

SPATIAL SYNCHRONY IN FOREST INSECT OUTBREAKS: ROLES OF REGIONAL STOCHASTICITY AND DISPERSAL

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Abstract. Spatial synchrony, that is, correlated population fluctuation over wide geographical areas, has been detected in diverse taxa and over various geographical scales. The most commonly suggested mechanisms to explain spatial synchrony include dispersal and regional stochasticity (i.e., “the Moran effect”). We analyzed landscape-scale historical outbreak data for six forest insect species: spruce budworm (*Choristoneura fumiferana*), western spruce budworm (*C. occidentalis*), larch bud moth (*Zeiraphera diniana*), forest tent caterpillar (*Malacosoma disstria*), mountain pine beetle (*Dendroctonus ponderosae*), and gypsy moth (*Lymantria dispar*). We used a recently developed statistical method (the nonparametric covariance function) for quantifying the magnitude and spatial range of synchrony in both outbreak and corresponding weather data. The varying dispersal capabilities of the species enabled us to speculate on the relative importance of dispersal vs. the Moran effect as potential mechanisms behind the observed patterns. Our results indicated that spatial synchrony was not directly associated with dispersal capabilities at the spatial scales considered. In contrast, the spatial correlation in weather variables was high enough to account for the levels of synchrony observed in the outbreak data. Therefore, the Moran effect appeared to be the more dominant process affecting the spatial dynamics of these species at the landscape scale. In general, however, the synchrony in outbreaks declined more steeply with geographical distance than the correlation in the weather variables, breaking with the predictions of Moran’s theorem. A more detailed analysis of gypsy moth outbreak data showed that local dynamics varied considerably in a spatially dependent manner. The existence of such variation violates one of the assumptions of the Moran’s theorem, namely, that the dynamic properties of disjunct populations are identical. We used a simple theoretical model to demonstrate that such geographical variation in local population dynamics may indeed force synchrony to decline more rapidly with distance than the correlation in the environment.

Key words: autocorrelation; *Choristoneura fumiferana*; *Choristoneura occidentalis*; defoliation; *Dendroctonus ponderosae*; landscape ecology; *Lymantria dispar*; *Malacosoma disstria*; population dynamics; spatial synchrony; *Zeiraphera diniana*.

INTRODUCTION

While there have been major advances in the theoretical development of how various population processes might interact to produce spatial patterns in the abundance of animal populations, this theory has largely remained untested due to the complexities of collecting and understanding extensive space–time data (Bascompte and Solé 1998, Liebhold and Kamata 2000). Recent developments in spatial statistics offer new tools for testing these theories (Koenig and Knops 1998, Lambin et al. 1998, Bjørnstad et al. 1999, Koenig 1999, Bjørnstad and Bascompte 2001, Buonaccorsi et

al. 2001). Probably the most frequently documented space–time pattern in ecological data is spatial synchrony, that is, correlated population fluctuations over localized or wide-scaled geographical areas (Ranta et al. 1995, Bjørnstad et al. 1999, Hudson and Cattadori 1999). Theoretical studies have shown that both regional stochasticity (i.e., spatially correlated, random forces that affect population growth in a density-independent fashion) and dispersal, together or separately, are plausible mechanisms in the explanation of spatial synchrony. A potential third mechanism is regional synchronization through the action of mobile natural enemies (Ydenberg 1987, Ims and Steen 1990).

The most obvious source of regional stochasticity is weather: many climatic variables are highly correlated over wide geographical areas (Koenig 2002). According to the theory developed by P. A. P. Moran (“the Moran effect”), spatially segregated populations with identical density-dependent dynamics will be synchro-

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nized if they are similarly affected by regionalized density-independent factors, such as weather perturbations (Moran 1953, Royama 1992). For populations with simple density-dependent growth, the spatial synchrony is predicted to mirror the correlation in the environment. This prediction holds, in theory, as long as local dynamics are not too nonlinear (Grenfell et al. 1998, Bjørnstad 2000). Dispersal may also induce synchrony by linking locally regulated populations. The spatial range of synchrony in abundance is thus controlled by the extent of synchrony in weather variation (e.g., Williams and Liebhold 2000a) and by the spatial range of dispersal (e.g., Bjørnstad and Bolker 2000). However, the type of density-dependent dynamics (e.g., stable equilibrium, cyclic, chaotic) may strongly influence the magnitude of spatial synchrony both when synchrony is caused by dispersal and when it is caused by the Moran effect (Ranta et al. 1998, Bjørnstad et al. 1999, Bjørnstad 2000, Ripa 2000). In principle, therefore, both mechanisms can produce nearly indistinguishable patterns of synchrony (Kendall et al. 2002). Confronting the existing theoretical framework with observational data on both abundance and climatic correlation is an important challenge in the quest to understand population processes (Lundberg et al. 2000).

Extensive outbreaks of a few insect species have dramatic ecological and economic effects on forests throughout the world. During the past 50 yr, efforts to predict and control outbreaks of these species have motivated government agencies to maintain extensive monitoring programs. These provide time series of outbreak data covering large geographical areas. Several analyses of these data have contributed greatly to our understanding of temporal patterns of population fluctuations (Myers 1988, Berryman 1996). We investigate synchrony in spatiotemporal outbreak data of six forest insect species with varying life history traits, dispersal abilities, and geographical ranges: (1) spruce budworm, *Choristoneura fumiferana* (Clemens), in eastern Canada and the state of Maine; (2) western spruce budworm, *Choristoneura occidentalis* Freeman, in the northwestern USA; (3) larch bud moth, *Zeiraphera diniana* Guéneé, in the European Alps; (4) mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in the northwestern USA; (5) forest tent caterpillar, *Malacosoma disstria* Hübner, in western Canada; and (6) gypsy moth, *Lymantria dispar* (L.), in the northeastern USA. The overall aim of our study is to seek a common explanation of the relative roles of weather and dispersal in the synchrony of forest insect outbreaks. We address this problem by contrasting space-time patterns among species with different mobility and by comparing patterns of spatial synchrony in outbreaks to the correlation seen in weather data.

Moran's theorem assumes that all geographical subpopulations adhere to the same density-dependent model (Moran 1953). However, this may not be always true

in nature. For both vertebrates and invertebrates, there is mounting evidence that population dynamics may differ geographically within a given species (Bjørnstad et al. 1998, Stenseth et al. 1999, Williams and Liebhold 2000b). One might intuitively expect, for example, that habitat quality would affect population growth rate and this would result in geographical variation in growth rate over large areas. We use gypsy moth as a case study to quantify geographic variation in local dynamics. We further use a strategic ("proof-of-concept") simulation to explore how geographical heterogeneity in local dynamics affects synchrony and speculate on how such heterogeneity may account for patterns in our case studies. We show that when the heterogeneity is spatially structured synchrony drops more rapidly with distance than the correlation in dominant climatic variables.

METHODS

Outbreak data

The outbreak data originated as aerial sketch maps (Fig. 1, Table 1). These maps were made by observers manually transcribing damaged areas observed from aerial surveys. The maps were subsequently digitized and ultimately transferred to raster GIS layers depicting the presence/absence (0/1) of outbreaks (Williams and Liebhold 2000a). In general, detectable defoliation in aerial surveys is considered to be >30% canopy defoliation (Webb et al. 1961). Aerial spraying of insecticides could potentially alter space-time patterns of outbreaks. However, most such treatments have historically been applied to a small fraction of the land area, and we consider their effects to be negligible at the scale of our analyses. Annual outbreak maps for mountain pine beetle, a bark beetle colonizing inner bark tissues, describe the distribution of tree mortality instead of defoliation and were also derived from aerial surveys. The resolution of original raster maps was 1 × 1 km for larch bud moth and forest tent caterpillar, 2 × 2 km for gypsy moth, mountain pine beetle, and western spruce budworm, and 5 × 5 km for spruce budworm.

The original raster cells were aggregated to produce 100 × 100 km cells, and the fraction of defoliated original cells was used as a proxy for abundance within the aggregate cells. Time series for each aggregate were obtained from maps from sequential years. Aggregates were excluded from analysis if they had a maximum value <0.01 or if >90% of years were completely undefoliated. These excluded data were typically located at the geographic margins of the outbreak regions (Fig. 1). The aggregation across 100 × 100 km spatial units will inevitably smooth out fine-scaled spatial variability in the data but will tend to average out the most rampant observational variability (we will return to this in the *Discussion*). However, meaningful comparisons

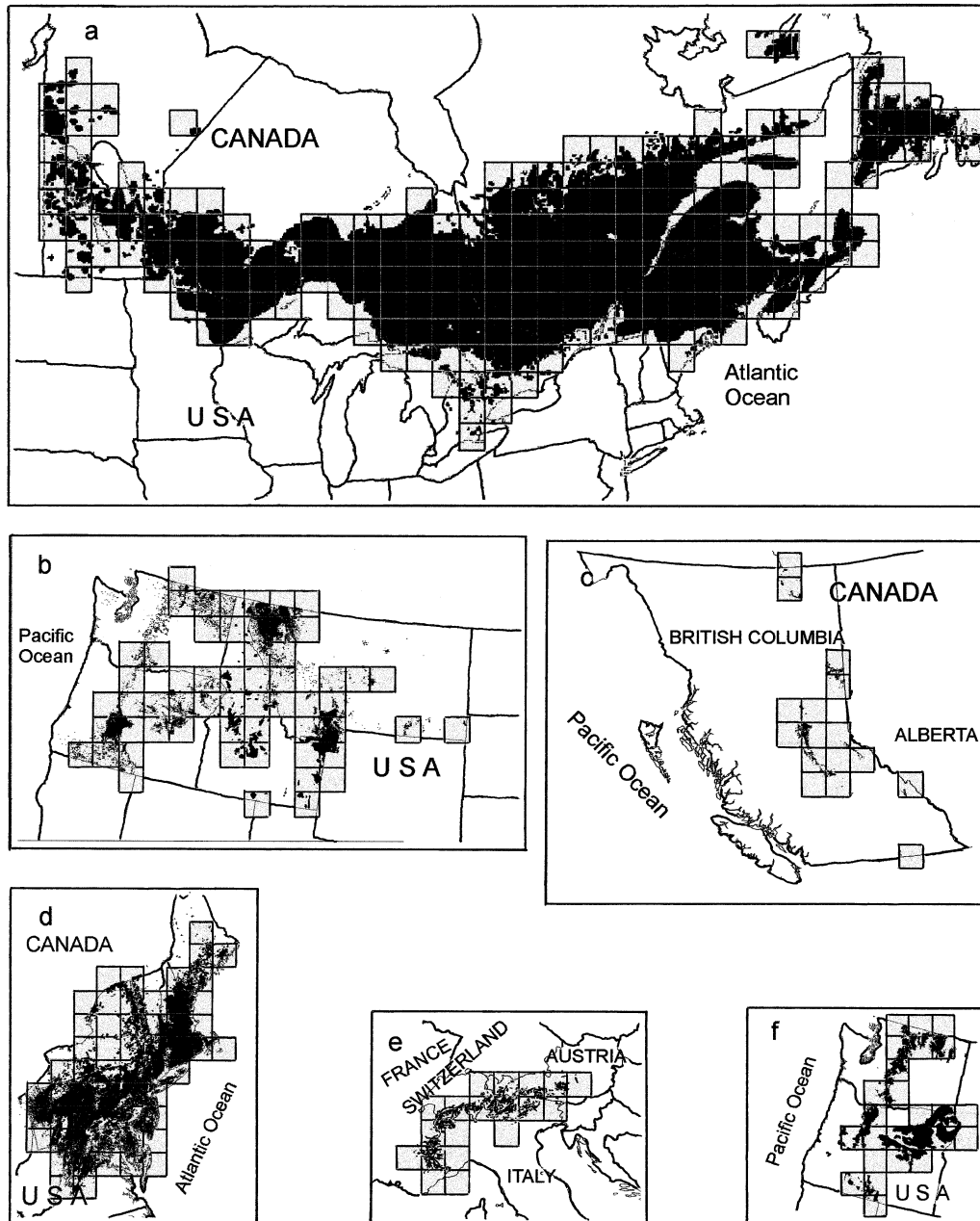


FIG. 1. Summary of the annual defoliation and tree mortality maps of the studies species: (a) the spruce budworm, (b) the mountain pine beetle, (c) the forest tent caterpillar, (d) the gypsy moth, (e) the larch bud moth, and (f) the western spruce budworm. Black corresponds to areas with ≥ 1 yr of detectable defoliation or tree mortality; gray indicates the location of aggregated 100×100 km cells used in the analyses.

among species required the use of a constant scale of resolution.

Weather data

Temperature and precipitation variables were analyzed to assess their spatial correlation and their potential to generate spatial synchrony in insect outbreaks (through the Moran effect). Monthly mean temperature and precipitation data were obtained from The Global

Historical Climatology Network provided by National Climatic Data Center, Arizona State University, Tempe, Arizona, USA, and The Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA (Peterson and Vose 1997). The temporal and spatial ranges of observations were selected to coincide with the data range of each insect species separately. Only observations from weather stations falling within the 100×100 km aggregates were

TABLE 1. Description of data sets of forest insect outbreaks used in the analyses.

Species	Location	Time range	Geographic extent (km) (E–W × N–S)	No. sub-populations†	No. weather stations‡	Source of outbreak data
High dispersal ability						
Spruce budworm <i>Choristoneura fumiferana</i> (Clemens)	Eastern Canada, Maine	1945–1988	1600 × 3600	212	161/152	Canadian Forest Service, USDA Forest Service (Williams and Liebhold 2000a)
Western spruce budworm <i>Choristoneura occidentalis</i> Freeman	Washington, Oregon	1947–1996	900 × 600	25	42/64	USDA Forest Service (Dolph 1980, Sheehan 1996)
Larch bud moth <i>Zeiraphera diniana</i> Guénéé	Alps, Central Europe	1961–1998	500 × 800	20	16/22	Swiss Federal Research Institute (Baltensweiler and Rubli 1999)
Moderate dispersal ability						
Forest tent caterpillar <i>Malacosoma disstria</i> Hübner	British Columbia (Canada)	1994–1996	1330 × 900	16	20/19	Canadian Forest Service
Mountain pine beetle <i>Dendroctonus ponderosae</i> Hopkins	Northwest USA	1980–1995	1000 × 1600	58	140/176	USDA Forest Service (Williams and Liebhold 2002)
Low dispersal ability						
Gypsy moth <i>Lymantria dispar</i> (L.)	Northeast USA	1975–1994	900 × 1200	57	207/214	USDA Forest Service (Liebhold et al. 1997)

† Per 100 × 100 km area.

‡ The first number reported is the number of weather stations for temperature data; the second number is the number of stations for precipitation data.

used in the analyses. The precipitation data were transformed as $\ln(n + 1)$ before analyses since this is a variance-stabilizing transformation of gamma variates such as rainfall (Coe and Stern 1982).

Previous studies have shown that the spatial synchrony of weather variables (monthly mean temperature and precipitation) does not vary substantially among months (Williams and Liebhold 2000a). Thus, we used June mean temperature and June precipitation time series to describe the regional weather patterns. All species considered here are in the larval stage in June, and environmental disturbances during that period are likely to be especially critical for their population growth.

Quantification of spatial synchrony

A simple method to quantify spatial synchrony among populations is to calculate pair-wise correlation of time series in spatially disjunct subpopulations (Buonaccorsi et al. 2001). A regional level of synchrony can then be estimated as the overall mean correlation for the entire study area. However, previous studies of spatial synchrony indicate that synchrony is not homogeneous; populations located near each other tend to be more synchronous than those located farther apart (Ranta et al. 1995, Bjørnstad et al. 1999, Koenig 1999). We obtain a more detailed understanding of spa-

tial synchrony by describing how correlation between populations varies as a function of the geographical distance between them. We used the nonparametric covariance function (NCF) to explore how synchrony decreases with increasing distance (Bjørnstad et al. 1999). The NCF uses a smoothing spline to produce direct, continuous estimates of the spatial covariance as a function of lag distance. Confidence intervals for the estimated functions were calculated using bootstrap resampling (500 iterations; see Bjørnstad and Falck 2001).

Aggregated 100 × 100 km cells and individual weather stations were used as “subpopulations” in this analysis. The estimated spatial covariance functions are likely to be biased at the longest lag distances, due to the selective location of subpopulations at the periphery of the sample area (Isaaks and Srivastava 1989). Thus, the maximum lag distance for the spatial covariance function was selected as the shorter geographical dimension (north–south or east–west) of the range of each species considered.

Spatial variation in local dynamics

We used gypsy moth as a case study to explore how spatially structured heterogeneity in local dynamics (such variation would violate a key assumption of Moran’s theorem) affects patterns of synchronization. First,

we described the local dynamics of each 100×100 km aggregate by fitting separate time series models to each of the log-transformed time series for each aggregate. The second-order autoregressive (AR) model was our choice of phenomenological model:

$$N_t = \alpha + \beta_1 N_{t-1} + \beta_2 N_{t-2} + \varepsilon_t \quad (1)$$

where N_t is log-abundance at time t , α is the intercept, β_1 and β_2 are autoregressive parameters, and ε is the error term (Royama 1992). First, we tested for significant spatial variation in the autoregressive parameters using spline correlograms (the univariate analogue of the nonparametric covariance function [Bjørnstad and Falck 2001]). (See Bjørnstad et al. [1995] for a discussion of how the log-AR model [Eq. 1] may be used to elucidate spatial variation in dynamics.)

Next we simulated the stochastic dynamics of a set of model populations centered on the same spatial coordinates as the 57 gypsy moth subpopulations. However, we wanted to emulate a situation where local dynamics varied geographically (in a spatially correlated fashion). In order to create such spatially dependent variation, the β_1 and β_2 coefficients were each drawn from a spatially correlated "distribution of parameters": A target covariance matrix, \mathbf{A} , between the 57 subpopulations was generated by calculating the distances between the locations and then fitting a Gaussian spatial covariance as a function of distance (Isaaks and Srivastava 1989). The range of the covariance function was arbitrarily set to 500 km in this exploratory study. A vector, \mathbf{Z} , of spatially correlated normal deviates with the target covariance was subsequently generated using the eigendecomposition method (see Ripley [1987] for details). A mean of zero and a variance of one were used initially. However, since the autoregressive coefficients must be constrained within a region (the "unit-root" region) to ensure non-divergent dynamics (see Royama 1992, Bjørnstad et al. 1995), we decreased the range in β_1 and β_2 until this criterion was met.

Spatially correlated error terms (ε_t), representing the regionally correlated stochastic influence ("climatic forcing"), were generated using the same eigendecomposition method. We chose a range of 1500 km for the covariance function of the error values in order to mimic the observed range of synchrony in weather data. For each time step in the ensuing simulation of the autoregressive models, we used a mean of zero and a variance of one for each error term. The intercept (α) was given a value of zero, because it does not affect the dynamics of the model or the level of spatial synchrony. We performed 200 replicate simulations of 500 generations each. The last 50 generations were used to estimate the spatial covariance functions for both outbreak data and "climate" (error values).

RESULTS

Spatial synchrony in outbreak and weather data

In general, spatial synchrony decreased with increasing lag distance both in outbreak and weather data (Fig.

2). The spatial covariance functions of the weather variables were very similar among the different geographical areas. On the whole, outbreak synchrony declined more rapidly with distance than the spatial correlation in precipitation and temperature data. Synchrony in the outbreak data at 100-km lag distance tended to be similar to the level of synchrony in temperature data at 500–700-km lag distance in most cases (Tables 2, 3, and 4).

The spatial correlation in mean June temperatures was considerably higher than that in the precipitation and the outbreak time series measured over the same geographical area (Tables 2, 3, and 4). The local synchrony of forest tent caterpillar, gypsy moth, and mountain pine beetle was slightly lower than that seen locally in the precipitation data. The local correlation did not differ significantly between precipitation and spruce budworm and western spruce budworm time series. At 100–200-km lag distance, larch bud moth outbreaks appeared to be slightly more synchronous than precipitation.

The extent and level of spatial synchrony of outbreaks did not differ dramatically between insect species (Fig. 2). None of the species showed significantly higher or lower levels of synchrony than the others throughout the compared range of lag distances (Table 2). Therefore, dispersal ability does not appear to have a pronounced effect on synchrony at the present resolution (100–500+ km). Highly mobile spruce budworm and much more sedentary gypsy moth showed about the same level of synchrony at the 100-km lag distance, but at the 150–750-km scale range, spruce budworm tended to be more synchronized. Larch bud moth, also known as a very mobile species, seemed to be slightly more synchronous than gypsy moth within the first 170 km, but the difference was not statistically significant. Western spruce budworm is also a considerably more mobile species than gypsy moth, but the 95% confidence envelopes of their covariance functions overlapped almost completely. The level of synchrony (within 100-km lag distance) of gypsy moth outbreaks was equal to that of forest tent caterpillar. The decline of synchrony was steeper in forest tent caterpillar than in gypsy moth outbreaks, even though forest tent caterpillar has better dispersal ability than gypsy moth.

The lowest overall level of spatial synchrony was found in mountain pine beetle outbreak time series. Species with good dispersal capabilities, such as spruce budworm, larch bud moth, and western spruce budworm, were spatially more synchronous than mountain pine beetle up to 600-, 400-, and 200-km lag distances, respectively. The level of synchrony in gypsy moth, forest tent caterpillar, and mountain pine beetle outbreaks was generally equivalent at the 100–200-km spatial scales, with some minor differences at longer distances (Table 2).

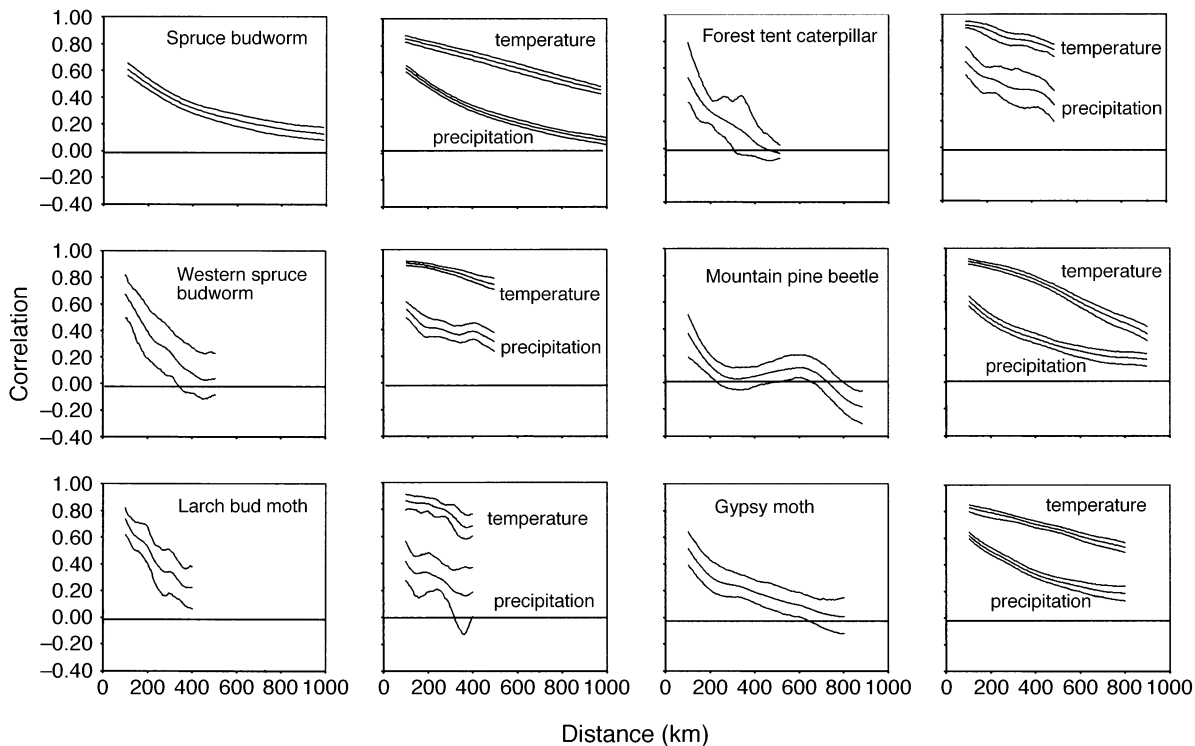


FIG. 2. The spatial covariance functions estimated from outbreak and weather data. The upper and lower lines in each group represent the 95% bootstrap confidence intervals.

Spatial variation in local dynamics

Detailed analysis of outbreak time series showed that the assumption of identical local dynamics does not hold. For instance, gypsy moth dynamics varied considerably and in a spatially dependent manner. The parameters of the second-order autoregressive models fitted to gypsy moth outbreak time series varied significantly across the entire geographical range. The mean values for parameters β_1 and β_2 were 0.55 (SD = 0.28, minimum = -0.20, maximum = 1.19) and -0.22 (SD = 0.31, minimum = -0.62, maximum = 0.31), respectively. Spline correlograms indicated that variation in the second-order autoregressive parameter, β_2 , was spatially autocorrelated at lag distances <500 km (Fig. 3).

Thus, we generated spatially dependent variation in model parameters for the simulations and allowed the local dynamics to vary with the range of spatial correlation in β_1 and β_2 set at 500 km. Moran's theorem, under the assumption of identical local dynamics, predicts that the spatial covariance function (SCF) curves describing population synchrony and weather synchrony should be parallel. However, our simulations showed that violation of the assumption of identical models for all locations affected patterns of spatial synchrony. The SCF curve estimated from simulated population data declined significantly more steeply with distance than the correlation in the stochastic influence

("climate") that we imposed (Fig. 4). This difference in the slopes of simulated outbreak and weather SCFs was similar to differences in SCF slopes observed in the actual outbreak and weather data (Fig. 2).

DISCUSSION

Due to a lack of consistent quantitative studies of dispersal, we relied on a qualitative classification of the six insect species according to their mobility. The dispersal capability of the species ranged from sedentary to highly mobile. Gypsy moth has the lowest level of dispersal. Females of this species are completely incapable of flight, and the windborne dispersal range of first instar larvae, hanging on silk threads, is usually much <1 km (Mason and McManus 1981). Spruce budworm, western spruce budworm, and larch bud moth are strong flyers; during outbreaks, large numbers of adult moths can fly considerable distances (up to several hundreds of kilometers), carried downwind by above-canopy air movements (Greenbank et al. 1980, Campbell 1993, Baltensweiler and Rubli 1999). Dispersing females of these species may carry significant numbers of their eggs to new habitats. The dispersal capabilities of mountain pine beetle and forest tent caterpillar are lower than spruce budworm, western spruce budworm, and larch bud moth, but higher than gypsy moth (Furniss and Carolin 1977, Raffa and Berryman 1979).

TABLE 2. Spatial synchrony in outbreak data at different lag distances.

Species	Distance (km)			
	100	300	500	700
Spruce budworm	0.61 [0.56, 0.66]	0.40 [0.35, 0.43]	0.27 [0.23, 0.31]	0.20 [0.15, 0.25]
Western spruce budworm	0.68 [0.50, 0.82]	0.24 [0.06, 0.41]	0.04 [-0.09, 0.23]	...
Larch bud moth	0.74 [0.62, 0.82]	0.34 [0.18, 0.50]
Forest tent caterpillar	0.53 [0.35, 0.79]	0.18 [0.00, 0.35]	-0.03 [-0.08, 0.04]	...
Mountain pine beetle	0.37 [0.19, 0.51]	0.03 [-0.05, 0.11]	0.09 [0.00, 0.17]	0.04 [-0.05, 0.14]
Gypsy moth	0.52 [0.40, 0.64]	0.24 [0.15, 0.34]	0.13 [0.05, 0.24]	0.03 [-0.07, 0.14]

Note: Numbers in square brackets are 95% confidence intervals.

Despite clear differences in dispersal capabilities, a general pattern of population synchrony was shared among the insect species. All species showed locally high levels of synchrony, which decreased with increasing distance and finally decayed completely at long distances. A similar pattern has been found in a wide range of other taxa, including insects, birds, and mammals (Hanski and Woiwod 1993, Ranta et al. 1995, 1997, Sutcliffe et al. 1996).

Two explanations have been suggested for the pattern of decreasing synchrony with increasing distance: spatially autocorrelated environmental variability (Grenfell et al. 1998, Williams and Liebhold 2000a), and distance-dependent dispersal (Ranta et al. 1997, Swanson and Johnson 1999). In the present analyses, both weather variables exhibited surprisingly uniform patterns of spatial correlation regardless of the geographical area over which they were recorded. This result is in accordance with a recent study on the global patterns of environmental correlation (Koenig 2002). However, the negative slope of spatial covariance functions of the weather variables testifies to how the correlation in climatic fluctuations also declines with distance, particularly at extensive geographical scales (Williams and Liebhold 2000a).

Even though close examination of the spatial covariance functions revealed some slight differences between species, they could not be directly associated with differences in dispersal capability. This indicates that dispersal is probably not a dominant process behind the observed population synchrony at the regional scale (100+ km). Theoretical models have shown that synchrony can be enhanced when populations have cyclic dynamics (Bjørnstad 2000). Larch bud moth is one

of the classical examples of species with very regular cyclic dynamics. It is also known to undergo mass flights over long distances (Baltensweiler and Rubli 1999). However, the spatial covariance function of larch bud moth was surprisingly similar to that of gypsy moth, which practically does not disperse at all. Sutcliffe et al. (1996), who studied synchrony in a number of butterfly species, concluded that dispersal had a significant effect on local synchrony. However, at the regional level, mobility was found not to be a significant factor (Sutcliffe et al. 1996), implying that widespread environmental stochasticity is of overriding importance at large scales. This may provide a proximate explanation for the similarity in long-range synchronization seen in the very mobile larch bud moth compared to the almost stationary gypsy moth. A further complication for our comparison is that the larch bud moth data arise from very mountainous regions of central Europe, while the gypsy moth data arise from more continuous forests of the eastern USA. We are currently undertaking a more detailed analysis of the larch bud moth data to elucidate some of these issues (Bjørnstad et al. 2002).

Mobile predators or parasitoids are a third type of process that has been invoked to explain regionwide synchrony (e.g., Ydenberg 1987, Ims and Steen 1990, Bjørnstad et al. 1999). However, trophic interactants are less likely to have a significant role in the large-scale synchrony of the insect species studied here because the most notable enemies of these insect species (small mammals, parasitoids, viruses) are likely to have mobility comparable to or less than the outbreaking insects themselves. (This may not be true for the gypsy moth because females are practically immobile.) How-

TABLE 3. Spatial synchrony in June mean temperatures at different lag distances.

Species	Distance (km)			
	100	300	500	700
Spruce budworm	0.85 [0.83, 0.88]	0.77 [0.74, 0.80]	0.68 [0.65, 0.71]	0.59 [0.56, 0.62]
Western spruce budworm	0.90 [0.89, 0.92]	0.84 [0.81, 0.86]	0.73 [0.68, 0.78]	...
Larch bud moth	0.88 [0.83, 0.93]	0.80 [0.72, 0.86]	0.69 [0.53, 0.96]	...
Forest tent caterpillar	0.92 [0.90, 0.95]	0.82 [0.76, 0.85]	0.73 [0.68, 0.77]	0.62 [0.56, 0.68]
Mountain pine beetle	0.91 [0.89, 0.92]	0.82 [0.80, 0.85]	0.69 [0.66, 0.72]	0.51 [0.46, 0.55]
Gypsy moth	0.83 [0.81, 0.85]	0.75 [0.73, 0.77]	0.67 [0.64, 0.69]	0.57 [0.54, 0.61]

Note: Numbers in square brackets are 95% confidence intervals.

TABLE 4. Spatial synchrony in June precipitation at different lag distances.

Species	Distance (km)			
	100	300	500	700
Spruce budworm	0.63 [0.61, 0.66]	0.42 [0.39, 0.44]	0.27 [0.25, 0.30]	0.19 [0.16, 0.21]
Western spruce budworm	0.56 [0.49, 0.61]	0.38 [0.32, 0.44]	0.31 [0.23, 0.38]	...
Larch bud moth	0.42 [0.28, 0.57]	0.22 [0.07, 0.36]
Forest tent caterpillar	0.64 [0.54, 0.76]	0.45 [0.33, 0.58]	0.32 [0.19, 0.42]	...
Mountain pine beetle	0.61 [0.57, 0.65]	0.38 [0.35, 0.42]	0.27 [0.23, 0.30]	0.20 [0.15, 0.24]
Gypsy moth	0.62 [0.60, 0.65]	0.41 [0.39, 0.44]	0.27 [0.24, 0.30]	0.20 [0.16, 0.25]

Note: Numbers in square brackets are 95% confidence intervals.

ever, it is possible that spatial synchrony is more subtly affected by trophic interactions through the emergence of self-organized spatial dynamics (e.g., Bascompte and Solé 1998, Bjørnstad and Bascompte 2001). This is an important area for future data analyses.

When Williams and Liebhold (2000a) analyzed synchrony of spruce budworm outbreaks, they used the same raw data that we analyzed here. Their method of detecting synchrony among 160×160 km aggregated cell units was based on cross-correlation analyses of “prewhitened” population values (i.e., residuals after fitting first- and second-order autoregressive models to time series), and the spatial covariance function was approximated by linear regression. Both studies revealed the same general pattern of spatial covariance. However, the present results suggest a somewhat higher

level of “local” synchrony in spruce budworm outbreaks. This difference may be because of our finer scale of observation (100×100 km cell units) and the prewhitening procedure used in the earlier study.

One distinctive pattern in our results was that the spatial correlation functions in the outbreak data generally declined significantly more rapidly with distance than the spatial correlation functions of the weather data (Fig. 2). This pattern broke with the predictions of Moran’s (1953) theorem, which states that the synchrony in the dynamics of populations following identical (linear autoregressive) models will equal the correlation in the environmental perturbations. Thus, whenever spatial correlation in weather declines with distance, Moran’s theorem predicts that the synchrony in dynamics should drop in an identical (if ϵ_t in Eq. 1

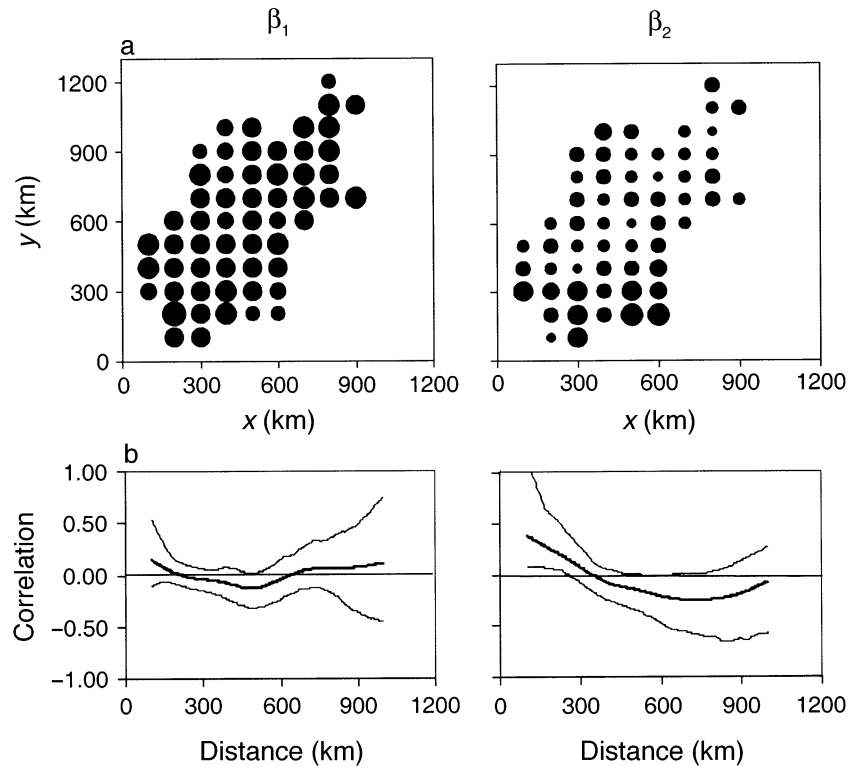


FIG. 3. Spatial continuity of autoregressive-model parameters estimated from the 57 gypsy moth outbreak time series: (a) bigger bubbles correspond to higher parameter values; (b) univariate spline correlograms (with 95% bootstrap confidence intervals) describe the spatial autocorrelation functions of parameter values.

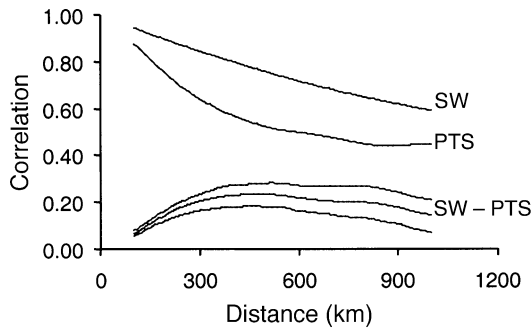


FIG. 4. The mean spatial covariance functions (SCFs) of simulated gypsy moth population time series (PTS) and spatially autocorrelated disturbance, that is, simulated weather (SW). Mean SCFs were calculated from 200 replicated simulations. Difference SW – PTS as a function of distance is presented with crude confidence intervals (estimated by subtracting the confidence intervals for the individual functions).

is completely due to weather) or parallel (if some fraction of ε_t is caused by weather) fashion.

There is mounting evidence that density-dependent dynamics vary regionally in a number of systems (Bjørnstad et al. 1998, Stenseth et al. 1999, Williams and Liebhold 2000b). Our analysis indicated that the outbreak dynamics of gypsy moth varies in a spatially dependent fashion (Fig. 3). The reasons for geographical variation in the local dynamics is not yet clear but probably reflect geographical variation in habitat quality. For example, one of the most evident measures of gypsy moth habitat quality is tree species composition, especially the proportion of oaks, the most favored host species of the gypsy moth in North America (Elkinton and Liebhold 1990).

We hypothesize that spatially dependent variation in density-dependent dynamics may be the mechanism to account for synchrony decaying more rapidly with distance than the correlation in the dominant climatic variables. Our simulations with spatially heterogeneous models supported this new hypothesis. The simulations demonstrated that when the assumption of identical density-dependent dynamics is violated and the dynamic parameters vary in a spatially dependent manner, synchrony will decline more steeply with distance than the correlation in weather (Fig. 4). These results from our exploratory simulations provide motivation for more detailed future research on the subject. The issue of geographical variation in local dynamics is probably of critical importance to understanding spatial synchrony and other spatiotemporal patterns in many animal populations.

In conclusion, our results indicate that the Moran effect is likely to be the dominant mechanism causing spatial synchrony in forest insect outbreaks across the regional scales considered here (100 + km). Dispersal as a synchronizing agent appears to be of less importance than regional stochasticity. At more local scales, the relative influences of these agents remain an open

question. One of the core assumptions of Moran's theorem, identical density-dependent dynamics for all populations, does not appear to be true in our case studies. The extent to which this assumption is violated, the underlying cause of such variation, and more detailed studies of how this affects regional dynamics of forest pest insects are three important areas for future research.

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