Population Dynamics

III. Spatial Models

So far we have considered the time evolution of systems at discrete time steps, from time n to time $n+1$. Also, we have only been concerned with the total number of individuals of each species involved.

If the populations are large and if individual may die or be born at any time, it makes more sense to use a continuous time approach. In the case of the logistic equation, for example, we could write

$$\frac{dN}{dt} = rN(1 - N/K) \qquad (1)$$

where r now is the average number of offspring per individual per unit time (for example 2 offspring per individual per year).

The methods we developed for discrete time models apply to continuous models with minor

changes, are we are going to see in a moment.
However, the dynamics of discrete models can be <u>very</u> different from that of a similar continuous model. The continuous logistic equation (1) illustrates this dramatically: while its discrete counterpart exhibits bifurcations and chaos, eq. (1) has a simple analytic solution

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}}$$

that converges to K for any initial condition.

<u>ONE VARIABLE</u> — The general equation describing a single population has the form

$$\frac{dN}{dt} = f(N) \qquad (2)$$

- equilibrium requires $f(\bar{N}) = 0$
- stability is obtained by setting $N = \bar{N} + n$ and expanding to first order

$$\frac{dn}{dt} = \frac{\partial f}{\partial N}(\bar{N})\, n \equiv \xi n$$

or

$$n(t) = n_0 e^{\xi t}$$

Therefore $\bar{N}$ is stable if $\xi < 0$ and unstable if $\xi > 0$ (compare with $\ln r$ in eq. I.(2))

TWO VARIABLES – If P and Q represent two interacting populations, then

$$\frac{dP}{dt} = f(P, Q)$$
$$\frac{dQ}{dt} = g(P, Q) \qquad (3)$$

– equilibrium corresponds to solutions of

$$f(\bar{P}, \bar{Q}) = g(\bar{P}, \bar{Q}) = 0$$

– setting $P = \bar{P} + p$, $Q = \bar{Q} + q$ we obtain

$$\frac{dW}{dt} = AW \quad ; \quad W = \begin{pmatrix} p \\ q \end{pmatrix}$$

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial P} & \frac{\partial f}{\partial Q} \\ \frac{\partial g}{\partial P} & \frac{\partial g}{\partial Q} \end{pmatrix}_{\bar{P}, \bar{Q}} \qquad (4)$$

The solution is

$$w(t) = c_1 v_1 e^{\lambda_1 t} + c_2 v_2 e^{\lambda_2 t}$$

$$A v_1 = \lambda_1 v_1 \qquad (5)$$

$$A v_2 = \lambda_2 v_2$$

$$w(0) = w_0 = c_1 v_1 + c_2 v_2 .$$

The equilibrium $\bar{P}, \bar{Q}$ is stable if the real part of both λ_1 and λ_2 are negative.

For more variables the method is the same, only the Jacobian matrix A gets larger.

A classic example is the Lotka-Volterra model for a prey P and a predator Q:

$$\frac{dP}{dt} = \underbrace{\alpha P}_{\text{exponential growth}} - \underbrace{\beta P Q}_{\text{decrease due to predation}} \qquad (6)$$

$$\frac{dQ}{dt} = \underbrace{-\gamma Q}_{\text{death in the absence of food}} + \underbrace{\delta P Q}_{\text{population growth if there are prey.}}$$

The two equilibria and corresponding Jacobian matrices are:

(a) Extinction $\bar{P} = \bar{Q} = 0$ $\quad A = \begin{pmatrix} \alpha & 0 \\ 0 & -\gamma \end{pmatrix}$

eigenvalues $\lambda_1 = \alpha > 0$, $\lambda_2 = -\gamma < 0$ $\Rightarrow$ unstable equilibrium

(b) Co-existence $\bar{P} = \gamma/\delta$ $\quad \bar{Q} = \alpha/\beta$

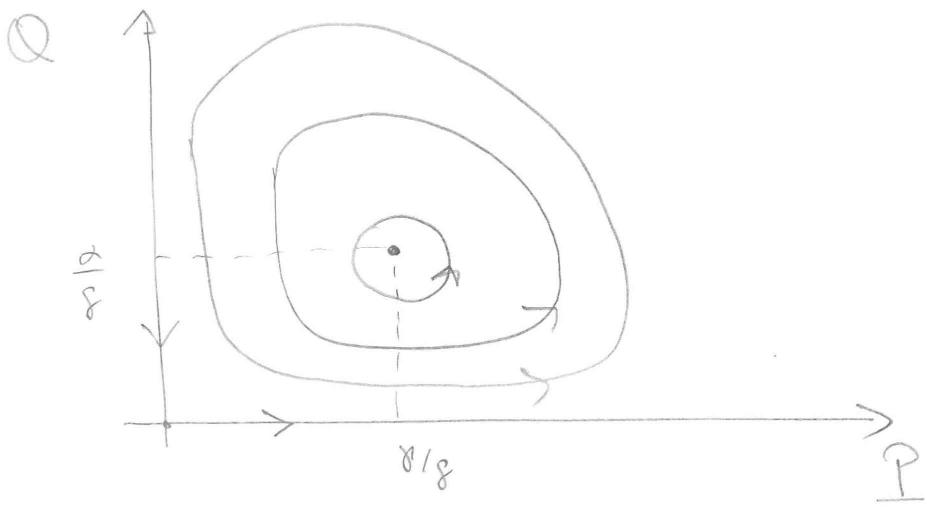
$$A = \begin{pmatrix} 0 & -\beta\gamma/\delta \\ \frac{\alpha\delta}{\beta} & 0 \end{pmatrix} \rightarrow \begin{array}{l} \lambda_1 = i\sqrt{\alpha\gamma} \\ \lambda_2 = -i\sqrt{\alpha\gamma} \end{array}$$

The equilibrium is "marginally stable", with nearby solutions oscillating around it.

Equations (6) can actually be integrated and we find that

$$Q^{\alpha} e^{-\beta Q} = \frac{C e^{\delta P}}{P^{\gamma}}$$

where C is a constant. The behavior is illustrated below:



SPACE AND DIFFUSION

In many situations it is not enough to know the total populations and information about its spatial distribution may be important. The usual approach to include space is to assume that interactions between individuals occur locally and that individual move around by diffusing, or by other mechanisms, such as following scents or other cues. For the logistic equation we would write

$$\frac{\partial N(x,t)}{\partial t} = r\,N(x,t)\left[1 - N(x,t)/K\right] + D\,\frac{\partial^2 N(x,t)}{\partial x^2}$$

for um space-dimension x and where D is the diffusion coefficient.

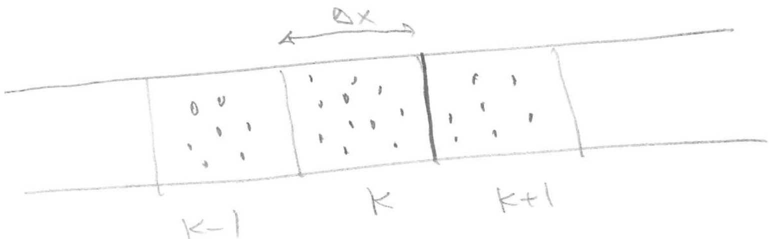
This equation has the interesting property that the homogeneous (space independent) solution we wrote down in page 2 is still a solution, since $\partial^2 N/\partial x^2 = 0$. The question is really whether the presence of diffusion changes the stability character of the solution.

When a stable solution of a space independent problem becomes unstable because of diffusion, non trivial space dependent solutions may arise, generating what is known as TURING PATTERNS.

DIFFUSION

Diffusion is the re-arrangement of particles (or individuals) due to their random motion. In a gás, for example, particles move around randomly and particles on a dense region will naturally move towards regions with lower densities..

Consider a one-dimensional pipe that we divide into little segments of size Δx



We define the flow at k as the number of particles that cross the boundary $k/k+1$ per unit time:

$$J(k) = \frac{\Delta N(k, k+1)}{\Delta t}$$

And the density of particles at segment k as

$$\rho(k) = \frac{N(k)}{\Delta x} .$$

If $\rho(k)$ varies in time is because there are particles crossing the $k-1/k$ and $k/k+1$ boundaries:

$$\frac{\Delta \rho(k)}{\Delta t} = \frac{-\Delta N(k, k+1) + \Delta N(k-1, k)}{\Delta x \, \Delta t}$$

$$= -\frac{J(k) - J(k-1)}{\Delta x} = -\frac{\Delta J}{\Delta x} .$$

If the number of particles coming in and out is the same the density does not change. In the limit when $\Delta x \to 0$, $\Delta t \to 0$ this becomes the "continuity equation"

$$\frac{\partial \rho}{\partial t} + \frac{\partial J}{\partial x} = 0 \quad . \qquad (7)$$

We now use "Fick's law" which say that the flow of particles is proportional to the spatial variation of the density:

$$J(x) = -D \frac{\partial \rho}{\partial x} \qquad (8)$$

so that if ρ is constant there is no flow. If the "diffusion coefficient" D is constant we find

$$\frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} \quad . \qquad (9)$$

Notice the minus sign in eq. (8), saying that the flow is from the high density to the low density regions. In 3-D this generalizes to

$$\frac{\partial \rho}{\partial t} = D\left(\frac{\partial^2 \rho}{\partial x^2} + \frac{\partial^2 \rho}{\partial y^2} + \frac{\partial^2 \rho}{\partial z^2}\right) \equiv D \nabla^2 \rho \, .$$

Exercise : show that

$$\rho(x,t) = \frac{1}{\sqrt{4\pi D t}} e^{-x^2/4Dt}$$

is a solution of eq. (9) and draw $\rho(x,t)$ for $t \approx 0$ and $t > 0$.

TURING PATTERNS

We are going to see how Turing patterns arise using the model of Mimura & Murray (J. Theor. Biol. 75 (1978) 249). It is similar to the Lotka-Volterra model of prey P and predators Q:

$$\frac{\partial P}{\partial t} = \left(\frac{a + bP - P^2}{c}\right) P - QP + D_P \frac{\partial^2 P}{\partial x^2} \qquad (10)$$

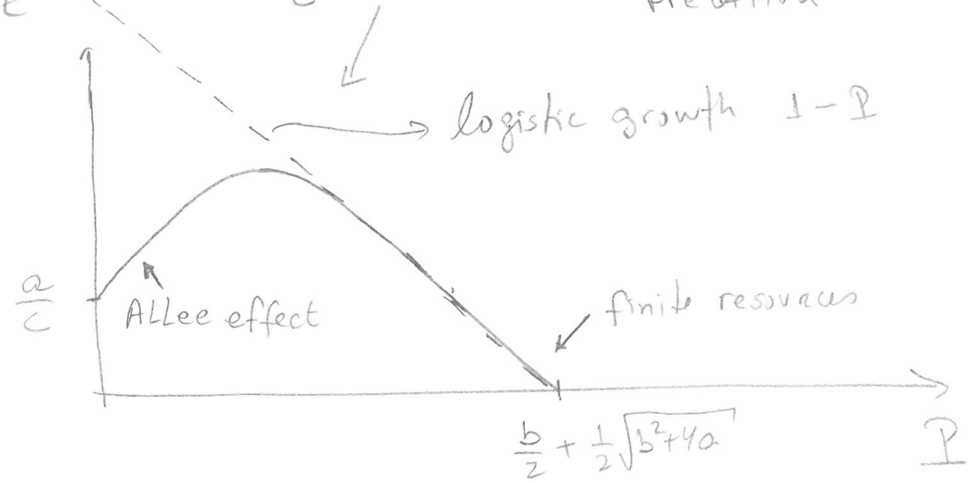
$$\frac{\partial Q}{\partial t} = -(1 + eQ) Q + PQ + D_Q \frac{\partial^2 Q}{\partial x^2}$$

where $P(x,t)$ and $Q(x,t)$ are densities of preys and predators at position x and time t;

D_P and D_Q are the diffusion coefficients and $0 \le x \le L$.

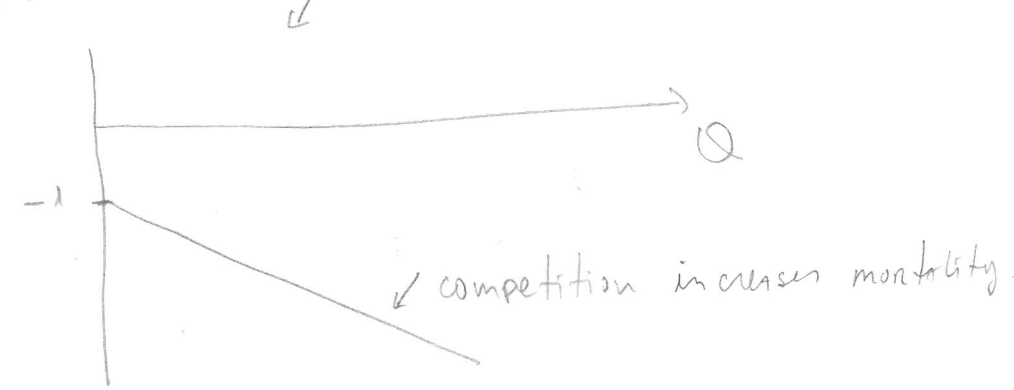
For the prey, the per-capita growth rate is

$$\frac{1}{P}\frac{\partial P}{\partial t} = \frac{a+bP-P^2}{c} - Q \rightarrow \text{predation}$$



For the predators

$$\frac{1}{Q}\frac{\partial Q}{\partial t} = -(1+eQ) + P \rightarrow \text{predation}$$



The constant coefficients will be fixed at

$$a = 35 \;, \quad b = 16 \;, \quad c = 9 \;, \quad e = 2/5 \,.$$

Homogeneous Equilibrium

Setting $\frac{\partial P}{\partial t} = \frac{\partial Q}{\partial t} = 0$ leads to equilibrium solutions.

Setting further $\frac{\partial P}{\partial x} = \frac{\partial Q}{\partial x} = 0$ leads to spatially homogeneous solutions $\bar{P}, \bar{Q}$:

$$\bar{P}\left[\left(\frac{a + b\bar{P} - \bar{P}^2}{c}\right) - \bar{Q}\right] = 0$$

$$\bar{Q}\left[-1 - e\bar{Q} + \bar{P}\right] = 0$$

There are 3 solutions:

$(\bar{P}, \bar{Q}) = (0, 0) \rightarrow$ extinction

$(\bar{P}, \bar{Q}) = \left(\frac{b}{2} + \frac{1}{2}\sqrt{b^2+4a}, 0\right) = (8+\sqrt{99}, 0) \rightarrow$ only preys

$(\bar{P}, \bar{Q}) = (5, 10) \rightarrow$ co-existence, solution of

$$\begin{cases} P^2 + P(c/e - b) - (a + c/e) = 0 \\ Q = \dfrac{P-1}{e} \end{cases}$$

In order to study the stability of these solutions we need to specify the boundary conditions at $x=0$ and $x=L$. We assume that there is no flow of individuals through the boundaries (see eq. (8)) i.e.,

$$\frac{\partial P}{\partial x}(0) = \frac{\partial P}{\partial x}(L) = \frac{\partial Q}{\partial x}(0) = \frac{\partial Q}{\partial x}(L) = 0$$

These conditions are obviously satisfied by the homogeneous solutions, since they do not depend on x. Therefore we look for perturbations

$$Q = \bar{Q} + q$$
$$P = \bar{P} + p \qquad (11)$$

with

$$\frac{\partial q}{\partial x} = \frac{\partial p}{\partial x} = 0 \quad \text{at} \quad x = 0, L.$$

The most general smooth form of q and p can be written in terms of "Fourier Modes":

$$p(x,t) = \sum_{n=1}^{\infty} a_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) \equiv \sum_{n=1}^{\infty} p_n(x,t)$$

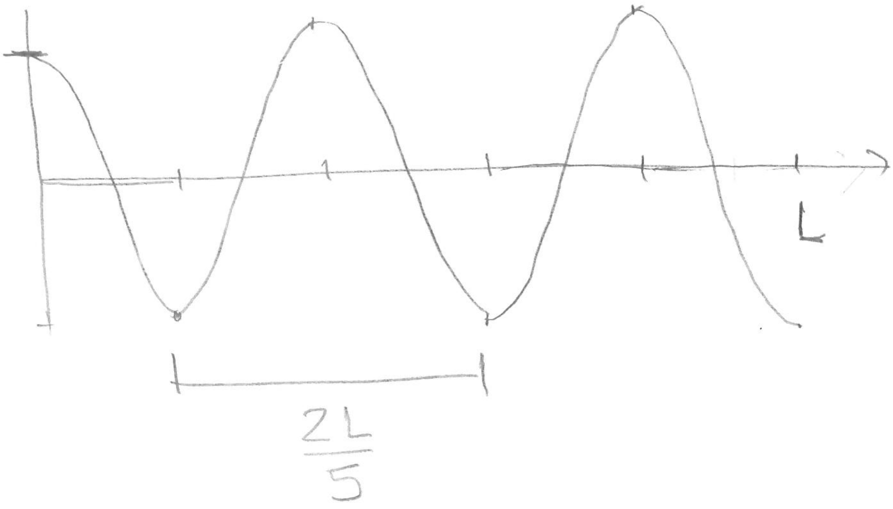
$$q(x,t) = \sum_{n=1}^{\infty} b_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) \equiv \sum_{n=1}^{\infty} q_n(x,t) \tag{12}$$

This corresponds to the decomposition of a general noisy function into a sum of simple periodic functions, each of them satisfying the boundary conditions. Moreover we can think of these modes as acting one at a time and the effect of the total perturbation is going to be the sum of the effects of each mode separately (prove this!).

Each mode (p_n, q_n) has a typical "size", or wavelength

$$L_n = \frac{2L}{n} \tag{13}$$

For $n = 5$, for example, we find



What we want to find is for what values of n, or for what Lenght L_n, the exponent λ becomes positive and the perturbation grows, destroying the homogeneous solutions and creating regions of high density separated by regions of low density, i.e., patterns.

We set $D_O = \alpha$ and $D_I = \beta$ for simplicity.
Later we will set $\alpha = 1$ so that β is the diffusion of preys measured in term of the diffusion rate of the predators.

Substituting eq. (11) into (10) and keeping only first order terms we obtain

$$\frac{\partial P_n}{\partial t} = a_{11} P_n + a_{12} q_n + \beta \frac{\partial^2 P_n}{\partial x^2}$$

$$\frac{\partial q_n}{\partial t} = a_{21} P_n + a_{22} q_n + \alpha \frac{\partial^2 q_n}{\partial x^2} \qquad (14)$$

where

$$a_{11} = \frac{a + b\bar{P} - \bar{P}^2}{c} + \bar{P}\left(\frac{b - 2\bar{P}}{c}\right)$$

$$a_{12} = -\bar{P}$$

$$a_{21} = \bar{Q} \qquad (15)$$

$$a_{22} = \left[\bar{P} - (1 + e\bar{Q})\right] - e\bar{Q}$$

$$\frac{\partial^2 P_n}{\partial x^2} = -a_n e^{\lambda t} \left(\frac{n\pi}{L}\right)^2 \cos\left(\frac{n\pi x}{L}\right)$$

$$\equiv -a_n e^{\lambda t} \sigma_n \cos\left(\frac{2\pi x}{L_n}\right) = -\sigma_n P_n$$

$$\frac{\partial^2 q_n}{\partial x^2} = -\sigma_n q_n$$

$$\sigma_n = \left(\frac{n\pi}{L}\right)^2 = \left(\frac{2\pi}{L_n}\right)^2$$

$$\frac{\partial p_n}{\partial t} = \left[a_{11} - \beta \sigma_n \right] p_n + a_{12} q_n$$

$$\frac{\partial q_n}{\partial t} = a_{21} p_n + \left[a_{22} - \alpha \sigma_n \right] q_n$$

If there were no diffusion, $\alpha = \beta = 0$ we would be back at the non-linear non-spatial case.

In this case we find that:

- EXTINCTION is unstable
- only preys is unstable
- co-existence is stable

For this last equilibrium we find

$$a_{11} = 30/9$$

$$a_{12} = -5$$

$$a_{21} = 10$$

$$a_{22} = -4$$

The Jacobian matrix has eigenvalues

$$\lambda = -\frac{1}{3} \pm i\sqrt{329}$$

showing that the population "spirals" back to the homogeneous equilibrium.

Setting $\alpha = 1$ we obtain, for the full Jacobian matrix,

$$\lambda_\pm = \frac{b}{2} \pm \frac{1}{2}\sqrt{b^2-4c}$$

$$b = a_{11} + a_{22} - \sigma_n(1+\beta) = -2/3 - \sigma_n(1+\beta)$$

$$c = (a_{11} - \beta\sigma_n)(a_{22} - \sigma_n) - a_{12}a_{21} = \frac{110}{3} - \sigma_n\left(\frac{30}{9} - 4\beta\right) + \beta\sigma_n^2$$

The idea is to calculate $\lambda_\pm$ for each value of n and check if $|\lambda_+|$ or $|\lambda_-|$ can be larger than 0, destabilizing the homogeneous solution.

Results from the paper are shown next:

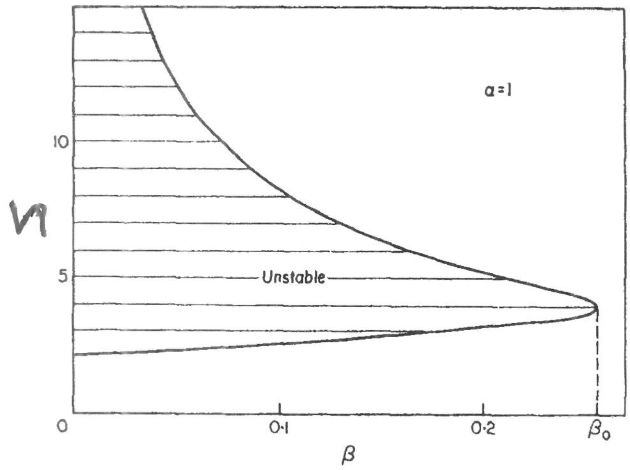


FIG. 4. Linear stability diagram: mode n as a function of β with fixed $a = 1$. The shaded region gives the linearly unstable modes for a given β.

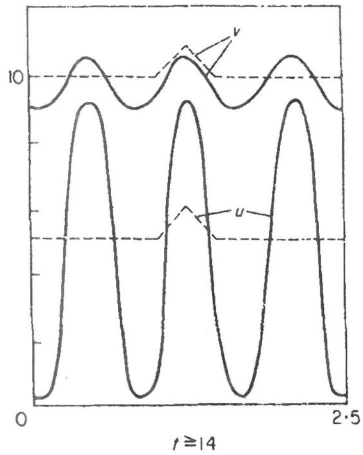


FIG. 3. Initial (– – –) and final spatial distributions for the equation system (9) with $a = 1$, $\beta = 0{\cdot}0125$ and $f(u)$, $g(v)$ as in Fig. 1: zero flux boundary conditions obtain at $x = 0$, $L(= 2{\cdot}5)$.

$u \to$ Prey
$v \to$ Q = predator

Therefore, if the predators diffuse sufficiently faster than the preys (small β) there is a range of modes that cause the homogeneous distribution to go unstable.

For small β, like $\beta = 0.0125$ in figure 3, the lowest mode to generate instability is $n = 3$. The simulation in fig. 3 shows the initial perturbation to the homogeneous solution $\bar{P} = 5$, $\bar{Q} = 10$ as two kinks at $x = L/2$ and the resulting stationary pattern, with 3 regions of high prey density and 3 with low prey density.

It is surprising that diffusion, which tends to homogenize the distribution has exactly the opposite effect here, of creating non-homogeneities. This phenomenon was discovered by Alan Turing and is known as Turing Patterns and the mechanism TURING INSTABILITIES.

Start from

$$\dot{p} = f(p, q) + D_p \frac{\partial^2 p}{\partial x^2}$$

PROOF OF STATEMENT IN PAGE 14

$$\dot{q} = g(p, q) + D_q \frac{\partial^2 q}{\partial x^2}$$

and set
$$p = p_0 + \sum_n p_n$$
$$q = q_0 + \sum_n q_n$$

Linearising we obtain

$$\sum_n \dot{p}_n = f_p \sum_n p_n + f_q \sum_n q_n + D_p \sum_n \frac{\partial^2 p_n}{\partial x^2}$$

$$\sum_n \dot{q}_n = g_p \sum_n p_n + g_q \sum_n q_n + D_Q \sum_n \frac{\partial^2 q_n}{\partial x^2}$$

or

$$\sum_n \left[\dot{p}_n - f_p p_n - f_q q_n - D_p \frac{\partial^2 p_n}{\partial x^2} \right] = 0$$

$$\sum_n \left[\dot{q}_n - g_p p_n - g_q q_n - D_Q \frac{\partial^2 q_n}{\partial x^2} \right] = 0$$

Therefore, if

$$\dot{p}_n = f_p p_n + f_q q_n + D_p \frac{\partial^2 p_n}{\partial x^2}$$

$$\dot{q}_n = g_p p_n + g_q q_n + D_Q \frac{\partial^2 q_n}{\partial x^2}$$

for each n, the full equation is satisfied.