Popul Ecol (2006) 48:131–138
DOI 10.1007/s10144-005-0248-6

ORIGINAL ARTICLE

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Geographic variation in density-dependent dynamics impacts the synchronizing effect of dispersal and regional stochasticity

Received: 2 June 2005 / Accepted: 25 October 2005 / Published online: 26 January 2006

Abstract Explanations for the ubiquitous presence of spatially synchronous population dynamics have assumed that density-dependent processes governing the dynamics of local populations are identical among disjunct populations, and low levels of dispersal or small amounts of regionalized stochasticity ("Moran effect") can act to synchronize populations. In this study we used historical spatially referenced data on gypsy moth (*Lymantria dispar*) outbreaks to document that density-dependent processes can vary substantially across geographical landscapes. This variation may be due in part to geographical variation in habitat (e.g., variation in forest composition). We then used a second-order log-linear stochastic model to explore how inter-population variation in density-dependent processes affects synchronization via either synchronous stochastic forcing or dispersal. We found that geographical variation in direct density-dependence (first order) greatly diminishes synchrony caused by stochasticity but only slightly decreases synchronization via dispersal. Variation in delayed density-dependence (second order) diluted synchrony caused by regional stochasticity to a lesser extent than first-order variation, but it did not have any influence on synchrony caused by dispersal. In general, synchronization caused by dispersal was primarily dependent upon the instability of populations and only weakly, if at all, affected by similarities in density-dependence among populations. We conclude that studies of synchrony should carefully consider both the nature of the synchronizing agents and the pattern of local density-dependent processes, including how these vary geographically.

Keywords Spatial synchrony · Moran effect · Gypsy moth · Population cycle · Stability · *Lymantria dispar* · Outbreak

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s10144-005-0248-6 and is accessible for authorized users.

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Introduction

The field of population dynamics focuses on quantifying and understanding variation in abundance through space and time. Among these patterns, population cycles and spatial synchrony have received considerable attention (Royama 1992; Liebhold and Kamata 2000; Turchin 2003). Population cycles refer to periodic oscillations in abundance though there may be considerable variation in both the strength and period of these cycles (Berryman 1996; Kendall et al. 1998). Spatial synchrony refers to changes in abundance that are coincident among geographically disjunct populations (Hanski and Woiwod 1993; Ranta et al. 1995; Bjørnstad et al. 1999; Liebhold et al. 2004).

The apparent ubiquity of synchronous population dynamics across a spectrum of animal taxa has recently attracted considerable attention. While synchrony is easily detected, the causes can be debatable. This is because similar patterns of synchrony can be caused either by (1) dispersal of individuals between populations, (2) movement of natural enemies (e.g., predators) among populations or (3) correlation in exogenous stochastic forces. The latter phenomenon, often termed "regional stochasticity" or the "Moran effect" after the Australian statistician who was credited with first recognizing this source of synchrony (Moran 1953), will result from climatic fluctuations impacting (often in a subtle way) the dynamics of populations; analyses of historical weather time series demonstrate that virtually all weather variables are geographically synchronous. Furthermore, this climatic correlation declines with distance in a manner that often resembles the distance-dependent decline in population synchrony of diverse taxa (Koenig 2002; Liebhold et al. 2004).

Substantial theory on spatially synchronous dynamics is centered on how oscillations driven by density-dependent interactions can be spatially synchronized as a result of dispersal or regionalized stochastic forcing (Royama 1992; Ranta et al. 1995; Kendall et al. 2000; Royama 2005). Moran (1953) used a stochastic second-order autoregressive model to represent local population dynamics and showed that any spatial correlation in stochastic forcing would result in synchronization of the dynamics of spatially disjunct populations. In detail, Moran (1953) showed that whenever local dynamics are linear (or 'log-linear') then the synchrony in dynamics would equal the correlation in the stochastic forcing. A key assumption in his analysis was that the density-dependent processes affecting local population growth are identical among the spatially disjunct populations. Such an assumption is inherent in many of the recent investigations of the synchronizing effects of regionalized stochasticity as well as dispersal (Ranta et al. 1995; Kendall et al. 2000; Cazelles and Boudjema 2001). However, paralleling the theoretical and empirical inquiries into population synchrony, there are recent studies documenting substantial geographical variation in density-dependent processes (Saitoh et al. 1998; Williams and Liebhold 2000; Tkadlec and Stenseth 2001). Geographic variation in density-dependence will usually result in geographic variation in dynamics, particularly with respect to intensity of outbreaks and periodicity (Henttonen et al. 1992; Bjørnstad et al. 1998). These differences in periodicity and dynamics may be expected to affect the tendency of populations to "phase lock" (Rosenblum et al. 1996; Blasius and Stone 2000). As a result, such geographical variability may dramatically affect synchronization. Blasius et al. (1999), using a tri-trophic model of multiple patches coupled via dispersal, showed that even in the presence of geographical variation in model parameters, synchronization may still occur but they did not explore the extent to which this geographical variation impacted synchronization.

Motivated by Peltonen et al.'s (2002) analysis of spatial variation in gypsy moth dynamics, we investigated how geographical variation in density-dependence impacts spatial synchrony. First, we illustrate geographical variation in density-dependence using historical data on gypsy moth, *Lymantria dispar*, outbreaks in North America. Next we use theoretical models to explore how variation in density-dependence will mould the synchronizing effects of dispersal and regionalized stochastic forcing.

A simple model

We used a stochastic second-order log-linear model to represent population dynamics. Although the dynamics of most populations are inherently nonlinear (Turchin 2003), log-linear models often accurately approximate the stochastic dynamics of many populations (Roughgarden 1975). The model is of the same family as the model that Moran (1953) introduced to discuss synchronization via regional stochasticity [and this class has recently been used to study synchronization via dispersal (e.g., Barbour 1990; Kendall et al. 2000)]. Within this formulation, the dynamics of two populations whose densities in year t are represented by X_t and Y_t will be given by:

$$\begin{aligned} X_t &= X_{t-1}\mathrm{e}^{\alpha_1\log(X_{t-1})+\alpha_2\log(X_{t-2})+\varepsilon_{x,t}}, \\ Y_t &= Y_{t-1}\mathrm{e}^{\beta_1\log(Y_{t-1})+\beta_2\log(Y_{t-2})+\varepsilon_{y,t}}. \end{aligned} \tag{1}$$

where $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ are random normal deviates with means of zero and standard deviations σ_X and σ_Y, respectively. For log-transformed values, these dynamics translate to the paired second-order autoregressive model:

$$\begin{aligned} x_t &= a_1\, x_{t-1} + a_2\, x_{t-2} + \varepsilon_{x,t}, \\ y_t &= b_1\, y_{t-1} + b_2\, y_{t-2} + \varepsilon_{y,t}, \end{aligned} \tag{2}$$

where $x=\ln(X)$, $y=\ln(Y)$, $a_1=\alpha_1+1$, $a_2=\alpha_2$, $b_1=\beta_1+1$ and $b_2=\beta_2$. The parameters a_1 (or b_1) and a_2 (or b_2) represent the strength of direct (first-order) and delayed (second-order) density-dependent effects on population 1 (or population 2). The first function in Eq. 2 can be rearranged as:

$$\begin{aligned} R_{x,t} &= \ln(X_t/X_{t-1}) = (x_t - x_{t-1}) \\ &= (a_1 - 1)x_{t-1} + a_2\, x_{t-2} + \varepsilon_{x,t}. \end{aligned} \tag{3}$$

That is, the change in population 1's density, $R_{x,t}$, is linearly related to the log of population density in the current (direct density-dependence) and previous (delayed density-dependence) generations. This second-order model has been widely used as an approximation of the oscillatory dynamics of a variety of taxa and is known to embrace a diversity of behaviors ranging from periodic oscillations to random walks, etc. (Royama 1992). Figure 1a maps the dynamics of the second-order stochastic model under various parameter values [parameters outside of the triangle result in divergent dynamics (Royama 1992)]. Parameter values falling within the upper portion of the triangle result in bounded random-walk dynamics. Inside the arch within the lower portion of the triangle, the dynamics will be periodic (in the presence of stochastic excitation).

Geographical variation in gypsy moth dynamics

The gypsy moth, *L. dispar*, is a leaf-feeding insect, native to most of temperate Europe and Asia but introduced in

North America. Throughout much of its range, gypsy moth populations exhibit episodic outbreaks; previous analyses indicate a statistical tendency for either a 10- or 5-year periodicity (Johnson et al. 2005, 2006). Furthermore, outbreaks are partially synchronized throughout North America (Williams and Liebhold 1995b; Peltonen et al. 2002). We fit the second-order log-linear (autoregressive) model to 150 geographically disjunct gypsy moth time series from the northeastern USA. The time series spanned the period 1975–2002 and represented the proportion of land area defoliated in 25×25 km cells. The details of time-series construction from annual aerial survey maps are given in Peltonen et al. (2002). The 150 locations used here were the most frequently defoliated areas of the northeastern USA during the 1975–2002 interval.

Figure 1b shows the estimated second-order model parameter values mapped in parameter space. Both the first- and second-order parameters exhibited considerable variation. Most parameter values fell within the slow period oscillatory region of parameter space in concordance with the overall 10-year periodicity of these populations, but with significant spatial variation. Geographic mapping of parameter values (Fig. 2) indicated that values at nearby locations were similar [a detailed statistical analysis of this autocorrelation is presented in Peltonen et al. (2002)]. In Fig. 1b, the 150 time series are coded according to the dominant forest type in which the populations were located. These forest types were determined by overlaying time-series locations with a forest-type group map (Eyre 1980). Though there was general overlap in the parameter values among the various forest types, there were some clear trends. For example, populations located in the white pine

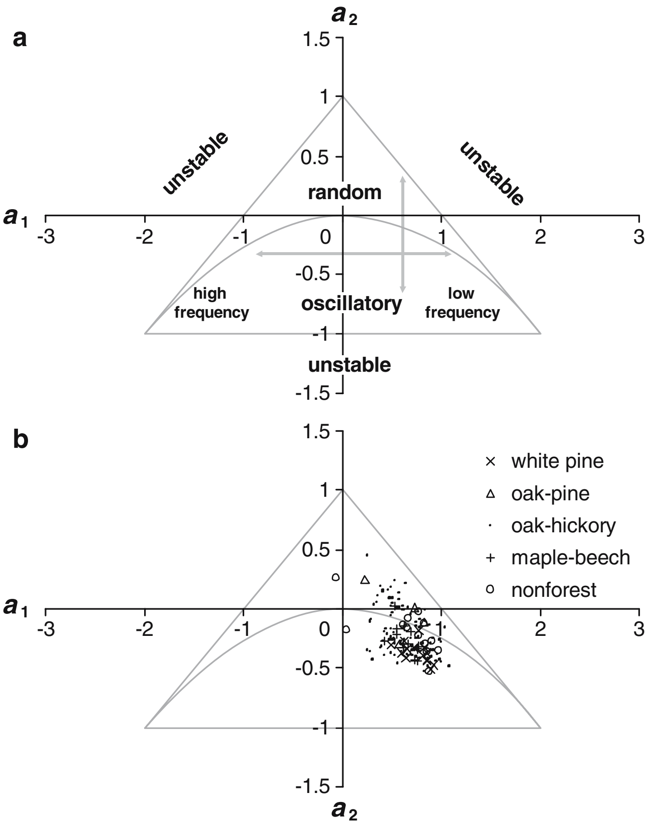

Fig. 1a, b Parameter space for the second-order linear model, Eq. 2. **a** Population behavior in various regions of the parameter space. *Gray lines with arrows* correspond to the range of parameters explored in simulations. **b** Parameter values fit to time series of yearly area defoliated by the gypsy moth in individual 25×25 km cells in the northeastern USA, coded by the dominant forest type classified in a map published by Eyre (1980)

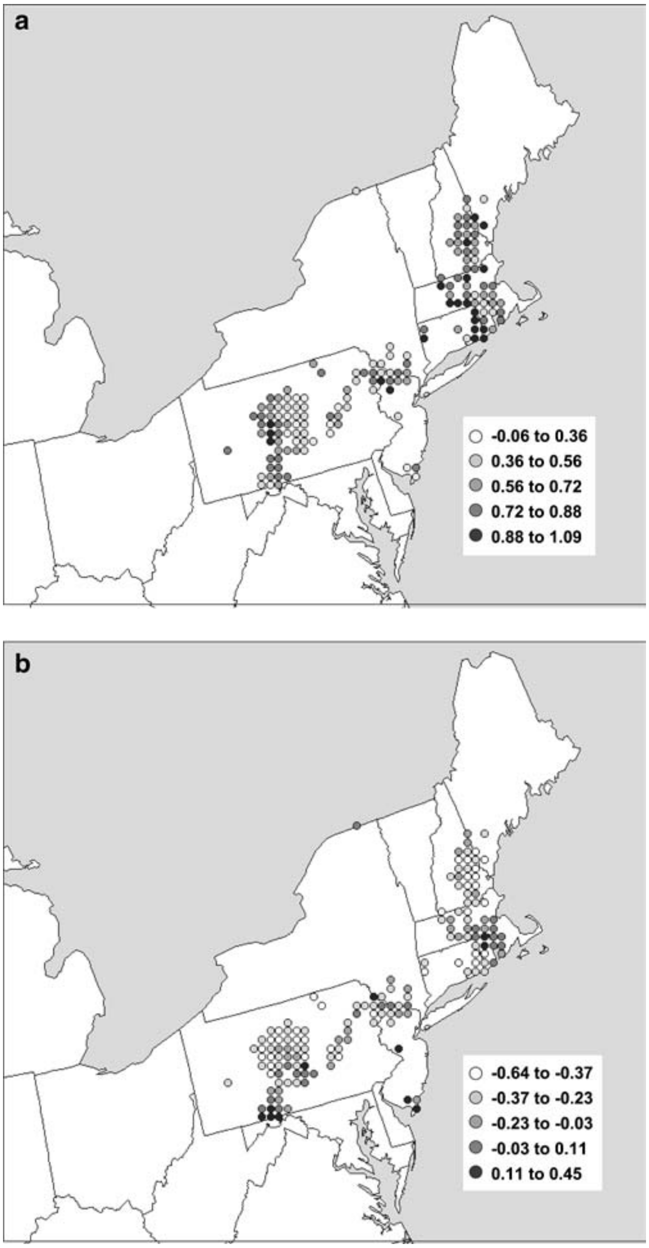

Fig. 2a, b Map showing geographical variation in second-order model parameters fit to time series of yearly area defoliated by the gypsy moth in individual 25×25 km cells in the northeastern US. **a** First-order parameter (a_1) values. **b** Second-order parameter (a_2) values group tended to have low second-order parameter values and may consequently be expected to exhibit more strongly periodic dynamics.

Synchrony and geographical variation

Given the geographic variation in density-dependence, we ask what is the consequence of this variation on synchronization of populations? The North American gypsy moth has very limited dispersal capabilities (females are flightless). It is therefore natural to consider regional stochasticity to be the crucial determinant of spatial synchrony (Williams and Liebhold 1995b; Peltonen et al. 2002). Given our time-series analyses, we inquire into how geographical variation in density-dependence affects synchronization through regionalized stochasticity. For generality, we also investigate synchronization through dispersal.

We simulated the dynamics of two linked populations using Eq. 2. First we conducted a series of simulations in which the first-order parameters, a_1 and b_1, were varied from -0.9 to 1.1 in increments of 0.4 (second-order parameters were held constant at $a_2=b_2=-0.3$). Then second-order parameters were varied from -0.7 to 0.3 in increments of 0.2 (first-order parameters were held constant at $a_1=b_1=0.6$). These values encompass a portion of the parameter space that represents both periodic and random dynamics in the stochastic second-order model (Fig. 1a) and encompass the range of parameter values observed among North American gypsy moth populations (Fig. 1b). For each parameter combination, populations were initiated out-of-phase and then simulated for 500 generations. The stochastic term, ε_t, was simulated as a random normal deviate with mean = 0, standard deviation $\sigma=0.5$, and the correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ fixed at 0.5. For such parameters, Moran's theorem provides the baseline correlation of 0.5 between populations with identical dynamics. We used the final 100 generations of each simulation to calculate periodograms (to quantify patterns of periodicity) and measure synchrony, using the Pearson correlation coefficient, between the two series. Each parameter combination was replicated 500 times, and results were summarized as averages across these replicates.

As described above, simulations incorporated a Moran effect in that $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ were correlated (50%). In order to simulate the effect of parameter variation when synchronization occurred via dispersal, we replicated all simulations with $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ uncorrelated, but with a constant 10% transfer of individuals between populations each generation. Synchrony was always measured directly following the dispersal step in simulations.

As according to theory (Fig. 1a), first-order parameter values (a_1, b_1) greatly influenced the period of oscillations in the simulated series (online supplementary Fig. 1). Oscillations had dominant frequencies of around 0.45 (period≈2) when $a_1=-0.9$ and dominant frequencies around 0.1 (period≈10) when $a_1=0.7$. Obviously, when both populations were governed by identical parameter values (i.e., $a_1=b_1$, the diagonal cells in online supplementary Fig. 1) their spectra were identical, and as parameters diverged, the two populations exhibited divergent spectra and different dominant frequencies. Also, when first-order parameters were identical, the synchrony of the two populations mirrored Moran's theorem (50%: the same level as correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$) but when the parameters increasingly differed, the level of synchrony eroded to zero (Fig. 3).

The parameter map (Fig. 1a) shows how the second-order parameter is inversely related to the strength of the periodicity. The online supplementary material (Fig. 2) illustrates this. The synchrony was greatest when second-order parameters were identical (diagonal of Fig. 4) and diminished as parameter values diverged. However, this effect was not as strong as the effect of variation in first-order parameters. Thus, it appears that the Moran effect is more sensitive to variation in first-order parameters than it is to variation in second-order parameters.

Interestingly, the impact of geographical variation in density-dependence on synchronization was quite different for dispersal-driven systems. As for environmental correlation, differences in first-order parameters led to spectra with divergent periods (online supplementary Fig. 3) and diminished synchrony (Fig. 5). However, this decrease in synchrony was much less than in populations synchronized via regional stochasticity (Fig. 3).

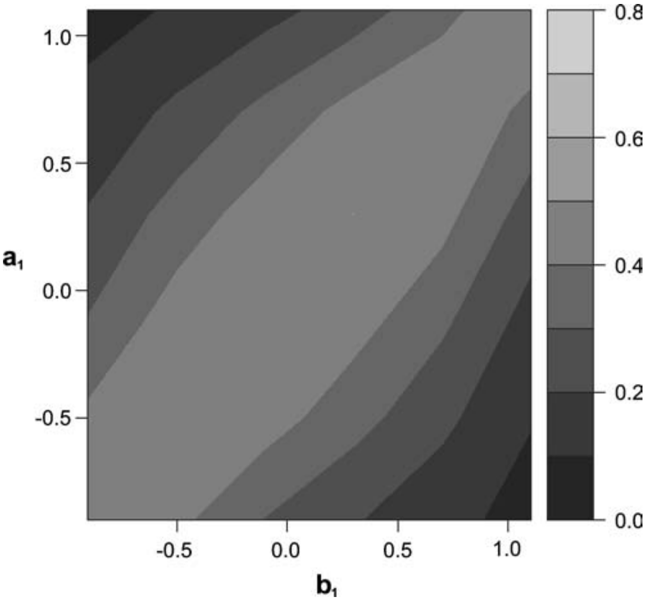

Fig. 3 Surface depicting synchrony (correlation) between time series of populations *a* and *b* simulated with various values of the first-order parameter in a second-order linear stochastic model (Eq. 2) under regional stochasticity. (Standard deviation of ε_t, $\sigma=0.5$, correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ was 50%; second-order parameters $a_2=b_2=-0.8$)

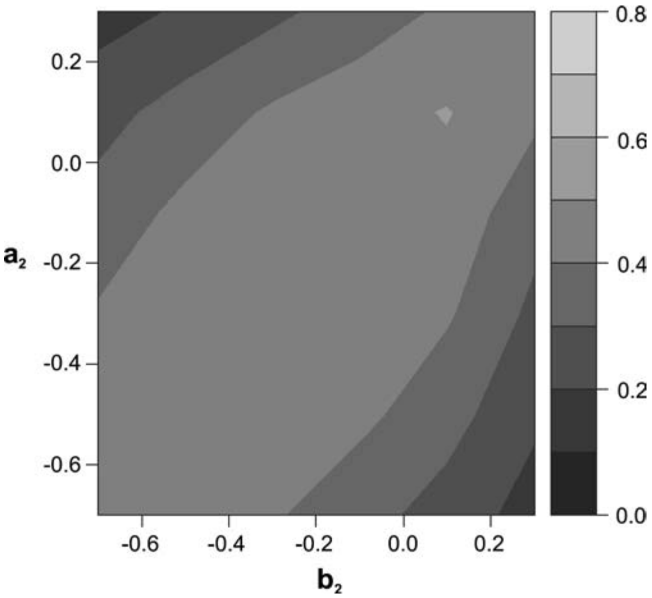

Fig. 4 Surface depicting synchrony (correlation) between time series of populations *a* and *b* simulated with various values of the second-order parameter in a second-order linear stochastic model (Eq. 2) under regional stochasticity. (Standard deviation of ε_t, $\sigma = 0.5$, correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ was 50%; first-order parameters $a_1 = b_1 = 0.2$)

Comparing dispersal and regional stochasticity, the effect of variability in second-order parameters was even more divergent. Variability in second-order parameters had no discernable effect on synchronization via dispersal (Fig. 6) even though it did dilute synchrony among populations subjected to the Moran effect (Fig. 4). The finding that populations with different second-order parameters were as synchronous as populations with identical second-order parameters is surprising given that this causes conspicuous divergence of the spectra (online supplementary Fig. 4).

While it is evident from Fig. 6 that differing second-order parameters did not cause two populations linked via dispersal to be less synchronous than when they had identical parameters, the figure does show that synchrony was greatest when both populations had either low or high second-order parameter values. This trend is also seen in extreme values of the first-order parameters (Fig. 5), but it is never evident in populations synchronized via regional stochasticity (Figs. 3, 4).

Discussion

Synchronization of disjunct populations through dispersal is well documented. So also is the “Moran effect,” in which populations governed by identical density-dependent mechanisms will tend to synchronize when influenced by regionalized stochastic effects. However, in the real world, geographically disjunct populations are often regulated by “non-identical” patterns of density-dependent feedbacks: spatial heterogeneity is pervasive in natural environments, and this can often lead to geographic variation in intrinsic dynamics (Bjørnstad et al. 1995, 1998; Tkadlec and Stenseth 2001). The effect

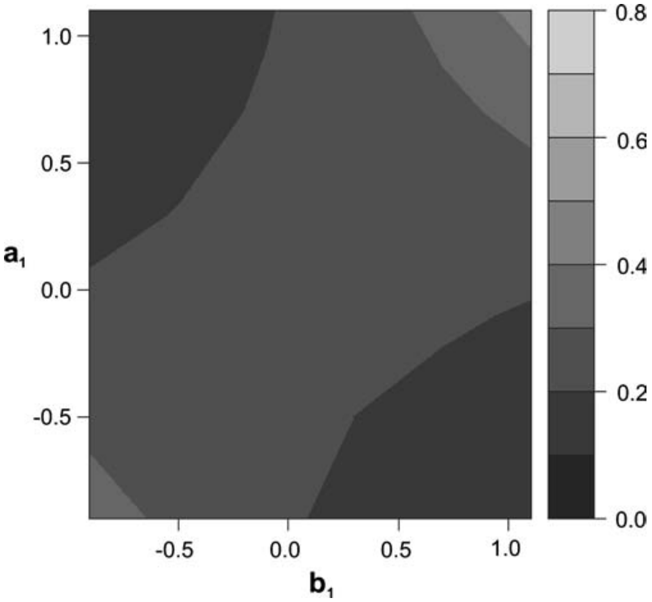

Fig. 5 Surface depicting synchrony (correlation) between time series of populations *a* and *b* simulated with various values of the first-order parameter in a second-order linear stochastic model (Eq. 2) with 10% dispersal between populations. (Standard deviation of ε_t, $\sigma = 0.5$, correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ was 0%; second-order parameters $a_2 = b_2 = -0.8$)

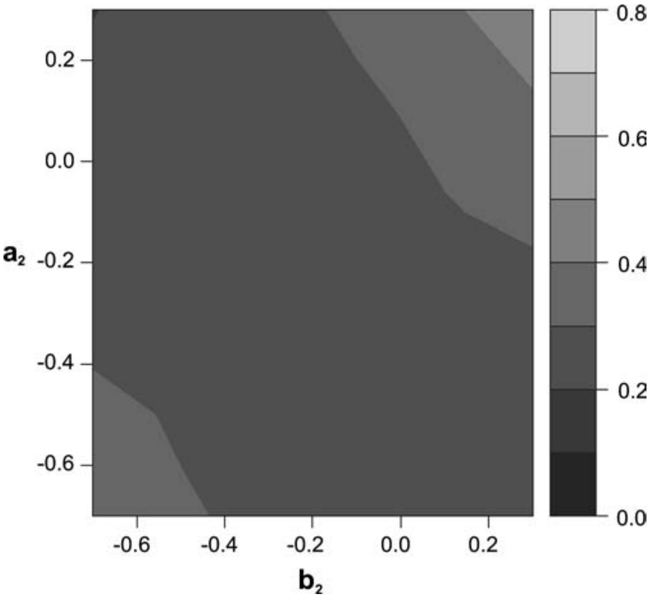

Fig. 6 Surface depicting synchrony (correlation) between time series of populations *a* and *b* simulated with various values of the second-order parameter in a second-order linear stochastic model (Eq. 2) with 10% dispersal between populations. (Standard deviation of ε_t, $\sigma = 0.5$, correlation between $\varepsilon_{x,t}$ and $\varepsilon_{y,t}$ was 0%; first-order parameters $a_1 = b_1 = 0.2$)

on synchrony of such spatial variation is an area that clearly deserves more attention.

The gypsy moth populations discussed here exhibit marked geographical variation in dynamics. The variation is spatially autocorrelated (Peltonen et al. 2002) and associated—at least to some extent—with forest vegetation (Fig. 1b), testifying that observed variability is not simply the result of sampling error, but the result of habitat characteristics affecting interactions between the gypsy moth, its hosts, and/or natural enemies. A more extensive analysis of how gypsy moth dynamics are affected by habitat variation is discussed by Johnson (2006).

Using computational models we found that differences in density-dependent feedbacks among populations led to lower levels of synchrony than expected under Moran's theorem (Figs. 3, 4). Moreover, synchronization through the Moran effect appears to be more sensitive to variation in direct density-dependence (first-order parameters) than to variation in delayed density-dependence (second-order parameters). The first-order parameter is a determinant of the period of oscillations (as long as parameters are in the cyclic part of the parameter space), while the second-order parameter determines the strength of periodicity (Fig. 1a); thus, the finding that variability in first-order parameters more strongly dilutes synchronization than does variability in second-order parameters indicates that variability in oscillation period more strongly impacts synchronization than does variability in periodicity strength.

Given the all-pervasive spatial autocorrelation in habitats and community compositions (Legendre 1993), nearby populations will tend to have similar density-dependent processes (Peltonen et al. 2002) (Fig. 2). As a consequence, we may expect greater heterogeneity-induced erosion of the Moran effect among more distantly located populations. Moreover, since climatic correlation tends to decline with distance (Koenig 2002), Moran's theorem alone predicts synchrony to decay with distance even in the absence of variation in density-dependence. The critical message here is that variation in density-dependence among populations should cause synchrony to decline more rapidly with distance than would be expected from environmental correlation alone, and that the details of this divergence depend critically on whether the geographic variation is in the direct or delayed feedbacks. This prediction was confirmed in simulations incorporating variation in density-dependence using linear models fit to gypsy moth data (Peltonen et al. 2002). Our present simulations refine this prediction.

Aanes et al. (2003) studied time series of three geographically disjunct Svalbard reindeer populations and concluded that populations were synchronized via regional stochasticity; synchrony was diminished by geographic variation in density-dependent dynamics, though they did not explicitly test for this. Ripa and Ives (2003), as part of a larger study of trophic interactions and synchronization via regional stochasticity, developed equations that predict synchrony between two populations under a Moran effect, corrected for the effect of variable first-order dynamics. They found that variability generally diluted synchronization; our simulations illustrate their conclusion and extend these relationships to the second-order model.

The simulations reported here indicate that there are both similarities and important differences in the way variation in density-dependence affects synchronization via regionalized stochasticity versus dispersal. When direct density-dependence (as measured by first-order parameters of the linear model) varies between populations, differences in the period of oscillations dilute synchronization due to stochasticity, and to a lesser extent, synchronization due to dispersal (Figs. 3, 5). However, in the case of delayed density-dependence (measured by second-order parameters), variability can cause a slight decrease in synchronization due to regional stochasticity (Fig. 4), but variation does not appear to influence synchronization via dispersal (Fig. 6).

Ripa (2000) explored how parameters of the second-order linear model affected synchronization induced by dispersal and found that that synchrony increased with increasing instability. Ripa (2000) also demonstrated that instability increases in the parameter space shown in Fig. 1a as one moves from the center of the triangle toward the margins. It follows from Ripa's (2000) findings that population instability can be expected to increase at extreme values of the parameter space that we explored (defined by the gray, arrowed lines in Fig. 1a). We confirmed this conclusion by calculating the dominant eigenvalues for each set of parameters as described by Royama (1992). Instability increases with the dominant eigenvalues (Yodzis 1989) and the higher dominant eigenvalues are at the extreme values of a_1 and a_2 (online supplementary Fig. 5). These relationships, thus, explain our finding that synchrony increased with extreme values of either a_1 or a_2 in populations linked via dispersal (Figs. 5, 6).

The simulations presented here were all based on log-linear population models. However, most real populations are probably inherently nonlinear (Turchin 2003; Royama 2005). Lande et al. (1999) used a stochastic nonlinear model to show that synchrony was proportional to the ratio of dispersal rate to the strength of density-dependence, though they only considered direct density-dependent effects. Ranta et al. (1997) compared synchronization caused by regional stochasticity under a first-order stochastic Ricker model with a similar second-order model, and they found that the second-order model generally produced greater levels of synchrony though they did not explore a large range of parameter values. Subsequently Ripa (2000) used linearized stochastic models to arrive at the opposite conclusion: the order of density-dependence had little effect on synchronization. Engen et al. (2002) used a logistic model to show that variation in carrying capacity generally diluted synchrony caused by either regional stochasticity or by dispersal.

Royama (2005) recently conducted an extensive analysis of the effect of regional stochasticity on synchronization in another type of non-linear model. Royama's model was based upon the standard second-order linear model but introduced nonlinearity via a constraint on the net reproductive rate. He found that populations governed by parameter combinations that produce population convergence to equilibrium values tended to exhibit levels of synchrony close to those predicted by Moran (1953) for linear models. However when his nonlinear model produced oscillating populations, synchrony was greatly diminished or non-existent. While Royama (2005) did not specifically address variation in density dynamics among populations, he did consider variation among populations in the magnitude of the regionally stochastic effect; such variation can greatly dilute synchronization.

In addition to the linear model described above, we conducted limited simulations using a stochastic nonlinear Ricker-like second-order model. Simulations indicated that both first-order and second-order parameters influenced both oscillation period and the strength of periodicity so it was less obvious how to separate the effect of each. Also, we found the associations between degree of periodicity and degree of synchronization were opposite for first- and second-order parameters. Considering these results, as well as similar studies described from the literature (op. cit.), it would appear that there remains considerable uncertainty about how differing types of density-dependence affect synchronization in nonlinear systems (Grenfell et al. 1998; Bjørnstad 2000). Different approaches to modeling nonlinear population behavior seem to produce contradictory results; the ultimate resolution to this question may necessitate empirical or experimental approaches.

Any comparison of first-order effects with second-order effects is only relevant if we can ascribe these effects to specific types of biotic interactions. The types of interactions that can cause first-order effects include competition, generalist enemies, resource depletion, etc. The types of interactions leading to second-order effects are perhaps more difficult to identify because they include both specific interactions with a clear time lag (e.g., the numerical response of a specialist predator, maternal effects), as well as a variety of interactions that are more complex (Royama 1992; Williams and Liebhold 1995a) Thus, while it is easy to document geographical variability in first- and second-order density-dependence from time series, deducing the reasons for this variation requires detailed observation or field experimentation.

In conclusion, the results here demonstrate that geographical variation in density-dependence should be considered when attempting to explain observed patterns of spatial synchrony in field populations. Clearly, synchrony is influenced by the degree of correlation in stochastic effects and by geographical patterns of dispersal. But perhaps more interestingly, the type of density-dependent effects, especially the extent to which they produce periodic behavior, and the manner in which these effects vary geographically, will also influence patterns.

Acknowledgements We thank E. Luzader for technical assistance. Esa Ranta and Jörgen Ripa provided very useful comments on an earlier version of this paper for which we are grateful. This work was supported by United States Department of Agriculture National Research Initiative Grant #2002-35302-12656.

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