Stochastic Processes and Insect Outbreak Systems: Application to Olive Fruit Fly

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Abstract: - The aim of the present work is to bring together new tools and developments in physics and computer science with new aspects in applied entomology. Our work elaborates on well known studies on applied entomology in population insect dynamics. A spatial evolution equation for olive fly population is proposed in order to describe more accurately outbreaks of insect populations by incorporating random movement or dispersion of the population. It turns out that dispersion causes both acceleration of population growth and shift of the high stable population equilibrium to even higher values thus producing population outbreak. Simulation results are also presented confirming theoretically predicted behavior of outbreaks in earlier times.

Key-Words: - population ecology, dispersion, insect outbreak

1. Introduction

Interactions between the mathematical and biological sciences have been increasing rapidly in recent years [1, 2]. Many problems arising in ecology may be described, in a first formulation, using differential equations with or without dispersion terms or noise induced terms (stochastic differential equations) which in their general form are known as the population dynamic equations [3, 4, 5, 6]. One can find numerous examples from ecology, which aim at understanding the relations between organisms themselves and their environment. According to the phenomenological theory of population ecology, a population of forest insects may be regarded as a bistable system characterized by various population densities and the possibility of transition from one state (low density) to another (bursting) [7]. This sort of ecological dynamics is called nowadays outbreak dynamics.

Nonlinear ecological dynamical systems have been studied extensively in terms of reaction-diffusion equations and the patterns they generate. These kinds of equations have occupied an important place in the literature of theoretical ecology. The present work elaborates on reaction-diffusion equations by studying the role of the diffusion terms which arise as a random motion in space (this belongs to a general class of well studied stochastic processes), both in the corresponding rate of growth and the transition of bursting state to even higher values.

An application of the proposed model is presented for the olive fruit fly (dacus). The duration of the life cycle of dacus is almost one year. During this time period 3 to 4 generations may arise. The population growth is strongly affected by climate conditions (while there is a temperature zone inside of which growth of dacus is possible, there is an almost linear relation between growth rate and temperature) and the presence of olive fruits since dacus recline their eggs only in olive fruits [8]. While earlier simulation attempts address the aforementioned factors in detail (e.g. [9]), in this work it is emphasized that building a robust model for the evolution of dacus population, dispersion of dacus is a crucial parameter. Indeed, experiments in real fields and with no new season fruit crop show that adult dacus may travel a mean distance over of 400m during a week [10].

The paper is organized as follows: In Section 2, a well known mathematic model for population growth (the case of spruce budworm [11]) is revisited and explored in order to correctly describe the dynamics of dacus population growth. In Section 3 the model is completed by the introduction of the diffusion term. Analysis of the dynamic properties of the resulting model as well as new insights in robust prediction of population outbreaks is also presented. Finally in Section 4 simulation results for the evolution of dacus population are presented while in Section 5 the main results of the paper are summarized.

2. Insect outbreak systems: Application to olive fruit fly

Qualitative and quantitative analysis follows similar lines as in [11]. It is noted that the model in [11] describes a similar ecosystem, the evolution of budworm population. Although certain differences are present (e.g. the time over which an outbreak takes place is of the order of years for budworm population), the main features of the evolution equation presented there are still valid for the evolution population of dacus. Indeed, a logistic equation which incorporates a predation term, is adopted,

$$\dot{N} = RN\left(1-\frac{N}{K}\right) - p\left(N\right) \qquad (1)$$

where, N is the dacus population, R is the growth rate and K is the carrying capacity of the ecosystem in terms of dacus. The predation term is given as,

$$p(N) = B\frac{N^2}{A^2+N^2}, \quad A, B > 0 \qquad (2)$$

Thus, there is almost no predation when budworms are scarce and so the birds seek food elsewhere. However, once the population exceeds a certain critical level $N = A$ the predation turns on sharply and then saturates (the birds are eating as fast as they can). The final evolution equation has the following form,

$$\frac{dN}{dt} = RN\left(1-\frac{N}{K}\right) - B\frac{N^2}{A^2+N^2} = f(N) \qquad (3)$$

The linear stability analysis consists of finding the fixed points of Equation (3) e.g. the roots for the equation,

$$f(N) = 0 \qquad (4)$$

One root or fixed point is, $N = 0$ which is always unstable since, $f'(N)\big|_{N=0} = R > 0$. This in turn means that for $N = 0$ the predation is very small so the budworm population grows exponentially. The other fixed points are given by the solution of the equation,

$$R\left(1-\frac{N}{K}\right) = B\frac{N}{A^2+N^2} \qquad (5)$$

While for the evolution of budworm population the analysis for the case of constant rate R and varying capacity K has physical meaning (Fig. 1), for the evolution of dacus population the opposite is true (Fig. 2).

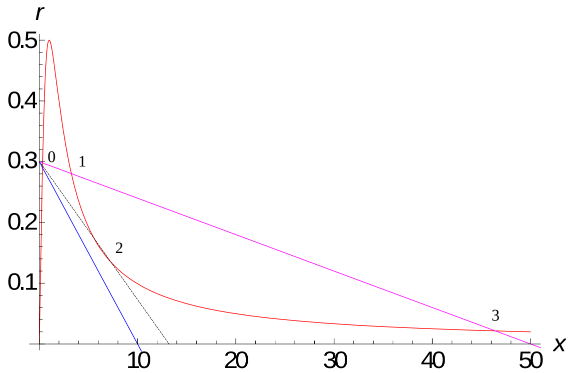

Figure 1 The red curve depicts the predation term. The blue line depicts the logistic term for fixed growth rate and small values of carrying capacity. The purple line depicts the logistic term for fixed growth rate and large values of carrying capacity.

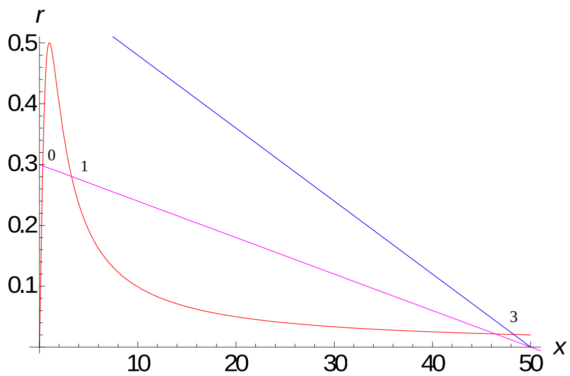

Figure 2 The red curve depicts the predation term. The blue line depicts the logistic term for fixed dimensionless carrying capacity and large values of the dimensionless growth rate. The purple line depicts the logistic term for fixed dimensionless carrying capacity and small values of the dimensionless growth rate.

As the parameter R is increased, points 0 and 1 coalescence into a saddle node (Fig. 2) and by a slight increase of R this node is vanished, so the population level jumps onto the stable equilibrium point 3 (outbreak level). Note that as we increase the value of R the purple line rotates around the fixed value of K clockwise towards the blue line.

It is the aim of the present work to study the effect of random motion in space (or dispersion) of dacus population. From the theory of stochastic processes, it is well known that this results into a diffusion term in the corresponding evolution equation (Eq. 3). In the next section, a detailed analysis of the role of the diffusion term in the evolution of dacus population is presented.

3. The Proposed Model with Dispersion

The role of olive fruit fly (dacus) dispersion in the behavior of the population it is not new. Indeed, experimental data in real field have shown that dacus may travel an average distance of 400 m per week in order to find new season fruit crop, despite the prevailing hot dry conditions [10]. However, no analytical model has been introduced where a dispersion term is taken into account explicitly. In the following, a reaction-diffusion model is proposed in order to incorporate dispersion behavior of dacus flies, e.g.,

$$\frac{dN}{dt} = RN\left(1-\frac{N}{K}\right) - B\frac{N^2}{A^2+N^2} + D\frac{\partial^2 N}{\partial x^2} \qquad (6)$$

where D is the corresponding diffusion coefficient which in general may be a function of environmental conditions. In this preliminary study we treat diffusion coefficient as a constant.

In order to predict the spatial pattern of dacus population we study the steady-state solutions of the above evolution equation. The steady state version of Eq. (6) is

$$D\frac{\partial^2 N}{\partial x^2} = p(N),$$

$$p(N) = -RN\left(1-\frac{N}{K}\right) + B\frac{N^2}{A^2+N^2} \qquad (7)$$

This last equation belongs to a general class of equations, which has been studied in detail in [12]. Three types of stationary spatial solutions are possible: reversals, localized and periodic solutions as depicted in Fig. 3. Noting that observations in real fields show a more or less random emergence of population nucleus, in the present work we are mainly interested in localized solutions which gradually fill up the entire space.

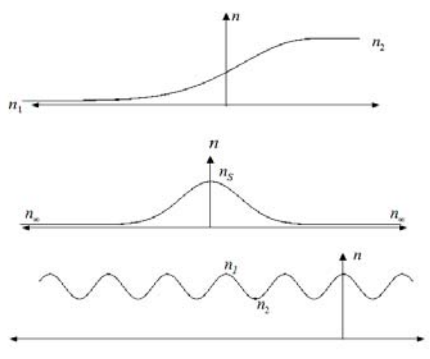

Figure 3 Reversals, localized and periodic solutions of Eq. (7).

Indeed, localized solutions exist for all N that are in the range where the $p(N)$ plot exhibits a negative slope. When integrating Eq. (6) twice gives,

$$x - x_0 = \int_{N(x_0)}^{N} \frac{1}{\sqrt{2F(u)}} du \quad (8)$$

where

$$F(u) = \int_{N_1}^{u} p(y) \frac{1}{D} dy \quad (9)$$

x_0 arbitrary constant and N_1 is the first equilibrium point of Eq. (6). Then, N_2 are determined by,

$$\int_{N_1}^{N_2} p(y) \frac{1}{D} dy = 0 \quad (10)$$

For $N \in [N_1, N_2]$ reversing Eq. (8) a stationary solution $N(x)$ can be estimated. For appropriate set of parameters a class of solutions of the type,

$$N(x) = a \cosh^{-2}(x/b) + c \quad (11)$$

emerges, where the constants a, b, c are functions of the model parameters R, K, B, A and D.

In order to study the effect of the diffusion term in the initial evolution equation we may enter the solution of Eq. (11) into the differential Eq. (6). For this scenario we redraw Fig. (2).

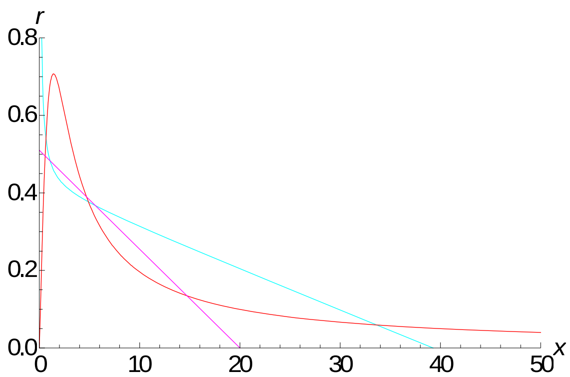

Figure 4 Equilibrium points of Eq. (7) with and without the diffusion term. Only one equilibrium point changes drastically under the presence of a diffusion term.

In Fig. 4 the green line depicts the correction because of the presence of the diffusion term. It is evident that while the position of the first two (one stable and one unstable) points are not strongly affected, the crucial position for outbreak of the second equilibrium is relocated to higher values of dacus population. That is, dacus population may increase to values that would not have been able to be predicted by previous model, so in our case an outbreak takes place. In order to check the relative value of growth rate with and without diffusion the second part of the corresponding evolution equation is depicted in Fig. 5. It is noted that while for the range under consideration and for low values of dacus population growth rate without diffusion is slightly smaller, the situation changes drastically to higher values where the growth rate with diffusion is grater and with the appropriate sign.

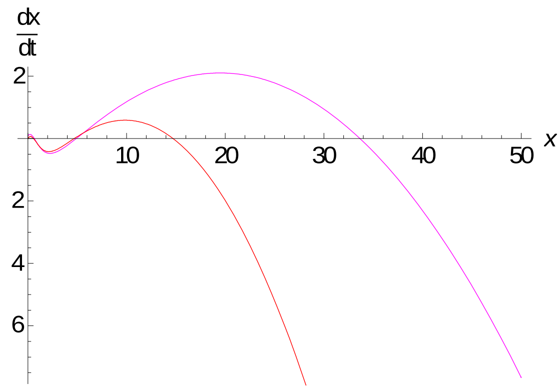

Figure 5 Growth rate of Eq. (7) with and without the diffusion term.

4. Simulation results

In order to validate the proposed model a simulated environment for studying the growth and dispersion of dacus population was built. It is noted that in order to distinguish the effect of diffusion term in growth rate increase and shift of the second equilibrium point, the predation term was not taken into account. Thus, it is expected that only increase of the growth rate of dacus population will be realised. We consider a continuous and homogeneous field with initial insect population coverage of 5% of the whole available area.

The simulated environment iterates in discrete time steps over the total available area and tracks the evolution of dacus population, according to the following rules:

- New insects can be born in neighborhoods already populated by previous generations of insects, and in particular, in an adequate number to enable new generations.
- While food availability is assumed to be homogeneous into the simulated environment, its presence is taken into account for the rate of simultaneous insect births. Under this consideration,

a limiting probability factor of 1/1000 is used to control the rate of simultaneous population growth in each iteration step.

Simulation results of insect population evolution over time in a continuous field of a million possible locations are depicted in Fig. (6):

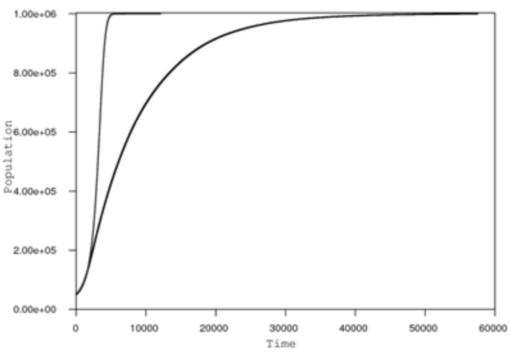

Figure 6 Simulation results of insect population evolution over time for Eq. (7) without the predation term.

The combined results of two simulation setups are shown in Fig. (6):

- In the first case (black line on Fig. (6)), the population of dacus is considered stationary, that is, it retains its original birth position on the field throughout the simulated period. As it can be seen from the above graph, the inability of insects to move to new locations limits the birth rate and results into a prolonged time period (over 50k simulated time steps), until the total insect population reaches final saturation in the field.
- In the second case (gray line on Fig. (6)), during simulation steps insects have a limited ability to migrate to neighboring locations of the field. This effect, although does not allow for dramatic population migrations during time but enables a sharper distribution of dacus populations over the field locations. This augmented distribution enables the creation of greater number of “reproductive” neighborhoods, resulting in a steep curve of total population growth. According to simulation results, a little over 10k time steps are required for the total insect population to reach saturation limit.

5. Conclusions

Even though the existence and modeling of population dispersion for insect dynamics has been noticed and formulated in the past by means of reaction diffusion equations, no clear picture about the effect of this mechanism to the evolution of population in time and space has been given. In this work, an integrated theoretical framework is provided where the effect of population dispersion enters in the corresponding evolution equation in the form of a second order diffusion term. In this framework it is possible to extract analytical solutions for the equilibrium population in space, giving thus the possibility to monitor and predict the emergence of critical nucleus of insect population in space which may trigger outbreaks.

More over, in the context of the proposed methodology the effect of the population dispersion has been clarified in detail: It turns out that the introduction of the diffusion term into the corresponding evolution equation both accelerates the overall increasing rate and moves the second stable population point of the bistable dynamic to higher values thus resulting to outbreaks. As a result, the introduction of the diffusion term (modeling dispersion of insect population) may be crucial for monitoring and early detection of population outbreaks where earlier models would not be able to predict those.

The above theoretical outcomes were confirmed with simulation results. For the simulation code, model parameters were chosen appropriately for the evolution of dacus population. It is noted that in this work the simulation code was build in a first approximation and it does not take into account many parameters emerging in real fields. It will be shown in a forthcoming paper that when a more precise interpretation is adapted the effect of population dispersion is even stronger.

Finally, it is noted that the extension of the proposed methodology to two dimensions is possible. Moreover, random fluctuations of model parameters can also be incorporated. It is expected that for this scenario stochastic differential equation for the evolution of population will result. The role of the emerging randomness to early detection of population outbreaks will be addressed in a future paper as well.

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