Outbreak regulation mechanisms play different roles at different stages of an Eastern spruce budworm (Choristoneura fumiferana) outbreak.

Pierce McNie (mcnie.pierce@courrier.uqam.ca)
Université du Québec à Montréal
Élise Filotas
TÉLUQ University
Daniel Kneeshaw
Université du Québec à Montréal

Research Article

Keywords: risk, scale, insect outbreak, defoliation, fragmentation

Posted Date: October 24th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-2180560/v1

Outbreak regulation mechanisms play different roles at different stages of an Eastern spruce budworm (*Choristoneura fumiferana*) outbreak

Pierce M^{c}Nie [1], Élise Filotas [2], and Daniel Kneeshaw [1]

[1]Center for Forest Research, Université du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, QC, H3C 3P8, Canada
[2]Center for Forest Research, Université du Québec (TELUQ), 5800 Saint-Denis, Montreal, QC, H2S 3L5, Canada

October 22, 2022

Abstract

Context: The stand level risk of defoliation and mortality due to the spruce budworm (*Choristoneura fumiferana*, SBW) is mainly linked to the host species content such that stands dominated by the primary host species, balsam fir (*Abies balsamea*), are considered the most vulnerable. At the landscape scale there is much less information but some work suggests that risk may decrease when landscapes are dominated by secondary hosts, such as black spruce(*Picea mariana*) or when landscapes are fragmented.

Objectives: We aim to determine risk of defoliation onset and of tree mortality due to SBW at a landscape scale due to factors that have been associated with SBW defoliation at the stand scale. We hypothesise that outbreak onset will occur earlier in landscapes dominated by host species and that fragmentation and black spruce content will not affect onset but will be associated with subsequent lower mortality.

Methods: We employed Cox hazard models to estimate the relative risk of different landscape configuration and species composition patterns on the onset and risk of mortality of a spruce budworm outbreak in Cote Nord, Quebec, Eastern Canada, using government data bases of forest tree species composition and of SBW defoliation across Québec. In particular, we measured the risks associated with primary host proportion, the relative amounts of secondary host and hardwood trees to fir trees, the structure of balsam fir in the landscape, and the structure of the forest overall.

Results: Our results show that defoliation onset is more related to the configuration of the landscape than to the species composition while mortality is ultimately influenced by the tree species present. Defoliation

onset risk is increased the most by a more complex configuration of fir patches in the landscape. Mortality risk on the other hand is unaffected by fir configuration, with the greatest change being a decrease in risk due to increased black spruce presence in the landscape.

Conclusions: Maintaining black spruce abundance and forest connectivity across forested landscapes could reduce SBW related mortality and delay defoliation onset. Forestry management strategies should avoid clear cuts and the development of fir monocultures in the forest.

Keywords— risk, scale, insect outbreak, defoliation, fragmentation

1 Introduction

Much of our understanding of spruce budworm (*Choristoneura fumiferana*, SBW) outbreaks stems from observations of tree mortality at a stand scale. However, the mechanisms generating local mortality patterns are not necessarily the same as those mechanisms involved at a landscape scale. SBW outbreaks in eastern North America are long-lasting and cover vast areas (Jardon et al., 2003; Williams and Liebhold, 2000), with the outbreak in the 1970's causing upwards of 50 million hectares of severe defoliation and lasting 15-20 years (Pureswaran et al., 2016). Despite the spatial extent of these outbreaks, most research done to date resolves stand scale mechanisms to stand scale defoliation and mortality patterns, assuming that the link to the broader outbreak follows the same patterns. Questioning this assumption leads us to ask whether the processes influencing defoliation at the stand scale are relevant at the scale of the outbreak, where processes such as dispersal, colonisation, and population growth are expressed.

Stand scale defoliation tends to follow the feeding preferences of the SBW, but this is altered by the presence of other tree species. In most cases, fir trees (*Abies balsamea*) and white spruce (*Picea glauca*) are more heavily defoliated than black spruce (*Picea mariana*) (Bellemin-Noël et al., 2021; Thomas, 1989). While black spruce is a host species for the SBW, the relationship is complex and its quality as a host for the SBW is marginal due to leaf toughness and mismatched timing in the phenology of budburst and larval emergence; both of which reduce SBW population growth (Fuentealba et al., 2020; Greenbank, 1963). Contrary to black spruce, the phenology of bud burst for balsam fir and white spruce is in greater synchrony with SBW larvae emergence in the spring (Nealis and Régnière, 2004b; Pureswaran et al., 2015). Moreover, the presence of black spruce in a stand may reduce, at least in the beginning phase of an outbreak, the defoliation of fir in the same stand (Bognounou et al., 2017). This associational resistance emerges due to lower fecundity of SBW on black spruce due to budburst timing limiting population growth, and ultimately reducing defoliation. How feeding preference and associational resistance scales from stand level to landscape level defoliation patterns is unknown.

Increased hardwood content of a stand has also been shown to decrease the defoliation and mortality of fir trees within stands (Campbell et al., 2008; Cappuccino et al., 1998; Su et al., 1996; Zhang et al., 2018). Although at a stand scale, the protective effect of hardwoods has been associated with greater parasitism from generalist parasitoids feeding on alternative Lepidoteran hosts (Cappuccino et al., 1998), at a smaller scale, hardwood interspersed among host trees reduces the likelihood of SBW larvae landing on a suitable host when dispersing, reducing the incidence

of defoliation (Zhang, 2020). While SBW larvae disperse by ballooning short distances on silk threads, adult SBW are capable of long distance flights (Anderson and Sturtevant, 2011; Batzer, 1968). In mixed host and non-host stands the ability of the female moth to target hosts may increase defoliation of host species as these are targeted by female moths during egg laying. Different dispersal methods at different life stages may result in the protection offered to fir by hardwood trees at the stand scale not being as influential at a landscape scale (Campbell et al., 2008).

The spatial distribution of host and non-host dominated stands is likely important in predicting the severity of SBW outbreaks across the landscape (Robert et al., 2018). More spatially homogeneous fir dominated stands tend to be associated with greater defoliation and severity of outbreaks of the SBW at the edge of the main range of SBW outbreaks (Robert et al., 2018). Other insect outbreaks are influenced by landscape configuration. For instance, Roland (1993) suggests that the disruption of parasitoid relationships with the forest tent caterpillar in fragmented environments results in outbreaks of a longer duration. However, a dearth of SBW studies at a landscape scale prevents us from drawing firm conclusions about the relative importance of forest structure on defoliation and mortality.

Understanding the progression of SBW outbreaks at any scale is further complicated by the interplay of top-down and bottom-up factors that control SBW populations (Pureswaran et al., 2016). Over recent decades, emphasis has been on the role of top-down effects, but landscape level studies suggest that bottom-up factors are important (Bouchard and Pothier, 2011; Robert et al., 2018). The effects of landscape factors may also differ between early and late phases of an outbreak (Pureswaran et al., 2016). Defoliation onset is likely more influenced by features of the landscape that limit dispersal and/or colonisation success of SBW such as fragmentation or non-host presence. After colonisation, tree mortality due to SBW could depend more on factors influencing SBW fecundity and population growth such as associational resistance or forage quality (Bognounou et al., 2017; Fuentealba et al., 2020). Separating the phases of the outbreak into onset and mortality phases when investigating the role of different landscape factors can offer a finer understanding of the role of landscape configuration and forest composition in SBW outbreak dynamics.

Given the likely role of landscape structure on the beginning and development of the current SBW outbreak in Quebec, Eastern Canada, we quantify the risk to defoliation onset and to mortality relative to the composition and configuration of the forest at a landscape scale. We investigated the factors influencing the landscape scale tree defoliation and mortality responses to the SBW using data from the Québec Ministry of Forests, Wildlife, and Parks that span 7 million ha across 14 years. More precisely, we evaluated the level at which onset of tree defoliation and mortality could be explained by five risk factors that are known to be associated with increased defoliation at the stand scale, or are linked to mechanisms known to influence defoliation at the landscape scale. These five factors are (Table 1): the proportion of fir, the relative proportion of spruce to fir, the relative proportion of hardwood to fir, the spatial configuration of fir-dominated patches, and the spatial configuration of forest patches (regardless of tree species composition).

We used Cox's proportional hazards (PH) regression models (Cox, 1972) to evaluate the risk factors of defoliation onset and tree mortality. The Cox PH model is a semi-parametric survival model that takes its distribution from the empirical data. Cox PH models do not require that a baseline hazard rate be specified. This is advantageous in that possibly incorrect assumptions about the baseline survival

times are avoided (Cyr et al., 2016). Cox PH models are widely used to assess morbidity risk of health interventions and lifestyle factors to disease outcomes (Kumar and Klefsjö, 1994), and the technique has been used to assess the risk of fire spread in landscapes (Cyr et al., 2016; Morin et al., 2015; Tremblay et al., 2018), but to our knowledge, this is the first application of the method to studying the spread of an insect epidemic.

Table 1: Risk factors likely to influence SBW defoliation onset and mortality with measurement metrics and hypotheses for landscape scale patterns based on their influence on SBW outbreaks at a stand scale.

		Landscape Scale Hypotheses	
Risk Factor	Landscape Metric (measured in each sampling window)	Defoliation onset	Mortality
Proportion of fir	Fraction of cells with fir composition greater than 50%	A landscape composition dominated by the preferred host should increase the likelihood of SBW finding the area (Bellemin-Noël et al., 2021).	A landscape composition dominated by the preferred host should increase the growth rate of the SBW population through increased food supply and overwintering habitat, hence increasing mortality (Bellemin-Noël et al., 2021).
Proportion of spruce relative to fir	Fraction of cells with black spruce composition greater than 50% relative to cells with fir composition greater than 50%	More black spruce in the landscape relative to fir increases associational resistance in the landscape, hence decreasing outbreak onset and mortality (Bognounou et al., 2017).	
Proportion of hardwood relative to fir	Fraction of cells with hardwood species composition greater than 50% relative to cells with fir composition greater than 50%	More hardwood in the landscape relative to fir increases associational resistance in the landscape, hence decreasing outbreak onset and mortality (Cappuccino et al., 1998; Zhang et al., 2018)	
Spatial configuration of forest cover	Number of forest patches and Landscape Shape index of forest patches .	Landscapes with greater heterogeneity in forest composition may be less easily traversed by parasitoid species than the more mobile SBW resulting in the SBW establishing and defoliating more quickly in the absence of predation (Murakami et al., 2008).	Patchy landscapes may reduce the ability of parasitoids to control the population growth of the SBW increasing mortality (Roland, 1993). Resource dilution may lead to reduced mortality (Bognounou et al., 2017).
Spatial configuration of fir patches	Number of forest patches and Landscape Shape index of forest patches	Landscapes with more complex configurations of fir patches reduce SBW movement and dispersal success, increasing time to defoliation onset.	Resource dilution results in increased defoliation at the landscape scale leading to greater mortality (Bognounou et al., 2017). Patchy landscapes may reduce the ability of parasitoids to control the population growth of the SBW increasing mortality (Roland, 1993).

2 Methods

2.1 Study Area

The study area is located in the Côte-Nord region of Québec, Canada, and covers approximately 7.05 million ha of predominantly balsam fir and black spruce forest. This area contains a large portion of the current spruce budworm outbreak and is centred on the initial epicentres of the outbreak (fig. 1).

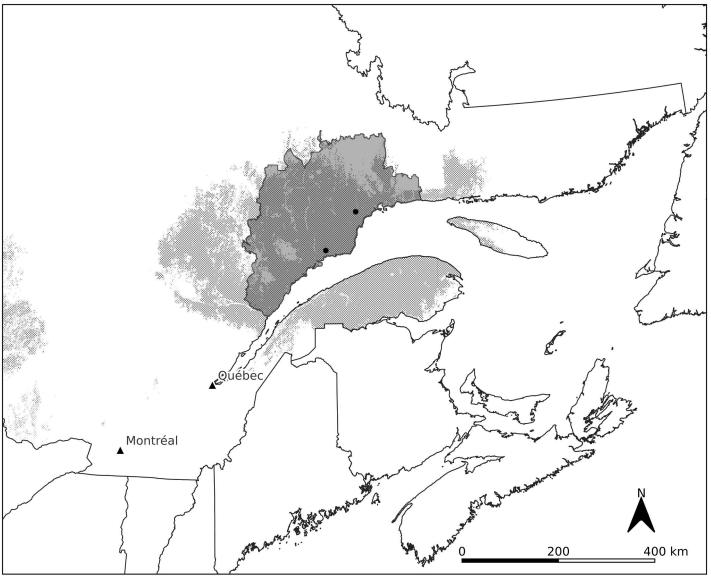

Figure 1: Study area (shaded in grey) on the north coast of the Saint-Lawrence river in Québec, Canada. Unlabelled black points within the shaded study area are the approximate centres of heavy defoliation in 2007, used as an estimate of the the origin of the outbreak in this study. Cross hatch shading shows the maximum extent of the SBW outbreak from its onset in 2007 until 2020.

2.2 Data collection

We assessed forest composition and SBW defoliation severity within our study area using a dendrometric LiDAR map (MFFP (2021a), and natural disturbance data for the spruce budworm (MFFP, 2021b) from the Québec Ministry of Forests, Fauna, and Parks (MFFP).

The dendrometric LiDAR data (MFFP, 2021a) are polygons, with average size of 0.8 ha, describing composition, wood volumes, and species of trees in forests across Quebec in 2021. The forest composition data were rasterised to a resolution of 0.0025ha to quantify risk factors using standard composition and configuration grid-based metrics (Bosch, 2019)(examle in fig. 2A).

Defoliation data are categorical polygons, with median size of 2.66 ha, characterized by one of four levels of annual defoliation severity estimated from aerial surveys

(example in fig. 2B). The defoliation classes are: no defoliation (none), defoliation of the upper few tiers of the crown (light), defoliation of the upper half of the crown (moderate), and almost complete defoliation of the crown (severe) (MFFP, 2021b). The collected defoliation data covers the years 2007 to 2020 inclusively.

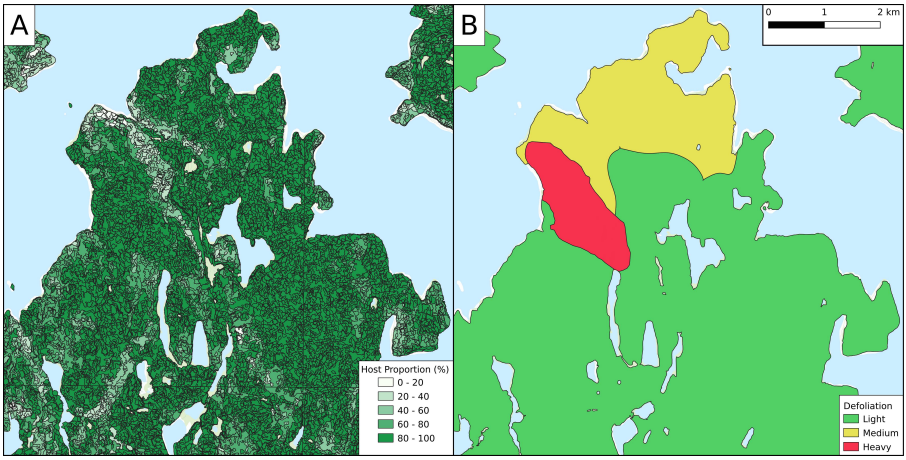

Figure 2: Examples of data used for forest composition (A) and defoliation (B) for an 800 ha sector within our study area in year 2021. Host proportion in map A is the sum of fir, black spruce, and white spruce.

2.3 Measuring defoliation and mortality

We measured defoliation and mortality at the landscape scale from the defoliation maps. First, we randomly distributed 2500 sampling windows of 2500 ha each across our 7.05 million ha study area. We assigned each window as a landscape. This 2500 ha landscape scale was chosen as a compromise between windows being large enough to encompass heterogeneous structure and allow computational efficiency in the subsequent analysis. Moreover, the 2500 windows allowed us to capture the variability in the risk factors (Table 1) hypothesized to influence defoliation onset and mortality due to SBW defoliation.

Second, for each year from 2007 to 2020, we calculated the average defoliation within each window. The spatial distribution of the windows allowed us to measure defoliation at different stages of the outbreak i.e. different zones of the study area have been affected for different lengths of time. Average defoliation in each window is calculated as the area-weighted mean over the four defoliation classes. Defoliation classes (MFFP (2021b)) were translated into percentages of defoliation using the mid point in each third of 100% (i.e. 1 = 16%, 2=50%, and 3 = 82%). Average defoliation in a given window is used as the principal index of damage when estimating the onset of an outbreak at the landscape scale. We define onset of the outbreak as the first year of moderate or severe average defoliation (>50%) in any given window. Light defoliation, was not used as it is a class category more subject to errors and confusion with causes other than the SBW.

Third, we estimated year of mortality using cumulative defoliation to account for the survival of trees up to approximately 6 years of 100% defoliation of new foliage

(Blais, 1958; Sainte-Marie et al., 2015). As SBW host trees carry 5-7 years of foliage 600% Cumulative defoliation is a proxy for complete loss of foliage and tree death (Blais, 1958; Sainte-Marie et al., 2015). Cumulative defoliation was measured in each window by summing the average defoliation year after year. As an example, if over three years of defoliation in a given window there was one year of light, one year of moderate and one year of severe defoliation, then using the mid-point of each defoliation class the cumulative defoliation for this three year period would be 16+50+82% or 148% cumulative defoliation. Cumulative defoliation score was calculated over successive years until 600% was reached at which point we estimated that mortality occurred in the window.

2.4 Estimating Risk Factors

We sampled rasterized dendrometric LiDAR maps at year 2021 using the same 2500 sampling windows used to estimate average defoliation and mortality at the landscape scale. In each sampling window, we analysed landscape composition and configuration factors known to increase defoliation or mortality risks at the stand scale or factors known to limit dispersal at the landscape scale (Table 1). We estimated five risk factors: 1) the proportion of fir, as the primary host of the SBW, fir is often associated with greater defoliation at the stand scale; 2) the relative proportion of spruce to fir, a factor associated with reduced defoliation at the stand scale due to associational resistance; 3) the relative proportion of hardwood to fir, also a factor associated with associational resistance at the stand scale; 4) landscape configuration of the forest cover, and 5) the landscape configuration of fir, regardless of composition, as both features are likely to limit SBW dispersal.

We calculated the proportion of fir in a sampling window as a fraction of its area covered by cells that contain more than 50% fir. Similarly, we calculated the relative spruce and hardwood content within a window by the fraction of cells with black spruce or hardwood composition greater than 50% relative to cells with fir composition greater than 50% .

We assessed landscape configuration using two indicators, the number of patches and the landscape shape index (LSI), both measured within each window using the python package pylandstats (Bosch, 2019). In this study, a patch is defined by contiguous cells of the same type and contiguity is measured using an eight-neighbor rule. The number of patches in a window is a simple way to capture how subdivided a landscape is. However, it does not account for patch area nor patch shape. LSI, on the other hand, is an indicator of landscape complexity: it measures how the shape of patches depart from a square shape, in relation to the size of the landscape. A landscape with high LSI implies that it encompasses patches with intricate edges or patches that are spatially distinct. As such, LSI can be described as a measure of patch aggregation (McGarigal, 1995) that complements the number of patches by capturing the effects of patch area, density and edginess at the landscape scale (Wang et al., 2014). These factors all have the potential to limit SBW movement through the landscape. Fir landscape configuration is calculated as the LSI over patches of cells containing greater than 50% fir in a window. Forest landscape configuration is the LSI of patches of cells where the dominant cover (>50%) is any type of forest (either hardwood or coniferous).

2.5 Analysis of Risk

We used Cox proportional hazards models to assess how the level of risk in each window varied according to the factors described above. The Cox proportional hazards model estimates how the change in one factor impacts the risk of an event occurring. Due to the expansion of the outbreak, the risk of defoliation was not equal at all points across the study area. As a result, we used a stratified model to account for the different baseline risks due to the distance between the source of the outbreak and the windows in which the five factors where measured. To assign strata we drew a polygon over the defoliation maps encompassing all defoliation experienced in the study area for each year of the 2007-2020 period. This resulted in 14 polygons of increasing size. We then estimated R, the average year on year increase in radius of the polygons, as an approximation of outbreak spread per year. In each window, we calculated the minimum distance d from the centre of the window to the nearest of the two origin points of the outbreak in 2007. The distance d of a window from the origin of the outbreaks was then rounded to the nearest multiple of R to group the data into strata based on binned distances from the outbreak origin.

We then used a stratified Cox's proportional hazards model (eqn 1) to understand the risk from our five different factors on two events: A) onset of defoliation by the SBW and B) mortality (represented by 600% cumulative defoliation). These two event criterion were used to censor the defoliation data so that windows unaffected by defoliation onset or tree mortality at the end of the study period (2020) did not unduly influence the results (Austin, 2017).

We modelled the hazard rate $\lambda(t)$ at time t as a function of the stratified baseline hazard rate $\lambda_g(t)$ and the risk factors of interest, x_i. The baseline hazard rate $\lambda_g(t)$ represents the hazard if all x_i are equal to zero in a strata g. The coefficient β_i represents the effect size of the risk factor x_i as a proportional change in hazard per change in 1 unit of the risk factor. The coefficients β_i are then compared to the null model based only on time.

$$\lambda(t) = \lambda_{g,i}(t) \exp(\beta_i x_i) \tag{1}$$

β_i values were modelled for defoliation onset and mortality risk for each risk factor in table 1. For interpretation, β_i values are presented as hazards ratios (log of β_i) which represents risk relative to the baseline risk.

2.5.1 Visualisation and Interpretation

Hazard ratios (HR) and 95%CI for each factor are visualised using a forest plot (fig. 3). Factors with proportional hazards greater than 1 and with confidence intervals not overlapping 1 are associated with a greater risk of defoliation onset or mortality while those below 1 a reduce risk. Cox model HR values are interpreted as a proportion change per unit change in the risk factor. For instance, a HR of 1.1 for the proportion of fir in the landscape would be interpreted as a 10% increase in risk per 1% increase in proportion of fir in the landscape, whereas a HR of 0.98 would translate to a reduction in risk of 2% per 1% increase in the proportion of fir in the landscape.

3 Results

The average spread of the outbreak was 23 km/yr as measured by the year to year growth in convex hull radius. This resulted in 8 strata of approximately 400 windows each.

3.1 Onset and Mortality

A 10% increase in the proportion of fir in a window increased the probability of onset by 9.2% and the risk of mortality by 17.7% (Proportion Fir in Table 2, fig. 3, p-values <= 0.001). On the other hand, an increase of 10% in relative spruciness had the opposite effect and decreased the risk of onset by 6.7% (Relative Spruciness in Table 2, fig. 3, p = 0.001) and mortality by 32.6% (Table 2, fig. 3, p < 0.001). Relative spruciness had the largest single effect of any factors on mortality and was also the only negative influence on both onset and mortality.

The risk of defoliation onset increased by 34.5% per 10% increase in hardwood proportion relative to fir (Relative Hardwood in Table 2, fig. 3, p= 0.013). However, relative hardwood had no effect on tree mortality.

A 10% increase in forest patch LSI increased the risk of defoliation onset by 26.4% (Forest Configuration in table 2, fig. 3, p = 0.001). The number of forest patches had no effect on defoliation of mortality risk (Forest Number of Patches in Table 2, fig. 3, p > 0.001). A 10% increase in fir patch LSI in a window increased the risk of defoliation onset by 36.5% (Fir Configuration in Table 2, fig. 3, p < 0.001), but at no effect either on mortality risk. The number of fir patches in the window increases the risk of defoliation onset by 3.8% per 10% increase in patch numbers, but had no effect on mortality risk (Fir Number of Patches in Table 2, fig. 3, p < 0.001).

Table 2: Cox's proportional hazards ratios (HR) and significant per 10 % increase in risk for different risk factors associated with onset of SBW defoliation and mortality of SBW host trees.

	Onset			Mortality		
Factor	HR	Per 10%	p	HR	Per 10%	p
Proportion Fir	1.01	9.2	< 0.001	1.02	17.7	0.001
Relative Spruciness	0.99	−6.7	0.001	0.96	−32.6	< 0.001
Relative Hardwood	1.03	34.5	0.013	0.97	–	0.379
Fir Configuration	1.03	36.5	< 0.001	1.00	–	0.96
Forest Configuration	1.02	26.4	0.001	0.97	–	0.26
Fir Patch Number	1.00	3.8	< 0.001	1.00	–	0.466
Forest Patch Number	1.00	1.2	0.539	1.00	–	0.543

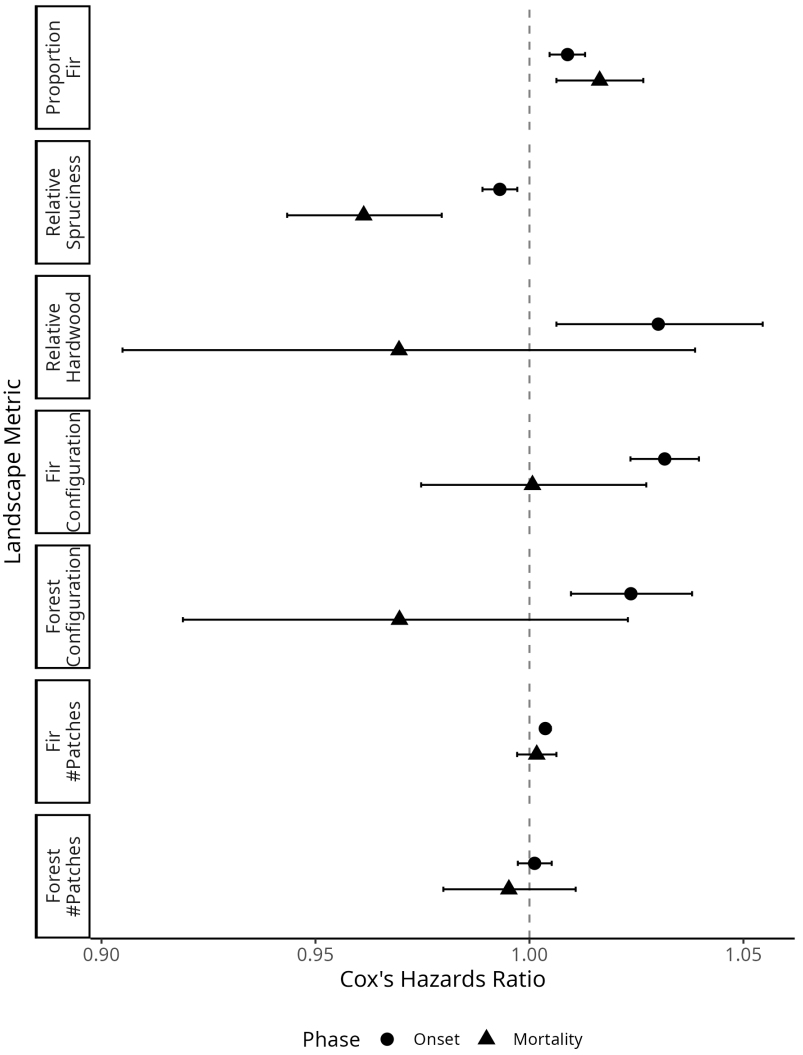

Figure 3: Hazards ratios of landscape risk factors (Table 1) to SBW defoliation onset and mortality from Cox's proportional hazards models. HR values represent risk of onset of epidemic (circles) or risk of tree mortality after onset (triangles) proportional to baseline risk where the factor of interest is zero. Factors where the 95% CI's overlap 1 are considered significant.

4 Discussion

The results presented here show that both the spatial and temporal scales of observation are important in understanding how local mechanisms influence SBW defoliation onset and mortality. Defoliation onset is mainly influenced by the ability for SBW

to locate and colonise patches; while tree species composition and host suitability is more important in determining the risk of tree mortality. Recognising that these mechanisms play different roles at different stages of an outbreak creates a finer temporal understanding of the progression of SBW outbreaks to tree mortality. Our results show that landscape configuration of forest patches influence the risk of defoliation onset (fig. 3). More precisely, landscapes containing forest patches with more complex shapes, or more fir trees and fewer black spruce stands in the forest, increase the risk of defoliation onset (fig. 3). This pattern is not seen when investigating the risk of mortality in the same landscapes with high LSI (fig. 3). Once SBW are established, tree species composition is the only factor that influences mortality (fig. 3).

4.1 Defoliation onset and landscape configuration

Increased risk of defoliation onset was most associated with increased complexity in the configuration of fir patches at the landscape scale. The smaller increase in the risk of defoliation onset due to the number of fir patches in relation to the LSI of fir patches suggests that movement about the landscape for the SBW is limited not only by non-contiguous fir patches, but by their irregular shapes. Cappuccino et al. (1998) suggested that small patches of fir would be more protected than large ones from parasitism and that this effect would be stronger than isolation alone. However, our results show that it is not only the islands of fir in a forested landscape that influence the onset of SBW defoliation but also the configuration of forest patches (regardless of their composition). This result suggests a potential role for parasitoid escape, as the SBW can move between patches more easily and over greater distances than its parasitoids (Cappuccino et al., 1998; Stireman et al., 2005). A similar mechanism of parasitoid escape was evoked to explain the greater impact of another defoliator, the forest tent caterpillar, in fragmented trembling aspen forests (Roland, 1993).

The importance of landscape configuration for defoliation onset could also be associated with a crowding effect. This effect occurs when the concentration of a resource or habitat in a fragmented landscape leads to greater use of that resource as it is the only suitable habitat remaining, leading to greater defoliation due to increased herbivore concentration on fewer host patches (Yamamura, 2002). As forest harvesting is influencing the shape and reducing the number of forest patches such a crowding effect is a possibility for defoliation onset. Subsequent relaxation of the crowding effect, as observed in fragmentation studies (Debinski and Holt, 2000), is also consistent with the fact that we did not observe an increase in mortality in these patches.

Long distance dispersal of the SBW from areas of high density into areas of low density are common, and likely form a key part of the dynamics of the SBW outbreak (Régnière and Nealis, 2019). Although Anderson and Sturtevant (2011) found less support for a SBW dispersal model that included forest patches of host species than a directional wind based model, they only looked at moth dispersal and not subsequent establishment and defoliation. Our work thus suggests that establishment and defoliation onset are subsequently influenced by forest structure. This is compatible with work that suggests that egg and larval survival influence the subsequent defoliating generation and thus onset, although not long-term temporal trends (i.e. mortality) (Debinski and Holt, 2000). This result may support a type of modified crowding effect where dispersing SBW moths hone in on patches of the most vulnerable hosts. As with many ecological phenomena these potential mechanisms

may be complementary rather than competing, and resource concentration as well as parasitoid escape by density dependant long-distance dispersal may be contributing to the observed effects on defoliation onset.

Though the configuration of the landscape elicited the greatest risk increase to defoliation onset, forest composition was also important. More fir is associated with greater SBW defoliation at the stand scale (Hennigar et al., 2008; Thomas, 1989); a pattern that scales up to the landscape in the present study. The SBW is more fecund where it has a better quality diet (Delisle and Hardy, 1997; Nealis and Régnière, 2004a). This is conistent with our results where composition had a smaller effect on onset than on mortality, which requires high populations. A greater relative spruce proportion in relation to fir in the landscape reduces risk of onset and also subsequent mortality. Reduce onset may be due to the phenological mismatch between the SBW and black spruce and thus more difficulty in establishing in a black spruce forest. Unsynchronised phenology om combination with poorer forage quality will subsequently lead to fewer SBW and lower fecundity (Bognounou et al., 2017; Fuentealba et al., 2020). When interspersed amongst fir in a landscape, black spruce trees draw egg laying SBW females, and divert some herbivory pressure from the more edible fir trees (Bognounou et al., 2017).

An interesting result of the current study is the increased risk of onset in forests with a high relative hardwood proportion. At the stand scale, increasing hardwood content of a forest tends to decrease observed defoliation. At this scale, isolated fir trees amongst hardwood benefit from the protective effect of non-hosts (Zhang, 2020) However, as we scale our observations this relationship reverses. The protective effect of hardwoods found at a stand scale may be attributed to the reduced likelihood of landing on an appropriate hosts, the dilution effect, in a mixed stand during pre- or post-winter dispersal of early stage SBW larvae (Régnière and Nealis, 2008; Zhang, 2020). With larval SBW dispersal often not exceeding 30m (Batzer, 1968), this mechanism may act only at a local scale and not be influential at a landscape scale where dispersing moths may focus on the any hosts that are present to lay eggs and thus influence onset.

4.2 Mortality and forest composition

Unlike defoliation onset, tree mortality is not associated with the configuration of the landscape. Instead, species composition becomes relatively more influential for predicting tree mortality. This suggests that the role of landscape level forest composition is more critical for population growth than for its role in migration and establishment. This is reflected in the results with the only significant factors for mortality being the proportion of fir and the relative spruciness; the factors related directly to reproductive success and not related to dispersal or migration. The proportion of fir in the landscape increases the risk of defoliation in the same manner as before the onset of defoliation (Hennigar et al., 2008; Thomas, 1989). A greater proportion of fir in the landscape translates into greater food availability and fecundity for the SBW (Delisle and Hardy, 1997; Nealis and Régnière, 2004a). Likewise, the associational resistance effects of black spruce may reduce the risk of mortality in landscapes with more spruce (Bognounou et al., 2017; Fuentealba et al., 2020). However, as populations are well established by this stage, additional SBW dispersal into the population may not do so in numbers that affect the risk of tree mortality, reducing the role of host and forest configuration in determining mortality.

4.3 Interpretation for forest management

All together, our results show that the roles of different landscape factors change as the outbreak progresses. Forest configuration is a key factor in determining where outbreaks will occur in a forested landscape and thus in risk analyses for pest management. Forest harvesting that isolates stands or creates complexity in the shapes of tree patches increases risk that defoliation will begin. The creation of smaller, less regular patches, especially of fir, should thus be avoided especially when black spruce are also harvested. This observation is in agreement with a recent study showing that a decrease in forest patch size after harvesting increases losses to the SBW (Kneeshaw et al., 2022). Landscapes with fir dominated patches, either in cut-blocks or in forests are likely to be the first defoliated.

However, once the SBW is established, forest composition is the dominant factor influencing subsequent severity but this offers foresters the opportunity to reduce mortality by manipulating composition at the landscape level (Sainte-Marie et al., 2015). Kneeshaw et al. (2021), however, listed impediments to doing so and the present study quantifies the difficulty related to the proposal as a reduction of 32.6% risk would require a 10% increase in the proportion of spruce across the landscape. In other words in a 100 000 ha landscape over 10 000 ha of spruce would need to be planted to reduce risk by 1/3. However, our analysis, similarly to Kneeshaw et al. (2022), highlights that the loss of black spruce would increase mortality risk and if this loss is accompanied by a conversion to fir then a 50% increase in damage could occur (i.e. a conversion of 10% of the landscape from spruce to fir). As it is difficult to replace fir with spruce while relatively easy to convert spruce to fir due to abundant advance fir regeneration it is easier to increase risk than to decrease it at the landscape scale. Forests rich in spruce and those where fir abundance is limited, have the lowest risk of mortality. Nonetheless, planting spruce to create SBW resistant landscapes would require a phenomenal effort. However, maintaining spruce abundance in forests can prevent the establishment of forests that are greatly at risk of SBW defoliation and mortality (Sainte-Marie et al., 2015). Forest harvesting today seems to be creating at risk forests through the preferential harvesting of spruce, which may result in greater tree mortality and defoliation in the future.

4.4 Limitations

As a first approximation of SBW defoliation patterns at a landscape scale, our study suffers from a few limitations. The first is that the forest composition data is a static data set from a single year (2021). Though a more accurate representation of the forest community each year would undoubtedly increase confidence in the results of this study, the use of a single year does not necessarily invalidate our results. Changes in forest composition tend to happen on the scale of decades and not years. Given young trees may take 40 years to reach maturity, the 14 year time span of the present study is short enough to limit the influence of tree community changes on the result. The second is a lack of abundance data for the SBW. Using defoliation as a proxy for SBW abundance can help us understand the patterns that emerge due to dipseral and successful colonisation but can leave us with a results that are ambiguous regarding the mechanisms for successful onset or mortality. A more direct measure of the abundance of the SBW over the study area, while far more difficult to collect, would help to tease apart mechanisms from patterns, allowing us to distinguish between hypotheses where multiple explanations exist. Future work

at the landscape scale, whether modelling or empirical, would benefit focusing on SBW parasitoids to determine mechanisms underlying these patterns.

4.5 Conclusions

In conclusion, our analysis provides a key demonstration of the influence of landscape-scale forest configuration on SBW outbreaks and landscape-scale forest composition on tree mortality during outbreaks of the SBW. Additionally, this result is the first to show the importance of landscape-scale patterns to the progression of SBW outbreaks. Isolated forest patches and particularly stands of pure fir, whether amongst other tree species, or standing alone, have the greatest risk of being early epicentres of defoliation. Increasing the proportion of spruce and decreasing the proportion of fir are the strongest measures for reducing mortality losses to the SBW. Well designed and future proof forestry management strategies should avoid clear cuts and the development of fir monoculture in the forest.

5 Acknowledgments

We would like to thank Audrey Smargiassi for invaluable help in applying the Cox model to the ecological data.

6 Ethical Statements

6.1 Competing interests

The authors have no relevant financial or non-financial interests to disclose.

6.2 Conflicts Interest

The authors have no conflicts of interest to declare.

7 Author Contributions

P.M.: Writing - Original Draft, Conceptualization, Formal analysis, Visualization. E.F: Supervision, Writing - Review & Editing, Methodology. D.K.: Supervision, Writing - Review & Editing, Methodology.

8 Funding

Funding was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a Discovery grant awarded to E.F. (RGPIN: 2018-06156) and and an NSERC Dicovery grant awarded to D.K. (RGPIN: 2017-06616)

9 Data Availability

The data sets generated during and/or analysed during the current study are available from the Quebec Ministry for forests, fauna, and parks, (MFFP, 2021a,b).

References

Anderson, D. P. and Sturtevant, B. R. (2011). Pattern analysis of eastern spruce budworm Choristoneura fumiferana dispersal. *Ecography*, 34(3):488–497. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1600-0587.2010.06326.x.

Austin, P. C. (2017). A Tutorial on Multilevel Survival Analysis: Methods, Models and Applications. *International Statistical Review*, 85(2):185–203. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/insr.12214.

Batzer, H. O. (1968). Hibernation Site and Dispersal of Spruce Budworm Larvae as Related to Damage of Sapling Balsam Fir. *Journal of Economic Entomology*, 61(1):216–220.

Bellemin-Noël, B., Bourassa, S., Despland, E., De Grandpré, L., and Pureswaran, D. S. (2021). Improved performance of the eastern spruce budworm on black spruce as warming temperatures disrupt phenological defences. *Global Change Biology*, 27(14):3358–3366. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.15643.

Blais, J. R. (1958). The vulnerability of balsam fir to spruce budworm attack in northwestern ontario, with special reference to the physiological age of the tree. *The Forestry Chronicle*, 34(4):405–422. Publisher: Canadian Institute of Forestry.

Bognounou, F., De Grandpré, L., Pureswaran, D. S., and Kneeshaw, D. (2017). Temporal variation in plant neighborhood effects on the defoliation of primary and secondary hosts by an insect pest. *Ecosphere*, 8(3):e01759. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/ecs2.1759.

Bosch, M. (2019). PyLandStats: An open-source Pythonic library to compute landscape metrics. *PLOS ONE*, 14(12):e0225734. Publisher: Public Library of Science.

Bouchard, M. and Pothier, D. (2011). Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern Québec. *Forest Ecology and Management*, 261(4):811–820.

Campbell, E. M., MacLean, D. A., and Bergeron, Y. (2008). The Severity of Budworm-Caused Growth Reductions in Balsam Fir/Spruce Stands Varies with the Hardwood Content of Surrounding Forest Landscapes. *Forest Science*, 54(2):195–205.

Cappuccino, N., Lavertu, D., Bergeron, Y., and Régnière, J. (1998). Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, 114:236–242.

Cox, D. R. (1972). Regression Models and Life-Tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, 34(2):187–202. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.2517-6161.1972.tb00899.x.

Cyr, D., Gauthier, S., Boulanger, Y., and Bergeron, Y. (2016). Quantifying Fire Cycle from Dendroecological Records Using Survival Analyses. *Forests*, 7(7):131. Number: 7 Publisher: Multidisciplinary Digital Publishing Institute.

Debinski, D. M. and Holt, R. D. (2000). A Survey and Overview of Habitat Fragmentation Experiments. *Conservation Biology*, 14(2):342–355. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1523-1739.2000.98081.x.

Delisle, J. and Hardy, M. (1997). Male larval nutrition influences the reproductive success of both sexes of the Spruce Budworm, Choristoneura fumiferana (Lepidoptera: Tortricidae). *Functional Ecology*, 11(4):451–463. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1365-2435.1997.00114.x.

Fuentealba, A., Sagne, S., Legendre, G., Pureswaran, D., Bauce, E., and Despland, E. (2020). Leaf toughness as a mechanism of defence against spruce budworm. *Arthropod-Plant Interactions*, 14(4):481–489.

Greenbank, D. O. (1963). Host Species And The Spruce Budworm. *The Memoirs of the Entomological Society of Canada*, 95(S31):219–223. Publisher: Cambridge University Press.

Hennigar, C. R., MacLean, D. A., Quiring, D. T., and Kershaw, Jr., J. A. (2008). Differences in Spruce Budworm Defoliation among Balsam Fir and White, Red, and Black Spruce. *Forest Science*, 54(2):158–166.

Jardon, Y., Morin, H., and Dutilleul, P. (2003). Périodicité et synchronisme des épidémies de la tordeuse des bourgeons de l'épinette au Québec. *Canadian Journal of Forest Research*, 33(10):1947–1961. Publisher: NRC Research Press.

Kneeshaw, D. D., De Grandpré, L., D'Orangeville, L., Marchand, M., Moisan-Perrier, J., Robert, L.-E., and Bouchard, M. (2022). Forest Structure and Composition Diverge Following Harvesting Compared to a Spruce Budworm Choristoneura fumiferana (Clem.) Outbreak. *Frontiers in Forests and Global Change*, 5.

Kneeshaw, D. D., Sturtevant, B. R., DeGrandpé, L., Doblas-Miranda, E., James, P. M. A., Tardif, D., and Burton, P. J. (2021). The Vision of Managing for Pest-Resistant Landscapes: Realistic or Utopic? *Current Forestry Reports*, 7(2):97–113.

Kumar, D. and Klefsjö, B. (1994). Proportional hazards model: a review. *Reliability Engineering & System Safety*, 44(2):177–188.

McGarigal, K. (1995). *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Google-Books-ID: FsI_GzPd5UUC.

MFFP (2021a). Carte dendrométrique LiDAR - Données Québec.

MFFP (2021b). Données sur les perturbations naturelles - Insecte : Tordeuse des bourgeons de l'épinette - Données Québec.

Morin, A. A., Albert-Green, A., Woolford, D. G., Martell, D. L., Morin, A. A., Albert-Green, A., Woolford, D. G., and Martell, D. L. (2015). The use of survival analysis methods to model the control time of forest fires in Ontario, Canada. *International Journal of Wildland Fire*, 24(7):964–973. Publisher: CSIRO PUBLISHING.

Murakami, M., Hirao, T., and Kasei, A. (2008). Effects of habitat configuration on host–parasitoid food web structure. *Ecological Research*, 23(6):1039–1049. _eprint: https://esj-journals.onlinelibrary.wiley.com/doi/pdf/10.1007/s11284-008-0478-0.

Nealis, V. G. and Régnière, J. (2004a). Fecundity and recruitment of eggs during outbreaks of the spruce budworm. *The Canadian Entomologist*, 136(4):591–604. Publisher: Cambridge University Press.

Nealis, V. G. and Régnière, J. (2004b). Insect host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. *Canadian Journal of Forest Research*, 34(9):1870–1882. Publisher: NRC Research Press.

Pureswaran, D. S., De Grandpré, L., Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., and Kneeshaw, D. D. (2015). Climate-induced changes in host tree–insect phenology may drive ecological state-shift in boreal forests. *Ecology*, 96(6):1480–1491.

Pureswaran, D. S., Johns, R., Heard, S. B., and Quiring, D. (2016). Paradigms in Eastern Spruce Budworm (Lepidoptera: Tortricidae) Population Ecology: A Century of Debate. *Environmental Entomology*, 45(6):1333–1342.

Robert, L.-E., Sturtevant, B. R., Cooke, B. J., James, P. M. A., Fortin, M.-J., Townsend, P. A., Wolter, P. T., and Kneeshaw, D. (2018). Landscape host abundance and configuration regulate periodic outbreak behavior in spruce budworm Choristoneura fumiferana. *Ecography*, 41(9):1556–1571. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/ecog.03553.

Roland, J. (1993). Large scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, 93(1):25–30.

Régnière, J. and Nealis, V. G. (2008). The fine scale population dynamics of spruce budworm: survival of early instars related to forest condition. *Ecological Entomology*, 33(3):362–373. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-2311.2007.00977.x.

Régnière, J. and Nealis, V. G. (2019). Density Dependence of Egg Recruitment and Moth Dispersal in Spruce Budworms. *Forests*, 10(8):706. Number: 8 Publisher: Multidisciplinary Digital Publishing Institute.

Sainte-Marie, G. B., Kneeshaw, D. D., MacLean, D. A., and Hennigar, C. R. (2015). Estimating forest vulnerability to the next spruce budworm outbreak: will past silvicultural efforts pay dividends? *Canadian Journal of Forest Research*, 45(3):314–324. Publisher: NRC Research Press.

Stireman, J. O., Dyer, L. A., Janzen, D. H., Singer, M. S., Lill, J. T., Marquis, R. J., Ricklefs, R. E., Gentry, G. L., Hallwachs, W., Coley, P. D., Barone, J. A., Greeney, H. F., Connahs, H., Barbosa, P., Morais, H. C., and Diniz, I. R. (2005). Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proceedings of the National Academy of Sciences*, 102(48):17384–17387.

Su, Q., Needham, T. D., and MacLean, D. A. (1996). The influence of hardwood content on balsam fir defoliation by spruce budworm. *Canadian Journal of Forest Research*, 26(9):1620–1628. Publisher: NRC Research Press.

Thomas, A. W. (1989). Food consumption and utilization by 6th-instar larvae of spruce budworm, Choristoneura fumiferana: a comparison on three Picea (spruce) species. *Entomologia Experimentalis et Applicata*, 52(3):205–214. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1570-7458.1989.tb01269.x.

Tremblay, P.-O., Duchesne, T., and Cumming, S. (2018). Survival analysis and classification methods for forest fire size. *PLOS ONE*, 13:e0189860.

Wang, X., Blanchet, F. G., and Koper, N. (2014). Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in Ecology and Evolution*, 5(7):634–646. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/2041-210X.12198.

Williams, D. W. and Liebhold, A. M. (2000). Spatial Synchrony of Spruce Budworm Outbreaks in Eastern North America. *Ecology*, 81(10):2753–2766. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1890/0012-9658%282000%29081%5B2753%3ASSOSBO%5D2.0.CO%3B2.

Yamamura, K. (2002). Biodiversity and stability of herbivore populations: influences of the spatial sparseness of food plants. *Population Ecology*, 44(1):33–40. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1007/s101440200004.

Zhang, B. (2020). *Determining the mechanism of impact of hardwood content on spruce budworm defoliation of balsam fir*. PhD thesis, University of New Brunswick.

Zhang, B., MacLean, D. A., Johns, R. C., and Eveleigh, E. S. (2018). Effects of Hardwood Content on Balsam Fir Defoliation during the Building Phase of a Spruce Budworm Outbreak. *Forests*, 9(9):530. Number: 9 Publisher: Multidisciplinary Digital Publishing Institute.