

Fluctuations in a coupled population model

This article has been downloaded from IOPscience. Please scroll down to see the full text article.

2005 J. Phys. A: Math. Gen. 38 6447

(<http://iopscience.iop.org/0305-4470/38/29/002>)

View [the table of contents for this issue](#), or go to the [journal homepage](#) for more

Download details:

IP Address: 171.66.16.92

The article was downloaded on 03/06/2010 at 03:50

Please note that [terms and conditions apply](#).

Fluctuations in a coupled population model

E Jakeman^{1,2}, K I Hopcraft² and J O Matthews²

¹ School of Electrical and Electronic Engineering, University of Nottingham, University Park, Nottingham NG7 2RD, UK

² School of Mathematical Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK

Received 21 April 2005, in final form 10 June 2005

Published 6 July 2005

Online at stacks.iop.org/JPhysA/38/6447

Abstract

We investigate a discrete Markov process in which the immigration of individuals into one population is controlled by the fluctuations in another. We examine the effect of coupling back the second population to the first through a similar mechanism and derive exact solutions for the generating functions of the population statistics. We show that a stationary state exists over a certain parameter range and obtain expressions for moments and correlation functions in this regime. When more than two populations are coupled, cyclically transient oscillations and periodic behaviour of correlation functions are predicted. We demonstrate that if the initial distribution of either population is stable, or more generally has a power-law tail that falls off like $N^{-(1+\alpha)}$ ($0 < \alpha < 1$), then for certain parameter values there exists a stationary state that is also power law but not stable. This stationary state cannot be accessed from a single multiple immigrant population model, but arises solely from the nonlinear interaction of the coupled system.

PACS numbers: 02.50.-r, 02.50.Ey, 89.75.-k

1. Introduction

Continuous variables characterized by Lévy-stable distributions have been invoked to characterize data from a wide range of complex systems [1–3]. However, many real phenomena are intrinsically discrete (e.g. [4]), with integer numbers of individuals or events characterizing a process that evolves with time. This has recently led us to develop a time-dependent population process whose equilibrium distribution is stable such that, by analogy with the continuous variable case, the sum of independent populations has the same distribution as that of each constituent population. By allowing individuals to leave the population, we were also able to generate a series of events that displayed the power-law characteristics normally associated with scale-free behaviour [5–7]. This emigration mechanism more

generally provides a means for the external monitoring of an evolving population [6] and has stimulated an investigation of the statistical accuracy expected in measurements [8].

The population model investigated in our previous papers is a simple process involving just deaths and multiple immigrations. The rate of demise of individuals is a conventional death process with rate μN governed by the instantaneous number N present in the population at a given time. However, the immigration process consists of multiple events that occur according to pre-determined coefficients $\{\alpha_r\}$ independent of the incumbent population. We have shown how these coefficients determine the evolution of the population and its equilibrium statistics and how indeed they can be chosen to generate a population with specific properties of interest such as an equilibrium distribution that is stable [5, 7]. More generally, it enables the time evolution of a chosen type of discrete noise or series of events to be simulated numerically—a useful tool in the evaluation of signal processing algorithms and system performance. One important property of the model is disconnection of the equilibrium distribution of the population from its time evolution. The latter is always characterized by exponential decay, even when the equilibrium distribution is scale-free, because the population evolution is a first-order Markov process with P_N , the probability of finding N individuals in the population at time t , being governed by the rate equation

$$\frac{dP_N}{dt} = \mu(N+1)P_{N+1} - \mu N P_N - P_N \sum_{r=1}^{\infty} \alpha_r + \sum_{r=1}^N \alpha_r P_{N-r}. \quad (1)$$

The choice of $\{\alpha_r\}$ in this equation determines the form of the equilibrium distribution that is attained asymptotically at long times whatever the initial state of the population. For example, we showed previously [5, 7] that when $\alpha_r \propto [\Gamma(r-\nu)/\Gamma(-\nu)r!]$ with $0 < \nu < 1$, a class of stable discrete distributions is obtained. In general, the $\{\alpha_r\}$ can themselves be normalized to form a discrete probability distribution of the *multiplicity* of the immigrants. Our original model can therefore be generalized by drawing these probabilities from a second population that may itself be evolving with time. Thus immigration into population 1 is moderated by the fluctuations in population 2. In this model, population 1 is still ‘driven’ by population 2 that evolves completely independently according to its own process.

Although this driven problem is of interest in its own right, it suggests a more symmetric configuration in which population 1 also influences population 2 through a similar multiple immigrant mechanism. It is this *coupled* population model that will be investigated in the present paper.

In the next section, a mathematical formulation of the model will be given, with a general solution derived for the generating function of the conditional population distribution in section 3. In section 4, the evolution of the moments will be derived using an alternative approach and correlation functions will be obtained. Section 5 will report an investigation of the effect of interactions between more than two populations whilst section 6 considers the case when one population is initially governed by a discrete stable distribution. A summary and discussion of future directions is presented in section 7.

2. Two populations coupled by multiple immigration

The terms containing $\{\alpha_r\}$ in equation (1) constitute a simple convolution and the problem is more simply expressed in terms of the generating function

$$Q^{(1)}(s, t) \equiv \sum_{N_1=0}^{\infty} (1-s)^{N_1} P_{N_1} = \langle (1-s)^{N_1} \rangle. \quad (2)$$

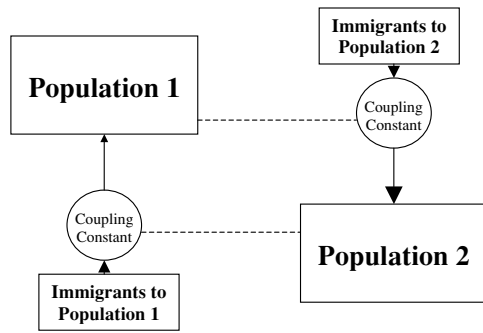


Figure 1. Diagram of two coupled multiple immigrant population models.

Thus, the convolution in (1) transforms into a product:

$$\frac{\partial Q^{(1)}}{\partial t} = -\mu_1 s \frac{\partial Q^{(1)}}{\partial s} + Q^{(1)} \left(\sum_{r=0}^{\infty} \alpha_r (1-s)^r - \sum_{r=0}^{\infty} \alpha_r \right). \tag{3}$$

The superscript on Q and the subscript on μ have been introduced to identify population 1. We now generalize this process by drawing the $\{\alpha_r\}$ from a second population governed by the generating function

$$\varepsilon_1 Q^{(2)}(s, t) = \sum_{r=0}^{\infty} \alpha_r (1-s)^r. \tag{4}$$

Here, ε_1 is a parameter required to convert α_r into a normalized discrete distribution, and plays the role of a coupling constant. Equation (3) may now be written as

$$\frac{\partial Q^{(1)}}{\partial t} = -\mu_1 s \frac{\partial Q^{(1)}}{\partial s} + \varepsilon_1 Q^{(1)} [Q^{(2)} - 1]. \tag{5}$$

The model that will be investigated in the present paper envisages that the second population is coupled back to the first population by a similar process:

$$\frac{\partial Q^{(2)}}{\partial t} = -\mu_2 s \frac{\partial Q^{(2)}}{\partial s} + \varepsilon_2 Q^{(2)} [Q^{(1)} - 1]. \tag{6}$$

It is important to emphasize that in this model members of the two populations are not exchanged nor are they necessarily of the same type, but the number in one population merely affects the likelihood of a particular number of immigrants arriving in the other, see figure 1.

Full solutions of equations (5) and (6) can be obtained in certain cases, the simplest of which is where two populations have the same coupling constants ε and the same death parameters μ . It is easy to show that the two populations then either grow without limit or become extinct unless $\mu = \varepsilon$. In order to retain some generality in the model, therefore, each population will be stabilized by introducing a conventional, independent, single immigration term ([6] and references therein). Equations (5) and (6) then become

$$\frac{\partial Q^{(1)}}{\partial t} = -\mu_1 s \frac{\partial Q^{(1)}}{\partial s} + \varepsilon_1 Q^{(1)} [Q^{(2)} - 1] - \nu_1 s Q^{(1)} \tag{7}$$

$$\frac{\partial Q^{(2)}}{\partial t} = -\mu_2 s \frac{\partial Q^{(2)}}{\partial s} + \varepsilon_2 Q^{(2)} [Q^{(1)} - 1] - \nu_2 s Q^{(2)}. \tag{8}$$

When $\varepsilon_1 = \varepsilon_2 = 0$, these equations describe two independent death-immigration processes characterized by Poisson equilibrium distributions. However, when coupling is present the

solution is evidently more complicated. In what follows, we shall usually specialize to the case $\mu_1 = \mu_2 = \mu$, $\varepsilon_1 = \varepsilon_2 = \varepsilon$, $\nu_1 = \nu_2 = \nu$ although the more general case can be solved for quantities such as the evolution of the mean and variance of the populations without too much difficulty.

3. Solution for the conditional generating function

When $\mu_1 = \mu_2 = \mu$, $\varepsilon_1 = \varepsilon_2 = \varepsilon$, $\nu_1 = \nu_2 = \nu$, equations (7) and (8) may be solved through removal of the nonlinear term by subtraction. This leads to

$$\begin{aligned}\frac{\partial D}{\partial t} &= -\mu s \frac{\partial D}{\partial s} - (\varepsilon + \nu s)D \\ D &= Q^{(1)} - Q^{(2)}.\end{aligned}\quad (9)$$

This equation has the solution

$$\begin{aligned}D(s, t) &= \exp\left[-\frac{\nu s}{\mu}(1 - \theta) - \varepsilon t\right] D(s\theta, 0) \\ \theta(t) &= \exp(-\mu t).\end{aligned}\quad (10)$$

For example if initially there are N_1 individuals in population 1 and N_2 in population 2 then

$$D(s\theta, 0) = (1 - s\theta)^{N_1} - (1 - s\theta)^{N_2}.\quad (11)$$

Equation (7) can be expressed as an inhomogeneous partial differential equation for $Q^{(1)}$ in terms of this difference solution:

$$\frac{\partial Q^{(1)}}{\partial t} = -\mu s \frac{\partial Q^{(1)}}{\partial s} + \varepsilon(Q^{(1)} - D - 1) - \nu s Q^{(1)}.\quad (12)$$

The transformation

$$Q^{(1)} = \frac{D}{1 - \exp(X)}\quad (13)$$

reduces equation (12) to the standard form

$$\frac{\partial X}{\partial t} + \mu s \frac{\partial X}{\partial s} = \varepsilon D.\quad (14)$$

The particular integral of this equation can be obtained in terms of the initial value of X by Laplace transformation with respect to the time variable. The result may be expressed in terms of an incomplete gamma function [9]

$$X(s, t) = X(s\theta, 0) - D(s\theta, 0) \frac{\varepsilon}{\mu} \left(\frac{\nu s}{\mu}\right)^{\varepsilon/\mu} \exp\left(\frac{\nu s}{\mu}\theta - \varepsilon t\right) \Gamma\left(-\frac{\varepsilon}{\mu}, \frac{\nu s}{\mu}\right).\quad (15)$$

In order to satisfy the boundary condition at $t = 0$, it is necessary to add a complementary solution of equation (14), namely, an appropriate function of $s\theta$. This obtains the full solution for the generating function:

$$\begin{aligned}Q^{(1)}(s, t) &= \frac{Q_0^{(1)} D_0 f}{Q_0^{(1)} - Q_0^{(2)} \exp\{D_0(1 - f + R)\}} \\ R &= \left(\frac{\nu s}{\mu}\right)^{\varepsilon/\mu} \exp\left(\frac{\nu s}{\mu}\theta - \varepsilon t\right) \left[\Gamma\left(1 - \frac{\varepsilon}{\mu}, \frac{\nu s}{\mu}\right) - \Gamma\left(1 - \frac{\varepsilon}{\mu}, \frac{\nu s}{\mu}\theta\right)\right]\end{aligned}\quad (16)$$

$$f = \exp\left[-\frac{\nu s}{\mu}(1 - \theta) - \varepsilon t\right].$$

In these formulae, we have used the abbreviations

$$D_0 = D(s\theta, 0) = Q_0^{(1)} - Q_0^{(2)} = Q^{(1)}(s\theta, 0) - Q^{(2)}(s\theta, 0). \tag{17}$$

It is simple to check that this solution satisfies the appropriate initial conditions. The generating function for the second population is obtained by transposing $Q_0^{(1)}$ and $Q_0^{(2)}$ in (16) and it is easy to demonstrate that the result obtained is identical to that using the identity $Q^{(2)} = D - Q^{(1)} = fD_0 - Q^{(1)}$. Note that result (16) reduces to that for a simple death-immigration process when the coupling constant, ε , is set equal to 0.

In the absence of the single immigrant terms, $\nu = 0$, the generating function reduces to

$$Q^{(1)}(s, t) = \frac{Q_0^{(1)} D_0 \exp(-\varepsilon t)}{Q_0^{(1)} - Q_0^{(2)} \exp\{D_0[1 - \exp(-\varepsilon t)]\}}. \tag{18}$$

Assuming that there are N_1 individuals present in population 1 initially and N_2 in population 2 using initial condition (11) the predicted means, $n_1(t), n_2(t)$ of the populations, are thereby found to be

$$\begin{aligned} n_1(t) &= \frac{1}{2}(N_1 + N_2) \exp[(\varepsilon - \mu)t] + \frac{1}{2}(N_2 - N_1) \exp[-(\varepsilon + \mu)t] \\ n_2(t) &= \frac{1}{2}(N_1 + N_2) \exp[(\varepsilon - \mu)t] + \frac{1}{2}(N_1 - N_2) \exp[-(\varepsilon + \mu)t]. \end{aligned} \tag{19}$$

Thus, the populations become extinct if $\mu > \varepsilon$ and increase without limit if $\mu < \varepsilon$. In the special case $\varepsilon = \mu$, the populations equalize at long times, preserving the total number of individuals present initially, and the generating functions for both populations approach the form

$$Q_\infty^{(1,2)}(s) = \frac{1}{1 + \frac{1}{2}(N_1 + N_2)s}. \tag{20}$$

This solution *remembers the initial condition* and is the generating function for a geometric or thermal distribution,

$$p(N) = \frac{\langle N \rangle^N}{(1 + \langle N \rangle)^{N+1}} \tag{21}$$

with mean $\langle N \rangle = \frac{1}{2}(N_1 + N_2)$. It is worth emphasizing again, however, that the two populations are not necessarily made up from the *same kind* of individuals.

A non-trivial stationary solution to the more general problem when $\nu \neq 0$ is obtained from equation (16) provided that $\varepsilon < \mu$. By exploiting the relationship $\Gamma(a, x) = \Gamma(a) - \gamma(a, x)$, we then find at long times

$$Q_\infty^{(1,2)}(s) = \frac{1}{1 + \left(\frac{\nu s}{\mu}\right)^{\varepsilon/\mu} \exp\left(\frac{\nu s}{\mu}\right) \gamma\left(1 - \frac{\varepsilon}{\mu}, \frac{\nu s}{\mu}\right)}. \tag{22}$$

In principle, the probability distribution of the populations and their factorial moments can be found from the derivatives of this function at $s = 1$ and $s = 0$, respectively,

$$\begin{aligned} p^{(1,2)}(N) &= \frac{1}{N!} \left(-\frac{\partial}{\partial s}\right)^N Q_\infty^{(1,2)} \Big|_{s=1}; \\ N^{[r]} &= \langle N(N-1)(N-2) \cdots (N-r+1) \rangle = \left(-\frac{\partial}{\partial s}\right)^r Q_\infty^{(1,2)} \Big|_{s=0} \\ n^{[r]} &= N^{[r]} / \langle N \rangle^r. \end{aligned} \tag{23}$$

It will be shown in the next section that in practice the time evolution of low moments can be obtained in a more direct way from the basic rate equations (7) and (8). Figure 2 shows the thermal probability distribution, given by equation (20), and the coupled population,

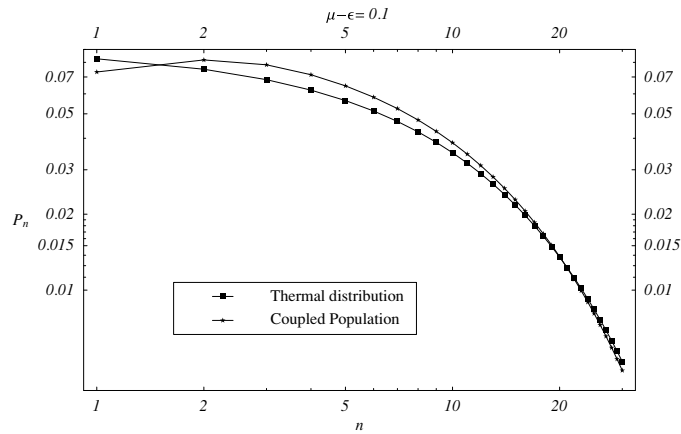


Figure 2. Plot of the probability distributions for the thermal distribution, with mean 10, and that for the coupled population also with mean 10. The constants that give these values are $\mu = 1.1, \epsilon = 1$ and $\nu = 1$.

equation (22). It can be seen that in this instance the probability distribution for the coupled population approaches that of the thermal distribution as $\epsilon \rightarrow \mu$.

The marginal case, $\epsilon = \mu$, when $\nu \neq 0$ is of some interest. The difference in gamma functions in the solution (16) then becomes a difference of exponential integrals [8] so that R takes the form

$$R = \frac{\nu s}{\mu} \theta \exp\left(\frac{\nu s}{\mu} \theta - \mu t\right) - \sum_{k=1}^{\infty} \left(-\frac{\nu s}{\mu}\right)^k (1 - \theta^k) / k k!. \tag{24}$$

After some manipulation, it can be shown upon using initial condition (11), that

$$\lim_{t \rightarrow \infty} Q^{(1)}(s, t) \rightarrow \frac{1}{1 + s \exp\left(\frac{\nu s}{\mu}\right) \left[\nu t + \frac{1}{2}(N_1 + N_2)\right]}. \tag{25}$$

This result reduces to (20) upon setting $\nu = 0$. At sufficiently long times the mean value predicted by (25), $\langle N \rangle = \nu t$, increases linearly with time. However, the *normalized* factorial moments are asymptotically independent of time, again taking the values $n^{[r]} = r!$ expected for a thermal or geometric distribution.

4. Moments and correlation functions

More insight into the evolution of the fluctuation statistics and correlation properties of the coupled population model can be gleaned by calculating the low moments of the population distribution directly from the rate equations for the generating functions (7), (8) using relation (23).

Denoting $n_i(t)$ as the mean and $m_i(t)$ as the second factorial moment of population i gives for the case $\mu_1 = \mu_2 = \mu, \epsilon_1 = \epsilon_2 = \epsilon, \nu_1 = \nu_2 = \nu$:

$$\dot{n}_1 = -\mu n_1 + \epsilon n_2 + \nu, \quad \dot{n}_2 = -\mu n_2 + \epsilon n_1 + \nu \tag{26}$$

$$\dot{m}_1 = -2\mu m_1 + \epsilon m_2 + 2n_1(\epsilon n_2 + \nu) \quad \dot{m}_2 = -2\mu m_2 + \epsilon m_1 + 2n_2(\epsilon n_1 + \nu) \tag{27}$$

where the over-dot denotes differentiation with respect to time.

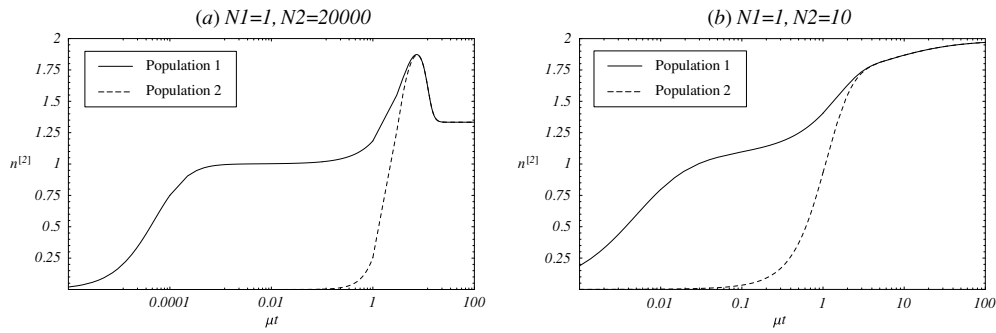


Figure 3. (a) A plot of the temporal behaviour of the normalized second moment with initial conditions $N_1 = 1, N_2 = 20000, \bar{N} = 20$ and $\varepsilon/\mu = 1/2$. (b) A plot of the temporal behaviour of the normalized second moment with initial conditions $N_1 = 1, N_2 = 10, \bar{N} = 1000$ and $\varepsilon/\mu = 0.99$.

The structure of these equations is noteworthy for two reasons. Firstly, equations (26), which determine the evolution of the mean, do not explicitly reflect the existence of the nonlinear coupling of the populations. This is in fact first manifest in the evolution of the fluctuations (27) and emphasizes an important general point: that the dynamics of the mean of a population does not necessarily provide a good guide to the full range of its behaviour. The second noteworthy feature is that the evolution of the m th order factorial moment does not depend on the $(m + 1)$ th order fluctuations, so that these stochastic systems do not have the usual BBGKY hierarchical structure [10–12] requiring an *ad hoc* model to facilitate closure. The fluctuations of any order can be determined for these systems without approximation.

In the case when there are N_1 individuals present initially in population 1 and N_2 in population 2, the solution of equation (26) is readily found to be

$$\begin{aligned} n_1(t) &= \bar{N}(1 - e^{(\varepsilon-\mu)t}) + e^{-\mu t}[N_1 \cosh \varepsilon t + N_2 \sinh \varepsilon t] \\ n_2(t) &= \bar{N}(1 - e^{(\varepsilon-\mu)t}) + e^{-\mu t}[N_2 \cosh \varepsilon t + N_1 \sinh \varepsilon t] \end{aligned} \tag{28}$$

where

$$\bar{N} = \langle N \rangle = \frac{\nu}{\mu - \varepsilon}. \tag{29}$$

Result (28) reduces to (19) in the absence of stabilization, $\nu = 0$. When $\nu \neq 0, \bar{N}$ is the equilibrium mean of each population that is approached at long times *provided that* $\mu > \varepsilon$. However, as we have already seen, the mean of each population grows linearly with time as $\varepsilon \rightarrow \mu$ and increases exponentially for $\varepsilon > \mu$.

When $\mu > \varepsilon$, the second normalized factorial moment approaches

$$n^{[2]} = \frac{2\mu}{2\mu - \varepsilon} \tag{30}$$

independent of the parameter ν . This value lies between the normalized second factorial moment of a Poisson distribution (expected for the simple death-immigration process when $\varepsilon = 0$) and that of a thermal or geometric distribution which it approaches as $\mu \rightarrow \varepsilon$ in accordance with result (21).

Figure 3 illustrates the temporal behaviour of the second moment for a selection of parameters and initial conditions. Of especial interest is the case when the initial sizes of the populations differ significantly from each other and with the final equilibrated mean size, given by equation (29). Note that the size of the second normalized factorial moment depends

essentially only on the ratio ε/μ . Figure 3(a) shows the evolution of the second moment for when $N_1 = 1$, $N_2 = 20\,000$, $\bar{N} = 20$, for which $\varepsilon/\mu = 1/2$. The relative fluctuations both commence at zero, but those of population 1, which has a smaller initial number present, rises and then appears to saturate close to 1, whilst those of population 2 remain close to 0. Thus, the fluctuations would indicate that population 1's fluctuations are characteristic with the Poisson distribution, whereas 2 evolves in an essentially deterministic manner until $\mu t \sim 0.1$. Thereafter the fluctuations in both populations rise, peaking in excess 1.8, at which time the fluctuations in both populations are broadly synchronous. Thereafter, the fluctuations simultaneously decline to the equilibrium value of $4/3$. Another situation of interest is when $\varepsilon \rightarrow \mu$, for then the mean of the stationary state diverges according to equation (29), and the relative fluctuations have value 2. Figure 3(b) shows the evolution of the second moment for when $N_1 = 1$, $N_2 = 10$, $\bar{N} = 1000$ and $\varepsilon/\mu = 0.99$. Again the relative fluctuations commence at zero, with the fluctuations in the population of smaller initial size rising first. There is a vestige of the plateau region when the second moment nears 1, but the characteristics of both populations is a monotonic rise to the equilibrium value, which is only attained at a very slow rate, concomitant with the divergence of the scale time $(\mu - \varepsilon)^{-1}$ that features in the evolution.

The auto- and cross-correlation functions for the two populations can be determined from the above results for the evolution of the mean values, conditional on initial numbers present, using the relation ($i, j = 1, 2$)

$$G_{ij}(\tau) = \langle N_i n_j(\tau) | N_i, N_j, \tau = 0 \rangle. \quad (31)$$

The normalized correlation functions

$$g_{ij}(\tau) = \frac{G_{ij}(\tau)}{\bar{N}^2} \quad (32)$$

are easily determined as

$$\begin{aligned} g_{11}(\tau) = g_{22}(\tau) &= 1 - \exp(-\mu\tau) \sinh(\varepsilon\tau) + \frac{\text{var } N}{\bar{N}^2} \exp(-\mu\tau) \cosh(\varepsilon\tau) \\ g_{12}(\tau) = g_{21}(\tau) &= 1 - \exp(-\mu\tau) \sinh(\varepsilon\tau) + \frac{\text{var } N}{\bar{N}^2} \exp(-\mu\tau) \sinh(\varepsilon\tau) \end{aligned} \quad (33)$$

where the relative variance of N is defined by (29) and (30). These expressions show that, like the time evolution of the means, the correlation functions are characterized by two distinct time scales, $(\mu + \varepsilon)^{-1}$ and $(\mu - \varepsilon)^{-1}$. Moreover, as $\varepsilon \rightarrow \mu$, the latter time scale diverges, indicating a slowing down of one contribution to the fluctuations. When $\varepsilon = \mu$, result (33) reduces to

$$g_{11}(\tau) = g_{22}(\tau) = 1 + \exp(-2\mu\tau) \quad g_{12}(\tau) = g_{21}(\tau) = 1. \quad (34)$$

Figure 4 shows the correlation functions for two populations, note the slow convergence to 1 as ε tends towards μ . It is noteworthy that these formulae are again independent of the normal immigration parameter, ν . They may be contrasted with the result expected for a simple death-immigration process ($\varepsilon = 0$):

$$g(\tau) = 1 + \left(1 + \frac{\mu}{\nu}\right) \exp(-\mu\tau). \quad (35)$$

The fluctuation time when $\varepsilon = 0$ is thus twice that characterizing the case $\varepsilon = \mu$. The factor μ/ν in result (35) is the reciprocal of the population mean for the reduced problem and is a manifestation of the discrete nature of the process. An analogous term is present in (33) but does not appear in (34) because $\bar{N} \rightarrow \infty$ when $\varepsilon \rightarrow \mu$ (equation (29)) and the process is asymptotically continuous in this case.

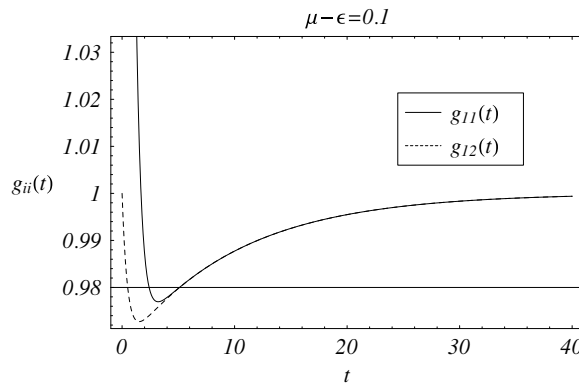


Figure 4. Plot of the normalized correlation functions g_{11} and g_{12} for two coupled populations. The constant values were the same as those used in figure 1.

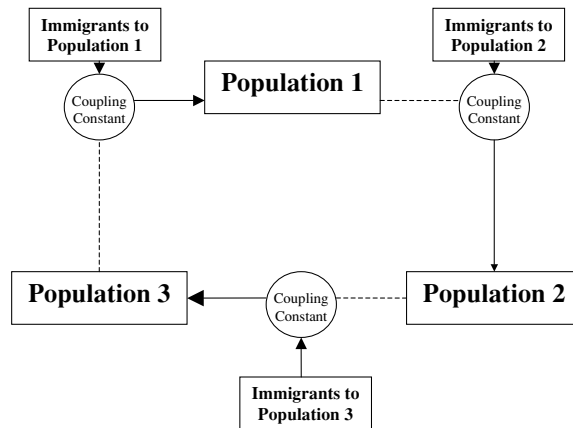


Figure 5. Diagram of three coupled multiple immigrant population models.

5. Cyclically coupled populations

The coupled population model discussed above can be generalized to the case when more than two populations are coupled in a cyclic fashion. A triple population process is illustrated in figure 5, for example. Rate equations for the generating functions governing the behaviour of this process may be written

$$\frac{\partial Q^{(i)}}{\partial t} = -\mu_i s \frac{\partial Q^{(i)}}{\partial s} + \varepsilon_i Q^{(i)} [Q^{(i+1)} - 1] - \nu_i s Q^{(i)}. \tag{36}$$

Here, $i = 1, 2, 3$ and $Q^{(4)} = Q^{(1)}$. We shall specialize to the case where the death and immigration parameters are the same for each population, as before. It is then simple to demonstrate that the same stationary state is obtained as in the case of two populations provided that $\mu > \varepsilon$. However, the evolution of the statistics to this state is now oscillatory. Thus, for the mean of each population we obtain

$$\bar{N}(t) = \frac{\nu}{\mu - \varepsilon} + \sum_{j=1}^M A_j \exp(a_j t) \tag{37}$$

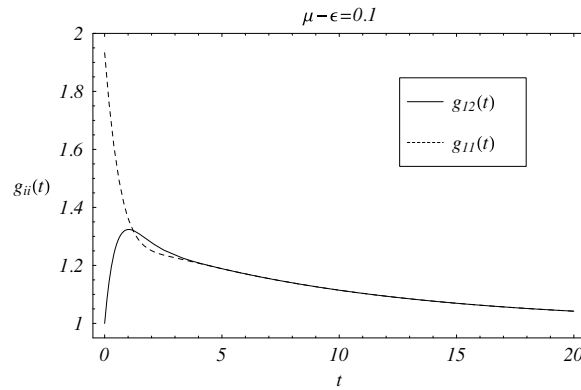


Figure 6. Plot of the normalized correlation functions for g_{11} and g_{12} for three coupled populations. The constant values were the same as those used in figure 1.

where $M = 3$ and the time constants in the exponent are given by

$$a_1 = -(\mu - \varepsilon) \quad a_2 = a_3^* = -\mu - \varepsilon(1 - i\sqrt{3})/2. \quad (38)$$

Since the real parts of these constants are negative, at long times a non-periodic stationary state of the form (22) is obtained. However, transient oscillations are generally manifest in the evolution to this state and these are reflected in the behaviour of the correlation functions:

$$\begin{aligned} n_1(t) &= \bar{N} + \frac{1}{3}(N_1 + N_2 + N_3 - 3\bar{N}) \exp[(\varepsilon - \mu)t] + \frac{1}{3}[(2N_1 - N_2 - N_3) \cos(\varepsilon t \sqrt{3}/2) \\ &\quad + (N_2 - N_3) \sin(\varepsilon t \sqrt{3}/2)] \exp[-(\mu + \varepsilon/2)t] \\ g_{ii}(\tau) &= 1 + \frac{\text{var } N}{3\bar{N}^2} \{ \exp[(\varepsilon - \mu)\tau] + 2 \exp[-(\mu + \varepsilon/2)\tau] \cos(\varepsilon \sqrt{3}\tau/2) \} \\ g_{ij}(\tau) &= 1 + \frac{\text{var } N}{3\bar{N}^2} \{ \exp[(\varepsilon - \mu)\tau] - 2 \exp[-(\mu + \varepsilon/2)\tau] \cos(\varepsilon \sqrt{3}\tau/2 + \pi/3) \}. \end{aligned} \quad (39)$$

The relative variance here is calculated from results (29) and (30) whilst results for the means of populations 2 and 3 can be obtained by simply permuting the indices. Note that the oscillation period is longer than the decay time of the same term and is therefore barely discernible in plot in figure 6 when the coupling constant ε approaches the death rate, μ . In the special situation where the populations are initially identical no transient oscillations of the mean will be observed although the correlation functions will still exhibit periodicities. This is a consequence of assuming that the immigration and death parameters of the three populations are identical.

In the case of four coupled populations, the exponents in (37) are given by

$$\begin{aligned} a_1 &= -(\mu - \varepsilon), & a_3 &= -(\mu + \varepsilon) \\ a_2 &= a_4^* = -\mu + i\varepsilon \end{aligned} \quad (40)$$

The correlation functions of the stationary solution again exhibit an oscillatory structure:

$$\begin{aligned} g_{12}(t) &= g_{23}(t) = g_{34}(t) = g_{41}(t) = 1 + \frac{\text{var } N}{2\bar{N}^2} \exp(-\mu t) [\sinh(\varepsilon t) - \sin(\varepsilon t)] \\ g_{13}(t) &= g_{24}(t) = 1 + \frac{\text{var } N}{2\bar{N}^2} \exp(-\mu t) [\cosh(\varepsilon t) - \cos(\varepsilon t)] \end{aligned} \quad (41)$$

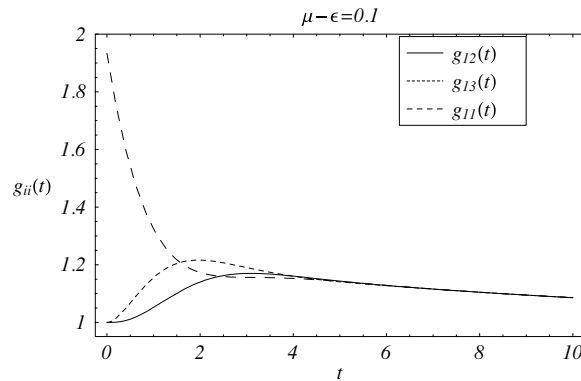


Figure 7. Plot of the normalized correlation functions for g_{11} and g_{12} for three coupled populations. The constant values were the same as those used in figure 1.

$$g_{ii}(t) = 1 + \frac{\text{var } N}{2\bar{N}^2} \exp[-\mu t](\cosh[\epsilon t] + \cos[\epsilon t]). \tag{42}$$

These results are invariant to reversal of the subscript ordering, i.e. $g_{12} = g_{21}$, etc.

The ratio of decay time to period of the oscillating terms in these results is now a factor $(2 + \epsilon/\mu)/\sqrt{3}$ greater than that of the case of three coupled populations. This effect can be seen clearly in figure 7, the oscillations becoming more pronounced and the correlations taking longer to decay to unity. This trend continues as the number of coupled populations is increased and may be demonstrated by consideration of the general case of a ring of M interacting populations. If the death and immigration parameters are identical for each population there is a stationary solution of the form (22) as before, and the mean of each population is governed by the transient solution (37) with

$$a_j = -\mu + \epsilon \cos(2\pi(j - 1)/M) + i\epsilon \sin(2\pi(j - 1)/M); \quad j = 1, 2, \dots, M. \tag{43}$$

It is easy to check that this formula generates the values (40) when $M = 4$, for example. When there are very many populations so that $M \gg 1$, the solution (37) contains terms that exhibit many oscillations during the approach to a stationary state. To see this consider the time constant a_2 :

$$a_2 = -\mu + \epsilon \cos(2\pi/M) + i\epsilon \sin(2\pi/M). \tag{44}$$

Let $\mu = \epsilon + \delta/M$ and scale the immigration parameters with the number of populations $\epsilon \rightarrow \epsilon M, v \rightarrow v/M$ so that $\bar{N} \rightarrow v/\delta$ is finite at long times. Substituting into (45) and expanding the trigonometric functions for small argument obtains

$$a_2 \approx -\frac{\delta + 2\pi^2\epsilon}{M} + 2\pi i\epsilon \tag{45}$$

so that the solution (37) has at least one term of the form

$$A \exp[-(\delta + 2\pi^2\epsilon)t/M] \cos(2\pi\epsilon t) \tag{46}$$

that has a decay time that is much greater than the period of oscillation. This behaviour will also be manifest in the correlation functions of the corresponding stationary state.

6. Evolution of populations that are initially stable

So far we have investigated the predictions of the coupled population model when each population contained a fixed number of individuals at time $t = 0$ (initial condition (11)).

Although the evolution of the populations is evidently different when the initial state is different, the conclusions reached above regarding the existence and characteristics of a stationary solution remain valid provided that the moments of the initial population distributions are finite. However, the situation is different if the moments of either of the population distributions are not defined at $t = 0$. We have recently investigated discrete distributions of this kind that occur in the study of complex systems [5, 7]. For example, the discrete *stable* distributions are an important class of statistical models that provide a discrete analogue of the Lévy-stable distributions which characterize continuous variables.

The class of discrete stable distributions are governed by the generating function

$$Q(s) = \exp(-as^\alpha); \quad 0 < \alpha < 1. \quad (47)$$

Since $Q(0) = 1$, the related distribution is correctly normalized. However, the integer moments and correlation functions defined through (23) and (31), respectively, are infinite because the distribution has a power-law tail that decreases like $N^{-(\alpha+1)}$. The sum of independent populations governed by the distribution corresponding to (47) obeys the same distribution: hence the term ‘stable’. The special case $\alpha = 1$ corresponds to the Poisson distribution, which is also a member of the discrete stable class.

Solution (16) of the two coupled population problem is valid for all initial states of the populations and the evolution of the system when the initial state is stable can be investigated by setting $Q_0^{(2)} = \exp(-as^\alpha \exp(-\alpha\mu t))$. Examination of the large time limit now reveals that the stationary state (22) is obtained as before only within the restricted parameter range $\alpha\mu > \varepsilon$. Exponential growth occurs if $\alpha\mu < \varepsilon$ whilst if $\alpha\mu = \varepsilon$ a stationary state of the following form is obtained:

$$Q^{(1)}(s) = \frac{1}{1 + \exp(\nu s/\mu) \left[\frac{1}{2}as^\alpha + (\nu s/\mu)^\alpha \gamma(1 - \alpha, \nu s/\mu) \right]}. \quad (48)$$

When the single immigrant term is omitted, $\nu = 0$, a stationary state is obtained only when $\alpha\mu = \varepsilon$ and takes the simple form

$$Q^{(1)}(s) = \frac{1}{1 + \frac{1}{2}as^\alpha} \quad (49)$$

The distributions corresponding to (48) and (49) are again characterized by power-law tails that decrease like $N^{-(\alpha+1)}$ and have infinite integer moments, but unlike the distribution corresponding to (47) they are not stable. Figure 8 shows the probability distributions for equations (47)–(49). The tail of the distribution for equation (48) approaches that of (49), and they both share the same asymptote as the stable distribution. The coupled population model indeed has the general property of converting any initial distribution of individuals that falls off like $N^{-(1+\alpha)}$ in the tail (with $0 < \alpha < 1$) into a population governed by (48) or (49) at long times when $\alpha\mu = \varepsilon$. An important point to note is that the solution (48) is truly stationary. This may be contrasted with the earlier result (25) that was obtained when $\varepsilon = \mu$ assuming that the initial distribution of each population had finite moments. In that case the generating function changed with time, although the normalized factorial moments were time independent.

Although (49) does not correspond to a stable discrete distribution, it is a stationary invariant of the convolution equation (1). In other words, if the static coefficients $\{\alpha_r\}$ are probabilities corresponding to (49) then the stationary solution of (1) is also of this form. It should also be further observed that if the time-dependent terms in equations (5) and (6) are discarded then a ‘stationary’ solution of the form (49) with $\alpha = \varepsilon/\mu$ is predicted if it is assumed that $Q^{(1)} = Q^{(2)}$. However, full time-dependent solution of the problem confirms that even

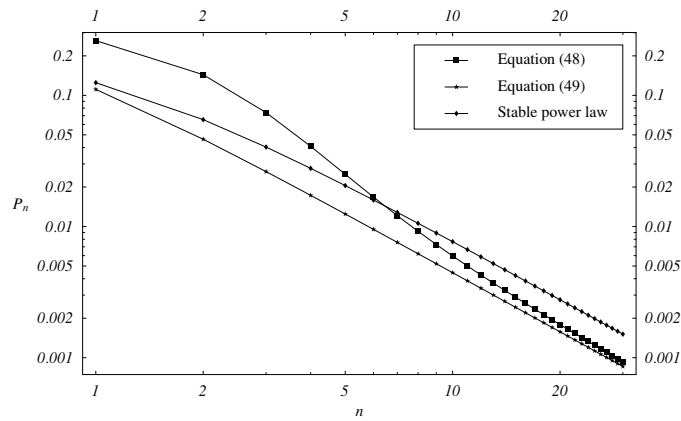


Figure 8. Plot of the probability distributions for: the two coupled populations with deterministic and stable power-law initial conditions, equation (48), the aforementioned system with $\nu = 0$, equation (49), and the stable power law described by equation (47). The constant values used are $\nu = 1, \mu = 2, \varepsilon = 1$ and $\alpha = 1/2$.

with this special assumption the class of generating functions (49) can only be accessed when $\varepsilon = \mu$ (equation (20)) or when the initial generating function is also of the form (49) with $\alpha\mu = \varepsilon$ as found above.

It is interesting that distributions corresponding to the generating function (49) would characterize the *total* number of individuals in many independent stably distributed populations the number of which fluctuates according to a thermal (geometric) distribution. Thus, the distribution of a fixed number W of independent stable populations is governed by the generating function (47) raised to the power W . However, if W is itself varying according to a thermal distribution

$$P(W) = \overline{W}^W / (1 + \overline{W})^{W+1} \tag{50}$$

then

$$\langle \exp(-aWs^\alpha) \rangle_W = \{1 + \overline{W}[1 - \exp(-as^\alpha)]\}^{-1}. \tag{51}$$

The high population number density limit is now obtained by scaling s with \overline{W} , i.e., $s^\alpha \rightarrow s^\alpha/\overline{W}$, and then taking $\overline{W} \rightarrow \infty$ leading immediately to (49). A variant of this type of mechanism is encountered in the case of continuous variables. Thus, if the number of independent Gaussian variables that are vector-summed is itself distributed according to a negative binomial distribution then the amplitude of the resultant is found to be K -distributed [13] in the high density limit. This is a very useful class of non-Gaussian statistical distributions that have found wide application in modelling electromagnetic scattering phenomena (see [14] for a brief review). More recently, the sum of a negative binomial distributed number of independent Lévy variables has been investigated in the context of scale-free and self-organized critical systems [15, 16], and leads to a probability density with distinct regions of power-law behaviour characterized by different indices. This suggests that the above class (49) of discrete distributions could be enlarged by varying the number of populations according to a negative binomial distribution of which the thermal or geometric distribution is only one member. The more general class would not be a natural outcome of the freely coupled population model considered here, but a time-dependent process could be generated by suitable choice of the multiple immigration parameters in equation (1).

7. Concluding remarks

In this paper, we have carried out a preliminary investigation of a discrete Markov process in which the immigration of individuals into one population is controlled by the fluctuations in another. In this model, there is no *exchange* of individuals, which can be of different types. We have examined the effect of coupling back the second population to the first through a similar mechanism and have derived exact solutions for the generating functions of the population statistics in this case. We have shown that a stationary state exists over a certain parameter range and have obtained expressions for moments and correlation functions in this regime. An investigation of cyclic coupling of more than two populations in this way has revealed transient oscillations and periodic behaviour of correlation functions. We have also demonstrated that if the initial distribution of either population is stable, or more generally has a power-law tail that falls off like $N^{-(1+\alpha)}$ ($0 < \alpha < 1$), then for certain parameter values there exists a stationary state that is also power law but not stable. Furthermore, this stationary state cannot be accessed from a single multiple immigrant population model, it arises solely from the nonlinear interaction of the coupled system.

The model that we have investigated in this paper was stimulated by our previous work on the role of discrete processes in complex systems such as the Internet and WWW, protein interactions and social networks. We have not sought to address a specific application here, but our preliminary results provide useful insights into the wide range of behaviour that coupled discrete populations of non-identical individuals can exhibit and offer an excellent prospect for applications in the future. This expectation is supported by the number of relatively simple generalizations that can be envisaged. For example, the populations could be characterized by different parameters as originally conceived in equations (7) and (8). The effect of one population on the other could be subject to delay: a preliminary study shows that, unlike the results presented in section 4 (equation (28)), this leads to transient oscillations of the population means even in the case of only two coupled populations. Single and multiple births can also be included in the model. In contrast to equation (26), this leads to nonlinear equations for the evolution of the mean of the type encountered in Smoluchowski coagulation [17, 18]. An important priority will be to include modulation of deaths in one population by fluctuations in the other in order to model predator-prey processes in small populations.

Acknowledgment

JOM acknowledges the support of the Leverhulme Trust.

References

- [1] Schlesinger M F, Zaslavsky G M and Frisch U (ed) 1995 *Lévy Flights and Related Topics in Physics* (Berlin: Springer)
- [2] Stanley H E and Ostrowsky N (ed) 1986 *On Growth and Form* (Dordrecht: Nijhoff)
- [3] Gopikrishnan P, Plerou V, Nunes Amaral L A, Meyer M and Stanley H E 1999 *Phys. Rev. E* **60** 5305–16
- [4] Albert R and Barabási A L 2002 *Rev. Mod. Phys.* **74** 47
- [5] Hopcraft K I, Jakeman E and Matthews J O 2002 *J. Phys. A: Math. Gen.* **35** L745–51
- [6] Jakeman E, Hopcraft K I and Matthews J O 2003 *Proc. R. Soc. A* **459** 623–39
- [7] Matthews J O, Hopcraft K I and Jakeman E 2003 *J. Phys. A: Math. Gen.* **36** 11585–603
- [8] Matthews J O, Hopcraft K I and Jakeman E 2005 *Phys. Rev. E* submitted
- [9] Abramowitz M and Stegun I A 1970 *Handbook of Mathematical Functions* 9th edn (New York: Dover)
- [10] Bogolyubov N N 1962 Problems of a dynamical theory in statistical physics *Studies in Statistical Mechanics* vol 1, ed J de Boer and G E Uhlenbeck (Amsterdam: North-Holland)
- [11] Born M and Green H S 1949 *A General Kinetic Theory of Liquids* (London: Cambridge University Press)

-
- [12] Green H S 1952 *The Molecular Theory of Fluids* (New York: Wiley-Interscience)
 - [13] Jakeman E and Pusey P N 1978 *Phys. Rev. Lett.* **40** 546–8
 - [14] Jakeman E 1999 *J. Opt. A: Pure Appl. Opt.* **1** 784–9
 - [15] Hopcraft K I, Jakeman E and Tanner R M J 1999 *Phys. Rev. E* **60** 5327–43
 - [16] Hopcraft K I, Jakeman E and Tanner R M J 2002 Random walks with fluctuating step number, scale invariant behaviour and self-organised criticality *Fractal Geometry: Mathematical Methods, Algorithms, Applications* ed J M Blackledge, A K Evans and J Turner (Chichester: Ellis Horwood)
 - [17] Davies S C, King J R and Wattis A D 1999 *J. Phys. A: Math. Gen.* **32** 7745–63
 - [18] Pushkin D O and Arel H 2002 *Phys. Fluids* **14** 694–703