Circumpolar variation in periodicity and synchrony among gypsy moth populations

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Summary

1. Previous studies of insect dynamics have detected spatial synchrony in intraspecific population dynamics up to, but not exceeding, 1000 km. Oddly, interspecific synchrony has recently been reported at distances well over 1000 km (at continental and circumpolar scales). While the authors implicated climatic effects as the cause for the apparent large-scale interspecific synchrony, there is no evidence that weather data are synchronized over such great distances.

2. In the present study, intraspecific circumpolar synchrony in the gypsy moth, *Lymantria dispar* (L.), was tested for among 11 regions across three continents (North America, Europe and Asia). Analyses indicate that most gypsy moth populations around the world tend to oscillate at periodicities between 8 and 12 years.

3. These oscillations were synchronized at distances up to *c.* 1200 km within continents. There was no evidence for intraspecific synchrony of gypsy moth populations between continents.

4. We suggest that previous reports of interspecific synchrony among insects at scales much greater than 1000 km may suffer from spurious correlations among oscillating populations.

Key-words: insect outbreaks, *Lymantria dispar*, periodicity, spatial synchrony, wavelet analysis.

Introduction

A common characteristic of the population dynamics of most animal populations is the apparent synchrony of oscillations among geographically disjunct populations (Smith 1983; Ranta *et al*. 1995a; Ranta, Lindstrom & Linden 1995b; Lambin *et al*. 1998; Bjørnstad, Ims & Lambin 1999; Zhang & Alfaro 2003; Liebhold, Koenig & Bjørnstad 2004). Three explanations are frequently posed to explain this synchrony: (1) small numbers of individuals dispersing among populations, (2) small numbers of individuals of enemies dispersing among populations and (3) a relatively small but synchronous random exogenous effect. An example of a synchronizing exogenous effect is random fluctuations

in weather, referred to as the 'Moran effect' (Moran 1953). Studies have demonstrated the existence of intraspecific synchrony over spatial scales up to 1000 km in several forest insect species (Liebhold, Kamata & Jacob 1996; Liebhold & Kamata 2000; Williams & Liebhold 2000; Peltonen *et al*. 2002; Zhang & Alfaro 2003; Økland & Bjørnstad 2004). In addition, synchrony between sympatric populations of two or more species of forest insects has also been noted in several cases (Miller & Epstein 1986; Hawkins & Holyoak 1998; Myers 1998; Raimondo *et al*. 2004a; Raimondo *et al*. 2004b). An extraordinary theory was advanced by Myers (1998) that populations of different forest insect species throughout the northern hemisphere are synchronized. Myers reported that outbreaks were associated with specific weather conditions (cool springs) and specific stages in the solar cycle (troughs) and concluded that this circumpolar interspecific synchronization was an example of the Moran effect. Technically, the phenomenon

observed by Myers should not be classified as a Moran effect; in Moran's original work, he hypothesized that the dynamics of two populations were determined primarily by density-dependent processes, but a small but synchronized exogenous stochastic effect (i.e. weather) could synchronize the populations. In contrast, Myers (1998) envisioned a system in which outbreaks were primarily caused by specific weather events. Hawkins & Holyoak (1998) found similar synchronization of populations of different species of forest insects over thousands of kilometres. This transcontinental synchrony in fluctuations of populations was also ascribed to synchrony in specific weather events.

The question remains as to whether the synchrony among populations separated by thousands of kilometres reported by Myers (1998) and Hawkins & Holyoak (1998) are exceptions or the rule; most other studies of population synchrony in forest insects (Liebhold *et al.* 1996; Liebhold & Kamata 2000; Williams & Liebhold 2000; Peltonen *et al.* 2002; Zhang & Alfaro 2003; Økland & Bjørnstad 2004) report more limited synchrony (up to approximately 1000 km). This more restricted scale of synchrony compares with the findings of Koenig (2002), that in most parts of the world synchrony in weather is generally limited to *c.* 1000 km.

One major difference between the studies of Myers (1998) and Hawkins & Holyoak (1998) and the other studies of forest insect spatial synchrony is that the former measured interspecific synchrony while the latter studied intraspecific synchrony. In the present study we address the transcontinental synchrony of a single species: the gypsy moth, *Lymantria dispar* (L.), which is distributed through most of the northern hemisphere and exhibits outbreaks through much of its range (Giese & Schneider 1979). If transcontinental synchrony were present, it is surmised that it would be stronger within a single species in contrast to interspecific comparisons. Two aspects of synchrony among populations are addressed: synchrony in population fluctuations and phase synchrony (= phase coherence).

Populations of many animal species fluctuate with regular cycles in the order of 10 years. Numerous mammal species in Canada, for example, have long been known to cycle at approximately 10-year periodicities

(Keith 1963). Forest Lepidoptera from the northern hemisphere often cycle with periodicities of 8–11 years (Kendall, Prendergast & Bjørnstad 1998; Myers 1998; Liebhold & Kamata 2000). The most common hypotheses to explain population oscillations are based on density dependent biotic interactions, i.e. predator–prey dynamics (Andersson & Erlinge 1977), maternal effects (Rossiter 1994), induced plant defences (Baltensweiler & Fischlin 1988), host–parasitoid interactions (Berryman 1996) and disease dynamics (Myers 1993). Solar cycles have also been proposed as causal agents in oscillations of snowshoe hare and lynx in Canada (Moran 1949; Sinclair *et al.* 1993). However, the concept of climatic release as a cause of periodic population cycles has been questioned both because of statistical concerns and the lack of periodicity in the climatic deviations that are thought to trigger outbreaks (Martinat 1987; Turchin & Berryman 2000). Although many processes are known to be capable of producing oscillations, identifying the specific mechanism operating in a given system is often difficult.

Materials and methods

Time-series that recorded the yearly forest area defoliated as a result of gypsy moth outbreaks were obtained from 11 regions of the northern hemisphere: five states in the North-eastern United States (Connecticut, Massachusetts, New Hampshire, New Jersey, and Vermont, USA), five European countries (Croatia, Hungary, Romania, Slovakia and Ukraine) and Japan. See Table 1 for descriptions of the origins of the data and areas of each region and Appendix I for raw values of these time series. The gypsy moth is not native to North America but it has been gradually expanding its range. Time series of defoliation in US states included only years after the entire state was infested at potentially defoliating levels (this was determined by only using data from 5 years after the entire state was designated by USDA quarantine regulations to be generally infested. Previous studies (Liebhold *et al.* 1994; Sharov, Liebhold & Roberts 1996) showed that at any location there is a typical 5-year lag between the time that a municipality is declared 'infested' and when defoliation commences.

Table 1. Description of historical records of gypsy moth defoliation

Country/state	Years	Land area (km²)	Source of data
Croatia	1970–2003	56 414	University of Zagreb, Zagreb, Croatia
Hungary	1962–2003	92 340	Forest Research Institute, Matrafured, Hungary
Romania	1953–2004	230 340	Forest Research and Management Institute, Brasov, Romania
Slovakia	1972–2003	48 800	Forest Research Institute, Zvolen, Slovakia
Ukraine	1947–2004	603 700	Ukrainian Research Institute of Forestry & Forest Melioration, Kharkov, Ukraine
Connecticut, USA	1955–2003	12 550	USDA Forest Service, State and Private Forestry, Morgantown, WV
Massachusetts, USA	1924–2003	20 300	USDA Forest Service, State and Private Forestry, Morgantown, WV
New Hampshire, USA	1924–2003	23 231	USDA Forest Service, State and Private Forestry, Morgantown, WV
Vermont, USA	1935–2003	23 956	USDA Forest Service, State and Private Forestry, Morgantown, WV
New Jersey, USA	1972–2003	19 215	USDA Forest Service, State and Private Forestry, Morgantown, WV
Japan	1951–1997	374 744	Japan Forestry Agency, Tokyo

Analysis of periodicity in defoliation intensity within each region was performed through wavelet analysis (Torrence & Compo 1998). Data from each location were log transformed ($\log_{10} + 1$) and normalized to a mean of zero and a variance of one. The Morlet wavelet, a damped complex exponential, was used in the analysis. Global wavelet power spectra for all regions are presented to illustrate graphically the strength of signal across periodicities. The temporally averaged dominant periodicity for each region was also reported. Similarly, periodicity analyses were performed using discrete Fourier transforms for comparison.

Wavelet phase relationships were compared among regions to quantify spatial synchrony in gypsy moth cycles. In a cyclical population, as the population cycles from a trough to a peak and back to a trough again, the phase angle (measured in radians) changes from $-\pi$ to 0 to π, respectively. The π then changes to $-\pi$ and the cycle is repeated. We measured the correlation in these phase angles as an indicator of spatial synchrony among the gypsy moth populations (Grenfell, Bjørnstad & Kappey 2001; Johnson, Bjørnstad & Leibhold 2004; Liebhold *et al.* 2004). Phase values between 8- and 10-year periodicities were focused upon in this analysis because nearly all the regions (except Japan) had strong periodicities within this range (see Results). Because phase states are circular, circular correlation estimates were used to measure inter-regional synchrony (Jammalamadaka & SenGupta 2001). Inter-regional distances from 0 to 1400 km (intracontinental) and from 6000 to 11 000 km (intercontinental) were compared separately because there were no inter-regional distances between these two ranges. Correlation coefficients were calculated between the vectors of phase values at discrete periodicities between all regional pairings. These data were bootstrapped 1000 times by randomly sampling correlation coefficients (from between the 8–10-year periodicity range) from all pairs of regions whose separation distance fell within the specified intra- or intercontinental distances. From these 1000 sets of bootstrapped data, we created 1000 spatial smoothing spline correlograms of correlation as a function of distance with a smoothing parameter equal to 10^{-7}. The autocorrelation values at each smoothing spline break (each representing a lag distance) in each of the 1000 smoothing splines were calculated and then sorted in ascending order. Thus, the median autocorrelation values (500th sorted value at each break) was used to estimate median correlation while the 25th and 975th values were used to estimate the 95% confidence interval of the correlogram. Smoothing splines were then fitted to each of these three sets of values to estimate the median and 95% confidence intervals of correlation as a function of distance.

As a third measure of spatial synchrony, a spatial spline correlogram (Bjørnstad & Falck 2001) was constructed from pairwise comparisons of changes in intensity of gypsy moth defoliation [$\log_{10}(N_{t+1} + 1) - \log_{10}(N_t + 1)$]. Because all data were normalized, the sample autocorrelation $\rho_{ij,t}$ between two sites i and j at time t was the product of the normalized data of the two samples at time t:

$$\rho_{ij,t} = z_{i,t} * z_{j,t}$$

where $z_{i,t}$ is the normalized change in defoliation intensity in region i at time t. Across all pairwise comparisons of the 11 regions (with multiple temporal components) there were 2140 values of ρ. These data were bootstrapped 1000 times by randomly sampling 2140 values of ρ with replacement and recording the corresponding great circle distances (δ) between the respective regions. Two spatial correlograms with median and 95% confidence intervals were created for the two ranges of interpatch distance, as described above.

Results

Time-series of defoliation intensity by the gypsy moth in 11 regions of the northern hemisphere are presented in Fig. 1. Dominant periodicities in eight of the 11 regions ranged between 8 and 12 years (Table 2). The exceptions were Ukraine, with a dominant periodicity = 16·53 year, New Jersey with a dominant periodicity of 4·91 year, and Japan with a dominant periodicity of 5·84 year. Note that even these exceptions had secondarily strong periodicities between 8 and 12 years (Fig. 2) (although that for Japan was only of moderate strength). Thus, all five US states had modes of strong periodicity between 8 and 12 years [although the periodicities were only significant ($Ps < 0·05$) in New Hampshire and Vermont]. Connecticut had two other modes of strong periodicity, one around 5 years ($P < 0·05$) and the other at 16 years ($P > 0·05$). All five of the European countries had modes of strong periodicity between 7 and 10 years [four of which were significant ($P < 0·05$): Croatia, Hungary, Romania and Slovakia]. Croatia had a second periodicity that was significant around 2–3 years ($P < 0·05$) and a third non-significant mode of

Table 2. Dominant periodicities of gypsy moth population dynamics around the world based on wavelet analysis with the Morlet wavelet function

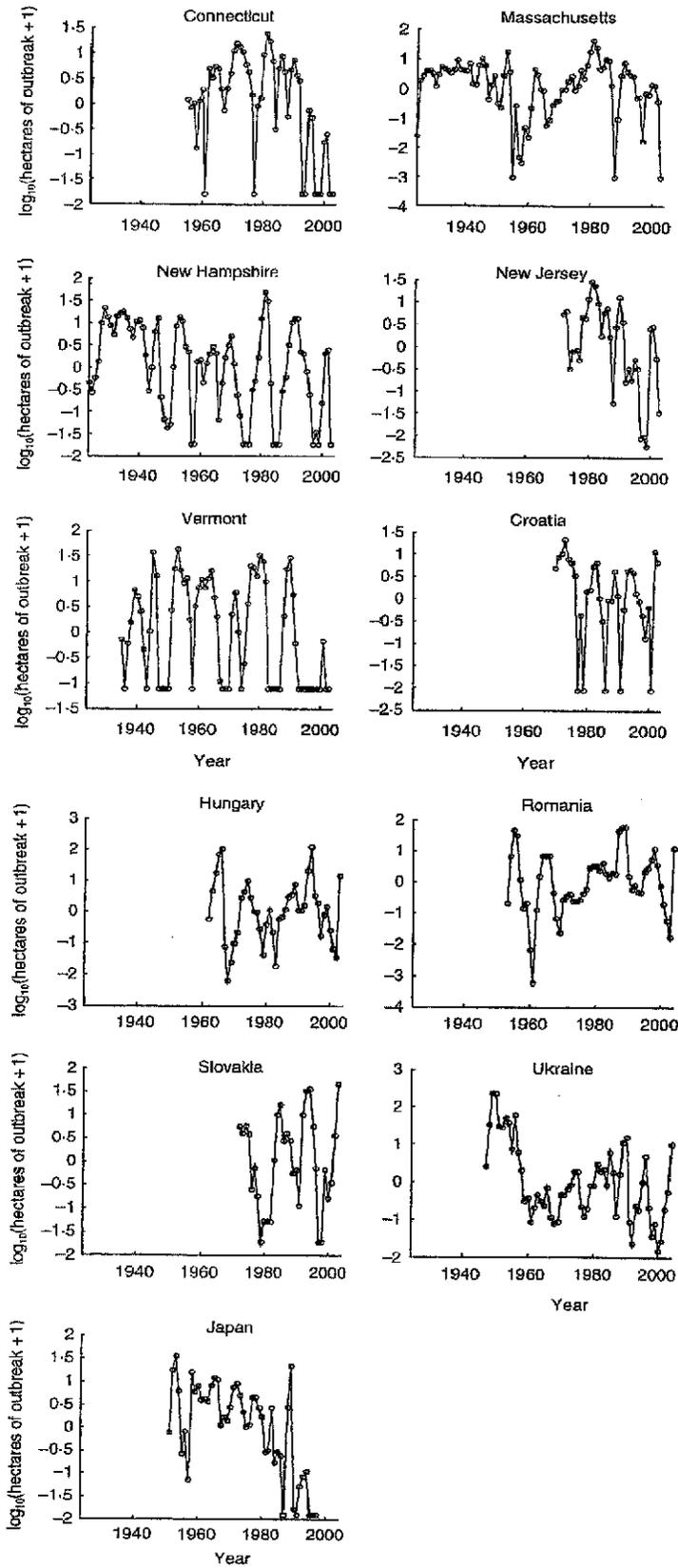| Region	Dominant periodicity (years)
USA	
Connecticut	8·26
Massachusetts	9·83
New Hampshire	11·69
New Jersey	4·91
Vermont	9·83
Europe	
Croatia	9·83
Hungary	9·83
Romania	8·26
Slovakia	9·83
Ukraine	$\geq 16·53$
Asia	
Japan	5·84

Fig. 1. $Log_{10} + 1$ transformed defoliation intensity data of the gypsy moth in 11 regions across the northern hemisphere (data are standardized to $\bar{x} = 0$ and variance = 1).

886
D. M. Johnson
et al.

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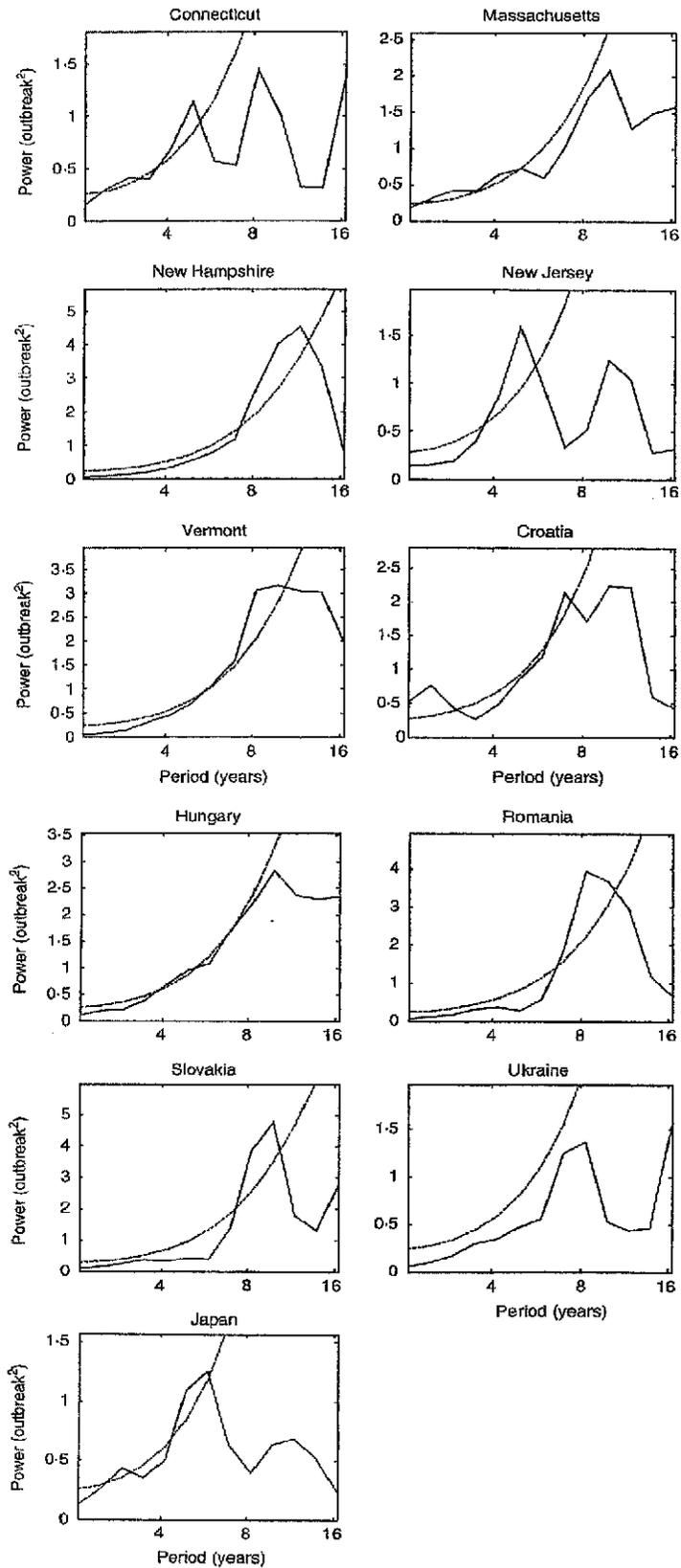*Journal of Animal
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Fig. 2. Global periodicity spectrum of gypsy moth outbreaks across 11 regions in the northern hemisphere. The solid line indicates strength of periodicities. Periodicity strengths above the dashed line indicate significant periodicities at the 95% confidence level.

strong periodicity at around 10 years. Japan had two significantly strong periodicities, one at around 3 years and the second at around 5–6 years. Overall, the periodograms reveal that the periodicity of gypsy moth dynamics were similar among the states of the US and the countries of Europe. Japan, on the other hand, had a shorter dominant periodicity. Despite the strong periodicities in the 8–12-year range most were insignificant, possibly because some of the time-series were somewhat limited in scale. For example, the shortest time series would capture only three cycles at a 10-year periodicity, at which scale only a very strong periodic signal would be significant. Periodograms constructed from discrete Fourier transforms also revealed strong periodicities at the 8–12-year range at all sites, and secondary periodicities from 4 to 7 years at most sites.

Fluctuations in gypsy moth defoliation intensity was positively correlated between regions that were less than 1300 km apart in 18 of 20 pairwise comparisons. The spatial correlogram indicates that defoliation in regions that were less than *c.* 1200 km apart were

positively correlated ($P < 0.05$, Fig. 3a). In comparison, there was significant positive correlation between wavelet phase values at interpatch distances only up to 600 km (intracontinental comparisons, Fig. 4a). At great circle distances greater than 6000 km, however, 19 of 35 pairwise comparisons of changes in defoliation intensity were positively correlated, which is close to the 50% of comparisons that could be expected to be positive by chance. The spatial correlogram at these distances indicates no synchrony in fluctuations at distances greater than 6000 km (Fig. 3b). The average correlation of comparisons between 6000 and 11 000 km was approximately 0·01 and was not significantly different from zero. Similarly, in transcontinental comparisons of phase values, the average correlation was less than 0·1 and revealed no significant synchrony between 6000 and 11 000 km (Fig. 4b). In short, these results reflect synchrony in the population dynamics of the gypsy moth within a continent (the US and Europe), but no evidence for synchrony at transcontinental distances between 6000 and 11 000 km.
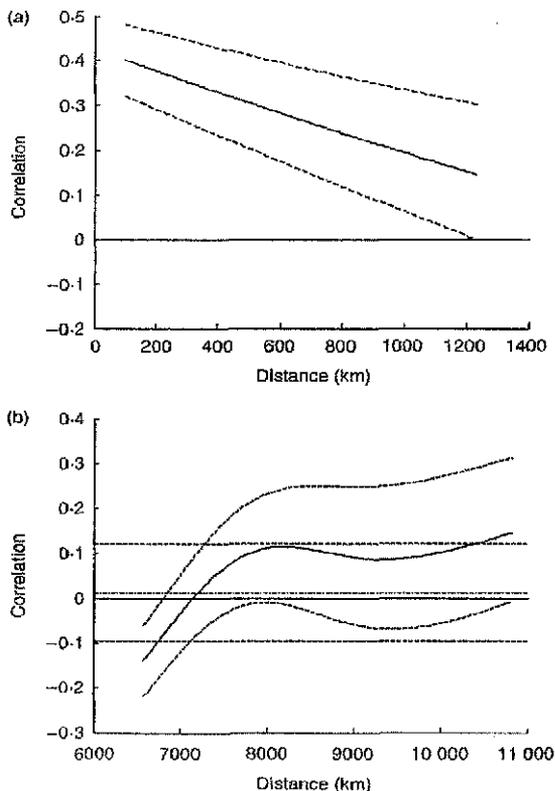

Fig. 3. Spatial covariance function (solid lines) estimated from gypsy moth defoliation data with 95% confidence intervals (dashed lines). The horizontal solid line represents no correlation (= 0). Intracontinental comparisons are presented in (a) and intercontinental comparisons are presented in (b). The horizontal dash-dotted line in (b) indicates the average correlation across the entire range of intercontinental distances (6000–11 000 km) and the horizontal dashed lines represent the 95% confidence interval.

Fig. 4. Spatial covariance function (solid lines) estimated from wavelet phase values with 95% confidence intervals (dashed lines). The thick horizontal solid line represents no correlation (= 0). Intracontinental comparisons are presented in (a) and intercontinental comparisons are presented in (b). The horizontal dash-dotted line in (b) indicates the average correlation across the entire range of intercontinental distances (6000–11 000 km) and the horizontal dashed lines represent the 95% confidence interval.
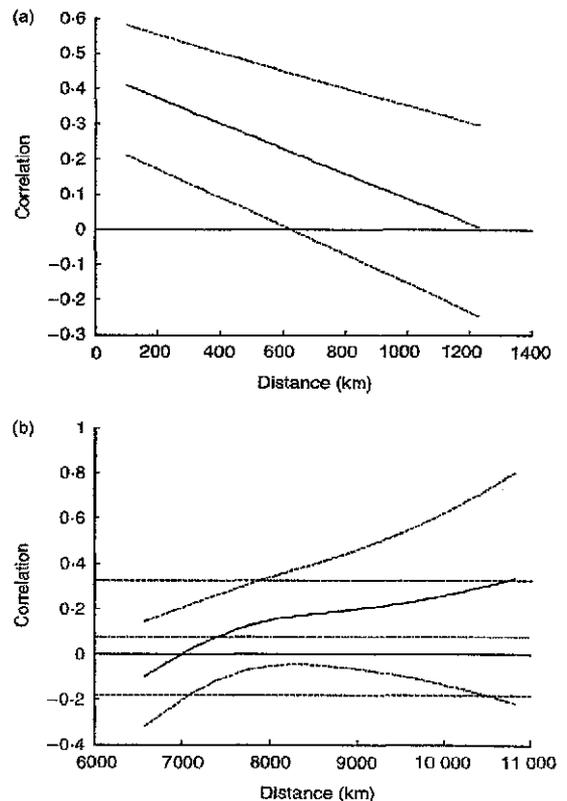
Discussion

Spatial synchrony among geographically disjunct populations of the same species is a common pattern among many species and could be the result of a number of processes, such as the Moran effect (Moran 1953) or dispersal (Bjørnstad *et al.* 1999). Peltonen *et al.* (2002) analysed historical maps of defoliation and compared patterns of intraspecific spatial synchrony among six species of forest insects (including the gypsy moth). Because they found that synchrony was not extended over longer distances in species of insects with capacities for movement much greater than North American gypsy moths (which have limited movement capabilities due to the lack of flight by adult females), they concluded that regional stochasticity (Moran effect) is a more dominant synchronizing agent of forest insect populations. The historical gypsy moth defoliation time series that Peltonen *et al.* (2002) analysed were slightly different than the series analysed here. Their series were shorter (1976–99) and were aggregated in 100 × 100 km cells. The analysis of Peltonen *et al.* (2002) indicated that gypsy moth outbreaks were synchronized over distances up to 600 km. Temperature and precipitation across the gypsy moth's range in the north-eastern US was synchronized over lag distances up to and greater than 800 km (Peltonen *et al.* 2002), thus suggesting that the regional stochasticity could be synchronizing gypsy moth outbreaks at this regional scale. They found no significant synchrony at distances greater than 1000 km. The results of our analysis of populations across the northern hemisphere were varied, where significant synchrony was detected up to 1200 km using spatial covariance analysis of defoliation series, but only up to 600 km using wavelet phase analysis. These results suggest that analysis of fluctuations in defoliation was a more powerful method for detecting synchrony than wavelet phase angle analysis. There was no evidence for synchrony in gypsy moth outbreaks at intercontinental distances between 6000 and 11 000 km.

Thus, there is no evidence for intercontinental synchrony among gypsy moth populations in this study. This is surprising, considering the finding of interspecific synchrony in forest insect outbreaks (including the gypsy moth) over thousands of kilometres by Myers (1998) and Hawkins & Holyoak (1998). Moreover, Selas *et al.* (2004) propose that forest insect outbreaks may be caused indirectly by low sunspot activity, which would result in global synchrony. The authors reason that UV-B radiation from the sun peaks in periods of low sunspot activity (Rozema *et al.* 2002), causing trees to respond by increasing the production of UV-B protective phenolics at the expense of production of chemicals for herbivore resistance. This possible mechanism for global synchrony in forest insect outbreaks requires further scrutiny, and apparently does not apply to the outbreak dynamics of the gypsy moth based on the results of the current study. Myers (1998) reported seven gypsy moth outbreaks in Europe from 1934 and

1985, and seven outbreaks in Vermont from 1941 to 1990. In 2 years outbreaks were simultaneous in both regions. To test whether this is a significant number of synchronous outbreaks, a Monte Carlo simulation model was run and outbreak series were replicated 10 000 times for each region (Vermont and Europe). In the model, the first outbreak was restricted to occur in each region independently somewhere between 1934 and 1941 (this range was selected because it is the empirical range of the first outbreaks, and 8 years is the mean interval between outbreaks). Then six more outbreak years were selected randomly based on the observed distributions of time intervals between outbreaks (from the empirical data) in Vermont and Europe, respectively. For example, if the first outbreak occurred in Vermont in 1940, and the randomly selected time interval was 10 years, then the next outbreak occurred in 1950, and so forth until each region had had seven outbreaks. Time intervals between outbreaks were selected with replacement. The distribution of the number of co-occurring outbreaks in each replicate was calculated. The result indicated that at least two co-occurring outbreaks could occur randomly 18% of the time; thus, the observed coincidence could occur by chance without any synchronizing effect. The analyses used by both Myers (1998) and Hawkins & Holyoak (1998) are based on the probability of coincidence of outbreaks and did not take into account the periodic behaviour of populations. However, it is well known that two time-series that are serially dependent and/or oscillatory are prone to spurious correlation (Royama 1992; Buonaccorsi *et al.* 2001; Brockwell & Davis 2002). Temporal auto-correlation violates the assumption of independence among samples that is implicit when testing the significance of correlation between two series. Furthermore, many insect species oscillate with similar periods (Kendall *et al.* 1998) and coincidence of peaks is likely to occur by simple chance. Thus, the conclusions of global synchrony proposed by Myers (1998) and Hawkins & Holyoak (1998) must be questioned.

Periodic fluctuations in population size are pervasive across many species. Of nearly 700 time-series of 25 years or longer, 30% exhibited periodic cycles (Kendall *et al.* 1998). Interestingly, an inordinate number of species around the world appear to have periodic cycles of approximately 10 years (Keith 1963; Myers 1998). As stated above, there are many arguments against the idea that insect populations are merely tracking some periodic weather phenomenon. If not because of weather, then why are the dominant periodicities among gypsy moth populations consistently between 8 and 12 years in eight of the 11 regions across the northern hemisphere ($\bar{x} = 11·25 \pm 3·31$ years)? Theoretical models demonstrate that host–parasitoid (Nicholson & Bailey 1935), host–pathogen (Anderson & May 1981) and predator–prey interactions (Rosenzweig & MacArthur 1963) can cause periodic cycles. Thus, one hypothesis is that something intrinsic in the trophic interactions of the gypsy moth and other forest insect populations is

the cause of 10-year cycles. In fact, some consumer–resource models consistently exhibit periodicities with a minimum of 6 years (Lauwerier & Metz 1986; Ginzburg & Taneyhill 1994), supporting this hypothesis. Dwyer, Dushoff & Yee (2004) proposed a model that incorporated virus epizootics, induced host plant responses and a type III functional response by small mammal predators, and this model was capable of producing the characteristic 10-year cycles seen in gypsy moth populations. Liebhold & Kamata (2000) hypothesized that gypsy moth outbreaks are triggered by periodic total mast failures in oak-dominated forests. Extensive ecological studies (Campbell & Sloan 1977; Elkinton *et al.* 1996) have implicated predation by small mammals as a critical regulating agent in the dynamics of low density gypsy moth populations. Small mammal population dynamics are highly influenced by the availability of mast during winters and thus function to link gypsy moth populations to mast abundance (Elkinton *et al.* 1996; Jones *et al.* 1998; Liebhold *et al.* 2000). Because mast seeding is known to be periodic, this could serve as the source of periodicity in gypsy moth populations.

While the precise identity of the mechanisms causing gypsy moth oscillations is not certain, it seems most likely that these oscillations are results of one or more of its trophic interactions, and that these interactions are similar (but not necessarily synchronized) between the US and Europe. The shorter periodicity in cycles of the gypsy moth in Japan may indicate different trophic interactions in this region. There are no studies utilizing identical methods available for comparing the trophic factors affecting gypsy moth populations in North America, Europe and Japan. However, there is evidence that the important role of small mammals that has been identified in the dynamics of North American gypsy moth populations may also be operating in Japan (Liebhold, Higashiura & Unno 1998) and Europe (Gschwantner, Hoch & Schopf 2002). Population dynamics of small mammals, in turn, respond to mast seeding fluctuations in forest trees (Hansen & Batzli 1978). It is possible that the variation in periodicity of gypsy moth populations observed among regions around the northern hemisphere may reflect the varying periodicities of mast seeding in the forests where they occur.

Acknowledgements

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Appendix I.

Raw data of hectares of forest defoliated by the gypsy moth by region

	Europe					North America					Asia
Year	Croatia	Hungary	Romania	Slovakia	Ukraine	CT	MA	NH	VT	NJ	Japan
1924							66	239			
1925							19 563	97			
1926							31 657	389			
1927							53 393	1 588			
1928							55 515	48 485			
1929							38 493	178 480			
1930							11 278	83 047			
1931							35 099	39 146			
1932							81 128	17 525			
1933							63 564	87 720			
1934							51 918	115 741			
1935							42 954	133 682	43		
1936							61 728	77 779	0		
1937							159 357	29 544	33		
1938							62 489	13 815	168		
1939							58 013	55 373	2 150		
1940							50 845	61 861	1 279		
1941							106 627	32 623	397		
1942							14 864	2 819	20		
1943							13 960	117	0		
1944							91 351	950	85		
1945							184 952	23 691	38 036		
1946							87 908	74 471	6 437		
1947					11 400		2 938	67	0		
1948					37 000		13 112	9	0		
1949					93 000		31 848	3	0		
1950					90 700		2 016	5	0		
1951					35 700		1 289	1 003	449		585
1952					34 900		33 349	38 451	10 925		68 896
1953			24 900		45 700		371 658	84 751	48 902		197 776
1954			189 584		38 700		47 812	62 354	9 980		14 781
1955			594 458		18 700	2 770	0	6 063	3 593		116
1956			473 233		48 800	1 400	1 551	3 767	5 115		651
1957			69 641		16 900	1 987	6	0	200		15
1958			20 164		10 200	47	3	0	0		58 841
1959			24 900		4 300	2 421	155	1 619	607		13 986
1960			3 300		4 700	6 073	61	1 862	2 483		21 365
1961			800		2 400	0	1 215	251	4 791		7 443
1962		2 200	18 800		3 600	33 721	60 729	1 372	2 547		7 984
1963		6 310	79 600		5 100	16 251	35 566	3 379	4 866		6 786
1964		12 597	195 900		4 300	39 900	8 416	5 874	9 523		21 967
1965		25 912	196 000		3 800	34 821	6 977	3 421	1 175		39 474
1966		31 923	196 000		6 300	6 435	202	8	263		34 098
1967		755	39 000		2 700	1 106	368	227	1		1 070
1968		211	12 800		2 300	6 646	1 589	2 360	0		1 951
1969		427	6 900		2 400	23 029	2 453	6 947	0		1 456
1970	9 438	853	29 000		5 100	149 274	2 767	15 597	0		4 307
1971	21 186	1 339	33 300		5 100	265 226	7 606	1 316	320		19 070
1972	27 882	4 909	37 500	1 450	6 000	208 049	8 291	81	1 706	91 555	26 237
1973	79 832	6 221	27 300	1 100	6 800	134 905	17 802	12	81	103 184	10 646
1974	19 431	9 530	27 500	1 500	9 900	48 980	31 135	0	0	11 377	2 913
1975	14 162	4 956	29 310	1 050	9 900	25 672	7 245	0	6	22 441	924
1976	5 538	2 938	37 700	100	3 700	3 971	12 073	0	709	23 332	1 076
1977	0	2 812	45 900	250	2 800	0	53 879	130	13 536	15 864	8 924
1978	271	1 510	117 400	75	3 500	1 553	25 523	294	12 047	82 927	8 773
1979	0	562	124 300	10	6 700	3 031	91 603	2 421	6 239	78 421	4 115
1980	1 633	1 801	123 400	25	6 700	110 208	367 237	74 494	30 402	166 791	2 021
1981	1 843	3 080	102 400	25	12 200	600 087	1 144 168	788 355	19 830	323 397	134
1982	10 816	1 326	142 500	25	10 000	325 426	560 026	355 576	3 994	273 678	150
1983	14 046	372	92 600	350	10 500	62 040	59 973	227	0	137 767	4 003
1984	966	2 186	77 100	2 450	6 800	220	75 109	0	0	39 957	58
1985	173	2 403	94 500	3 700	17 100	36 253	167 645	0	0	96 903	139
1986	0	3 167	89 100	800	9 800	96 047	138 903	0	0	113 478	101

Appendix I. *Continued*

Year	Europe					North America					Asia
	Croatia	Hungary	Romania	Slovakia	Ukraine	CT	MA	NH	VT	NJ	Japan
1987	841	5 167	582 012	1 100	2 800	26 463	11 635	117	0	38 504	0
1988	829	5 615	695 105	800	9 300	664	0	411	285	3 008	4 255
1989	7 640	8 283	687 400	200	22 400	31 753	385	7 447	11 067	55 591	97 860
1990	1 206	3 084	81 100	225	26 500	71 488	33 844	53 927	25 506	174 589	1
1991	0	3 055	46 400	50	2 400	20 305	114 228	73 227	1 456	68 785	0
1992	431	3 703	54 147	2 400	1 300	12 809	50 119	73 917	34	6 717	9
1993	7 738	13 960	40 672	6 750	3 800	0	35 904	4 079	0	11 219	20
1994	8 406	34 326	39 900	7 450	3 400	0	31 117	3 283	0	7 225	30
1995	6 636	5 390	98 800	1 500	7 400	1 095	3 525	688	0	16 024	0
1996	1 375	4 078	116 600	250	15 200	568	3 755	85	0	11 332	0
1997	774	1 173	168 700	10	3 600	0	41	0	0	773	0
1998	276	2 610	267 300	10	1 600	0	5 250	2	0	808	
1999	49	3 566	133 700	231	2 288	0	4 792	0	0	559	
2000	500	1 463	53 900	70	1 044	75	13 081	40	0	53 933	
2001	0	712	24 120	135	1 396	149	12 169	3 563	40	57 019	
2002	32 696	518	11 961	1 000	3 408	0	2 462	4 783	0	16 928	
2003	14 286	11 580	5 800	8 931	5 610	0	0	0	0	2 081	
2004			270 500		21 519						