# Analytical methods for a stochastic mainland-island metapopulation model

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**Abstract:** The term 'metapopulation' is used to describe individuals of a species living as a group of local populations in geographically separate, but connected, habitat patches (Levins 1970, Hanski 1999). Patches may become empty through local extinction and empty patches may be recolonised by migrants from other local populations. A balance between local extinction and colonisation may be reached which allows the metapopulation to persist (Hanski 1999). The relationship between these two processes is therefore an important consideration when formulating mathematical metapopulation models. We suppose that events of the same type occur in seasonal *phases*, so that extinction events only occur during the *extinction phase* and colonisation events only occur during the *colonisation phase*, and that these phases alternate over time. They may correspond to two parts of an annual cycle, for example, where local populations are prone to extinction during winter while new populations establish during spring.

We assume that a census takes place either at the end of the colonisation phase (...-extinction-colonisation-census-...) or at the end of the extinction phase (...-colonisation-extinction-census-...), and thus fits naturally within a discrete-time modelling framework. If extinction and colonisation events were to occur in random order, then a continuous-time model would of course be preferred. Here we use a discrete-time Markov chain whose state $n_t$ is the observed number of occupied patches at the $t$-th census. Its transition matrix is the product of two transition matrices that govern the individual extinction and colonisation processes. This approach has been used previously and several models have been proposed (Akçakaya and Ginzburg 1991, Day and Possingham 1995, Hill and Caswell 2001, Klok and De Roos 1998, Tenhumberg et al. 2004, Rout et al. 2007). Each model accounts for local extinction in the same way, but different methods are used to model the colonisation process, reflecting the differing breeding habits and means of propagation of the particular species under investigation. Whilst they account for a range of colonisation behaviour, the models were examined using numerical methods and simulation, and few explicit analytical results were obtained. Furthermore, only the extinction-colonisation-census scenario was considered. Whilst it is certainly true that timing of the census is arbitrary in that it does not affect the dynamics of the metapopulation (Day and Possingham 1995), its timing may affect the efficiency of any statistical procedures used to calibrate the models and successful implementation of management actions.

We present a new and quite general approach to modelling the colonisation process, one that permits explicit expressions for a variety of quantities of interest. We concentrate here on a *mainland-island* configuration: the patches (*islands*) receive migrants from an external source (the *mainland*), assumed to be immune from extinction. We evaluate the distribution of $n_t$ at any census time $t$. We then establish a *law of large numbers*, which identifies a deterministic trajectory that can be used to approximate $(n_t, t \geq 0)$ at any time $t$ when the number of patches is large. We also establish a *central limit theorem*, which shows that the fluctuations about this trajectory are approximately normally distributed. These results are useful in understanding the patch occupancy process when the parameters of the model are known. For example, the mean and variance of $n_t$, and the expected time to first total extinction, can be exhibited explicitly. We describe briefly much finer results that can be used for model calibration.

*Keywords: Metapopulation; discrete-time Markov chain; phase; mainland-island; chain-binomial model*

## 1. INTRODUCTION

Stochastic patch-occupancy models (SPOMs) which assume that extinction and colonisation occur in distinct phases in discrete-time can be categorised as (i) heterogeneous SPOMs (Akçakaya and Ginzburg 1991, Day and Possingham 1995) or (ii) homogeneous SPOMs (Daley and Gani 1999, Hill and Caswell 2001, Klok and De Roos 1998, Rout et al. 2007, Tenhumberg et al. 2004).

Heterogeneous SPOMs use a vector of size $N$ to describe the presence/absence of occupants in an $N$-patch metapopulation, the $k$-th component being 1 or 0 according to whether the $k$-th patch is occupied or empty. Local extinction and colonisation event probabilities can be patch-specific, such as in Akçakaya and Ginzburg's (1991) 3-patch model for the endangered Mountain Gorilla (*Gorilla gorilla beringei*) metapopulation in Uganda, or vary according to patch size and position as demonstrated in Day and Possingham's (1995) 8-patch model for the malleefowl (*Leipoa ocellata*) metapopulation in South Australia. Since there are $2^N$ possible states, the analysis of these models quickly becomes computationally expensive as $N$ increases. Homogeneous SPOMs on the other hand simply record the number of occupied patches and therefore have only $N+1$ states for an $N$-patch metapopulation, entailing computationally inexpensive analysis even for large ($N = 50$) networks. Whilst patches are assumed to behave in the same way, these models can account implicitly for spatial arrangement by allowing the colonisation probabilities to depend on the number of occupied patches. They have additional appeal because, as we shall see, they can be analytically tractable. Two-phase homogeneous SPOMs are usually based on the following approach to modelling the extinction and colonisation processes.

**Extinction and colonisation**. Occupied patches are assumed to go extinct independently, each with the same probability $e$. Hence, given $i$ patches initially occupied, the number that survive the extinction process follows a binomial $\mathsf{B}(i, 1 - e)$ law. With $j$ patches remaining after the extinction phase, the $N - j$ empty patches either remain empty or are colonised during the subsequent colonisation phase. In modelling the colonisation process one must consider how individuals disperse through the metapopulation network. Hill and Caswell (2001) assume implicitly that propagules arrive at each patch according to a homogeneous Poisson process with rate $\beta i/N$, where $i$ is number of patches currently occupied and $\beta$ is the expected number of propagules produced by each occupied patch. Thus, the probability that one or more propagules arrive at any given patch is $c_i = 1 - \exp(-\beta i/N)$, and so, given $i$ patches occupied, the total number of colonisation events follows a binomial $\mathsf{B}(N - i, c_i)$ law. Their model goes one step further in allowing only a fixed subset of the $N$ patches to be suitable for habitation.

Klok and De Roos (1998) suppose that colonisation comprises two separate processes: (i) reproduction, which determines the number of juveniles born to adults that survive the preceding extinction phase (each adult occupying one patch or 'territory'), and (ii) settlement, which determines how many patches are colonised by juveniles. Each process is governed by its own transition matrix and these are multiplied to produce the overall transition matrix for the colonisation phase. Their model was designed to study the common shrew (*Sorex araneus* L.), which exhibits the three-phase (extinction-reproduction-settlement) behaviour described.

Tenhumberg et al. (2004) and Rout et al. (2007) model a single population of individuals with an assumed fixed population ceiling. Their models track the number of female individuals, each producing either a maximum of one offspring (Tenhumberg et al. 2004), or a number of offspring (Rout et al. 2007) determined by the binomial distribution. The total number of females resulting from the colonisation process is then determined by a recursive formula.

These Markov chain models are often referred to as *chain-binomial models* (Daley and Gani 1999, Hill and Caswell 2001), because the numbers of patches/individuals remaining after each phase is determined by a binomial distribution whose parameters are determined by the result of the previous phase.

**Timing of the census**. Whilst the choice between taking the census after colonisation or after extinction does not affect the dynamics of the metapopulation, it is certainly important from an empirical perspective. For example, Klok and De Roos (1998) chose to census after the colonisation phase because the real shrew population was known to be more stable at this time.

In this paper we introduce a homogeneous stochastic patch-occupancy model of a similar design to those described, but with a new and quite general approach to modelling colonisation. We study both census scenarios and present analytical results for both, concentrating here on the mainland-island configuration.

## 2. THE MODEL

Suppose there are $N$ patches. Let $n_t$ be the observed number occupied at census time $t \in \{0, 1, \dots \}$ and suppose that $(n_t, t \geq 0)$ is a discrete-time Markov chain that takes values in $S = \{0, 1, \dots, N\}$ with transition probabilities $P = (p_{ij})$. The colonisation and extinction processes are governed by their own transition matrices, $E = (e_{ij})$ and $C = (c_{ij})$, respectively, so that $P = EC$ (the EC model) if the census is taken just after the colonisation phase or $P = CE$ (the CE model) if the census is taken just after the extinction phase.

*Extinction phase*. Occupied patches are assumed to go extinct independently, each with the same probability $e$ ($0 < e < 1$). Thus, given $i$ occupied at the start of the extinction phase, the number that survive extinction follows a $\mathsf{B}(i, 1 - e)$ law. Therefore, $e_{ij} = \binom{i}{j}(1 - e)^j e^{i-j}$ for $j = 0, \dots, i$, and $e_{ij} = 0$ for $j > i$.

*Colonisation phase*. Suppose that, given $i$ occupied patches at the start of the colonisation phase, the empty patches are colonised independently, each with probability $c_i$ ($0 < c_i < 1$). We call $c_i$ the *colonisation potential* (of $i$ occupied patches). Thus, given $i$ occupied (and hence $N - i$ unoccupied), the number of empty patches colonised during this phase follows a $\mathsf{B}(N - i, c_i)$ law. Therefore, $c_{ij} = \binom{N-i}{j-i}(1 - c_i)^{N-j} c_i^{j-i}$ for $j = i, i+1, \dots, N$, and $c_{ij} = 0$ for $j < i$. This general setup accommodates (among other choices):

(i) $c_i = 1 - \exp(-\beta i / N)$, which is Hill and Caswell's (2001) specification with $\beta$ being the propagation rate;

(ii) $c_i = (i/N)c$, where the colonisation potential is *proportional to* the number of occupied patches up to a fixed maximum colonization potential $c \in (0, 1]$, the (hypothetical) probability that a single unoccupied patch would be colonized by the fully occupied network;

(iii) $c_i = c^*(1 - (1 - c_1/c^*)^i)$, so that a 'law of decreasing returns' operates (the colonization potential of the occupied group increases by less and less with each addition of an occupied patch), and $c_1 \leq c^*$ ($\leq 1$) where $c_1$ is the probability that an empty patch will be colonised given there is one patch occupied ($i = 1$) and $c^*$ is the limiting colonisation potential ($c_N \to c^*$ as $N \to \infty$);

(iv) $c_i = c$, the same for all $i = 0, \dots, N$ (in particular $i = 0$), which corresponds to there being a 'mainland' providing overwhelming colonization potential, the potential of colonized patches being insignificant in comparison;

(v) A combination of (iv) with any of (i)–(iii), for example $c_i = c_0 + (i/N)c$, which would correspond to there being a mainland, but with a significant internal colonisation process operating according to (ii).

If desired, we can evaluate $P$ elementwise using $p_{ij} = \sum_{k=0}^{\min(i,j)} e_{ik} c_{kj}$ for the EC model and $p_{ij} = \sum_{k=\max(i,j)}^{N} c_{ik} e_{kj}$ for the CE model. Notice that $E$ is lower-triangular and $C$ is upper-triangular, but that $P$ is dense. Notice also that $p_{i0} = e^i(1 - c_0)^N$ for the EC model and $p_{i0} = e^i(1 - c_i(1 - e))^{N-i}$ for the CE model, and that $p_{0j} = \binom{N}{j}(1 - p_0)^{N-j} p_0^j$, where $p_0 = c_0$ for the EC model and $p_0 = c_0(1 - e)$ for the CE model. Thus, in cases (i)–(iii), we have $p_{0j} = \delta_{0j}$, implying that 0 is the (sole) absorbing state (corresponding to total extinction) with $\{1, \dots, N\}$ being a communicating class from which 0 is accessible. We will content ourselves with a detailed analysis of Case (iv).

In Case (iv) it is useful to think of the patches as being islands that receive migrants from a mainland: hence the term *mainland-island* model. Now $S$ is irreducible and aperiodic, and so the Markov chain has a unique stationary (and hence limiting) distribution. We will evaluate this below in Corollary 1. We begin by exhibiting explicitly the distribution of $n_t$, the number of occupied patches at time $t$. We then establish a *law of large numbers*, which identifies a deterministic trajectory that can be used to approximate $(n_t)$, and then a *central limit theorem*, which shows that the fluctuations about this trajectory are approximately normally distributed. With $c_i = c$, our model can be reinterpreted as a chain-binomial SIS (susceptible-infected-susceptible) epidemic model that incorporates immigration-emigration episodes; see Section 4.4 of Daley and Gani (1999). Our results apply equally to their model, with $n_t$ interpreted as the number of susceptibles.

## 3. RESULTS FOR THE MAINLAND-ISLAND MODEL

The simplicity of the mainland-island model is exemplified by the following lemma. We see that the behaviour of both models (EC and CE) can be summarized in terms of a *single pair* of parameters $(p, q)$: for the EC model $p = 1 - e(1 - c)$ and $q = c$, while for the CE model $p = 1 - e$ and $q = (1 - e)c$. It will be clear from the statement of Lemma 1 that $p$ and $q$ can be interpreted as 'effective' survival and colonisation probabilities.

**Lemma 1** *Given $n_t = i$, $n_{t+1}$ has the same distribution as the sum of two independent binomial random variables, $B_1$ and $B_2$, with $B_1 \sim \mathsf{B}(i, p)$ and $B_2 \sim \mathsf{B}(N - i, q)$.*

*Remark*: It is *as if* each of the $i$ currently occupied patches remains occupied with probability $p$ and each of the $N - i$ currently unoccupied patches becomes occupied with probability $q$, all patches being affected independently.

Our main result gives the distribution of $n_t$ at any time $t$, conditional on the initial ($t = 0$) number of occupied patches. Set $a = p - q = (1 - e)(1 - c)$, being the same for both models, and $q^* = q/(1 - a)$, noting that $0 < a < 1$ and $0 < q^* < 1$. It will be clear from the statement of Theorem 1 that $q^*$ is the equilibrium expected proportion of occupied patches, and that $a$ is the rate of (geometric) approach to equilibrium.

**Theorem 1** *Define sequences $(p_t)$ and $(q_t)$ by $q_t = q^*(1 - a^t)$ and $p_t = q_t + a^t$ ($t \geq 0$). Then, given $n_0 = i$, $n_t$ has the same distribution as the sum of two independent binomial random variables, $B_t^{(1)}$ and $B_t^{(2)}$, with $B_t^{(1)} \sim \mathsf{B}(i, p_t)$ and $B_t^{(2)} \sim \mathsf{B}(N - i, q_t)$.*

*Remark*: It is as if each of the $i$ initially occupied patches remains occupied with probability $p_t$ and each of the $N - i$ initially unoccupied patches becomes occupied with probability $q_t$, all patches being affected independently.

We may conclude that $\mathbb{E}(n_t|n_0 = i) = ip_t + (N - i)q_t$ and, since $B_t^{(1)}$ and $B_t^{(2)}$ are independent, $\mathrm{Var}\,(n_t|n_0 = i) = ip_t(1 - p_t) + (N - i)q_t(1 - q_t)$. Note also that the sequences $(p_t)$ and $(q_t)$ satisfy $p_0 = 1$ and $q_0 = 0$, $p_1 = p$ and $q_1 = q$, and, both have limit $q^*$. Theorem 1 is therefore consistent with Lemma 1 and, furthermore, the equilibrium behaviour of our model is very simple to describe. It is as if each of the $N$ patches is occupied independently with probability $q^*$:

**Corollary 1** *Given $n_0 = i$, $n_t$ converges in distribution to a binomial $\mathsf{B}(N, q^*)$ random variable as $t \to \infty$.*

This is illustrated in Figure 1, along with a simulation of the EC model. It is important to realise that it is the equilibrium *observed* occupancy that follows the binomial $\mathsf{B}(N, q^*)$ law, and that the expected equilibrium observed proportion $q^*$ depends on *when* the census is taken; it is smaller for the CE model than for the EC model by a factor of $1 - e$. Indeed, because the extinction and colonisation processes are assumed to occur as distinct phases, the long-term proportions fluctuate between high and low.

Next we examine the proportion $X_t^{(N)}(= n_t/N)$ of occupied patches at time $t$, and consider what happens for *fixed* $t$ as $N$ gets large. The following law of large numbers shows that the (random) proportion of occupied patches can be approximated using a deterministic process $(x_t)$. Here and henceforth $\overset{D}{\to}$ denotes convergence in distribution.

**Theorem 2** *Let $(i_N)$ be a sequence of initial states such that $i_N/N \to x_0$ as $N \to \infty$. Then, for any $t \geq 1$, $X_t^{(N)} \overset{D}{\to} x_t$ as $N \to \infty$, where $x_t = p_t x_0 + q_t(1 - x_0) = q^* + a^t(x_0 - q^*)$.*

The limiting ($t \to \infty$) proportion of occupied patches for the deterministic process $(x_t)$ is $q^*$. Indeed, the limiting *expected* proportion is also $q^*$. Thus, for both models (EC and CE), the proportion of occupied patches converges to the same limit regardless of the order in which limits are taken. However, note that $q^*$ is different for each model. Indeed, $q^*$ is uniformly *greater* for the EC model, which is not surprising because even in equilibrium the process is observed immediately after colonisation.

We also note a connection with the incidence function model of Hanski (1994), which describes the occupancy of a single patch using a two-state Markov chain. Hanski uses the term 'rescue effect' to describe the deleterious effect of colonisation on extinction when colonisation is frequent, and intuits that the extinction probability should be $(1 - c)e$ rather than $e$ (in our notation). However, Lemma 1 (above) establishes that, for the EC model, $(1 - c)e$ *is* the effective extinction probability resulting from our assumed two-phase behaviour, and Corollary 1 establishes that the expected equilibrium observed proportion is $q^* = q/(1 - a) = c/(c + (1 - c)e)$, being precisely Equation 7 of Hanski (1994). Furthermore, our Theorem 1 gives a more detailed interpretation of the rescue effect. The 'effective' extinction probability at time $t$ is $1 - p_t = (1 - q^*)(1 - a^t)$, which for the EC model is $1 - p_t = (1 - c)e(1 - a^t)/(1 - a)$, being $(1 - c)e$ when $t = 1$ and $(1 - e)c/(c + (1 - c)e)$ in the long term.

The following central limit theorem establishes that, for large $N$, the fluctuations about the deterministic trajectory determined by Theorem 2 have an approximate normal (Gaussian) distribution.

**Theorem 3** *In addition to the conditions of Theorem 2 suppose that $\sqrt{N}(x^{(N)} - x_0) \to z_0$, as $N \to \infty$, where $x^{(N)} = i_N/N$. Let $Z_t^{(N)} = \sqrt{N}(X_t^{(N)} - x_t)$. Then, for any $t \geq 1$, $Z_t^{(N)} \xrightarrow{D} \mathsf{N}(a^t z_0, v_t)$ as $N \to \infty$, where $v_t = p_t(1 - p_t)x_0 + q_t(1 - q_t)(1 - x_0)$.*

Notice that the approximating variance given in Theorem 3 is consistent with the exact variance given by Theorem 1: $\operatorname{Var} Z_t^{(N)} = N \operatorname{Var} X_t^{(N)} = p_t(1 - p_t)x^{(N)} + q_t(1 - q_t)(1 - x^{(N)}) \to v_t$ as $N \to \infty$. They will be identical if $x^{(N)} = x_0$. This is illustrated in Figure 2, along with a simulation of the EC model.

We can also assess the fluctuations about the deterministic equilibrium $q^*$, provided that the initial proportion occupied is sufficiently close to $q^*$, thus giving a much simpler distributional approximation that is appropriate once equilibrium is reached. On setting $x_0 = q^*$ in Theorems 2 and 3 we obtain the following result.

**Corollary 2** *Let $(i_N)$ be a sequence of initial states such $i_N/N \to q^*$ as $N \to \infty$. Then, for any $t \geq 1$, $X_t^{(N)} \xrightarrow{D} q^*$ as $N \to \infty$. Let $Z_t^{(N)} = \sqrt{N}(X_t^{(N)} - q^*)$. If $\sqrt{N}(i_N/N - q^*) \to z_0$, then, for any $t \geq 1$, $Z_t^{(N)} \xrightarrow{D} \mathsf{N}(a^t z_0, q^*(1 - q^*))$.*

*Remarks.* Aficionados will realise that strong laws of large numbers hold, because convergence in Theorem 2 and the first part Corollary 2 can be strengthened to convergence almost sure. Theorem 3 and the second part of Corollary 2 allow us to assess the quality of the deterministic approximation. For example, Theorem 3 implies that, for $N$ sufficiently large, $\Pr(|X_t^{(N)} - x_t| > \epsilon_t) \simeq 2(1 - \Phi(\epsilon_t \sqrt{N/v_t}))$, where $\Phi$ is the standard normal distribution function.

## 4. DISCUSSION

Our results are useful for understanding the patch occupancy process when the effective survival and colonization parameters $p$ and $q$ are known. Much finer results would be needed for model calibration, because data would typically be collected at successive census times, and thus observations would be dependent (even in equilibrium). We have been able to show that the finite-dimensional distributions of the scaled process $(Z_t^{(N)})$ defined in Theorem 3 converge to those of a Gaussian Markov chain $(Z_t)$ defined by $Z_{t+1} = aZ_t + E_t$ $(Z_0 = z_0)$, where the 'errors' $E_t$ $(t \geq 0)$ are independent random variables with $E_t \sim \mathsf{N}(0, \sigma_t^2)$ and $\sigma_t^2 = x_t p(1 - p) + (1 - x_t)q(1 - q)$. A similar result holds for the scaled process defined in Corollary 2, but now $E_t \sim \mathsf{N}(0, q^*(1 - q^*)(1 - a^2))$, and so $(Z_t)$ is a standard (autoregressive) AR-1 process with identically distributed errors. Thus, standard time-series methods can be used to estimate $p$ and $q$. These results will be reported elsewhere.
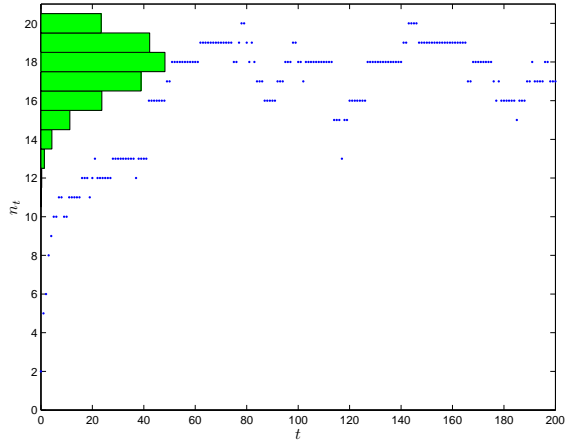


**Figure 1.** A single simulation of the EC model with $N = 20$, $e = 0.01$ and $c = 0.05$, starting with $n_0 = 2$ patches occupied. The number $n_t$ of occupied patches is plotted at times $t = 0, \ldots, 200$. The bar graph in green is the $\mathsf{B}(N, q^*)$ stationary distribution ($q^* = 0.84034$).
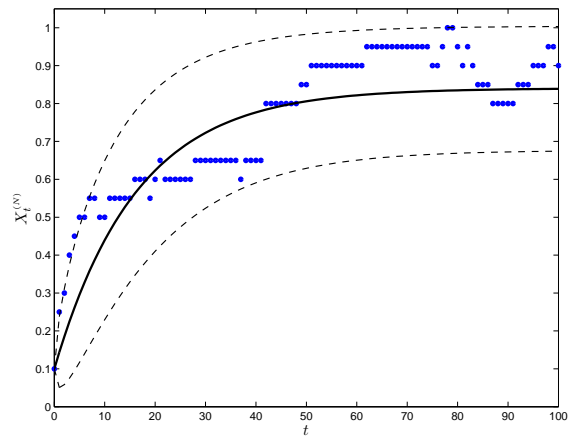


**Figure 2.** A single simulation of the EC model with $N = 20$, $e = 0.01$ and $c = 0.05$, starting with $n_0 = 2$ patches occupied ($x^{(N)} = x_0 = 0.1$). The proportion $X_t^{(N)}$ of occupied patches is plotted at times $t = 0, \ldots, 100$. The solid curve joins points on the limiting deterministic trajectory. The the dashed curve is $\pm 2$ standard deviations as predicted by the normal approximation.

In addition to the present mainland-island model (Case (iv) above), we have studied Cases (i) and (iii), evaluating the expected time to total extinction, extinction probabilities, and quasi-stationary distributions. For models with $c_i = g(i/N)$ for some function $g$, we have developed limit laws which allow one to approximate the proportion of occupied patches over time by a discrete-time Gaussian (autoregressive) process. These results, which are based largely on the analytical methods introduced in this paper, will be reported elsewhere.

## 5. CONCLUSION

We have presented a two-phase discrete-time Markov chain model that describes the dynamics of a metapopulation network. A new and quite general approach to modelling the colonisation process was presented, one that substantially subsumes earlier models. Despite its generality, explicit results can be obtained for several quantities of interest. We concentrated here on the mainland-island case, where the colonization probability was constant. The distribution of the observed number of occupied patches after the extinction and colonization phases was obtained (both the time-dependent and equilibrium distribution) and a law of large numbers and a central limit law were established that permit these distributions to be approximated by a normal distribution whose parameters were given explicitly.

## 6. APPENDIX

*Proof of Lemma 1.* Suppose that $n_t = i$. We will use conditional expectation to evaluate $G$, the probability generating function (pgf) of $n_{t+1}$. For the EC model, $n_{t+1} = U + Z$, where $U \sim B(i, 1 - e)$ and $Z \sim B(N - U, c)$, and so

$$
\begin{aligned}
G(z) &= \mathbb{E}(z^{U+Z}) = \mathbb{E}\left(\mathbb{E}(z^{U+Z}|U)\right) = \mathbb{E}\left(z^U \mathbb{E}(z^Z|U)\right) = \mathbb{E}\left(z^U(1 - c + cz)^{N-U}\right) \\
&= (1 - c + cz)^N \mathbb{E}\left((z/(1 - c + cz))^U\right) = (1 - c + cz)^N (e + (1 - e)z/(1 - c + cz))^i \\
&= (e(1 - c) + [1 - e(1 - c)]z)^i (1 - c + cz)^{N-i}.
\end{aligned}
$$

For the CE model, $n_{t+1} \sim B(i + Z, 1 - e)$, where $Z \sim B(N - i, c)$, and so

$$
\begin{aligned}
G(z) &= \mathbb{E}\left(\mathbb{E}(z^{n_{t+1}}|Z)\right) = \mathbb{E}\left((e + (1 - e)z)^{i+Z}\right) \\
&= (e + (1 - e)z)^i \mathbb{E}\left((e + (1 - e)z)^Z\right) = (e + (1 - e)z)^i (1 - c + c(e + (1 - e)z))^{N-i} \\
&= (e + (1 - e)z)^i (1 - c(1 - e) + c(1 - e)z)^{N-i}.
\end{aligned}
$$

Therefore $G(z) = (1 - p + pz)^i (1 - q + qz)^{N-i}$, where $p = 1 - e(1 - c)$ and $q = c$ for the EC model, and $p = 1 - e$ and $q = (1 - e)c$ for the CE model. The result follows.

*Proof of Theorem 1.* Suppose that $n_0 = i$ and let $G_t$ be the pgf of $n_t$. Then, $G_0(z) = z^i$ and, from Lemma 1,

$$
\begin{aligned}
G_{t+1}(z) &= \mathbb{E}\left((1 - p + pz)^{n_t}(1 - q + qz)^{N-n_t}\right) = (1 - q + qz)^N \mathbb{E}\left(\left(\frac{1 - p + pz}{1 - q + qz}\right)^{n_t}\right) \\
&= (1 - q + qz)^N G_t\left(\frac{1 - p + pz}{1 - q + qz}\right),
\end{aligned}
\tag{1}
$$

for all $t \geq 0$. The proof will be complete if we can show that

$$
G_t(z) = (1 - p_t + p_t z)^i (1 - q_t + q_t z)^{N-i}
\tag{2}
$$

for all $t \geq 0$, where $(p_t)$ and $(q_t)$ are the given sequences. Recall that $q_t = q^*(1 - a^t)$ and $p_t = q_t + a^t$ ($t \geq 0$), where $a = p - q = (1 - e)(1 - c)$ and $q^* = q/(1 - a)$. Clearly (2) is true for $t = 0$ because $p_0 = 1$ and $q_0 = 0$. But, if (2) is true for some fixed $t \geq 0$, then a simple calculation involving (1) shows that

$$
\begin{aligned}
G_{t+1}(z) &= (1 - (q + ap_t) + (q + ap_t)z)^i (1 - (q + aq_t) + (q + aq_t)z)^{N-i} \\
&= (1 - p_{t+1} + p_{t+1}z)^i (1 - q_{t+1} + q_{t+1}z)^{N-i},
\end{aligned}
$$

and so the result follows by Mathematical Induction.

*Proof of Corollary 1.* Suppose that $n_0 = i$. Then, Theorem 1 states that $n_t$ has the same distribution as $B_t^{(1)} + B_t^{(2)}$, where $B_t^{(1)}$ and $B_t^{(2)}$ are independent random variables with $B_t^{(1)} \sim B(i, p_t)$ and $B_t^{(2)} \sim B(N - i, q_t)$.

We have already remarked that $(p_t)$ and $(q_t)$ have common limit $q^*$. Therefore, it is clear that $B_t^{(1)} \xrightarrow{D} B^{(1)} \sim \mathsf{B}(i, q^*)$ and $B_t^{(2)} \xrightarrow{D} B^{(2)} \sim \mathsf{B}(N - i, q^*)$, as $t \to \infty$, because the corresponding sequences of characteristic functions converge point wise to the appropriate limits. Then, since $B_t^{(1)}$ and $B_t^{(2)}$ are independent (for each $t$), so are $B^{(1)}$ and $B^{(2)}$, and, moreover, $B_t^{(1)} + B_t^{(2)} \xrightarrow{D} B^{(1)} + B^{(2)}$. But, clearly $B^{(1)} + B^{(2)} \sim \mathsf{B}(N, q^*)$, and the result follows.

*Proof of Theorem 2.* From Theorem 1, $X_t^{(N)}$ has the same distribution as $K_t^{(N)} + L_t^{(N)}$, where $K_t^{(N)}$ and $L_t^{(N)}$ are independent random variables given by $K_t^{(N)} = B_t^{(1)}/N = x^{(N)}B_t^{(1)}/i_N$ and $L_t^{(N)} = B_t^{(2)}/N = (1 - x^{(N)})B_t^{(2)}/j_N$, where $j_N = N - i_N$ and $x^{(N)} = i_N/N$. We are told that $x^{(N)} \to x_0$ as $N \to \infty$, and so $i_N \to \infty$ and $j_N \to \infty$. It follows from the standard Weak Law of Large Numbers that $B_t^{(1)}/i_N \xrightarrow{D} p_t$ and $B_t^{(2)}/j_N \xrightarrow{D} q_t$. Hence, $K_t^{(N)} \xrightarrow{D} x_0 p_t$ and $L_t^{(N)} \xrightarrow{D} (1 - x_0)q_t$, and so $K_t^{(N)} + L_t^{(N)} \xrightarrow{D} p_t x_0 + q_t(1 - x_0)$ ($= q^* + a^t(x_0 - q^*)$), which is the stated result.

*Proof of Theorem 3.* Again we exploit the independence exhibited in Theorem 1. First notice that

$$X_t^{(N)} - x_t = x^{(N)}B_t^{(1)}/i_N - x_0 p_t + (1 - x^{(N)})B_t^{(2)}/j_N - (1 - x_0)q_t$$
$$= x^{(N)}(B_t^{(1)}/i_N - p_t) + (1 - x^{(N)})(B_t^{(2)}/j_N - q_t) + (x^{(N)} - x_0)(p_t - q_t),$$

and so, on multiplying by $\sqrt{N}$ and noting that $p_t - q_t = a^t$, we find that

$$Z_t^{(N)} = \sqrt{x^{(N)}}\sqrt{i_N}(B_t^{(1)}/i_N - p_t) + \sqrt{1 - x^{(N)}}\sqrt{j_N}(B_t^{(2)}/j_N - q_t) + z^{(N)}a^t, \qquad (3)$$

where $z^{(N)} = \sqrt{N}(x^{(N)} - x_0)$. By the standard Central Limit Theorem $\sqrt{i_N}(B_t^{(1)}/i_N - p_t) \xrightarrow{D} \mathsf{N}(0, p_t(1 - p_t))$ and $\sqrt{j_N}(B_t^{(2)}/j_N - q_t) \xrightarrow{D} \mathsf{N}(0, q_t(1 - q_t))$. Therefore, the first and second terms of (3) define independent sequences that converge in distribution to $\mathsf{N}(0, x_0 p_t(1 - p_t))$ and $\mathsf{N}(0, (1 - x_0)q_t(1 - q_t))$ random variables, respectively. But, we are told that $z^{(N)} \to z_0$ as $N \to \infty$. Therefore, $Z_t^{(N)} \xrightarrow{D} \mathsf{N}(z_0 a^t, v_t)$, where $v_t = p_t(1 - p_t)x_0 + q_t(1 - q_t)(1 - x_0)$.

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