



Short communication

Increases and decreases in network synchrony associated with local population extinction and recolonization



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ARTICLE INFO

Article history:

Received 24 April 2013

Received in revised form 14 June 2013

Accepted 17 June 2013

Keywords:

Colonization
Dispersal
Extinction
Metapopulation
Migration
Synchrony

ABSTRACT

Synchronous population dynamics, a positive correlation in growth rates among populations, is of interest from basic and applied perspectives. Synchronous dynamics are ubiquitous in nature thus understanding the mechanisms producing synchrony is fundamental. Population networks with synchronous dynamics have shorter persistence times than asynchronous networks, thus understanding its sources may aid conservation. Previous research has shown that the extinction and recolonization of local populations within a spatial population network produces a decrease in synchrony; however, models investigating extinction alone have shown increases in synchrony and the potential for increased network wide extinction risk. Here, I investigated these contrasting results. At low population growth rates, $r = 1.1$, the extinction and recolonization of a local population increased the synchrony of surrounding populations. Also in contrast to previous results, at higher growth rates, $r > 2.1$, extinction–recolonization dynamics resulted in a range of results – increasing, decreasing, and no change in synchrony. In all cases, the impact of extinction and recolonization dynamics on synchrony depended on whether dispersal was local or global, the population growth rate, the emigration rate, and the amount of local stochasticity. Results indicate that there is a high potential for positive feedback of local extinction and recolonization on network-wide extinction risk for patchy populations of species with low intrinsic growth rates.

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1. Introduction

Synchronous population dynamics, a positive correlation in growth rates among populations, is of interest from basic and applied perspectives. Synchronous dynamics are ubiquitous in nature, thus understanding the mechanisms producing synchrony is fundamental. Population networks with synchronous dynamics have shorter persistence times than asynchronous networks, thus understanding its sources may aid conservation. Previous research has shown that the extinction and recolonization of local populations within a spatial population network produces a decrease in synchrony; however, models investigating extinction alone have shown increases in synchrony and the potential for increased network wide extinction risk. Here, I investigated these contrasting results. At low population growth rates, $r = 1.1$, the extinction and recolonization of a local population increased the synchrony of surrounding populations. Also in contrast to previous results, at higher growth rates, $r > 2.1$, extinction–recolonization dynamics resulted in a range of results – increasing, decreasing, and no change in synchrony. In all cases, the impact of extinction and recolonization dynamics on synchrony depended on whether dispersal was

local or global, the population growth rate, the emigration rate, and the amount of local stochasticity. Results indicate that there is a high potential for positive feedback of local extinction and recolonization on network-wide extinction risk for patchy populations of species with low intrinsic growth rates.

Synchronous population dynamics, a correlation in population growth among spatially isolated populations of the same species, has been shown across an array of taxa and at a wide range of spatial scales (Hanski and Woiwod, 1993; Ranta et al., 1995; Liebhold et al., 2004). Given its prevalence in nature, understanding the mechanisms responsible for synchrony is of basic interest. Synchrony is thought to arise through different mechanisms. First, many studies (e.g., Abbott, 2011; Hanski and Woiwod, 1993; Matter, 2001; Sutcliffe et al., 1996) have shown that dispersal among local populations unites their dynamics producing synchrony. Second, exogenous forcing can synchronize dynamics. Moran (1953) proposed that populations with similar, linear density-dependent structures would become synchronized by spatially correlated forcing. In particular, Moran emphasized the effects of weather; a phenomenon dubbed the “Moran effect” by Royama (1992). Correlated weather or climate has been shown to affect synchrony in many studies, at many spatial scales (e.g., Macias-Fauria and Johnson, 2009; Roland and Matter, 2007). Correlated predation rates can synchronize dynamics of prey populations (Huitu et al., 2005; Ydenberg, 1987), and spatially correlated fluctuations

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in resources can synchronize populations of trophically related species (Haynes et al., 2009; Ripa and Ranta, 2007). Matter and Roland (2010) demonstrated from experimental and theoretical perspectives that the extinction of a local population can increase the synchrony of remaining populations within a spatial population network. Mechanistically, they hypothesized that increased synchrony could result from a simultaneous decrease in the number of immigrants to populations surrounding the population undergoing extinction, lowering abundance below carrying capacity producing a simultaneous increase in population size and a short-term increase in synchrony (Matter and Roland, 2010). Changes in landscape configuration resulting from the local extinction may also affect synchrony through changes in the relative attraction of immigrants by remaining populations (Matter and Roland, 2010).

In addition to its basic importance, synchrony also pertains to conservation. Synchronous population networks are predicted to have lower persistence than networks with more asynchronous dynamics (Allen et al., 1993; Ben-Zion et al., 2011; Dey and Joshi, 2006a; Harrison and Quinn, 1989; Matter, 2001). If local populations are synchronous, their risk of extinction is correlated. This correlation exists because of the strong inverse relationship between extinction risk and population size (Hanski, 1994). When populations are synchronous all populations experience simultaneously low abundance and high extinction risk, increasing the risk that all local populations go extinct, i.e. network extinction. Similarly, and particularly important in stochastic environments, all populations may be at simultaneously low abundance during a catastrophic event.

Although Matter and Roland (2010) showed that local population extinction can increase synchrony in spatial population networks, they did not investigate the effects of extinction/recolonization dynamics. Dey and Joshi (2006b, 2007) demonstrated that extinction/recolonization dynamics reduces synchrony. However, this was not the focus of their studies and they did not investigate the effects of extinction and recolonization on synchrony across an array of conditions. Thus, the general effects of extinction recolonization dynamics on synchrony remain unclear. Here, I explore the effects of extinction–recolonization dynamics on synchrony in spatial population networks across a broader range of conditions.

2. Materials and methods

The modeling here is general, but based on the biology of the butterfly, *Parnassius smintheus* and data collected for populations along Jumping pound Ridge (Matter et al., 2004; Matter and Roland, 2010). Because of the butterflies' univoltine life history and evidence for direct (lag one) density-dependence, but little evidence for natural enemies playing a strong role in population dynamics (Matter and Roland, 2013; Roland and Matter, 2013), I used a discrete, logistic model (Ricker, 1954):

$$N_{t+1} = N_t e^r \left(1 - \frac{N_t}{K}\right),$$

where N is population size, r is the rate of population growth, and K is the carrying capacity. This approach contrasts with other insect systems where synchrony has been studied but natural enemies play a role, necessitating a model incorporating delayed density-dependence (Liebhold et al., 2006). The carrying capacity for all populations was set at $K=100$. A maximum of ± 2.5 , 5, 10, or 15 individuals per generation, drawn from a uniform distribution, was added to each population, each generation to add local stochasticity (var).

Dispersal followed population growth. Because the effects of extinction on synchrony can differ based on spatial structure (Matter and Roland, 2010), I simulated two extremes of spatial

structure. Dispersal among populations was either global or local. Immigration to each population was based on its connectivity:

$$S_j = \sum_{k, k \neq j}^n e^{-\alpha d_{jk}}$$

where S_j is the connectivity of population j and d is the distance between populations j and k (Matter et al., 2004). The five populations were arranged linearly with a distance of one unit between populations. For global dispersal, the inverse of the mean dispersal distance, α , was set at 0.0001 and dispersers were allotted nearly equally among all populations, i.e., a lack of spatially structured dispersal. For local dispersal, α was set at 1.0000. The overall sequence of the model was: reproduction (survival to adult) $\rightarrow N_{i,t}$ (pre-migration) \rightarrow dispersal (adults) \rightarrow extinction $\rightarrow N_{i,t}$ (used for calculation).

Population abundance was initialized at a uniform random value between zero and K . Populations were allowed to “burn in” for 100 generations, after which time the center population in the linear array was allowed to undergo random extinction. The extinction risk was randomized based on a uniform distribution with an extinction occurring at values less than or equal to the set rate. Given the patchy population structure, recolonization occurred in the following generation provided the population was not subject to a subsequent random extinction event. Simulations were run for a total of 500 generations.

As the goal was to determine if extinction recolonization dynamics could result in increased synchrony, I investigated factors shown to be important (Dey and Joshi, 2006b, 2007; Matter and Roland, 2010), or of possibly influential here. The first was the rate of population extinction, which ranged from a probability of 0.00 to 0.50 extinctions per generation, incrementing by 0.05. The second factor was the rate of population growth which varied from $r=1.1$, 2.1, 3.1, and 4.1, simulating a range of dynamics (Dey and Joshi, 2007; May, 1974). Third, the effects of dispersal were examined as described above, with rates of emigration ranging from 0.05 to 0.35, incrementing by 0.05. All factors were investigated in a factorial manner. Synchrony was calculated as the mean Pearson correlation in population growth ($\log N_{t+1} - \log N_t$) from generation 101 to 500 among the four populations not subject to extinction and recolonization. One-hundred replicates were run under each set of parameter combinations.

3. Results and discussion

The results clearly demonstrate that the extinction and recolonization of a local population can increase, decrease, or have little effect on synchrony under specific conditions (Fig. 1). For populations with low growth rates, $r=1.1$, extinction/recolonization dynamics increased synchrony under all conditions where $em > var$, although the magnitude of the increase varied with other factors. There were generally larger increases in synchrony as the emigration rate increased and for global versus local dispersal. Greater local variation in population growth resulted in smaller increases in synchrony. At higher population growth rates ($r=2.1$, 3.1, and 4.1), the effects of extinction/recolonization dynamics were much more variable, producing increases, decreases, or little change in network-wide synchrony. In general, there was less change in synchrony when dispersal was global rather than spatially structured. Global dispersal under many of the simulated conditions resulted in near complete synchrony despite the perturbation of extinction and recolonization.

Mechanistically, extinction/recolonization at low population growth increased synchrony because the loss of immigrants in the generation following extinction was sufficiently large relative

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