Extinction and persistence of populations in a random environment: generalization to density-dependent noise intensities

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The purpose is to extend to density-dependent noise intensities the results previously obtained for constant noise intensities concerning extinction and persistence of populations in a randomly varying environment. We will also look at the question of which stochastic calculus should one use.

Previous model and results

Denote by $N = N(t)$ the size at time $t \geq 0$ of a population (animals, bacteria, cells) living in a randomly varying environment and assume $N(0) = N_0 > 0$ is given. The *per capita growth rate* (abbrev. *growth rate*) of the population can be described by the general stochastic differential equation (SDE) model

$$\frac{1}{N}\frac{dN}{dt} = g(N) + \sigma\varepsilon(t)$$

or, in standard notation with $W(t) = \int_0^t \varepsilon(s)ds$ being the standard Wiener process,

$$dN = g(N)Ndt + \sigma N dW(t).$$

Here, $g(N)$ is interpreted as the "average" per capita growth rate and the effect of the environmental fluctuations (noise) is approximated by $\sigma\varepsilon(t)$, $\varepsilon(t)$ being a standard white noise and $\sigma > 0$ being the *noise intensity*. We will assume that $g(\cdot) : (0, +\infty) \mapsto (-\infty, +\infty)$ is a continuously differentiable function such that the limit $g(0^+) := \lim_{N \downarrow 0} g(N)$ exists (may be infinite) and $G(0^+) = 0$ (no spontaneous generation), where $G(N) = Ng(N)$ is the *total growth rate* of the population. We will assume g to be a strictly decreasing function, assuming no Allee effects and translating the fact that, under limited resources, as the population gets larger, the harder it is for individuals to survive and reproduce. This is a generalization of a variety of models that have appeared in the literature using specific forms of g functions.

In Braumann (1999a), we have studied this general model using Stratonovich calculus. We have shown the existence and uniqueness of the solution and that it stays in the interval $(0, +\infty)$. The solution is a homogeneous diffusion process with diffusion coefficient $b(x) = \sigma^2 x^2$ and drift coefficient $a(x) = g(x)x + \frac{1}{4}db^2(x)/dx = (g(x) + \sigma^2/2)x$.

We have concluded that ("mathematical") extinction ($N(t) \to 0$ as $t \to +\infty$) occurs with probability one if $g(0^+)$ ("average" growth rate at low population densities) is negative. When $g(0^+)$ is positive, there is no risk of extinction and there is a stationary density $p(n)$ (the process $N(t)$ is also ergodic). Denoting by N_∞ a random variable (r.v.) with p.d.f. $p(n)$, this means that $N(t)$ converges in distribution to N_∞ as $t \to +\infty$. The proof of the existence of a stationary density rests on showing, under such few assumptions, that the boundaries $N = 0$ and $N = +\infty$ are non-attractive (using the scale measure) and that the speed measure is finite.

Results of a similar sort on extinction and on existence of a stationary density were also obtained for harvesting models (same models with an extra density-dependent harvesting term) in Braumann (1999b).

Under Itô calculus, however, the drift coefficient is $a(x) = g(x)x$ and there is extinction or a stationary density according to whether $g(0^+)$ is smaller or larger than $\sigma^2/2$. So, we may have extinction even for positive values of the "average" growth rate at low densities. This qualitatively different prediction, and the general fact that the two calculi give different solutions, is puzzling and the question of which calculus gives the correct predictions is paramount. Similar issues for specific g functions have raised a controversy on the literature over which calculus is appropriate to model population growth in a random environment. The controversy is solved in Braumann (2007a) (see also Braumann, 2007b, for the same issue for harvesting models). In fact, $g(x)$, contrary to what has been presumed in the literature, does not represent the same type of "average" growth rate. It rather represents the geometric average growth rate (when the population size is x) if Stratonovich calculus is used and the arithmetic average growth rate if the Itô calculus is used. Considering the different meanings of G, the two calculi yield exactly the same qualitative and quantitative results. For both calculi, the population will become extinct when the geometric average growth rate at low densities is negative.

Generalization to density-dependent noise intensities

We now allow the noise intensity to depend on population size. Denote it by $\sigma(N)$. We now have the even more general SDE model

$$dN = g(N)Ndt + \sigma(N)NdW(t).$$

We will assume that $\sigma(\cdot) : (0,+\infty) \mapsto (0,+\infty)$ is a positive continuously differentiable function such that the limit $\sigma(0^+)$ exists and is finite and $V(0^+) = 0$ where $V(N) = \sigma(N)N$ is the *total noise intensity*.

Now, the diffusion coefficient is $b(x) = \sigma^2(N)x^2$ and the drift coefficient is $a(x) = g(x)x$ for Itô calculus and $a(x) = g(x)x + \frac{1}{4}\frac{db(x)}{dx} = \left(g(x) + \sigma^2(x)/2 + x\sigma(x)\sigma'(x)/2\right)x$ for Stratonovich calculus.

A refinement of the techniques previously used still work and we are able to show similar results on extinction and existence of a stationary density for well-behaved $\sigma(N)$. Having $\sigma(N)$ bounded below and above by positive numbers works, but we manage to obtain a much weaker sufficient condition.

The resolution of the controversy on whether Itô or Stratonovich calculus is more appropriate proceeds as previously by showing that g means different types of average under the two calculi and that results are completely coincidental if we take into account the difference between the two averages. However, while g is still the arithmetic average growth rate under Itô calculus, it is what we call a ϕ-average growth rate under Stratonovich calculus, where $\phi(x) = \int_c^x \frac{1}{z\sigma(z)}dz$ (with $c > 0$ an arbitrarily chosen constant). In the particular case where $\sigma(N)$ is constant, ϕ is a logarithmic function (apart a location and a scale parameter) and the ϕ-average becomes a geometric average. At any rate, in what concerns extinction, the sign of the geometric average growth rate at low population densities can still be used as a deciding criteria for both calculi because the ϕ-average approaches the geometric average as $x \to 0^+$.

Conclusions

We had previously considered SDE models for the growth of a population in a randomly varying environment that have very general growth rate functions and constant noise intensities. We have proved that we would get ("mathematical") extinction or a stationary density according to whether the geometric average growth rate at low population densities is negative or positive. That result does not depend upon the stochastic calculus used, Itô or Stratonovich; to reach this conclusion we have resolved a long-standing controversy due to the apparent different results of the two calculi. The differences are apparent and due to the wrong presumption made in the literature that the so-called "average" growth rate meant the same type of average under the two calculi. Taking into account the differences in the two averages, the results of the two calculi completely coincide. Here, we show that these results can be extended to the case of density-dependent noise intensities.

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