Coupled phase-amplitude dynamics in heterogeneous metacommunities

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Abstract

Within metacommunity theory, stability of ecosystems is a fundamental concept. Synchrony between populations is known to cause greater regional variability and diminish the possibility of rescue effects after a catastrophe, and thus it negatively affects stability. However, much of the underlying dynamics of synchrony as applied to ecology are not yet known. It is mathematically predicted that populations may move closer to and farther away from synchrony in cycles, a phenomenon known as phase difference modulation, but this has not been tested in ecological models. Here, we test for phase difference modulation using a mathematical model of metapopulations, and evaluate its effects on stability. We find that intermediate values of dispersal and habitat heterogeneity produce phase difference modulation. Additionally, we show that it can occur in simulated metacommunities where all populations naturally fluctuate as well as in those with one that is naturally at equilibrium but fluctuates due to dispersal. Phase difference modulation was found to cause populations' amplitudes to vary, leading to cyclic patterns of local and regional variability. Our results highlight the importance of viewing synchrony as a dynamic phenomenon, with implications for how synchrony between populations is measured in the field.

Résumé

Dans la théorie métacommunautaire, la stabilité des écosystèmes est un concept fondamental. La synchronisation entre les populations est connue pour provoquer une plus grande variabilité régionale et diminuer la possibilité d'effets de sauvetage après une catastrophe, et ainsi affecter négativement la stabilité. Cependant, une grande partie de la dynamique sous-jacente de la synchronie appliquée à l'écologie n'est pas encore connue. Il est prédit mathématiquement que les populations peuvent se rapprocher et s'éloigner de la synchronie en cycles, un phénomène connu sous le nom de modulation de différence de phase, mais cela n'a pas été testé dans des modèles écologiques. Ici, nous testons la modulation de différence de phase en utilisant un modèle mathématique de métapopulations, et évaluons ses effets sur la stabilité. Nous trouvons que les valeurs intermédiaires de dispersion et d'hétérogénéité de l'habitat produisent une modulation par différence de phase. De plus, nous montrons qu'il peut se produire dans des métacommunautés simulées où toutes les populations fluctuent naturellement aussi bien que dans celles qui en ont une qui est naturellement à l'équilibre mais qui fluctue en raison de la dispersion. La modulation de la différence de phase a fait varier les amplitudes des populations, ce qui a entraîné des variations cycliques de la variabilité locale et régionale. Nos résultats soulignent l'importance de considérer la synchronie comme un phénomène dynamique, avec des implications sur la façon dont la synchronie entre les populations est mesurée sur le terrain.

Preface

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Contributions of authors

All material contained in this thesis was written by Russell Milne, under the guidance of Prof. Frederic Guichard.

1 Introduction

1.1 Stability of natural and modelled metapopulations

Over the course of the development of the field, ecologists have always been interested in the stability of natural populations. Indeed, the concept of stability has been on the minds of ecologists since the early days of the discipline (Elton, 1958). While stability has many definitions (Grimm et al., 1992; Ives and Carpenter, 2007), two particular ones that have been of great importance to ecologists are persistence and variability. Persistence is defined as the ability of an ecosystem to retain some fundamental quality it possesses over time (Harrison, 1979; Pimm, 1984; Grimm and Wissel, 1997), which can be further specified to the ability of an ecosystem to maintain a relatively constant species composition (Donohue et al., 2016). It follows that a natural system with high persistence will see its species go extinct at low rates. Variability, in turn, is defined as the ability of a species or group of species to maintain steady population levels and avoid large fluctuations (Harrison, 1979; Pimm, 1984; Grimm and Wissel, 1997). Both of these concepts of stability have motivated extensive volumes of work both in the field (Donohue et al., 2016) and of a more theoretical nature (Austin and Cook, 1974; DeAngelis and Waterhouse, 1987; McCann et al., 1998; Ives and Carpenter, 2007; Gellner et al., 2016).

A common thread between persistence and variability is that both can be thought of as the likelihood that a given population will reach critically low levels, low enough for that population to go extinct. Indeed, variability and time to extinction have been shown to correlate with each other (Inchausti and Halley, 2003). This means that there exist metrics that can effectively measure both of these stability concepts. The coefficient of variation (CV) of a time series, defined as its standard deviation divided by its mean, is a leading measurement of variability used both theoretically (Doak et al., 1998; Cottingham et al., 2001; Loreau and de Mazancourt, 2013) and in the field (e.g. Bai et al., 2004; Grman et al., 2010; Mrowicki et al., 2016). However, since both decreasing the mean and increasing the standard deviation of a species's population levels heighten the chance that that species will decline to critical levels, and both also increase the CV of the corresponding population time series, CV has been used as an effective metric for determining extinction risk (Gellner et al., 2016).

Theoretical studies of natural populations have been undertaken using a variety of different models, but the Rosenzweig-MacArthur predator-prey model (Rosenzweig and MacArthur, 1963) is among the most commonly used for interacting species both within a patch and in metapopulations (e.g. Koelle and Vandermeer, 2005; Vasseur and Fox, 2009; Garvie and Golinski, 2010). This model features a Hopf bifurcation and the potential for oscillatory solutions (Rosenzweig and MacArthur, 1963; Kuang and Freedman, 1988). Properties (including oscillatory behaviour) consistent with low-dimensional deterministic models, and specifically the Rosenzweig-MacArthur model, have been shown by experimental populations (Vasseur and Fox, 2009) and long-term field data (Schaffer, 1984; Holmengen et al., 2009). The Rosenzweig-MacArthur model can be iterated over multiple patches (in other words, turned into a metapopulation model). In this case, the oscillatory behaviour of the populations modelled lends itself to analysis of persistence and variability, just as is done in observed populations.

Within the context of metapopulation stability, synchrony has been widely studied and found to have a negative effect. More specifically, this is because of the decline of the rescue effect among synchronous populations. If a species goes extinct in one patch, migration from another patch where the species is more abundant may rescue that population (Hanski, 1998; Gonzalez et al., 1998). This is, intuitively, more likely if the various local populations hit their minima at different times, or in other words if they exhibit population asynchrony (Allen et al., 1993; Ruxton, 1994). The relationship between synchrony and stability is underscored by the effect of dispersal on both. Theoretical results show that dispersal can facilitate the rescue effect (Abbott, 2011), but also has the effect of inducing synchrony (Winfree, 1967). If enough dispersal to fully synchronize a system is present, the magnitude of the rescue effect becomes minimal (Briggs and Hoopes, 2004; Abbott, 2011). In the same vein, synchrony across populations causes the aggregate of those populations to possess high variability, while less synchronous communities have more dampened fluctuations; a graphical explanation of these effects is available in figure 1.1c.

1.2 Synchronization in metapopulation ecology

In ecology, synchronization of oscillatory population abundances has long been of interest, both theoretically (Winfree, 1967) and in the field (Elton and Nicholson, 1942). The number of field studies showing synchrony across populations is large, and encompasses a diverse range of organisms such as mammals (Moran, 1953; Mackin-Rogalska and Nabagło, 1990; Ranta et al., 1995), birds (Ranta et al., 1995; Paradis et al., 1999; Koenig and Liebhold, 2016; Eberhart-Phillips et al., 2016), fish (Cheal et al., 2007; Frank et al., 2016), and insects (Hanski and Woiwod, 1993; Bouchard et al., 2017). Field literature has postulated a variety of potential causes for synchrony, including the Moran effect of environmental fluctuations (Moran, 1953; see figure 1.1b) as well as dispersal (see figure 1.1a). High dispersal has been explicitly linked to synchrony in populations observed in the field (Matter and Roland, 2010) and in laboratory-based experiments (Dey and Joshi, 2006; Vogwill et al., 2009; Duncan et al., 2015). Additionally, synchrony between populations has been found to decrease with increasing distance for many different species (Ranta et al., 1995), which has been interpreted as a relationship between dispersal and synchrony. The observation of greater spatial synchrony in species with greater dispersal ability (Paradis et al., 1999) supports this, as does synchronization among populations separated by less distance than species' known dispersal ranges (Cheal et al., 2007; Eberhart-Phillips et al., 2016).

The degree of synchrony between ecological populations measured in the field has mainly been described in terms of correlations between time series (Paradis et al., 1999; Buonaccorsi et al., 2001; Liebhold et al., 2004; Loreau and de Mazancourt, 2013). This method does have some advantages, for instance being easy to compute given field data (Loreau and de Mazancourt, 2013). However, it is an imperfect metric. It marks as “asynchronous” any pair of populations with low or no correlation between each other, including pairs of populations where one always peaks shortly after the other, leading to a constant and predictable phase difference between the two but low correlation (Liebhold et al., 2004). This has the consequence of pairs of two populations, or a population and an environmental signal, being declared asynchronous despite a strong appearance of being associated with each other (Milner et al., 1999). Using a static correlation also disregards any changes in synchrony that may occur over time, and masks different patterns of synchrony that happen over different time scales (Defriez et al., 2016). As a result, while a correlation-based approach has its uses when dealing with field data, theoretical papers in biology that deal with synchrony have instead used other methods (Blasius et al., 1999; Goldwyn and Hastings, 2008, 2009; Wall et al., 2013; Zhang et al., 2015).

1.3 Measuring synchrony across populations

Analysis of phase differences and asynchrony between periodic signals is done in a wide variety of disciplines, for instance astronomy (Zolotova and Ponyavin, 2006), medicine (Chao et al., 1997), and physics (Rosenblum et al., 1996; Pikovsky et al., 1997), and has many applications within biology (Winfree, 1967). In the broad field of biology, much of the early work on phase dynamics was conducted in the context of neuronal oscillators (Ermentrout, 1981; Ermentrout and Kopell, 1991; Somers and Kopell, 1993, 1995), including the rigorous derivation of equations describing the phase of such oscillators (Ermentrout, 1981).

From this derivation, it is possible to obtain equations for the phase difference between pairs of oscillators, and the rate of change of this difference (this last one is referred to as the “G-function”) (Goldwyn and Hastings, 2009). This derivation assumes a number of constraints, namely that the levels of coupling between oscillators and heterogeneity among oscillators are weak and of the same order of magnitude, and that without coupling the system produces a strongly attracting limit cycle (Ermentrout, 1981; Kuramoto, 1984). Further work has led to the derivation of the time it takes coupled oscillators to reach a state of unchanging phase (Izhikevich, 2000), and the finding that oscillators with more than one time scale (referred to as pulse-relaxation oscillators) do so more quickly than those with only one (called sinusoidal or regular oscillators) (Somers and Kopell, 1993, 1995; Izhikevich, 2000). Mathematically, this shows up in the higher magnitude of pulse-relaxation oscillators' G-functions (Goldwyn and Hastings, 2008). Additionally, it has been shown that manipulating parameters in a system of oscillators has effects on the G-function: increasing heterogeneity between oscillators may remove its zeros, causing the system to undergo phase drift (Goldwyn and Hastings, 2009). In a similar vein, the G-function of the Rosenzweig-MacArthur model in two patches has been shown to have stable zeros at values other than 0 and 2π for parameter values leading to pulse-relaxation oscillations, but not sinusoidal ones, meaning that the former but not the latter can converge to stable out-of-phase states (Goldwyn and Hastings, 2008).

As literature on synchrony has proliferated, the number of ways to measure it has as well. The rigorously-derived differential equations for phase and phase difference discussed above are powerful tools, but may not be applicable for most scenarios due to their inherent conditions. As a result, other methods of measuring phase have been utilized in the literature (Pikovsky et al., 1997). One simple method of calculating phase of an oscillator is to assume that the phase function is 2π-periodic and is zero at each local maximum (representing the beginning of a period), then increases linearly until the next local maximum (Blasius et al., 1999; Cazelles and Stone, 2003), which has been referred to as the method of marker events (Glass et al., 1983; Lotrič and Stefanovska, 2000). This method is light on computation, but does not account for dynamics between local maxima, and is therefore good for measuring phase with respect to oscillators that move approximately in a circle in the phase plane (Pikovsky et al., 1997) but less so for more irregular oscillations such as pulse-relaxation ones (Liebhold et al., 2004). Another way of measuring phase relies on angular momentum (Pikovsky et al., 1997; Allefeld and Kurths, 2004; Liebhold et al., 2004); this addresses the problem of accuracy for non-sinusoidal waveforms. A third method, taken from the field of signal processing, involves finding the phase of a presumedly oscillatory function by adding its Hilbert transform multiplied by i to it (Rosenblum et al., 1996; Pikovsky et al., 1997). Additionally, techniques such as measuring the correlations between time series (Liebhold et al., 2004; Loreau and de Mazancourt, 2013) and spectral analysis (Grenfell et al., 2001; Sheppard et al., 2016; Defriez et al., 2016) have been used to evaluate synchrony, mainly from field data, although those metrics do not measure phase directly.

1.4 Linking ecological synchrony with mathematical theory

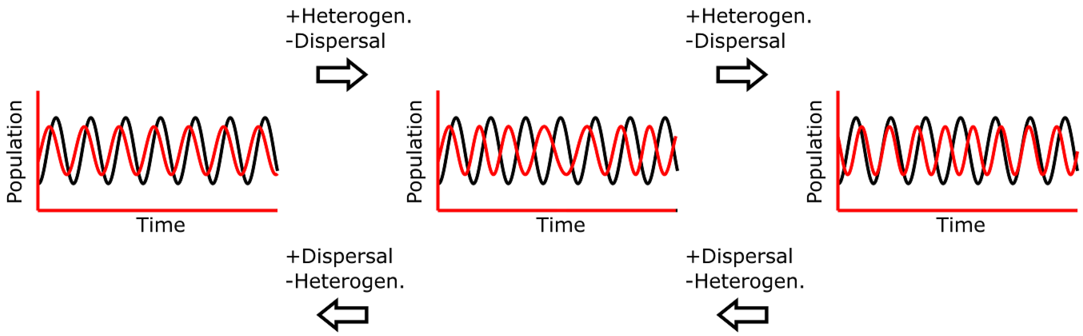
While it is without question that synchrony has been thoroughly discussed in ecology, much of the mathematically possible phenomena related to synchrony remain untested. At the heart of this lie the dynamics of phase, and by extension phase difference between populations. By definition, populations that are becoming synchronized will see their phase difference approach zero; anti-synchronous populations will have their phase difference at $\frac{\pi}{2}$, or 50%. Consequentially, it is possible for the phase difference between two fluctuating populations to itself fluctuate, or modulate, around a certain value. Since field studies have tended to use synchrony metrics that forgo direct measurements of phase, they have not yet explored the dynamics of synchrony through the lens of phase difference. Likewise, although phase dynamics are regularly talked about in the theoretical ecology literature, phase difference modulation has not been, despite its mathematical justification being straightforward. To wit, if three oscillatory populations exist with phases of θ_1, θ_2 and θ_3, then two linearly independent phase differences exist in the system, e.g. $\theta_1 - \theta_2$ and $\theta_2 - \theta_3$ (in this example, $\theta_1 - \theta_3$ is a linear combination of the other two). If these two quantities are considered as varying temporally, then we are left with two ordinary differential equations in time. This may admit a limit cycle, which would cause both $\theta_1 - \theta_2$ and $\theta_2 - \theta_3$ to fluctuate around an equilibrium. The implications for this are that populations would move closer to being synchronous, then farther away, in an ongoing cycle. Groups of three and more populations that exhibit these variable, bounded phase differences have already been theorized in the physics literature (Aronson et al., 1990; Aeyels and Rogge, 2004). Additionally, theoretical ecology papers have found transitions between various kinds of phase dynamics at intermediate levels of dispersal (Blasius et al., 1999) and habitat heterogeneity (Goldwyn and Hastings, 2009), suggesting that dynamics such as phase difference modulation may potentially be possible in such ranges. (See figure 1.1a for a theorized system exhibiting PDM at levels of dispersal and heterogeneity between those producing synchronous and uncorrelated populations.) Viewing synchrony in this way could alter views of what it means for populations to be synchronous, as well as impacting the way synchrony is measured in the field.

Thus, within this thesis, I investigate the question of whether phase difference modulation is expected in ecological systems. I use the Rosenzweig-MacArthur predator-prey model to simulate a metacommunity full of oscillatory populations, and examine the change over time in phase difference between pairs of populations of each species. With the documented effects of synchrony on stability in mind, I observe the CVs of synchronous and asynchronous metapopulations, including one exhibiting phase difference modulation. This allows me to integrate phase difference modulation into the existing body of work on synchrony and variability. Additionally, I establish signatures of populations undergoing phase difference modulation, assisting its identification in the field. Ultimately, my work will advance both theoretical and field ecology, by adding another aspect to the theoretical knowledge on synchrony and providing ways of verifying it in nature.

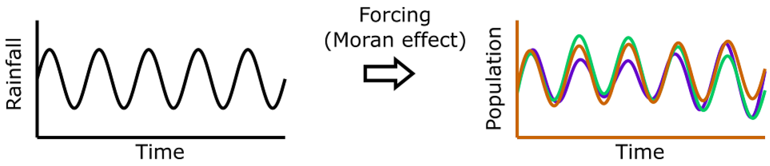
1.5 Figures

Figure 1.1: Conceptual diagrams illustrating how synchrony can be generated through dispersal, habitat heterogeneity and the Moran effect, as well as the effects of synchrony and asynchrony on regional stability. A theorized community showing phase difference modulation is included, at intermediate rates of dispersal between synchronous and uncorrelated populations.

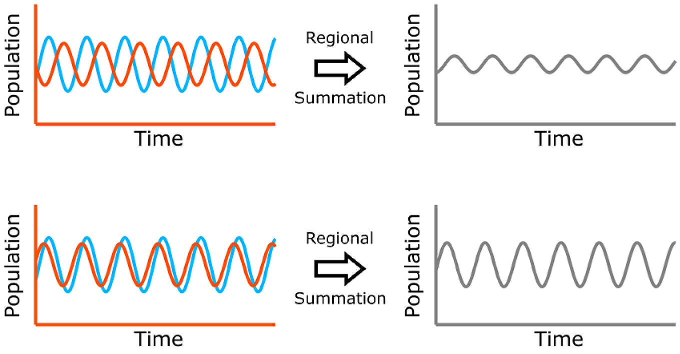
(a) Dispersal and habitat heterogeneity



(b) The Moran effect



(c) Effects of synchrony on variability



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2 Chapter 1: Modulation in phase and amplitude in heterogeneous metacommunities and effects on stability

2.1 Abstract

Within metacommunity theory, stability of ecosystems is a fundamental concept. Synchrony between populations is known to cause greater regional variability and diminish the possibility of rescue effects after a catastrophe, and thus it negatively affects stability. However, much of the underlying dynamics of synchrony and phase dynamics as applied to ecology are not yet known. The ability of oscillating populations to undergo modulation in their phase difference is mathematically predicted but has not been tested in ecological models. Here, we test for the robustness of phase difference modulation in the Rosenzweig-MacArthur predator-prey model in three patches, and evaluate its effects on stability. We find that phase difference modulation occurs at intermediate values of interpatch coupling and habitat heterogeneity. Additionally, we show that phase difference modulation can happen in metacommunities where all populations autonomously oscillate as well as those with one at equilibrium that is forced into oscillation. Phase difference modulation was found to produce temporal variation in populations' amplitudes, leading to cyclic patterns of local and regional variability. Our results highlight the importance of viewing synchrony as a nonstationary phenomenon, with implications for how synchrony between populations is measured in the field.

2.2 Introduction

Greater understanding of synchronization among oscillating populations, including effects of coupling and heterogeneity, have led to advances in understanding the variability and extinction risk of metacommunities (Liebhold et al., 2004). However, the existing literature in theoretical and field ecology has treated synchrony as a fixed property. Considering the phase dynamics between oscillatory populations allows us to view temporal variation in their synchrony, and specifically fluctuations in synchrony not caused by any environmental disturbance. This treatment of synchrony as dynamic is predicted to affect the amplitudes of population fluctuations, and thus allow us to reconsider stability concepts related to synchrony such as persistence and variability. Here, we examine the robustness of this dynamic synchrony, which we call phase difference modulation, with respect to dispersal and habitat heterogeneity. Additionally, we look at the coupling of phase difference modulation with variation in population amplitudes, and how this affects stability of metacommunities.

When evaluating metacommunity stability, much attention has been paid to synchrony among local populations. In-phase dynamics have been linked to higher extinction rates due to cotemporality of local population minima (Ruxton, 1994; Earn et al., 1998; Liebhold et al., 2004), while uncorrelated populations show less regional variability due to statistical averaging (the "portfolio effect") (Doak et al., 1998; Cottingham et al., 2001). Hence, the question of how oscillatory populations in a metacommunity can synchronize has arisen. Dispersal between populations has been found to synchronize them (Blasius et al., 1999; Goldwyn and Hastings, 2008), consistent with the mathematical finding of time to synchrony between oscillators bearing an inverse relationship with the strength of their coupling (Izhikevich, 2000). However, the relationship between dispersal and synchrony is far from being clear-cut. In their study of synchronization in large networks of communities, Blasius *et al.* (1999) found that low levels of dispersal led to phase drift among the populations concerned and high levels synchronized them, but intermediate levels of dispersal synchronized local populations' periods but not amplitudes. This was distinguished from the "complete synchronization" present at higher coupling rates, and deemed to closely resemble population patterns found in nature. These results stress the importance of both phase and amplitude when evaluating synchrony versus interpatch variation.

Spatial synchrony theory in ecology has mostly emphasized phase-locking as the equilibrium phase difference, either in or out of phase. Recently, it has been shown that dispersal can drive non-equilibrium phase difference depending on the size of metacommunities. In two-patch heterogeneous systems, the phase dynamics are known: increasing dispersal moves phase drifting systems to a phase-locked state, and heterogeneity in patch parameters (carrying capacity, predator death rate) has been found to shift systems between synchronization and obligate phase drifting (Goldwyn and Hastings, 2009). These correspond to the phase difference between two like oscillators ($\theta_1 - \theta_2$) either converging to a stable equilibrium point (locking) or not converging at all (drift) (see e.g. Strogatz, 2000); these two cases represent the bulk of observable phase dynamics in a low-dimensional system. In contrast, a system of three patches yields two linearly independent phase differences (e.g. $\theta_1 - \theta_2$ and $\theta_2 - \theta_3$). Considering these phase differences as a system of two coupled differential equations means that they can admit a cyclic solution (such as limit cycles in a phase plane of phase differences). This possibility of a modulation in phase difference suggests that phase dynamics beyond drift and locking may have a much larger presence in systems with three patches than those with two. Limit cycles in phase difference stemming from high system dimensionality also bear ecological relevance as metacommunities found in nature are often far more complex than only two patches. Modulation of phase differences has been mentioned in the existing physics literature (Kim and Shaw, 1984; Aronson et al., 1990; Rosenblum et al., 1996; Aeyels and Rogge, 2004). However, the phenomenon has so far gone unexplored in ecology, where research has instead focused on synchronizing drifting systems within the paradigm of phase-locked synchrony.

While phase difference modulation itself has not been looked at in ecology, we do have some clues as to where it might appear. Transitions in phase dynamics occurred when heterogeneity between patches was varied (Goldwyn and Hastings, 2009). In very heterogeneous systems, one population may converge to a stable limit in the absence of coupling, but oscillate due to forcing by other patches when coupled to them. Non-stationary signals have been found in systems containing such forced oscillators (Leroux and Loreau, 2012), providing another potential location for phase difference modulation. Coupling is also known to produce transitions in phase regimes (Ermentrout and Kopell, 1991; Goldwyn and Hastings, 2008), and the "more unusual form of synchronization" of Blasius *et al.* (1999) took place in coupling ranges between those that produced phase drift and pure synchronization. This suggests that coupling as well as heterogeneity may play an important role in leading to non-equilibrium phase and amplitude dynamics.

Signs of the interrelatedness of synchrony and variability, and hence of phase and amplitude, have been produced in the ecological literature. The portfolio effect found by Doak *et al.* (1998) means that a regional time series will have smaller amplitudes if its constituent populations are out of phase. On a local level, it is known that weak coupling between out-of-phase populations causes immigration into these populations to become inversely correlated with their abundances, which has a damping effect on each population's amplitude (Briggs and Hoopes, 2004). Both of these effects rely on how close to being out of phase the populations in a metacommunity are. If that property changes over time, as it would in a system exhibiting phase difference modulation, the strengths of the portfolio effect and immigration-local abundance decoupling would also both vary. Hence, it is intuitive that if there is modulation in phase difference, there should also be modulation in amplitude.

In this paper, we establish the existence, robustness, and implications for stability of modulation in phase difference and amplitude. To do this, we investigate a model featuring one predator and one prey iterated over two and three patches. We use a simple linear model of phase (Blasius et al., 1999; Cazelles and Stone, 2003) to check pairs of oscillators for phase differences, and establish relationships between coupling strength and patchwise parameter heterogeneity (i.e. migration rates and habitat heterogeneity) and the type of phase dynamics expected. Additionally, we use a common measure of ecological stability, namely the coefficient of variation, to determine how local and regional stability respond to synchrony regimes. The establishment of phase difference and amplitude modulation as distinct types of dynamics, separate from locked systems and phase drift, provides new insight as to how oscillatory natural populations can be evaluated. Also, the wide parameter ranges considered offer information about phase dynamics beyond the restrictions of weak coupling and weak heterogeneity.

2.3 Methods

2.3.1 Terminology and model

In this study, the following terminology related to phase dynamics was used: phase-locking refers to the phase difference between two oscillators converging to a constant value, phase difference modulation (PDM) refers to that phase difference converging to a limit cycle, and phase drift is when phase difference does not converge.

The Rosenzweig-MacArthur model (1) was used to simulate predator and prey populations:

$$\begin{aligned} \frac{dN_i}{dt} &= r_i N_i \left(1 - \frac{N_i}{K_i}\right) - \frac{s_i N_i P_i}{1 + s_i \tau_i N_i} + \sum_{j \neq i} m_{ij}^N N_j - \sum_{j \neq i} m_{ji}^N N_i \\ \frac{dP_i}{dt} &= \frac{b_i s_i N_i P_i}{1 + s_i \tau_i N_i} - c_i P_i + \sum_{j \neq i} m_{ij}^P P_j - \sum_{j \neq i} m_{ji}^P P_i \end{aligned} \tag{1}$$

This model was iterated over two and three patches ($i = 1, 2, 3$). Within the model, for each patch, r_i represented the intrinsic prey growth rate, K_i represented the carrying capacity of the prey, s_i was the predator's search rate for prey, τ_i was the time taken for the predator to handle a captured prey organism, b_i indicated how much energy gained from predation went towards predator reproduction, and c_i was the predator's death rate. In all simulations, each patch was assumed to have identical values of each parameter other than K. Specifically, these were $r_i = 10$, $s_i = 0.5$, $\tau_i = 1$, $b_i = 1$ and $c_i = 0.4$, which were chosen based on previous studies of out-of-phase dynamics (Goldwyn and Hastings, 2009). For simplicity, the prey migration rates m_{ij}^N and predator migration rates m_{ij}^P were assumed to be equal within simulations. K was chosen as the parameter of habitat heterogeneity because it was shown to drive a transition from phase drift to synchronization in a two-patch system (Goldwyn and Hastings, 2009).

We set parameter values, including those of K, that would produce sinusoidal waves rather than pulse-relaxation ones. This was done in order to test for the roles of habitat heterogeneity and coupling on the emergence of PDM and amplitude varaition while controlling for the effect of pulse-relaxation oscillations (Izhikevich, 2000).

In order to produce sinusoidal waves with the non-K parameters set to the values mentioned above, K was needed to be fairly low. Hence, for the three-patch system, one of the patches (the "middle-K" patch) was assumed to have a value of 5 for K, while the other two (the "high-K" and "low-K" patches) had K-values of $5 + \Delta K$ and $5 - \Delta K$ for some specified ΔK. For the two patch system, the patches in question instead had K-values of $5 + \Delta K$ and $5 - \Delta K$. The particular choice of 5 for the average value of K across patches allowed for studying forced systems. When all other parameters are as previously specified, one patch will cross the Hopf bifurcation and will thus only oscillate as a result of being coupled to the other patches.

The system was integrated in MATLAB, using the ODE45 function. In each simulation, the system was integrated until $t = 3000$ and the results up until $t = 1000$ were thereafter discarded in order to eliminate transient dynamics. The periods of the oscillations generated by running the system with the parameters as above were determined to be approximately $5t$, with some variation depending on K. As a result, the integration step size was set to $h = \frac{3}{100}t$ (i.e. 0.001% of the simulation length) in order to minimize computation time while keeping numerical error low.

2.3.2 Measuring phase difference and amplitude modulation

The phase of each oscillator in the Rosenzweig-MacArthur system (1) was measured. To do this, the local maxima of each oscillator was identified and that oscillator's phase was assumed to linearly increase from 0 to 2π from one local maximum to the next. This method has been used in ecology (Blasius et al., 1999; Cazelles and Stone, 2003); its advantages include that it is not very computationally intensive compared to the Hilbert transform method used in Rosenblum et al., 1996 and that it does not require assuming weak coupling and weak heterogeneity, as the derivation of phase equations does (Ermentrout, 1981; Goldwyn and Hastings, 2009). Although this method neglects the behaviour of the oscillators between local maxima (Liebhold et al., 2004), the assumption of regular, sinusoidal waveforms mitigates this concern. In previous simulations, the phases extracted with the method of marker events and with other methods have had minimal differences (Pikovsky et al., 1997; Lotrič and Stefanovska, 2000).

The resulting time series of phase difference between pairs of oscillators (see figure 2.2) were analyzed for phase synchrony. If, after transient dynamics, the minimum phase difference was 0 and the maximum was 2π, indicating one oscillator steadily moving past the other owing to a faster intrinsic frequency, the oscillators were said to be exhibiting phase drift (figure 2.2a). If instead the time series of phase difference stabilized at a constant value and thus the maximum and minimum phase differences were the same, the two oscillators were said to be phase-locked (figure 2.2c), in phase if this value was 0 and out of phase if it was greater than 0. Any intermediate behaviour involving the phase difference varying, but neither oscillator overtaking the other, was deemed to be PDM (figure 2.2b). In other words, modulatory behaviour in the phase difference between two oscillators was characterized by a spread between the maximum and minimum phase differences that was greater than 0 but less than 2π.

Amplitudes were extracted from time series by identifying local minima and maxima and measuring the vertical distance from a local minimum to the succeeding local maximum. The amplitudes in a time series were said to be at equilibrium if there was no difference between the greatest and least amplitude, and non-equilibrium if there was.

2.3.3 Habitat heterogeneity and coupling strength

To evaluate the response of phase dynamics to habitat heterogeneity and coupling strength, we analyzed the plotting the pairwise spread in phase difference between oscillators in relation to variations in coupling strength (m) and interpatch heterogeneity in carrying capacity (ΔK). Parameter spaces were created for each pair of oscillators. Since the assumptions of weak coupling and weak heterogeneity were relaxed, wide ranges of values for these parameters could be looked at. Specifically, in each parameter space, ΔK took values in the range $[0, 0.5]$ in order to capture areas on both sides of the Hopf bifurcation, which occurs at $K = \frac{14}{3}$ when the other system parameters are as specified above (Kuang and Freedman, 1988). Likewise, the migration rate m took values in the range $[0, 0.045]$ in order to represent weak, intermediate and strong coupling scenarios.We additionally compared the three-patch results with a two-patch control over a similar parameter space.

2.3.4 Effects on local and regional stability

In order to test for the effect of regimes of spatial synchrony on community stability both within and among patches, the regional and average local coefficients of variation (CV) were calculated for simulated time series from parameter sets leading to phase drift, PDM and phase-locking. The oscillators in a system exhibiting PDM should have cyclical periods, and thus PDM is predicted to show non-stationary signals. To capture these, the CV needed to be taken over a window that would be long enough to include multiple periods of the oscillators, but too short to contain an entire period of the oscillators' periods. Specifically, the CV was taken over windows of 20 and 200 time steps. Regional CV (CV_{reg}) was calculated by summing the populations of a single species across patches, then taking the CV of the resulting time series within the aforementioned window, an approach consistent with past studies (Holyoak and Lawler, 1996; Romanuk and Kolasa, 2004). Average local CV (CV_{loc}) was obtained by averaging the CV from each patch in a single species over the same window (Campbell et al., 2011).

2.4 Results

2.4.1 Emergence of phase difference modulation

As expected, increasing coupling strength while holding heterogeneity constant caused the system to synchronize (figure 2.1, figure 2.4). In the three-patch system, holding coupling strength constant while increasing heterogeneity caused the same shift in reverse, also according to expectations (figure 2.1, figure 2.4). In contrast, increasing heterogeneity in the two-patch system caused phase-locked oscillators to start drifting as their proper frequencies diverged, but it also caused the low-K oscillator to approach the Hopf bifurcation and thus have lower amplitudes. This meant that the low-K oscillator could be dominated by the high-K oscillator, leading to phase-locking, with the ease of such domination depending on the coupling strength (figure 2.3).

Phase difference modulation (PDM) was found to be present in the three-patch system, and regions in parameter space where it was present were located between areas of phase drift and phase-locking (figure 2.4, figure 2.5). There existed parameter ranges where phase difference was bounded within $]0, 2\pi[$, corresponding to PDM (figure 2.4). PDM was present regardless of the pair of oscillators being compared (figure 2.4a, figure 2.4b), and this region occupied a smaller but comparable range of parameters than the region of unbounded phase difference (figure 2.5).

The two-patch system also exhibited PDM (figure 2.3), but it occurred in different and more restricted regions of parameter space compared to the three-patch one (figure 2.3, figure 2.4). Specifically, PDM occurred where the low-K oscillator was just close enough to the Hopf bifurcation to transition between drifting and locking relative to the high-K oscillator (figure 2.3). This way of arriving at PDM was not observed in three-patch metacommunities (figure 2.4).

2.4.2 Phase difference modulation in forced systems

Within the three-patch system, PDM was present in forced systems as well as systems of three autonomous oscillators. Large areas of PDM occurred where the low-K patch did not oscillate on its own but had a significant amplitude due to dispersal (figure 2.4a, figure 2.4b). This contrasts with the two-patch system, in which systems where one patch was forced by the other had the forced oscillator matching the phase dynamics of the natural oscillator, i.e. it was entrained into phase-locking (figure 2.3).

Forced systems showing PDM had stronger variation in phase difference than systems with three autonomous oscillators (figure 2.4a, figure 2.4b). The phase difference fluctuations in these forced systems could have amplitudes close to π, i.e. the high-K and low-K oscillators could cycle from being almost in phase to almost anti-synchronous.

2.4.3 Relations between phase and amplitude

There were three distinct regions in parameter space with regards to amplitude variation, which corresponded to regimes of phase dynamics (figure 2.6a, figure 2.5). In phase-drifting systems, a given oscillator's maximum amplitude showed no difference from its intrinsic amplitude but its minimum amplitude decreased with increases in coupling. For systems showing PDM, the maximum and minimum amplitude changed together, and the difference between them remained constant regardless of coupling strength. If coupling was strong enough to phase-lock the system, the maximum amplitude of each oscillator was the same as its minimum amplitude. As with phase difference, the transitions between the different regimes of period and amplitude were sharp (figure 2.5, figure 2.6).

In the three-patch system, PDM was closely tied to temporal variation in amplitude (figure 2.8). Each population in a drifting system stayed at its own intrinsic amplitude and period (figure 2.8a). In phase-locked systems, all populations converged to a common period and showed no temporal variation in period or amplitude (figure 2.8c). However, populations in systems showing PDM showed cyclic patterns of period and amplitude (figure 2.8b), dynamics not seen in the other two regimes.

2.4.4 Effect of phase difference and amplitude modulation on stability

Systems undergoing PDM showed lower average local CV, and therefore greater local stability, than either phase drifting or phase-locked systems (figure 2.7a). This is despite PDM typically being intermediate between drift and locking in terms of coupling strength and heterogeneity, and also intermediate between them in terms of regional CV. These results held regardless of the length of the window that CV was calculated over (figure 2.7b). The reason for this is that when PDM was present, all populations in the system had lower amplitudes than they did in the other two phase regimes (figure 2.8).

Systems with PDM also had the distinct signature of oscillating in both CV_{loc} and CV_{reg} (figure 2.7a), in keeping with PDM being a non-stationary phenomenon. This enabled these systems to loop around in a cycle in CV_{loc}-CV_{reg} parameter space, similar to their cyclic patterns of period and amplitude. The higher the amplitude of the fluctuation in phase difference, the larger this loop was (figure 2.7c). In contrast, the parts of parameter space governed by phase drift had highly variable CV_{reg} but comparatively little change in CV_{loc}, and phase-locked systems had no temporal variation in CV_{loc} or CV_{reg} beyond that from artifacts related to the sampling window (figure 2.7a). Greatly lengthening the window to minimize these artifacts yielded no CV variation at all in phase-locked systems (figure 2.7b), as would be expected from a system of completely synchronized oscillators.

2.5 Discussion

2.5.1 Emergence and robustness of phase difference modulation

In both two-patch and three-patch models, increasing coupling led to drifting populations being synchronized. Prior observations have shown this pattern both under the assumptions of weak coupling (Goldwyn and Hastings, 2008) and with higher rates of dispersal (Ranta et al., 1998). Field studies have also shown that connecting populations can lead to synchrony

(Haddad et al., 2014), and that populations of species with greater ability to disperse were more synchronous (Paradis et al., 1999). The same broad pattern of synchronization through coupling holds for other biological oscillators, for instance those found in neuroscience (Shuai and Durand, 1999; Ferrari et al., 2015) and epidemiology (Xia et al., 2004). Increasing heterogeneity in the three-patch system had the opposite effect, namely changing locked systems to drifting ones. This also is consistent with expectations (Goldwyn and Hastings, 2009).

Different patterns of synchronization were found in the two-patch system, with the high-K oscillator dominating the low-K one if the latter was near or past the Hopf bifurcation. In that setup, the intrinsic amplitude of the low-K patch is small or zero, and it can thus be dominated by signals from the high-K patch. The fact that coupling can alter the dynamics of oscillators near a Hopf bifurcation is well-known (Aronson et al., 1990). This is also similar to the concept of "master-slave" oscillators found in the mathematical and physical literature, where one oscillator can be entrained by another by means of unidirectional coupling (Lee et al., 2010; Pisarchik and Jaimes-Reátegui, 2015).

The presence of phase difference modulation is itself notable, as it implies that spatial synchrony can be a non-equilibrium, oscillatory phenomenon in the absence of stochastic environmental fluctuations. The convergence of drifting populations to a phase-locked state is more commonly talked about in the existing theoretical literature (Blasius et al., 1999; Goldwyn and Hastings, 2008; Wall et al., 2013; Zhang et al., 2015), and discussion of any temporal changes in synchrony is rare in field-based work (Koenig and Liebhold, 2016). However, our results suggest a new way of thinking about population synchrony as a dynamic process.

2.5.2 Entrainment and forcing

In a two-patch metacommunity, forced oscillations led to entrainment and phase-locking. However, in a three-patch system, forcing of one community leads to complex interactions between forced and autonomous oscillators and results in PDM over a broad range of heterogeneity and dispersal values. This suggests that patches at equilibrium may play an important role in maintaining stability in metacommunities.

Unconditional sink populations by definition approach equilibrium (i.e. zero) in the absence of dispersal (Pulliam, 1988; Loreau et al., 2013) and provide a limiting case for our research on PDM with forced oscillations. Much of the existing source-sink literature focuses on systems where all patches are at equilibrium, but many examples of source-sink landscapes with fluctuating dynamics have been identified (Loreau et al., 2013). Indeed, theory predicts that sink populations with regular oscillations can be driven by migration from sources (Howe et al., 1991; Holt et al., 2003; Schreiber et al., 2006; Amarasekare, 2016). As illustrated by our findings that populations at equilibrium can induce PDM by receiving migration from multiple patches, it is possible that the presence of sinks will make a larger metacommunity more stable, although more research in this area is required.

2.5.3 Coupled phase-amplitude dynamics in strongly coupled metacommunities

We found a strong relationship between the phase dynamics present and the behaviour of the amplitudes of the populations in a system. In systems undergoing phase drift, populations that were out of phase could temporarily dampen each other's amplitudes, a phenomenon referred to as immigration-local abundance decoupling (Briggs and Hoopes, 2004; Amarasekare, 2008). Within the regime of phase drift, greater coupling increased the strength of this effect (figure 2.6). Systems with PDM also showed variation in amplitude over time: the amplitudes of oscillators rose and fell in limit cycles similar to what was concurrently happening with phase difference (figure 2.8b). This was caused by the oscillators moving closer to and farther away from synchrony, and hence the strength of the damping varying temporally.

In contrast, increasing coupling to values capable of phase-locking the system caused the end of temporal amplitude variation. This is consistent with past findings on groups of oscillators entraining each other's amplitudes via strong coupling (Kuramoto and Nishikawa, 1987). Previous studies under the assumptions of weak coupling have found dynamics with uniform phase and chaotic amplitude in both bitrophic (Goldwyn and Hastings, 2009) and tritrophic models (Blasius et al., 1999), but under strong coupling we did not find dynamics of that nature.

2.5.4 A dynamic theory of coupled local-regional stability

Phase difference modulation has the potential to reduce variability by damping the amplitudes of both local and regional time series (figure 2.7a). In coupled oscillatory systems, the amplitudes of local time series can be damped via coupling of out-of-phase oscillators (Briggs and Hoopes, 2004), and variability in regional averaged time series can be damped by statistical averaging (Doak et al., 1998; Cottingham et al., 2001). Our results show that systems undergoing PDM combine both local damping and regional averaging, leading to fluctuations between local and regional stability in metacommunities.

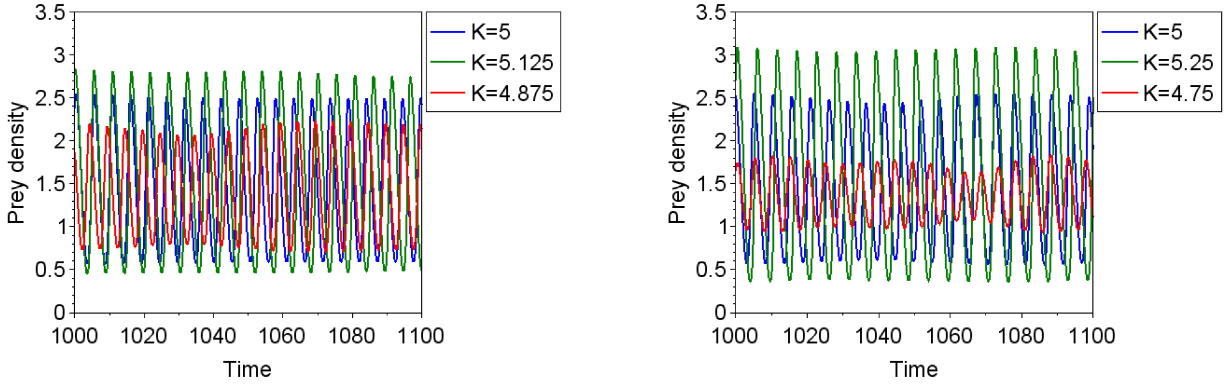
We have shown that phase difference modulation can provide more local stability than phase drift or phase-locking (figure 2.7a). At regional scales, the consensus is that out-of-phase dynamics maximize stability, while in-phase dynamics lead to greater regional variability and extinction risk (Hanski, 1998). Our findings revealed oscillators undergoing PDM that were always at least somewhat out of phase, and reached high regional stability when phase difference approached π. Hence, our work suggests that drifting systems may not be the most stable type. The rationale for this is that while the oscillators in a drifting system may damp each other via the decoupling of immigration and local abundance (Briggs and Hoopes, 2004; Gouhier et al., 2010), and thus approach steady-state dynamics (Amarasekare, 2008), this effect is lessened as the drifting oscillators become more synchronous and zero when they are in phase.

2.6 Conclusion

In this paper, we have shown that synchrony of phase and amplitude can be viewed as non-stationary properties, and improved our understanding of spatial synchrony in ecology. Our investigation of phase difference modulation has established it as a phenomenon robust to strong coupling and heterogeneity. Additionally, we have found phase difference modulation to damp amplitudes of local populations in a metacommunity. These coupled phase-amplitude dynamics lead to similarly coupled fluctuations in local and regional stability, and induce greater local stability. The coupling of phase and amplitude dynamics provides for a distinct signal of phase difference modulation, which should aid its identification in the field.

2.7 Figures

Figure 2.1: Example time series of systems of prey populations for varying levels of migration and habitat heterogeneity. When heterogeneity and migration are both low, the oscillators have frequencies close to their intrinsic ones and changes in phase difference are gradual. Increasing heterogeneity leads to greater interpatch differences between the oscillators' intrinsic frequencies and amplitudes. Stronger migration leads to a phase-locked system where all oscillators' periods are identical.



(a) Low migration and heterogeneity: $\Delta K = 0.125$, $m_{ij} = 0.005$

(b) Low migration, high heterogeneity: $\Delta K = 0.25$, $m_{ij} = 0.005$

(c) High migration and heterogeneity: $\Delta K = 0.25$, $m_{ij} = 0.03$

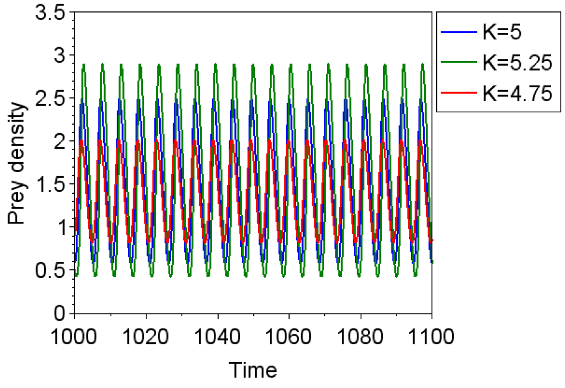
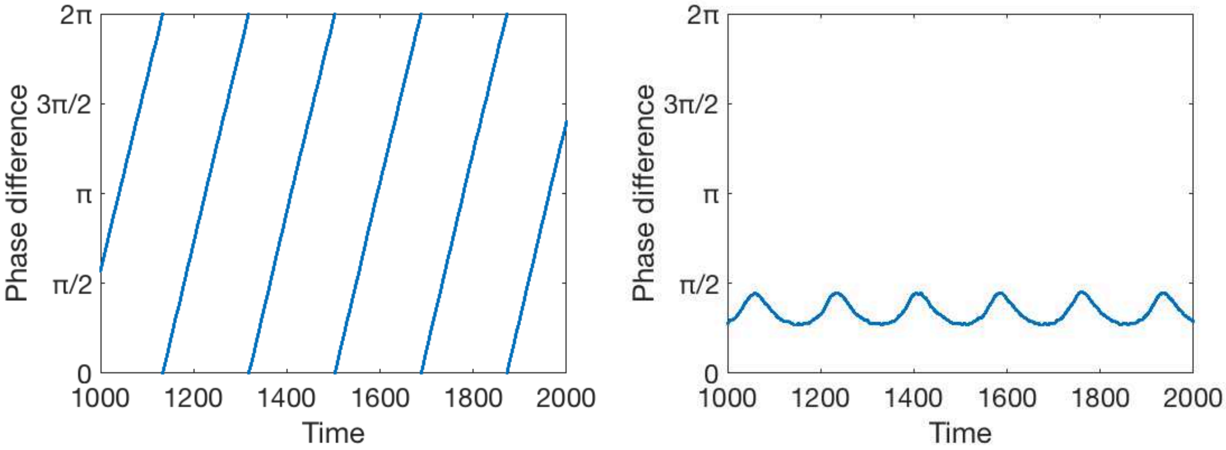
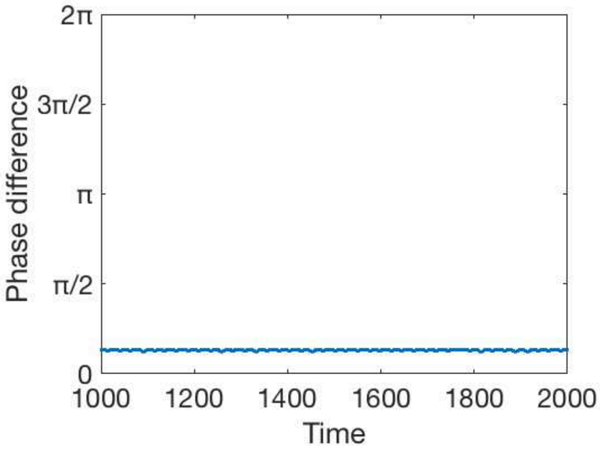


Figure 2.2: Example time series of phase difference between two given oscillators, showing the three different kinds of dynamics. $\Delta K = 0.1$ in each time series. Absent migration, the oscillators' intrinsic frequencies are dominant, causing the faster one to steadily move past the slower one and their phase difference to increase linearly. With strong migration, phase-locking occurs: the two oscillators are always at the same point in phase relative to one another, so phase difference is constant. However, with intermediate migration levels, the oscillators move closer to and farther away from each other in a cycle without one ever overtaking the other. This is phase difference modulation.



(a) Phase drift: $m_{ij} = 0$

(b) Phase difference modulation: $m_{ij} = 0.012$



(c) Phase-locking: $m_{ij} = 0.02$

Figure 2.3: Spread in phase difference (maximum minus minimum) between the patches in the two-patch system as a function of migration and heterogeneity. The green line represents the amount of heterogeneity necessary for the low-K patch to cross the Hopf bifurcation. Areas in white (with a spread of 2π) are where one oscillator has overtaken the other at least once, indicating phase drift. Grey areas are where the phase difference between the two oscillators never changes, i.e. they are phase-locked. Any other colour represents areas where the phase difference changes over time but neither oscillator overtakes the other, defined as PDM.

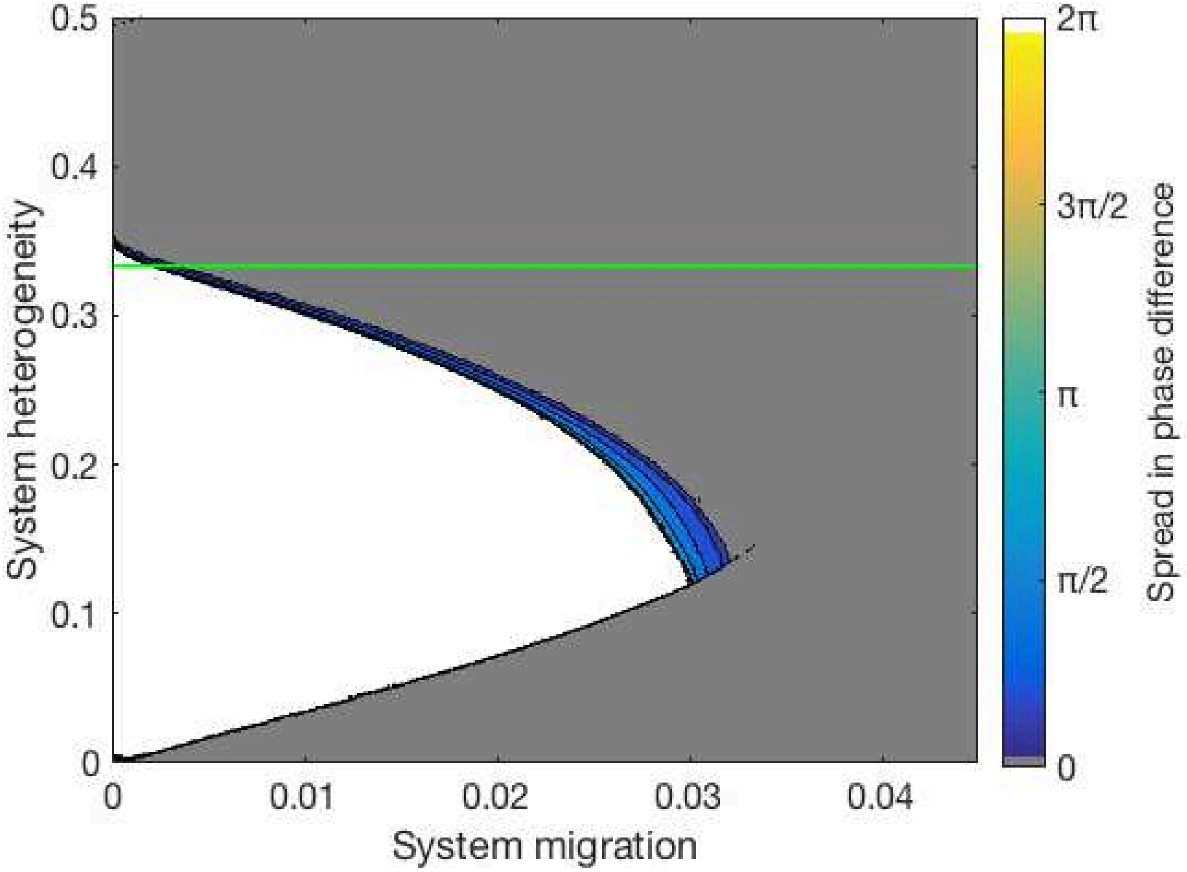
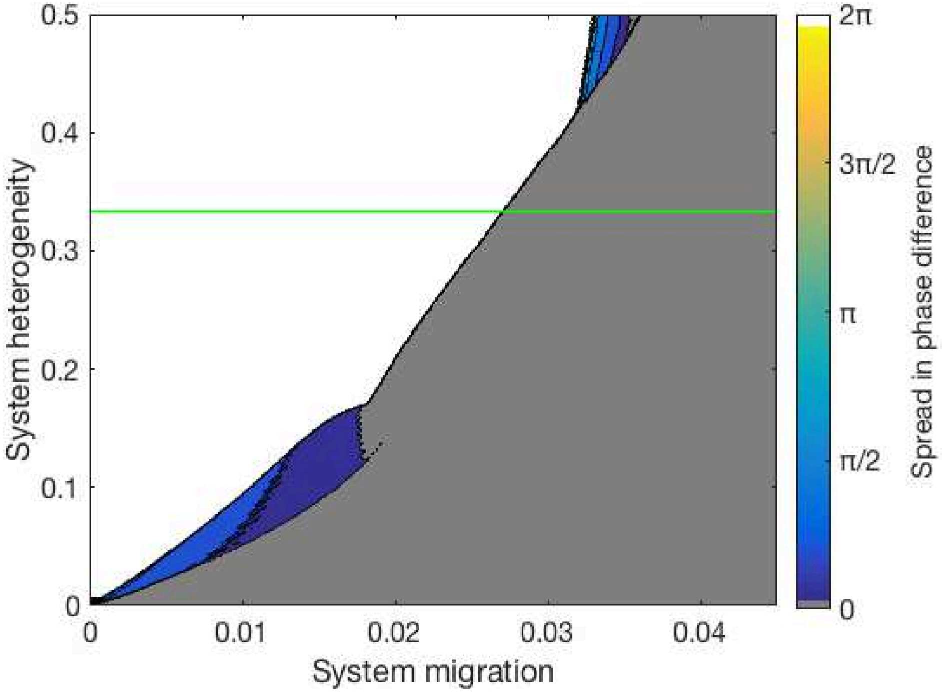


Figure 2.4: Spread in phase difference between two given patches in the three-patch system as a function of migration and heterogeneity. The green line represents the amount of heterogeneity necessary for the low-K patch to cross the Hopf bifurcation.

(a) Middle-K versus high-K patches



(b) High-K versus low-K patches

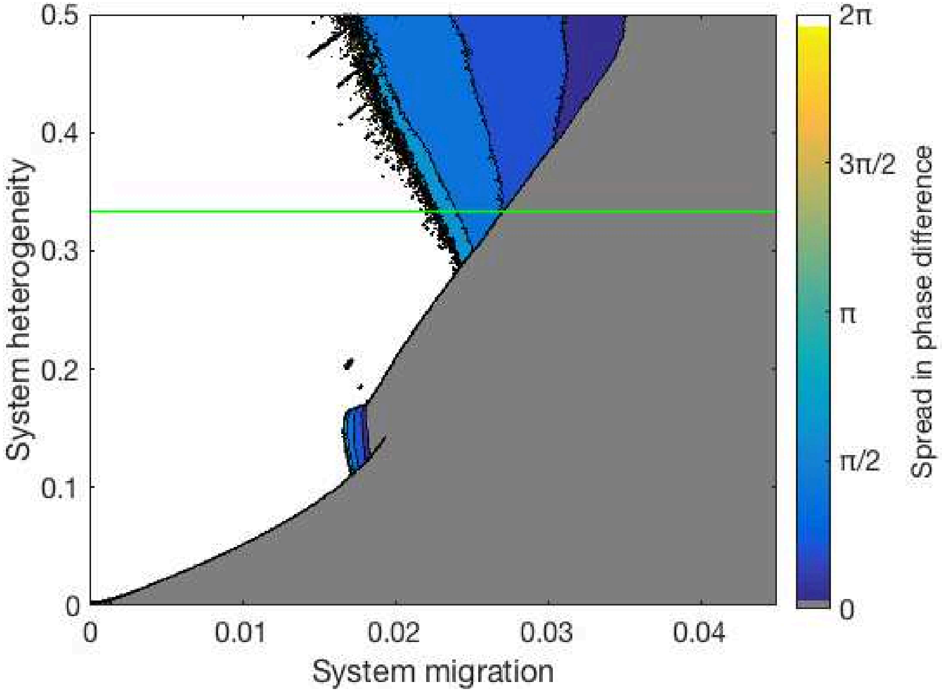


Figure 2.5: Bifurcation plot of maximum and minimum phase difference between the middle-K and high-K patches as a function of coupling strength, with $\Delta K = 0.1$. This graph is equivalent to a horizontal slice through figure 2.4a; the three regimes of phase drift, PDM and phase-locking are visible from left to right.

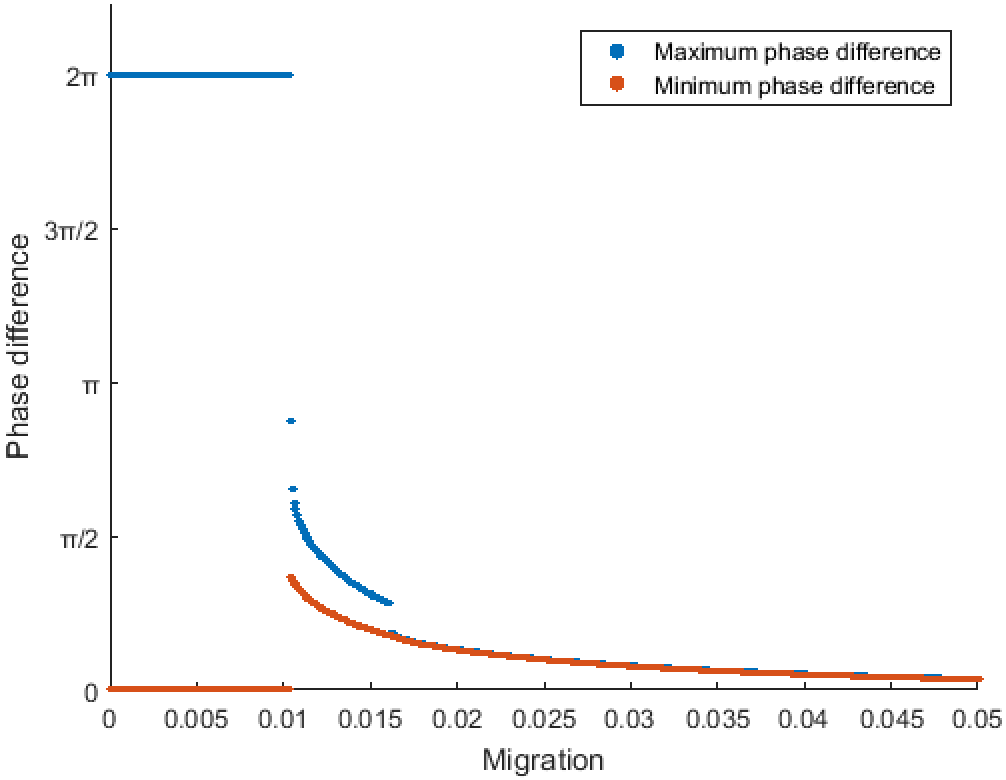
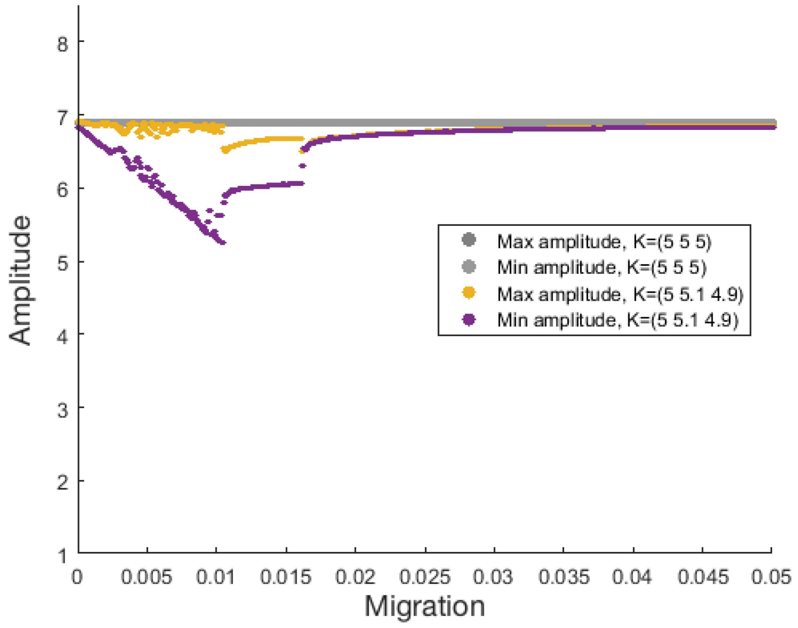


Figure 2.6: Bifurcation plots of maximum and minimum amplitude and period for the middle-K patch as functions of coupling strength. $\Delta K = 0.1$, as in figure 2.5, and the transitions between amplitude and period regimes fall in the same places as those between phase drift, PDM and phase-locking. The case where $\Delta K = 0$ (all oscillators have identical intrinsic dynamics) is included for reference.

(a) Bifurcation of amplitude



(b) Bifurcation of period

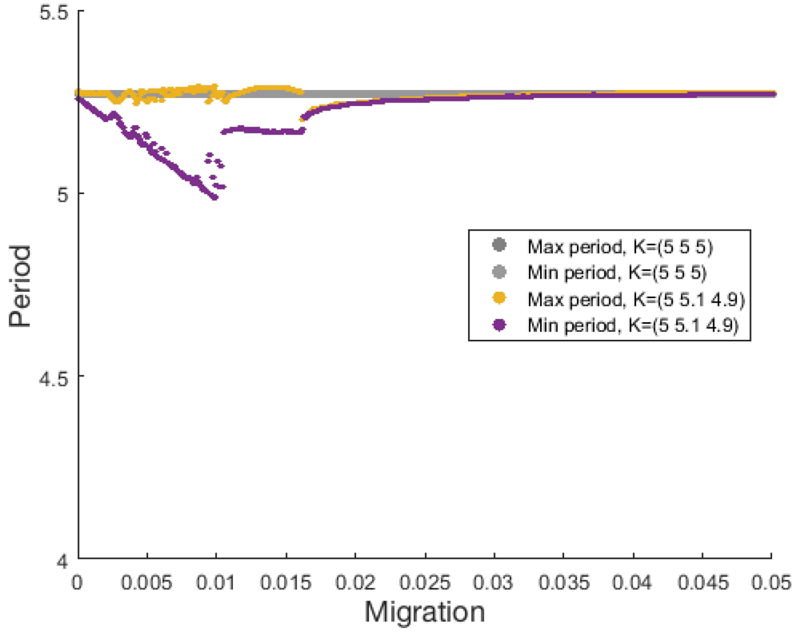
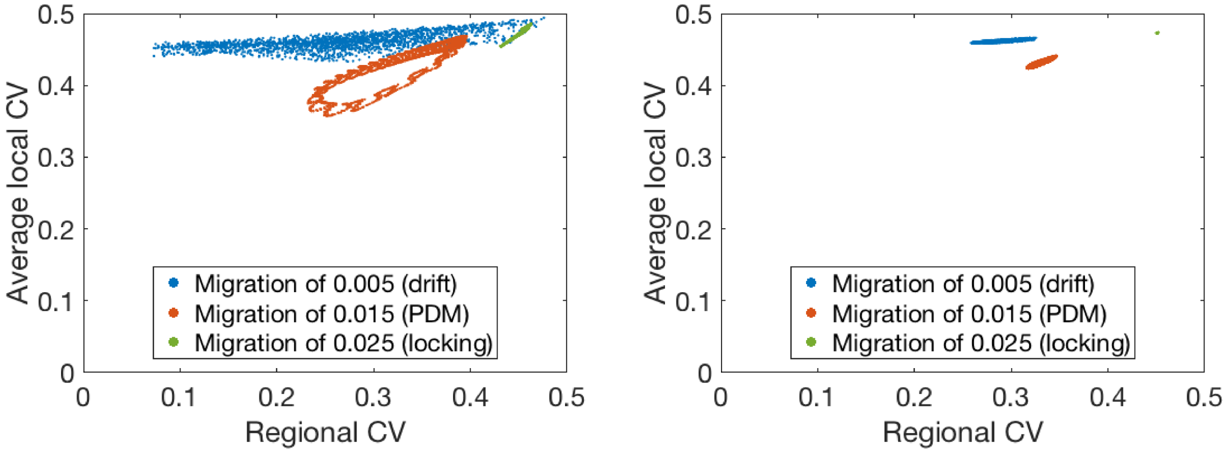


Figure 2.7: Regional and average local CV over time in the three-patch system for a variety of parameter values, representing different types of phase dynamics. $\Delta K = 0.125$ in all scenarios unless otherwise noted. A drifting system has its oscillators move in and out of phase with each other, which translates to times of both high and low regional variability. However, the oscillators therein largely maintain their heterogeneous intrinsic frequencies, which keeps local variability roughly constant. In a phase-locked system, all oscillators have the same period and thus how synchronous the oscillators are never changes. Because of this, both local and regional CV are unchanging in phase-locked systems (discouting window-related artifacts). A system with PDM, however, has a cyclic pattern of local and regional CV that mirrors its non-stationarity in phase difference.



(a) Rolling window 20 time steps long

(b) Rolling window 200 time steps long

(c) Autonomous versus forced oscillations

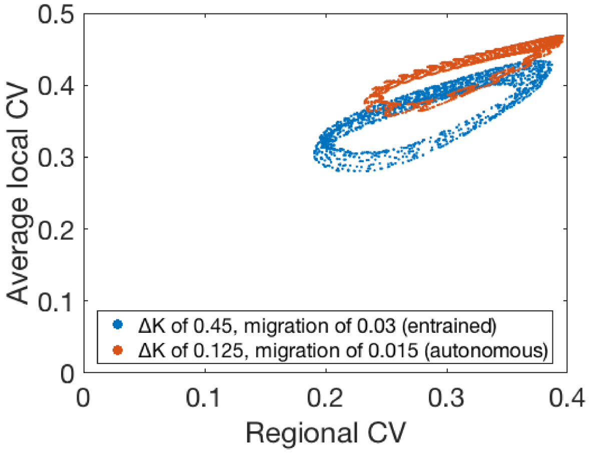
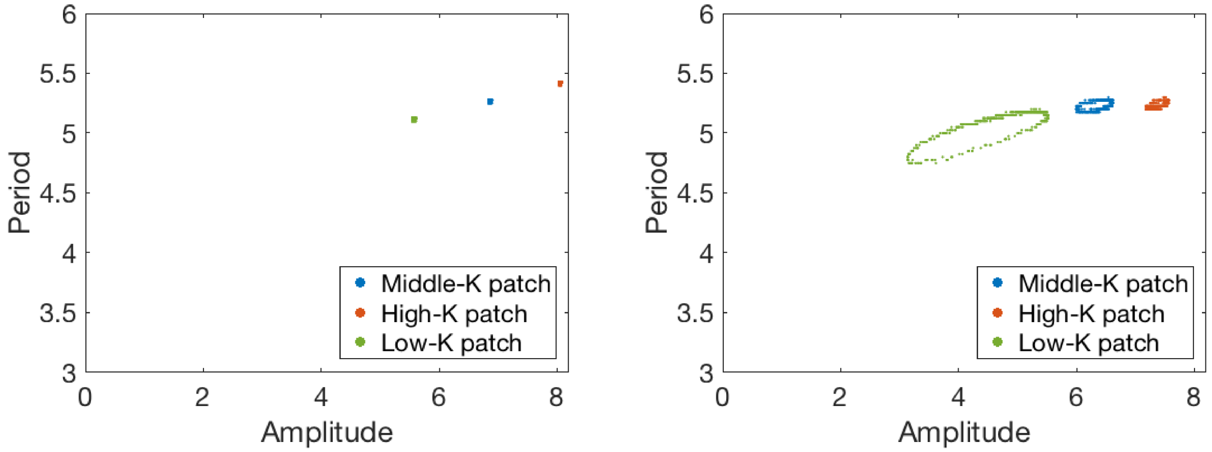
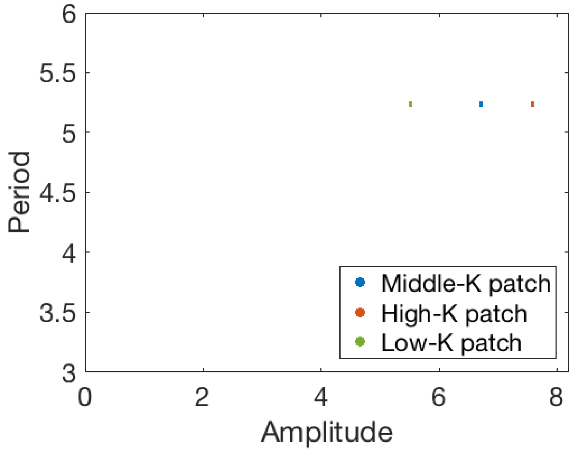


Figure 2.8: Amplitudes and periods of populations in the three-patch system over time. $\Delta K = 0.1$ in each graph. Cyclic period-amplitude signals occur solely in the case of phase difference modulation, as in figure 2.7. In drifting and phase-locked systems the periods and amplitudes of oscillators are fixed, meaning the graphs of period and amplitude over time in these systems collapse to a single point. The fact that all oscillators in a phase-locked system have the same period is also evident.



(a) Phase drift: $m_{ij} = 0$

(b) Phase difference modulation: $m_{ij} = 0.012$



(c) Phase-locking: $m_{ij} = 0.02$

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3 Conclusion

Synchrony in natural systems is vital in influencing their stability and extinction risk. Migration has been identified as a driver of synchronization, both in nature (Paradis et al., 1999; Haddad et al., 2014) and in theoretical literature (Blasius et al., 1999; Goldwyn and Hastings, 2008). Moreover, several other theoretical predictions on synchrony have been made, such as its hampering by habitat heterogeneity (Goldwyn and Hastings, 2009) and travel time between different patches (Wall et al., 2013; Zhang et al., 2015). However, much of the existing theoretical literature focuses on small (i.e. two-patch) metacommunities, suggesting that many phenomena that primarily occur in more complicated systems are yet to be uncovered. Having a greater understanding of the synchrony-related patterns that emerge in larger and more lifelike systems will enable us to make better, more informed predictions, ultimately enhancing the knowledge of theoreticians and field biologists alike.

The goal of this project was to observe one such theoretically predicted phenomenon, phase difference modulation, incorporate it into the paradigm of synchrony, and determine how it affects ecosystem stability. To do this, I have simulated ecological time series and extracted their phase dynamics, then ascertained the effects of said dynamics on the system's local and regional variability. Mathematical results in metacommunity theory have predicted dynamics midway between full synchronization and drifting populations when interpatch migration and habitat heterogeneity are both present but not strong (Blasius et al., 1999). My results have shown that under similar conditions (intermediate levels of migration and habitat heterogeneity) in systems of three patches, phase difference modulation is possible. The ability thus expressed of synchrony to vary over time has consequences of how we measure it in the field, as measuring the evolution of synchrony over time is currently rare (Koenig and Liebhold, 2016). I have also shown that systems where one patch is at equilibrium but responds to fluctuations in another connected patch can show the same dynamics. This suggests that phase difference modulation can play an important role across varied landscapes, particularly in connected networks of sources and sinks.

In addition to predicting the existence of phase difference modulation, my work also has put it in the framework of synchronization and stability. It is known that asynchronous populations are more stable than synchronous ones, with anti-synchronous populations at the apex of stability. In terms of regional stability, my results support this. However, I found that phase difference modulation produced the lowest levels of average local variability, and thus the highest local stability, of any of the regimes of synchrony or asynchrony examined. Additionally, I showed that a system undergoing phase difference modulation will have a distinctive signature in terms of variability: in such a system, both local and regional CV were shown to oscillate over time. This means that variability, like synchrony, is best viewed as a dynamic property. Related to variability is temporal change in amplitude, which I have also shown is linked to phase difference modulation. If phase difference modulation is to be found in a metapopulation in nature, looking for varying amplitudes may be an easy way to discover it.

3.1 Phase difference modulation in the field

In ecology, it is important for theoretical and field literature to be in accordance (Donohue et al., 2016). Phase difference modulation represents a new paradigm that has not been tested in the wild yet, so a logical next step from our work would be to do so. In the past, field studies dealing with stability have typically measured it using either correlation-based measures or spectral analysis of time series (Defriez et al., 2016), including when explicitly testing theoretical predictions (Paradis et al., 1999). These methods are not optimal for detecting PDM, as they do not explicitly measure phase as a function of time. Hence, in order to properly capture temporal variation in phase difference across populations in a metacommunity, different techniques should be used. The method of marker events (Glass et al., 1983; Pikovsky et al., 1997; Lotrič and Stefanovska, 2000) used in our work is easy to implement in the field, as it only involves identifying the local maxima of a time series and little computation beyond that. Most importantly with regards to PDM, it measures phase over time rather than just as a stationary signal. Therefore, if PDM is to be measured in the field, we recommend the method of marker events (or others that measure phase) to do it.

Testing for PDM could also be done with existing time series from the field. Because of the nature of PDM, identifying it would require time series from populations in a metacommunity (so they could be compared) that were long enough to go through several oscillations. Metacommunity-related studies have been done on, for instance, populations of mosquitoes (Ellis et al., 2015), bacteria (Cadotte et al., 2006) and crayfish (Almeida et al., 2014); bacteria and invertebrates may be ideal for uncovering PDM as their shorter generation times mean that many population cycles can be observed in short time frames.

In our work, we tested for the presence of PDM with a relatively straightforward patch topology, namely three globally connected patches. Altering that topology may have an affect on how and when PDM arises. This is part of a broader question of how connectivity affects synchrony, which has been looked at in the field (Haddad et al., 2014) as well as in theoretical work (Yeakel et al., 2014). As with the theory behind PDM, this is an area where mathematical findings can be readily adapted to ecological settings. For instance, the concept of "master-slave" oscillators, where one oscillator entrains another by way of unidirectional coupling (Lee et al., 2010; Pisarchik and Jaimes-Reátegui, 2015), has an ecological analogue in one-way migratory flows, such as riparian organisms moving downstream. A set of oscillators arranged in a ring, as in (Ermentrout and Kopell, 1991), is similar to a group of subpopulations that surround a large geographical feature such as a mountain or lake. While some work has been done on how the topology of a metacommunity affects synchronization and stability, as mentioned above, the question as specifically applied to PDM remains open.

3.2 Integration into metacommunity theory

The synchrony or asynchrony of populations has long been a focus of metapopulation studies (Elton and Nicholson, 1942). This has typically involved calculating spatial autocorrelations (e.g. Paradis et al., 1999; Buonaccorsi et al., 2001; Morton et al., 2016; Oliver et al., 2017; Tredennick et al., 2017), treating synchrony as a value varying with distance but not time (Liebhold et al., 2004). Loreau and de Mazancourt (2013) have produced the following formula for degree of synchrony, ϕ_N, of an arbitrary number of sampled populations N_i, for N_T the total biomass:

$$\phi_N = \frac{\sigma^2_{N_T}}{\left(\sum_i \sigma_{N_i}\right)^2}$$

However, an important finding in our research is the non-stationarity of synchrony. Temporal changes in synchrony are rarely measured in the field (Koenig and Liebhold, 2016), but our work has shown that synchrony is dynamic and using stationary metrics to quantify it leaves out important information. This is especially pertinent for natural systems with high levels of variability, given the association of CV with ecosystem instability and extinction. Correlation-based measures also neglect the possibility of synchrony or anti-synchrony on multiple timescales (Defriez et al., 2016). Their ability to detect systems that are phase-locked out of phase is also poor (Liebhold et al., 2004): the patches in these may show similar (albeit phase-shifted) dynamics but have correlations near zero. With these factors in mind, we recommend that field ecologists use other metrics to measure synchrony. As mentioned earlier, the method of marker events that we use is easily implementable given field data, requires little computation, and has the added bonus of representing the phase of an oscillatory population as a function of time. Other methods based on spectral analysis, which also represent an improvement over correlation-based measures, have been applied as well (Grenfell et al., 2001; Sheppard et al., 2016; Defriez et al., 2016). Either of these would represent an improvement over correlation-based metrics.

Time series in ecology tend to be short (Bence, 1995; Clark et al., 2015), and those used to determine synchrony are no exception (Turchin and Taylor, 1992). The preference for longer time series has already been noted in the metacommunity literature (Pandit et al., 2009), and this indeed holds when synchrony is considered. If patches in a metapopulation are assumed to move in and out of phase with one another in a cyclical motion, calculating synchrony based on a short time series may mask the presence of dissimilar dynamics outside the sampling window. Attempts have been made to reconstruct hypothesized dynamical systems behind field time series and thus predict future dynamics with mathematical rigour (Turchin and Taylor, 1992). This had the effect of lengthening relatively short time series and unveiling the potential for complex oscillatory patterns, which may feature PDM. Because of the potential for changes in synchrony to emerge with time, we strongly suggest that researchers studying metacommunities in the field produce long time series, either by mathematical reconstruction or by sampling for longer periods of time.

Regional stability is important in metacommunity research, and the portfolio effect is one of the concepts dealing with regional stability that is mentioned the most (e.g. Tilman et al., 2006; Schindler et al., 2010). Previously, the portfolio effect has been invoked when talking about uncorrelated systems (Doak et al., 1998). The strength of the portfolio effect in a system with PDM would change over time, meaning that as with other phenomena that depend heavily on synchrony, the portfolio effect should be looked at as a dynamic quantity. As the stability of ecosystems has been used in formulating policy decisions (Donohue et al., 2016), accurately characterizing fluctuating variability is imperative for more than just academic reasons. Additionally, our work has shown that systems exhibiting PDM have greater local stability than those in other phase regimes, including phase drifting (i.e. uncorrelated) systems. This suggests that within a metapopulation, average local variability should be looked at in tandem with regional variability.

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