Population Dynamics in Diffusive Coupled Insect Population

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Abstract

A variety of ecological models exhibit chaotic dynamics because of nonlinearities in population growth and interactions. Here, we will study the LPA model (beetle Tribolium). The LPA model is known to exhibit chaos. In this project, we investigate two things which are the effect of noise constant and the effect of diffusion combined with the LPA model. The effect of noise is not only to change the dynamics of total population density but also to blur the bifurcation diagram. Numerical simulations of the model have shown that diffusion can drive the total population of insects into complex patterns of variability in time. We will compare these simulations with simulations without diffusion. And we conclude that the diffusion coefficient is a bifurcation parameter and that there exist parameter regions with chaotic behavior and periodic solutions. This study demonstrates how diffusion term can be used to influence the chaotic dynamics of an insect population.

Keywords: diffusion, LPA model, insect population, Chaos, periodic behavior

1. Introduction

A variety of ecological models exhibit various patterns in population dynamics such as equilibrium steady state, periodic or chaotic dynamics caused by their nonlinearities in population growth and interactions. Sensitivity to initial conditions (initial population or control parameter) is a key characteristic of dynamics in population system. Many researchers have investigated how small perturbations of the control parameters have affected the ecology system to exhibit the chaotic behavior [1,2,3]. Population fluctuations are the result of stable points (node or spiral), stable periodic and aperiodic cycles, chaos, stable and unstable manifolds of invariant sets and multiple attractors. Population fluctuations depend on the stability of fixed points; stable points are where every trajectory goes to a fixed point, stable periodic trajectories occur when population numbers oscillate among a finite number of values and there is a limit cycle around the fixed point, aperiodic cycles occur when populations oscillate but the characteristics of the oscillation can change, and chaos which provides an unusual, apparently random, and intuitively unexpected prediction of population behavior.

The LPA model, describes the dynamics of larval, pupal, and adult Tribolium population, is known to exhibit chaotic pattern in their population. Many studies have examined the effect of small perturbations of the parameters, such as the survival rate of a pupa in the presence of an adult or the survival rate of an egg in the presence of both larvae and adults, on the dynamics of the total population density [4, 5]. A nonlinear mathematical model, LPA model, was used to identify a sensitive region of phase space where the addition of a few adult insects would result in a dampening of the life stage fluctuations.

The few ecological studies of chaos in spatial systems consider models in discrete time and space [6,7] or in discrete time and continuous space [8]. In all these models, the diffusive dispersal of organisms drives the biological system (prey-predator or host-parasitoid system) into chaotic dynamics. The results of discrete models cannot be applied directly to nonlinear interactions and dispersal in continuous time and space. It is well known that discrete models exhibit chaos more readily than their continuous counterparts. In this paper, A nonlinear mathematical model, LPA model, was used to identify a sensitive region of phase space where the addition of a few adult insects would result in a dampening of the life stage fluctuations. In other words, we investigate the effect of diffusion on the diffusive coupled LPA model. Numerical simulations of the model have shown that diffusion can drive adults into complex patterns of variability in time. The main point of this study is to determine whether these patterns are chaotic. We will demonstrate that there is diffusion induced chaos and diffusion induced periodicity in the LPA model with diffusion. And we conclude that the diffusion coefficient is a bifurcation parameter and that there exist parameter regions with chaotic behavior and periodic solutions.

2. Model

2. 1 LPA Model with Stochastic Terms

Many species of Tribolium (flour beetle) are cannibalistic, including the species Tribolium castaneum. The following model, which is called the LPA model, describes the dynamics of larval, pupal, and adult Tribolium populations at time *t* + 1 as a function of the populations at time *t* by means of a system of three difference equations

$$L_{t+1} = bA_t \exp(-C_{el}L_t - C_{ea}A_t + E_{1t}) \quad (1)$$

$$P_{t+1} = L_t(1-\mu_l)\exp(E_{2t}) \quad (2)$$

$$A_{t+1} = [P_t \exp\left(-C_{pa}A_t\right) + A_t(1-\mu_a)]\exp(E_{3t}) \quad (3)$$

where is L_t is the number of feeding larvae (referred to as the L-stage) at time t, P_t is the number of large larvae, non-feeding larvae, pupae, and callow adults (collectively the P-stage) and A_t is the number of sexually mature adults (A-stage animals). The unit of time is taken to be the feeding larval maturation interval so that after one unit of time a larva either dies or survives and pupates. The unit of time is 2 weeks and is, approximately, the average amount of time spent in the feeding larval stage under standard experimental conditions described in the reference [5]. The unit of time is also approximately the average duration of the P-stage. The quantity *b* is the number of larval recruits per adult per unit time in the absence of cannibalism. The fractions μ_l and μ_a are the larval and adult rates of mortality, respectively, in one-time unit.

The exponential nonlinearities account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fractions $A_t\exp(-C_{el})$ and $\exp(-C_{ea}A_t)$ are the probabilities that an egg is not eaten in the presence of L_t larvae and adults, respectively, in one-time unit [4]. The fraction $\exp\left(-C_{pa}A_t\right)$ is the survival probability of a pupa in the presence of A_t adults in one-time unit. The terms E_{1t}, E_{2t} and E_{3t} are random noise variables assumed to have a joint multivariate normal distribution with a mean vector of zeros and a variance-covariance matrix denoted by Σ (The variance-covariance matrix is estimated from experimental data in [5]. The maximum likelihood estimates in the variance- covariance matrices are σ11 = 0.3412, 2 = 0.2488, 3 = 1.627 × 14, 2 = 7.312 × 12, 3 = 34−1.719 × P1, and σ23 = 3.374 × 1). The deterministic skeleton of the model is identified by setting Σ = 0, or equivalently, by letting E_{1t}, E_{2t} and E_{3t}equal to zero in Eqs. 1–3.

The noise variables represent unpredictable departures of the observations from the deterministic behavior (resulting from environmental and other causes) and are assumed to be correlated with each other within a time unit but uncorrelated on longer time scales. These assumptions were found acceptable for many previous data sets by standard diagnostic analysis of time-series residuals. The adult mortality rate, μ_a, may be experimentally set to 0.96 by removing or adding adults at time of census. In Costantino et al. 1997 [4], recruitment into the adult stage was manipulated by removing or adding young adults at the time of census to make the number of new adult recruits consistent with the treatment value of C_{pa}.

2. 2 Diffusive coupled LPA Model

To pose the problem in its simplest form, we will assume that we are investigating the deterministic skeleton and Σ = 0. We will also assume that only adults move to other insect niches and no unpredictable external factors are acting. We set the rate of diffusion, *d*, to be the same for all niches. With these assumptions, we can generalize the LPA model to include the effects of diffusion. Consider a single dimension along which adults diffuse at the same constant rate d. Larvae and pupae do not move. Thus, there is no diffusion term in the populations of larvae and pupae.

$$L_{t+1}^{j} = bA_t^{j}\exp(-C_{el}L_t^{j} - C_{ea}A_t^{j}) \tag{4}$$

$$P_{t+1}^{j} = L_t^{j}(1-\mu_l) \tag{5}$$

where *j* is *jth* bin and *t* is the time

Now, consider the dynamics of the adult population. We will assume that adults can diffuse between bins. The equations in this case become

$$A_{t+1}^{j} = P_{t}^{j}\exp\left(-C_{pa}A_{t}^{j}\right) + A_{t}^{j}(1-\mu_a) + d(A_{t}^{j+1} - 2A_{t}^{j} + A_{t}^{j-1}) \tag{6}$$

$$A_{t+1}^{j} = P_{t}^{j}\exp\left(-C_{pa}A_{t}^{j}\right) + A_{t}^{j}(1-\mu_a) + d(A_{t}^{j-1} - A_{t}^{j}) \tag{7}$$

$$A_{t+1}^{j} = P_{t}^{j}\exp\left(-C_{pa}A_{t}^{j}\right) + A_{t}^{j}(1-\mu_a) + d(A_{t}^{j+1} - A_{t}^{j}) \tag{8}$$

where d is a diffusion coefficient. Eq. (6) is the case for interior bins, Eq. (7) and (8) are the case for the right and left boundary, respectively.

2. 3 Numerical Methods

For the computational simulation, the computer software (MATLAB) has been used. We iterated the LPA model for 64000 steps to see the long-term behavior of the total population. By changing the parameter, C_{pa}, the population dynamics changes giving rise to bifurcations in dynamics. In the case where $\Sigma = 0$ (in the absence of noise terms), for each C_{pa}, the dynamics of the adult population shows a stable equilibrium, periodic cycles or chaos. We simulated the LPA model with both the deterministic skeleton (without noise term) and stochastic terms (with noise term) to study the effect of noise on the dynamics of insect total population. For the simulation of LPA model with diffusion term, we used the deterministic skeleton to investigate the effect of diffusion on the dynamics. The evolution of the total population will be changed from steady state (equilibrium) to periodic cycles or periodic cycles to chaos with different value of bifurcation parameter, C_{pa} (Fig. 1).

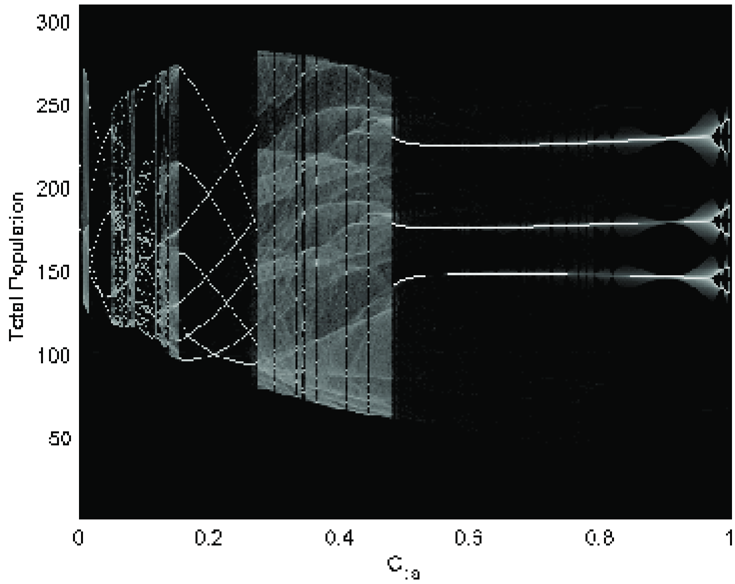

Figure 1: Density Bifurcation diagram for total population numbers (L-stage+P-stage+A-stage) using deterministic skeleton $\Sigma = 0$). For deterministic skeleton, the total population exhibits various patterns of

populations with respect to C_{pa}. We used the following parameter values b=10.45, 1 C_{el} = 0.01731, C_{ea} = 0.01310, μ_l = 0.2 and μ_a = 0.96.

2. 4 Dynamics of the Insect Population

The bifurcation diagram conveys information about how the dynamics of the total population changes as a function of the parameter, C_{pa}. The LPA model displays various patterns of populations for different values of C_{pa}. Fig. 1 shows is the density bifurcation diagram of the total population for the LPA model. The black color represents zero population, whereas white indicates high populations with gray scales in between. Smoothly distributed regions are evidence of quasi-periodicity or chaos, and the sharp lines represent periodic cycles. For C_{pa} = 0.0, the population dynamics shows a stable equilibrium. For $C_{pa} \in (0, 2.7]$, the different periodic cycles are shown and the most chaotic behaviors are shown in the range of $C_{pa} \in [2.8, 4.7]$ except some values of C_{pa}. The population dynamics over time is shown in Fig. 2. It is clearly observed that the total population is oscillating with different period for $C_{pa} = 0, 0.2$ and 0.7. However, the aperiodic cycle or chaotic pattern is shown for $C_{pa} = 0.4$

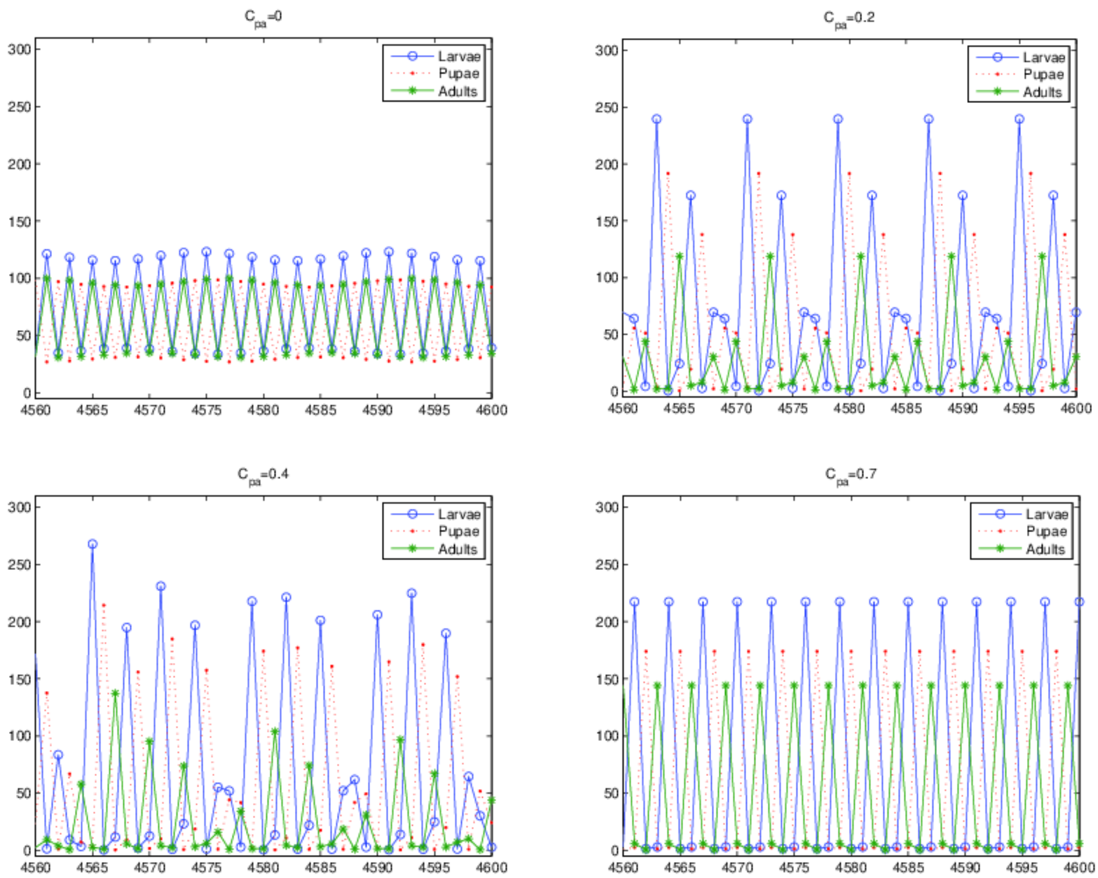

Figure 2: Dynamics of the LPA model for different values of C_{pa}. For C_{pa} = 0, 0.2 and 0.7, these graphs show periodic cycles. The total population is oscillating periodically; there are 8 periodic cycles and 3 periodic cycles, respectively. For a = 0.4, the population shows aperiodic or chaotic pattern.

3. Results

3.1 Density Bifurcation Diagram with Noise

There are several interesting things that can happen when the system is receiving noises. One of things is the pattern of noise-induced chaos in ecological system [5,9]. In general, the noise-induced chaotic pattern is referred to as an attractor with sensitive dependence on initial conditions, which changes the structure of the system upon switching off the noise. Here, we investigate the effect of noises on the LPA model.

For very small amplitude noise, the density bifurcation diagram shows qualitative changes in structures of the total population. In the deterministic skeleton, both periodic cycles and chaotic pattern co-exist in the region of $C_{pa} \in [2.8, 4.7]$. However, for the amplitude of noise $(\epsilon) = 0.00001$, the region of $C_{pa} \in [2.8, 4.7]$ is completely chaotic region, that is, no periodic cycles in the total population exist. This implies the noise can induce the chaotic pattern in an insect population. Furthermore, increasing the amplitude of noise is to blur the bifurcation diagram. Structure is still apparent even for $\epsilon = 0.0001$. However, increasing the amplitude results in destroying the structure of bifurcation diagram.

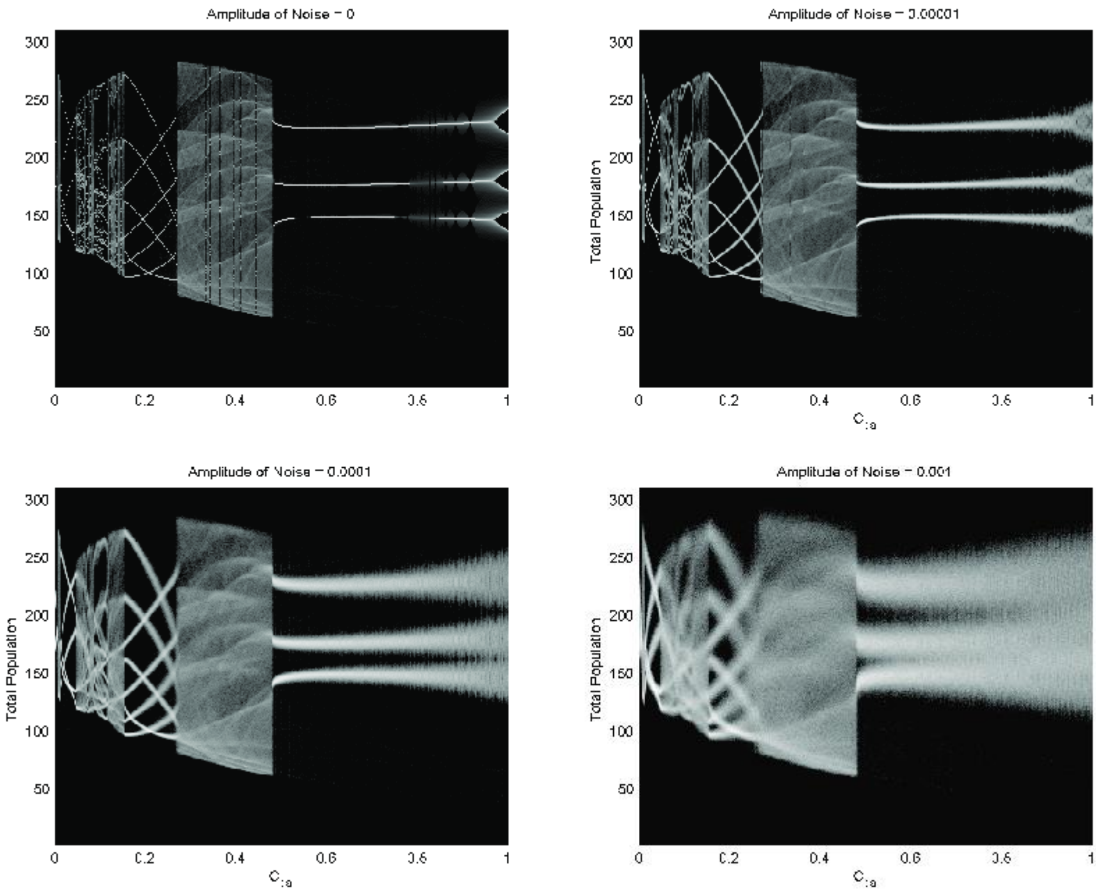

Figure 3: The effect of noise on the total population. Noise induces chaos and blur the bifurcation diagram.

3.2 Density Bifurcation Diagram for Diffusive Coupled System.

Numerous studies have demonstrated that diffusion changes dynamics patterns in biological and ecological systems. A continuous predator-prey model in which two populations diffuse along a spatial gradient is shown to exhibit temporal chaotic pattern at a fixed point in space. In other words, low diffusion values induce a periodic system to aperiodic or chaotic behavior with sensitivity to initial conditions [10]. In neuroscience, a strong diffusive connection in a diffusive coupled system induces synchronization of connected neurons in a complex neural network [11]. Here, we study the effect of diffusion in an insect population.

Figure 4 shows the bifurcation diagram for the control parameter C_{pa} with different values of the diffusion amplitude coefficient (d = 0, 0.0001, 0.001, 0.005, 0.02 and 0.03, respectively). The figures show the effect of the diffusion on the total population density. Different values of the diffusion coefficient induce either chaotic or periodic population fluctuation. We used the following parameter values b=10.45, C_{el} = 0.01731, C_{ea}= 0.01310, μ_l = 0.2 and μ_a= 0.96. For the control case (before the system is diffusive coupled or the diffusion coefficient= 0), the mixed population fluctuation (periodic and chaotic pattern in the total population) exhibits mostly in the range of C_{pa} $\in$ [0.28 0.47]. However, increasing the diffusion amplitude up to d = 0.005 results in expanding the range of C_{pa} where the population fluctuation exhibits the chaotic behavior. Furthermore, for the higher value of d=0.005, the density bifurcation diagram is shown to exhibit the different structure from the one with lower values of the diffusion coefficient.

Figure 5 shows the dynamics of the LPA model for different values of the diffusion coefficient with fixed C_{pa}=0.02, 0.2, 0.4, and 0.7, respectively. In the deterministic skeleton, the total population density exhibits 4 periodic cycles for C_{pa}= 0.02. However, increasing the diffusion coefficient values results in changing the dynamics from the periodic cycles to chaos and chaos to periodic pattern in their total population density diagram. For C_{pa}= 0.4, the total population shows aperiodic cycles or chaos. The diffusion term derives the total population density to the periodic pattern with 7 periodic cycles in the region of the diffusion coefficient between 0.033 and 0.038. Figure 6 shows how small change in diffusion coefficient induces chaotic pattern from periodic cycles.

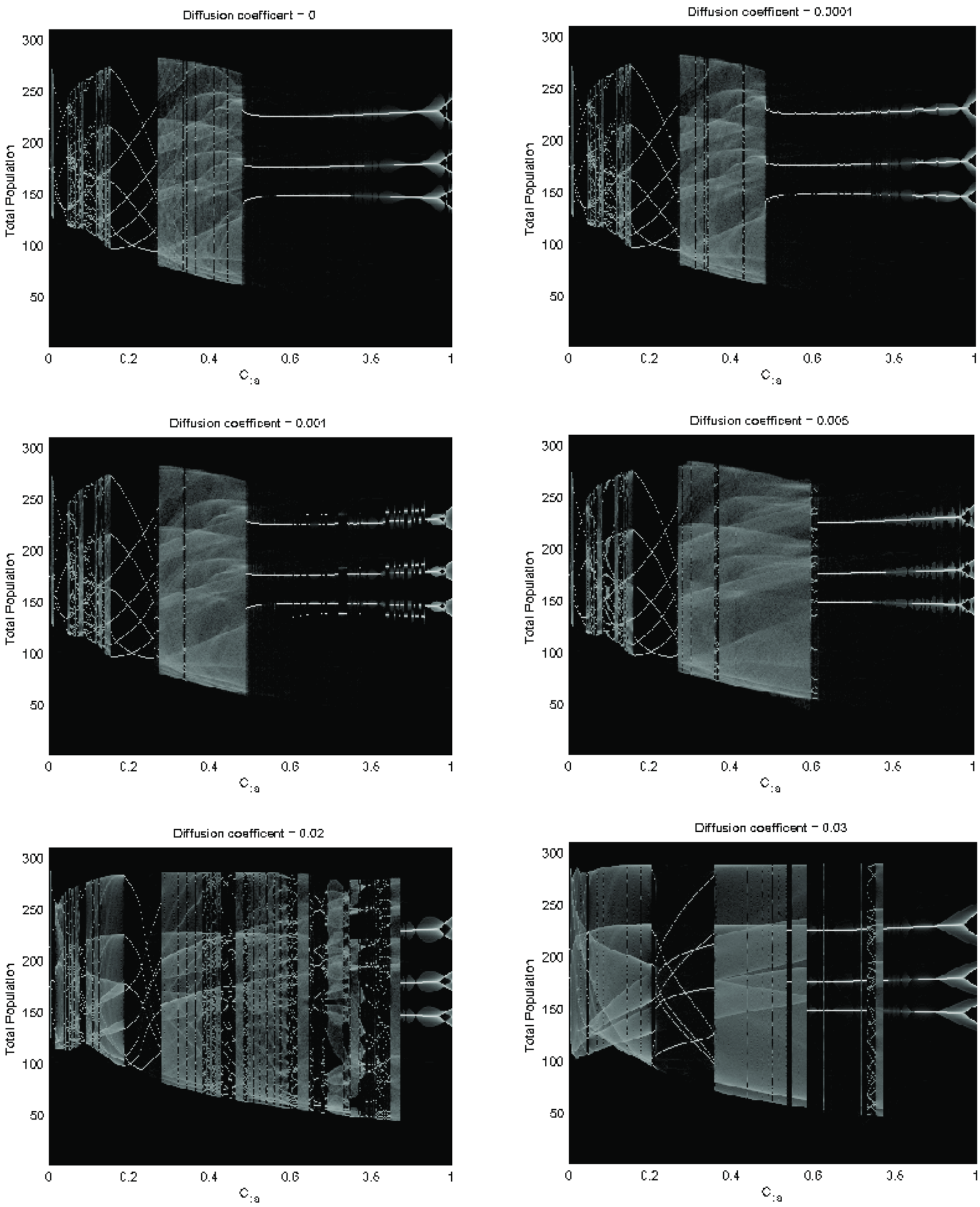

Figure 4: The bifurcation diagram for the control parameter C_{pa} (x-axis) with different values of the diffusion amplitude coefficient (*d* = 0, 0.0001, 0.001, 0.005, 0.02 and 0.03, respectively).

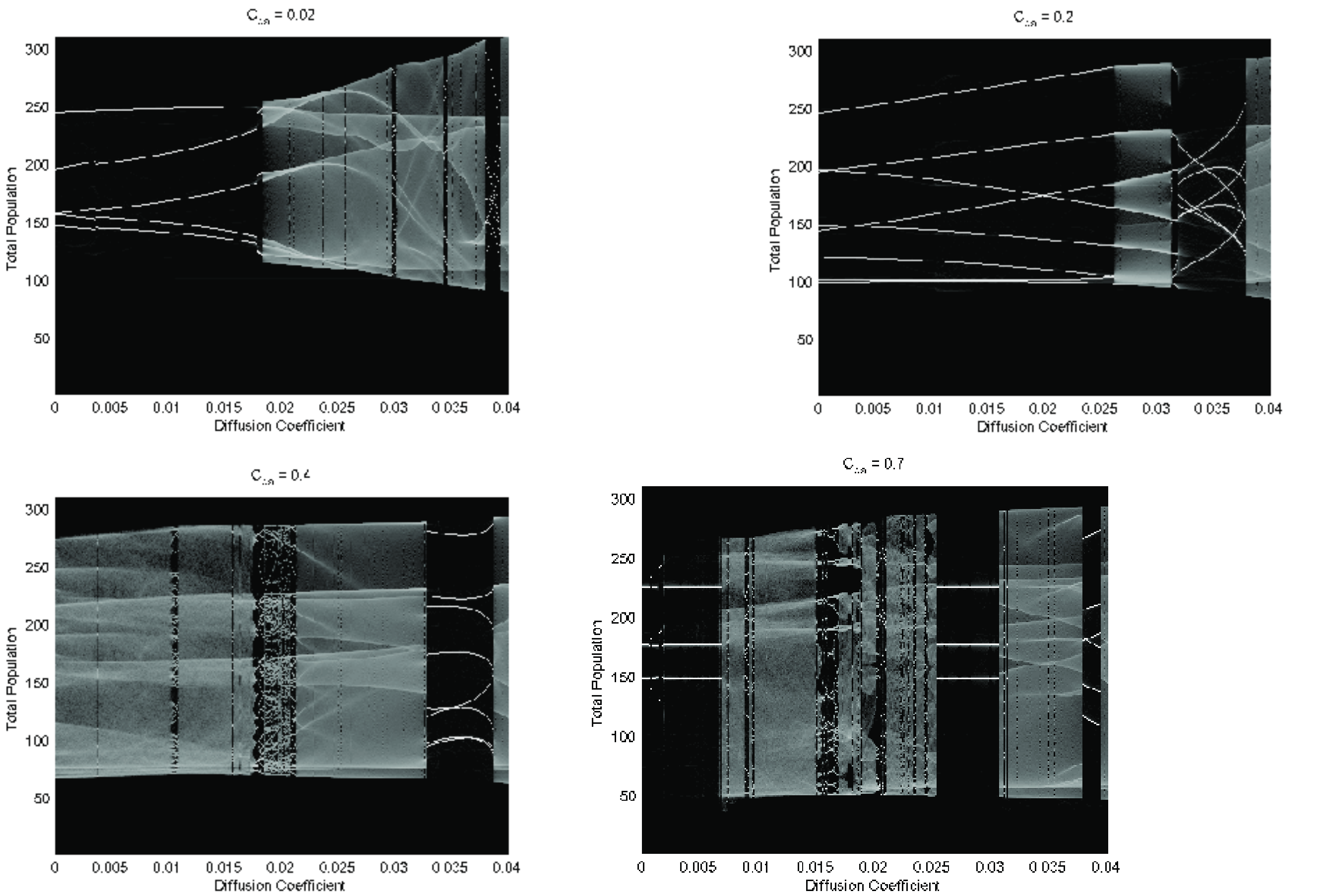

Figure 5: Dynamics of the LPA model for different values of the diffusion coefficient with fixed C_{pa}=0.02, 0.2, 0.4, and 0.7, respectively

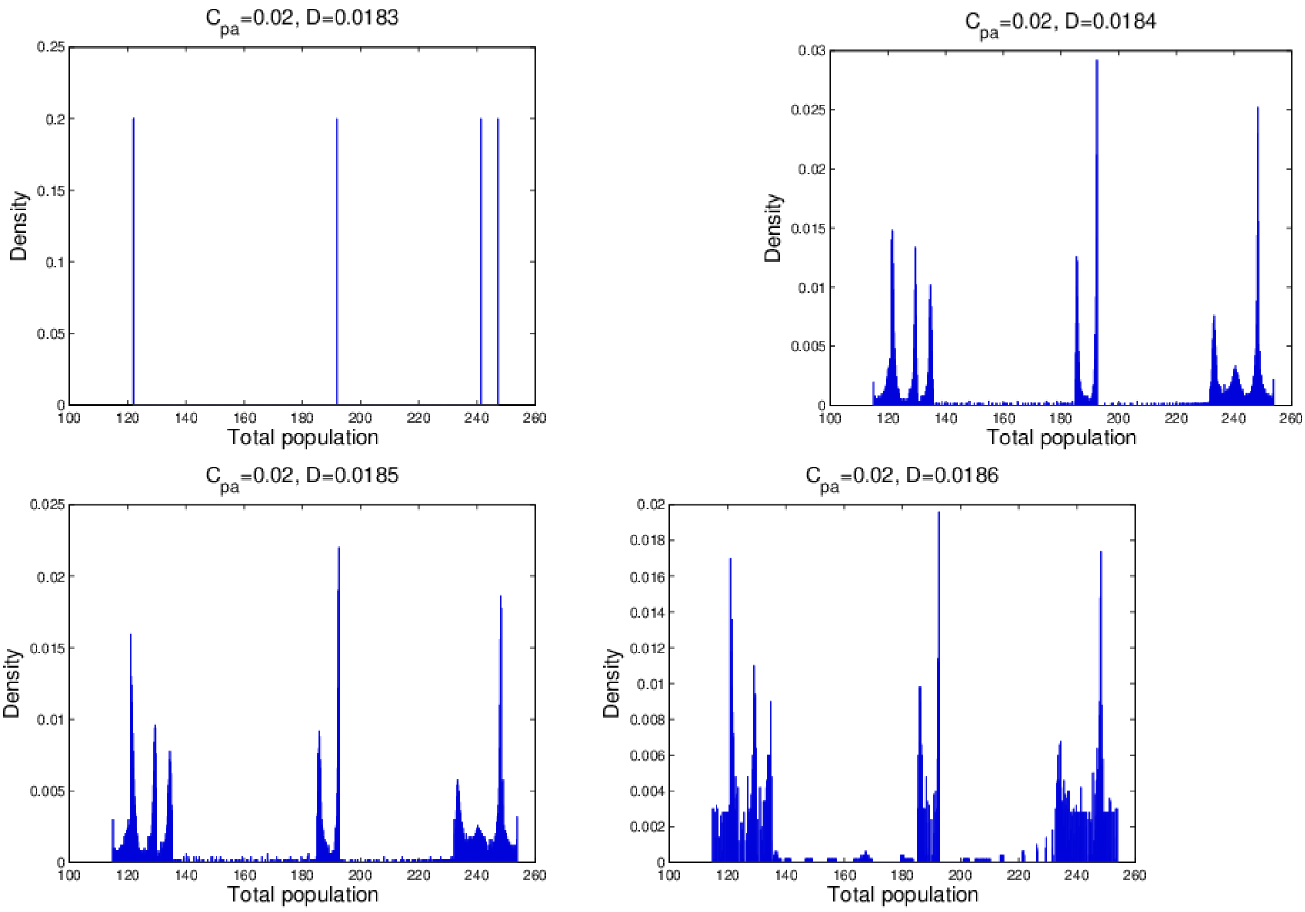

Figure 6: Histograms of how the small perturbation of the diffusion amplitude affects the population fluctuation and how the periodic cycles of the total population changes into a chaotic pattern by a small change in diffusion.

5. Conclusion

We discussed the dynamics of total population with the LPA model. In this discussion, we used the density bifurcation diagram (without noise and with noise) to see the dynamics. The effect of noise is to blur the density bifurcation diagram. Small-scale features blur most easily and large-scale features retain their characteristics longer as the amplitude of noise increases. In the experimental setting, therefore, in the last panel of Figure 3, we show predicted population densities for C_{pa} = 0 to 1. No fine detail is visible. The only relic of the solution is the change in the lower population limit as a function of C_{pa}. Even if the noise constant is large enough, the dynamics of total population is not extinct. In the diffusion case, we have shown that there is another parameter that may induce chaos, the diffusion coefficient. Conversely, we have also shown that diffusion can also induce periodicity in a previously chaotic system.

Can diffusion induced chaos be observed? In an experimental setting, if the equations for the evolution of the system are unknown, then one is at most able to determine if the dynamics is chaotic or not. However, in deliberately designed experiment, when the equations for the dynamics are known and the diffusion coefficient can be freely control, one can certainly study if diffusion induced chaos has occurred and what diffusion coefficient level can induce chaos.

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