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Spatial scale and the detection of density dependence in spruce budworm outbreaks in eastern North America

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Abstract Using two tests for direct density dependence and standard techniques of time series analysis, we identified density dependence in defoliation time series of the spruce budworm across its outbreak range in eastern North America over the years 1945–1988. We carried out analyses for the entire region and for grid cells of defoliation maps at five spatial scales created by aggregating the smallest grid cells. The rate of detection of direct density dependence, as assessed by two previously published methods, decreased with increasing spatial scale. Using both methods, density dependence was detected more frequently at the periphery of the outbreak range, where defoliation rate was lower. This result suggested that density-dependent regulation may be stronger in those areas. The first order autoregressive process was the basic model for defoliation dynamics overall and the most common model across spatial scales. Second-order processes were encountered much less frequently, and those commonly identified as resulting from delayed density dependence generally occurred across spatial scales at a rate expected by chance alone. Our results were similar to those of other published studies, which have found the detection of density dependence to decrease at larger spatial scales. The results also reinforced the importance of considering spatial scale when diagnosing population processes using time series of abundance for single species.

Key words Autoregressive model · *Choristoneura fumiferana* · Density dependence · Spatial scale · Time series analysis

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Introduction

Spatial scale is important in many population processes. For example, relationships between hosts and parasitoids vary across spatial scales, and scale is an important factor that must be considered in detecting density-dependent control by parasitoids (Heads and Lawton 1983; Walde and Murdoch 1988). Attention to spatial scale is critical because investigation of host-parasitoid interactions at an inappropriate scale can result in failure to identify density dependence. In an analysis of 79 published studies of density dependence, Ray and Hastings (1996) reported that density dependence was identified more frequently at relatively small spatial scales (i.e., generally <1 ha but varying among species) than at larger ones. Differences presumably resulted from the relative ranges of movement of individuals within the spatial units. At smaller scales, study units encompassed most of the potential movement ranges of individuals, whereas at larger scales, units might encompass many such ranges. Thus, dynamics of small subpopulations might tend to “average out” in the larger spatial units, reducing the detection of density dependence. In a field study of density dependence in a gall-forming insect, Hails and Crawley (1992) also found a lower frequency of density dependence at larger spatial scales and suggested this phenomenon as a possible explanation. Similarly, Hastings (1993) demonstrated the potential for inter-patch movement to decrease detection of density dependence at larger spatial scales in a modeling study.

Time series analysis (Box and Jenkins 1976) has been used recently to infer delayed density dependence in time series of single-species censuses of animal populations (Turchin 1990; Royama 1992). The form of the autocorrelation function and the strength of partial autocorrelations at the first and second lags have been considered diagnostic of the order of density dependence (Turchin 1990; Royama 1992). This technique and those developed to detect direct density dependence, such as the tests proposed by Bulmer (1975) and Pollard et al. (1987), are generally limited in their application by the

paucity of time series from natural populations of sufficient length to give statistically significant results (Royama 1992). Moreover, multiple series are rarely available for individual species to permit investigation of spatial variability in density-dependent processes.

The spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is native to eastern North America and inhabits spruce-fir forests (Royama 1984; Mattson et al. 1988). It has one generation per year. When abundant, larvae can defoliate trees, and outbreaks may extend over millions of hectares. Several theories about the dynamics of budworm populations have been advanced based alternatively on the effects of weather, hosts, and natural enemies (Wellington 1950; Greenbank 1956, 1957; Morris 1963; Hardy et al. 1983; Royama 1984, 1992; Blais 1985; Régnière and Lysyk 1995). Most of the theories were developed from intensive life table data collected in specific forest stands (Morris 1963).

In this paper, we analyze budworm dynamics from a landscape perspective and attempt to diagnose the underlying dynamics by examining historical population dynamics over most of the outbreak range. The size of that range and the relatively fine resolution of our outbreak maps permitted us to create many time series of defoliation area (i.e., a proxy for abundance) for analysis at each of five spatial scales via aggregation of spatial units. The spatial units used here were vastly larger (e.g., 10 km×10 km at the smallest) than those typically considered in field studies of spatial density dependence (Ray and Hastings 1996; Hails and Crawley 1992). However, we wished to investigate how detection of direct and delayed density dependence may be affected by changes in spatial scale at the landscape level, and our data sets were of sufficient spatial range and temporal duration to allow us to do so.

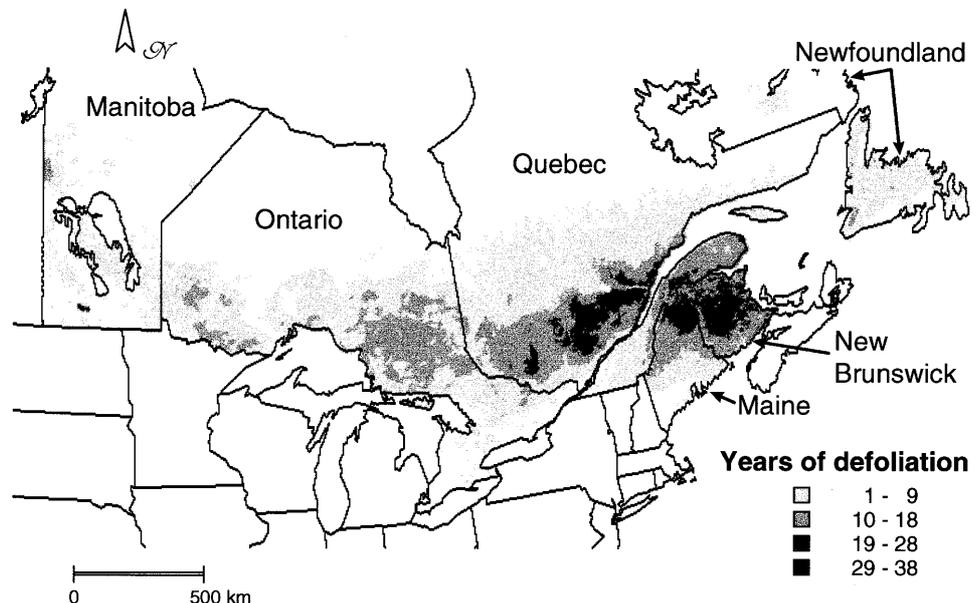
Materials and methods

Basic data for the analyses consisted of a time series of 44 annual digital maps of spruce budworm defoliation in eastern North America over the time interval 1945–1988. The maps covered an area that included the Canadian provinces of Newfoundland, Quebec, New Brunswick, Ontario, and Manitoba, and the state of Maine (Fig. 1). Although the southern margin of the outbreak range of spruce budworm extends into the states of Minnesota, Michigan, New York, New Hampshire, and Vermont and the provinces of Nova Scotia and Prince Edward Island, we did not have defoliation maps for those areas over the entire study interval.

We produced digital maps of defoliation during the period 1945–1980 by scanning paper maps published by Hardy et al. (1986) with a digital scanner at a resolution of 300 dots per inch (2.5 cm). We produced maps for the period 1981–1988 by scanning unpublished paper maps of defoliation obtained from provincial and state agencies and assembling them in a geographic information system. Williams and Liebhold (1995a) provided details of map scanning and processing. We stored and manipulated digital maps using the IDRISI geographic information system (Eastman 1989). Grid cells, the basic units of the annual defoliation maps, represented square land areas 5 km×5 km in extent. Because the original paper maps were developed from aerial sketch map surveys of pest damage, characterization of defoliation was necessarily qualitative, with forest stands classified simply as exhibiting defoliation detectable from the air (i.e., ≥30% canopy defoliation) or as without detectable defoliation (<30%). Using a binary classification, we assigned defoliated grid cells a value of 1 and undefoliated cells a value of 0.

To create maps at various spatial scales, we aggregated the cells into larger cells consisting of 2×2, 4×4, 8×8, 16×16, and 32×32 of the basic cell units. Thus, the larger cells represented land areas of 100, 400, 1,600, 6,400, and 25,600 km², respectively. The dimensions (i.e., rows×columns) of those maps were 370×186, 185×93, 92×46, 46×23, and 23×11, respectively. We calculated defoliation in the larger cells simply as the sum of the binary-valued unit cells contained in each aggregated cell. When all of the annual maps were placed in temporal sequence, the defoliation means at individual geographical locations formed time series of defoliation in their respective cells. The “populations” in the larger grid cells were the sums of the smallest (5×5 km) unit cells that were defoliated within each larger cell. As a caveat it must be noted that aggregation in the 2×2 cells resulted in just five possible population values. Because of the discrete nature of the ele-

Fig. 1 Number of years of detectable defoliation by eastern spruce budworm in eastern North America over the 44-year period 1945–1988



ments in those series, it is questionable whether the data were normally distributed. The results of analyses on the time series of 2x2 cells should be regarded with caution because of their discrete character.

Because the smallest units of the larger cells were binary, some defoliation series contained many zero elements. We chose to analyze only series exhibiting 4 or more years of defoliation (i.e., containing $\geq 9\%$ non-zero elements). Following the general practice for the analysis of time series of population density (Royama 1992), we transformed the defoliation sums as $x = \ln(n+1)$.

We evaluated the defoliation time series for direct density dependence using tests developed by Bulmer (1975) and Pollard et al. (1987). The test of Bulmer (1975) compares a model containing density dependence with a random walk. Bulmer's test uses the criterion $R=V/U$, where

$$V = \sum_{t=1}^{N-1} (x_{t+1} - x_t)^2$$

and

$$U = \sum_{t=1}^N (x_t - \bar{x})^2$$

where x_t is the logarithm of the population size at time t and N is the length of the time series. Density dependence is associated with small values of the criterion. It is detected as significant at the 5% level of probability for $R \leq 0.25 + 0.0366(N-2)$.

The test of Pollard et al. (1987) is a randomization test that compares the criterion for the original time series with those for many random orderings of the original data. The criterion is the Pearson correlation between the population growth rate between successive years, $d_t = x_{t+1} - x_t$, and x_t , the log of population size. We computed the test criterion for 25,000 random orderings of each defoliation time series. Density dependence was indicated if the criterion for an original series lay in the lower 5% of criteria for all of the random series.

We also analyzed the defoliation time series using the standard tools of time series analysis, the autocorrelation function (ACF) and the partial autocorrelation function (PACF) (Box and Jenkins 1976). The ACF is the set of autocorrelations between series values separated by time lags over the range, 1 to k , which is plotted as a function of lag length. For time lags greater than 1, partial autocorrelations are correlations between series elements k lags apart with the effects of the intervening $k-1$ lags removed. Similar to an ACF, the PACF is the set of partial autocorrelations plotted against lag length.

One common time series process, the autoregressive process, provides a simple model of a biological population (Royama 1992). In the autoregressive model, the magnitude of a series element depends linearly upon the value of one or more previous elements plus the magnitude of a random element:

$$x_t = a + b_1 x_{t-1} + b_2 x_{t-2} + \dots + b_k x_{t-k} + z_{t-1}$$

where, in our case, x_t is the defoliation area in successive years and z_t is the random variable, which may be exemplified by the effects of weather. The "order" of a process corresponds to the highest lag having a significant partial autocorrelation. Thus, inspection of the PACF is useful for identifying the order of an autoregressive process. Animal population dynamics are generally characterized by first or second order autoregressive processes (Royama 1992). Diagnosis of a second-order model for a sample time series has been used to infer population regulation by delayed density dependence (Turchin 1990). Specifically, delayed density dependence is characterized as a second order process with the ACF often exhibiting damped oscillations and the PACF having a significant positive lag 1 autocorrelation and a significant negative lag 2 partial autocorrelation (Turchin 1990; Royama 1992; Williams and Liebhold 1995b). We did not investigate lags longer than 2.

We approximated 95% confidence intervals for the partial autocorrelations as Bartlett bands, defined as $\pm 2/\sqrt{N}$, where N is the length of the time series (Royama 1992). As our time series were all 44 years in length, the confidence interval was ± 0.3015 , and

we considered partial autocorrelations of greater absolute value to be significant. We also tested time series generally for the presence of autocorrelation using a chi-square test proposed by Ljung and Box (1978). We used the critical values of the ACF and PACF, as well as those of the tests for direct density dependence of Bulmer (1975) and Pollard et al. (1987), mainly for evaluating the relative magnitude of observed values rather than for hypothesis testing per se. Considering the very large number of series tested, it would be impossible to control experiment-wide error levels.

Results

Defoliation by spruce budworm extended longitudinally over a range exceeding 3,000 km in southeastern Canada and the northeastern United States (Fig. 1). The number of years of defoliation ranged from 0 to 38 out of the 44 years investigated, with areas of highest numbers of years of defoliation in northern Maine and central New Brunswick. Throughout the longitudinal range, there were areas with defoliation in nearly half of the 44 years of the study. Areas of longest-term defoliation generally occurred in the middle of the latitudinal range of outbreaks, with the number of years of defoliation tapering off to the northern and southern margins.

When aggregated over the entire geographical range, the time series of defoliation exhibited two broad peaks separated by a wide trough during the 1960s (Fig. 2a). Thus, the study included about one and one half population oscillations. The total area defoliated ranged from as low as 21,000 km² to as high as 640,000 km². Neither the method of Bulmer (1975) nor that of Pollard et al. (1987) detected direct density dependence at the 5% level in the aggregated series. The ACF for the time series exhibited an approximately linear decrease from high

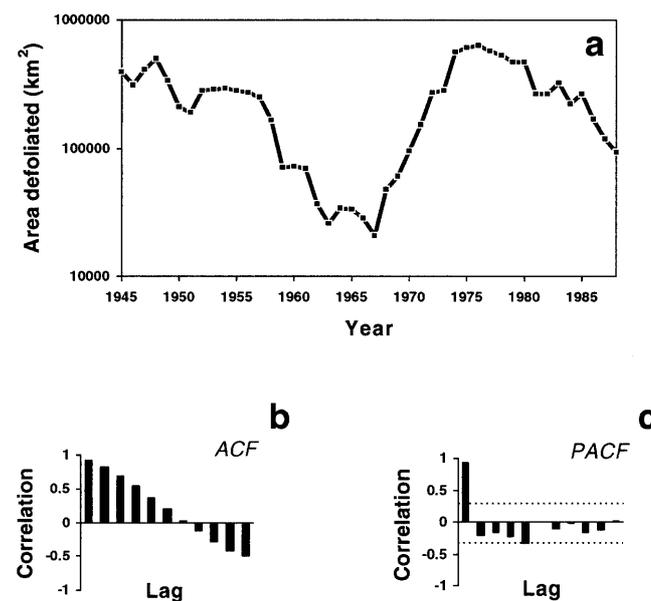


Fig. 2 a Time series of total area defoliated by eastern spruce budworm in eastern North America from 1945 to 1988, and the b autocorrelation (ACF) and c partial autocorrelation (PACF) functions estimated for that series

Fig. 3a–e Values of Bulmer's R statistic for defoliation time series at five levels of spatial resolution. R -values ≤ 1.7872 were significant at the 5% level. **a** 10 km \times 10 km, **b** 20 km \times 20 km, **c** 40 km \times 40 km, **d** 80 km \times 80 km, **e** 160 km \times 160 km

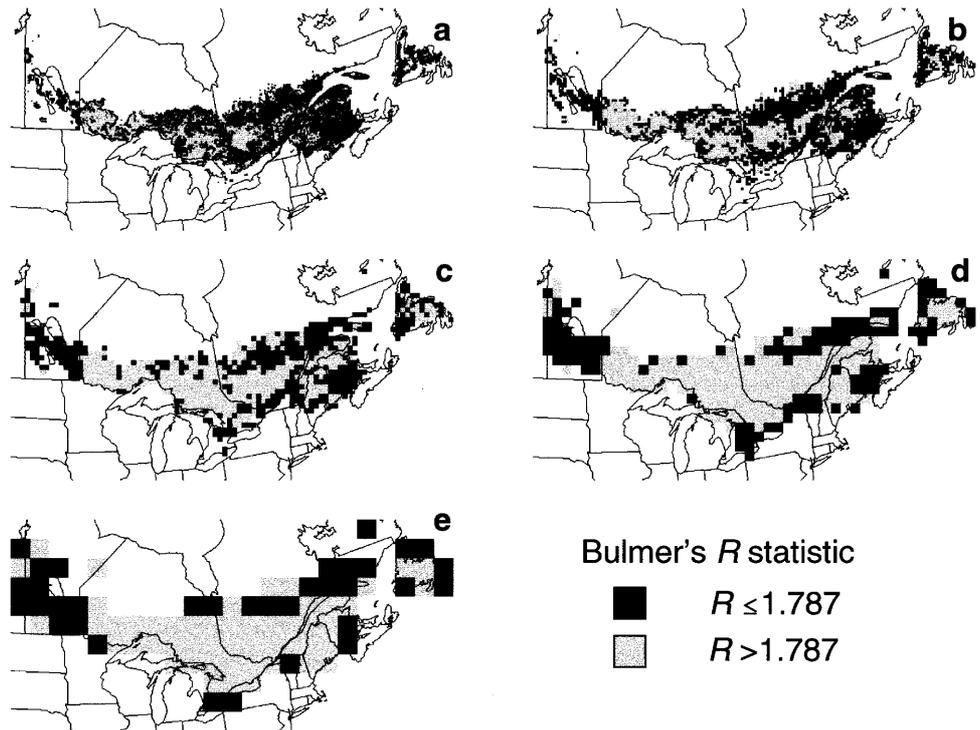
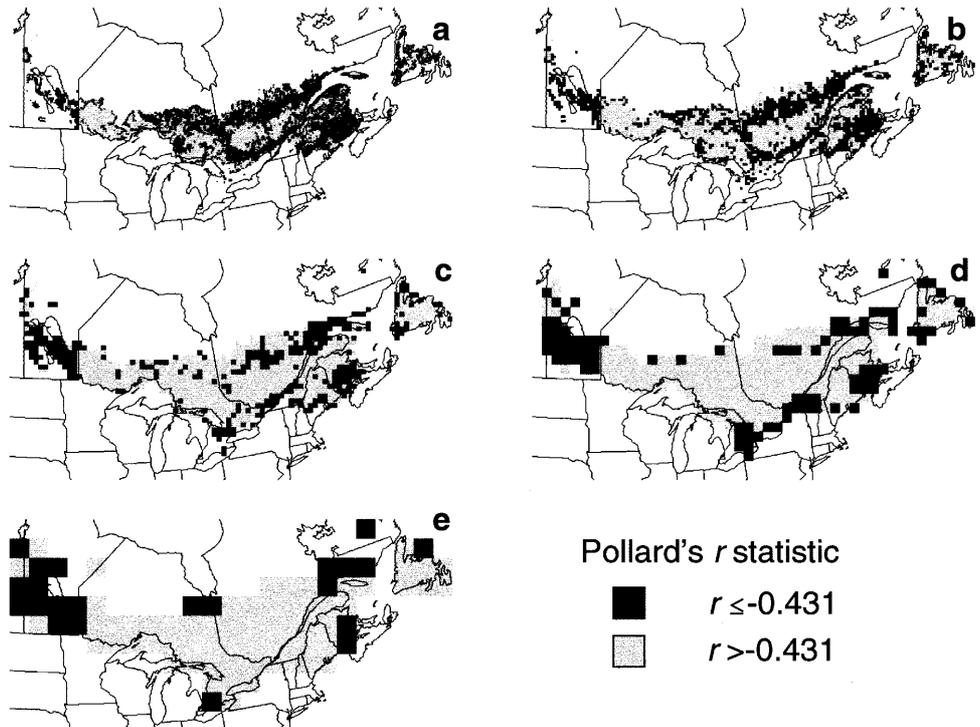


Fig. 4a–e Values of Pollard's r statistic for defoliation time series at five levels of spatial resolution. Values of $r \leq -0.431$ were significant at the 5% level. **a** 10 km \times 10 km, **b** 20 km \times 20 km, **c** 40 km \times 40 km, **d** 80 km \times 80 km, **e** 160 km \times 160 km



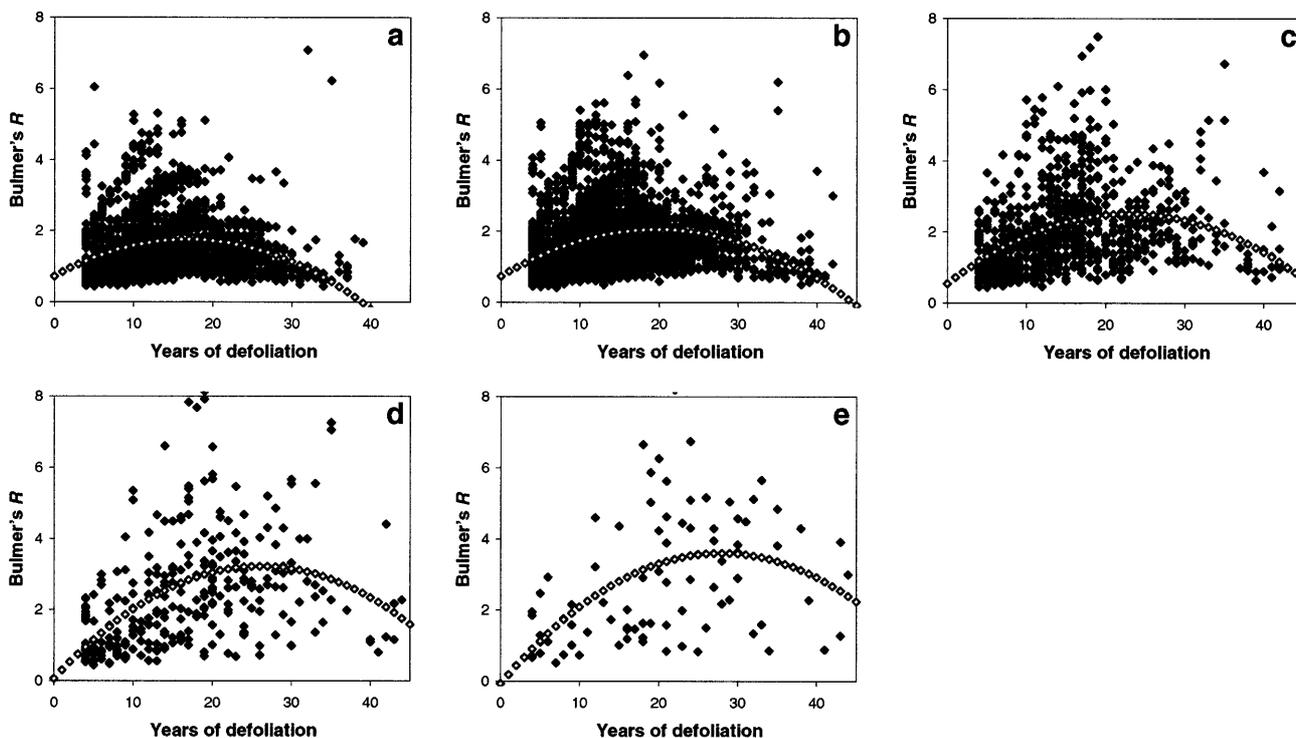
positive autocorrelations to high negative autocorrelations over 11 lags (Fig. 2b). The PACF had one strong positive autocorrelation at lag 1, a marginally significant negative partial autocorrelation at lag 5 (which we did not consider further), and insignificant partial autocorrelations at other lags (Fig. 2c). Thus, the PACF suggested a first order autoregressive process. The decline of the

ACF into negative values suggested the possibility of a higher-order process although it did not oscillate over the range of lags observed (Box and Jenkins 1976).

The geographical distribution of density dependence as detected by the method of Bulmer (1975) exhibited a consistent pattern across multiple spatial scales (Fig. 3): cases of density dependence tended to occur toward the

Table 1 Percentage of all map grid cells exhibiting defoliation, percentage of defoliated cells having significant values of Bulmer's R (Bulmer 1975) and Pollard's r (Pollard et al. 1987), and means and SEs of R and r for defoliated cells at five spatial resolutions

Resolution (numbers of unit cells)	% All cells defoliated	Bulmer			Pollard		
		% Defoliated cells with significant R value	Mean R	SE	% Defoliated cells with significant r value	Mean r	SE
2×2	14.7	71.4	1.529	0.008	58.5	-0.454	0.001
4×4	17.1	61.2	1.732	0.017	46.9	-0.429	0.002
8×8	20.8	49.3	2.034	0.039	35.5	-0.402	0.004
16×16	26.7	40.4	2.441	0.095	31.6	-0.380	0.008
32×32	33.6	40.0	2.855	0.193	25.9	-0.348	0.016

**Fig. 5a–e** Relationship between the value of Bulmer's R statistic and the number of years of defoliation experienced by grid cells at five levels of spatial resolution. The *open boxes* plot quadratic functions fit to the data points. **a** 10 km×10 km, **b** 20 km×20 km, **c** 40 km×40 km, **d** 80 km×80 km, **e** 160 km×160 km

edges of the outbreak distributions. The latitudinal and longitudinal centers of the distributions generally had large areas with apparent density independence. Similar patterns were obtained using the method of Pollard et al. (1987) although that method detected fewer cases of density dependence overall (Fig. 4).

Cursory comparison of the patterns in Fig. 3 and Fig. 4 suggested that cells with lower values of the R statistic of Bulmer (1975) and the r statistic of Pollard et al. (1987) (which will be referred to simply as Bulmer's R and Pollard's r in the rest of the paper) decreased in frequency as spatial scale increased (e.g., compare the relative areas of the black cells in Fig. 3a and Fig. 4a

with those in Fig. 3e and Fig. 4e, respectively). The percentages of defoliated cells with significant values for the two test statistics confirmed this pattern (Table 1). Bulmer's method detected density dependence in 71.4% of all defoliated 2×2 cells and just 40% of 32×32 cells. Similarly, Pollard's method detected density dependence in 58.5% of all 2×2 cells but only 25.9% of 32×32 cells. Conversely, mean values of the test criteria increased with increasing spatial scale. Mean values of Bulmer's R rose steadily from 1.529 in the smallest cells to 2.855 in the largest, whereas mean values of Pollard's r rose from -0.454 to -0.348 over the same range. Thus, direct density dependence was detected at the highest rate in the smallest cells and at successively lower rates in larger cells.

Comparison of Fig. 1 with Fig. 3 and Fig. 4 suggested qualitatively that values of Bulmer's R and Pollard's r were highest in the middle ranges of the number of years of defoliation with lower values occurring in the ex-

Table 2 Numbers of defoliation time series used in the analyses and percentages of those without significant autocorrelation (AC) and exceeding the significance value of 0.3015 ($P=0.05$) for three categories of autoregressive models at five spatial resolutions, where a unit grid cell is 5 km \times 5 km (PAC partial autocorrelation)

Resolution	Series with >3 non-zero elements	% Series with significant positive lag 1 AC but non-significant lag 2 PAC	% Series with significant positive lag 1 AC and significant negative lag 2 PAC	% Series with significant positive lag 1 AC and significant positive lag 2 PAC
2 \times 2	10,136	76.0	0.6	8.1
4 \times 4	2,947	80.2	1.1	5.8
8 \times 8	881	82.3	2.0	4.1
16 \times 16	282	79.8	2.8	5.0
32 \times 32	85	77.6	5.9	7.1

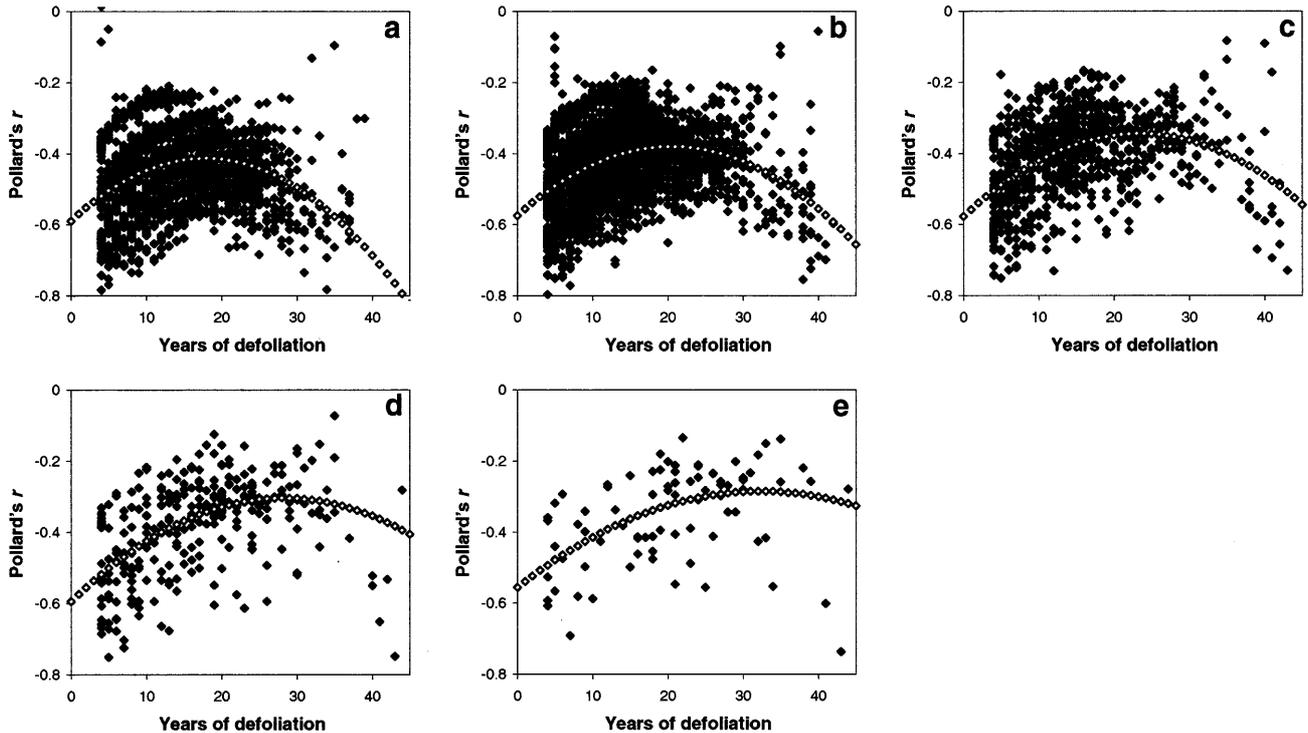


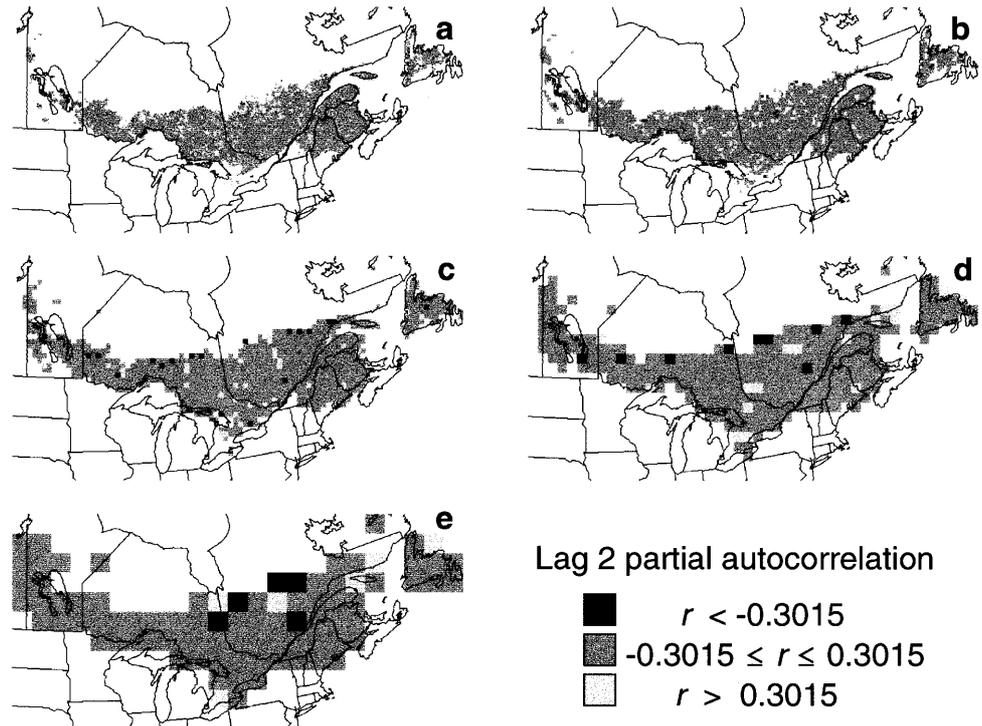
Fig. 6a–e Relationship between the value of Pollard's r statistic and the number of years of defoliation experienced by grid cells at five levels of spatial resolution. The *open boxes* plot quadratic functions fit to the data points. **a** 10 km \times 10 km, **b** 20 km \times 20 km, **c** 40 km \times 40 km, **d** 80 km \times 80 km, **e** 160 km \times 160 km

tremes. To examine this relationship more closely, we graphed values of Bulmer's R and Pollard's r against the numbers of years of defoliation for individual cells (Figs. 5, 6, respectively). These graphs exhibited general concave downward patterns of the test criteria over the range of years of defoliation, suggesting that the detection of density dependence was highest at the two extremes of years of defoliation and lowest in the middle range. Regression analysis confirmed the general pattern. Multiple regressions of the two test criteria on the number of years defoliated and that variable squared were highly significant at all spatial scales. Although both the linear and quadratic models had low P values, quadratic regressions fit the data better than simple linear regres-

sions in all cases. Coefficients of determination (R^2 values) were 0.07, 0.09, 0.14, 0.21, and 0.24 for the quadratic regressions of Bulmer's R (Fig. 5a–e, respectively) and 0.12, 0.14, 0.18, 0.25, and 0.20 for Pollard's r (Fig. 6a–e, respectively).

Given the large number of time series analyses involved, especially at the smaller spatial scales, it was not possible to examine ACFs and PACFs for individual grid cells. Instead we summarized the results of analyses at each spatial scale as the percentages of cases in each of three autoregressive models (Table 2). In most time series across all spatial resolutions, autocorrelation was significant at lag 1 only; 76–82% exhibited significant autocorrelation at lag 1 and none at longer lags. Percentages of spruce budworm defoliation time series with absolute values of lag 2 partial autocorrelations greater than the critical value of 0.3015 were relatively low (Table 2), suggesting a lesser importance of second order effects. Numbers with positive partial autocorrelations, which ranged from 4% to 8% of all cases, exceeded

Fig. 7a–e Values of the lag 2 partial autocorrelation for defoliation time series at five levels of spatial resolution. Values ≤ -0.3015 or ≥ 0.3015 were significant at the 5% level. **a** 10 km×10 km, **b** 20 km×20 km, **c** 40 km×40 km, **d** 80 km×80 km, **e** 160 km×160 km



those with negative partial autocorrelations. With the exception of cases at the largest spatial scale, numbers of significantly negative lag 2 partial autocorrelations did not exceed the 5% level that might be expected purely by chance. Cells with positive lag 2 partial autocorrelations greater than 0.3015 were distributed more or less evenly over the outbreak range of spruce budworm across spatial scales (Fig. 7). By contrast, the fewer cells with negative lag 2 partial autocorrelations less than -0.3015 were most prevalent along the northern margin and in the northern part of the outbreak range (note Fig. 7c and d in particular).

Discussion

Our results compared well in concept with those of Ray and Hastings (1996). The overall frequency of cells exhibiting significant direct density dependence increased with decreasing spatial scale while the mean values of the test criteria decreased (Table 1). At the largest spatial scale, the methods of Bulmer (1975) and Pollard et al. (1987) both failed to detect direct density dependence in the defoliation time series aggregated over all of eastern North America. Density dependence clearly was more prevalent at smaller spatial scales. Although our study and those reviewed by Ray and Hastings (1996) focused on very different ranges of spatial scales, both appear to confirm the effect of averaging over subpopulations, which was postulated by those authors to lower the detection of density dependence at larger spatial scales. Our recent work on spatial synchrony of spruce budworm defoliation (Williams and Liebhold 2000) adds

strength to this argument. Across eastern North America, spatial synchrony of defoliation time series decreased with distance between the series. Thus, larger aggregations of cells probably contained increasingly larger proportions of component cells that were out of synchrony. Taking averages among cells that were out of phase probably obscured the density dependence present in the original series.

Density dependence was distributed geographically across spatial scales in a characteristic fashion. It tended to be detected around the margins of the outbreak distributions and not detected at the centers. The only other studies of which we are aware that examined geographical patterns of density dependence involved rodent populations. Saitoh et al. (1998) reported high rates of direct density dependence in populations of the gray-sided vole in northern sites on the island of Hokkaido and lower rates at their southernmost sites. Alternatively, Bjørnstad et al. (1995) detected a latitudinal gradient of direct density dependence in rodent populations in Fennoscandia that increased from north to south. Our data did not exhibit such latitudinal patterns: density dependence was most prevalent at the northern and southern extremes of the outbreak range.

It seems likely that such a discontinuous geographical pattern may be the result of interactions among three or more trophic levels in the spruce budworm system. As a possible explanation, we offer the following hypothesis involving the host forest and the natural enemy complex. The potential for regulation by natural enemies probably occurs everywhere. Royama (1992) noted that the two most common species of specialist hymenopterous parasitoids are found throughout the geographical range

of budworm. What changes most noticeably over the budworm distribution is forest species composition, which alters the habitat quality for growth of budworm populations. We speculate that habitat quality is highest in the center of the outbreak range, in which region we did not detect direct density dependence. Higher habitat quality may result in budworm populations' escaping regulation by natural enemies and undergoing long term population fluctuations in which large numbers of host trees die as a result of prolonged defoliation (Blais 1985). Such a long-term oscillation involving death and regrowth of forest stands is an extreme form of population regulation. Because of the long time lags involved, it is unlikely that direct density dependence would be detected. Alternatively, at the margins of the distribution, where habitat quality is lower, the density-dependent activity of the natural enemy complex may be more dominant resulting in more frequent detection of density dependence.

It is interesting that the few cases with significant negative lag 2 partial autocorrelations, which suggested delayed density dependence, primarily lay along the northern margin of the outbreak range (Fig. 7). This may have been a result of the patterns of time series in those regions, which may exhibit dynamics that appear cyclic. A similar situation has been reported in small rodent populations in Fennoscandia, where a latitudinal gradient in population dynamics is observed (Hansson and Henttonen 1985, 1988; Bjørnstad et al. 1995). Northern populations exhibit cyclic behavior whereas southern populations do not. However, we cannot speculate too much on this pattern because the occurrence of negative lag 2 partial autocorrelations did not generally exceed that expected by chance.

The occurrence of second order cases with positive lag 2 partial autocorrelations was puzzling because that model has not been given a mechanistic interpretation in the ecological literature. Their apparently random occurrence in the outbreak distributions (Fig. 7) suggests that they were due to chance variations in the large number of series.

The number of years of defoliation affected the detection of density dependence. The lowest levels of detection occurred in the middle ranges of number of years of defoliation (Figs. 5, 6). Cases with fewer years of defoliation had time series consisting of non-zero values interspersed between runs of zeros, and conversely, cases with more years of defoliation had time series consisting primarily of runs of non-zero values. Such cases apparently had more detectable density dependence.

Lag 1 autocorrelation was by far the most prevalent form of autocorrelation over the outbreak range of spruce budworm in eastern North America. The results of our time series analyses for the entire outbreak range (Fig. 2) were similar to those reported by Turchin (1990) for a 28-year time series of spruce budworm densities in New Brunswick (Royama 1984) and Candau et al. (1998) for four 56-year time series of defoliation from Ontario. Similarly, the ACFs in both studies exhibited an almost linear decrease from positive to negative autocor-

relation values over the first 10 lags. Moreover, the ACFs reported by Candau et al. (1998) exhibited long-period cyclical behavior when computed for lags over 30 years. In the series analyzed by Turchin (1990), the PACF also had a strong lag 1 autocorrelation with non-significant partial autocorrelations at subsequent lags.

Relatively few cases of second-order models were observed. This was particularly true for models with significantly positive lag 1 autocorrelations and significantly negative lag 2 partial autocorrelations, which have been characterized as resulting from delayed density dependence (Turchin 1990; Royama 1992). Royama (1992) suggested that spruce budworm oscillations are probably driven by delayed density-dependent factors, especially by the activities of a guild of specialist parasitoids. However, he noted that the 28-year population density series that he analyzed was too short relative to the typical length of a budworm outbreak cycle to detect second order effects. Although our defoliation time series was over 50% longer, the length problem was still evident. There are no specific criteria for determining the minimum time series length necessary to detect second order effects, but Royama (1992, p. 102) remarked that "Some populations, e.g., spruce budworm, exhibit an unusually long cycle of 30–40 years. It may require ten such consecutive cycles for a meaningful statistical analysis of the generating process."

It is important to keep one point in mind regarding our time series data when evaluating the results of the analyses. In using defoliation data, we assumed that they reflected, at least roughly, the dynamics of the defoliating spruce budworm populations. It was encouraging that our aggregated defoliation time series (Fig. 2) was similar qualitatively to the time series of actual population densities in New Brunswick presented by Royama (1984, Fig. 1). However, it must be noted as a caveat that the relationship between level of defoliation and defoliator population density is generally nonlinear and subject to considerable variation (Williams et al. 1991; Liebhold et al. 1993). Thus, precise interpretations of population dynamics cannot be inferred from our results. Nevertheless, defoliation is a good qualitative indicator of budworm abundance, particularly at high densities. It is of lesser value at low densities that produce undetectable defoliation, which was classified as zero defoliation in our data.

In conclusion, direct density dependence was detected across much of the range of spruce budworm outbreaks in eastern North America. Moreover, similar time series models dominated defoliation dynamics across spatial scales over a large region of North America, suggesting common population processes over the outbreak range. The detection of direct density dependence decreased uniformly as the smallest grid cells were aggregated to larger spatial scales for analysis. The decreasing detection of density dependence with increasing spatial scale suggests the need for attention to spatial scale in inferring population processes from the analysis of time series of single species population abundance.

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