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LETTER

Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model system

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Abstract

Spatially separated populations of many species fluctuate synchronously. Synchrony typically decays with increasing interpopulation distance. Spatial synchrony, and its distance decay, might reflect distance decay of environmental synchrony (the Moran effect), and/or short-distance dispersal. However, short-distance dispersal can synchronize entire metapopulations if within-patch dynamics are cyclic, a phenomenon known as phase locking. We manipulated the presence/absence of short-distance dispersal and spatially decaying environmental synchrony and examined their separate and interactive effects on the synchrony of the protist prey species *Tetrahymena pyriformis* growing in spatial arrays of patches (laboratory microcosms). The protist predator *Euplotes patella consumed Tetrahymena* and generated predator–prey cycles. Dispersal increased prey synchrony uniformly over both short and long distances, and did so by entraining the phases of the predator–prey cycles. The Moran effect also increased prey synchrony, but only over short distances where environmental synchrony was strongest, and did so by increasing the synchrony of stochastic fluctuations superimposed on the predator–prey cycle. Our results provide the first experimental demonstration of distance decay of synchrony due to distance decay of the Moran effect. Distance decay of the Moran effect likely explains distance decay of synchrony in many natural systems. Our results also provide an experimental demonstration of long-distance phase locking, and explain why cyclic populations provide many of the most dramatic examples of long-distance spatial synchrony in nature.

Keywords

Dispersal, metapopulations, microcosms, Moran effect, phase locking, predator–prey cycles, protists, spatial synchrony.

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INTRODUCTION

Spatial synchrony refers to spatially separated populations which exhibit correlated fluctuations in abundance or some other population property. Spatial synchrony has been reported in many species, including insects, fish, birds, mammals and human pathogens (reviewed in Liebhold *et al.* 2004). Spatial synchrony, especially across long distances (synchrony has been reported for populations separated by > 100 km) is a surprising phenomenon that requires explanation. Spatial synchrony also has strong implications for metapopulation persistence (Heino *et al.* 1997).

Spatial synchrony typically decays with distance: more widely separated populations tend to be less synchronous (Ranta *et al.* 1999; Koenig 2002). Distance decay of synchrony presumably reflects distance decay in the underlying causes of synchrony. For instance, if populations are synchronized because of dispersal of organisms, synchrony might be expected to decay with distance because widely separated populations should exchange few or no dispersers (Ranta *et al.* 1995; Sutcliffe *et al.* 1996; Lande *et al.* 1999; Paradis *et al.* 1999). Populations which are synchronized because they experience synchronous environmental fluctuations (the Moran effect; Moran 1953) also should exhibit distance decay of synchrony, as environmental fluctuations themselves exhibit distance decay of synchrony (Lande *et al.* 1999; Ranta *et al.* 1999; Koenig 2002). However, dispersal and the Moran effect are not mutually exclusive. Teasing apart their separate effects in nature has proven challenging, except in the rare cases where dispersal does not occur (Grenfell *et al.* 1998). Furthermore, theory predicts that even in very simple ecological situations, dispersal and the Moran effect can have non-independent effects on synchrony, further complicating the challenge of explaining synchrony and its spatial decay (Ranta *et al.* 1995, 1999; Kendall *et al.* 2000; Ripa 2000; Abbott 2007).

Synchrony can exhibit more complicated spatiotemporal patterns than simple distance decay. In particular, even low rates of dispersal among populations exhibiting cyclic dynamics can cause those populations to cycle perfectly in phase; such populations are said to be phase locked (Blasius *et al.* 1999; Jansen 1999, 2001). Because phase locking is an all-or-nothing phenomenon, phase locking is a mechanism by which short-distance dispersal can produce long-distance synchrony. For instance, consider a linear system of n patches connected by nearest-neighbour 'stepping stone' dispersal. If dispersal phase-locks neighbouring patches, then all n patches necessarily are phase locked with one another. In practice, dispersal is unlikely to maintain perfect, global phase locking, due to among-patch heterogeneity of population dynamics (e.g. among-population variation in cycle periods and amplitudes), and to the effects of perturbations that kick populations out of phase (e.g. Ranta *et al.* 1997). The resulting complex spatiotemporal population dynamics can exhibit complex behaviours such as 'travelling waves' of synchrony and anti-synchrony, due to local population cycles shifting into and out of phase (e.g. Comins *et al.* 1992; Blasius *et al.* 1999).

Here, we complement observational and comparative studies of synchrony in nature by conducting a manipulative experiment in laboratory microcosms. In previous work (Vasseur & Fox 2009), we

examined the effects of dispersal, the Moran effect and the predatory ciliate *Euplotes patella* on the synchrony of the ciliate prey species *Tetrahymena pyriformis* in a 'minimally spatial' system (pairs of microcosms). We found that dispersal phase-locks predator–prey cycles, leading to high prey synchrony, and that the Moran effect also increases prey synchrony, independently of dispersal (Vasseur & Fox 2009). Dispersal has little effect on synchrony in the absence of predators because in the absence of predators there are no cycles to phase lock. The present experiment builds on our previous work by considering spatial arrays of microcosms, linked by spatially realistic patterns of short-distance dispersal and environmental fluctuations. We asked the following questions: (1) How do dispersal and environmental synchrony affect the pattern of distance decay of population synchrony? (2) Can short-distance 'stepping stone' dispersal produce phase locking of widely separated predator–prey cycles? and (3) Do dispersal and the Moran effect exhibit interactive or independent effects on synchrony?

METHODS

Experimental methods

The experiment was a 2 × 2 factorial design crossing the presence/absence of spatially correlated environmental fluctuations with the presence/absence of dispersal. The experimental units were linear spatial arrays of six culture bottles (microcosms). There were four replicate arrays/treatment combinations for a total of 16 arrays and 16 × 6 = 96 bottles.

The experiment used established culture methods, with minor modifications (Vasseur & Fox 2009). Culture vessels (patches) were screw-capped 100 mL glass bottles containing 80 mL of nutrient medium and one wheat seed. Nutrient medium comprised Protozoan Pellets (PP; Carolina Biological Supply, Burlington, NC, USA) at a concentration of 0.15 g PP L^{-1} spring water. Protozoan Pellets are standardized pellets of crushed, dried plant matter. The PP concentration used here is slightly lower than that used in Vasseur & Fox (2009) because pilot experiments indicated that higher PP concentration increased the risk of prey extinction. Bottles were loosely capped to allow gas exchange while preventing contamination by unwanted microbes. All materials were autoclaved before use.

Forty-eight hours before use the medium was inoculated with three bacterial species (*Enterobacter aerogenes*, *Bacillus cereus*, *Bacillus subtilis*) known to be edible to *Tetrahymena*. Other unidentified bacteria were inoculated along with the protists. On day 0 of the experiment, each bottle was inoculated with small volumes of medium from stock cultures of *Tetrahymena* and *Euplotes*. Volumes were chosen so as to give expected initial *Euplotes* densities of 0.5 mL^{-1} in all bottles, and expected initial *Tetrahymena* densities of either 22 or 225 mL^{-1} in alternate bottles within each array. Initial *Tetrahymena* densities varied among bottles so that adjacent bottles would begin predator–prey cycles slightly out of phase with one another. We expected that slight phase differences between patches near the nadir of the predator–prey cycle would develop into large differences in synchrony under the influence of demographic and environmental stochasticity, unless counteracted by the Moran effect and/or dispersal (Vasseur & Fox 2009). However, all bottles exhibited a highly synchronous increase in *Tetrahymena* early in the experiment, possibly because the initial *Euplotes* density was too low (see Results). The experiment therefore tested whether the Moran effect and dispersal could prevent this high initial synchrony from decaying over time.

Methods for manipulating environmental fluctuations and dispersal followed Vasseur & Fox (2009), with appropriate extensions to the multi-patch arrays considered here. Daily temperature fluctuations were achieved by assigning bottles between two incubators set at 20 and 30 °C. Each bottle followed a specific temporal sequence generated by permuting a reference vector which coded for 30 days at 20 °C and 20 days at 30 °C (thereby ensuring that each jar experienced fluctuations with the same mean, 24 °C and variance, 24.5). For each spatial array of jars, we used a multivariate adaptation of the method of Vasseur (2007) to generate a matrix of six permutation vectors which were serially autocorrelated (possessing a $1/f^{0.5}$ power spectrum). Eight of the arrays experienced environmental fluctuations with spatially decaying synchrony. In these arrays, temperature vectors had a cross-correlation which declined linearly from 0.8 for adjacent pairs of patches to zero for patches at opposite ends of the array. These arrays potentially exhibit a spatially decaying Moran effect. In the other eight arrays, all temperature vectors were spatially independent (cross-correlation equal to zero). The multivariate extension of Vasseur (2007) yields very accurate cross-correlations between the first, and each successive vector, but suffers from reductions in the accuracy of successive cross-correlations (David A. Vasseur, unpublished work). To combat this issue, we selected the permutation matrix for each array which most closely matched the desired cross-correlation structure from 10 000 independent iterations of the method. Inspection of the resultant temperature sequences ensured that they yielded the desired serial and cross-correlation structure.

Each of the four replicate arrays comprising the −environmental synchrony/−dispersal treatment experienced a unique set of temperature fluctuations, which were re-used for the arrays comprising the −environmental synchrony/+dispersal treatment. Similarly, the four unique sets of temperature time series used for the +environmental synchrony/−dispersal treatment were re-used for the +environmental synchrony/+dispersal treatment. Using different sets of temperature time series for the replicate arrays within a treatment ensured that treatment effects were not confounded with unique features of a single set of temperature time series. Using the same temperature time series across dispersal treatments ensured that the effects of dispersal were more effectively isolated from those of temperature fluctuations.

Dispersal occurred in a 'stepping stone' pattern: only adjacent bottles within an array exchanged dispersers. On Mondays, Wednesdays and Fridays, the bottles were agitated and 8 mL (=10%) of medium from each bottle, and the organisms in it, was exchanged with 8 mL from an adjacent bottle. This procedure was repeated for all pairs of adjacent bottles. Bottles at either end of the array therefore exchanged dispersers only with a single adjacent bottle, whereas other bottles exchanged dispersers with two adjacent bottles, one on either side. All medium to be dispersed was removed from all bottles within an array before any was added back to any bottle, thereby ensuring that organisms could not be dispersed more than a single 'step'. Dispersal events occurred after sampling. Vasseur & Fox (2009) used the same dispersal regime, and showed that thrice-weekly dispersal events are sufficiently frequent for the treatment effects of dispersal to be captured by a theoretical predator–prey model assuming continuous dispersal. While a per-capita dispersal rate of 10% per dispersal event might seem high, the protists used in this experiment have generation times of *c.* 4 h (*Tetrahymena*) or *c.* 24 h (*Euplotes*), implying

per-capita dispersal rates substantially < 10% per generation. Studies of interpatch movement in fragmented habitats in nature find mean interpatch movement rates of *c.* 15% per generation (minimum 0%), hence our dispersal rate is not unrealistic (Bowne & Bowers 2004).

Bottles were sampled on weekdays starting on day 1, using established procedures (Vasseur & Fox 2009). Briefly, bottles were agitated and *c.* 0.3 mL samples were withdrawn and the protists counted under a binocular microscope. Dense populations were diluted and subsampled. The experiment lasted 50 days.

Once every 7 days beginning on day 7, bottles were mixed and 8.5 mL of medium was withdrawn from each, replaced by 10 mL of fresh medium. This procedure replaced medium lost to sampling and prevented exhaustion of the resource base and accumulation of waste products. To prevent prey extinction, sterile replacement medium was inoculated immediately before use with a small known volume of medium drawn from a 5-day-old *Tetrahymena* stock culture, resulting in *c.* 10 *Tetrahymena* being added to each bottle. Medium replacement occurred after sampling, on a day with no dispersal. Medium removal comprises a small synchronous perturbation which might slightly increase mean synchrony across all jars, but cannot create differences in synchrony among treatments.

Data analysis

All statistical analyses were performed using R 2.12.0. (www.R-project.org). *Tetrahymena* densities (x) were transformed as $\log_{10}(x + 1)$ before analysis. We measured prey synchrony between each pair of bottles within each array as the cross-correlation of prey densities (Vasseur & Fox 2009). We then calculated the mean cross-correlation at each spatial lag within each array. Spatial lag is the number of dispersal 'steps' separating paired bottles. Adjacent bottles are separated by one step (spatial lag 1), whereas bottles at opposite ends of the array are separated by five steps (spatial lag 5). The resulting vector of five cross-correlations, one for each spatial lag, comprises a multivariate response variable. We applied Fisher's z-transformation to this vector to normalize it, and used MANOVA to test for effects of dispersal, environmental synchrony, and their interaction, with the Pillai trace as the test statistic (other test statistics gave similar results). We conducted univariate ANOVAs on the cross-correlations at each spatial lag to aid interpretation of the MANOVA. Inspection of residuals indicated conformity with statistical assumptions.

To directly test for treatment effects on the spatial decay of synchrony, we regressed the mean cross-correlations from each array on spatial lag. The estimated regression slope from each array summarizes the spatial decay of synchrony (negative slope) or the spatial increase of synchrony (positive slope). We used ANOVA to test for treatment effects on the regression slope, and two-tailed single-sample t-tests to test whether the mean regression slope in each treatment differed significantly from zero.

We used spectral analysis to test for predator–prey cycles, and test whether dispersal synchronized prey populations by entraining the phases of these cycles. For each prey population, we calculated the Lomb–Scargle periodogram (Lomb 1976; Scargle 1982). The Lomb–Scargle periodogram is a standard technique for spectral analysis of unevenly spaced time series data. The Lomb–Scargle periodogram gives the reduction in the sum of squares of the time series that would result from removal or 'detrending' of an oscillation with a given frequency. Distinct peaks in the periodogram correspond to regular oscillations with distinct frequencies [see Vasseur & Gaedke (2007) for further discussion in an ecological context]. A predator–prey cycle should generate a distinct low-frequency peak in the periodogram due to the long period of the predator–prey cycle (e.g. Fig. 1). We estimated the Lomb–Scargle periodograms using R code developed by Glynn *et al.* (2006), available from http://research.stowers-institute.org/efg/2005/LombScargle/R/index.htm. Time series of $\log(x + 1)$-transformed prey densities were linearly detrended before spectral analysis. For every prey population for which the periodogram indicated the existence of a distinct predator–prey cycle, we estimated the phase of this cycle by fitting a cosine wave to the linearly detrended prey dynamics [Vasseur *et al.* 2005; estimating the phase from the periodogram using the method of Glynn *et al.* (2006) gave similar results]. This approach to estimate cycle phase is appropriate for cycles with a constant period. Our time series were too short to allow the use of wavelets to formally test for temporal shifts in cycle period. We had no reason to expect such shifts, and the periodograms revealed no hint of such shifts. For each array, we calculated the variance in phase among the prey populations using the var function

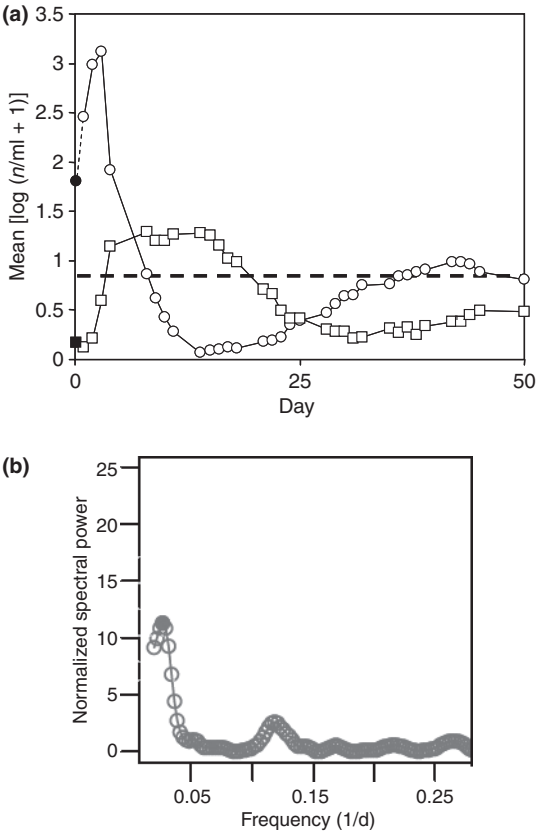

Figure 1 (a) Mean log-transformed densities of *Tetrahymena* (circles) and *Euplotes* (squares) over time, across all jars in all arrays. Filled symbols on day 0 indicate initial conditions (mean initial conditions for *Tetrahymena*). Horizontal dashed line indicates the approximate density corresponding to a sample containing one individual, given our sampling protocol. Error bars would be large, due to both sampling error and to asynchrony across jars, and are omitted for clarity. (b) Normalized Lomb–Scargle spectrogram for an illustrative prey population. The y-axis gives the proportion of the total variability of the (detrended) prey dynamics explained by fluctuations with a given period. The distinct low-frequency peak arises from the predator–prey cycle, which has an estimated period of 36.8 days in this population. The remaining variability represents random, stochastic, low-amplitude variability superimposed on the predator–prey cycle.

from R package circular (phase is a circular statistic). We used ANOVA to test for effects of dispersal, the Moran effect and their interaction on the variance in phase. We expected that dispersal would reduce the variance in phase among prey populations within arrays, but that the Moran effect would not. We expected the Moran effect to synchronize higher frequency stochastic variability in prey dynamics generated by stochastic temperature fluctuations, not entrain the low-frequency cycle generated by the predator–prey interaction.

Euplotes densities were very low on average, resulting in dynamics dominated by sampling error and preventing analysis of synchrony (see Results).

RESULTS

As in previous work (Vasseur & Fox 2009), *Tetrahymena* and *Euplotes* exhibited a predator–prey cycle (Fig. 1). Plotting the dynamics of average predator and prey densities across all jars in all arrays revealed a clear cyclic pattern (Fig. 1a). The spectral analyses provided a more rigorous and precise quantification of cyclic dynamics at the population level (e.g. Fig. 1b). Lomb–Scargle periodograms revealed a single dominant, low-frequency peak for 87 of 96 prey populations and for three other populations revealed a distinct low-frequency peak along with one or more high frequency peaks. The period of fluctuation associated with the low-frequency peak averaged 37 days (minimum 20 days).

Dispersal significantly increased prey synchrony (MANOVA; $F_{1,12} = 8.82$, $P = 0.004$), and did so at every spatial lag (follow-up ANOVAs; all $F_{1,12} > 9.75$, all $P < 0.009$). Inspection of the data indicated that dispersal increased synchrony by approximately the same amount at all spatial lags (Fig. 2). Environmental synchrony significantly increased prey synchrony (MANOVA; $F_{1,12} = 6.62$, $P = 0.010$), but only at the two shortest spatial lags (follow-up ANOVAs; $F_{1,12} > 5.56$, $P < 0.037$ for lags 1 and 2; $P > 0.6$ for other lags; Fig. 2). There was no dispersal × environmental synchrony interaction in the MANOVA ($P = 0.748$) or in any of the follow-up ANOVAs (all $P > 0.390$).

Dispersal significantly reduced the variance in phase among prey populations within arrays (ANOVA; $F_{1,12} = 7.34$, $P = 0.019$; Fig. 3). Environmental synchrony did not significantly affect the variance in phase among prey populations, either on its own or in interaction with dispersal (ANOVA, both $P > 0.76$; Fig. 3).

Regression of prey synchrony on spatial lag within each array quantified the spatial decay of prey synchrony within each array. ANOVA on the slopes of these regressions found that environmental synchrony significantly increased the rate of spatial decay of synchrony ($F_{1,12} = 5.54$, $P = 0.036$; Fig. 2). There was no significant effect of dispersal or the interaction term on the rate of spatial decay of synchrony (ANOVA, $P > 0.2$; Fig. 2). This result occurred because environmental synchrony significantly increased prey synchrony only at short spatial lags (where environmental synchrony itself was highest), while dispersal increased prey synchrony by approximately the same amount at all spatial lags (Fig. 2). The mean regression slope was significantly < 0 in the presence of environmental synchrony (two-tailed single-sample *t*-test, $P = 0.001$), but not in its absence ($P = 0.081$), indicating that only spatially decaying environmental synchrony produced spatially decaying population synchrony.

Our results also reveal effects of initial conditions on prey synchrony. Prey synchrony was quite high even in the absence of environmental synchrony and dispersal (Fig. 2), reflecting the fact that

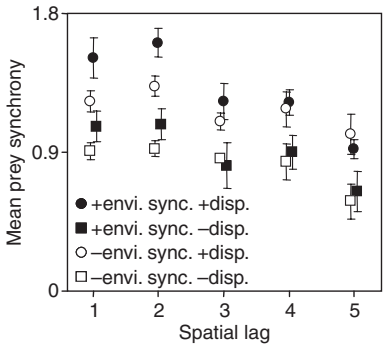

Figure 2 Mean prey synchrony (± SE, as a function of spatial lag (separation distance between microcosms). Prey synchrony is measured as the Fisher's *z*-transformed cross-correlation of log-transformed prey abundances and so can exceed one on the transformed scale; see text for details.

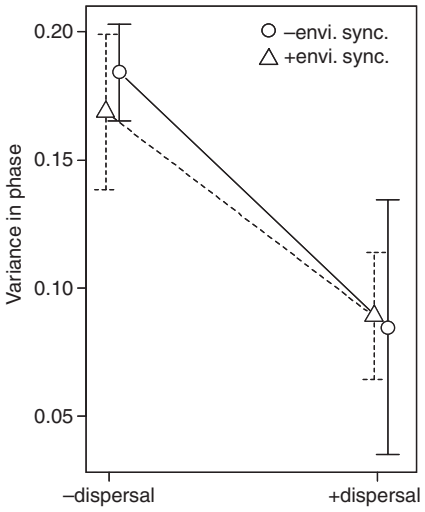

Figure 3 Effects of dispersal, environmental synchrony and their interaction on the mean (± SE) of the variance in phase of prey cycles.

all jars started in perfect or near-perfect synchrony (i.e. with the same or very similar initial conditions). Furthermore, within 15 of 16 arrays, mean prey synchrony at even-numbered spatial lags was higher than mean prey synchrony at odd-numbered spatial lags, a significant difference (sign test, $P < 0.001$; Fig. 2). Bottles separated by an even number of steps began with identical initial conditions, and so maintained slightly higher synchrony than bottles separated by an odd number of steps, which began with slightly different initial conditions.

DISCUSSION

Distance decay of the Moran effect, but not short-distance dispersal, generated distance decay of population synchrony. To our knowledge, this is the first experimental demonstration of distance decay of synchrony due to distance decay of the Moran effect. Previous experimental tests of the Moran effect have considered only pairs of patches, or else have not varied the strength of the Moran effect over space (Benton *et al.* 2001; Fontaine & Gonzalez 2005; Vasseur & Fox 2009).

Prey synchrony at a given spatial lag in the absence of dispersal did not equal environmental synchrony at that lag, contrary to the

predictions of simple linear spatial population models with a Moran effect (Moran 1953). Rather, prey synchrony was consistently higher than environmental synchrony even in the absence of dispersal, presumably because the populations began in or near-perfect synchrony. Whether prey synchrony in the absence of dispersal would have eventually decayed to the level of environmental synchrony is an open question. We hypothesize that, in the long run and in the absence of dispersal, prey would fluctuate less synchronously than the environment, due to the nonlinear density dependence generated by the predator–prey interaction (Grenfell *et al.* 1998; Greenman & Benton 2001; Vasseur 2007).

Rather than generating distance decay of synchrony, short-distance dispersal increased synchrony equally at all spatial lags. That is, dispersal synchronized distant patches only indirectly connected by dispersal just as much as adjacent patches directly connected by dispersal. This striking result reflects phase locking. By entraining the phases of adjacent patches, dispersal caused all patches in the array to oscillate in phase. Vasseur & Fox (2009) showed that dispersal phase-locks predator–prey cycles in patches directly connected by dispersal; here, we extend this result to indirectly connected patches. Vogwill *et al.* (2009) also showed the short-distance dispersal can produce long-distance phase locking of enemy-victim (phage-bacteria) cycles, albeit with a much higher per-generation dispersal rate than used here. Our results show that dispersal rates on the order of *c.* 1% per prey generation can produce long-distance phase locking, and raise the question of how low dispersal rates can be while still producing phase locking. Our experimental results complement and lend credence to observational and model-based evidence for long-distance phase locking of population cycles in nature (Ranta *et al.* 1997; Bjørnstad 2000).

The Moran effect did not affect the phases of predator–prey cycles within arrays. This result implies that the Moran effect increased synchrony by synchronizing prey fluctuations at other, higher frequencies. This result is consistent with theory predicting that stochastic, non-periodic external forcing will not entrain the phases of intrinsically generated oscillations (e.g. Blasius *et al.* 1999).

As short-distance dispersal generated long-distance phase locking, short-distance dispersal did not lead to distance decay of synchrony. Our results caution against the intuitive but incorrect assumption that, because most organisms move only short distances during their lifetimes, widely separated populations can only by synchronized by the Moran effect. Our results, together with those of previous theoretical and empirical studies, suggest that dispersal will generate distance decay of synchrony in nature only in limited circumstances. Dispersal either produces phase locking (leading to high, non-decaying synchrony) if population dynamics are cyclic, or else little synchrony at all if dynamics are not cyclic (this study; Bjørnstad 2000; Ripa 2000; Vasseur & Fox 2009; Vogwill *et al.* 2009). However, short-distance dispersal can contribute to distance decay of synchrony if cycling populations drift into and out of phase under the influence of strong stochasticity, as in the Canadian lynx-hare system (Ranta *et al.* 1997; Blasius *et al.* 1999). Our experiment did not last long enough to test this possibility. The needed experiment likely would require a minimum of several hundred days, given the estimated predator–prey cycle period of 37 days. Similarly, our metapopulations did not include enough patches to test for more complex spatiotemporal patterns, such as 'spiral waves' and 'crystal lattices' (Comins *et al.* 1992).

Dispersal and the Moran effect affect synchrony independently of one another in this system (this study; Vasseur & Fox 2009). The Moran effect and dispersal operate independently because they operate via distinct mechanisms which affected population fluctuations at different frequencies. Dispersal phase-locks deterministic, intrinsically generated, low-frequency cycles, while the Moran effect synchronizes stochastic, extrinsically generated, high frequency fluctuations superimposed on those cycles. This lack of interaction contrasts with the predictions of several theoretical models (Ranta *et al.* 1995, 1999; Kendall *et al.* 2000; Ripa 2000; Abbott 2007). Identifying the reasons for this contrast requires further theoretical and experimental work, as previous theory does not consider nonlinear predator–prey cycles of the sort studied here. It would be interesting to test whether this independence continues to hold over much longer timeframes, over which environmental stochasticity combined with dispersal might cause predator–prey cycles to temporarily drift out of phase (Ranta *et al.* 1997).

It would be interesting to incorporate additional species into our experiment, and to sample bacterial as well as protist dynamics. Adding additional species would increase the potential for complex spatiotemporal patterns of synchrony (Gouhier *et al.* 2010).

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