

Variable synchrony in insect outbreak cycling across a forest landscape gradient: multi-scale evidence from trembling aspen in Alberta

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Abstract

Using multi-scale trembling aspen tree-ring width data from Alberta, we show that scaling has a profound influence on dendroecological inferencing. At all scales of sampling, there is a significant climatological signal whose strength is nevertheless superseded by the pervasive effect of insect herbivory. At the smallest spatial scale, $20 \text{ km} \times 20 \text{ km}$, we demonstrate a quasiperiodic pattern of sharp growth reductions and the existence of negative spatial correlations among successive outbreaks. At the intermediate spatial scale of $20 \text{ km} \times 80 \text{ km}$, we show that the period 1930–1963 was marked by extremely low correlations in aspen ring widths, with much higher correlations occurring both before and after, despite high variance in precipitation that might have caused ring widths to correlate under moisture limitation. At the largest spatial scale of the entire province, aspen ring widths in the boreal forest became decorrelated abruptly in 1916, after cycling synchronously for the previous 80 years. This occurred despite a warming climate that heightened moisture limitation. Something in the environment prevents some outbreak cycles from rising to maximum intensity and from spreading to maximum extent. This appears to be the key to better predictability and management of forest insects and forests at short and long time-scales.

Key words: forest tent caterpillar, insect dendroecology, outbreak periodicity, synchronization, trembling aspen

Introduction

Resources, such as food and shelter, are distributed patchily in space, affecting the dynamics of both animal population growth and movement (Wiens 1976; Baker 1978; Hanski 1999). In the case of northern forest insects, it is increasingly clear that many cycling Lepidopteran species are under the influence of spatial variation in forest structure (Johnson et al. 2004; Haynes et al. 2013), with host forest landscape structure determining parameters of frequency, severity, and extent of outbreaks (Robert et al. 2018). These effects of landscape structure on outbreak dynamics are layered on top of additional effects of weather variability and climate change on outbreak dynamics, resulting in a complex spatiotemporal mosaic of concomitant effects (Cooke and Roland 2000).

Forest tent caterpillar (FTC), *Malacosoma disstria* (Hbn.), is a periodic defoliator of broad-leaved trees throughout North America (Witter 1979). In eastern North America, FTC outbreaks cycle somewhat regularly with a periodicity of 13 years (Cooke et al. 2012, 2022). Curiously, FTC outbreaks in the prairie provinces of western Canada exhibit poorly synchronized, aperiodic fluctuations (Hildahl and Campbell 1975). Recurring outbreaks of FTC are thought to be the result of a deterministic host–parasitoid interaction subject to stochastic meteorological perturbations (Hodson 1977; Roland 2005). However, it is not clear to what extent each of these forces is responsible for induction of population cyclicity and synchrony, and whether they are responsible for local departures from perfectly synchronized, cyclic behaviour.

Roland (1993) showed that outbreaks of FTC in much of Ontario, over the period 1948-1984, tended to last longest in forests fragmented as part of agricultural settlement. Daniel and Myers (1995) showed that the cumulative spatial pattern of defoliation in Ontario was shaped by key climatic thresholds. Both climatic and landscape factors were essential to understanding the spatial distribution of defoliation in Ontario (Roland et al. 1998). In Alberta, Roland et al. (1997) and Roland and Taylor (1997) used short-term population data 1993–1995 to show that landscape influences dispersal patterns of FTC parasitoids implicated in cycling. Similarly, forest landscape structure directly affects the frequency of FTC population cycling over the course of a cycle (Roland 2005), potentially through its effects on parasitism-this in spite of severe winter weather acting as a significant perturbation influencing population cycle collapse (Cooke and Roland 2003).

Trembling aspen (*Populus tremuloides* Michx.) is the principal host tree species consumed by FTC larvae, and tent caterpillar defoliation is the major factor accounting for temporal variation in aspen ring widths, outweighing, by far, any effect of drought (Hogg 1999). Outbreaks of FTC can thus be inferred from careful measurements of aspen ring widths (Hogg and Schwarz 1999) and the presence of "white rings" (Hogg et al. 2002), although separation of entomological from climatic signal, based on ring widths alone, becomes difficult in drier environments (Cooke 2001).

Using trembling aspen tree-ring records from Alberta, Cooke and Roland (2018) addressed the long-term history of FTC outbreaks, demonstrating a curious switch in cycling behaviour at the start of the 20th century, from periodic and synchronous to aperiodic and asynchronous, coinciding with a latitudinal gradient in dynamic stability that matched spatial patterning in historical climate data. Such variable patterns in spatial synchrony were subsequently confirmed in Manitoba (Haynes et al. 2018), where, again using trembling aspen tree-ring data, both drought and surface radiation influence FTC outbreak dynamics. Just south of Manitoba, in Minnesota, both climate and forest structure influence trembling aspen tree-ring patterns (Itter et al. 2017), through indirect effects on defoliation by FTC and through direct effects on trees and tree competition. Finally, in the Border Lakes region of Minnesota and Ontario, spatial complexity in FTC cycling outbreaks based on tree-rings was associated variation in forest landscape structure (Robert et al. 2020): more aspen was associated with stronger synchrony. Collectively, these studies illustrate that context matters greatly in spatial landscape ecology: there are multiple factors affecting trees and insects simultaneously. Careful attention must be paid to both scale and ecological context when making inferences about which factors regulate which processes.

With this surge in interest in FTC landscape dendroecology, we revisit the Alberta trembling aspen tree-ring data of Cooke and Roland (2018). Here, we focus on the finer, meso-scale (20–80 km) structures not attributable to spatial variations in weather or climate, but which can only be attributable to a spatially asynchronous disturbance, such as insect outbreak. We focus on the southern aspen parkland subset of data to identify gradients in forest landscape associated with breakdown in synchrony of periodic growth fluctuations.

A central problem in dendroecology is the separation of climatological signal from entomological signal when using a single chronology. Sophisticated, process-oriented, causal mathematical models of tree-ring increment can be used to separate and quantify the two signal types. Haynes et al. (2018) emphasized such models for estimating independent effects in multi-causal systems. Itter et al. (2019) developed an ecological model of ring width response emphasizing cumulative effects of multiple interacting disturbances over a 10-year interval. Both studies focus on FTC effects in aspen tree-ring data from the Manitoba/Minnesota region of central North America. The modeling studies demonstrate that the greater the entanglement of environmental factors affecting tree growth and insect populations, the greater the challenge in estimating effects using statistical models of individual time-series data.

A complementary approach explored here is to use spatially extended sampling to differentiate entomological and climatological signals across environmental gradients. By sampling tree-rings in spatially extended networks across meso-scale (20–80 km) gradients in forest landscape structure, we sought to identify periodic ring width fluctuations not attributable to climatic inputs (which are aperiodic and synchronous at this scale), i.e., those of non-climatic, entomological, inputs. Our objective was to determine whether heterogeneous forest landscapes serve to desynchronize periodic fluctuations in FTC dynamics.

Methods

Radial increment was measured in 420 trembling aspen stems gathered from across Alberta at three spatial scales: municipal (20 km \times 20 km), regional (40 km \times 80 km), and provincial (400 km \times 400 km) (Fig. 1). Two or three stems were felled in each of 246 plots. A section was taken at the base of each tree. Sections were dried at 40 °C for several days, sanded, and polished. Annual growth rings were resolved using a 10–60 \times magnification stereo-microscope with a variety of light sources. Each ring was dated and measured to the nearest 0.01 mm using an ocular micrometer. Sectional chronologies were cross-dated by examining the crosscorrelation among ring width profiles, particularly with regard to high-frequency fluctuations in ring width. Detailed methods of sample collection, preparation, and data processing are presented in Cooke and Roland (2018).

Study design proceeded in stages, with the finest scale sampling ($20 \text{ km} \times 20 \text{ km}$) occurring in 1995, and the largest scale sampling ($400 \text{ km} \times 400 \text{ km}$) in 1999. Here, we use preliminary results from the finest scale to inform sampling at the two larger scales. The largest scale data were published first (in Cooke and Roland 2018) simply because results were the least difficult to interpret. Interpretation of the finer scale results required a lengthy foray into spatial FTC dendroecology in other, warmer and more humid, parts of the continent: Quebec (Cooke and Lorenzetti 2006), Ontario (Cooke and Roland 2007; Cooke et al. 2009, 2012), and Minnesota (Robert et al. 2020; Cooke et al. 2022).

The municipal-scale sampling at Cooking Lake was done over the same study grid of 128 sites described by Roland and Taylor (1997) and Roland (2005), wherein forest landscape structure had a strong influence on spatial patterns of parasitism of FTC, and on cycling dynamics. In the current study, we ask whether short-term landscape-driven variations in cycle-frequency (revealed in population data collected over tens of kilometres) would accumulate through time to reveal meso-scale structure in asynchronous dynamics in longer term tree-ring data. We reasoned that it should, but subject to the caveat that fine-scale variations in longterm dynamics might be suppressed through the synchronizing effects of dispersal and spatially autocorrelated weather disturbances at those meso-scales of 20–80 km.

Analyses of spatial patterns of precipitation in North America reveal correlations in long, annually aggregated timeseries typically exceed r = 0.9 inside of 50 km (Tabios III and Salas 1985) and r = 0.8 inside of 200 km (Groisman and Easterling 1994). We verified that spring precipitation and annual moisture in Alberta follow similar patterns of spatial correlation (Fig. SI1), supporting the supposition that annual precip-

Fig. 1. Sample locations in Alberta, with sampling done at three scales: a provincial grid (3×3 , 400 km \times 400 km), a pair of boreal–parkland ecotonal gradients (at Whitecourt and Drayton Valley, 20 plots each, over areas 40 km \times 80 km), and a municipal grid of 128 plots (at Cooking Lake, 20 km \times 20 km). Each square represents a sample of three trees. Forest regions redrawn from Rowe (1972).



itation across the 20 km \times 20 km study area likely exceeds r = 0.9. Instrumental records are not available for any place in Canada at such a fine spatial scale. However, instrumental records of total March–June precipitation at two points—Edmonton International Airport and Tofield (separated by 60 km, and each located 30 km west and east of Cooking Lake, respectively, Fig. SI2)—were 418 and 424 mm, respectively, in 1995, suggesting similar precipitation across the intervening 20 km \times 20 km grid.

A preliminary analysis of the fine-scale tree-ring data revealed strong phase-synchronization of growth anomalies consistent with synchronization by weather disturbances (e.g., Cooke and Roland 2003), but also a clear, and hitherto-unreported, amplitude decoherence—a systematic pulsating motion in the intensity of outbreaks that was not smooth like a traveling wave (as in Johnson et al. 2004), but choppy, such as a cycling process being periodically interrupted. These patterns are described further in the "Results" section. An initial examination of data from the 20 km \times 20 km grid (Cooke and Roland 2003) suggested examining outbreaks at a larger scale (40 km \times 80 km), a forest landscape gradient stronger

in contrast. To do so, we additionally sampled points in the fragmented and continuous forests surrounding Whitecourt and Drayton Valley (Fig. 1). Here, we ask whether amplitude decoherence observed at Cooking Lake over 20 km \times 20 km grew to even stronger patterns of phase decoherence at larger scales. We expected that a larger extent of sampling would not only allow for clearer contrast in forest landscape types, but also might reduce the number of female moths flying the full extent of the study area. This expectation was based on our 1994–1996 observations that female moths respond to forest conditions at localized spatial scales (Cooke 2022).

Finally, because Alberta is heterogeneous with respect to both forest and climate, it was decided in 1999 to extend sampling to the spatial scale of 400 km \times 400 km, using a 3 \times 3 grid of nine chronologies. We specifically sought to sample more humid (albeit colder) areas of Alberta where a drought signal might be weaker and not impinge on outbreak inferencing, a pattern apparent in the driest parts of the aspen parkland. These large-scale data were presented in Cooke and Roland (2018), focusing on the nature of the breakdown in periodicity and synchrony that occurred in the early 20th cen-

tury. We subject these data to a more complete spatial and temporal response function analysis, consisting of a multiple linear regression of ring width on indices of drought (March–June precipitation) and indices of insect abundance (based on Canadian Forest Insect and Disease Surveys (FIDS)) 1957–1998. Our objective was to evaluate the relative contributions of drought and FTC to aspen ring width fluctuations across the climatic gradient from the dry aspen parkland region to the northern boreal region. We predicted that strong phase coherence seen at 20 km \times 20 km scale would weaken considerably over an area 400 times larger, with mild amplitude decoherence at the finest meso-scale giving way to phase decoherence with a loss of synchrony at the largest macro-scale.

Macro-scale provincial data were subject to time-series spectral analysis as part of Cooke and Roland (2018). We showed a gradient of periodicity, with low-frequency FTC outbreaks every 20 years in the north (Dixonville and Fort Mc-Murray) and high-frequency outbreaks every 7–10 years in the south (Drayton Valley, Cooking Lake, and Frog Lake), with a mixed, multi-frequency pattern of FTC outbreaks in the central region (Whitecourt, Peerless Lake, Athabasca, and Conklin). In the current analysis, we use a moving wavelet analysis in a continuous-time data framework to further clarify the change in dynamics in the three longest chronologies (Whitecourt, Peerless Lake, and Conklin), originating in 1837. Our primary focus, however, is on time-series behaviour and spatial asynchrony in the aspen parkland region (Drayton Valley, Whitecourt, and Cooking Lake). We did not formally reconstruct the historical pattern of FTC outbreaks at these three parkland locations, as the analysis of the macro-scale tree-ring and climate data suggested that cleanly separating the climatic signal from the entomological signal might be difficult in this dry region. Rather, we sought to answer a more tractable question about the relationship between spatial variations in forest structure and spatial synchrony in raw ring- width fluctuations: could we identify periods where meso-scale ring width fluctuations were sufficiently asynchronous that they were not associated with a common climatic process, and therefore instead must be associated with an asynchronous biological process, such as insect outbreak?

Analysis of synchrony at the Whitecourt and Drayton Valley locations consisted of simply separating the two chronologies into paired sets: the first for sites in the "white zone" of Alberta-areas where private-land farming dominates land use, and where forest pest surveys are not generally conducted, the second for the "green zone"-areas where commercial forestry and forest land conservation dominate on public land, and where forest pest surveys are usually conducted annually. These chronology pairs, separated by roughly 40-80 km, were then compared by examining the pattern of correlation within pairs over time, to determine whether major growth reductions were positively correlated within the pair, or whether there were periods where correlations declined to zero. The latter would occur if outbreaks tended to bounce back and forth between the continuously forested ("green zone") versus the fragmented forest ("white zone") regions, but could not occur as a result of climatic inputs, such as drought, which are spatially autocorrelated over hundreds of kilometres.

Analysis of synchrony on the Cooking Lake data grid was more complicated, because the study area did not span a linear gradient of forest structure, but rather a network of sites across a more subtle U-shaped forest gradient, with fragmented forest on its east and west sides, and more continuous forest in the centre. We also characterized the spatial pattern of synchronization at Cooking Lake, because sites spanned a smaller area, only 20 km \times 20 km. The pairwise inter-series correlation coefficient is too blunt a tool to characterize spatio-temporal patterning in such a dense network, particularly when moths could readily disperse among sites.

Instead of separating Cooking Lake chronologies into two discrete cover classes ("green zone" versus "white zone"), and simply comparing inter-series correlations (as done for Drayton Valley and Whitecourt), we first analyzed the spatial pattern of synchronization independent of forest landscape, examining spatial correlations in growth both within growth reduction intervals and between them. By examining temporal correlations within intervals, and then spatial correlations between intervals, we determine whether outbreak intensities are regulated by some slow variable operating asynchronously in space, as this is one potential reason why outbreaks in Ontario and Quebec typically span less than 40% of the total area historically defoliated (Cooke et al. 2009). We then treated forest cover as a continuous variable, and analyzed the spatial correlation between interval impacts and forest cover. In doing so, we determine whether forest cover shapes spatial pattern of synchronization in interval impacts (as observed at the intermediate-scale analysis of Whitecourt and Drayton Valley).

In theory, growth reductions entirely attributable to climatic fluctuations, such as a drought signal, may produce a "red" spectrum with strong, positive, first-order autocorrelations, the result of so-called "physiological pre-conditioning" (Fritts 2012). However, if growth reductions result in a "pink" spectrum, characterized by an additional component of strongly negative second-order autocorrelation, it increases the chances that periodic growth signal is a result of a cycling herbivore population. We knew that the Cooking Lake study area was undergoing outbreak by FTC in 1993-1995 (Roland 2005), even though provincial pest data indicated limited defoliation in the area at that time. One limitation of aerial surveys of forest insect pests is they are insensitive to defoliation of trembling aspen below the detection threshold of 50%-a fact we suspected in 1995, and demonstrated later for Ontario (Cooke and Roland 2007) and Minnesota (Cooke et al. 2022), places where the entomological signal in trembling aspen is far stronger than the climatological signal.

For Cooking Lake, we conducted a time-series analysis of tree-ring widths, to detect periodic behaviour consistent with a periodic herbivore. Once established, we used R package *ampd ()* to identify cycle peaks and troughs (as in Cooke et al. 2022). A "growth reduction interval" was defined as the time between successive peaks. We then quantified (a) the pairwise correlation among time-series within intervals, and contrasted that with (b) the spatial correlation between suc-

cessive mapped intervals. If weather effects on trees and insects are spatially autocorrelated at this scale, and if FTC populations are perfectly synchronized at this scale, then correlations should be uniformly strong and positive. There would therefore be both phase coherence within intervals in the time domain (all areas experience similar defoliation during the same interval) and amplitude coherence between intervals in the spatial domain (the same area shows similar patterns in successive intervals). In such an ideal case, the recent past would prove to be a reliable indicator of the near future, useful for forecast modeling.

The average spatial pattern of growth reduction during each interval was analyzed for (a) spatial contagion, i.e., similarity in the magnitude of reduction across neighbouring sample points, and (b) spatial correlation with forest cover. Forest cover was measured from digital aerial photography as the proportion of pixels covered with forest at multiple spatial scales within neighbourhoods around sample points (212, 425, 850, and 1700 m; Roland and Taylor 1997). Centred in the aspen parkland region, this landscape is comprised of mostly trembling aspen, with balsam poplar (indistinguishable in aerial photography) as a minor component. Coniferous species are rare. We were not certain at what scale FTC and their parasitoids might respond to forest cover, and chose to examine correlations between interval impacts and forest cover, at multiple spatial scales. The mean distance between the 128 sample points on the 20 km \times 20 km grid was roughly 1700 m. If growth reduction in any interval was due to a weather effect, such as drought, then its spatial pattern should be less spatially autocorrelated than if caused by a contagious process such as insect outbreak. Spatial contagion was characterized for each interval using Moran's I, as a function of distance. We determined whether spatial patterns were dispersed broadly across the grid, or were more spatially restricted, and whether areas of heavier impact were more forested.

We were also interested in the statistical distribution of peak interval impacts (lowest mean tree-ring growth) during each interval. If growth reductions result from simple oscillating herbivore populations, then a unimodal distribution of peak impact intensities is expected (same severity each year). A more complex distribution of impact intensities would suggest complex causation—either more complex herbivore dynamics or more complex mosaic of causes. Either was considered possible because FTC in Alberta from 1957 to 1998 did not exhibit the periodicity seen in eastern Canada (Cooke and Roland 2018).

When our study was initiated, 1995–1999, there were no reports of such complex spatial dynamics in the cycling forest Lepidoptera. However, such patterns are now apparent for spongy moth (SM) (Johnson et al. 2005; Haynes et al. 2013, 2019, 2022). We considered at the time whether the suggested pattern of responses was robust and universal, and so sought to characterize the complex patterns more fully.

Results

At the smallest spatial scale (20 km \times 20 km), in the aspen parkland, growth reductions were sharp, complex, and quasi-



periodic (Fig. 2). Eleven growth reduction intervals were identified over the 80 years, ranging from 5- to 15-year duration (Fig. 2). Within-interval time-series correlations were positive (averaging +0.45), indicating high local synchrony via high phase coherence at the fastest time-scale (1-7 years). Between-interval spatial correlations were negative (averaging -0.45), indicating that peak growth suppression occurred in different places in subsequent outbreaks. Low amplitude coherence at the dominant frequency (7-10 years, an intermediate time-scale corresponding to the average interval length) represents a significant departure from perfectly synchronous behaviour. The distribution of ring width troughs was bimodal: four of the 11 were deeper than the critical 0.65 mm threshold, and seven higher (Fig. 2b). The periodicity of growth reductions was split between 7 and 10 years, with an ambiguous autocorrelation function (ACF) rising at a lag of 7 years, but failing to peak at a lag of 10 years (Fig. 2c), a partial autocorrelation function (PACF) that failed to truncate after the second lag (Fig. 2d), and a spectrum that included strong peaks at 10 and 7 years and a lower peak at 5 years (Fig. 2e). The degree of time-series correlation within intervals was also directly dependent on the depth of the intensity of the interval trough (Fig. 2f): the deeper the trough, the higher the synchrony.

Negative spatial correlation between successive growth reduction intervals was often the result of a single large area of growth reduction moving systematically between intervals (Fig. 3). The spatial pattern of growth reduction within intervals was variable in the degree of contagion exhibited (Fig. 4). Intervals 1, 2, 5, and 8 were generally patternless. Intervals 3, 4, 6, 7, 9, 10, and 11 exhibited positive spatial autocorrelation at short distances (10–20 km)—the patchy pattern of a contagious gradient. Some of these gradients were linear across the study area (intervals 4, 7, and 11); others were more U-shaped (intervals 3, 6, 9, and 10).

The spatial pattern of aspen forest cover was saddle-shaped (Fig. 5), resulting in positive spatial autocorrelations at both short- and long-distance classes and negative autocorrelations at intermediate distances (Fig. 6). The spatial patterns of ring width impact within intervals (Fig. 3) were correlated with forest cover (Fig. 5), but in a divergent way. The distribution of forest-growth-reduction correlations was bimodal. During six intervals (1, 2, 5, 7, 9, and 11), growth reduction and forest were positively correlated (greater reduction in heavier forest). During the other five intervals (3, 4, 6, 8, and 10), growth reduction and forest negatively correlated (greater reduction in lighter forest cover). The sequence of correlations formed a regular pattern. When one growth reduction event dominated a less-forested part of the study area (east and west), the next would dominate the more-forested area (north and south). This systematic motion in peak impacts accounts for the bimodal distribution of correlation coefficients, with modes centering on r = -0.2 and +0.1 (Fig. 7).

At the intermediate spatial scale of the aspen parkland, the period 1930–1963 was characterized by extremely low correlations in aspen ring widths and much higher correlations before and after this interval (Fig. 8). During the low synchrony period (1930–1963), there was no survey effort until 1957,

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Fig. 2. Patterns of radial increment measured at 128 plots over the Cooking Lake study area. The time-series was divided into 11 growth reduction intervals and time-series correlations computed for ring widths within intervals (squares, at mid-interval); spatial correlations were computed between intervals for mean intervallic ring widths (circles, at peaks). The horizontal line in (*a*) indicates 0.65 mm, the threshold at which 50% defoliation by forest tent caterpillar (FTC) commonly occurs in Minnesota (Cooke et al. 2022). Troughs occurring at or below this line are almost certainly a result of herbivory.



and hence no evidence of heavy defoliator activity until the large-scale outbreak of 1961–1963. Low synchrony occurred despite high variance in precipitation (Fig. SI3) correlated between sample areas, which therefore should have caused ring widths to correlate under a common moisture limitation. These patterns are consistent with sub-epidemic fluctuations in herbivore populations, whereby aperiodic pulses of low-intensity defoliation are associated with asynchronous patterns of growth reduction between land cover types—much as we illustrated on the municipal grid (Figs. 3 and 7).

At the largest spatial scale (400 km \times 400 km) of the entire province, response function analysis showed that precipitation had a positive impact on growth in all nine locations and was strongly significant (p < 0.01) at three locations (all in the aspen parkland: Dixonville, Cooking L., and Frog L.) and marginally significant (p < 0.1) at two additional locations (Whitecourt and Conklin) (Table 1). Defoliation had a significant negative impact on growth at every location except Fort McMurray, where no defoliation was officially recorded during the period 1957–1998. The negative effect of defoliation was weakest (p < 0.1) at Athabasca and Cooking Lake, where defoliation the previous year had a slightly stronger negative impact than did defoliation in the current year. Overall, the analysis supported the contention that most variation in aspen radial increment was due to defoliation by FTC.

Wavelet analysis of provincial-scale data indicated that aspen ring widths across the boreal forest region lost periodicity abruptly in 1916, after cycling synchronously for the previous 80 years (Fig. 9). The change in dynamics was dramatic, with mean inter-series correlations halving, from 0.32 to 0.15. We note that covariances were higher before 1916 than after, and the variances were also higher before than after. So: (1) the reduced level of synchrony after 1916 was associated with decreased variance not a rise, which, all things being equal, is expected given that an inter-series correlation is the ratio of its covariance to its variance, and (2) the lowered variance and lowered covariance after 1916 came despite a warming climate that should result in moisture limitation and increased coherence in the drought signal, common to all three chronologies. That the opposite was observed (reduced coherence in the drought signal) implies that something in the non-climatological signal changed, i.e., the dendroentomological signal. Notably, this provincial-scale 1916 decorrelation event occurred despite a warming climate that heightened the moisture limitation in trembling aspen in the **Fig. 3.** Mean radial increment measured at 128 plots (circles) over the Cooking Lake study grid, averaged over each of the 11 intervals in Fig. 2. Surfaces beneath plot data generated by inverse-distance weighting (power = 1.5).



parkland region, evident in an increasingly sensitive drought response at Cooking Lake after 1920 (Fig. SI4).

Discussion

Our study was constructed in stages, starting with 20 km \times 20 km (municipal-scale) sampling at Cooking Lake in 1995,

followed by sampling at the intermediate (regional) scale in 1998, and finally the largest (provincial) scale in 1999. To understand the key findings, it helps to review results in reverse order, starting at the largest spatial scale, where results are perhaps least surprising or contentious. To understand the more controversial and substantive results arising at the finest scale of observation—municipal grid at Cooking





Lake—it is necessary to jointly consider the full range of FTC dendroecology literature that emerged between Cooke and Roland (2003) and Cooke et al. (2022), so this discussion point comes last.

There is a ubiquitous climatological signal in Alberta trembling aspen—evidenced in ring widths that are moderately variable, but well correlated, and particular with March-June precipitation in the aspen parkland region (Dixonville, Cooking L., and Frog L.). This signal strength is nevertheless superseded, at all spatial scales, by pervasive herbivory by FTC. At all scales, ring width chronologies exhibit remarkably variable patterns of inter-series correlationsometimes highly positive, but often near zero-a pattern consistent with trembling aspen data from Ontario, where radial increment is far more limited by herbivory than by moisture availability (Cooke and Roland 2007). This speaks to an overriding influence of herbivore population dynamics dominating the dendroecological signal in trembling aspen. The most parsimonious conclusion is that patterns of decorrelation in growth in Alberta result from complex spatial dynamics of mobile herbivores-outbreaks that are only somewhat cyclic and only somewhat synchronized, and which often occur as localized pulses separated in space and time from the primary outbreak cycle.

Provincial-scale response function analysis indicates a strong drought signal in the aspen parkland of Alberta providing justification for not attempting to reconstruct outbreaks in that dry region, but rather to ask clear questions about spatial patterns of synchronization within and among growth reduction intervals-questions robust to the possible co-occurrence of a drought signal that cannot be separated from an entomological signal. Extending sampling from the drought-prone Cooking Lake region westward to the farmforest interface at Whitecourt and Drayton Valley was done to decrease the drought response signal and increase the likelihood of detecting a landscape effect on the entomological signal. Similarly, the decision to scale up once again to the provincial level was an attempt to further limit the influence of the drought signal, helping to put the Cooking Lake drought response in context. In fact, our 3×3 provincial sampling grid extended beyond the northern limit of recorded FTC outbreaks, and yet we saw evidence of outbreaks at Fort McMurray, in the form of narrow white rings (Hogg et al. 2002) in a time frame (1981–1982) where FTC outbreak was occurring across Alberta's boreal forest. This is further evi-

Fig. 5. The pattern of forest cover measured at 212 m across the 20 km \times 20 km Cooking L. grid (*a*). Large blue patches are the heavily forested Cooking Lake Blackfoot Grazing Reserve (CLBGR) and Ministik Hills Bird Sanctuary (MHBS).



dence that operational aerial surveys are insensitive to defoliation occurring below some threshold where impacts are nevertheless recorded in tree-rings, as in Ontario (Cooke and Roland 2007) and Minnesota (Cooke et al. 2022).

At the intermediate scale, at Whitecourt and Drayton Valley, major growth reduction events (1924-1925, 1968-1969, 1977-1982, and 1988-1989) coincided with large-scale outbreaks mapped after 1957 and were fairly well synchronized between land cover types (Fig. 8; green zone versus white zone). There were, however, extended periods (e.g., 1930-1963) when growth disturbances were of lower intensity; reductions were poorly synchronized between cover types. This asynchronous pattern of mild disturbance is consistent with the hypothesis of a low-intensity defoliation event where populations do not rise to the detectable level of 50% defoliation, but still exhibit some periodicity and impact on radial increment. Instead of being synchronous, these light disturbances bounce back and forth between land cover types, with slightly greater frequency in fragmented than continuous forests (Fig. 8). These episodes are (a) poorly spatially synchronized among plots, (b) difficult to detect aerially, and (c) produce only light impact in tree-rings-a pattern not identified in the literature when these data were collected, but which has since been reported for eastcentral North America (Cooke and Roland 2007; Cooke et al. 2012, 2022). The current study demonstrates that similar complexity in herbivore dynamics occurs in western Canada. Although these herbivore populations fluctuate somewhat periodically, the periodicity is complex and indistinct, and cycles are not spatially synchronized.

At the finest spatial scale of the Cooking L. grid, growth disruptions varied discretely between mild episodes where increment did not drop below 0.65 mm and severe episodes where increment dropped below this threshold. Despite this strong phase coherence *within* 5–15-year intervals (coefficients in Fig. 2*a* outlined with squares), there was strong amplitude decoherence resulting in negative spatial correlations *between* successive 5–15-year intervals, averaging r = -0.45 (coefficients in Fig. 2*a* outlined with circles). What explains this remarkable pattern of decorrelation within versus between growth reduction intervals?

First, it must be noted that such a pattern is inconsistent with the inference of diffuse, dispersed, abiotic causation (e.g., weather that is highly spatially autocorrelated at the scale). Impacts exhibit spatial contagion in most intervals, and correlate strongly with forest cover, sometimes positively, sometimes negatively, but rarely neutral. This is reminiscent of the pattern described for Drayton Valley and Whitecourt, and is, again, consistent with the hypothesis of a contagious biotic disturbance agent whose cycling is synchronous across land cover types when intense, but asynchronous when weak. Parsimony suggests the same cause in all three cases: a cycling herbivore, fluctuating with variable amplitude, and with slightly faster frequencies in fragmented forests than in continuous forests. As such, these os-

Fig. 6. Correlogram of forest cover mapped in Fig. 5. Filled circles indicate significant spatial autocorrelations.



cillations are not amenable to full synchronization over distances of 40–80 km. Even at shorter distances of 20 km, they are resistant to amplitude coherence. Weather effects, such as drought, cannot produce such complex meso-scale patterns and dynamic landscape responses in tree-ring data, but mobile herbivores can.

Are there any population data indicating forest insect populations actually behave this way? Hodson (1977) showed that FTC populations in Minnesota can peak below a density that causes 50% defoliation. These are not aerially detectable, yet still produce depressed ring widths between 0.65 and 1.0 mm (Cooke et al. 2022; Fig. 5). Higher frequency (5-7-year) fluctuations in wavelength are common in aspen tree-ring data in Minnesota (Cooke et al. 2022; Fig. 6), Ontario (Cooke and Roland 2007; Fig. 3), and Manitoba (Haynes et al. 2018; Fig. 2). These fluctuations are not tightly associated with major outbreaks of FTC, although there is often mapped defoliation nearby, as discussed for Fort McMurray 1981-1982. Individual outbreaks in Ontario and Quebec (Cooke et al. 2009; Fig. 3) always fail to extend over the full range of trembling aspen; the average extent of defoliation during a 10-15-year outbreak is only \sim 40% of the area historically defoliated. Similar failure of cycles of low amplitude to synchronize is apparent from tree-ring data from Ontario and Minnesota (Robert et al. 2020; Fig. 5).

Our meso-scale results from Alberta indicate that either environment or landscape prevents complete synchronization of herbivore population cycles, despite the theoretical synchronizing effects of dispersal and of spatially autocorrelated weather disturbances (Peltonen et al. 2002). The smaller the landscape area, the tighter the pattern of synchronization, consistent with dispersal controlling synchronization, and yet, even at the smallest scale, with just 1.6 km between sampling plots, amplitude decoherence remains, and successive growth reduction events skip discretely from one part of the study area to the next (Fig. 3). Something systematic is preventing outbreaks from expanding across the entire study area. Populations consistently collapse before they spread to their fullest extent. This is similar as noted in Ontario and Quebec (Cooke et al. 2009) where aerial defoliation data were used. Oscillations evident in aerial defoliation data from eastern Canada are seemingly not amenable to full synchronization, i.e., coherence in both phase and amplitude. The same is apparently true of tree-ring data in western Canada, so what is the common mechanism?

One obvious candidate is that fragmented forests—because they alter parasite hunting efficiency and dispersal—tend to produce faster, lower amplitude population oscillations than in continuous forests (Roland 2005), and the resulting difference in frequency is too great to be reconciled via the synchronizing effect of inter-population dispersal. Differential cycling was not yet demonstrated in 1995–1999, when our data were collected, but it was one hypothesis being explored.

A second possibility is that the effects of extreme winter cold—which is a significant consideration in Alberta FTC (Cooke and Roland 2003)—are neither density independent (as often assumed) nor spatially autocorrelated (as also often assumed), but are, instead, partly density dependent. In being **Fig. 7.** The distribution of forest-impact correlations measured in the 11 intervals defined in Fig. 2, with forest cover estimated around plots at six different spatial scales, from 53 m (For53) to 1700 m (For1700).



so, correlations would be lost as population that rises variably and slowly enough that the earliest rising elements can be forced suddenly to collapse, with these epidemic-phase populations suffering heavy mortality and the endemic populations lagging behind remaining relatively unaffected. This would happen if, for example, high-density populations compete intensely for the best-protected overwintering sites. For FTC, this is the case, where egg survival is best in the limited upper canopy and least in the abundant shrub layer that is vulnerable to frost pooling (Cooke and Roland 2003). Partial density dependence of overwintering mortality also occurs for SM, *Lymantria dispar dispar*, which also competes in-

tensely for low overwintering sites—on bark, insulated under snow (Madrid and Stewart 1981); Smitley et al. 1998; Nealis et al. 1999; Andresen et al. 2001). In outbreaks, the highest density SM populations suffer the greatest mortality from winter cold, and areas with endemic populations will largely be spared. The difference between the two species' overwintering biology is FTC's habit of laying egg bands in a single cluster around twigs in the upper canopy, and SM's habit of laying eggs in a single cluster on bark below snow. The similarity is that both are vulnerable to outbreakterminating winter cold, and both exhibit complex spatial dynamics. **Fig. 8.** Individual plot locations for forested (green squares) and fragmented (red circles) cover types at Whitecourt (top) and Drayton Valley (bottom), overlaid on 1:250 000 national topographic system (NTS) topographic maps (source: Natural Resources Canada) that show forest as green ("green zone") and clearing as white ("white zone"). Each map covers an area of 40 km \times 80 km. The distance between heavily forested and fragmented sample clusters is roughly 40 km in each case. Mean ring width chronologies for the four locations shown at centre. Intervals of low synchrony highlighted in yellow. (See Fig. 1 for the complete map of sites.)



A third possibility is the hypothesis that an unidentified, slow, "long-term memory" or "long-term persistence" process modulates herbivore population cycle amplitude. For example, persistence of a soil-borne pathogen, such as a nuclear polyhedrosis virus, has a lingering effect on repercussion cycles, or a lingering host-plant quality effect causes herbivore fecundity to stay low for 5–15 years while the forest recovers. Both "top-down" and "bottom-up" possibilities exist. In the top-down category, another possibility is long-lived generalist predators that build up during one cycle, and carry over to the next, some 5–7 years later (but no longer). Mobility of many candidate predators, including carabids, vespids, and birds, would allow them to quickly shift spatial distribution in response to food availability, and be less likely to linger in a way that could dampen early population growth in a subsequent cycle. Cycle amplitude modulation could also be caused by more distal elements in the food web, such as agents from the higher trophic levels. These are currently not known.

Identifying the agent responsible for the negative mesoscale spatial correlations in impacts among outbreak intervals should be a priority for forest insect ecology. Without

Table 1. Response function analysis of trembling aspen ring widths 1957–1998 regressed on defoliation, lagged defoliation,and March–June precipitation.

Municipality	Defoliation (s.e.)	Lagged defoliation (s.e.)	Precipitation (s.e.)	r^2
Dixonville	-0.122 (0.173)	- 0.519*** (0.173)	0.406*** (0.116)	0.49
Peerless L.	- 0.444*** (0.141)	- 0.178 (0.139)	0.130 (0.139)	0.23
Fort McMurray	0.000 (0.164)	0.060 (0.160)	0.162 (0.164)	-0.04
Whitecourt	- 0.398** (0.166)	- 0.255 (0.166)	0.220* (0.127)	0.34
Athabasca	- 0.461* (0.176)	- 0.110 (0.176)	0.205 (0.132)	0.29
Conklin	- 0.328** (0.146)	- 0.826**** (0.157)	0.317* (0.115)	0.48
Drayton Valley	- 0.365** (0.173)	- 0.396 ^{**} (0.175)	0.111 (0.121)	0.45
Cooking L.	-0.221 (0.141)	0.255* (0.146)	0.552**** (0.133)	0.36
Frog L.	- 0.331* (0.172)	- 0.614**** (0.172)	0.420*** (0.130)	0.31

⁻

****p < 0.001.***p < 0.01.**p < 0.05.*p < 0.1.

it, a "history repeats" hazard modeling heuristic leaves us in the paradoxical state where the worst possible predictor of the spatial distribution of meso-scale impacts during the next outbreak interval is what happened during the last interval. History does not repeat, and assuming it does results in incorrect predictions. It is an open question the extent to which this finding relates to other forest insect species, and at what spatial scales, but this would have obvious implications for pest risk assessment and forecasting.

Finally, trembling aspen has a reputation among dendrochronologists as a species whose ring widths: (a) do not correlate particularly well among sites and (b) exhibit a weak response to weather fluctuations. We show, however, that trembling aspen does indeed respond in a consistent manner to moisture limitation, but that this limitation alone cannot explain the asynchronous entomological signal arising from the complex spatiotemporal dynamics of insect herbivory. This appears particularly so with respect to the complex synchronization dynamics of quasi-periodic outbreaks by the FTC. We would not have come to this important conclusion had we not sampled the southernmost landscape, Cooking L., at a rate of 128 plots over 20 km \times 20 km (=0.32 plots per km²), and had we not upscaled our sampling on two occasions, first to capture spatial dynamics across a sharp forest-farm gradient (40 km \times 80 km) and second to capture temporal dynamics across an even larger boreal-parkland forest-climate gradient (400 km \times 400 km). This speaks to the dendroecological value in sampling at both high intensity and across a sufficiently large spatial extent. Sparse sampling hides important meso-scale structure, and limited spatial extents hide important parts of the environmental response surface. All dendroecology needs to be understood within a generalized framework of landscape ecology that is species specific: scale and context matter greatly, such that no study can go uncaveated.

Conclusions

Trembling aspen in Alberta exhibits complex patterns of periodic growth reduction frequently associated with mapped defoliation caused by FTC. Some growth reduction events are intense, well synchronized spatially, and coincide with easily mapped outbreaks of FTC. However, more than half of these growth reductions are of diminished intensity (drops between 0.65 and 1.0 mm), are not spatially synchronized, and yet do not rise above the defoliation detectability threshold of 50% defoliation. If growth reductions were the result of a drought signal common to all sites, these lowintensity events would be synchronized among sites, but they are not. They most likely result from sub-epidemic population fluctuations that peak before attaining the threshold for detection over large areas.

Indeed, the breakdown in spatial synchrony at all spatial scales, from meso to macro, is associated with the forestfarm interface. The more complex the landscape, the more complex the cycling and synchronization dynamics of these growth reduction events. If, as in the Whitecourt and Drayton Valley plots, the forest landscape contrast is stark enough, and the distance between sampled cover types is sufficiently large (>40 km), ring widths show long periods of complete decorrelation. If, as in the Cooking L. plots, forest landscape contrast is weakened due to intermingling of cover types, and distance across sampled cover types is small enough (<20 km), ring widths will not go through any periods of temporal decorrelation, but may nevertheless exhibit amplitude decoherence, whereby successive growth reductions attain maximum impact in disparate parts of the study area, i.e., spatial decorrelation. In neither case would we describe the growth reduction episodes as "synchronized". The Whitecourt and Drayton Valley growth patterns were uncorrelated 1930-1963 because they were decoherent with respect to cycle phasing. The Cooking Lake growth patterns were correlated because they were coherent with respect to cycle phasing, but decoherent with respect to cycle amplitude, causing systematic movement of the growth reduction epicenter. Strong synchronization requires both phase coherence over fast time-scales (within intervals) and amplitude coherence over intermediate time-scales (between intervals). The latter, however, does not seem to occur anywhere in the FTC's range in North America. Nowhere do cycles ever grow in intensity to reach their potential extent defined by host availability.

Fig. 9. Ring widths in the three longest chronologies at Whitecourt (W), Peerless Lake (P), and Conklin (C), compared to wavelet power spectra. Note the abrupt decorrelation and loss of amplitude variance, covariance, and periodicity at 1916. Horizontal line in top frame is the 0.65 mm threshold below which growth reduction is likely a result of >50% defoliation by forest tent caterpillar (FTC).



Spatial ecologists studying periodic outbreaks of forest insects often begin with the notion that outbreaks are spatially synchronized. This is a useful starting point for thinking about spatial forest pest population dynamics, but, clearly, it is not a robust premise for spatial sampling designs that seek to answer quantitative questions about factors influencing spatial dynamics, including cycle synchrony. Dendroecology studies seeking to legitimize lowintensity spatial sampling by presuming periodic disturbances risk begging the question. We show that meso-scale asynchrony in defoliator cycling is revealed only in highintensity sampling at a rate of one outbreak chronology per 0.32 km². Dendroecologists may be misled by the large extent of outbreaks reported in aerial surveys performed by fixed-wing aircraft. These surveys are, however, insensitive to light defoliation occurring below the detectability threshold of 50%, when population fluctuations are most likely to be asynchronous. Spatial synchrony should not be presumed if this is the research question being investigated. We cannot say why FTC outbreaks exhibit such powerful resistance to synchronization, even at small scales of 20 km \times 20 km, where extreme winter weather events are uniform and moth flight is sufficient to connect all sub-populations. Our results provide the unfortunate situation where the best predictor of impacts during the next outbreak may well be the opposite of what happened during the previous outbreak. If the last outbreak was intense, the next likely won't be. If the last outbreak focused on one area, the next will focus on a different area. The common assumption in forest insect pest hazard rating is that the past is a good indicator of the future. We show the opposite: the recent past is the worst possible predictor of the near future.

The management implications are twofold. First, identifying the agents responsible for constraining the growth of cycles in time and the spread of eruptions in space would offer new hope for practical forest pest management. If one were to falsely accept that all cycles are equally intense and equally well synchronized, then one would falsely conclude there are no agents that can stop a synchronously cycling outbreak. Second, although there may be limits to short-term population predictability relevant to the time-scales of operational pest management (e.g., the pest population cycle), this may give way to enhanced predictability at time-scales more relevant to forest management objectives (e.g., the forest harvest cycle). To move forward in forest pest predictive ecology and integrated forest and pest management, new investment is required in basic spatial population sampling and operational monitoring.

The idea that forests may be "pest-proofed" by diversifying forest tree species compositions at a landscape scale has considerable policy allure (Kneeshaw et al. 2021). Our results suggest that, indeed, a more complex and diverse forest landscape may be less prone to synchronized and intense forest insect pest damage. However, we also demonstrate that care is required in any study that purports to quantify the precise spatial relationship between forest landscape structure and forest insect pest dynamics. Context and scale appear to matter rather critically.

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Data availability

Data generated or analyzed during this study are available in the Dryad repository, https://doi.org/10.5061/ dryad.pzgmsbcqm.

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Competing interests

The authors declare no competing interests.

Supplementary material

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