



Ecosystem management based on large-scale disturbance pulses: A case study from sub-boreal forests of western Quebec (Canada)

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ABSTRACT

The northern Témiscamingue region (western Québec) sustained regional-scale pulses of natural disturbances during the 1850–2000 period, such as severe fires during the 1908–1926 period, two severe spruce budworm outbreaks that occurred in 1909–1918 and 1974–1984, and two birch dieback episodes around 1940 and 1980. These disturbances produced synchronous fluctuations in forest characteristics over large spatial scales. In this paper, we review possible responses of flora and fauna to pulsed large-scale disturbance events and speculate on whether they should be emulated to reduce the impacts of forest management on non-timber resources. The importance of large-scale disturbance pulses for biodiversity and forest ecosystem integrity is potentially great, but this aspect has been poorly investigated by previous research, and thus there is little information available to guide forest management. Large-scale, synchronous disturbances could be emulated by clustering harvesting activities in time, for example by creating “harvest pulses” of 10–20 years, separated by periods of 50–100 years or so with low harvest rates. A potential disadvantage of this strategy is that when our capacity to predict future natural disturbances is low, there is a higher probability of accidentally taking the forest ecosystem outside of the range of natural variability compared with a *status quo* forest management scenario. From a socio-economic perspective, another potential disadvantage is in creating irregular wood flows to the forest transformation industry. Nonetheless, in a context where the forest has been over-disturbed in the recent past, a forest management strategy involving fluctuating harvest rates could provide the means for faster ecosystem recovery compared with a *status quo* strategy. We recommend that the potential importance of disturbance pulses for boreal and sub-boreal ecosystems be more thoroughly investigated by future research to inform management and conservation policies.

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1. Introduction

Forest management activities can significantly alter natural ecosystems, and may pose serious threats to the persistence of some animal or plant species. One way to address this problem is to implement management practices that have impacts that are as similar as possible to those of the natural disturbances that have moulded these ecosystems, based on the assumption that local species are relatively well adapted to the range of natural variability (Hunter, 1999; Landres et al., 1999; Bergeron et al.,

1999). Even though the spatial variability introduced by natural disturbances is generally addressed in detail by such strategies, the temporal distribution (pulsed or even) of disturbances is rarely considered.

Natural forest disturbances can be described at various spatial scales. Studies conducted over continental or sub-continental spatial scales usually focus on the relationships between disturbances and climate (Williams and Liebhold, 2000; Bergeron et al., 2006). By contrast, regional studies tend to insist more on the relationship between disturbance characteristics (patch size, mean frequency, intensity, effects on forest succession, etc.) and pre-disturbance forest composition or site characteristics (Seymour et al., 2002; Frelich, 2002). Regional studies facilitate the identification of disturbance features that are locally very strong and important, but that would be averaged out or overlooked in more general studies. Also, because each disturbance type (fires, insect outbreaks, hurricanes, floods, etc.) has a specific geographical

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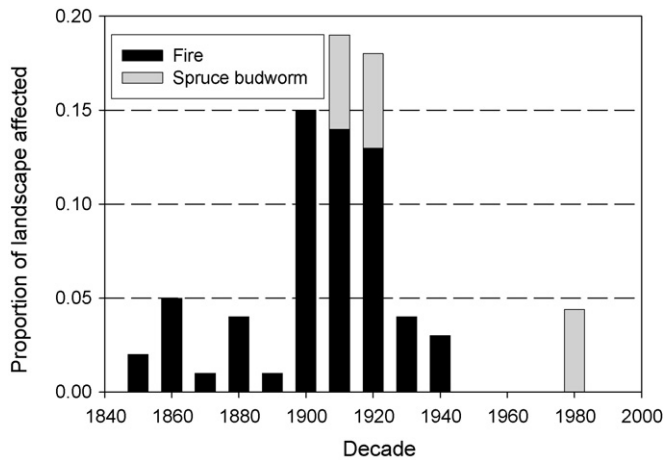


Fig. 1. Proportion of the region affected by major disturbances during the 1850–2000 period. For fire disturbance, only the most recent fires are considered, based on Grenier et al. (2005). The area affected by the 1972–1984 spruce budworm outbreak was measured on forest maps, and area covered by the 1910–20 outbreak was estimated based on old aerial photographs. Only the impact of stand-replacing disturbances is shown.

distribution over continental spatial scales, their interactions are probably more adequately described by using a regional scale case-study approach. Such an approach also facilitates the formulation of realistic and testable ecosystem forest management scenarios (Dale et al., 1998).

Our approach in this paper is to summarize salient features of the natural disturbance regimes in a region for which pre-industrial disturbance patterns have already been studied for two major disturbance types, fires and spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks. These disturbances present considerable temporal fluctuations in intensity, causing synchronous fluctuations in forest structure and composition over large spatial

scales. Based on a literature review, we evaluate how important these temporal fluctuations could be for ecosystem integrity or functioning, develop a basic ecosystem forest management scenario based on the emulation of these features, and we critically examine the feasibility of such a scenario for the study area. We expect that ideas presented here will also be of interest in other regions of the boreal or sub-boreal forest, or in any region where large-scale synchrony in natural disturbances is important.

2. Natural disturbances and forest dynamics in northern Témiscamingue

The effect of episodic disturbance regimes will be illustrated using an example from a territory located in northern Témiscamingue (Province of Quebec, Canada) (Fig. 1), where natural disturbance patterns are relatively well known for the 1850–2000 period. This territory is located in the yellow-birch/balsam fir bioclimatic domain according to the most recent bioclimatic classification in Québec (Saucier et al., 1998), a transitional zone that is also described as southern mixedwoods, temperate-boreal, or sub-boreal forest (Pastor and Mladenoff, 1992). A feature of this zone is that disturbance processes typical of boreal forests (i.e. fires and insect outbreaks), and their associated tree species (*Pinus banksiana*, *Picea* spp., *Abies balsamea*, *Populus* spp., *Betula papyrifera*), co-occur with a smaller proportion of stands dominated by species usually found in the temperate zone farther south (*Acer* spp., *Betula alleghaniensis*, *Pinus strobus*).

The history of large stand-replacing fires in the study area was reconstructed by Grenier et al. (2005), who found that fires that occurred during the years 1908–1926 covered nearly 40% of the total 280 000 ha forested area (Figs. 1 and 2). Even if some of these fires were ignited by humans, it is believed that weather conditions during that period were the dominant factor explaining their extent (Grenier et al., 2005). Taking potential human influences into account, Grenier et al. (2005) estimated that the average natural fire return interval is 200–250 years for this region. Fires

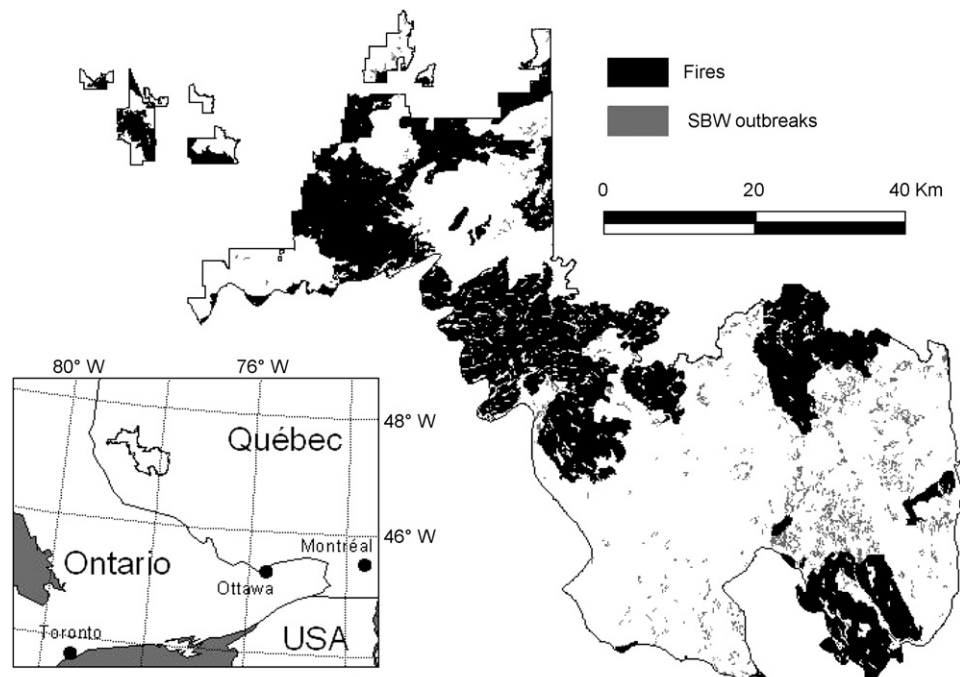


Fig. 2. Spatial distribution of severe fires during the 1890–2000 period, and of stands killed (>75% tree mortality) by the last spruce budworm outbreak (SBW) in the studied area. Mortality following the 1910–1920 severe spruce budworm outbreak is not shown.

created mortality patches extending from tens to thousands of hectares. Based on observations made using aerial photographs taken a few decades after the fires occurred, clumps of green trees survived in some locations, but mortality was often near total on areas covering several hundreds of hectares. In general, the area affected by these fires appeared similar to the pattern described by Kafka et al. (2001) in a boreal forest of western Quebec, namely heterogeneously shaped patches of mortality containing residual clumps of green trees. Tree species such as black spruce (*Picea mariana*), jack pine (*P. banksiana*), trembling aspen (*Populus tremuloides*) and white birch (*B. papyrifera*) commonly dominate young stands of fire origin in this region.

The history of spruce budworm outbreaks was also reconstructed (Bouchard et al., 2005, 2006a, 2006b). Past outbreaks caused extensive mortality in stands dominated by the primary host species of this insect, balsam fir (*A. balsamea*) and to a lesser degree white spruce (*Picea glauca*). These late-successional tree species become dominant in stands that have not burned for periods of 150 years or more (Bergeron, 2000; Bouchard et al., 2005). Severe outbreaks occurred in this region around 1980 and 1910, and perhaps 1830 (Bouchard et al., 2006a). The impacts of the 1910 and 1980 outbreaks have been described (Bouchard et al., 2005, 2006a), and in the region it has been found these two outbreaks led to near total mortality in all stands dominated by mature balsam fir trees. According to information derived from forest maps and permanent plots, it is estimated that the 1980 outbreak alone caused stand-replacement mortality in about 8% of the total forested area (in stands dominated by balsam fir), and partial mortality in at least 15% of the total forested area (in stands co-dominated by balsam fir). In contrast with fire, the spatial pattern of mortality caused by the spruce budworm was generally more diffuse, and patches of stand-replacing mortality rarely exceeded 50 ha. Following stand mortality, a mixture of shade-tolerant (*Abies*, *Picea*, *Thuja*) and shade-intolerant tree species (*Betula*) established (Bouchard et al., 2006b).

A synchronous dieback of birch (*B. alleghaniensis* and *B. papyrifera*) was also observed during the 1940 and 1980 decades, probably facilitated in part by meteorological events (i.e. thaw-frost events in winter time) and the synchronous arrival of some birch cohorts at senescence (Braathe, 1995; Bouchard et al., 2006a). At the regional scale, these diebacks caused important fluctuations in the abundance of dominant birch trees, at least in forests that had not been recently affected by fire (Bouchard et al., 2006a). However, the mortality caused by these diebacks was even more diffuse spatially than the mortality caused by spruce budworm outbreaks, and it was not sufficient at the stand scale to generate stand-replacement.

Some interactions between different disturbance types are likely to take place through forest composition or structure. For example, fires tend to promote the recruitment of tree species that are not preferentially attacked by the spruce budworm, and thus areas that have been recently affected by fire are less vulnerable to this insect (Bergeron and Leduc, 1998). Theoretically, pulses of dead wood following spruce budworm outbreaks could also temporarily increase the fire hazard, but the real influence of spruce budworm outbreaks on fire occurrence or spread is still debated, and probably varies temporally as stands degrade and lose fine fuels as well as on a region-to-region basis according to the prevailing climate (MacLean, 2004). In the northern Témiscamingue study area, the 1908–1926 fire pulse occurred more or less simultaneously with the 1909–1919 outbreak, but we have no evidence that the fires affected areas that were previously dominated by balsam fir. The risk of fire after a spruce budworm outbreak is also likely to be less important in regions where a thick broadleaved undergrowth develops after the outbreak (MacLean,

2004), which is the case in this region (Bouchard et al., 2005). For all concerns, it is more likely that the tremendous extent of fires during this period was mainly a consequence of unusually dry and warm meteorological conditions (Grenier et al., 2005; Girardin et al., 2004), rather than an indirect effect of spruce budworm outbreaks. Like spruce budworm outbreaks, large-scale birch diebacks are also potentially affected by other disturbance types through forest composition, because this disturbance takes place in senescent even-aged white birch cohorts that recruited after fire or spruce budworm outbreaks.

In summary, even if the spatial pattern of mortality patches created by disturbances such as fire, insect outbreaks and diebacks varies from one disturbance type to the other, they share a common characteristic in that during the 1850–2000 period they all occurred in pulses that lasted from one decade (spruce budworm outbreaks, birch dieback) to a few (fire). Moreover, these pulses were probably caused by natural factors, and not anthropogenic influences (Grenier et al., 2005; Bouchard et al., 2006a).

3. A review of disturbance pulses and their ecological consequences

3.1. Large-scale composition fluctuations

Large scale natural disturbances are important to ecosystem functioning on an evolutionary perspective (Thompson and Harestad, 2004). In boreal or sub-boreal ecosystems of north-eastern North America, spruce budworm outbreaks and fires are two disturbance types that have occurred for millennia (Carcaillet et al., 2001; Simard et al., 2006). Large-scale fluctuations in disturbance intensity have also been reported for a variety of other disturbances. In North-America, some examples of native insect species with recurrent and destructive outbreak patterns include the mountain pine beetle (Taylor and Carroll, 2004), the spruce beetle (Matsuoka et al., 2001), the forest tent caterpillar (Cooke and Lorenzetti, 2006) as well as others insect species (MacLean, 2004). Other disturbance types such as earthquakes (Wells et al., 2001), windthrow (Lorimer, 1980) or hurricanes (Boose et al., 2001) also have the potential of causing large-scale mortality pulses on a recurrent basis.

The large-scale synchronism exhibited by these episodic disturbances is mostly a product of climatic factors. For example, severe droughts increase the potential for fire over large areas (Weisberg and Swanson, 2003; Girardin et al., 2004). Meteorological factors also play a role in the synchronization of spruce budworm outbreaks over large areas (Williams and Liebhold, 2000), and other disturbances, such as large-scale forest declines or diebacks, are also known to correlate with climatic oscillations or meteorological events (Auclair et al., 1996).

3.2. Importance for biodiversity

3.2.1. The effects of episodic disturbances on habitat availability

For simplification, the effects of episodic disturbance regimes on regional forest characteristics can be separated into three components: their effects on forest age structure, on forest composition and on the spatial arrangement of the forest mosaic.

Synchronous disturbance regimes result in the episodic regeneration of large swaths of forests following pulses of tree mortality, and will cause temporal fluctuations in forest age-class structure at the regional scale (Boychuk and Perera, 1997; Wimberly et al., 2000; Armstrong et al., 2003; Agee, 2003), and also other related features such as dead wood (Sturtevant et al., 1997; Wright et al., 2002). In the immediate aftermath of a

disturbance pulse, there is probably a decrease of abundance for populations of organisms associated with older forest types (birds, mammals, plants, arthropods, fungi, etc). For example, it has been suggested that large scale pulses of fire might be responsible for widespread declines of woodland caribou (*Rangifer tarandus*) abundance in western Ontario around the year 1800 (Fritz et al., 1993), and around 1910 in Quebec (Audet, 1979), presumably in part because of a large-scale rarefaction of terrestrial lichens for a period of several decades following the fires (Audet, 1979; Fritz et al., 1993). On the other hand, synchronous large-scale disturbances create short-term pulses of coarse woody debris (Sturtevant et al., 1997; Wright et al., 2002; Crête and Marzell, 2006) which benefit some saproxylic insects and fungi (Saint-Germain et al., 2004), or birds such as woodpeckers (Imbeau et al., 2001; Hoyt and Hannon, 2002; Drever and Martin, 2007). A few years after these disturbance pulses, young thickets and decomposing logs form habitats suitable for different communities of bird and mammal species (Crête et al., 1995; Imbeau et al., 1999). An example of a trophic effect on community structure is an increased abundance of the snowshoe hare (*Lepus americanus*) (Hodges, 2000) in regenerating habitats may in turn lead to population increases in some predators, e.g., Canada lynx (*Lynx canadensis*) (Mowat and Slough, 2003) or marten (*Martes martes*) (Potvin et al., 2000; Thompson and Harestad, 2004).

Large-scale synchronous disturbances also cause large-scale oscillations in forest composition. Post-fire succession has been well described at the stand scale in southern mixedwood forests, where it leads to the initial establishment of fire-adapted tree species (i.e. pine–black spruce–aspen mixtures), which are gradually replaced by late-successional species (typically a mixture of stands dominated by spruce–fir–cedar–birch) (Frelich and Reich, 1995; Bergeron, 2000). Following large-scale fire pulses, a similar phenomenon can be observed, but this time at the regional scale. Large-scale changes in composition also occur following spruce budworm outbreaks. In forest mosaics that have not been affected by fire for 150 years or more, the analysis of old aerial photographs reveals that episodic outbreaks can result in alternate periods of relative dominance by coniferous tree species and relative dominance by hardwoods (Bouchard et al., 2006a). Large-scale shifts in tree-species composition can alter community structure for animal species that live therein, one well-studied example from western Quebec being bird assemblages (Drapeau et al., 2000). Shifts in forest composition over large spatial scales are may also be partly responsible for the gradual disappearance of woodland caribou in southern Quebec, because moose (*Alces alces*) and its associated predators (e.g. bear and wolf) tend to increase in importance in landscapes dominated by young deciduous stands of clearcut origin (Crête and Marzell, 2006; Courtois, 2003).

Finally, another difference between pulsed disturbances compared with disturbances that are more evenly distributed in time is the spatial size and arrangement of disturbed patches. This can be easily grasped intuitively by contrasting, for example, the effects of 25 000 ha fires occurring every 50 years (in a relatively unstable climate), with fires of 500 ha occurring every year (in more stable climatic conditions). Even if these two fire regimes could result in similar average stand age structures or forest composition for large landscapes, the first fire regime will probably result in the formation of larger habitat patches (Hunter, 1993). The occurrence of severe spruce budworm outbreaks in close succession (i.e. 30 years or less) may also produce patches of relatively small sizes, whereas outbreaks that occur at intervals of 60 years or more are more likely to result in the creation of large patches (Bouchard et al., 2006a). Thus, for a given disturbance cycle (cf. time necessary to disturb an area the size of the reference area), episodic large-scale disturbances will usually result in a coarser

grained forest mosaic (Gustafson, 1996). These patches might also be qualitatively different, as disturbances affecting larger patches are usually more lethal: notably, large fires leave fewer residual trees or stands than small fires (Turner and Romme, 1994; Bergeron et al., 2004). Some animal species might be threatened by the disappearance of landscapes dominated by large, relatively homogenous patches, but there is a lack of well replicated studies clearly separating the effects of habitat loss from those of changing spatial patterns (i.e. fragmentation) (Fahrig, 2003).

3.2.2. Other factors influencing population fluctuations

Even if fluctuations in population sizes of plant and animal species are influenced by habitat abundance, which in turn is controlled by disturbance rates, several other factors can regulate population abundances. Inter-specific relations (competition, predation, parasitism), demographic factors, or climate can determine large-scale cyclic population fluctuations of key mammal species such as the snowshoe hare or red-backed voles (*Clethrionomys gapperi*) and their predators (Boutin et al., 1995; Cheveau et al., 2004; Stenseth et al., 2004). Such large-scale population fluctuations are typical in boreal forests (Danell et al., 1998; Hodges, 2000), and also probably correspond to the situation in northern Témiscamingue, at least for the snowshoe hare and lynx (Fortin and Tardif, 2003). Temporal population fluctuations also exist for a multitude of smaller organisms such as insects, but these fluctuations and their possible causes have rarely been investigated for species that do not have a direct economic importance (Danks and Footitt, 1989).

It is reasonable to expect that in general, species that depend specifically on habitats created by recent disturbances will be the ones that are affected most directly by temporal fluctuations in disturbance intensity. This includes for example a range of insect species that colonize charred wood (Saint-Germain et al., 2004), fire-adapted bird species such as the black-backed woodpecker (*Picoides arcticus*; Imbeau et al., 2001), warblers that feed preferentially on spruce budworm larvae during outbreak periods (Patten and Burger, 1998). For species that do not depend primarily on such habitats, pulsed large-scale disturbances may influence population abundances in a more indirect manner, for instance by creating variable environmental conditions, which are relatively unfavourable for stable density-dependent regulation and the maintenance of stable population levels (Liebhold et al., 2004).

3.2.3. Potential importance of episodic disturbances for the maintenance of species diversity

For a given animal or plant species, fluctuations in population sizes induced by variations in habitat abundance are generally considered to increase extinction risk (Johst and Drechsler, 2003; Liebhold et al., 2004). Such negative effects are particularly likely to occur when the amplitude of the fluctuations is beyond the range of natural variability. Within that range however, it can be assumed that most plant and animal species have either adapted to these fluctuations or been extirpated.

It might be interesting to think of fluctuations in habitat abundance not as a risk factor for long-term persistence of populations and communities, but rather as an important component of large-scale ecosystem processes in sub-boreal forests. For example, in the case of tree species, large-scale disturbances such as fires do not only regulate the recruitment of shade-intolerant (aspen) or fire-adapted species (such as pines or black spruce) at the stand scale but they are also important for maintaining coarse-scale patchiness (Hunter, 1993; DeLong and Tanner, 1996). In this context, species with low dispersal potential such as cedar and balsam fir are disadvantaged when it comes to re-colonizing large fire patches (Bergeron et al., 2004), but can still

maintain a presence at the landscape or regional scales. Hence, a pulsed disturbance regime characterized by large mortality patches can cause a decline in tree species diversity at the stand scale, but may contribute to higher stand type diversity at the regional scale. Spruce budworm outbreaks, however, will have a different effect. During an outbreak, seed production of surviving host trees is inhibited over whole regions, which may hamper the capacity of balsam fir and spruces (the primary hosts of the budworm) to recolonize stands that sustained severe mortality (Blais, 1954; Simard and Payette, 2005), particularly when advance regeneration is absent. Frequent outbreak pulses can thus favour the entry of non-host species and lead to a higher tree species diversity at the stand scale (Bouchard et al., 2006b).

For animal species, the possibility that fluctuations in habitat abundance might have a positive effect for the persistence of rare species has rarely been explored. In non-boreal ecosystems, it has been suggested resource pulses can allow reproductive potential to persist in some populations (Chesson et al., 2004). In a boreal context, one possible advantage of fluctuating populations for some animal species is that the peak abundances that are reached at times, either caused by changing habitat abundance or density-dependent regulation, might contribute to the maintenance of viable metapopulations. For the Canada lynx, one of the rare species that has been studied in this respect, high population levels might lead individuals to leave over-populated areas to prospect elsewhere for more favourable environments (Schwartz et al., 2002). This dispersal may allow for gene flow among populations within the range of distribution of this species in North-America (Stenseth et al., 2004), and might even coincide with periodic replenishment of populations located at the margin of the main distribution that might not maintain themselves otherwise (Schwartz et al., 2002).

The importance of pulsed disturbances might not be so much in the creation of temporally fluctuating habitat abundances, but in the coarse grained spatial pattern of contiguous habitats created at large spatial scales, particularly in the case of forest fires. Theoretically, this spatial structure would be advantageous to species with relatively high dispersal rates and tolerance for habitats created by recent disturbances (Tilman, 1994). In contrast, more generalist species might increase in importance in the fine-grained forest mosaic resulting from evenly distributed disturbance regimes such as forest management, and some organisms specializing on recently disturbed habitats might be outcompeted in this situation (Thompson and Harestad, 2004). One limitation of this hypothesis is that most animals with large home ranges are generalists, and may not particularly benefit from large homogenous patches (Hunter, 1990). Nonetheless, some evidence exist that spatial structure has an importance for some larger species, e.g. Canada Lynx which can be displaced by coyote (*Canis latrans*) in fine-grained forest mosaics (Buskirk et al., 2000).

4. Emulating large-scale synchronous disturbances

Assuming that pulsed disturbances are important for the maintenance of natural ecosystems, forest management practices must be adapted accordingly. One simple way of re-creating the large-scale synchronism typical of severe disturbances would be to concentrate disturbance-emulation cuts during certain periods, followed by no-harvest intervals. The following section proposes a basic forest management scenario inspired by this simple rationale, followed by its critical examination. For simplification, only two disturbance parameters are illustrated (total area disturbed and temporal variability), but other correlated parameters such as disturbance intensity or patch size are discussed.

We also insist mostly on the emulation of severe disturbances, e.g. those that have the ability to cause severe mortality over continuous areas of 50 ha or more.

4.1. Initial scenario and key assumptions

To determine the frequency of harvest pulses we used available knowledge about natural disturbance regimes, and other information relevant for forest management such as tree species longevity. In the case of spruce budworm outbreaks in Témiscamingue, harvesting every 60–70 years on average would be reasonably close to the natural interval between the 1910 and 1980 outbreaks, and marginally longer than the economic rotation for even-aged balsam fir stands. Because something like a “natural frequency” has not been found yet for pulses of fire in this region (Girardin et al., 2004), there is no way to obtain an ecologically relevant rotation period for this disturbance type. A rotation of ca. 80–100 years could be practical because this period is relatively close to the economic rotation for post-fire species such as aspen, black spruce and jack pine in sub-boreal forests. Deciding in advance on the timing of regional harvest pulses based on economic stand maturity might lack ecological realism, but may be closer to conventional approaches in forestry and allow some forecasting of future wood supplies. Such an approach might also be relatively easy to implement in a region such as Northern Témiscamingue, where extensive forest management has not yet completely obliterated the pre-industrial, unbalanced forest age-class structures. The average decadal rates of severe natural disturbances in this region were respectively of 1.3% per decade and 5% per decade for spruce budworm outbreaks and fires (Table 1). We thus based the disturbance-emulation cutting rates on these averages, but we also arbitrarily reduced the rates of disturbance-emulation cuts by 20%, to account for unexpected natural disturbances during the 2000–2150 horizon that would otherwise lead to an additive effect of natural and harvesting disturbances (Table 1). Therefore, for this scenario the amplitude of harvest pulses was maintained between 2% and 10% per decade, which is lower than the natural amplitude observed for the 20th century (compare Figs. 2 and 3), but probably more realistic from a socio-economic perspective. The two reductions proposed (i.e. a 20% reduction overall, and a maximum decadal rate of 10% during harvest pulses) are complementary, because they address two distinct temporal features of natural

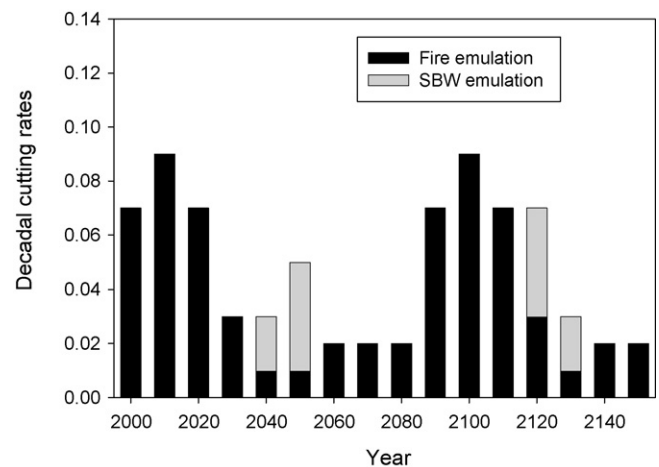


Fig. 3. Example of projected clearcutting rates based on the scenario emulating temporal fluctuations in natural disturbances regimes. This scenario is based on parameters defined in Table 1. The average rate of disturbance-emulation cuts is 5.1% for both disturbances combined (Table 1). This figure does not illustrate the emulation of non-stand-replacing disturbances.

Table 1

Parameters values used for setting decadal clearcutting rates based on natural disturbance patterns in mixed forests of Western Québec

Disturbance emulated	Parameter	Parameter values
Severe fires	Last fire optimum (year)	1920
	Period length ^a (year)	90
	Average rate of natural disturbance ^b (%)	5
	Average rate of emulation clearcuts ^c (%)	4
Severe spruce budworm outbreaks	Last SBW optimum (year)	1980
	Period length ^a (year)	70
	Average rate of natural disturbance ^d (%)	1.3
	Average rate of emulation clearcuts ^c (%)	1.1
Bounds ^e	Maximal decadal rate (%)	10
	Minimal decadal rate (%)	2

All percentages represent the proportion of total forest area affected by decade.

^a Period length: based on an approximate mean rotation age for the post-disturbance tree species for each disturbance type.

^b Based on the mean fire return interval (200 years).

^c Harvest rates were reduced by 20% compared with natural disturbance rates, to account for unexpected natural disturbances and reduce the risk of additivity.

^d Based on severe outbreak return interval (70 years) and mean area affected per outbreak (8% of total landbase).

^e Socio-economically and ecologically “acceptable” maximal and minimal clearcutting rates were defined empirically for the studied region.

disturbances: the mean disturbance rate, and peak disturbance rate during pulses.

4.2. Critical examination of the scenario

4.2.1. Degree of emulation

At the stand scale, the capacity for emulating natural disturbance pulses is of course constrained by the capacity of silvicultural techniques to mimic natural disturbance processes (Perera and Buse, 2004 termed this the *degree of emulation*). In this section, we concentrate on regional-scale effects of natural disturbances, and hence we will not directly address the question of whether stand-scale effects of severe natural and anthropogenic disturbances are similar (but see Haeussler and Kneeshaw, 2003 for a thorough review on the topic). However, it is important to remember that most stand scale limitations in disturbance emulation will translate directly at the landscape or regional scales. For example, emulating regional-scale fluctuations in forest characteristics such as forest composition or age-class structure should be possible, because standard silvicultural techniques are relatively efficient in influencing forest composition at the stand-scale. However, the reproduction of regional-scale pulses of dead wood is more difficult to achieve. To maintain this attribute, it might be necessary to maintain some level of natural disturbances, a possibility that depends on the type of disturbances to be maintained and on our ability to control them. For disturbances such as synchronous diebacks or spruce budworm outbreaks, we know that they are more likely to occur when there is a great abundance of overmature stands; hence, in this case, the occurrence of large-scale disturbances can be predicted and controlled indirectly (up to a point) by properly managing forest characteristics such as composition and structure at the regional scale. For a disturbance type such as severe fires, which in Temiscamingue are largely controlled by weather, the occurrence of a disturbance event is more unpredictable, and our ability to control disturbance occurrence through forest characteristics such as species composition or structure is limited.

4.2.2. Complementarity between natural disturbances and disturbance-emulation cuts

Forest management strategies are generally based on the assumption that future natural disturbances can be controlled, and mostly replaced by harvesting operations. However, it is clear that in boreal forest conditions in Canada, some natural disturbances

will continue to occur in addition to anthropogenic disturbances. Spatially, there is a risk that areas affected by natural disturbances will juxtapose or superimpose with areas affected by cuts, which has the potential to carry the ecosystem outside the range of natural variability (Paine et al., 1998; Perera and Buse, 2004; Suffling and Perera, 2004). Once again, this risk is of a different nature when we compare one disturbance type to another. For insect outbreaks and diebacks, which are generally diffuse spatially, their spatial additivity will mostly occur at local spatial scales, in interaction with partial cuts (Seymour et al., 2002). For crown fires and severe outbreaks, the risk also occurs at larger spatial scales, for instance the juxtaposition of a fire-emulation clearcut of 100 km² with a real fire of 100 km² will result in a 200 km² disturbed area that might end up being outside the range of natural variability. The spatial superimposition of fires and cuts can also result in un-natural permanent shifts in species composition (Radeloff et al., 2000).

Substituting emulation-cuts to natural disturbances is easier when there is some form of guarantee that disturbance return intervals will decrease over time, for example due to direct forest protection measures such as the use of water bombers or insecticide sprayings. Under these expectations, there is a lower probability that a natural disturbance pulse will occur simultaneously with a harvest pulse. When a lower occurrence of natural fires compared with historical rates is expected in the future due to climate changes (see Bergeron et al. (2006) for western Quebec), this further decreases the risk of additive disturbances. In the case of spruce budworm outbreaks, global warming is expected to cause an increase in outbreak severity (Logan et al., 2003). In the specific case of the Témiscamingue region however, future outbreaks are not expected to have a more drastic effect than the 1910 and 1980 outbreaks, each of which already lead to an almost complete depletion of mature balsam fir stands (Bouchard et al., 2006a).

Another factor that facilitates the substitution of natural disturbances by anthropogenic disturbances is when the natural disturbance pulses affect a circumscribed component of the ecosystem. For example, a severe spruce budworm outbreak will affect most balsam fir stands older than 50 years in a given region. In such conditions, it would be easier to use silvicultural treatments as substitutes by specifically targeting balsam fir stands. Substitution is more difficult for crown fires, because this disturbance creates large patches of severe mortality in locations that are impossible to predict. The probability of proceeding to a successful substitution is thus lower for fire-emulation cuts.

4.2.3. Wood flows

The corner stone of most current forest management plans in Quebec and elsewhere in Canada is finding an optimal, “perpetually” sustainable level of harvesting that can be expressed on an annual basis. These even-flow policies are mostly implemented to maintain stable employment levels in local communities that depend exclusively on the forest industry. In reality, in spite of these official even-flow policies, ups and downs in wood flows and employment are historically frequent, either due to socio-economic upheavals or mismanagement (cf. Baskerville, 1995; Adamowicz et al., 2003). The utility of even-flow policies has also been criticized from a purely economical perspective, as fluctuating harvest rates that match with economical cycles could be much more profitable over the long term (Pearse, 1990). Thus, even if rapid variations in wood flows can have dramatic effects on the forest industry and employment, progressive variations such as those illustrated in Fig. 3 could be more acceptable, especially in regions where the economy does not depend exclusively on the forest sector.

Alternatively, a more regular wood input to transformation industries could be achieved by adopting intensive forms of silviculture on restricted areas to provide timber in-between disturbance-emulation harvest pulses, for example so as to attenuate the fluctuations observed in Fig. 3. To be coherent, such areas should be identified by using a methodology taking the long-term impacts on biodiversity into account. Areas that are already deforested such as abandoned agricultural lands should probably be prioritized. Importing lumber from other management units is another possible solution, assuming that they are not affected as well by synchronous disturbance-emulation cuts. In this respect, a true ecosystem management strategy might force foresters and governments to consider spatial scales that are far larger than what they are generally used to.

4.2.4. Road networks

Minimizing the extent of the road network is often considered a priority to mitigate the effects of harvesting on biodiversity, particularly for large carnivores and ungulate species such as the woodland caribou (Bourgeois et al., 2005). This can be done more easily when disturbances like large forest fires are emulated, because in this case the area harvested per km of road is maximized (Andison, 2003). Other disturbances such as spruce budworm outbreaks and large-scale diebacks are much more diffuse, and a slavish emulation of these patterns could necessitate the creation or the maintenance of extensive forest road networks, which could have a negative effect on some animal species that depend on “deep forest” attributes. This would be the case if a pulse of fire-emulation cuts is synchronous with a temporal pulse of spruce budworm-emulation cuts (Fig. 3). Thus, pulsed harvesting of spatially circumscribed disturbances such as fire could have favourable effects on reducing the negative impacts of roads, but the emulation of diffuse disturbances could have an adverse effect.

5. Conclusion

The proposed approach to emulate large-scale disturbance pulses is simple, but presents several potential disadvantages, including a high level of scientific uncertainty. Notably, the benefits of episodic large-scale disturbances and fluctuating habitat abundance for biodiversity are mostly theoretical at the moment, because current research has not yet directly investigated these issues, except for a few larger mammals (e.g. caribou or lynx in North-America). Another question is whether the disturbance regime that is used as reference is really representative of forest dynamics over evolutionary time scales (Thompson

and Harestad, 2004). For example, there are indications that spruce budworm outbreaks of the 20th century have been of exceptional severity compared with those of earlier centuries (Simard et al., 2006), which raises the question of whether this disturbance should be emulated at all. Also, the assumptions we used in this study to determine the frequency and amplitude of disturbance pulses are somewhat arbitrary, and might lead to a form of ecosystem homogenization (i.e. periodic fluctuations instead of the stochastic fluctuations that are more likely in natural ecosystems). Such questions are complex to address, but crucial topics for further reflection and future research.

Nonetheless, under the provision that they are carefully planned and compatible with other conservation issues such as protection of old-growth forests (Crête and Marzell, 2006), it would be possible and even desirable to implement some form of temporal fluctuations in forest management activities. In areas where disturbances in past decades have been low compared to historical levels, and where natural disturbance severity is expected to decrease due to human influences, there is probably room to introduce temporal pulses of disturbance-emulation cuts. The strategy could be even more useful in regions that have been over-disturbed in recent decades due to a combination of anthropogenic and natural disturbances, as it would force the adoption of harvesting levels that are below the average natural-disturbance rate (5.3% per decade for disturbances emulated by clearcuts in the Témiscamingue region; Table 1) for several consecutive decades.

Maintaining large-scale fluctuations in forest characteristics would also probably mean increased levels of mortality due to pathogens and insect outbreaks, especially during periods in which stands arrive synchronously at maturity over whole regions. Thus, ultimately, the adoption of a pulsed harvesting pattern probably depends on the general willingness to “sacrifice” some timber revenues for biodiversity, as is probably the case for any ecosystem forest management strategy (Le Goff et al., 2005).

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