Journal of Theoretical Biology ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

A possible mechanism for the attainment of out-of-phase periodic dynamics in two chaotic subpopulations coupled at low dispersal rate

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HIGHLIGHTS

Q2

- An hypothesis for the onset and maintenance of out-of-phase periodic dynamics in two inherently chaotic subpopulations coupled with low dispersal is proposed.
- The propensity of chaotic dynamics in single species population growth models to visit very low sizes is critical to the onset of out-of-phase dynamics in two coupled inherently chaotic subpopulations.
- The stabilization of chaotic to periodic dynamics is likely due to dispersal placing upper and lower limiters to subpopulation size.
- The components of the hypothesis are supported by the results of simulations of the various proposed effects using the Ricker (with and without extinction), logistic and Hassell models.

ARTICLE INFO

Article history:
Received 13 April 2014
Received in revised form
16 October 2014
Accepted 25 November 2014

Q3 *Keywords:*
Metapopulation
Ricker model
Logistic model
Hassell model
Extinction
Limiters
Stability
Chaos

ABSTRACT

Much research in metapopulation dynamics has concentrated on identifying factors that affect coherence in spatially structured systems. In this regard, conditions for the attainment of out-of-phase dynamics have received considerable attention, due to the stabilizing effect of asynchrony on global dynamics. At low to moderate rates of dispersal, two coupled subpopulations with intrinsically chaotic dynamics tend to go out-of-phase with one another and also become periodic in their dynamics. The onset of out-of-phase dynamics and periodicity typically coincide. Here, we propose a possible mechanism for the onset of out-of-phase dynamics, and also the stabilization of chaos to periodicity, in two coupled subpopulations with intrinsically chaotic dynamics. We suggest that the onset of out-of-phase dynamics is due to the propensity of chaotic subpopulations governed by a steep, single-humped one-dimensional population growth model to repeatedly reach low subpopulation sizes that are close to a value $N_t = A$ ($A \neq$ equilibrium population size, K) for which $N_{t+1} = K$. Subpopulations with very similar low sizes, but on opposite sides of A, will become out-of-phase in the next generation, as they will end up at sizes on opposite sides of K, resulting in positive growth for one subpopulation and negative growth for the other. The key to the stabilization of out-of-phase periodic dynamics in this mechanism is the net effect of dispersal placing upper and lower bounds to subpopulation size in the two coupled subpopulations, once they have become out-of-phase. We tested various components of this proposed mechanism by simulations using the Ricker model, and the results of the simulations are consistent with predictions from the hypothesized mechanism. Similar results were also obtained using the logistic and Hassell models, and with the Ricker model incorporating the possibility of extinction, suggesting that the proposed mechanism could be key to the attainment and maintenance of out-of-phase periodicity in two-patch metapopulations where each patch has local dynamics governed by a single-humped population growth model.

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http://dx.doi.org/10.1016/j.jtbi.2014.11.028
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1. Introduction

Many theoretical and empirical studies have indicated that synchronous dynamics among the constituent subpopulations can affect the stability of metapopulations, and that dispersal among subpopulations is a major factor affecting the spatial synchrony of subpopulation dynamics (Allen et al., 1993; Hastings, 1993; Gyllenberg et al., 1993; Kendall and Fox, 1998; Ruxton, 1994; Heino et al., 1997; Ranta et al., 1998; Earn et al., 2000; Ylikarjula et al., 2000; Molofsky and Ferdy, 2005; Dey and Joshi, 2006a; Ben-Zion et al., 2010, 2012). Theoretical studies have shown that subpopulations with inherently chaotic dynamics can exhibit out-of-phase periodic dynamics when coupled at low to intermediate rates of dispersal, whereas higher rates of dispersal can result in local synchronization and a simultaneous shift to chaos from periodicity (Ben-Zion et al., 2010; Dey et al., 2014). Interestingly, in systems of two coupled populations with inherently chaotic dynamics, the attainment of out-of-phase dynamics typically coincides with the stabilization of local dynamics of both populations to periodicity (Ben-Zion et al., 2010; Dey et al., 2014). However, the mechanism for the attainment of out-of-phase dynamics and simultaneous stabilization of local dynamics from chaos to periodicity in two coupled populations is not clear. Here, we propose a possible explanation for both the onset and maintenance of out-of-phase periodic population dynamics in single-species two-patch metapopulations with low levels of dispersal, and test the postulated components of this explanation using simulations largely based on two coupled Ricker (1954) maps, although we also verified the results with other single-species population growth models. We chose the Ricker model to test our hypothesis because this is a simple two-parameter model routinely used to study the synchrony and dynamics of single-species discrete-time metapopulations (Ruxton, 1994; Earn et al., 2000; Ben-Zion et al., 2010; Braverman and Haroutunian, 2010; Singh et al., 2011, Livadiotis and Elaydi, 2012; Poria et al., 2013). Moreover, the Ricker model has been shown to successfully capture the gross dynamics of a wide variety of natural and laboratory populations, despite its simplicity (Dey and Joshi, 2006a; Cheke and Holt, 1993; Sheeba and Joshi, 1998; Ives et al., 2004). In addition, to explore the generality of our results, we also examined the behaviour of similar coupled two-patch systems with local dynamics governed by the logistic and Hassell et al. (1976) models, or by Ricker models with probabilistic extinction thresholds introduced. Although more complex metapopulation models composed of coupled two-species models have also been reported to have the propensity to exhibit out-of-phase dynamics at lower rates of coupling (Goldwyn and Hastings, 2011), the hypothesis proposed in this paper focuses exclusively on single-species metapopulations modeled by coupled Ricker or related single-humped discrete population growth models.

2. The hypothesis

We consider a two-patch metapopulation, with each subpopulation following Ricker (1954) dynamics [$N_{t+1} = N_t \exp(r(1-N_t/K))$; where N_t = population size at generation t, r = maximum per-capita growth rate, and K = equilibrium population size] at identical high (chaotic) values of r and identical values of K. The qualitative dependence of Ricker dynamics on r is depicted in Fig. S1. The two subpopulations are coupled by symmetric fixed-fraction dispersal at some rate $0 \le m \le 1$. Therefore, the iterative equations for the per-generation change in the sizes N_1 and N_2 of the model subpopulations are:

$$N_{1,t+1}{}^* = N_{1,t}\exp(r(1-N_{1,t}/K)) \quad (1.1)$$

$$N_{2,t+1}{}^* = N_{2,t}\exp(r(1-N_{2,t}/K)) \quad (1.2)$$

$$N_{1,t+1} = (1-m)N_{1,t+1}{}^* + mN_{2,t+1}{}^* \quad (1.3)$$

$$N_{2,t+1} = (1-m)N_{2,t+1}{}^* + mN_{1,t+1}{}^* \quad (1.4)$$

Following Ben-Zion et al., 2010, 2012, we treat the two subpopulations as being out-of-phase when they show opposite directions of growth from a given generation to the next, i.e. one subpopulation reduced in size (negative growth) while the other increased in size (positive growth). Thus, the onset of such out-of-phase dynamics at generation t requires that the two subpopulations should have sizes $N_{1,t}$ and $N_{2,t}$ on opposite sides of K, respectively. This is trivially achieved if the two subpopulations start at sizes $N_{1,0}$ and $N_{2,0}$ on opposite sides of K (henceforth, inherently out-of-phase initial conditions). However, simulations of the system described above revealed that two coupled chaotic subpopulations can go out-of-phase even if they start with sizes $N_{1,0}$ and $N_{2,0}$ on the same side of K. Moreover, we found that synchrony in such two-patch systems does not depend on initial conditions when the two subpopulations have high r: two coupled chaotic subpopulations go out-of-phase irrespective of the relationship of their initial sizes $N_{1,0}$ and $N_{2,0}$ to K (data not shown). Our hypothesis aims to explain the onset of out-of-phase dynamics, and its subsequent maintenance over generations, in metapopulations consisting of two coupled subpopulations with Ricker dynamics that do not start from inherently out-of-phase initial conditions.

For the Ricker model at chaotic r values, return maps (plots of N_{t+1} versus N_t) show a portion with very steep positive slope at very low values of N_t (Fig. 1). Therefore, slight differences between two populations in very low N_t values can lead to considerable differences in their population sizes at generation $t+1$. As can be seen in Fig. 1, the point A represents the value of N_t ($N_t \neq K$) yielding $N_{t+1} = K$. Hence, in a given generation, if two populations, both of size quite low compared to K, happen to attain sizes on opposite sides of point A, in the next generation, the size of the subpopulation to the left of A in Fig. 1 will remain below K whereas the size of the subpopulation to the right of A will increase above K, even though their sizes were not very different in the previous generation. Inspection of time series revealed that isolated chaotic subpopulations with high r values often drop to this low population size zone around A from high sizes in the previous generation (data not shown). This scenario, where the two subpopulations have very similar sizes, but on opposite sides of point A, can lead to the onset of out-of-phase dynamics as the two subpopulations will have sizes on opposite sides of K in the next generation. Note that a prerequisite for the operation of this phenomenon is an inherent propensity of the populations to reach very low sizes around point A frequently. Unlike in chaotic dynamics, in the case of relatively

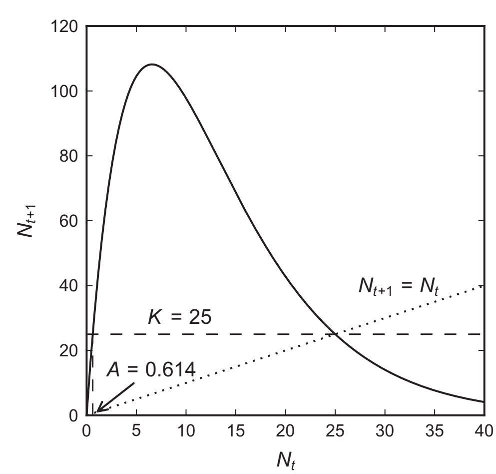

Fig. 1. Return map of the Ricker equation (r=3.8) showing the position of the sensitive point A for K=25. Note that if the sizes of two populations fall on opposite sides of A in generation t, they will reach opposite sides of K in generation $t+1$.

Please cite this article as: Dey, S., et al., A possible mechanism for the attainment of out-of-phase periodic dynamics in two chaotic subpopulations coupled at low dispersal rate. J. Theor. Biol. (2014), http://dx.doi.org/10.1016/j.jtbi.2014.11.028