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The dynamics of forest tent caterpillar outbreaks in Québec, Canada

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Abstract

Historical patterns of forest tent caterpillar defoliation over the period 1938–2002 in the province of Québec, eastern Canada, were analyzed in relation to forest inventory data. The extent of defoliation over time was largely nonstationary and only somewhat periodic; however six major defoliation episodes could be identified. Individual outbreaks tended to span only 36.6% (±13.1% S.E.) of the total area defoliated, suggesting they are frequently terminated before attaining their maximum potential extent. Although outbreaks tended to recur periodically, they were not perfectly synchronized across the province. Two core regions, 14 000 and 20 000 km^2 in size, located in the northwestern, aspen-dominated boreal forest region and the southeastern, maple-dominated mixedwood forest region, were found to exhibit cyclic patterns of defoliation, with periodicities of 9 and 13 years, respectively. These oscillations were characterized by strong second-order negative feedback, suggesting regulation by lagged density-dependent processes. Outbreak cycles in the two core regions were in phase with one another ($r = 0.39$) until 1963, when a sudden, large-scale outbreak collapse occurred in the North during the initial phase of the third cycle. Since that time outbreak oscillations have been completely out of phase ($r = -0.16$), leading to a persistent wave-like pattern of outbreak spread back and forth between regions along a northwest–southeast axis. Within core regions, cycle amplitude varied in a slow and smooth manner, with the phasing pattern of amplitude modulation differing substantially between regions. Although the timing of population cycle peaks appears to be highly predictable, at least within the core regions, the levels of defoliation experienced during these peaks appears to be unpredictable and may be modulated by factors yet to be identified.

Keywords: Insect outbreaks; Spatiotemporal dynamics; Population cycles; Synchronization; Cluster analysis; Time-series analysis; Stationarity; Natural disturbance forecasting

1. Introduction

Insects are a major source of disturbance in the boreal forest; however there are very few species whose dynamics are sufficiently well understood that the timing and extent of outbreaks can be predicted with any reliability (Cooke et al., 2006). The most destructive species, such as the conifer-feeding budworms of the genus *Choristoneura* (Lepidoptera: Tortricidae), are unquestionably the best studied (MacLean, 1980; Royama, 1984; Volney, 1989; Campbell, 1993). However, these species, compared to the less destructive hardwood defoliators, tend to outbreak so infrequently – every 20–40 years (Blais, 1983; Swetnam and Lynch, 1993; Burleigh et al., 2002; Boulanger and Arseneault, 2004) – that it takes that much more time and effort to study and understand their dynamics. For example, although we have been studying budworms in eastern and western North America for nearly a century, there are still disagreements as to how and why outbreaks occur (Ludwig et al., 1978; Royama, 1992; Hassell et al., 1999; Royama et al., 2005), and whether or not their occurrence and impact is at all predictable (MacLean and MacKinnon, 1997; Gray et al., 2000; Jardon et al., 2003).

It is in this vein that we consider the case of the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae), a major defoliator of trembling aspen, *Populus tremuloides* Michx., and sugar maple, *Acer saccharum* Marsh, in mixedwood and hardwood forests throughout North America (Witter, 1979). Compared to the relatively wasteful needle-feeding insects, the forest tent caterpillar is an efficient forager that consumes most of the foliage it destroys (Fitzgerald, 1995). Consequently, there is a strong linear relationship between

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population density and defoliation (Hodson, 1941) which breaks down only as population densities exceed the 100% defoliation threshold.

In eastcentral Canada (i.e. Ontario), forest tent caterpillar outbreaks are fairly well-synchronized and recur every decade or so (Sippell, 1962). However, in westcentral Canada (i.e. Saskatchewan and Manitoba), outbreaks are so asynchronous as to lack any distinct periodicity (Hildahl and Reeks, 1960). The forest tent caterpillar, though not as destructive as the conifer-feeding budworms, can cause substantial mortality of trembling aspen over large areas (Candau et al., 2002), suggesting it could be a source of much insight into the dynamics of other periodically outbreaking, forest-disturbing *Lepidopteran* species. However a significant challenge is to reconcile these major regional differences in outbreak patterns. If outbreak occurrence is truly periodic, then why should the long-term dynamics differ so strongly between regions?

Spatial analyses of defoliation data from Ontario indicate that outbreak duration varies regionally in response to landscape variables such as forest structure, climate, and elevation (Roland, 1993; Roland et al., 1998; Cooke and Roland, 2000)—all of which are known, from survivorship studies in Alberta, to influence temporal processes governing population growth, including early larval overwintering survival (Blais et al., 1955; Cooke and Roland, 2003) and late larval and pupal parasitism (Roland and Taylor, 1997). In particular, a decade-long survivorship study from Alberta indicates that outbreaks develop more rapidly in fragmented forests (Roland, 2005), while a parallel modeling study suggests this may translate, in the long-run, into more rapid population cycling (Cobbold et al., 2005).

In this paper we analyze the spatiotemporal pattern of forest tent caterpillar outbreaks across a large, and different, area – the province of Québec, in eastern Canada – over the period 1938–2002. We show how a purely temporal analysis of the aggregate province-wide data leads to the conclusion that forest tent caterpillar populations are at best marginally cyclic. Using cluster analysis on the full space–time data set, we show that outbreaks are actually highly periodic within certain regions, but only weakly synchronous between regions. We conclude that periodic outbreaks are a result of spatially synchronized oscillatory population fluctuations, but that the cycle-synchronization process varies in strength in time and space.

2. Methods

2.1. Historical insect data

Our analyses were based on the historical forest insect data base maintained by the Ministère des Ressources Naturelles et de la Faune du Québec. This is a synthetic data base summarizing, for the entire province of Québec, the presence/absence of a large number of forest insect species, as determined by a variety of federal and provincial institutions, using a variety of sampling methods and survey criteria that have varied since the program began in 1938. We focused on the defoliation mapping component of the database—this having been measured with the greatest degree of consistency among years and across the landscape. We selected the subset of data related to forest tent caterpillar, which are gridded at a spatial resolution of 5 min $\times$ 5 min of longitude and latitude, and binary-coded as ‘defoliated’ or ‘not defoliated’. Our data set comprised 6630 observational cells spanning some 400 000 km^2, over the period 1938–2002 (Fig. 1). As illustrated by Gray et al. (2000), who analyzed the spruce budworm component of the defoliator database, the coarse-resolution aerial survey data, though inappropriate for high-resolution applications, such as stand-level risk assessment, are well-suited to large-scale pattern analysis. Consequently we report here on dynamics occurring in fairly large, contiguous regions between 14 000 and 100 000 km^2 in surface area, even though the database has a spatial resolution of $\sim$58 km^2.

2.2. Pattern analysis

Temporal patterns of fluctuation in defoliation were summarized using classical time-series analysis methods, including spectral analysis and autocorrelation analysis. Classical time-series methods, however, are very sensitive to nonstationarity (Chatfield, 1989). Stationarity – the degree of temporal (or spatial) homogeneity in means (first-order stationarity) and variances (second-order stationarity) – is a condition that is often assumed in ecological time-series analysis, but rarely checked (Turchin, 1990). This is unfortunate because nonstationarity is a serious impediment to the interpretation of results from time-series analysis (Berryman and Turchin, 2001).

Nonstationarity was an immediate concern in this study because, according to historical fire-tower surveys maps, forest tent caterpillar outbreaks in 1952 and 1953 were unusually extensive. Assuming these maps were accurate, we calculated the area defoliated across the province during six roughly decadal time intervals and, using a one-sample *t*-test, computed the probability that the extensive outbreak of 1948–1957 was within the range of variability expected from this sample (Minitab, Minitab Inc., College Station, PA).

Having demonstrated the importance of gross nonstationarity in the aggregate provincial-scale data, we proceeded to a regional scale analysis, in an attempt to factor out any nonstationarity and get a clearer picture of the spatiotemporal dynamics of outbreaks within regions of stationarity. Our hypothesis was that temporal nonstationarity in the provincial-scale time-series was a result of spatial nonstationarity (i.e. regional variability) in tent caterpillar outbreak dynamics. In other words, we expected it might be possible to decompose the nonstationary provincial time-series into well-defined spatial regions of stationary and nonstationary dynamics. Within the regions of stationarity, we fully expected to find cyclical patterns of outbreaks, such as have been reported for the neighboring province of Ontario, over a similar time period (Fleming et al., 2000).

Cluster analysis was used to partition the province into areas where forest tent caterpillar fluctuated synchronously between epidemic and endemic levels. The temporal dynamics of