MODELLING THE LONG-TERM BEHAVIOUR OF EVANESCENT ECOLOGICAL SYSTEMS[1]

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1. INTRODUCTION

There are many ecological systems which eventually “die out”, yet over any reasonable time scale appear to settle down to a stable equilibrium. For example, it is not unusual for animal populations to be subject to large-scale mortality or emigration. This can occur when disease, such as a new virus, affects the population, or when food shortages occur, such as those induced by overbrowsing or dramatic changes in climatic conditions. However, although these populations may eventually become extinct, they can survive for long periods in an apparently stable state. The notion of a quasistationary distribution has proved to be a potent tool in modelling this behaviour. It is potentially useful in wildlife management, for it allows one to predict persistence times and the distribution of population size. Here we present simple conditions for the existence of quasistationary distributions for a variety of evanescent processes. We shall use these conditions to obtain quasistationary distributions for two models which arise frequently in ecological modelling, namely the birth-death process and the linear birth-death and catastrophe process. Additionally, we shall draw attention to a recently developed computational algorithm for evaluating quasistationary distributions for large-scale models with a sparse transition structure.

2. QUASISTATIONARY DISTRIBUTIONS

The idea can be traced back to Yaglom [19], but we shall use the definition of a quasistationary distribution introduced by van Doorn [3]. We shall suppose that the system in question can be modelled as a time-homogeneous Markov chain, $(X(t),\ t \geq 0)$, taking values in a discrete set S. Let $Q = (q_{ij},\ i,j \in S)$ be the q-matrix of transition rates (assumed to be stable and conservative), so that $q_{ij}\ (\geq 0)$, for $j \neq i$, represents the transition rate from state i to state j and $q_{ii} = -q_i$, where $q_i = \sum_{j \neq i} q_{ij}\ (< \infty)$ represents the transition rate out of state i. Additionally, we shall suppose that Q is regular, so that $X(\cdot)$ is the unique chain with these rates. We shall be concerned with evanescent chains, so, for simplicity, let us take 0 to be the sole absorbing state, that is, $q_0 = 0$, and suppose that $S = \{0\} \cup C$, where $C = \{1, 2, \dots\}$ is an irreducible transient class. In order that there be a positive probability of ever reaching 0 starting in C, we shall suppose that $q_{i0} > 0$ for at least one $i \in C$. Finally, let $P(\cdot) = (p_{ij}(\cdot),\ i,j \in S)$ be the transition function of the chain, so that $p_{ij}(t) = \Pr(X(t) = j | X(0) = i)$, for $t \geq 0$.

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Definition. *Let $m = (m_j,\ j \in C)$ be a probability distribution and let $p_j(t) = \sum_{i\in C} m_i p_{ij}(t)$, for $j \in S$ and $t \geq 0$. Then, m is a quasistationary distribution if, for all $t > 0$ and $j \in C$, $p_j(t)/(\sum_{i\in C} p_i(t)) = m_j$. That is, if the chain has m as its initial distribution, then m is a quasistationary distribution if the state probabilities at time t, conditional on the chain being in C at t, are the same for all t.*

The relationship between quasistationary distributions and the transition probabilities of the chain can be made more precise as follows:

Proposition 1 (Nair and Pollett [9])**.** *Let $m = (m_j,\ j \in C)$ be a probability distribution. Then, m is a quasistationary distribution if and only if, for some $\mu > 0$, m is μ-invariant for P, that is*

$$\sum_{i\in C} m_i p_{ij}(t) = e^{-\mu t} m_j, \qquad j \in C,\ t \geq 0. \tag{1}$$

Thus, in a way which mirrors the familiar theory of *stationary distributions*, one can interpret quasistationary distributions as eigenvectors of the transition function. However, the transition function is available explicitly in only a few simple cases, and so one requires a means of determining quasistationary distributions directly from transition rates of the chain. Since q_{ij} is the right-hand derivative of $p_{ij}(\cdot)$ near 0, an obvious first step is to rewrite (1) as

$$\sum_{i\in C:\, i\neq j} m_i p_{ij}(t) = \big((1 - p_{jj}(t)) - (1 - e^{-\mu t})\big)\, m_j, \qquad j \in C,\ t \geq 0,$$

and then divide by t and let $t \downarrow 0$. Proceeding formally, we get

$$\sum_{i\in C:\, i\neq j} m_i q_{ij} = (q_j - \mu) m_j, \qquad j \in C,$$

or, equivalently,

$$\sum_{i\in C} m_i q_{ij} = -\mu m_j, \qquad j \in C. \tag{2}$$

Accordingly, we shall say that m is *μ-invariant for Q* whenever (2) holds. The above argument can be justified rigorously (see Proposition 2 of [18]), and so, in view of Proposition 1, we have proved that if m is a quasistationary distribution then, for some $\mu > 0$, m is μ-invariant for Q. The more interesting question of when a probability distribution, m, which satisfies (2) also satisfies (1) is answered in the statement of our major result. It can be deduced from Theorems 3.2, 3.4 and 4.1 of [9].

Proposition 2. *Let $m = (m_j,\ j \in C)$ be a probability distribution and suppose that m is μ-invariant for Q. Then, $\mu \leq \sum_{j\in C} m_j q_{j0}$, with equality if and only if m is a quasistationary distribution. A sufficient condition for m to be a quasistationary distribution is that $\sum_{j\in C} m_j q_j < \infty$.*

3. APPLICATIONS

3.1 Finite-state systems

If S is a finite set, then clearly $\sum_{j\in C} m_j q_j < \infty$ and so every μ-invariant probability distribution for Q is a quasistationary distribution. Indeed, classical matrix theory can be used to show that the q-matrix restricted to C has eigenvalues with negative real parts, that $-\mu$ is the dominant eigenvalue (it has maximal real part), that this eigenvalue always has multiplicity 1, and, that both the corresponding left- and right-eigenvectors have positive entries (see [2] and [7]) ; the left eigenvector is, of course, the quasistationary distribution. Thus, for example, in closed (finite) population models, the stationary conditional distribution of the number in the population (conditional on non-extinction) can be obtained as the normalized dominant left-eigenvector of the transition-rate matrix restricted to the transient states. In most cases one is forced to evaluate the dominant eigenvector numerically. If the number of states is reasonably small, say 100, then one can use any of the standard methods (inverse iteration, for example) which are widely available as part of matrix packages, such as MATLAB. If the number of states is even moderately large, these methods are ineffective, both in respect of storage and CPU time. For example, if there are 10^4 states (which would be the case in a predator-prey system with of the order of 100 individuals), Q requires 400 Mbytes of storage! If Q is sparse, or if it possesses a banded structure that can be usefully exploited, then moderately large systems can be handled without difficulty. Pollett and Stewart [14] have developed an iterative version of Arnoldi's algorithm for dealing with sparse q-matrices, and this has been used to evaluate the quasistationary distribution, to within a tolerance of 10^{-6}, for a variety of systems with of the order of 10^4 states, in times ranging from 7 to 15 CPU minutes on a Sun SPARC 10. If the number of states is very large, say 10^8, then it is frequently the case that deterministic approximations [13] or diffusion approximations [12] can be used to provide accurate estimates of the quasistationary distribution.

3.2 Birth-death processes

These are widely used in modelling ecological systems. The q-matrix of an absorbing birth-death process is of the form

$$q_{ij} = \begin{cases} \lambda_i, & \text{if } j = i+1, \\ -(\lambda_i + \mu_i), & \text{if } j = i, \\ \mu_i, & \text{if } j = i-1, \\ 0, & \text{otherwise,} \end{cases}$$

where the birth rates, $(\lambda_i,\ i \geq 0)$, and the death rates, $(\mu_i,\ i \geq 0)$, satisfy $\lambda_i,\ \mu_i > 0$, for $i \geq 1$, and $\lambda_0 = \mu_0 = 0$. Thus, 0 is an absorbing state and $C = \{1, 2, \dots\}$ is an irreducible class. The classical theory of these processes involves the recursive construction of a sequence of orthogonal polynomials (see van Doorn [3]). Define $(\phi_i(\cdot),\ i \geq 1)$, where $\phi_i : \mathrm{R} \to \mathrm{R}$, by $\phi_1(x) = 1$, $\lambda_1\phi_2(x) = \lambda_1 + \mu_1 - x$, and, for $i \geq 2$,

$$\lambda_i\phi_{i+1}(x) - (\lambda_i + \mu_i)\phi_i(x) + \mu_i\phi_{i-1}(x) = -x\phi_i(x).$$

Now define $\pi = (\pi_i,\ i \geq 1)$ by $\pi_1 = 1$ and $\pi_i = \prod_{j=2}^{i} \lambda_{j-1}/\mu_j$, for $i \geq 2$, and let $m_i = \pi_i \phi_i(x)$. It can be shown [3] that $\phi_i(x) > 0$ for x in the range $0 \leq x \leq \lambda$, where λ (≥ 0) is the decay parameter of C (see [5]). Since $\sum_{i \in S} \pi_i q_{ij} \leq 0$, $j \in S$, it follows, from Theorem 4.1 b(ii) of [11], that, for each fixed x in the above range, $m = (m_i,\ i \geq 1)$ satisfies (2) with $\mu = x$. Indeed, m is uniquely determined up to constant multiples. Proposition 2 tells us that if m can be normalized, that is, $\sum_{i=1}^{\infty} \pi_i \phi_i(x) < \infty$, then the normalized m will be a quasistationary distribution if and only if

$$\sum_{i=1}^{\infty} r_i(x) = 1, \tag{3}$$

where $r_i(x) = \mu_1^{-1} \pi_i x \phi_i(x)$, a conclusion reached by van Doorn using direct methods. Van Doorn's Theorem 3.2 can then be used to determine all the values of x for which (3) holds, at least under the condition $\sum_{i=1}^{\infty} \frac{1}{\lambda_i \pi_i} = \infty$, which ensures that absorption occurs with probability 1. If, in addition, the series $A = \sum_{i=1}^{\infty} \frac{1}{\lambda_i \pi_i} \sum_{j=i+1}^{\infty} \pi_j$ diverges, then (3) holds for *all* x in $(0, \lambda]$, while if it converges then (3) holds if and only if $x = \lambda$. Proposition 2 then tells us that, in either case, $r(x) = (r_i(x),\ i \geq 1)$ is a quasistationary distribution. Indeed, because m is uniquely determined for each x, *all* quasistationary distributions have been obtained; if $A < \infty$, then there is only one, namely $r(\lambda)$, otherwise $(r(x),\ 0 < x \leq \lambda)$ comprises a one-parameter family of quasistationary distributions.

3.3 The birth-death and catastrophe process

The introduction of a catastrophe component allows one to model populations which are subject to large-scale mortality or emigration. See, for example, [6] and [15] for studies of populations of reindeer and moose, which, after introduction into Alaska, suffered substantial reductions in numbers owing to overbrowsing combined with effects of severe winters; the moose population was additionally subjected to Spruce Budworm infestation and later fire. Further contrasting examples are described in [4] and [8]. The q-matrix of the birth-death and catastrophe process is given by

$$\begin{aligned} q_{i,i+1} &= a q_i, & i &\geq 0, \\ q_{i,i} &= -q_i, & i &\geq 0, \\ q_{i,i-k} &= q_i b_k, & i &\geq 2,\ k = 1, 2 \ldots i-1, \\ q_{i,0} &= q_i \sum_{k=i}^{\infty} b_k, & i &\geq 1, \end{aligned}$$

where $q_0 = 0$, $q_i > 0$, for $i \geq 1$, $a > 0$, $b_i > 0$ for at least one value of $i \geq 1$ and $a + \sum_{i=1}^{\infty} b_i = 1$. Thus, at a jump time, a birth occurs with probability a, or otherwise a catastrophe occurs, the size of which is determined by the probabilities b_i, $i \geq 1$. Clearly, 0 is an absorbing state and $C = \{1, 2, \ldots\}$ is an irreducible class. It is usual to set $q_i = \rho i$, where $\rho > 0$, so that jumps occur at a constant "per capita" rate ρ. It is

well known [10] that the probability of absorption, starting in state i, is 1 if and only if $D := a - \sum_{i \in C} ib_i \leq 0$. Note that the process is said to be subcritical, critical or supercritical according as D is negative, zero or positive. An important role is played by the probability generating function, f, given by $f(s) = a + \sum_{i \in C} b_i s^{i+1}$, $|s| < 1$, and the related function, b, given by $b(s) = f(s) - s$. In identifying the quasistationary distribution, we shall need the following facts from branching process theory (see [1]): b is convex on $[0, 1]$, $b(s) = 0$ has a unique solution, σ, on this interval, $\sigma = 1$ or $0 < \sigma < 1$ according as $D \geq 0$ or $D < 0$, and, $b(s) \geq 0$ on $[0, \sigma]$.
On substituting the transition rates in (2), we get

$$-(\rho - \mu)m_1 + \sum_{k=2}^{\infty} k\rho b_{k-1} m_k = 0,$$

$$(j-1)\rho a m_{j-1} - (j\rho - \mu)m_j + \sum_{k=j+1}^{\infty} k\rho b_{k-j} m_k = 0, \qquad j \geq 2.$$

If we try a solution of the form $m_j = t^j$, the first equation tells us that $\mu = -\rho b'(t)$, and, on substituting both of *these* quantities in the second equation, we find that $b(t) = 0$. Hence, we may set $t = \sigma$, thus providing a positive solution to (2) with $\sum_{j \in C} m_j < \infty$ whenever $\sigma < 1$. Under this latter condition, we also have $\sum_{j \in C} m_j q_j = \sum_{j \in C} \sigma^j j\rho < \infty$. Thus, using Proposition 2, we have proved that the subcritical linear birth-death and catastrophe process has a geometric quasistationary distribution, given by $m_j = (1 - \sigma)\sigma^{j-1}$, $j \in C$, a result which is implicit in the proof of Theorem 5.1 of [10].

3.4 Computational methods for infinite-state systems

For the two infinite-state models considered above, we were able to exhibit the quasistationary distribution explicitly. In cases where it cannot be, or where the form of the quasistationary distribution is not amenable to numerical evaluation, one is forced to use a direct computational approach. One widely used method is to truncate the restricted q-matrix to an $n \times n$ matrix, $Q^{(n)}$, and construct a sequence, $\{m^{(n)}\}$, such that $m^{(n)}$ is the left-eigenvector of $Q^{(n)}$ associated with the eigenvalue with maximum real part. Then, one estimates the quasistationary distribution by taking successively larger truncations until the difference in the normalized eigenvectors is as small as desired. For a detailed account of these procedures, see [16] and [17]. When this approach is used, the iterative Arnoldi method, referred to above, provides an efficient means of determining the sequence $\{m^{(n)}\}$.

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