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A METHOD FOR THE APPROXIMATE SOLUTION OF SOME STOCHASTIC EQUATIONS OF POPULATION BIOLOGY

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ABSTRACT. A method is presented for analyzing several types of equations describing interacting species in a random environment. Approximate solutions of the models are obtained under the assumption that the stochastic fluctuations of the environment are rapidly varying.

1. This paper contains a brief description of a method which has been used to analyze several types of stochastic models of interacting species. Theorems justifying the method are in [1, 4, 6], and a more detailed discussion of the applications is in [5, 2].

Among the simplest deterministic models of interacting species is the ordinary differential equation. Let $x(t) = (x_1(t), x_2(t), \cdots, x_n(t))$ be a vector of (scaled) population sizes $x_1, x_2, \cdots, x_n$ of a system of n species. Then in a non-random environment, the equations are

$$\frac{d}{dt}\, x(t) = F(x(t), \gamma),\ x(0) = x_0 \text{ given.} \tag{1.1}$$

Here F is some non-linear function describing the species interaction dynamics, and $\gamma = (\gamma_1, \cdots, \gamma_m)$ is a vector of m parameters occurring in the equations, e.g., growth rates, carrying capacities, inter-species competition coefficients, etc. More realistic models than (1.1) may also incorporate time-delays, as well as an environment which is itself changing in time. Further generalizations of (1.1) may treat spatial inhomogeneities in the environment.

In a stochastic environment, the parameters γ may be expected to fluctuate randomly in time. The fundamental assumption that we make here is that the random environmental fluctuations are on a time scale which is much faster than any other time scale in the sytem. Mathematically, we assume that $\gamma = \gamma(\tau)$ is a stochastic process, and that

$$\tau = t/\epsilon,\ 0 < \epsilon \ll 1. \tag{1.2}$$

The small parameter ϵ is then the ratio of the time scale t for which the equations are written to the time scale τ of the noisy fluctuations. The idea is to exploit this disparity of time scales to derive an approx-

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imate solution of the equations. A heuristic argument will be given here for equation (1.1).

Denoting the solution for fixed ϵ by $x^\epsilon(t)$, (1.1) now becomes

$$\begin{aligned} &\frac{d}{dt}\ x^\epsilon(t) = F(x^\epsilon(t),\ \gamma(t/\epsilon)) \\ &x^\epsilon(0) = x_0 \text{ given.} \end{aligned} \tag{1.1'}$$

We assume that for fixed, non-random x, the random process $F(x, \gamma(\tau))$ satisfies the law of large numbers, i.e., that there is a limit $\overline{F}(x)$ to which the time averages of F converge in the mean.

$$\frac{1}{T}\int_{t_0}^{t_0+T} F(x,\ \gamma(\tau))\,d\tau \xrightarrow[T\to\infty]{} \overline{F}(x). \tag{1.3}$$

By (1.3) we mean that for all t_0,

$$\lim_{T\to\infty} E\left|\frac{1}{T}\int_{t_0}^{t_0+\tau} F(x,\ \gamma(t))\,d\tau - \overline{F}(x)\right| = 0. \tag{1.3'}$$

It is furthermore assumed that the limit is approached uniformly in x, t_0. Clearly, if such an $\overline{F}$ exists, it may be computed by

$$\overline{F}(x) = \lim_{T\to\infty}\frac{1}{T}\int_0^T E[F(x,\ \gamma(\tau))]\,d\tau. \tag{1.4}$$

To clarify what is necessary for (1.3'), consider the example $F(x, \gamma(\tau)) = f(x) + g(x)\gamma(\tau)$ with x, f, g, γ scalars, and $\gamma(\tau)$ a stationary stochastic process with mean zero and correlation function $R(u)$. Then (1.3') will be satisfied with $\overline{F}(x) = f(x)$ if

$$E\left|\frac{1}{T}\int_{t_0}^{t_0+T} g(x)\gamma(\tau)\,d\tau\right| \xrightarrow[T\to\infty]{} 0$$

uniformly in x and t_0. If $|g(x)|$ is bounded, we need that

$$E\left|\frac{1}{T}\int_{t_0}^{t_0+T} \gamma(\tau)\,d\tau\right| \xrightarrow[T\to\infty]{} 0$$

uniformly in t_0. But by the Schwarz inequality,

$$\left(E\left|\frac{1}{T}\int_{t_0}^{t_0+T}\gamma(\tau)\,d\tau\right|\right)^2 \leqq \frac{1}{T^2}E\int_{t_0}^{t_0+T} d\tau_1\int_{T_0}^{t_0+T} d\tau_2\gamma(\tau_1)\gamma(\tau_2)$$

$$\leqq \frac{1}{T^2} \int_{t_0}^{t_0+T} d\tau_1 \int_{t_0}^{t_0+T} d\tau_2 \, |R(\tau_1 - \tau_2)|$$

$$\leqq \frac{2}{T} \int_0^T \left(1 - \frac{u}{T}\right) |R(u)| \, du \leqq \frac{2}{T} \int_0^\infty |R(u)| \, du.$$

Thus (1.3′) is satisfied in this case if $\int_0^\infty |R(u)| \, du < \infty$.

A sufficient condition for this example is therefore that the correlation $R(u)$, of $\gamma(\tau)$ and $\gamma(\tau + u)$, goes to zero sufficiently rapidly as the time separation u becomes large. For the results that follow, what must be assumed is a "mixing condition"—roughly, that events separated by a large time gap u become asymptotically independent as $u \to \infty$.

Returning to (1.1′), let $x^0(t)$ be the (wholly deterministic) solution of

$$\frac{d}{dt} x^0(t) = \overline{F}(x^0(t)), \; x^0(0) = x_0. \tag{1.5}$$

The claim now is that $x^0(t)$ is a good first approximation to $x^\epsilon(t)$ for small ϵ.

Equation (1.1′) may be written in integrated form as

$$x^\epsilon(t) = x_0 + \int_0^t F(x^\epsilon(s), \, \gamma(s/\epsilon)) \, ds. \tag{1.1″}$$

For simplicity, we argue heuristically here that if F is bounded, and has a bounded first derivative with respect to x, then x^0 is approximately a solution of (1.1″) as $\epsilon \to 0$. Let n be a large integer, and for $t > 0$, define $\Delta = t/n$. Then

$$x_0 + \int_0^t F(x^0(s), \, \gamma(s/\epsilon)) \, ds$$

$$= x_0 + \sum_{i=0}^{n-1} \int_{i\Delta}^{i\Delta+\Delta} F(x^0(s), \, \gamma(s/\epsilon)) \, ds$$

$$= x_0 + \sum_{i=0}^{n-1} \int_{i\Delta}^{i\Delta+\Delta} F(x^0(i\Delta), \, s/\epsilon) \, ds + O(\Delta)$$

$$\approx x_0 + \sum_{i=0}^{n-1} \Delta \left[\frac{\epsilon}{\Delta} \int_{i\Delta/\epsilon}^{i\Delta/\epsilon+\Delta/\epsilon} F(x^0(i\Delta), \, \tau) \, d\tau \right].$$

Comparing the quantity in brackets above to (1.3), and identifying $T = \Delta/\epsilon \to \infty$ as $\epsilon \to 0$, we have

$$x_0 + \int_0^t F(x^0(s), \, \gamma(s/\epsilon)) \, ds \approx x_0 + \left[\sum_{i=0}^{n-1} \Delta \overline{F}(x^0(i\Delta)) \right].$$

The quantity in brackets above is a Riemann sum approximation to an integral. Therefore

$$x_0 + \int_0^t F(x^0(s), \gamma(s/\epsilon))\, ds$$

$$\approx x_0 + \int_0^t \bar{F}(x^0(s))\, ds = x^0(t).$$

This last equality follows from integration of (1.5).

Then to first approximation, the stochastic function F may be replaced by its average (both with respect to time and probability) $\bar{F}$, and the stochastic equation (1.1′) replaced by the deterministic one (1.5). The non-linear equation (1.5) may still pose formidable mathematical problems, but the analysis lies outside the domain of probability. Thus it will be possible to utilize any pre-existing theory of interacting species based on equation (1.5) in constructing an approximate solution to the stochastic problem (1.1′).

We next construct the second term in a perturbation expansion of $x^\epsilon(t)$. The first term is evidently $x^0(t)$, so that we seek a solution of the form

$$x^\epsilon(t) \approx x^0(t) + \epsilon^\alpha y^0(t) + \cdots . \tag{1.6}$$

The parameter $\alpha > 0$ is to be chosen to make such an expansion possible. Putting (1.6) into (1.1′) and using a Taylor series of F gives

$$\frac{d}{dt}\, x^0(t) + \epsilon^\alpha \frac{d}{dt}\, y^0(t) + \cdots \tag{1.7}$$

$$= F(x^0(t), \gamma(t/\epsilon)) + \epsilon^\alpha \frac{\partial F}{\partial x}(x^0(t), \gamma(t/\epsilon)) y^0(t) + \cdots .$$

Note that equating coefficients of powers of ϵ does *not* give the correct result (1.5). This is because epsilons still occur in the equation as the time scale of γ. Instead, we drop terms higher than ϵ^α, and use equation (1.5). After re-arrangement, the result is

$$\frac{d}{dt}\, y^0(t) = \frac{\partial F}{\partial x}(x^0(t)\ \gamma(t/\epsilon)) y^0(t)$$

$$+ \frac{1}{\epsilon^\alpha}[F(x^0(t), \gamma(t/\epsilon)) - \bar{F}(x^0(t))] \tag{1.8}$$

$$+ o(1).$$

Since $x^\epsilon(0) = x_0 = x^0(0)$, evidently $y^0(0) = 0$. Integration of (1.8) then gives the integral equation

$$y^0(t) = \int_0^t \frac{\partial F}{\partial x}(x^0(s), \gamma(s/\epsilon))y^0(s)\,ds$$

$$+ \frac{1}{\epsilon^\alpha}\int_0^t [F(x^0(s), \gamma(s/\epsilon)) \tag{1.9}$$

$$- \bar{F}(x^0(s))]\,ds + o(1).$$

A central limit theorem for mixing processes now dictates the choice $\alpha = 1/2$, for which the last integral in (1.9) converges (weakly) to a gaussian process, whose derivative is formally a white noise. By reasoning similar to that used in deriving (1.5) the term $\partial F/\partial x$ in (1.9) can be replaced by $\partial \bar{F}/\partial x$. Omitting the details, the resulting stochastic equation is

$$\frac{d}{dt}\, y^0(t) = \frac{\partial \bar{F}}{\partial x}(x^0(t))y^0(t) + \sigma(x^0(t))W(t),\ y^0(0) = 0. \tag{1.10}$$

Here $W(t)$ is a vector of gaussian white noises with covariance

$$E[W(t)W^T(t')] = \delta(t - t')I.$$

I is the nxn identity matrix, and δ is the Dirac delta function. The matrix $\sigma(x)$ is to be calculated as follows. First, the matrix function $A(x)$ is calculated by the formula (with x fixed).

$$A(x) = \lim_{T\to\infty} \frac{1}{T}\int_0^T ds_1 \int_0^T ds_2$$

$$E\{[F(x, \gamma(s_1)) - EF(x, \gamma(s_1))]\,[F(x, \gamma(s_2)) - EF(x, \gamma(s_2))]^T\}. \tag{1.11}$$

$\sigma(x)$ is then any matrix such that

$$\sigma\sigma^T = A. \tag{1.12}$$

To summarize, the solution of (1.1′) is constructed as follows. First F is averaged according to (1.4), and x^0 determined from (1.5). Next $\sigma(x)$ is calculated from (1.11) and (1.12), and evaluated along $x^0(t)$ for use in (1.10). Since (1.10) is a linear white noise equation, its solution y^0 will be a gaussian process with mean zero. Its covariance will be calculated in the next section.

From (1.6) we have that

$$x^\epsilon(t) \approx x^0(t) + \sqrt{\epsilon}\, y^0(t). \tag{1.10}$$

Therefore the approximate solution will be a deterministic function with small superimposed gaussian fluctuations.

2. Equation (1.10) may be integrated in terms of the fundamental solution matrix $Y(t)$ of the linear deterministic system

$$\frac{d}{dt}\, Y(t) = \frac{\partial \overline{F}}{\partial x}\,(x^0(t))\; Y(t), \quad Y(0) = I. \tag{2.1}$$

Variation of parameters then gives

$$y^0(t) = Y(t) \int_0^t Y^{-1}(s)\sigma(x^0(s))W(s)\, ds. \tag{2.2}$$

Since y^0 is gaussian, its statistics are completely determined by its covariance. From (2.2), this may be calculated by (for $t' \geqq 0$),

$$E[y^0(t + t')y^0(t)] = Y(t + t') \int_0^t Y^{-1}(s)A(s)Y^{-1T}(s)\, ds\; Y^T(t). \tag{2.3}$$

We define the covariance of the components of y^0 at one instant of time by

$$D(t) = E[y^0(t)y^{0T}(t)]. \tag{2.4}$$

$D(t)$ may be calculated from (2.3) by setting $t' = 0$. By differentiating this expression, and using (2.1) we obtain

$$\begin{aligned} \frac{d}{dt}\, D(t) &= C(t)D(t) + D(t)C^T(t) + A(x^0(t)) \\ D(0) &= 0 \end{aligned} \tag{2.5}$$

where

$$C(t) = \frac{\partial \overline{F}}{\partial x}\,(x^0(t)). \tag{2.6}$$

Thus we may solve directly a linear system of matrix differential equations for D.

First, we consider the equilibrium point model. That is, we assume that the deterministic system (1.5) has a linearly stable equilibrium point, at some population point $\bar{x}$. Then for a starting point $x^\epsilon(0) = \bar{x}$, we have $x^0(t) = \bar{x}$, a constant for all time. Therefore $C = (\partial \overline{F}/\partial x)(\bar{x})$, $A = A(\bar{x})$ are constant matrices, and (2.3) may be put in the form

$$E[y^0(t + t')y^{0T}(t)] = e^{Ct'} \int_0^t e^{Cs}Ae^{C^Ts}\, ds. \tag{2.7}$$

In this case, C is what has been called the "community matrix". Since the deterministic system is linearly stable, the eigenvalues of C have

negative real parts. Therefore, from (2.7), the covariance of the random fluctuations goes to zero exponentially in t' as t' becomes large. The exponential decay rates, or, roughly, the rates of forgetfulness of the system, are the eigenvalues of C.

Furthermore, setting $t' = 0$ in (2.7), we see that at t gets large, $D(t)$ converges exponentially (with rates that are sums of eigenvalues of C) to a limit $D(\infty)$. More graphically, we may picture the contour lines of the gaussian density of $x^\epsilon(t)$ as ellipsoids centered at $\bar{x}$ with axes determined by $D(t)$. These ellipsoids expand as time increases and uncertainty in the position of $x^\epsilon(t)$ also increases. The ellipsoids do not, however, expand indefinitely, but converge to a limiting ellipsoid determined by $D(\infty)$. This limit can be calculated simply by solving a system of linear algebraic equations; we set $(d/dt)D(t) = 0$ in (2.5) to get

$$0 = CD(\infty) + D(\infty)C^T + A. \tag{2.8}$$

Another type of model is the limit cycle. We assume here that x^ϵ is 2-dimensional, and that the solution $x^0(t)$ of (1.5) is a limit cycle in the plane. Then

$$C(t) = \frac{\partial \overline{F}}{\partial x}(x^0(t)),\ A(t) = A(x^0(t))$$

are periodic functions of time, and Floquet theory is applicable to the analysis of (2.1). We include here only the results. Details are in [5].

It is convenient to change coordinates in the plane to (r, s), where r is distance from the limit cycle, and s is arc-length along the limit cycle. Then it can be shown that the variance of the random fluctuations along the limit cycle (s) diverge slowly (that is, linearly) as time gets large, i.e., the fluctuations in "phase" of the approximately cyclical populations $x^\epsilon(t)$ become considerable after long time. The variance of the distance from the limit cycle (r) converges, however, in the following way. Let $r^\epsilon(t)$ be the perpendicular distance of $x^\epsilon(t)$ from the limit cycle, and α the period of $x^0(t)$. Then the variance of $r^\epsilon(t + n\alpha)$ converges to a limiting value as $n \to \infty$ through integer values. The convergence is geometric in the square of the Floquet multiplier of equation (2.1).

An illustration of the theory, as well as comparison with Monte-Carlo results of May [3] is in [5].

3. The methods of the previous sections may be modified to handle time-delays and non-autonomous systems. The equations then are

$$\frac{d}{dt}x^\epsilon(t) = F(x^\epsilon(t), x^\epsilon(t - \delta_1), x^\epsilon(t - \delta_2), \cdots x^\epsilon(t - \delta_N), t, \gamma(t/\epsilon)). \tag{3.1}$$

Here $0 \equiv \delta_0 < \delta_1 < \delta_2 < \cdots < \delta_N$ are time delays, $\gamma(t/\epsilon)$ is the vector of rapidly-varying stochastic parameters, and time t may occur explicitly in the equations. Initial conditions are specified as

$$x^\epsilon(t) = \phi(t), \text{ given for } -\delta_N \leqq t \leqq 0. \tag{3.2}$$

The solution may be approximated by a method similar to that of the preceding sections. First, the function F is averaged, both with respect to time and probability

$$\begin{aligned} &\overline{F}(x_0, x_1, \cdots, x_N, t) \\ &\qquad \equiv \lim_{T\to\infty} \frac{1}{T} \int_0^T E[F(x_0, \cdots, x_N, t, \gamma(s))]\, ds. \end{aligned} \tag{3.3}$$

One then solves the deterministic system

$$\begin{aligned} &\frac{d}{dt}\, x^0(t) = \overline{F}(x^0(t), x^0(t-\delta_1), \cdots, x^0(t-\delta_N), t), \quad t > 0, \\ &x^0(t) = \phi(t), \quad -\delta_N \leqq t \leqq 0. \end{aligned} \tag{3.4}$$

The matrices $C_i(t)$ are defined by

$$C_i(t) = \frac{\partial \overline{F}}{\partial x_i}(x^0(t), x^0(t-\delta_1), \cdots, x^0(t-\delta_N), t), \quad i = 0, 1, \cdots, N. \tag{3.5}$$

The solution $x^\epsilon(t)$ is then approximately of the form

$$x^\epsilon(t) \approx x^0(t) + \sqrt{\epsilon}\, y^0(t). \tag{3.6}$$

$y^0(t)$ is a gaussian stochastic process, the solution of the linear white noise delay-differential equation

$$\begin{aligned} &\frac{d}{dt}\, y^0(t) = \sum_{i=0}^{N} C_i(t) y^0(t-\delta_i) + \sigma(t) W(t) \\ &y^0(t) \equiv 0 \text{ for } t \leqq 0. \end{aligned} \tag{3.7}$$

Here $W(t)$ is a vector of independent white noises, and the matrix $\sigma(t)$ is calculated as follows. First, one calculates the matrix

$$\begin{aligned} &A(x_0, x_1, \cdots, x_N, t) \\ &= \lim_{T\to\infty} \frac{1}{T} \int_0^T ds_1 \int_0^T ds_2\, E\{[F(x_0, x_1, \cdots, x_N, t, \gamma(s_1)) \\ &\quad - EF(x_0, x_1, \cdots x_N, t, \gamma(s_1))] \\ &\quad [F(x_0, x_1, \cdots, x_N, t, \gamma(s_2)) - EF(x_0, x_1, \cdots, x_N, t, \gamma(s_2))]^T\}. \end{aligned} \tag{3.8}$$

A matrix $\sigma(x_0, x_1, \cdots x_N, t)$ is then chosen so that

$$\sigma\sigma^T = A. \tag{3.9}$$

$\sigma(t)$ in equation (3.7) is then defined by $\sigma(t) \equiv \sigma(x^0(t), x^0(t - \delta_1), \cdots, x^0(t - \delta_N), t)$, and $A(t) \equiv \sigma(t)\sigma^T(t)$.

As in the non-delay case, the solution of (3.7) may be written in terms of a deterministic fundamental solution matrix. Here this matrix is the solution of

$$\begin{gathered}\frac{d}{dt} Y(t, s) = \sum_{i=0}^{N} C_i(t)Y(t - \delta_i, s) \quad t > s \\ Y(t, s) = 0 \text{ for } t < s, \quad Y(s, s) = I.\end{gathered} \tag{3.10}$$

The solution of (3.7) may then be written as

$$y^0(t) = \int_0^t Y(t, s)\sigma(s)W(s)\, ds. \tag{3.11}$$

The covariance of $y^0(t)$ is then calculated as (for $t' \geqq 0$)

$$E[y^0(t + t')y^{0T}(t)] = \int_0^t Y(t + t', s)A(s)Y^T(t, s)\, ds. \tag{3.12}$$

Unfortunately in the delay case there appears to be no analogue of equation (2.5) for calculating the covariance (with $t' = 0$) directly.
The analysis of equilibrium point models now proceeds along lines quite similar to that for the non-delay case. It is assumed that time t does not appear explicitly in equation (3.1), and that the corresponding deterministic equations (3.4) have a solution $x^0(t) = \bar{x}$ a constant. If this solution of (3.4) is linearly stable, then the covariance of the gaussian distribution of $y^0(t)$ converges exponentially to a limit, and the general qualitative features are the same as in the non-delay case, although explicit calculations are more difficult. Methods for calculating the covariance, and applications to a specific example are in [4]. A comparison with Monte-Carlo results is in [2].

4. The methods of § 3 may be extended to handle several other types of models. First, the fixed delays of § 3 may be replaced by delays which are themselves rapidly-varying random functions of time. We may consider, for instance, the equations

$$\frac{d}{dt}x^\epsilon(t) = f(x^\epsilon(t - \delta(t/\epsilon))) \tag{4.1}$$

where $\delta(\tau)$ is a stochastic process. We consider first the case where

there are only a finite number of possible values $\{\delta_0, \delta_1, \cdots, \delta_N\}$ for δ.

$$\delta(\tau) = \delta_i \text{ for some } i = 0, 1, \cdots, N \text{ with probability 1.} \tag{4.2}$$

This may be reduced to the problem of fixed delays by the following device. Define the "random switches"

$$\gamma_i(\tau) = \begin{cases} 1 \text{ if } \delta(\tau) = \delta_i \\ 0 \text{ otherwise.} \end{cases} \tag{4.3}$$

Then for vector $\gamma(\tau) = (\gamma_0(\tau), \cdots, \gamma_N(\tau))$ we have the identity

$$\begin{aligned} \frac{d}{dt}\, x^\epsilon(t) &= \sum_{i=0}^{N} f(x^\epsilon(t - \delta_i))\gamma_i(t/\epsilon) \\ &\equiv F(x^\epsilon(t - \delta_0), \cdots, x^\epsilon(t - \delta_N), \gamma(t/\epsilon)). \end{aligned} \tag{4.4}$$

The methods of § 3 may now be applied directly to (4.4).

The case of random delays with a continuum of possible values may also be treated, but a further extension is needed [see **2**, 3]. The approximation $x^\epsilon(t) \approx x^0(t) + \sqrt{\epsilon}y^0(t)$ with x^0 deterministic and y^0 gaussian is still valid. Calculation of the relevant quantities, however, involves the solution of integrodifferential equations.

Further generalizations of these types of models may involve integral memory terms rather than point time delays. That is, the non-linear function F may depend on terms of the form

$$y(t) = \int_{-\infty}^{t} k(t - s)g(x_i(s))\, ds, \tag{4.5}$$

where $x_i(s)$ is one of the components of the population vector x^ϵ. These models may be treated by the methods of § 2 in the special case when the kernel $k(t)$ has a Fourier transform $\hat{k}(\omega)$ which is a rational function of ω. Actually, any reasonably well-behaved kernel can be approximated by such a function by means of an expansion in Laguerre functions [see 7]. The idea is to introduce new dependent variables $y_1(t) \equiv y(t)$, $y_2(t)$, $y_3(t)$, $\cdots$, $y_d(t)$, so that $(y_1, y_2, \cdots, y_d)$, x^ϵ together form a system of coupled ordinary differential equations.

As an example, consider the single stochastic equation for scalar $x^\epsilon(t)$

$$\frac{d}{dt}\, x^\epsilon(t) = f\left(\int_{-\infty}^{t} k(t - s)g(x^\epsilon(s))\, ds,\ \gamma(t/\epsilon) \right). \tag{4.6}$$

We define

$$y_1(t) = \int_{-\infty}^{t} k(t - s)g(x^\epsilon(s))\, ds. \tag{4.8}$$

For the case of exponentially decaying memory, $k(t) = e^{-t}$, we have that

$$\frac{d}{dt} y_1(t) = -y_1(t) + g(x^\epsilon(t)).$$

We may therefore solve the 2-dimensional system

$$\frac{d}{dt}\begin{bmatrix} x^\epsilon(t) \\ y_1(t) \end{bmatrix} = \begin{bmatrix} f(y_1(t), \gamma(t/\epsilon)) \\ -y_1(t) + g(x^\epsilon(t)) \end{bmatrix}$$
$$= F(x^\epsilon(t), y_1(t), \gamma(t/\epsilon)).$$

For the kernel $k(t) = t e^{-t}$, we define

$$y_2(t) = \int_{-\infty}^{t} e^{-(t-s)} g(x^\epsilon(s))\, ds.$$

We may then solve the 3-dimensional system

$$\frac{d}{dt}\begin{bmatrix} x^\epsilon(t) \\ y_1(t) \\ y_2(t) \end{bmatrix} = \begin{bmatrix} f(y_1(t), \gamma(t/\epsilon)) \\ -y_1(t) + y_2(t) \\ -y_2(t) + g(x^\epsilon(t)) \end{bmatrix}.$$

The main difficulty that arises is that, depending on the form of k, there may be considerable enlargement of the number of simultaneous equations to be solved.

Recent theoretical work [see **6**] has extended these methods to handle some boundary value problems of the type that occur in models of interacting species in random spatial environments. More specifically, we assume that the populations are distributed along a one-dimensional space, and that the environment does *not* change with time. It has, however, a random spatial structure that may give rise to random "patches" where some species are favored more than others. While any one such community may reach its own equilibrium, there will be significant differences due to chance if many such communities are observed.

Let $u_i(t, x)$ be the density of species i at position x in space, at time t. The population vector is then defined as $u = (u_1, u_2, \cdots, u_n)$. If the stochastic fluctuations are on a small space scale, then models allowing for diffusive migration can be written in the form

$$\frac{\partial}{\partial t} u(t, x) = \frac{\partial}{\partial x} a(x, \gamma(x/\epsilon)) \frac{\partial}{\partial x} u(t, x)$$
$$+ f(u(t, x), \frac{\partial}{\partial x} u(t, x), x, \gamma(x/\epsilon)) \text{ for } x \in [0, L]. \tag{4.6}$$

Here a is the diffusion matrix, and f gives the form of the local interaction dynamics. $\gamma(x/\epsilon)$ is a spatial stochastic process, and $\epsilon > 0$ is small. In addition to (4.6), some boundary conditions must be specified for $u(t, x)$ at the limits of the finite environment at $x = 0$ and $x = L$.

While interesting dynamical behavior may well occur in (4.6), we consider here only possible steady states, solutions of the equation

$$\frac{\partial}{\partial x}\, a(x, \gamma(x/\epsilon))\, \frac{\partial}{\partial x}\, v(x) + f(v(x), \frac{\partial}{\partial x} v(x), x, \gamma(x/\epsilon)) = 0. \tag{4.7}$$

Since (4.7) is to be solved as a boundary-value problem, fundamental questions of existence and uniqueness of the stochastic solution need to be considered.

There is a deterministic equation relevent to the solution of (4.7). It is of the form

$$\frac{\partial}{\partial x}\, \bar{a}(x)\, \frac{\partial}{\partial x}\, \bar{v}(x) + \bar{f}(v(x), \frac{\partial}{\partial x} v(x), x) = 0, \tag{4.8}$$

where $\bar{a}$, $\bar{f}$ are determined by explicit averaging formulae analogous to those for the initial value problems considered earlier. The expression for $\bar{a}$ is a sort of harmonic mean of a (which is assumed invertible):

$$\bar{a}(x) = \left[\lim_{T\to\infty} \frac{1}{T} \int_0^T E[a^{-1}(x, \gamma(y))]\, dy \right]^{-1}. \tag{4.9}$$

If f does not depend on $(\partial/\partial x)v(x)$, then $\bar{f}$ is computed simply by

$$\bar{f}(v, x) = \lim_{T\to\infty} \frac{1}{T} \int_0^T E[f(v, x, \gamma(y))]\, dy. \tag{4.10}$$

Under general hypotheses, it can be shown that for any solution $\bar{v}(x)$ of (4.8) there exists, with probability arbitrarily close to one as $\epsilon \to 0$, a unique solution of (4.7) that is close to $\bar{v}$ in an appropriate sense, and satisfies the same boundary conditions. This solution, $v(x)$, can then be written approximately for small ϵ as $v(x) \approx \bar{v}(x) + \sqrt{\epsilon}\, v_1(x)$. Furthermore, $v_1(x)$ is gaussian, and can be characterized as the solution of a linear stochastic boundary value problem.

Bibliography

1. R. Z. Khasminskii, *Stochastic processes defined by differential equations*, Theory Prob. Appl. **9** (1966), 211–228.

2. M. Levandowsky and B. S. White, *Randomness, time scales, and the evolution of biological communities*, Evol. Biol. (to appear).

3. R. M. May, *Stability in randomly fluctuating versus deterministic environments*, American Naturalist, **107** (1973).

4. B. S. White, *Some limit theorems for stochastic delay-differential equations*, Comm. Pure. Appl. Math. **29** (1976), 113–141.

5. ———, *The effects of a rapidly-fluctuating random environment on systems of interacting species*, SIAM J. Appl. Math. **32** (1977), 666–693.

6. B. S. White and J. N. Franklin, *A limit theorem for stochastic two-point boundary value problems of ordinary differential equations*, Comm. Pure Appl. Math. (to appear).

7. N. Wiener, *Extrapolation, Interpolation and Smoothing of Stationary Time Series*, M.I.T. Press, 1966.

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