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Effects of symmetric and asymmetric dispersal on the dynamics of heterogeneous metapopulations: Two-patch systems revisited

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HIGHLIGHTS

- Effect of dispersal on heterogeneous two-patch Ricker metapopulations was studied.
- Net asymmetric dispersal into the more stable subpopulation was destabilizing.
- Net asymmetric dispersal into the more unstable subpopulation was stabilizing.
- Symmetric dispersal was more stabilizing when both subpopulations were chaotic.
- Three zones of chaos varied in how readily they were stabilized by dispersal.

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ABSTRACT

Although the effects of dispersal on the dynamics of two-patch metapopulations are well studied, potential interactions between local dynamics and asymmetric dispersal remain unexplored. We examined the dynamics of two Ricker models coupled by symmetric or asymmetric constant-fraction dispersal at different rates. Unlike previous studies, we extensively sampled the $r_1 - r_2$ space and found that stability of the coupled system was markedly affected by interactions between dispersal (in terms of strength and asymmetry) and local dynamics. When both subpopulations were intrinsically chaotic, increased symmetry in the exchange of individuals had a greater stabilizing impact on the dynamics of the system. When one subpopulation showed considerably more unstable dynamics than the other, higher asymmetry in the exchange of individuals had a stabilizing or destabilizing effect on the dynamics depending on whether the net dispersal bias was from the relatively stable to the relatively unstable subpopulation, or vice versa. The sensitivity of chaotic dynamics to stabilization due to dispersal varied with r-value in the chaotic subpopulation. Under unidirectional or bidirectional symmetric dispersal, when one subpopulation was intrinsically chaotic and the other had stable dynamics, the stabilization of chaotic subpopulations with $r \sim 3.3$–4.0 occurred at the lowest dispersal rates, followed by chaotic subpopulations with $r \sim 2.7$–2.95 and, finally, chaotic subpopulations with $r \sim 2.95$–3.3. The mechanism for this pattern is not known but might be related to the range and number of different attainable population sizes possible in different r-value zones.

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1. Introduction

Following the appreciation that many natural populations show spatial structuring into metapopulations, groups of semi-independent subpopulations connected by dispersal (Clobert et al., 2012), earlier often referred to as migration (Levins, 1969; Hanski, 1999; Dey and Joshi, 2006), the study of spatiotemporal dynamics of population size has received considerable attention from population ecologists. Much of this work has focused on understanding the factors affecting metapopulation stability (Abbott, 2011). The stability of metapopulations depends on the inherent dynamics of the constituent subpopulations and also on their synchrony. Consequently, dispersal is a major factor affecting metapopulation stability, as it can influence both subpopulation dynamics and synchrony (Abbott, 2011). The role of dispersal in mediating metapopulation stability has also been experimentally verified (Ellner et al., 2001; Bonsall et al., 2002; Dey and Joshi, 2006; Dey, 2012), although only two of these studies specifically

imposed pre-determined dispersal rates and examined their effects on local and global dynamics and synchrony in a single-species system (Dey and Joshi, 2006; Dey, 2012). The other two studies used varying degrees of linkage between patches hosting multiple interacting species, and focused primarily on local extinction rather than dynamics per se (Ellner et al., 2001; Bonsall et al., 2002).

Theoretical studies using coupled map lattices have focused more sharply on the narrower question of how coupling affects local dynamics of linked simple difference equations (maps), and have shown that connected maps can exhibit a wide spectrum of dynamic behaviors depending on the strength and form of the coupling (Kaneko, 1993). Many studies focused on the simplest such coupled systems consisting of two single-species subpopulations linked by dispersal, in order to examine the effects of dispersal rate on the dynamics and stability of coupled populations with minimum distraction (Gonzalez-Andujar and Perry, 1993; Gyllenberg et al., 1993; Hastings, 1993; Doebeli, 1995; Lloyd, 1995; Kendall and Fox, 1998). A few studies also compared results from a two-patch system to those from a larger number of patches (Ylikarjula et al., 2000; Ben Zion et al., 2010). While these studies elucidated important effects of dispersal, especially the stabilizing effects of coupling two subpopulations with chaotic dynamics, they did not typically consider a large range of local dynamics and dispersal rates in a factorial manner, thus precluding a proper investigation of possible interactions between rate and (a)symmetry of dispersal on the one hand and spatial heterogeneity, as reflected in different local dynamics in the two subpopulations, on the other. For example, some studies considered homogeneous patches (same values of the parameter determining dynamics in both subpopulations) and symmetric dispersal (Lloyd, 1995; Ben Zion et al., 2010), whereas other studies allowed the value of the parameter determining dynamics to differ between the two subpopulations but kept dispersal symmetric (Gyllenberg et al., 1993; Hastings, 1993; Kendall and Fox, 1998). Conversely, yet other studies allowed for asymmetric dispersal but restricted the analysis to the case of identical values of the parameter determining qualitative dynamics in the two subpopulations (Gonzalez-Andujar and Perry, 1993; Doebeli, 1995; Ylikarjula et al., 2000).

A further limitation of many of these studies is that only one or a few discrete values of the parameter determining qualitative dynamics in the two subpopulations were considered (Gonzalez-Andujar and Perry, 1993; Doebeli, 1995; Lloyd, 1995; Ylikarjula et al., 2000; Ben Zion et al., 2010). The three studies that examined a wide range of values of the parameter determining qualitative dynamics used two coupled logistic models with symmetric dispersal only (Hastings, 1993; Gyllenberg et al., 1993; Kendall and Fox, 1998). Much of the analysis in these earlier studies focused on the dynamic behavior of the system of coupled subpopulations when the local dynamics were intrinsically chaotic i.e. the value(s) of the parameter determining qualitative dynamics in the two subpopulations would have yielded chaos in a single population. Other than the general observation that coupling intrinsically chaotic subpopulations by dispersal tended to stabilize their dynamics to low-period cycles (Gyllenberg et al., 1993; Hastings, 1993; Lloyd, 1995; Kendall and Fox, 1998), and that often the resultant system dynamics depended on initial conditions (Hastings, 1993; Lloyd, 1995), studies examining asymmetric dispersal between intrinsically chaotic coupled logistic models (Gonzalez-Andujar and Perry, 1993), Ricker (1954) models (Ylikarjula et al., 2000), and Maynard Smith and Slatkin (1973) models (Doebeli, 1995), all suggested that dispersal was more stabilizing when asymmetric. However, in all three of these studies, identical local dynamics were assumed in the two patches. Experimental work on nine-patch and two-patch metapopulations of fruitflies, nevertheless, suggests that dispersal rate and local dynamics can interact in their effects on dynamics of both spatially homogeneous and heterogeneous systems (Dey and Joshi, 2006; Dey, 2012).

Consequently, we decided to revisit systems of two coupled subpopulations to examine how dispersal rate might interact with local dynamics across a much wider range of parameter space than considered in the above-mentioned studies. We examined systems of two subpopulations following Ricker (1954) dynamics, coupled by either unidirectional, bidirectional symmetric or bidirectional asymmetric dispersal, wherein a constant fraction of a subpopulation dispersed every generation. We examined the dynamics of the system for a wide range of combinations of r-values (the dynamics determining parameter) in the two subpopulations, thereby permitting an assessment of the potential interactions between local dynamics and their spatial heterogeneity on the one hand and dispersal rate and its (a)symmetry, on the other. Our results extend the findings of the previous studies on the dynamics of coupled subpopulations in two major respects. First, we found that in the case of unidirectional or bidirectional symmetric dispersal, three broad zones of chaos can be discerned that differed in their sensitivity to getting stabilized by dispersal. When one subpopulation was intrinsically chaotic and the other had stable dynamics, the stabilization of a chaotic subpopulation with $r \sim 3.3$–4.0 occurred at the lowest dispersal rates, followed by chaotic subpopulations with $r \sim 2.7$–2.95 and, finally, chaotic subpopulations with $r \sim 2.95$–3.3 got stabilized at the highest dispersal rates. Second, when dispersal was asymmetric and there was spatial heterogeneity, such that the local dynamics were qualitatively different in the two subpopulations, the critical factor determining whether dispersal was stabilizing or destabilizing was the direction of the net dispersal bias towards or away from the relatively unstable subpopulation, respectively. Thus, the notion that asymmetric dispersal is stabilizing is not always true, depending on how the net dispersal bias maps onto the gradient of stability between the two subpopulations.

2. Model description

The populations were modeled using the Ricker (1954) equation, a simple discrete time population model that gives the number of individuals in a particular generation as a function of the number of individuals in the previous generation:

$$N_{t+1} = N_t \exp(r(1 - N_t/K)) \tag{1}$$

In Eq. (1), N_t = population size at generation t, e^r = maximal per capita growth rate and K = equilibrium population size. The qualitative dynamic behavior of the Ricker model depends solely on r, with stable point behavior for $r < 2.000$, periodic dynamics for $2.000 < r < 2.693$, and chaotic dynamics for $r > 2.693$ (May and Oster, 1976). The Ricker model was chosen because it is a simple model with only one bifurcation parameter (r), making interpretation and depiction of the simulation results relatively simple. Despite its simplicity, this model captures the gross features of the dynamics of single populations and metapopulations of different species reasonably well (Ricker, 1954; Cheke and Holt, 1993; Sheeba and Joshi, 1998; Fryxell et al., 2005; Ponciano et al., 2005; Dey and Joshi, 2006), and can be derived from first principles under the assumptions of scramble competition and a uniform random distribution of individuals in space (Brännström and Sumpter, 2005). Moreover, unlike the commonly used logistic model, whose qualitative dynamics are also solely determined by the maximal per capita rate of increase r, the Ricker model does not take negative values of N_{t+1} even for very high values of N_t, rendering it somewhat more realistic. Thus, results obtained from simulations using the Ricker model apply to real populations to a reasonable degree (e.g. see discussion in Sah et al., 2013) even though the latter are normally subject to demographic stochasticity and their sizes are limited to integer values, the so-called lattice effect (Henson et al., 2001; Domokos and Scheuring, 2004). In our simulations, two