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Modelling Spatial Interactions Among Fire, Spruce Budworm, and Logging in the Boreal Forest

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ABSTRACT

In the boreal forest, fire, insects, and logging all affect spatial patterns in forest age and species composition. In turn, spatial legacies in age and composition can facilitate or constrain further disturbances and have important consequences for forest spatial structure and sustainability. However, the complex three-way interactions among fire, insects, and logging and their combined effects on forest spatial structure have seldom been investigated. We used a spatially explicit landscape simulation model to examine these interactions. Specifically, we investigated how the amount and the spatial scale of logging (cutblock size) in combination with succession, fire, and spruce budworm outbreaks affect area burned and area defoliated. Simulations included 30 replicates of 300 years for each of 19 different disturbance scenarios. More disturbances increased both the fragmentation and the proportion of coniferous species and imposed additional constraints on the extent of each disturbance. We also found that harvesting legacies affect fire and budworm differently due to differences in forest types consumed by each disturbance. Contrary to expectation, budworm defoliation did not affect area burned at the temporal scales studied and neither amount of logging nor cutblock size influenced defoliation extent. Logging increased fire size through conversion of more of the landscape to early seral, highly flammable forest types. Although logging increased the amount of budworm host species, spruce budworm caused mortality was reduced due to reductions in forest age. In general, we found that spatial legacies do not influence all disturbances equally and the duration of a spatial legacy is limited when multiple disturbances are present. Further information on post-disturbance succession is still needed to refine our understanding of long-term disturbance interactions.

Key words: dynamic feedbacks; forest management; landscape legacies; forest disturbance; spatial modelling; landscape pattern metrics.

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Introduction

Interactions among contemporary forest disturbances and the legacies of previous events are essential components of the spatio-temporal dynamics of forest landscapes (Turner 1989). In the eastern boreal and mixed-wood forests of Canada, the historically dominant disturbances were stand-replacing fire (Bergeron and others 2001) and periodic outbreaks of the spruce budworm (SBW—*Choristoneura fumiferana*) (Bouchard and others 2006; Gray and MacKinnon 2006). Presently, logging also contributes significantly to forest change. In combination with forest succession, forest disturbances create a mosaic of spatial pattern in forest composition and age (Shugart and others 1992). These patterns affect ecosystem dynamics and forest sustainability through their influence on nutrient dynamics (Foster and others 1998), timber availability (Wallin and others 1994), biodiversity (Fahrig 2003), and future disturbance events (Turner 1989; Tang and others 1997).

Understanding how forest patterns created through logging affect other disturbances is of central importance to sustainable forest management (Turner 1989; Tang and others 1997). Forest management changes forest spatial structure (Franklin and Forman 1987; Fall and others 2004; James and others 2007) and affects forest composition and forest succession (Carleton 2000; Friedman and Reich 2005). Not only can patterns and intensities of logging constrain future management options (Wallin and others 1994; James and others 2007) but they can also influence fire behavior and SBW defoliation patterns through changes in patterns of forest age and composition.

Disturbance interactions are difficult to analyze and few studies have examined the combined influence of human and natural disturbances (Gustafson and others 2000; Radeloff and others 2000; Fall and others 2004; Didion and others 2007). However, none of these examples examines interactions among the three dominant boreal disturbances (that is, fire, SBW, and logging). Challenges to examining such interactions include the broad spatial and temporal scales involved, the lack of large-scale spatial and temporal data, and the fact that dynamic feedbacks among fire, insects, logging, and persisting spatial legacies make it difficult to identify clear cause and effect relationships. Furthermore, non-linear and cross-scale interactions also make identifying relationships among human and natural disturbances difficult (Peters and others 2004; Raffa and others 2008). Nonetheless, understanding these spatial feedback processes at coarse spatial and temporal scales is important to sustainable long-term management of forest resources (Cooke and others 2007; Puettmann and others 2009).

Individual disturbance events are typically not independent (Veblen and others 1994). Instead, disturbances are constrained or facilitated by the legacies of previous events. Disturbances and persisting legacies can combine to produce patterns distinct from those generated by any one disturbance on its own (Paine and others 1998). In eastern boreal forests, fires can reduce the abundance of SBW host (that is, fir and spruce) on the landscape and reduce the effects of budworm outbreaks (Bergeron and others 1995). Budworm outbreaks can also temporarily increase the risk of wildfire by increasing fuel availability (Stocks 1987; Fleming and others 2002). In the western US, spruce beetle activity may be influenced by forest structure created by previous fires and avalanches (Veblen and others 1994), and in turn spruce beetle outbreaks have the potential to increase forest flammability (Knight and Wallace 1989).

SBW defoliation creates complex patterns of forest mortality and volume loss (MacLean and Mackinnon 1997; Candau and Fleming 2005) over millions of hectares with important economic and ecological consequences (MacLean 1990). Over the last century, outbreaks have become more extensive and severe, possibly due to changes in forest composition (that is, species homogenization) and configuration (that is, spatial pattern) due to logging and fire suppression (Blais 1983; Cooke and others 2007). Here, homogenization refers to increases in the amount of host fir and spruce on the landscape and increased connectivity among host patches. These changes have altered forest stand and landscape level susceptibility (that is, the likelihood that a stand will be attacked) and vulnerability (that is, the likelihood that a stand once attacked will be killed). Because SBW is host-specific, it has the potential to be strongly affected by feedbacks with forest succession and forest management (Bergeron and Leduc 1998).

From the premise that logging has potentially increased forest vulnerability to SBW outbreaks, the ‘‘silvicultural hypothesis’’ (Miller and Rusnock 1993) posits that increasing forest diversity through management could be used to reduce the impacts of future outbreaks. Several studies have shown that an increased proportion of hardwood can reduce stand vulnerability (Bergeron and others 1995; Su and others 1996) as can the amount of hardwood in the surrounding neighborhood (Cappuccino and others 1998; Campbell and others 2008). Landscape structure (that is, fragmentation) has also been shown to affect population dynamics in another important forest defoliator, the forest tent caterpillar (*Malacosoma disstria*) (Roland and Taylor 1997).

We used a spatially explicit simulation model to examine the relationships among forest condition, fire, spruce budworm defoliation, and forest management at different spatial scales. We asked the following four questions: (1) How does logging alter forest susceptibility to SBW defoliation through changes in forest composition and landscape structure? (2) How does logging influence fire dynamics? (3) What effect does SBW defoliation have on area burned? (4) How do the three-way interactions among forest management, fire, and SBW affect forest age, composition, and spatial structure?

Methods

Study Area

The Vermillion study area consists of boreal mixedwood forest in Québec (Figure 1) that covers approximately 430,000 ha, 392,000 ha of which is forested. The study area contains two forest types. The northern portion consists of 180,000 ha within the ''Missinabi-Cabonga'' region (Rowe 1972). Dominant species include black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and white birch (*Betula papyrifera*). The southern portion consists of approximately 210,000 ha and is classified as ''Laurentian'' forest which is a transition zone between the boreal and the temperate forest regions (Rowe 1972). Characteristic species of this region include, balsam fir, white spruce (*Picea glauca*), and yellow birch (*Betula alleghaniensis*). The region has moderately rugged topography and a high density of lakes and wetlands (approx. 15% in total). Current patterns in forest age and composition reflect the region's history of forest management and interactions with succession and natural disturbance.

Vermillion Landscape Model

The Vermillion Landscape Model (VLM) is a spatially explicit stochastic model that simulates landscape scale forest dynamics and includes sub-models for fire, SBW, logging, forest growth, and forest succession. The VLM shares many characteristics with other landscape simulation tools and can be classified as a forest landscape simulation model that includes spatial interactions, dynamic communities, but excludes explicit detailed ecosystem processes (Scheller and Mladenoff 2007). The VLM is comparable to the LANDIS simulation model (He and Mladenoff 1999) in that multiple processes are iteratively simulated using a fixed timestep in a spatial, raster context. The VLM was implemented using SELES (Fall and Fall 2001) and has been previously used to investigate interactions between forest management and fire (Fall and others 2004; Didion and others 2007), the consequences of shifting management regimes on forest age (James and others 2007), and TRIAD management zoning (Côté and others 2009). In the following sections, we employ the model description protocol of Grimm and others (2006) to describe the VLM.

Model Overview

Purpose

The purpose of the VLM is to examine dynamic interactions and mutual constraints among multi-

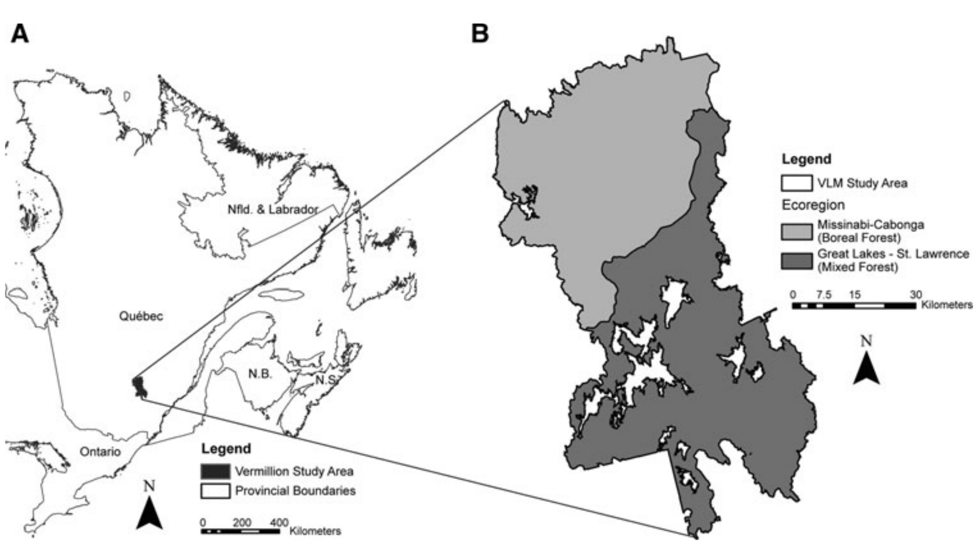

Figure 1. Vermillion landscape study region in context in Québec, Canada (**A**). The region straddles two forest ecoregions classified according to Rowe (1972) (**B**). The study area is approximately 430,000 ha, 392,000 ha of which is forested. Data are represented in raster format at a pixel resolution of 50 m × 50 m.

ple forest disturbance agents and regeneration. The VLM was designed to permit investigations into the indirect long-term consequences of different forest management strategies on natural disturbance dynamics (that is, fire and SBW) as mediated through the direct influence of forest management on spatial patterns of forest age and composition.

State Variables and Scale

State variables in the VLM fall into two categories: (1) spatial variables that describe landscape context and condition at each individual raster cell location; and (2) variables that describe aspects of the disturbance processes that spread and interact with the set of spatial variables. The dynamic interactions among processes and spatial variables produce dynamic landscapes.

Spatial variables are represented in raster format and cover the full extent of the study area at a 50-m resolution. Each raster cell is characterized by the state variables age, tree species, and site stratum. Site stratum describes the successional type of a cell and is based on soil, drainage, and productivity conditions. Successional dynamics are determined using these base variables as well as last disturbance type. All other spatial variables such as flammability (fuel type), SBW susceptibility (host type), and logging potential (volume/ha) are derived from these variables.

Forested cells in the VLM contain information on the presence and proportion of up to four tree species that correspond to the dominant and secondary species in both a canopy and a sub-canopy cohort. Spatial relationships between cohorts and species within a cell are not tracked. Initial conditions for the VLM only contain information for a single cohort (dominant and secondary species), and cohort age. Secondary cohorts can be initiated after partial disturbance by SBW defoliation, and a cell may return to a single cohort through stand-replacing disturbance and succession (Online supplemental appendix).

State variables that pertain to spatial processes can be further subdivided into those relevant to (1) fire, (2) SBW, and (3) logging. Fires are characterized by the maximum duration, maximum size, return interval, mean duration, and initial spread index (weather conditions). Many of these variables are specified as distributions (Table 1). SBW outbreaks are characterized by return interval, outbreak duration, number of initiation sites, and a random variable used to simulate stochasticity (Table 1). Logging is characterized by a minimum and maximum cutblock size, annual allowable cut (AAC), and site-specific minimum harvest age.

The current VLM (VLM.v5; Figure 2, Online appendix) represents an updated version (VLM.v4; James and others 2007; Didion and others 2007). Changes were made to facilitate interactions among disturbances through their mutual dependence on forest conditions. These changes include a duration-based fire model (Pennanen and Kuuluvainen 2002) in which forest fuels determine fire spread rates and eventual size, a spruce budworm disturbance model that produces patterns of defoliation that reflect patterns of susceptible hosts (Sturtevant and others 2004), and an adjusted succession sub-model that responds uniquely to different disturbances (Table 2; see Online appendix for further details).

Table 1. Summary of Simulation Parameters used for Fire and SBW Sub-Models

Sub-Model	Variable	Distribution	Value	Source
Fire	Max. duration	–	500	LFD, calibration
	Max. size	–	40 000 ha	LFD
	Return interval	–	250 years	Bergeron and others (2001)
	Mean number per decade	Neg. exp.	Mean = 6.4	Calculated; Van Wagner (1978)
	Mean duration (fire size)	Truncated neg. exp.	Mean = 200	LFD, Bergeron and others (2001), calibration
	Initial spread index (weather)	Truncated neg. exp.	Mean = 5, Min. = 4, Max. = 40	Env. Can. weather database, calibration
SBW	Return interval	Normal	Mean = 35, SD = 5	Candau and others (1998)
	Outbreak duration	Normal	Mean = 10, SD = 3	Candau and others (1998)
	Number of ignition sites per outbreak	Normal	Mean = 2, SD = 5	Calibration
	Patch variable (PV)	Uniform	Min. = 0, Max. = 100	Sturtevant and others (2004)

Maximum and mean fire duration are expressed in simulation time units. Calibration using these units yields the desired fire size distribution.
LFD = large fire database (Stocks and others 2002).

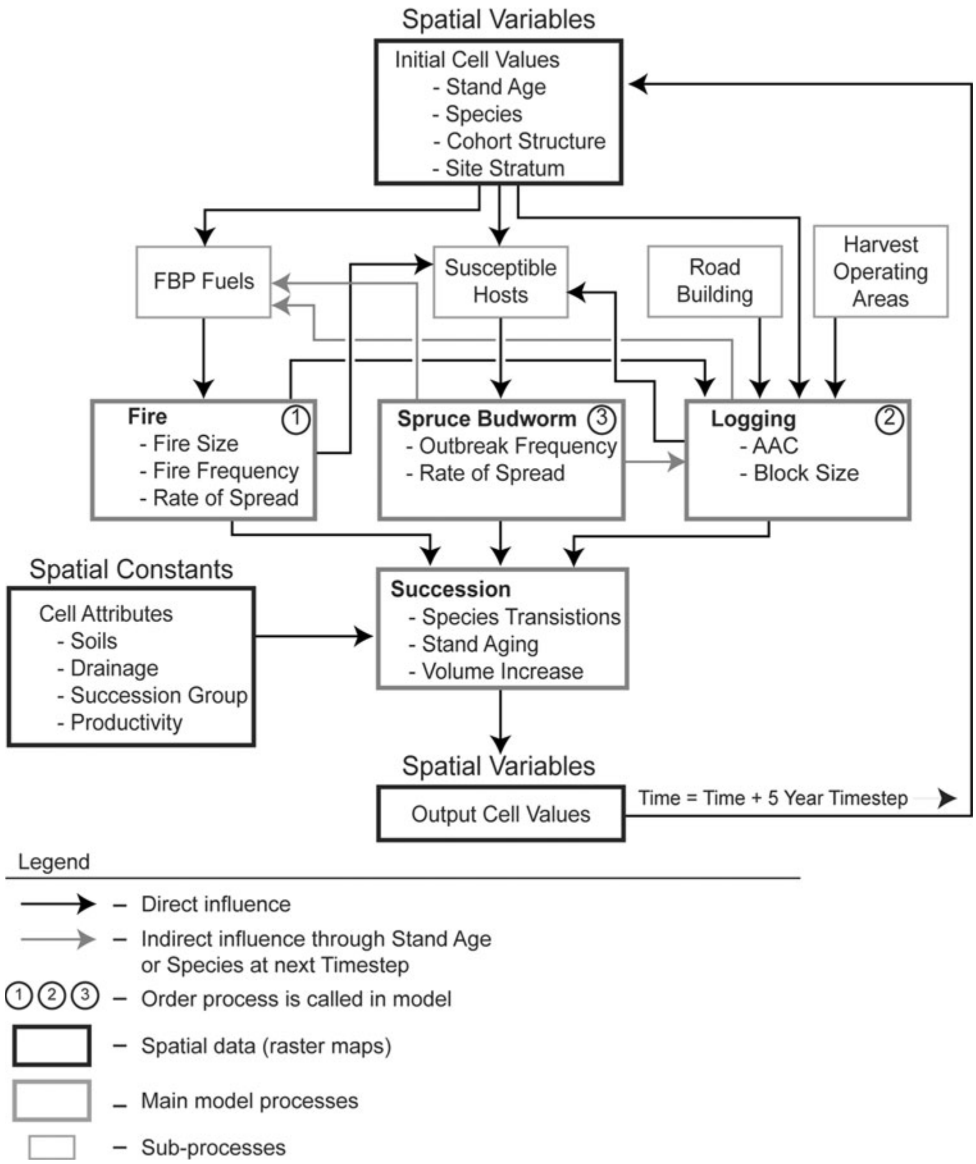

Figure 2. VLM v.5 conceptual model. Schema representing the main processes and flows for the VLM simulation model. Spatial variables and spatial constants represent raster maps of initial conditions that interact with simulated forest disturbance and succession processes to produce output, or consequent forest conditions using a 5-year time step. The three main processes are fire, spruce budworm outbreak, and logging, each of which has its own sub-model. The sub-process ''FBP Fuels'' refers to forest fuel classification using the Canadian Fire Behavior Prediction System (FBP—Forestry Canada Fire Danger Group 1992; see text for further details).

Process Overview and Scheduling

The VLM is designed to operate in fixed time steps (user defined between 1 and 10 years). Each process is scheduled to occur in the following sequence (Figure 2):

(i) Aging and succession.
(ii) Planning (assess growing stock, fuels, and management constraints).
(iii) Update roads.
(iv) Fire.
(v) Harvest operating areas and logging.
(vi) Spruce budworm disturbance.

Each process sub-model is designed to complete before the next one starts. Most reporting is done after the planning step.

Design Concepts

The forest succession sub-model was designed as an empirical semi-Markov chain based on the proportions of species in different age classes in the inventory data. This model was designed to capture similar trajectories that arose in the historical record using a space-for-time substitution within a stratification based on site characteristics (site stratum), where we assumed that the different cells in a given site type were subject to the same conditions and have the same species available to them. Species variation across the landscape results from changes in age structure from disturbance and aging, and from stochastic selection along a trajectory.

Table 2. Disturbance-Specific Initial Species Assignments for Succession Trajectories

Disturbance	Previous dominant species	Initial species assigned
Fire	All	Site-type lookup
Logging	Fir	Fir
	Aspen	Aspen
	Spruce	Spruce; fir or aspen if present
	Jack pine	Jack pine; fir or aspen if present
SBW	Other	Spruce; fir or aspen if present
	All host	Host
	Mixed	Released non-host

These assignments persist for 40 years, after which time other species are assigned based on an empirical semi-Markov succession model that uses site stratum, current and previous composition, and neighborhood context (see text and Online appendix for details on post-SBW species assignment).

The logging model was designed to be consistent with harvest models used in timber supply analyses. This model uses input growth and yield data (indexed by stand age and site stratum), spatial constraints (road access), and management constraints (minimum harvest age, harvest targets, zoning constraints for some scenarios). It was also designed for use with natural disturbance simulation. The roading sub-model captures the basic layout of road development and control on harvest access but was not designed to predict where roads would actually be built.

The fire model was designed to allow the rate of spread to depend on fuel type, but also to be partially controlled by empirical fire regime data. We chose a duration-based approach, where the time duration of each fire is selected from an input distribution, and fires spread for the selected length of time. Fire size, and hence overall fire rotation, is emergent and depends on the flammability and connectivity of fuels. This approach allows some top-down control on fire size, where the duration distribution can be calibrated from fire data (as in Pennanen and Kuuluvainen 2002), but interacts more with landscape patterns than empirical models.

The spruce budworm sub-model was designed to capture the pattern, timing, and effects of outbreaks, but with a level of detail consistent with the other sub-models. The main aim was to capture the loss of growth and mortality caused by spruce budworm that influence fuels (and hence fire), timber volume (and hence logging and roading), and tree species (and hence succession).

Details

Initialization

Initial spatial conditions were the same for all simulation runs based on inventory data (see next section). All forested cells were assumed to have a single cohort. The initialization of all process models was the same in terms of initial parameters.

Input

Data for the initial conditions in all modelling scenarios were derived from the third decadal forest inventory (1990s) carried out by Système d'Information FORestière par Tesselle (SIFORT) in collaboration with the Québec Ministry of Natural Resources and Wildlife and Abitibi-Bowater.

Wood volume in each cell is based on yield curves calculated using multivariate regression analysis of plot data (SIFORT) stratified by site type (productivity, ecoregion). Existing and planned future roads were broken into segments represented by an input grid (road segment id) and a table (with start and end locations and type), so the road update sub-model could activate segments as logging proceeded.

Sub-Model Descriptions

Detailed sub-model descriptions and their parameterization can be found in the Online appendix. Specific parameters used in the sub-models can be found in Table 1.

Experimental Design

Nineteen scenarios were simulated that included different combinations of fire, insects, and logging. This set of scenarios includes each disturbance on its own, in pairs, and combined as three disturbances (Table 3). Logging effects were varied by changing the intensity and spatial scale of logging where intensity refers to the amount of forest harvested annually. The VLM uses an area-based AAC that describes the percentage of the landscape accessed in a given year. Two levels of this factor were simulated: (1) low—0.65% (~2550 ha/year), and (2) high—1% (~3900 ha/year). Scale of logging refers to the simulated cutblock size distribution that is specified as a uniform distribution with a maximum and minimum size. Two levels of this factor were simulated: (1) small cut-blocks (60–80 ha), and (2) large cut-blocks (180–220 ha), which reflect the

Table 3. List of Simulation Scenarios

Number	Summary	Code	Factors			AAC (%)	Cutblock size
			Fire	SBW	Logging		
1	Only fire	F	Yes	No	No	X	X
2	Only SBW	s	No	yes	No	X	X
	Only logging	Lla	No	No	Yes	0.65	Small
4	Only logging	Lib	No	No	Yes	0.65	Large
5	Only logging	L2a	No	No	Yes	1.0	Small
6	Only logging	L2b	No	No	Yes	1.0	Large
7	SBW + fire	SF	Yes	Yes	No	X	X
8	SBW + logging	SLla	No	Yes	Yes	0.65	Small
9	SBW + logging	SLlb	No	Yes	Yes	0.65	Large
10	SBW + logging	SL2a	No	Yes	Yes	1.0	Small
11	SBW + logging	SL2b	No	Yes	Yes	1.0	Large
12	Fire + logging	FLla	Yes	No	Yes	0.65	Small
13	Fire + logging	FLlb	Yes	No	Yes	0.65	Large
14	Fire + logging	FL2a	Yes	No	Yes	1.0	Small
15	Fire + logging	FL2b	Yes	No	Yes	1.0	Large
16	SBW + fire + logging	SFLla	Yes	Yes	Yes	0.65	Small
17	SBW + fire + logging	SFLlb	Yes	Yes	Yes	0.65	Large
18	SBW + fire + logging	SFL2a	Yes	Yes	Yes	1.0	Small
19	SBW + fire + logging	SFL2b	Yes	Yes	Yes	1.0	Large

All scenarios were run for 300 years and 30 replicates.
SBW = spruce budworm; AAC = annual allowable cut expressed as a percentage of the harvestable landbase.

approximate range of cutblock sizes typically applied in managed forests in Québec (Sougavinski and Doyon 2005). Stand-replacing fires and high severity SBW outbreaks were either included or excluded. Thirty replicates of each scenario were simulated for 300 years using a 5-year timestep.

Analysis—ANOVA

Three ANOVA models were created to examine the effects of fire, spruce budworm defoliation, and logging (that is, AAC and cutblock size) on total area burned and total area defoliated using the set of mean response values over 30 replicates as the analysis unit. All output was restricted to simulated year 100 and later to minimize the effects of initial conditions. ANOVA results were summarized using output tables and boxplots. In cases where interaction effects were significant, interaction plots illustrate how the mean values of the samples vary in response to different combinations of factors.

Analysis—Principal Components Analysis (PCA)

Two landscape metrics: (1) mean patch size (MPS), and (2) percentage of the landscape (PCT), were used to compare changes in the spatial structure of forest age and species in response to different disturbance combinations. Although many metrics are available, MPS and PCT represent simple and meaningful indicators of landscape pattern that describe both amount and fragmentation of the different forest classes on the landscape. Metrics were calculated using output maps for age and species at simulation year 300 classified into three age classes [1—young (1–100 years); 2—medium (101–200 years); 3—old (201+ years)], and five dominant forest tree species (1—birch; 2—aspen; 3—spruce; 4—pine; 5—fir).

PCA was used to summarize landscape pattern metrics and to compare landscape patterns among scenarios (James and others 2007). Points in the PCA biplots summarize spatial patterns of the different scenarios after 300 years of simulation. PCA was performed on the correlation matrix using the ''princomp'' function in R (R Development Core Team 2008). The broken stick criterion was used to assess significance of ordination axes and significance of loadings within significant axes (Jackson 1993; Peres-Neto and others 2003).

Results

Area Defoliated

As expected, total area defoliated was significantly influenced by the presence of fire and changes in

AAC (Figure 3). Individually, both fire and a higher AAC (1%) reduced area defoliated. Analysis of variance also revealed a significant interaction between AAC and fire (Table 4) in which the presence of fire reduced the effect of a higher AAC on area defoliated (Figure 4). The range of area defoliated over the 30 replicates was clearly reduced in the presence of fire, particularly at a higher AAC (Figure 3). Although both logging and fire reduce area defoliated through removal of mature host, the extent to which AAC affects defoliation appears limited by the amount of forest disturbed by fire.

Area Burned

Contrary to expectation, total area burned was not significantly affected by SBW defoliation (Table 5). Although the influence of SBW was not significant, median area burned was slightly higher with SBW for all factor combinations (Figure 5). Area logged (AAC) had a significant effect in that an AAC of 1% resulted in more area burned than an AAC of 0.65% (Table 5; Figure 5). No significant interactions between logging and SBW were identified although interaction plots did reveal some subtle, potentially interesting interactions (that is, different slopes) between AAC and SBW (Figure 6A) and between cutblock size and SBW (Figure 6B). Specifically, the presence of SBW increases area burned at a low AAC but not at a higher AAC. Similarly, SBW results in more area burned with small cutblocks than with larger cutblocks.

Landscape Pattern—Forest Age

Differences in landscape pattern metrics among scenarios are summarized in PCA biplots for (1) forest age structure (Figure 7), and (2) dominant species composition (Figure 8). In ordination of forest age structure metrics (Figure 7), 82 and 12% of the total variance was captured by the first and second axes, respectively. However, only the first axis is significant and can be used for interpretation. The broken stick criterion applied to factor loadings shows that this axis represents a gradient in forest age and fragmentation. Scenarios that resulted in continuous, old forest occupy the right quadrants and scenarios that resulted in younger, more fragmented forest occupy the left quadrants.

When more area was disturbed, either through an increase in AAC or through multiple disturbances, the forest was younger and characterized by smaller patch sizes. Budworm on its own creates the oldest and most connected (that is, large patch) forest landscapes. Fire on its own also creates older forest, but less so than SBW. As expected, a combination of fire and SBW further decreases age and increases fragmentation. Logging at a lower AAC produces more young forest than either fire or SBW, but is still in the right half (older) of the biplot. When AAC is increased to 1% or multiple

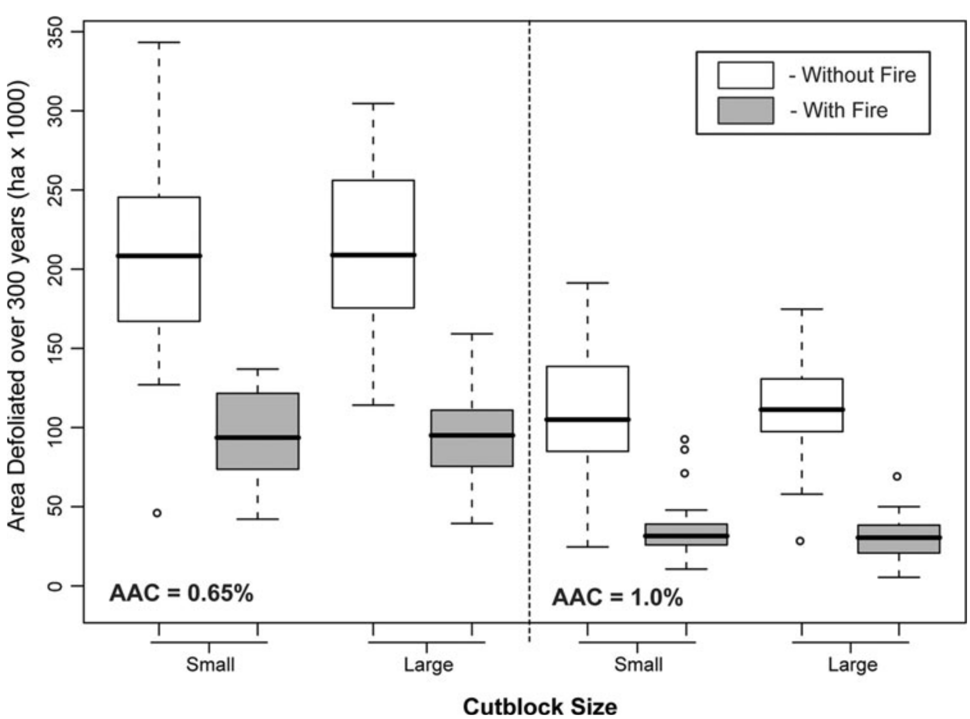

Figure 3. Effects of Fire, AAC, and Cutblock size, on *Total Area Defoliated*. *Bold horizontal bars* represent median total area defoliated over 30 simulated replicates and *vertical whiskers* represent 1.5 times the interquartile range. Cutblock sizes were specified as uniform distributions between 60 and 80 ha for the ‘‘small’’ treatment and between 180 and 200 ha for the ‘‘large’’ treatment. AAC percentages describe the annual area cut, expressed as a proportion of the total study area.

Table 4. ANOVA Table Summarizing the Main Effects and Interactions Between Fire and Logging on *Total Area Defoliated* by the Spruce Budworm

Factor	Df	Sum of squares	Mean squares	*F* value	Pr(>*F*)
AAC	1	383453534555.440	383453534555.440	259.342	**0.000**
Cutblock size	1	267957458.496	267957458.496	0.181	0.671
Fire	1	603186444398.313	603186444398.313	407.955	**0.000**
AAC:cutblock size	1	62963977.700	62963977.700	0.043	0.837
AAC:fire	1	22257669742.438	22257669742.438	15.054	**0.000**
Cutblock size:fire	1	90685.657	90685.657	0.000	0.994
AAC:cutblock size:fire	1	176052290.388	176052290.388	0.119	0.730
Residuals	232	343026432786.556	1478562210.287		
Total	239	1352431145894.990	1010883275318.720		

Bold values represent $p < 0.001$.

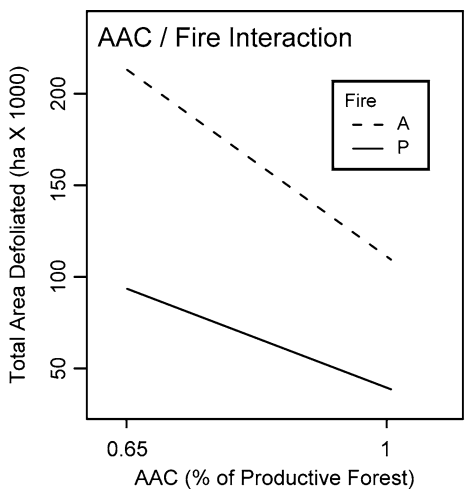

Figure 4. Interactions between fire and AAC on mean *total area defoliated*. End points of the *bars* represent the mean value for *total area defoliated* summarized over 30 replicates. Higher AAC interacts with fire to significantly reduce *total area defoliated* (Table 4). *Dashed lines* indicate the absence of fire (*A*) and *solid lines* indicate presence (*P*).

disturbances are present, scenarios become increasingly associated with fragmented, younger forest.

An interesting result was that the degree of change in age structure due to an increase in AAC is greatest when only logging is included, and barely present when other disturbances were included (Figure 7). When only logging (L) is present, the change in AAC from 0.65 to 1% results in a large shift toward younger forest (that is, from L1a to L2a). However, when SBW and fire are also present this change in AAC (that is, SFL1a to SFL2a) causes a shift in ordination space that is less than half that of logging alone. This reduced movement in ordination space illustrates the constraints that additional disturbances can impose on logging. That is, with more disturbances, the logging model is not able to take advantage of the increase in AAC because of a reduced availability of mature forest. The target AAC would only be met though violation of other logging constraints (that is, minimum harvest age and adjacency). When fire

Table 5. ANOVA Table Summarizing the Main Effects of and Interactions between Logging and Spruce Budworm Defoliation on *Total Area Burned*

Factor	Df	Sum of squares	Mean squares	*F* value	Vr(>*F*)
SBW	1	1206624234.834	1206624234.834	0.346	0.557
AAC	1	178305018114.384	178305018114.384	51.135	**0.000**
Cutblock size	1	2916446862.551	2916446862.551	0.836	0.361
SBW:AAC	1	2136508222.817	2136508222.817	0.613	0.435
SBW:cutblock size	1	1356948637.204	1356948637.204	0.389	0.533
AAC:cutblock size	**1**	1116269100.104	1116269100.104	0.320	0.572
SBW:AAC:cutblock size	1	19177520.026	19177520.026	0.005	0.941
Residuals	232	808970003166.725	3486939668.822		
Total	239	996026995858.645	190543932360.742		

For this analysis and all subsequent ANOVAs, $n = 30$.
Bold values represent $p < 0.001$.

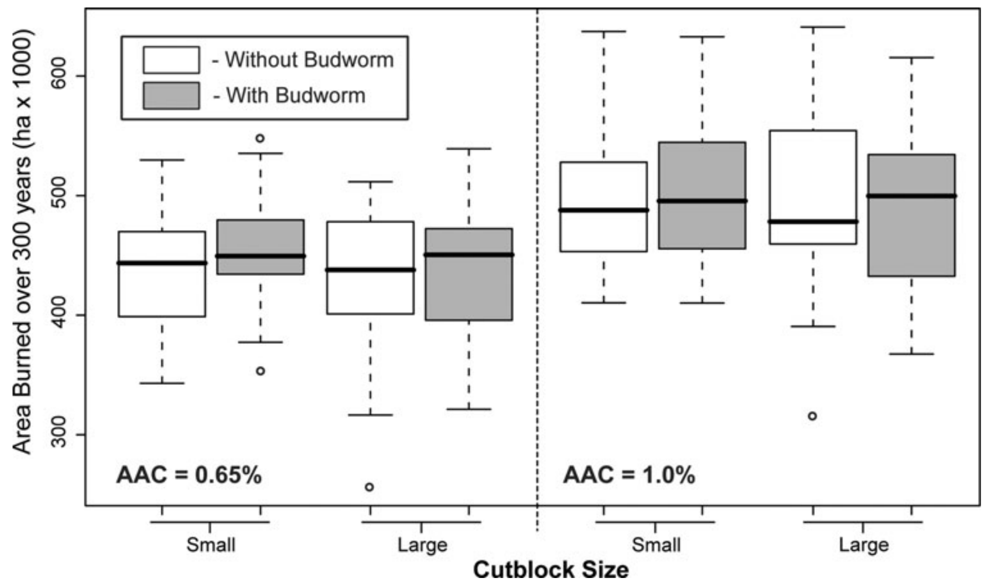

Figure 5. Effects of AAC, cutblock size, and spruce budworm defoliation on *total area burned*. *Bold horizontal bars* represent median total area burned over 30 simulated replicates and *vertical whiskers* represent 1.5 times the interquartile range. Cutblock sizes were specified as uniform distributions between 60 and 80 ha for the ''small'' treatment and between 180 and 200 ha for the ''large'' treatment. AAC percentages describe the annual area cut, expressed as a proportion of the total study area.

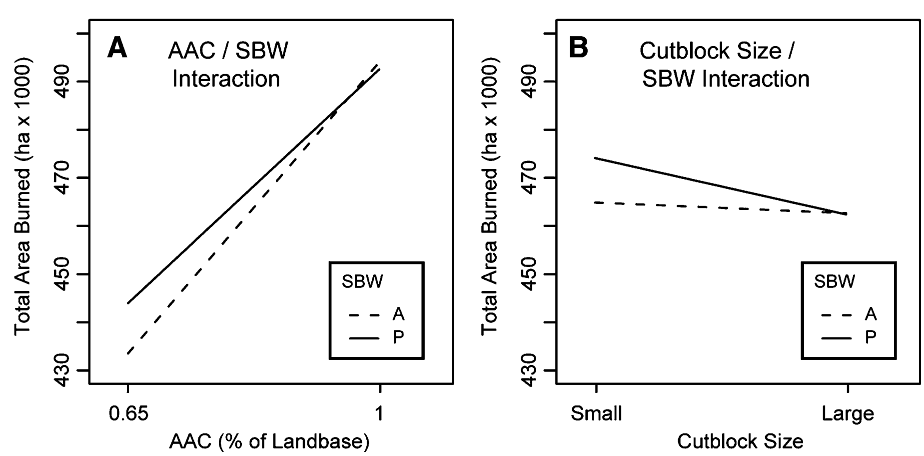

Figure 6. Interaction plot illustrating the effects of fire and logging on *total area burned*. End points of the *bars* represent the mean value for *total area burned* summarized over 30 replicates. Neither interactions depicted were identified as statistically significant (Table 4) but do suggest subtle interaction effects (that is, different slopes) between AAC and SBW (**A**) as well as between cutblock size and SBW (**B**). *Dashed lines* indicate the absence of SBW defoliation (*A*) and *solid lines* indicate SBW presence (*P*).

is included with the highest AAC, no additional changes are observed in spatial age structure due to the addition of SBW (that is, no difference between FL2a and SFL2a). Cutblock size appears to have had little effect on age structure shown by the overlap of ordination points representing scenarios that only differ in cutblock size.

Landscape Pattern—Species

Ordination of species landscape metrics revealed nearly identical groupings as those found for forest age (Figure 8). Here, 56 and 37% of the total variance was captured by the first two axes and both are significant. The first axis represents a

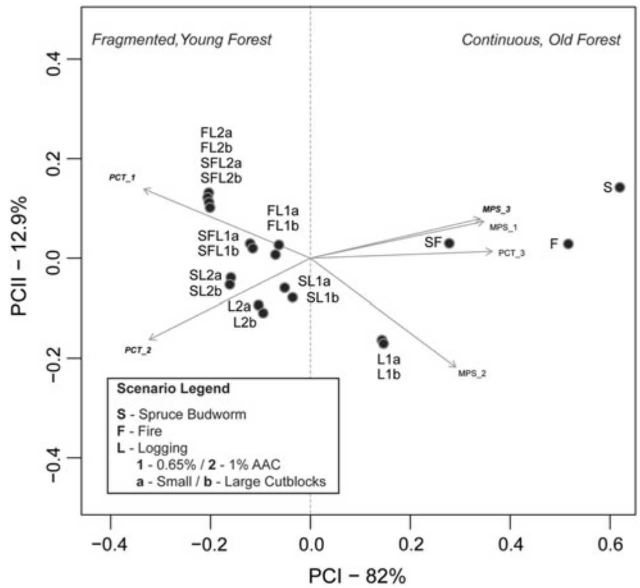

Figure 7. Biplot summarizing principal components analysis (PCA) of the landscape pattern metrics *mean patch size* and *percent of landscape* for forest age classified into three categories: 1—young (0–100 years), 2—intermediate (101–200 years), and 3—old (201+ years). *Points* represent simulation scenarios plotted in ordination space and are labelled according to the convention described in the legend. The broken stick criterion identified only the first (*horizontal*) axis as significant. The percentage of the total variance captured by each axis is indicated in the axis label. Text in the top left and top right denote the gradient associated with this single significant axis. *Arrows* represent factor loadings and labels in *bold* indicate those loadings that are significantly associated with the horizontal axis and were used to interpret the main gradient.

hardwood/mixed-wood—conifer gradient, and the second axis represents a pine—spruce gradient.

More disturbances resulted in greater compositional homogenization of the landscape and conifer dominance, particularly by pine, which reflects the dominance of fire and logging relative to SBW (Figure 8). However, increased disturbance also increased the amount of fir. Scenarios without logging (S, F, and SF) were associated with higher amounts of hardwood (that is, birch and aspen) than conifer, and more pine than spruce. SBW on its own resulted in more hardwood (birch and aspen) due to its relatively infrequent occurrence, host specificity, ability to release non-host trees, and initial mixed forest conditions. Logging on its own resulted in more spruce relative to all other scenarios and more conifers relative to the other scenarios with only one disturbance. Scenarios that combined logging with additional disturbances are also associated with more conifers. SBW and logging scenarios with a low AAC (SL1a and SL1b) are near the boundary between conifer and mixed with a tendency to be dominated by spruce. An increase in AAC moved similar scenarios towards greater conifer dominance. The addition of fire to multiple disturbance scenarios created landscapes more dominated by jack pine. An AAC of 1% had more of an effect than did an AAC of 0.65%. Cutblock size did not affect spatial patterns.

Discussion

Understanding how natural and human disturbances mutually influence forest composition and spatial structure is important to effective and sustainable forest management. Developing this knowledge is challenging because forest disturbances typically do not occur in isolation and are instead connected to previous and future disturbances through spatial legacies in age and composition. In this study, we examined interactions among the three main boreal forest disturbances using a spatially explicit simulation model.

Spruce Budworm Defoliation

As the area affected by fire and logging increases, SBW appears restricted in its access to resources (that is, mature host species). Furthermore, the combined influence of fire and logging is greater than the sum of their individual effects. This result highlights the competition among disturbances for limited resources and is particularly pronounced for SBW due to its specificity and age dependence.

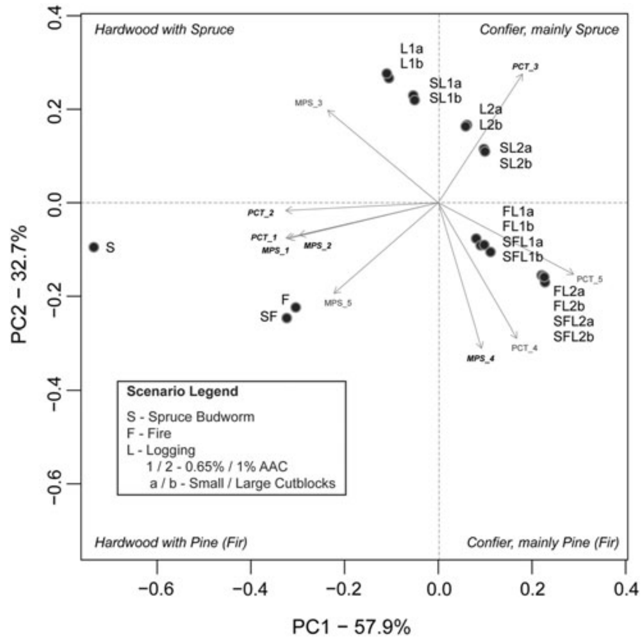

Figure 8. Biplot summarizing principal components analysis (PCA) of the landscape pattern metrics *mean patch size* and *percent of landscape* for forest species composition classified into five categories according to dominant species: 1—birch, 2—aspen, 3—spruce, 4—pine, and 5—fire. Points represent simulation scenarios plotted in ordination space and are labelled according to the convention described in the legend. The broken stick criterion identified both the first and second axes as significant. The percentage of the total variance captured by each axis is indicated in the axis label. Text in the corners of the biplot indicates which species are associated with the different quadrants. *Arrows* represent factor loadings and labels in *bold* indicate those loadings that are significantly associated with the two axis and were used to interpret the main gradients and assign the labels to the four quadrants.

Competition for resources among disturbances is also relevant for forest sustainability as it may become increasingly difficult to meet management objectives when interactions among disturbances create novel and unexpected forest conditions.

As a result of SBW's selectivity, logging affects SBW negatively in the short term, but has the potential to increase it in the long term. Although there may be selection through logging for preferred host species, it is not guaranteed that host sites will reach a susceptible age class and will result in larger outbreaks. In contrast, in the boreal forest fire can respond quickly to changes in forest composition (for example, increased flammability) created by logging because it is relatively age-independent; forest type, and weather are of greater importance than age in determining rate of spread and fires (Forestry Canada Fire Danger Group 1992). This suggests that fire may be less sensitive to spatial legacies than spruce budworm or logging. However, delayed regeneration (Vasiliauskas and Chen 2002) may reduce the rate at which fire can respond to post-disturbance successional trajectories. In this model, we did not specifically simulate regeneration delay but expect that inclusion of such an effect would change the relative rate at which fire can respond to new patterns in forest composition. Nonetheless, the temporal lag between forest alteration and the manifestation of large continuous areas of susceptible SBW host can be several decades and this lag reduces the likelihood of a detectable interaction between SBW and logging because forest conditions can be further altered by disturbance and succession during that time period (Veblen and others 1994).

Manipulation of cutblock size was hypothesized to affect the scale of forest patchiness in host and non-host species and to influence the total area affected by budworm (Miller and Rusnock 1993). Increased proportions of hardwood and other non-host species can reduce the effects of budworm through a reduction of the amount of available foliage, increased rates of parasitism, or a combination of the two (Roland and Taylor 1997; Cappuccino and others 1998; Campbell and others 2008). We coarsely mimicked these effects through a reduction in the rate of defoliation patch spread with greater proportions of non-host. Although the effects of cutblock size on defoliation were not significant (Table 4), our results do suggest that when cutblocks are small or there is a lower rate of harvesting, defoliation may increase area burned because defoliated sites are more flammable (Figure 6). An increased availability of SBW host accompanies a less intense management regime and may translate into larger continuous areas of defoliated sites with associated increased flammability. Similarly, we expect that a longer fire return interval will increase the availability of SBW host and hence increase defoliation risk.

Although we varied cutblock size, we did not see a response in forest patchiness in age or species (Figures 7, 8). This is important because unless the cutblock size has a direct and lasting effect on the spatial scale of forest structure, it seems unlikely that forest management will influence defoliator dynamics. However, it is possible that due to spatial constraints on the landscape, adjacent small patches behaved as though they were singular large patches and obscured local fine-scale patchiness. The coarse resolution at which forest age was classified may also have obscured these patterns. Furthermore, forest succession operates on a pixel by pixel basis in the VLM where each cell is assigned a successional trajectory following disturbance. Even though the composition of neighboring cells influences the successional trajectories, the stochastic assignment results in a heterogeneous forest that may obscure legacies in species composition. Our results are indeed influenced by these aspects of the succession sub-model and also by our assumptions regarding the consequences of forest management on forest composition. Further study will involve refining the spatial response of forest succession.

Biologically, there are many fine-scale factors that determine patterns of forest mortality and morbidity that are not included in this model. One of the most important is the complex food web of predators and parasitoids associated with the SBW (Eveleigh and others 2007). Multi-trophic population and community level dynamics were not modelled although local SBW population dynamics can be potentially coupled with predator and parasitoid responses to changes in forest structure (Roland and Taylor 1997). Additional factors such as stochastic variation in weather (Royama and others 2005), the timing of variation in weather (Veblen and others 1994), and lengthening fires cycles (Bouchard and Pothier 2008) have also been implicated in the supposed increases in outbreak extent in the twentieth century and were not modelled here. The inclusion of these factors may produce different results and represent a limitation of the current model. However, whether a change in outbreak dynamics has occurred and the cause of such changes, if present, remains controversial (Fleming 2000; Royama and others 2005). A central challenge to understanding these complex interactions and the degree to which human activity has influenced SBW outbreaks is the different spatial and temporal scales at which these processes operate and represent worthwhile future modelling challenges.

Fire

Total area burned increased with an increased AAC (Figure 5) but was not affected by SBW, as we hypothesized. These results were unexpected for two reasons. First, logging was expected to reduce area burned through reduction of age and removal of fuels. However, because rate of spread and fire intensity in this system are determined through the interaction between composition and weather conditions (ISI), and not age (Johnson 1992), the increase in coniferous fuels with greater AAC (Figure 8) resulted in increased flammability and significantly more area burned. In this way, the effects of fire and management were additive, and not compensatory (Didion and others 2007). The increase in coniferous forest in response to logging reflects our model assumptions regarding silviculture following logging. That is, dominant coniferous species that were removed are often replanted and fir and aspen only establish if present before logging. With these assumptions, forest composition over time is strongly influenced by the legacies of initial conditions which included 19% jack pine and 23% spruce, both of which represent highly flammable fuel classes (Forestry Canada Fire Danger Group 1992).

This increase in flammability is highly contingent on our assumptions regarding species recruitment following logging. Indeed, it has been shown that fir and aspen tend to increase following logging more frequently than following fire (Carleton and MacLellan 1994). We tried to capture this effect through priority colonization of post-logged stands by fir and aspen if they were present prior to the disturbance. However, given initial forest conditions and our assumptions regarding silviculture, this approach may underestimate the probability of colonization by fir and aspen. Similarly, our finding that logging did not lead to increases in the extent of SBW defoliation may be a result of our simplified succession model and reduced colonization by host fir.

The second way that these results were unexpected was that the presence of SBW did not increase area burned. Although median area burned was slightly higher with SBW in all cases (Figure 5), these increases were not significant. Defoliation effects on fire risk have been shown to last for at most 15 years following defoliation (Stocks 1987; Fleming and others 2002). The ephemeral nature of increased fire risk due to budworm damage combined with the infrequency of budworm outbreaks relative to fire (every 35 years vs. every year) may explain why no signal was detected for the interaction between insects and fire over the entire 300-year simulation horizon. Finer-scale analyses such as examination of fire sizes in regions recently defoliated or correlating time series of fire sizes and budworm defoliation could help reveal transient effects of and interactions among disturbances that are obscured by other events and patterns that accrue over time. It is important to note that our results are dependent on our assumptions regarding outbreaks and their effects and that uncertain climatic conditions and local variability may influence both the frequency of outbreaks and the length of time that SBW killed forests represent an increased fire risk. Developing more region and context-specific models of budworm–fire interactions will be very useful to further refining our understanding of these dynamics.

The amount of logging, represented as AAC, had different effects on fire than it did on SBW. Through its effect on species composition, logging creates more flammable forests (Figures 6, 8). With regards to budworm, although logging encourages a greater proportion of vulnerable species (Figure 8), it also reduces forest age (Figure 7), which has the net effect of reducing forest vulnerability to budworm (Figure 3). This highlights the important differences between disturbances that are relatively selective agents of ''creative destruction'' such as the SBW (Cooke and others 2007) and those that are relatively indiscriminate, such as fire.

Model Considerations

Several simplifying assumptions were made in this simulation study. The challenge of integrating multiple disturbances and succession processes into a single spatial simulation model requires some sacrifice of realism. As such, simulation outputs should be regarded as the consequence of interactions among assumptions, hypotheses, and initial conditions rather than an attempt to predict the future state of the forest (Baker 1992). The forest patterns that were simulated reflect interactions among simplified models of forest disturbance and demonstrate the potential long-term consequences of these assumptions and the importance of landscape-scale spatial legacies to forest dynamics and sustainability.

The results of this study also depend strongly on the forest succession sub-model and the successional trajectories derived from forest inventory data. A major challenge to using these trajectories in combination with multiple disturbances is a lack of differentiation among causes of stand initiation in the original data used to construct the semi-Markov transition model. To include unique forest responses to different disturbances, we made several assumptions regarding initial composition following logging and SBW outbreaks based on what was possible and logical given the scale of the model (Table 2). Different frameworks for immediate post-disturbance succession could produce different qualitative results using this model and will be investigated in the future. Additionally, because our model of forest succession is not process-based (as in LANDIS-II; Scheller and Mladenoff 2007) the model is constrained by original forest inventory data, and important rare transitions may not be included. Nonetheless, a broad range of possible trajectories are simulated. In general, the response of large-scale vegetation patterns to different disturbances in boreal forests is complex and highly variable (Schroeder and Perera 2002). Additional empirical information on post-disturbance succession would improve the reliability of landscape level forest succession models such as the VLM, whereas future analysis could further explore the sensitivity of model results to post-disturbance regeneration parameters.

Conclusions

In this research, we examined the dynamic feedbacks among three dominant boreal forest disturbances in a spatially explicit context. Many challenges remain to understanding the interactions among multiple disturbances, their spatial legacies, and forest succession. Several hypothesized effects of logging on natural disturbances were not observed, including the influence of forest management on the extent of spruce budworm defoliation. However, for both fire and spruce budworm it remains possible that although global differences were not detected, spatially and temporally localized consequences of different management strategies over short time periods may still be relevant to timber production and biodiversity conservation and require further investigation. Uncertainty in model parameters, modelling assumptions, and the varying scales of the different disturbances simulated represent important challenges to modelling these spatial processes and their interactions.

Contrary to expectation, forest management had a greater influence on fire than on spruce budworm, at least at coarse spatial and temporal scales. The differences in response to management depend on the relative specificities of these two disturbances in the boreal forest; fire is frequent and relatively age-independent, whereas spruce budworm is infrequent, highly selective, and age-dependent. The potentially ephemeral nature of disturbance legacies relative to the periodicity of SBW outbreaks (for example, once every 35 years) may account for the lack of observed increases in outbreak extent in response to management. If, as hypothesized, forest management affects SBW outbreak dynamics, we would expect to see more links among changes in forest structure, host availability, and area defoliated. This study emphasizes that spatial disturbance legacies do not influence all disturbances equally, that legacies in age and composition may affect forest dynamics differently, and that spatial management legacies may not persist indefinitely, especially when multiple disturbances are present.

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