case previously. This recent change in the fire cycle is positive for the forest industry, as it implies that some old-growth forest is available for harvest that would previously have been burnt (Bergeron et al. 2006). For example, forest harvest could be used to create forest age structures that would exist under a 140-year fire cycle by harvesting old-growth stands with low-productivity and regenerating productive even-aged stands.

Despite the potential of partial cuts for maintaining structural complexity in boreal forests, there are few experimental or operational trials underway, and the relatively short time span (<10 years) of this work makes it difficult to determine whether the desired results are achieved (cf. Deans et al. 2003). This is because the simple creation or preservation of irregular structure does not guarantee that these stands will be used by old-growth specialist species. There are therefore two levels of uncertainty: (1) does partial harvest recreate irregular and uneven structure? and (2) do species use the created habitat?

To answer these questions, partial harvest trials have been undertaken on the Clay Belt of Québec and Ontario over the last 10 years (Fenton et al. 2008). The partial cuts were carried out in stands that already had an irregular structure, and therefore represent a transition from the second to the third cohort as described above. Preliminary results indicate that the treatments succeeded in maintaining an uneven-age structure and that for some organisms the created structure was a satisfactory habitat. However, for others such as epiphytic lichens, the newly created third cohort stands were not satisfactory, although they were preferable to clear-cuts where no habitat was available. These trials indicate that partial and selection cuts are viable options in these forests, but that the specifics of the silvicultural treatments need to be further studied.

Solution 2: restarting succession and creating even-aged stands through severe soil disturbance

To maintain long-term forest productivity on the Clay Belt, forest harvest must be accompanied by soil disturbance, particularly in stands with a high degree of paludification. Like fire, disturbing the soil in such a way that the layers are mixed and aerated should stimulate decomposition of the accumulated organic material (Sutton and Weldon 1993; Lavoie et al. 2005). Physically reducing the thickness of the organic material is not absolutely necessary, as well-decomposed organic material, unlike poorly decomposed organic material (humic vs fibric) provides a nutrient-rich environment for tree growth (Lavoie et al. 2007). Ultimately, a reduction in the cover of sphagna and an increase in the cover of *Pleurozium schreberi* and other feathermosses is desirable, as sphagna decompose much more slowly than feathermosses, and create a predominantly fibric organic layer while feathermosses create humic organic layers (Lavoie et al. 2007).

Not all paludified stands have the same potential for recovery of productivity, however. Stands that are primarily affected by successional paludification were once productive, and as such have a productivity potential that may be recovered if the appropriate site preparation technique is applied. However, edaphic paludification resulting from primary succession is a permanent feature of a site and would require major investments to be altered (e.g., forest drainage). It is therefore crucial to be able to identify not only whether a stand is paludified or not but also whether paludification is primarily due to edaphic or successional factors.

At the landscape level, slope and time since fire were found to be good predictors of organic layer depth, allowing the separate estimation of topographic and successional effects on paludification (Simard et al. 2009). Therefore, by mapping slope and stand age across the Clay Belt, it could be possible to identify sectors that are likely to be paludified, allowing an appropriate planning. It was also found that, compared to steeper sites, flat sites had thicker organic layers that accumulated at faster rates, which would make any productivity gains in these stands very short-lived (Simard et al. 2009). Therefore, intensive management efforts should be focused on paludified stands with a gentle slope, which show a higher potential for productivity recovery.

Conclusion

We recognize that we are suggesting seemingly contradicting silvicultural practices, partial and selection cuts with little soil disturbance and aggressive site preparation). While these two strategies appear to be contradictory, they are in reality the logical outcome of a management strategy based on natural disturbances. Both severe stand-replacing disturbances (i.e., fire) and secondary disturbances (tree mortality by blow downs, insect outbreaks, etc.) are important on this landscape, creating a complex mosaic of both even- and irregularly-aged/sized stands. As a result, any management strategy that aims at maintaining biodiversity and ecosystem function by emulating natural disturbances needs to take both of these types of disturbances into account. Globally, old-growth stands should be managed to limit paludification, while young productive stands should be managed to ultimately reach an old-growth structure.

The analysis carried out for the Clay Belt of eastern Canada illustrates that a thorough understanding of the natural dynamics of a landscape can be used to determine how forest management practices should be modified in order to more closely emulate the natural disturbance regime. Particularly, it illustrates that both stand-replacing and secondary disturbances can be incorporated into the management plan of a forested landscape.

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