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ARTICLE

Forest tent caterpillar (Lepidoptera: Lasiocampidae) across Canada, 1938–2001: II. Emergent periodicity from asynchronous eruptive anomalies

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Abstract

Using aerial sketch map data spanning more than 1 000 000 km^2 across Canada, I use cluster analysis to show that outbreaks of forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), through the 20th century have occurred regularly every decade or so; however, there are two distinct aspects to the patterning of outbreaks. The dominant mode of variability is a nonrecurring pattern of singular spike anomalies, lasting just a few years, that are regional in extent but are not synchronised across the country. The regional time series derived from cluster analysis that are dominated by these singular spike eruptions exhibit extreme skewness and kurtosis, are not stationary in mean or variance, and are not amenable to classical time-series analysis. Although these regional-scale eruptive anomalies tend to occur periodically in aggregate, their central location always varies in an unpredictable manner, resulting in aperiodic local behaviour. Range-wide periodicity is thus an emergent property from asynchronous, aperiodic eruptions aggregated across regions. The second mode of variability is a low-amplitude fluctuation of weak periodicity that is weakly synchronised across the country. These observations support a hybrid cyclic–eruptive theory of outbreak occurrence that is not consistent with the simpler idea of spatially synchronised cycling.

Introduction

The forest tent caterpillar, *Malacosoma disstria* (Hübner) (Lepidoptera: Lasiocampidae), is a recurrent defoliator of broad-leaved trees throughout North America (Sippell 1962). Trembling aspen, *Populus tremuloides* Michaux (Salicaceae), is the principal host tree species consumed by forest tent caterpillar larvae in the boreal forest of North America (Witter 1979). Over the period 1938–2001, forest tent caterpillar outbreaks across Canada have recurred periodically every decade or so; however, despite the regular periodicity of outbreak occurrence, the pattern of forest tent caterpillar-caused host forest decline appears to be rather episodic (Cooke 2024). Outbreaks that collapse after just one to two years of moderate-to-severe defoliation are typical (Cooke *et al.* 2009), and these appear to have no discernible impact on host forests (Kulman 1971; Hall and Moody 1994; Thompson 2000; Schowalter 2017). However, long-term forest health monitoring following the occasional outbreak lasting three years or longer of moderate-to-severe defoliation reveals consistent syndromic patterns of cumulative mortality that continue to grow years after the outbreak has passed (Batzer 1955; Ghent 1958; Churchill *et al.* 1964; Witter *et al.* 1975; Bauce and Allen 1991; Gross 1991; Payette *et al.* 1996; Candau *et al.* 2002; Brandt *et al.* 2003; Wood *et al.* 2009; Man and Rice 2010; Moulinier *et al.* 2013; Charbonneau *et al.* 2012; Perrette *et al.* 2014).

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Recurring outbreaks of forest tent caterpillar are conjectured to be the result of a deterministic host–parasitoid interaction (Cobbold *et al.* 2005; Roland 2005) that is subject to stochastic meteorological perturbations (Hodson 1941, 1977; Blais *et al.* 1955; Witter 1979; Cooke and Roland 2003). However, the duration of a given outbreak cycle appears to be determined by several factors, including climatic conditions (Daniel and Myers 1995) and a top–down/bottom–up interaction arising from the influence of forest landscape structure on the foraging and dispersal abilities of key members of the natural enemy community (Roland and Taylor 1997). On the one hand, forest fragmentation by commercial development in rural Ontario, Canada, tends to increase the duration of outbreaks (Roland 1993; Roland *et al.* 1998; Cooke and Roland 2000), making them, in theory, that much more impactful. On the other hand, in more intact, less-disturbed forest landscapes, rising host forest abundance tends to generate better-synchronised, higher-amplitude population cycling (Robert *et al.* 2020), thereby suggesting a second dynamical pathway by which host forest landscape structure could influence large-scale measures of outbreak duration and impact.

A key question that remains unanswered is how periodic population fluctuations caused by top–down and/or bottom–up trophic interactions are spatially organised to generate large-scale outbreaks. Coupled oscillator theory suggests that if populations are regulated identically and are therefore cycling at a common frequency, they may be readily brought into phase with one another by a so-called "Moran effect" if the random variables that influence population fluctuations are even mildly correlated amongst populations (Moran 1953; Royama 1997; Royama *et al.* 2005). An extension to this theory suggests that even if the populations are regulated differently by different suites of factors, any resulting differences in cycling frequency may be homogenised if these independently cycling populations are linked to one another through interpopulation migration (Barbour 1990). According to this theory, the more extensive the host forest landscape, the greater the number of dispersers amongst populations, the greater their rate of dispersal success, and the greater the dispersal connectivity between subpopulations.

However, at this point, a serious paradox emerges: if cycling populations of forest Lepidoptera are synchronised through spatially autocorrelated weather perturbations and/or interpopulation migration (Peltonen *et al.* 2002), why are outbreaks so difficult to forecast? Why do forest tent caterpillar outbreaks, when summed across decadal intervals, routinely fail to spread to cover more than 40% of the insect's outbreak range (Cooke *et al.* 2009)? Sturtevant *et al.* (2023) suggested that this is a central paradox in applied forest entomology: how populations that are supposedly cycling synchronously – like "clockwork," some have suggested (Bjørnstad 2000) – can result in "cross-scale" (*sensu* Holling 1973; Raffa *et al.* 2008) "catastrophes" (*sensu* Thom 1975; Ludwig *et al.* 1978; Rose and Harmsen 1981) with utterly unpredictable timing and extent. How do we reconcile such widely divergent models of forest insect population dynamics? Returning to the specific case of forest tent caterpillar outbreak dynamics: which of these paradigms is more applicable?

Sippell (1962) described the forest tent caterpillar in Ontario as periodic going back to 1834 and introduced the practice of numbering outbreaks using Roman numerals. In contrast, Hildahl and Reeks (1960) described outbreaks in neighbouring Manitoba and Saskatchewan as highly irregular and disputed the existence of predictable cycling. However, the two divergent groups from eastern and western Canada never combined their disparate regional data sets to take a national perspective on the question of whether the cycling was sufficiently regular to enable predictive forecasting. In a companion paper (Cooke 2024), I show that despite the overall periodic occurrence of short-duration outbreaks across Canada, large-scale host declines have occurred episodically in every part of the country in response to unusually long-lasting eruptive anomalies. In this paper, I take a spatially explicit view of the insect's historical pattern of occurrence in Canada and ask whether the patterns are as divergent between western and eastern Canada as commonly supposed and whether the regional-scale time series of outbreak occurrence are amenable to linear autocorrelation analysis and autoregressive modelling or whether the presence

of anomalously intense outbreak cycles violates the assumptions of stationarity and normality that are so pivotal to time-series analysis (Chatfield 2003). I show that, indeed, the regional time series are largely nonstationary, being dominated by singular spike anomalies that carry high skewness and kurtosis. And yet, despite the asynchronous occurrence of these spike anomalies, they nevertheless fall into a national-scale pattern sequence that, collectively, generates periodic outbreaks in aggregate. This is a mysterious pattern of spatial scaling that has never been reported before and may help to explain why divergent schools of thought have emerged and persisted on the nature and cause of periodic outbreaks. I speculate on factors that might be responsible for the spike anomalies and attempt to explain how these might be sequenced as to generate periodic behaviour in aggregate.

Methods

In a companion paper, I describe in detail the methods by which forest tent caterpillar outbreak activity in Canada has been monitored historically (Cooke 2024). In brief, each year, from 1938 to 1995, the Forest Insect and Disease Surveys unit of the Government of Canada used fixed-wing aircraft to map areas of moderate-to-severe defoliation of trembling aspen in each province. The identity of the defoliator was typically confirmed using a sparse and constantly varying network of spot ground checks. After 1995, survey responsibility in Canada was transferred to the appropriate provincial authorities, and survey methods began to change, especially after 2001, with the advent of modern digital technologies, including global positioning systems and recording "tablets."

In 2002, these data were assembled to create separate eastern and western Canadian databases, and in 2014, these were fused into a single database with annual national coverage for 1938–2001. Rasterised to a common resolution of approximately 58 km^2 per cell (equivalent to 7.6 km × 7.6 km, the resolution of archived spatial data in Québec, which serves as the limiting factor), these national-scale data, comprising 29 994 cells over 1 739 652 km^2, were submitted to a hierarchical cluster analysis using R package "cluster" (Kaufman and Rousseeuw 2009) in order to determine the dominant modes of variability in space and time. Hierarchical time-series cluster analysis works by identifying groups of pixels where time series are fluctuating in a similar fashion. It has been applied successfully to defoliation survey data in several cases in Québec (Cooke and Lorenzetti 2006) and Ontario (Cooke *et al.* 2012) and to tree-ring data from Alberta (Cooke and Roland 2018) and Ontario (Robert *et al.* 2020). The goal in the current paper was to determine whether periodic or aperiodic behaviour would dominate these patterns and whether the putative difference between western and eastern Canada stood up to formal scrutiny.

For the cluster analysis, I first used a stopping criterion of six clusters because six cycles (I–VI) were occurring in six major regions of Canada (Alberta, Saskatchewan, Manitoba, Ontario, Québec, and the Maritime Provinces) and, with six independent survey crews amongst regions, it made sense to determine if cluster time series tended to be distinguished longitudinally, being shaped by provincial boundaries and provincial survey methods, or latitudinally, as a function of biophysical gradient variables that span provincial boundaries. When I failed to observe strong periodic behaviour in the six derived clusters, I increased the number of clusters up to the point where periodic behaviour was finally observed at more localised spatial scales, matching earlier publications from eastern Canada on the subject (Cooke and Lorenzetti 2006; Cooke *et al.* 2012).

Violent, episodic time-series behaviour is not consistent with the cycling behaviour prescribed by the Royamian autoregressive modelling framework (Royama 1992) that has been used in a number of papers to describe the cyclic dynamics of forest tent caterpillar outbreaks in both western Canada (Roland 2005) and eastern Canada (Cooke *et al.* 2012). An important question to consider, therefore, in modelling such time series is whether they conform to the two most

important assumptions in time-series analysis: (1) the normal distribution of residual error and (2) stationarity in the principal parameters governing central tendency and dispersion (Chatfield 2003).

Strictly speaking, any process that is bound on the interval [0, 1] is, by definition, distributed nonnormally because the normal distribution is unbounded on either tail. This is unquestionably the case for a variable such as the proportion of cells defoliated in any given year, which cannot exceed 1 or drop below 0. However, most of the defoliation cluster time-series values from east–central Canada are dominated by fractional values below unity (Cooke *et al.* 2012). When autocorrelation models are fitted to these data, the residuals are often close to normal; that is, they largely do not egregiously violate this part of the normality assumption. On the other hand, some of the northern cluster time series do exhibit signs of an asymmetric distribution of values, with many zeroes during a long endemic phase and the odd sequence of values near unity during unusually intense epidemics. Autocorrelation models of such series do not lead to residuals that are normally distributed. Cooke and Lorenzetti (2006) considered these series to be nonstationary with respect to local mean and variance and thus ill-suited to time-series analysis. I therefore sought to examine the statistical attributes of western and eastern Canadian time series derived from regional cluster analysis.

One could argue that time series that exhibit rare and random spiking are not well characterised by the first and second moments alone, which deal with central tendency (mean) and dispersion (variance) in a process. In contrast, skewness is a quantitative measure of distributional asymmetry, and kurtosis is a quantitative measure of distributional "tailedness." These are the third and fourth moments of any process, comparable to the first and second moments, the mean and variance. When we require normality and stationarity of a process, we are requiring a constant mean and variance through time, but we are also requiring reasonably low skewness and low kurtosis throughout the series. These higher-order distributional assumptions often go unchecked.

I therefore calculated skewness and kurtosis for all of the derived forest tent caterpillar cluster time series across Canada (see Cooke 2024 for a detailed discussion of results from the 12-cluster model), to determine if this part of the normality assumption was seriously violated. These parameters were computed using the *skewness*() and *kurtosis*() functions from the R package "moments" (Komsta and Novomestky 2022). A high-order breach of the normality assumption would indicate an even more fundamental problem beyond the well-recognised requirement for stationarity in mean and variance. I predicted that many of the forest tent caterpillar time-series clusters would exhibit problematically nonnormal levels of skewness and kurtosis.

For comparative purposes, the aggregate time series for all clusters was compiled and submitted to the same analysis. I predicted that the aggregate series, unlike the disaggregated series, would be comparatively well behaved, with lower skewness and kurtosis, with regular periodicity evidenced in spectral analysis and autocorrelation function (ACF) analysis, and with low-order feedback evidenced in the partial ACF.

Finally, I computed pairwise correlations amongst all pairs of the regional time-series clusters in order to determine if and how regular cycling in aggregate might give way to asynchronous eruption (marked by high skewness and kurtosis) at the regional scale. All analyses were conducted using R, version 4.2.3 (R Core Team 2023).

Results

As expected, the aggregate mean time series for forest tent caterpillar across Canada in 1938–2001 exhibited six regular cycles, each one peaking to cover no more than 35% of the total area defoliated through time in any one year (Fig. 1A). Three of the cycles (I, IV, and V) covered less than 15% of the insect's outbreak range. Skewness, s, was 1.77 and kurtosis, k, was 6.36 in the
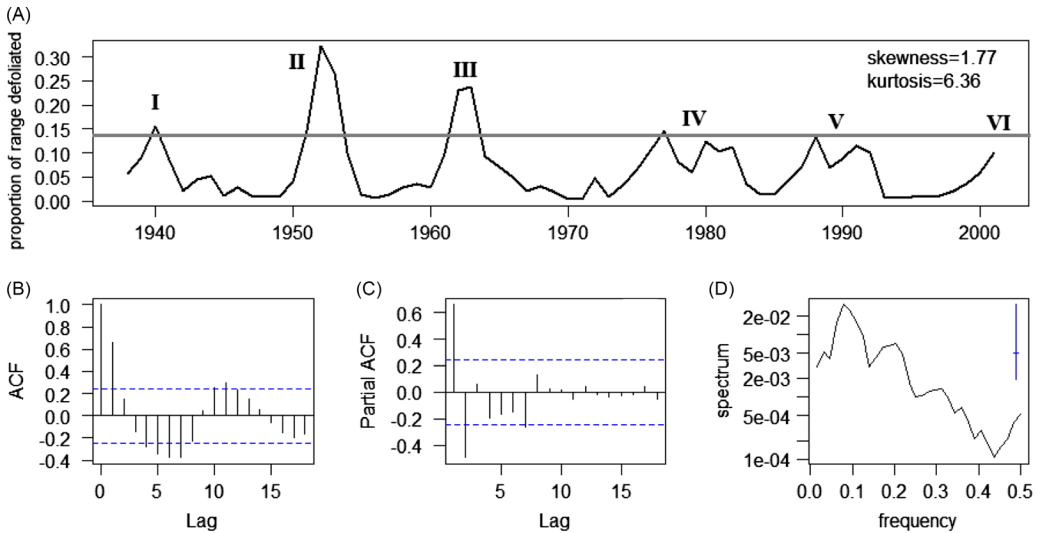
Figure 1. Analysis of the aggregate time series for forest tent caterpillar outbreak occurrence across Canada; skewness, $s = 1.77$; kurtosis, $k = 6.36$. Autocorrelation function (ACF), partial ACF, and spectrum indicating regular, low-order cycling are shown in **A**, **C**, and **D**. Horizontal line in **A** indicates where 14% of range is defoliated. Roman numerals in **A** refer to range-wide outbreak cycles.

aggregate time series. This is much higher than one expects for a sinusoid ($s = 0$, $k = 1.5$) but is as expected for a periodic pest data process that is suppressed through the population trough due to a lack of sensitivity of aerial surveys to low levels of defoliation. The ACF suggested an 11-year cycle (Fig. 1B), and the partial ACF exhibited significant positive and negative feedback at lags one and two, respectively (Fig. 1C). Spectral analysis confirmed a strong spectral peak at 12.8 years (Fig. 1D).

The sum area defoliated by forest tent caterpillar over the period 1938–2001 was 1 739 652 km^2, occurring mostly between Alberta and New Brunswick, with just trace occurrences in British Columbia, Northwest Territories, and Nova Scotia (Fig. 2A). However, the highest levels of defoliation – cells experiencing more than 20 years of outbreak over 64 total years – were concentrated in a few small areas less than 50 000 km^2 in extent, near Entwistle, Alberta, Dryden, Ontario, and Témiscamingue, Québec (Fig. 2A, red circles). The bulk of the country experienced less than five years of defoliation over this period, indicating a contagious, or clumped, distribution of impact. All six of the derived clusters were distributed across more than one province; however, the dispersion pattern of cluster assignments was highly clumped, with each cluster tending to focus on a specific region of the country (Fig. 2B). Cluster 1 focusing on cycle II in the early 1950s was somewhat more well dispersed across the country, with strong representation in Québec, New Brunswick, and Saskatchewan. The individual cluster time series (Fig. 2C) contrasted sharply with the aggregate pattern (Fig. 1): they were not periodic but were instead dominated by singular spike anomalies that often spanned more than 80% of a given cluster (Fig. 2C) and were a source of significant skewness (mean $s = 4.0$, standard deviation $= 0.5$) and kurtosis (mean $k = 21.2$, standard deviation $= 4.3$).

Periodic behaviour was not observed in individual clusters until the number of clusters was raised to 12, thereby reducing the average size of clusters by one-half and thus increasing the opportunity to detect rare, localised behaviour (Supplementary material, Fig. S1). At this point, the 12th and smallest cluster (but still quite large: 862 cells, 50 000 km^2), located in northwestern Ontario, exhibited a pattern of skewness, s, and kurtosis, k ($s = 1.5$, $k = 3.8$) similar to and lower than the aggregate ($s = 1.77$, $k = 6.36$). The other time series – that is, the six-cluster classification – exhibited
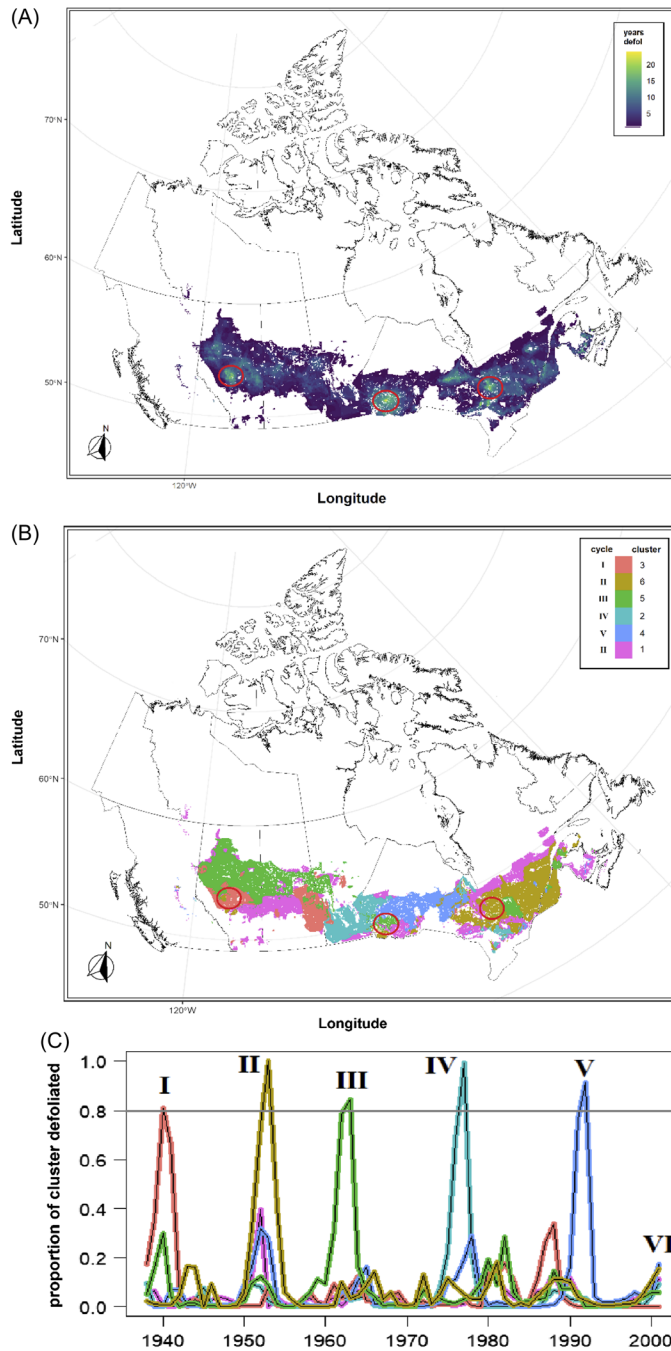
Figure 2. A, The total number of years of defoliation by forest tent caterpillar, **B**, the six-cluster map, and **C**, the six-cluster time series of proportion of cluster defoliated. Red circles **(A, B)** outlining "hot spots" where defoliation exceeds 20 of 64 years are 50 000 km^2 in extent. The colour legend in **B** also applies to **C.** Horizontal line in **C** indicates 80% of cells in a cluster defoliated. Cluster time series in **C** aggregate to the range-wide time series of Fig. 1A. Roman numerals I–VI associated with anomalous eruptive pulses in **C** match those of cycles in Fig. 1A. *Note*: cycle VI had started only in 2001 and does not affiliate uniquely with any one cluster.

much higher levels of skewness and kurtosis, making them ill-suited to time-series autocorrelation analysis (Supplementary material, Fig. S1). Eight of the 12 clusters exhibited extremely high levels of skewness and kurtosis ($s > 4$, $k > 20$), all arising from a single spike – a single outbreak of anomalous intensity and extent occurring just once in a series and within a brief one- to four-year interval. Skewness and kurtosis were highly correlated amongst the 12 clusters ($r = 0.98$); the more a series was dominated by a single spike, the more nonnormal its condition was. These series cannot be considered stationary in mean or variance because the autocorrelation information contained during the brief outbreak spike is distinct from the autocorrelation information contained during the long endemic phase of the remainder of the series.

Notably, all of the spikes that were the source of high skewness and kurtosis aligned closely with outbreak cycles in aggregate (Supplementary material, Fig. S1, black lines for individual clusters *versus* grey line for aggregate series). Although individual spikes in the regional clusters tended to align with one of the six national-scale cycles, I–VI, the degree of correlation between regional cluster time series was low (mean = 0.10, median = 0.02; histogram in Supplementary material, Fig. S2). Patterns in clusters 2, 4, 6, 7, and 12 did not correlate highly with any of the other clusters. The five time-series pairs that did exhibit correlations greater than 0.5 were 1 *versus* 8, 3 *versus* 5, 3 *versus* 10, 5 *versus* 10, and 9 *versus* 11. The other 55 cluster pairs exhibited correlations well below 0.5. Eruptive spiking behaviour was thus highly asynchronous between clusters. If the five years surrounding each of the spike anomalies were removed from the analysis, the mean correlation between time-series pairs doubled to 0.20, indicating a significant rise in cycle synchrony.

Discussion

Although forest tent caterpillar outbreak cycling is weakly synchronised across Canada, the spike eruptions that dominate its major regions are not; these tend to be regional, not national, in distribution (Fig. 2B). Their central location varies unpredictably, and they do not recur periodically within regions but, rather, across regions (Fig. 2C). This complex behaviour is inconsistent with the primary prediction of coupled oscillator theory of the emergence of spatially synchronised cycling (Royama 1992). It is somewhat consistent with the generalised catastrophe theory of insect outbreaks (Holling 1973; Ludwig *et al.* 1978) that has been postulated for forest tent caterpillar (Rose and Harmsen 1981); however, it is even more consistent with a hybrid cyclic–eruptive theory of outbreak occurrence (Sturtevant *et al.* 2015) because, despite the asynchrony of the aperiodic eruptive spikes, they nevertheless emerge according to a periodic schedule.

Whether we use a six-cluster model (Fig. 2) or a 12-cluster model (Supplementary material, Fig. S1) to characterise forest tent caterpillar outbreak dynamics across Canada, the patterns are qualitatively similar and the interpretations do not change. Indeed, the high pairwise time-series correlations that occasionally resulted from coincident spiking across the 12-cluster model are what led to six clusters being the natural basis for the grouping of clusters into broader regions. Increasing the number of clusters from six to 12 revealed just one small region in northwestern Ontario (50 000 km^2; <3% of the insect's outbreak range) where the dynamics were periodic. This area lies at a nexus where a number of distinct clusters swirl together (Fig. 2A *versus* 2B), implying that fluctuations here are borderline periodic/aperiodic and synchronous/asynchronous. These cells may be assigned one way or the other, depending on the density of the cluster model. If the insect were cycling regularly and synchronously across Canada, one would expect a larger size and number of such clusters.

In a study of just Québec (384 540 km^2 of area defoliated), the use of a nine-cluster model for that one province alone (384 540 km^2/9 clusters = 26 222 km^2/cluster) revealed three locations (Abitibi, 41 000 km^2; Témiscamingue, 14 000 km^2; Estrie, 25 000 km^2) where the insect was cycling somewhat regularly but with amplitudes that were not sustained through time (Cooke and Lorenzetti 2006). Across Canada (1 739 652 km^2 of area defoliated), raising the number of clusters higher than 12 (1 739 652 km^2/12 clusters = 144 971 km^2/cluster) reveals additional periodic

behaviour; however, the total area exhibiting periodicity increases very little because increasing the number of clusters decreases their average size. The occurrence of asynchronous spike anomalies that cover tremendous areas – 74 000 to 236 000 km^2 in extent – tends to dwarf any localised periodic behaviour occurring at scales less than 50 000 km^2 in extent. Detecting clusters of periodic behaviour that are as small as 26 222 km^2 on average over an area of 1 739 652 km^2 would require a 66-cluster model – a density of clusters that could fairly be criticised as a "fishing expedition." Isolated instances of somewhat periodic behaviour can be detected if one searches hard enough for it.

The complex pattern of weak periodicity, weak synchrony, and asynchronous regional-scale anomalies constitutes relatively weak support for the clockwork theory of outbreak occurrence and relatively strong evidence for the catastrophe theory of outbreak occurrence, consistent with inferences from fine-scale tree-ring studies of trembling aspen defoliated by forest tent caterpillar in Alberta (Cooke and Roland 2023) and northwestern Ontario (Cooke *et al.* 2024). The fact that two modes of variability were detected – with low-amplitude cycling that is so weakly synchronised that it is dwarfed by regional-scale eruptive anomalies – supports a hybrid "clockwork–catastrophe" theory of outbreaks (Sturtevant *et al.* 2023) that combines elements of Royama's (1992) clockwork theory of harmonic oscillation and Holling's (1973) catastrophe theory of relaxation oscillation.

Time-series autocorrelation analysis methods that seem to work well for short series of population data in central Alberta (Roland 2005) or longer series of defoliation data in much of east–central Canada (Cooke *et al.* 2012) appear to apply well to the aggregated national-scale data (Fig. 1) but are ill-suited to the disaggregated data representing the asynchronous regional-scale patterns of outbreaks in 97% of the insect's outbreak range in Canada (Fig. 2B). This, too, is inconsistent with Royama's (1992) theory of insect outbreaks as an emergent feature of spatially synchronised population cycling. Outbreak patterns west of Ontario are dominated by single spikes of prolonged outbreak that rise at unpredictable times and are not correlated amongst the various regions (Supplementary material, Fig. S3). These eruptions collapse just as quickly and are not seen again in the period studied (Fig. 2C). This wildly anomalous eruptive behaviour is characterised by extremely skewed and kurtotic distributions of defoliation intensities (Supplementary material, Fig. S2). In fact, examples of such wild behaviour can also be found throughout the eastern provinces. Stable cycling appears to be the exception, not the norm, in the whole of Canada.

Even in that small part of northwestern Ontario where, using a 12-cluster model, forest tent caterpillar outbreaks occur with regular periodicity once a decade (cluster 12, Supplementary material, Fig. S1), the skewness and kurtosis values greatly exceed the expectation for a sinusoid. This is attributable to the low level of sensitivity of aerial defoliation sketch mapping to defoliation occurring below the 50% detectability threshold (Cooke *et al.* 2022). Between cycle peaks, when defoliation is not being detected, populations may be cycling smoothly through a trough but at a low enough level that no cyclic variation is observed. This leads to an accumulation of zero values between outbreak cycles, resulting in highly skewed distributions as a baseline. The additional skewness and kurtosis observed in the more spiked series (clusters 1–11) are not attributable to survey insensitivity: they are a real product of insect population dynamics. Clusters 1 and 2, for example, resulting from a late-1970s anomaly focused in central Manitoba and an early-1950s anomaly focused in northern Québec (for maps of the 12-cluster partition, see Cooke 2024, Supplementary material, Fig. S1), exhibit skewness levels of $s > 5$ and kurtosis levels of $k > 50$. These anomalies cannot be dismissed as mere provincial survey errors nor as isolated incidents because they have extensions into two disparate parts of Ontario and they occurred 30 years apart from one another. Different survey crews in different decades are independently observing the same anomalous pattern of rare spike eruptions. In sum, it appears that such anomalously intense eruptions are a regular feature of this species' population dynamics.

That forest tent caterpillar outbreaks are highly periodic in aggregate across Canada (Fig. 1) might be seen as lending support to the Royamian framework used so successfully by Roland (2005) for short-term population data over a 400-km^2 grid in Alberta in 1993–2005 and by Cooke *et al.* (2012) for longer-term defoliation data for 1938–2001 across Ontario and Québec. On the other hand, the disaggregated regional-scale data reveal a high degree of nonstationary behaviour (Fig. 2C) that would suggest this framework may be inappropriate for local use in most of the insect's range. The bulk of the cluster time series are too skewed and too sharply tailed – because of a serious inhomogeneity of some nature in the outbreak-generating process – to be treated with standard time-series methods such as autocorrelation analysis.

Much of academic forest entomology focuses on the cause of synchronous population cycling. Yet it appears that the mysterious departures from synchronous normality are what really require explanation. The regional patterns of anomaly dominated endemic cycling are highly asynchronous despite the appearance of regular cycling at the national scale (Fig. 2). This is reminiscent of the so-called "skipping behaviour" of forest tent caterpillar outbreaks observed in trembling aspen tree-ring records from central Alberta (Cooke and Roland 2023): pulse eruptions that are phase-synchronised with some larger-scale cycling process but which have much higher intensity and which shift about asynchronously from one area and interval to the next as if some local ecological memory effect were regulating cycle amplitude. Apparently, this asynchronous behaviour occurs at the smallest and the largest of spatial and temporal scales. This raises the questions: "what is responsible for generating such wild anomalies that dwarf any cycling and are able to firmly resist the many forces of synchronisation?" and, spatially, "how can populations go so readily from stable and innocuous cycling in one area to wicked anomalies that cause large-scale forest decline in the rest of the country?" Until now, we were not aware these were the questions that needed answering. We were under the illusion that the pertinent question was "what synchronises independently cycling forest tent caterpillar populations?"

A careful scan of the six-cluster partition in Figure 2 provides some guidance as to some potentially fruitful approaches to these more pertinent questions. In the six-cluster model (*i.e.*, Fig. 2B, C), clusters 3 and 6 associate with spike anomalies during cycles I and II, peaking in 1940 and 1953 in the southern boreal region of the prairie provinces and of central Québec, respectively. Meanwhile, clusters 5, 2, and 4 associate with spike anomalies during cycles III, IV, and V, peaking in 1963, 1977, and 1992 in the northern boreal region of Alberta–Saskatchewan, of Manitoba, and of Ontario, respectively. This effectively constitutes two longitudinal, belt-shaped waves of cyclic pulses travelling west to east in the direction of prevailing winds, with the first wave, 1938–1957, occurring before and positioned more than 100 km to the south of the second wave, 1958–1995. It is possible that the northward shift between the two longitudinal belts is a product of climate warming. Next, the regional spike anomalies within each longitudinal wave tend to occur during a time when populations in northwestern Ontario are peaking, even though the anomalies are centred hundreds or thousands of kilometres to the west and east. This could be a result of ordinary synchronised population cycling caused by moth migration if there is also an additional effect caused by, say, local forest or weather conditions that tend to amplify local cycling within the anomalous zone but do not unduly affect northwestern Ontario. A regional-scale attenuation of natural enemy numbers could also result in intense eruptive spikes that are effectively disequilibrium transients that require a decade to equilibrate.

A clue to the origins of the spiking behaviour may lie in the history of forest landscape disturbance across Canada. In western Canada, homesteading, selective harvest of spruce, fire suppression, and bison extirpation during the first quarter of the 20th century all may have contributed to a rapid rise in trembling aspen hosts available for forest tent caterpillar (Bird 1961; Strong 1977; Campbell *et al.* 1994). In eastern Canada, clear-cutting of spruce, outbreaks of spruce budworm (*Choristoneura fumiferana* Clemens) (Lepidoptera: Tortricidae), and spruce budworm salvage logging, all of which favour stand conversion to balsam fir, *Abies balsamea* (Linnaeus) Miller, or trembling aspen, reached their peak in the last quarter of the 20th century (Carleton 2000; Girona *et al.* 2023).

The purple and gold clusters 1 and 6 (Fig. 2B, C) emphasising the 1952–1953 spike anomaly of cycle II in central Québec would appear to be an exception to this formula, but different patterns and timing of development and industrialisation in that Québec region provide a likely explanation. The Catholic Church was actively colonising and industrialising that area at the turn of the century (Ryan 1966), with a much stronger rural forest and agricultural economy occurring there than across the provincial border in Ontario (McDermott 1961). The resulting clear-cut conifer harvesting on the Québec side left a legacy of superabundant aspen that preceded the same effect in Ontario for several decades (Cooke et al. 2006). All of these colonial industrial economic forces may have restructured the forest landscape in a way that created pulse-ready, cycle-amplifying pockets of host trees that could generate enemy-free disequilibrium eruption dynamics.

This speculative scenario depends critically on the existence of some periodic source of migrating moths to generate the asynchronous spike eruptions, and yet I found little support for this possibility because it is not realistic for a single 50 000 km² area in northwestern Ontario to serve as a source of gravid females for areas 200 000 km² in extent located 1500 km to the east and west. On the other hand, as discussed previously in the present paper, increasing the number of clusters in the model will identify smaller areas of cycling behaviour that lie below the radar of a six- or 12-cluster model. In fact, the small areas where defoliation is most frequent tend to lie at the interface of multiple cluster boundaries, near places such as Entwistle, Alberta, Dryden, Ontario, and Témiscamingue, Québec (Fig. 2A, red circles). The cells in and around these areas are ambiguous in their near-periodic behaviour and therefore are readily separated from the nonstationary spiking patterns of clusters 1–6 (Fig. 2B, red circles). Regardless, three widely dispersed sources of moths may be insufficient to generate periodic anomalies that collectively span the country. It is possible there are more than these three multiple-cluster interface areas because aerial sketch mapping data carry two negative biases that tend to attenuate the intermediate-to-low-density population signal and could be a source of diminished periodic signal: (1) aerial sketch mapping tends to miss defoliation occurring below the 50% detectability threshold (Cooke et al. 2022), and (2) this miss rate is heightened as the concentration of trembling aspen in the landscape decreases (Cooke and Roland 2007). The use of population and tree-ring data instead of aerial sketch mapping data could yield a greater representation of periodic and synchronous behaviour across the landscape and, thus, a greater number and size of periodic sources of M. disstria moths.

Supposing there are periodic sources of moths dispersed across the country in places where spike clusters meet and mingle, and supposing that these periodic dynamics occur below the detectability threshold of fixed-wing aircraft, it is then possible that when these cycles peak, the dispersing moths from these areas land in neighbouring areas tens to hundreds of kilometres away (Brown 1965; Cooke 2022), leading to spike eruptions in places where host abundance is abnormally high or natural enemies are abnormally low. These eruptive pulses might kill some of the host forests and render the surviving component nutritionally suboptimal (e.g., too high a concentration of leaf tannins and phenolic glycosides and thus conducive to malnutrition and the expression of infections by the microsporidian Nosema disstriae (Nosematidae) (Flaherty et al. 2024) and nuclear polyhedrosis virus (Baculoviridae) (Cory and Myers 2003). With the reduction in host forest cover and with severely reduced fitness parameters in the wake of the outbreak, perhaps these eruptive pulses are not seen again in survey data for an entire forest cycle.

Obviously, it is not possible with the limited data available to evaluate the degree to which spatially synchronised cycling is being heavily perturbed by disequilibrium forces operating from the top down (natural enemies) or the bottom up (host plant effects); it is little more than speculation. On the other hand, these data do provide an essential basis for contextualising any population or tree-ring study purporting to address the question. One cannot assume that spatiotemporal context does not matter to the patterns one will find in a population process study. These data clearly indicate that one study done at one time and place and in one ecological context is unlikely to yield a comparable result to another conducted at a different time and place and

under different circumstances. Each region tends to have its own peculiar dynamic pattern of outbreaks. Context therefore appears to matter as much as scale.

The distinction in views between Sippell (1962) in Ontario and Hildahl and Reeks (1960) in the Prairie Provinces on the periodicity of forest tent caterpillar outbreaks, alluded to in the closing paragraph of the introduction of the present paper, appears to hinge on the robust cycling observed in just one small location: a 50 000 km^2 area located in northwestern Ontario. Everywhere else in the country, populations do not cycle with high amplitude but with highly variable amplitude. The differing views of western *versus* eastern Canadian entomologists therefore appear to be rooted in a hybrid cyclic–eruptive dynamic that can be discerned only when the data are collated at a national scale over the course of six cycles. It is only at this large spatial and temporal scale that the periodic occurrence of nonrecurring eruptive anomalies becomes evident. Estimates of outbreak periodicity in the literature therefore appear to be highly context-dependent, varying according to the spatial and temporal scales used in sampling and the methods used to estimate periodicity.

Finally, although the focus of this paper is forest tent caterpillar, it is reasonable to ask whether similar patterns and processes might govern the dynamics of other major forest Lepidopteran species, such as spruce budworm. Cooke *et al.* (2024) showed that the sort of complexity described here at the national scale also occurs at finer spatial scales – even in northwestern Ontario, where periodicity and synchrony are maximal. Moreover, they showed that *M. disstria* and *C. fumiferana* exhibit the same qualitative responses to variations in forest landscape structure, with greater host abundance leading to more synchronous high-amplitude cycling. It is a reasonable expectation that spruce budworm cycling and spatial dynamics may be as complex as those of forest tent caterpillar, particularly as the large-scale, long-term patterns of outbreak can be quite distinct between regions (Berguet *et al.* 2021). This paper may serve as a template on what pattern responses to look for in long-term studies of any forest Lepidopteran species.

Conclusions

Over the period, 1938–2001, forest tent caterpillar populations in aggregate have tended to cycle periodically across Canada every decade or so; however, during each outbreak cycle, there has always been one location, somewhere in Canada, where the outbreak tends to be so extensive and so long-lasting that it runs into the next. In these areas, it is the anomalous spike in outbreak intensity during that brief interval that dominates the time series, leading to highly asymmetric and sharp-tailed distribution of defoliation intensity through time. These series are ill-suited to the standard methods of time-series autocorrelation analysis, violating the assumptions of normality of residuals and of stationarity in means, variances, skewness, and kurtosis.

It is perhaps not fair to categorically state that forest tent caterpillar outbreaks do not occur periodically or synchronously: during the long intervals when regional populations are not spiking eruptively, they do fluctuate with weak periodicity and weak synchrony. The level of synchrony simply appears to be proportional to the amplitude of regular cycling: both are low, lurking in the background, dwarfed by the occurrence of extensive pulse eruptions that do not recur, and yet are sequenced on a periodic schedule. It is not clear what role forest conditions, weather conditions, or the absence of natural enemies may play in driving synchronisation-resistant spike anomalies, but we now know that this is the question that needs answering.

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