Chapter 6: Modelling Extreme Environmental Stochasticity

6.1) Introduction

The environmental models studied in Chapter 5 displayed environmental trajectories that changed gradually over time. Real world environments experience gradual changes nearly all of the time. However, the environment is occasionally subject to very large shocks. Even though such shocks rarely occur; the (often great) magnitude of such shocks warrants special attention. Extreme events affect the risk of extinction; the variability of the population size, as well as the ideal survival strategies for a population (amongst other things).

6.2) Levy Processes

One way of modelling extreme environmental events would be to re-use the model introduced in Section 5.3. In this case, instead of having the environment represented by a diffusion process, one would use a Levy process to characterize variations in the environment. A Levy process has stationary, independent increments and its sample path has at most jump discontinuities (i.e. the sample path is continuous from the right and the left-hand limit always exists). The Levy process may be decomposed into three independent components:

\[ X_t = \theta_t + \sigma B_t + J_t \]  \hspace{1cm} (6.2.1)

\( \theta_t \) is a purely deterministic component whilst \( \sigma B_t \) is a continuous random component and \( J_t \) is a purely discontinuous random component. A Levy process can be interpreted as the sum of Brownian motion with drift and a compound Poisson process. No references to population models were found which used Levy processes to model the environment, but it does seem to be a natural way to incorporate extreme environmental changes within a population model.

By modelling the environment as a Levy process, we are assuming that the environment is not affected by the population. This may or may not be a realistic assumption depending on one’s definition of the environment. I wish to explore the impact that a two-way interaction between the environment and the population would have on the system dynamics. Since Levy processes will not allow for such an interaction, I will not explore Levy processes in further detail.
6.3) Using transition rates to model the environment

In this section, a model is developed that allows the population to affect the environment. Both the implications and the behaviour of the model are considered in some detail. If we consider the environment to be a universal entity, which is distinct from the population we are modelling and whose history affects the population trajectory, then it is probably unrealistic to prevent the population from affecting the environment. For example, if we were interested in the number of lions within an area, then under the aforementioned definition of the environment, the lion’s prey would be viewed as part of the environment. In this case, we would clearly expect the ‘environment’ to decrease (all other things being equal) as the lion numbers increased.

In order to model the environment-population system by a Markov Jump process, we choose to represent the environment as a random process with sample space, \( S \in \{1, 2, \ldots \} \) and, in addition, we let \( \phi^* > 0 \). The environment is restricted to the positive domain as it makes it easier to ensure that the transition rates (introduced in equation (6.3.1)) are always positive. The environment-population system is modelled using transition rates for each of the possible events that can occur in a time interval, \( \Delta t \). We assume that the environment can only experience one of the following outcomes in the interval \( \Delta t \): the environment could improve by one environmental unit; the environment could deteriorate by one environmental unit; the environment could experience a shock of size \( D \) or nothing could happen. As before, we assume that the only possible changes that the population can experience in that same interval are -1, 0 and +1. If the shock \( D \) is negative, we need to make the environmental condition after the shock equal \( \max(1, N + D) \) so as to ensure that the environment is always positive. We can thus fully characterize the model by defining the transition rates for each of the possible changes to both the population and the environment that could occur as follows:

\[
\phi_{jk}(N, \phi)\Delta t = P\{\Delta N(t) = j, \Delta \phi(t) = k|N(t), \phi(t)\} \quad \text{where } j = -1, 0, 1; \quad k \in \mathbb{Z}
\]

(6.3.1)

It follows that \( \phi_{jk}(N, \phi) \) is the transition rate for the event that the population size increases by \( j \) units whilst the environmental condition improves by \( k \) units. Bailey (1964) stated that the differential equation for the moment generating function of such a two dimensional process is:

\[
\frac{\partial M(\theta, \lambda, t)}{\partial t} = \sum (e^{\lambda \phi_{jk} \Delta t} - 1)\phi_{jk}\left(\frac{\partial}{\partial \theta}, \frac{\partial}{\partial \lambda}\right)M(\theta, \lambda, t)
\]

(6.3.2)
Ideally, we wish to have functional forms for the transition rates that ensure that both the population and the environment have a stable equilibrium state. It is surprisingly difficult to come up with transition rates that remain positive over all possible (or at least likely) values of $N$ and $\phi$ whilst, at the same time, ensuring that the system has a stable equilibrium state. Consider the case where the birth and death rates are proportional to the population size:

$$B(N) = a_1 N; \quad D(N) = a_2 N$$  

(6.3.3)

In this case, depending on the values of the constants $a_1$ and $a_2$, either $B(N)$ is always greater than $D(N)$ or $D(N)$ is always greater than $B(N)$. The implication in both cases is the same: the population cannot have a positive, stable equilibrium state. In the case where $a_1 = a_2$, the population has an infinite number of equilibrium states (since $B(N) - D(N) = 0 \quad \forall N$) but it is only the extinction state that is stable.

We assume that the population's birth and death rates have the following form:

$$B(N) = f_{10}(N, \phi) = c_1 N \phi - a_1 N$$
$$D(N) = f_{-1,0}(N, \phi) = -c_2 N \phi + a_2 N$$

(6.3.4)

At the same time, we assume that the transition rates for the environment are:

$$f_{0,1}(N, \phi) = d_1 \phi - g_1 \phi^2 - b_1 N \phi$$
$$f_{0,-1}(N, \phi) = d_2 \phi + g_2 \phi^2 + b_2 N \phi$$
$$f_{0,0}(N, \phi) = \mu$$

where $D$ is a constant

(6.3.5)

Empirically, the transition rates given in (6.3.4) and (6.3.5) seem to ensure that the population and the environment have stable equilibrium states. Regrettably, (6.3.4) and (6.3.5) allow the transition rates to be negative under certain values of $N$ and $\phi$. In choosing the parameter values for the model, one needs to ensure that the transition rates are always positive for all possible (or at least all likely) values of $N$ and $\phi$. The transition rates for both the population and the environment have an interaction term between $N$ and $\phi$. Thus, the population's future trajectory is influenced by the current state of the environment and vice versa. In addition we model the rate at which environmental shocks occur by the transition rate $\mu$. Intuitively, we would expect the occurrence of an environmental shock to be independent of the current state of the system. Thus, $\mu$ is assumed to be a constant. It is assumed that all environmental shocks are of the same size $D$. This is not very realistic, but it does enable one to study the qualitative effects that an environmental shock has on the population. For the above
transition rates, an application of equation (6.3.2) gives us the following differential equation for the moment generating function:

\[
\frac{\partial M(\theta, \lambda, t)}{\partial t} = (e^\theta - 1) \left[ c_1 \frac{\partial^2 M}{\partial \theta \partial \lambda} - a_1 \frac{\partial M}{\partial \theta} \right] + (e^{-\theta} - 1) \left[ -c_2 \frac{\partial^2 M}{\partial \theta \partial \lambda} + a_2 \frac{\partial M}{\partial \theta} \right] + (e^{-\lambda t} - 1) \mu M \\
+ (e^{-\lambda t} - 1) \left[ d_1 \frac{\partial M}{\partial \lambda} - g_1 \frac{\partial^2 M}{\partial \lambda^2} - b_1 \frac{\partial^2 M}{\partial \theta \partial \lambda} \right] + (e^{-\lambda t} - 1) \left[ d_2 \frac{\partial M}{\partial \lambda} + g_2 \frac{\partial^2 M}{\partial \lambda^2} + b_2 \frac{\partial^2 M}{\partial \theta \partial \lambda} \right]
\]

(6.3.6)

Naturally, one can apply the cumulant truncation procedure to find approximate values for the first few cumulants.

Suppose the parameter values are as follows:

\[
a_1 = 0.05; \quad a_2 = 0.11; \quad b_1 = 0.002; \quad b_2 = 0.0006; \quad c_1 = 0.007; \quad c_2 = 0.003; \quad d_1 = 0.1; \quad d_2 = 0.026; \quad g_1 = 0.0008; \quad g_2 = 0.0003
\]

These set of parameter were chosen as the resulting transition rates were positive for the likely population and environmental values. The deterministic equivalent of the stochastic model (ignoring the jumps in the environmental model) can be found by substituting these parameter values into (6.3.4) and (6.3.5) respectively. The resulting expressions represent the rates at which the population and the environment are changing. These rates of change (namely, \( \dot{N} \) and \( \dot{\phi} \)) are as follows:

\[
\dot{N} = 0.01N\dot{\phi} - 0.16N \\
\dot{\phi} = 0.074\dot{\phi} - 0.0011\dot{\phi}^2 - 0.0026N\dot{\phi}
\]

A plot of the above differential equations is given below where the starting environmental and population sizes are 3 and 8 respectively.

![Environment trajectory](image1)

![Population trajectory](image2)

**Figure 6.1 The deterministic Population and Environmental trajectories**
Figure 6.1 shows that the above transition rates cause the population and the environment to decay cyclically towards equilibrium after any perturbation. The diagram below shows a stochastic run of the above model when the size of the environmental jumps, $D = -5$ and the initial conditions of the system is as before:

![Trajectories](image)

**Figure 6.2 The Population and Environmental trajectory**

One can clearly see the interaction between the population and the environment in the above diagram. The trajectory of the population tends to follow that of the environment with a small time lag. The cyclic decays to equilibrium that can be clearly seen in the deterministic equivalent of the model cannot be seen in Figure 6.2. This is because the stochastic fluctuations of both the environment and the population tend to obscure this decay. In the above trajectory, environmental shocks occurred at times 30.08, 162 and 210.95.

We now examine how the population responds to varying magnitudes and likelihoods of an environmental ‘disaster’. (I use the term ‘disaster’ here to signify a large, sudden change in the environment; whether it be a drastic improvement or a drastic deterioration of the environmental condition.) Suppose the parameter values are as follows:

\[
\begin{align*}
  a_1 &= 1.2; \quad a_2 = 8.3; \quad b_1 = 0.05; \quad b_2 = 0.05; \quad c_1 = 0.14; \quad c_2 = 0.02; \\
  d_1 &= 41; \quad d_2 = 30; \quad g_1 = 0.02; \quad g_2 = 0.05
\end{align*}
\]

The equilibrium state for the above system has $N^* = 68.4; \phi^* = 59.4$. (The equilibrium state was found by creating a plot of both the environment and the population – as in Figure 6.1 – with some arbitrary initial values for the system and seeing which values both the population and the environment settled to after a period of time.) We wish to
study how the probability distribution for the population changes as we vary the magnitude (and the likelihood) of the environmental ‘disaster’. In order to estimate the population’s probability distribution, 25000 simulations were run for each for the different levels of likelihood and magnitude of the disaster, and the population size and the environmental condition at time 5 was recorded. We firstly consider an environment that is free from disasters. That is, the rate at which disasters occur, $\mu$, is equal to zero. The probability distribution for the population derived from 25000 simulations was:

![Population Probability Distribution Function]

**Figure 6.3 The estimated probability distribution for a population at time 5 where $\mu = 0$**

One can see from Figure 6.3 that the mode of the population occurs in the region of the population’s deterministic equilibrium state (whose value is 68.4). There is also a mode close to zero. This secondary mode is a measure of the extinction risk. We now consider the cases where the rate of disaster occurrence, $\mu = 0.1.1$ and when the magnitude of the disaster, $D$ can take on the values $D = -40, 40$. When $D = 40$, the environment has improved drastically, whilst when $D = -40$, the environment has undergone a major deterioration. When performing the simulation when $D = -40$, care was taken to ensure that the environmental condition did not fall below one (as negative numbers are outside $\phi$’s sample space).
The distributions are shown below:

**Figure 6.4 Estimated probability distributions for different values of $\mu$ and $D$ at time 5**

For all the parameter values considered, the population is skew to the right, whilst there is a peak in the distribution near zero. This is because the population size cannot drop below zero, so whenever the environment is harsh, the population will be pushed towards this secondary mode under which the population is on the brink of (or is at) extinction. The table below summarises the key features for each of the five distributions considered:

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Extinction Probability</th>
<th>Mean</th>
<th>Variance</th>
<th>Skewness</th>
<th>Conditional Mean</th>
<th>Conditional Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Disaster</td>
<td>0.1409</td>
<td>51.1817</td>
<td>1368.594</td>
<td>21809.96</td>
<td>59.575952</td>
<td>1593.05586</td>
</tr>
<tr>
<td>$\mu=1, D=-40$:</td>
<td>0.57788</td>
<td>20.39704</td>
<td>1098.893</td>
<td>60942.85</td>
<td>48.320478</td>
<td>2603.27253</td>
</tr>
<tr>
<td>$\mu=0.1, D=-40$:</td>
<td>0.20516</td>
<td>46.445</td>
<td>1472.243</td>
<td>30436.45</td>
<td>58.433144</td>
<td>1852.25053</td>
</tr>
<tr>
<td>$\mu=1, D=+40$:</td>
<td>0.05924</td>
<td>63.22124</td>
<td>1460.585</td>
<td>30191.39</td>
<td>67.202305</td>
<td>1552.55884</td>
</tr>
<tr>
<td>$\mu=0.1, D=+40$:</td>
<td>0.04172</td>
<td>58.63388</td>
<td>1136.527</td>
<td>15991.19</td>
<td>61.186584</td>
<td>1186.00743</td>
</tr>
</tbody>
</table>

**Table 6.1: Selected statistics of the population at time 5**
The conditional mean and variance are both conditioned on the event that the population is not extinct. One can see from the table that the more likely a disaster is, the greater the extinction risk. Perhaps surprisingly, this is also true in the case when the environment is only subject to a sudden improvement – this is because, the resulting population behaviour is more erratic. Both the mean and the conditional mean seem to increase with $D$. In addition, the two statistics increase with the rate of disaster occurrence, $\mu$ if $D > 0$; but decrease as $\mu$ increases if $D < 0$. The empirical behaviour of the mean and the conditional mean thus confirms to our intuition.

We now look at the corresponding probability distributions for the environment. As before, the probability distributions were observed from 25000 simulations. For an environment free of disasters, the probability distribution is:

![Environmental Probability Distribution Function](image)

**Figure 6.5: The estimated probability distribution for an environment at time 5 where $\mu = 0$**

One can see from Figure 6.5 that the mode of the environment is in the region of the environment’s deterministic equilibrium state (the value of which is 59.4). There is a slight peak near zero. An unfavourable environmental condition is probably indicative of the population exerting a lot of strain on the environment by virtue of its large size. As before, we also consider the cases where the rate of disaster occurrence, $\mu = 0.1, 1$ and
when the magnitude of the disaster, $D$ can take on the values $D = -40, 40$. The resulting probability distributions for the environment are shown below for time 5:

![Environmental Probability Distribution Function](image1)

![Environmental Probability Distribution Function](image2)

![Environmental Probability Distribution Function](image3)

![Environmental Probability Distribution Function](image4)

**Figure 6.6 Estimated probability distributions for different values of $\mu$ and $D$**

As with Figure 6.5, there is a peak of the environmental distribution around the environment’s deterministic equilibrium state. Furthermore, from the first two graphs (under which the extinction risk is considerable), one can clearly see a second peak in the population. This peak is in the region of the deterministic equilibrium state for the environment when the population is extinct (the value of this second equilibrium state is 157.1).

The Jump models covered in this Chapter add an extra dimension to our population models. Such models enable us to study how the population responds to disasters and consequently how the probability of events like extinction changes as the severity and frequency of occurrence of such disasters increases. Regrettably, little work seems to have been done in incorporating such discontinuous environmental models.