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The spruce budworm from Minnesota and Manitoba to Maine and the Maritimes: Blais and budworm paradigms revisited

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Abstract

We revisit the research legacy of J.R. Blais and re-evaluate his contributions to spruce budworm—forest dynamics in light of a century of research, 1924–2025. We trace the evolution of scientific thought on outbreak ecology and reassess Blais' foundational insights using contemporary data and methods. Blais' alignment with a bottom-up, host-driven outbreak paradigm—centered on forest composition and epicentric spread—anticipated many findings now supported by modern research. Reanalysis of Blais' historical outbreak maps (1802–1940) reveals a longitudinal gradient in outbreak frequency aligned with balsam fir distribution, a pattern only visible with century-scale data. While individual outbreaks emerge fragmented and asynchronous, aggregate patterns exhibit long-term trends of increasing periodicity, intensity, and synchrony—consistent with Blais' suggestion that cycling behavior has shifted, with greater outbreak extents emerging in the 20th century. A paradigm revolution toward Royama in the 1980s discounted forest structure as a driver, shaping interpretations for decades. Yet tree-ring, defoliation, and population data today converge on four conclusions: outbreak periodicity is weak and complex; synchrony is variable; spatial patterns are non-repeating; and host forest structure strongly influences outbreak dynamics. These revelations—many crystallizing in the last decade—validate Blais' interpretation and support his argument that promoting forest diversity through silviculture remains the most effective strategy for managing budworm risk.

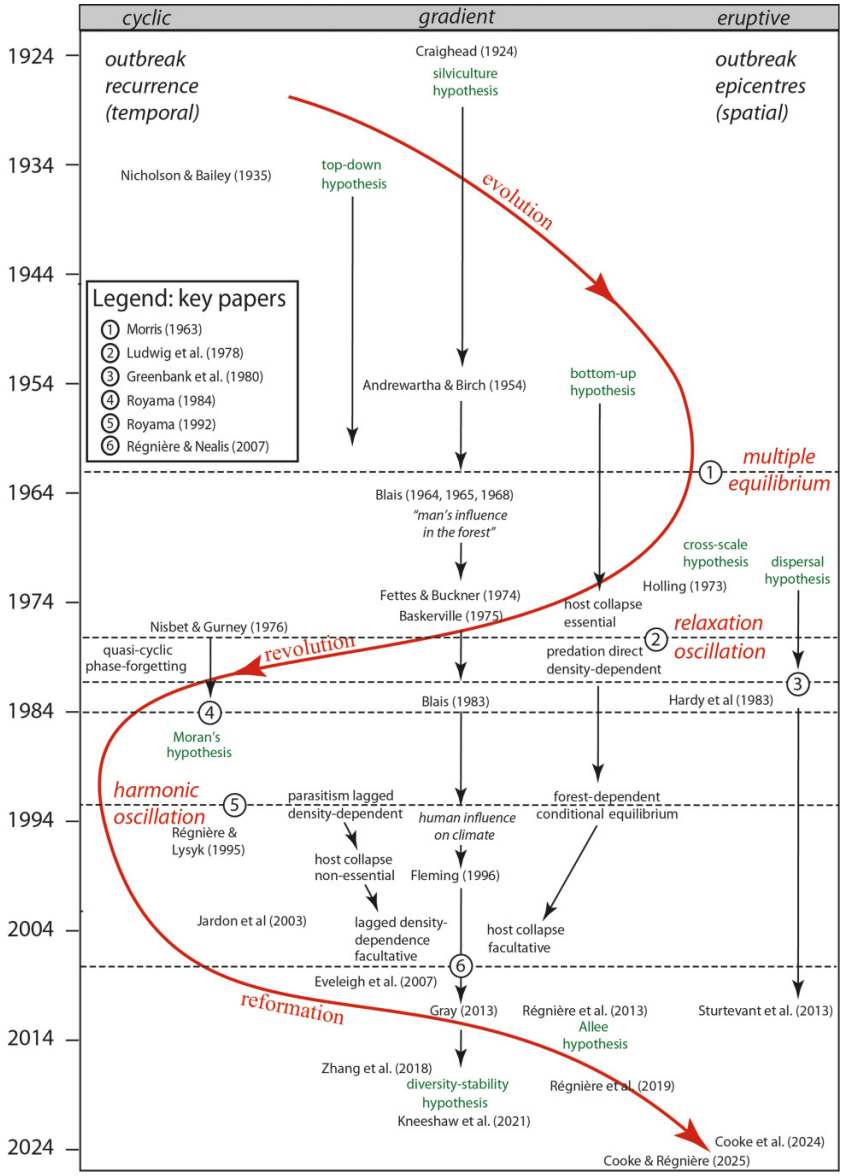
Key words: Blais, spruce budworm, dendrochronology, population dynamics, silvicultural hypothesis, cycle synchronization theory

Introduction

As the most devastating forest pest in eastern North America, the spruce budworm needs little introduction. Outbreaks tend to recur at semi-regular intervals; however, the cause of the "cycle", and of spatial and temporal variability around that basic pattern (Kneeshaw et al. 2015), have been the subject of much study and debate over the last 100 years (Sturtevant et al. 2015). The last large-scale outbreak in the 1970s and 1980s had devastating consequences for wide swaths of the North American boreal and hemiboreal and was particularly concentrated in the Atlantic Canadian forest sector (MacLean 1980) and adjacent Maine (USA) (Irland et al. 1988). In 2025, we are now deep into the next interregional outbreak (Ministère des Ressources Naturelles et des Forêts Québec 2023; Ontario Ministry of Natural Resources and Forestry 2023; Maine Department of Agriculture, Conservation and Forestry 2024; Minnesota Department of Natural Resources 2024; Newfoundland and Labrador Fisheries, Forestry and Agriculture 2025), as predicted by Gray et al. (2000) at the end of the last outbreak. As we contemplate what comes next and how best to manage, there is value in re-examining the century of research behind us.

The purpose of this Perspectives piece is twofold: (i) to summarize in broad terms the evolution of thought around spruce budworm population dynamics through the century, and (ii) to review the major findings of Blais in context of the last four decades of research since his retirement. What we seek to illustrate is that Blais was an intuitive visionary, ahead of his time. Our approach is to first outline the broad contours of the century of research, which puts Blais, in the centre of the timeline, in historical context. We then reconsider his quintessential (1968) dataset, to show how patterns revealed in a formal re-analysis strongly support his central argument. Finally, we return to our historical timeline, to document the fundamental detour in scientific consensus that emerged around the time of Blais's retirement, followed by the fissures in that paradigm that began to crack in the ensuing decades as the latest major outbreak unfolded—ultimately validating what Blais had intuited, but could not quantitatively defend. We close with some

Fig. 1. A century investigating drivers underlying spruce budworm outbreak dynamics in time and space. Across the top are three broad paradigms: "cyclic" vs. "eruptive", with "gradient" in between. The red vector indicates the evolving research trajectory over the century, as the weight of evidence swayed from cycling theory to eruption theory ("evolution") to cycling theory ("revolution") and back ("reformation"). Specific models and modeling papers associated with each phase are indicated red text ("multiple equilibrium", "relaxation oscillation", "harmonic oscillation"). Key papers driving momentum shift are indicated by horizontal dashed lines and in the legend as numbered circles. Additionally, 24 other papers are depicted, which help define the shape of the arc. Eight key hypotheses are depicted in green. The black arrows tie together related themes (also in black) through time. Each of these papers, paradigms, hypotheses, themes are referenced in the main text (Craighead 1924; Nicholson and Bailey 1935; Andrewartha and Birch 1954; Blais 1964, 1965, 1968; Nisbet and Gurney 1976; Fettes and Buckner 1974; Baskerville 1975; Holling 1973; Blais 1983; Hardy et al. 1983; Régnière and Lysk 1995; Fleming 1996; Jardon et al. 2003; Everleigh et al. 2007; Gray 2013; Régnière et al. 2013; Sturtevant et al. 2013; Zhang et al. 2018; Kneeshaw et al. 2021).



thoughts on spruce budworm management as inspired by Blais and his place in history.

A century of competing paradigms

It was 100 years ago that Craighead (1924) presented the first formal analysis of the "bionomics" of spruce budworm population ecology (Fig. 1). Fifty years later, precisely at the halfway point in our century-long timeline, Fettes and Buckner (1974, p. 57) offered a critical perspective on progress to date:

> *"Studies concerning the insect are now in the fifth generation of Canadian researchers: First by Tothill, Craighead, and Swaine in about 1912; the second generation, Graham, Dowden, Flieger, Balch, and Atwood; thence to the third: Blais, Belyea, Fettes, Morris, Henson,*

Table 1. Top significant and sweeping innovations originating from spruce budworm research.

Citation	Innovation
Morris 1959	Formalized life table analysis
Blais 1965	Tree-ring-based outbreak reconstructions
Holling 1973	Resilience theory
Jones 1974	Aspatial computer-based forest-insect simulation models
Clark and Holling 1979	Spatial computer-based forest-insect simulation models
Greenbank et al. 1980	Aerobiology of insect dispersal
Régnière 1982	Life-stage phenology models
Royama 1984	Cycling and synchronization theory
Sanders 1988	Monitoring with pheromone traps
van Frankenhuyzen 1990	Development and optimized use of bacterial insecticide
Royama 2001	Quantitative life table analysis
Sturtevant et al. 2013	Agent-based aerobiology model
Nealis 2015	Formalized pest risk analysis
James et al. 2015	Genetic investigation of irruptive insect dynamics
Cooke et al. 2024	Formalized multi-scale spatiotemporal analysis

Wellington, and Angus; then to the fourth of Miller, Randall, Greenbank, and Buckner; and finally to the fifth and presently active group, consisting of Kettela, Sanders, Howse, and Desaulniers. Many innovative approaches have been taken over the years: management practices, chemical protection, and biological and integrated control. Canadian researchers have undoubtedly led the way in research on the life history, ecology, physiology, and population dynamics of this and other economically important insects. Nonetheless we must report that our scientists, in a study pre-dating World War I, have learned very little about infestation dynamics."

Since then, successive generations that include world-renowned scientists on the international stage have both refined and shifted in their support of competing theories on the mechanisms driving the quasi-periodic rise and fall of budworm populations, with two emergent conclusions: (1) immense datasets and different approaches are necessary to disentangle these processes, and (2) the budworm–forest system may be best characterized through a hybrid model (Sturtevant et al. 2015) that includes natural enemies, forest structure, and climate.

The spruce budworm has been the source of a number of sweeping, impactful innovations through the decades (Table 1), far beyond the 50-year old list supplied by Fettes and Buckner (1974). Between 1955 and 2022, researchers produced 1281 articles—averaging 19 per year (Sturtevant et al. 2023, SI1). But what is remarkable is that even after another four decades of innovation after Fettes and Buckner (1974), the community was still mired in a "century-long debate" about the very question that Fettes and Buckner (1974) had flagged: "infestation dynamics" (Pureswaran et al. 2016). In 1974, we were asking: did outbreaks come and go with periodic predictability (as per Blackman 1919), or did they boom and bust unpredictably (as per Morris 1963; Watt 1963)? In 2016, we were still undecided whether the "oscillatory hypothesis" of Royama (1984) was superior to its eruptive predecessors: the "multiple equilibrium hypothesis" of Watt (1963), and the closely related "bistability manifold hypothesis" of Ludwig et al. (1978). Nearly a decade later, has any progress been made?

The reason this question matters as much today as it did decades ago is that if the budworm cycle carries with it such momentum that it cannot be stopped or prevented, then we must manage around it. If it is, instead, dependent on a sensitive triggering mechanism, then perhaps it is possible to disable the trigger. This explains the enduring commitment to answer this question over a century of research (Fig. 1).

Through this century of research, the prevailing paradigm drifted from an oscillatory paradigm to an eruption/manifold paradigm (Morris 1963; Ludwig et al. 1978) back to a cycling paradigm (Royama 1984) and swinging back again in the most recent decade (Fig. 1). Through it all remained a central paradigm—the "silvicultural hypothesis" of Craighead (1924)—which suggested that regardless what drives population "cycling", outbreak intensity and extent tend to follow fluctuations in host abundance, thus forming gradients though space and time. This paradigm found its strongest support in J.R. Blais, though his published works 1954–1985, which dominated the central third of the century-long timeline. Blais argued that it was "man's influence in the forest", with the proliferation of balsam fir regeneration following spruce harvest, that was exacerbating outbreaks.

No one today debates that the forest plays some role in budworm outbreak dynamics. Outbreaks cannot occur where host is not present and must terminate if the host food resource collapses. What has been the subject of long-standing debate is the nature of the forest–insect interaction between these extremes. The silvicultural hypothesis held that host forest landscape structure influences spruce budworm population growth rates (not just numbers or densities) in time and space and thus can be used as a lever to manage long-term forest outbreak risk. Aligned with the "bottom-up"

paradigm, this idea was subsequently investigated most vigorously by Blais (1964, 1965, 1968, 1974), well before Ludwig et al. (1978) encoded it in the mathematical framework of "catastrophe theory". Hardy et al. (1983) argued for an "epicenter theory" of outbreak initiation and spread, where long-range mass-migration of female moths (Greenbank et al. 1980) was the key driver of eruptive waves of spot growth and spread, much as Blais (1954) had illustrated decades earlier using tree-ring data (Fig. 1).

After 50–60 years of serious observation, analysis, and modeling over two regional-scale outbreaks, the spruce budworm forest research sector was honing a consensus around a fusion between the "silviculture hypothesis" and the "multiple equilibrium hypothesis", leading to the penultimate synthesis: the "cross-scale hypothesis" of Holling (1973), Clark (1987), and Clark and Holling (1979), which held that nonlinear growth dynamics (i.e., catastrophe theory) and mass migration (as per Greenbank et al. 1980) are the means by which such tiny insects can generate such extensive damage so simultaneously. Under this paradigm, there are several mechanisms by which the amount of host forest cover determines budworm population growth rates, not just numbers or densities, at a point in space and time, thereby shaping every aspect of outbreak "cycling" dynamics in time and space: intensity, duration, extent, periodicity, frequency, and synchrony.

However, a distinctly different idea unexpectedly emerged in the form of Royama's (1984) re-analysis of the infamous "Green River" spruce budworm population data from northern New Brunswick originally used to develop the multiple equilibrium model of Watt (1963). Royama's oscillation hypothesis suggested that (i) spruce budworm populations cycle sinusoidally due to delayed feedback coming from the "top-down", through the action of a wide array of parasites, pathogens, and predators, many of them unknown, (ii) immigration and emigration were random variables that generated significant noise around the cycle, and (iii) the forest played at most a secondary role in shaping the primary predator–prey cycle. Inspired by Moran (1953) and Nisbet and Gurney (1976), he surmised that the periodic spruce budworm outbreak was primarily a "phase-forgetting quasi-cycle", and the massive extent of outbreaks could easily be explained by the "Moran Effect", whereby independently cycling populations may be brought into phase with one another by the density-independent effects of random weather drivers that are spatially correlated amongst locations and thus have a similar cumulative influence on cycle phasing across locations (Cooke et al. 2007).

A key distinction between paradigms is whether host abundance indirectly and weakly affects cycling dynamics, and hence impacts, through its effects on the natural enemy community (top-down oscillation hypothesis), or whether it directly determines nonlinear growth rates of budworm populations by influencing dispersal behavior and success around eruption thresholds (bottom-up multiple equilibrium hypothesis). Dispersal plays a role in generating large-scale outbreaks in both cases. The difference is that under the multiple equilibrium hypothesis, dispersal is actively driving asynchronous traveling waves of eruption, to the extent that regional host abundance can amplify or attenuate local dynamics via cross-scale dynamics. Whereas under Royama's oscillation hypothesis, it is spatially correlated weather-driven dispersal losses that are passively bringing predator–prey-driven cycles into phase alignment as a stochastic process. As an overly simplistic metaphor, the forest is a key driver under the multiple equilibrium paradigm, whereas it is a mere passenger under the oscillation paradigm.

The emergence of Royama's (1984) new theory of synchronized spruce budworm population cycling represented a watershed moment in spruce budworm population ecology and occurred at the precise time when Blais was retiring. Blais' final publication (Blais 1985*b*) was a remarkable *tour de force* in its clarity and depth of vision, because it covered every aspect of spruce budworm population dynamics—origin of outbreaks, outbreak cycles, weather, dispersal, biocontrol, and the forest–insect relationship. However, Blais was not in agreement with Royama (1984), arguing in favour of the bottom-up silvicultural hypothesis, and the epicentric hypothesis of outbreak emergence and spread.

We will complete the historical timeline on modern research findings both under and after Royama (1984, 1992). But before we do this, it is imperative to revisit Blais' weighty (1968) paper, as it was so central to his perspective. A quantitative analysis using tools not available to him at the time elevates the strength of his findings, and helps re-situate his work when viewed with a modern lens.

Blais 1968 revisited

Scientific hypotheses emerge from perceived patterns and assumptions about underlying processes. If understanding past outbreaks is essential for predicting future outbreaks, then Blais stands as the foremost innovator in spruce budworm predictive ecology of the 20th century. By 1968, Blais had reconstructed six historical outbreaks (1802–1940) spanning from the Ontario–Manitoba border to Nova Scotia, including parts of Minnesota and Maine. His work provided the first specific large-scale hypothesis on the drivers of outbreak behavior, focusing on the dominance of balsam fir in eastern North American boreal forests versus the drier, fir-scarce central boreal forests.

While earlier research focused on local biotic drivers (Morris 1963), Blais used tree-ring analysis to uncover outbreak patterns across much larger spatial and temporal scales. He emphasized the lack of periodicity and synchrony in these cycles—assertions clearly stated in his 1968 study (p. 17):

> *"Past outbreaks, instead of embracing the whole area subject to the most recent series of outbreaks, occurred in separate parts of the area. Epidemics of this insect did not recur regularly within regions. The time of occurrence of future outbreaks therefore cannot be predicted with accuracy on the basis of the periodicity of past ones."*

Blais' (1968) choice of words is significant, because his success would go on to inspire many dendrochronologists in the years to come (Table 2). Blais (1968) was unprecedented then or since in the scale of his sampling work, his study area spanning 13 800 000 000 km^2-years of space–time (Table 2). But before we revisit his data, a few caveats are required. Blais

Table 2. The breadth of space and time covered by the 10 most highly cited studies in forest insect dendroecology.

Citation	Citations[a]	Species	Space (km^2)	Time (years)	Space–time (10^3 km^2-years)
Swetnam and Lynch 1993	455	Western spruce budworm	150 × 150	390	2925
Boulanger and Arseneault 2004	245	Spruce budworm	60 × 10	450	270
Morin 1994	242	Spruce budworm	120 × 240	200	5760
Speer et al. 2001	216	Pandora moth	20 × 5	622	62.2
Bouchard et al. 2006	170	Spruce budworm	60 × 80	180	864
Blais 1965	136	Spruce budworm	160 × 80	281	1348.8
Boulanger et al. 2012	115	Spruce budworm	60 × 100	400	2400
Weber 1997	90	Larch budmoth	30 × 20	571	342.6
Blais 1968	86	Spruce budworm	2000 × 500	138	13 800 000
Cooke and Roland 2007	63	Forest tent caterpillar	100 × 100	73	730

[a]Google scholar, accessed 2 November 2024.

was an empiricist, not a modeler. He was a dendrochronologist, not a time-series analyst. Blais worked without the benefit of geographic information systems, statistical software, or an established framework for spatiotemporal statistical ecology, which was only just forming (Moran 1948; Skellam 1952; Knox and Bartlett 1964). Digital archiving, too, was not yet practised. It is therefore not possible to replicate his work. It is not even entirely clear exactly how he delimited his (1968) "outbreak" extents, although there are significant clues in his earlier work indicating how he probably did this. Blais (1958) showed that inter-annual growth suppressions on the order of 20%–50% on either fir or spruce tended to occur 2–4 years after the onset of visible defoliation and 1–3 years after the onset of severe defoliation. Blais (1954) showed that this "first year of suppression" during an 1860s outbreak did not occur synchronously across northwestern Ontario. When the year of initiation was mapped with isolines, it indicated a smooth radial expansion of the outbreak from an epicenter over the years 1866–1872. The cumulative area experiencing at least one year of suppression would thus constitute the extent of the "area of outbreak" during that time interval. This method is likely what he used to generate additional regional-scale maps in later studies (Blais 1961, 1962, 1964, 1965), which were then consolidated in his remarkable 1968 presentation. Table 2.

Blais' (1968) final outbreak maps—hand-sketched in black-and-white (Fig. 2)—introduce a cognitive bias to the casual viewer. The visual presentation, with solid black denoting outbreaks, dashed lines for outbreak-free areas, and thick black strokes outlining political boundaries, inadvertently reinforces a human cognitive preference for pattern consistency, rather than the irregularity Blais aimed to highlight.

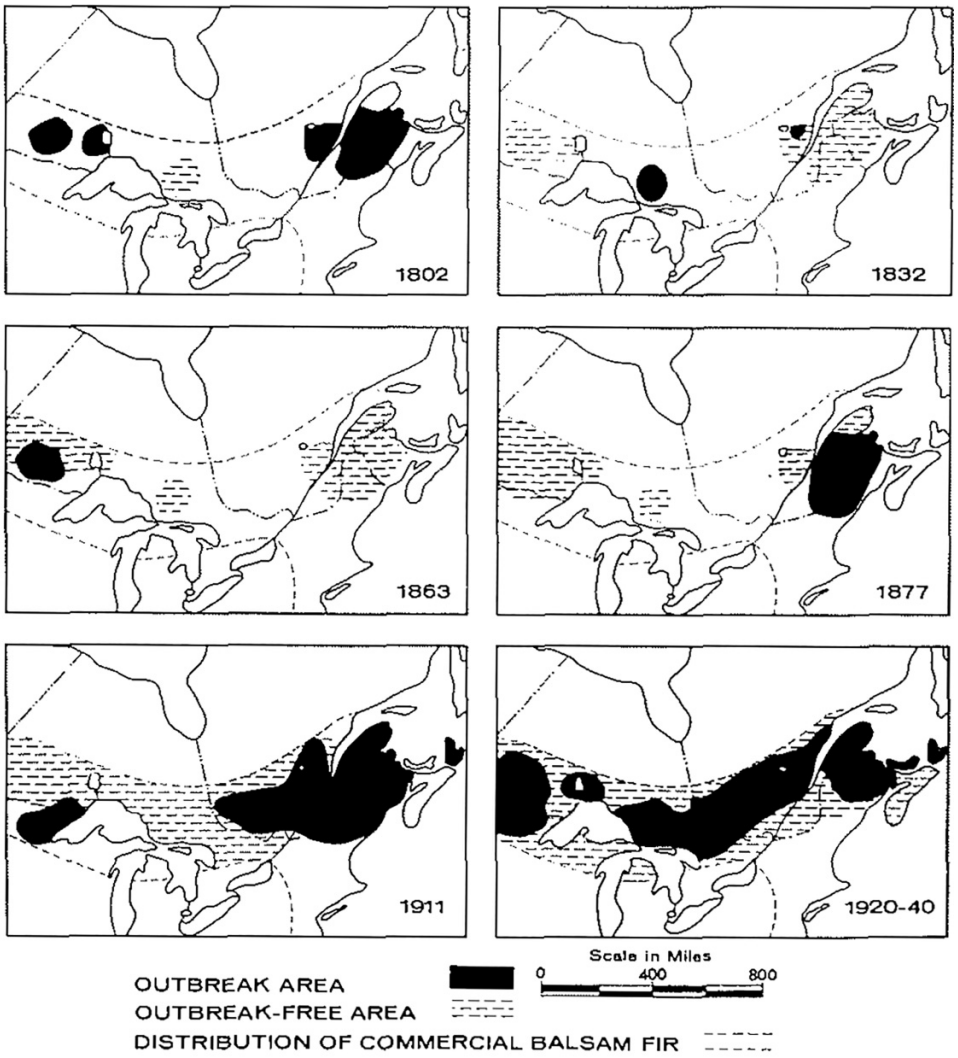
To reassess Blais' conclusions with contemporary methods, we digitized and rasterized his maps in QGIS (v.3.36.3), applying a color-coded system (Fig. 3):

- Red: outbreak present.
- Blue: no outbreak.
- Cream: areas affected by the "historical effect" (under-sampling bias).
- Transparent/white: no sampling effort.

Assigning quantitative values (+1, −1, 0, NA) enabled an unbiased statistical analysis of outbreak patterns. Digital rasters were summed cellwise across time intervals in R (v. 4.4.2; R Core Team 2024) and submitted to correlogram analysis (Bjornstad 2022). The digitized rasters confirm Blais' original observation: outbreak presence and absence follow a latitudinal belt-like pattern, consistent across six historical intervals. However, outbreak frequency is markedly higher in Quebec, Maine, and the Maritime provinces, compared to Ontario and the Lake States. Summing outbreak presence across the six interval rasters (Fig. 3, bottom) reveals a clear longitudinal gradient. In Québec and New Brunswick, summed outbreak values rarely exceed two, reflecting alternating outbreak presence and absence. In Ontario, summed values rarely exceed zero, suggesting outbreaks seldom persist through successive cycles. Minnesota emerges as an outlying epicenter that contrasts with the overall gradient, although it is not clear why, according to Blais—whose raw data were never archived—there was an absence of evidence for outbreaks in Minnesota during the first four intervals 1802–1877. Overall, this method of summation clarifies Blais central point about the importance of the dashed "outbreak-free area"—areas the outbreak has skipped over for some reason. These areas that are skipped cover large swaths of space and time. These "skips" are what are responsible for the "regional variation" in outbreak patterning. Blais central argument is that because of the lack of systematic patterning in space and time one cannot predict if an area will be skipped or not. But it appeared to him that the areas being skipped were shrinking. Blais (1968) also stated, without supporting quantitative analysis, that:

> *"The degree of intensity and the extent of one budworm outbreak can influence the time of occurrence of the next one. If an outbreak is prolonged and extensive, it will cause greater and more wide-spread mortality of mature fir than if it is of short duration or restricted in size. Since a second outbreak is not likely to develop within an area until it is reoccupied by mature fir, it will take longer before this condition is realized in an area where mature fir stands were destroyed than in one where the stands were not so seriously affected."*

Fig. 2. Reprinted from Blais (1968) with permission from *The Forestry Chronicle*: his fig. 2 map of the extent of six distinct outbreaks of the spruce budworm in eastern North America, based on interpreted tree-ring records.



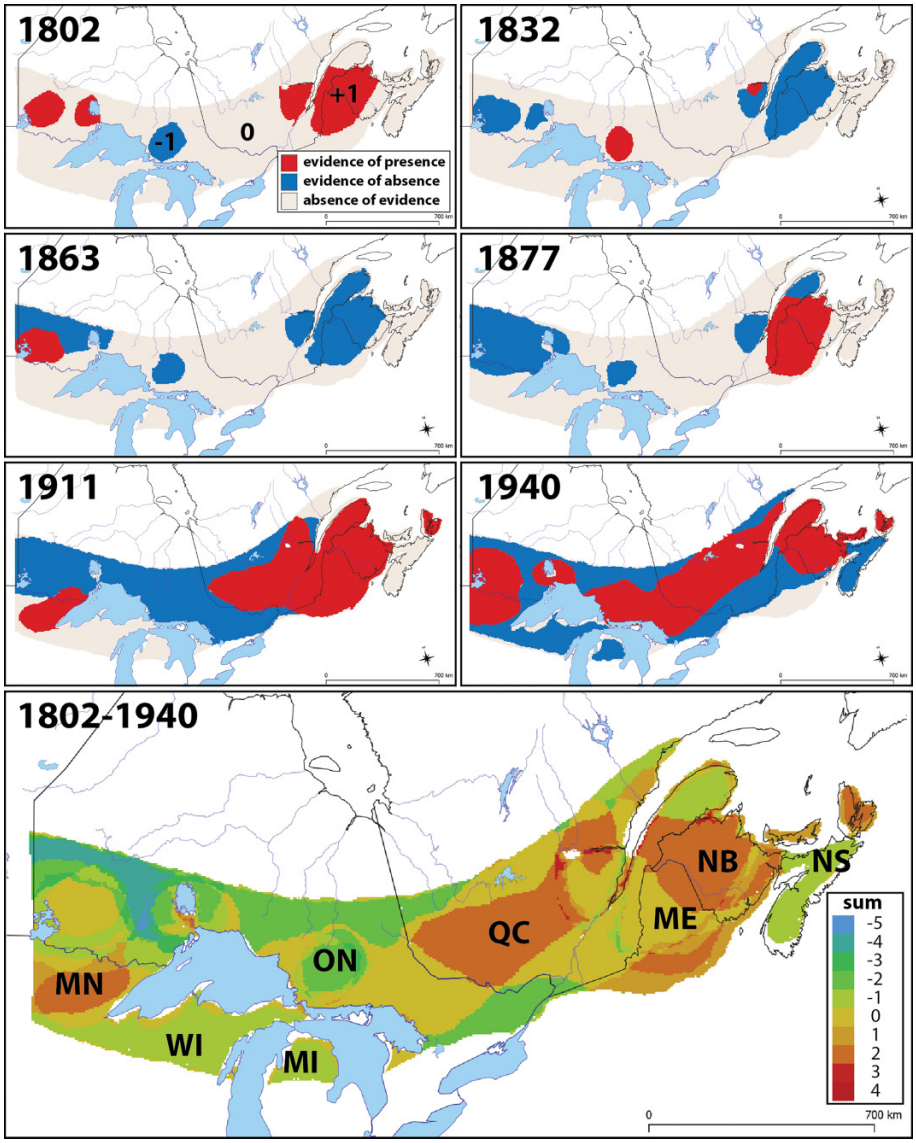
There are insufficient data to determine whether this skipping behavior is caused by an absence of hosts from outbreak-caused mortality, or from fire, or from something else. But the areas skipped are extensive, suggesting it may not be any one factor alone.

Avoiding the pitfalls of pattern cognition, we used correlation analysis to statistically test whether spatial patterns of one outbreak could predict the next. Spearman correlation between outbreak maps across successive intervals averages −0.02, ranging from +0.40 (1877 vs. 1911) to −0.74 (1802 vs. 1832). The lack of consistent spatial repeatability supports Blais' claim that future outbreaks cannot be reliably predicted from past ones. In particular, the large-scale gradient in budworm impact that emerges at the slow timescale, 1802–1940, 138 years, is not evident at the faster timescale of individual outbreaks, ∼23 years, where regional-scale patchy structures are more evident. Today, we can use correlograms to quantify the gradient structure at the slow cumulative timescale and the patchy structure at the faster timescale (Fig. 4).

Correlograms for individual outbreaks show a rapid decline in correlation as distance increases from 0 to 400 km, after which correlation values largely stabilize or truncate (Fig. 4, top panels). The spatial extent of outbreaks varies considerably, ranging from 250 km (1940 outbreak) to 900 km (1877 outbreak). Beyond this range, long-distance correlations behave inconsistently—sometimes turning negative (suggesting a broad-scale gradient structure), sometimes remaining near zero (indicating patchy regional outbreaks), and occasionally rising back to positive values (suggesting a "dish" structure with distant areas following similar patterns).

When outbreak frequency is aggregated across 138 years (1802–1940), a smooth spatial gradient emerges (Fig. 4, bottom), with significant correlation extending up to 800 km and strong negative correlation beyond 1000 km. This shift confirms that while individual outbreaks display fragmented, regional-scale patchiness, long-term outbreak dynamics form a coherent longitudinal gradient that only becomes apparent with century-scale data accumulation. Blais did not use

Fig. 3. The fig. 1 data of Blais (1968), digitized, rectified, rasterized, re-coded, and collated. Cells in red patches are coded as +1, blue patches as –1, cream as 0, transparent as "NA". Figure was created using QGIS version 3.36.3 and assembled from the following data sources: Province boundaries from ESRI Data & Maps "province.shp" layer (vendor: DMTI Spatial Inc.; https://www.esri.com, accessed 2026–01–06); Lakes features from ESRI Data & Maps ("World Lakes" dataset; publisher: ESRI; https://www.esri.com, accessed 2026–01–06); base map courtesy of ESRI shapefiles © ESRI.



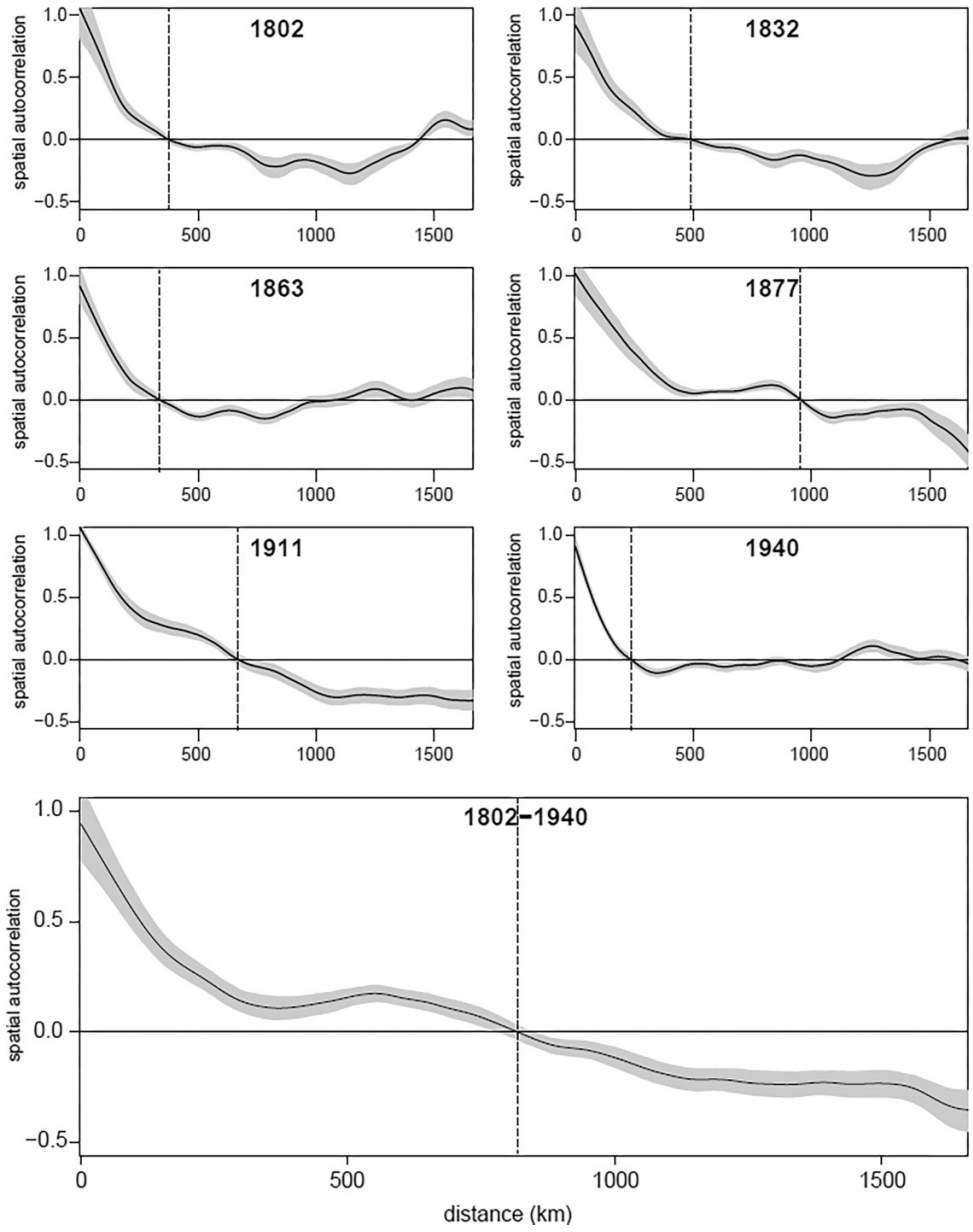
this language of spatial statistics, yet he was clear as to the surprising complexity—the "regional variation"—revealed in the data.

Blais argued that human-driven changes in forest composition, particularly the proliferation of balsam fir, were amplifying budworm impact. His emphasis on balsam fir was justified by the fact that it is the most vulnerable of the hosts to mortality given defoliation, followed by white spruce, red spruce, and finally black spruce, which is comparatively invulnerable (Blais 1985*b*). Our correlation analysis between Blais' outbreak data (Fig. 3) and the coarse-scale balsam fir distribution he documented (Fig. 5) yields a Spearman rank correlation of $r = 0.45$—supporting at least the contention that balsam fir abundance plays a role in aggregate outbreak behavior.

Given the strength of this result, it seems a puzzling oversight that in their retrospective summary of 50 years of research, Buckner and Fettes (1974) mentioned Blais by name, yet concluded that little was known of spruce budworm infestation dynamics. While it is true that the factors affecting cycling behavior still hadn't been identified at that time, Blais had enough material to convincingly argue that fir abundance was driving long-term eruption dynamics.

Still, there were many unresolved questions. If balsam fir abundance explains long-term outbreak risk, what accounts for asynchronous patch dynamics at shorter time scales? Why do outbreaks (red) often fail to spread across surrounding regions (blue)? What stops outbreak expansion from epicenters (the smaller red polygons)? What terminates the population cycle in areas where there is still an abundance of

Fig. 4. Correlograms of the data in Fig. 4. Vertical dashed lines indicate the distances at which correlations drop to zero. Correlograms built using R package ncf running on a random sample of 1200 points from each 1116 × 2680 raster.



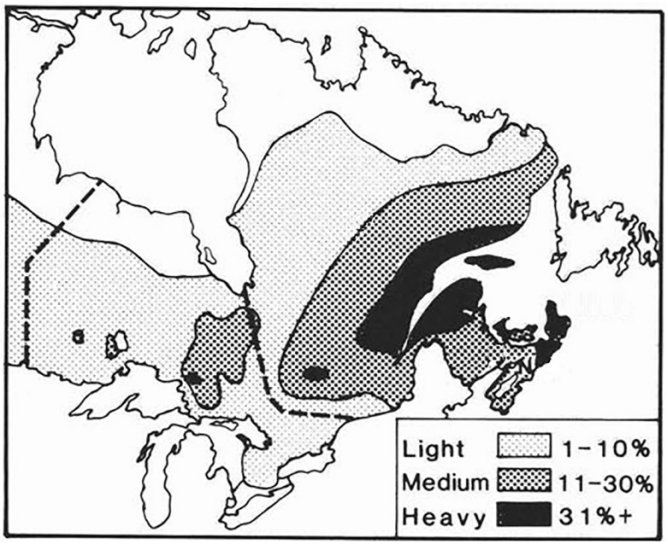
host trees on the landscape? What explains the large gaps where outbreaks fail to materialize despite suitable host conditions? To what degree does forest management affect these dynamics? The interplay between forest composition, climate variability, and local ecological resistance remained an open question—one that demanded further exploration.

Royama's Arc

After the publication of Royama (1984), Blais began to recede in prominence, as the top-down oscillatory hypothesis began to displace the bottom-up multiple equilibrium hypothesis (Fig. 1). The power of Royama's influence can be seen in the temporal pattern of citations of Moran (1953). Starting with the publication of Royama's (1992) "Analytical Population Dynamics", the number of citations of Moran (1953) began rising sharply, after 40 years of dormancy (Fig. 6).

The impact of this paradigm shift went well beyond spruce budworm and was felt broadly across the taxonomic spectrum (Ranta et al. 1997; Myers 1998; Peltonen et al. 2002). Here was a simple, universal mechanism that could explain the upscaling of herbivore impacts without appeal to any "catastrophe theory" that invoked huge numbers of dispersers causing a domino effect of traveling eruption waves due to nonlinear population growth dynamics. The Moran Effect was an exciting new paradigm that gave population pattern analysts and dendroentomologists a clear, pattern-focused hypothesis to target—one that could side-step detailed mechanistic considerations of what was

Fig. 5. Reprinted from Blais (1985*a*) with permission from *The Forestry Chronicle*: his fig. 3 map indicating the "population density of balsam fir in eastern Canada according to Halliday and Brown (1943)".



ultimately responsible for the cycling. Population ecologists, pattern analysts, and dendroentomologists began citing Moran (1953), following Nisbet and Gurney (1976), and, especially Royama (1992) and Swetnam and Lynch (1993) in the early 1990s.

Was it the academic fascination with cycle synchronization theory that led to the declining interest in Blais hypothesis? Blais (1983) has been cited 544 times, which ranks highly in spruce budworm ecology, though not as highly as the three most highly cited papers from the 1960s, 1970s, and 1980s dealing most squarely with the theory and data of the outbreak mechanism (Table 3). In this regard—past and contemporary interpretations of outbreak reconstructions that applied Blais' tree-ring methodology are particularly enlightening.

Quebec tree-ring data post-Blais

Despite being inspired by Blais' outbreak reconstructions via tree-ring analyses, a shift in interpretation of historical budworm outbreak dynamics emerged in the 1990s, coincident with the publication of Royama's (1992) formidable monograph "Analytical Population Dynamics" (Fig. 1). Starting with Swetnam and Lynch (1993), dendroentomologists increasingly reported strong spatial synchrony in forest insect outbreaks worldwide. Jardon et al. (2003) commented on the complex periodicity and lack of synchrony in spruce budworm outbreaks in Quebec—a view that was aligned with that of Blais. However, subsequent studies on spruce budworm in eastern and southern Québec (Boulanger and Arseneault 2004; Boulanger et al. 2012) described consistent outbreak intervals (~40 years) and an enduring multi-century stability. This supposed stability contradicted Blais' (1983) assertion that outbreak dynamics were changing, with outbreaks becoming more extensive and synchronized due to human influence.

The contradiction could not be more glaring. The same split amongst spruce budworm population ecologists that Pureswaran et al. (2016) documented regarding the silviculture hypothesis, the multiple-equilibrium hypothesis, and the oscillatory hypothesis was now reflected in the forest dendroecology literature. In both cases, the idea of synchronized cycling of outbreaks was gaining traction through the end of the 20th century. Blais was being swamped; and yet it is not clear that he was being refuted.

Jardon et al. (2003) conducted one of the largest post-Blais tree-ring studies in Quebec (500 km × 400 km). Writing in French, they introduced the concept of "complex periodicity"—noting that the most recent three budworm cycles were highly synchronized, whereas earlier cycles were not. The source of this complexity, they found, was the early lack of outbreak synchrony and extreme variability in cycle amplitude. Jardon et al. characterized a "stable" 32-year outbreak cycle, but this stability applied far more to 20th-century data than to 19th-century records, a trend Blais (1983) himself illustrated (his Fig. 2). They reported: "*All series have a very strong periodic component that emerges at the first or second step of the analysis, varying between 25 and 38 years. This range in periodicities for epidemics is within the limits proposed by Royama (1984, 1992), which he estimates to be between 25 and 45 years.*" (Translated from French).

Curiously, Jardon et al. (2003) did not cite Blais (1968), despite clear study area overlap. At a glance, the two papers appear to reach opposite conclusions, but deeper analysis reveals an underlying agreement: the periodicity and synchrony that marks that 20th century was absent during the 19th century.

Indeed, this is an important commonality across all century-scale spruce budworm studies published before 2012 that has gone unnoticed. Blais (1983) suggested that the area experiencing moderate-to-severe defoliation by spruce budworm was not only periodic, but that the peak cycle intensity was rising through time. This rising trend in the extent, intensity, and synchrony of outbreaks between the 19th and 20th century was independently identified four more times. Bouchard et al. (2006) showed that cycle peak intensities in the per stem impact of spruce budworm on host-tree growth suppressions was rising from the 19th to the 20th centuries in southwestern Québec. Fraver et al. (2007) showed the same in Maine, that the 19th century was a time when outbreaks were poorly synchronized, often "missing" under the assumption of a cycling outbreak process. Finally, although Boulanger and Arseneault (2004) and Boulanger et al. (2012) reported stable, periodic, and synchronous outbreak behavior in eastern and southern Quebec, an overlaid comparison of these two datasets reveals that the cycling is less regular than initially implied (Cooke 2024*a*). The two datasets taken together indicate a rising level of periodicity, intensity, duration, and synchrony of outbreaks. Blais had already suggested that predictive modeling based on outbreak periodicity might be unreliable—and indeed, when tested formally, past outbreaks in eastern and southern Québec fail to provide sufficient regularity for forecasting

Fig. 6. Citations of Moran (1953) over time, indicating a 40-year lag between its publication and a sudden rise in citations after Royama (1984, 1992).

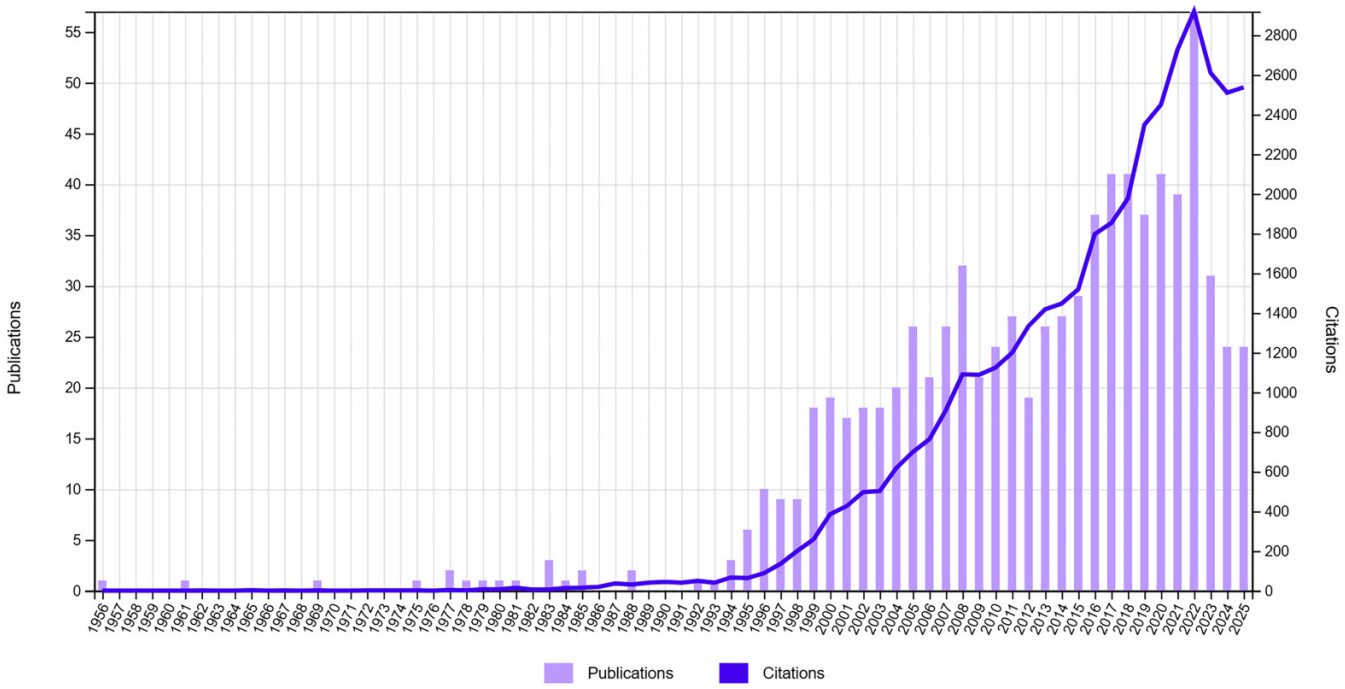


Table 3. The top 10 cited papers in spruce budworm population outbreak ecology.

Citation	Citations[a]	Title
Ludwig et al. 1978	1170	Qualitative analysis of insect outbreak systems: the spruce budworm and forest
Morris 1963	691	The dynamics of epidemic spruce budworm populations
Royama 1984	593	Population dynamics of the spruce budworm
Blais 1983	544	Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada
Régnière, St-Amant, Duval 2012	246	Predicting insect distributions under climate change from physiological responses: spruce budworm as an example
Boulanger and Arseneault 2004	245	Spruce budworm outbreaks in eastern Quebec over the last 450 years
Nealis and Régnière 2004	177	Insect host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest
Bouchard et al. 2006	170	Forest dynamics after successive spruce budworm outbreaks in mixedwood forests
Gray et al. 2000	126	Analysis and use of historical patterns of spruce budworm defoliation to forecast outbreak patterns in Quebec
Régnière and Nealis 2007	118	Ecological mechanisms of population change during outbreaks of the spruce budworm

[a]Google scholar, accessed 2 November 2024.

future cycles with precision (Cooke 2024*b*). As Blais noted: scale matters.

These revelations reinforce why Blais' 1968 study deserves renewed attention—his dataset was vastly larger in scale than all subsequent studies (Table 2), offering broader insights into regional variations. Yet, frequent citations of his 1983 summary paper have overshadowed the deeper insights of his earlier work—underscoring the need to revisit his original findings.

Validation from the Canada–US Border Lakes Landscape study

If Blais was correct that host forest composition influences outbreak dynamics, then this pattern should also appear outside Quebec—beyond the focus of most modern treering studies (Table 2). The Border Lakes Landscape Project, launched by the U.S. Forest Service in 2005, examined spruce budworm dynamics across Ontario and Minnesota, investi-

gating how mixedwood forest structures affected outbreaks over the 19th and 20th centuries. Project proponents predicted that budworm cycle intensity and synchrony would be conditioned by the amount of spruce and fir in the landscape. The results confirmed this: host-rich unmanaged forests saw increasing outbreak intensity and synchrony over time, while host-poor managed forests—especially in Minnesota—saw diminishing outbreak intensity and synchrony (Robert et al. 2018).

In sum, while the underlying outbreak cycle driver remains unresolved, budworm behavior is clearly modified at multiple spatial and temporal scales by forest composition and species succession. This conclusion gains further weight from comparative analysis with a different herbivore system in the same landscape, under identical environmental conditions (Cooke et al. 2024). In each defoliator species, forest host abundance drives outbreak patterning, providing empirical support for Blais' argument. Indeed, Cooke et al. (2024) introduced a formalized framework to more explicitly distinguish among the spatio-temporal patterns of anticipated under the competing paradigms of outbreak dynamics, and benefitted specifically from modern-day remote sensing technology not available to Blais. Such formalism serves as an important counterweight to the analytical rigor of Royama, suggesting that budworm growth and spread models must incorporate host forest condition and successional dynamics to remain testable in real-world conditions.

Comparison with alternative data sources

It is important to consider how dendroecological data of the type Blais collected align with other data sources, such as operational defoliation survey data and population data. Gray (2013) analyzed the 1941–1998 outbreak cycles over a 1.7 million km^2 area of eastern Canada, slightly larger than Blais' (1968) study. His findings confirmed that forest composition strongly shapes outbreak patterns. Gray accounted for both climate influences and forest composition, identifying the ratio of fir to spruce as the second-strongest explanatory variable (p. 1192): "*The abundance (m^3/ha) of the host has a significant influence on outbreaks, as suggested by many authors. Locations with higher volumes of the more vulnerable host group (balsam fir + red spruce + white spruce) experience longer outbreak duration and higher severity.*"

Gray did not cite Blais explicitly, yet his results independently validate Blais' core insights—defoliation surveys show the same host-driven outbreak dynamics Blais inferred via tree-ring data. Because their datasets span different time periods (Blais before 1940, Gray after 1940), this serves as a thoroughly independent confirmation of Blais' conclusions.

Blais' (1968) maps of presence/absence of outbreak did not support Royama's (1984) theory of spruce budworm outbreaks as a highly periodic process that was well-synchronized. But Royama's (1984) theory of cycling was based almost entirely on a single population sub-plot (G4), and his theory of spatial synchronization was based on just New Brunswick. In contrast, Blais (1968) study of tree-ring data was orders of magnitude more extensive (from Minnesota to Maine) than the base of data underlying Royama (1984). Blais' expansive tree-ring studies clearly highlighted regional contrasts in outbreak behavior. If spruce budworm outbreaks in eastern North America had exhibited consistent periodicity and high spatial synchrony in the 19th century, Blais (1968) would have noted it. His study was explicitly testing for such predictability. Instead, his findings emphasized regional variation, questioning the feasibility of long-term forecasting. Today, this paper remains undercited (86 times), falling short of inclusion in the most cited works in Table 3, despite representing one of the most ambitious feats of insect dendroecology (Table 2).

Population studies that span a significant swath of space and time are rare; however, Nealis and Régnière (2004) documented a 16-year spruce budworm outbreak (1983–1997) at Black Sturgeon Lake, Ontario—an outbreak lasting several years longer than the 1947–1958 Green River study (Morris 1963; re-analyzed by Royama 1984). This budworm population outbreak, which started just as Blais was retiring, was intense, causing 100% defoliation of balsam fir in 4 of the 16 years: 1984, 1989, 1990, 1993. By the end of the outbreak in 1997, so much fir had died that its basal area was reduced by 90%, as the basal area of trembling aspen, in response, more than doubled. Early larval mortality during dispersal consistently increased over time as the forest transitioned from fir-dominated to aspen-dominated (Régnière and Nealis 2007). The outbreak ended abruptly in 1997, rather than declining smoothly, in accordance with a predator–prey cycle as per Royama (1984). These findings suggest that Royama was not entirely wrong—natural enemies do play some role in terminating outbreak. However, the larger-scale population crash aligns more closely with Blais' perspective—forest structure fundamentally influences population growth rates and hence outbreak dynamics across multiple time scales, including the cycle itself.

Spruce budworm population studies since this time have continually shown an additional feature that is not consistent with Royama's oscillatory hypothesis, but is consistent with both the silvicultural hypothesis of Craighead, Blais, Baskerville, and Gordon, and the multiple equilibrium/epicenter hypothesis of Morris, Watt, Ludwig, Holling, Greenbank, and Hardy (see Fig. 1). Spruce budworm population recruitment functions are nonlinearly density-dependent at the low end of the density spectrum. This was shown in northwestern Ontario during the decline of the last outbreak (Régnière and Nealis 2007), in more recent experimental work (Régnière et al. 2013), and also in the Lower St. Lawrence region of Québec during the rise of the current outbreak (Régnière et al. 2019). It is the alternating phases of positive and negative density-dependent population growth and decline that generate the boom–bust dynamics of outbreak consistent with the idea of a bottom-up driven system, with natural enemies playing a significant, but secondary, modifying role. Moreover, Cooke and Régnière (2025) subsequently re-analyzed historical datasets from three widely dispersed locations in Canada (Black Sturgeon Lake, northwestern Ontario; Chapleau, northeastern Ontario; Green River plot G4, New Brunswick), concluding that spruce budworm outbreaks are ultimately triggered by an eruptive process that makes them resistant to the weak forces of phase synchronization—

an interpretation that conflicts deeply with that of Royama (1984, Royama et al. 2005, 2017), but is aligned with earlier theories (Morris 1963; Ludwig et al. 1978). This revelation does not just validate Blais' (1968) conclusion; it also validates his career path, to move from the study of natural enemies (1960) to focus on the long-term tree-ring research (1954, 1958, 1961, 1964, 1965, 1968) that revealed regionalized patterns of asynchronous eruption and spread.

Dispersal is central to both paradigms in explaining cross-scale dynamics and the emergence of large outbreak extents. However, Royama's cycle synchronization hypothesis suggests spatially correlated weather-driven dispersal losses throughout the cycle (high in some years, low in others, and random overall) tend to bring independently cycling populations into phase alignment, thus explaining the extent of synchronized outbreaks; whereas in the epicentre hypothesis, mass long-range dispersal of egg-bearing females is a direct trigger of nonlinear eruption, thus explaining the extent of asynchronously occurring outbreak waves. Validated dispersal models now confirm that long-range advection is common in spruce budworm (Sturtevant et al. 2013; Garcia et al. 2022). Meanwhile, modern genetic analyses confirm that genetic spatial structure is created during long endemic bottleneck phases—where mutation and founder effects dominate—and then destroyed, post-eruption due to mass migration (James et al. 2015). This proves that it is not just the males that are mass-advecting, but also egg-bearing females. The result is a pattern of spot eruption and spread that is consistent with how the current outbreak in Québec started (Bouchard and Auger 2014), how it spread (James et al. 2025), and indeed what Blais documented 70 years ago in northwestern Ontario (Blais 1954), precisely as Hardy et al. (1983) emphasized.

In summary, the tree-ring data, the defoliation data, and the population data all point to a common conclusion: (1) periodicity in the spruce budworm system is weak and complex, (2) synchrony is weak and variable, (3) spatial patterns are regionally variable and non-repeating, and (4) regardless what drives period eruption, host forest landscape structure affects outbreak cycle intensity, duration, extent, and synchrony. We emphasize that different data sources and different metrics all yield the same conclusion: the proportion of vulnerable fir in the landscape is affecting per stem population densities and their proxies, regardless if these proxies are measured instantaneously in time or at a point, or if they are aggregated through time or space. It does not matter how "outbreak" is defined; all analyses point in the same direction. So, while it is trivially true that host trees are necessary to support outbreak-level population numbers, these data together suggest that the proportion of vulnerable host is having an active effect, not a passive effect, on population growth rates, and thus every conceivable metric of any proxy of population density integrated at any spatial and temporal scale. That spruce budworm population growth functions are both nonlinearly density-dependent (Régnière and Nealis 2007; Régnière et al. 2019; Cooke and Régnière 2025) and host-dependent means that host forest landscape structure is powerfully influencing nonlinear cross-scale eruption dynamics.

Managing spruce budworm

If spruce budworm outbreaks are heavily conditioned by forest composition, then they do not follow the rigid momentum of a predator–prey cycle, where oscillations are difficult to disrupt. This suggests that silviculture should provide an effective long-term strategy for managing outbreaks. Miller and Rusnock (1993) declared the silvicultural hypothesis "fallen", yet subsequent empirical work has strongly reinforced the case that mixedwood management—incorporating hardwoods—can significantly reduce budworm impacts at local scales and impact outbreak behavior at broader scales (Kneeshaw et al. 2021; Cooke et al. 2024).

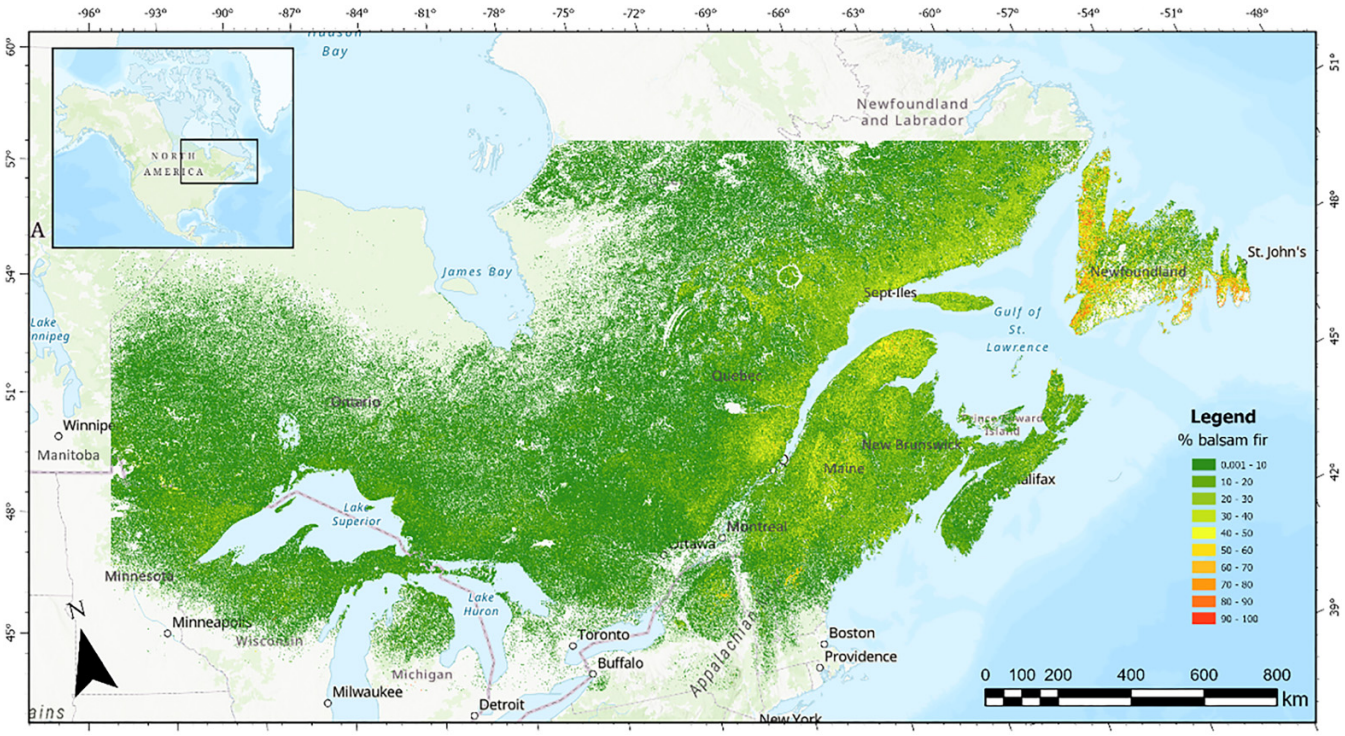
Nealis and Ortiz (1996) were the first to clarify how the presence of hardwoods in budworm-infested mixedwoods could (a) raise the mortality levels of dispersing larvae and (b) provide refuge for hardwood defoliators, fostering natural enemies that spill over onto spruce budworm populations. This theme was later expanded by Cappuccino et al. (1998), Campbell et al. (2008), and Zhang et al. (2018, 2020), amongst others. Cooke et al. (2007) illustrated how budworm cycles can be co-driven by (a) loss of host material at the outbreak peak, followed by (b) natural enemy control in the final years—exactly what happened in the 1980s outbreak in northwestern Ontario (Régnière and Nealis 2007). The silvicultural approach, once dismissed, now aligns with the budworm's own behavior: the "super silviculturist" spruce budworm (Baskerville 1975) has the capacity to promote diverse tree species regeneration, particularly after a series of stand-altering severe outbreaks (Sturtevant, unpublished manuscript). Blais (1983) warned against replacing spruce with fir, as it heightened budworm risk, but replacing fir with birch, aspen, or pine wherever feasible can diminish outbreak intensity, duration, extent, and synchrony.

If fir dominance drives outbreak risk, then assessing current balsam fir distribution is critical. Blais' (1985*a*) sketch map of balsam fir abundance circa 1970 can now be updated using modern remote sensing. Contemporary mapping reveals a significantly higher proportion of fir in the Maine–Maritime region than in the Minnesota–Manitoba Border Lakes region (Fig. 7)—consistent with Blais' earlier findings (Fig. 5). Notably, western and southern Newfoundland now exhibit proportionally high fir content, an area excluded from earlier assessments. These results suggest that Maine and Newfoundland could benefit from formalized pest risk assessments, given the ongoing spread of the current outbreak from Québec. Meanwhile, New Brunswick appears to contain less fir than in previous decades, though outbreak risk also depends on white and red spruce distributions and overall forest composition. Indeed, Blais (1985*b*) lists white spruce plantations among that current practices that contribute toward amplified outbreaks.

One last critical question remains: the role of insecticides in population management. Blais, in 1974, reasoned (p. 20) that:

> *"if the forest is kept alive through chemical treatment during a budworm outbreak, a second outbreak can develop in the same region in*

Fig. 7. Percent balsam fir in eastern North America. Figure was created using ESRI ArcGIS Pro version 3.3.6 using Canadian data from Hermosilla et al. (2022), and US data from Wilson et al. (2018). Administrative boundaries from ESRI Data & Maps (https://www.esri.com, accessed 2026–01–06).



a relatively short period of time, as is now the case in northern New Brunswick and the Gaspé Peninsula, where the first widespread application of insecticides against spruce budworm took place."

If budworm cycles are co-driven by host depletion followed by natural enemy control, indiscriminate insecticide use could prolong outbreaks indefinitely, especially if broad-spectrum insecticides suppress both budworm and its predators. A more sustainable and integrated strategy is to harvest protected timber quickly, to help promote dispersal mortality, which then reduces budworm numbers to levels where natural enemies can regain control. Modern insecticide applications in Québec and Ontario use narrow-spectrum bacterial treatments, deployed only in commercially viable stands nearing harvest—avoiding large-scale suppression of natural enemies. This aligns with Integrated Pest Management principles, reinforcing that forest management—not solely insecticide application—is essential for outbreak control (Blais 1974; Baskerville 1975; Gordon 1985).

Finally, it is interesting to consider what Blais would have made of relatively recent confirmation that spruce budworm populations exhibit nonlinear, eruptive population growth dynamics, not just during the current outbreak (Régnière et al. 2019), but even during the last outbreak (Cooke and Régnière 2025). This would suggest that outbreaks, on the front end, could be forestalled, at least in theory, even if they could not be altogether "stopped", by an "early intervention" strategy (Johns et al. 2019). His musings on the origin of outbreaks suggest that he would have marvelled at our modern ability to monitor budworm populations at pre-irruption densities across broad areas (Blais 1985*b*). Nonetheless, he concludes his review (p. 56) with the paragraph:

"Although much remains to be learned, we, nevertheless, possess a considerable amount of information on the budworm itself. It is the insect-forest relationship that still holds many mysteries. This is the relationship that is the most fascinating aspect of the budworm problem, and it is only when it is better understood, that a solution to the problem may be found."

Regarding the current outbreak, we surmise that Blais might well ask: *are we paying attention to the state of the forest in the course of our interventions*? If a population process is cyclic, then the absence of a cycle following insecticide intervention can be taken as proof that outbreaks are preventable. But if the population process is eruptive, then the absence of a cycle may simply indicate an absence of immigration at the levels required to trigger eruption. In the latter case, the forest condition will be a powerful determinant of the intensity and duration of the next outbreak, if and when it is triggered.

This is where "paradigms" really matter. If we assume that outbreaks are strongly periodic (cyclical), then we simply need to mitigate the outbreak via early intervention, and await the next "cycle" decades later. But if they are more eruptive in nature, then we must vigilantly suppress any emergent sources of moths as long as susceptible forest remains.

Conclusion

Budworm ecology has evolved under shifting paradigms, where different schools of thought—from weather to forest-driven to predator–prey cycling outbreak models—have guided interpretations of population dynamics over decades. Blais was convinced that balsam fir abundance was a key driver of spruce budworm outbreak intensity and duration, shaping differences in outbreak severity from Minnesota to Maine. While he did not explicitly speculate on fir's role in cycle amplitude and synchrony, he was not fully convinced that budworm populations exhibited a true cyclic pattern at any scale—except in aggregate trends.

The bulk of research conducted since his retirement has reinforced his perspective: mixedwood landscapes are less prone to budworm outbreaks than spruce–fir-dominated forests. While this relationship might be difficult to discern in any one short-term analysis, the evidence supporting this claim becomes overwhelming as data accrue over time and across studies. While natural enemies may influence budworm population cycling, the role of forest composition in modulating that cycling behavior cannot be dismissed; it shapes outbreak intensity, extent, and persistence across slow, intermediate, and fast time scales. Future budworm population risk models therefore must integrate forest dynamics into their frameworks.

When research paradigms or schools of thought oppose one another, the pressure to publish can sometimes conflict with the need for deep reflection. Blais exemplified a researcher willing to let the data shape his conclusions, rather than forcing observations to fit neatly into existing theories. His approach stands as a cautionary tale—a reminder that ecological complexity often resists simple answers and that careful synthesis requires patience. Future advancements in budworm ecology will depend not just on refining models, but on allowing space for critical reassessment and open dialogue.

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