

Small Heterogeneity Has Large Effects on Synchronization of Ecological Oscillators

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Abstract Heterogeneity in habitat plays a crucial role in the dynamics of spatially extended populations and is often ignored by both empiricists and theoreticians. A common assumption made is that spatially homogeneous systems and those with slight heterogeneity will behave similarly and, therefore, the results and data from studies of the former can be applied to the latter. Here, we test this assumption by deriving a phase model from two weakly coupled predator-prey oscillators and analyze the effect of spatial heterogeneity on the phase dynamics of this system. We find that even small heterogeneity between the two patches causes substantial changes in the phase dynamics of the system which can have dramatic effects on both population dynamics and persistence. Additionally, if the prey and predator time scales are similar, the effect of heterogeneity is much greater.

Keywords Heterogeneity · Synchrony · Dispersal · Population persistence · Predator-prey dynamics · Phase response curve · Moran effect

1. Introduction

Heterogeneity in habitat plays a crucial role in population dynamics and is too frequently ignored by ecologists and population biologists studying populations in space. Frequently, both laboratory experiments and theoretical work are conducted in spatially homogeneous settings, even though these conditions are unlikely to occur in natural systems. Qualitative results and conclusions from these studies are then often generalized to hold for systems with slight spatial heterogeneity. The assumption that these two types of systems produce similar dynamics is not necessarily an accurate one. Here, we test this assumption by studying a two patch heterogeneous predator-prey system and analyze the effect of small heterogeneity on the phase dynamics of this system.

Incorporating the effect of spatial dynamics on ecological populations is essential in order to understand the dynamics of many natural populations. An interesting and well-observed phenomenon is that of spatial synchrony in oscillating populations, as reviewed

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for ecological populations in Liebhold et al. (2004), and for disease dynamics in Earn et al. (1998). Spatial population structure influences the dynamics of a population both because individuals may be more likely to interact with nearby neighbors and because spatial heterogeneity of habitat may exist. Liebhold et al. (2006) and Hugueny (2006) simulated linear and log-linear discrete time models, with the result that spatial heterogeneity decreases the level of synchrony, regardless of whether the mechanism inducing this synchrony is spatially correlated noise or dispersal. Kendall and Fox (1998) found that in a two patch, one population, discrete time logistic map, small heterogeneity affects the ratio of the population levels in each patch as well as the qualitative dynamical behavior. Earlier work on heterogeneity in ecological systems has emphasized the role that heterogeneity might play in stabilizing unstable interactions among hosts and parasitoids by looking at stability of steady states (Hassell and May, 1974). A focus on dynamics of oscillatory behavior is a way to complement and extend these studies.

Empiricists and theoreticians have shown much interest in understanding what factor or factors are most important in causing the observed instances of spatial synchrony. The two most common explanations of synchronous behavior are stochastic exogenous influences, such as climate, known as the Moran effect (Moran, 1953), and endogenous factors, such as dispersal. Ranta et al. (1995) analyzed three different discrete time, one species population models and found that dispersal alone can lead to synchrony. While Peltonen et al. (2002) analyzed data for six forest insect species and found that dispersal was not likely to be the primary process behind synchrony at larger spatial scales for any of the six species. The interest in explaining synchronous behavior comes primarily from the observed and theoretical phenomenon that persistence and synchrony are inversely related to each other in metapopulations, as can be seen for predator and prey protists in Holyoak (2000).

In this paper, we study a two patch predator-prey model and analyze how spatial heterogeneity affects the phase dynamics of a system coupled by small amounts of migration. Specifically, we look at both heterogeneities in the intrinsic dynamics and the coupling of the two oscillators. While the mathematical derivation of phase models only holds for small amounts of intrinsic heterogeneity, simulations show that these results can often be extended to systems with moderate heterogeneity. This case of small migration is biologically relevant since for populations characterized by large migration rates, this migration would be directly observable or measurable and rapid convergence to synchrony would be the expected outcome.

Much of the theoretical work involving phase dynamics of ecological oscillators has been focused on coupled predator-prey oscillators (Blasius and Stone, 2000; Hastings, 2001; Jansen, 2001), which is the system we will study. We focus on the case where both predator and prey are limited in their dispersal. This allows us to use the theory of weakly coupled oscillators (Malkin, 1949, 1956; Ermentrout, 1981; Kuramoto, 1984) to derive a phase model from our original population model, and then to determine the type of phase locking occurring and the rates of convergence to these phase locked states. We follow the method for this model as introduced in Goldwyn and Hastings (2008) for the homogeneous system, now allowing for and focusing on the important effects of spatial heterogeneity. The key result from this previous study and from Izhikevich (2000) is that a difference in characteristic time scale between the predator and the prey is necessary for convergence to phase locking to occur on a biologically relevant time scale. Here,

we investigate this difference in time scale in the context of spatial heterogeneity and its effects on the phase locking behavior.

We analyze a spatially heterogeneous model to determine whether small levels of heterogeneity can alter the dynamics of a population in a way that has ecological consequences. The consequences we are examining are a change in phase behavior of the system and a decrease in synchrony, presumably leading to an increase in persistence. We incorporate heterogeneity into both the local dynamics of the system (intrinsic heterogeneity) and into the dispersal rates (asymmetrical coupling). Our analysis is quite general, aside from the assumptions of weak coupling and weak intrinsic heterogeneity (clearly strong heterogeneity would have a larger effect). In particular, the results should apply to any predator prey model that is cyclic, with varying effect depending on the existence of a separation in time scales that we analyze.

2. Model

2.1. Population model

We study a model containing one predator and one prey species in two spatial patches. This yields a system of four coupled ordinary differential equations. The prey (victims) and predator populations are described by the variables V_i and P_i , respectively, with the subscript i referring to the patch. We assume logistic growth of the prey species in the absence of predation with r_i as the intrinsic rate of increase and K_i as the carrying capacity. Predation follows a Holling Type II functional response, with predation rate a_i and half saturation coefficient b_i . The loss of prey due to predation also depends linearly on c_i ($c_i > 1$), a measurement of the ratio of the loss of prey to the gain in predators. The predator has a linear death rate m_i . Migration is a linear per capita rate and since we assume no immigration or emigration out of the system, we have two small coupling parameters per species, D_{ij}^V and D_{ji}^V (not necessarily equal), which represent the prey migration from patch i to j and j to i , respectively (analogous for predator migration). These terms need to be sufficiently small in order for the system to be weakly coupled and allow for the derivation to the phase model that we do in the next section. Each patch represents a hunting region for the predator and a foraging region for the prey such that migration is independent from these activities. This is the Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963) in two patches

$$\begin{aligned} \frac{dV_i}{dt} &= r_i V_i (1 - V_i/K_i) - \frac{c_i a_i P_i V_i}{b_i + V_i} + D_{ji}^V V_j - D_{ij}^V V_i, \\ \frac{dP_i}{dt} &= \frac{a_i P_i V_i}{b_i + V_i} - m_i P_i + D_{ji}^P P_j - D_{ij}^P P_i, \end{aligned} \quad (1)$$

$$i, j = 1, 2; i \neq j.$$

There are two different types of heterogeneity in (1). Intrinsic heterogeneities arise from the parameters, a_i , b_i , c_i , K_i , m_i , and r_i , not being equal in both patches, asymmetrical coupling occurs when parameters $D_{ij}^V \neq D_{ji}^V$ and/or $D_{ij}^P \neq D_{ji}^P$. It is the dynamics created by these differences in intrinsic and coupling parameter values that we analyze and compare to those for the homogeneous case.

Equation (1) can be rescaled, reducing the number of parameters and leaving only dimensionless quantities. This simplifies the analysis of the system by reducing the number of parameters and allows us to see more specifically how heterogeneity affects each term in the population model. We first express the heterogeneity by letting the intrinsic parameters $q_1 = q$ and $q_2 = q + \sigma_q q$ ($q = a, b, c, K, m, r$), and the coupling parameters $D_{12}^V = D^V$ and $D_{21}^V = D^V + \sigma_{DV} D^V$ (same for coupling in P). The parameter σ_q is the percentage difference between the value of the parameters in the two patches. We then use the following substitutions as in Goldwyn and Hastings (2008)

$$v_i = V_i/b, \quad p_i = [(ac)/(rb)]P_i, \quad \tau = at, \quad \alpha = b/K, \quad \eta = m/a, \\ \epsilon = a/r, \quad d_{ij}^v = D_{ij}^V/a, \quad d_{ij}^p = D_{ij}^P/a.$$

With the above substitutions, (1) can now be written

$$\begin{aligned} \frac{dv_1}{d\tau} &= 7\frac{1}{\epsilon} \left(v_1(1 - \alpha v_1) - \frac{p_1 v_1}{1 + v_1} \right) + d^v((1 + \sigma_{dv})v_2 - v_1), \\ \frac{dv_2}{d\tau} &= \frac{1}{\epsilon} \left((1 + \sigma_r)v_2(1 - (1 - \sigma_k)\alpha v_2) - (1 + \sigma_a + \sigma_c) \left(1 - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} \right) \\ &\quad + d^v(v_1 - (1 + \sigma_{dv})v_2), \tag{2} \\ \frac{dp_1}{d\tau} &= \frac{p_1 v_1}{1 + v_1} - \eta p_1 + d^p((1 + \sigma_{dp})p_2 - p_1), \\ \frac{dp_2}{d\tau} &= (1 + \sigma_a) \left(1 - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} - (1 + \sigma_m)\eta p_2 + d^p(p_1 - (1 + \sigma_{dp})p_2). \end{aligned}$$

Our analysis focuses only on the case where the intrinsic dynamics lead to oscillatory behavior. This occurs when $\alpha < 1$ and $\eta < \frac{1-\alpha}{1+\alpha}$ (Hastings, 1997). The smaller each of α , η , and $\epsilon < 1$ are, the greater the separation in characteristic time scales between the prey and predator species, with the prey operating on a faster time scale.

2.2. Phase model

Before formulating the phase model, we note the following definitions: the phase of the oscillator, θ , is measured in the interval $[0, 2\pi)$ and represents the location in the cycle of the predator-prey populations; phase locking indicates that the difference in the phase between the two oscillators is constant over time; synchrony occurs when the phases are equal; asynchrony is any nonsynchronous phase locked behavior; and antisynchrony is a particular case of asynchrony occurring when the phases are exactly opposite from one another. If phase locking does not occur, then the system experiences phase drift. Figure 1 shows the behavior of the prey populations in patches one and two relative to each other for each of synchronous, asynchronous, and phase drift behavior.

A system of ordinary differential equations modeling individual populations, such as (1) or (2), can be transformed to a system of phase equations describing the phase of the oscillators so long as the original model produces a strongly attracting limit cycle in the absence of coupling, the coupling is sufficiently weak, the oscillators are only weakly

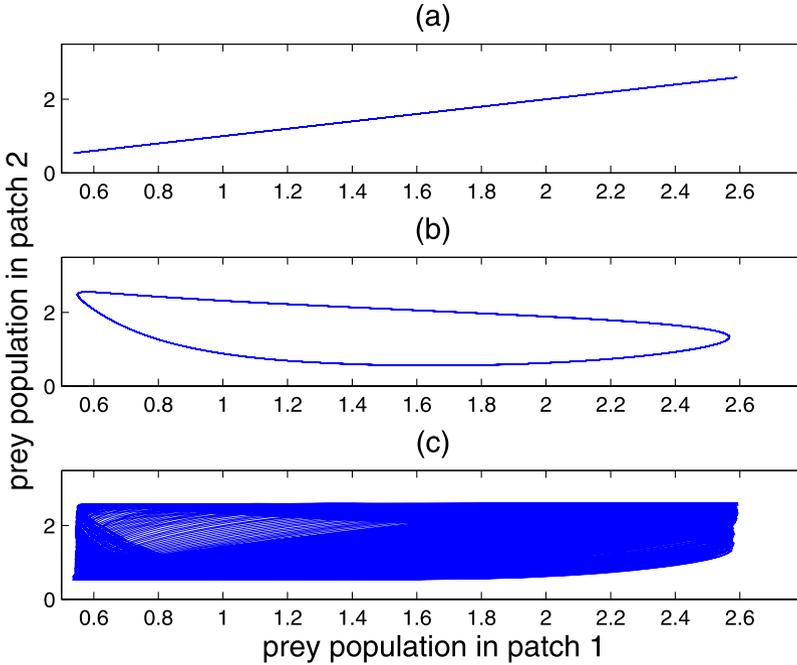


Fig. 1 Plots of the prey populations in patch one versus patch two after the transient behavior is finished. The parameters in (a) are $a = 1$, $b = 2$, $c = 4$, $K = 5$, $m = .4$, and $r = 10$. This yields a synchronous steady state and equal populations in the two patches. In (b), asynchronous behavior occurs due to heterogeneity in the predator death rate, m , and the populations form a closed loop. In (c), heterogeneity in the carrying capacity, K , causes phase drift which results in no correlation between the populations in patches one and two.

heterogeneous, and these heterogeneities are the same order of magnitude as the coupling (Ermentrout, 1981; Kuramoto, 1984; Winfree, 2001). Weak coupling implies that the intrinsic dynamics of the system are at least one order of magnitude larger than the coupling dynamics. For the parameter ranges used in our study, we find that this small migration leads to about 1% of the population migrating per cycle. A derivation of the phase model for the spatially homogeneous system of the Rosenzweig–MacArthur model can be found in Goldwyn and Hastings (2008). With the appropriate function F_i and W_i , the model of two weakly asymmetrically coupled nonidentical oscillators, as formulated in (1) and (2), can be written as the general model

$$\begin{aligned} \frac{dX_1}{dt} &= F_1(X_1) + \delta W_1(X_2, X_1), \\ \frac{dX_2}{dt} &= F_2(X_2) + \delta W_2(X_1, X_2). \end{aligned} \tag{3}$$

The variable $X_i = (v_i, p_i)^T$ is the vector of the population sizes in patch i . The functions F_i and W_i represent the intrinsic dynamics of the populations and the migration in

the i th patch, respectively. The dimensionless quantity δ measures the strength of dispersal.

In order to apply the theory of weakly coupled oscillators, we must first rewrite (3),

$$\begin{aligned}\frac{dX_1}{dt} &= F(X_1) + \delta W_1(X_2, X_1), \\ \frac{dX_2}{dt} &= F(X_2) + \delta f_2(X_2) + \delta W_2(X_1, X_2).\end{aligned}\tag{4}$$

Equation (4) is obtained directly from Eq. (3) if $F_1(X_1) = F(X_1)$ and $F_2(X) = F(X_2) + \delta f_2(X_2)$. We let $f_1(X_1) = 0$, so that the intrinsic heterogeneity is expressed only in the equation of patch 2. The assumption of weak intrinsic heterogeneity implies that $\delta f_2(X_2)$ needs to be an order of magnitude smaller than $F(X_2)$ and the same order of magnitude as $\delta W_2(X_1, X_2)$. This implies that $\sigma_q < .01$, which yields a difference in intrinsic parameters on the order of 1%. We now asymptotically expand the nondimensional population model (2) around $q_2 = q + \sigma_q q$ for each parameter. After ignoring higher order terms in σ_q , we find $f_2(X)$. Writing our specific system (2) in the general form of (4) requires

$$\begin{aligned}X_i &= [v_i, p_i]^T, \\ F(X_i) &= \left[\frac{1}{\epsilon} \left(v_i(1 - \alpha v_i) - \frac{p_i v_i}{1 + v_i} \right), \frac{p_i v_i}{1 + v_i} - \eta p_i \right]^T, \\ W_1(X_2, X_1) &= \left[\frac{d^v}{\delta} (v_2 - v_1 + \sigma_{dv} v_2), \frac{d^p}{\delta} (p_2 - p_1 + \sigma_{dp} p_2) \right]^T, \\ W_2(X_1, X_2) &= \left[\frac{d^v}{\delta} (v_1 - v_2 - \sigma_{dv} v_2), \frac{d^p}{\delta} (p_1 - p_2 - \sigma_{dp} p_2) \right]^T, \\ f_2(X_2) &= \left[\frac{1}{\epsilon} \left(v_2(\sigma_r - (\sigma_r - \sigma_K)\alpha v_2) \right. \right. \\ &\quad \left. \left. - \left(\sigma_a + \sigma_c - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} \right), \left(\sigma_a - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} - \sigma_m \eta p_2 \right]^T, \\ \delta &= \max(d^v, d^p).\end{aligned}\tag{5}$$

Now, we can derive a phase model describing the change in the phase, θ_i , of each oscillator over time. The phase model consists of two equations describing the phase of each oscillator as opposed to our original four equation population model.

$$\begin{aligned}\frac{d\theta_1}{dt} &= \omega_1 + \delta H_1(\theta_2 - \theta_1), \\ \frac{d\theta_2}{dt} &= \omega_2 + \delta H_2(\theta_1 - \theta_2).\end{aligned}\tag{6}$$

The term ω_i is the frequency of the i th oscillator without coupling and is found by adding the scaled intrinsic frequency of the unperturbed homogeneous oscillator to the effect of heterogeneity on the frequency of the oscillator. This effect can be found by

exploiting a difference in time scales between the unperturbed period and the difference of the homogeneous and heterogeneous periods through the method of averaging (Kuramoto, 1984),

$$\omega_i = 1 + \frac{\delta}{T} \int_0^T z(t) \cdot f_i(X_i^0(t)) dt. \quad (7)$$

This average is the integral of the dot product of the functions $z(t)$ (the sensitivity of the phase of the oscillator to perturbations, described below) and $f_i(X_i^0(t))$ taken over one period. The dot product is used because this is a sum of the effects of heterogeneity on the prey and predator populations. The functions $X_i^0(t)$ are the limit cycle solutions to the unperturbed oscillator in patch i and are different if the intrinsic parameter values are different.

The functions, $H_i(\phi)$, measure the effect of coupling on the phase of the oscillator. These functions are found by averaging the coupling and the sensitivity of the phase to coupling for each population over one cycle,

$$H_i(\phi) = \frac{1}{T} \int_0^T z(t) \cdot W_i(X_i^0(t), X_i^0(t - \phi)) dt. \quad (8)$$

The key function in determining both ω_i and $H_i(\phi)$ is $z(t)$, also known as the infinitesimal phase response curve or the PRC (Winfree, 1967; Kuramoto, 1984). The PRC measures the effect of an infinitesimally small and arbitrarily short perturbation on the phase dynamics. Positive values for the PRC indicate that a perturbation will advance the phase of the oscillator, while negative values indicate a delay in the phase. The magnitude of this function measures the degree to which the phase is altered. The PRC can be found by evaluating the following differential equation and normalization (Kuramoto, 1984).

$$\begin{aligned} \frac{dz(t)}{dt} &= -[D_x F(X^0(t))]^T z(t), \\ 1 &= z(t) \cdot (X^0)'(t). \end{aligned} \quad (9)$$

The term $D_x F$ refers to the derivative of F , the function $X^0(t)$ is the periodic solution to the unperturbed oscillator, and the superscript T indicates the transpose of the matrix.

2.3. Steady states

We are ultimately interested in the difference in phase between the two oscillators, defined as $\phi = \theta_1 - \theta_2$. This difference is the time lag between the phase of the two oscillators and not the spatial lag. Our goal is to analyze how this quantity changes over time by studying its time derivative, $\frac{d\phi}{dt}$. To determine $\frac{d\phi}{dt}$, we simply take the difference of the two equations in (6),

$$G(\phi) = \frac{d\phi}{dt} = \omega + \delta(H_1(-\phi) - H_2(\phi)) = \omega + H(\phi). \quad (10)$$

The steady states of the phase model, ϕ^* , called the phase locked states, occur when the difference in the two phases remains constant over time, $\frac{d\phi}{dt} = G(\phi) = 0$. The function $G(\phi)$, called the G-function, is a one dimensional function and, therefore, the phase

locked states are stable when its slope is negative at a fixed point and unstable when the slope is positive. The rate of convergence to a phase locked state at any given difference in phase is the magnitude of the G-function. Convergence to these phase locked states can then be found by integrating this G-function.

The effects of intrinsic heterogeneity and asymmetrical coupling are separated into the term $\omega = \omega_1 - \omega_2$, see (7), and $H(\phi)$, called the H-function (8), respectively. The PRC is used to find both ω and the H-function and, therefore, controls both the effects of migration and heterogeneity on the phase dynamics of each oscillator.

If the two oscillators have identical intrinsic dynamics, then $\omega = 0$, if coupling is symmetric then $H_1 = H_2$. If both of these events occur, the change in time of the phases difference is equal to negative two times the odd part of $H_i(\phi)$, as is the case in Goldwyn and Hastings (2008).

3. Results

We use the theory of weakly coupled oscillators (Ermentrout, 1981; Kuramoto, 1984) to derive a phase model from the two patch predator-prey system in Eq. (1) in order to analyze the effect of heterogeneities on the phase behavior of this system. The crucial function in studying the phase dynamics of an oscillatory system is the phase response curve (PRC or $z(t)$, Eq. (9)). This function measures the degree to which an outside perturbation advances or delays the phase. Because this system is nonlinear, the PRC cannot be found analytically. We use the numerical program XPP to find a numerical approximation for the PRC (for details on XPP, see Ermentrout, 2002). Using this approximation, we analyze how intrinsic heterogeneities and small (possibly asymmetrical) coupling affect the change in phase difference over time between the two oscillators (see Fig. 1 in Goldwyn and Hastings, 2008 for graphs of the PRC for this system with the same parameter values used in Figs. 2, 3, 4).

Heterogeneity in intrinsic dynamics creates a frequency difference, ω from Eq. (7), between the two oscillators. The effect of coupling on the phase difference is quantified by the H-function (8). Using the term ω and the H-function, we find the differential equation (10), known as the G-function which governs the change in the phase difference between the two oscillators over time. We see from this equation the very important result that the effect of intrinsic heterogeneities and asymmetrical coupling are independent from one another and, therefore, can be examined separately. Because the G-function is a one dimensional, continuous, 2π periodic function, finding the phase locked states (when $G(\phi) = 0$) and their convergence rates is easily done. Several different arrangements of phase locked states can occur, depending on the parameter values of the system (Figs. 2, 3, 4). The phase locking behavior for the special case of two spatially homogeneous predator-prey oscillators is examined in Goldwyn and Hastings (2008). The important result from that paper is that in order for convergence to a phase locked state to occur on a biologically relevant time scale, a separation between the characteristic time scales of the prey and predator must exist. Decreasing any of the three parameters α , η , or ϵ from Eq. (2) increases this separation in time scales. Furthermore, prey migration is much more important than predator migration in driving the system to phase locked behavior when this difference in time scales exist. Specifically, positive perturbations to the prey population when it is at very low density greatly increase the phase of the oscillator. Here,

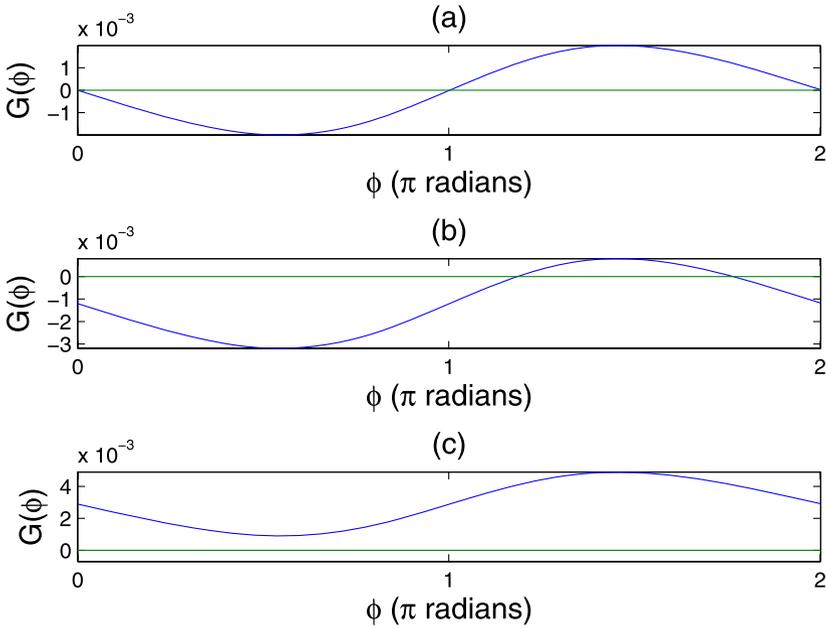


Fig. 2 Plots of the G-function which describes the rate of change of the phase differences between two oscillators. The parameters in each of the graphs are the same as in Fig. 1. (b) includes a 0.1% increase in the predator death rate, m , in patch 2, increasing the frequency of oscillation in that patch and shifting the G-function down. (c) has the same percentage increase in the carrying capacity, K . The sensitivity of the oscillators to the heterogeneity in carrying capacity, leads to a sufficiently large difference in frequency, to lead to phase drift, whereas the change in the predator death rate in (b) still leaves a stable phase locked state, though it is no longer perfectly synchronous.

we restrict our focus to the differences in the G-function and, therefore, on the dynamics of the system, created by intrinsic heterogeneity and asymmetrical coupling.

3.1. Heterogeneity in intrinsic dynamics

In order to examine the effect of heterogeneity in intrinsic dynamics on the two oscillators, we first look at the phase behavior in the special case of homogeneous oscillators with symmetric coupling. Homogeneous oscillators arising from (1) always have a synchronous stable steady state and a (stable or unstable) antisynchronous steady state. Other asynchronous states may or may not exist depending on the parameter values. The term arising from intrinsic heterogeneity is $\omega = \omega_1 - \omega_2$, and it vertically shifts the G-function by that difference (Figs. 2, 3, and 4).

In the case where stable synchrony and unstable antisynchrony are the only phase locked states, a saddle node bifurcation occurs at the critical value of $\omega_c = |\max(H(\phi))|$, where the maximum is taken over the values of ϕ , the difference in phase between the two oscillators. The two phase locked solutions disappear when $|\omega| > \omega_c$. This occurs if either the effect of coupling on the change in phase difference is small for all phase differences or the effect of heterogeneity is large. The shift resulting in no phase locked states is known

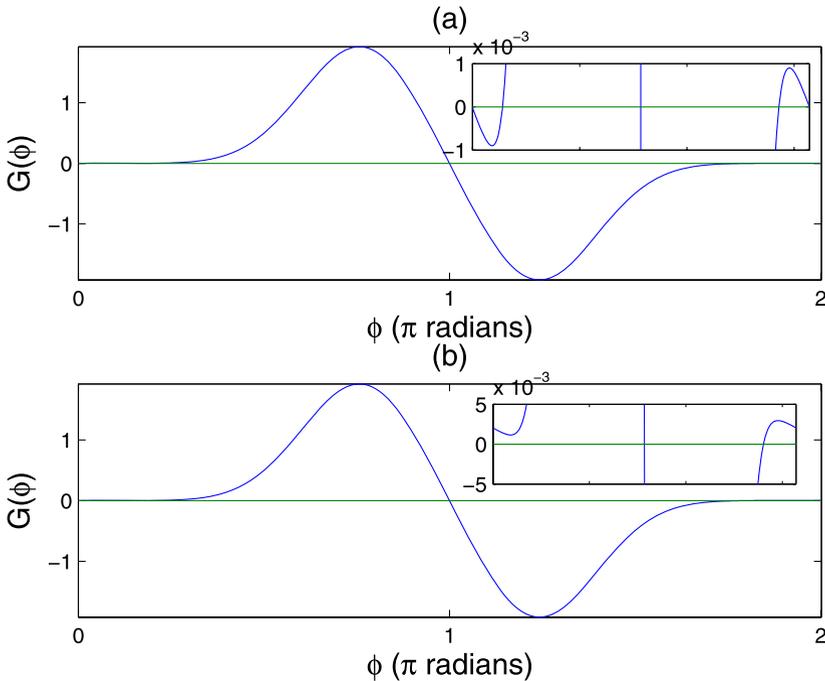


Fig. 3 Plots of the G-function with (a) having parameter values $a = 1$, $b = 2$, $c = 5$, $K = 5$, $m = .15$, and $r = 10$. Inset shows behavior near $G(\phi) = 0$. Heterogeneity is introduced in (b) with the carrying capacity, K , increased by 0.1%. In the homogeneous case (a), there are stable phase locked states at synchrony and antisynchrony. The difference in frequency created by the heterogeneity removes the synchronous stable state and leaves the system with only one near antisynchronous stable phase locked state.

as phase drift and can be seen in Fig. 2(c). If $|\omega| < \omega_c$, then the shift will move the steady states away from their original locations of synchrony and antisynchrony as in Fig. 2(b). This bifurcation in steady states of phase locking due to heterogeneity in frequency of oscillation is discussed in Chap. 4 of Strogatz (1994) for the flashing of male fireflies.

In Blasius et al. (1999), a tritrophic predator-prey resource model that was able to generate dynamics having uniform phase chaotic amplitude (UPCA) was used to study the well-known Canadian hare-lynx cycle. With a two patch coupled model, they found that increasing the coupling rate from no coupling past two numerically determined thresholds led from phase drift, to asynchrony, to synchrony (see Fig. 2 in that paper). This is the same phenomenon that we see in Fig. 3 in this paper when the effect of intrinsic heterogeneity on the frequency of the oscillator is decreased.

If the homogeneous system has stable asynchronous phase locked states in addition to the stable synchronous state, then shifting the H-function by ω can eliminate, by means of a saddle node bifurcation, some, but not all of the phase locked states. This occurs when ω is larger than one or more of the local extrema of the H-function. The synchronous stable states are usually the first to be eliminated by this saddle node bifurcation, leaving only asynchronous stable steady states as in Fig. 3. This shift will also move the other steady states away from their original locations. We find that differences as small as 0.1% in a

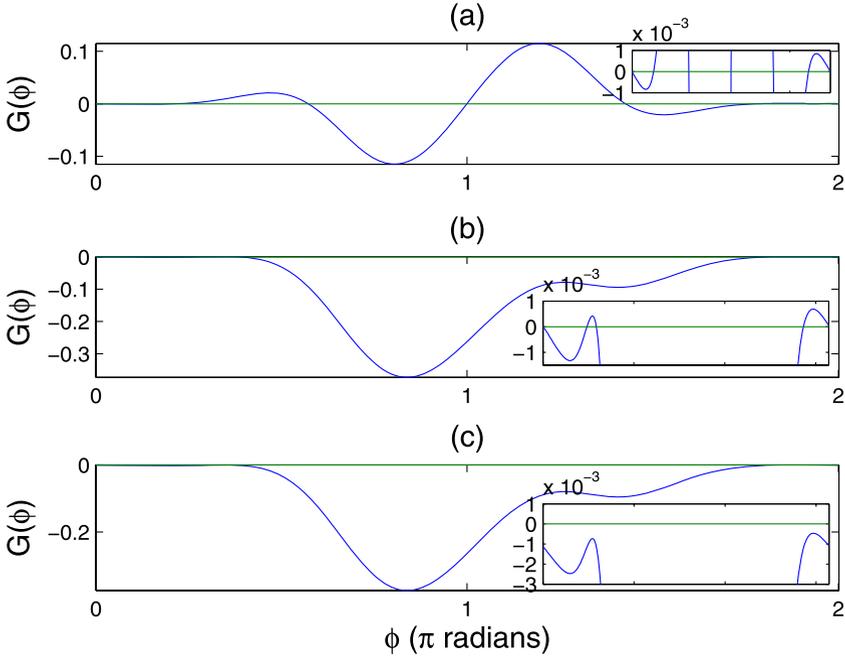


Fig. 4 Plots of the G-function with (a) having parameter values $a = 1$, $b = 1.5$, $c = 4$, $K = 5$, $m = .3$, and $r = 10$. Graphs (b) and (c) have asymmetry with 40% less migration going from patch 2 to patch 1 than the opposite direction. In graph (c), intrinsic heterogeneity is introduced with the predation rate, a , decreased by 0.1% in patch 2. Inset shows behavior near $G(\phi) = 0$. In graph (a), there are stable steady states at synchrony and asynchrony, and unstable steady states at antisynchrony and near synchrony. Asymmetry alone leads to stable synchronous and near synchronous states. Adding heterogeneity by decreasing the predation rate in patch two slows the frequency of oscillation of that patch and shifts the G-function downward. This removes all phase locked states and yields phase drift.

given parameter value can be sufficient to allow for either type of saddle-node bifurcation discussed above and, therefore, lead to qualitative changes in the behavior of the system.

As discussed in Goldwyn and Hastings (2008), the H-function has a larger maximum magnitude when there is a difference in time scales between the prey and predator populations and this maximum magnitude can vary by many orders of magnitude, as is the case in Figs. 3 and 4 as opposed to Fig. 2. The reason behind these differences in the maximum magnitude of the H-function in the case of a large difference in time scales is because the unperturbed dynamics have a saddle steady state point at the origin (where both the prey and predator populations are zero). The dynamics of the system are very slow when the populations are near the stable manifold of this saddle steady state. Larger differences in time scales between the predator and the prey lead to the dynamics of the system getting closer to this stable manifold, where the effect of an external perturbations to the prey is very large. This yields a large maximum magnitude of the H-function.

Our analysis shows that while the magnitude of ω varies due to the type of intrinsic heterogeneity and the specific dynamics of the system, it is not necessarily larger when there is a difference in time scale between the two populations. For our range of parameter

values, the maximum value of $|\omega|$ is on the order of 10^{-2} . This indicates that for intrinsic heterogeneity to cause phase drift in our model with symmetric coupling, it is necessary both that there is not a separation of time scales between the two predator and prey species, and the heterogeneities produce large sufficiently ω .

3.2. Asymmetric coupling

We analyzed two different types of asymmetric coupling. One occurs when a larger percentage of the population of predator or prey migrates from patch i to patch j , than patch j to patch i . The most extreme case of this is one directional migration. The other type of asymmetric coupling occurs when the two patches are of different sizes (these patches can still have homogeneous intrinsic dynamics as the populations can be thought of as densities). While the rates of migration may be the same in either direction, clearly migration occurring from the larger patch to the smaller patch has more of an impact than migration occurring in the opposite direction. A greater migration rate from patch i to j behaves qualitatively similarly to a system with patch i being larger than j . These two types of asymmetrical coupling are similar in their effects on the phase behavior of the system, so we will only explain the details of asymmetries in direction of coupling here.

In this model, small levels of asymmetrical coupling do not have large effects on the G-function and, therefore, the phase dynamics. This is in contrast with intrinsic heterogeneity where even very small levels of heterogeneity can have large effects on the G-function and qualitatively change the phase dynamics of the system.

Whereas heterogeneity in intrinsic dynamics shifts the G-function vertically by the term ω , the effect of asymmetric coupling depends on the phase difference and, therefore, it alters the shape of the G-function as in Fig. 4(b). We also notice that for the case of a difference in time scale between the prey and predator species, asymmetries in prey migration have a larger effect on the G-function than those in predator migration. As the asymmetry in coupling is increased, the steady states of phase locking will go through saddle node bifurcations similarly to what occurs when intrinsic heterogeneity is increased. In this case, the most asynchronous steady states are the first to be eliminated. For systems that are very strongly asymmetrically coupled (as is the case in one directional migration), $H(\phi) = 0$ occurs only when ϕ is near synchrony. This indicates that an intrinsically homogeneous, strongly asymmetrically coupled system will only have one stable steady state which is very near to synchrony. This steady state will correspond to patch 1 being slightly ahead in phase of patch 2 if all the migration is moving from patch 1 to patch 2. In that sense, patch 1 is pulling or synchronizing patch 2 to itself. We can see from Fig. 4(b), that the G-function is very small when positive. Therefore, if this asymmetrically coupled system has intrinsic heterogeneity that increases the frequency of oscillator 2 (shifting the G-function down), such as a smaller predation rate in patch 2 than in patch 1, there will be no phase locked states and the system will exhibit phase drift; see Fig. 4(c). This is a consequence of the PRC being almost entirely positive for this range of parameter values. Oscillator 2 will be only positively perturbed by oscillator 1, increasing its frequency. If oscillator 2 has a higher frequency than oscillator 1, then the coupling will never allow for oscillator 1 to slow it down sufficiently to allow for phase locking. Notice that phase drift was not a possible outcome with the parameters used in Fig. 4 with intrinsic heterogeneity alone.

4. Discussion

The fundamental question that we address in this paper is: What are the effects of intrinsic heterogeneity and asymmetrical coupling on the dynamics of spatially extended populations? Specifically, we analyze the difference in behavior between spatially heterogeneous and homogeneous populations to see if even small heterogeneity can produce qualitatively different behavior. Since it is much easier to formulate and analyze spatially homogeneous populations in a theoretical setting, it is these models that have been more extensively studied. The results from these studies are then often generalized and assumed to hold for systems having slight heterogeneities. For the phase model analyzed here, just a 0.1% difference in parameter values can produce qualitatively different phase behavior. This shows the power and importance of small heterogeneity to produce dynamics that are observably different. It also indicates the risk of assuming that results for a homogeneous model or experiment will also hold for heterogeneous environments.

In our two patch model, intrinsic heterogeneity can manifest itself through different prey birth rates, prey carrying capacities, predation rates, predator half saturation coefficients, or predator death rates. These differences between the two model patches can result from a variety of biological factors including unequal amounts of resources for prey to consume, varying habitat which impacts the ability of the prey to evade predation, varying population densities, and others.

Results from our analysis indicate that even slight differences in any of these attributes can yield dramatically different behavior for the heterogeneous case as opposed to the homogeneous one. The differences become more pronounced when the prey and predator operate on similar characteristic time scales, at which point even small intrinsic heterogeneity prevents synchronous behavior from occurring. While the results based on the phase model strictly hold only in the case of small heterogeneities, simulations indicate that the qualitative results will also hold for larger heterogeneities.

Another possible heterogeneity in the system is the occurrence of asymmetrical coupling or dispersal. Unlike with intrinsic heterogeneity, in order for asymmetric coupling to have a qualitative effect on the system, the asymmetry must be somewhat large (on the order of 10%), before qualitative changes in the dynamics occur. One example of asymmetrical coupling is when migration does not flow evenly in both directions, as would occur in the presence of air or water currents. Another possibility is patches having different sizes but identical population densities. The combination of asymmetrical coupling and intrinsic heterogeneity is also very likely to reduce or prevent synchrony from occurring.

One type of behavior that is possible with two heterogeneous patches is that there will be no phase locked states and the system will have phase drift. Phase drift behavior is qualitatively different from any type of phase locking, and heterogeneity which creates this behavior is clearly much different from the homogeneous case. The exception is if the drifting of the phases is slow. Natural populations are often observed on short time scales and if the phase drift is sufficiently slow, which occurs when the G -function is close to zero for some given phase difference (as occurs for the ϕ value corresponding with the minimum of $G(\phi)$ in Fig. 2 and the local maxima of $G(\phi)$ in Fig. 4), it may be difficult to differentiate from phase locked behavior.

Careful studies of spatiotemporal dynamics of coupled predator-prey systems in nature are, of course, very difficult so the current results must be used as more of a guide. However, more careful studies have been made of the dynamics of a different exploiter-victim

system, namely human childhood diseases. A particularly well-studied case is measles in the UK. This is essentially an exploiter victim system having heterogeneities caused by extreme differences in city size from London to the very smallest cities. In this case, the result is a traveling wave of disease outbreaks, as analyzed by Grenfell et al. (2001). Although the systems may seem extremely different, our results on asynchronous phase locking with heterogeneity are consistent with the idea of traveling waves. Our work approaches the problem from the view of a simple model whose behavior we attempt to understand using analytic tools to characterize classes of dynamic behavior, and thus complements the data based approach of Grenfell et al. (2001). One theme we emphasize, namely the importance of perturbations at the “trough” of the cycle, is consistent with the discussion of the importance of cases that set off epidemics. Also, we focus here on the role of heterogeneity. Future work extending our analytical approach to look at epidemic systems would be very interesting.

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