

Metapopulation dynamics for spatially extended predator–prey interactions

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ABSTRACT

Traditional metapopulation theory classifies a metapopulation as a spatially homogeneous population that persists on neighboring habitat patches. The fate of each population on a habitat patch is a function of a balance between births and deaths via establishment of new populations through migration to neighboring patches. In this study, we expand upon traditional metapopulation models by incorporating spatial heterogeneity into a previously studied two-patch nonlinear ordinary differential equation metapopulation model, in which the growth of a general prey species is logistic and growth of a general predator species displays a Holling type II functional response. The model described in this work assumes that migration by generalist predator and prey populations between habitat patches occurs via a migratory corridor. Thus, persistence of species is a function of local population dynamics and migration between spatially heterogeneous habitat patches. Numerical results generated by our model demonstrate that population densities exhibit periodic plane-wave phenomena, which appear to be functions of differences in migration rates between generalist predator and prey populations. We compare results generated from our model to results generated by similar, but less ecologically realistic work, and to observed population dynamics in natural metapopulations.

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1. Introduction

Traditional metapopulation theory proposes mechanisms that explain how species persist regionally despite small local populations that are susceptible to extinction (Levins, 1969). The foundation upon which current metapopulation theory rests is based on Levins' mathematical model that describes a metapopulation as a spatially homogeneous population of unstable local populations, inhabiting discrete habitat patches (Hanski, 1998). Metapopulations persist through a balance between 'births' (establishment of new populations at unoccupied sites, Hanski, 1998) and 'deaths' (local extinctions). Processes influencing extinction in metapopulations operate at different scales: if the scale of extinction is local, demographic, environmental, and genetic stochasticity can lead to the extinction of populations (Hanski and Singer, 2001). Extinction of local populations can also be caused by extrinsic factors such as habitat loss or the presence of generalist predators and prey (Hanski and Singer, 2001). At the metapopulation scale, stochastically driven extinction can be caused by migration in small populations, and dynamics generated by extinction–colonization events. Extrinsic factors such as the

presence of specialist enemies and competitors can also lead to metapopulation extinction (Hanski and Singer, 2001).

1.1. Levins' metapopulation model

Mathematical models based on traditional metapopulation theory, usually assume that the metapopulation is made up of many neighboring spatially homogeneous habitat patches (e.g., Levins, 1969; Kareiva, 1990; Taylor, 1990; Hanski and Gilpin, 1997) connected via dispersal. Consequently, testing the predictions of traditional metapopulation theory against the predictions of metapopulation models that define a small number of spatially heterogeneous habitat patches connected via a migratory corridor remains relatively unexplored. Because these types of models do not usually include explicit spatial structure, there is a natural opening for exploring qualitative dynamics of a metapopulation model that takes into account spatial heterogeneity and differences in migration between generalist predator and prey populations. Moreover, limiting the number of habitat patches makes numerical investigations of the dynamics of a spatially explicit metapopulation model more tractable.

Past theoretical work has demonstrated that if the metapopulation patch network is spatially homogeneous, a number of factors can influence metapopulation persistence of a generalist predator and its prey. These factors have been examined using mathematical models with Lotka–Volterra (reaction–diffusion) and Nichol-

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son–Bailey dynamics within patches and spatially independent ‘diffusive’ migration between patches (see Kareiva, 1987, 1990; Taylor, 1990; Harrison and Taylor, 1997; Nee et al., 1997). Numerical investigations of these models demonstrate that populations persist longer in comparison to non-traditional models when within-patch dynamics are independent in different patches, and if re-colonization is possible (Kareiva, 1990; Comins et al., 1992).

1.2. Metapopulation models: spatial heterogeneity and migration

Mathematical models derived from traditional models demonstrate that there is potential for metapopulation persistence via a balance between patch extinction and colonization (Levins, 1969; Hanski, 1996; Hassell et al., 1991) or through local populations being rescued from extinction by immigration (i.e., rescue effects; Brown and Kodric-Brown, 1977). Simulations with large numbers of spatially homogeneous habitat patches demonstrate that at low migration rates, predators go extinct from local patches more frequently than they recolonize, causing regional predator extinction. Either low or high migration rates may cause dependence among predator or prey dynamics within a patch or across all patches and allow predators to drive prey regionally extinct (Blasius et al., 1999). However, at intermediate migration rates, both predator and prey may be able to persist through rescue effects and a balance between patch extinction and recolonization (Crowley, 1981; Kareiva, 1990; Taylor, 1990). In this study, we explore these findings with an alternative model that incorporates spatial heterogeneity and migration into a previously studied two-patch nonlinear ordinary differential equation metapopulation model. The model described herein is novel because spatial heterogeneity and migration between patches is modeled explicitly.

1.3. A spatially explicit metapopulation model: predator and prey migration

In this study, we compare qualitative results of models derived from traditional metapopulation theory with results from a spatially explicit system. The spatially explicit (reaction–diffusion) system models diffusively coupled predator–prey populations that migrate between two spatially heterogeneous patches by means of a migration corridor. The model builds on previous work that explored the dynamics of two spatially homogeneous patches coupled by migration. For these models, the dynamics in each patch were given by the Lotka–Volterra predator–prey equations without self-limitation (Jansen, 1995; Czárán, 1998; Jansen and Lloyd, 2000; Jansen and de Roos, 2000; Jansen, 2001). In our model, we undertake numerical experiments to test if the qualitative dynamics generated by the reaction–diffusion system match predictions made by an ordinary differential equation metapopulation model (Jansen, 2001). We explore the qualitative behavior of the model when the initial densities of predator and prey in neighboring patches are at steady state equilibrium, and in the case when predators become regionally extinct. Lastly, we determine if patterns generated by our model match patterns observed in naturally occurring metapopulations.

1.4. The single patch predator–prey model of Rosenzweig–MacArthur form

Before discussing the two patch predator–prey model coupled by migration it is advantageous to initially recall the single patch predator–prey model without migration. We consider a spatially extended system of Rosenzweig–MacArthur form, which in the

spatially homogeneous case is arguably the most well-known nonlinear predator–prey model. The basic predator–prey model in a single patch Ω has the following nondimensional form:

$$\begin{cases} \frac{\partial u}{\partial t} = \Delta u + u(1 - u) - \frac{uv}{u + \alpha}, \\ \frac{\partial v}{\partial t} = \delta \Delta v + \frac{\beta uv}{u + \alpha} - \gamma v, \end{cases} \quad (1)$$

where $u(\vec{x}, t)$ and $v(\vec{x}, t)$ are the population densities of prey and predators at time t and (vector) position \vec{x} , Δ is the usual Laplacian operator, and the parameters α , β , γ , and δ , are strictly positive. In the above model the local growth of the prey is logistic and the predator shows the ‘Holling type II functional response’ (Holling, 1959), which is well-documented in empirical studies (Gentleman et al., 2003; Jeschke et al., 2002; Skalski and Gilliam, 2001). Models of this class have been intensively studied (see, for example Medvinsky et al., 2002; Murray, 1993; Sherratt et al., 1997, 1995; Sherratt, 2001; Gurney et al., 1998) and have been successfully used to model a variety of ecological phenomena. The solutions of this model possess rich spatiotemporal dynamics with implications for waves of invasion, persistence of species and biological chaos, which makes this model an interesting and fruitful source of study.

2. Model description

In this paper we study the numerical solutions of a two-patch metapopulation model, where each subpopulation is governed by the spatially extended predator–prey system (1). The two-patch metapopulation model has the following nondimensional form

$$\begin{cases} \frac{\partial u_1}{\partial t} = \Delta u_1 + u_1(1 - u_1) - \frac{u_1 v_1}{u_1 + \alpha_1} + d_u(u_2 - u_1), \\ \frac{\partial v_1}{\partial t} = \delta_1 \Delta v_1 + \frac{\beta_1 u_1 v_1}{u_1 + \alpha_1} - \gamma_1 v_1 + d_v(v_2 - v_1), \\ \frac{\partial u_2}{\partial t} = \Delta u_2 + u_2(1 - u_2) - \frac{u_2 v_2}{u_2 + \alpha_2} + d_u(u_1 - u_2), \\ \frac{\partial v_2}{\partial t} = \delta_2 \Delta v_2 + \frac{\beta_2 u_2 v_2}{u_2 + \alpha_2} - \gamma_2 v_2 + d_v(v_1 - v_2), \end{cases} \quad (2)$$

where $u_i(\vec{x}, t)$ and $v_i(\vec{x}, t)$ are the population densities of prey and predators at time t and (vector) position \vec{x} within patch Ω_i ($i = 1, 2$). $\Delta = \sum_{j=1}^d (\partial^2 / \partial x_j^2)$ is the usual Laplacian operator in $d \leq 3$ space dimensions, and the parameters α_i , β_i , γ_i , and δ_i ($i = 1, 2$) are strictly positive. The parameters d_u and d_v represent the *per capita* migration rates between the two patches for the prey and predators respectively. Observe that in the absence of migration (i.e., $d_u = 0$ and $d_v = 0$) the metapopulation model effectively decouples into two separate predator–prey systems (Garvie, 2007). The parameters δ_i ($i = 1, 2$) are the ratios of dispersion (diffusion) coefficients of predators and prey in patch i .

The above system generalizes a predator–prey metapopulation model investigated by Jansen (2001) in two ways. Firstly, unlike the model studied by Jansen, system (2) is spatially explicit within each patch. In our model the predators and prey, in addition to interacting subject to the specifics forms of the reaction kinetics, disperse in space. Furthermore, Jansen’s model involved migration between patches of the predators only, while the model studied here incorporates migration of both predators and prey. System (2) is augmented with appropriate initial conditions

$$u_i(\vec{x}, 0) := u_{i0}(\vec{x}), \quad v_i(\vec{x}, 0) := v_{i0}(\vec{x}) \quad \text{for } \vec{x} \in \Omega_i, \quad i = 1, 2,$$

and the zero-flux boundary conditions

$$\frac{\partial u_i}{\partial n} = \frac{\partial v_i}{\partial n} = 0, \quad \text{on } \partial \Omega_i \times T, \quad i = 1, 2,$$

where n is an outward normal vector to the boundary of each patch $\partial\Omega_i$, which reflects the fact that species cannot leave their respective patches, except via migration.

3. Numerical results

3.1. Discretization

In order to approximate the solutions of the two-patch metapopulation system we employed an implicit–explicit (IMEX) finite difference scheme. IMEX schemes for reaction–diffusion equations employ an implicit discretization of the Laplacian with an explicit discretization of the reaction kinetics. The IMEX scheme used in this paper is similar to Scheme 2 discussed in Garvie (2007). The only difference is that the finite difference scheme for the metapopulation system involves additional linear terms for the migration of predators and prey, which couples the predator–prey interactions in the two patches. An advantage of the finite difference scheme is that it is stable and convergent provided the time step is below a (non-restrictive) critical value (see Garvie, 2007 for further details).

Denoting the patches by Ω_i ($i = 1, 2$), we employed a uniform subdivision of the squares $\Omega_i = [a, b] \times [a, b]$, with grid points $(x_i, y_i) = (ih + a, jh + a)$, $i, j = 0, \dots, J$, where the space step is given by $h = (b - a)/J$. We also take a uniform subdivision of the time interval $[0, T]$ with time levels $t_n = n\Delta t$, $n = 1, \dots, N$, where the time step is $\Delta t = T/N$. Migration of predators and prey was restricted in both patches to a circle in the middle of the square domains with radius $(b - a)/60$, corresponding to a corridor connecting the two patches (see Fig. 1). It is a simplifying feature of the model that the migratory corridor maps pointwise from inside a circle of one domain to inside a circle in the second domain. We did not use a corridor that joins parts of the edges of the two domains together to avoid boundary effects polluting the solution (see Section 4 for more details.)

We comment that for the experiments on the largest domain ($[0, 300] \times [0, 300]$) the resulting sparse linear systems have on the order of one million unknowns, which are solved 96,000 times as we march forward in time from $t = 0$ –250. Thus the computations are numerically intensive, taking about a day to compute with the sparse GMRES algorithm in MATLAB (on a Mac Pro with a 2×3 GHz Dual-Core Intel Xeon processor).

3.2. Experimental results

We investigated the numerical solutions of (2) in 2D using the IMEX scheme described in Section 3.1 via four experiments discussed below. Experiments 1 and 2 involve predator migration only ($d_u = 0$), while Experiments 3 and 4 allow the migration of predators and prey. In all experiments the stationary states correspond to the spatially homogeneous systems of the decoupled equations (i.e., in the absence of migration). Details concerning the parameter values and initial data are given in the captions of the relevant figures.

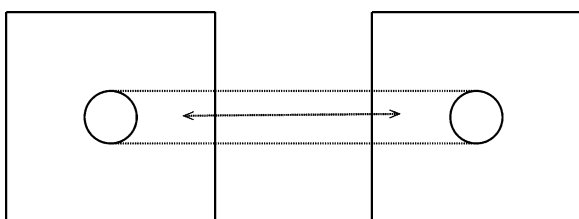


Fig. 1. Two-patch domain with connecting corridor.

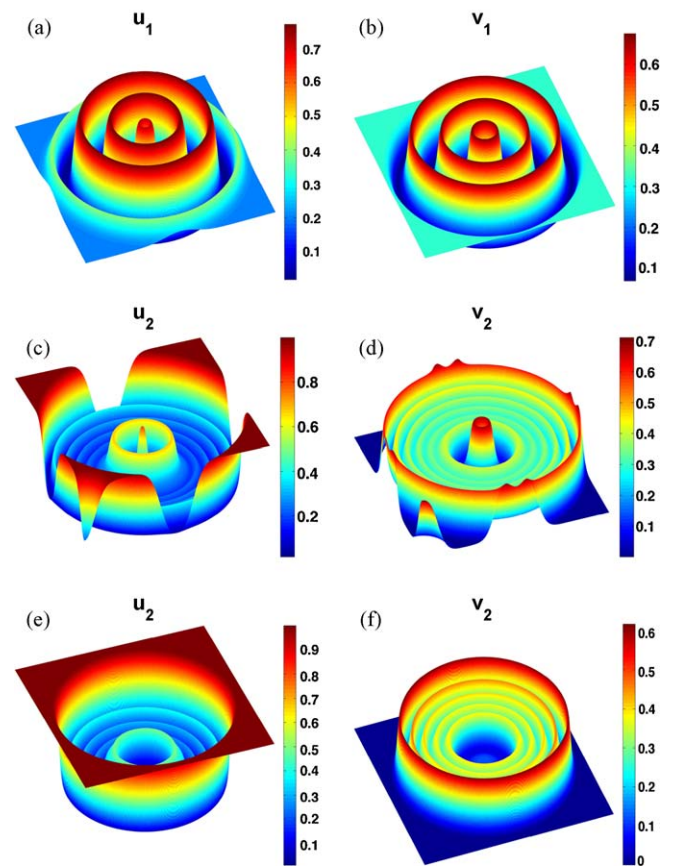


Fig. 2. Case (i): Approximate prey densities (1st column figures) and predator densities (2nd column figures) within patch 1 at $T = 250$ (row 1 figures) and patch 2 at $T = 140$ (rows 2 and 3 figures) on the square $[0, 300] \times [0, 300]$ with temporal and spatial discretization parameters of $1/384$ and $1/2$ respectively. Parameter values in both patches: $\alpha_i = 1/5$, $\beta_i = 1$, $\gamma_i = 1/2$, $\delta_i = 1$ ($i = 1, 2$). Initial data: $u_{10} = 0.2$, $v_{10} = 0.32$, $u_{20} = 0.2$, $v_{20} = 0$ (local extinction). Migration rates: figures (a)–(d) $d_v = 1$, $d_u = 0$; figures (e) and (f) $d_v = 1 \times 10^{-6}$, $d_u = 0$.

3.2.1. Predator migration only

In Fig. 2(a)–(f) the initial data are the stationary states of predators and prey in patch 1 and the stationary state of prey in patch 2, but with the local extinction of predators in patch 2. The parameter values were chosen to be the same in both patches. We note that the particular choice of initial conditions causes an initial migration of predators from patch 1 to patch 2.

3.2.1.1. Experiment 1. With migration rates $d_v = 1$ and $d_u = 0$ the evolution of the system rapidly led to the spread of predators and prey throughout the two patches (Fig. 2(a)–(d)). Behind the wave front the circular bands of regular peaks and troughs are clearly visible corresponding to the generation of ‘target patterns’.

3.2.1.2. Experiment 2. With migration rates $d_v = 1 \times 10^{-6}$ and $d_u = 0$ the stationary states of predators and prey in patch 1 persisted (not shown), while in patch 2 we see ‘target patterns’ (Fig. 2(e)–(f)), similar to those observed in Experiment 1.

3.2.2. Predator and prey migration

In Fig. 3(a)–(d) the initial data are the stationary states of predators and prey. Different parameter sets were chosen in the two patches. We note that the particular choice of initial conditions causes an initial migration of predators from patch 2 to patch 1, and an initial migration of prey from patch 1 to patch 2.

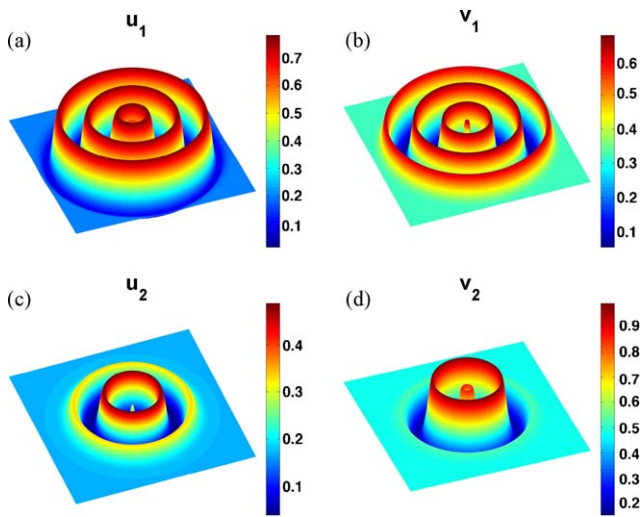


Fig. 3. Case (ii): Approximate prey densities (1st column figures) and predator densities (2nd column figures) within patch 1 at time $T = 250$ (row 1 figures) and patch 2 at $T = 350$ (row 2 figures) on the square $[0, 300] \times [0, 300]$ with temporal and spatial discretization parameters of $1/384$ and $1/2$ respectively. Parameter values in patch 1: $\alpha_1 = 1/5$, $\beta_1 = 1$, $\gamma_1 = 1/2$, $\delta_1 = 1$. Parameter values in patch 2: $\alpha_2 = 2/5$, $\beta_2 = 2$, $\gamma_2 = 3/5$, $\delta_2 = 1$. Initial data: $u_{10} = 0.2$, $v_{10} = 0.32$, $u_{20} = 0.1714$, $v_{20} = 0.4735$. Migration rates: $d_v = 1$, $d_u = 1$.

3.2.2.1. Experiment 3. With migration rates $d_v = d_u = 1$ the evolution of the system rapidly led to the spread of predators and prey throughout both patches (Fig. 3(a)–(d)) corresponding to ‘target patterns’, however, the wavefront speed of the target patterns are faster in patch 1 than in patch 2.

3.2.2.2. Experiment 4. With migration rates $d_v = d_u = 1 \times 10^{-6}$ the stationary states of predators and prey in both patches persisted (results not shown).

4. Conclusions and discussion

It is tempting to try and interpret the numerical results from the experiments in the previous section in the light of traditional metapopulation theory, namely, that low migration rates lead to asynchronous population dynamics, while high migration rates generate synchronous population dynamics (see Koelle and Vandermeer, 2005; and the references therein). In this context the synchrony of local populations refers to the extent that local populations are the same at different locations. However, the results generated in this paper are not strictly comparable with results predicted by the traditional theory. This is because studies aimed at understanding when dispersal (or migration in our context) lead to synchrony focus on the long-time (or ‘asymptotic’) behavior of population dynamics (Hastings and Goldwyn, 2008). However, our results represent the *transient* dynamics of fluctuating local populations. Furthermore, due to the artificial nature of the zero-flux boundary conditions on a square domain, it makes little sense to run the simulations for a long time. This is because once the wavefront of a target wave reaches the edge of the domain the boundary conditions artificially pollute and damp the solution. In spite of this drawback the results are interesting for various reasons. Firstly, researchers are only recently becoming aware of the role that transient dynamics play in understanding ecological systems (Hastings, 2004). Secondly, although there have been a number of studies investigating metapopulation dynamics using just two spatially homogeneous patches (see, for example Hastings, 2001; Jansen, 2001; Blasius et al., 1999; Koelle and Vandermeer, 2005; El Abdllaoui et al., 2007), to the best of our knowledge the results in this paper generalize for the first time

such studies to the partial differential equation setting as the patches in our model are spatially heterogeneous. We now discuss some specific implications of the numerical results.

For the first set of experiments, using two different migration rates, we investigated the ability of predators to recolonize a patch where predators have undergone an extinction event. With predator migration high, and prey migration absent (Experiment 1), we observe rapid recolonization via the spread of periodic traveling waves (‘target waves’). Target waves are observed for both species in both patches. With predator migration low, and prey migration absent (Experiment 2), we observe target waves for predators and prey in patch 2, but *no new dynamics are initiated in patch 1*. The second set of experiments were designed to further elucidate the conditions under which target waves are generated with both predator and prey migration. Starting from the stationary states in both patches, and high migration rates of both predators and prey (Experiment 3), the evolution of the system led to the rapid spread of target waves throughout both patches. If the migration rates of predators and prey are low (Experiment 4), the stationary states persist in both patches, and *no new dynamics are observed in either patch*. We also ran additional experiments on a smaller domain ($[0, 100] \times [0, 100]$) and confirmed that the stationary states persist until the large final time $T = 1000$.

One might argue that the target waves in our experiments are simply due to a new way of generating invasion, rather than the result of a new mechanism. However, the absence of new dynamics in patch 1 with a low predator migration rate (Experiment 2), and the absence of new dynamics in either patch with low migration rates (Experiment 4) suggests otherwise. It is well-known that for predator–prey models with logistic growth of the prey (and hence no Allee effect) and standard functional response of the predators (e.g., Holling Type II), any infinitesimal initial distribution of prey results in its successful invasion (Malchow et al., 2008). Thus with the traditional theory of invasion small predator migration rates should always lead to invasion in our model, which is not the case in Experiment 4. Furthermore, additional preliminary numerical results on a smaller domain ($[0, 100] \times [0, 100]$) with a range of intermediate predator migration rates ($d = 10^{-n}$, $n = 1-4$), suggest that the generation of new dynamics depends on a threshold migration rate somewhere between $d = 10^{-2}$ and $d = 10^{-3}$, rather than on a gradual onset. However, additional experiments are needed to clarify these findings.

These essentially new dynamics have some interesting ecological implications with regard to the spatiotemporal dynamics of predators and prey. In terrestrial environments spatiotemporal patterns resembling periodic traveling waves have been observed in several natural populations, for example, field voles (MacKinnon et al., 2001) and red grouse (Moss et al., 2000). The mechanisms that lead to these periodic traveling wave phenomena in natural populations are still unknown, however the use of mathematical models to simulate predator–prey dynamics has provided some suggestive possibilities. Periodic traveling wave phenomena in 2D, for example, spiral waves and target patterns, are fundamental solution forms in oscillatory reaction–diffusion equations. Oscillatory reaction–diffusion equations possess a stable limit cycle in the reaction kinetics, and for appropriate parameters and initial data include the predator–prey models studied here. Previous results from numerical simulations of the solutions to oscillatory reaction–diffusion equations has provided two main conjectures for the generation of periodic traveling wave phenomena in natural populations, which are: invasion of a population of prey by predators (Sherratt et al., 1997); and the effect of landscape features that inhibit the movement of species (Sherratt et al., 2002). The results in this paper suggest a third new mechanism for the generation of periodic plane wave phenomena

in natural populations, namely, migration of predators and/or prey between subpopulations.

With the above considerations in mind we now make the following tentative conclusions:

- (i) For appropriate parameter sets, the generation of new dynamics relies on sufficiently high migration rates of predators (and or prey).
- (ii) The results suggest a possible new mechanism for the spread of periodic traveling waves in natural populations.
- (iii) There may be a threshold level of migration rates needed for (i) above.

It is interesting that the transient dynamics show the reverse of what is predicted by traditional metapopulation dynamics for the long-term situation, namely, that dispersal leads to synchrony. However, our results are consistent with results from the coupled two-patch model by (Jansen, 2001) who found that low migration rates led to synchrony, while large predator migration rates give rise to more complicated dynamics.

With regard to evidence of predator–prey metapopulation dynamics in the field, or in laboratory experiments, there are few studies (Holyoak and Lawler, 1996), thus the importance of using modeling and numerical simulation to help understand metapopulation dynamics. For example, Gonzalez et al. (1998) tested the rescue effect hypothesis for an entire fragmented moss-based ecosystem, and demonstrated that immigration stopped the decline in both abundance and distribution of species. In a different laboratory study Holyoak and Lawler (1996) investigated bottles containing protistan predator–prey pairs connected by tubes. The researchers found that dispersal made local dynamics more prone to extinction, yet promoted regional persistence. Several older laboratory studies demonstrated that habitat subdivision promotes coexistence of predators and prey, however these investigations failed to distinguish between regional and local dynamics (see Holyoak and Lawler, 1996 and the references therein).

The results presented here provide new insights into how the transient dynamics of dispersal in true spatially structured metapopulations possess features not held by models with coupled spatially homogeneous patches. Future work will need to investigate further the transient dynamics, in particular, the possible threshold level of migration in point (iii) above. It is also not clear to us why the target waves of Experiment 2 in patch 2 do not initiate new dynamics in patch 1. Future studies will need to investigate how both the size and placement of the migratory corridor affects metapopulation dynamics. More realistic models will also need to include a greater number of patches, and incorporate time-delays in the migration terms.

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References

- Blasius, B., Huppert, A., Stone, L., 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature* 399 (6734), 354–359.
- Brown, J., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449.
- Comins, H., Hassell, M., May, R., 1992. The spatial dynamics of host–parasitoid systems. *J. Anim. Ecol.* 61 (3), 735–748.
- Crowley, P., 1981. Dispersal and the stability of predator–prey interactions. *Am. Nat.* 118 (5), 673–701.
- Czárán, T., 1998. *Spatiotemporal Models of Population and Community Dynamics*. Population and Community Biology Series, vol. 21. Chapman and Hall.
- El Abdllaoui, A., Auger, P., Kooi, B., Bravo de la Parra, B., Mchich, R., 2007. Effects of density-dependent migrations on stability of a two-patch predator–prey model. *Math. Biosci.* 210, 335–354.
- Garvie, M., 2007. Finite difference schemes for reaction–diffusion equations modelling predator–prey interactions in MATLAB. *Bull. Math. Biol.* 69 (3), 931–956.
- Gentleman, W., Leising, A., Frost, B., Strom, S., Murray, J., 2003. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep-Sea Res. Pt. II* 50, 2847–2875.
- Gonzalez, A., Lawton, J., Gilbert, F., Blackburn, T., Evans-Freke, I., 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* 281, 2045–2047.
- Gurney, W., Veitch, A., Cruickshank, I., McGeachin, G., 1998. Circles and spirals: population persistence in a spatially explicit predator–prey model. *Ecology* 79 (7), 2516–2530.
- Hanski, I., 1996. *Metapopulation ecology*. In: Rhodes, Jr., O., Chesser, R.K., Smith, M.H. (Eds.), *Population Dynamics in Ecological Space and Time*. University of Chicago Press, Chicago, pp. 13–43.
- Hanski, I., 1998. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I., Gilpin, M., 1997. *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego.
- Hanski, I., Singer, M., 2001. Extinction–colonization dynamics and host–plant choice in butterfly metapopulations. *Am. Nat.* 158 (4), 341–353.
- Harrison, S., Taylor, A., 1997. Empirical evidence for metapopulation dynamics. In: Hanski, I., Gilpin, M. (Eds.), *Metapopulation Biology*. Academic Press, San Diego, pp. 27–42.
- Hassell, M., Comins, H., May, R., 1991. Spatial structure and chaos in insect population-dynamics. *Nature* 353 (6341), 255–258.
- Hastings, A., 2001. Transient dynamics and persistence. *Ecol. Lett.* 4, 215–220.
- Hastings, A., 2004. Transients: the key to long-term ecological understanding? *Trends Ecol. Evol.* 19, 39–45.
- Hastings, A., Goldwyn, E., 2008. When can dispersal synchronize populations? *Theor. Popul. Biol.* 73, 395–402.
- Holling, C., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Holyoak, M., Lawler, S., 1996. Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. *Ecology* 77 (6), 1867–1879.
- Jansen, V., 1995. Regulation of predator–prey systems through spatial interactions: a possible solution to the paradox of enrichment. *OIKOS* 74 (3), 384–390.
- Jansen, V., 2001. The dynamics of two diffusively coupled predator–prey populations. *Theor. Popul. Ecol.* 59, 119–131.
- Jansen, V., de Roos, A., 2000. The role of space in reducing predator–prey cycles. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, Cambridge, pp. 183–201.
- Jansen, V., Lloyd, A., 2000. Local stability analysis of spatially homogeneous solutions of multi-patch systems. *J. Math. Biol.* 41, 232–252.
- Jeschke, J., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72 (1), 95–112.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* 326 (6111), 388–390.
- Kareiva, P., 1990. Population dynamics in spatially complex environments—theory and data. *Phil. Trans. R. Soc. Lond. Series B* 330 (1257), 175–190.
- Koelle, K., Vandermeer, J., 2005. Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecol. Lett.* 8, 167–175.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15 (3), 237–240.
- MacKinnon, J., Lambin, X., Elston, D., Thomas, C., Sherratt, T., Petty, S., 2001. Scale invariant spatio-temporal patterns of field vole density. *J. Anim. Ecol.* 70, 101–111.
- Malchow, H., Petrovskii, S., Venturino, E., 2008. *Spatiotemporal Patterns in Ecology and Epidemiology: Theory, Models, and Simulation*. Mathematical & Computational Biology, vol. 17. Chapman & Hall/CRC.
- Medvinsky, A., Petrovskii, S., Tikhonova, I., Malchow, H., Li, B.-L., 2002. Spatiotemporal complexity of plankton and fish dynamics. *SIAM Rev.* 44 (3), 311–370.
- Moss, R., Elston, D., Watson, A., 2000. Spatial asynchrony and demographic traveling waves during red grouse population cycles. *Ecology* 81, 981–989.
- Murray, J., 1993. *Mathematical Biology of Biomathematics Texts*, vol. 19. Springer, Berlin.
- Nee, S., May, R., Hassell, M., 1997. Two-species metapopulation models. In: Hanski, I., Gilpin, M. (Eds.), *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, pp. 123–147.
- Sherratt, J., 2001. Periodic travelling waves in cyclic predator–prey systems. *Ecol. Lett.* 4, 30–37.
- Sherratt, J., Eagan, B., Lewis, M., 1997. Oscillations and chaos behind predator–prey invasion: mathematical artifact or ecological reality? *Phil. Trans. R. Soc. Lond. B* 352, 21–38.
- Sherratt, J., Lambin, X., Thomas, C., Sherratt, T., 2002. Generation of periodic waves by landscape features in cyclic predator–prey systems. *Proc. R. Soc. Lond. B* 269, 327–334.
- Sherratt, J., Lewis, M., Fowler, A., 1995. Ecological chaos in the wake of invasion. *Proc. Natl. Acad. Sci.* 92, 2524–2528.
- Skalski, G., Gilliam, J.F., 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* 82 (11), 3083–3092.
- Taylor, A., 1990. Metapopulations, dispersal, and predator–prey dynamics—an overview. *Ecology* 71 (2), 429–433.