Discrete Time Coupled Logistic Equations with Symmetric Dispersal

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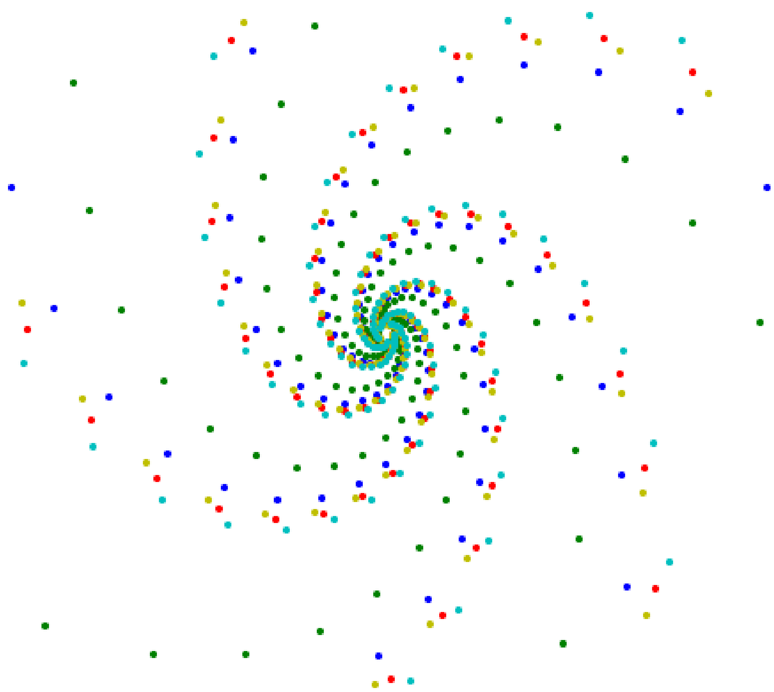


Abstract: A simple two patch logistic model with symmetric dispersal between patches is explored and compared with a single patch model. Numerical simulations show that stable attractors cannot only be conserved when a moderate amount of dispersal is added to the system, but dispersal can also be a mechanism of organization in a two patch system. Furthermore, the two patch system is extremely sensitive to initial conditions.

Introduction

Most ecological environments are not spatially uniform. The simplest way to account for a spatially heterogeneous environment is to divide a given area into patches which may differ in resource quality. In the simplest case, one can look at a two patch system. Because dispersal allows for gene flow, more advantageous exploitation of the environment and determines the ability of invasive species to displace resident species, it is of much interest to conservation biology and restoration biology; it is therefore essential that dispersal be accounted for when modeling an ecological system. This can be done in a many ways, each varying greatly in complexity. The simplest way to include dispersal dynamics is to include a constant dispersal parameter which represents the fraction of the population in each patch which leaves after the growth event at each time step. When this parameter is larger than zero, the patches are said to be coupled.

Background

Much is known about the dynamics of the one dimensional logistic map, $x(n+1) = rx(n)[1 - x(n)]$. For example, for r∈[3,1+$\sqrt{6}$] the map exhibits a stable period-2 cycle; thereafter a series of period doublings occur as r increases, with chaos setting in at just below r=3.57[2]. Another notable interval of the growth parameter is around r=1+$\sqrt{8}$, where a superstable period-3 cycle occurs[2].

If one models a species with non overlapping generations in a heterogeneous environment by considering a two patch system, each experiencing logistic growth followed by symmetric dispersal event, many questions arise. One can consider how including dispersal affects the previously mentioned stable cycles, as well as what affect dispersal will have in a setting where a single logistic patch experiences chaos.

Dynamical System

The dynamics of a two patch model with logistic growth in each patch can be described by the following equations:

$$x_1(n+1) = \hat{x_1}(n) + d[\hat{x_2}(n) - \hat{x_1}(n)]$$
$$x_2(n+1) = \hat{x_2}(n) + d[\hat{x_1}(n) - \hat{x_2}(n)]$$

Where the dispersal parameter, d∈[0,0.5] and

$$\hat{x_1}(n) = r_1 x_1(n)[1 - x_1(n)]$$
$$\hat{x_2}(n) = r_2 x_2(n)[1 - x_2(n)]$$

describe the dynamics before dispersal is accounted for.

Here, x_1 and x_2, which take values in [0,1], are the populations levels of patch 1 and patch 2, respectively, and r_1 >0 and r_2 >0 are the logistic growth rates for each patch. The behavior for different parameter sets (r_1,r_2,d) is explored and compared to a one patch logistic system. Unless noted otherwise, all results are for $r_1 = r_2$, and all initial conditions are chosen randomly from a uniform [0,1] distribution.

Methods

A variety of numerical methods can be employed when investigating the behavior of this system. Using the pylab module of matplotlib to create bifurcation diagrams is particularly useful for identifying parameter sets which may lead to significant behavior. Using pylab to plot the time series for various parameter sets allows one to analyze the range of behavior of the two patch system. Furthermore, Lyapunov characteristic exponents can be numerically estimated in order to measure the degree of chaos in the system for various parameter sets. Plotting the time series starting from a cluster of different initial conditions demonstrates how sensitive the system is to initial conditions.

Results:

Behavior

Bifurcation diagrams of r vs $x_1 + x_2$ and r vs $x_1 - x_2$ for various fixed values of d reveal that for larger values of d the dynamics of the total population is analogous to that of a single logistic patch, and for intermediate values of d behavior unique to the two patch system may occur. A few notable parameter sets discovered from bifurcation diagrams for a range of d values are (3.7,3.7.0.1) (shown below) and (3.8,3.8.0.15). The dynamics of these parameter sets are further investigated with other numerical methods.

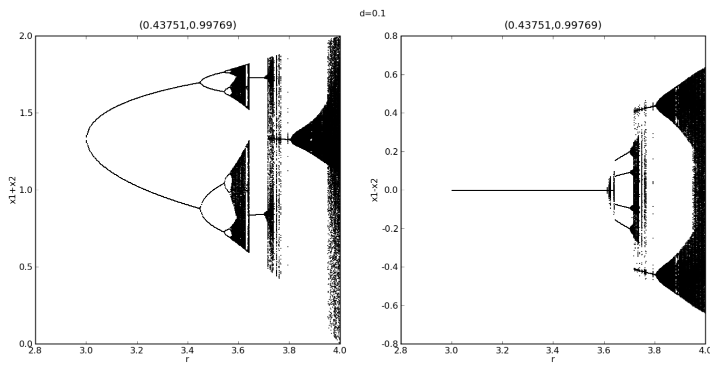
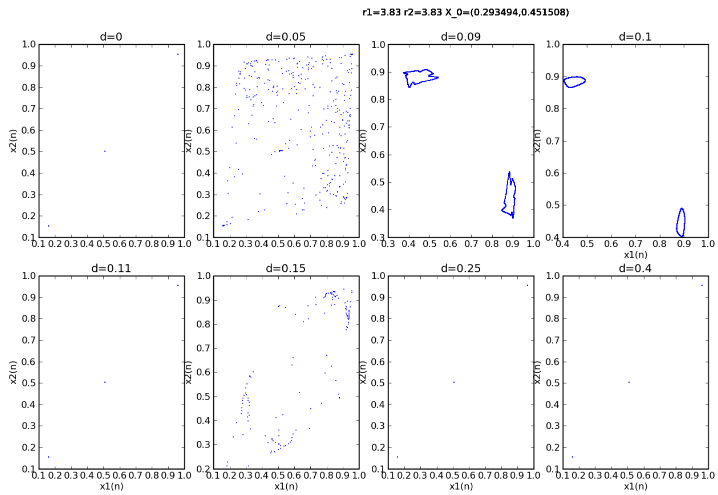


Figure 1: There is an interval around r=3.7 where the total population has a period-2 cycle and the difference has a period-4 cycle. Similar behavior is seen in a smaller window, starting at r=3.8, for d=0.15.

The attractors of the two patch system can be revealed by plotting the time series $x_1(n)$ vs $x_2(n)$. By allowing d to vary, plotting the time series for a fixed value of r elucidates the affect of the coupling parameter. Recall that in the case of a single logistic patch with r=3.3 there is a stable period-2 cycle. Plotting the time series for various values of demonstrates that even as the fraction of the population dispersing at each time step is increased from zero, the period-2 cycle remains. The corresponding Lyapunov characteristic exponents*[0]are all negative, indicating that both organization and stability are maintained as d is increased to it's maximum allowed value. Similarly, if one plots the time series for r=3.83, the stable period-3 cycle remains stable for large values of d:

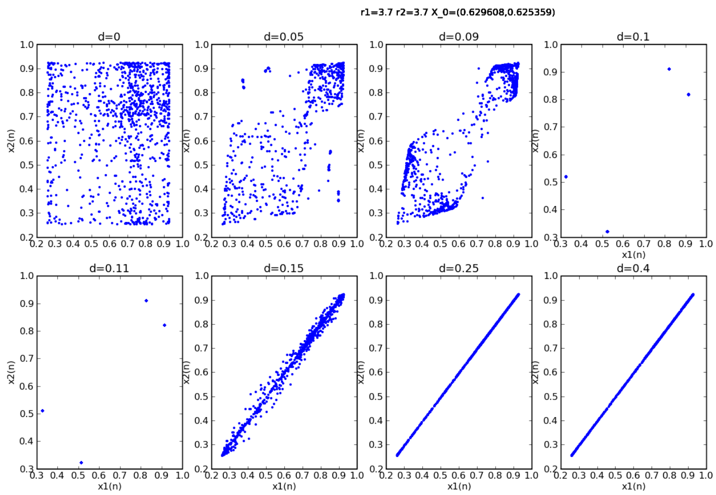
[0]Lyapunov characteristic exponent tables are included in the supporting information



r=3.83: Stability is maintained for large values of coupling.

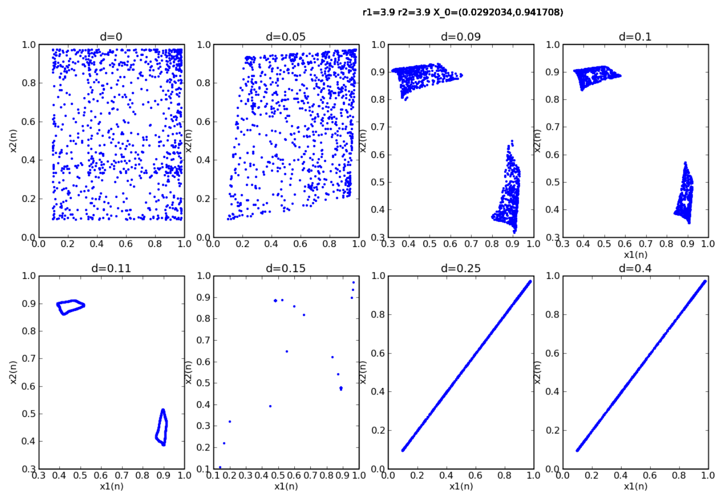
This case is more interesting, however, as for some intermediate values organization is lost and then regained in the form of closed trajectories. The Lyapunov characteristic exponents indicate that these closed trajectories are chaotic attractors. This occurrence of multiple attractors is different from the behavior seen in a single patch.

Another interesting behavior unique to the two patch system can be seen by plotting the time series for values of r which lead to chaotic behavior in the one patch system. For example, consider the previously mentioned parameter value r=3.7:



For r=3.7, increasing d creates organization.

As expected, for d=0 the iterates are scattered about the unit square. Notice though, as d is increased slightly to 0.05, organization already starts to occur and as it is increased further, iterates cluster around four values. The Lyapunov characteristic exponents for d=0.1 and 0.11 are negative indicating that this is a stable solution. Further increasing d leads to solutions on the line $x_1 = x_2$. This is very intriguing as increasing movement between patches each exhibiting chaotic behavior leads to both organization and stability. Another such example occurs for r=3.9:

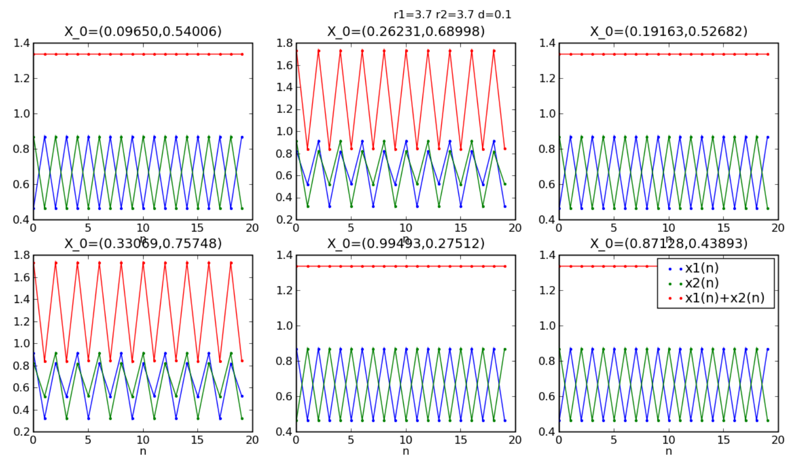


For r=3.9, increasing d creates both organization and stability.

As in the case for r=3.7, increasing d leads to organization. The two patches in the time series for d=0.09 and 0.1 are chaotic attractors, however, the closed trajectories obtained for d=0.11 have negative Lyapunov exponents and are thus *stable* attractors. The case of two stable quasiperiodic attractors is not possible in the one patch system.

Sensitivity to Initial Conditions

As previously mentioned, the initial conditions for all numerical simulations are chosen at random from a uniform [0,1] distribution. Running these simulations multiple times for any given parameter set may lead to different behavior, indicating a sensitivity to initial condition. For example, consider the parameter set (3.7,3.7,0.1). The bifurcation diagram shown above indicates that the total population has a period-2 cycle while the difference in the populations has a period-4 cycle. Also, the time series plot shows (x_1, x_2) accumulate around four points. However, if a different initial condition is chosen, the total population is constant, while the difference in the population has a period-2 cycle. In this case the time series plots shows (x_1, x_2) accumulate around two points, rather than four (see supporting information). This can be visualized in a different manner by plotting n vs x_1, x_2 and the total population:



Time series for r=3.7, d=0.1 starting from 6 different random initial conditions

The above figure shows that for this parameter setting there are several possible behavioral outcomes. There are two different out of phase solutions: one in which each time series is of period-2 and the total population is constant and another where each time series is of period-4 and the total population has a period-2 cycle. In the former case, the two populations bounce back and fourth between the same to values leading to a constant total population. In the latter case, the two populations oscillate between the same four values in such a way that the total population is of period two. Even when initial conditions are clustered, both solutions are seen, indicating that the basin of attraction for these two stable solutions do not have a nice shape. If one considers the parameter set (3.8,3.8,0.15) solutions starting from a cluster of initial conditions either exhibit one of the two out of phase solutions previously described, or chaotic behavior (see supporting information). The basin of attraction of these three outcomes is not apparent revealing that this system is extremely sensitive to initial condition.

Conclusions

Despite the fact that this model is the simplest model that accounts for spatial heterogeneity and dispersal, it exhibits behavior which is much more complicated than a single patch model. Furthermore, the differences occur when varying the coupling parameter only, as the growth rates for each patch were assumed to be identical. This mathematically strengthens the assertion that dispersal plays a key role in determining the long term dynamics of a population. Adding dispersal to a system in which each patch exhibits stable oscillatory behavior does not necessarily add chaos or disorder, but can preserve stable behavior. Interestingly, in a system where each individual patch has chaotic behavior, increasing the dispersal parameter can add order and stability.

Supporting Information

Lyapunov Characteristic Exponents

r_1=3.3 r_2=3.3 X_0=(0.651382,0.655136)

d	minLCE	maxLCE	Contraction	Difference
0.00	-0.618937	-0.618937	1.23787	1.55431e-015
0.05	-0.724298	-0.618937	-1.34323	0.0
0.09	-0.817388	-0.618937	-1.43633	4.52971e-014
0.10	-0.842081	-0.618937	-1.46102	1.08802e-014
0.11	-0.867399	-0.618937	-1.48634	1.53211e-014
0.15	-0.975612	-0.618937	-1.59455	9.76996e-015
0.25	-1.31208	-0.618937	-1.93102	1.68754e-014
0.40	-2.22838	-0.618937	-2.84731	1.64313e-014

r_1=3.83 r_2=3.83 X_0=(0.293494,0.451508)

d	minLCE	maxLCE	Contraction	Difference
0.00	-0.36805	-0.36805	-0.7361	0.0
0.05	-0.221206	-0.128426	-0.349632	4.996e-016
0.09	-0.192739	0.00088242	-0.191857	4.16334e-016
0.10	-0.165714	0.000539196	-0.165174	2.77556e-017
0.11	-0.616512	-0.36805	-0.984562	7.43849e-015
0.15	-1.31946	-1.27764	-2.5971	3.9968e-015
0.25	-1.06578	-0.372635	-1.43842	8.88178e-015
0.40	-1.98207	-0.372635	-2.35471	1.95399e-014

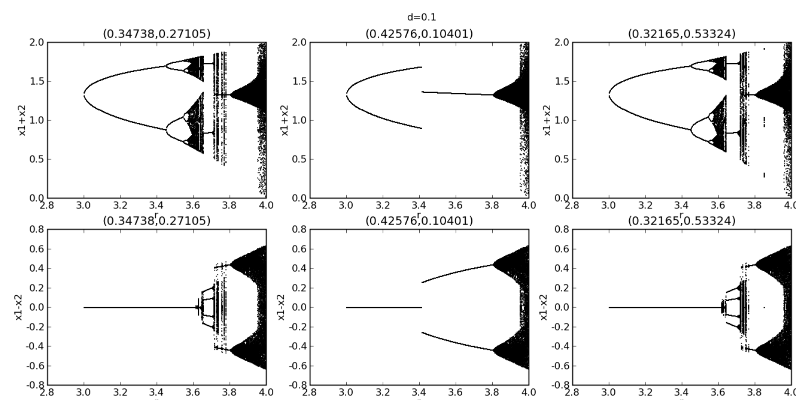
r_1=3.7 r_2=3.7 X_0=(0.629608,0.625359)

d	minLCE	maxLCE	Contraction	Difference
0.00	.357063	.356934	0.713997	3.33067e-016
0.05	0.0358699	0.14107	0.17694	2.77556e-016
0.09	.0838933	0.15496	0.238853	1.11022e-016
0.10	-0.0086781	-0.00823005	-0.0169082	1.17961e-016
0.11	-0.15356	-0.155202	-0.308763	1.9984e-015
0.15	0.0209622	0.349685	0.370647	1.11022e-016
0.25	-0.345175	0.347972	0.00279733	3.7817e-016
0.40	-1.25149	0.357947	-0.893544	7.77156e-016

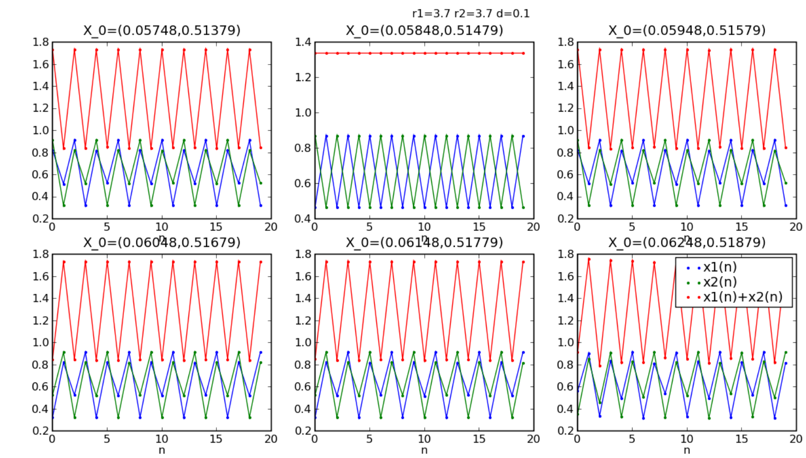
r_1=3.9 r_2=3.9 X_0=(0.0292034,0.941708)

d	minLCE	maxLCE	Contraction	Difference
0.00	0.489512	0.497681	0.987193	1.11022e-016
0.05	0.379957	0.441035	0.820992	8.88178e-016
0.09	0.100473	0.174591	0.275064	1.11022e-016
0.10	-0.00523404	0.0662479	0.0610139	5.55112e-017
0.11	-0.218253	-0.000680373	-0.218933	1.66533e-016
0.15	-0.546104	-0.540334	-1.08644	1.02141e-014
0.25	-0.194547	0.4986	0.304052	4.996e-016
0.40	-1.1219	0.487543	-0.634353	4.44089e-016

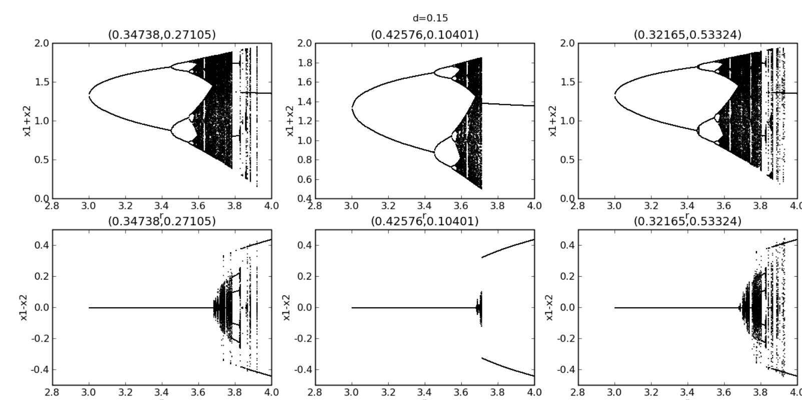
Sensitivity to Initial Conditions



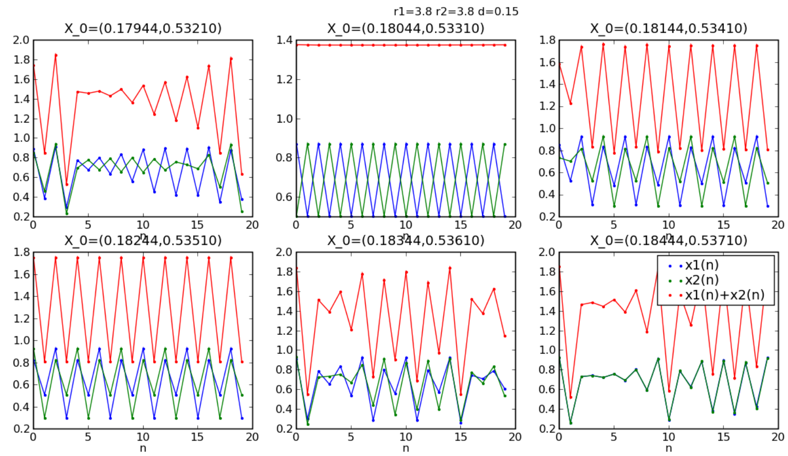
The first and third bifurcation diagram correspond to the out of phase period-4 solution, while the middle corresponds to the out of phase period-2 solution. All three initial conditions where chosen from a uniform [0,1] distribution.



For a cluster of initial conditions we see both types of out of phase solutions.



We see that the first and third diagrams correspond to out of phase period-4 solutions and that the window for this behavior is smaller in the third diagram.



For a cluster of initial conditions both types of out of phase solution as well as more chaotic behavior are exhibited.

References

1. Hastings,A.(1993) *Complex Interactions between dispersal and dynamics: Lessons from coupled logistic equations.* Ecology.74, 1362-1372.
2. Strogatz, Steven H. Nonlinear Dynamics and Chaos. Westview Press,2001.