

Derek M. Johnson · Ottar N. Bjørnstad
Andrew M. Liebhold

Landscape mosaic induces traveling waves of insect outbreaks

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Abstract The effect of landscape mosaic on recurrent traveling waves in spatial population dynamics was studied via simulation modeling across a theoretical landscape with varying levels of connectivity. Phase angle analysis was used to identify locations of wave epicenters on patchy landscapes. Simulations of a tri-trophic model of the larch budmoth (*Zeiraphera diniana*) with cyclic population dynamics on landscapes with a single focus of high-density habitat produced traveling waves generally radiating outwardly from single and multiple foci and spreading to isolated habitats. We have proposed two hypotheses for this result: (1) immigration subsidies inflate population growth rates in the high connectivity habitat and, thus, reduce the time from valleys to peaks in population cycles; (2) populations in the high connectivity habitat crash from peaks to valleys faster than in an isolated habitat due to over-compensatory density dependence. While population growth rates in the high connectivity habitat benefitted from immigration subsidies, times from population valleys to peaks were greater in high connectivity habitat due to a greater magnitude of fluctuations. Conversely, the mean time of the crash from population peaks to valleys was shorter in high connectivity habitat, supporting the

second hypothesis. Results of this study suggest over-compensatory density dependence as an underlying mechanism for recurrent traveling waves originating in high connectivity habitats aggregated around a single focus.

Keywords Connectivity · Epicenter hypothesis · Larch budmoth · Spatial model · Synchrony · *Zeiraphera diniana*

Introduction

Theoretical studies have demonstrated that oscillating populations in a spatial arena can produce a range of patterns including crystal lattices, spiral waves, and spatial chaos (Hassell et al. 1991), although examples of many of these patterns in nature are generally lacking. The exception is that recurrent traveling waves have been described in a number of biological systems, including forest insect outbreaks (Bjørnstad et al. 2002), epidemics (Grenfell et al. 2001), voles (Lambin et al. 1998; Mackinnon et al. 2001), Grouse (Moss et al. 2000), snowshoe hare (Smith 1983), and lynx (Ranta et al. 1997). By traveling waves in population dynamics, we refer to peak densities moving across a spatial gradient over time. Despite substantial evidence for traveling waves in nature, the mechanism(s) driving such dynamics remain unclear. The ‘epicenter hypothesis’ states that traveling waves originate in specific epicenters and subsequently spread to neighboring habitats (Berryman 1987; Wallner 1987; Liebhold and McManus 1991; Johnson et al. 2004). Models of specific systems that incorporate spatially heterogeneous landscapes with differences in patch quality have proven resistant to epicenter dynamics (Liebhold and McManus 1991). As an alternative, we have provided evidence that epicenters of traveling waves in the larch budmoth (*Zeiraphera diniana* Guenee; syn. *Z. griseana* Hübner) were shaped by landscape geometry, originating in areas of high habitat density and subsequently spreading to more

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D. M. Johnson (✉)
Department of Biology, University of Louisiana at Lafayette,
P.O. Box 42451, Lafayette, LA 70504, USA
E-mail: derekjohnson@louisiana.edu

O. N. Bjørnstad
Department of Entomology, Pennsylvania State University,
505 ASI Building, University Park, PA 16802, USA

A. M. Liebhold
Northeastern Research Station, USDA Forest Service,
180 Canfield St, Morgantown, WV 26505, USA

peripheral habitats in the European Alps (Johnson et al. 2004). Based on this evidence we have proposed that the critical feature of landscape geometry that induces traveling waves is that the high-density habitat has a high connectivity to the neighboring habitat; connectivity being defined as the potential for immigration subsidies to population size (Johnson et al. 2004). However, the demographic mechanism by which habitat geometry produces traveling waves from epicenters remained unclear. We have provided a theoretical model that mimicked the patterns in the data, even with spatially-constant parameters. The epicenter, therefore, must somehow reflect differential immigration and/or emigration rates. In the present study, we conduct a detailed analysis of model dynamics (based on the larch budmoth system) to critically contrast hypotheses for the precise mechanism by which habitat connectivity induces epicenter dynamics.

Recent theoretical studies have shown that landscape geometry can greatly affect outbreak waves. Sherratt et al. (2002) studied how outbreaks may originate at the edges of obstacles to movement. In contrast, Johnson et al. (2004) showed that historical larch budmoth outbreaks in the Alps originate in epicenters of high connectivity habitat and then subsequently spread to low connectivity habitat. Spatial analysis of 38 year of larch budmoth outbreak records revealed that outbreaks in areas of low connectivity habitat lagged behind those in high connectivity habitat. Identifying the mechanism causing these patterns is difficult because outbreaks often result from highly non-linear reaction-diffusion dynamics involving multiple trophic levels.

To understand the influence of habitat geometry, we need to consider the conditions that are associated with recurrent traveling waves in population dynamics. Three properties are necessary: locally fluctuating populations, phase-locking among locations, and a spatial gradient in phase state. Local population cycles in abundance have been demonstrated in a variety of species across a range of taxa (Bulmer 1974; Kendall et al. 1999; Liebhold and Kamata 2000; Hansson 2002). Phase-locking refers to the state when the phase differences between multiple locations are fixed; thus, each location exhibits similar temporal fluctuations, but they are not necessarily in synchrony. When locations are phase-locked, but not in perfect synchrony, a variety of theoretical patterns of outbreak spread can emerge including spiral waves and spatial chaos (Hassell et al. 1991). A traveling wave originating at an epicenter, for example, occurs when the temporal lags in phase increase with increasing radial distance from that central location (Johnson et al. 2004).

A goal of the study reported here was to elucidate the demographic mechanism(s) responsible for inducing outbreak waves across heterogeneous landscapes with particular reference to cyclic populations. We present two hypotheses for the location of wave epicenters in high connectivity habitat. One hypothesis is that higher immigration into high connectivity habitat results in

faster growth from low population densities. We proposed the following mechanism for this hypothesis; first, that emigration acts as a drain on local population dynamics across the entire landscape (Kean and Barlow 2000). Areas of high-density habitat tend to have high connectivity and thus receive higher immigration subsidies than more isolated habitat. Immigration, in turn, inflates the apparent population growth rates in the high connectivity habitat compared to low connectivity habitat. We define apparent population growth rate as the change in local population size (N_{t+1}/N_t), thus, including immigrants and excluding emigrants. Under this hypothesis, it should be expected that areas with the highest apparent population growth rates transition from valleys to peaks faster than those with lower apparent population growth rates. An alternative hypothesis is that populations in high connectivity habitat peak at higher levels, which causes a quicker population crash, thereby shifting the population phase forward and causing traveling waves to originate in epicenters in high connectivity habitat and then subsequently spread to low connectivity habitat. We confront these two hypotheses through spatial simulations of a tri-trophic model specific to the population dynamics of the larch budmoth in the Alps (Turchin 2003; Johnson et al. 2004).

Lastly, we extend our analyses of traveling waves to landscapes with multiple foci of high-density habitat. We demonstrate that in these more complex patch arrangements, outbreaks still generally spread radially from epicenters in high-density habitat, but with occasional shifts to somewhat directional waves where a traveling wave from one focus overcomes that of another focus.

Methods

Herein, we apply a tri-trophic model of interacting parasitoids, consumers, and vegetation on theoretical landscapes to explore the underlying mechanism relating connectivity to traveling wave dynamics. The model is based on the larch budmoth system in the Alps and represents both induced defenses in budmoth hosts and the numerical response of budmoth parasitoids (Turchin 2003). Dynamics of this model are consistent with the behavior of larch budmoth populations, exhibiting local cyclical dynamics and, when extended spatially onto a theoretical landscape, exhibiting phase-locking, spatial gradients in phase states, and recurrent outbreak waves in consumer abundance (Johnson et al. 2004). Because the larch budmoth is a mobile insect species capable of undirected flight over large geographic areas (Baltensweiler and Rubli 1999), we assume absorbing boundaries; that is, individuals that disperse into unsuitable habitat do not contribute to population growth. In this study, we apply the model to five theoretical landscapes to decipher the underlying mechanism(s) producing the outbreak waves. We compare spatial dynamics and cycle

periods of the host across a range of host and parasitoid dispersal abilities.

First, to determine the spatial dynamics of the tri-trophic model with unvarying levels of connectivity, we ran a model simulation of 1000 time steps on a 50×50 -patch landscape. Patches were uniformly spaced in a square map lattice. Wavelet phase angle analysis (Grenfell et al. 2001; Johnson et al. 2004) (see below for details) was then performed on the interior 25×25 patches (625 patches in total), where levels of connectivity were relatively constant, to test for epicenter dynamics across a homogeneous landscape.

We next created five other coupled map lattices with different patterns containing one, two, or four foci of high densities of patches surrounded by lower patch densities. In one landscape, the highest connectivity habitat was in the center of a square landscape. In the second, a single focus was off-center on a square landscape. In the third and fourth landscapes, there were two foci, spatially proximate in one of the landscapes and far apart in the other landscape. In the fifth landscape, four foci were evenly spread across a landscape in a square pattern. The landscapes were created by probabilistically generating either a suitable patch or an unsuitable one in each location based on a decaying probability function of the distance between the given patch and the focus/foci so as to produce a wide range of connectivity levels. Wavelet phase angle analysis was used to identify outbreak waves and their epicenters of spread in the landscape. Animations of the spatial dynamics were viewed to confirm these wave dynamics. We further compared patch-specific qualities (number of immigrants, maximum apparent population growth rates, and times from cycle valley to peak and vice versa) to levels of connectivity in one of the landscapes to better understand the underlying mechanism causing traveling waves of outbreaks in the larch budmoth. A shorter average time from a valley to peak in high connectivity habitat would indicate that epicenters of traveling waves result from higher apparent population growth rates due to immigration subsidies. On the other hand, if the average time from peak to valley were shorter in high connectivity habitat, this would indicate that epicenters in outbreaks are actually the result of faster crashes in population sizes in high connectivity habitat.

The tri-trophic model was applied to a three-patch system where there were two nearby (high connectivity) patches located at the X - Y coordinates (0,0) and (10,0) and where the location of a third more isolated (lower connectivity) patch was varied [location coordinates were (5,10), (5,15), (5,20), (5,25), (5,30), (5,35) on an arbitrary scale]. This system was used to determine the effects of connectivity on the phase-locking among the patches and on the phase lag of the isolated patch compared to the two high connectivity patches. Connectivity is defined below. This analysis allowed us to describe the effects of connectivity on the phase angles of population trajectories of each habitat patch and synchrony relationships. The host dispersal parameter was

standardized at $\alpha_H = 10$ and the parasitoid dispersal parameter was arbitrarily set at half that of the host ($\alpha_P = 5$).

Herein we define relative connectivity (Ω) as the fraction of immigrants received by an isolated habitat patch per immigrants received in the most connected patch in the landscape according to the redistribution equation assuming a Gaussian dispersal kernel. The fraction of immigrants was calculated by averaging the fraction of immigrants over the final 100 time steps of the model simulation. Thus, the most connected patch has a relative connectivity equal to one ($\Omega = 1$), and all patches have connectivity values bounded by zero and one.

The models

We selected a spatial population model that robustly retains limit cycles across a range of connectivity levels: a spatially-extended version of the tri-trophic model for the larch budmoth (parasitoid-herbivore-patch quality: Turchin 2003; Johnson et al. 2004). The equations for the local dynamics of the moth (H), parasitoid (P), and habitat quality (Q) at location I are

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

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

$$Q_{i,t+1} = (1 - \beta) + \beta Q_{i,t} - \frac{uH_{i,t}}{v + H_{i,t}}, \quad (1c)$$

where t represents time, r_0 is the intrinsic rate of increase of the host, δ determines the rate at which growth plateaus, k is host carrying capacity, a is the prey saturation parameter, w is a parasitoid mutual interference parameter, β determines the dependence of habitat quality at time $t+1$ on habitat quality at time t (i.e., when $\beta=0$ the qualities at the two time steps are independently calculated), and u and v are patch quality parameters (Table 1). All parameter values were taken from Turchin (2003). The prime signs in Eqs. 1a and 1b indicate that these are pre-dispersal host and parasitoid population sizes. Habitat quality (Q) can be viewed as any habitat feature that affects the vital rates of the host species (for example, in the case of the larch budmoth, the length of the larch needles has been shown to be a good indicator of habitat quality). Low levels of demographic and regional stochasticity were added to the model by varying the values of r_0 for each patch at each time step. In the model simulations, initial population sizes of H_I and P_I were randomly generated for each patch from a uniform distribution between 0 and 500, while the initial values of all Q_I were randomly generated from a uniform distribution between 0 and 1.

Table 1 Parameter values for the tri-trophic model based on the larch budmoth (Turchin 2003)

Parameters	Tri-trophic model
r_0	2.5
K	250
A	2.5
W	0.17
A	0.5
C	0.9
D	100
δ	0.22

We modeled the dispersal of the hosts and the parasitoids in the tri-trophic model with a two-dimensional Gaussian model with absorbing boundaries,

$$N_{i,t+1} = \frac{\sum_{j=1}^n \exp \left[-N'_{j,t+1} \left(\frac{d_{ij}}{\alpha} \right)^2 \right]}{C}. \quad (2)$$

The parameter N is population size of the organism (in the case of the LBM model, N corresponds to H in the case of moth dispersal and P in the case of parasitoid dispersal). The parameter α is the dispersal parameter and d is the Euclidean distance between patches. The parameter C is the normalization constant so the total proportion of dispersal across suitable and unsuitable habitat sums to one. The Gaussian model was selected because it is an approximation of redistribution based on a random-walk dispersal mode (Okubo 1980). In all simulations on the various landscapes, the dispersal parameters for the hosts and parasitoids in the tri-trophic model were arbitrarily set at $\alpha_H = 10$ and $\alpha_P = 5$, respectively.

Wavelet and phase angle analysis

Wavelet analysis is a method of quantifying the magnitude of periodicity in temporal data across a range of periods based on a given wavelet function (in this case we used the Morlet wavelet function). The dominant period in the system can then be identified and the corresponding complex vector (where each number is composed of a real and an imaginary component) of wavelet decomposition isolated for phase angle analysis. The phase angles (ranging from -180 to 180°) of the dominant period are then calculated from radians, which are represented by the arctangent of the ratio of the imaginary number over the real number. More simply, a population that is at a valley in its cycle has a phase angle of -180° . As the population size increases to a peak, the phase angle increases to 0° . Then, as the population size decreases to a valley the phase angle increases to 180° , where it switches to -180° and the cycle is repeated. This procedure was carried out for the population in each habitat patch in this study. We compared phase angles

among populations to elucidate the effects of connectivity on spatial dynamics; for example, a population with a phase angle of 0 degrees is peaking before a population with a phase angle of -45° . Thus, the highest phase angle is indicative of the wave epicenter and a gradient of decreasing phase angles is indicative of the direction and speed of traveling waves (Grenfell et al. 2001; Johnson et al. 2004).

Results

A comparison across a range of host and parasitoid dispersal abilities (all combinations of α values ranging from 1 to 10 at integer intervals for each organism – 100 combinations in all) on a landscape with one focused center (Fig. 1a) revealed a number of different patterns of host spatial dynamics (Fig. 2a). The predominant dynamic, however, was radial outbreak waves emanating from the areas of high connectivity. Less common, at low host and/or parasitoid dispersal abilities, were waves emanating directionally from low/medium connectivity habitat at one side of the landscape, across the high connectivity habitat in the center of the landscape, and then into low/medium connectivity habitat on the other side of the landscape. At very low host and parasitoid dispersal abilities, either spiral waves originating in high connectivity habitat, chaotic waves, or radial waves formed depending on the exact parameterization. In a restricted range at high host dispersal ability and low parasitoid dispersal ability, host populations reached equilibrium. Overall, however, cyclical population dynamics was the norm in local dynamics, and radial waves were the most common spatial dynamic (the focus of this study was on radial wave dynamics). Figure 2b illustrates the combined effects of host and parasitoid dispersal kernels on the dominant period in the system. High host dispersal ability combined with low parasitoid dispersal ability resulted in the shortest periods (6–7 years), while high dispersal ability of both the host and parasitoid resulted in the longest periods (11–12 years). In general, the dominant period increased with increasing dispersal ability of the parasitoid.

In the three-patch model, as the third patch was increasingly isolated from the two proximate patches, the cycles of the third patch increasingly lagged behind those of the proximate patches, but remained phase-locked at all but the lowest level of connectivity (Fig. 3a–f). Thus, the population cycle in the area of low connectivity trailed that in the high connectivity area. At a high connectivity level of 0.78, the number of immigrants into the isolated patch was relatively high, and the three patches were very nearly synchronized with the phase of the isolated patch lagging by approximately 1° . This is a small difference; in a system with 8-year-cycles, a 45° shift in phase angle would translate into a 1-year lag. At connectivity levels of 0.22 and 0.04, the isolated patch lagged averages of approximately 25° and 45° ,

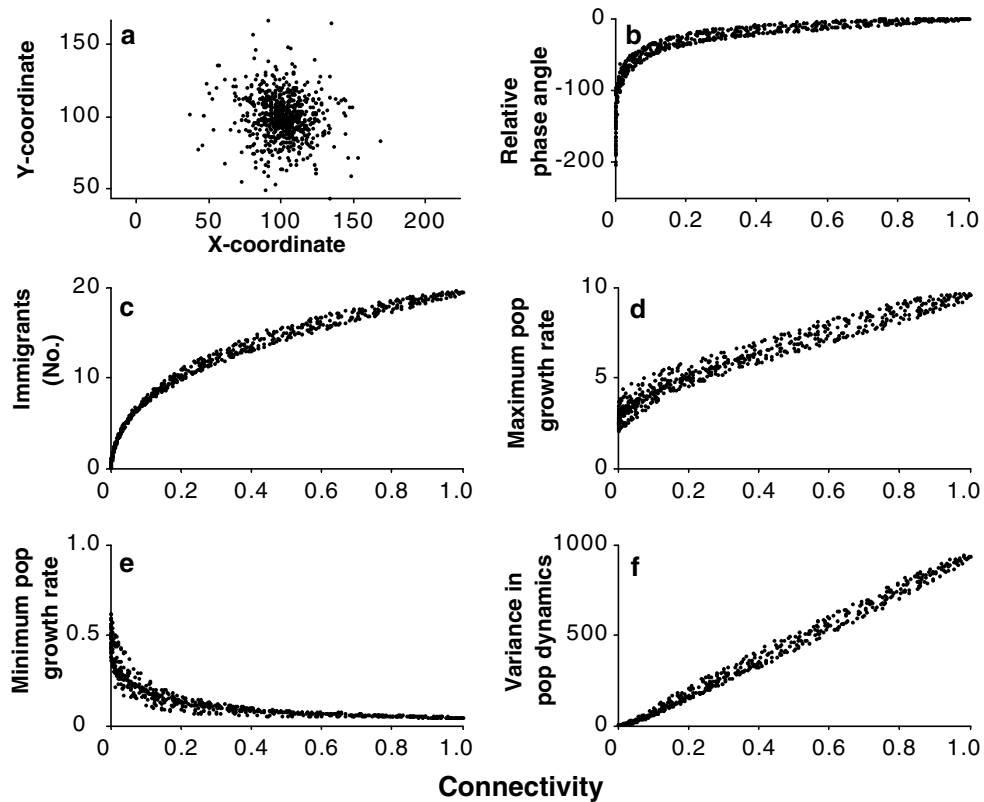


Fig. 1 **a** Habitat distribution of theoretical patches on a coupled map lattice with high density in the center and decreasing density outward. **b** Positive relationship between the mean relative phase angle (over 50 simulations) and connectivity across patches ($r^2=0.76$, $n=616$, $p<0.001$). **c** Relationship between the mean number of immigrants into each patch and connectivity ($r^2=0.99$,

$n=616$, $p<0.001$). **d** Relationship between mean maximum apparent population (pop) growth rate (N_{t+1}/N_t), and connectivity ($r^2=0.96$, $n=616$, $p<0.001$). **e** Relationship between mean minimum apparent population growth rate and connectivity ($r^2=0.91$, $n=616$, $p<0.001$). **f** Relationship between variance in population dynamics and connectivity ($r^2=0.92$, $n=616$, $p<0.001$)

respectively. At connectivity levels of 0.004 and 0.0003 the cycles remained phase-locked but in approximate anti-synchrony with the high connectivity patches (lagging approximately 160° and 190° , respectively). Only at a very low connectivity level, 0.00001, did the period of the isolated patch fall out of phase, into a longer period than the two proximate patches. These results illustrate three points: (1) periodic cycles in the isolated habitat increasingly lag as the level of connectivity decreases, (2) very modest levels of inter-patch movement are sufficient to induce phase-locking among the habitat patches, and (3) when isolation is sufficiently high, period length in the isolated patch is greater than in the more connected patches. This simple model illustrates that traveling waves from high to low connectivity habitat in the tri-trophic model are robust to a wide range of levels of connectivity.

A simulation of tri-trophic dynamics on habitat with very little variation in connectivity produced only a slight hint of wave dynamics from across the landscape (Fig. 4). Instead, all of the 625 patches in the center of the landscape were nearly completely synchronized. The spatial layout of the theoretical landscape of habitat with high levels of variation in connectivity, and a single focus of high connectivity in the center of the landscape,

is shown in Fig. 1a. The mean phase angles of populations simulated on this landscape were positively correlated with level of connectivity (Fig. 1b), indicating a wave traveling from the epicenter in high connectivity habitat. As expected, there was a strong positive relationship between the measure of connectivity and the number of immigrants into a patch (Fig. 1c), thereby reflecting increasing immigration subsidies and suggesting that immigration subsidies shorten the time from population valleys to peaks in low fragmentation habitats. Moreover, areas of high connectivity had higher maximum apparent growth rates (Fig. 1d), which is also consistent with the immigration subsidies hypothesis. However, the alternative mechanism – that traveling waves result from quicker population crashes in low fragmentation habitat – was supported by the fact that minimum population growth rate was negatively related to the level of connectivity (Fig. 1e). Neither of these results, therefore, are conclusive evidence for either hypothesis because the magnitude of the fluctuation in population densities was greater in high connectivity habitat (Fig. 1f). This means that a greater maximum population growth rate, and a lesser minimum population growth rate, would be required for high connectivity habitat to have the same period as low

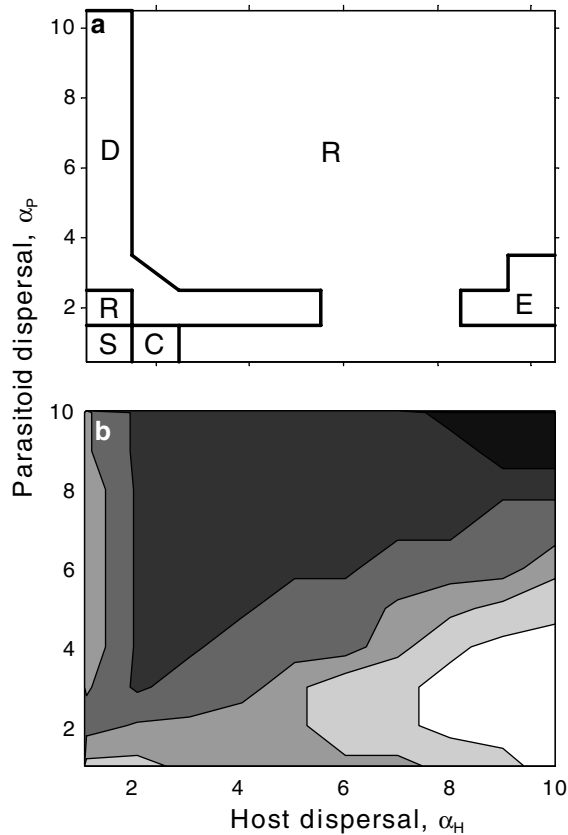


Fig. 2 **a** Map of the varying types of spatial dynamics in the simulated tri-trophic model as the dispersal parameters α_H and α_P , for the host and parasitoid, respectively, were varied. *R* Radial waves emanating from the high connectivity habitat, *D* directional waves moving across the landscape, *S* spiral waves emanating from the high connectivity habitat, *C* chaotic waves, *E* host population settled at an equilibrium population size. One hundred combinations of values of α_H and α_P were tested (all possible combinations of integer values between 1 and 10 for both the host and the parasitoid). **b** Contour plot of the dominant periods of the simulated host dynamics at varying host (α_H) and parasitoid (α_P) dispersal parameters. *White* 6–7 years, *very light gray* 7–8 years, *light gray* 8–9 year, *medium gray* 9–10 years, *dark gray* 10–11 years, *black* 11–12 years

connectivity habitat. A detailed examination of the population oscillations revealed that the time from population valleys to peaks was greater in high connectivity habitat (Fig. 5a), thus, immigration subsidies are not sufficient to shorten a period length in high connectivity habitat. In contrast, time from population peaks to valleys was quicker in high connectivity habitat (Fig. 5b), a result which supports the second hypothesized mechanism: traveling waves result from quicker population crashes in high connectivity habitat. Note that because all populations in this model simulation were phase-locked (that is, all periods were the same length), a quicker time from a peak to a valley necessitates a compensatory slower time from a valley to a peak, and vice versa.

In the landscapes with both one central focus and an off-center focus [Electronic Supplementary Material (ESM): Animation A and B], outbreak waves radiated

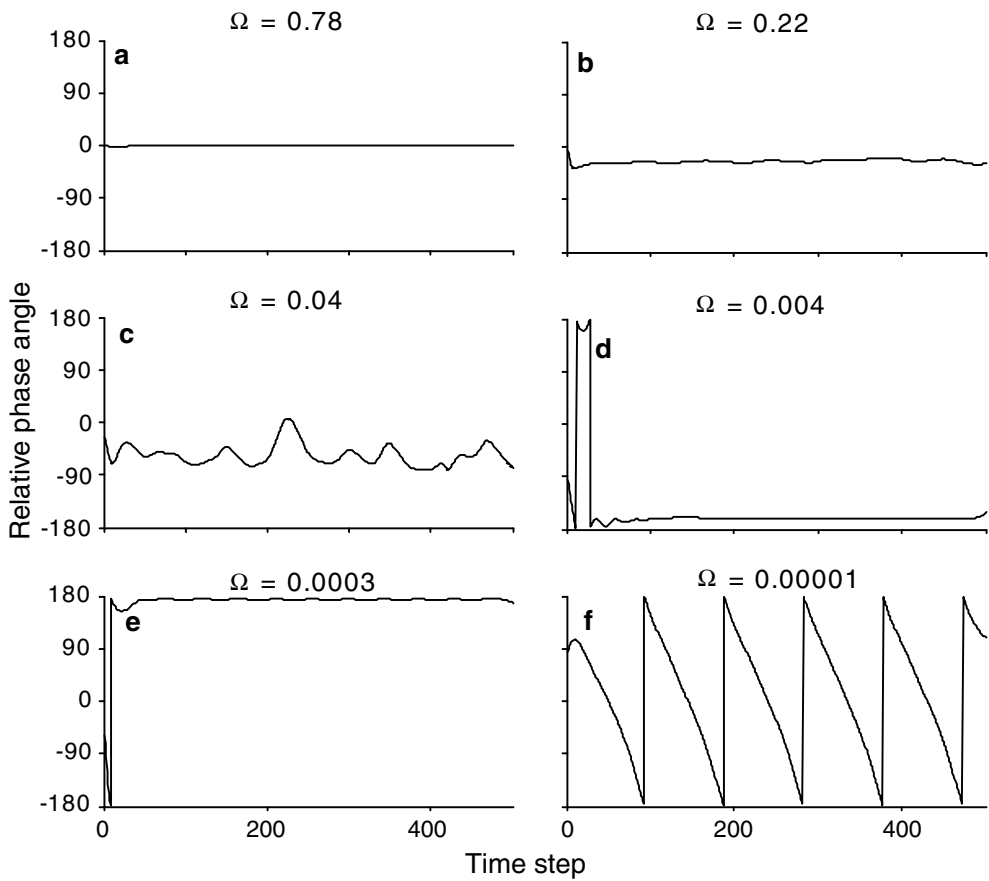
from the high-density habitat. However, the relationship between connectivity and mean phase angle in the landscape with two spatially proximate foci (ESM: Animation C) was more complex and temporally variable. While the dominant dynamic was traveling waves radiating from the high-density habitat around each focus, the traveling waves from one focus sometimes dominated the other focus, and epicenters sometimes shifted to moderate density habitat, causing somewhat directional waves. In the landscape with two spatially distant foci (ESM: Animation D), radial waves consistently emanated from each focus, and the outbreaks around each focus remained somewhat in synchrony. Lastly, on a landscape with four evenly dispersed foci of high-density habitat (ESM: Animation E), traveling waves radiated outwardly from all of the foci, but not always in synchrony with the outbreaks in patches around the other foci.

Discussion

In a previous study, we presented empirical (from historical records of larch budmoth outbreaks) and theoretical evidence that epicenters of traveling population waves were located in areas of high connectivity and that waves subsequently spread to more isolated areas (Johnson et al. 2004). In the present study, we investigated this general pattern with a tri-trophic model specific to the larch budmoth. We showed that patches of habitat remained phase-locked, a prerequisite for recurrent traveling waves, at all but very low levels of connectivity. Finally, on landscapes with a single focus of high-density habitat, recurrent traveling waves emanating from high-density (high connectivity) habitat were robust across most of a range of both host and parasitoid dispersal abilities. These results suggest that epicenter dynamics from high to low connectivity habitat may be predicted for many naturally cycling populations. In fact, we know of two other population systems with qualitatively similar spatial dynamics. Cycles of the Canada lynx were reported to first peak near west central Canada with peaks in the extreme locations of the country lagging 2–4 years behind more centrally located areas (Smith and Davis 1981). Likewise, traveling waves of the Red Grouse in northern Scotland originated in the center of suitable moorland habitat and subsequently spread to margins where moorland bordered unsuitable habitat (Moss et al. 2000).

One goal of this study was to reveal the mechanism underlying the previous empirical observation of traveling waves in spatial population dynamics from high to low connectivity habitat. We proposed here two possible mechanisms: (1) that immigration subsidies in high connectivity habitat inflate population growth rates and, thus, reduce the time from valleys to peaks in cyclical population dynamics and (2) that populations in high connectivity habitat crash from peaks to valleys quicker than in more isolated habitat. Our simulations did not

Fig. 3 The relationship between relative phase angle of the isolated patch compared to the two well-connected patches ($\Omega = 1.00$) across a range of levels of lesser connectivity. The symbol Ω is a measure of connectivity relative to the most highly connected patches. *Time step* is an arbitrary time unit over which the model was repeatedly iterated



support the first hypothesis because, while immigration subsidies did inflate population growth rates in high connectivity habitat, the inflation was not sufficient to reduce the time from valleys to peaks. In fact, because high connectivity habitat had much greater variances in population sizes, times from population valleys to peaks were actually greater than in isolated habitat. Instead we found support for the second hypothesis, that popula-

tions crashed more quickly in high connectivity habitats. Minimum apparent population growth rates were smallest in high connectivity habitats, in accordance with the second hypothesis. This stronger population crash in high connectivity habitat is likely to be tied to over-compensatory density dependence.

From these results, we can generate testable predictions about the nature of population dynamics across a landscape. First, when traveling waves are present in a cyclic system, we predict that one will find a gradient in minimum λ 's (H_{t+1}/H_t) (during the decrease phase of a cycle) where populations at the beginning of a wave would have the smallest minimum λ 's while those at the end of the wave would have the largest minimum λ 's. On the other hand, in cyclic systems with no evidence of traveling waves, one would expect to find no spatial gradient in minimum λ 's among declining populations. Our model suggests that the minimum λ of a habitat is negatively associated with the level of habitat connectivity; thereby causing waves radiating from high connectivity habitat. A recent study of the larch budmoth found this traveling wave-connectivity relationship (Johnson et al. 2004). Whether this hypothesis conforms to other population systems remains to be empirically tested.

Previous theoretical analyses have demonstrated traveling waves spreading outward from the edges of obstacles in an otherwise homogeneous landscape

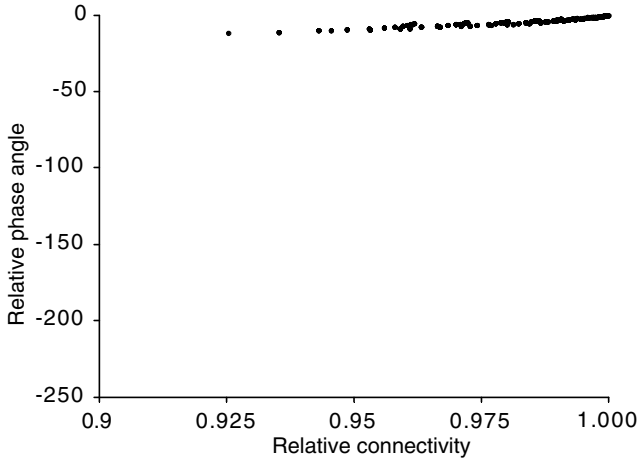


Fig. 4 Relationship between relative phase angle and the relative connectivity of 625 patches embedded in a uniformly spaced 50×50 patch matrix

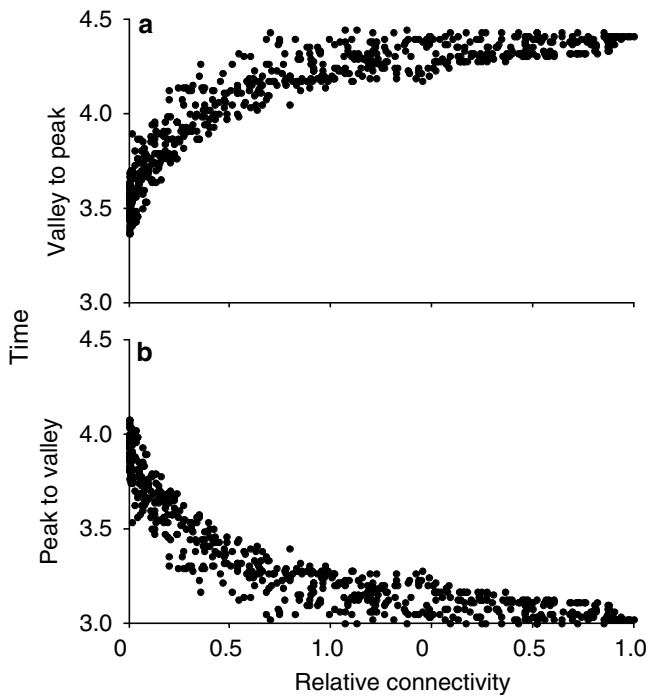


Fig. 5 **a** Relationship between the mean time period from a valley to a peak in population cycles and connectivity ($r^2=0.85$, $n=616$, $p<0.001$). **b** Relationship between the mean time period from a peak to a valley in population cycles and connectivity ($r^2=0.85$, $n=616$, $p<0.001$)

(Sherratt et al. 2002, 2003). In these models, the boundaries between suitable habitat and the obstacles had ‘zero flux’ conditions, which means that individuals dispersing into the unsuitable habitat did not reproduce and effectively died (analogous to the absorbing boundary condition in the present study). The results of Sherratt et al. (2002, 2003), however, are in apparent contrast to the results of the present study for the following reason. In the Sherratt et al. (2002, 2003) models, there was no emigration from the obstacles so that habitat at the edge of the obstacle received lower immigration subsidies than habitat away from the obstacle; yet traveling waves emanated from these habitats with relatively low connectivities. In the present study, outbreak waves emanated from the habitat with a single focus of high connectivity to the lower connectivity habitat, and empirical data on waves of larch budmoth outbreaks supported this result (Johnson et al. 2004). However, we did not specifically investigate the effects of landscape obstacles on spatial dynamics. Thus, the apparent conflict between our results and those of Sherratt et al. (2002, 2003) may be due to specific effects of landscape obstacles on spatial dynamics, independent of connectivity effects, or due to differences in local dynamics specified in the models. Moreover, our results suggest some variation in wave patterns when there are multiple foci of high-density habitat – most commonly outwardly radiating waves – but also somewhat directional waves. It is clear that more analyses are necessary

to understand the complex spatiotemporal patterns in these more complex landscapes.

The effect of variation in habitat connectivity on spatial population dynamics has important implications for dynamics on fragmented landscapes. Habitat fragmentation refers to the isolation of patches of suitable habitat in a matrix of unsuitable habitat. Whether habitat fragmentation is natural or human-induced, it can have a number of significant effects on population dynamics, including lowering population densities (Andr n 1994; Fitzgibbon 1997; Davies and Margules 1998; Didham et al. 1998), increasing population densities (Cappuccino and Martin 1997; Dooley and Bowers 1998; Lecomte et al. 2004), increasing population fluctuations (Fitzgibbon 1997; Lecomte et al. 2004), increasing local extinction probabilities (Hames et al. 2001; Lecomte et al. 2004), decreasing local colonization probabilities (Hames et al. 2001), reducing gene flow (Bacles et al. 2004), and decreasing genetic variation (Young et al. 1993). On a regional scale, metapopulation theory makes the prediction that organisms living in highly fragmented habitats are more prone to regional extinction than those in well-connected habitats (Thomas and Harrison 1992; Hanski and Ovaskainen 2000), resulting in lower species diversity in highly fragmented habitats (Ferraz et al. 2003). Habitat fragmentation has also been shown to influence population processes during biological invasions by altering the speed by which populations expand into new areas (Shigesada et al. 1986; Kinezaki et al. 2003). Despite this wealth of knowledge on how habitat heterogeneity influences various population processes, little is known about its influences on the dynamics of resource-consumer populations. Roland (1993) reported that outbreaks of tent caterpillars (*Malacosoma distria*) were more pronounced in areas of high forest fragmentation and argued that this relationship was caused by decreased parasitoid effectiveness in fragmented habitats (Roland and Taylor 1997). However, relatively little is known about how geographical variation in habitat fragmentation affects the spatial dynamics of populations. The present study suggests that variation in fragmentation across a landscape can induce epicenter dynamics and traveling waves from areas with low levels of fragmentation in cyclic populations. This provides a foundation from which one can generate hypotheses about the effects of habitat fragmentation on spatial population dynamics.

Outbreaks of herbivorous insects can have dramatic effects on forests, causing defoliation over large geographical areas, and this may lead to decreased tree growth and/or tree mortality which may trigger a multitude of other ecological effects (Myers 1993; Lovett et al. 2002). There is a general trend of increased impacts on forests with increasing frequencies and duration of outbreaks, thus illustrating the importance of understanding the causes of outbreak durations. Interestingly, outbreak frequencies of the tent caterpillar in North America were found to be

greater in high fragmentation habitats than in low fragmentation habitats (Roland 1993). Results from the present study are contradictory with respect to the tent caterpillar finding because when the level of fragmentation surpassed an upper threshold the populations in highly fragmented habitat fell into a longer period than those in less fragmented habitats; consequently, outbreaks were less frequent in high fragmentation (low connectivity) habitat.

Outbreak waves of population dynamics have been demonstrated in numerous organisms, but their causes have remained elusive to ecologists. We have presented evidence here that recurrent traveling waves can originate in epicenters in low fragmentation habitat under certain conditions. When there are multiple areas of low fragmentation, however, the spatial dynamics can vary temporally between radiating and directional waves. As habitat fragmentation is pervasive in both natural and human-altered landscapes, the results of this analysis could have wide-ranging implications. In highly mobile outbreaking forest pests – such as the larch budmoth, for example – focusing outbreak control efforts on the epicenters may disrupt the wave of outbreak to adjacent habitat. In addition, we have demonstrated that traveling waves persist across a wide range of levels of connectivity. Thus, for species of conservation concern, preserving high-density habitat may insure the persistence of naturally occurring traveling waves across varying levels of connectivity. Both the theoretical evidence presented here and the analytical data of Johnson et al. (2004) indicate an association between connectivity and traveling waves emanating from epicenters. Further analyses of the spatial dynamics of oscillatory populations of other species are needed to determine the ubiquity of this association.

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