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RESEARCH ARTICLE

Forest landscapes determine their pests: jack pine budworm spatial dynamics under host scarcity

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Abstract

Context Jack pine budworm (JPBW), Choristoneura pinus pinus, is a major defoliator in Canada, yet remains absent from theoretical discourse on outbreak synchrony, despite sharing key life history traits with the archetypal "cross-scale" pest, spruce budworm (C. fumiferana). JPBW has primarily been studied in host-rich landscapes, raising questions about its behavior in host-sparse regions.

Objectives We asked whether scale-crossing JPBW outbreaks are contingent on host density, and whether reduced outbreak incidence in host-sparse landscapes reflects synchronized or desynchronized population limitation.

Methods We applied a systematic framework for analyzing spatiotemporal tree-ring data, adapted from recent reconstructions of spruce budworm and forest tent caterpillar. This framework integrates temporal and spatial methods to evaluate periodicity, coherence, and landscape-scale synchrony.

Results In the pine-sparse Border Lakes region (~30,000 km^2), we identified 14 growth disturbances between 1910 and 2006, typically recurring every seven years and affecting 30% of trees annually at peak. Reanalysis of data from a host-rich site in Manitoba confirmed strong correspondence between JPBW defoliation and growth reductions. Nine episodes in the host-rich site coincided with published outbreaks, whereas signals in the host-sparse Border Lakes remained spatially variable and weakly correlated across sample areas.

Conclusions Despite high fecundity and dispersal potential, JPBW in host-sparse landscapes behaves endemically. Pest status, we argue, is not a fixed insect trait but an emergent property of host availability and spatial scale. The JPBW system constitutes a third example from the Border Lakes region where the "catastrophe" theory of outbreak origin is more consistent with data than a "clockwork" theory of spatially synchronized cycling.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-026-02485-x.

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Introduction

Large-scale insect forest outbreaks are ecologically disruptive and economically costly, leading to a long-standing question in insect ecology: "what is a pest?" (Nothnagle and Schulz. 1987). Rising pest behaviour in North America has been linked in several key cases to climate warming (Bentz et al. 2010; Boulanger et al. 2025); however, the role of the forest itself in regulating outbreak dynamics remains underexplored (Campbell et al. 2008; Senf et al. 2017; Kneeshaw et al. 2021). Complicating matters, historical land use and fire suppression have altered forest age structure and composition (Boucher et al. 2014), while climate change has introduced novel ecological conditions across the continent (Stralberg et al. 2020), making it difficult to evaluate the relative contributions of each to changing pest dynamics (Gougherty et al. 2024).

The forest-defoliating Lepidoptera often exhibit spatially synchronized population cycling (Myers 1988, 1998). Among the periodic outbreak species, the spruce budworm (*Choristoneura fumiferana* Clem., SBW) is the primary model for cross-scale insect outbreak dynamics (Holling 1973; Royama 1984; Williams & Liebhold 2000), while the closely related jack pine budworm (*Choristoneura pinus pinus* Freeman, JPBW) is nearly absent from broad conceptual treatments (Volney 1988; McCullough 2000). Although the two species share similar life histories—including high fecundity, dispersal capacity, and interactions with comparable natural enemy communities (Nealis 2016)—they differ in key aspects of host-mediated feedbacks. JPBW relies on early access to pollen cones for survival (Nealis & Lomic 1994), whereas SBW can mine older foliage (McGugan 1954), enabling populations to persist through multi-year episodes of defoliation (Régnière & Nealis 2007). These contrasting feedbacks contribute to distinct population behaviours: infrequent, prolonged outbreaks in SBW versus more rapid, collapsible eruptions in JPBW (Cooke et al. 2007).

This divergence raises an important question: why is SBW widely recognized as a quintessential cross-scale pest (Holling 1986), whereas JPBW remains peripheral to outbreak theory? The question is timely given substantial investments in JPBW suppression (Rawat et al. 1987; Cadogan 1993; Meating et al. 1995; Holmlund 2020) and evidence that both species exhibited rising outbreak activity in the 1980 s (Blais 1983; Volney 1988).

Everything that is known about JPBW comes from host-rich landscapes where jack pine is abundant and defoliation occurs at near-decadal intervals (Dixon & Benjamin 1963, Foltz et al. 1972, Clancy et al. 1980, Batzer & Jennings 1980, Volney & McCullough 1994, McCullough 2000). Far less is understood about how JPBW behaves in host sparse systems, where populations may remain suppressed, cycle at low amplitude, or fluctuate asynchronously across space—a question made more pressing by ongoing shifts in forest composition under climate and disturbance change.

To evaluate how host abundance shapes JPBW dynamics, we draw on two contrasting paradigms of Lepidopteran outbreak behaviour (Sturtevant et al. 2023): "clockwork" models emphasizing weather synchronized cycles driven by fast acting natural enemies (Royama 1984), and "catastrophe" models emphasizing asynchronous, nonlinear population eruptions driven by host mediated feedbacks (Ludwig et al. 1978). These perspectives frame a key working hypothesis: that host density influences the intensity, periodicity, and synchrony of defoliator outbreaks across space and time (Cooke et al. 2024).

To test this hypothesis, we used tree ring and forest composition data from the Border Lakes Landscape (BLL), a hemiboreal region of northeastern Minnesota and northwestern Ontario where jack pine is sparse, and we compared these results with those from Spruce Woods Provincial Forest (SWPF), Manitoba, a host rich system sampled by Robson et al. (2015). By leveraging the strong contrast in host abundance between these landscapes, we assess whether JPBW outbreak behaviour across the broader landscape is fundamentally shaped by forest context—and what this implies for understanding and managing defoliator dynamics at landscape scales.

To address these questions, our investigation was structured in two phases. In Study 1, we examined the spatiotemporal dynamics of jack pine growth disturbances in the Border Lakes Landscape (BLL) and evaluated their relationship to forest landscape attributes,

following analytical approaches applied previously to spruce budworm and forest tent caterpillar (*Malacosoma disstria* Hbn.) dynamics in the same study area (Cooke et al. 2024). When these analyses yielded unexpectedly weak relationships, we broadened the investigation in Study 2 by formally comparing the BLL results with those of Robson et al. (2015) from the host rich Spruce Woods Provincial Forest (SWPF), Manitoba. This comparative step proved essential for interpreting the BLL patterns and for evaluating whether JPBW dynamics aligned more closely with "clockwork" or "catastrophe" expectations. Because the contrasting landscapes required a staged and iterative analytical workflow—including a systematic framework for assessing synchrony, periodicity, and spatial structure (Table 1)—we provide expanded methodological detail, diagnostic analyses, and the full reasoning path connecting Studies 1 and 2 in the Supplementary Information.

Methods

The investigation was designed in two phases. In Study 1 we examined the spatiotemporal dynamics of jack pine growth disturbances in the Border Lakes Landscape (BLL) in relation to forest landscape attributes, following the straight-forward analytical designs of Robert al. (2018) for spruce budworm on white spruce (*Picea glauca* (Moench) Voss), and Robert et al. (2020) for forest tent caterpillar on trembling aspen (*Populus tremuloides* Michx). After obtaining an uninspiring result in Study 1, we broadened the scope of the investigation in a second phase of analysis to formally compare our Study 1 results to those of Robson et al. (2015) in Spruce Woods Provincial Forest (SWPF), Manitoba. The informative comparison between the two allowed us to go back to the results of Study 1 and re-interpret what we initially thought was a negative result. The Supplementary Information provides a complete accounting of the logical sequence of steps involved in iteratively moving back and forth between the methods and the results of the two studies.

Study areas

Border lakes landscape

The Border Lakes Landscape (BLL) encompasses a large (~30 000 km^2) ecoregion that straddles the border between Minnesota (USA) and Ontario (Canada) at the hemiboreal transition between the Laurentian mixed-wood and boreal forest regions. Forest composition is mixed (Heinselman 1973) with a high proportion of boreal tree species (e.g., jack pine, black spruce (*Picea mariana* (Mill.) B.S.P), white spruce, balsam fir, paper birch (*Betula papyrifera* Marsh.), aspens (*P. tremuloides* Michx., *P. grandidentata* Michaux), as well as several species near the northern limit of their range, such as white pine (*Pinus strobus* L.), red pine (*P. resinosa* Ait.), and red maple (*Acer rubrum* L.). Forest composition and structure vary in response to historical fire regimes and management legacies that differ spatially across the region (Sturtevant et al. 2014). Conifer abundance is higher in the central and northeastern BLL, while hardwoods dominate the southwestern portion, particularly in Minnesota (Cooke et al. 2024). Jack pine comprises roughly 7% of basal area across the landscape (Thapa et al. 2020), occurring patchily within this heterogeneous matrix.

Spruce woods provincial forest

Spruce Woods Provincial Forest (SWPF), located ~ 600 km northwest of BLL in Manitoba's Boreal Plains ecoregion, provides a contrasting landscape context (Fig. 1). Jack pine plantations dominate parts of this forest, reflecting an intensive reforestation program between 1930–1946 in which ~ 74% of seedlings planted were jack pine (Haig 1957; Henderson et al. 2002). The broader sandhills region comprises mixed aspen–oak (*Quercus* spp.)–grassland ecosystems, but the plantation network targeted by Robson et al. (2015) includes three sampling clusters (seven jack pine plots) separated by ~ 10 km. Although not spatially extensive enough to analyze broad-scale synchrony, these chronologies provide a valuable comparison for evaluating temporal JPBW dynamics relative to BLL.

Tree-ring data collection and preparation

Study 1: Border lakes landscape (BLL)

Jack pine in the BLL was not originally sampled to investigate jack pine budworm directly. Rather, jack pine cores were collected opportunistically as part of a broader, multispecies dendroecological program

Table 1 An overview guide to the analysis of synchrony in spatiotemporal patterning in forest insect and proxy data, as implemented in the next section

Dimension	Method	Algorithm	Purpose	**Prediction** vs null[1]	Evidence[2]
Temporal	Auto-regression analysis	acf, pacf	1. Identify autocorrelation structure in aggregated and disaggregated time-series	**Cycling is irregular**, not purely low-order	Figs. SI2, SI11, SI15
	Spectral analysis	spectrum	2. Identify dominant frequency of fluctuation in aggregated and disaggregated time-series	**Spectrum is multi-peaked**, not unimodal	Figs. SI3, SI11, SI15
	Peak detection	AMPD	3. Define intervals and characterize the severity of interval peaks in aggregated time-series, including the distribution of these cycle peak intensities	**Cycle peak intensities are highly variable, with no strong tendency toward a singular mode**, not tightly unimodal	Figure 2 (and SI5, SI15)
	Peak alignment	AMPD, hist	4. Define intervals and characterize the intensity of interval peaks in disaggregated time-series, including the coincidence of cycle peak phasings	**Peaks are poorly aligned across time-series, are over-dispersed in frequency count**, not well aligned and under-dispersed	Fig. SI2 (and Fig. 2 & SI 16)
	Continuous wavelet transform	CWT	5. Identify slow changes through time in periodic behaviour in aggregate time-series	**Periodicity changes with changes in climate or landscape structure** rather than stable over time	Figure 3
	Time-series cross-correlation analysis	cor	6. Compute the mean pairwise correlation, $\bar{r}$, between all pairs of disaggregated time-series	**Correlation is significant but lower than expected under Moran's hypothesis**	Figs. SI9 & SI15
		Sncf	7. Quantify correlation between time-series as a function of separation distance	Correlograms indicate a decline in correlation between series with increasing distance**, but the correlations are significantly lower in the host-sparse landscape**	Figure 5 & SI17

Table 1 (continued)

Dimension	Method	Algorithm	Purpose	**Prediction** vs null[1]	Evidence[2]
Spatial	Spatial auto-correlation analysis	correlog	1. Identify contagion in spatial maps of impact	**Impacts are contagious, as per catastrophe theory**, not diffuse as per clockwork theory	Fig. SI6
	Spatial cross-correlation between successive intervals	cor	2. Characterize strength of "ecological memory"	Even if spatial patterns are persistent at fast time-scales, at intermediate time-scales **previous spatial patterns are repulsive,** not forgotten	Figure 4 and SI7
	Landscape principal components analysis	princomp	3. Identify the dominant thematic factors influencing multivariate landscape structure	**There is systematic landscape structure associated with human and natural disturbance**	Fig. SI9
	Spatial regression analysis	lm	4. Quantify the influence of landscape structure on spatial maps of impact	**Impacts are extremely variable in how they correlate with landscape structure**, not consistent across intervals	Table SI1

[1]Specific predictions in bold font contrasted against null clockwork hypothesis in standard font

[2]Primary results are bolded. Standard font are results presented in Appendix or as Supplementary Information

designed to study spruce budworm (SBW) and forest tent caterpillar (FTC) dynamics (Robert et al. 2018, 2020). Because sampling for SBW and FTC required stands containing 5–10 sample trees of white spruce or trembling aspen, jack pine was cored only where it occurred within or adjacent to these targeted stands. Consequently, jack pine representation varied among sites, producing lower and uneven per-site replication (178 trees total; cf. 317 spruce and 374 aspen). Nonetheless, sample sites were well distributed geographically across the BLL, stratified by management legacy and broad geographic gradients (Supplementary Information Fig. SI1), ensuring landscape-level coverage despite local variability in jack pine density.

Core samples were processed following established protocols in the companion SBW study (Robert et al. 2018). All trees were at least 70 years old (oldest dated 1854). Ring-width series were cross-dated and detrended using ARSTAN, removing low-frequency trends while retaining mid-frequency variation (5–25 year) following Robson et al. (2015). The program OUTBREAK (Holmes & Swetnam 1986) was then applied to derive annual indices of growth suppression. We identified growth disturbances as $\geq$ 4-year negative anomalies exceeding – 1.28 SD, a threshold consistent with short-duration Lepidopteran defoliation signals. We did not employ a nonhost reference chronology because all long-lived species in the BLL are subject to episodic defoliation. Annual disturbance intensity was quantified as the percentage of trees affected (PTA).

Because jack pine occurred only intermittently within targeted stands, the resulting 40 jack pine chronologies could not support the finer subarea aggregation levels used in previous BLL studies (i.e., 15–16 subareas) the finer subarea aggregation (15–16 units) used in earlier BLL studies. Instead, we grouped these chronologies into eight area-level growth-disturbance chronologies, based on spatial clustering of sampling effort and established hierarchical groupings used in earlier work (Fig. 1; Supplementary Information Fig. SI1). This approach maintains spatial representation across the BLL while ensuring sufficient replication within each aggregated unit.

Study 2: Spruce woods provincial forest (SWPF)

Although BLL sampling was conducted in 2007, prior to the publication of Robson et al. (2015),

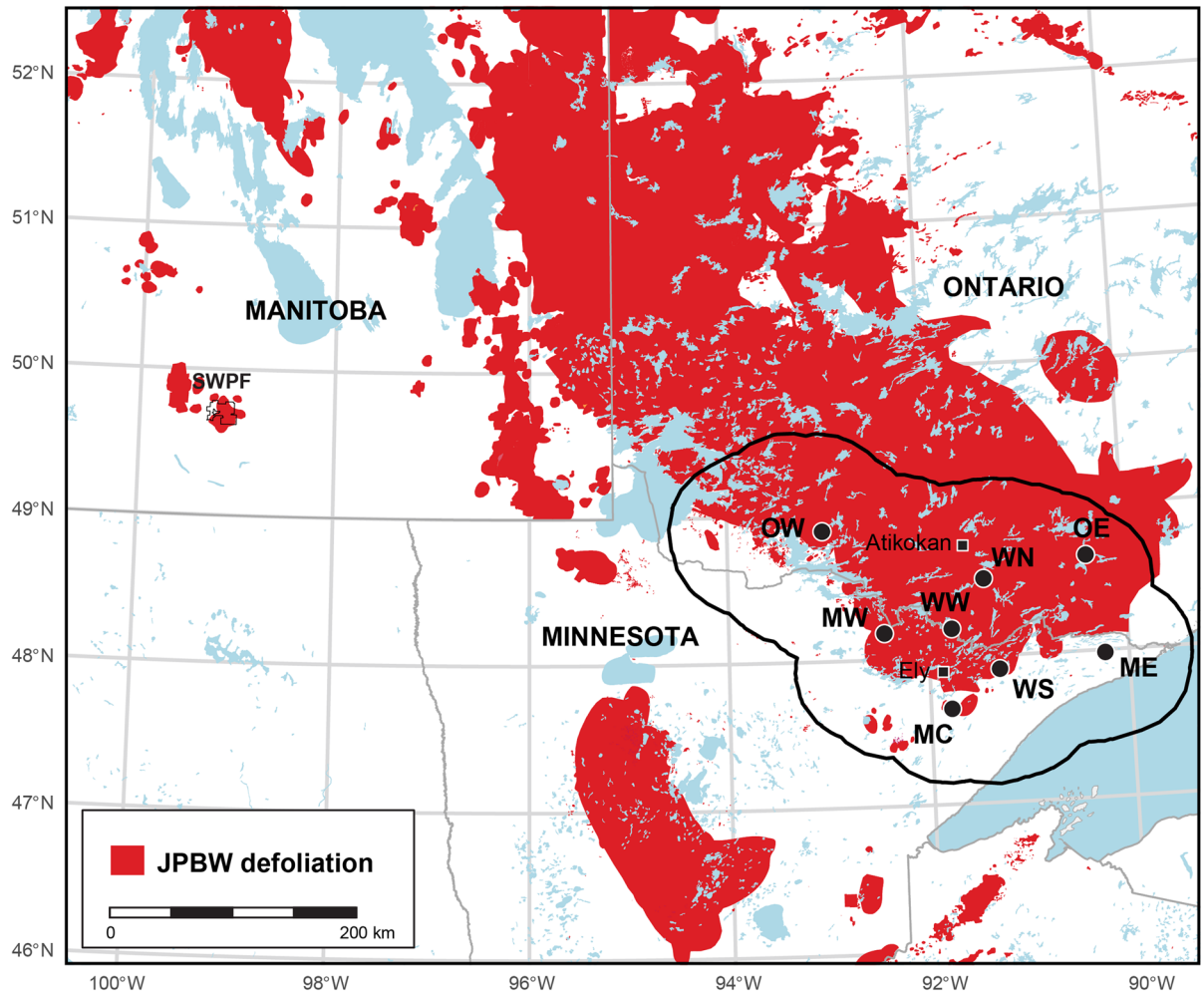


Fig. 1 The extent of jack pine budworm (JPBW) defoliation observed in Manitoba (1937–2020), Ontario (1937–2019), Minnesota (1954–2019), and Wisconsin (1997–2009). The "Border Lakes landscape" refers to a 50 km buffer (black oval) around the Border Lakes ecoregion (Sturtevant et al. 2015). Spruce Woods Provincial Forest (SWPF), Manitoba is also indicated, 600 km west of the BLL. The eight sampled areas (circles) are indicated by two-letter code: M, O, W = Minnesota, Ontario, Wilderness; N, E, W, S, C = North, East, West, South, Central. The area covered by the quadrilateral defined by the corners of the sample area (OW-OE-ME-MC) is roughly 30 000 km^2

and the two studies differ in extent, the small-scale SWPF dataset provides an essential baseline for interpreting Study 1 in the BLL. The sampled plantations in the SWPF were pure pine, whereas the BLL was considerably lower in pine content, offering an opportunity to assess how host abundance influence JPBW outbreak dynamics. To support direct comparison, we digitized the SWPF ring-width chronologies from Robson et al. (2015) using "plot digitizer"–a web-based application for digital data capture (https://plotdigitizer.com/)–and processed them using the same detrending, standardization, and OUTBREAK procedures applied in Study 1. These analyses served primarily as diagnostic context, enabling evaluation of climatic signal strength, periodicity, and disturbance detectability across the two systems. Full methodological details and sensitivity diagnostics are provided in the Supplementary Information.

Data analysis

Study 1: BLL

Our primary objective in Study 1 was to evaluate whether jack pine growth disturbances in the BLL exhibited temporal or spatial signatures consistent with a synchronized, near-linear population cycling process (sensu Moran 1953; Royama 1984, 2005), or whether they bore the hallmarks of asynchronous, locally driven, and weakly periodic disturbance dynamics. To do this, we implemented a structured analytical workflow that has proven effective in reconstructing outbreak histories for other defoliators in the same region (Cooke & Roland 2023; Cooke et al. 2024). The workflow proceeds hierarchically from temporal analyses, to spatial analyses, and finally to spatiotemporal synthesis, allowing us to assess how disturbance signals behave across scales and whether they conform to expectations associated with "clockwork" versus "catastrophe" outbreak models. The logic of each analytical step and its predicted outcome under synchronizing dynamics is summarized in Table 1.

Temporal dynamics We applied seven complementary temporal analyses to characterize disturbance behavior within each of the eight area-level jack pine chronologies (Table 1).

1. Autocorrelation and partial autocorrelation function (ACF, PACF) analyses provide a first diagnostic of temporal structure in time-series data. Under synchronized population cycling, disturbance chronologies should exhibit a positive first-order partial autocorrelation, often accompanied by a negative second-order partial autocorrelation, reflecting low-order feedbacks characteristic of nonlinear cycling processes (Chatfield 2003).
2. Spectral decomposition (i.e., spectral analyses) was used to identify dominant fluctuation frequencies and assess whether disturbances in jack pine chronologies express a coherent periodic signal (Volney 1988). A strong unimodal peak would support the presence of a characteristic outbreak cycle, while multiple weak peaks or broad spectra would support a more irregular or aperiodic disturbance regime—a pattern previously observed for JPBW in Wisconsin (Volney & McCullough 1994).
3. We applied the Automatic Multiscale Peak Detection (AMPD) algorithm (ampd package in R; Scholkmann et al. 2012) to identify peak disturbance years in each PTA series. AMPD is well suited for defoliator systems because it extracts peak/trough structure in noisy ecological data without assuming strict periodicity but requires sensitivity analyses applied to its scaling parameter (See Supplemental Information). Identified peaks define the boundaries of disturbance intervals and provide measures of peak intensity. We examined whether these intensities were unimodally or bimodally distributed, noting that SBW and FTC in the BLL show characteristic bimodality (Cooke et al. 2024).
4. We examined whether peak disturbance years were temporally clustered across the eight BLL areas. Spatially synchronized processes tend to produce strong clustering, whereas asynchronous processes generate over-dispersion. Over-dispersion indicates that growth reductions in different parts of the landscape arise at different times, which in turn implies weak spatial coupling or distinct local drivers.
5. We used Continuous wavelet transform (CWT) analysis (dplR package in R) to identify how disturbance periodicity changed through time, enabling a test for long-term shifts potentially attributable to changing climate, disturbance legacies, or host availability. Because early chronology years (1854–1910) contain fewer samples, we interpreted wavelet structure in this period cautiously. CWT is particularly useful for detecting transitions from strong to weak periodic behavior—an important diagnostic given the hypothesized decline in jack pine abundance over the twentieth century (Friedman & Reich 2005).
6. We computed mean pairwise correlation ($\bar{r}$) across all pairs of area-level chronologies. Under synchronized dynamics, we would expect moderate to high correlations among chronologies, reflecting spatial coherence in outbreak forcing. Low or negative correlations would indicate asynchronous disturbance regimes, potentially driven by localized host feedbacks or spatially heterogeneous resource distributions.

7. Finally, we assessed how time-series correlation decays with distance by constructing correlograms. Synchronizing disturbance processes typically produce a smooth decay with distance, whereas asynchronous processes produce low correlation at all but the smallest scales.

Spatial dynamics Because spatiotemporal patterning is central to distinguishing between competing outbreak models (Cooke et al. 2024), we applied four spatial analytical methods (Table 1), each capturing a different dimension of landscape-level behavior. To support spatial analyses—particularly those evaluating the influence of forest composition and structure on disturbance patterns—we assembled a suite of landscape metrics derived from available forest composition and land-cover datasets. These metrics included 12 tree-species composition variables, expressed as relative basal area (ash, birch, maple, poplar, balsam fir, white spruce, black spruce, cedar, larch, jack pine, "big pine" [red and white pine, occasional hosts of JPBW; V. Nealis, pers. comm.], and total pine) for two time periods (1985 and 2005) (Thapa et al. 2020). We also computed four structural variables—percent forest cover (PF), edge density (ED), cover diversity (CD), and the area-weighted mean patch size of forest openings (AWMP)—applied to a time series of land cover (1975–2000; Wolter et al. 2012). All landscape metrics were computed within 1-km circular neighborhoods surrounding the 40 jack pine sample locations ("J" in Fig. SI1), where structural variables averaged over the land cover time series to capture long-term spatial configuration. Mean landscape metric values were then calculated for the eight area-level units used in Study 1 (Fig. 1).

1. For each disturbance interval, we analyzed the spatial distribution of PTA using autocorrelograms. Spatially coherent outbreak fronts would yield positive autocorrelation at short distances, decaying outward (Tobin et al. 2023, citing Legendre (1993)). Conversely, spatial patchiness or disorder would yield minimal or negative autocorrelation.
2. We next computed spatial correlations between successive disturbance intervals to assess "ecological memory"–the occurrence of asynchronous eruption pulses that are driven by long-term memory processes arising from the bottom-up or top-down (Cooke et al. 2024). In systems where local conditions (e.g., host flowering status, residual defoliation, stored plant stress) carry forward through time, spatial configurations may repeat or exhibit systematic spatial repulsion. Negative correlations between successive intervals signal such repulsion and are inconsistent with simple periodic outbreak waves.
3. Given evidence from SBW and FTC that host abundance gradients strongly structure outbreak synchrony in BLL landscapes (Cooke et al. 2024), we tested whether jack pine abundance mapped for this landscape (Thapa et al. 2020) similarly influenced JPBW dynamics. Because jack pine is sparse in the BLL, we expected any such gradient effects to be weak, but their presence or absence is directly relevant to host-density hypotheses.
4. To evaluate whether forest composition or structure influences spatial patterns of disturbance intensity, we synthesized the landscape metrics summarized above using principal components analysis (PCA). We then used the first two PC axes—representing major compositional and structural gradients—as predictors predictors in a linear regression model of growth disturbance impact over the various time intervals available for analysis (i.e., two time periods for the compositional variables and one composite average for the structural variables).

Study 2: SWPF comparison and cross-system evaluation

The second phase of analysis evaluated how JPBW dynamics in the host-rich SWPF compared to those observed in the host-sparse BLL. While the SWPF dataset lacked the spatial breadth needed for a full application of the spatial methods described above, its temporal resolution provided an essential counterpoint for interpreting BLL patterns.

Climatic signal detection

Robson et al. (2015) identified both a JPBW pest signal and a drought signal in their pine samples. Using BioSIM (Régnière et al. 2014; Fortin et al. 2022),

we reconstructed climate moisture index (CMI) time series for both study areas and examined correlations between detrended ring-width chronologies and CMI. If drought dominates growth variability, ring-width and CMI series should be strongly correlated within and across regions.

Temporal signal comparability We applied the same suite of temporal analyses used in Study 1 (autocorrelation, spectra, AMPD peak detection, interval analysis, and correlation structure) to the SWPF chronologies in Study 2. This allowed us to evaluate whether the strong periodic signals observed in SWPF by Robson et al. (2015) remained apparent when processed identically to the BLL dataset.

Synchrony across spatial scales Given that spatial proximity often enhances correlation in ecological data (Legendre 1993), it was expected that the more spatially compact SWPF chronologies would exhibit stronger inter-series correlations than those from the more expansive BLL region (spanning ~ 30000 km^2). To enable a scale-sensitive comparison of spatial correlation structures, we computed a spline-based correlogram for the BLL dataset using the sncf package in R, which models correlation as a function of geographic distance. For SWPF, where only two sites contain multiple chronologies, we calculated mean within-site and between-site correlations (sites separated by ~ 10 km). This approach facilitated a direct comparison of the two correlation functions across distance classes. If the two correlation functions were well-aligned with one another (i.e. a smooth curve could be drawn between them), there would be no reason to suspect a difference in synchronization mechanics in the two study areas. If, instead, as we hypothesized, the higher proportion of pine in the SWPF plantations was leading to greater periodicity and synchrony in insect signal strength, then there would be a sharp discontinuity in the two correlations function arising at the exact gap in sampling extents–around 10–40 km, where the extent of the SWPF study area stopped, and the resolution of the BLL sample area started.

Data and workflow availability

Unless otherwise specified, all data transformations and analyses were conducted using the R statistical software package ver. 4.5.1 (R Core Team 2025). All data and R code are archived at: https://doi.org/10.5061/dryad.w9ghx3g2z.

Results

Study 1: BLL

In any tree-ring chronology the number of trees contributing to the record declines in reverse time, as not all trees have the same old age. Although 178 trees were sampled across the 40 sites and 8 area chronologies of the BLL, many originated in the early–mid twentieth century and do not extend far enough back to contribute to early chronology years. By 1910, the earliest year where there was at least one tree per area chronology, there were 38 sample trees available for spatial analysis, and these were distributed unevenly across the eight area chronologies (mean = 3.75 trees; s.d. = 3.3). This pattern is typical of opportunistic sampling in mixed-species studies and is illustrated in Supplemental Information Fig. SI1. Despite reduced depth in earlier years, the chronology remains adequate for evaluating broad spatiotemporal trends in jack pine growth disturbance from 1910–2006.

Temporal dynamics

Auto-regression and spectral analysis Temporal fluctuation patterns differed substantially among areas of the BLL. Autocorrelation functions showed only weak evidence of sustained cycling (Fig. SI2): only ME and OE exhibited significant positive autocorrelation at lags beyond 5 years (peaking at 14 and 17 years). Partial autocorrelation functions likewise indicated weak low-dimensional cycling, with only WN and WW showing a negative second-order lag. Spectral analyses were similarly variable (Fig. SI3). Only OE displayed the classic ~9-year JPBW cycle noted elsewhere (Volney 1988; McCullough 2000; Volney & McCullough 1994). Most spectra showed higher periodicities and multiple secondary peaks, indicating irregular or weakly periodic behavior. Non-stationarity also impaired cycle detection, with one series (WN) producing a spurious multi-century peak.

Peak alignment Peak years of growth disturbance identified via AMPD were widely dispersed across

areas (44 distinct peak years out of 97; Fig. 2). Under perfect synchrony, only ~ 13 years would contain peaks. Although over-dispersed, the peaks showed enough clustering to delineate 14 distinct disturbance intervals (Fig. 2). Mean pairwise correlation among area chronologies was low ($\bar{r} = 0.12$), with a bimodal distribution including several moderately positive correlations (> 0.3) and several negative ones (Fig. SI4). Peak intensities were consistently low compared to typical defoliator outbreaks. The bimodal distribution of PTA values (15–25%) (Fig. SI5) falls well below the thresholds typically associated with recognizable outbreaks in dendroentomological studies. The poor alignment of peaks was also reflected amongst trees within sites, where inter-series correlations actually declined with rising sample sizes within sites (Fig. SI6).

Continuous wavelet transform CWT analysis suggested a shift in disturbance dynamics around 1910–1920, coinciding with increased sample depth. There were only two growth disturbances before 1920, and their peak intensities exceeded 30 PTA, yielding a periodicity of ~ 35 years per cycle. After 1920, all growth disturbance peak intensities failed to cross this threshold, as the periodicity became indistinct (Fig. 3). These patterns are consistent with the observation that growth disturbance fluctuations were asynchronous across the eight areas (Fig. SI2). Examining a range of pivot years from 1920 to 1940 yielded similar patterns, suggesting no unique significance to any single year.

Spatial dynamics

Spatial cross-correlation Disturbance intensity varied markedly in space and time (Fig. 4). Spatial autocorrelograms lacked clear gradient structures and fluctuated widely with distance (Fig. SI7), reflecting the patchy and asynchronous disturbance patterns visible in Fig. 4. Pairwise spatial correlations across disturbance intervals ranged from strongly positive (> 0.5) to strongly negative (< – 0.5) (Fig. SI8), suggesting that spatial patterns sometimes repeated but often shifted or reversed between intervals. These negative correlations align with temporal cross-correlation results (Fig. SI9), further indicating weak ecological coupling among sample areas. The negative spatial correlations between intervals are direct evidence of an ecological memory process of some form that spans two successive intervals.

Landscape structure (PCA + regression) A PCA of landscape structure revealed clear compositional and structural gradients across the BLL (Fig. SI10). PC1 distinguished the Wilderness region (conifer-dominated, large openings) from the rest of the landscape (higher forest cover). PC2 reflected a moisture or mesic–xeric gradient, with birch, cedar, and balsam fir loading negatively, and "big pine," aspen, ED, and CD loading positively.

Linear regression of disturbance intensity on PC1 and PC2 revealed low explanatory power across intervals. Although several intervals (6, 11, 13, 14) showed moderate apparent correspondence with landscape axes (model $r^2 > 0.5$), none were statistically significant (SI Table 1). Regression coefficients frequently changed

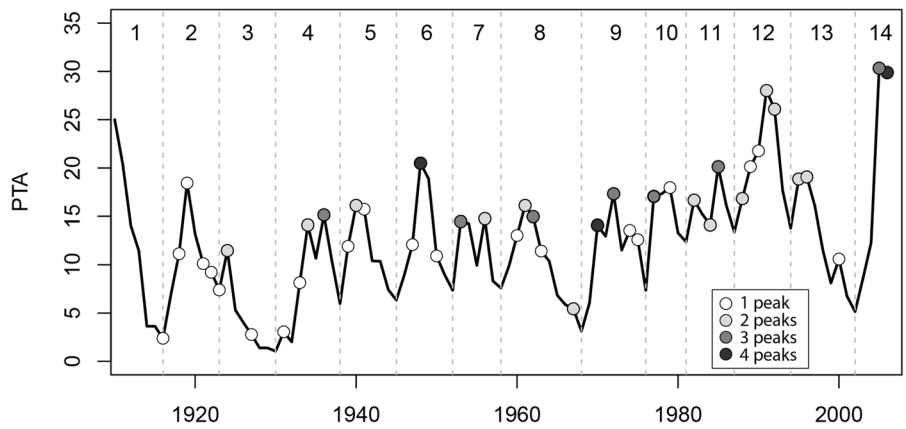


Fig. 2 Aggregated data for the growth disturbance chronologies for the BLL (see Fig. 1 map), 1910–2006. The circles indicate peak years identified by AMPD in Fig. SI2. Shading indicates the number of times a particular year was identified as a peak growth disturbance year across the eight area chronologies. PTA refers to % trees affected

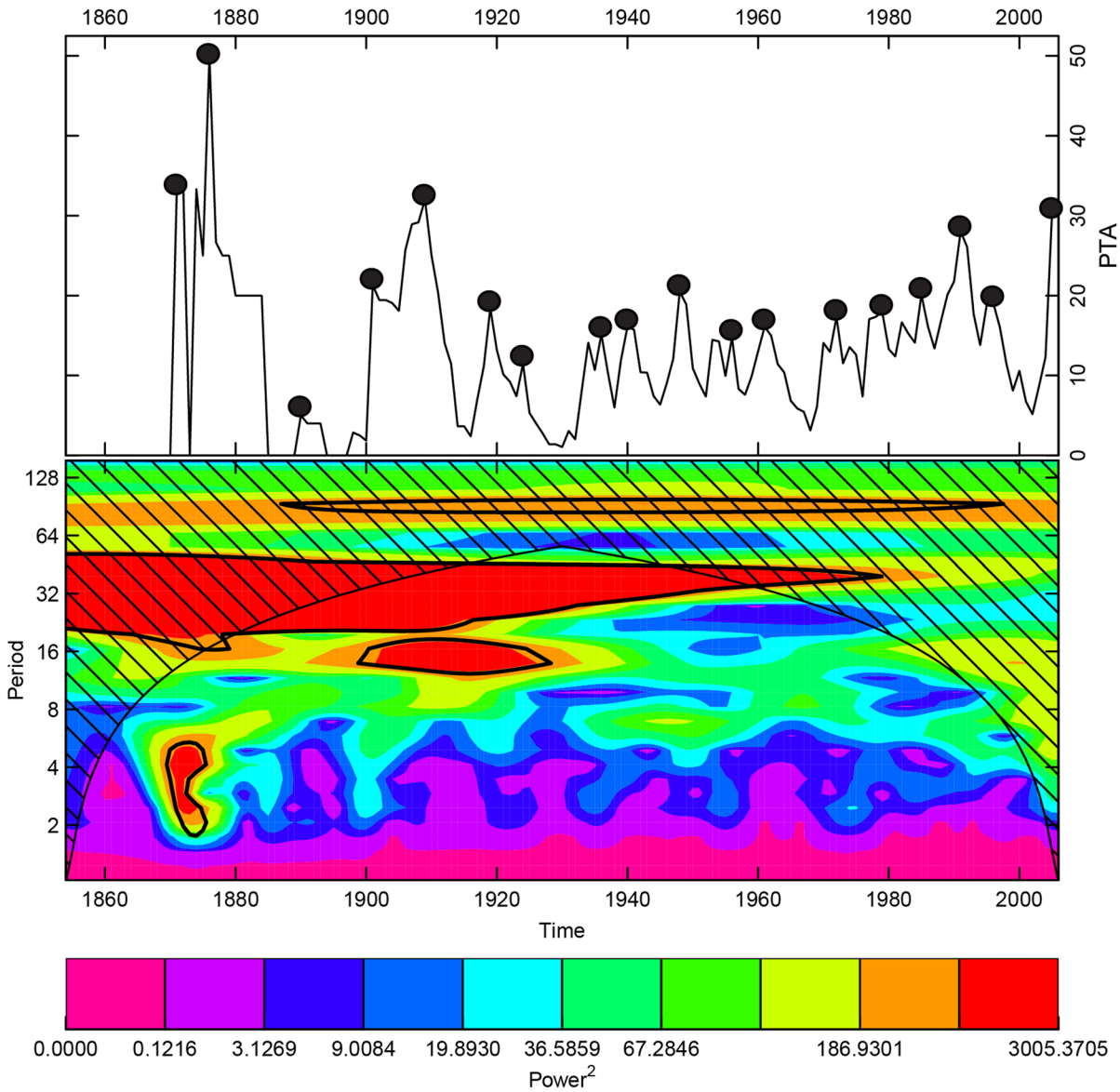


Fig. 3 Continuous wavelet transform (CWT) of the aggregated master growth disturbance chronology for the BLL (see Fig. 1 map), 1854–2006. Top frame: black circled years indicate cycle peaks identified by AMPD. Bottom frame: oceans and islands of red outlined in black are significant bouts of periodicity

sign across intervals, indicating inconsistent spatial patterning and reinforcing the overall asynchrony.

Study 2: SWPF comparison to BLL

Response function analysis

The common analysis window (1932–2006) enabled a direct temporal comparison between SWPF and BLL. Detrended ring-width series from the two regions were moderately correlated ($r = 0.28$; Fig. SI11a), as were CMI values ($r = 0.33$; Fig. SI11b). Within-region correlations between ring width and CMI were weak and nonsignificant (BLL: $r = 0.15$; SWPF: $r = -0.02$), despite SWPF being substantially drier (mean CMI = −5.0) than BLL (mean CMI = 17.9) (Table SI 2). The muted climatic signal at SWPF may reflect groundwater buffering, a

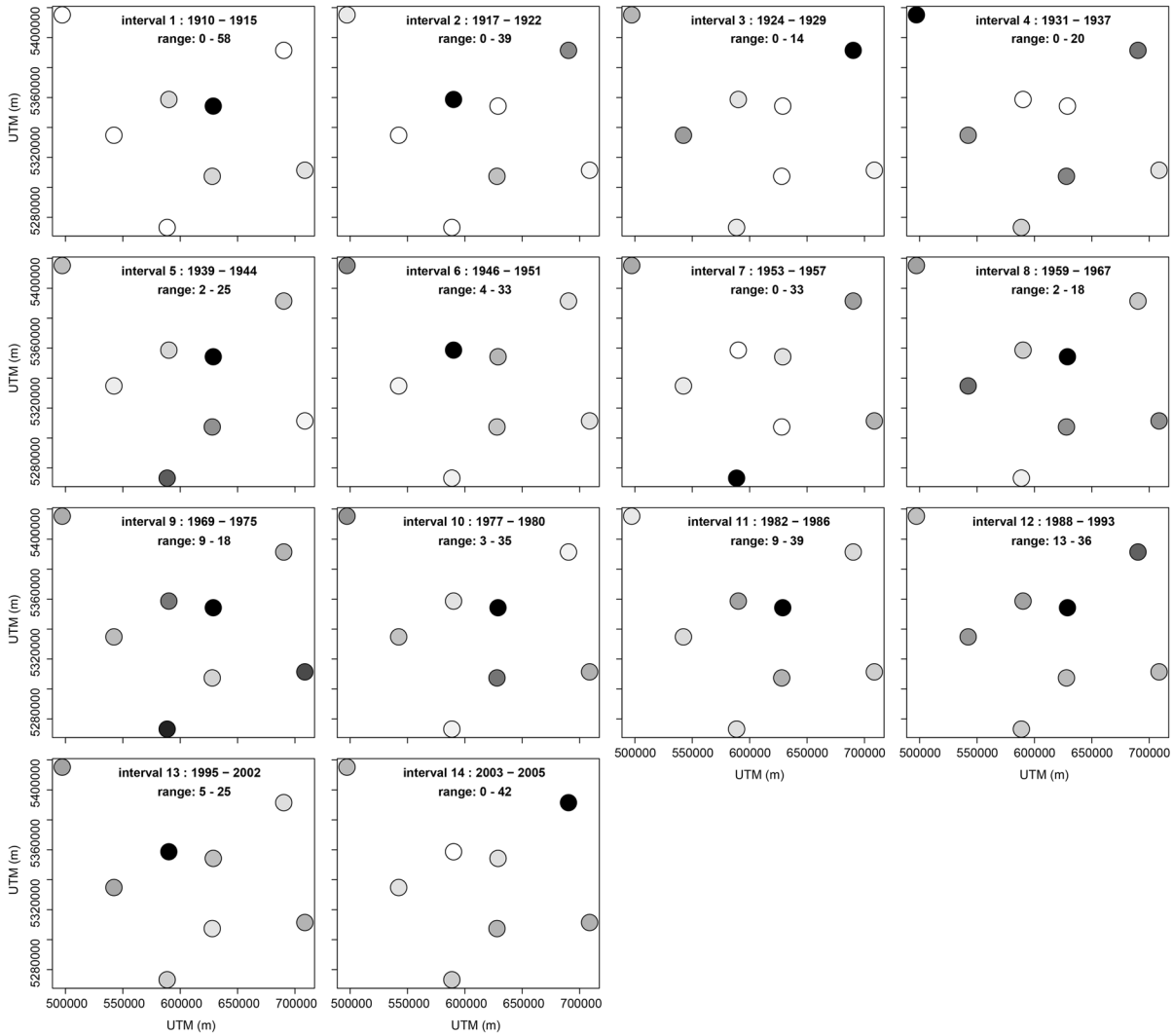


Fig. 4 The spatial distribution of growth disturbances across the 8 sample areas of the BLL (see Fig. 1 map) for each of 14 growth disturbance intervals identified in Fig. 2. White represents the minimum growth disturbance and black represents the maximum growth disturbance for the interval, with growth disturbance ranges labeled for each interval. One year is removed between frames to diminish any perception of negative spatial covariance that could arise from framing bias

factor historically associated with jack pine plantation viability (Henderson et al. 2002).

Spatial synchrony

The SWPF chronologies (seven plots across three clusters) showed markedly higher synchrony than the eight dispersed BLL area chronologies. The mean pairwise correlation was nearly twice as high in SWPF ($\bar{r} = 0.59$) than in BLL ($\bar{r} = 0.31$) (Study 1; Fig. SI10a). Comparison of the two correlograms revealed a sharp discontinuity at the spatial scales separating the studies: SWPF correlations remained high at < 10 km, whereas BLL correlations declined rapidly with distance (Fig. 5). Even accounting for differences in spatial extent, this indicates genuinely stronger synchronization in the host-rich SWPF landscape.

Discussion

In Study 1, conducted across the host sparse Border Lakes Landscape (BLL), we found no consistent relationship between jack pine growth disturbances and forest landscape attributes that we expected to influence jack pine budworm (JPBW) outbreak dynamics. This contrasts sharply with previous work in the same region showing strong landscape controls on the spatial synchronization of spruce budworm (SBW) and forest tent caterpillar (FTC) outbreaks (Robert et al. 2018, 2020). One common feature to all three of these studies is the presence of negative spatial correlations in outbreak patterning between successive intervals, suggesting that a form of memory process is regulating eruption potential at a give time and place. The unexpectedly weak patterns in jack pine prompted us to evaluate whether this result reflected ecological reality or methodological limitation, motivating a direct comparison with jack pine disturbance chronologies from the host rich Spruce Woods Provincial Forest (SWPF) of Manitoba (Robson et al. 2015).

Our comparative analyses demonstrate that the divergence between the two regions is not attributable to sampling error, insufficient replication, or algorithmic artifacts. Growth reductions consistent with JPBW herbivory occurred in both landscapes, and the timing of several disturbance episodes aligned between BLL and SWPF. However, the spatial behavior of these disturbances differed fundamentally. In the BLL, growth reductions were brief in duration and rarely affected more than a few sample areas at any time, reflecting the large distances between samples and the patchy distribution of jack pine. When these asynchronous disturbance signals were aggregated at broader spatial extents, the result was a diffuse, low intensity regional signal (Fig. 3; SI9). In contrast, the SWPF samples were collected from a compact (~ 50 km^2) plantation network, too small for such noise accumulation to occur. Within that limited spatial extent, disturbance signals were much more coherent.

Before exploring the ecological implications of these results, we address two common concerns associated with tree ring–based outbreak reconstruction. First, we acknowledge the lack of a climatic control chronology in our BLL reconstruction. Our alternative approach was to estimate the moisture response function directly, using instrumental weather data. This allowed us to avoid the problem that many, if not all, of the tree species of the BLL are affected by an associated defoliator species. Second, we conducted a suite of sensitivity analyses to evaluate the robustness of our OUTBREAK and AMPD data processing decisions. These tests confirmed that (a) periodicity in the raw ring width data was weak prior to outbreak detection, (b) AMPD-derived peaks were stable across parameter values, and (c) the low periodicity and weak synchrony observed in the BLL PTA series were not artifacts of either sampling effort or algorithmic settings (SI Sects. 3.2–3.3). In short, the asynchrony evident in the BLL is intrinsic to the ecological system.

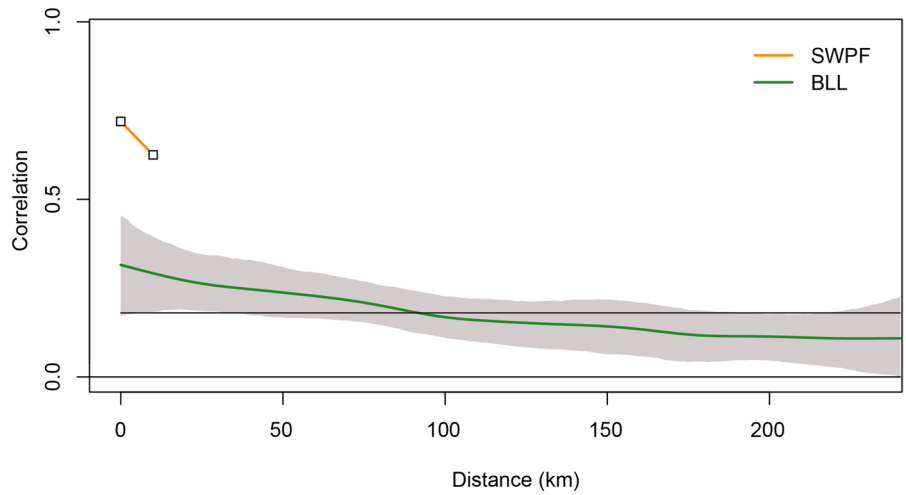


Fig. 5 Correlogram of the raw detrended ring width data for BLL, 1932–2006 (green). SWPF correlations (orange) are shown for comparison (squares): mean within-site (< 1 km) correlation $r = 0.72$; mean between-site correlations (~ 10 km) correlation $r = 0.62$. These values exceed the confidence envelope of BLL correlations. (Fig. 1 map indicates the locations of the BLL and SWPF study areas.)

Together, these results reinforce a foundational premise of landscape ecology: scale and context strongly influence the detectability and expression of ecological processes (Turner & Gardner 2015). In the BLL, jack pine is both sparse and patchily distributed, conditions not conducive to forming a landscape scale gradient in host availability capable of driving coherent outbreak dynamics. The study area itself was originally chosen to study SBW and FTC, whose hosts (spruce and aspen) are far more abundant. In contrast, the SWPF landscape—although sampled over a smaller spatial extent—is characterized by a very high local abundance of jack pine within plantations. These contrasting contexts fully account for the qualitative differences between the two datasets.

The lack of synchrony in the BLL is particularly telling. If growth disturbances there were driven by broad scale climatic anomalies or synchronized flowering events, we would expect temporal alignment and spatial coherence across large areas. Instead, the BLL disturbance chronologies show over dispersion of AMPD peaks, weak ACF/PACF signatures, multi peaked and inconsistent spectral structure, and a rapid decay of synchrony with distance. These patterns are inconsistent with any form of Moran-type synchronization or top-down regulated cycling. They are also inconsistent with periodic insect outbreaks that manifest as coherent spatial waves.

Rather, the BLL data align with a third possibility: asynchronous, low intensity defoliation governed by localized, weakly periodic JPBW dynamics that fail to scale across the landscape. In such host limited circumstances, JPBW populations may irrupt locally but cannot maintain phase alignment across space.

This interpretation gains support when viewed across scales. On one extreme, Volney (1988) reported strongly periodic regional JPBW outbreaks across ~ 1.3 million km^2 in Manitoba and Saskatchewan, where jack pine is far more abundant and contiguous. On the other extreme, Robson et al. (2015) documented strong periodic signals within small plantation clusters where host density is extremely high. The BLL, occupying an intermediate extent (~ 30,000 km^2) and characterized by low jack pine abundance, sits between these regimes and expresses neither landscape level periodicity nor strong local synchrony.

The cross-system contrast is further reflected in disturbance intensity. During the shared 1932–2006 interval, PTA values in the BLL never exceeded ~ 35%, whereas SWPF values frequently surpassed 50%. Moreover, synchrony in ring width and PTA series was substantially higher in SWPF than in BLL, even at comparable spatial scales (< 10 km). Synchrony in SWPF is robust even when accounting for scale differences; synchrony in BLL remains weak even when comparing the two datasets on equivalent spatial terms (Fig. SI6). Together, these findings underscore that host abundance modulates not only the detectability and intensity of defoliation, but also its capacity to synchronize across landscapes.

Consistent with patterns observed for SBW and FTC in the BLL, these results highlight the central influence of host availability in modulating outbreak dynamics (Cooke et al. 2024). However, unlike spruce or aspen—both relatively abundant in the BLL—jack pine is too sparse to sustain the nonlinear feedbacks required for coherent population cycling. As a result, JPBW dynamics in the BLL remain localized and weakly periodic. At larger scales, where jack pine abundance increases (e.g., Manitoba, Wisconsin), periodicity strengthens and outbreaks attain recognizable spatial extent.

The temporal shift in BLL periodicity—from pre 1920 bouts of stronger periodicity (~ 35 year cycles) to post 1920 irregularity—may reflect historical changes in host availability stemming from logging and fire suppression (Stearns 1997; Friedman & Reich 2005). Loss of red and white pine, occasional hosts of JPBW (Kulman & Hodson 1961), and reduced jack pine regeneration may have disrupted long term host feedbacks, diminishing outbreak coherence. Although sample depth is low prior to 1910, and such inferences should be treated cautiously, the temporal pattern is consistent with a system transitioning from host supported periodic dynamics to host limited asynchrony.

At a mechanistic level, the observed asynchrony and weak periodicity in the BLL align with population level studies indicating that JPBW dynamics are dominated by bottom-up processes. JPBW survival and fecundity depend heavily on the presence of staminate flowers, and defoliation suppresses future flowering (Nealis et al. 2003). This feedback creates a phase-remembering system, wherein population trajectories are governed locally by tree level state variables that do not disperse across space. In contrast, top-down regulators such as predators, parasitoids,

and pathogens are mobile and tend to scramble phase structure across sites, producing phase-forgetting dynamics more amenable to regional synchronization (Nisbet & Gurney 1976; Royama 2005). Thus, a bottom-up, host-limited system should resist regional synchrony—even under shared climatic perturbations—exactly as seen in the BLL.

These findings inform the broader debate between "clockwork" and "catastrophe" models of Lepidopteran outbreak dynamics (Pureswaran et al. 2016; Sturtevant et al. 2023). In the host-sparse BLL, neither paradigm fully explains the dynamics: outbreaks are too weak and asynchronous to align with clockwork expectations, yet too localized and non eruptive to reflect full catastrophe dynamics. The SWPF, by contrast, expresses periodicity and synchrony at small scales, making both paradigms more applicable depending on the lens of analysis. The hybrid model proposed by Sturtevant et al. (2015, 2023) therefore appears particularly relevant: JPBW demonstrates the capacity for periodic, eruptive behavior under high host abundance, but defaults to weak, noisy cycling when hosts are limiting.

Finally, our findings complement the "multi stable resilience complex" framework proposed by Sturtevant et al. (2026). The BLL appears to occupy a region of state space where spruce–fir/SBW and aspen/FTC dominate as forest–insect attractors, with jack pine/JPBW occupying a marginal and weakened basin of attraction. In more pine-dominated landscapes, the JPBW basin is deeper and more dynamically stable. We propose that host availability shapes not only defoliator behavior, but the stability and configuration of forest–insect attractor states themselves. According to this scheme, the depth and dynamic stability within each basin of attraction would depends on landscape-level host abundance, which governs how forest areas enter and persist within particular forest–insect regimes (Fig. 6). In other words, it seems it is the forest landscape that determines whether or not a given forest insect species exhibits pestiferous behavior.

Conclusion

Our results demonstrate that jack pine budworm (JPBW) outbreak behaviour is strongly contingent on landscape context. In the host sparse BLL, growth disturbances never achieved the intensity, periodicity, or spatial coherence characteristic of classical Lepidopteran outbreaks. Instead, disturbances were weak, irregular, and highly asynchronous across space, even at fine scales. By contrast, in the host rich SWPF, periodic signals were more robust and synchrony markedly higher. The

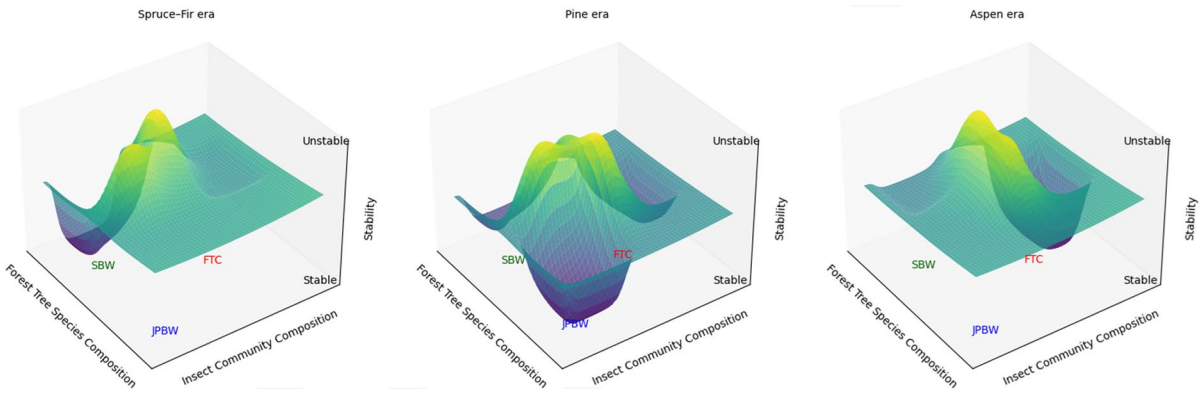


Fig. 6 A set of three stability surfaces each indicating three forest/insect basins of attraction in the Border Lakes forest ecosystem, one basin of attraction for each forest-insect complex. Figure adapted from Walker et al. (2004) and Sturtevant et al. (2026). As the forest tree species composition of the landscape changes, the dominant insect species complex also changes, including its propensity for high-severity outbreaks. Each panel shows the landscape potential as a function of forest tree-species composition (x-axis) and insect community composition (y-axis), with local stability increasing with basin depth (z-axis). The three attractor basins correspond to spruce–fir/SBW (spruce budworm; green), jack pine/JPBW (jack pine budworm; blue), and aspen/FTC (forest tent caterpillar; red). The sequence illustrates the shift in the dominant stable state as long-term changes in host composition move the system from SBW stability to JPBW stability to FTC stability

comparison makes clear that these differences are not methodological artifacts but reflect true variation in outbreak scaling potential tied to host abundance and distribution.

This landscape dependence has broader implications for understanding the mechanisms governing JPBW population dynamics. The weak temporal structure and inconsistent spatial patterns in the BLL align with a bottom up, "phase-remembering" system driven by local host feedbacks rather than top-down or climate-driven synchronizing forces. When host density is insufficient to sustain or propagate nonlinear population responses, disturbances remain localized and fail to synchronize across the landscape. Conversely, in host rich systems such as SWPF or the broader Canadian prairie provinces, periodicity and spatial coherence emerge more readily—consistent with hybrid cycle eruptive dynamics observed in other defoliators.

These findings reinforce emerging views of hemi boreal forests as multi-stable disturbance complexes in which insect regimes are structured by host abundance and spatial configuration. JPBW occupies a diminished basin of attraction in the BLL but a deeper, more stable one in pine rich regions. From a management perspective, this underscores that "pestiferous" behaviour is not a fixed property of a species but an emergent characteristic of forest composition and scale. Strategies that maintain or enhance host diversity—and avoid creating large, contiguous pine dominated landscapes—may reduce the likelihood of severe, synchronized JPBW outbreaks. At a broader scientific level, our results highlight the need to consider landscape context explicitly when interpreting dendroecological reconstructions and when generalizing outbreak theory across species and regions.

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Data availability All data and R code are archived at: https://doi.org/10.5061/dryad.w9ghx3g2z The link for the data used in this paper is: [https://datadryad.org/dataset/doi:10.5061/dryad.w9ghx3g2z]

Declarations

Conflict of interest The authors declare no competing interests.

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