

Chaotic waves and phase synchronization in spatially extended ecological systems

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Abstract. An ecological population model is presented for exploring complex synchronization phenomena in biological systems. The model describes a three level predator-prey-resource system which oscillates with Uniform Phase evolution yet has Chaotic Amplitudes (UPCA). We investigate the phase synchronization of two nonidentical diffusively coupled models, and a two dimensional lattice of chaotic population models coupled via nearest neighbors. With weak coupling, a collective phase synchronization emerges, and for the spatially extended system this gives rise to a circular travelling wave structure where population abundances remain chaotic and uncorrelated.

I AN ECOLOGICAL UPCA MODEL

Ecological and biological oscillations are often characterized by highly irregular amplitudes but nearly constant and amplitude-independent frequencies [1] - a behaviour very reminiscent of the oscillators with Uniform Phase evolution and Chaotic Amplitudes (UPCA) used for studies of phase synchronization [2]. Beside the (ecologically implausible) Rössler system very few models possessing UPCA dynamics are known. Here we present a simple chaotic model of a three species predator-prey-vegetation system which demonstrates UPCA, and which matches real data [3,4].

We use the model to study complex spatio-temporal synchronization effects observed in ecological systems [5]. The well known Canadian hare-lynx system, for example, has been documented over 100 years, with hare and lynx population across Canada synchronizing in phase to a collective 10-year cycle that manifests over millions of square kilometers [6]. Currently, however, theoretical understanding of such phenomena lags behind experimental and field studies.

The minimal model consists of a “vertical” food chain with predators (z) feeding on herbivores (y), which themselves consume vegetation (x):

$$\begin{aligned}\dot{x} &= a(x - x_0) - kxy \\ \dot{y} &= -b(y - y_0) + kxy - eyz \\ \dot{z} &= -c(z - z_0) + eyz.\end{aligned}\tag{1}$$

In the absence of interspecific interactions ($e = k = 0$) we assume the existence of a (stable or unstable) fixed point (x_0, y_0, z_0) , and expand the system linearly around this steady state. In contrast to other standard Lotka-Volterra models [7] the steady state is here not necessarily set to zero and may, for example, describe the indirect influence of alternative prey and other species that exist in the real foodweb [3,4]. The coefficients a, b and c represent the respective nett growth rates of each individual species. Predator-prey and consumer-resource Lotka-Volterra interactions are incorporated with strengths k, e .

Figure 1a displays a typical model run in the phase coherent chaotic regime. Observe that the top predator, z , oscillates at what appears to be a constant frequency although the maximum or peak amplitude of each cycle is highly unpredictable. Note, that the time series of the foodweb model and the attractor in the (x, y) plane (Fig.1b) closely resembles the UPCA found in the Rössler system [8].

II SPATIAL PHASE SYNCHRONIZATION

We now study the synchronization of an ensemble of nonidentical foodweb systems (1) which are coupled by diffusive migration [3,4].

$$\begin{aligned} \dot{x}_i &= a(x_i - x_0) - ex_i y_i \\ \dot{y}_i &= -b_i(y_i - y_0) + ex_i y_i - ky_i z_i + \epsilon \sum_j (y_j - y_i) \\ \dot{z}_i &= -c(z_i - z_0) + ky_i z_i. \end{aligned} \quad (2)$$

Here x_i, y_i and z_i represent the vegetation, herbivore and predator populations in patch- i , and ϵ sets the magnitude of diffusive migration summed over a predefined set of local nearest neighbours $\{j\}$. Here we restrict the analysis to the simplest scheme in which only the herbivores are coupled by migration. Similar results have been obtained for migration schemes that include all three species [3]. The systems are assumed to be nonidentical and to cycle with different natural frequencies, which are determined by the coefficients b_i .

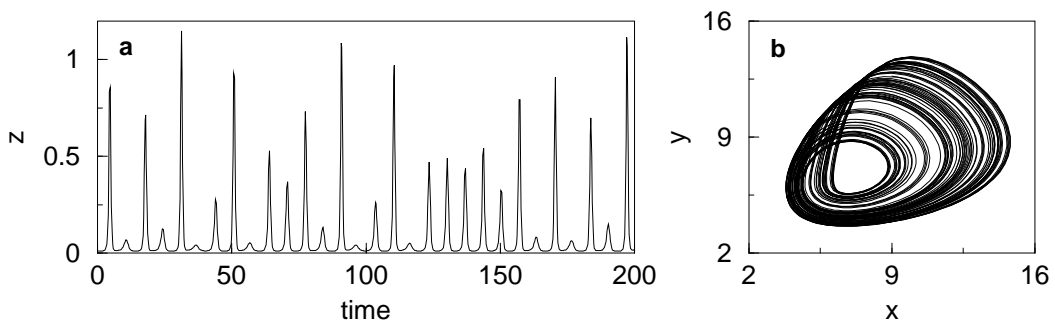


FIGURE 1. Simulation results of system (1). a) Time series of z b) Projection of attractor into the (x, y) plane. Parameters ($a = 1, b = 1, c = 10, k = 0.6, e = 0.1, x_0 = 1.5, y_0 = 0, z_0 = 0.01$).

In order to study phase synchronization, in practice one needs to decompose a chaotic signal into its phase and amplitude components [2]. Here, following [9], we let t_n be the time at which the top predator z reaches its n 'th maxima. Since the phase increases 2π between successive maxima, one can define the series of phases $\phi_n = \phi(t_n) = 2\pi n$. The discrete amplitudes A_n are defined as the values of z at these maxima i.e., $A_n = z(t_n)$.

A) Synchronization of Two Coupled Foodweb Models

First we study the synchronization of two coupled patch systems (2) with $i = 1, 2$. For the two UPCA models, we set growth rates of consumers to $b_1 = 0.98$ and $b_2 = 0.97$, leading to a frequency mismatch in the uncoupled system. Fig. 2 plots the relative frequency difference $\Delta\Omega(\epsilon)/\bar{\Omega}$ (i.e., as a percentage of the mean frequency $\bar{\Omega}$) as a function of coupling ϵ . The frequencies of the systems (and hence $\Delta\Omega$) are easily calculated by monitoring the phase growths ϕ_n . As ϵ increases, the frequency difference between the two patches drops and reaches zero at the critical coupling $\epsilon_c = 0.023$. At this point frequency locking is achieved ($\Delta\Omega = 0$), and the two systems are phase synchronized.

The correlation r between the two predator time-series z (i.e., the discretized maxima A_n) is also plotted as a function of ϵ . Fig.2 reveals that for relatively large coupling ($\epsilon > \epsilon_f = 0.07$) “full synchronization” both in phase and in amplitudes is achieved, since $r = 1$ and $\Delta\Omega = 0$. Note that for intermediate coupling levels ($\epsilon_c < \epsilon < \epsilon_f$) there is a distinct regime of “phase synchronization” where $\Delta\Omega = 0$, but the amplitudes of the two time-series are not strongly correlated. In Fig.2, we also plot the time lag τ between the two synchronized patch oscillations as a function of coupling ϵ . The time lag tends to decrease as full synchronization is approached [10].

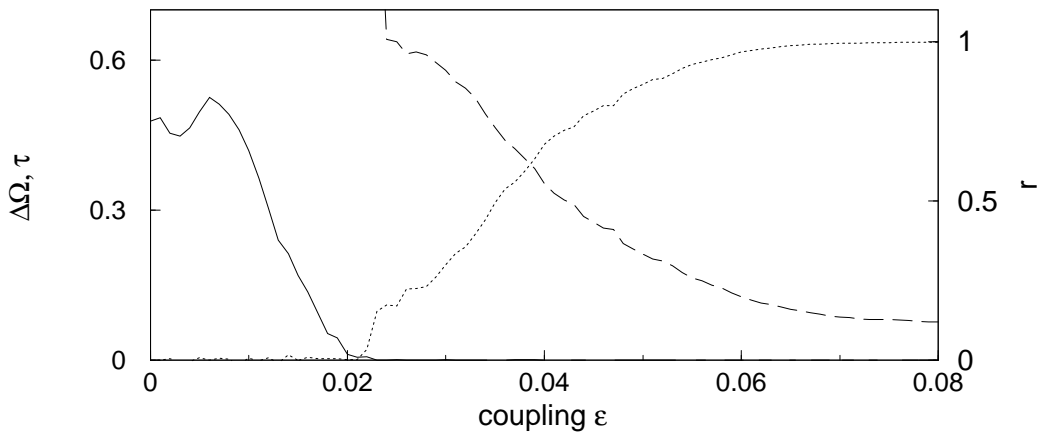


FIGURE 2. Transition to synchronization in two coupled models. Relative frequency difference, $\Delta\Omega$, (solid line), time lag, τ , (dashed line) and correlation between peaks A_n , r , (dotted line).

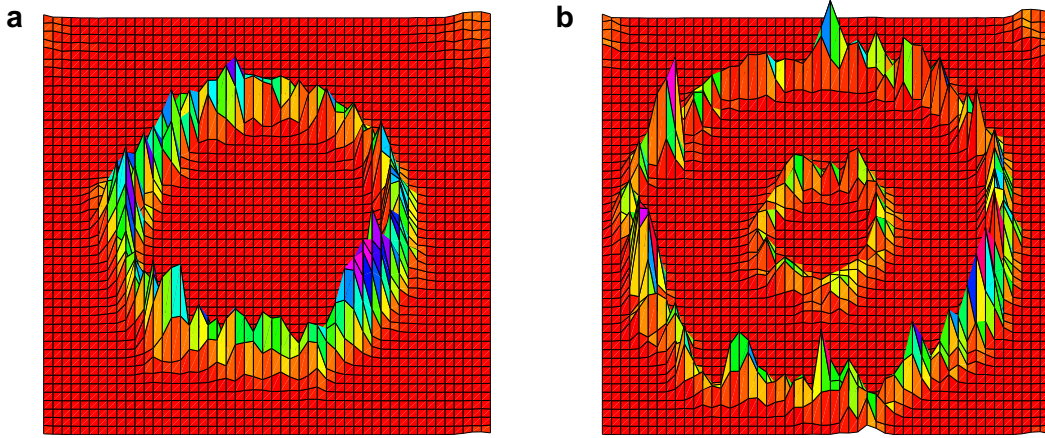


FIGURE 3. Circular chaotic wave in a 50×50 lattice. Snapshot of top predator z for two different values of the coupling strength a) $\epsilon = 0.075$, and b) $\epsilon = 0.05$. Note that the wavelength can be tuned by the coupling ϵ .

B) Phase Synchronization in Spatially Extended Lattice Systems

We now investigate synchronization in a spatial lattice of $N \times N$ patches ($N = 50$), each patch being a foodweb model. The models are taken to be nonidentical, having random natural frequencies that act as spatial inhomogeneity over the lattice. In order to achieve this, the consumer growth rates b_i are uniformly distributed lying within $\pm 7.5\%$ from the mean $\langle b_i \rangle = 1$. Each patch is connected to its eight nearest neighbours to take into account local migration ϵ . We performed a series of lattice simulations with different sizes N , boundary conditions, and number of nearest neighbors, but our main results were found to be robust to these changes.

With no migration between patches ($\epsilon = 0$), the populations display independent chaotic oscillations. On the other hand with large coupling ($\epsilon > 0.2$) global full synchronization is reached, and this leads to trivial spatial patterns, since phase and amplitude dynamics are then identical across the entire lattice.

The more interesting global phase synchronization occurs at intermediate levels of coupling ($\epsilon > 0.03$). Patch populations are again typically separated by a phase lag, but when viewed over the whole lattice the phase lags give rise to complex spatio-temporal patterns. Fig.3 demonstrates a remarkable coherent travelling wave structure where populations abundances remain chaotic, but unusual circular waves form and spread in time across the spatial landscape. The wave pattern repeats in an endless cycle, with patches having chaotic amplitudes, making each cycle different from the next. Recent ecological field studies have reported similar travelling wave structures [5].

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