The emergence of phase asynchrony and frequency modulation in metacommunities

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Abstract
Spatial synchrony can summarize complex patterns of population abundance. Studies of phase synchrony predict that limited dispersal can drive either in-phase or out-of-phase synchrony, characterized by a constant phase difference among populations. We still lack an understanding of ecological processes leading to the loss of phase synchrony. Here, we study the role of limited dispersal as a cause of phase asynchrony defined as fluctuating phase differences among populations. We adopt a minimal predator-prey model allowing for dispersal-induced phase asynchrony, and show its dependence on species traits. We show that phase asynchrony in a homogeneous metacommunity requires a minimum of three communities and is characterized by the emergence of regional frequency modulation of population fluctuations. This frequency modulation results in spectral signatures in local time series that can be used to infer the causes and properties of metacommunity dynamics. Dispersal-induced phase asynchrony extends the application of ecological theories of synchrony to nonstationary time series, and is consistent with observed spatiotemporal patterns in marine metacommunities.

Keywords Phase synchrony · Metacommunities · Spatial dynamics · Predator-prey dynamics · Self-organization · Weakly coupled oscillators

Introduction
A central challenge in ecology is to predict patterns of population abundance across spatial scales, especially for non-equilibrium dynamics. Predator-prey communities are known to exhibit stable cyclic dynamics, but our understanding of emerging patterns in metacommunities consisting of oscillating predatory-prey communities is still incomplete. The concept of spatial synchrony, the lack thereof, and the mechanisms of its emergence have provided an appropriate level of simplification to understand how spatiotemporal patterns affect population persistence (Abbott 2011), species coexistence (Lampert and Hastings 2016), community stability (Koelle and Vandermeer 2005), and ecosystem function (Marleau et al. 1777) over landscapes. Our work provides novel insights into drivers of asynchrony and identifies signatures in time series that distinguish these mechanisms from previously known ones.

In ecology, spatial synchrony can be measured as covariance among time series of population density (Koelle and Vandermeer 2005; Lande et al. 1999; Liebhold et al. 2004). When time series contain periodic components (Turchin 2003), synchrony can also be studied by extracting their phase, i.e., the angular position of the variable along each cycle. Spatial synchrony can then be measured (Bjørnstad et al. 1999; Blasius et al. 1999) or predicted (Goldwyn and Hastings 2007) as the phase difference among locations. Phase synchrony is defined as a constant phase difference among time series (i.e., phase-locking) (Hoppensteadt and Izhikevich 1997), which includes the special case of in-phase synchrony (zero phase difference). Phase synchrony is studied by contrasting in-phase (spatially homogeneous) to out-of-phase (spatially heterogeneous) phase-locked synchrony, and it has become central to the study of dispersal-driven heterogeneity in metapopulations and metacommunities (Blasius et al. 1999; Cazelles and Boudjema 2001).
Ecological theories of synchrony predict that limited dispersal, predator movement, or correlated environmental variation can lock identical, distant communities into in- or out-of-phase synchrony (Liebhold et al. 2004; Bjørnstad et al. 1999). However, natural (Henden et al. 2009; Cazelles et al. 2008) and model (Jansen and de Roos 2000) systems often fail to result in phase-locking. For example, a marine metacommunity model for *Mytilus californianus* (California mussel) distribution over 1800 km along the North East Pacific coast was used to simulate spatially coupled, identical locally oscillatory dynamics. The system did not phase lock but exhibited spatiotemporal variations in phase differences even though the coupling strength was in a regime where phase-locking would be expected. These spatiotemporal patterns were used to validate the model against short-term (7 years) spatial data (Gouhier et al. 2010), but we still lack a general understanding of ecological processes causing deviations from in- or out-of-phase-locking and non-stationary dynamics of phase difference.

With the above definition of phase synchrony (illustrated for two coupled communities in Fig. 1a, b), we can define phase asynchrony as a deviation from phase-locking. One form of phase asynchrony can arise from spatial heterogeneity when communities with different natural frequencies of local oscillations are (weakly) coupled and the heterogeneous frequencies persist (Fig. 1c, d). This asynchrony can be synchronized by (sufficiently strong) dispersal (Koelle and Vandermeer 2005; Blasius et al. 1999), or by a common environmental forcing (Cazelles and Boudjema 2001). A different form of phase asynchrony can arise when spatially heterogeneous environmental fluctuations modulate the frequencies of local population fluctuations (Allstadt et al. 2015) (Fig. 1e, f). Frequency modulation has been studied in chemical and physiological systems (Hoppensteadt and

![Fig. 1](https://example.com/fig1.png)
Izhikevich 1998; Kim et al. 1998; Baesens et al. 1991; Emelianova et al. 2013), and can more generally emerge from symmetric (Ashwin et al. 1990) and asymmetric (Montbrío et al. 2004) coupling. Here, we study how species dispersal and interactions can lead to phase asynchrony by frequency modulation with no environmental variations.

Our work extends current theories of ecological synchrony to dispersal-induced phase asynchrony. We study this phenomenon via a minimal dynamical metacommunity model consisting of three identical, spatially coupled predator-prey systems. We use two complementary approaches: one based on the theory of phase equations for weakly coupled networks and bifurcation theory, the other based on numerical simulations of the dynamical equations, and guided by the bifurcation results. We also characterize statistical properties of time series of asynchronous metacommunities and reveal signatures of nonstationary (modulated) phase differences. We finally illustrate the robustness of frequency modulation in larger systems by using the marine metacommunity model mentioned above. Our model predicts the dependence of dispersal-induced asynchrony on species traits, and could provide a statistical signature of ecological processes across scales. The latter aspect is particularly important since inferring causes of asynchrony from time series can be challenging: phase asynchrony leads to nonstationary time series and to spatial patterns that deviate from signatures of phase-locked systems such as regular traveling waves. Our results contribute to a more general ecological theory of synchrony, and in particular establish dispersal as a potential driver for spatial phase asynchrony, which has important consequences for rescue and compensatory effects between populations.

**Metacommunity model and phase equations**

We investigate spatial phase synchrony among weakly coupled predator-prey communities characterized by periodic fluctuations in their abundance. To study the stability of phase synchrony and the emergence of asynchrony, we consider three weakly coupled habitats as the minimum extension from previous studies on two-patch metacommunities (Goldwyn and Hastings 2007; Zhang et al. 2015). On patch $i$, we write the density of prey ($h_i$) and predator ($p_i$) as the vector $X_i = (h_i, p_i)^T$. We adopt the Rosenzweig-MacArthur model with logistic regulation of prey growth and saturating functional response of the predator. In nondimensional terms, the model on patch $i$ reads $dX_i/dt = F(X_i)$, where

$$F(X_i) = \left( \frac{1}{\epsilon} \left( h_i (1 - \alpha h_i) - \frac{h_i p_i}{1 + h_i} \right) \cdot \frac{h_i p_i}{1 + h_i} - \eta p_i \right)^T.$$  

Here, $\epsilon$ denotes a relative time scale of prey growth, $\alpha$ is the strength of prey-density regulation, and $\eta$ is the relative scale of predator death (for details please see Zhang et al. 2015).

Finally, we assume that all three habitats are identical and that dispersal is well-mixed and linear (density-independent) among all three local communities. Then, we study the following nondimensionalized model:

\[
\begin{align*}
\frac{dX_1}{dt} &= F(X_1) + \delta \left( \frac{X_2}{2} + \frac{X_3}{2} - X_1 \right), \\
\frac{dX_2}{dt} &= F(X_2) + \delta \left( \frac{X_1}{2} + \frac{X_3}{2} - X_2 \right), \\
\frac{dX_3}{dt} &= F(X_3) + \delta \left( \frac{X_1}{2} + \frac{X_2}{2} - X_3 \right),
\end{align*}
\]

(1)

where $\delta$ denotes the (relative) time scale of dispersal and $F$ describes the local dynamics as above.

We study the question of synchrony or asynchrony in this model in two complementary ways: via direct numerical simulations of system (1) and via qualitative analysis of the corresponding phase-difference equations. To obtain the phase-difference equations from our model equations, we follow the theory for weakly connected networks (Hoppensteadt and Izhikevech 1997) and previous work on predator-prey dynamics (Goldwyn and Hastings 2007; Zhang et al. 2015). We assume that parameters for the uncoupled Rosenzweig-MacArthur system $dX_i/dt = F(X)$ on each patch are chosen such that there is an exponentially stable $T$-periodic solution $\gamma = \gamma(t) \in \mathbb{R}^2$. We denote the frequency of this orbit by $\Omega = 2\pi/T$.

We denote by $\phi_i \in [0, 2\pi)$, $i = 1, 2, 3$ the phase variable on the $i$th patch. When the dispersal rate $\delta$ is small, the phase variables satisfy the following phase equations:

\[
\begin{align*}
\frac{d\phi_1}{dt} &= \frac{1}{2} H(\phi_2 - \phi_1) + \frac{1}{2} H(\phi_3 - \phi_1), \\
\frac{d\phi_2}{dt} &= \frac{1}{2} H(\phi_1 - \phi_2) + \frac{1}{2} H(\phi_3 - \phi_2), \\
\frac{d\phi_3}{dt} &= \frac{1}{2} H(\phi_1 - \phi_3) + \frac{1}{2} H(\phi_2 - \phi_3),
\end{align*}
\]

(2)

where the interaction function $H$ is given by

\[
H(x) = \frac{1}{T} \int_0^T \dot{\gamma}(t) \cdot (\gamma(t + x/\Omega) - \gamma(t)) dt.
\]

(3)

with $\dot{\gamma}(t)$ solving the system

\[
\frac{d\dot{\gamma}(t)}{dt} = -DF(\gamma(t))^T \dot{\gamma}(t)
\]

(4)

\[
\dot{\gamma}(t) \cdot \gamma'(t) = 1
\]

(5)

DF is the derivative matrix of the vector field $F$, evaluated at the periodic orbit $\gamma(t)$. The superscript $T$ refers to the transpose of the matrix, $\cdot$ indicates the dot product, and $\gamma(t)$ is the periodic solution on a single patch.
We can define two phase differences as $\psi_i := \phi_{i+1} - \phi_i$, $i = 1, 2$ between patches $i$ and $i+1$. These variables satisfy the equations

\[
\frac{d\psi_1}{dt} = \frac{1}{2}[H(-\psi_1) + H(\psi_2) - H(\psi_1) - H(\psi_1 + \psi_2)],
\]
\[
\frac{d\psi_2}{dt} = \frac{1}{2}[H(-\psi_1 - \psi_2) + H(-\psi_2) - H(-\psi_1) - H(-\psi_2)].
\]

These are the equations that we will study in detail via stability analysis.

**Model analysis**

We begin our model analysis with the phase-difference equations (6) and use the results as a guide for intensive numerical simulations of the full model system (1). We focus on $\eta$ as a bifurcation parameter for comparability with previous studies. We more specifically chose the range $0.15 < \eta < 0.4$ while all other parameters are fixed ($\epsilon = 0.1$, $\alpha = 0.4$, Fig. 2). Decreasing $\eta$ over that range contributes to a separation of temporal scales between predator and prey growth by decreasing predator mortality and/or increasing attack rate relative to prey growth. In a single patch, this separation leads to pulse-relaxation-type oscillations (Goldwyn and Hastings 2007). In a two-patch system, pulse-relaxation oscillations are known to promote the emergence of bistability: stable out-of-phase and in-phase synchronous states coexist (Goldwyn and Hastings 2007). We thus study how model parameters relating to traits of predators and prey influence phase asynchrony in a three-patch system.

**Phase-difference equations**

We summarize the most important results of our stability analysis of the phase-difference equations (6) in the bifurcation diagram in Fig. 2a. We explain the diagram and refer to the Appendix for details and calculations as well as further illustrations.

The phase-difference equations have $(0, 0)$ as a steady state, representing the “in-phase-locked” scenario. This state exists independently of parameter values, and it is locally stable for the range of parameter values in our study. It is represented by the thick line at the bottom of the bifurcation diagram.

When exactly one of the phase differences is zero initially, it will remain zero for all times. By symmetry, the model has three of these “two in-phase” states, independent of parameters, and they are unstable when the in-phase-locked states are stable. We excluded them from Fig. 2a but show them in the detailed plots in the Appendix.

The most important state in our study is that of equal phase differences between all three oscillators, sometimes called “traveling-wave state” (Goldwyn and Hastings 2011) or “rotating wave” (Ashwin et al. 1990). By symmetry, there are two of these states at $(2\pi/3, 2\pi/3)$ and $(4\pi/3, 4\pi/3)$. They are represented by the upper line in the bifurcation diagram in Fig. 2a. These states are foci that can be stable (thick line) or unstable (thin line), depending on parameter values. Numerical simulations indicate that the stability switch occurs via a Hopf bifurcation that can be subcritical (SH), where an unstable limit cycle surrounds a stable steady state, or supercritical (H), where a stable limit cycle surrounds an unstable steady state. Such a limit cycle corresponds to sustained oscillations of the phase differences in our model and thereby to phase asynchrony.
A limit cycle is represented in the bifurcation diagram only by the minimal phase difference along the orbit.

The bifurcation diagram shows a second scenario for the emergence of sustained phase oscillations. The scenario arises mathematically through a pair of saddle-node bifurcations of limit cycles (SNL) along the branch of the unstable limit cycle from the subcritical Hopf bifurcation. These bifurcations are extremely difficult to capture analytically since they are so-called “global” rather than “local” bifurcations (i.e., they depend not only on a single point), and since the interaction function $H$ is only defined implicitly. We provide numerical evidence in the Appendix. In such a bifurcation, two nested limit cycles, one stable and one unstable, collide and annihilate one another. In Fig. 2a, we see how a stable limit cycle (thick line)—corresponding to sustained phase oscillations—emerges in one saddle-node bifurcation with an unstable limit cycle (thin line) and disappears again in another such bifurcation.

In the next section, we explore how closely the full system (1) matches the results from the phase-difference system (6).

**Full model simulations**

We use results from the analysis of phase dynamics to guide our study of the stability of phase (a) synchrony and of its statistical properties in the full model system (1), thereby verifying that the phase dynamics model is a good approximation to the phases of the full model.

We performed numerical simulations of the full system (1) using the ode45 solver in MatLab (Mathworks). We ran 15 simulations until $t = 2 \cdot 10^6$ for each set of parameter values and extracted the phase over the second half of each time series. As suggested by coexistence of stable objects in the phase difference equations (Fig. 2a), initial conditions need to be chosen carefully in the basin of attraction to reveal these objects in simulations. Initial densities were semi-randomly sampled from the single-patch predator-prey limit-cycle for each set of parameter values, meaning that initial phase position along that orbit was constrained to be in the vicinity of one of four possible attractors: (i) < 1% deviation from all-in-phase (homogeneous phase-locking); (ii) < 1% deviation from two in-phase (asymmetrical phase-locking); (iii) < 1% deviation from equal, $2\pi/3$ phase differences (traveling-wave phase locked state); and (iv) a < 1% deviation from in-phase, and random initial phases for all three patches, in order to capture limit cycles in phase differences corresponding to phase asynchrony.

We extracted phases and calculated all local minima and maxima across pairwise phase-difference time series following Cazelles and Boudjema (2001). Local minima and maxima in phase differences reveal synchrony and asynchrony: if maxima are equal to minima of a time series then we have a locally stable phase-difference equilibrium (phase synchrony); if they differ, we have oscillatory dynamics of phase difference (phase asynchrony).

We first simulated the three-patch system across the same values of $\eta$ defined above, and for weak dispersal ($\delta = 10^{-4}$) in order to test for agreement between the full system and the analysis of phase equations (Fig. 2a). For $\eta > 0.3$, only the all-in-phase state (filled diamonds) is stable (Fig. 2b). For $0.175 < \eta < 0.3$, the traveling-wave states (red squares) also become locally stable, as predicted by the phase equations (Fig. 2a, top thick line). For $\eta < 0.2$, we see the appearance of a stable limit cycle of phase difference (asynchrony) through a saddle-node bifurcation of limit cycles (SNL) from initial conditions that are away from the in-phase and traveling-wave states (filled circles). For $\eta < 0.175$, the traveling-wave state loses its local stability as indicated by the divergence between maximum and minimum phase differences (open red squares), and is replaced with asynchrony through a Hopf bifurcation. For $0.171 < \eta < 0.174$, two asynchronous orbits coexist, one resulting from the Hopf bifurcation of the traveling wave at $\eta \approx 0.174$, and one at $\eta \approx 0.2$ from the saddle-node bifurcation (Fig. 2b). These results are compatible with the combination of a saddle-node and Hopf bifurcations obtained from phase equations (Fig. 2a and Appendix), except for the brief coexistence ($0.171 < \eta < 0.174$) between Hopf and saddle-node orbits that were only observed in numerical simulations of the full model.

Decreasing $\eta$ contributes to a separation of temporal scales between predator and prey growth. In a single patch, this separation leads to pulse-relaxation-type oscillations. In a two-patch system, pulse-relaxation oscillations are known to promote the emergence of bistability between out-of-phase and in-phase synchronous states (Goldwyn and Hastings 2007). Scaling up to three patches, these same properties, when $\eta < 0.2$ (Fig. 2b) predict phase asynchrony, characterized by stable periodic oscillations of phase differences between each pair of coupled predator-prey communities (Fig. 3b). For both two- and three-patch systems, the outcome is bistability: bistable (synchronous) steady states for two patches, and bistable steady state and orbit(s) for three patches. Bistability has been shown to be a general outcome for networks of homogeneous oscillators with symmetric (Ashwin et al. 1990) and asymmetric (Montbrió et al. 2004) coupling, where the generic bifurcation is a saddle-node, and symmetry forces trajectories onto cycles. This property means that the traveling wave among three patches can be interpreted as the analogue to the anti-phase synchrony between two patches. Coexistence of multiple stable states results in a dependence on initial conditions. However, for all $\eta$ values leading to asynchrony as one of the stable states, asynchrony was the only state reached from numerical simulations with
Fig. 3  Local and regional dynamics of system (1) under phase asynchrony ($\eta = 0.15, \delta = 10^{-4}$). a Time series of local abundance in each patch (colored lines) and of regional (average over three patches, black line). b Time series of phase difference ($\psi$) for each pair of patches. c Time series of frequency deviation (ratio of observed to a single-patch frequency) of oscillations in each patch (relative to frequency of the single orbit).

random initial phases for all patches or from 10% deviation from the in-phase state. All other synchronous states (in-phase and traveling wave) are reached by constraining initial conditions to their vicinity.

Dispersal-induced asynchrony leads to nonstationary local and regional dynamics that are distinct from the expected effect of environmental heterogeneity. Instead of heterogeneous frequencies that would result in continuous growth of phase difference across habitats, dispersal-induced phase asynchrony is associated with oscillations of phase differences (Fig. 2b) over much longer temporal scales than predator-prey cycles, as illustrated in Fig. 3 for $\eta = 0.15$ and $\delta = 10^{-4}$. In contrast with the averaging effect of phase-locking, each pair of habitats goes through periods of apparent in-phase or out-of-phase synchrony (Fig. 3b), and total metacommunity abundance periodically shifts between strong fluctuations during periods of weak phase differences, to periods of lower amplitude oscillations with transient frequency doubling (Fig. 3a).

The nonstationary dynamics of phase differences results from an endogenous modulation of frequencies induced by dispersal (Fig. 3c). Frequency modulation (Boashash 2016) explains nonstationary phase differences as the combination of 2 stationary signals: the “carrier” signal (single-patch dynamics), and the lower frequency “modulator” signal, which here emerges at the metacommunity level from spatial coupling. The magnitude of the modulator signal informs us about the maximum changes in frequency experienced by the carrier, while the modulator frequency sets the temporal scale of nonstationarity in phase differences. For example, carrier and modulator frequencies and amplitudes can be extracted numerically from their time series,
and for the parameter values used in Figs. 3 and 4, the frequency (measured in cycles/t) of the carrier (oscillations from the single-patch dynamics) is $C = 0.94$ (Figs. 3a and 4a). Oscillations in the frequency of the time series correspond to the modulation signal and have frequency $M = 0.0007$. The amplitude of that modulation signal then corresponds to the maximum modulation $D = 0.0104$ (Fig. 3c). The observed frequency modulation leads to phase asynchrony because frequencies are modulated with heterogeneous amplitudes (Fig. 3c).

Frequency modulation also leaves signatures on the spectral properties of both local and regional time series. In a frequency domain, asynchronous time series reveal nonharmonic side bands (peaks at frequencies that are not integer multiples of the fundamental) around harmonic peaks (Fig. 4b) that are missing from time series of single-patch dynamics (Fig. 4a). The presence of sidebands constitutes a signature of frequency modulation, but frequency modulation theory can more specifically predict that the modulator frequency $M$ corresponds to the distance between nonharmonic sidebands (Fig. 4b, inset). The magnitude and number of significant sidebands around the fundamental frequency could be obtained by deriving Bessel functions of the Fourier series (Boashash 2016). However, Carson’s rule (Boashash 2016) can be used to approximate the bandwidth of significant sidebands as $2(D + M) = 0.02$, which provides a good approximation of frequency modulation properties in our predator-prey system (Fig. 4b, inset).

**Application to a large-scale metacommunity**

We tested the robustness of phase asynchrony to the previous assumptions of small (three-patch) metacommunities, weak spatial coupling, and relaxation oscillators. We used a spatially continuous (integro-differential) predator-prey model previously applied to spatiotemporal dynamics of large-scale coastal ecosystems (Gouhier et al. 2010). This model corresponds to an infinite linear array of equally spaced communities, each governed by Rosenzweig-MacArthur dynamics $\frac{dX_i}{dt} = F(X_i)$ as in Eq. 1. Spatial coupling differed slightly from Eq. 1 in that coupling strength decreases exponentially with linear distance between communities. Distance-independent coupling is unrealistic for systems of this spatial extent.

To relax the assumptions of weak coupling and relaxation oscillators, we decreased the separation of temporal scales between predators and preys with $\epsilon = 0.7$, and increased coupling to $\delta = 0.1$. The resulting parameters were those used to validate short-term spatial synchrony with data.

![Fig. 4](image-url) Power spectrum of local predator abundance time series for a the single-patch (uncoupled) orbit and b phase asynchronous metacommunity dynamics. Parameter values as in Fig. 3. In a, only a single patch is considered, which constitute the “carrier” (unmodulated) signal with a fundamental frequency of 0.94 cycles/t. In b, random initial phases lead to phase asynchrony, which produces a frequency-modulated signal. The inset shows the nonharmonic sidebands around the distribution fundamental frequency at $\approx 0.1$ with sideband spacing of $\approx 7.10^{-4}$.
of *Mytilus californianus* (California mussel) distribution over 1800 km along the North East Pacific coast (Gouhier et al. 2010). We then tested for the presence of frequency modulation associated with validated spatiotemporal patterns characterized by spatial periodicity in phase coherence (Gouhier et al. 2010).

We simulated the integro-differential equations with periodic boundary conditions over $t = 12000$ time steps and kept the last 3000 time steps of each simulation output for analysis. We extracted phase from local time series and calculated local instantaneous period using the same method as for our three-patch simulations.

Results produce complex spatiotemporal patterns (Fig. 5a) reported in previous studies (Gouhier et al. 2010), which lead to similarly complex spatiotemporal modulation of frequency over an extended spatial domain (Fig. 5b). More specifically, large-scale aggregations of high frequency oscillations over the 1D domain explain the spatial periodicity in short-term phase coherence found in both numerical simulations and data of *Mytilus* from 1999–2007 (Gouhier et al. 2010). Over longer temporal scales, the distribution of these high frequency patches becomes dynamic, but leads to qualitatively similar regularity of local frequency modulation found in three-patch networks (Fig. 5c). We also analyzed the spatially continuous model with the same parameters that were used for our three-patch model in Figs. 3 and 4b, with $\epsilon = 0.1$ and $\delta = 10^{-4}$. Weak coupling and relaxation oscillators also predict frequency modulations (Fig. 5c), but of much smaller amplitude than nonrelaxation oscillators under strong coupling. These results suggest that frequency modulation is robust and even promoted by strongly coupled regular oscillators.

**Discussion**

Our study shows that spatial phase asynchrony, defined as the lack of a fixed-phase difference among fluctuating populations, can be driven by weak dispersal in a homogeneous predator-prey metacommunity with a small (three-patch) or large (infinite) number of patches. This endogenous phase asynchrony results in the emergence of a collective frequency modulation across the metacommunity. Frequency modulation is distinct from exogenous asynchrony that can arise from environmental heterogeneity, and can be detected from sufficiently long individual time series. Dispersal-induced asynchrony reveals a new mechanism for the maintenance of heterogeneity and nonstationarity driven by species interactions and movement. The detection of long-term fluctuations in frequency remains challenging with existing ecological datasets. However, the emergence of frequency modulation could lead to the development of
statistical tools for the inference of intrinsic and extrinsic causes of spatiotemporal heterogeneity from local (nonspatial) time series. Phase asynchrony and frequency modulation are compatible with spatiotemporal patterns of spatial synchrony previously observed in marine metacommunities, and have important implications for predicting population persistence and community stability in spatially structured habitats.

**Frequency modulation and the emergence of ecological asynchrony**

The loss of phase synchrony is central to predicting nonstationary properties of large-scale ecosystems, including their stability and productivity. Phase asynchrony can result from environmental heterogeneity in natural frequencies of populations (Blasius et al. 1999; Koelle and Vandermeer 2005) (Fig. 1c, d). Given no or weak dispersal, these heterogeneous frequencies can be maintained and lead to continuous changes in phase differences across the metacommunity. Uncorrelated environmental fluctuations can also cause heterogeneity in the frequency and phase difference of communities (Allstadt et al. 2015). Frequency modulation can be viewed as a special case where a periodic fluctuation imposes a periodic change in local frequencies (Fig. 1e, f). If the frequency modulation is spatially heterogeneous, it can cause phase asynchrony. Our results reveal that frequency modulation can emerge from weakly coupled homogeneous oscillations and is associated with phase asynchrony in the absence of any environmental heterogeneity. When compared to the environmental forcing of heterogeneous frequencies, one important implication of dispersal-driven frequency modulation is the nonstationarity of both local and regional time series, which can be used to infer spatial dynamics from local time series.

Frequency modulation is a common feature of natural and synthesized sounds, with many applications in signal processing (Boashash 2016). It has a long history in engineering to encode and decode complex signals into its carrier (the single-patch predator-prey orbit in the present study), and a modulator prescribing the rate and magnitude of frequency modulation to the carrier (Fig. 1e, f). In ecology, frequency modulation has been applied to ecological and behavioral studies of sound production by individuals (Morton 1975; Truax 2001). Its general spectral signature (in the frequency domain) is the presence of nonharmonic sidebands around harmonic peaks. The distribution of these sidebands depends on the frequency and amplitude of the modulator relative to the carrier signal. In that context, frequency modulation is usually considered an exogenous cause of phase asynchrony, where modulator signals force the carrier oscillation. Our results show that frequency modulation and the frequency modulator signal itself can be emerging properties of metacommunity dynamics. It is therefore possible to extract the modulator signal and infer regional phase asynchrony from local time series. Applying frequency modulation theory to our simulation results, we show how the spacing of nonharmonic sidebands (Fig. 4b, inset) from the local time series provides a good approximation of the regional frequency modulation signal. This result contributes an important tool to infer not only the emergence of dispersal-driven phase asynchrony, but also the temporal scales of both local and regional dynamics.

**Scaling up from species traits to metacommunities**

Ecological synchrony can help scaling up from individual traits to the dynamics of metacommunities. For example, phase synchrony can be predicted from individual traits such as birth, death, and consumption rates that respond to environmental heterogeneity (Blasius et al. 1999; Koelle and Vandermeer 2005; Goldwyn and Hastings 2009). Increasing the difference between predator and prey growth leads to relaxation-type oscillations that are more prone to phase-locked synchrony than regular oscillations in two-patch metacommunities (Goldwyn and Hastings 2007). While two-patch predator-prey systems display a limited range of spatial dynamics, larger ecological networks can exhibit very high complexity, including long transient (Ruxton and Doebeli 1996; Hastings 2001; Cazelles et al. 2001) and chaotic (Holland and Hastings 2008) dynamics. One approach to resolving this complexity consists in studying the emergence of dynamical behavior in networks of intermediate size (Marleau et al. 1777). Our results show that a qualitatively different dynamical behavior, phase asynchrony through frequency modulation, can emerge from a minimal increase of spatial complexity, from two to three discrete habitats. Our results thus support pulse-relaxation oscillations as an important dynamical behavior for predicting spatial synchrony in weakly coupled communities. Future studies should elucidate the role of pulse-relaxation oscillations and the robustness of phase asynchrony to more complex species interaction networks than predator-prey interactions, and to heterogeneous spatial networks.

Phase asynchrony leads to nonstationarity of individual predator-prey time series over local (frequency and phase difference) and regional (averaging effect on frequency doubling and amplitude dampening) spatial scales. Inferring dispersal-induced asynchrony from such complex time series can be guided by properties of the embedded frequency modulator. The periodic modulation of frequencies reported here for a small network provides an important foundation for understanding complex dynamics over larger
networks. In marine coastal ecosystems for example, the spatial dynamics of benthic invertebrates was predicted over regional scales using metacommunity models where local predator-prey fluctuations are strongly coupled by the passive transport of pelagic larvae (Gouhier et al. 2010). Predictions of dispersal-induced heterogeneity over large spatial networks (> 100 km) were tested using spatially extensive but short-term data (Gouhier et al. 2010). Here, we show that the same model also predicts dispersal-induced temporal non-stationarity, with long-term oscillations in the frequency of local population fluctuations (Guichard and Gouhier 2014), similarly to our analysis of three-patch networks. Frequency modulation constitutes a novel ecological mechanism linking species interactions and movement to the maintenance of spatiotemporal heterogeneity across scales, with important implications for linking metacommunity theory and data (Grainger and Gilbert 2016).

Inferring metacommunity dynamics from time series

Inferring endogenous and exogenous causes of variability from time series has been a long-standing goal of population and community ecology (Jassby and Powell 1990; Louca and Doebeli 2014; Cavanaugh et al. 2013). Detecting and interpreting spatial synchrony has proven especially challenging because most periodic time series also contain a strong stochastic component (Turchin 2003), in which case statistical correlation and phase synchrony can become confounded (Haydon and Greenwood 2000; Gouhier and Guichard 2014). Also, in the presence of long transient dynamics (Holland and Hastings 2008; Hastings 2004), resulting nonstationarity of spatial synchrony and of the period of fluctuations can be confounded with dispersal-induced phase asynchrony reported here. Nonstationarity in the period of ecological fluctuations and in spatial synchrony has been detected in a number of long-term time series of small mammal populations (Henden et al. 2009; Cazelles et al. 2008), and much progress has been made towards the statistical detection of such time-dependent frequency dynamics (Cazelles et al. 2008). However, nonstationary periods and synchrony are interpreted as the result of environmental drivers, through their spatial and/or temporal heterogeneity (e.g., spatially uncorrelated temporal fluctuations; Allstadt et al. 2015; Arumugam et al. 2015). Dispersal-induced frequency modulation provides a new interpretation for nonstationary frequency dynamics in ecological time series. We predict such modulation in the absence of any environmental heterogeneity using a spatially continuous metacommunity model applied to the regional dynamics of predator-prey fluctuations coupled by dispersal (Guichard and Gouhier 2014). These predictions were previously tested in a natural coastal ecosystem using short term but spatially extensive data on spatial synchrony of marine invertebrates (Gouhier et al. 2010). By predicting spatial and temporal signatures of dispersal-induced frequency fluctuations, our theory of endogenous asynchrony offers a method to infer ecological processes by using temporal or spatial data as a proxy for complex spatial dynamics. However, the availability of long-term ecological time series is still limited to a few natural systems. Also, more efforts are needed to develop inference methods based on a combination of shorter term spatial and temporal data, in order to assess the relative importance of abiotic and biotic drivers of frequency modulation.

Phase asynchrony contributes to a more general theory of ecological synchrony by defining endogenous and exogenous mechanisms causing the loss of phase synchrony, and by characterizing its dynamical and statistical properties. Phase synchrony provides an equilibrium theory (phase-locking) of non-equilibrium population dynamics. Phase asynchrony extends this theory to non-equilibrium dynamics of spatial heterogeneity (phase difference) itself. Because phase asynchronous time series contain characteristic statistical signatures across spatial and temporal scales, phase asynchrony improves the robustness of current inference frameworks used for studying the causes of nonstationary spatiotemporal fluctuations in natural ecosystems.

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Appendix: Model analysis

Here, we provide details on the qualitative analysis of the planar dynamical system given by the phase-difference equations (6), i.e.,

$$\frac{d\psi_1}{dr} = \frac{1}{2} [H(-\psi_1) + H(\psi_2) - H(\psi_1) - H(\psi_1 + \psi_2)],$$  \hspace{1cm} (A.1)

$$\frac{d\psi_2}{dr} = \frac{1}{2} [H(-\psi_1 - \psi_2) + H(-\psi_2) - H(-\psi_1) - H(\psi_2)].$$  

The most important ingredient of these equations is the $2\pi$-periodic function $H$. It is related to the so-called infinitesimal phase-response curve, $\dot{\gamma}$, along a periodic orbit (Goldwyn and Hastings 2007). The infinitesimal phase-response curve is the solution of the differential equation

$$\frac{d\dot{\gamma}}{dr} = -DF(\gamma(t))\dot{\gamma}$$  \hspace{1cm} (A.2)

with the normalization condition $\dot{\gamma}(t) \cdot \gamma'(t) = 1$. In other words, $\dot{\gamma}$ is given by the linearization equation of the
vector field $F$ around the stable periodic orbit $\gamma$. With this notation, function $H$ is given as the average:

$$H(x) = \frac{1}{T} \int_0^T \gamma'(t) \cdot (\gamma(t + x/\Omega) - \gamma(t)) \, dt,$$

(A.3)

where $T$ is the period of the periodic orbit $\gamma(t)$ of the Rosenzweig-MacArthur model and $\Omega = 2\pi/T$ is the frequency.

Even though function $H$ is not explicitly given, we can still proceed with the qualitative analysis of the phase-difference system by finding steady states and calculating their stability conditions. Periodicity of the function $H$ is an important aspect in almost all the considerations to follow.

**Zero phase differences**

The “all-in-phase” state $(\psi_1, \psi_2) = (0, 0)$ is a steady-state solution, independent of parameter values. Hence, all-in-phase synchrony is always possible. Moreover, this state is always locally asymptotically stable: if a metacommunity is initially close to in-phase synchrony, it will converge to in-phase synchrony. To see that $(0, 0)$ is locally stable, we linearize (A.1) and get the Jacobi matrix

$$J(0, 0) = \frac{H'(0)}{2} \begin{pmatrix} -3 & 0 \\ 0 & -3 \end{pmatrix}.$$  

Thus, the local stability of $(0, 0)$ is determined by the sign of $H'(0)$. If $H'(0) > 0$ ($H'(0) < 0$), the all-in-phase steady state is linearly stable (unstable). This condition is exactly the same as for the two-patch model studied in Goldwyn and Hastings (2007) and Zhang et al. (2015). Based on those results, the all-in-phase state will be locally stable for all parameter sets that we study here.

**Symmetry**

As we look for further steady states, we note that the phase-difference equations are $2\pi$-periodic and possess several symmetries. In particular, if $(\psi_1^*, \psi_2^*)$ is a steady state of system (A.1), then the following are also steady states:

$$(2\pi + \psi_1^*, \psi_2^*), (\psi_1^*, 2\pi + \psi_2^*), (2\pi + \psi_1^*, 2\pi + \psi_2^*),$$

and

$$(2\pi - \psi_2^*, 2\pi - \psi_1^*).$$

In fact, the vector field in Eq. A.1 on the square $[0, 2\pi] \times [0, 2\pi]$ is symmetric with respect to the diagonal $y = 2\pi - x$. It can therefore be completely represented by its value on the triangle $0 \leq \psi_1 + \psi_2 \leq 2\pi$. The schematic representations in Fig. 7 only show one such triangle for each case. The computationally generated phase-plane plots in Fig. 8 show the entire square $[0, 2\pi] \times [0, 2\pi]$ and illustrate the symmetry along the diagonal.

**Equal phase differences**

The next particular steady-state solution that we investigate has equal, non-zero phase differences between all three oscillators. Such a state is known as a “traveling-wave state” (Goldwyn and Hastings 2011) a “rotating wave” (Ashwin et al. 1990) or “splay state”. If we assume that $(\psi_1^*, \psi_2^*) = (x^*, x^*)$ is such a state, we have the equations:

$$0 = H(-x^*) + H(x^*) - H(2x^*),$$

$$0 = H(-2x^*) + H(-x^*) - H(-x^*) - H(x^*).$$

(A.4)

Hence, if $2x^* = -x^*$ modulo $2\pi$ then these equations are satisfied. Therefore, traveling-wave states with phase difference $x^* = 2\pi/3$ or $x^* = 4\pi/3$ exist independently of parameter values in the system.

Knowing the stability behavior of traveling-wave states will turn out crucial to understanding the dynamics of the system. The Jacobi matrix at the state $(x^*, x^*) = (2\pi/3, 2\pi/3)$ has the form

$$J = \frac{1}{2} \begin{pmatrix} -2H'(2x^*) - H'(x^*) & H'(x^*) - H'(2x^*) \\ H'(2x^*) - H'(x^*) & -H'(2x^*) - 2H'(x^*) \end{pmatrix}.$$  

(A.5)

To get this form, we used the fact that for $x^* = 2\pi/3$ we have $2x^* = -x^*$ mod $2\pi$ and that $H$ is $2\pi$-periodic. We calculate the trace and determinant of this matrix as follow:

$$\tr J = -3H'(x^*) + H'(2x^*),$$

$$\det J = 3[H'(x^*)^2 + H'(2x^*)^2 + H'(x^*)H'(2x^*)].$$

To evaluate the eigenvalues of $J$, we calculate the discriminant as following:

$$(\tr J)^2 - 4\det J = -3[H'(x^*) - H'(2x^*)]^2 \leq 0.$$  

Hence, the eigenvalues are not real (unless $H'(x^*) = H'(2x^*)$) and therefore, the point is a focus or spiral. This observation also follows from general symmetry considerations (Ashwin et al. 1990). The stability is then given by the sign of the trace of $J$. In particular, the traveling-wave state is stable if $\tr J < 0$ or

$$H'(x^*) + H'(2x^*) > 0.$$  

(A.6)

We evaluate this quantity numerically for our parameter set. The plot in Fig. 6 shows that the traveling-wave state is stable for intermediate values $\eta$ but unstable for small and for large values.

**Two in-phase states**

Finally, we will see steady-state solutions where one phase difference is zero, so-called “two in-phase states” (Ashwin et al. 1990), for example, $(\psi_1^*, \psi_2^*) = (y^*, 0)$. These arise when $y^*$ satisfies

$$2H(y^*) = H(-y^*).$$  

(A.7)
Fig. 6  Numerical evaluation of the stability condition (A.6) for our default parameter set. The traveling-wave state is stable when the quantity in the figure is positive.

Fig. 7  Schematic of the phase plane of system (6) for $0.15 < \eta < 0.4$. Blue dots correspond to the all-in-phase-locked state and are locally stable for all values. Red dots correspond to two in-phase states and are saddles. The green dot stands for the traveling-wave state. The latter state is an unstable spiral for $\eta \geq 0.35$ (top left). After a subcritical Hopf bifurcation, it becomes stable with a surrounding unstable limit cycle ($\eta = 0.31$, top right). After the first saddle-node bifurcation, there are three limit cycles of which the inner and outer are unstable ($\eta = 0.19$, bottom left). After the second saddle-node bifurcation, there is only a large unstable limit cycle (no plot). Then, a supercritical Hopf bifurcation generates a stable limit cycle and the traveling-wave state becomes unstable again ($\eta = 0.17$, bottom right). The other parameter values are $\epsilon = 0.1$, and $\alpha = 0.4$. 
Fig. 8 Phase planes of system (6) for different values of $\eta$, corresponding to Fig. 7. Plot (a) shows two complete trajectories, connecting the unstable traveling-wave state to the stable all-in-phase state. Plot (b) also shows two complete orbits, one located inside the unstable limit cycle (upper right triangle), one outside (lower left triangle). The upper right triangle in plot (c) shows how two forward trajectories approach two stable objects: the traveling-wave state and the stable periodic orbit of asynchronous phase. The lower left triangle in plot (d) highlights the single stable limit cycle as it is approached from the exterior (top right triangle) and the interior (bottom left triangle). The large unstable limit cycle is extremely difficult to capture because it is so close to the axes that numerical accuracy becomes an issue. These plots were obtained using Matlab (Mathworks), after generating an expression of the function $H$ from XPPAUT (Ermentrout 2002).

These states are located in an invariant set. In fact, if $\psi_2 = 0$ then $d\psi_2/dt = 0$. Hence, if the phase difference $\psi_2$ is zero initially, then it will be zero for all times. In that case, the dynamics reduce to the line $(\psi_1, 0)$, with $0 \leq \psi_1 \leq 2\pi$. The two end-points are locally stable, as we have seen above when studying the stability of $(0, 0)$. Since the dynamics are one-dimensional, there has to be at least one steady state on the line with $0 < \psi_1 < 2\pi$, and if there is only one it has to be unstable. Hence, the two in-phase state always exists.

By symmetry, the same reasoning holds for $\psi_1 = 0$ and $\psi_2 = 0$.

Fig. 9 Schematic summary of the bifurcation behavior of the phase-difference dynamics of Eq. 6 as $\eta$ varies in (0.15, 0.4). The straight horizontal lines correspond to the tall-in-phase state at (0, 0) and the traveling-wave state at $(2\pi/3, 2\pi/3)$; the curves represent amplitudes of limit cycles. Thicker lines are stable objects, thin lines unstable.

Letters H and SH indicate the Hopf and the subcritical Hopf bifurcation. SNL stands for the saddle-node bifurcation of limit cycles. The vertical lines correspond to the values of $\eta$ for which the phase plane schematic is given in Fig. 7.
there have to be at least three such states, namely \((y^*,0), (2\pi - y^*, y^*), \text{ and } (0, 2\pi - y^*)\).

### Stability changes

In the corresponding two-patch system, the antiphase-locked solution changes stability, and additional out-of-phase-locked solutions appeared, when parameters are varied in such a way that the relative temporal scales between different processes differed (Goldwyn and Hastings 2007; Zhang et al. 2015; Wall et al. 2013). We focus on how the dynamics of Eq. 6 change as parameter \(\eta\) decreases. We describe several scenarios in Figs. 7 (schematic) and 8 (actual) and summarize the results in a schematic bifurcation diagram (Fig. 9, see also Fig. 2 in the main text). For large values of \(\eta \geq 0.32\), the traveling-wave state is an unstable focus; all nonconstant solutions converge to the all-phase-locked state. As \(\eta\) decreases, the traveling-wave state becomes stable through a subcritical Hopf bifurcation (SH) and an unstable limit cycle emerges. Continuing to decrease \(\eta\), two additional limit cycles appear in a saddle-node bifurcation of limit cycles (SNL) so that there are now three limit cycles. The middle one is stable (e.g., \(\eta = 0.19\)). The two inner limit cycles eventually collide and disappear in another saddle-node bifurcation of limit cycles (near \(\eta = 0.175\)). The traveling-wave state undergoes another Hopf bifurcation (H), this time supercritical, so that a stable limit cycle emerges (\(\eta = 0.17\)). The stable limit cycles correspond to solutions that are not phase-locked, and hence show true asynchrony.

The situation is similar to the generic bifurcation diagram for three identical, weakly coupled oscillators in Ashwin et al. (1990). Those authors mention that the branch that emerges from the (subcritical) Hopf bifurcation can “fold back on itself and create saddle-node bifurcations of tori.” What we do not observe in our parameter range is the change of stability of the all-in-phase-locked state that is required for the global bifurcation that these authors observed.

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