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ARTICLE

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Insect defoliators trading spaces in a hemiboreal forest: Implications for diversity–stability and ecosystem resilience

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Abstract

Periodic outbreaks of forest insect pests shape northern forest dynamics, yet interactions between multiple insect–host systems—and their role in ecosystem metastability and resilience—remain poorly understood. To elucidate these spatiotemporal interactions, we investigated the coupled dynamics of two dominant insect–host systems—spruce budworm (SBW) associated with late-successional fir and spruce, and forest tent caterpillar (FTC) associated with early-successional aspen. We assess whether asynchronous outbreak patterns shift over time and whether those shifts are consistent with forest compositional change. Using tree-ring data from mixedwood sites across a 20,000-km^2 hemiboreal landscape at the United States–Canada border, we reconstructed outbreak histories (1928–2005) and applied multi-scaled analyses guided by resilience theory. We analyzed outbreak dynamics across a continuous range of temporal resolutions, summarizing patterns into short (years), intermediate (decade), and long (multi-decade) windows to evaluate spatial persistence and cross-species correlations, and examined whether patterns over the longest windows align with contemporary forest composition. SBW and FTC cycled independently over short windows, but cross-correlations became increasingly negative as windows lengthened to multi-decadal scales, consistent with compositional feedbacks. Spatial persistence within species shifted from positive over short windows to strongly negative over long windows, where outbreak centers reciprocally inverted between early and contemporary periods—a "trading spaces" dynamic indicative of metastability. These patterns show that insect outbreaks are not passive responses but feedback-driven agents interacting with anthropogenic legacies that accelerate compositional change. Our findings highlight how cross-scale feedbacks involving slow and fast regulatory processes shape disturbance regimes, thus supporting resilience theory and the concept of dynamic stability. Forest homogenization through fire

suppression and past logging may collapse the stability landscape into a biphasic regime dominated by SBW and FTC, whereas increasing compositional and structural diversity can expand it into multiphasic regimes that attenuate disturbance amplitudes and promote asynchronous dynamics—underscoring the role of diversity–stability and resilience principles in guiding forest management.

KEYWORDS
cross-scale dynamics, disturbance regime, diversity–stability, ecological memory, forest tent caterpillar, metastability, resilience theory, spatiotemporal analysis, spruce budworm, time series data

INTRODUCTION

Insect disturbances are among the most influential forces shaping the northern mixed forests of North America, spanning the boreal biome and its hemiboreal transition zones. Yet their role in governing ecosystem stability across scales—and the ways that multiple sympatric insect–host systems interact—remains poorly understood. Holling (1973) introduced the concept of ecosystem resilience, describing how ecosystems can be highly unstable yet persist in their capacity to absorb disturbance and reorganize while retaining function, structure, identity, and feedbacks (Walker et al., 2004). Among Holling's foundational case studies was the outbreak dynamics of the spruce budworm (SBW; *Choristoneura fumiferana*) feeding on balsam fir (*Abies balsamea*) and spruce (*Picea* spp.) (Ludwig et al., 1978). Contemporary perspectives emphasize that resilience emerges from interactions between fast processes (e.g., outbreaks) and slow processes (e.g., succession, nutrient cycling, disturbance legacies) (Beisner et al., 2003; Johnstone et al., 2016). Within this context, we examine two dominant outbreak systems—the SBW associated with spruce–fir and the forest tent caterpillar (FTC; *Malacosoma disstria*) associated with aspen (*Populus* spp.)—to test whether they exhibit long-term (multi-decadal) reciprocal linkages mediated by vegetation feedbacks, and how such linkages influence outbreak dynamics, forest metastability, and cross-scale resilience.

Resilience theory helps disentangle complexity via conceptual metaphors. Using the classical "ball in cup" metaphor, ecosystems occupy basins of attraction in a stability landscape whose contours change through the interplay of external shocks and internal feedbacks (Beisner et al., 2003; Walker et al., 2004). Applied to insect–host systems: fast disturbances (e.g., outbreaks) can displace the ball (position of a subarea in the stability landscape), whereas slow processes (e.g., biomass accumulation, succession, legacies) reshape host abundance and connectivity, altering basin depth and position over time. Cross-scale dynamics—reciprocal interactions among processes operating at different spatial and temporal scales—can amplify or dampen outbreak amplitude and extent (Peters et al., 2004; Raffa et al., 2008). Ecological memory—the information legacies (traits, landscape structure) and material legacies (survivors, propagules, residues, soils) left by past disturbances—mediates these interactions and influences whether a system remains within its current basin or transitions to an alternative substate (Johnstone et al., 2016). As an indicator of ecological memory at landscape scales, we consider spatial persistence (Cooke et al., 2024)—the degree to which outbreak patterning recurs versus inverts across time windows of decreasing resolution (short term ≈ years, intermediate ≈ decade, long term ≈ multi decade to century). These ideas frame a hemiboreal stability landscape with multiple basins of attraction—a metastable system capable of occupying more than one possible substate yet vulnerable to transitions triggered by fast or slow processes (Frelich, 2002). This perspective aligns with meta-regime resilience, the maintenance of system identity across shifting substates (Delettre, 2021), a concept rarely examined empirically in resilience research.

Understanding how these theoretical dynamics manifest empirically requires examining the mechanisms that govern outbreak behavior and potential interactions between species. SBW and FTC differ in their specialist natural enemy suites and larval exposure (Eveleigh et al., 2007; Schowalter, 2017), yet they also share generalist predators (birds, ants, spiders) that respond across host systems (Jennings & Crawford, 1985; Nixon & Roland, 2012; Figure 1). Outbreaks driven by trophic interactions and sensitivity to nonlinear Allee effects (e.g., mating success thresholds) (Kramer et al., 2009) lead to a blend of periodic, harmonic oscillations and irregular eruptive outbreak patterns (Cooke et al., 2024; Sturtevant et al., 2023). These "hybrid-cyclic-eruptive" outbreaks can feed back to alter forest composition, shifting dominance between spruce–fir and aspen substates—especially when compounded by fire or successional dynamics (Figure 1). We expect that cross system linkages

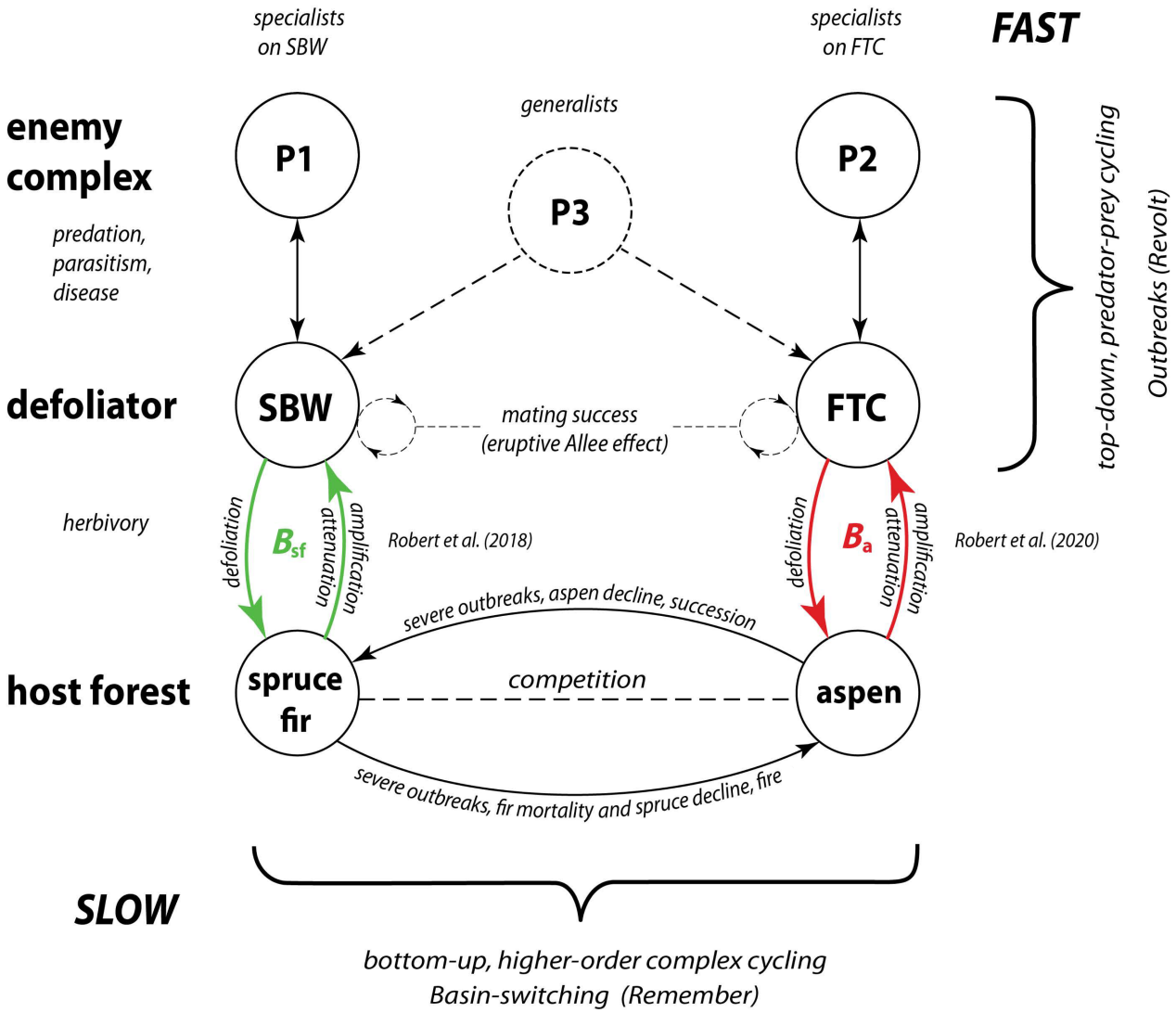

FIGURE 1 Mechanistic linkages between two forest insect systems and host feedbacks. Spruce budworm (SBW) and forest tent caterpillar (FTC) differ in specialist natural enemy suites and larval exposure. FTC larvae are exposed and often vulnerable to Dipteran parasitoids, whereas SBW larvae are more concealed and commonly targeted by Hymenoptera; overlap exists (Diptera also parasitize SBW). Shared generalist predators (birds, ants, spiders; dashed lines) have comparatively lower response capacity. Outbreak severity scales with host abundance, and outbreaks can feed back to alter forest composition, shifting dominance between spruce–fir and aspen substates—especially when compounded by fire or succession. Community level interactions (e.g., pathogens, parasitoid networks) add complexity beyond vegetation feedbacks. Mating success can introduce an eruptive Allee effect, contributing to a blend of harmonic oscillations with eruptive dynamics. These linkages provide the mechanistic basis for the stability landscape shown in Figure 2. Symbols B_{sf} and B_a correspond to spruce–fir and aspen basins of attraction.

are relatively weak at short predator–prey timescales but become stronger at long vegetation-mediated timescales, enabling metastability between spruce–fir and aspen substates (Figure 1). Returning to the stability landscape metaphor (Figure 2), basins of attraction are reshaped by fast disturbances ("revolt") and slow legacies ("remember") in a panarchy-like dynamic (Allen et al., 2014).

Disturbance regimes across these northern mixed forests are characterized by interactions between wildfire and insect defoliation, which influence forest successional trajectories over long timescales (Bergeron & Leduc, 1998; Shorohova et al., 2011). Frequent fires favor species adapted to rapid postfire regeneration, whereas extended fire return intervals favor balsam fir, increasing susceptibility to SBW outbreaks and reinforcing a self-sustaining disturbance cycle enabled by fir's advance regeneration strategy (Baskerville, 1975; Bergeron & Harvey, 1997). These dynamics shift along climatic gradients, with fire dominance decreasing and SBW-driven disturbance increasing from west to east (Blais, 1968; Fleming, 2000; Weber & Flannigan, 1997). FTC–aspen interactions add further

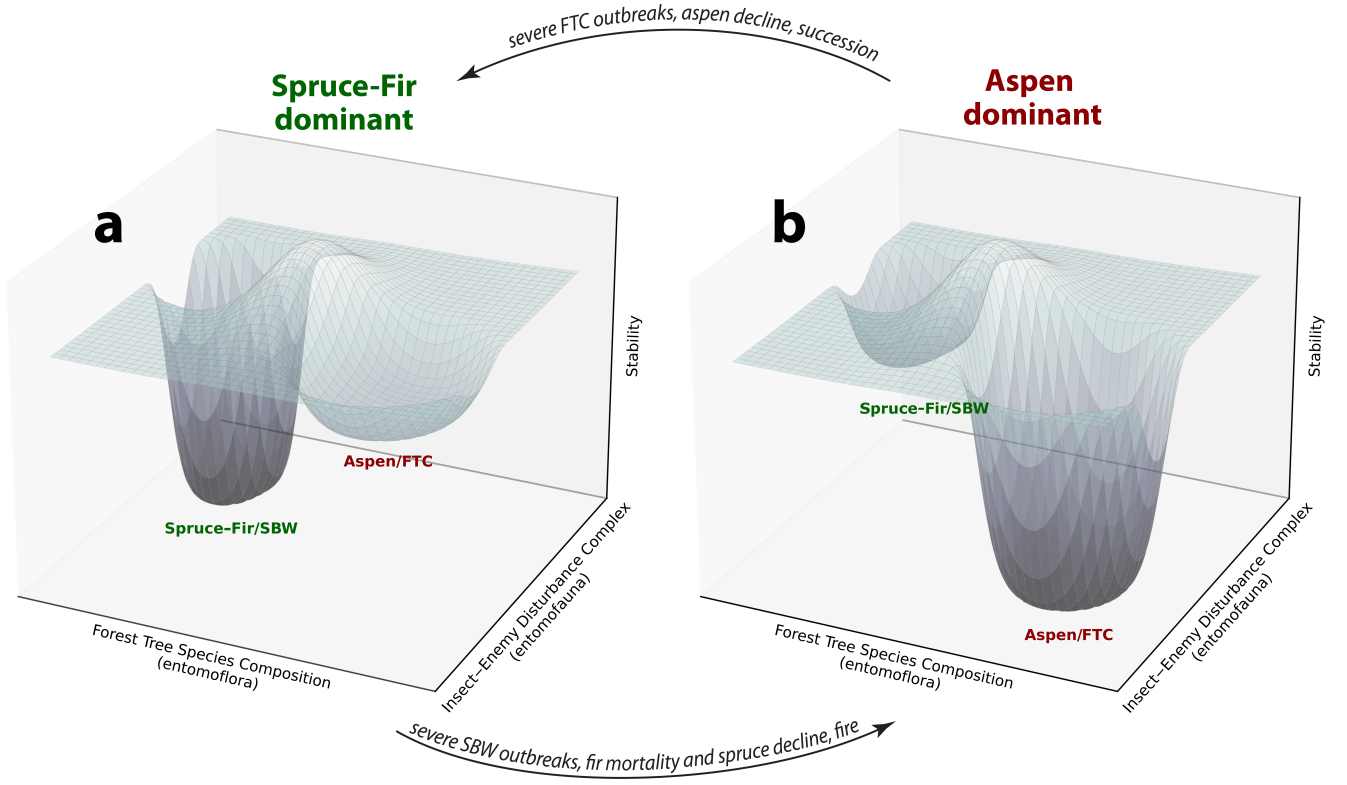

FIGURE 2 Dynamic stability and meta-regime resilience in hemiboreal mixedwoods. The simplified stability landscape illustrates two alternative landscape-level substates—spruce–fir/spruce budworm (SBW) (left rear) and aspen/forest tent caterpillar (FTC) (right front)—represented as basins of attraction whose relative depths (*z*-axis) denote their stability or dominance. Bidirectional arrows (as in Figure 1) indicate that cumulative changes in forest composition (*x*-axis) and associated insect–enemy communities (*y*-axis) can deepen one basin while shallowing the other. These shifts arise from the interaction of fast disturbances (insect outbreaks, fire events) that displace subareas within the stability landscape and slow feedbacks (succession, fire history, management legacies) that reshape host abundance, connectivity, and the underlying stability surface. Panel (a) depicts conditions that deepen the spruce–fir/SBW basin. Panel (b) shows conditions that deepen the aspen/FTC basin. Ecological memory—expressed through entomoflora and entomofauna legacies—mediates these cross-scale feedbacks and contributes to dynamic stability, where outbreak patterns may recur or invert over decades as subareas drift among substates, consistent with the reciprocal interactions illustrated in Figure 1.

complexity: FTC preferentially defoliates aspen but can affect a broader suite of hardwoods during intense outbreaks (Witter, 1979). While widespread mortality is uncommon (Schowalter, 2017), prolonged or frequent events can kill aspen (Man, 2024), and short-duration events can temporarily open canopies, favoring release of shade-tolerant fir (Wellington et al., 1950). Severe SBW outbreaks may likewise disrupt fir regeneration enough to enable aspen expansion (Leduc et al., 2021; Nealis & Régnière, 2004). Whether the SBW–spruce–fir system operates independently of, or is interlinked with, the FTC–aspen system remains an open question; theory suggests that such multispecies interactions should contribute to the metastability and resilience of disturbance-prone forests (Ludwig et al., 1997).

Human legacies amplify and sometimes accelerate these trajectories. Over a century of fire suppression and logging practices have altered composition and structure, often homogenizing landscapes and potentially increasing outbreak amplitude and synchrony (Blais, 1983; Boucher et al., 2009; Burton et al., 2003; McCullough et al., 1998). These effects are pronounced in the hemiboreal transition zone (sensu Brandt, 2009), where boreal forests grade into northern hardwood and pine–oak systems. In northern Minnesota, for example, fire suppression and logging have reduced pine while increasing balsam fir and aspen (Friedman & Reich, 2005), with consequences for subsequent SBW and FTC activity. Such legacies constitute ecological memory at landscape scales, reshaping host abundance, connectivity, and the structure of the stability landscape (Allen et al., 2014; Johnstone et al., 2016).

The Border Lakes mixedwood region spanning Minnesota and Ontario provides a natural experiment for probing these dynamics (Sturtevant et al., 2014; Figure 3). Previous analyses in this landscape showed that outbreak intensity and synchrony were sensitive to host abundance and pattern for SBW (Robert et al., 2018) and FTC (Robert et al., 2020). Cooke et al. (2024) further

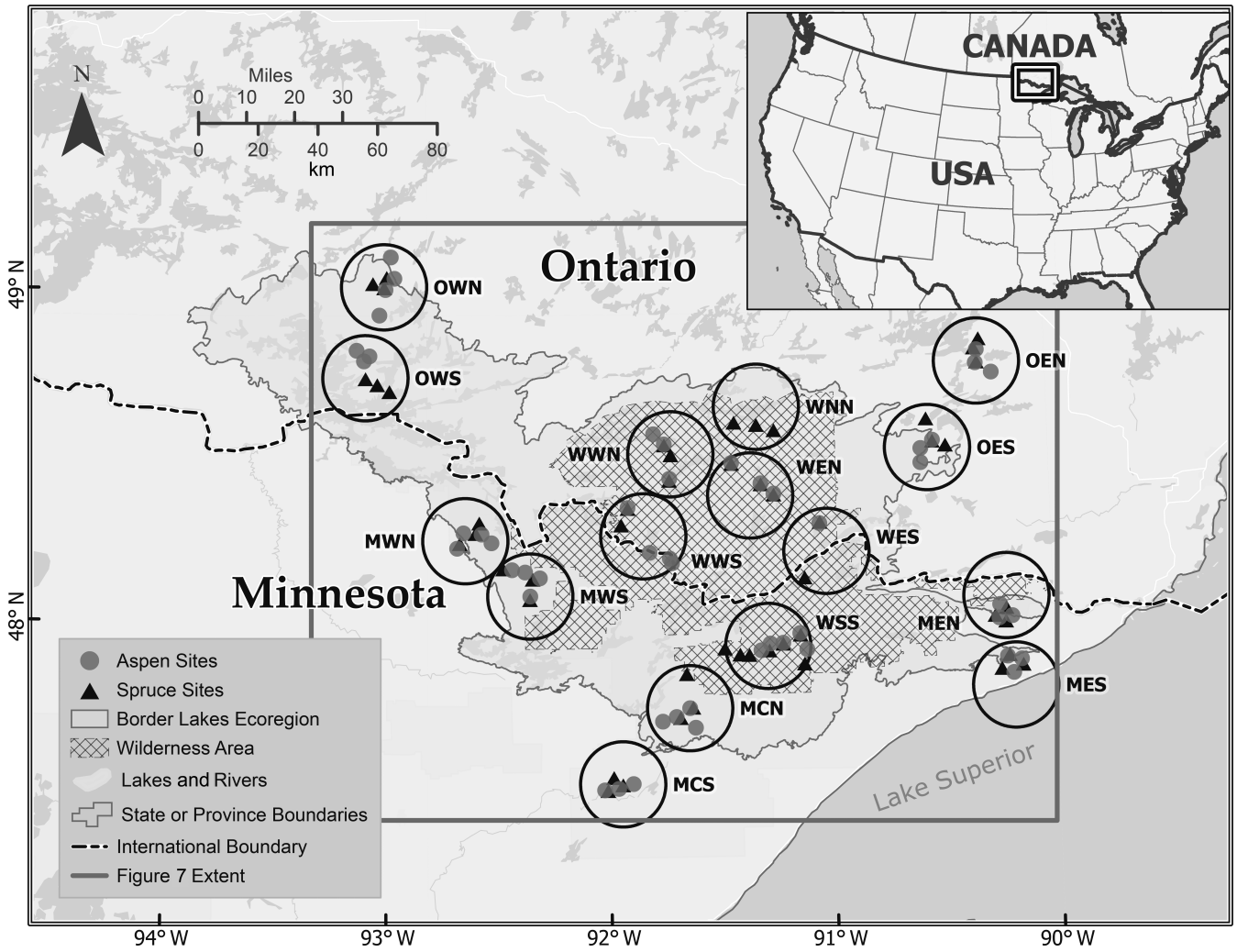

FIGURE 3 Spatial distribution of host species and sampling sites (2006–2007) across the study area. Circles denote subareas used to aggregate tree level data into outbreak chronologies: 15 for aspen/forest tent caterpillar (FTC) and 16 for spruce/spruce budworm (SBW). Labels follow a three-letter code: first = management (M, Minnesota managed; O, Ontario managed; W, wilderness); second = longitudinal position (E, east; C, center; W, west); third = latitudinal position (N, north; S, south).

demonstrated that FTC cycled at roughly twice the rate of SBW, that both systems combined cyclic and eruptive traits, and that spatial persistence tended to invert between outbreaks for each species. Building on these findings, we ask whether such inversions strengthen at multi-decadal timescales, whether cross-species correlations emerge at similarly long timescales, and whether long-term outbreak patterns align with contemporary composition—questions not addressed in prior work. Contrasting conditions—fir–spruce wilderness versus aspen-dominated managed landscapes (Cooke et al., 2024)—offer a unique context for exploring how SBW–spruce–fir and FTC–aspen substates interact across long timescales.

Guided by our conceptual framework (Figures 1 and 2), we address three questions. (1) At short timescales, do SBW and FTC operate independently, with little cross-correlation? (2) At intermediate timescales, does short-term spatial persistence start to give way to pattern inversion, as vegetation-driven feedbacks start to reverse where outbreaks occur? (3) At long timescales, do spatial patterns of outbreak activity align with contemporary host composition and configuration, indicating slow, vegetation-mediated legacies? To address these questions, we quantify spatial persistence within species and cross correlation between species across short-term (within outbreak), intermediate (between outbreak), and long-term (multi-decadal) time windows. We conduct inference at the landscape level (subareas; Figure 3), rather than the stand level, to capture broad scale outbreak–composition feedbacks and slow compositional change. Our approach separates fast pulses from slow drifts without presupposing periodic behavior and evaluates whether outbreak patterns (i.e., subarea impacts

aggregated within temporal windows of varying size) shift across time in ways consistent with dynamic stability and ecological memory (Figures 1 and 2). Clarifying whether SBW and FTC interact across ecological timescales has implications for diversity–stability relationships and for pest management strategies that emphasize landscape diversification (Kneeshaw et al., 2021), especially given the phylogenetic and functional contrasts between spruce–fir and aspen (Jactel et al., 2021).

METHODS

Study area

The Border Lakes landscape contains a large (~20,000 km^2) ecoregion that spans the Minnesota (United States)–Ontario (Canada) border at the hemiboreal transition between the northern hardwood and boreal forests (Figure 3). The region experiences a humid continental climate with cold winters and short warm summers, shaped by glacially carved terrain, abundant lakes and wetlands, and Canadian Shield bedrock (Heinselman, 1996). The mixed Laurentian Forest includes boreal species (e.g., jack pine [*Pinus banksiana*], black spruce [*Picea mariana*], white spruce [*Picea glauca*], balsam fir, paper birch [*Betula papyrifera*], and aspens [*Populus tremuloides*, *Populus grandidentata*]), along with range-edge species such as white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and red maple (*Acer rubrum*).

Railways arrived by the late 1800s, initiating exploitative logging focused on pine along waterways (Heinselman, 1996), while fires increased due to settlement, logging slash, and dry weather (White & Host, 2008). Extensive fire damage spurred rigid fire policies that effectively ended cultural burning as common practice (Kipfmueller et al., 2021). By the mid-1930s, new infrastructure enabled an emerging pulpwood industry, coincident with the development of fire surveillance and suppression systems and technology (Heinselman, 1996). Industrial forestry expanded post World War II (Stearns, 1997), when management practices diverged among managed (Minnesota vs. Ontario) and unmanaged (wilderness) zones shown in Figure 3. Minnesota's fragmented ownership and land management policies produced dispersed small-sized cut-blocks, whereas Ontario's Crown forest resulted in more aggregated cut-blocks 10 times larger in size (Haley & Nelson, 2007; Stearns, 1997; Sturtevant et al., 2014). Recreational interest in the core wilderness area limited pulp logging that officially ceased in the Quetico Provincial Park in 1973 and in the Boundary Waters Canoe Area Wilderness in 1978 (Heinselman, 1996; Nelson, 2009).

Sample design and outbreak reconstruction

We reconstructed spatiotemporal outbreak histories of SBW and FTC from the mid-1800s–2006 by sampling tree rings from 100 mixedwood sites containing 50 white spruce and 50 trembling aspen sample locations, each distributed according to a consistent sampling design throughout the Border Lakes landscape. Sample sites were stratified by management legacy (Minnesota managed, Ontario managed, and unmanaged Wilderness), then by longitude (east, center, west), and latitude (north, south) (Figure 3). Five to 10 host trees were sampled from each sample location. Outbreaks were defined annually at the individual tree level by tree-ring growth reductions according to established methods for each respective insect species on their respective host trees (Robert et al., 2018, 2020; Appendix S1: Table S1). These data were aggregated as the percentage of trees affected by either insect species across "subareas" of sites in close proximity (i.e., within 25 km), thereby generating 16 spatially distributed SBW outbreak chronologies, and 15 spatially distributed FTC outbreak chronologies, with a high degree of congruency in the spatial distribution of reconstruction chronologies (Figure 3). Subarea-scale analyses were limited to 1928–2005, when 5 or more trees were available for each subarea.

Data analysis

We designed a series of multi-scale analyses applied to subarea-scale time series of insect impacts derived from the tree-ring reconstructions described above. In our approach, we deliberately avoided frequency-based continuous-time methods (e.g., wavelet transforms) because the time series were relatively short and we sought to avoid any assumption regarding oscillatory behavior. We applied a bootstrapping approach to partition time series into windows of variable length, generating a continuous range of temporal resolutions binned by the number of windows. The first window always began in 1928, and the last window ended in 2005, but otherwise the window framing varied freely. For interpretation, we summarize patterns across three broad categories of temporal resolution: short windows (finer resolution, roughly within outbreak, governed by fast processes), intermediate windows (between-outbreak), and long windows (coarser resolution, multi-decadal,

governed by slow processes). The categorical labels are intended only to assist with interpretation; the underlying analysis treats the number and size of window intervals as a continuous variable. For each temporal resolution, we computed spatial cross-correlations in interval impacts within and between species.

We began by evaluating interdependence using whole time series cross-correlations of annual percent trees affected by SBW and FTC, followed by spatial cross-correlation analyses of interval impact maps aggregated by window length. We then quantified spatial pattern persistence (SPP) within species across successive windows (lags of one window) using autocorrelograms and examined how persistence changed with window length. Finally, we assessed patterns at the longest mean window size by relating interval impacts to contemporary forest composition and by testing spatial correlations between linear trend coefficients of annual outbreak severity for SBW and FTC. Our goal was to determine whether anti-persistence patterns observed at intermediate windows (Cooke et al., 2024) extend to the longest windows and whether they align with contemporary forest cover attributes or cross-species correlations—patterns consistent with a metastable interaction between disturbance subsystems.

The detailed methods of analysis follow, where all data transformations and analyses were conducted using the R statistical software package ver. 4.1.2 (R Core Team, 2023). All data and code are archived at https://doi.org/10.13140/RG.2.2.10080.44801/2.

Annual-scale time series cross-correlations

We used time series cross-correlation analysis to determine the likelihood that the two outbreaking insect species' fluctuations in percent trees affected were independent. Fifteen of the published SBW and FTC subarea outbreak chronologies could be paired as colocated in a common sample subarea (Figure 3). Interspecies correlations were therefore computed at the level of the study area as a whole and the level of the individual subarea. The common interval between species for the global time series was 1875–2005. Among individual subareas, the common interval was shorter: 1928–2005.

Multi-scale spatial cross-correlations

The degree of dependence between the two insect species was also examined spatially, by comparing impacts at the subarea level aggregated across various temporal resolutions, using the windowing scheme to partition the 78-year-long time series (1928–2005) into a sequence of random-length intervals as described above. These time series windows varied from 13 intervals averaging 6 years in length to two intervals, averaging 39 years in length. To eliminate the possibility of subjectivity in bias arising in the interval partitioning of time series, we used a bootstrapping approach to compute 1000 random windows, each partition using a random variable-length windowing scheme for defining intervals. For each time interval, average impact (percent trees affected) was computed for each of the 15 subareas, producing an interval impact map for each species. Spatial cross-correlations were then computed on these pairs of impact maps. Loess curves were fit to the correlation outputs, one curve for each type of partition, measured by the number of windows per partition. We examined the patterns of cross-correlations both as a function of mean window size and SD of the window size.

SPP as a function of mean window size

To examine how the ecological memory of insect impacts (i.e., percent trees affected) changed as a function of mean window size, we computed autocorrelogram functions for each insect species that we refer to as SPP functions. These SPP functions evaluate how spatial patterns of outbreak severity, as measured by subarea impacts (percent trees affected) aggregated within a given time interval for a given insect species, tend to persist between intervals through time. If persistence is strong, then spatial cross-correlations between successive time intervals will be strongly positive. If spatial patterns degrade quickly between successive intervals, then these spatial cross-correlations will be near zero. "Anti-persistence" is indicated by negative spatial cross-correlations and could result from some residual top-down influence of natural enemies operating as faster dynamics, or through the slower action of bottom-up forces, such as successional changes in host forest landscape structure (Figures 1 and 2).

To develop these SPP functions, we applied the same windowing scheme described above for the multi-scale spatial cross-correlations to allow the outbreak intervals to vary widely and freely. For each species, we computed the strength of spatial cross-correlation between successive intervals in impacts aggregated over time at the subarea scale. We used a full range of interval lengths, from short intervals consistent with fast eruption events (13 windows averaging 6 years in length) to long intervals consistent with slow forest change (2 windows averaging 39 years in length). Plotting the between-interval

correlations allowed us to evaluate the strength and sign (i.e., persistence vs. anti-persistence) of spatial cross-correlations through time, with impact aggregated across various mean window sizes. These SPP autocorrelogram functions could then be compared between species to determine whether SPP was similar or different between insect species.

Insect species outbreak trend analyses

For each species' outbreak chronology 1928–2005, we computed linear time series trends at the subarea level to determine if there were places where defoliator outbreak cycles were systematically rising or falling in amplitude through time. We then plotted these trend statistics for each species to see if the places where one species was falling were where the other was rising, and vice versa.

Relating slow outbreak dynamics to forest attributes

We built upon the results of the previously described analyses to examine whether spatial patterns of outbreak at longest mean window size were related to contemporary forest attributes. The outbreak data (beginning in 1928, to obtain adequate spatial coverage of samples) were split into early versus contemporary time periods. Since the earliest Landsat data (MSS) were first available in 1972, we reviewed the subarea-scale chronologies to seek the most consistent "trough year" (i.e., low point in percent trees affected; see Figure 4) for each defoliator species around that year to focus on early versus contemporary outbreak events. The dividing year was defined as 1977/1978 and 1974/1975 for SBW and FTC, respectively. Site-level annual percent trees affected were then averaged across early and contemporary time periods for each defoliator species ($n = 50$ per species). Results were visualized in space using spatial interpolation (inverse distance-weighting, power = 2) implemented in R (packages: gstat, sp., sf, raster).

Forest composition was derived from Thapa et al. (2020) to represent the relative (i.e., percent) basal area for both preferred and the full host complement for SBW and FTC (preferred hosts: SBW = balsam fir, FTC = aspen species; full host complement: SBW = balsam fir and spruce species; FTC = all broadleaf species except red maple). Contemporary composition was mapped in two different years (1985 and 2005). Since patterns of host are strongly affected by the abundant lakes and open wetlands in this region (James et al., 2011), with uncertain consequences for insect dispersal dynamics, we ignored these two cover types in our calculation of relative basal area to focus on land area. Four land cover structure variables (area-weighted mean nonforest patch

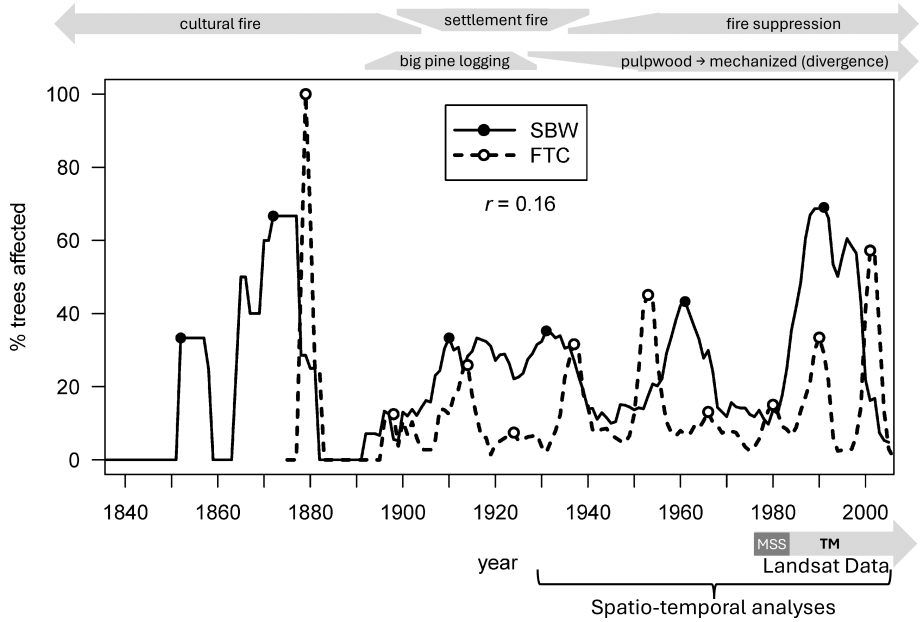

FIGURE 4 Master outbreak tree-ring chronologies for spruce budworm (SBW) (solid line), from Robert et al. (2018), and forest tent caterpillar (FTC, dashed line), from Robert et al. (2020) summarized over the full extent of the study area including all subareas (Figure 3). The interspecies correlation across the common interval, 1875–2005, is $r = 0.16$. Cycle peaks (circles) for each species were determined algorithmically, as described in Cooke et al. (2024). Arrows indicate major periods of human activities affecting forests (approximate, top) and the availability of satellite-based land cover and composition (bottom). Spatiotemporal data analyses were limited to 1928–2005.

size [in hectares], Shannon index of forest cover diversity, percent forest, and forest edge density [in meters per hectare]) were derived from a time series of land cover maps (Wolter et al., 2012), averaged across the time period 1975–2000. As above, nonforest patch size was limited to nonaquatic cover types, while percent forest did include water and open wetlands as nonforest cover. Four landscape structure variables and four species composition variables (the latter measured at two distinct time-points, 1985 and 2005) yielding a total of 12 forest landscape structure variables. These variables were sampled at a range of different radii (1, 5, and 10 km) from each of the tree-ring sample points and then averaged at the subarea level.

We reduced the dimensionality of the forest composition and landscape structure variables down to one or two dominant axes using principal components analysis (PCA) applied to each of the three sample radii. These PCA axes were then used as predictors in ordinary least squares regression models relating SBW and FTC outbreak severities (annual percent trees) aggregated across early and contemporary time periods. Inclusion of one or two axes in a given model was contingent on their statistical significance.

RESULTS

Annual-scale time series cross-correlations

With a 28-year cycle for SBW (6 outbreak cycles over 170 years, 1836–2005) and a 13-year cycle for FTC (10 outbreak cycles over 132 years, 1875–2006), the two systems appeared to be cycling independently of one another at the spatial scale of the entire study area (Figure 4). The aspen and spruce sample sites in Figure 3 are close enough in proximity for the two insect species' populations to be considered colocated. The interspecies correlation across the 131-year-long common interval, 1875–2005, was weakly positive ($r = 0.16$, 95% CI [−0.01, 0.32], $t(129) = 1.84$; $p = 0.067$), despite species cycling at different frequencies. A local minimum in the percentage of trees affected in both defoliator species coincides with the onset of the contemporary Landsat archive, providing a reference point for subsequent analyses comparing early and contemporary outbreak periods (Figure 4). Meanwhile, the 1928 start date for spatial analyses corresponds roughly with the end of both region-wide big pine logging, where cultural burn practices were ended even earlier (see *Study area* for details). The earliest decades of this tree-ring record include a transitional settlement period accompanied by widespread fire. Satellite-based landscape data were available starting in 1975 (Landsat MSS, distinguishing land cover types) and 1985 (Landsat TM, distinguishing forest composition)—following decades of divergence in logging practices among management zones (Figure 4).

The fact that the two systems cycle at different primary frequencies, globally, does not imply an absence of interdependencies at more localized spatial scales. Nevertheless, at the level of the subarea, we expected no correlation between any of the interspecies series pairs. The shortest series began in 1928, so the common interval for this finer scale analysis was 1928–2005 (i.e., 78 years). Three SBW cycles and six FTC cycles were observed during this interval. For each subarea, we calculated Pearson's correlations between annual outbreak severity (% trees affected) for SBW and FTC across the common time interval. These averaged close to zero and showed no systematic trend (Appendix S1: Figure S1), indicating that any local interaction between species outbreak severity is not evident at the annual time resolution.

Multi-scale spatial cross-correlations

Cross-correlations between SBW and FTC were most negative at the longest mean window sizes ($r \approx -0.4$; Appendix S1: Figure S2) and weakened gradually as windows shortened, reflecting a shift from strong divergence at slow scales to near independence at fast scales. The wide spread in data points was the result of randomness in window partitioning and stochasticity in insect dynamics (Appendix S1: Figure S2).

SPP as a function of mean window size

SPP shifted smoothly across scales (Figure 5). SBW moved from moderate persistence at short windows to strong anti-persistence at long windows, while FTC transitioned from neutral persistence to strong anti-persistence, matching SBW at the longest windows.

Insect species outbreak trend analyses

For each species, we estimated linear trend coefficients for outbreak severity through time within each subarea using Pearson's correlation. We then applied Pearson's correlation to these paired trend coefficients (FTC vs. SBW) to assess the relationship between species-specific trends, finding a marginally significant

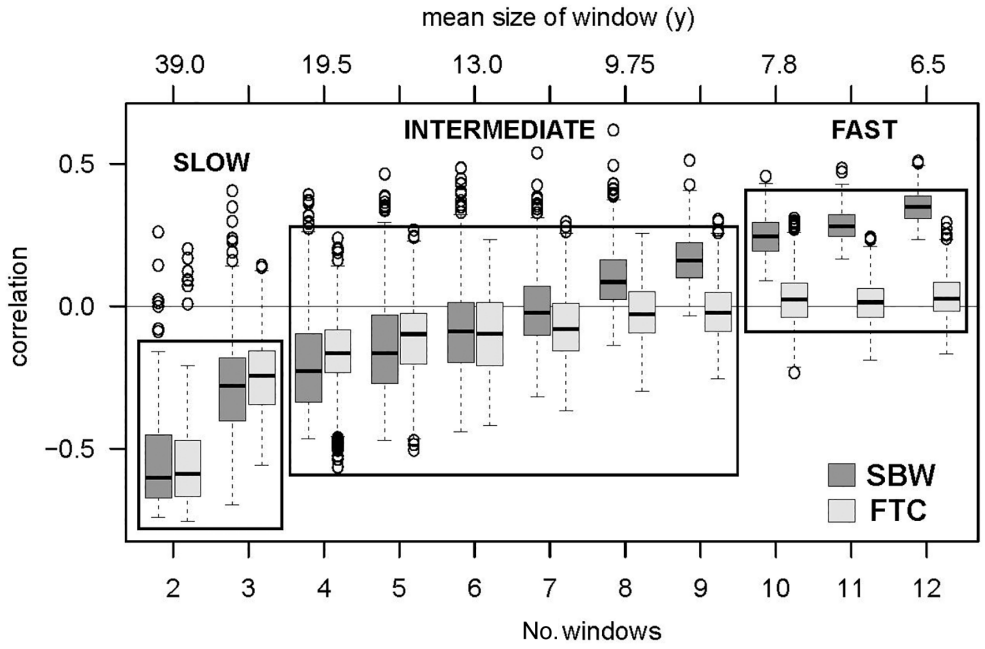

FIGURE 5 The effect of number of windows on spatial persistence patterning in spruce budworm (SBW) and forest tent caterpillar (FTC). Corresponding mean size of window (y = years) on upper *x*-axis labels. Box plots represent distributions of correlations when the 20% most evenly spaced windows are used to partition the time series (i.e., censoring the bulk of partitionings that are unlikely to contain a cycle peak). Mean window size on the upper *x*-axis provides context for long, intermediate, and short windows corresponding with slow to fast processes underlying outbreak dynamics, where this article focuses on the longest windows best associated with slow vegetation change.

negative correlation ($r = -0.41$, 95% CI [−0.74, 0.02], $t(13) = -1.62$, $p = 0.064$, $n = 15$; Figure 6a). The full set of outbreak trendlines underlying these correlation coefficients can be found in Appendix S1: Figure S3. Extremes in these opposing trendlines are illustrated by a comparison of the Minnesota central south (MCS) subarea versus the Ontario east north (OEN) subarea (Figure 6b,c). In MCS (part of the broader landscape grouping that is more dominated today by aspen and fragmented forest [see Figure 8 below]), SBW outbreaks diminished in severity through time. By comparison, in OEN (part of the broader landscape grouping where spruce–fir dominates [see Figure 8 below]), SBW outbreaks increased in severity through time. All four trends, in isolation, were weak, as one would expect compared to the high amplitude of cycling in the master outbreak chronologies (Figure 4). Still, the four trends, combined with the broader negative correlation in outbreak trends across defoliator species (Figure 6a), indicate a consistent emergent result: the focal area of high-severity, synchronous cycling has switched locations over the 78 years of observations. Where the SBW was once the dominant outbreak cycling herbivore, the FTC has taken its place, and vice versa. We suggest the overall pattern in trendlines across locations and defoliator species implies the existence of a pest-species successional "see-saw."

Relating slow outbreak dynamics to forest attributes

As foreshadowed in Figure 6 in the pattern of see-saw cycling, as well as in the strong negative autocorrelations observed for both species at multi-decadal time scales (Figure 5), the spatial correlation between the areas impacted by SBW versus FTC was inversely related during early versus contemporary time periods. During the contemporary period, the spatial correlation between the areas impacted by SBW versus FTC was $r = -0.54$ (95% CI [−0.82, −0.04], $p = 0.038$, $n = 15$). In the earlier period, the correlation was similar ($r = -0.61$, 95% CI [−0.86, −0.14], $p = 0.016$, $n = 15$), but the two spatial distributions appear opposite (Figure 7). Consistent with this reversal pattern, the spatial patterns of impact in the earlier versus the later period were strongly and negatively correlated for both species (SBW: $r = -0.73$, 95% CI [−0.90, −0.37], $p = 0.001$, $n = 16$; FTC: $r = -0.70$, 95% CI [−0.89, −0.37], $p = 0.004$, $n = 15$). We note that SBW impact (% trees affected) was roughly double the impact of FTC because SBW outbreaks had greater duration, leading to higher impacts when measured over each respective time period (Figure 7). As expected, the correlation between SBW and FTC in opposing time periods was positive, averaging +0.58 (Appendix S1: Table S3). This correlation reflects the tendency for impact by one

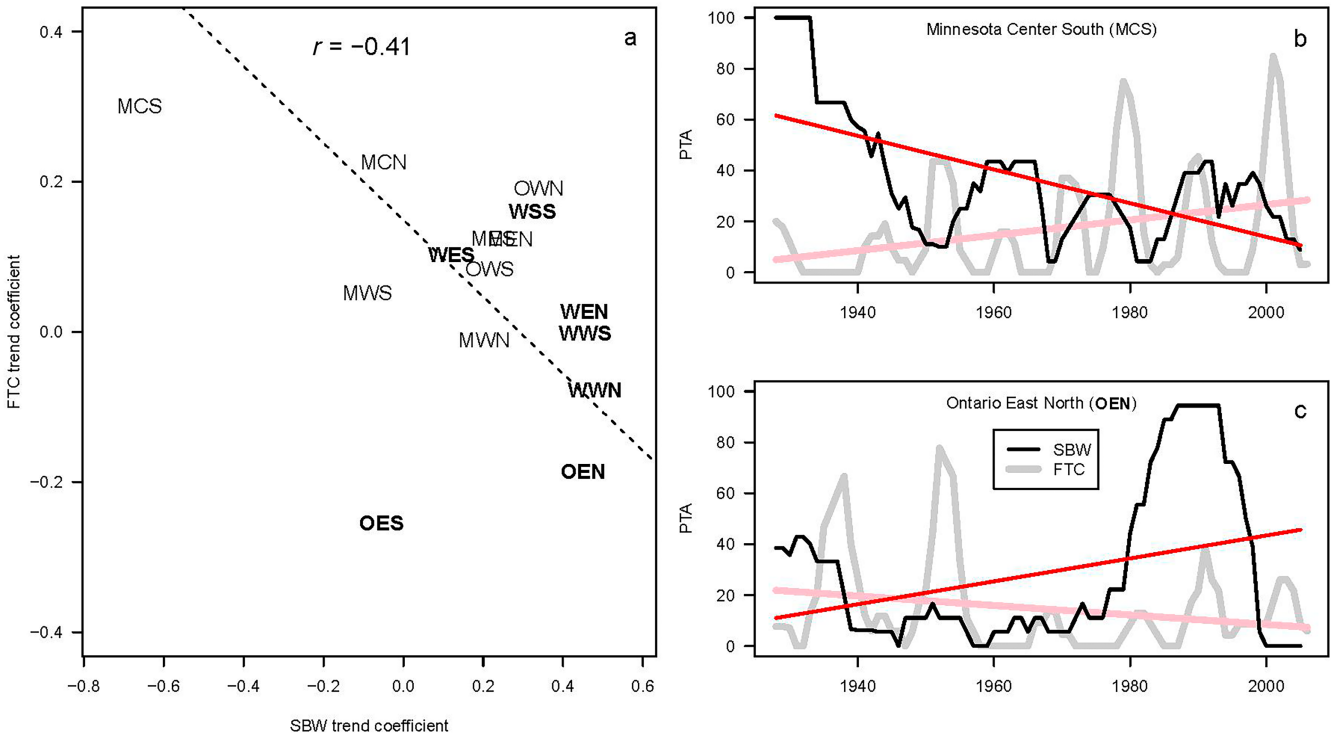

FIGURE 6 (a) Pearson's correlation coefficients estimated for linear trends in outbreak severity (percent trees affected; PTA) for spruce budworm (SBW) versus forest tent caterpillar (FTC), indicating these linear trends tend to be negatively correlated across defoliator species. Subarea acronyms correspond to locations defined in Figure 3, where bold font corresponds with negative loadings on the principal components analysis (PCA) applied to forest landscape structure variables (see Figure 8) that indicate comparably more forested, less fragmented, and with higher spruce–fir content than the plain font in the subareas of managed Minnesota and Ontario West locations. Comparative trendlines in PTA are shown for the extreme cases (b) Minnesota central south (MCS) and (c) Ontario eastern north (OEN), illustrating not only how the trends can oppose each other at a given location, but also how those same trends can be reversed across species (i.e., "see-saw pattern") at different locations in a way that appears related to contemporary forest landscape structure.

species in one multi-decadal time period to be followed by the opposite species in the next time period. In essence, the two insects are trading places with one another at a time scale that is similar to the speed of cycling of SBW outbreaks, and half the speed of cycling of the FTC outbreaks.

The PCA ordination of the forest landscape structure variables measured using a 1-km radius at the site level and then averaged to the subarea level reveals a primary axis that explained 53% of the variation, indicating a general separation of subareas into those with higher fir and spruce content (wilderness and Ontario east), and those with higher aspen and hardwood content (Minnesota and Ontario west; Figure 8). A second component that explained an increasing amount of variance (from 0.14% to 0.23%) with increasing length of sampling radius (Appendix S1: Table S4) was oriented primarily on forest structure, separating Minnesota from Ontario subareas (Appendix S1: Figure S4).

We found that SBW outbreaks in early and contemporary time periods were strongly related to the PC1 axis defining contemporary spruce and fir versus aspen and hardwood composition, but with opposing regression coefficients (Table 1). Contemporary SBW impacts were negatively correlated with PC1 reflecting the gradient from spruce and fir to aspen and hardwood (Figure 8), whereas SBW impacts in the early period show an equally strong but positive association with this axis (Table 1). For FTC, the situation was the opposite, though the strength of the association in both periods was weaker (Table 1). Increasing the spatial scale of sampling increased the relative importance of the second axis (PC2) related to landscape structure for both insect species, but the sign of the regression coefficients consistently switched between periods within species, as well as within periods between species (Appendix S1: Tables S4 and S5).

DISCUSSION

Empirical interpretations

SBW and FTC are two of the most significant biotic disturbances in boreal and hemiboreal mixedwoods. Their

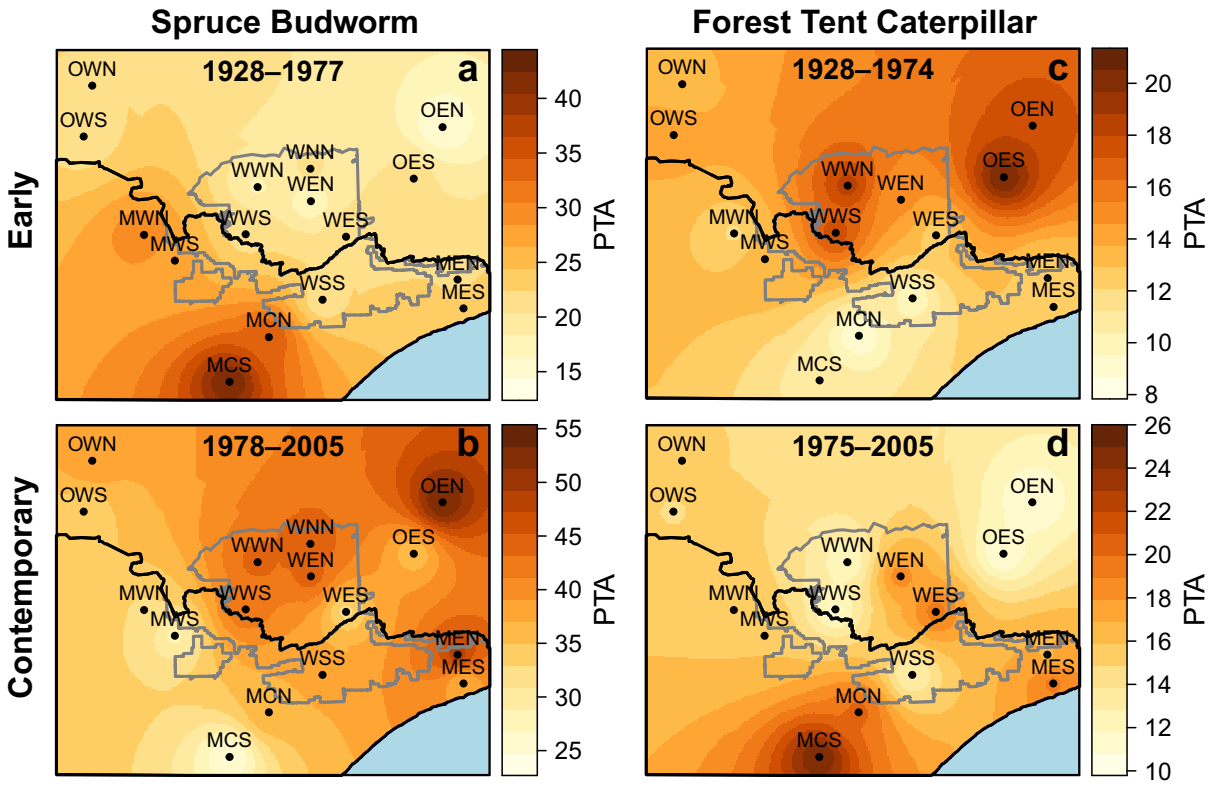

FIGURE 7 Spatial interpolation (inverse distance-weighting, power = 2) of the average impact (percent trees affected; PTA) of spruce budworm (SBW) on white spruce and forest tent caterpillar (FTC) on trembling aspen (columns) during the early time period (late 1920s to mid-1970s) versus the contemporary time period (mid-1970s to 2005) (rows). Subarea acronyms correspond to locations defined in Figure 3, black dots are subarea centroids used for interpolation. Black line represents the Minnesota–Ontario border, gray line represents the sampled wilderness area. Ranges in color maps vary between panels according to minimum and maximum PTA values: (a) SBW early: 14.34–42.49, (b) SBW-contemporary: 24.69–53.37, (c) FTC early: 8.67–20.53, (d) FTC-contemporary: 10.78–25.01.

ranges overlap and outbreaks often co-occur, but do they simply coincide, or interact through disturbance-driven succession? Across short windows, the species cycle independently (Appendix S1: Figure 4). As windows lengthen, spatial cross-correlations become increasingly negative (Appendix S1: Figure S2), and at the longest, multi-decadal windows outbreak centers trade places between the early (1928–1970s) and contemporary (1970s–2005) periods; within-species spatial persistence inverts from positive to strongly negative, and cross-species severity trends exhibit a see-saw pattern (Figures 5–7; Appendix S1: Figure S3). These patterns align with contemporary forest composition and structure (Figure 8; Table 1), supporting vegetation-mediated indirect interactions between SBW and FTC (Figure 1). Interpreting these window-based results in dynamical terms, the independence seen in short windows reflects fast outbreak pulses, whereas the inversions and reciprocal displacement evident at long windows emerge from slow, vegetation-driven feedbacks—so the long-term perspective is a necessary complement to the short-term view for understanding cross-species disturbance ecology.

These findings extend prior work by explicitly examining within- and between-species relationships across temporal scales. At fast scales—most evident in the high-frequency dynamics of FTC—outbreak pulses shift rapidly across the landscape, producing quasi synchronous patterns that obscure durable associations with forest composition (Robert et al., 2020). At intermediate scales, a "skipping" behavior emerges—severity alternates across consecutive outbreaks in space and time, consistent with earlier observations (Bouchard et al., 2006; Cooke et al., 2024) and with the distribution of correlations in Figure 5. At the slowest scales, the layering of faster eruptive pulses over top a slow invasion process has been described in the case of spongy moth (*Lymantria dispar dispar*) as "pulsed invasion" (Johnson et al., 2006). While SBW and FTC are not invasive, the analogy highlights a shared dynamic feature: when each species slowly expands into areas formerly occupied by the other, that reciprocal exchange unfolds in discrete stages. The underlying population processes are continuous across scales (Figure 5), but their expression is pulsed, and over longer periods each species displaces the

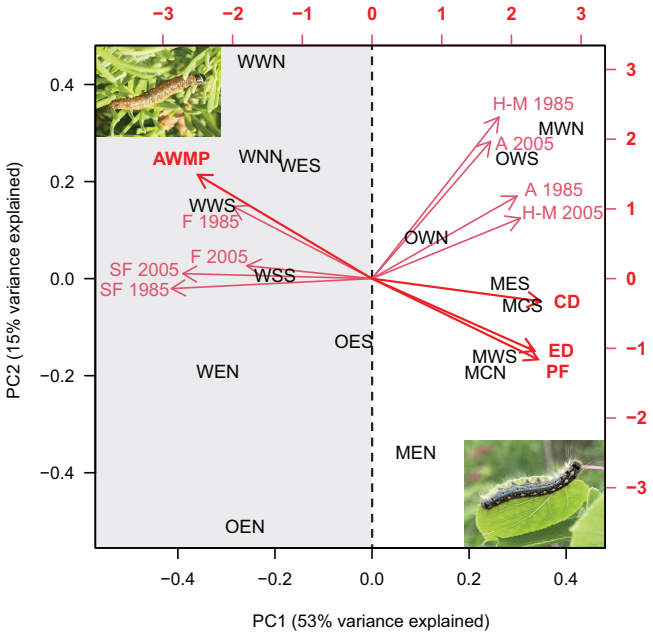

FIGURE 8 Principal components analysis applied to forest structure variables at the 1 km radius scale. First principal component (PC1) explained the dividing lines indicate subarea-scale defoliator activity (spruce budworm [SBW]: gray, forest tent caterpillar [FTC]: white) most active in the contemporary period that overlaps the satellite-based estimates of forest landscape structure (Figure 7). Composition variables include a year (A, aspen; F, fir; H-M, hardwood except maple; SF, spruce–fir); structural variables in bold (AWMP, area-weighted mean patch size of forest openings; CD, cover diversity; ED, edge density; PF, percent forest). SBW photo by christine123 via iNaturalist at https://www.inaturalist.org/observations/221658017; FTC photo by Ian Manning via iNaturalist at https://www.inaturalist.org/observations/166770638. Both photos are provided under a CC BY 4.0 license (https://creativecommons.org/licenses/by/4.0/).

other (Figure 6), producing a final spatial pattern (Figure 7) that is dictated by contemporary host distributions (Table 1). Taken together, these cross-scale patterns position SBW and FTC not as passive followers of succession but as disturbance agents whose pulsed dynamics both respond to—and accelerate—vegetation change through selective herbivory and landscape-level feedbacks (Holling, 1973; Raffa et al., 2008). The result is a "trading spaces" dynamic in which the positive correlations evident at fast scales invert at slow scales, reflecting the reciprocal displacement of SBW and FTC and the host-dictated endpoints that define this system.

Although we cannot directly reconstruct early-century forest composition (1928–1970), the strong inversion of SBW and FTC outbreak centers between early and contemporary periods implies a major compositional shift. This pattern likely reflects lagged insect response to anthropogenic legacies. Two assumptions underlie this interpretation: (1) insects respond most consistently to host abundance at slow scales (this study) and (2) vegetation reorganizes over decades following cumulative land management practices (Collins et al., 2017; Johnstone et al., 2016). Historical evidence supports this view: the early 1900s marked a transition from exploitative logging and settlement to mechanized forestry (Figure 4), with cut-over areas rapidly colonized by aspen (Heinselman, 1996) and widespread fires documented in 1930s air photos (White & Host, 2008). Early forests likely reflected these disturbance legacies (Stearns, 1997), whereas contemporary conditions reflect decades of industrial forestry (divergent in space) and coordinated fire suppression (consistent in space) (James et al., 2011; Sturtevant et al., 2014). More recent disturbances—including large fires and the massive 1999 derecho—have further promoted broadleaf expansion in wilderness (Anoszko et al., 2022). These events fall near the end or beyond our chronologies, but because insect–forest relationships emerge at slow scales, future SBW and FTC will likely respond as legacies propagate. This interpretation aligns with the conceptual framework of Figures 1 and 2 but placed in the context of the forces affecting compositional shifts across the timespan of the chronologies (Figure 4).

Theoretical and practical implications

Historical observations suggested that FTC outbreaks often precede SBW by a few years (Wellington et al., 1950), whereas subsequent work found limited evidence for such fast scale linkages (Ghent, 1958). Our results reconcile these views by shifting the lens to slow timescales: when insect–host systems are linked via vegetation feedbacks, causal correlations emerge over decades, not years. The reciprocal trading of spaces we document exemplifies metastability—cumulative disturbances by one herbivore prepare conditions that later favor the other and vice versa (cf. Ludwig et al., 1997). In resilience terms, these dynamics reflect "revolt and remember" (Allen et al., 2014): fast disturbances (outbreaks) drive nonlinear transitions, while slow legacies (composition, connectivity, and management history) remember and mediate subsequent cycles (Johnstone et al., 2016).

This behavior challenges static interpretations of stability landscapes. The classical ball-in-cup metaphor (Beisner et al., 2003; Walker et al., 2004) assumes systems settle toward basin minima governed by gravity-like forces. In our system, the attributes that define basins of attraction—host abundance and connectivity—also govern the disturbances (SBW and FTC), making the

TABLE 1 Results of ordinary least squares regression relating average annual percent trees affected by each herbivore species (FTC, forest tent caterpillar; SBW, spruce budworm) and in each period to the scores from the first component (PC1) of the principal components analysis applied to forest landscape structure variables (Figure 8), where increasing score indicates a higher proportion of aspen and hardwood relative to spruce and fir in recent decades.

Species–period	Model or predictor	R^2	Coefficient[a]	95% CI[b]	t(df)	F(df)	p
SBW early	Model	0.50				13.74 (1, 14)	0.002
	Intercept		23.74	[20.97, 26.51]	18.36 (14)		<0.001
	PC1		1.96	[0.83, 3.10]	3.71 (14)		0.002
SBW late	Model	0.45				11.26 (1, 14)	0.005
	Intercept		38.39	[35.29, 41.48]	26.59 (14)		<0.001
	PC1		−1.98	[−3.25, −0.72]	−3.35 (14)		0.005
FTC early[c]	Model	0.25				4.41 (1, 13)	0.056
	Intercept		13.99	[12.28, 15.69]	17.73 (13)		<0.001
	PC1		−0.68	[−1.37, 0.02]	−2.10 (13)		0.056
FTC late[c]	Model	0.25				4.34 (1, 13)	0.058
	Intercept		15.72	[13.69, 17.74]	16.76 (13)		<0.001
	PC1		0.80	[−0.03, 1.63]	2.08 (13)		0.058

[a]Coefficients represent regression estimates: Intercept = expected outbreak severity when PC1 = 0; PC1 = change in outbreak severity per unit increase in PC1 score.
[b]CIs computed with t critical values (df = 14: 2.145; df = 13: 2.160).
[c]FTC models exclude wilderness north north (WNN) subarea (15 subareas).

disturbance intrinsic rather than exogenous. The result is dynamic stability: trajectories that oscillate within substates (intermediate anti-persistence; Figure 5) and invert between substates (Figure 7), echoing strange-attractor-like dynamics (Lorenz, 1963) and aligning with recent advances that frame resilience through ecological dynamic regimes—non-equilibrium trajectories within multidimensional basins of attraction (Sánchez-Pinillos et al., 2024). This distinction underscores two complementary notions of stability: structural stability, represented by shifting basins in a stability landscape (Beisner et al., 2003), and dynamic stability, represented by trajectories that loop and invert across scales. Emphasizing this duality moves beyond metaphor toward a unified understanding of resilience that integrates structural stability with dynamic, trajectory-based regimes (Sánchez-Pinillos et al., 2024).

Placing insects alongside other disturbance drivers clarifies their unique role. Wind is largely exogenous—its severity is filtered by stand structure, species traits, and density—factors that govern wind susceptibility even as wind events themselves remain independent of landscape composition (Gardiner, 2021). Fire blends exogenous ignitions and weather with endogenous fuel characteristics, producing strong interactions with vegetation structure and landscape arrangement (Peters et al., 2004). In contrast, native eruptive defoliators like SBW and FTC are tightly bound to forest composition: Outbreak patterning reflects host abundance and connectivity, and selective herbivory in turn reshapes those same hosts. Climate may modulate outbreak dynamics—particularly near range margins (e.g., Büntgen et al., 2020)—but our study area lies within the core bioclimatic envelope of both species (Régnière et al., 2012; Schowalter, 2017), and the dominant spatial signal in our analysis is vegetation mediated rather than climate driven (Robert et al., 2018, 2020).

These interactions have occurred within a landscape profoundly shaped by human legacies, and they frequently compound one another (sensu Burton et al., 2020). The role of FTC in accelerating transitions from aspen to fir–spruce is well supported (Man, 2024; Moulinier et al., 2013), whereas the degree to which SBW alone triggers retrogressive succession back to broadleaf dominance is less consistent (Leduc et al., 2021; Nealis & Régnière, 2004; Sánchez-Pinillos et al., 2019). Linked disturbances can magnify SBW impacts: Fire activity often increases following SBW outbreaks (James et al., 2017), and logging frequently accelerates during outbreaks to mitigate the loss of wood fiber (Mushakhian et al., 2020; Radeloff et al., 2000). Historically, jack pine was maintained by stand-replacing crown fires, while mixed-severity fire regimes favored red and white pine—disturbance dynamics that once buffered against dominance by spruce–fir or aspen (Frelich, 2002; Kipfmueller et al., 2021). In recent decades, large fires and windstorms have further shifted trajectories; jack pine increasingly being replaced by either aspen (after severe or frequent burns, or wind then fire) or spruce–fir

(succession, or wind not followed by fire), reinforcing a biphasic aspen versus spruce–fir landscape (Anoszko et al., 2022). This synthesis places insect disturbance in proper context relative to wind, fire, and land use—each shaping, filtering, or amplifying the vegetation template that insects both read and rewrite.

These insights connect directly to diversity–stability principles. The hemiboreal Border Lakes region is more compositionally diverse than the true boreal forest, which makes our detection of a biphasic shift even more notable. Disturbance legacies persist—pine decline, fir increase, and aspen expansion (Friedman & Reich, 2005; James et al., 2011)—and both fir and aspen exhibit life history traits that sustain population persistence (fir seedling banks; aspen refoliation and suckering). Ecosystems simplified by anthropogenic stressors tend to favor "weedy" species (Folke et al., 2004), incurring resilience debt through the loss of information legacies (Johnstone et al., 2016). Under such homogenization, native eruptive insects can dominate the disturbance regime, producing low-dimensional dynamics—a biphasic attractor centered on SBW and FTC. This contraction of the stability landscape—the degradation or loss of basins—reflects the kind of nonlinear threshold behavior described by cusp catastrophe formulations for forest mosaics (Frelich, 2002) and observed in recent decades as jack pine has been replaced by either aspen or spruce–fir (Anoszko et al., 2022). Conversely, increasing compositional and structural diversity could expand the previous century's stability landscape into more robust multiphasic regimes, attenuating outbreak amplitudes and promoting asynchrony (see Appendix S1: Figure S5 for a conceptual synthesis).

Coupled dynamics of two defoliators targeting different hosts highlight why pest risk is best assessed in a broader context rather than in isolation. Traditional approaches often focus on single species (Kneeshaw et al., 2021), yet our findings show that interactions among herbivores can shape disturbance regimes over decades. For instance, increasing hardwood content reduces SBW damage (Campbell et al., 2008; Cappuccino et al., 1998; Zhang et al., 2018), and mixing phylogenetically distant species can lower overall herbivory (Jactel et al., 2021). However, what counts as "diversification" matters: mixtures dominated by aspen and fir may simply reinforce the same biphasic substates rather than expand the stability landscape. Management that moves beyond generic diversity targets toward strategies that create multiphasic regimes—landscapes with multiple basins of attraction (Appendix S1: Figure S5)—can help dampen eruptive behavior of outbreaks, promote asynchronous dynamics, and reduce the amplitude of looped disturbances where one herbivore sets the stage for another (Burton et al., 2020). These strategies emphasize diversifying functional traits—not just taxonomic richness—along with structural heterogeneity and spatial patterns that reduce host abundance and connectivity (Messier et al., 2019).

CONCLUSIONS

Metastability describes systems that shift among multiple basins of attraction without requiring catastrophic change. In the hemiboreal Border Lakes landscape, SBW and FTC traded places over multi-decadal periods, tracking slow shifts in host composition. These reciprocal inversions represent the spatial expression of a biphasic attractor structure shaped by disturbance legacies and feedback-driven insect dynamics, as evidenced by slow-scale negative correlations, inversions in spatial persistence, and sign-switching associations with composition (Figures 5 and 7; Table 1). This interpretation aligns with emerging perspectives that frame resilience through ecological dynamic regimes.

For management, the implications are clear. Homogenization—via fire exclusion, simplified silviculture, or legacy effects—tends to collapse the stability landscape into a low-dimensional, biphasic regime dominated by SBW and FTC. In contrast, increasing compositional and structural diversity—such as restoring historically important species (e.g., pine), supporting mixed-severity fire where feasible, and avoiding mixtures that reinforce aspen–fir dominance—can expand the stability landscape into multiphasic regimes, dampen disturbance amplitudes, and promote asynchronous dynamics. Integrating diversity–stability principles with resilience theory and an explicit view of cross-scale feedbacks can help guide boreal and hemiboreal forests toward more stable, multiphasic disturbance regimes that sustain ecological complexity and long-term forest health.

AUTHOR CONTRIBUTIONS

Brian R. Sturtevant, Barry J. Cooke, Daniel Kneeshaw, and Louis-Etienne Robert conceived the ideas and designed methodology. Louis-Etienne Robert, Brian R. Sturtevant, Daniel Kneeshaw, Patrick M. A. James, Peter T. Wolter, and Philip A. Townsend collected the field data. Barry J. Cooke, Brian R. Sturtevant, and Louis-Etienne Robert analyzed the data with input by Daniel Kneeshaw, Patrick M. A. James, and Marie-Josee Fortin. Peter T. Wolter developed the land cover data layers, and Peter T. Wolter, Philip A. Townsend, and Brian R. Sturtevant developed the forest composition layers. Brian R. Sturtevant and Barry J. Cooke co-led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Cooke et al., 2026) are available in ResearchGate at https://doi.org/10.13140/RG.2.2.10080.44801/2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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