The roles of the Moran effect and dispersal in synchronizing oscillating populations

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A B S T R A C T

Patterns of spatial synchrony of population dynamics are dramatic phenomena that provide the potential for unraveling forces controlling the dynamics of natural populations in time and space. Prior ecological research has focused on attention to either deterministic or stochastic forces acting separately, with an emphasis on long term behavior, or on small systems consisting often of two interacting spatial locations. Using ideas from the dynamics of weakly coupled oscillators with an emphasis on the temporal dynamics of synchrony we develop a synthetic approach that explains patterns of synchrony as the result of an interplay between deterministic and stochastic forces. The temporal scale of convergence can provide a useful tool for determining the relative importance of deterministic and stochastic influences. Our approach applies both to specific systems that have been previously analyzed such as disease dynamics, and to a range of exploiter victim systems.

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1. Introduction

A striking dynamical phenomenon observed in many oscillating plant and animal populations is intraspecific species synchrony (as measured by correlation in abundance) across a large spatial domain. While there is no general consensus on the cause or causes of observed spatial synchrony in natural populations, the two most common explanations are spatially correlated extrinsic effects such as weather, often referred to as the Moran (1953) effect, and intrinsic factors such as migration. Determining which of these two phenomena (or the relationship between the two) is the leading cause of spatial synchrony has proven to be a difficult challenge, as reviewed by Liebhold et al. (2004). In order to determine the importance of both migration and the Moran effect as mechanisms leading to synchrony, we take a more integrated view of this problem than is done in previous modeling studies by using approaches that can deal with relatively large systems that include both nonlinearities (density dependence) in the deterministic intrinsic dynamics and realistic levels of stochastic extrinsic influences.

The interest in studying spatial synchrony arises in large part because increased spatial synchrony in oscillating populations leads to a decrease in expected global persistence (Huffaker, 1958; Harrison and Quinn, 1989; Holyoak, 2000). Asynchronous dynamics in these population can prevent extinction through either recolonization or the "Rescue Effect" (Brown and Kodric-Brown, 1977). Additionally, understanding the causes of synchrony can potentially provide a deeper understanding of what regulates natural populations, with applications including managing species conservation (Earn et al., 1998), minimizing outbreak of pests (Abbott and Dwyer, 2008), and controlling infectious diseases (Grenfell et al., 2001). This understanding can shed light on the relationship between the effects of biotic and abiotic forces in addition to explaining the degree of impact that synchrony or asynchrony may have on population dynamics at a larger scale. Since synchrony typically decreases with distance (Bjørnstad et al., 1999), the spatial scale of synchrony may have implications for the management of spatial populations.

To study the effect of migration on synchrony, we draw upon the study of coupled oscillators. In this case the oscillators, patches with one predator and one prey species, are coupled together by migration. The phenomenon of synchrony arising from coupled oscillators was first observed in two pendulum clocks attached to the same support beam by Christiaan Huygens in the 17th century. Since this observation, coupled oscillators have been studied in a variety of physical, chemical, and biological applications (Winfree, 2001; Pikovsky et al., 2001). Recently the use of coupled oscillator models in determining synchrony has been extended to ecological predator–prey populations (Jansen, 2001; Blasius et al., 1999), masting in trees (Satake and Iwasa, 2002), and the spread of epidemics (Grenfell et al., 2001; Lloyd and Jansen, 2004).

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Cycles in biological systems are described by amplitude (i.e., ratio of the maximum value to the minimum value) and frequency. Essentially, the phase of a given single cycle can be mapped onto a circle (Winfree, 2001), such that its phase is defined as a number between 0 and 2π describing the system's location within the given cycle. In many instances the amplitude of a cycle is relatively insensitive to other influences, and knowing the phase of each oscillating population in a collection of interacting populations gives a good description of the system. We use the theory of weakly coupled oscillators (Kuramoto, 1984) to derive a phase model from our original population model. The phase model has fewer equations and is therefore easier to analyze and measure synchrony with than the population model. This derivation and the study of a phase model from a system of weakly coupled oscillators have been extensively used to model networks of neurons (Ermentrout, 1981; Somers and Kopell, 1993) and have also been used for the same predator–prey model studied here (but without the Moran effect) with two weekly coupled patches (Goldwyn and Hastings, 2008). Weakly coupled systems are of ecological interest and importance because we expect that if coupling (migration) is large, then its effect would be directly observable or measurable, and that the expected outcome would be synchrony on a fast time scale.

A model consisting of populations in discrete patches is an effective representation of populations existing in patchy habitats and is often a good approximation for habitats existing in continuous space (Hanski, 1998). While continuous space models have been used to study synchrony in natural population (Engen et al., 2002), discretizing these populations often allows for more detailed analysis. In either case, the goal is to find a model that best approximates the actual spatio-temporal dynamics of the system. The choice of patch size (and therefore the number of patches) in a theoretical model is crucial and is usually determined by the dominant process in the regulation of the population dynamics, as is done by Bjørnstad et al. (1999) in a study of the voles and mice of Hokkaido. Williams and Liebhold (2000) varied the size of patches (cells) in a study of the defoliation by the spruce budworm in Eastern North America. They found that taking larger cells obscured the density dependence present in the dynamics of the budworm, possibly due to asynchrony within these cells. Ray and Hastings (1996) found this same phenomenon in their review of 79 insect populations with variable spatial scales. When studying the effect of migration occurring on a continuous landscape with a discrete patch approximation, careful attention needs to be paid to the relationship between the number of patches used and the migration rate. Intuitively, increasing the number of patches in a theoretical study (decreasing the size of each patch) increases the migration rate. As we show, increasing the number of patches in a model without also increasing the migration rate leads to a much slower rate of convergence to the steady state behavior.

Unlike global (spatially correlated) perturbations that can either increase or decrease synchrony (Hastings, 2004), natural populations are also subject to spatially varying perturbations which tend to destroy synchrony. Due to these external perturbations, any realistic explanation of the cause of observed synchronous behavior in natural systems must allow for convergence to synchrony to occur on a faster time scale than that of these spatially uncorrelated external perturbations. While in general, weakly coupled systems often take many more unperturbed cycles to converge to synchrony than are likely in natural systems, relaxation type oscillators can converge to synchrony much faster (Izhikevich, 2000). These types of systems do occur in ecology when there is a difference in the characteristic time scale of the interacting populations, as explored by Ludwig et al. (1978), and in the context of a weakly coupled system in Goldwyn and Hastings (2008). As we find here, adding in the Moran effect can also help decrease the time until synchrony. Since perfect synchrony is not a common occurrence in natural populations, our explanation need only yield near synchronous behavior on some short time scale. The idea is to determine the circumstances under which migration, the Moran effect, or some combination of the two, can bring the system to some near synchronous behavior, even while it is being perturbed by some uncorrelated extrinsic stochastic effects. As we will see, system size can be very important, so our use here of large systems of (rather than just two) coupled spatial patches will shed new light on the dynamics of synchrony in ecological systems.

2. Model

Our model is a predator–prey system in N patches coupled by density independent migration and subject to external perturbations. The variables V_i and P_i represent the number of prey (victims) and predators respectively in patch i ($1 \leq i \leq N$). We assume that the intrinsic dynamics of each patch are identical with logistic growth of the prey species, predation following a Holling Type II functional response, and a linear predator death rate. The increase of the prey population is described by growth parameter s and carrying capacity K. Predation is described by the parameters a and b, with the latter being the half saturation coefficient. The loss of prey due to predation also depends linearly on c ($c > 1$), a measurement of the ratio of the loss of prey to the gain in predators, implying that the loss in prey population due to predation is faster than the gain in predators. The parameter m represents the mortality rate of the predator.

Migration of the prey and predator species are determined by the per capita rates D_V and D_P and the connectivity matrix $M_{i,j}$. The matrix $M_{i,j}$ has entries 0 and 1 (before being scaled by the number of other oscillators to which each oscillator is coupled), is symmetric, and describes the coupling configuration of the system. Each patch represents a hunting region for the predator and a foraging region for the prey such that migration is independent from these activities. We model the Moran effect through instantaneous spatially correlated Poisson perturbations. These perturbations depend on the prey and predator population sizes and are Dirac delta impulses with amplitudes $A_V(V)$ and $A_P(P)$. This model is the Rosenzweig and MacArthur (1963) model, in N patches with extrinsic perturbations, and consists of $2N$ differential equations:

$$\frac{dV_i}{dt} = sV_i(1-V_i/K) - \frac{caP_iV_i}{b+V_i} + D_V \sum_{j=1}^{N} M_{i,j}(V_j - V_i) + A_V(V_i)\delta(t-t_1)$$

$$\frac{dP_i}{dt} = \frac{aP_iV_i}{b+V_i} - mP_i + D_P \sum_{j=1}^{N} M_{i,j}(P_j - P_i) + A_P(P_i)\delta(t-t_1) \quad i,j = 1,2,\ldots,N; i \neq j.$$

$$(1)$$

To study the role of migration in leading to synchrony in a predator–prey system we vary the number of discrete patches and the manner in which the patches are coupled together (i.e. nearest neighbor or all-to-all). To include the Moran effect, we vary the strength and timing (t_1) of the spatially correlated external perturbations.

Eq. (1) can be non-dimensionalized, as is done by Goldwyn and Hastings (2008), reducing the number of intrinsic parameters to the following three dimensionless quantities:

$$\varepsilon = a/s,$$

$$\alpha = b/K,$$

$$\eta = m/a. \tag{2}$$

These three dimensionless parameters completely describe the entire range of parameter space for the intrinsic dynamics (there is also a new time scale $\tau = at$, and the prey and predator populations are rescaled).

If the intrinsic dynamics of the system described in Eq. (1) produce an asymptotically stable limit cycle ($\alpha < 1$ and $\eta < (1-\alpha)/(1+\alpha)$ Hastings, 1997), then there will be a saddle steady state point at the origin of the phase plane (where the prey and predator populations are both extinct), with the predator axis (corresponding to prey extinction) acting as the stable manifold. Smaller values of any of the three dimensionless parameters in (2) correspond to the system spending more time close to this stable manifold, which is the mechanism which creates a separation in time scales between the two species and large amplitude oscillations of the prey population. Dynamics of different interacting ecological populations often occur on separate time scales, as in the class of models studied by Rinaldi and Scheffer (2000). This difference in characteristic time scale between the two species modeled in Eq. (1) plays a crucial role in the rate of convergence of the system to a phase locked state, as we see below.

2.1. Weakly coupled oscillators and the iPRC

We can use the theory of weakly coupled oscillators to derive a phase model from Eq. (1) if certain conditions are met. First, the system must have an asymptotically stable limit cycle. Next, either the perturbations must be sufficiently small or there must be sufficient time after a perturbation and before the system is perturbed again. In the former case, the effect of these perturbations (which describe migration) on the dynamics of the systems needs to be an order of magnitude smaller than that of the intrinsic dynamics. In the latter case, the populations must be allowed to relax back to the limit cycle, before the next

(small or large) perturbation occurs. In Eq. (1), and for the range of parameters that we use, weak coupling implies that about 1% of the population migrates per cycle and that between one and ten unperturbed cycles occur after a large perturbation and before migration or another large perturbation occur. As reviewed in Chapter 10 of Izhikevich (2007), the phase model can be derived using any of three different methods: Kuramoto (1984), Winfree (2001) or Malkin (1949, 1956), see Chapter 9 of Hoppensteadt and Izhikevich (1997) for a proof of Malkin's theorem.

The derivation of a phase model for weakly coupled oscillators reduces this system of 2N ordinary differential equations modeling the prey and the predator populations in each patch, to a system of N ordinary differential equations modeling the phase of the oscillation in each patch. The phase model with weak coupling is commonly written as:

$$\frac{d\theta_i}{dt} = 1 + \delta \sum_{j=1}^{N} H_{i,j}(\theta_j - \theta_i). \tag{3}$$

The variable $\theta_i \in [0, 2\pi)$ refers to the phase of the oscillator in the ith patch, with the intrinsic frequency of each oscillator scaled to 1. The parameter δ is related to the dispersal rates, D_V and D_P in Eq. (1), and needs to be sufficiently small to ensure weak coupling (it is naturally scaled by one divided by the number of oscillators to which it is coupled). The function $H_{i,j}$ (often called the interaction function, Izhikevich, 2007) quantifies the effect of migration between oscillators i and j on the phase of the ith oscillator, and is a function of the difference in phase between the two oscillators. The interaction function depends on the coupling function (we use diffusive coupling, Eq. (1)), and on a nonlinear function called the infinitesimal phase response curve or iPRC (Kuramoto, 1984). The iPRC measures the sensitivity of the oscillator to an infinitesimally small, instantaneous external perturbation (weak migration), and is a function only of the phase of the oscillator. Graphically, the sensitivity of the oscillator
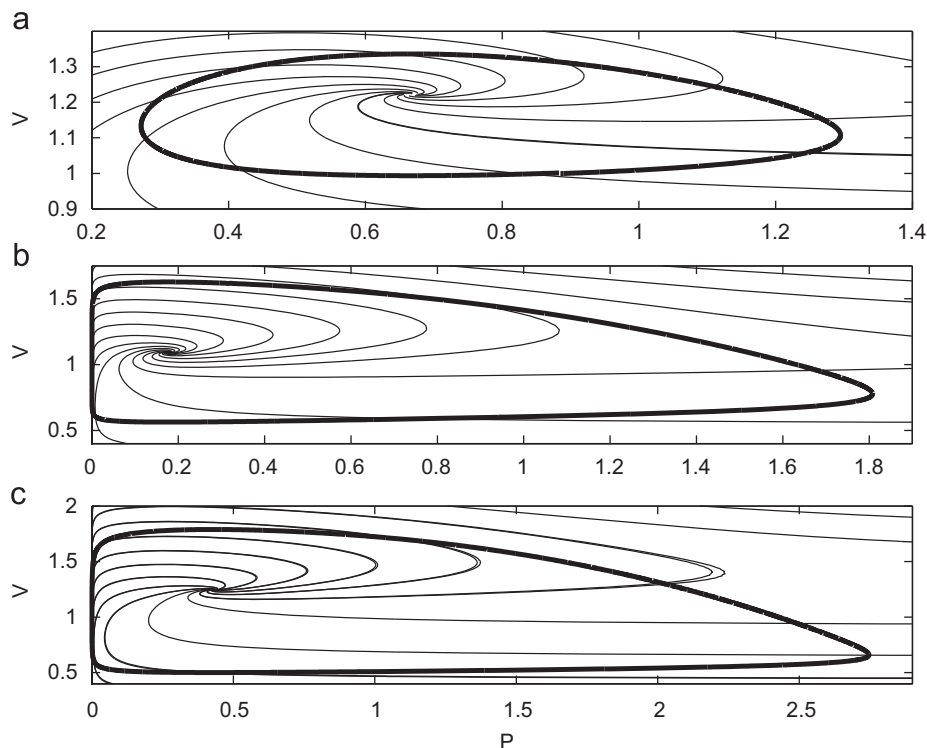

Fig. 1. The phase plane dynamics of the dimensionless version of Eq. (1) with parameter values (a) from scenario 1, $\varepsilon = 0.1$, $\alpha = 0.4$, and $\eta = 0.4$, (b) from scenario 2, $\varepsilon = 0.1$, $\alpha = 0.4$, and $\eta = 0.15$, and (c) from scenario 3, $\varepsilon = 0.1$, $\alpha = 0.3$, and $\eta = 0.3$, Eq. (2). The thick line is the limit cycle and the thinner lines are numerical approximations of 12 isochrons (lines of constant asymptotic phase).
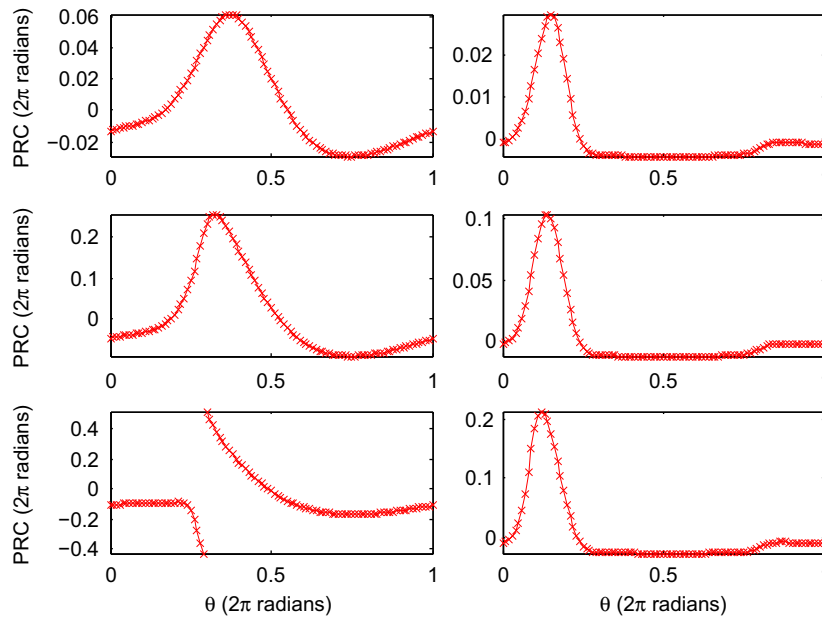
Fig. 2. Phase response curves (sensitivity of each oscillator to external perturbations) for parameters yielding a system where the prey and predator operate on similar characteristic time scales (parameter values from scenario 1, $\varepsilon = 0.1$, $\alpha = 0.4$, and $\eta = 0.4$, left side) and on different time scales (scenario 3, parameter values of $\varepsilon = 0.1$, $\alpha = 0.3$, and $\eta = 0.3$, right side). The perturbations correspond to reductions in the prey population by 10% (top row), 30% (middle row), and 50% (bottom row). The y-axis is the number of 2π radians that the oscillator is perturbed forward and the x-axis is the phase of the oscillator before the perturbation (phase of zero is chosen to correspond to they prey population increasing past (1). The 50% perturbation for the system with no difference in time scales between the two species is qualitatively different than the other perturbations because the perturbed system no longer contains the fixed point and therefore does not intersect all of the isochrons. This PRC is often referred to as being Type 0, as opposed to Type 1 (Winfree, 2001).

at a given phase to an external perturbation can be seen by the density of the isochrons (Fig. 1). An isochron is a collection of points that have the same asymptotic phase: every point on a given isochron converges to the same point on the limit cycle of the oscillator (Winfree, 2001). Several numerical approximations of the iPRC for different parameter values of Eq. (1), as well as a more detailed derivation of Eq. (3), can be seen by Goldwyn and Hastings (2008).

2.2. External perturbations and the PRC

When studying the Moran effect with an instantaneous external perturbation (pulse), we use the following equation to describe the phase of the ith oscillating predator–prey patch:

$$\theta_i^{new} = \theta_i^{old} + Z(\theta_i^{old}, A_\theta) \tag{4}$$

The function $Z(\theta, A_\theta)$ measures the degree to which this external pulse advances or delays the phase of the oscillator, as measured by how many isochrons are crossed (Fig. 1). This function is often referred to as the phase response curve (PRC) and it is a function of the timing within the cycle of the external pulse and, unlike the iPRC, the magnitude of the pulse, A_θ (Fig. 2).

2.3. Defining synchrony

Phase locking occurs when the difference in phase between each oscillator remains constant over time and can be either in-phase (the difference in phase between the oscillators is zero) or out-of-phase (a range of non-zero phase differences). In a two oscillator system, for $\theta_1(t) - \theta_2(t) = \rho$, full in-phase behavior occurs when $\rho = 0$, and out-of-phase behavior occurs when $\rho \neq 0$, with $\rho = \pi$ describing anti-phase behavior. Defining in-phase vs. out-of-phase behavior is less straightforward for larger systems. Instead of looking at the pairwise phase difference between oscillators, we want a global measurement of the coherence of

the system. The derived phase models, Eqs. (3) and (4), allow us to find the following sequence of order parameters, r_k $(0 \leq r_k(t) \leq 1)$:

$$r_k e^{i\psi} = \frac{1}{N} \sum_{j=1}^{N} e^{ik\theta_j}. \tag{5}$$

The first order parameter, $r_1(t)$, is the Kuramoto (1984) Synchronization Index and $\psi(t)$ is the average phase of the N oscillators. If $r_1(t) = 1$, the system is in-phase, with smaller values of $r_1(t)$ indicating a less coherent system. Unlike the two oscillator case which has a clear definition of anti-phase, $r_1(t) = 0$ can be caused by different configurations of the oscillators: the phases of each oscillator can be equally spaced apart (often referred to as splay phase), or there can be clusters of multiple oscillators that have a particular distance in phase from the other clusters, balancing each other, as can occur in a system of nearest neighbor coupled chaotic oscillators (Belykh et al., 2000). Higher order values of r_k explain clustering of the oscillators. An $r_k = 1$, with all lower order parameter values equal to zero, indicates oscillators that are equally spaced in k clusters. Using these order parameters as a measurement of synchrony enables deeper analysis than is possible with other measurements of synchrony that are used in the absence of a mathematically derived phase model, such as the Pearson product-moment correlation coefficient or lag 0 cross-correlation coefficient. Like the study of Gil et al. (2009), who analyzed many globally coupled phase oscillators affected by common white noise, we were unable to find states containing greater than three clusters (excepting splay phase).

3. Results

3.1. Separation of time scales

We previously (Goldwyn and Hastings, 2008) used the method of phase reduction to study the Rosenzweig–MacArthur model in

two patches coupled together by migration. We found that for biologically realistic parameters (and no extrinsic perturbations), there were three distinct qualitatively different steady state configurations for the system described in Eq. (1).

Here, through many simulations, we find that there are also exactly three different steady state configurations in the N oscillator case covering the same regions of parameter space (assuming all-to-all coupling). As we explain below and can be seen in Fig. 3, the actual behavior of the N oscillator system is much richer than it is in the two oscillator system. Our approach takes advantage of the known property that the rate of convergence to a phase locked state in any weakly coupled oscillating system depends only on the strength of the coupling and on the sensitivity of the oscillators to this coupling, as described by the iPRC (Winfree, 2001; Kuramoto, 1984).

We refer to the range of parameters where the prey and predator operate on similar characteristic time scales (sinusoidal dynamics of the populations through time) as scenario 1. In scenario 1, the only stable phase locked state for the two oscillator system is an in-phase solution (a phase locked state at anti-phase is unstable). The N oscillator system with all-to-all coupling will also always converge to the in-phase solution (left column of Fig. 3). This system is relatively insensitive to the small perturbations (Fig. 1a) coming from migration, and therefore the iPRC has small magnitude throughout the cycle (Goldwyn and Hastings, 2008), leading to slow convergence to synchrony. Furthermore, Strogatz (2000) showed that a large number of all-to-all coupled Kuramoto oscillators (which fall under scenario 1),

having a unimodal symmetric distribution of frequencies, will also experience phase locking and near in-phase behavior of all the oscillators with natural frequencies close to the mean frequency. Only the oscillators with frequencies on the tails of the distribution will not experience near in-phase behavior and will exhibit phase drift.

Increasing the separation in time scales between the two populations leads to the prey population experiencing short time interval outbreaks separated by longer time intervals of lower population levels. This behavior occurs when any of the three non-dimensional parameters, ε, α, or η in Eq. (2), are decreased and is caused dynamically by an increase in time spent near the stable manifold of the system. A system with this separation in time scales is very sensitive to small perturbations occurring near this stable manifold (as can be seen by the high density of isochrons, Fig. 1) and therefore migration has a larger effect on the phase of the oscillators. This increased sensitivity leads to a larger maximum magnitude of the iPRC and increases the rate of convergence to phase locking (Goldwyn and Hastings, 2008). This increase in the separation of time scales yields either a pitchfork (scenario 2) or saddle-node (scenario 3) bifurcation of the phase locked states in the two oscillator system, depending on the other parameter values. Both of these bifurcations create an additional stable steady state (out-of-phase in the case of a saddle-node bifurcation, and anti-phase for a pitchfork bifurcation) that does not occur when the populations operate on similar time scales (Goldwyn and Hastings, 2008).
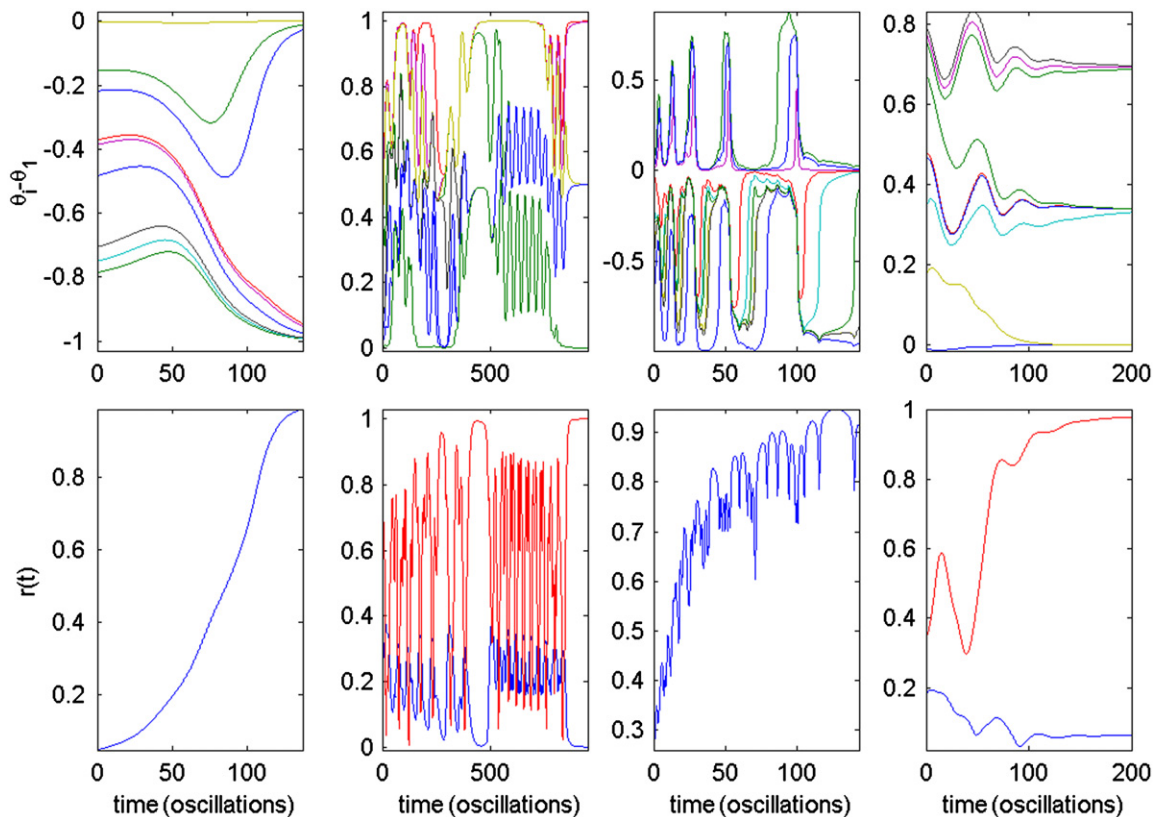

Fig. 3. Typical simulation results for 10 oscillators with all to all weak coupling, as written in Eq. (3). The top row shows the phase difference (Eq. (3)) between one arbitrarily chosen oscillator and the other nine. These phase differences are scaled by 2π, i.e. a value of 1 corresponds to being one cycle ahead of the arbitrarily chosen oscillator. The bottom row shows the Kuramoto Synchronization Index ($r_1(t)$) of the system in blue and higher order parameters ($r_2(t)$ in the second panel from the left and $r_3(t)$ in the far right) in red, Eq. (5). The left column corresponds to a system with no separation in characteristic time scales between the prey and the predator (scenario 1, with the same parameter values in Fig. 1(a), and $D_V = D_P = 10^{-3}$). The other figures all correspond to parameters where there is a difference in time scales between the populations. The second column from the left (scenario 2, has parameters as in Fig. 1(b) with $D_V = D_P = 10^{-5}$) and leads to anti-phase behavior. The right two columns have the same parameters (scenario 3, Fig. 1c with $D_V = D_P = 10^{-6}$) and experience bistability, full in-phase behavior, and multiple (three in this example) distinct out-of-phase clusters. While the left column appears to phase lock in a similar time frame as the other columns, the migration parameters are actually two and three orders of magnitude larger. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Scenario 2 occurs when the parameters are in the region where both anti-phase and in-phase stable steady states are possible in the two oscillator case. Our simulations found that for many oscillators in-phase behavior is a very unlikely outcome, much more unlikely than it is with two oscillators. Numerous simulations showed that there is a transient behavior with a low and fluctuating synchronization index, but larger values for the second orders of $r_2(t)$. These oscillators group in few distinct (nearly anti-phase) clusters that are not phase locked with each other. This transient period can have various lengths before the system eventually converges to anti-phase with the oscillators in two clusters half an oscillation apart from each other in phase space, (second column from the left Fig. 3).

As in scenario 2, the region of parameter space yielding stable out-of-phase (but not anti-phase) steady states in the two patch model has bistability in the many oscillator system. We refer to the region of parameter space leading to this out-of-phase behavior as scenario 3. The asymptotic state for these parameter values depends on the initial conditions. If the system starts in a sufficiently incoherent state, then it is likely to converge to an out-of-phase state containing several clusters of oscillators that are in-phase with each other. This behavior can be considered partially synchronized. While the Kuramoto Synchronization Index, $r_1(t)$ is quite low, the third order term approaches one (right column of Fig. 3). The other possibility for this range of parameters is full synchrony, which occurs when the initial phases are more coherent (second column from the right of Fig. 3). In this case the oscillators approach a synchronization index of close to one relatively quickly, but take a long time to actually converge to one. For this range of parameter values, if an external perturbation increases the synchrony of the system, it can shift it from a state that would have deterministically approached the state containing clusters of oscillators, to a state

that deterministically approaches the synchronous state (Fig. 4). A perturbation that significantly decreases the level of synchrony can do the opposite.

The other possible behavior that can occur in each of the above cases (but is very rare for all-to-all coupling) is when the oscillators are all equally spaced in phase space, often referred to as splay phase. Strogatz and Mirollo (1991) found that a system of homogeneous phase oscillators in splay phase will remain stable until a bifurcation occurs when either heterogeneity or noise becomes sufficiently large. Both splay phase and the two cluster solutions yield first order synchronization indexes of zero.

While decreasing any of these dimensionless parameters increases the effect of migration on the phase behavior due to the sensitivity of these types of systems at low prey density populations, we find here that it decreases the Moran effect. This can be seen by the smaller values of the PRC (Fig. 2) and their impact on Eq. (4). This agrees with the results from Vasseur and Fox (2009), who simulated a stochastic Rosenzweig–MacArthur model and found that the Moran effect alone was unlikely to synchronize populations due to its small impact on low density populations. On the other hand, as mentioned above, decreasing these parameters leads to a large magnitude of the iPRC when the system is near the stable manifold, indicating that the system will be very sensitive to noise or spatially uncorrelated perturbations at that time in the cycle and is likely to become desynchronized by these effects, also agreeing with the results of Vasseur and Fox (2009).

We also analyze nearest neighbor coupling, where migration occurs only between adjacent patches in a one dimensional lattice. We allow for the structure to be either a ring or a chain of oscillators, with the former occurring if the first and last patch are connected. This is written by changing $M_{i,j}$ in Eq. (1) to a tri-diagonal matrix with entries of $1/2$ above and below the main diagonal and all other entries (including the main diagonal) are 0.
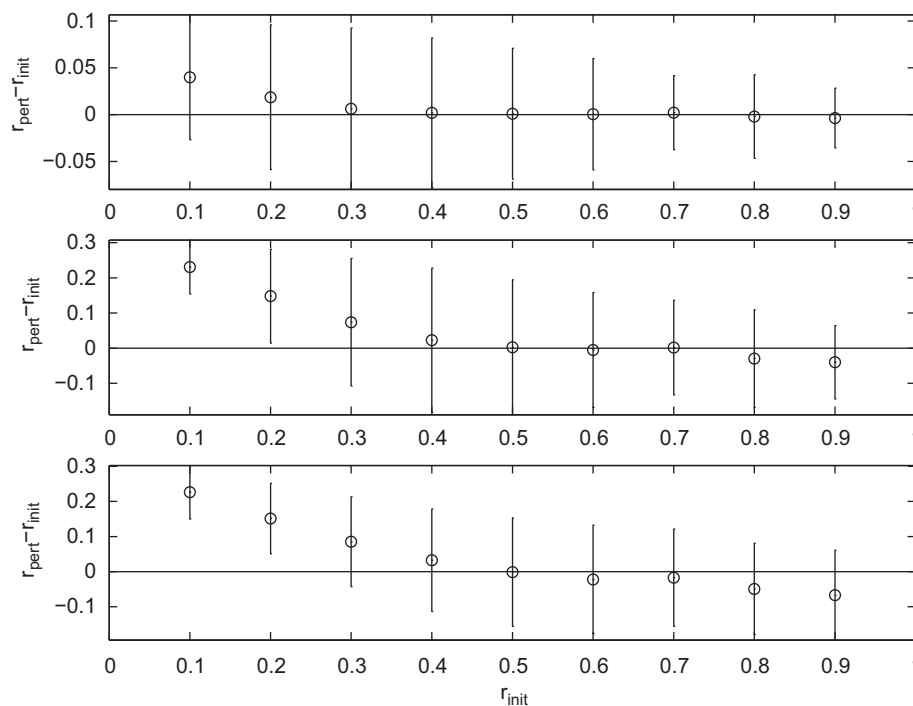

Fig. 4. The strength of the Moran effect with spatially correlated perturbations decreasing the prey population in each of 10 patches by 10% (top row), 30% (middle row), and 50% (bottom row). Each simulation is taken with the phase of each oscillator as it is in the left column of Fig. 3, with its associated Kuramoto Synchronization Index ($r_1(t)$, Eq. (5)). We performed 1000 simulations for each level of synchrony with the initial phases of each oscillator shifted in for every simulation. The mean results of the simulations are the open circles, and the error bars represent one standard deviation above and below the mean. The x-axis shows the synchronization index before a perturbation and the y-axis shows the difference between the perturbed index (based on the asymptotic phase, Fig. 1) and the original index. For incoherent states, a perturbation is likely to increase the coherence of the system while systems with greater coherence tend to be desynchronized by these perturbations, though the opposite can happen depending on the where in the cycle these predator–prey oscillators are at the time of the perturbations.

Our simulations show that the time until the system is synchronous is larger for nearest neighbor coupling than it is for all-to-all coupling, even though the coupling might seem stronger (individual entries in $M_{i,j}$ are larger for nearest neighbor coupling). The larger convergence time for nearest neighbor coupling occurs because each oscillator is only communicating with nearby oscillators as opposed to the whole system. This introduces a distance between the model patches that corresponds to an actual distance in a natural system. Synchrony taking longer for nearest neighbor coupling is consistent with data showing that degree of synchrony decreases as distance increases (Hanski and Woiwod, 1993; Ranta et al., 1995). Goldwyn and Hastings (2009) showed that increased spatial heterogeneity in a weakly coupled system also reduces synchrony. These two observations lead us to believe that if migration is the primary cause of synchrony, either some type of nearest neighbor coupling must be occurring or spatial heterogeneity exists in a way that increases with distance.

With nearest neighbor coupling, there exists another possible spatial population structure, a traveling wave solution. In a nearest-neighbor model coupled on a one dimensional lattice, this occurs when the phase difference between the $i+$1st and the ith oscillator is the same as the phase difference in phase between the ith and the $i-$1st oscillator. The occurrence of a traveling wave solution is not an artifact of the discrete patch model, Crook et al. (1997) found a traveling wave solution in a model with a continuum of neural oscillators. Traveling wave solutions have been found in natural populations of voles in Finland (Ranta and Kaitala, 1997) and in measles epidemics in England and Wales (Grenfell et al., 2001). Blasius et al. (1999) found a U-shaped traveling wave solution to a tritrophic population model with nearest neighbor coupling on a two dimensional lattice, and Grenfell et al. (2001) found traveling waves for their model of the above mentioned measles epidemic. Ermentrout and Kopell (1984) found that nearest neighbor coupled oscillators with a linear gradient in frequency will have multiple phase locked clusters of oscillators with jumps in frequency between the clusters.

3.2. The effect of changing the number of oscillators on convergence rates

In addition to studying the asymptotic behavior of the system, we examine how increasing the number of oscillators and altering the connectivity of the patches affect the rate of convergence to phase locking. For fixed intrinsic parameter values in Eq. (1), the rate of convergence in the two patch case depends linearly on the coupling strength, δ Eq. (3). In an N oscillator system, determining the actual coupling strength is more complicated than simply finding the D_V and D_P terms in Eq. (1). In the case of all-to-all coupling, the convergence of the oscillators to their phase locked states depends on the degree of coherence of the system, $r_1(t)$, and the weighted average phase, $\psi(t)$, Eq. (5), as discussed in Strogatz (2000). These averages often behave in a very non-linear way and are much more complicated than the migration rate parameters from the two patch case.

Our simulations of the unperturbed model (done with initial phases of each oscillator distributed uniformly random, with the condition that the Kuramoto Synchronization index is less that 0.3) show that increasing the number of oscillators increases the time of convergence to the stable steady state of phase locking, regardless of whether this state is in-phase or out-of-phase. Fig. 5 shows the results from a system of varying numbers of oscillators when prey and predators operating on similar characteristic time scales (scenario 1). The time until the system converges to the synchronous steady state (here we define synchrony as a Kuramoto synchronization index $r_1(t) > .9$) is close to linear on a log scale of the number of oscillators. We can see from Eq. (3), and
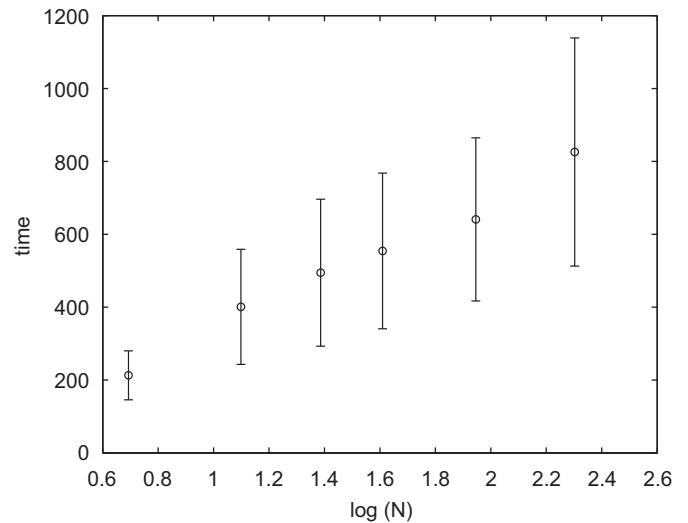

Fig. 5. This figure shows the relationship between the logarithm of the number of oscillators, N, and the time until the system converges to an in-phase for all-to-all coupling using Eq. (3) with parameters from Fig 1a, scenario 1. The populations have similar characteristic times scales and the system has exactly one (in-phase) steady stable state. We consider the system to be in-phase when the index $r_1(t) > 0.9$, see Eq. (5). We plot the mean after 1000 simulations with error bars representing one standard deviation in each direction. Initial conditions are chosen from a uniformly random distribution with the condition that the system is sufficiently incoherent, $r_1(0) < 0.3$.

as simulations show that if a mean field coupled system of in-phase oscillators has one patch perturbed away from the cluster of in-phase oscillators, then that patch will be pulled back to the main cluster with a force that is scaled by the number of patches coupled to it. Additionally, the greater the number of oscillators, the smaller the effect the one oscillator has on the big cluster leading to a longer time until full synchronization of the system.

We can analytically find the convergence rate to synchrony when the system is already near the synchronous steady state by linearizing around this state and finding the eigenvalues. To do this we expand the numerical approximation of the interaction function, H from Eq. (3), in a Fourier series. We find that if the prey and predator populations operate on similar time scales, then one of the eigenvalues will be equal to zero while all other eigenvalues will be identical and negative (the zero eigenvalues correspond to a phase shift of both oscillators which naturally will not affect their difference in phase, $\theta_1 - \theta_2$). Furthermore, the non-zero eigenvalues increase monotonically while remaining negative (their absolute value decreases) as the number of oscillators is increased. Smaller magnitude eigenvalues indicate a slower convergence to synchrony when the system is sufficiently close to synchrony. The eigenvalues of the Kuramoto oscillator, where the interaction function is simply the first sine mode of the Fourier series, can be calculated analytically. After finding the Jacobian of this system for a fixed number of oscillators N, we can see that the non-zero eigenvalues are $\lambda = -1 - 1/(N-1)$. If the system is not near the fixed point of synchrony, then linearization is not applicable, so we look at the results from our simulations (Fig. 5).

While we find that increasing the number of oscillators slows convergence to the phase locked steady states due to migration, this increase does not change the expected Moran effect in our model. The synchronization index of the system after a perturbation can be found using Eq. (5), by inputting the phase of each oscillator after the perturbation (Eq. (4)). We see that degree of synchrony of the system depends only on the initial phase of each oscillator and its PRC (which in turn depends on the magnitude and timing within the oscillation of the perturbation). Therefore,

for any given distribution of initial phases, the expected coherence of the system after a perturbation is independent of the number of oscillators, N, though the variance of the coherence will depend on N.

3.3. Stochasticity vs. determinism

Natural systems are subject to a great deal of stochasticity, such as the climatic events envisioned by Moran. While the model we study here has intrinsic dynamics that are strictly deterministic, the variabilities in individual trials of our simulation come from the random phases of each oscillator when the Poisson distributed extrinsic perturbation occurs. Incorporating other forms of stochasticity into the intrinsic dynamics of the population model makes the system too complicated to analyze in the detailed way that we do here. We can, however, use the results from our approach to understand the influence of random perturbations. We focus on large instantaneous Poisson perturbations as is done in Arai and Kakao (2008) and Ko and Ermentrout (2009). Perturbations in ecological systems can be spatially correlated, which can either increase or decrease synchrony (Fig. 4), or spatially uncorrelated, tending to destroy synchrony. The interplay between deterministic coupling and (correlated or uncorrelated) external perturbations leads to a variety of possible dynamics. The deterministic dynamics tend to synchronize populations in-phase (though they can lead to out-of-phase or anti-phase behavior depending on if the system falls under scenario 1, 2, or 3), while external forces can either encourage or discourage this convergence to in-phase synchrony depending on the strength of the perturbation, the synchronization index of the system, the specific phase of each oscillator, and the parameters of the system. The effect of these forces is shown schematically in Fig. 6.

Fig. 3 shows that if both populations have similar characteristic time scales (scenario 1), then migration alone deterministically increases synchrony in a sigmoidal fashion. If the system is either very coherent or very incoherent, the deterministic dynamics slowly increase the level of synchrony, whereas if this system has a moderate level of coherence, the synchronization index will be increased more quickly by migration. The system has an unstable steady state at a synchronization index of zero, therefore when the system in near this state, the deterministic coupling does little until a stochastic perturbation forces it away from this steady state to some moderate level on synchrony. Then the deterministic intrinsic dynamics can bring the system into some level of near synchrony. The system will stay synchronous until another perturbation (likely spatially uncorrelated) occurs and knocks the system out of synchrony again. This interaction between stochastic external perturbations and deterministic dynamics demonstrates how both processes can be necessary for this type of system to synchronize. Vasseur and Fox (2009) simulated a stochastic version of this same Rosenzweig–MacArthur model in two patches and found that both the Moran effect and dispersal were necessary for synchrony to occur. Their simulation results agreed with their experimental results in a system consisting of the protist *Tetrahymena pyriformis* and its predator *Euplotes patella*.

For systems where a separation in the characteristic time scales between the prey and the predator population exists (scenarios 2 and 3), the intrinsic dynamics can generate asymptotic behavior that will be either in-phase or out-of-phase, depending on the initial coherence of the system and the parameter values. For parameter values as in scenario 3, a sufficiently coherent system will approach synchrony by intrinsic dynamics alone, while an incoherent system will form multiple synchronized clusters that are out-of-phase with each other (Fig. 3).
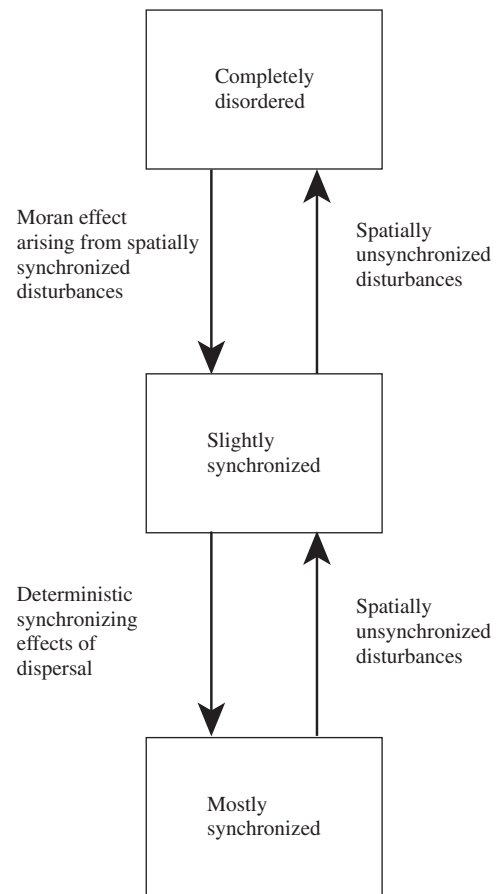

Fig. 6. This figure demonstrates when each of spatially correlated disturbances (the Moran effect), spatially uncorrelated disturbances, and dispersal play an important role in changing the level of synchrony of the system. While this figure shows the most common impacts of these three mechanisms, our results demonstrate that larger spatial synchronized disturbances can desynchronize mostly synchronized systems and small disturbances can push already mostly incoherent systems further incoherent. The deterministic synchronizing effect of dispersal plays a small role synchronizing the population unless there exists a separation in the characteristic time scales between the two species.

A synchronous natural system can therefore be explained either by extrinsic forces pushing the oscillators into a range of phases that are sufficiently coherent allowing for the intrinsic dynamics alone to lead to synchrony, or by the synchrony in each individual cluster in an otherwise seemingly incoherent population. Fig. 3 shows that when this system is very uncorrelated, weak deterministic migration will never lead to global synchronization. However, a spatially correlated perturbation can knock the system to a state where coupling can yield high global synchrony levels.

Additionally, for systems that are exhibiting a traveling wave solution (or splay phase), an external perturbation can knock the system away from that steady state to allow for the intrinsic dynamics to lead to an in-phase or out-of-phase solution. This can occur regardless of whether the system has all-to-all or nearest neighbor coupling.

4. Discussion

The ubiquity of synchronous oscillations in natural ecological populations and its potential impact on metapopulation persistence has led to a large number of theoretical and experimental studies (as reviewed in Liebhold et al., 2004) which have

attempted to determine its cause as well as its effect on persistence. Metapopulations exhibiting extreme oscillations are at risk for local extinction (Hastings, 2001), though migration from asynchronous populations can reduce this risk through recolonization or the 'Rescue Effect' (Brown and Kodric-Brown, 1977). The most likely causes of intraspecific species synchrony are either dispersal, the Moran effect (Moran, 1953), or some combination of both. The observed phenomenon that synchrony decreases with distance (Hanski and Woiwod, 1993; Ranta et al., 1995) has implications on the management of spatial populations.

The direct combination of dispersal and the Moran effect has been analyzed by Kendall et al. (2000). In a discrete time model where local dynamics, dispersal, and environmental stochasticity all enter linearly, they found that the effects of the two synchronizing forces are subadditive. Gouhier et al. (2010) examined the combined effects of dispersal and environmental fluctuations on synchrony and stability of a two prey, one predator, one resource system on a local and global level. They focused on the case where these effects are sufficiently large to disrupt the compensatory dynamics of the system, so their study complements our approach of focusing on the interaction between relatively weak migration and the Moran effect. As in Goldwyn and Hastings (2008), if the two species are operating on similar time scales, then convergence to synchrony from migration alone, will be quite slow and therefore the Moran effect is the likely cause (or one of the likely causes) of synchrony. However, if there exists difference in time scale between the prey and predator populations, as is the case with the spruce budworm (Ludwig et al., 1978), then convergence to synchrony from migration alone can occur in fewer cycles and can be a realistic explanation of synchrony. As in Fig. 3, for certain systems, convergence to synchrony due to migration occurs much faster when the system already has a moderate level of synchrony. This implies that spatially correlated external input plays an important role in taking a highly incoherent system and bringing in into some moderate level of synchrony (Fig. 6). The other important role that external input plays in synchronizing this system is shifting it between initial conditions yielding in-phase and out-of-phase behavior due to migration when this bistability occurs. The fact that both in-phase and out-of-phase solutions are possible with the same parameter values indicates the importance of the relationship between migration and extrinsic input. We also notice that near synchronous populations will be continually forced toward synchrony by dispersal. These populations are likely to stay synchronized unless there is a sufficiently large perturbation which knocks them far enough away from synchrony where dispersal will not immediately resynchronize them.

While studies of two oscillators, as in Goldwyn and Hastings (2008), give valuable insight into the necessity of the existence of a separation in time scale in order for synchrony to occur on a biologically relevant time scale, two patch results do not tell the entire story for the cases of out-of-phase behavior. Only through the use of many patches can we see that anti-phase and other out-of-phase behavior can actually contain clusters of patches that are themselves in-phase. These clusters of in-phase patches make the system partially in-phase, and depending on the spatial location of the patches in each cluster, can ultimately lead to many of the same ecological outcomes as a completely in-phase habitat. We recognize that there are many other ways to model the temporal behavior of spatially distributed systems (Durrett and Levin, 1994), including using partial differential equations in a reaction diffusion model, using systems similar to ours but with nearest neighbor coupling in two-dimensional lattices, as well as varying levels of distance dependent dispersal. We view our model as a good first approximation to these more complicated systems.

How would the results we generate here inform the analysis, interpretation, or collection of data from empirical systems? First, our results provide the general and important guidance that a much more nuanced approach to the causes of synchrony is needed: only through considering the relative combination of stochastic and deterministic forces can the forces leading to synchrony be unraveled. Other features of our results can be used directly to suggest manipulations or data interpretation. The results that the rate of convergence from deterministic forces slows as the number of patches goes up, in contrast to the fact that for the Moran effect this is determined only by the area of synchrony, suggests that developing tests to compare synchrony as a function of system size would be important. For example, if there are two systems in the same geographical area, our results would predict similar levels of synchrony if the Moran effect were operating, and greater synchrony for the species with fewer subpopulations than for the species that was more subdivided (which is different than saying that the species with the higher rate of connectivity) if migration were the principle driver of synchrony. For example, Liebhold et al. (2004) contrasted the studies of Paradis et al. (2000) on British breeding birds who found that synchrony was related to dispersal ability, Peltonen et al. (2002) on forest insects who found that dispersal was not related to synchrony, and Sutcliffe et al. (1996) who found a more complex pattern depending on spatial scale. Our results clearly indicate an important role for the number of subpopulations in determining the degree of synchrony which can help explain the appearance of contrasting results for systems where the only focus was on dispersal.

The analysis presented here provides new insights into the combined and contrasting roles of dispersal and the Moran effect in synchronizing populations. Our work is able to put a new emphasis on the importance of the interaction between stochasticity at different spatial scales and internal dynamics in generated patterns of synchrony observed in natural systems. This more synthetic view will provide a way to go beyond current studies (e.g. those reviewed in Liebhold et al., 2004) that have tended to emphasize the importance of one or the other explanation. Although the importance of this combined view of population dynamics has long been emphasized in understanding single populations (Hastings et al., 1993), the importance of the combined effects of stochasticity and deterministic forces in producing synchrony in spatial dynamics has received less attention. Studies of disease dynamics (Rohani et al., 1999) are an exception, but our study provides a much more general analysis that provides insights across a range of systems. While our work focuses on stochasticity as it relates to larger external perturbations, ecological populations are known to be affected by noise (Bjørnstad and Grenfell, 2001). More work on the nature of the interactions, both direct and indirect, between dispersal and extrinsic perturbations (both large and small) needs to be done to continue to flesh out their combined effect on the synchronization of these biological populations. Specifically, using the method of phase reduction to study the effect of noise, as has been done in the context of phase oscillators for white noise in Ly and Ermentrout (2009) and colored noise in Nakao et al. (2010), could prove very helpful in that regard.

Acknowledgments

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