Effects of forest management legacies on spruce budworm (*Choristoneura fumiferana*) outbreaks

Louis-Etienne Robert, Daniel Kneeshaw, and Brian R. Sturtevant

Abstract: The "silvicultural hypothesis" of spruce budworm (*Choristoneura fumiferana* Clem.) dynamics postulates that increasing severity of spruce budworm outbreaks over the last century resulted from forest conditions created by past management activities. Yet, definitive tests of the hypothesis remain elusive. We examined spruce budworm outbreak dynamics (synchrony, periodicity, and intensity) in the 20th century using historical reconstruction from tree-ring chronologies sampled within 19 sites in a large ecoregion located on the border of Minnesota and Ontario. The study encompassed three areas affected by contrasting management legacies: a fine-grained area (Minnesota, six sites, average cut size = 17 ha), a coarse-grained area (Ontario, six sites, average cut size 10 times that of Minnesota), and a conservation zone (seven sites) with little recent harvest activity overlapping the border. Results suggest important differences in outbreak dynamics between the forest management zones that cannot be explained by differences in climate among sample sites. Budworm outbreaks within the conservation zone were more synchronous, with more trees per site affected and less frequent outbreaks than sites sampled within fine-scale managed areas. Outbreak dynamics within forests managed at coarser scales suggest a mixture of the conservation and fine-scale management zone outbreak patterns. Potential factors affecting differences in the observed outbreak patterns include forest pattern, composition, and age. Our study generally supports the silvicultural hypothesis and emphasizes that management legacy effects on spruce budworm dynamics should be observable at landscape scales, as well as at local scales.

Résumé : L'hypothèse sylvicole de la dynamique de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) postule que l'augmentation de la sévérité des épidémies au siècle dernier est le résultat des conditions forestières créées par l'aménagement, mais un test définitif de cette hypothèse reste élusif. Nous avons examiné la dynamique des épidémies de la tordeuse des bourgeons de l'épinette du 20e siècle (synchronisme, périodicité et intensité) par la dendrochronologie, et ce sur 19 sites à l'intérieur d'une écorégion située à la frontière du Minnesota et de l'Ontario, où les frontières politiques ont créé un contraste entre l'héritage de l'aménagement : récolte à échelle fine au Minnesota (six sites, coupe de 17 ha en moyenne), récolte à échelle grossière en Ontario (six sites, coupe d'environ 10 fois la taille de coupe moyenne du Minnesota), zone de conservation (sept sites) traversée par la frontière où peu d'aménagements récents ont été effectués. Les résultats suggèrent des différences importantes dans la dynamique des épidémies entre les zones d'aménagement forestier. Ces différences sont difficilement explicables par les différences climatiques entre les sites. Les épidémies de tordeuse de bourgeons de l'épinette à l'intérieur de la zone de conservation étaient moins fréquentes, plus synchrones et avec un plus haut pourcentage d'arbres affectés que la zone aménagée à l'échelle fine. Les épidémies à l'intérieur de la zone d'aménagement grossier suggèrent un mélange de la zone de conservation et de la zone d'aménagement fin. Les facteurs potentiels pouvant affecter la dynamique des épidémies sont la composition, l'age et la configuration des espèces hôtes. Notre étude supporte donc l'hypothèse sylvicole et met en évidence que les effets observables de l'héritage forestier sur la dynamique des épidémies se produisent à l'échelle locale comme à l'échelle du paysage.

Introduction

Current landscapes are a legacy of disturbances created by both natural and human causes (Turner 1989). Forest management can radically change ecosystem dynamics, thereby creating legacy effects that persist for decades (Dale et al. 2001; Spies et al. 1994). Such changes in forest patterns and processes are hypothesized to influence insect outbreaks by affecting landscape abundance and connectivity of susceptible host (Raffa et al. 2008). As an example, clearcutting that protects advance regeneration increases the proportion of balsam fir (*Abies balsamea* (L.) Mill.) in the landscape (MacLean 1984), thereby increasing the abundance and connectivity of host species for the eastern spruce budworm (*Choristoneura fumiferana* Clem.). Researchers have speculated that logging and other management activities (e.g., fire suppression) have interfered with natural succession to increase forest susceptibility to spruce budworm, resulting in observed increases in severity of spruce budworm outbreaks during the 20th century (Blais 1983; Swetnam and Lynch 1993). This so-

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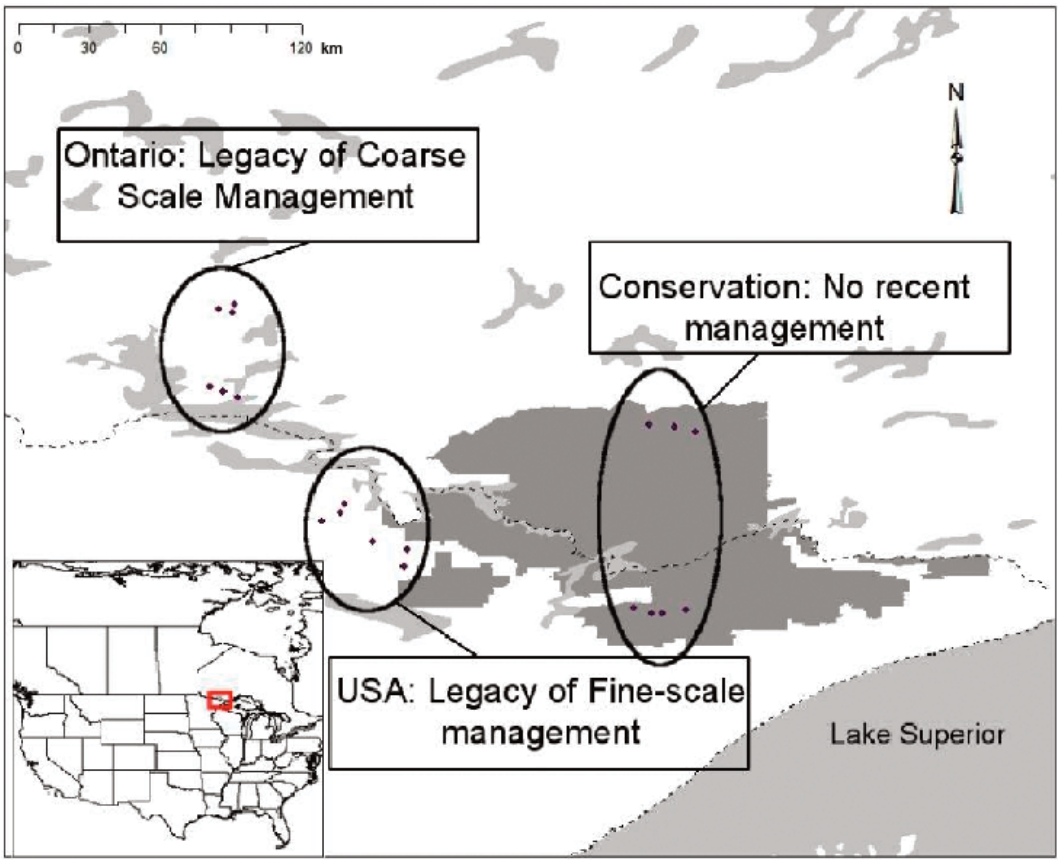
Fig. 1. The Border Lakes landscape study area located at the border between Ontario (Canada) and Minnesota (United States). Points represent sampling sites for dendrochronological reconstructions of outbreaks.



called "silvicultural hypothesis" suggests that the converse is also true, i.e., proactive forest land management could decrease forest susceptibility to spruce budworm outbreaks; however, this hypothesis has never been rigorously tested (Miller and Rusnock 1993).

Eastern spruce budworm is an economically important forest defoliator that readily disperses over long distances (Greenbank et al. 1980) and is well-known for the broad-scale spatial synchrony of its outbreaks. Outbreak synchrony of oscillating defoliator populations is thought to result from regionally correlated weather perturbations (Royama 2005) but may be influenced by landscape conditions at finer, landscape scales (Candau and Fleming 2005; Haynes et al. 2009*a*). Host connectivity may influence outbreak synchrony and limit associated forest damage by affecting defoliator dispersal (Ims et al. 2004), movement of natural enemies from adjacent habitats (Cappuccino et al. 1998; Eveleigh et al. 2007), or both.

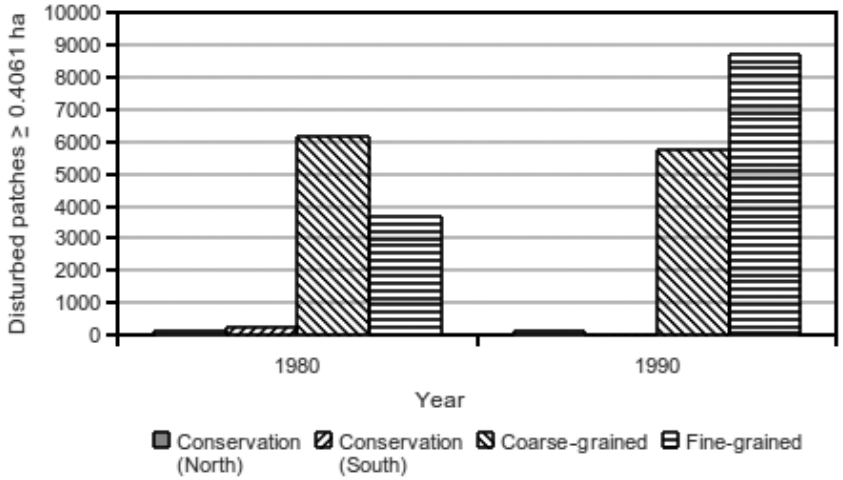
The impacts of host connectivity on insect outbreaks have been demonstrated in other insect species. As an example, the winter moth (*Operophtera brumata* L.) causes less defoliation during outbreaks in management-fragmented landscapes (Wesołowski and Rowiński 2006). Conversely, forest fragmentation led to longer more severe outbreaks in isolated stands containing host species of the forest tent caterpillar (*Malacosoma disstria* Hubn.) (Cooke and Roland 2000; Roland 1993; Roland et al. 1998). Although previous studies have investigated the effects of landscape composition on budworm impacts (Cappuccino et al. 1998; MacKinnon and MacLean 2004), no studies have been conducted on the effects of landscape pattern on budworm outbreak dynamics. This lack of study is perhaps due to the challenge of locating sufficiently large landscapes that differ with respect to land management but are similar with regard to weather gradients, forest composition, and other potentially confounding factors.

In this paper, we address the silvicultural hypothesis by contrasting spruce budworm outbreak patterns within a large (2 million ha) ecoregion containing three different forest land management legacies: a conservation zone (no active management), a fine-grained forest management zone with small cutblocks (17 ha average), and a coarse-grained forest management zone with large cutblocks (an order of magnitude larger). Our hypotheses are twofold: (*i*) outbreaks should be more synchronous and last longer in more connected natural forests in the conservation area as they have higher host connectivity and stand susceptibility compared with younger and more fragmented managed landscapes; and (*ii*) spruce budworm outbreaks should be more synchronous and of longer duration within coarse-grained managed areas with larger patches containing host species than within fine-grained managed areas.

Study area

The study area is defined by the Border Lakes ecoregion (BLE: 1 870 000 ha), where political boundaries have resulted in starkly contrasting management legacies (Fig. 1).

Fig. 2. Summary graph of land-cover remote sensing showing the quantity of disturbed patches (in hectares (ha)) that are larger than or equal to 0.4061 ha from 1980–1990. Disturbance refers to all disturbances (fire, harvest, insect, and wind) based on a change from a forested state to a nonforested state between image dates in the time series.



The combination of harvest regulations, road networks, and land ownership has created a fine-scale pattern of harvesting on the Minnesota side of the BLE, with harvest units averaging 17 ha from the 1930s to 1990 (Host and White 2003). By contrast, harvest units on the Ontario side of the BLE are an order of magnitude larger (Rempel et al. 1997; Suffling et al. 2003). Harvest rates over the last three decades were relatively similar between the managed zones of Minnesota and Ontario (B.R. Sturtevant, unpublished data, 2010). Between the two managed zones lies a conservation zone formed by Quetico Provincial Park in Ontario and the Boundary Water Canoe Area Wilderness in the United States. Although partial harvesting occurred in the past within the conservation area, clearcut harvesting was uncommon and all harvesting was permanently banned by the 1960s. To confirm the different legacies, we evaluated the average patch size (regardless of disturbance type) from remote sensing data of land cover maps in 1980 and 1990. Before evaluating the average patch size, distributions were area-weighted, i.e., the frequency of a patch of a given size observation was multiplied by the number of disturbed cells within the patch. We used weighted patch size distributions to reflect the relative likelihood of selecting a patch of a given size when randomly selecting a disturbed forest cell from the map. For the conservation zone, the average patch size was 13.34 ha (SD = 19.14). The coarse-grained Ontario zone had a higher number of larger patches, with an average patch size of 271.12 ha (SD = 440.17), and the fine-grained Minnesota area had an average patch size of 31.91 ha (SD = 42.78). Figure 2 also shows the similarity between the amount of land disturbed per time period for both the coarse-grained zone and the fine-grained zone. In comparison, the conservation zone has been subjected to less disturbance than the other managed areas.

The three management zones shared a common early management history. Region-wide forest harvest activity started at the end of the 19th century and focused on selective harvest of the "big pines" (*Pinus strobus* L., *Pinus resinosa* Ait.) using waterways across the majority of the BLE. This was followed in the 1910s by a campaign of fire suppression that may have varied both in efficacy and time of application depending upon the region (Heinselman 1973). After World War II, the broad use of heavy machinery for clearcut pulpwood harvesting and transportation by road was common on both sides of the border and signaled the beginning of modern industrial forestry. It was during this modern pulpwood era that management activities diverged among zones.

The forest matrix in the three study regions tends towards a coniferous mixed forest. Studies conducted in the Boundary Waters Canoe Area concluded that, since 1910, decreasing fire frequency has changed the dominant pathway of succession from even-aged jack pine (*Pinus banksiana* Lamb.) and aspen (*Populus* spp.) to an uneven age structure with a complex mixture of spruce (*Picea* spp.), paper birch (*Betula papyrifera* Marsh.), and balsam fir (Frelich and Reich 1995). In the absence of fire, small-scale disturbances such as wind, insects, and senescence have become the main disturbances, with the notable exception of a major blowdown event that occurred very recently (Mattson and Shriner 2001). The managed part of the landscape contains similar forest types but has a higher dominance of early successional forest classes due to forest management operations (Wolter and White 2002).

Methods

Data collection

Spruce budworm outbreaks were reconstructed using tree-ring chronologies of white spruce (*Picea glauca* (Moench) Voss). White spruce rather than balsam fir was selected because of its greater longevity and its higher probability of surviving spruce budworm defoliation (Hennigar et al. 2008). A total of 19 sites were located within mesic forest types to account for the potentially confounding effect of local environment on the dendronological reconstruction. These sites were separated into northern and southern areas within each zone to compare outbreak characteristics at different latitudes as a proxy for climatic conditions and also to compare differences in outbreak parameters within zones (Fig. 1). Northern sites in the conservation area were of the same approximate latitude as southern sites in the coarse-grained zone, whereas southern sites in the conservation area are

Table 1. COFECHA output of summary statistics (mean ring width, sensitivity, and intertree correlation) of the dendrochronological reconstruction for the northern and southern part of each management zone.

					Sensitivity		
Lattitude	Zone	No. of trees	Time span	Mean ring width (mm)	Mean	SD	Intertree correlation
North	Conservation	20	1906–2005	2.51	0.268	1.356	0.643
South	Conservation	24	1897–2005	1.93	0.277	1.026	0.604
North	Fine	22	1903–2005	2.45	0.277	1.363	0.63
South	Fine	22	1920–2005	2.87	0.263	1.508	0.61
North	Coarse	19	1895–2005	2.34	0.28	1.157	0.604
South	Coarse	17	1932–2005	2.45	0.272	1.159	0.571

even further south (by 12 km) than southern sites in the fine-grained zone. Northern and southern sites in the conservation area were separated by 75 km. Sample sites were selected for ease of access in stands located alongside roads or, in the roadless wilderness, along river corridors and lakeshores. A suitable stands was selected when 5–15 canopy white spruce were located from the road or river. While sampling, we avoided stands located on high slopes or in very humid areas. All sampled white spruce had a minimum of 30 cm diameter at breast height (DBH), and we sampled two cores taken at a perpendicular angle at 1 m height from a minimum of at least five host trees per site. At least 15 nonhost trees from stands located from the road or river (*P. banksiana* and *P. resinosa* of at least 30 cm DBH) were also cored at one site within each management zone (with the exception of the conservation zone in which 15 trees were cored in both the northern and southern sites) to serve as a comparison to host chronologies. Cores were stored in plastic straws to be mounted later and sanded (80, 150, 220 grit size).

Tree ring chronologies

Tree-ring widths were measured using a Velmex unislide measuring table with an accuracy of 0.001 mm connected to a computer (Velmex Incorporated, Bloomfield, New York). We visually crossdated cores within tree and sites and used the program COFECHA (Holmes 1997) to locate missing or false rings. Tree chronologies were aggregated by northern and southern parts of each management zone, and an additional COFECHA test was conducted to correct previously undetected errors at the site level and eliminate problem series. Index chronologies were calculated using the program ARSTAN (Cook 1985; Holmes 1997), with a cubic smoothing spline to detrend the series and remove the age-related trend in growth (Cook 1985). The spline parameters were set to a 50% frequency response cutoff of 60 years (Bouchard et al. 2006; Boulanger and Arseneault 2004). From 36 to 44 trees were used to develop mean chronologies for each of the three management zones, and Table 1 provides summary statistics for the northern and southern parts of each management zone.

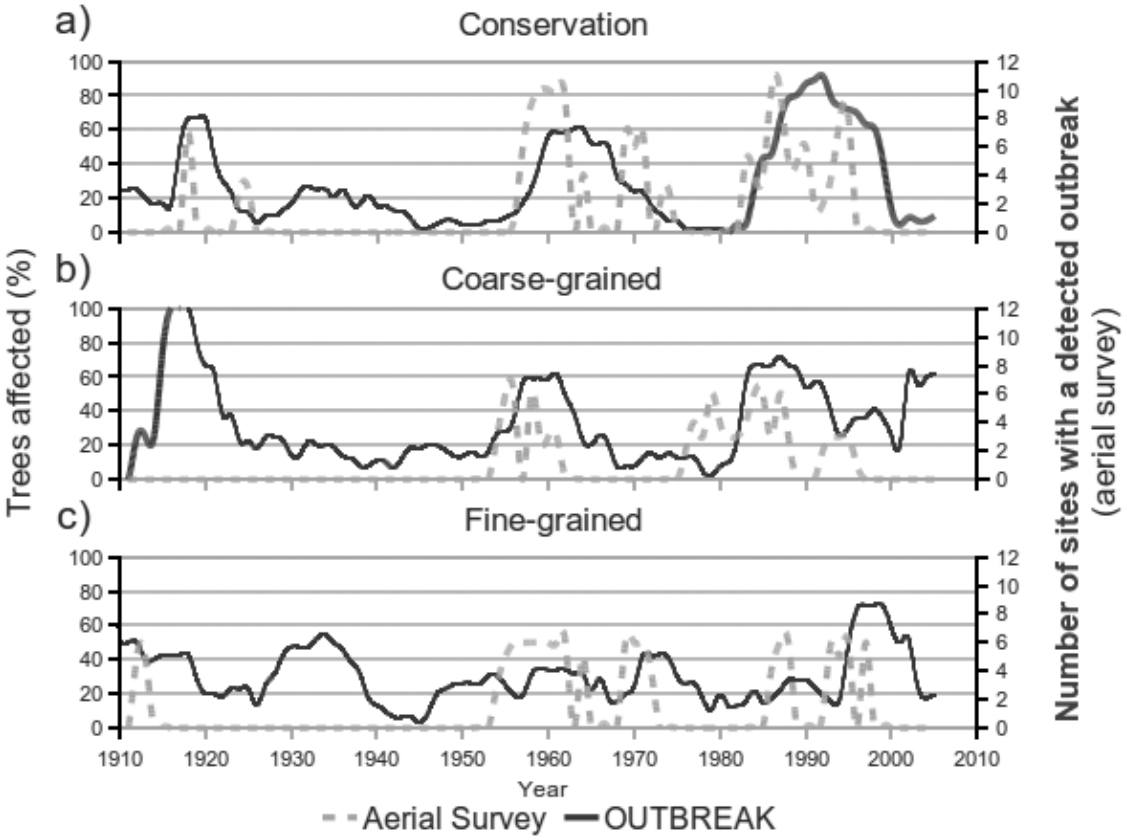
Outbreak reconstruction

A spruce budworm outbreak was defined for a given tree-ring chronology when a growth reduction was observed for more than 5 years with at least one year with a reduction greater than 1.28 SDs using the program OUTBREAK (Holmes and Swetnam 1996). This software has been used extensively in various spruce budworm outbreak reconstruction studies (Bouchard et al. 2006; Boulanger and Arseneault 2004). These thresholds should be sufficient to detect outbreaks of the spruce budworm and avoid confounding potential consequences of other defoliating insect. We are not aware of other defoliator species capable of causing growth reductions of sufficient magnitude in spruce to be identified as an outbreak in this region (W. Mattson, US Forest Service (retired), personal communication, 2010). This method has been widely used in researching past spruce budworm outbreaks (Blais 1983; Jardon et al. 2003; Morin 1994). Outbreak detection with the program OUTBREAK was more efficient when applied solely to host species (Bouchard et al. 2006). Thus nonhost chronologies were only used to validate detected outbreaks by visual comparison of the growth pattern during outbreak and nonoutbreak years. Because nonhost chronologies were introducing errors in the outbreak reconstruction, we validated our historical reconstruction using aerial survey data from 1910 to 2000 in a 1 km buffer around each dendrochronological site. We examined the correspondance between the two datasets as shown in Fig. 3, which indicates that the reconstruction is accurate for the conservation zone but a lag between survey data and the reconstruction for the other managed zones is present in the most recent outbreak.

Output from the program OUTBREAK was converted to a frequency graph to show the percentage of trees affected by each outbreak. Results were aggregated by each management zone and north–south groupings to evaluate our hypotheses and to ensure a reasonable number of tree replicates to define a given outbreak event. For the purpose of analysis, outbreaks were defined as occurring when the number of trees showing a growth reduction exceeded 25%. We found this value to allow an appropriate balance between identifying low-intensity outbreaks while minimizing the risks of including false outbreaks. We performed an additional sensitivity analysis by systematically varying this threshold value between 20% and 50% to evaluate the degree to which our conclusions were dependent on our definition of an outbreak.

Outbreak dynamics were characterized according to their relative spatial synchrony, periodicity, duration, and intensity. Synchrony, defined as spatial covariation in population density fluctuation (Bjørnstad et al. 1999), measures the degree of lag between outbreaks occurring in different areas. We used the degree of overlap in outbreaks between northern and southern sites within management zones as a relative indicator of spatial synchrony. Periodicity is the average interval between outbreaks, which we measured as the mean time period between the first year of successive outbreaks (Blais

Fig. 3. Comparison between the frequency graph from OUTBREAK and the aerial survey data taken at a 1 km buffer around each dendrochronological site: (*a*) conservation, (*b*) coarse-grained, and (*c*) fine-grained management zones. The left axis represents the output from OUTBREAK, and the right axis represents the number of sites experiencing outbreak for a given year.



1983). Intensity is often linked to population density and duration; for our study, we used the highest percentage of affected trees for each outbreak as a proxy to evaluate intensity. We also evaluated duration as the number of years that an outbreak lasted using our 25% cutoff definition of an outbreak.

Evaluation of confounding factors

The premise of our study is that forest management through its effect on forest fragmentation and composition will affect spruce budworm outbreaks among the different management zones. Different landscape structures of forests resulting from different management legacies (Minnesota, 17 ha cutblocks; Ontario, cutblocks 10 times the average of Minnesota; Conservation, no large-scale harvesting) have previously been established (James 2010; Wolter et al. 2008). To assess our premise, we measured forest composition both locally (local forest measurements were made using a metric factor 2 prism) and using remote sensing maps of basal area within 1 km neighborhoods (for balsam fir and for spruce species) for each dendrochronology sample site (Wolter et al. 2008). Spruce species were agglomerated as remote sensing was not specific enough to distinguish between white spruce and black spruce. However, it is important to note that these measurements represent current composition at the site selected for the presence of old white spruce. Hence the local (i.e., plot-scale) composition was expected to be biased toward higher white spruce content relative to the broader landscape. For this reason, the 1 km neighborhoods more accurately describe current composition for the study sites. The plot-level composition is, however, expected to best reflect local composition effects on spruce budworm outbreaks. For example, Campbell (2007) showed that although there was a weak effect of composition out to 1 km, the strongest composition effect occurred in the local stand and tree neighbourhoods. A nested MANOVA test was performed (north or south nested within zones) to detect differences in forest composition between sites, and ANOVA Tukey comparisons were performed when significant statistical differences were found. Current composition has, however, likely changed over the last century, i.e., the period for which outbreak patterns were estimated, and thus results should be interpreted prudently for effects in the past.

Climatic variation

Our sampling design was stratified by latitude to control for the influence of climate on spruce budworm outbreaks. Our assumption is that because sites are located in close proximity, the variation of climatic variables between sites should not be biologically meaningful. Because latitude is not a perfect proxy for climate, we summarized 10 key climatic variables that have been shown to influence budworm outbreaks and tested that assumption.

We summarized 10 key climatic variables (December, January, February, and May average and minimum mean monthly temperatures along with mean May and July precip-

itation) that have been shown to influence budworm outbreaks (Campbell 2007; Candau and Fleming 2005; Candau and Fleming 2011; Swetnam and Lynch 1993). Interpolated weather records were calculated for each year over the last century (1901–2000) using the geographic locations of each dendrochronoloy plot (McKenney et al. 2006). A nested MANOVA (north or south nested within zones) was performed to assess differences between sites, and ANOVA Tukey comparisons were performed when significant statistical differences were found.

Results

Outbreak reconstruction

The recurrence interval of spruce budworm outbreaks in the conservation zone was estimated to be 23 years, with average outbreak duration of 10 years, based on the 25% threshold of trees showing a growth reduction used to define outbreaks (Table 2). Four main outbreaks were detected in this zone over the last century: from 1917 to 1922, from 1932 to 1936, from 1958 to 1969, and from 1984 to 1999 (Fig. 4). The outbreak pattern was clear and well defined, with over 60% of the sampled white spruce trees in the conservation zone undergoing significant growth reductions during peak outbreak years with the exception of the 1932 outbreak.

The coarse-grained zone (Ontario) presented a recurrence interval of 32 years, with average outbreak duration of 15 years (Table 2). Data from the coarse-grained management zone indicated three main outbreaks during the 20th century (Fig. 4). The first outbreak started earlier than the chronology could detect but ended around 1928, and two other outbreaks can be identified from 1954 to 1963 and from 1983 to 2005.

In the fine-grained area (Minnesota), the recurrence interval for spruce budworm outbreaks was 14 years, with outbreak duration of 7 years (Table 2). The fine-grained area experienced three main outbreaks that were well defined. One of these outbreaks ended in 1919, another one occurred from 1928 to 1938, and the last occurred from 1995 to 2003 (Fig. 4). Additionally at least four smaller outbreaks were detected between these last two. These outbreaks mainly occurred from 1949 to 1955, 1958 to 1966, 1971 to 1977, and 1987 to 1991.

The number of outbreaks was similar for the coarse-grained and conservation zones (Table 2), whereas outbreaks were almost twice as frequent in the fine-grained zone. Duration was not similar between these zones but instead was similar between the conservation and fine-grained zone. The conservation zone thus seems to be less affected by outbreaks (i.e., few and of short duration) than the managed zones, where outbreaks were either more frequent or lasted longer. However, it should be noted that outbreaks observed in the coarse-grained zone were more severe, whereas outbreaks in the fine-grained zone were of lower intensity.

Sensitivity analysis

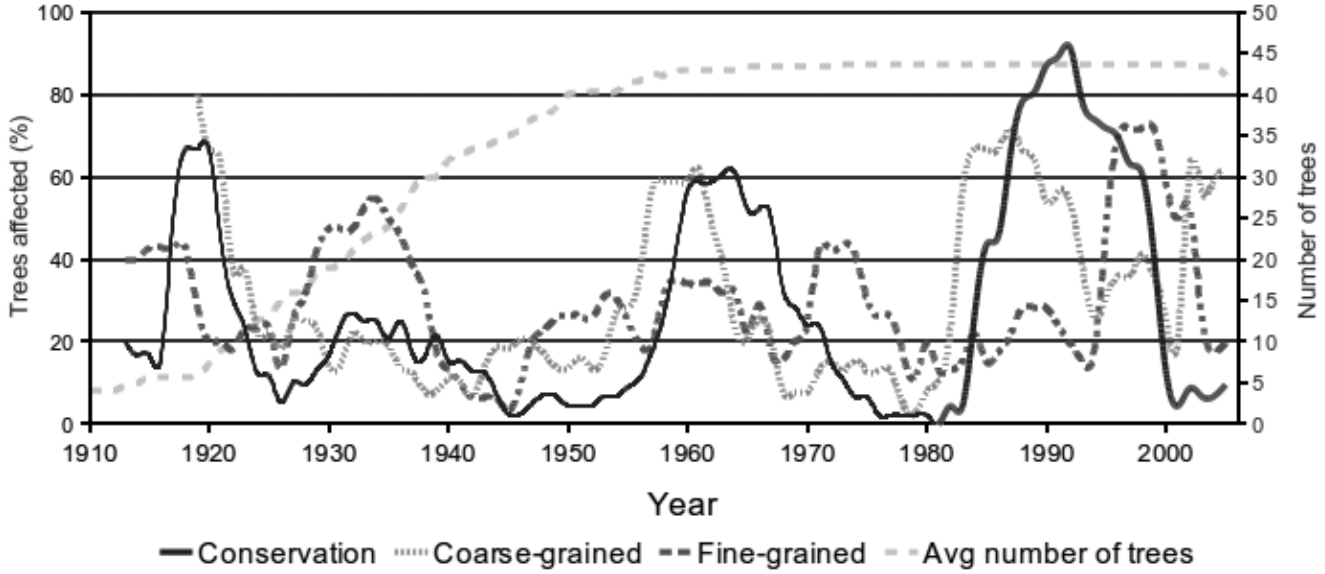
To verify whether the 25% cutoff of the number of trees showing a growth reduction led to robust results, we conducted a sensitivity analysis in which the cutoff percentage was varied. The number of outbreaks observed by zone was

Table 2. Changes in the number of outbreaks, their duration, their recurrence, and their intensity across landscapes with different land use based on different threshold criteria for the determination of outbreaks (20%, 25%, 30%, and 50%).

	No. of outbreaks				Average duration (years)				Recurrence interval				Average intensity (maximum % of trees affected)			
	20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%
Conservation	4	4	3	3	10.75	9.75	10.33	8	22.67	23	34	35	61.44	61.44	72.95	72.95
Coarse	3	3	3	4	17.67	15.33	11.67	5.25	32	33	31.5	27.33	66.67	66.67	66.67	65.39
Fine	9	7	5	2	7.333	7.571	7.4	5	10.25	13.67	20.5	63	39.04	43.79	49.5	63.15

Note: Statistics are for corrected outbreak data (outbreaks of 1–2 years in duration have been suppressed or integrated into other outbreaks). Note that the value used in this study is 25% (shaded).

Fig. 4. Frequency graph of the percentage of affected trees of the program OUTBREAK aggregated by management zones (conservation, coarse-grained, fine-grained) (shown on the left axis). The right axis shows the number of trees available for each year of the reconstruction.



generally insensitive to the threshold criteria (% of trees affected) used to define outbreaks, with the clear exception of the fine-scale management zone (Table 2). This result is consistent with the observation of lower intensity outbreaks within that zone, as a much lower number of outbreaks were detected with the 50% threshold. Average duration of outbreaks was stable with respect to the threshold criteria for the conservation and fine-scale management zones but declined with increasing threshold percentage of affected trees for the coarse-scale management zone (Table 2). The general pattern that the fine-scale management zone had more frequent but less intense outbreaks of shorter duration than the other two zones was consistent across thresholds, ranging from 20%–30%, but not at the highest threshold value examined (50%). Outbreak statistics differed consistently between the coarse-grained zone and the conservation zone at threshold values across the same range of values but were most distinctly different at lower threshold values (20% and 25%).

Outbreak synchrony

Separation of tree chronologies by latitude suggests that outbreak patterns in the northern and southern sites of the conservation zone were similar and well synchronized (Fig. 5*a*), despite a difference in latitude of 75 km. However, the patterns observed at sites at the same latitude but in different zones were dissimilar. For example, the northern conservation and southern coarse-grained sites were at the same latitude but outbreaks at these sites were not synchronous (Figs. 5*a*, 5*b*). Similarly, the southern conservation site, although being located at a latitude intermediate between the two fine-grained sites, did not exhibit an outbreak pattern similar to either. Outbreaks occurring in the northern part of the coarse-grained zone also occurred in its southern part but at a lower intensity, suggesting partial synchrony across this zone. Outbreaks in the southern sites of the coarse-grained zone were of lower intensity but had an outbreak recurrence interval similar to that of the fine-grained intensive zone. The earliest recorded outbreaks within the southern and northern sites of the fine-grained zone were synchronous; however, the outbreaks occurring between 1945 and 1985 were not synchronous despite their relatively close proximity (10 km) (Fig. 5*c*). The last outbreak (1995–2005) occurred synchronously in both northern and southern sites. Both the northern and southern sites of the fine-grained zone showed a pattern of frequent, low-intensity outbreaks.

Evaluation of confounding factors

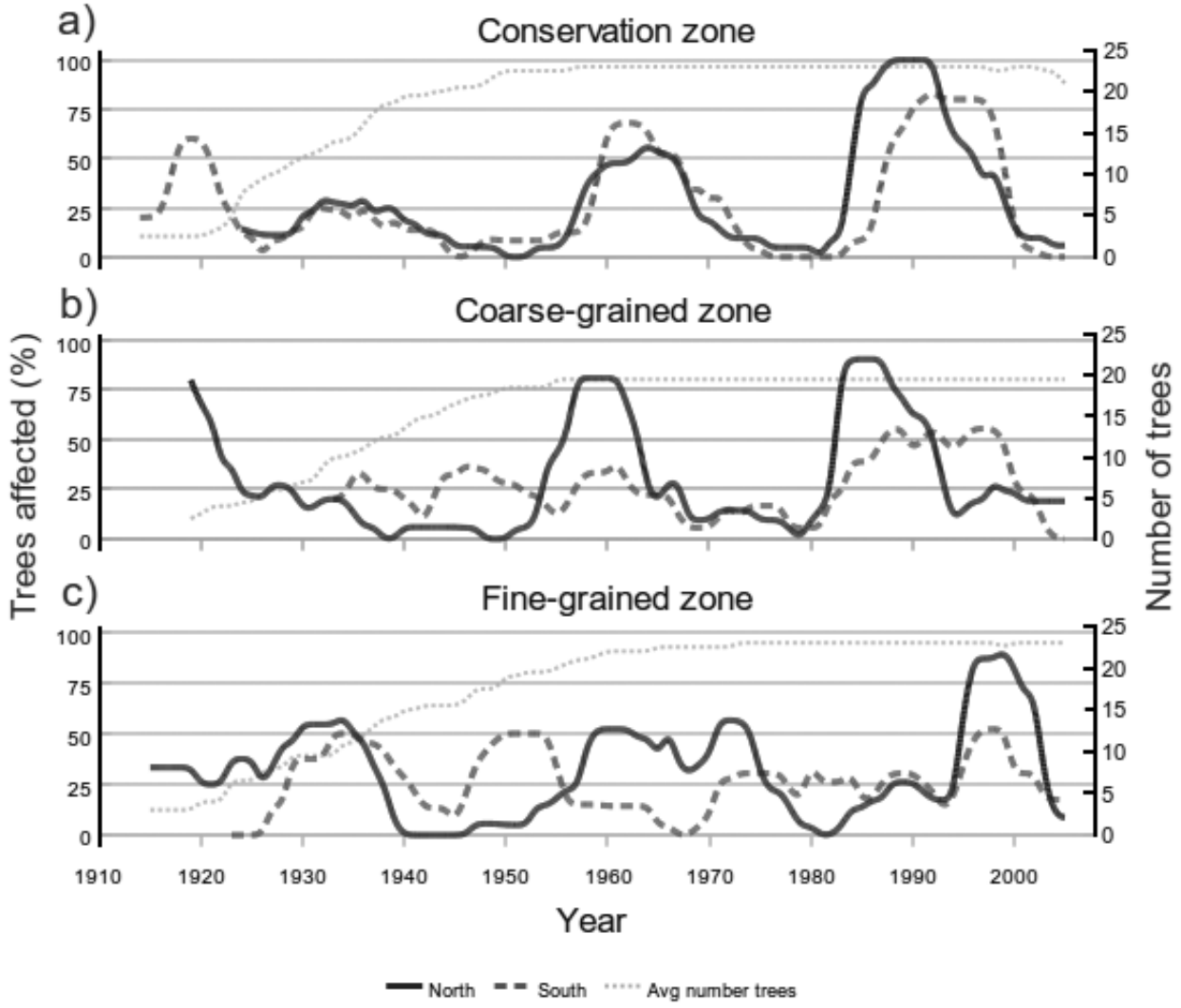
Forest composition

At the local scale, the amount of live host trees varied from 20% to 65%, but a higher percentage of host tree basal area was observed in the conservation north, coarse north, and fine south zones (Fig. 6*a*). MANOVA analysis of remotely sensed data at the 1 km scale indicates that the proportion of balsam fir differs between zones ($p = 0.0001$) but currently has very low abundance across all zones within the landscape (1%–4% of total basal area). The largest compositional difference between zones is for spruce species ($p = 0.0001$), which are most abundant within the conservation zone (26%–30% by basal area) but which make up a similar proportion of the forest across the two actively managed zones (2%–10%) (Fig. 6*b*). Deciduous content measured for its potentially protective effect against budworm outbreaks was not significantly different between zones or sites at different latitudes within zones ($p = 0.3377$).

Climate

A nested MANOVA (north–south nested within zones) shows that average and minimum winter temperatures (December, January, and February) in the southern conservation zone were warmer than all other sites, whereas winter temperature in the northern coarse zone were the coldest. Precipitation in May and July were similar for all sites except for the conservation zone, which received less precipitation than both the coarse- and fine-grained zones. The conservation zone also experienced colder springs (May temperature) in comparison with the actively managed zones. However, de-

Fig. 5. Frequency graph of the program OUTBREAK showing north and south percentage of affected trees for each management zone ((*a*) conservation, (*b*) coarse-grained, and (*c*) fine-grained) (shown on the left axis). Average number of trees for each zones (shown on the right axis) was 23 per year, except for prior to 1950.



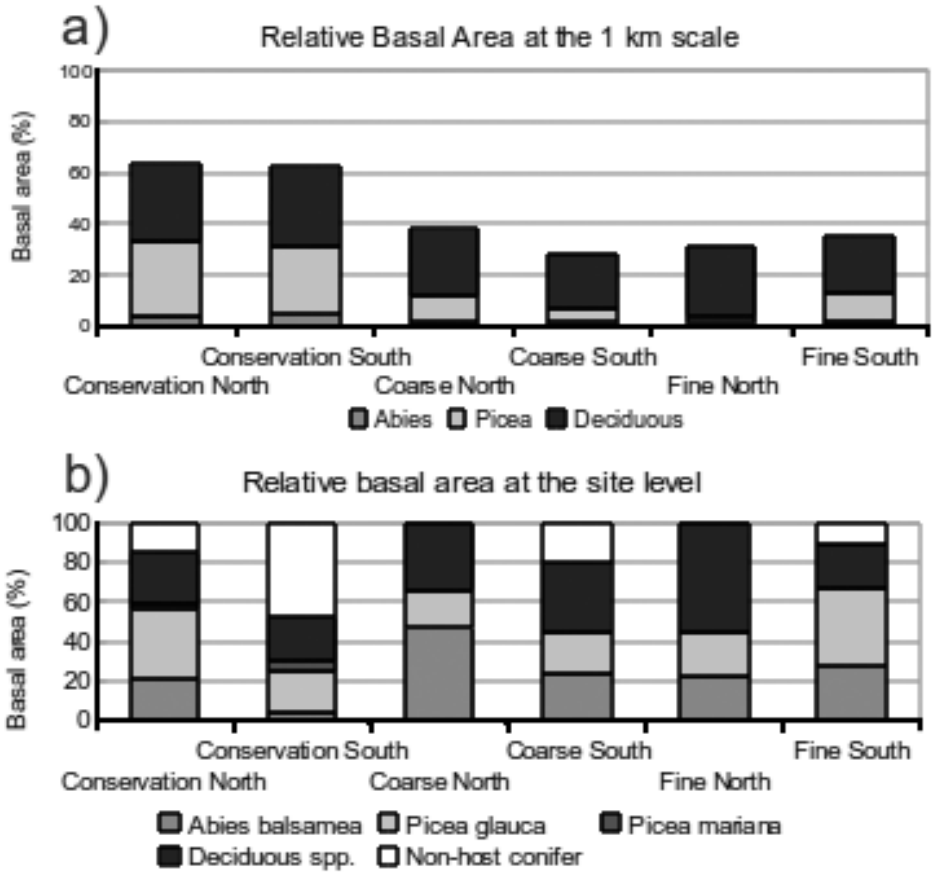
spite some significant differences in the weather data among zones, their respective mean values from 1900–2000 do not vary substantially (Table 3), suggesting that at our study scale, such weather differences have minor influence, if any, on the widely divergent spruce budworm outbreak behaviours observed across the different management zones.

Discussion

Our study lends support to the notion that management legacies that modify forest conditions can overcome regional drivers of outbreak synchrony. Outbreaks at the 25% affected tree threshold were more synchronous in the conservation zone than in the two managed zones, despite the considerable difference (75 km) of latitude between the northern and southern sites within this zone. By comparison, sites separated by a shorter latitudinal difference in the managed zones showed a lack of synchrony in outbreak occurrence. We observed this lack of spatial synchrony, despite the fact that outbreaks of defoliators are commonly synchronized across regions by minor but regionally correlated perturbations (such as weather events) (Bjørnstad et al. 1999; Bjørnstad et al. 2008) — a phenomena known as the Moran effect (Moran 1953). Further, we observed a lack of synchrony at sites located at similar latitude but within differently managed zones. Very slight differences in climate occurred between the sample sites, but no consistent relationship between climatic variables and outbreak dynamics could be observed. We therefore conclude that observed differences in outbreak behaviour resulted from differences in legacies of past management activities rather than from distance in space or climatic drivers.

Recent analyses of aerial survey data indicate that geographical variations in forest conditions may influence defoliator outbreak synchrony and temporal dynamics (Bellier et al. 2007; Candau and Fleming 2005; Haynes et al. 2009*b*). Processes such as dispersal by larvae and adults (Johnson et al. 2004) or spatial movements of natural enemies (Cappuccino et al. 1998; Eveleigh et al. 2007; Roland and Taylor 1997) may influence population dynamics at a scale that is intermediate between stand and regional scales. Our results suggest that management legacies may have affected spruce

Fig. 6. Difference in local forest composition for each management zone (*a*) at the 1 km scale by remote sensing and (*b*) at the site scale from local inventory.



budworm outbreaks within managed areas and desynchronized spruce budworm outbreaks relative to the conservation area, where the combination of fire suppression, historic removal of pines, and lack of recent harvest has left a legacy of older, spruce-dominated forest relative to managed forests (Heinselman 1996) (Fig. 6*b*). Unlike analyses of aerial surveys, our study minimized the confounding influence of environment and climate by focusing on a single ecoregion where differently managed zones were in close proximity.

Though outbreak synchrony is often correlated with outbreak intensity (i.e., impacts), we observed subtle but important deviations from that general pattern. The intensity of outbreaks (as indicated by the average of highest percentage of affected trees for each outbreak using the 25% threshold) (Table 2) was highest in the coarse-grained managed zone and lowest in the fine-grained managed zone. We also observed twice as many outbreaks within the fine-grained management zone (Minnesota) relative to the other two zones (Table 2), which decreased the recovery period of the forest. Outbreak duration is most correlated with actual damage to the forest, as multiple years of defoliation are generally required to kill the most vulnerable host species (i.e., balsam fir (MacLean 1980)). We found that the average outbreak duration at the 25% threshold within the coarse-grained management zone (Ontario) was roughly double that observed in the fine-grained zone. These results suggest trade-offs between different indicators of forest impacts in the two managed zones with either short-lived but frequent outbreaks of low intensity or long lasting but infrequent outbreaks of high intensity. By contrast, outbreaks in the conservation zone were both infrequent and of short duration, with intensities intermediate to the two managed zones.

Outbreak dynamics were less consistent between northern and southern sites of the coarse-grained managed zone relative to the other two zones. We had hypothesized that the degree of outbreak synchrony within this zone would be intermediate to that observed within finely fragmented managed areas of Minnesota (asynchronous) and the relatively unfragmented areas in the conservation zone (synchronous). Instead, we found divergent outbreak behavior within the coarsely fragmented Ontario zone, where data from southern sites indicated behaviour more similar to that observed in the fine-grained zone and data from northern sites indicated behaviour more similar to the conservation zone (Fig. 5). One potential explanation for this pattern is that harvest disturbances in Minnesota are more evenly distributed in time and space, whereas the more clustered harvest pattern in Ontario resulted in greater spatial heterogeneity in fragmentation, leading to divergent behaviour. Alternatively, harvest was more recent in the vicinity of the northern sites of the coarse-grained zone, and thus, effects on outbreak behavior may not yet be manifest. The greater abundance of white spruce plantations particularly in the southeast toward Lake Superior might be a further explanation, but they are scattered in the study area and could thus be expected to have a limited impact. A last possibility is that the southern sites are

Table 3. Mean weather data and their standard deviation (SD) for each management zone.

		May precipitation (mm)		July precipitation (mm)		December temperature (°C)		December minimum temperature (°C)		January temperature (°C)		January minimum temperature (°C)		February temperature (°C)		February minimum temperature (°C)		May temperature (°C)		May minimum temperature (°C)	
Latitude	Zone	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
North	Conservation	92.4	0.4	91.6	0.3	–13.0	0.1	–18.5	0.1	–16.9	0.1	–23.5	0.1	–14.1	0.0	–21.4	0.1	9.2	0.1	2.0	0.0
South	Conservation	95.2	0.2	92.7	0.1	–12.0	0.1	–17.2	0.1	–15.7	0.1	–21.9	0.1	–13.0	0.0	–19.9	0.0	9.0	0.1	2.0	0.1
North	Fine	97.4	0.2	93.6	0.2	–12.9	0.0	–18.1	0.0	–16.9	0.0	–23.0	0.0	–13.8	0.0	–20.6	0.0	10.4	0.0	3.4	0.0
South	Fine	97.3	0.3	93.0	0.2	–12.6	0.0	–18.0	0.0	–16.5	0.0	–22.9	0.0	–13.4	0.0	–20.5	0.0	10.2	0.0	2.9	0.0
North	Coarse	97.1	0.5	93.5	1.2	–13.1	0.6	–18.3	0.4	–17.1	0.7	–23.2	0.4	–14.0	0.7	–20.8	0.4	10.1	0.1	3.1	0.1
South	Coarse	97.6	0.3	93.7	0.3	–12.9	0.4	–18.3	0.2	–16.9	0.6	–23.1	0.3	–13.7	0.6	–20.7	0.3	9.9	0.1	2.7	0.4

Note: Source of data: McKenney et al. (2006).

influenced by their close proximity to a large lake (Fig. 1). Cappuccino et al. (1998) observed lower budworm damage on forested islands within lakes relative to forests within a land matrix. Analyses across a greater range of locations throughout the Border Lakes landscape, currently underway, will provide stronger insights into the effects of management legacies and other landscape features on budworm outbreak dynamics.

Observed divergences in budworm outbreak behaviour begs the question: at what spatial scale is fragmentation perceived by the spruce budworm? A detailed study of a European defoliator, winter moth (*Operophtera brumata* L.), which has a smaller dispersal capacity than the spruce budworm, found that fragmentation created by management increased dispersal mortality during outbreaks and may explain why less defoliation is experienced in fragmented landscapes (Wesołowski and Rowiński 2006). Spruce budworm adults can disperse long distances (i.e., 10s to 100s of km) during outbreaks (Greenbank et al. 1980), suggesting that this species may be less sensitive to fragmentation of host species than the less mobile winter moth. Yet dispersal of adults is only one process of many that may influence outbreak dynamics (Régnière and Nealis 2007). For example, Cappuccino et al. (1998) found that stands of budworm hosts isolated at the scale of 1 km neighborhoods experienced less damage than host species surrounded by forest dominated by host during an outbreak in Quebec, Canada.

Spatial influences on the natural enemy complex may have influenced the response time of budworm enemies in managed areas of the BLE to the point that outbreak dynamics were affected. The larger patch size of the coarse-grained zone may have created a lag in the response of natural enemies (Cappuccino et al. 1998). This would result in higher intensity and longer lasting outbreaks in this zone as spruce budworm population growth would be initially favored due to the lack of predators (Cooke et al. 2007). In contrast, we suspect that the natural enemy response may be more rapid in the fine-grained zone due to its lower mean patch sizes. If so, then this reduced lag time may have contributed to the observed lower intensity but frequent outbreaks observed there. However, although the different legacies of forest management are evident in disturbance patch sizes and forest ages observed across zones, corresponding differences in patterns of budworm host are far less obvious. This suggests that repeated budworm disturbances may have degraded this pattern over time (James 2010). Because our composition dataset represents only a snapshot of current composition, additional temporal data on age structure and abundance of host species is needed to discriminate between effects of host proportion, configuration, and age structure on spruce budworm outbreak dynamics.

Potential climatic influence

Climate is known to affect outbreaks and it is conceivable that some of the differences observed in the current data could be explained by differences in climate between sites (Campbell et al. 2006; Volney and Fleming 2000). Our study design aimed to control the effect of climatic variability by allowing us to compare sites in different zones but in close proximity and by explicitly considering northern and southern sites within zones. Winter temperature can limit the sur-

vival of second instar larvae (Candau and Fleming 2005), and as expected, northern latitude sites were consistently colder than southern latitude sites nested within management zones. If winter temperature had a significant influence over outbreak dynamics, we should have observed consistent budworm outbreak dynamics at similar latitudes, yet this was not the case. The most consistent climatic difference between management zones was the relatively colder springs and lower May–July precipitation observed within the conservation zone. If the slightly colder springs in this zone were to affect outbreaks, then we would have expected them to limit the duration and intensity of spruce budworm outbreaks compared with the other management zones. If there was an effect of the slightly drier beginning of summer, it would be to increase outbreak intensity as early summer moisture affects the beginning of the initial phase of outbreaks (Lucuik 1984). Instead, the most severe outbreaks were observed within northern sites in the coarse-grained zone, an area with higher July precipitation. Such inconsistencies in pattern when combined with the minor absolute differences in climate between zones relative to the divergent outbreak behavior observed suggest that at the scale of this study, climate is at best a minor factor underlying observed differences in outbreak behavior.

Conclusion

Our study is among the first to show that forest management can influence dynamics of outbreaks. A review of previous studies conducted at stand scales found no evidence to support the notion that stand-level treatments by themselves have any influence on defoliator outbreaks (Muzika and Liebhold 2000). Our study suggests that the cumulative effects of management at the landscape scale can modify spruce budworm outbreak patterns. Management legacies have changed the patch structure and the contiguity of older forests and, potentially, the composition of those forests. We observed clear differences between outbreak patterns in managed and unmanaged forests irrespective of distance and position between sample locations. Our results suggest that although the elimination of budworm outbreaks is unlikely to be achieved via forest management practices, such practices may influence the scale, periodicity, or duration of the outbreaks. It appears that a trade-off exists between frequent outbreaks of short duration versus less frequent but higher intensity outbreaks and that landscape-scale management legacies can influence realization of these two outbreak behaviors.

Miller and Rusnock (1993) suggested that evaluation of the silvicultural hypothesis may be beyond the limits of classic scientific method due to the long-term and large-scale experiments required to perform an adequate test of the hypothesis. Such an experiment is currently underway (Volney et al. 1999); however, it will be decades before any conclusions may be made. Landscape-scale "natural experiments" such as presented here offer a complimentary method that, in lieu of true large-scale controlled experiments, may be effectively applied to understand drivers underlying outbreak dynamics at scales relevant to the outbreak process.

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