RESEARCH ARTICLE

Influence of environmental factors and spatio-temporal covariates during the initial development of a spruce budworm outbreak

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Abstract Recurrent and synchronous spruce budworm (SBW) outbreaks have important impacts in boreal and sub-boreal forest ecosystems of North America. This study examines the early phase of an outbreak that was developing across a 268,000 km^2 area over a period of 9 years (2003–2011). The territory was subdivided in 225 km^2 cells, and the relative influence of forest composition, elevation, forest age, average degree-days and soil drainage were examined during three development phases of the outbreak: initial epicenter location, relatively long-distance spread (cell-to-cell expansion), and expansion inside individual cells (within-cell expansion). The results indicate that elevation is the most determinant variable for initial epicenter location. Other variables that were identified as important for outbreak development by previous studies, such as forest composition and average degree-days, were not so important during this phase. However, forest composition and average degree-days were important factors during the cell-to-cell and within-cell expansion phases. Separating outbreak development in distinct phases also allowed to integrate phase-specific spatial and temporal covariates that were highly significant in the models, such as distance from previous year defoliations during the cell-to-cell expansion phase, and the proportion of defoliated stands during the preceding year for the within-cell expansion phase. Overall, this study provides limited evidence that patterns of SBW outbreak expansion could be altered by reducing host tree species abundance in the forest [mainly balsam fir (*Abies balsamea*) in this region]. More generally, this study suggests that the influence of environmental variables on SBW outbreak development is clearly phase-dependent, and that this landscape-level, process-based approach could be useful to forecast insect outbreak development in forest ecosystems.

Keywords Insect outbreaks · Spruce budworm · Insect dispersal · Spatially explicit models · Defoliation surveys · Landscape-level disturbance model

Introduction

Understanding the effect of environmental factors on the development of forest insect outbreaks can have major implications for forest resource management. On one hand, if the patterns of initiation and spread of an outbreak are primarily influenced by biotic factors, in particular by parameters related to forest structure and composition, this could mean that the course of an outbreak could be altered indirectly through forest

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management policies. On the other hand, primary influence of abiotic factors, such as climate, or an absence of relationship between outbreak patterns and environmental factors, could mean that it would be difficult to alter the course of an outbreak by modifying forest characteristics.

The development of forest insect outbreaks is a complex phenomenon that can span across a wide range of spatial scales (Raffa et al. 2008), and involve highly complex multitrophic population processes (Eveleigh et al. 2007). Developing predictive models for such complex systems usually requires some simplifications that will depend on the main focus of the study (Levin and Pacala 1997). For studies that are mainly interested by the large-scale patterns of insect defoliation, it can be useful to separate outbreak development in successive phases (Jepsen et al. 2009), for example outbreak initiation, spread and collapse; each of these phases could be influenced differentially by environmental factors, and could be formulated as sub-models inside a more general disturbance model. By clarifying the relationship between environmental factors and particular phases of outbreak development, it also becomes feasible to build process-based models that will predict disturbance responses in situations that have no analog in the past (Williams and Jackson 2007).

The spruce budworm (SBW) [*Choristoneura fumiferana* (Clem.)] is a defoliating insect present across northern North America (MacLean 2004). In eastern Canada, it primarily defoliates balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), red spruce (*P. rubens* Sarg.) and black spruce (*P. mariana* (Mill.) B.S.P.). Large-scale synchronous outbreaks occur at intervals averaging 35 years in eastern Canada (Morin et al. 2007), and often result in major mortality episodes for host species. Forest characteristics such as the relative proportion of host and non-host tree species within the stand have been found to affect defoliation levels (MacKinnon and MacLean 2003), perhaps because they alter the structure of the natural enemy complex (Quayle et al. 2003), or because stand structure and composition affect the way larvae and moths disperse within the stand (Nealis and Régnière 2004). The physiological state of the host species has also been reported to influence outbreak development, as stands of host trees weakened by age (Erdle and MacLean 1999) or by unfavorable soil conditions (Fuentealba and Bauce 2012) are more susceptible or vulnerable to SBW defoliation. At larger spatial scales, forest composition might also influence the way an outbreak develops across a territory: the presence of large concentrations of mature stands of host tree species have been hypothesized to be important for the location of insect outbreak epicenters (Blais 1983; Johnson et al. 2006), whereas other studies pointed out that the presence of host species was primarily important during outbreak expansion (Aukema et al. 2006).

Climate has also been identified as an important factor in SBW population dynamics. Climatic controls, mostly associated with temperature, are thought to limit the geographical extent of severe SBW defoliation to the north, to the south and in elevation (Blais 1958; Candau and Fleming 2011; Régnière et al. 2012). Meteorological patterns, which synchronize the fluctuations in population abundances over large territories, are also important factors in population dynamics of the insect, its natural enemies, and its host species (Williams and Liebhold 2000; Royama et al. 2005). As a consequence of the complex relationships between climate and outbreak development, the effects of climate change on SBW outbreaks have recently received more attention by researchers (Gray 2008; Candau and Fleming 2011; Régnière et al. 2012).

In this study, we use the case of the SBW to examine the relationship between insect defoliations and environmental factors. The spatial and temporal progression of SBW defoliations was examined on a 268,000 km^2 territory subdivided in 225 km^2 cells. The study examines the influence of the main environmental factors vary during three outbreak development phases: initial location of defoliations (epicenter initiation), regional-scale expansion from epicenters (cell-to-cell expansion), and yearly increases in defoliation levels inside individual cells. More generally, the objectives were to examine whether development patterns of SBW outbreaks could be altered by modifying forest characteristics through forest management, and to evaluate if a modelling approach that separates distinct outbreak development phases could improve forecasting.

Methods

Study area

The study area includes the portion of the province of Quebec (Canada) that was affected by SBW

defoliations between 2002 and 2011. This area spans across a relatively large latitudinal and longitudinal gradient (Fig. 1), which overlaps three main forest zones along the latitudinal gradient (Rowe 1972): boreal forests in the northern part, mostly dominated by conifers (spruce and fir) with a much lower prevalence of intolerant hardwoods [trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*)], temperate forests in the southern part, mostly dominated by the tolerant sugar maple (*Acer saccharum*), and sub-boreal forests in between, which tend to be dominated by complex mixtures of boreal and temperate species. Broad latitudinal variations in the prevalence of the main tree species or species groups are shown on Fig. 2.

Defoliation surveys

In Quebec, systematic aerial forest surveys of insect defoliations have been conducted annually by the provincial ministry of natural resources (QMNR) since 1968 (QMNR 2011). In the most recent surveys, all polygons affected by light (1–34 % of the annual shoots), moderate (35–69 %) or severe (>69 %) defoliations were reported on maps using real-time GPS on a touch-screen tablet PC (QMNR 2011). Defoliation severity is based on host species defoliation, which means that a forest stand in which host species are sub-dominant can still be considered severely defoliated. In this study, no distinctions were made between defoliation levels: even if the separation of defoliation levels could lead to a more efficient prediction of tree growth reductions and tree mortality levels (Pothier et al. 2012), this separation is not necessarily relevant to develop an understanding of

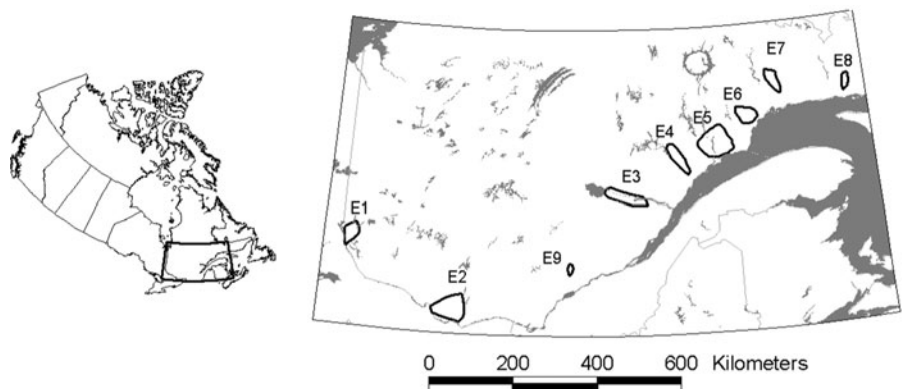the spatio-temporal patterns of outbreak development (Royama 1984).

Episodic SBW defoliations were reported in the western part of the province throughout the 1990–2000 decade, but began to expand more significantly after 2002 (QMNR 2011). During the 2003–2011 period, defoliation epicenters appeared and persisted in spatially-disjointed areas across the province. Nine of these epicenters, which are defined in this study as concentrated defoliations that are initially located at least 75 km from one another (Fig. 1), were identified. The notion of defoliation epicenter is somewhat controversial in studies of SBW outbreak dynamics, probably because it has been used in a relatively restrictive sense by particular schools of thought (see for example Hardy et al. 1983; Royama 1984). In this paper we use the term in a very broad sense, viz., a location where the first signs of a large-scale outbreak were detected by the aerial surveys.
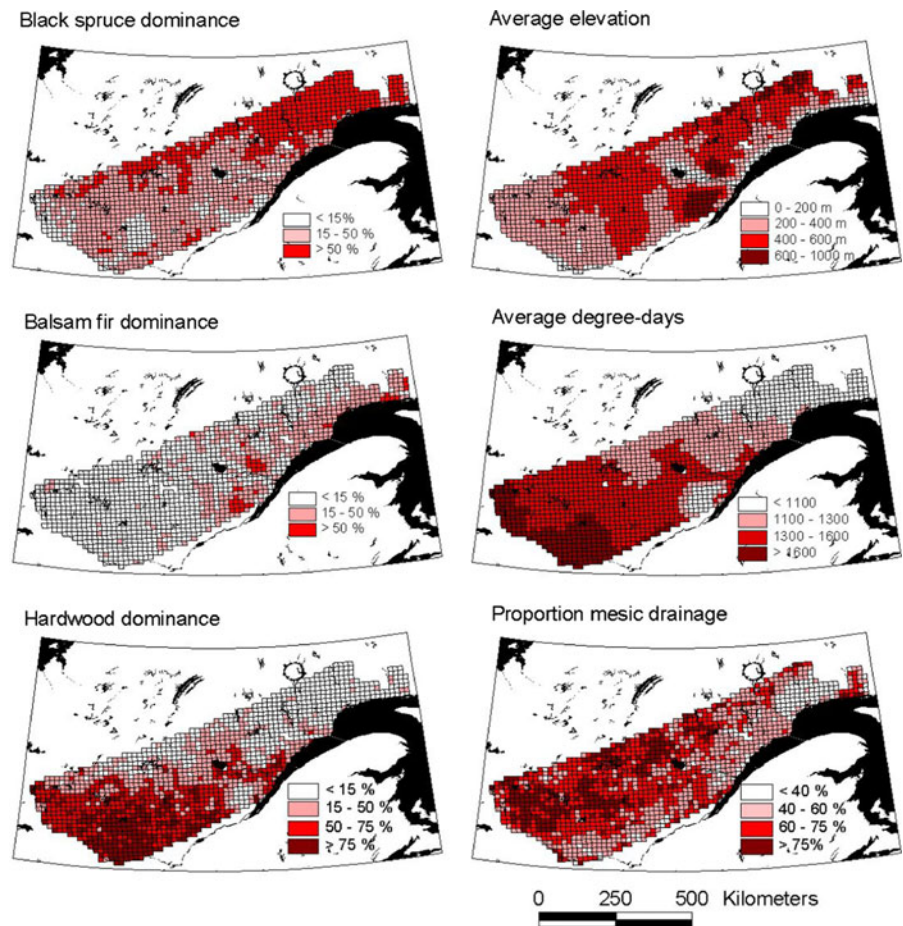
Environmental variables

A large polygon surrounding all the areas defoliated between 2003 and 2011 was delineated and used for environmental characterization. A 1 by 1 km grid was overlaid on the polygon, and each intersection point of this grid was described in terms of biotic and abiotic environmental characteristics. A defoliation code (defoliated or not) was also attributed to each point for each year.

Forest information was collected from forest inventory maps established by the QMNR, based on the interpretation of aerial photographs (1:15,400) taken between 2000 and 2010 across Quebec. During this inventory, all forest stands were delineated down

Fig. 1 Study area and location of the nine spruce budworm defoliation epicenters in the province of Québec, Canada

Fig. 2 Spatial distribution of environmental variables in the study area

Black spruce dominance

Average elevation

Balsam fir dominance

Average degree-days

Hardwood dominance

Proportion mesic drainage

0   250   500 Kilometers

to a minimal area of 4 ha (Lord and Faucher 2003). The resulting maps were subjected to a validation procedure ensuring that they were comparable throughout the province (Lord and Faucher 2003). In our study, we also updated this database to take into account the occurrence of stand-replacing disturbances (such as harvesting or fires) between the year of the photographs and 2010.

The information available on forest maps is categorical. Three compositional variables were created, based on the abundance of balsam fir, black spruce (the two main host species in terms of abundance in Québec), and non-host hardwood species. On the stand maps, tree species are mentioned in order of importance according to their abundance in the stands. The abundance of each species was put in one of two categories for the analyses: one category for stands dominated by the species, and one category for stands where the species is sub-dominant or not mentioned in the stand type. A stand type designation in which the species was not mentioned was interpreted as a stand where it could be present, but where it was not sufficiently abundant to warrant being mentioned. Stand age classes were grouped into two categories: young (<60 years) and old (>60 years), corresponding with different levels of vulnerability to SBW damage (Erdle and MacLean 1999). Points located in non-forested areas or in forest stands dominated by low regenerating vegetation (height <4 m) were excluded from the analyses, because of the lack of cartographic information about some stand characteristics, particularly species composition.

Because the study area is large, all climatic variables related with temperature (minimal winter temperature, degree-days, frost-free period, etc.) are strongly collinear, and at this scale they mostly reflect the latitudinal and elevation gradients. Sum of the average degree-days greater than 5 °C, which was

deemed an important variable for SBW outbreak development in previous studies (Gray 2008), was used as a summary climatic variable associated with temperature to reflect this geographical gradient. Degree-days greater than 5 °C were interpolated for each point of the dataset using BioSIM version 10.0.9.23 (Régnière and St-Amant 2011), by taking into account the influence of elevation and latitude. The interpolations used meteorological data for the years 2000–2011, obtained from the 8 weather stations located closest to each point. Because interannual variations in degree-days are relatively minor compared with spatial variations, we averaged all records for the period 2000–2011.

Two other abiotic independent variables were considered: elevation and drainage. Elevation was considered as a separate variable from climate because cursory visual analysis of the study area suggests that this factor might have an independent influence. The importance of elevation was sometimes mentioned with respect to SBW outbreaks (Blais 1958; Magnussen et al. 2004), and we wanted to verify if there was an effect that was independent from that of degree days or soil characteristics. Elevation (to the nearest 10 m) was inferred from topographic maps. Finally, we attributed a drainage class to each point, according to the information available on forest maps. It has been reported that balsam fir trees growing on xeric or hydric sites are more vulnerable to SBW damage compared with trees growing on mesic sites, presumably because they have lower energy reserves (Dupont et al. 1991; Fuentealba and Bauce 2012). To verify if drainage has an indirect effect on large-scale outbreak development patterns, we grouped drainage classes into two categories: mesic sites (drainage classes 2–3 according to Saucier et al. 1994), and excessively or poorly drained sites (classes 1 and 4–5–6).

Scale of analysis and data coding at the cell scale

Insect infestations are contagious by nature, and show spatially autocorrelated patterns. When outbreak development is analyzed, the influence of spatial autocorrelation should either be removed as much as possible from the data, or explicitly considered in the models, for example by adding a covariate (Peres-Neto and Legendre 2010). If the autocorrelation is not

acknowledged and dealt with, there is a risk that the effect of some environmental factors will be exaggerated or downplayed in the analyses (Legendre 1993; Peres-Neto and Legendre 2010).

Because spatial autocorrelation is expected to increase as the outbreak progresses, we elected to deal with it first by choosing an appropriate cell size for our regional-scale disturbance models, and then to integrate spatial covariates in the analyses (described in the next section). We adopted a cell size of 15×15 km (225 km^2), which is large enough to absorb some of the fine-scale variations observed in the dataset (Fig. 3). This cell size is also large enough to reflect the landscape-scale effect of forest composition on defoliation levels (Campbell et al. 2008), and probably large enough to account for the relatively coarse nature of some of the information (in particular, averaged temperatures interpolated with BIOSIM). Finally, a 15×15 km cell size is relatively close to the cell sizes used in similar analyses of SBW defoliation surveys across large spatial scales (Williams and Liebhold 2000; Gray 2008; Pothier et al. 2012). Hence, the 1 km point data were recompiled at the 15 km scale. This means that every 15 km cell contained a maximum of 225 points, but generally less, given that the non-forested points were discarded. For each cell, the total number of defoliated points for each year was defined as the independent variable. The presence or absence of defoliations inside individual cells for each year are shown in Fig. 4.

For independent variables, the categorical environmental variables were converted into continuous
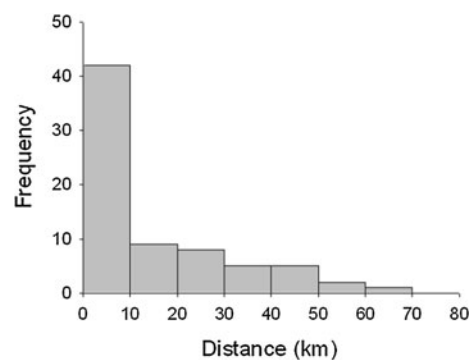
Fig. 3 Maximum yearly distance of expansion for defoliations observed in the nine epicenters. Frequencies are calculated on a set of 72 observations, each of which corresponds to a unique epicenter × year combination
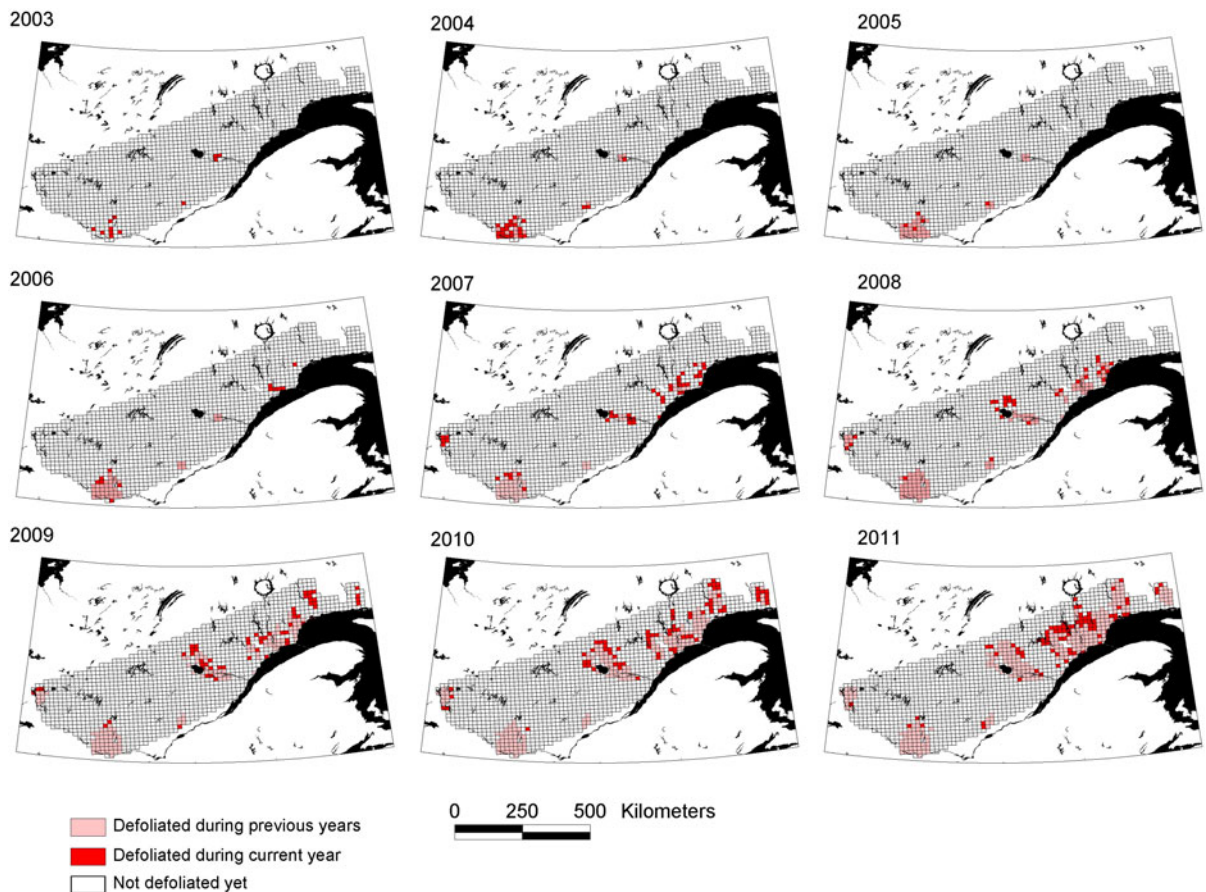
Fig. 4 Annual defoliations by the spruce budworm for the period 2003–2011

variables, based on the proportion of points within the cell associated to a given category. For example, 24 points located in stands dominated by balsam fir over a total of 200 forested points gives a value of 0.12 for this cell for this variable. Variables that were continuous in the initial 1 km point dataset (elevation, degree-days) were averaged to obtain the value for the 15 × 15 km cell. Spatial variations for the environmental variables are shown in Fig. 2. Initial characteristics of the 9 epicenters with respect to the main environmental variables are shown in Table 1.

Analyses

Overall, the defoliation data underwent three distinct types of analyses, which correspond with different phases of outbreak development. Specifically, these phases refer to sub-processes that are part of the overall outbreak development process. These sub-

processes can operate simultaneously when observed at the province level, but not at the cell level. For each analysis, a different subset from the basic dataset was constituted, as explained below.

The first analysis examined which factors determine the location of the cells that were initially defoliated. It was based on a dataset containing all 1,341 cells present in the territory, 62 of which were considered initially defoliated. The number of initially defoliated cells present in each epicenter is indicated in Table 1. In this analysis, a cell is considered defoliated when it comprises at least one defoliated point, else it is considered non defoliated. Only cells defoliated during the first years after the appearance of the epicenter were integrated in this analysis—these years are presented in Table 1.

The second analysis examined outbreak expansion from cell to cell. For this second analysis, separate datasets were constituted for each year between 2004

Table 1 Range of variation found for different environmental variables in the 15 × 15 km cells that are located near defoliation epicenters (Fig. 1)

Variable	Epicenter								
	E1	E2	E3	E4	E5	E6	E7	E8	E9
First year of defoliation	2007	2003[a]	2003[a]	2007	2006	2006	2009	2009	2003[a]
Number of initially defoliated cells	12	24	20	15	32	11	12	9	7
Balsam fir abundance (%)									
Mean	0.09	0.07	0.13	0.23	0.28	0.33	0.14	0.39	0.08
Range	0.01–0.16	0.01–0.19	0.04–0.20	0.08–0.47	0.08–0.50	0.17–0.64	0.06–0.79	0.08–0.56	0.02–0.42
Black spruce abundance (%)									
Mean	0.16	0.19	0.20	0.47	0.5	0.64	0.79	0.56	0.42
Range	0.02–0.29	0.02–0.43	0.06–0.41	0.14–0.84	0.25–0.86	0.28–0.83	0.53–0.92	0.42–0.67	0.33–0.54
Elevation (m.a.s.l.)									
Mean	279	210	213	413	304	315	483	314	265
Range	229–308	112–280	116–363	250–507	87–475	77–492	334–647	180–439	207–312
Mesic drainage (%)									
Mean	0.65	0.53	0.52	0.48	0.49	0.34	0.33	0.52	0.38
Range	0.49–0.75	0.34–0.81	0.31–0.69	0.36–0.67	0.37–0.59	0.25–0.48	0.17–0.52	0.32–0.73	0.29–0.44
Degree-days above 5 °C									
Mean	1,683	1,873	1,504	1,238	1,182	1,064	925	865	1,583
Range	1,646–1,709	1,770–2,079	1,370–1,590	1,120–1,359	1,061–1,261	1,005–1,144	899–967	844–879	1,530–1,641
Hardwood abundance (%)									
Mean	0.58	0.74	0.55	0.16	0.18	0.03	0.06	0.05	0.72
Range	0.36–0.72	0.47–0.92	0.35–0.72	0.00–0.63	0.00–0.55	0.00–0.12	0.00–0.19	0.00–0.29	0.56–0.79
Main hardwood species	SM, WB, YB, TA	SM, TA	YB, WB, TA	WB, TA	WB, TA	WB	WB	WB	SM, YB, TA, WB

SM sugar maple, *TA* trembling aspen, *WB* white birch, *YB* yellow birch

[a] Epicenters for which defoliations were also detected during aerial surveys done before 2003

and 2011. For any given year, only the cells that were not defoliated during the previous years but that were located at a maximal distance of 50 km from cells defoliated during the previous years were included. Each of these cells were attributed a binary code (1 or 0) depending if they were defoliated during the current year. The distance of 50 km was chosen because an examination of the overall dataset indicated that for 95 % of the epicenter/year combinations, the maximal distance of expansion was less than 50 km (Fig. 3). Hence, we assumed that comparison of environmental characteristics of defoliated versus non-defoliated cells was relevant only for cells that are located within this distance. Yearly datasets from 2004 to 2011 were pooled, and the statistical analyses were performed on this pooled dataset. As in the first analysis, the occurrence of one defoliated point within a cell was sufficient to consider it as defoliated.

The third analysis examined temporal changes in the proportion of defoliated stands inside the cells once they were colonized. Only the stands where host species were present were considered in order to calculate the dependent variable of interest, proportion of defoliated stands. As in the second analysis, separate datasets were constituted for each year between 2004 and 2011. For each year, cells that were not defoliated during the current year or during any of the preceding years were excluded from the analysis. Yearly datasets between 2004 and 2011 were pooled, and the statistical analyses were performed on this pooled dataset. For this third analysis, the dependent variable was the total number of defoliated points within each cell, thus giving a value that varies between 1 and 225.

The influence of environmental factors (summary statistics in Table 1) during the three outbreak development phases was examined using an information theoretic approach (Burnham and Anderson 2002) to select the most parsimonious fit to the data among a set of candidate models. We formulated a priori a set of 21 biologically reasonable and simple models, by making sure they are interpretable (Burnham and Anderson 2002). The fit of these same 21 models was compared for the three outbreak phases. The dependent variable was binary in analyses 1 and 2 (presence/absence of defoliation, binomially distributed), and a proportion analysis 3 (proportion of defoliated stands, binomially distributed). Spatial or temporal covariates were also added in analyses 2 and 3 in order to account for the contagious nature of outbreak progression. In analysis 2,

distance from the closest cell that was defoliated during any of the previous years was added as covariate. In analysis 3, two temporal covariates, quantity of defoliated points within the cell during the previous year and the number of years elapsed since the first year of defoliation in the cell, as well as a spatio-temporal covariate, the number of defoliated stands in a radius of 30 km from the center of the cell during the previous year, were also forced in all models. In analyses 2 and 3, we added an additional candidate model that included only the spatio-temporal covariates (no environmental variables).

For each analysis, the model that was most likely to explain the observed defoliation patterns was selected based on Akaike's information criterion corrected for small sample sizes (AIC$_c$). Model averaging (Burnham and Anderson 2002) was used when the AIC$_c$ weight of the top-ranking model was <0.9. Average parameter estimates and unconditional standard errors were calculated from all candidate models. Multicollinearity between the environmental variables was assessed using variance inflation factors (VIF). One model, which included hardwood content and degree-days, was excluded from all three analyzes because of a VIF >5, indicating the presence of collinear variables.

To facilitate assessment of their relative contribution in the models, all variables were standardized before the statistical analyses (Gelman 2008). We used the AICcmodavg package (Mazerolle 2011) in R (R Development Core Team 2011) to compare models and implement multimodel inferences to assess the effect of variables on defoliation probability.

We assessed more general patterns of outbreak synchrony using a non-parametric covariance function. This function allows estimating the scale at which defoliations are synchronous, based on a three dimensional matrix comprising the x and y coordinates of the central location of each cell, as well as the presence/absence of defoliations in a given cell for all years between 2003 and 2011. The analyses were done using the sncf function in package ncf in R (Bjornstad 2012). Because the estimated covariance functions are likely to be biased at the longest lag distances, we used a maximal distance of 1,000 km, which is shorter than the ca. 1,500 km distance that separates the extreme eastern and western defoliated cells. Confidence intervals around the function were built using a bootstrap resampling technique with 1,000 replications (Bjornstad 2012).

Results

Influence of environmental factors on defoliation epicenters at the regional scale

The most parsimonious model regarding the location of defoliation epicenters was the one which comprised elevation and abundance of balsam fir (w = 0.72, $r^2 = 0.19$) (Table 2). Higher elevations correspond with a lower probability of defoliation, and a higher balsam fir abundance corresponds with a higher probability of defoliation (Table 3). This model was six times more likely (0.72/0.12) to explain defoliations during the outbreak initiation phase than the second best model. The model-averaged standardized coefficients indicate that in the observed range of variation, initial location of defoliation epicenters is much more sensitive to variations in elevation than to variations in balsam fir abundance (Table 3). An AIC_c difference of 58 between the model with elevation alone and the model with balsam fir alone (Table 2), as well as the fact that the six top-ranking models include elevation (Table 2), support the hypothesis that elevation is the most important factor.

Influence of environmental factors on outbreak expansion at the regional scale

Regarding the influence of environmental variables on the expansion of defoliation epicenters, the most parsimonious model was the one comprising distance from previous defoliation (negative influence), abundance of hardwoods (negative) and elevation (negative) (w = 0.76, $r^2 = 0.34$) (Tables 4, 5). This model was 8.4 times more likely than the second best model (0.76/0.09) to explain defoliations during the outbreak expansion phase. For the observed range of variation for these three variables, the model-averaged standardized coefficients indicate that this model is more sensitive, by decreasing importance, to variations in distance from previous-year defoliations, abundance of hardwoods and elevation (Table 5).

Influence of environmental factors on population increases at the cell scale

The most parsimonious model for the prediction of defoliation level inside individual cells indicate that

Table 2 Relative support for candidate models describing the effect of environmental variables on initial location of spruce budworm epicenters

Candidate models	K	AICc	ΔAICc	w	LL
elevation+fir	3	371.9	0.0	0.72	−183.0
elevation+hardwoods	3	375.4	3.5	0.12	−184.7
elevation+drain+dd	4	376.2	4.3	0.08	−184.1
elevation+drain+age	4	377.6	5.7	0.04	−184.8
elevation	2	378.8	6.8	0.02	−187.4
elevation+spruce	3	380.3	8.3	0.01	−187.1
drain+spruce	3	425.4	53.5	0	−209.7
drain+fir	3	427.1	55.2	0	−210.6
dd+fir	3	430.6	58.6	0	−212.3
age+fir	3	433.0	61.0	0	−213.5
drain	2	433.5	61.5	0	−214.7
drain+hardwoods	3	435.3	63.4	0	−214.7
fir	2	436.4	64.4	0	−216.2
age	2	439.8	67.8	0	−217.9
age+hardwoods	3	440.0	68.1	0	−217.0
age+spruce	3	441.1	69.1	0	−217.5
spruce	2	441.4	69.5	0	−218.7
dd+spruce	3	443.4	71.5	0	−218.7
dd	2	443.4	71.5	0	−219.7
hardwoods	2	444.2	72.3	0	−220.1

The models are ranked according to Akaike's information criterion corrected for small sample size (AICc). Number of estimated parameters including the intercept (K), the difference in AIC_c (ΔAIC_c), AIC_c weight (w) and log-likelihodd (LL) are also provided. "fir", "spruce" and "hardwoods" are the proportion of stands dominated or co-dominated by balsam fir, black spruce and hardwoods inside each cell, respectively. "dd" is the average degree-days above 5 °C, "dist" is the distance from the closest previously defoliated cell, "age" is the proportion of mature and old stands, and "drain" is the proportion of stands with mesic drainage

abundance of balsam fir and degree-days above 5 °C are the most important environmental factors that explain defoliation patterns (Table 6). Defoliations increase faster when there is more balsam fir stands in the cell, and when the number of degree days above 5 °C is relatively low (Table 7). The most parsimonious model has a very high relative probability of w = 1 during this outbreak development stage (Table 6). The spatio-temporal covariates, the amount of defoliation inside the cell during the previous year, as well as the amount of defoliation in the surrounding cells, are also very important in the model (Table 7). Temporal changes in the proportion of defoliated

stands associated with representative values of the two environmental variables (amount of balsam fir, degree-days above 5 °C) are shown in Fig. 5.

Table 3 Averaged standardized coefficients of the environmental variables explaining the initial location of spruce budworm epicenters

Predictor	Average coefficient	95 % CL
elevation	−1.2080	(**−1.5426** to **−0.8735**)
fir	0.4101	(**0.1518** to **0.6683**)
hardwoods	−0.3409	(**−0.6332** to **−0.0486**)
drainage	−0.2469	(**−0.4697** to **−0.0242**)
dd	−0.1720	(−0.4395 to 0.0954)
age	−0.0806	(−0.3976 to 0.2365)

95 % confidence limits (CL) are shown (CL in bold exclude 0). Variables that were absent from the best models (sum of weights <0.95; Table 2) are not presented

Spatial synchrony

The spatial covariance function, which estimates spatial synchrony as a function of distance, is shown in Fig. 6, and indicates that synchrony is relatively high locally (0.65). Average correlation at the scale of the province (0.43) corresponds with the level of correlation observed at a distance of 400 km. Correlation declines with increasing distance up to a distance of 800 km, where spatial synchrony reaches a value near 0, but increases again for distances larger than 800 km, even if the 95 % bootstrap confidence interval is larger for these distances.

Discussion

The results of this study indicate that environmental factors can play a different role depending on how

Table 4 Relative support for candidate models describing the effect of environmental variables and distance from previously defoliated cells on the cell-to-cell expansion of spruce budworm defoliations

Model[a]	K	AIC$_c$	ΔAIC$_c$	w	LL
dist+elevation+hardwoods	4	1,218.08	0.00	0.83	−605.03
dist+hardwoods	3	1,223.01	4.93	0.07	−608.50
dist+age+hardwoods	4	1,223.58	5.50	0.05	−607.78
dist+drain+hardwoods	4	1,223.99	5.91	0.04	−607.98
dist+elevation+dra+dd	5	1,240.06	21.98	0.00	−615.02
dist+dd+fir	4	1,243.47	25.39	0.00	−617.73
dist+dd	3	1,244.82	26.74	0.00	−619.40
dist+dd+spruce	4	1,246.70	28.62	0.00	−619.34
dist+spruce	3	1,272.96	54.88	0.00	−633.47
dist+drain+spruce	4	1,273.86	55.78	0.00	−632.92
dist+age+spruce	4	1,274.75	56.67	0.00	−633.36
dist+elevation+spruce	4	1,274.96	56.88	0.00	−633.47
dist+drain	3	1,285.30	67.22	0.00	−639.64
dist+drain+fir	4	1,285.31	67.24	0.00	−638.65
dist+elevation+drain+age	3	1,285.54	67.46	0.00	−639.77
dist+age+fir	2	1,285.96	67.88	0.00	−640.98
dist+age	3	1,286.40	68.32	0.00	−640.19
dist+fir	4	1,286.97	68.89	0.00	−639.47
dist	4	1,287.37	69.29	0.00	−639.68
dist+elevation	3	1,287.43	69.35	0.00	−640.71
dist+elevation+fir	5	1,288.28	70.20	0.00	−639.13

The models are ranked according to Akaike's information criterion corrected for small sample size (AIC$_c$). Variable "dist" is distance from the closest previously defoliated cell. Other variables are as in Table 2

defoliation surveys are examined. Elevation was more determinant with respect to the initial location of defoliation epicenters, whereas variables associated with forest composition were determinant during the cell-to-cell and within-cell expansion phases. A phase-based approach also allowed us to include some phase-specific covariates in the models, such as distance from previous-year defoliations, which is determinant during the cell-to-cell expansion phase, and defoliation level during the previous year, which is important to explain defoliation expansion inside individual cells. The spatial covariance function also indicates that even if there is a drop in correlation between distances of 600 and 900 km (Fig. 6), which is probably explained by different defoliation patterns in the epicenters located in the central portion of the territory (E2 and E9), defoliations are correlated for distances shorter and longer than this interval. However, correlations are much stronger for distances <400 km, which is probably explained in part by the fact that by contrast with the relatively large longitudinal gradient, the latitudinal gradient is generally shorter than this distance (Fig. 4).

Table 5 Averaged standardized coefficients of the variables explaining the cell-to-cell expansion of spruce budworm defoliations

Predictor	Average coefficient	95 % CL
dist	−1.5222	(**−1.7365** to **−1.3080**)
elevation	−0.2194	(**−0.3858** to **−0.0531**)
hardwoods	−0.6656	(**−0.8758** to **−0.4554**)
dd	0.2536	(−0.0587 to 0.5658)
age	−0.0677	(−0.2076 to 0.0721)

95 % confidence limits (CL) are shown (CL in bold exclude 0). Variables that were absent from the best models (sum of weights <0.95; Table 4) are not presented

Table 6 Relative support for candidate models describing the effect of environmental variables and spatio-temporal covariates on within-cell defoliation levels
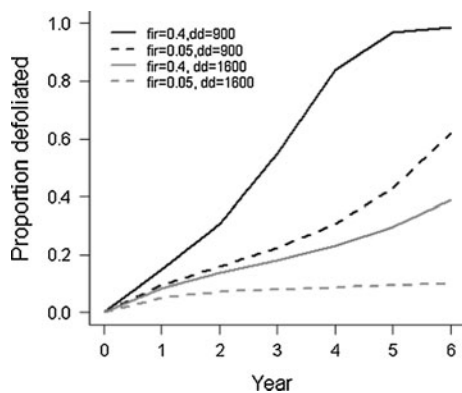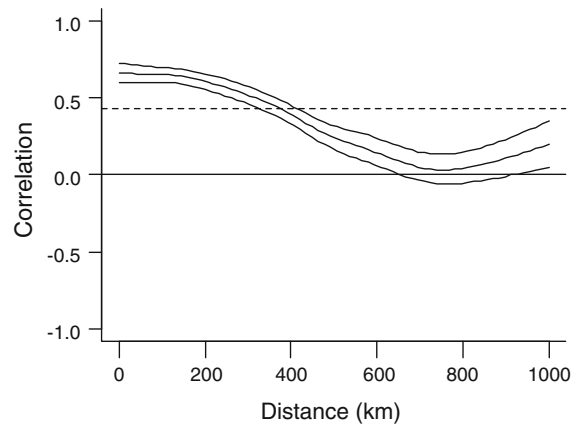
Model	K	AICC	DeltaAICC	w
time+prev_def+surr_def+dd+fir	6	21,274	0	1.00
time+prev_def+surr_def+age+hardwoods	6	21,479	205	0.00
time+prev_def+surr_def+drain+hardwoods	6	21,481	206	0.00
time+prev_def+surr_def+hardwoods	5	21,500	226	0.00
time+prev_def+surr_def+elevation+hardwoods	6	21,500	226	0.00
time+prev_def+surr_def+elevation+drain+dd	7	21,594	320	0.00
time+prev_def+surr_def+dd+spruce	6	21,604	330	0.00
time+prev_def+surr_def+dd	5	21,625	351	0.00
time+prev_def+surr_def+elevation+fir	6	21,627	353	0.00
time+prev_def+surr_def+drain+fir	6	21,694	420	0.00
time+prev_def+surr_def+age+fir	6	21,705	431	0.00
time+prev_def+surr_def+fir	5	21,713	439	0.00
time+prev_def+surr_def+age+spruce	6	22,448	1,174	0.00
time+prev_def+surr_def+drain+spruce	6	22,474	1,200	0.00
time+prev_def+surr_def+elevation+spruce	6	22,474	1,200	0.00
time+prev_def+surr_def+spruce	5	22,479	1,205	0.00
time+prev_def+surr_def+elevation+drain+age	7	22,618	1,344	0.00
time+prev_def+surr_def+elevation	5	22,633	1,359	0.00
time+prev_def+surr_def+age	5	22,683	1,409	0.00
time+prev_def+surr_def	4	22,785	1,510	0.00
time+prev_def+surr_def+drain	5	22,786	1,512	0.00

The models are ranked according to Akaike's information criterion corrected for small sample size (AIC_c). "time" is the number of years since the first year of defoliation in the cell, "prev_def" is the proportion of defoliated stands inside the cell during the previous year, "surr_def" is the cumulative area covered by defoliated stands during the previous period inside a 30 km buffer surrounding the cell. Other variables are as in Table 2

Table 7 Averaged standardized coefficients of the environmental variables explaining the within-cell expansion of spruce budworm defoliations

Parm	Coef	SE	Lower CL	Upper CL
prev_def	0.957	0.010	**0.938**	**0.976**
surr_def	0.262	0.008	**0.246**	**0.278**
fir	0.173	0.009	**0.155**	**0.191**
dd	−0.271	0.013	**−0.296**	**−0.245**
time	−0.042	0.013	**−0.067**	**−0.017**

95 % confidence limits (CL) are shown (CL in bold exclude 0). Variables that were absent from the best models (sum of weights <0.95; Table 4) are not presented

Fig. 6 Nonparametric spatial covariance function estimated from spruce budworm defoliation data. The *upper* and *lower lines* refer to the 95 % bootstrap confidence interval, and the *dashed horizontal line* indicates the level of average synchrony

Fig. 5 Increases in defoliation levels within cells as a function of proportion of balsam fir (fir) and average degree days above 5 °C (dd). The values were obtained from the best model presented in Table 6, with the coefficients estimated from the non-standardized data. Year 1 corresponds with the year when defoliations were first observed in the cell. The variable corresponding with the abundance of defoliations in the surrounding cells was fixed at surr_def = 100

Influence of environmental factors on outbreak development

Epicenters can be defined empirically as the first places where defoliations are observed at the beginning of a large-scale outbreak (Hardy et al. 1983; Royama 1984; Aukema et al. 2006). In the case of the SBW, the emergence of defoliations in such epicenters is explained by local population dynamics, notably the relationship between SBW populations and their natural enemies (Royama 1984; Royama et al. 2005). In this study, elevation was the environmental factor that had the most influence on the location of initial defoliations. This is surprising, considering how

rarely this factor is mentioned in the insect outbreak literature. Most studies refer to the importance of the elevational gradient for insects in connection with its effect on temperature (Blais 1958; Hodkinson 2005; Raffa et al. 2012), but because a variable relating to average degree-days was integrated directly in the models and was not present in the most parsimonious models, this explanation seems unlikely. Magnussen et al. (2004) have proposed that in western Canada the effect of elevation on SBW defoliation is explained by different forest compositions and edaphic characteristics in valley bottoms, but variables related to these two factors—abundance of hardwoods, spruce and fir and drainage—had a weak direct effect in the most parsimonious models (Table 2). Daily temperature variations, wind patterns and humidity levels close to river courses, are other examples of climatic parameters that could vary according to topographic position (Geiger et al. 2003), and that could influence insect populations (Pedgley et al. 1990; Hodkinson 2005).

Expansion of defoliations from cell to cell was strongly contagious, as indicated by the high coefficient associated with the spatial covariate (Table 3). One obvious explanation for this contagious pattern is the role of insect dispersal. Relatively short-distance immigration of moths from adjacent cells is likely to increase the probability that local SBW populations escape density dependent regulation mechanisms (Johnson et al. 2006; Régnière and Nealis 2007). More long-distance flights could also play a similar role, or lead to the establishment of defoliation

hotspots relatively far from the main epicenters (Greenbank et al. 1980; Anderson and Sturtevant 2011). These spots could eventually act as source populations during subsequent years, thus accelerating overall outbreak progression. Nonetheless, the role of dispersal in the expansion of SBW outbreaks is debated, because what appears as a contagious process could be the result of slightly asynchronous but relatively independent local population increases (Royama 1984). Even though defoliation data obtained from aerial surveys is of limited use to separate the respective contributions of moth immigration and local increases, the very strong effect of the spatial covariate suggests that dispersal played an important role during the studied outbreak.

Outbreak expansion from epicenters is also influenced by hardwood abundance (negative influence) and elevation (negative influence). The negative effect of hardwood content on defoliation expansion becomes particularly obvious after 2007, when the outbreak clearly progressed much slower in the western part of the province (Fig. 2), where hardwood abundance was dramatically higher (Table 1). Less explosive population increases in forests dominated by non-hosts have been mentioned in the past, and may be explained by a lower probability that dispersing moths and larvae land on suitable hosts (Nealis and Régnière 2004), and by more favorable conditions for natural enemies and density-dependent regulation when hardwoods are present (Quayle et al. 2003). Different hardwood species might have a different value in this respect, but the effect of variations in hardwood species composition (Table 1) was not examined in this study.

Our analyses indicate that within the 15 × 15 km cells, the proportion of defoliated stands is strongly and positively related to the amount of defoliation during the previous year, emphasizing the probable role of a relatively short-distance type of dispersal during this phase. Defoliations also increase faster if the cell contains an important amount of stands dominated by balsam fir, reinforcing the notion that balsam fir remains a tree species of major importance for the expansion of budworm populations in eastern Canada (MacLean 2004). Average degree-days above 5 °C also play a significant role at this scale, indicating that the proportion of defoliated stands increases more rapidly in colder locations. This could indicate that within the latitudinal climatic gradient that was

sampled in this study, optimal conditions for SBW population development are found in the north, and that conditions in the south are sub-optimal. This would be consistent with the findings of Régnière et al. (2012), who indicated that relatively warm conditions recently observed or projected in southern Quebec as a consequence of climate change could be detrimental for SBW populations.

Long-term implications

The current study examines only one synchronized outbreak, which could be considered as a form of pseudo-replication. It has been demonstrated that even if insect outbreaks sometimes occur at relatively regular temporal intervals (ca. 30–40 years for the SBW), they can exhibit staggeringly variable development patterns, particularly regarding the speed at which they initially expand (Morin et al. 2007). When the development of the current outbreak is compared with the previous ones on the same territory, its expansion seems to be relatively slow and local, comparable to the 1950s outbreak, whereas the two other large scale outbreaks of the twentieth century (1910s and 1970s) appeared to exhibit much more explosive and synchronous expansions (Morin et al. 2007). Thus, the range of environmental conditions and defoliation patterns sampled in this study probably remains relatively narrow when compared with historical variability. This could also mean that the role of insect dispersal was disproportionately important during the initial development of the current outbreak compared with some previous outbreaks.

Nonetheless, the combined effect of compositional and climatic factors during the phases associated with defoliation expansion (analyses 2 and 3) strongly suggest that the development of a SBW outbreak is sensitive to environmental changes. When one compares the defoliation patterns observed during the current outbreak with those observed during the previous one (c.f. Morin et al. 2007), it appears that outbreak progression is relatively slow in the southwestern part of the province during the current outbreak. This could be explained by changes in environmental conditions from one outbreak to the next. For example, it is possible that this zone is now warmer and less optimal for SBW population development (Régnière et al. 2012). There is also a possibility that outbreak progression was slowed in

this part of the province because it now has a higher content of hardwood stands than in the past: an increase in hardwood content during the last decades has been observed in connection with the cumulative effect of past SBW outbreaks on forest composition (Bouchard et al. 2006, 2007; Duchesne and Ouimet 2006), and with the preferential harvesting of coniferous stands for sawlogs and for the pulp and paper industries (Ortuño and Doyon 2010). Temperature and composition are two factors that, combined with the fact that the outbreak began earlier in epicenter E2, could explain why density dependent regulation mechanisms caught up first with SBW populations in this location.

Ultimately, the duration and severity of defoliation episodes will also determine the amount of host mortality (MacLean 2004; Pothier et al. 2012). Outbreak duration and collapse could not be examined in this study because SBW populations were still in expansion in most epicenters. There is some evidence that the collapse of insect outbreaks is determined by factors that are not necessarily important in early outbreak development; for example, an increased synchrony has been observed as the outbreak progresses and epicenters coalesce (Aukema et al. 2006). The occurrence of disruptive meteorological patterns (Royama 1984), the action of natural enemies (Royama 1984) or changes in the health status of host plants (Régnière and Nealis 2007), could also play a role during outbreak collapse.

Management implications

The question of how much the development of an insect outbreak can be influenced by human-induced modifications in forest composition has obvious implications for natural resource management (Robert et al. 2012). In the case of the SBW, it seems that both the periodicity of outbreaks (Royama et al. 2005) and epicenter location (this study) would be difficult to control through preventive management actions, as they are apparently not very sensitive to variations in forest characteristics. However, the fact that forest composition is important during outbreak expansion (between and within cells) reinforces the notion that reducing host species content could decrease the risk associated with future outbreak damage. The study also generally supports that northern stands of host

species that were little affected during previous outbreaks (Blais 1983) are more susceptible to budworm attack during the current outbreak, perhaps due to the effect of climate warming (Régnière et al. 2012). On the other hand, balsam fir dominated stands and landscapes remain a crucial habitat for many plant and animal species in boreal forests (Desponts et al. 2004), including when they have been affected by SBW-caused mortality (Tremblay et al. 2007). Hence, replacing balsam fir with non-hosts, particularly on the massive scales that would be required to have an effect on SBW dynamics, could be costly, and have negative implications for biodiversity conservation. This potential trade-off between ecological and economic interests should be fully acknowledged by forest managers before making decisions regarding the reduction of SBW host species content.

More generally, this study proposes a different way of modelling insect outbreaks, breaking up outbreak development in distinct landscape-level sub-processes. This allows emphasizing the differential influence of the environmental factors and of specific population processes such as dispersal during different phases of outbreak development. Some previous studies have implied that the influence of environmental factors can vary during outbreak development, for example in connection with the increased synchrony that is generally observed in the later phases of outbreak development (Nealis and Régnière 2004; Aukema et al. 2006), but this was never modelled explicitly at the landscape level to our knowledge. Even if landscape-level models lack in mechanistic details compared with population-level models (e.g. Royama 1984; Régnière and Nealis 2007), they present the advantage of being more easy to parameterize for large regions and a wide range of environmental conditions (Sturtevant et al. 2004; James et al. 2011). How the type of landscape-level model used in this study would perform to reconstruct past outbreaks, improve our understanding of inter-outbreak variability, and help predict the development of future outbreaks, remains an open but very important question.

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