

Article

Ecoregional Patterns of Spruce Budworm—Wildfire Interactions in Central Canada's Forests

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Abstract: Wildfires and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), are the two dominant natural disturbances in Canada's boreal forest. While both disturbances have specific impacts on forest ecosystems, it is increasingly recognized that their interactions also have the potential for non-linear behavior and long-lasting legacies on forest ecosystems' structures and functions. Previously, we showed that, in central Canada, fires occurred with a disproportionately higher frequency during a 'window of opportunity' following spruce budworm defoliation. In this study, we use Ontario's spatial databases for large fires and spruce budworm defoliation to locate where these two disturbances likely interacted. Classification tree and Random Forest procedures were then applied to find how spruce budworm defoliation history, climate, and forest conditions best predict the location of such budworm–fire interactions. Results indicate that such interactions likely occurred in areas geographically bound by hardwood content in the south, the prevalence of the three major spruce budworm host species (balsam fir, white spruce and black spruce) in the north, and climate moisture in the west. The occurrence of a spruce budworm–fire interaction inside these boundaries is related to the frequency of spruce budworm defoliation. These patterns provide a means of distinguishing regions where spruce budworm attacks are likely to increase fire risk.

Keywords: spruce budworm defoliation; forest fire; disturbance interactions; forest composition; weather

1. Introduction

Historically, two main types of natural disturbances have dominated Canada's boreal forest: wildfire and outbreaks of spruce budworm (SBW), *Choristoneura fumiferana* (Clem.) [1,2]. While each type has specific impacts on forest composition and dynamics, biogeochemical cycling and numerous ecological processes, there is an increasing recognition that the interaction of these types of disturbance can also have dramatic long-term effects on the ecosystem's structure and functioning [3,4].

As climate change is expected to affect both types of disturbance regimes (e.g., [5,6]), understanding their interactions will also be critical for appropriate risk-assessment and management planning in the future. In the simplest and most direct form of these interactions, a warmer, drier climate is expected to increase the tendency of SBW-killed stands to burn [7]. This effect would likely be magnified by the fact that the spatial extent of SBW outbreaks, and thus the availability of SBW-attacked stands, already much greater than the extent of fires [2], may increase with climate change [5].

When considered together, these factors suggest that in a drier, warmer climate, the boreal forest may experience accelerated carbon releases due to the interaction of SBW and wildfire disturbance regimes. Indeed, recent carbon budget studies have shown that climate change-induced modifications of disturbance regimes have critical impacts on the net atmospheric carbon exchange [8,9].

The idea that SBW-damaged stands represent an increased risk of wildfire has long been based on anecdotal observations of severe forest fires occurring shortly after SBW outbreaks (e.g., [10–13]).

The first attempt to examine empirical evidence of an interaction between SBW defoliation and fire was carried out through a series of experimental burns in northern Ontario from 1976 to 1982 [14,15]. Although the number of experimental plots successfully burnt was low ($n = 5$) and no control plots were established, the results suggested that the abundance of ‘ladder fuels’ could make SBW-killed stands an extreme fire risk [14,15]. ‘Ladder fuels’ are dead and broken treetops and branches that became snagged and entangled by other branches before falling completely to the ground. These ‘ladder fuels’ present a vertical structure that increases the risk of conducting relatively harmless surface fires up into the crown where the fires can become much more dangerous. In practice, wildfire risk assessment uses a separate class of fuel types for SBW-killed conifers (i.e., M3 and M4: Dead Balsam Fir Mixedwood, leafless and Green respectively [7]). The presence of this class testifies to the importance of the relation between SBW damage and the risk of wildfire for fire managers, but the calculation of risk is still based almost entirely on the results from Stocks’ single experiment.

Following Stocks’ experiment, Péché [16] conducted a long-term monitoring of fuel distribution in plots affected by extensive spruce budworm defoliation in Cape Breton (Nova Scotia). The study showed that, despite heavy mortality, there was no accumulation of fine fuels, and fuel loadings were decreasing after the outbreak except for the larger, less flammable, size class. The risk of fire was further decreased by the proliferation of new growth quickly after the stand was opened. Differences between Stocks [14,15] and Péché’s [16] results were attributed to cooler, wetter weather in Cape Breton compared to Ontario that would accelerate the decomposition of spruce budworm-related fuels and decrease the overall fire risk. The comparison of these studies highlighted the importance of local conditions in mediating the influence of insect damage on subsequent fire risk.

Later, a statistical analysis of the spatio-temporal patterns of spruce budworm defoliation and large (i.e., crown) wildfires in Ontario [17] revealed that, within the area defoliated at least once by spruce budworm since 1941, (1) areas that suffered moderate frequencies of defoliation (9–11 years) were the most likely to be burnt; (2) large fires ($>2 \text{ km}^2$) rarely occur shortly before defoliation (presumably because spruce budworm populations cannot reach outbreak level in burnt stands); (3) large fires tended to occur disproportionately more often during a ‘window of opportunity’ of 3–9 years after a spruce budworm outbreak. Fleming et al. [17] hypothesized that this ‘window of opportunity’ was related to the accumulation of ‘ladder fuel’ from the breakage of SBW-killed top trees and windthrow of SBW-killed trees. To test this hypothesis, Watt [18] investigated differences in the vertical fuel structure of boreal mixedwood stands that suffered varying durations of SBW defoliation. The results of this investigation show that vertical fuel continuity (i.e., “ladder fuel”) increases with the duration of continuous defoliation. Using his estimates of stand fuel characteristics in a crown fire model, Watt was then able to demonstrate how the potential for surface fires to reach the canopy and become crown fires increases with the duration of SBW defoliation. More recently, in a landscape-scale analysis of SBW–fire interaction in Central Canada, James et al. [19] found that lagged cumulative defoliation increased the risk of fire ignition, thus supporting further Fleming et al.’s [17] conceptual model.

The notion of “window of opportunity” is a key component of Fleming et al.’s [17] model. In their analysis, they found that the timing and the duration of this time window both vary geographically, presumably because regional biogeographical factors affect fuel dynamics after defoliation. James et al. [19] reached the same conclusion. More specifically, regional differences in the lag between the end of the defoliation and the start of the “window of opportunity” are thought to be related to the varying speeds at which SBW-killed trees break down depending on weather and forest composition while the end of the “window of opportunity” (i.e., a reduction of the fire risk to each pre-defoliation level) might be more related to decomposition of the accumulated fine fuel and the ‘greening up’ of the understory as herbaceous plants and suppressed trees fill in the opening created in the stand by SBW defoliation.

In this paper, we expand on the analyses of Fleming et al. [17] and James et al. [19] by examining how the timing and duration of the “window of opportunity” vary over the landscape as a function of factors related to insect damage history, climate, and fire.

2. Data and Methods

Our study area covers a latitudinal belt that spans across the province of Ontario between the 45th and 52nd parallels. The area corresponds to an updated version of what Candau et al. [20] referred to as the ‘defoliation belt’, i.e., the area within which moderate to severe SBW defoliation occurred at least once between 1941 and 2005. Large-scale, spatially explicit data of historical SBW defoliation, large fires (>2 km²), forest composition and climate were compiled for the entire study area. Since 2005, SBW defoliation in Central Canada has been limited to small areas and sporadic but historical patterns suggest that a new outbreak is to be expected in the next few years [20]. All the data were entered into a Geographic Information System (GIS) and transformed into a 10-km grid before analysis. Once areas covering large lakes and those with missing data were removed, the remaining study area covered 386×10^3 km².

2.1. Spruce Budworm Defoliation Data

The Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service conducted aerial reconnaissance of large-scale defoliation events throughout Ontario’s productive, exploitable forest from 1941 to 2005. Each year, survey flights are organized as soon as the current season’s defoliation is completed, usually in mid- to late-July. In the aircraft, areas within which defoliation has occurred are sketched on 1:125,000 or 1:250,000 maps [21]. For each area, the level of defoliation is recorded as light, moderate or severe, based on the percentage of new foliage lost (0–25%, 26–75%, 76–100%, respectively). All the maps collected one year were later compiled and transferred to smaller scale maps (e.g., 1:600,000). In the early 1990s, annual maps of defoliation since 1941 were digitized and stored into a spatial database. Since then, areas sketched on 1:125,000 or 1:250,000 maps are directly digitized and stored in the database. Records of light defoliation are often considered relatively unreliable [21,22], so only records of moderate and severe defoliation were included in the present analyses.

The map of the frequency of defoliation by spruce budworm converted to a 10-km grid (Figure 1A) shows the patterns reported in Candau et al. [20]: areas defoliated at least one year during the period 1941–2005 extend over a continuous east–west ‘defoliation belt’ divided into three zones centered around ‘hot spots’ of frequent defoliation which are separated longitudinally by two corridors where defoliation is less frequent. In a previous study, Candau and Fleming [23] showed that areas of high defoliation frequency were associated with dry Junes and cool springs. Conversely, low frequencies were associated with cold winters in the north and a low abundance of host species in the south.

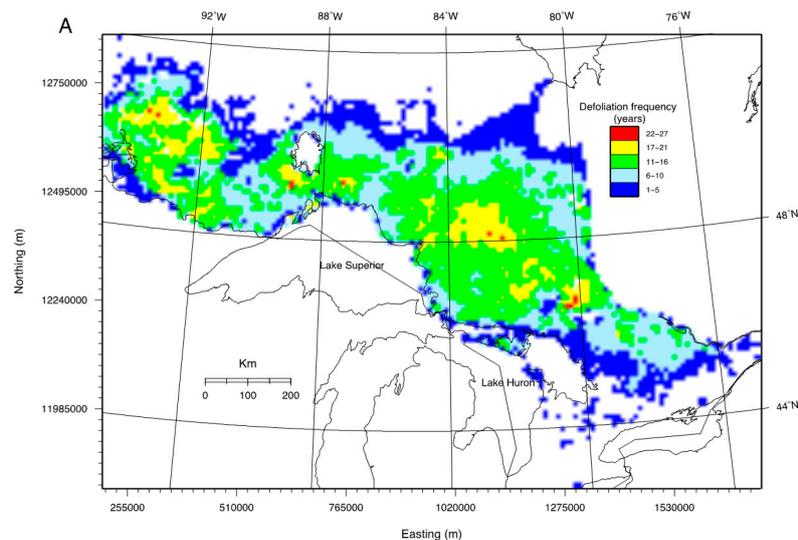


Figure 1. Cont.

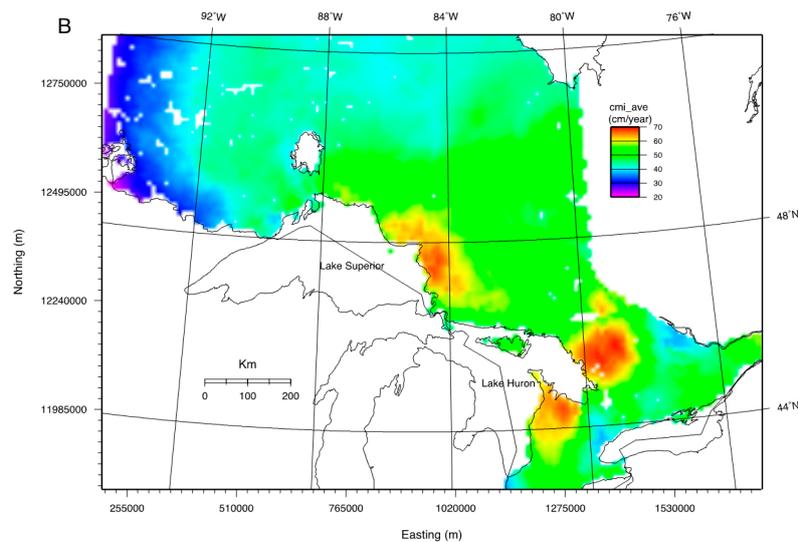


Figure 1. (A) Frequency (number of years) of moderate to severe defoliation by spruce budworm between 1941 and 2005 on a 10-km grid; (B) Average climate moisture index (cm/year) between 1 November and 31 October on a 10-km grid from 1941 to 2003. (See text for calculating algorithm).

2.2. Fire Data

Fire data were extracted from the same spatial database used in Fleming et al. [17] updated to 2005. Two different sources were used to compile fire data. B.J. Stocks (Canadian Forest Service) provided records extracted from microfiche compiled by the Ontario Ministry of Natural Resources for the period 1941–1979. The rest of the records (i.e., for fires from 1980 to 2005) were extracted from an updated version of the Canadian Large Fire Database [24]. Although the database contains less than 5% of fires reported in Canada, these large fires account for more than 97% of the area burned and thus represent the vast majority of the fire impacts [24].

Independently of their origin, fire polygons included in the final database are fire perimeters mapped from aerial photography, satellite imagery, and aircraft observation (more recently using global positioning system units). Indeed, although most large fires leave unburned islands [25], only a small percentage of the polygons have this information [26], as only the outside perimeter was mapped for most of the fires. Fire data accuracy has likely improved through time, as recent technological developments facilitate mapping and increase accuracy. The area where fires were recorded has probably varied considerably between 1941–2005 with new areas being monitored, particularly in the north of the province. However, most of these areas are located north of the spruce budworm ‘defoliation belt’ so they were excluded in our analyses.

Previously, Fleming et al. [17] showed that, inside the spruce budworm defoliation belt, large fires occurred disproportionately more often during a period of a few years after a spruce budworm outbreak. This period of time, hereafter called the spruce budworm–fire interaction period (or SFIP), during which fire probability increases in areas previously defoliated does not occur immediately after the defoliation ends but with a delay of a few years. Therefore, SFIPs can be characterized by their duration and by the delay between the end of the outbreak (defined as the last year of moderate–severe defoliation there) and the onset of the SFIP. Both the duration and the delay of the SFIP, varied geographically. In the eastern part of the defoliation belt, the SFIP occurs between 3 and 6 years after an outbreak; in the western part of the defoliation belt, it occurs between 6 and 16 years after an outbreak; in the central part, it occurs between 4 and 9 years.

In this paper, we use both spatial and temporal conditions to define a ‘likely interaction’ between spruce budworm defoliation and a large fire. First, there must be geographical overlap between the fire and defoliation. Second, the fire must have occurred within the SFIP for the region of concern.

The spruce budworm defoliation and fire spatial databases were merged so every fire could be assessed against these two conditions. Fires that met both conditions were classified as ‘likely interaction’. Clearly, this classification system has shortcomings. A fire falling within the SFIP may have occurred regardless of any previous defoliation. On the other hand, a fire occurring after the SFIP finished may have been promoted by longer-term effects of defoliation than were recognized by Fleming et al. [17]. A fire starting inside (or outside) a defoliated area may have spread widely in a non-defoliated (or defoliated) area. Perhaps, without starting where it did, no fire would have occurred at all. Perhaps there were special conditions (e.g., previous defoliation) that allowed the fire to spread as well as it did. The problem is that even with ‘boots on the ground’ it is often extremely difficult to distinguish between these possibilities. Consequently, we view our approach to defining a ‘likely interaction’ as a practical compromise, which is not without difficulties. The opposite interaction (of fire affecting the likelihood of subsequent spruce budworm defoliation) has received more attention [17,27–29].

Several hypotheses have been proposed to explain the spatial variation in the timing and duration of SFIPs. In particular, forest composition and climate may play an important role by affecting the decomposition rate of surface fuel and the duration of vertical continuity of ‘ladder fuel’ after a spruce budworm outbreak.

2.3. Forest Data

Forest composition has been found to affect the distribution of spruce budworm defoliation [23] and fire hazard [30] and was thus considered as a potential factor in explaining the location of spruce budworm–fire interactions. The northern part of the study area is part of the Boreal forest region, dominated by conifer (mainly spruce, jack pine and fir), while the southern part is in the Great Lakes—St Lawrence region, dominated by hardwoods (mainly tolerant hardwoods, birch, poplar). Forest data were extracted from the forest resource inventory (FRI) conducted by the Ontario Ministry of Natural Resources [31]. In the FRI, forest characteristics are determined at the stand level with a combination of aerial photo interpretation and ground surveys. We used a large-scale version of the inventory summarized over grid cells varying in size between 5×5 km and 20×20 km. For each grid cell, the data include the percentage of the total basal area of balsam fir and white spruce (i.e., ‘FbSw’), and of balsam fir, white spruce and black spruce (i.e., ‘FbSwSb’), and hardwood (i.e., ‘hw’). FbSw accounts for the tree species (balsam fir and white spruce) on which spruce budworm feeds primarily, while FbSwSb covers all major hosts in Ontario. Hardwood content was included as it may affect fire behavior [30]. Forest resource inventory data are not available in the northernmost part of the province, but aerially visible defoliation is quite rare there (G. Howse, personal communication). For this study, we used the earliest large-scale Ontario forest inventory available on GIS. This inventory was compiled in 1996 [31] from data acquired between 1988 and 1992. Although, at the stand level, forest composition has likely changed during the 65 years of the study, we assumed that at the large scale, low resolution of our study, the relative proportions of each broad forest type remained relatively stable.

2.4. Climate Data

The historical climate data are spatial interpolations of monthly minimums and maximums for temperature ($^{\circ}\text{C}$) and precipitation (mm) from 471 meteorological stations across Ontario, eastern Manitoba, and western Quebec, over the period 1901–2000 [32] updated with data from 2001 to 2003.

These data were used to calculate a climate moisture index (cmi) according to the algorithm published by Hogg [33] modified to replace $T_{\text{dew}} = T_{\text{min}} - 2.5$ $^{\circ}\text{C}$ with $T_{\text{dew}} = T_{\text{min}}$ (T_{dew} is the mean dew point temperature and T_{min} the mean daily minimum temperature) to take into account moister conditions in Ontario than in Alberta (E. Hogg, personal communication).

Annual CMI were calculated from 1941 to 2003 for years starting 1 November and ending 31 October [i.e., $\text{CMI}(\text{year}) = \sum \text{CMI}(m)$, $m = \text{Nov}(\text{year} - 1) - \text{Oct}(\text{year})$]. This division of months into years follows Girardin et al. [34] and highlights how annual moisture fluctuations relate to the seasonal fire cycle.

The average of the annual CMI (*cmi_ave*) was then calculated over the period 1941–2003 for each cell of a 10-km grid. Based on this variable, the province is clearly partitioned into a dryer (*cmi_ave* < 40 cm/year) zone in the West along the Manitoba border, wet (*cmi_ave* > 60 cm/year) areas along the eastern shores of Lakes Huron and Superior and average areas in the north and northeast (Figure 1B).

2.5. Classification Tree (CART) Analysis

We used classification trees (CART, [35]) to model how climate, forest composition and spruce budworm defoliation history affect wildfire potential. Such models belong to the classification and regression tree family of analysis methods. Compared to classical methods for predictive modelling (e.g., Generalized Linear Models), CART models do not require the restrictive assumptions of (a) Gaussian relations between response and predictor variables; (b) uniform effects of predictors and their interactions on the response over their range of values; and (c) constant interactions among predictors over their range of values. Classification trees also have several advantages over linear discriminant and multiple regression analyses. They can capture non-linear and non-additive behavior, as well as general interactions among predictors, such as when relationships between a response variable and certain predictors are conditional on the values of other predictors. Classification trees can also accommodate both continuous and categorical predictor variables without transformation.

Classification trees can be unstable in the variables retained, in their branching patterns, and in the values of their split points. In this sense, a particular classification tree is but one realization of an ensemble of possible trees and the issue then centers on how well this particular classification tree represents the ensemble. To address this question, we assessed the robustness of this classification tree against each possible source of variation and verified that it was representative of the general relation between the predictor and the response variables.

The first source of instability stems from the fact that the pruning procedure used to reduce the size of a classification tree is based on a 10-fold cross-validation. The cross-validation algorithm separates the original data set into 10 mutually exclusive random subsets and then uses each subset once to independently calculate a cross-validation relative error for the subtrees grown on the 9 remaining subsets. The algorithm uses the cross-validation error to determine at which level (i.e., split) the pruning is performed. Different random samples taken during the cross-validation procedure could produce classification trees of different sizes (but with the same split variables and values up the point of pruning) because the procedure is based on samples drawn randomly from the dataset. We performed 50 independent pruning procedures on the classification tree described above to test the stability of classification tree size after pruning.

The second source of instability, i.e., multicollinearity in explanatory variables, often produces misleading coefficients in linear or nonlinear regressions [36]. One common approach to dealing with multicollinearity is to drop collinear explanatory variables from the analysis but in CART this approach reduces efficiency in finding the best explanatory variable at each split. For this reason, we did not drop collinear explanatory variables. Instead, we verified how representative the variables included in the model were by testing their importance with the randomForest procedure [37,38]. In this procedure, classification trees are constructed using different random subsamples of the originally selected pixels used to build the original tree. At each split, the randomForest procedure finds the best split possible that can be found among the randomly chosen subset of explanatory variables that are available. We constructed 500 classification trees, with two explanatory variables randomly chosen at each split. The importance of each explanatory variable was estimated as the mean decrease in accuracy in the test sample (the 10% of the data held back for testing the classification tree) when data for only that variable are randomized. The random selection of explanatory variables in each classification tree of the randomForest alleviates the instability related to multicollinearity.

Using a different random sample of cells from the dataset might produce different classification trees. To test the stability of our results over variation in the cells sampled, we used a resampling

process which involved drawing 50 random samples from the original grids (Figure 1) and then fitting a classification tree and a randomForest to each of these samples. This allowed us to build distributions of the various classification tree ‘characteristics’ (e.g., misclassification error rates, number of terminal leaves after pruning, the explanatory variables used in the splits) and variable importance rankings as measured by the mean decrease in accuracy in the randomForests procedure.

We also assessed the spatial variability among the areas of likely spruce budworm–fire interaction that were predicted by the classification trees built on the 50 random samples. We used each of these 50 classification trees to predict areas of likely spruce budworm–fire interaction. The probability of spruce budworm–fire interaction was calculated based on the 50 predictions for each 10-km grid cell.

3. Results

3.1. Locating Where Spruce Budworm Defoliation Contributed to Fire Potential

We began by distinguishing the bioclimatic conditions in the areas of the spruce budworm belt where a ‘likely interaction’ (as defined above) between spruce budworm defoliation and a large fire occurred, from those areas of the belt where there was no ‘likely interaction’. These latter areas may have never been burnt, or large fires may have occurred there but not during the SFIP. ‘Likely interactions’ occurred in 450 of the 3865 cells used to map the spruce budworm belt on a 10-km resolution grid (Figure 2). Unbalanced samples can affect the performance of CART models, particularly in the prediction of the minority class, which is of particular importance in this analysis. For this reason, we re-balanced the sample by keeping all the observations of the minority class (i.e., 450 cells of ‘likely interactions’) and randomly sampling (without replacement) an equivalent number of cells with no ‘likely interactions’.

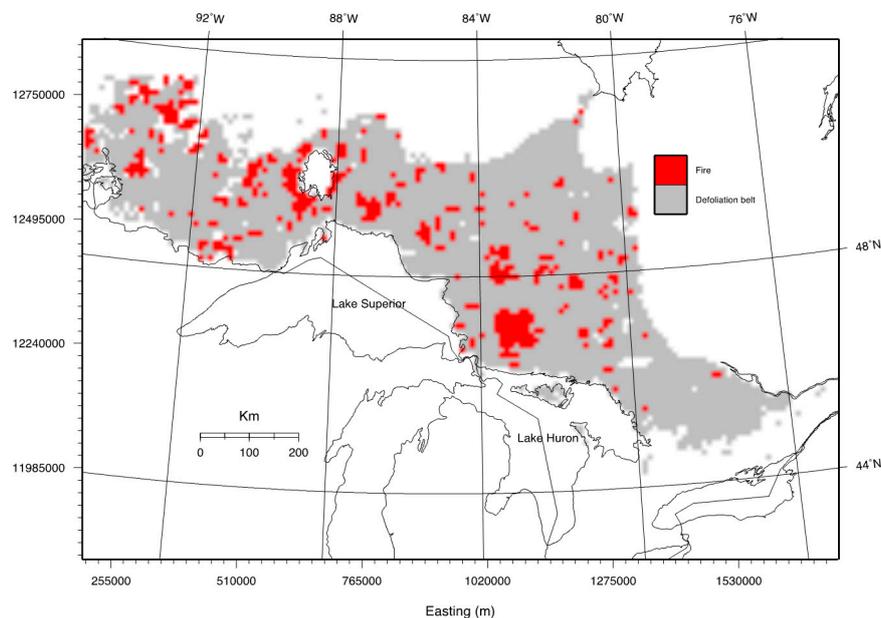


Figure 2. ‘Likely interactions’ (in red) of spruce budworm defoliation and large (>2 km²) fires in the spruce budworm belt (gray) mapped on a 10-km grid for 1941–2005.

The classification tree used to distinguish areas of the defoliation belt with ‘likely interactions’ from those areas without is shown in Figure 3. Four bioclimatic variables were retained: the percentage of the total basal area contributed by hardwood species (hw), and by balsam fir, white spruce and black spruce combined (fbswsb), the average climate moisture index (cmi_ave), and the frequency of defoliation (sbwfreq).

The classification tree has six leaves (colored circles numbered 1–6 from left to right) and an overall rate of correct classification of 69.2%. The number ‘1’ directly under the circles for leaves 5 (red) and 6 (brown) indicates the presence of ‘likely interactions’ between spruce budworm defoliation and large fires. Working down from the top of the classification tree (Figure 3) toward these leaves reveals the predicted conditions for these interactions. Areas where such interaction likely occurred are characterized by a mix of tree species according to the top two splits in Figure 3 (total basal area was less than 54.4% hardwood (highest split) but also less than 77.6% of the spruce budworm’s host species in Ontario (balsam fir, white spruce and black spruce)). The third split ($\text{cmi_ave} > 33.2$) eliminates roughly 4% of the driest remaining areas from further consideration as locations where ‘likely interaction’ occurred. The fourth split, leads to leaf 6 (brown) suggesting that one condition for ‘likely interaction’ in the spruce budworm belt was moderate climate moisture ($33.2 < \text{cmi_ave} < 45.1$). The fifth split leads to leaf 5 (red) which suggests that likely spruce budworm–fire interaction also tended to occur in moist areas ($\text{cmi_ave} > 45.1$) which had experienced at least 8 years of defoliation from 1941 to 2003.

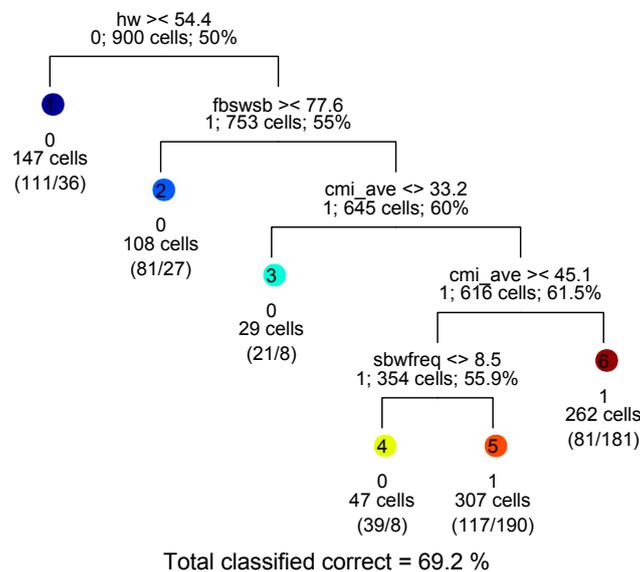


Figure 3. Classification tree of the presence (1) or absence (0) of ‘likely interaction’ between large fires and spruce budworm defoliation in Ontario’s spruce budworm belt (Figure 1A) from 1941 to 2005. Five splits (horizontal bars) and six leaves (circles numbered 1–6 from left to right) are shown. A variable is shown above each bar followed by the two inequality signs, ‘>’ and ‘<’. The inequality sign on the left (right) applies to the left (right) end of the bar. The variables are the number of years of moderate–severe defoliation (sbwfreq), the average climate moisture index (cmi_ave), the percentage of the total basal area that is hardwood (hw) or balsam fir, white spruce and black spruce combined (fbswsb). The ‘0’ or ‘1’ directly below the circle at each leaf and leading the second line above each bar indicate whether the previous split classified this group of cells as having conditions conducive to the presence (1) or absence (0) of interaction. The ‘0’ or ‘1’ is followed by the group size (# cells) and then, for the bars, the correct classification %, and for leaves, parentheses enclosing the numbers of cells where absence/presence [of a “likely interaction”] is predicted. See text for further explanation.

Misclassification error rates can be calculated for each leaf using the two numbers there (Figure 3) in parentheses (number of cells where absence/presence (of a ‘likely interaction’) is predicted). The misclassification error inside the terminal leaves is generally higher in the leaves predicting a ‘likely interaction’ between spruce budworm defoliation and fire (38.1% in leaf 5 and 30.9% in leaf 6) than in the leaves predicting no interaction (from 17.0% in leaf 4 to 25.5% in leaf 3).

Figure 4 maps the unique area defined by each leaf of the classification tree (Figure 3). Leaves 1 and 2 respectively demark areas with high content of either hardwood or Ontario’s spruce budworm

host trees (balsam fir, white spruce and black spruce). These areas largely define the southern and northern boundaries of spruce budworm defoliation, respectively, particularly in the eastern part of the province. The areas defined by these two splits are also characterized by a low frequency of defoliation (Figure 1A). The third leaf identifies the dry western edge of the defoliation belt where the climate moisture index is lowest. The boundary between this western edge and the rest of the defoliation belt is closely associated with a gradient in the climate moisture index (Figure 1B). Leaf 4 defines a scattered group of moist areas that experienced relatively little defoliation from 1941 to 2005. Leaf 5 accounts for the largest area in Figure 4. It is moist and has at least 9 years of moderate–severe defoliation in its 1941–2005 history. Spatially, leaf 6 identifies a largely contiguous area of moderate climate moisture in the western part of the defoliation belt. Defoliation history does not factor in delimiting leaf 6. The classification tree suggests that the areas defined by leaves 5 and 6 were conducive to spruce budworm–fire interaction.

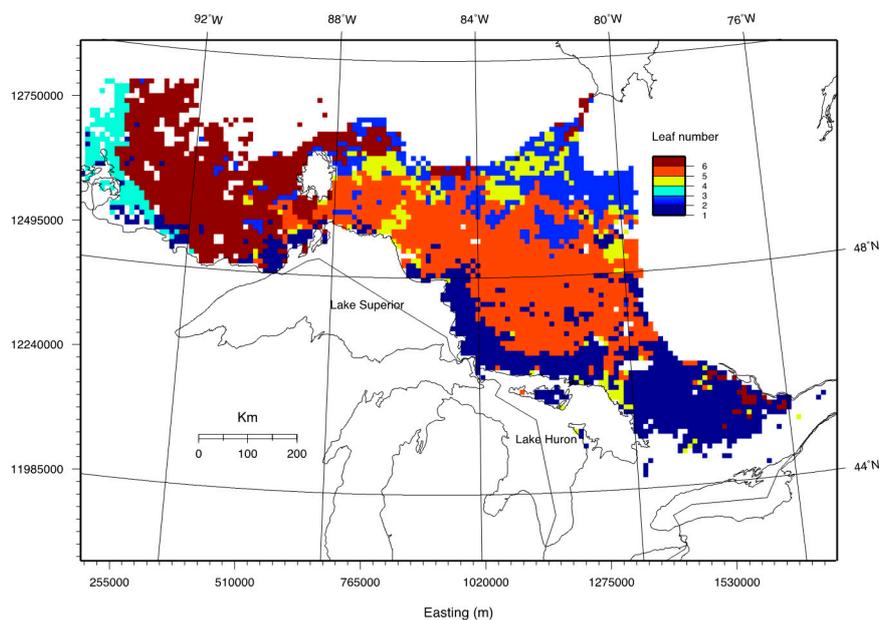


Figure 4. Areas uniquely associated with each leaf of the classification tree in Figure 3.

3.2. Error Analysis

The representiveness of the classification tree in Figure 3 was assessed against three sources of instability. To test for variations in tree size after pruning, 50 independent pruning procedures were performed. The final 50 classification trees ranged in size from 6 to 14 leaves with 6 being the most common (i.e., 48% of the time). Multicollinearity in explanatory variables (Table 1) was addressed by running a randomForest procedure which produces a measure of variable importance based on the mean decrease in accuracy of the model when the data for a variable is randomized. According to this criterion, the climate moisture index and the frequency of defoliation were the most important explanatory variables (Figure 5). When a classification tree was run using only these two explanatory variables (Figure 6), the cross-validated misclassification rate was $100\% - 69.4\% = 30.6\%$. This is only 0.2% lower than the misclassification rate of the original classification tree (Figure 3).

The misclassification error rates of the 50-fold random sample ranged from 25–35%. The 30.8% rate produced by our classification tree (Figure 3) is near the middle of this range. The distribution of the number of leaves after pruning ranged from three to 24 leaves, with most of the classification trees having either three or, as in the initial tree (Figure 3), six leaves. Both of these results suggest that our classification tree (Figure 3) is representative of other potential trees for these characteristics.

Table 1. Cross-correlations between explanatory variables. These variables are the average climate moisture index (cmi_ave); the percentages of the total basal area, that is, hardwood (hw), balsam fir and white spruce combined (FbSw), or balsam fir, white spruce and black spruce combined (FbSwSb); and the number of years of moderate–severe defoliation (sbwfreq).

	cmi_ave	FbSw	FbSwSb	hw	sbwfreq
cmi_ave	1	−0.02	−0.09	0.33	−0.09
FbSw	−0.02	1	0.22	0.01	0.18
FbSwSb	−0.09	0.22	1	−0.77	−0.03
Hw	0.33	0.01	−0.77	1	−0.07
sbwfreq	−0.09	0.18	−0.03	−0.07	1

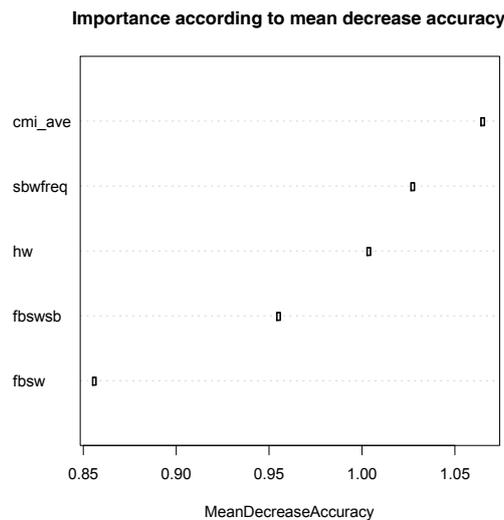


Figure 5. Importance of the explanatory variables used to construct the classification tree (Figure 3), as assessed by the randomForest procedure. These variables are the average climate moisture index (cmi_ave); the number of years of moderate–severe defoliation (sbwfreq); and the percentages of the total basal area, that is, hardwood (hw), balsam fir and white spruce combined (fbsw), or balsam fir, white spruce and black spruce combined (FbSwSb).

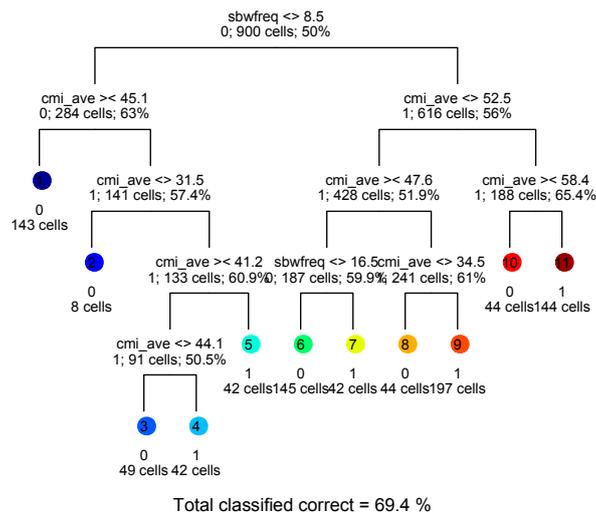


Figure 6. Classification tree of the presence (1) or absence (0) of the interaction between fire and spruce budworm defoliation as a function of just the two most important explanatory variables (Figure 5) from the data used to grow the tree shown in Figure 3. These two variables are the frequency of defoliation by spruce budworm (sbwfreq) and the annual average climate moisture index (cmi_ave). See the caption to Figure 3 for additional detail.

On the other hand, the identity and importance of the explanatory variables retained in the final 50 classification trees after pruning vary slightly from the corresponding results for our original classification tree (Figure 3). In the classification trees based on the 50 random samples, climate moisture index (cmi_ave) and hardwood content (hw) were the explanatory variables most often retained. The proportion of balsam fir, white spruce and black spruce (FbSwSb) and the proportion of balsam fir and white spruce (FbSw) were next. Defoliation frequency (sbwfreq) was the least often selected. However, selection frequency is only one of many possible measures of importance. As shown above, an explanatory variable selected near the bottom of a classification tree (e.g., defoliation frequency in Figure 3), and consequently susceptible to pruning, can have a considerable importance for the accuracy of the classification tree (Figure 5).

For each of these 50 classification trees, the explanatory variables were ranked according to their importance. Figure 7 shows the distribution of these ranks. The importance of average climate moisture index (cmi_ave) and hardwood content (hw) is confirmed as they tend to rank first or second. In contrast, the proportion of balsam fir, white spruce and black spruce combined (FbSwSb), and defoliation frequency (sbwfreq) tend to rank third or fourth. The proportion of balsam fir and white spruce combined (FbSw) almost always ranks fifth (last) in importance in this analysis.

Figure 8 maps the location-specific probabilities of likely spruce budworm–fire interaction based on predictions from 50 random samples. Areas with a high probability of interaction (0.8–1) are mostly located in large patches in (1) the northwest of the province; (2) on the southwestern side of Lake Nipigon and (3) in a fairly narrow band running NW to SE from the southeastern side of Lake Nipigon to the Mississagi river watershed. In between these areas, the probability of predicting an area of interaction is still high (80%) or medium (60%).

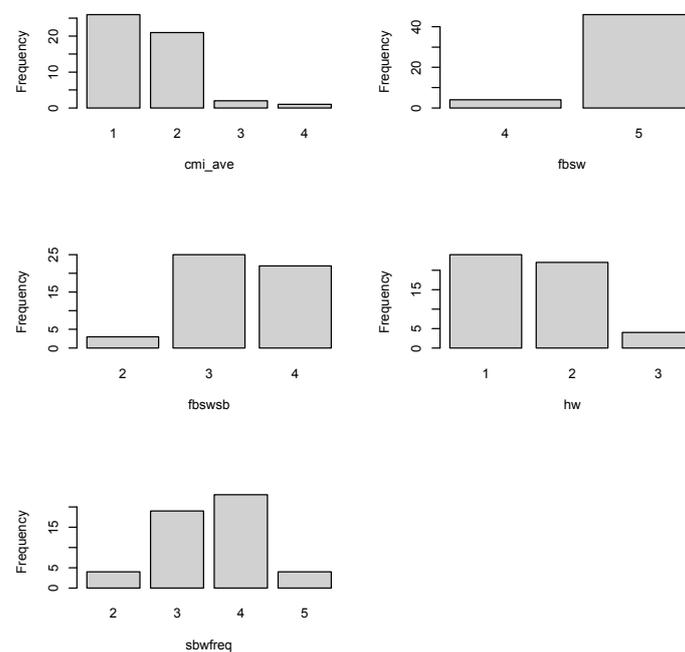


Figure 7. Distributions of the importance rankings of the explanatory variables in 50 classification trees calculated on random samples of the original dataset. Importance was measured by the mean decrease accuracy in the randomForests procedure.

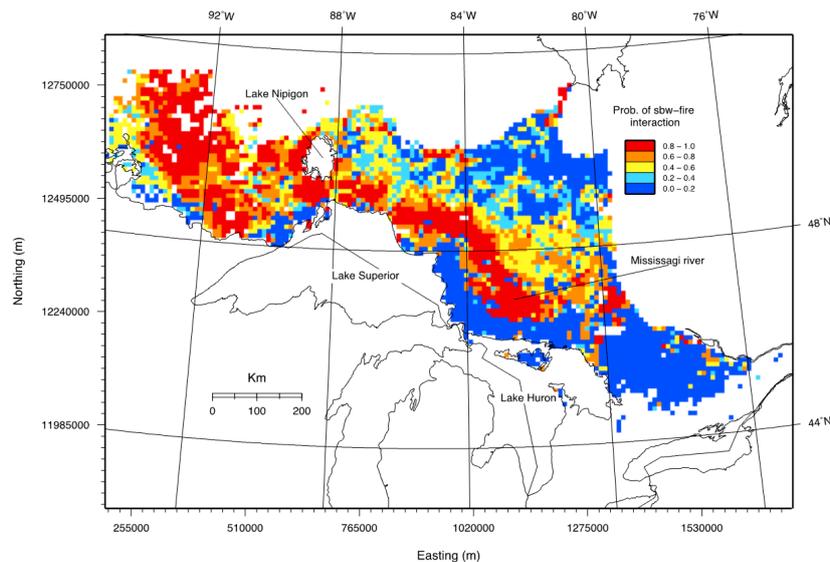


Figure 8. Probability of interaction between spruce budworm and fire based on predictions from 50 classification trees calculated on random samples of the original dataset.

4. Discussion

In our analysis, hardwood content, closely followed by climate moisture (Figure 1B), were the two dominant explanatory variables for predicting where spruce budworm defoliation most likely promoted subsequent large fires in Ontario (Figure 7). The third most important explanatory variable was the prevalence of the spruce budworm's host species (i.e., balsam fir and white and black spruce, combined) and fourth, by the propensity (number of years recorded) for spruce budworm defoliation to occur at that location (Figure 1A). Of least importance was the content of just the two principal spruce budworm host species (i.e., balsam fir and white spruce, combined).

The relative importance of these explanatory variables is evident in (a) the maps (Figures 4 and 8) showing the estimated likelihoods that spruce budworm defoliation will promote subsequent large fires; and (b), the classification trees on which these maps are based (e.g., Figure 3). The areas where spruce budworm defoliation most likely promoted subsequent large fires are best defined by a geographical limit related to hardwood content in the south, balsam fir, white spruce and black spruce together in the north, and moisture in the west. Inside these limits, areas of spruce budworm–fire interaction are related to spruce budworm defoliation frequency. There is little evidence that spruce budworm defoliation promotes subsequent large (>2 km²) fires in the southeast where hardwood content was high and SBW defoliation rare, in the northeast where there was also little history of defoliation, and in the dry western and southwestern regions. Within the area defined by these boundaries and towards the northern limit of the spruce budworm belt in the west, spruce budworm–fire interaction seems likely.

The steepness of the probability gradients in Figure 8 indicates the relative spatial certainty in locating the borders that separate regions where spruce budworm–fire interaction is likely from those where it is not. For instance, the abrupt shift from a probability of 1 to a probability of 0 in the southeast clearly defines the border's location there. The location of the border is not as easily located in the northeast where the shift from probability 1 to 0 is gradual, nor in the west where few cells have a probability less than 0.4. In the northwest, areas of likely spruce budworm–fire interaction reach the northern limit of the data, suggesting that they could extend further north, beyond the data, if SBW defoliation occurs there.

These results appear robust against several sources of variation: over the ensemble of regression trees examined, hardwood content is consistently one of the most important variables in explaining the areas of spruce budworm–fire interaction (Figure 7). In southeastern Ontario, the latitudinal gradient

of hardwood content matches a gradient of increasing urbanization and, as a result, of increasing fire protection that might also explain the absence of fire in these areas [17]. At the northeastern limit of the spruce budworm belt, the high proportion of balsam fir, white spruce and black spruce (FbSwSb > 77.6%) is mainly due to the high proportion of black spruce, a tree that is less supportive of large spruce budworm populations than balsam fir or white spruce [39], and a tree which can proliferate on the wet soils there. In addition, these wet soils coupled with weather patterns bringing cold, moist air from Hudson's Bay limit the occurrence of fire (Figure 2 in [17]). Consequently, it is unlikely that spruce budworm defoliation will promote fire here.

After hardwood content, the climate moisture index is the explanatory variable most consistently high in importance over the ensemble of 50 regression trees constructed (Figure 7). Climate moisture affects the risk of fire directly, but also indirectly through its influence on the rate of decomposition of dead trees and branches and other fuels following spruce budworm defoliation. For instance, compared to western Ontario, Fleming et al. [17] suggest that it is increased rates of decomposition in the wetter climates of eastern Ontario (Figure 1B) which shorten the time-window (their Figure 6) following spruce budworm defoliation during which fire potential remains high. In dry climates (low climate moisture index) such as in the western reaches of the province (Figure 1B), large fires are relatively common (their Figure 2) and seem to burn independently of spruce budworm defoliation (Figure 8). In wetter climates such as in the red zone in Figure 1B east of Lake Superior, large fires are rare (their Figure 2), presumably often prevented by this climate despite the prevalence of spruce budworm defoliation there (Figure 1A). It is in the areas of moderate climate moisture that the presence of spruce budworm defoliation is most likely to elevate the subsequent risk of large fires.

The prevalence (number of years recorded) of spruce budworm defoliation at a given location ranks fourth in importance over the ensemble of 50 regression trees constructed (Figure 7). Hardwood content, climate moisture, and the prevalence of spruce budworm host species all rank higher. The relatively poor explanatory power of defoliation prevalence is partly explained by its curvilinear relationship with fire (Figure 4 in [17]). In this relationship, areas within the spruce budworm belt that experienced moderate frequencies of defoliation were the most likely burned. After a large fire, the forest needs time to recover before it is again suitable for spruce budworm defoliation, so fires tend to be relatively rare in areas with high frequencies of defoliation. Defoliation prevalence is also low in the northeast (due to black spruce prevalence, as explained above), and in the southeast of the defoliation belt where farms and large pockets of dense deciduous forest interrupt the continuity of host trees species that is otherwise found further north. Large fire is rare in these areas due to climate (northeast, see above) and aggressive fire response in the relatively urbanized southeast.

In this analysis, we searched for broad tendencies in the patterns of budworm–fire interaction over decades of historical records at very large spatial scales. Local, instantaneous conditions such as fire weather, topography, and fuel condition at the ignition point are important factors that directly affect fire ignition and spread in particular sites at specific times [40,41], but over the large spatio-temporal scales of this study, variations in weather, topography and fuel condition become so 'smoothed out' that they are no longer useful predictors. Hence such variables were not included in our analysis. However, other ecological and climate factors may affect ecoregional patterns of spruce budworm and fire interactions. The nature of understory vegetation (composition, age, and structure) is likely one of these factors as it could affect the inter- and intra-annual dynamics of fuel moisture. Early on [15,17], it was hypothesized that crown breakage following sustained defoliation would release the understory by opening the canopy. The proliferation of the understory would then increase surface fuel moisture, thus decreasing the risk of surface fire and the risk for surface fires to reach the canopy. As such, the nature of the understory vegetation (composition, age, and structure) would likely affect its post-release dynamics and its effect on fire intra-annually in the timing of leaf-out in the spring (fire risk is generally thought to be higher prior to leaf-out), and inter-annually in the time that it will require to grow enough in size and complexity to achieve a reduction in fire risk. Understory composition, age and structure could not be included in this analysis for lack of data over the study

area. Although the three classes of overstory vegetation we used in this analysis may somewhat correspond to broad classes of understory vegetation [42], a better characterization of the understory would certainly be desirable. Wind is another factor that was not included in our analysis for lack of data although it likely increases the risk of crown breakage, which may accelerate the accumulation of “ladder fuel”. Long-term mean wind speed in the spring and summer is spatially homogeneous over our study area and has low inter-annual variability [43].

The elevation of fire risk by spruce budworm defoliation may seem to be a relatively small problem. For instance, Fleming et al. [17] reported that of the 417,000 km² defoliated by spruce budworm in Ontario at least once between 1941 and 1996, only about 5% experienced large fires. In this paper, we have shown that from 1941 to 2005, spruce budworm defoliated 418,000 km² at least once, of which 21% constitutes areas where the probability of spruce budworm–fire interaction is greater than 0.8 (Figure 8). This percentage is larger than the former because, with only 1.5 outbreaks in our data, many of these areas with elevated fire risk have yet to realize their spruce budworm-related fires.

According to our results, climate change could potentially affect spruce budworm–fire interaction through changes in the bioclimatic variables that were retained in the model. Global circulation models predict temperature increases in southern Ontario of 3–5 °C in summer and 4–6 °C in winter before the end of the century. The corresponding predictions in northern Ontario are for seasonal temperature increases of 3–6 °C and 4–10 °C, respectively. Precipitation is predicted (with less certainty than temperature) to decrease by 20% in the summer and 10–20% in the winter (20% and 20–30% decrease in northern Ontario, respectively) [44]. An increase in temperature combined with a decrease (or even no change) in precipitation can be expected to decrease climate moisture. As a result, some areas of moderate climate moisture might experience a drier climate under which spruce budworm defoliation has less influence on the subsequent risk of large fires. Climate change can also potentially affect the distribution of the frequency of spruce budworm defoliation. The application of climate projections for 2011–2040 to a bioclimatic model of spruce budworm defoliation in Ontario suggests (1) a northern extension of the area of defoliation combined with a persistence of the southern limit, effectively increasing the total area of defoliation by more than 20% compared to the area observed in the last outbreak (1967–1998); and (2) a decrease of the frequency of defoliation in the center of the historical defoliation belt [5]. A northward extension of the area of defoliation could create more opportunity for interactions with fire, especially because historically, more area has been burnt by large fires north of the defoliation belt (particularly in the northwest) than in it [45].

Changes in temperature and precipitation regimes are also expected to affect forest composition and distribution through their effects on the physiology and ecology of tree species. For instance, white and black spruce respond negatively to temperature increases [46], and Lenihan and Neilson [47] predict that future climate warming could potentially reduce their area of dominance by 20–30%. Balsam fir has a wide distribution that could be displaced by the combination of the northward expansion of the temperate conifer and hardwood species of the Great Lakes—St Lawrence Forest Region south of the Boreal zone, and a northward shift of its climatically optimal habitat. While there is certainty that changes in forest composition and distribution will occur, the rate, magnitude, and location of such changes are all highly uncertain. In the boreal forest, changes in natural disturbance regimes are expected to exert a stronger effect than changes in the climate itself. There is potential for positive (or negative) feedback: disturbances may accelerate changes in forest composition and distribution ‘imposed’ by a different climate which, in turn, may create new conditions which favor (or hinder) more disturbances and even further forest changes.

While climate change adds another level of complexity to the interactions between spruce budworm defoliation and fire, and the forests in which they occur, the likelihood that it will affect these interactions and the potential impacts of spruce budworm-caused fires as described above, point to the need for further research in this area.

5. Conclusions

The existence of an interaction between spruce budworm defoliation and wildfire in central Canada's boreal forests is supported by an increasing body of experimental [14,15,18] and statistical [17,19] results. The driving factor behind this interaction is the accumulation of "ladder fuel" (i.e., highly flammable tree tops and branches arranged vertically) that increases the probability for surface fires to reach the canopy, thus increasing the risk of severe fires.

In this study, we integrate and extend previous work on the influence of spruce budworm outbreaks on the subsequent potential for wildfire. We show that factors such as climate, defoliation history, and forest condition all help explain characteristics of this influence and its spatial variation across the region. We use this new information to distinguish, at the landscape scale, those areas of Central Canada's boreal forest where spruce budworm defoliation is likely to increase subsequent fire risk from those areas where it is not.

In the short term, these results may help fire managers in geographically allocating resources among areas that were previously considered as having similar fire risk. In the long term, further research is required to better understand how the increase in fire risk and changes in spruce budworm defoliation patterns predicted under climate change will affect the interaction between these two disturbances.

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