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Landscape host abundance and configuration regulate periodic outbreak behavior in spruce budworm *Choristoneura fumiferana*

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Landscape-level forest management has long been hypothesized to affect forest insect outbreak dynamics, but empirical evidence remains elusive. We hypothesized that the combination of increased hardwood relative to host tree species, prevalence of younger forests, and fragmentation of those forests due to forest harvesting legacies would reduce outbreak intensity, increase outbreak frequency, and decrease spatial synchrony in spruce budworm *Choristoneura fumiferana* outbreaks. We investigated these hypotheses using tree ring samples collected across 51 sites pooled into 16 subareas distributed across a large ecoregion spanning the international border between Ontario (Canada), and Minnesota (USA). This ecoregion contains contrasting land management zones with clear differences in forest landscape structure (i.e. forest composition and spatial configuration) while minimizing the confounding influence of climate. Cluster analyses of the 76-yr time-series generally grouped by subareas found within the same land management zone. Spatial nonparametric covariance analysis indicated that the highest and lowest degree of spatial synchrony of spruce budworm outbreaks were found within unmanaged wilderness and lands managed at fine spatial scales in Minnesota, respectively. Using multivariate analysis, we also found that forest composition, configuration, and climate together accounted for a total of 40% of the variance in outbreak chronologies, with a high level of shared variance between composition and configuration (13%) and between composition and climate (9%). At the scale of our study, climate on its own did not explain any of the spatial variation in outbreaks. Outbreaks were of higher frequency, lower intensity, and less spatially synchronized in more fragmented, younger forests with a lower proportion of host species, with opposing outbreak characteristics observed in regions characterised by older forests with more concentrated host species. Our study is the first quantitative evaluation of the long-standing 'silvicultural hypothesis' of spruce budworm management specifically conducted at a spatio-temporal scale for which it was intended.

Keywords: spruce budworm, harvest disturbance, landscape ecology, forest management legacies, dendrochronology, outbreak synchrony

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Introduction

Outbreaks of boreal forest insects are a major forest disturbance that have significant ecological and economic consequences. Insect outbreaks affect biogeochemical processes and can influence nutrient cycling, hydrology, and atmospheric carbon cycling, all of which can affect climate at a global scale (Kurz et al. 2008, Dymond et al. 2010). Insect outbreaks also affect forest landscape structure (i.e. stand species composition and spatial configuration) with consequences for forest succession (Baskerville 1975), timber production (Chang et al. 2012), and the risk of future disturbances such as fire (James et al. 2017).

The notion that reciprocal feedback between forest and insects at least partially drives periodic population eruption was central to the earliest formalized concepts of forest-insect ecosystem dynamics (Holling 1973), and continues to be a central theme in ecosystems ecology (Raffa et al. 2008). An important role of the forest on outbreaks has been demonstrated in multiple defoliator systems, including the jack pine budworm *Choristoneura pinus* (Volney and McCullough 1994), forest tent caterpillar *Malacosoma disstria* (Roland 2005), gypsy moth *Lymantria dispar* (Haynes et al. 2009), and winter moth *Operophtera brumata* (Wesołowski and Rowiński 2006). Although the top-down effects of natural enemies typically underlie cyclic outbreak behaviour (Berryman 2002, Turchin 2003), there is also evidence that some of this outbreak behaviour may be attributable to bottom-up host-plant effects (Price et al. 1984, Nealis and Lomic 1994, White 2012). For example, impact of the European spruce bark beetle *Ips typographus* is determined by available deadwood and its spatial distribution (Lausch et al. 2013). Another example is the larch budmoth *Zeiraphera griseana* in the European Alps, where gradients in density of host tree species induced epicenter formation and travelling waves within outbreaks (Johnson et al. 2004). Further, the ability of natural enemy communities to respond to population irruptions appears to be linked to forest landscape conditions (Roland and Taylor 1997, Cappuccino et al. 1998), suggesting there are important interactions among trophic levels affecting outbreak dynamics.

The spruce budworm *Choristoneura fumiferana* is the most damaging forest insect defoliator in North America, with balsam fir *Abies balsamea* and white spruce *Picea glauca* being especially vulnerable (MacLean 1980, Hennigar et al. 2008). This native insect is a strong flier capable of long distance dispersal (Greenbank et al. 1980) and best known for the broad-scale spatial synchrony, comparatively low frequency, and long duration of its outbreaks (Blais 1983, Royama 1984, Williams and Liebhold 2000, Jardon et al. 2003).

The spruce budworm inspired much of the foundational thinking about forest-insect feedbacks as the cause of cross-scale eruptive dynamics (Ludwig et al. 1978). Indeed, the early 'multiple equilibrium' models of spruce budworm outbreaks hypothesized that abundance of host foliage was a principle bottom-up driver enabling budworm escape from top-down control (Jones 1977, Hassell et al. 1999). What was missing from these early models was robust empirical evidence for the hypothesized effect of the forest on the budworm.

In parallel, the 'silvicultural hypothesis' of spruce budworm management posited that the impact of the spruce budworm in the 20th century was accentuated by 'man's influence in the forest' – i.e. regional-scale commercial harvesting of spruce (*Picea* spp.), and its replacement by balsam fir – that concentrated preferred host abundance and increased outbreak extent and intensity (Blais 1965, 1983). Baskerville (1975) argued that the reciprocal feedback between the budworm and the forest was strong, although Miller and Rusnock (1993), who accepted the impact of budworm on the forest and that broad-scaled concentrations of mature balsam fir were more vulnerable to budworm damage, emphasized the lack of supporting evidence for any influence of such concentrations of balsam fir on budworm outbreak dynamics. More recent empirical studies have shown that: 1) budworm defoliation consistently tends to be lower when hardwoods are abundant (Bergeron et al. 1995, Su et al. 1996, Campbell et al. 2008, Gray 2013), and 2) this effect is due, in part, to an increased abundance of key parasitoid species associated with this hardwood component (Cappuccino et al. 1998, Quayle et al. 2003). This has led to a broadening of the silvicultural hypothesis to include the effect of forest composition on natural enemy interactions. Still missing is convincing evidence for the penultimate effect of forest landscape structure (i.e. the age, amount, and spatial arrangement of host vs nonhost tree species) on the dynamics of spruce budworm outbreaks.

The relative importance of top-down versus bottom-up processes in budworm outbreak dynamics has been a subject of intense empirical debate for nearly a century (Sturtevant et al. 2015, Pureswaran et al. 2016). The idea of forest-driven feedback to budworm outbreaks was dismissed by Royama (1984), who argued that the core population oscillation underlying periodic outbreaks is produced by delayed density-dependent mortality due to natural enemies, and that spatial outbreak synchrony is produced by regionally-correlated factors such as weather (i.e. the Moran effect (Moran 1953, Royama 2005)). However, more recent research suggests that complex cycling of outbreaks may emerge from a combination of both top-down and bottom-up reciprocal feedback processes (Cooke et al. 2007, Régnière and Nealis 2007, Sturtevant et al. 2015).

Considering the full weight of the evidence, both empirical and theoretical, one would expect that reducing host forest cover might affect the frequency and intensity of budworm outbreak cycles, through its effects on local budworm dispersal success (Nealis 2016) and on natural enemies (Royama 1984, Eveleigh et al. 2007). One might also expect a reduction in host to reduce spatial synchrony, through its effect on long-range dispersal success (Régnière and Lysyk 1995, Peltonen et al. 2002) and cycle amplitude (Barbour 1990, Cooke et al. 2007). This would represent a coherent multivariate response of outbreak characteristics that are functionally related to one another, and modified

through changes in forest landscape structure. Robert et al. (2012) used tree-ring data from Ontario and Minnesota to show that spruce budworm outbreaks during the 20th century tended to affect fewer trees in managed landscapes than in unharvested wilderness areas. In particular, they found that outbreak intensity was reduced in areas where the spatial pattern of forest harvesting was diffuse rather than spatially aggregated. These results were qualitatively consistent with a forest landscape structure feedback to outbreak dynamics. Outbreaks within older, less fragmented forests (wilderness) exhibited infrequent, spatially synchronous outbreaks. In contrast, younger, managed forests containing a greater proportion of hardwood species exhibited outbreaks that were more frequent, but less synchronized – all in accordance with the predictions of the silvicultural hypothesis.

In this paper, we extend the study of Robert et al. (2012) to quantitatively investigate the effect of forest landscape structure on spatio-temporal variation in budworm outbreak dynamics. We hypothesized that attributes of forest landscape structure related to landscape management practices, including forest composition (host abundance, hardwood content, forest age) and configuration (disturbance rates, host connectivity), influence budworm outbreak behavior (i.e. cycle intensity, cycle frequency, and spatial synchrony) according to the expectations of a multi-variate response outlined above. We further wished to distinguish the effects of forest landscape structure on outbreaks from the effects of climate (Gray 2008, 2013). Although other studies have examined the effects of forest landscape structure on the characteristics of a single outbreak (Bergeron et al. 1995, Su et al. 1996, Candau and Fleming 2005, Campbell et al. 2008, Gray 2013), our goal is to examine the long-term (i.e. over multiple outbreaks) effects of forest landscape structure on outbreak dynamics at scales both relevant to that of dispersing spruce budworm (i.e. 10's to 100's of km; (Greenbank et al. 1980, Anderson and Sturtevant 2011) and consistent with the silvicultural hypothesis more generally (Miller and Rusnock 1993).

Methods

Study area

The Border Lakes Landscape (BLL) contains a large (~20 000 km²) ecoregion that straddles the border between Minnesota (USA) and Ontario (Canada) (Fig. 1; (Sturtevant et al. 2014)) at the transition between the Great Lakes-St Lawrence mixed-wood and boreal forest regions. The full extent of the BLL includes a 50 km buffer to address potential edge-effects related to insect movement (Anderson and Sturtevant 2011). Forest composition is mixed 'near boreal' (Heinselman 1973) with a high proportion of boreal tree species (e.g. jack pine *Pinus banksiana*, black spruce *Picea mariana*, white spruce *Picea glauca*, balsam fir *A. balsamea*, birch *Betula papyrifera*, trembling aspen *Populus tremuloides*), as well as several species near the northern limit of their range,
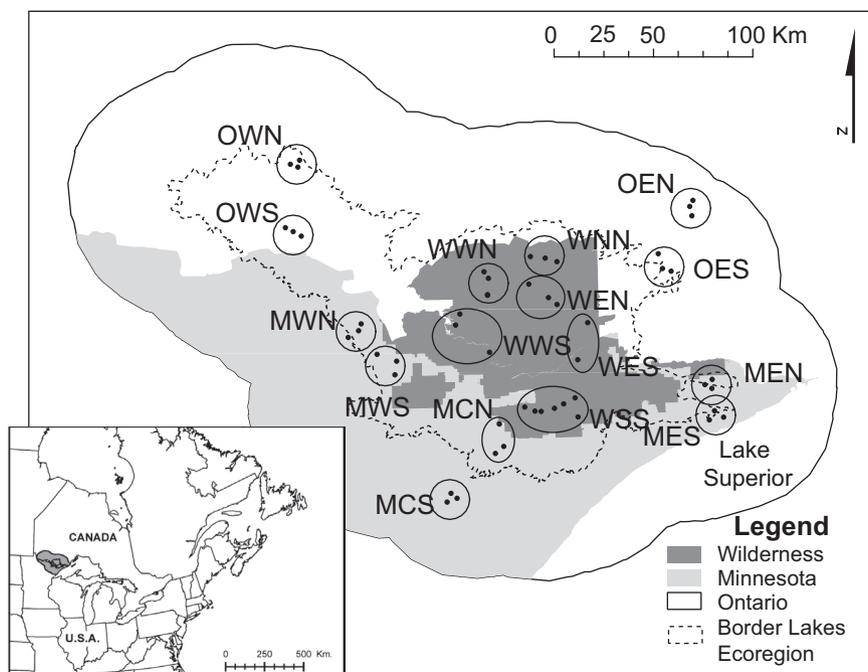
Figure 1. The Border lakes landscape (BLL) study area located at the border between Ontario (Canada) and Minnesota (United States). Points represent sampling sites for dendrochronological reconstructions of outbreaks that are grouped by the subarea unit of analysis. Subarea labels: 1st letter = management zone (Ontario, Wilderness, Minnesota); 2nd letter = area (East, West, 'Central', South, North); 3rd letter = subarea (North, South).

such as white pine *Pinus strobus*, red pine *Pinus resinosa*, and red maple *Acer rubrum*.

The entire BLL shares a common early logging history. Region-wide logging started at the end of the 19th century and focused on selective harvest of the 'big pines' (*P. strobus, P. resinosa*). Logging patterns diverged sharply between Minnesota and Ontario approximately 70 yr ago, coinciding with the advent of mechanized harvesting on both sides of the border. Cut-block sizes in managed Canadian forests are an order of magnitude larger in size than managed American forests, though the rates of harvest have been historically similar (James et al. 2011, Sturtevant et al. 2014). Between these managed regions lies an approximately 10 000 km² wilderness area that includes Quetico Provincial Park in Ontario and the Boundary Waters Canoe Area Wilderness in Minnesota, where no timber harvest has occurred since the early 1970s (Heinselman 1996), referred to henceforth as 'Wilderness'. Forest fires have decreased over the last century (Ahlgren and Ahlgren 2001), enhancing succession toward spruce and fir. Periodic defoliation by spruce budworm often kills balsam fir in this region (Frelich and Reich 1995).

Forest landscape structure of the study area

Divergence in the spatial patterning of disturbances between management zones in the BLL has been documented by a time-series of Landsat-derived land cover maps from (1975–2000, (Wolter et al. 2012) (Supplementary material Appendix 1 Fig. A1A). Prior analyses of these data by Sturtevant et al. (2014) showed that: 1) disturbance patch-size distributions in the BLL were the most consistent through time in Minnesota managed zones, and least consistent spatially and temporally within the Wilderness; 2) Minnesota cut-blocks were both small in size and more diffuse than the aggregated, large-sized cut-block patterns in Ontario; 3) natural, stand-replacing disturbances in the Wilderness were comparably rare, with the exception of a few recent large wind and fire disturbances. Forest composition (i.e. tree species basal area) was also mapped via remote sensing by Wolter et al. (2008) ca 2002 (Supplementary material Appendix 1 Fig. A1B) and also ca 1985 (Wolter unpubl.) using archived Landsat TM imagery. Wavelet analysis applied to the 2002 dataset (James et al. 2011) indicated that management zones differed somewhat in terms of the basal area of spruce budworm hosts (spruce and fir), especially between Minnesota and Wilderness (Supplementary material Appendix 1 Fig. A1B). The managed parts of the landscape (Ontario and Minnesota) contained similar forest types, but had more early-successional, deciduous forest relative to the Wilderness (James et al. 2011).

Sampling design

We reconstructed spruce budworm outbreak histories using tree-ring analyses of white spruce tree cores sampled from 51 sites distributed throughout the BLL (Fig. 1). White spruce was selected because it is as susceptible as balsam fir to defoliation by spruce budworm, but has a higher probability of surviving attack (Hennigar et al. 2008). We targeted mesic sites that contained five to fifteen old, large canopy white spruce (> 30 cm DBH) on flat or mid-slope topographic positions. Two cores were taken from each spruce tree at a height of 1 m. Between 5 and 10 trees were sampled per site (Table 1). Groups of three neighbouring sites were then aggregated into 'subareas' to provide sufficient sample size (n > 15 trees) for outbreak reconstruction (Fig. 1). In total we created 16 subareas that represent a stratified sampling of the BLL based on forest management region (Ontario = 'O', Wilderness = 'W', Minnesota = 'M'), longitude (East = 'E', Central = 'C', West = 'W'), and latitude (North = 'N', South = 'S'). The goal of this stratification was to account for climatic gradients across the study area. The minimum distance between subarea centroids was 15 km and the maximum distance was 250 km. A minimum of fifteen

Table 1. Summary statistics of the dendrochronological reconstruction for all subareas produced by the program COFECHA.

Zone	Area	Subarea	Label	No. of trees	Time span	Sensitivity		
						Mean	SD	Inter-tree correlation
Ontario	Eastern	North	OEN	18	1849–2005	0.25	1.13	0.496
	Eastern	South	OES	22	1883–2005	0.226	1.024	0.472
	Western	North	OWN	19	1895–2005	0.28	1.157	0.604
	Western	South	OWS	17	1926–2005	0.272	1.159	0.571
Wilderness	Eastern	North	WEN	16	1924–2006	0.279	1.029	0.661
	Eastern	South	WES	13	1902–2006	0.25	1.105	0.506
	North	North	WNN	20	1906–2005	0.268	1.356	0.643
	South	South	WSS	24	1897–2005	0.277	1.026	0.604
	Western	North	WWN	21	1836–2006	0.259	0.92	0.426
	Western	South	WWS	15	1880–2006	0.253	0.826	0.594
Minnesota	Center	North	MCN	21	1915–2005	0.208	1.351	0.636
	Center	South	MCS	23	1928–2005	0.207	1.413	0.583
	Eastern	North	MEN	22	1836–2005	0.238	1.403	0.368
	Eastern	South	MES	22	1872–2005	0.249	1.075	0.609
	Western	North	MWN	22	1903–2005	0.277	1.363	0.63
	Western	South	MWS	22	1920–2005	0.263	1.508	0.61

non-host coniferous trees (i.e. jack pine and red pine; > 30 cm DBH) per subarea were also cored to serve as a control for local climatic variation. All cores were stored in plastic straws and were later mounted and sanded using progressively finer grit (80, 150, and 220).

Outbreak history reconstruction

Budworm outbreaks were reconstructed from spruce tree ring data using the methods described in Robert et al. (2012). Site-level chronologies were built using tree-ring widths measured using a Velmex uni-slide measuring table with an accuracy of 0.001 mm connected to a computer (Velmex Incorporated, Bloomfield, New York, USA). Widths were cross-dated using the program COFECHA (Holmes et al. 1986) which was also used to locate missing or false rings and to test for measurement errors. Chronologies were then aggregated into their respective subareas as described above. Index chronologies were calculated using the program ARSTAN (Cook 1985, Holmes 1992) with a cubic smoothing spline to detrend the series and remove age-related growth trends (Cook 1985). Spline parameters were set to a 50% frequency response cut-off of 60 yr, which is standard for spruce budworm outbreak reconstruction (Boulanger and Arseneault 2004, Bouchard et al. 2006, Robert et al. 2012). Between 13 and 24 trees (mean = 19.8 trees; SD = 3.2 trees) were used to develop chronologies for each subarea (Table 1).

At the level of an individual tree, outbreaks were defined when a tree-ring growth reduction was observed for more than 5 yr and at least one year showed a reduction greater than 1.28 standard deviations from the mean chronology ring width (Boulanger and Arseneault 2004, Bouchard et al. 2006). Outbreak histories, based on the percentage of trees classified as affected by an outbreak at a given year and scale, were reconstructed using these parameters and the program OUTBREAK (Holmes and Swetnam 1996). OUTBREAK has been previously used in spruce budworm outbreak reconstruction and can detect outbreaks while avoiding confounding consequences of other defoliating insects (Boulanger and Arseneault 2004, Bouchard et al. 2006). No other defoliators are known in the region that are capable of causing growth reductions over multiple years such that they would be identified as an outbreak. Outbreak detection with the program OUTBREAK was more efficient when applied solely to host species (Bouchard et al. 2006). Non-host chronologies were only used to validate detected outbreaks by visual comparison of the growth pattern (not shown). The percentage affected trees by outbreaks each year at either the site or subarea scales were used as the response variable for cluster analysis, redundancy analysis, and analysis of spatial synchrony (described below).

Predictor variables

Forest landscape structure

Forest landscape structure was spatially quantified in two ways, each using separate sets of multi-temporal Landsat sensor data (Table 2): 1) forest configuration was quantified

Table 2. Summary of potential and selected predictor variables to describe variation in SBW outbreak attributes at each sample subarea (Fig. 1; see text for details). Dates refer to the time periods for which this predictor was available. Predictors indicated as being calculated at multiple spatial scales were calculated at using multiple extracted buffers of increasing radii (0.5, 1, 5, 10, 20, 30 km) centered on each subarea.

Category	Variable	Unit	Abbreviation	Time period	Multi-scale	Data source
			Candidate landscape factors affecting budworm dynamics			
Composition	Balsam fir basal area	Mean	Fir[SpatialScale][Year]	1985 and 2002	Yes	Landsat TM
	Spruce and fir basal area	Mean	Hst[SpatialScale][Year]	1985 and 2002	Yes	Landsat TM
	Deciduous basal area	Mean	Decid[SpatialScale][Year]	1985 and 2002	Yes	Landsat TM
	Proportion of forest	%	PFor[SpatialScale][Year]	1975	Yes	Landsat TM
	Proportion of old forest	%	POld[SpatialScale][Year]	2000	Yes	Landsat TM
Configuration	Area-weighted patch size of forest disturbance	Mean	AwmPtch[SpatialScale]	Average of 1980–2000, 5 yr increment	Yes	Landsat MSS and Landsat TM
	Proportion of forest disturbance	%	PDist[SpatialScale]	Average of 1980–2000, 5 yr increment	Yes	Landsat MSS and Landsat TM
	Area-weighted patch size of openings	Mean	AWMOpn[SpatialScale]	Average of 1980–2000, 5 yr increment	Yes	Landsat MSS and Landsat TM
	Proportion of forest opening	%	POpn[SpatialScale]	Average of 1980–2000, 5 yr increment	Yes	Landsat MSS and Landsat TM
	COHESION of fir patches	Mean	CoheFir[SpatialScale][Year]	1985 and 2002	Yes	Landsat MSS and Landsat TM
	COHESION of spruce-fir patches	Mean	CoheHst[SpatialScale][Year]	1985 and 2002	Yes	Landsat MSS and Landsat TM
Climate	Spruce budworm growth index	Index	ClimInd	Average of 1971–2000	No	BIOSIM
	Min. winter temperature	Mean	WintTmp	Average of 1900–2000	No	McKenney et al. 2007
	Min. spring temperature	Mean	SpTmp	Average of 1900–2000	No	McKenney et al. 2007
	Min. summer temperature	Mean	SumTmp	Average of 1900–2000	No	McKenney et al. 2007

using discrete land use land cover time series maps at five-year intervals from 1975–2000 (i.e. 6 points in time) (Wolter et al. 2012); and 2) forest composition was quantified using use maps of spatially continuous estimates of basal areas (m^2 ha^{-1}) for balsam fir, combined budworm host species (i.e. fir and spruce), and deciduous tree species. Composition was quantified at only two points in time (1985 and 2002) due to the availability of forest plot data necessary to develop the underlying tree species models (Wolter et al. unpubl. and Wolter et al. (2008)).

Because we do not know a priori the scales at which budworm outbreaks respond to forest conditions, we quantified our forest landscape structure predictor variables at multiple scales using a range of sample radii (i.e. 0.5, 1, 5, 10, 20, 30 km), where each predictor variable was measured within a circle defined by a given sample radius for each site, and site-level variables were then averaged across sites within a subarea (approximately 3 sites per subareas).

Both forest composition and configuration were characterized using multiple metrics, where the specifics of each metric were contingent on the corresponding data available at different points in time. Forest composition was represented using the basal area of combinations of budworm host and non-host species, and the proportion of either forest area (circa 1975) or 'old forest' area in 2000 (see below). We calculated the average basal area of balsam fir, spruce combined with fir, and the combination of all deciduous tree species for each sample radius for both 1985 and 2002. We measured the proportion of forest in 1975 and then the proportion of pixels that were classified as mature forest in 1975 and remained so in 2000 as our estimate of old forest coverage in 2000. Given the constraints of the available datasets, these latter variables were the best available surrogates for forest age at each time period, with clear limitations limiting the degree of inference linking forest age to budworm outbreak dynamics.

Forest configuration was quantified using landscape pattern metrics that capture the spatial connectivity of budworm host patches as well as the amount and size of forest openings (i.e. forest fragmentation). Connectivity of fir and spruce-fir patches was calculated for each sample radius based on basal area for each of the two map dates (1985 and 2002) using the COHESION landscape metric (Schumaker 1996). Forest openings (non-forest) were represented using 'disturbed' and 'open' land classifications. 'Disturbed' land included pixels that were classified as mature forest during one 5-yr interval, but were then classified as open, grass, brush, or regenerating in the next year interval (Sturtevant et al. 2014), representing the disturbance rate. 'Open' land combined all non-forest land cover types (i.e. ignoring water and open wetlands) (Sturtevant et al. 2014) with disturbed cover types to estimate cumulative fragmentation of forest. We calculated the area-weighted mean patch size (AWMPS) and proportion of area for both disturbed and open categories across all sample radii averaged over all 5-yr intervals between 1975 and 2000. AWMPS and

COHESION were calculated using FRAGSTATS (McGarigal et al. 2012).

Climate

We assessed the potential effect of climate on outbreaks within our study area using mean minimum seasonal (winter, summer, spring) historical (1901–2000) temperature for each subarea (McKenney et al. 2007) (Table 2). Minimum seasonal temperatures have been previously shown to influence spruce budworm outbreaks (Swetnam and Lynch 1993, Candau and Fleming 2005, 2011). We also examined the influence of a spruce budworm population growth index (Table 2, Supplementary material Appendix 1 Fig. A1C) on outbreaks averaged between 1970 and 2000. This generation survival probability index is based on a model of budworm physiological development and in response to climatic variation (Régnière et al. 2012).

Statistical analysis

Time-series clustering

Using complete linkage cluster analysis (Keogh and Kasetty 2003) applied to time series of raw percentage affected trees, we identified subareas that exhibited similar historical outbreak dynamics. Prior to clustering, time series were trimmed so that each year examined with a subarea time series contained information on at least five individual trees, resulting in series spanning the common interval 1928–2005. Clustering was based on the Euclidean distance between time-series (Keogh and Kasetty 2003) using the 'hclust' function in R. The statistical significance of the identified clustering was assessed using distance-based redundancy analysis (dbRDA; (Legendre and Legendre 2012)) as implemented using the 'adonis' function in the vegan (Oksanen et al. 2017) package in R. Here, the matrix of Euclidean distances was used as the response variable and cluster identification was used as a predictor.

To determine the degree of periodicity and the primary frequency of oscillation in outbreak chronologies we conducted spectral analyses on the cluster-level time-series (function 'spec.pgram' in R; Daniell kernel; smoothing parameter=3).

Spatial synchrony

We characterized the spatial synchrony of site-level outbreak time-series (n=51) using spatial nonparametric covariance functions (SNCF), as implemented in the ncf package in R (Bjørnstad 2009). SNCF measures the covariance amongst pairs of sites close together versus those further apart, and typically produces smooth decay patterns for pairs of sites further apart. SNCFs were computed for all pairs of sites within each management zone (M, W, O), and for all sites within the study area (i.e. a global SNCF). We used site level data instead of subareas despite relatively fewer replicates per site (5–15 trees) to maximize the number of pairwise comparisons within management zones. We predicted that, for any given distance class, there would be

greater synchrony (i.e. covariance) within the less-disturbed, more host-rich Wilderness (W) than in the managed forest landscapes (M, O).

Multivariate analysis

Constrained ordination (RDA) was used to model how forest landscape structure and climate affect variation in subarea outbreak chronologies. Our multivariate response matrix consisted of the annual % of trees affected by budworm outbreak, 1928–2005, for each subarea (rows; n = 16; Fig. 1). Potential predictor variables (total n = 101; Table 2), were of three types: 1) forest configuration (n = 48); 2) forest composition (n = 48); and 3) climate (n = 5). A greater number of predictors are included for forest configuration and composition due the multiple spatial scales at which these predictors were calculated, and in some cases multiple dates (Table 2). Prior to analysis, all predictors were standardized to zero mean and unit variance. We first identified a parsimonious subset of predictors within each predictor type using forward selection and adjusted R^2 as the selection criterion (Dray et al. 2007, Oksanen et al. 2017). Forward selection was implemented using the 'forward.sel' function in the 'packfor' package in R.

Once predictor subsets were identified for each type, we combined them into a final ordination model. We further reduced the retained predictors by removing those that were identified as collinear based on the variance inflation factor (VIF). Collinearity among predictors can result in biased models and can confound coefficient direction and interpretation. Predictors with a VIF greater than 10 were removed from the model (Zuur et al. 2009). VIFs were calculated using the 'vif.cca' function in the vegan package in R (Borcard et al. 2011). The relative importance of each predictor type (i.e. forest composition, configuration, and climate) was assessed using variance partitioning (Peres-Neto et al. 2006). Variance partitioning was undertaken using the 'varpart' function in the vegan package in R (Oksanen et al. 2017).

Our analysis is the first to relate forest landscape structure to budworm outbreak dynamics over multiple outbreaks. This objective presents two important challenges. First, individual outbreaks may respond more strongly to forest landscape structure at the time of each outbreak than the aggregate response of multiple outbreaks to either average structure or structure at any specific point in time. Second, data on forest landscape structure becomes more limited as one goes back in time; the most comprehensive remote sensing data is associated with the most recent budworm cycle. To better understand how outbreak timing and the availability of spatial data affect our ability to infer outbreak drivers, we repeated the RDA procedure outlined above for three shorter windows of roughly equal length, each spanning one outbreak cycle: 1928–1957 (cycle II, 28 yr), 1958–1983 (cycle III, 26 yr), 1984–2005 (cycle IV, 22 yr). According to our logic above, we predicted that the variance explained by the predictors applied to the latest cycle (i.e. IV) would be greater than either the aggregate, multi-cycle analysis or disaggregated analyses applied to either of the earlier cycles.

Data deposition

Results

Outbreak temporal patterns

The overall chronology contained four complete, major outbreak cycles between 1850 and 2005, yielding a region-wide estimate of cycle periodicity of 39 yr (Fig. 2). The first (peak ~ 1872, cycle I) and last (peak ~ 1991, cycle IV) of these four cycles were intense, and synchronous, affecting more than 65% of host trees at the cycle peak. While the first outbreak (cycle I) was not used in the analysis because it was defined by very few sample trees, an outbreak at this time is consistent with previous studies (Blais 1954). The second cycle (II) came in discrete pulses with variable timing (peaks ~ 1910, 1916, and 1931, spanning a long interval, but never rising to affect more than 40% of trees in any one year). The third cycle (III; peak ~ 1961), was more synchronous in its timing, but affected just over 40% of trees at the cycle peak.

Clustering of outbreak time-series

The 16 subarea chronologies (see Supplementary material Appendix 2 for raw subarea-level chronologies) grouped into four significant clusters on the basis of raw outbreak chronologies of percent trees affected (Fig. 3A) (dbRDA; F = 2.44; $p < 0.05$). The clusters corresponded largely to management zone, although they were also oriented along a southwest to northeast axis (Fig. 3B). Cluster 1 was comprised of a single subarea in the central part of the study area, in northern Minnesota, where just two, long-lasting outbreaks were observed (Fig. 4C). Cluster 2, restricted to the southwestern part of the study area, and entirely in Minnesota, exhibited irregular, high-frequency, low-amplitude behaviour that was poorly synchronized within-cluster (Fig. 4D). Clusters 3 and

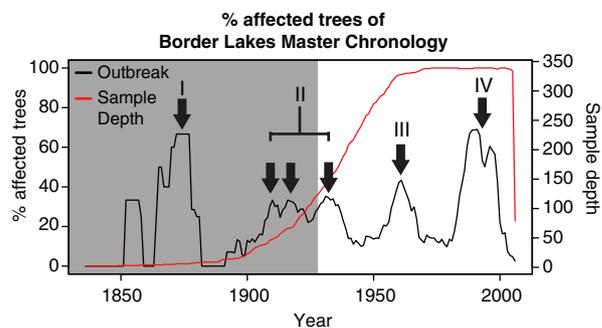Figure 2. Master chronology for the full BLL study area. The grey section was excluded from formal analyses due to low sample size at the level of the sample unit (i.e. subarea). Sample depth (red line) refers to the number of trees upon which the disturbance chronology (percent affected trees; black line) is based. Cycle peaks associated with four major cycles (I–IV) are indicated with arrows.
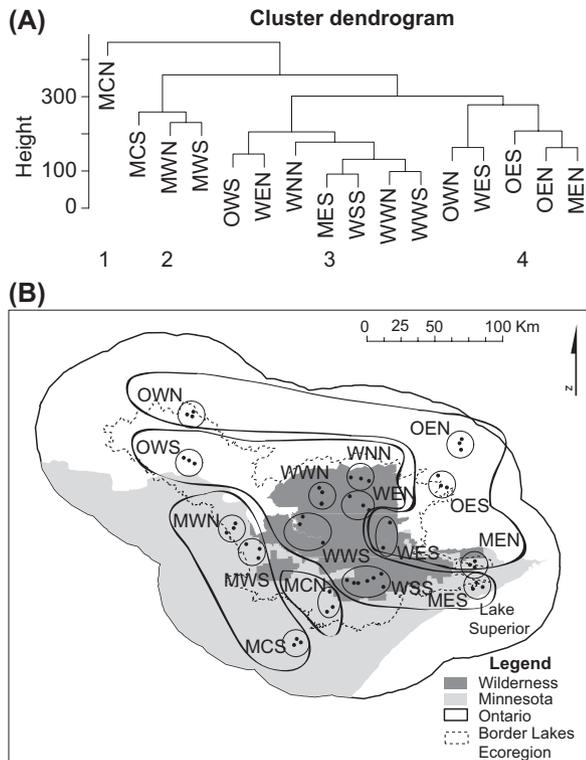
Figure 3. (A) Results of the cluster analysis (n = 4) of the percentage of trees affected by defoliation in the 16 subareas. (B) The four clusters overlaid in geographical space. See Table 1 for subarea acronyms.

4 each experienced three periodic outbreaks, with relatively high synchrony (narrow confidence interval) in cluster 3 and lower synchrony (wider confidence interval) in cluster 4 (Fig. 4A, B). Clusters 3 and 4 were slightly out-of-phase, with cluster 3 cycles consistently occurring three years later than cluster 4 cycles, as evidenced in a cross-correlation tabulation conducted a posteriori ($r_{lag\ 3} = 0.891$). This minor shift in phasing simply indicates some potential directionality in the expansion of outbreaks (e.g. travelling waves) that cannot be further evaluated without analysis of spatial dynamics at scales larger than the study area.

Spectral analyses applied to the mean chronologies for the clusters showed that clusters 1, 3, and 4 exhibited a single spectral peak at 40, 33, and 33 yr, respectively (Fig. 4). Cluster 2, in contrast, exhibited non-stationary behavior, including two major cycles at the start and end of the series (in the 1930s and 1990s), and four minor cycles occurring at regular intervals in between the major cycles. This resulted in weak periodicity in the 12–15 yr frequency range. Over the interval 1940–1990 the % of trees affected in cluster 2 never rose higher than 40%.

Outbreak spatial synchrony

Spatial covariance in outbreak occurrence generally decreased with increasing geographic distance between sites, whether measured at the scale of the whole study area (Fig. 5, red curves), or within the three management zones (Fig. 5A, B, C, black curves). As expected, spatial covariance within any given distance class was higher (i.e. more synchronous) in the less-disturbed, more host-rich Wilderness (Fig. 5B) than in the other two areas (Fig. 5A, C). This was especially true for distances greater than 40 km, where covariance actually increased with distance in the Wilderness (Fig. 5B).

Forest landscape structure and climate influence on outbreak dynamics

The final RDA model applied to the full chronology (1928–2005) contained seven variables distributed among the three predictor types (Table 3). Forest configuration was included as the proportion of forest disturbance at scales of 30 and 5 km. Forest composition was included as the basal area of balsam fir at scales of 5 and 1 km in the year 2005, and the proportion of old forest in 2005 at 10 and 20 km. Climate was included as the budworm growth index (Fig. 6).

In total, this model captured 40% of the variance in outbreak pattern among the 16 subareas over 76 yr. 20% of the total variance was attributable to forest configuration and forest composition alone, representing roughly half of the variance explained. The other half of the explained variance was shared among predictors, with half of that (13%) shared between forest composition or configuration, and most of the other half (9%) shared between forest composition and climate. Climate alone accounted for none of the variation (Fig. 6).

In analysing each outbreak cycle independently (cycles II–IV; Fig. 2), we found that, as expected, our models captured a greater proportion of variance as we moved forward in time. During cycle II (1928–1957; Fig. 7A) 14% of the variance in outbreak pattern could be explained by forest configuration; no other predictors were retained. During cycle III (1958–1983; Fig. 7B) 46% of the variance in outbreak pattern was explained by forest composition and configuration. During cycle IV (1984–2005; Fig. 7C) 66% of the variance in outbreak pattern was explained by a combination of all three classes of predictors, with 40% of the variance explained by forest landscape structure (inclusive) and the remainder shared between climate and forest landscape structure variables, with none of the variance attributed to climate alone.

Discussion

Our results indicate that historical outbreak dynamics were affected by differences in forest landscape structure that resulted from different land management legacies in the BLL. We found that the greater the basal area of host tree species and the proportion of older forest on the landscape, the lower the frequency of outbreaks and the higher their amplitude, resulting in outbreaks that are more intense, more extensive, of longer duration, and of greater synchrony.

We did not expect an important effect of climate on outbreak behavior because we predicted that climate was
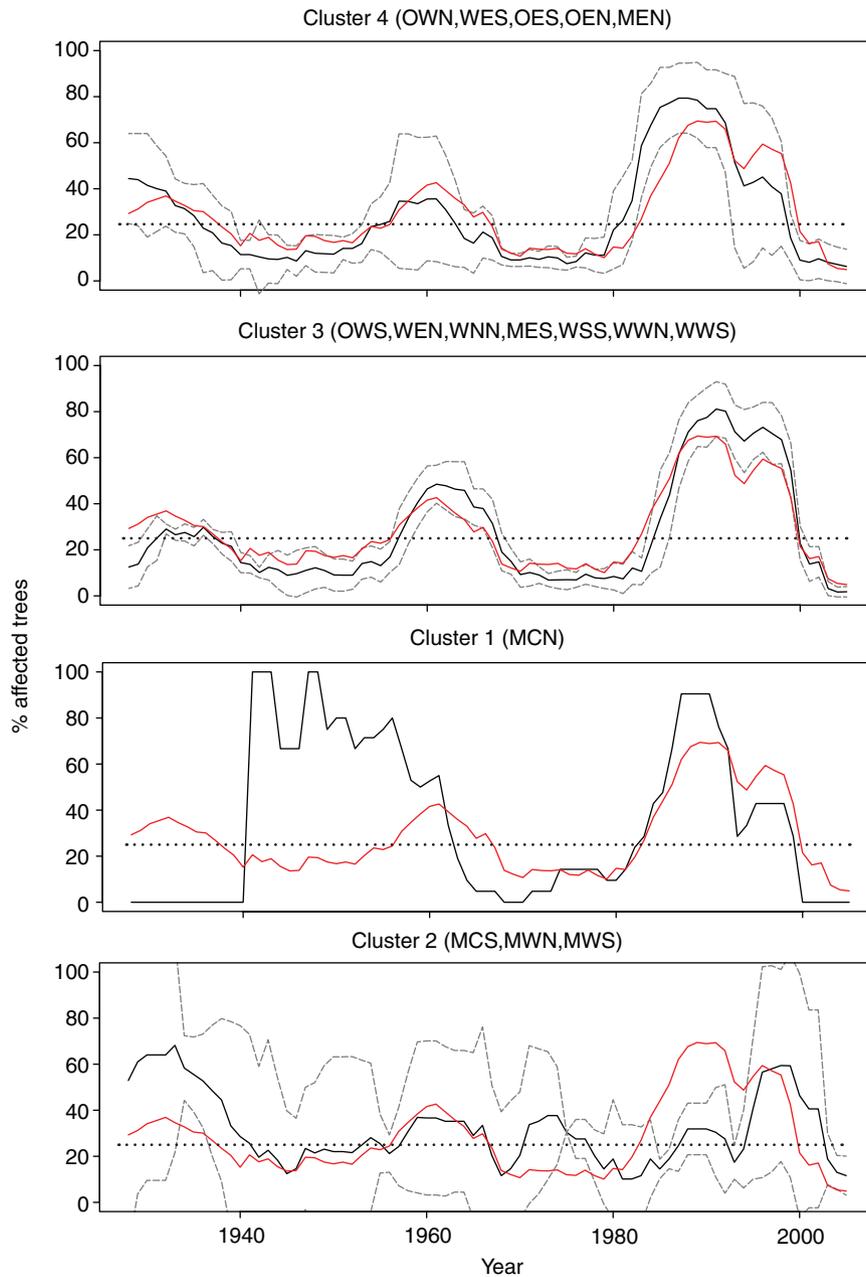
Figure 4. Combined chronologies for each of the four clusters shown in Fig. 3, listed from the southwest (bottom) to the northeast (top). Black = average percentage of trees affected for the cluster. Dashed gray = 95% confidence intervals for the cluster. Red = average percentage of trees affected for the entire study area (Fig. 1). Dotted horizontal line indicates the 25% threshold defining outbreaks in prior study (Robert et al. 2012) – but this line is used for reference only and not applied in any analysis. Difference between red and black curves shows the deviation of a cluster from the broader BLL temporal pattern. See Table 1 for subarea acronyms, and Supplementary material Appendix 2 for raw subarea-level chronologies. Spectral peak from spectral analysis is the following for each cluster: cluster 4 and 3: 33 yr, cluster 2: 12–15 yr, cluster 1: 44 yr.

not sufficiently variable within our study area. However, we learned that climate does vary somewhat with distance from Lake Superior such that subareas that are closer to the lake have cooler springs and summers (Fig. 7C). Indeed, the spruce budworm population growth index indicates that the cooler climate closest to Lake Superior could produce higher population growth rates, whereas progressively interior sites and sites south of our study area may be too warm for optimal reproduction (Régnière et al. 2012) (Supplementary material Appendix 1 Fig. A1C). Although some of the variation in outbreak histories was due to climate, this variance was consistently shared with, and therefore indistinguishable

(A) Ontario

(B) Wilderness

(C) Minnesota

Distance (km)
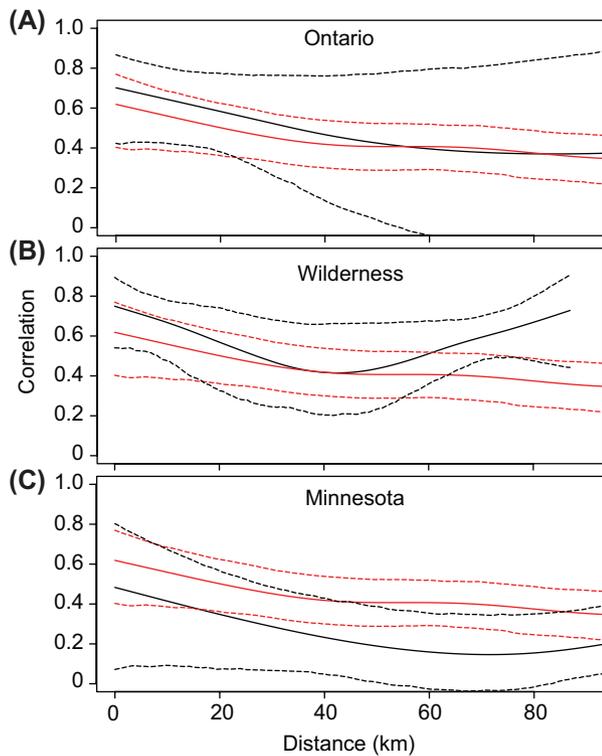
Figure 5. Spatial non parametric covariance functions (SNCF) for the different management zones in the BLL. Each management zone (black) is represented individually on separate graph (A, B, C) with their 95% confidence interval (dashed lines) and overlaid with the SNCF calculated for the entire BLL (red).

Cycle frequency, amplitude, and synchrony

We predicted that outbreak cycle frequencies, amplitudes, and synchrony would be related to one another in a systematic way, and that this multi-variate response would be related to forest landscape structure, and this is precisely what we observed. Outbreak behavior within clusters 3 and 4 in Wilderness and in Ontario was consistent with most other tree-ring based studies of spruce budworm outbreaks: outbreaks were periodic, and evenly spaced, with 33 yr between cycle peaks (Fig. 4A, B). They were well-synchronized at the scale of both clusters (Fig. 5A, B), which were extensive, spanning 75% of the subareas (Fig. 3B: 7 subareas in cluster 3, 5 subareas in cluster 4). Such strong periodicity and synchrony are also consistent with Royama's (1984) theory of harmonic oscillations in the spruce budworm system.

The contrast in observed outbreak behavior between clusters 1 and 2 was striking even though both clusters are in Minnesota. Here, a greater diversity of cycling behavior was observed relative to the other zones. We found evidence for high-amplitude, low-frequency, 40-yr cycles in tiny cluster 1 (Fig. 4C: 1 subarea), and low-amplitude, high-frequency cycling in cluster 2 (Fig. 4D: 3 subareas). It is possible that our statistical test of climatic effects on outbreak patterning was weak, and that the anomalously low amplitude and high frequency of irregular cycling within Minnesota's cluster 2 is consistent with the environment being too warm to promote regular, high-amplitude cycling. However, this would not explain the opposite pattern being observed in Minnesota's adjacent cluster 1.

What might explain these divergent patterns within a single management zone is spatial variation in forest fragmentation of host forests in Minnesota, including the decreased abundance and contagion of host cover. This in turn would be wholly consistent with the growing number of results that have emerged in the last two decades supporting

from, that due to forest landscape structure. Thus, at the scale of our uniquely structured study area, it appears that forest landscape structure is more important than climate in shaping of spruce budworm outbreak dynamics.

Table 3. Summary of variables selected for inclusion in the final RDA models at each outbreak time window. Multiple time periods and/or spatial scales selected for a given variable indicated by multiple values separated by the '/' character.

Temporal window	Variable family	Variable selected	Time period	Spatial scale
Full	Composition	Balsam fir basal area	2002/2002	1 km/5 km
		Proportion of old forest	2000/2000	10 km/20 km
	Configuration	Proportion of forest disturbance	Time-series average	5 km/30 km
	Climate	Spruce budworm growth index	Time-series average	Subarea average
1928–1957	Configuration	Area-weighted patch size of forest disturbance	Time-series average	Subarea average
1958–1983	Composition	Spruce and fir basal area	2002	30 km
		Proportion of forest	1975	0.5 km/5km
		Proportion of old Forest	2000	5 km
	Configuration	Proportion of forest disturbance	Time-series average	5 km
1984–2005	Composition	Fir basal area	2002	1 km
		Proportion of forest	1975	0.5 km
		Proportion of old forest	2000	30 km
	Configuration	Proportion of forest disturbance	Time-series average	1 km/30 km
		COHESION of fir patches	Time-series average	1 km
	Climate	Min. spring temperature	Time-series average	Subarea average
		Min. summer temperature	Time-series average	Subarea average

Figure 6. Redundancy analysis (RDA) and variance partitioning relating dissimilarity in the annual percent trees affected to independent variables chosen by forward selection for each of our three hypotheses: 1) forest configuration; 2) forest composition; and 3) climate. See Table 1 for subarea acronyms in black font. Inset bubble diagrams indicate the independent and shared variance explained by each class of variables (see Table 2 for predictor variable descriptions, where the color label corresponds to the class of variables in the bubble diagram). The RDA is applied to the full chronology is contrasted with separate RDAs applied to each of the three major outbreak periods (Fig. 7).

the 'silvicultural hypothesis', which suggests that outbreak dynamics may be stabilized (i.e. lower amplitude and higher frequency) through the removal of susceptible host forest from the landscape.

The contrast in outbreak synchrony among management zones indicates that forest management legacies influence spatial synchrony (Fig. 5). This result is interesting given the known long-range dispersal capacity of the spruce budworm (Greenbank et al. 1980, Anderson and Sturtevant 2011). Our study purposefully selected contrasts in forest management legacies at spatial scales large enough to overcome the large scale spatial correlation of outbreak dynamics created by the cycle synchronization process. West and central areas of Minnesota that contained the least amount of budworm host exhibited the lowest degree of synchrony of the three management zones (i.e. cluster 2; Fig. 4). In contrast, the Wilderness, where host was most abundant and forests were least disturbed, exhibited the highest degree of synchrony (Fig. 4–6). Ontario, which had similar rates of disturbance as Minnesota but where disturbances were more aggregated in space, was intermediate in its degree of synchrony (Fig. 5). Notably, outbreak dynamics of subareas from Minnesota that contained more host (i.e. eastern Minnesota; Fig. 6) tended to follow the dynamics of the broader study area (i.e. clusters 3 and 4; Fig. 3) – demonstrating the importance of treating forest landscape structure as a continuous variable that does not necessarily follow political boundaries (James et al. 2011).

In our study, the concentration and connectivity of preferred budworm host, rather than deciduous content, emerged as the important compositional factors in our RDA analyses (Fig. 6). This result suggests that it is the effect of host forest on dispersal success, and not the effect of non-host forest on natural enemy communities, through which cycling behavior is modified. While one might speculate that these factors could be negatively correlated with each other,

Pearson correlations between balsam fir basal area and deciduous basal area were low ($r = 0.08$ and $r = 0.34$ at 1 and 5 km radius, respectively). It is possible that balsam fir is the limiting factor in this region, relative to the geographic locations where negative relationships between hardwood content and budworm damage have been documented (i.e. southeastern Canada; (Cappuccino et al. 1998, Campbell et al. 2008)). Further research will be required to identify which of the mechanisms are responsible for the interesting asynchronous high-frequency oscillations observed in cluster 2.

Contrast with other studies

The patterns we report compare well to other reported patterns in the spruce budworm dendroecology literature, but are perhaps more directly interpretable because we specifically chose a spatially structured landscape with clear contrasts forest landscape structure associated with divergent land management legacies (Sturtevant et al. 2014). On the one hand we observed a relatively stable cycle that was fairly well synchronized throughout the bulk of the study area, which is consistent with (Boulanger et al. 2012), in their small-scale, multi-century study in southern Quebec. On the other hand, we also observed persistent asynchrony at finer temporal and spatial scales, as did Jardon et al. (2003), in their large-scale study from across Quebec. We found that spatial synchrony varied the most among management zones with different forest landscape structures. Our study supports Jardon et al. (2003)'s assertion that a study area needs to be extensive to reliably estimate outbreak frequency. Our observation of a wide range of outbreak intensities (Fig. 2, 4) is further consistent with a small-scale, multi-century study in Maine (Fraver et al. 2007) that described a relatively low outbreak frequency (~67 yr), but with alternating major and minor cycles of defoliation intensity, where only the major cycles were counted as 'outbreaks'.

Figure 7. Redundancy analysis (RDA) and variance partitioning relating dissimilarity in the annual percent trees affected to independent variables chosen by forward selection for each of our three hypotheses: 1) forest configuration; 2) forest composition; and 3) climate. See Table 1 for subarea acronyms in black font. Inset bubble diagrams indicate the independent and shared variance explained by each class of variables (see Table 2 for predictor variable descriptions, where the color label corresponds to the class of variables in the bubble diagram). The RDA is applied to each of the three major outbreak periods (A–C).

Previous investigators have reported on large-scale patterns in outbreak synchrony as a function of distance, and have inferred that the Moran effect is a ubiquitous phenomenon in both spruce budworm (Williams and Liebhold 2000) and other forest insect systems (Peltonen et al. 2002). More recent study of synchrony in the spruce budworm demonstrates that different causal factors – including bottom-up factors such as host tree cone production – can contribute to the Moran effect at different times in the outbreak cycle, and concluded that synchrony is unlikely to be caused by any one factor (Bouchard et al. 2017). While their study focused on the effect of high frequency fluctuation of factors related to food availability and budworm survival on synchrony, our study focused on the effect of slow changes in forest composition and structure on cycling behavior. Our results suggest that in spite of the Moran effect, the process of outbreak

synchronization can break down due to strong transitions in forest landscape structure.

Looking beyond the spruce budworm, there is evidence for reciprocal insect–host plant feedback operating in other periodic defoliator systems, namely: forest tent caterpillar in boreal Canada (Roland 1993, Roland and Taylor 1997); gypsy moth in the northeastern United States (Haynes et al. 2009); jack pine budworm in central North America (Nealis and Lomic 1994); larch budmoth in the Swiss alps (Johnson et al. 2004); and winter moth in Fennoscandia (Ims et al. 2004). Collectively, this suggests that the research community should consider re-evaluating the idea that population outbreak cycles are driven strictly by reciprocal feedback occurring in either the upper or lower trophic levels of a tritrophic (host plant–herbivore–natural enemy) interaction. Wherever both trophic levels seem to be implicated in cycling

behaviour, there may be some opportunity for manipulating long-term outbreak dynamics by manipulating landscape structure, which is in accordance with the silvicultural hypothesis.

Study limitations

While tree-ring data is a good proxy to quantify the temporal dynamics of budworm outbreaks within a given location, it is not a perfect proxy. Indeed, the use of the percentage of trees with radial growth sufficient to indicate defoliation damage may not capture some of the fine-scaled variation in population dynamics that may be occurring at the tree-level. Nonetheless, a comparison with aerial defoliation surveys suggests that tree ring data do capture larger scale variation in tree damage associated with budworm outbreaks (Bouchard et al. 2006). Clearly, intensive population studies provide the best local understanding of the underlying processes that may not be detectable using impact proxies such as tree ring and aerial survey data (Royama 1984). There are, however, no practical methods available to quantify such fine-scaled population dynamics at the spatiotemporal scale necessary to evaluate landscape-scale feedbacks of the forest on budworm outbreaks.

Our study is the first to explicitly examine effects of forest landscape structure on budworm outbreak dynamics across multiple outbreak cycles. A challenge facing any approach such as ours is the absence of detailed historic data on forest conditions during earlier cycles. The availability of Landsat-derived spatial data extends back only to the early 1970s. Further, the earlier Landsat Multispectral Scanner sensors did not have the spectral resolution necessary to distinguish tree species composition (Moore and Bauer 1990) which was enabled later by launch of the Landsat Thematic Mapper sensors in 1982 and 1984. However, we know that small-sized and spatially-diffuse clearcut harvest disturbances have been applied consistently in Minnesota since the 1930s (White and Host 2003, Sturtevant et al. 2014), and that the Wilderness had a lower disturbance rate during the last century than surrounding managed forests (Heinselman 1996). Forestry operations in northern Ontario have been traditionally road-limited and applied to lands leased from the provincial government (Rempel et al. 1997) – so there is no reason to suspect the spatial pattern of mechanized forestry operations prior to 1975 were markedly different from those observed in the 1970s and 1980s. Nonetheless, balsam fir is clearly sensitive to budworm disturbance in the region (Frelich and Reich 1995), and it is likely that this host species is more dynamic than the otherwise dominant legacy of forest management activities because spruce budworm is simultaneously killing the fir (James et al. 2011).

We found that the analysis specific to cycle IV (i.e. the most recent; Fig. 7) provided a more robust estimate of the forest response than both a) the aggregated analysis of all cycles, and b) analysis of earlier cycles (cycle II and III) (Fig. 6, 7). This greater robustness is likely due to the increased quantity and quality of remote sensing data used to generate relevant forest landscape structure variables through time. Alternatively, a stronger effect of forest landscape structure on outbreaks moving forward through time (Fig. 7) might also be the consequence of increasingly divergent landscape structure as the legacies of forest management activities accumulated over time (Sturtevant et al. 2014). That is, budworm outbreak behavior may simply be tracking forest landscape structure as it diverges among management zones through time. Without access to high quality data of population abundance and landscape structure at earlier time periods, we cannot yet distinguish between these two plausible explanations for the results from the outbreak-specific analyses, and, indeed, they are not mutually exclusive.

Conclusions

We found that spatial variation in forest landscape structure, including species composition and spatial configuration influences spruce budworm outbreak cycle frequency, intensity, and synchrony. In areas with reduced fir abundance and connectivity, spruce budworm outbreaks had low intensity and high frequency, and were not well synchronized. The opposite was observed in areas where host was more abundant, as in the relatively undisturbed Wilderness. This result is consistent with the 'silvicultural hypothesis' that increasing severity of spruce budworm outbreaks over the last century resulted from past management activities that enhanced fir, in this case by demonstrating the reverse situation is true – i.e. a reduction in landscape-level host mitigates the cycling behavior of budworm outbreaks. This paradigm of strong forest-insect reciprocal feedback is generally more accepted for bark beetle systems in western North America (Whitehead and Russo 2005) and western Europe (Temperli et al. 2013), but until now has been considered controversial for defoliators such as the spruce budworm (Miller and Rusnock 1993, Muzika and Liebhold 2000).

Relationships between forest landscape structure and outbreak patterns appear to be intertwined with weak responses to a climatic gradient, which highlights the challenge of identifying the unique contributions of forest landscape structure on spruce budworm outbreaks. Our results also did not directly support the notion that deciduous content affected outbreak behavior, a surprising result given the mixed forest conditions of the BLL. Nevertheless, ongoing land management and consequent land-use changes at large scales has the potential to have significant unintended effects on spatial ecological processes. Continued sustainable stewardship of forest ecosystems requires that more attention be given to spatial legacies in forest landscape structure as these legacies affect insect outbreak dynamics over broad spatial scales.

Our results support the synthetic view that while budworm outbreaks are generally cyclic, these cycles may be muted in host-deficient forests. To the extent that the budworm itself, through stand-replacing disturbances, is responsible for significant changes in forest species composition and forest spatial configuration, our study implies that there is a reciprocal feedback relationship between the budworm and forest

that occurs at the landscape scale, as hypothesized decades ago (Baskerville 1975). This provides considerable qualitative validation to the earliest models of spruce budworm dynamics, which hypothesized that forest renewal was a key process affecting spruce budworm cycling (Jones 1977). Even if, as hypothesized by Royama (1984), reciprocal feedback with natural enemies is a primary source of outbreak cycling behaviour, it appears that the budworm–forest reciprocal feedback cannot be ruled out as a significant component of the full complexity in outbreak patterning. Additional study in different ecological contexts is needed to better quantify the influence of forest landscape structure on budworm outbreak cycling as well as how forest landscape structure may indirectly affect top-down control by natural enemies. Additionally, we think there would be enormous value in examining the strength of the insect–host relationship in other defoliator systems to determine if reciprocal forest–insect feedback is a universal feature of forest defoliator outbreak systems.

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