

REPORT

Landscape geometry and travelling waves in the larch budmoth

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Abstract

Travelling waves in cyclic populations refer to temporal shifts in peak densities moving across space in a wave-like fashion. The epicentre hypothesis states that peak densities begin in specific geographic foci and then spread into adjoining areas. Travelling waves have been confirmed in a number of population systems, begging questions about their causes. Herein we apply a newly developed statistical technique, wavelet phase analysis, to historical data to document that the travelling waves in larch budmoth (LBM) outbreaks arise from two epicentres, both located in areas with high concentrations of favourable habitat. We propose that the spatial arrangement of the landscape mosaic is responsible for initiating the travelling waves. We use a tri-trophic model of LBM dynamics to demonstrate that landscape heterogeneity (specifically gradients in density of favourable habitat) alone, is capable of inducing waves from epicentres. Our study provides unique evidence of how landscape features can mould travelling waves.

Keywords

Connectivity, epicentre hypothesis, insect outbreaks, landscape geometry, larch budmoth, travelling waves, tri-trophic model, wavelet phase analysis, *Zeiraphera diniana*.

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INTRODUCTION

Several species of forest insects are known to reach outbreak levels, often resulting in large-scale forest defoliation and/or tree mortality. While considerable progress has been made in quantifying temporal patterns and understanding their underlying mechanisms (Turchin 1990; Berryman 1996), much less is known about causes of complex spatial patterns that often characterize these outbreaks. Theoretical ecologists have long demonstrated that relatively simple spatial interactions (e.g. interactions between predators and prey with different relative mobilities) are capable of generating a variety of possible spatial patterns (Hassell *et al.* 1991; Bjørnstad & Bascompte 2001). One particularly compelling characteristic of outbreak patterns is the phenomenon of moving outbreaks or ‘travelling waves’ (Okubo 1980; Bjørnstad *et al.* 1999). Travelling waves are characterized by temporal lags in spatial synchrony where outbreaks shift from one location to an adjacent location in successive years (Bjørnstad *et al.* 2002).

The so-called ‘epicentre’ hypothesis states that regional outbreaks begin in specific *foci* and then spread into adjoining areas. This hypothesis has been advanced for

many forest insect species, including the spruce budworm, gypsy moth, and mountain pine beetle (Berryman 1987; Wallner 1987; Liebhold & McManus 1991; Royama 1992). Various hypotheses attempt to explain epicentre dynamics (outbreak spread from foci) in forest insect populations. The most common version of this hypothesis is that regional outbreaks start in the habitats of the highest quality (where pest population growth is greatest) and spread via dispersal to elevate pest densities in the surrounding suboptimal habitats to induce secondary outbreaks (Royama 1992). Despite substantial efforts, models of specific systems that incorporate spatial heterogeneity are surprisingly resistant to producing outbreaks that expand from epicentres (Liebhold & McManus 1991). What is more, a previous model for larch budmoth (LBM) host–parasitoid dynamics revealed the counter-intuitive result that theoretical outbreaks spread from low quality (from the point of view of the moth) to high habitat quality (Bjørnstad *et al.* 2002). This is in apparent contradiction to classic epicentre hypotheses.

The field of landscape ecology addresses how landscape mosaics – i.e. the spatial interspersions of favourable habitats (*‘patches’*) and non-favourable habitats (*‘matrix’*) – affect ecological processes (Turner *et al.* 1989; Wiens *et al.* 1993). The idea here is that proximity of favourable habitats,

and/or ‘permeability’ (Stamps *et al.* 1987) of any intermediate (matrix) habitat, will enhance interdispersal (‘connectivity’) between such habitats. In this way, immigration will subsidize and enhance population growth in central habitats. Indeed, previous studies suggest that landscape heterogeneity and fragmentation affect the dynamics of pest populations (Shigesada *et al.* 1986; Roland 1993).

In this study we propose a revised epicentre hypothesis based on landscape geometry, that habitat fragmentation interacts with dispersal to form outbreak foci. We examine a population system [the LBM (*Zeiraphera diniana* Guenee, syn. *Z. griseana* Hübner) in the European Alps] where travelling waves of outbreak have been previously identified (Baltensweiler & Rubli 1999; Bjørnstad *et al.* 2002). By combining wavelet phase analysis with spline gradient estimation, we demonstrate that the outbreaks originate in two distinct epicentres and these epicentres are located in the most habitat dense and well-connected landscapes. Thereafter the outbreaks spread to peripheral areas of more sparse and poorly connected habitat. We use a spatially extended tri-trophic model to demonstrate that such habitat geometry alone can induce these travelling waves.

METHODS

Data description

The LBM undergoes 8–9-year cycles in abundance that have been theorized to result from interactions with its larch food-resource and a guild of parasitoids (Turchin *et al.* 2003). Populations of the LBM have high reproductive potential, leading to rapid population growth when resources are plenty and enemies are few (Baltensweiler & Rubli 1999). Furthermore, because of the moth’s high

mobility, local population growth is sometimes significantly enhanced by immigration (Baltensweiler & Rubli 1999). The LBM is primarily found in the mixed larch forests that are found in an altitudinal band between 500 and 2000 m across the European Alps. The optimal habitat appears to be the mixed larch–cembran pine forests in the subalpine zone above 1500 m (Baltensweiler & Rubli 1999). Because of the jagged nature of the Alps, this habitat is fragmented and interspersed by valleys and higher mountains. This is important because geographic variation in landscape mosaic and climatic patterns may potentially affect the extent to which local populations of the LBM can be enhanced through immigration ‘subsidies’ from neighbouring areas (Baltensweiler & Rubli 1999).

The main forest habitat of the LBM extends in a predominantly east–west direction across the Alps, but with important geographic variation in habitat breadth and density within the landscape mosaic (Fig. 1). This variation results in local differences in how dispersal ‘connects’ local habitats to other suitable habitats across the LBM range. By connectivity, we specifically mean the potential for immigration subsidies into a patch of suitable habitat from other suitable habitat patches. We measured connectivity (Ω) with a Gaussian distribution function describing the pairwise connectivity of quadrats as a function of inter-quadrat distance (x_{ij}) and moth dispersal ability (reflected in the parameter α),

$$\Omega_i = \frac{\sum_{j=1}^n e^{-(x_{ij}\alpha^{-1})^2}}{C}, \quad (1)$$

where C is the normalization constant that scales $\Omega = 1$ when there is no habitat fragmentation. Obviously, the

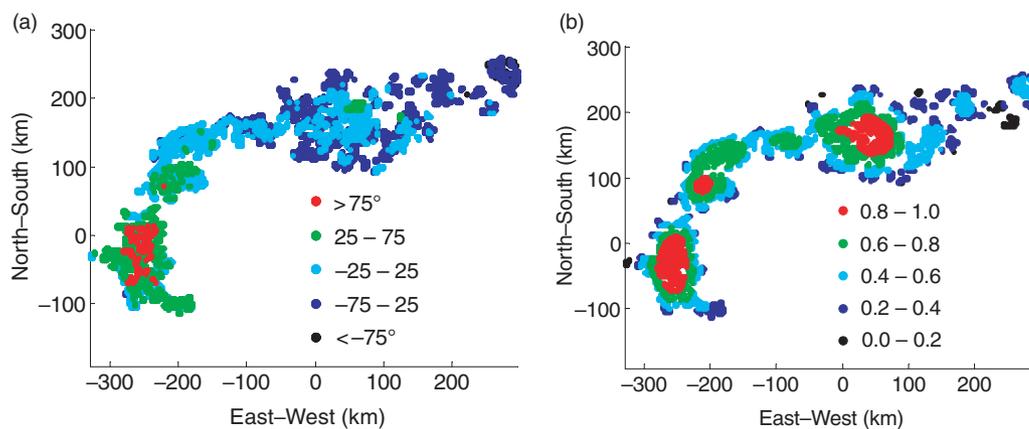


Figure 1 (a) Time-averaged phase angles of larch budmoth (LBM) outbreaks. Highest phase angles (red) indicate epicentre locations and lower phase angles indicate subsequent areas of spread. (b) Relative connectivity measures of LBM habitat across the Alps based on Gaussian dispersal with $\alpha = 25$. The connectivity measures were rescaled where the location with the highest connectivity equals 1.

effect of 'landscape features' on population dynamics depends on the dispersal ability as measured by the dispersal kernel of the study species and the geometry of the habitat. This kernel can be approximated based upon data from the literature on LBM dispersal (Furuta 1978; Baltensweiler & Rubli 1999).

At peak densities, the LBM defoliates large tracts of the larch-cembra pine forest, leaving an easily recognizable signature. From 1961 to 1998, yearly defoliation was mapped during aerial surveys of the entire Alps region (Baltensweiler & Rubli 1999). The presence/absence of defoliation was recorded in each 1×1 km area of the Alps. For this study, we aggregated the defoliation data into 3×3 km quadrats, thus intensity of defoliation was rated at one of 10 possible levels, ranging from 0/9 to 9/9. We restricted our analyses to quadrats with at least two LBM outbreaks over the 38-year period (3122 quadrats in total). Quadrats with fewer than two outbreaks were excluded from the analysis because they are likely to represent marginal or unsuitable habitat for the LBM.

The presence of LBM habitat in each 3×3 km cell was classified based on the historical (1961–1998) presence of defoliation at least once over that interval. The data from Baltensweiler & Rubli (1999) and Furuta (1978) were used to estimate a Gaussian dispersal kernel and to calculate connectivity for each 3×3 km cell.

Wavelet phase analysis

We used wavelet phase analysis (Grenfell *et al.* 2001) to characterize spatial waves in LBM outbreaks. An advantage to wavelet analysis is that, in addition to calculating a temporally averaged power spectrum across periodicities, it can detect temporal shifts in periodicity. The Morlet wavelet function (a damped complex exponential) appeared to be an adequate describer of periodicities in the data. Wavelet analysis was initially performed on the time series of yearly spatial averages (over the entire Alps) of outbreak intensity to identify the dominant periodicity (*c.* 8–9 years). Next, the time series from each of the 3122 3×3 km quadrats across the Alps were subjected to wavelet decomposition. From the wavelet decomposition for the 8-year scale, ψ , we calculated time series of wavelet phase angles [in degrees as $(180/\pi) \times \arctan(\text{Im}(\psi)/\text{Re}(\psi))$] where $\text{Im}(\psi)$ and $\text{Re}(\psi)$ represent the imaginary and the real part of the wavelet decomposition, respectively (Grenfell *et al.* 2001). Phase angle values range from -180° to 180° . As a population cycles from a trough to a peak, the phase angle increases from -180° to 0° . As a population cycles from a peak to a trough, the phase angle continues to increase from 0° to 180° . Time series of relative phase angles were calculated for each quadrat by subtracting the temporal vector of spatial mean phase angles from the corresponding temporal vector

of phase angles for each quadrat. Lastly, a mean relative phase angle (MPA) was calculated for each quadrat by averaging the vector of time-specific relative phase angles. Thus, the MPA is the average phase angle of a given location relative to the spatial average across the entire Alps. The MPAs summarized the spatial wave dynamics; for example, if two populations have MPAs of 0° and -90° , respectively, and the cycle periodicity is 8 years (over 360° , thus a 45° change equals 1 year), then the cycle of the second population trails that of the first by 2 years. The quadrats with the highest MPAs, thus, represent the locations of outbreak origins (epicentres), while smaller MPAs indicate areas of subsequent outbreaks. Because phase angles are circular, we used the largest gap among the sorted MPAs to identify the leading location (primary epicentre).

Epicentres and wave speeds

To estimate the two-dimensional direction and speed of the outbreak waves, we fit a thin-plate spline (smoothing parameter $s = 1 \times 10^{-6}$) to the MPA data (3122 quadrats) with northing and easting as 'covariates'. Partial derivatives of the smoothing spline provided local estimates of wave (vector) directions and speeds (slopes) for each location on the map of the European Alps. Epicentres were identified as locations from which waves emanated radially. The smoothing spline slopes that characterized changes in MPA over space were used to estimate wave speeds per yr (in this case of an 8-year cycle), by determining the distance spanned over a 45° change in MPA. Temporal variation in mean wave speed was examined by dividing the first 32 years of data into four parts, each consisting of 8 years of data, and repeating the analysis of smoothing splines described above.

RESULTS

Spatial comparisons of wavelet phase angles indicate multiple wave epicentres: a primary wave focus located in the south-western Alps and secondary foci in the central south-western and central north-eastern Alps (Fig. 1a). These epicentres coincide with the three areas of high connectivity (Fig. 1b). The vector plot of wave direction and speed (based on the derivatives of thin-plate spline of MPA on latitude and longitude) illustrates how LBM waves originate from two dominant foci that correspond with two of the three areas of high connectivity (Fig. 2). The locations of the wave foci suggest that connectivity influences and/or determines the epicentre dynamics. The association was confirmed by the positive relationship between MPA and connectivity in both the south-western and north-eastern portions of the Alps (Fig. 3).

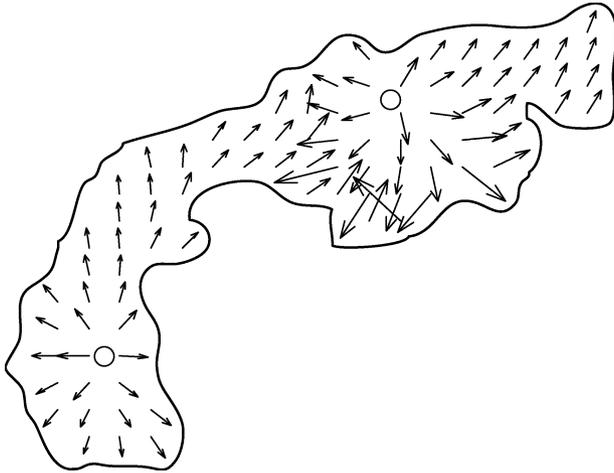


Figure 2 Vector plot indicating local relative speeds and directions of larch budmoth wave movement across the Alps. The circles indicate two-wave epicentres.

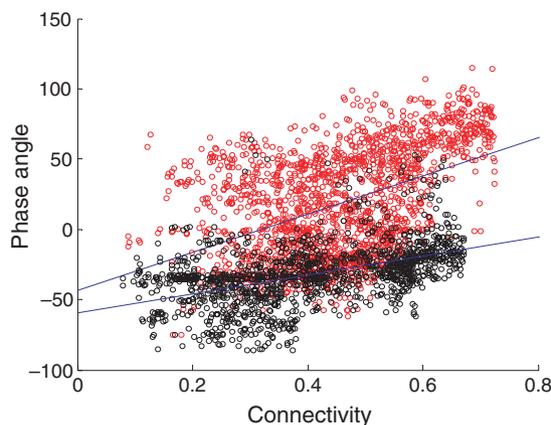


Figure 3 Regression plot of location-specific phase angles on location connectivity in the southwest (red, $r^2 = 0.21$, $p < 0.001$) and northeast (black, $r^2 = 0.23$, $p < 0.001$) portions of the Alps. Connectivity values are based on the Gaussian dispersal kernel with the parameter $\alpha = 25$ km and are relative to the connectivity value of a quadrat in unfragmented habitat (which would have a connectivity value = 1). A sensitivity analysis indicated that the relationship between phase angle and connectivity is robust to changes in the dispersal parameter used to calculate connectivity α (in values ranging from $c. 20$ to 60 , r^2 range from 0.15 to 0.23 ; see Appendix S1 in Supplementary Material).

A two-dimensional analysis of the MPAs revealed a mean wave speed of 254 ± 283 km year⁻¹ (range: 84–1593 km year⁻¹ among the 3122 quadrats), somewhat faster than a previous estimate of 220 km year⁻¹ using time-lagged cross-correlation functions (Bjørnstad *et al.* 2002). The spatial mean wave speed varied through time; values for

the first through fourth temporal periods were 299, 196, 171 and 180 km year⁻¹, respectively. Three of the four time-specific wave speeds were less than the spatiotemporal average wave speed for the Alps, suggesting that the estimated average wave speed of 254 km year⁻¹ may be an overestimate. Despite some temporal variation in wave speed, the locations of the epicentres were remarkably constant through time (see Appendix S1 in Supplementary Material).

A SPATIALLY EXPLICIT MODEL

In order to explore how habitat geometry affects dynamics, and specifically to determine the effect of connectivity on epicentre dynamics, we constructed a spatially extended model to simulate LBM dynamics on theoretical landscapes with varying patch configurations. Many theories have been advanced to explain LBM population cycles but the two dominant theories are that LBM dynamics are determined by (1) LBM-induced cycles in plant quality (Baltensweiler 1993) and/or (2) Nicholson–Bailey type host–parasitoid interactions (Hassell 1978; Turchin 2003). Outbreak-level damage to larch trees is known to reduce foliage quality (indirectly measured as length of the larch needles) in subsequent years, which has a negative effect on LBM survival and reproduction (Baltensweiler 1993). Additionally, theoretical modelling and cursory evidence suggest that interactions between the LBM and its parasitoids can result in observed population cycling (Hassell 1978; Turchin 2003). To embrace both of these interactions, we used a spatially extended version of Turchin's (Turchin 2003) tri-trophic model for local LBM dynamics. The equations for the local dynamics of the moth (H), parasitoid (P) and habitat quality (Q) at location i are

$$H'_{i,t+1} = H_{i,t} \exp \left\{ (r_0 + u) \left(1 - \exp \left[-\frac{Q_{i,t}}{\delta} \right] \right) - \frac{r_0}{k} H_{i,t} - \frac{aP_{i,t}}{1 + awP_{i,t}} \right\}, \quad (2a)$$

$$P'_{i,t+1} = H_t \left\{ 1 - \exp \left[\frac{aP_{i,t}}{1 + awP_{i,t}} \right] \right\}, \quad (2b)$$

$$Q_{i,t+1} = (1 - \beta) + \beta Q_{i,t} - \frac{cH_{i,t}}{d + H_{i,t}}, \quad (2c)$$

where t represents time, r_0 is the intrinsic rate of increase of the moth, δ determines the rate at which growth plateaus, k is moth carrying capacity, a is the prey saturation parameter, w is a parasitoid mutual interference parameter, β determines the rate at which patch quality decays, and c and d are patch quality parameters (Table 1). The parameter u , which

Table 1 Parameter values for the tri-trophic larch budmoth model

Parameters
$r_0 = 2.5$
$w = 0.17$
$\delta = 0.22$
$c = 0.9$
$k = 250$
$d = 100$
$\alpha = 2.5$
$\beta = 0.5$

All values were taken from Turchin (2003).

measures the demographic stochasticity in intrinsic rate of increase, was arbitrarily set to 0.1. The prime signs in eqns 2a and 2b indicate that these are pre-dispersal host and parasitoid population sizes.

Dispersal is also an important process in the system because the LBM is highly mobile (Baltensweiler & Rubli 1999). We modelled dispersal in the moth and the parasitoids with a two-dimensional discretized Gaussian model.

$$N_{i,t+1} = \frac{\sum_{j=1}^n N'_{j,t+1} e^{-(x_{ij}\alpha^{-1})^2}}{C}. \quad (3)$$

The Gaussian model was selected because it is an approximation of redistribution based on a random-walk dispersal mode (Okubo 1980). The parameter N is population size of the organism (host or parasitoid). The parameter α is the dispersal parameter. The parameter x is the Euclidean distance between patches and is dependent on the geometry of the landscape used in the simulation. The parameter C is a normalization constant. There is little empirical information on LBM dispersal, thus, the parameter α was set at 25 km for the LBM to roughly approximate the distances flown by LBMs in a flight mill over their lifetimes (Furuta 1978). Intriguingly, sensitivity analysis revealed that the highest correlation between connectivity and phase angles occurred around this value of α (see Appendix S1). Equation 3, thus, approximates the redistribution of the moths over one-time step on a theoretical landscape. Because parasitoids disperse less than the LBM, the parasitoid dispersal parameter was arbitrarily set at a low level ($\alpha = 2$ km).

To elucidate our refined epicentre hypothesis, the tri-trophic model was simulated on two different theoretical landscapes consisting of 3×3 km patches of suitable habitat and unsuitable matrix. In one landscape, habitat was most dense in the center and at decreasing densities towards the periphery (Fig. 4a). In the other landscape, habitat was most dense in a corner and at decreasing densities with distance from that corner (Fig. 4b). Both

habitat configurations were created by assuming that the probability of a patch being suitable declined exponentially with the distance from the focal location. The two scenarios were used to separate the effects of connectivity from edge effects. Fifty replicate tri-trophic models were simulated for 500 time steps (year). Initial conditions for host, parasitoid and patch quality were selected from a random uniform distribution (host and parasitoid ranged between 0 and 500, and patch quality ranged between 0 and 1) separately for each quadrat in each replicate. The last 38 time steps of each simulation were analysed using wavelet phase analysis and subsequent calculation of MPAs. For both configurations there was a positive relationship between habitat connectivity and MPA (Fig. 4c,d). This gradient of decreasing MPAs with decreasing connectivity provides strong supporting evidence for the hypothesis that epicentres originate in areas of high connectivity and subsequently spread to areas of lower connectivity.

We ran sensitivity analyses to test the robustness of travelling waves to ± 2 SD variation in the eight parameters in eqns 2a–2c (except for the parameter d for which 2 SD was a biologically unrealistic value less than zero). Standard deviations were taken from Turchin (2003). The model simulations consistently created travelling waves from high to low connectivity habitats in all cases except two: (1) when w was decreased by 2 SD, and (2) when d was decreased by 1 SD. In these two cases there was no detectable relationship between phase angle and connectivity. Thus, the travelling waves were robust to reasonable variation in most of the parameters.

DISCUSSION

Interest in the LBM and its defoliation of subalpine larch cembran forests was initially motivated by a concern for its negative effects on tourism in the Engadine region of the Alps (Baltensweiler & Rubli 1999). More recently, population biologists have taken a keen interest in the LBM because of its regular oscillations (Turchin 2003) and recurring travelling waves (Bjørnstad *et al.* 2002). Previous theoretical analyses have demonstrated that spatial gradients in habitat quality (reflected in LBM population growth rate) or advective (directional) dispersal can result in recurring directional waves (Bjørnstad *et al.* 2002). Herein we present evidence supporting an alternative hypothesis based on habitat geometry; that habitat connectivity plays a key role in shaping spatial dynamics and, in particular, epicentre dynamics in the LBM. The outbreak epicentres consistently recurred in the same two areas of high connectivity in each of the cycles during the 38-year sample period, indicating that this is more than a transient relationship. Interestingly, in Red Grouse populations in northern Scotland, waves travelled from the center of suitable habitat (moorland)

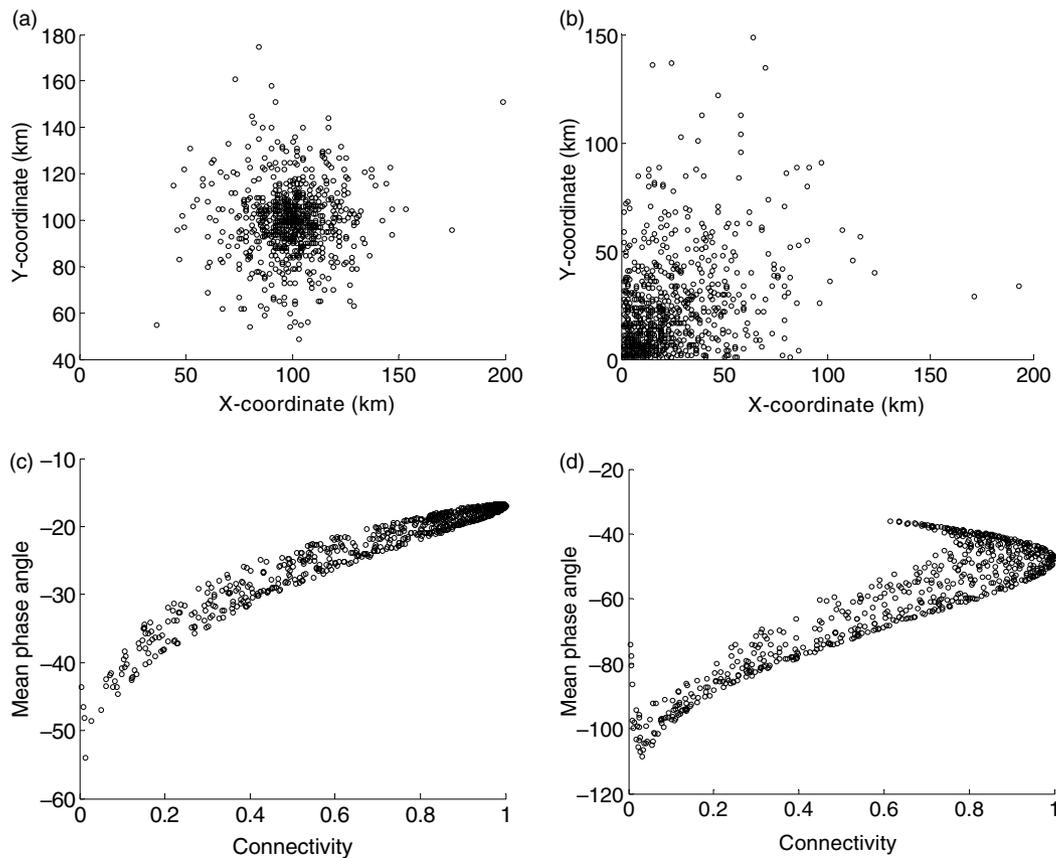


Figure 4 Distributions of theoretical patches with highest density in the (a) center and (b) lower left corner of theoretical landscapes. Simulations of tri-trophic larch budmoth models with absorbing boundaries on these two distributions revealed a positive relationship between connectivity and mean phase angle in both habitat distributions [(c) and (d) correspond to (a) and (b), respectively].

towards the margins where the moorland bordered unsuitable habitat (Moss *et al.* 2000).

We extended Turchin's *et al.* (2003) tri-trophic model into a spatial realm, modelling LBM dynamics over habitat geometries with heterogeneous connectivities. Simulations of the model demonstrated qualitatively similar results to the empirical data; epicentres were located in areas of high connectivity, with outbreaks spreading to areas of lower connectivity.

In general, three possible spatial patterns can emerge in cyclic population dynamics: (1) spatial synchrony, (2) spatial asynchrony and (3) travelling waves. We used wavelet phase analysis to distinguish between these three spatial dynamics. Populations in complete spatial synchrony would have identical phase angles regardless of their spatial locations. Populations in complete asynchrony would have varying phase angles with no consistent spatial pattern. Thus, while some populations would peak earlier than others in the case of spatial asynchrony, there would be no spatial gradient in the timing of the cycles. Travelling waves, on the other

hand, are typified by populations in partial synchrony with a gradient in phase angle differences as a function of distance. The wavelet phase analysis of both LBM empirical and simulated data revealed spatial gradients in phase angles, clearly illustrating travelling waves in LBM outbreaks moving from areas of high connectivity to areas of lower connectivity.

The LBM is one of the most notable examples of travelling waves in population dynamics (Baltensweiler & Rubli 1999; Bjørnstad *et al.* 2002). However, as the number of spatial data sets over multiple years increases, travelling waves are being detected in more and more species, suggesting that it may be a common pattern in cyclic populations. For example, travelling waves have been described for lynx and hare populations (Smith 1983; Ranta *et al.* 1997), voles (Lambin *et al.* 1998) and Red Grouse (Moss *et al.* 2000). Wavelet phase angles were previously used to identify travelling waves of measles (Grenfell *et al.* 2001) and dengue (Cummings *et al.* 2004). Thus, travelling waves have been detected in a variety of systems.

For LBM we hypothesize that areas with the highest immigration subsidies are the epicentres of travelling waves. We hypothesized that immigration subsidies inflate the population growth rate during the increase phase, thus, causing highly connected habitat to reach peaks faster than less connected habitat. In the theoretical model, the mean time from a population trough to a peak, however, was greater in high connectivity habitat than in low connectivity habitat ($r^2 = 0.84$, see Appendix S1). In contrast, populations in high connectivity habitats transitioned from peaks to troughs faster than in low connectivity habitats ($r^2 = 0.84$, Appendix S1), suggesting that more rapid crashes in population sizes cause high connectivity habitats to be epicentres of travelling waves. The underlying mechanism for these quicker crashes in population sizes appears to be subsequent population responses to greater 'overshooting' of the carrying capacity because of immigration subsidies in high connectivity habitat.

Interestingly, there was a negative relationship between connectivity and phase angle in a model with reflecting boundaries (see Appendix S1); thus, outbreaks originated in low connectivity habitat. The stark contrast of wave dynamics in the model with absorbing vs. reflecting boundaries begs the question of which dispersal mode is more appropriate for the LBM? Because LBM are known to disperse long distances via passive wind-borne movement of flying adults, we assumed that they do not track the resource tightly. This behaviour would result in a certain proportion of individuals dispersing into unsuitable habitat without reproducing, and is more consistent with the absorbing boundary model. Royama *et al.* (in press) interpreted spatially coincidental negative rates of change in the spruce budworm as being due to synchronous pulses in moth dispersal. The logic is that during these dispersal pulses, many spruce budworm moths either dispersed beyond the borders of the study area or suffered a high mortality; thus, resulting in a low per capita recruitment rate. This mechanism, which may act to synchronize disjunct populations (Royama *et al.* in press), is consistent with an absorbing boundary model.

The appropriate measure of 'connectivity' among populations has been a point of contention in ecology (Tischendorf & Fahrig 2000b; Moilanen & Hanski 2001; Tischendorf & Fahrig 2001). In the present study, the term 'connectivity' was used to describe the potential number of immigrants into equal sized habitat cells in the landscape, analogous to the 'cell immigration' measure endorsed by Tischendorf & Fahrig (2000a). In this way, habitat connectivity is a function of inter-patch distances and the dispersal distance distribution. Thus, based on the definitions of Tischendorf & Fahrig (2001), our 'connectivity' is a hybrid between a functional and structural definition in that it considers both dispersal behaviour (functional) and habitat geometry (structural).

Wavelet phase analysis is a powerful tool for elucidating spatiotemporal dynamics of complex systems (Grenfell *et al.* 2001). Previous phase analyses of spatiotemporal dynamics of measles in England and Wales (Grenfell *et al.* 2001) and dengue in Thailand (Cummings *et al.* 2004) reveal that recurrent epidemics originated in large urban areas, with subsequent spread to smaller towns and rural areas. This interestingly parallels the findings of the current study, in which LBM outbreaks tended to begin in areas of higher habitat density areas and then spread to less dense areas. The mechanisms causing waves in the diseases, however, may differ from that of the LBM. High density areas, such as cities, seemed to act as reservoirs for outbreaks of measles and dengue. Conversely, our model indicated that quickened population crashes in high density habitat cause the recurrent travelling waves in the LBM model.

The importance of habitat geometry in shaping complex spatial dynamics has been suggested but not vigorously quantified in ecological analyses. Two notable theoretical exceptions showed waves emanating outward from dispersal barriers in otherwise homogeneous landscapes (Sherratt *et al.* 2002, 2003). A necessary condition for this result was that the edge of the dispersal barrier had 'zero population density conditions', meaning that individuals attempting to cross the barrier always died. This is similar to the condition of absorbing boundaries as was used in the present study, yet produced the opposite result. Specifically, habitat at the edge of the dispersal barriers had a lower 'connectivity' than other habitat in the landscape, yet travelling waves originated in these low connectivity areas. We found that epicentres were located in areas of high connectivity, but did not consider the effects of dispersal barriers *per se*. Herein, we demonstrated that epicentre dynamics were sensitive to the biology at habitat edges. The difference between our result and those of Sherratt *et al.* (2002, 2003) illustrates the need for better understanding of the dual role of dispersal behaviour and landscape geometry in generating travelling waves.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE659/ELE659sm.htm>

Appendix S1 LBM spatial dynamics.

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