A stochastic model for the evolution of the influenza virus

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Abstract. Consider a birth and death chain to model the number of types of a given virus. Each type gives birth to a new type at rate $\lambda$ and dies at rate 1. Each type is also assigned a fitness. When a death occurs either the least fit type dies (with probability $1 - r$) or we kill a type at random (with probability $r$). We show that this random killing has a large effect (for any $r > 0$) on the behavior of the model when $\lambda < 1$. The behavior of the model with $r > 0$ and $\lambda < 1$ is consistent with features of the phylogenetic tree of influenza.

Key words: phylogenetic tree, influenza, stochastic model, mutation

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1 Introduction.

Consider the following model for the evolution of a virus. The model depends on two parameters, $\lambda > 0$ and $r \in [0, 1]$. We think of $\lambda$ as the mutation rate. The number of types at time $t$ is denoted by $X(t)$, a birth-death process which makes transitions

$$n \rightarrow \begin{cases} 
  n + 1 & \text{at rate } n\lambda \text{ for } n \geq 1 \\
  n - 1 & \text{at rate } n \text{ for } n \geq 2
\end{cases}$$

(the number of types is never less than one). Each virus type has a fitness $\phi$, chosen at random from the uniform $(0,1)$ distribution when it is created (so each new type is different from all previous types). When a type dies the type that is chosen to die is, with probability $r$, selected uniformly among the existing types, and with probability $1 - r$ the type with minimal fitness. We will say that with probability $r$ a random killing occurs.

The model with $r = 0$ (the least fit type type is always killed) was introduced by Liggett and Schinazi in [7]. Several articles have since been written on closely related models, see [3], [5], [6] and [8]. “Kill the least fit” models go back to at least [2]. The model with random killing (i.e. $r > 0$) is a natural extension for at least two reasons. From a modeling perspective “Kill the least fit” is quite natural. However, assuming that this is always the case is not. Random events should occasionally prevent this transition from happening. Furthermore, from a mathematical perspective it seems interesting to study the effect of small random perturbations of the basic model. As we will see they can have major effects on the behavior of the model.

We are interested in

$$\phi_t = \phi^*_t = \text{ the maximal fitness of the types alive at time } t,$$
$$a_t = a^*_t = \text{ the age of the type with maximal fitness at time } t$$

(if a type is created at time $s$ then its age at time $t > s$ is $t - s$). We start the process with a single individual. We assume that its fitness $\phi_0$ is uniformly distributed on $(0,1)$, and initially we take $a_0 = 0$.

Let $\Rightarrow$ denote weak convergence and $\rightarrow_p$ denote convergence in probability. The following theorem summarizes the main results of [7].

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Theorem 1 ([7]). Assume \( r = 0 \), and \( Y \) is uniformly distributed on the interval \((0,1)\).

(a) If \( \lambda \leq 1 \) then \( a_t/t \Rightarrow Y \) as \( t \to \infty \).

(b) If \( \lambda > 1 \) then \( a_t/t \to_p 0 \) as \( t \to \infty \).

When \( \lambda < 1 \), \( X(t) \) converges in distribution to its stationary distribution, and hence at any given time there will not be many types. In this case, (a) above shows that the fittest type at time \( t \) will have been around for order of time \( t \). As noted in [7], this is consistent with the observed structure of an influenza tree. When \( \lambda > 1 \), \( X(t) \) tends to infinity as \( t \to \infty \), and (b) shows that the fittest type at time \( t \) has been around only for only \( o(t) \) time. As noted in [7], this is consistent with the observed structure of an HIV tree. In the critical case \( \lambda = 1 \) we have something inbetween these two pictures. It is easy to see that in all cases the maximal fitness \( \phi_t \to 1 \) as \( t \to \infty \).

Theorem 1 shows that the model with \( r = 0 \) can, by adjusting \( \lambda \), describe rather different evolutions. Nevertheless, it has some limitations. The maximal fitness always tends to 1, and for \( \lambda \leq 1 \) the age \( a_t \) tends to infinity. As shown below, the model with random killing \( (r > 0) \) allows for the possibilities that \( \phi_t \not\to 1 \) and \( a_t \not\to \infty \).

Before proceeding to our results for the \( r > 0 \) case we resolve one question left open by Theorem 1. Namely, (b) leaves open the two possibilities: \( a_t \) is (stochastically) bounded as \( t \to \infty \), or \( a_t \to \infty \). It turns out that \( a_t \) does not tend to infinity, instead it converges in distribution. For the sake of completeness, we include the behavior of the maximal fitness in the following result.

Theorem 2. Assume \( r = 0 \), and let \( E \) be a mean one exponential random variable.

(a) For \( \lambda > 0 \), \( \phi_t \to 1 \) a.s. as \( t \to \infty \).

(b) For \( \lambda > 1 \), \( a_t \Rightarrow \frac{1}{\lambda} E \) as \( t \to \infty \).

We turn to the case of random killings \( (r > 0) \) and focus on the \( \lambda < 1 \) case. We see that the behaviors of the maximal fitness and age processes are quite different from the \( r = 0 \) case.

Theorem 3. Assume \( r > 0 \) and \( \lambda < 1 \). Then

(a) \( \phi_t \) converges in distribution as \( t \to \infty \) to a nondegenerate limit law, and

(b) \( a_t \) converges in distribution as \( t \to \infty \) to a nondegenerate limit law.

Theorem 3 is consistent with features of the influenza phylogenetic tree. The most fit type lasts a finite random time and then is replaced by a new most fit type and so on. As desired \( a_t \) does not go to infinity with \( t \) and \( \phi_t \) does not go to 1. Instead they converge to nondegenerate limits.

Turning to the \( r > 0, \lambda > 1 \) case, our results are less complete. We can show that the fitness \( \phi_t \) tends to one as \( t \to \infty \), but we cannot show, as we conjecture, that the age \( a_t \) does not tend to infinity.

Theorem 4. For \( r > 0 \) and \( \lambda \geq 1 \), \( \phi_t \to_p 1 \) as \( t \to \infty \).

In the next section we give the proof of Theorem 2. In Section 3 we give a construction that we use to prove Theorem 3. The construction allows us to write down a renewal type description of the limit laws for both the fitness and age processes. In Section 4 we use a different construction to prove Theorem 4.

2 Proof of Theorem 2

Let us dispense with the easy convergence \( \phi_t \to 1 \). Let \( B(t) \) be the number of types created by time \( t \), and let \( U_1, U_2, \ldots \) be the successive iid uniform \((0,1)\) random variables created as the process evolves. Then \( \phi_t = \max\{U_1, \ldots, U_{B(t)}\} \). It is easy to see that \( \max\{U_1, \ldots, U_n\} \to 1 \) a.s. as \( n \to \infty \). Since \( B(t) \to \infty \) a.s. we get \( \phi_t \to 1 \) a.s.
For (b), fix $\lambda > 1$ and recall the notation of Section 3 of [7]. Following the notation there, let $T_n$ be the first time $X_t$ reaches $n$, let $N(t) = \sup\{n : T_n \leq t\}$, and set

$$\zeta(n) = T_n - \frac{\log n}{\lambda - 1}.$$  

We need an improvement of Lemma 1 of [7].

**Lemma 1.** With probability one, $\lim_{t \to \infty} N(t)e^{-(\lambda - 1)t} = e^{-(\lambda - 1)\zeta_\infty}$, a strictly positive finite limit.

**Proof.** It was shown at the end of the proof of Lemma 1 in [7] that $\zeta(n) \to \zeta_\infty$ a.s. as $n \to \infty$ for some finite random variable $\zeta_\infty$. Since $N(t) \to \infty$ as $t \to \infty$ we also have $\zeta(N(t)) \to \zeta_\infty$ a.s. as $t \to \infty$. By definition,

$$T_{N(t)} \leq t < T_{N(t)+1}$$

so

$$\zeta_N(t) \leq t - \frac{\log(N(t))}{\lambda - 1}$$

or

$$\log(N(t)) - (\lambda - 1)t \leq -(\lambda - 1)\zeta(N(t)).$$

This implies $N(t)e^{-(\lambda - 1)t} \leq e^{-(\lambda - 1)\zeta(N(t))}$ and therefore

$$\limsup_{t \to \infty} N(t)e^{-(\lambda - 1)t} \leq e^{-(\lambda - 1)\zeta_\infty} \text{ a.s.}$$

To get an inequality in the reverse direction we note that (2.1) implies

$$t - \frac{\log(N(t) + 1)}{\lambda - 1} \leq \zeta(N(t) + 1),$$

or

$$\log(N(t) + 1) - (\lambda - 1)t \leq -(\lambda - 1)\zeta(N(t) + 1).$$

This implies $(N(t) + 1)e^{-(\lambda - 1)t} > e^{-(\lambda - 1)\zeta(N(t)+1)}$ and therefore

$$\liminf_{t \to \infty} N(t)e^{-(\lambda - 1)t} \geq e^{-(\lambda - 1)\zeta_\infty} \text{ a.s.}$$

This completes the proof, since $\zeta_\infty$ is positive and finite with probability one. \hfill \square

When $r = 0$ the maximal fitness $\phi_1$ is increasing in $t$. This implies that for $s < t$, $a_t \geq t - s$ if and only if $\phi_s = \phi_t$. Let $S_n$ be the number of types produced up to time $T_n$. By (1) and (2) in [7],

$$E\left[\frac{S_{N(s)}}{S_{N(t)+1}}, N(s) < N(t)\right] \leq P(\phi_s = \phi_t, N(s) < N(t)) \leq E\left[\frac{S_{N(s)+1}}{S_{N(t)}}, N(s) < N(t)\right].$$

(2.2)

Fix $u > 0$ and let $s = t - u$. By Lemma 4, $P(N(s) < N(t)) \to 1$ as $t \to \infty$, so it suffices to prove that both the left-side and right-side of (2.2) converge to $e^{-(\lambda - 1)u}$.

It was shown in [7] that $S_n/n$ converges a.s. to a finite positive limit as $n \to \infty$. By this fact, $N(t) \to \infty$, and Lemma 1,

$$\frac{S_{N(s)+1}}{S_{N(t)}} = \frac{S_{N(s)+1}}{N(s) + 1} \frac{N(t)}{S_{N(t)}} \frac{N(s) + 1}{N(t)} \to e^{-(\lambda - 1)u} \text{ a.s.}$$

It follows that the right-side of (2.2) converges to $e^{-(\lambda - 1)u}$ as $t \to \infty$. A similar argument handles the left-side of (2.2). This completes the proof of Theorem 2.
3 Proof of Theorem 3.

Throughout this section $0 < r \leq 1$ and $0 < \lambda < 1$ are fixed. We first extend the notation of Section 2 of [7] making the following definitions and observations.

(1) Put $T_0 = 0$ and for $n \geq 1$ let $T_n$ be the time of the $n$th return of $X(t)$ to state 1. The “interarrival times” times \{ $T_n - T_{n-1}, n \geq 1$ \} are iid random variables.

(2) For $n \geq 1$ let $\xi_n$ be the duration of the $n$th sojourn time in state 1,

\[ \xi_n = \inf \{ t > T_{n-1} : X_t \neq 1 \}. \]

The random variables \{ $\xi_n, n \geq 1$ \} are iid exponential with parameter $\lambda$. Note also that for $n \geq 0 \sigma(T_0, \ldots, T_n)$ is independent of $\sigma(\xi_{n+1}, \xi_{n+2}, \ldots)$.

(3) For $n \geq 1$ let $u_n$ be the uniform random variable created at time $T_{n-1} + \xi_n$, when $X(t)$ jumps from 1 to 2. At time $T_{n-1} + \xi_n$ there are two types, with fitnesses $\phi(T_{n-1}), u_n$. The \{ $u_n, n \geq 1$ \} are iid uniform (0,1) rv’s, independent of the sequences \{ $T_n, n \geq 0$ \} and \{ $\xi_n, n \geq 1$ \}.

(4) For $n \geq 1$ let $\eta_n$ be the duration of the sojourn time in 2 starting at time $T_{n-1} + \xi_n$,

\[ \eta_n = \inf \{ t > T_{n-1} + \xi_n : X_t \neq 2 \}. \]

The random variables \{ $\eta_n, n \geq 1$ \} are iid exponential with parameter $2\lambda + 2$, independent of \{ $\xi_n, n \geq 1$ \} and \{ $u_n, n \geq 1$ \}. Furthermore, $\sigma(T_0, \ldots, T_n)$ is independent of $\sigma(\eta_{n+1}, \eta_{n+2}, \ldots)$.

(5) For $n \geq 1$ let $T'_n = T_{n-1} + \xi_n + \eta_n$. For all $t \in [T_{n-1} + \xi_n, T'_n)$ here are exactly two types, the fitnesses are $\phi(T_{n-1}), u_n$.

(6) At time $T'_n$, if $X(t)$ jumps to 1, with probability $r$ one of the types $u_n, \phi(T_{n-1})$ is chosen to be killed. For $n \geq 1$ let

\[ \varepsilon_n = \begin{cases} 
1 & \text{at time } T'_n, X_t \text{ jumps to 1 and the type } \phi(T_{n-1}) \text{ is killed by random killing } \\
0 & \text{otherwise.} 
\end{cases} \]

Note that we do not include in the event \{ $\varepsilon_n = 1$ \} the possibility that $\phi(T_{n-1}) < u_n$ and the least fit type is killed with probability $1 - r$. The random variables \{ $\varepsilon_n, n \geq 1$ \} are iid Bernoulli with mean

\[ p = \frac{2}{2(1+\lambda)} \frac{r}{2} = \frac{r}{2(1+\lambda)} > 0. \]

Also, the sequence \{ $\varepsilon_n, n \geq 1$ \} is independent of the sequence \{ $u_n, n \geq 1$ \}, and $\sigma(T_k, \xi_k, \eta_k, k \leq n)$ is independent of $\sigma(\varepsilon_{n+1}, \varepsilon_{n+2}, \ldots)$.

(7) To consider the return times $T_j$ corresponding to the event \{ $\varepsilon_n = 1$ \}, put $\kappa_0 = 0$, $R_0 = 0$, and for $n \geq 1$ define

\[ \kappa_n = \inf \{ k > \kappa_{n-1} : \varepsilon_k = 1 \} \text{ and } R_n = T_{\kappa_n}. \]

The random variables \{ $R_n - R_{n-1}, n \geq 1$ \} are iid, with $\mu = ER_1 \in (0, \infty)$ and at the times $R_n$, $n \geq 1$,

\[
\begin{align*}
\phi_{R_n} &= u_{\kappa_n} \text{ is uniform on } (0,1) \\
\sigma_{R_n} &= \eta_{\kappa_n} \text{ is exponential with parameter } 2(\lambda + 1). 
\end{align*}
\] (3.1)

The construction is illustrated in Figure 1 below, in which $\varepsilon_1 = 0$, $\varepsilon_2 = 1$ and $R_1 = T_2$. 


By (3.1), at time $R_1$ there is a single type, its fitness has the uniform distribution on $(0, 1)$, and its age has the exponential distribution with parameter $2(\lambda + 1)$. Furthermore, given this information, the distribution of our process for $t \geq R_1$ is independent of what has happened before time $R_1$. It follows that if we start at time 0 with a single type with fitness uniformly distributed on $(0, 1)$ and age exponentially distributed with parameter $2(\lambda + 1)$ then $R_1$ is a regeneration time. The strong Markov property now implies the following result.

**Lemma 2.** If $\phi_0$ is uniformly distributed on $(0, 1)$ and $a_0$ is exponentially distributed with parameter $2(\lambda + 2)$ then for $t > 0$,

$$P(\phi_t \leq v, R_1 \leq t) = \int_0^t P(R_1 \in ds)P(\phi_{t-s} \leq v), \quad 0 < v < 1,$$

and

$$P(a_t \leq x, R_1 \leq t) = \int_0^t P(R_1 \in ds)P(a_{t-s} \leq x), \quad x > 0.$$

**Remark 1.** The fitness process does not depend on the age process, so (3.2) holds regardless of the distribution of $a_0$.

In order to make use of (3.2) and (3.3) we will need information on the tail of the distribution of $R_1$, which is provided by our next result.

**Lemma 3.** For $\lambda < 1$ there are constants $C, \gamma$ such that $P(R_1 > t) \leq Ce^{-\gamma t}$. In particular, $E(R_1) < \infty$.

**Proof.** We are going to use Gronwall’s inequality. Let $\tilde{X}(t)$ denote $X(t)$ starting at 3 instead of 1, let $\tilde{T}_1$ be the first time $\tilde{X}(t)$ reaches 1, and let $\tilde{R}_1$ be defined analogously to $R_1$. By a simple coupling it is clear that $P(R_1 > t) \leq P(\tilde{R}_1 > t)$ for all $t > 0$. Let $\tau$ be the first time $\tilde{X}(t)$ reaches 2 after reaching 0,

$$\tau = \inf\{t > \tilde{T}_1 : \tilde{X}(t) = 2\},$$

and let $\tilde{\eta}$ be an independent exponential random variable with parameter $2\lambda + 2$. Finally, let $\tau' = \tau + \tilde{\eta}$. By the Markov property,

$$P(\tilde{R}_1 > t) = P(\tau' > t) + (1 - p) \int_0^t P(\tau' \in ds)P(\tilde{R}_1 > t - s).$$

It follows now from Gronwall’s inequality that

$$P(\tilde{R}_1 > t) \leq P(\tau' > t)e^{(1-p)\int_0^t P(\tau' \leq s)} \leq eP(\tilde{R}_1 > t).$$
It follows that 
\[ s, t \in \text{the time interval } \left[ 0, \infty \right) \]

or \( t = \) a continuous function of \( s = 0 \) we obtain 
\[ s \]

We claim that 
\[ \mu \]

By the branching property, we get 
\[ X \]

It follows from Theorem 4.4.4 of \[ U \]

or decomposing the event defining \( U \) at rate 1, and treat 0 as a trap. If we let \( \tau_0 \) be the first hitting time of 0, then \( \tau_0 > \tau \), so the final reduction is to prove that for some constants \( C, \gamma \), 
\[ P(\tau_0 > t | X(0) = 3) = P(X(t) = 0 | X(0) = 3) \leq Ce^{-\gamma t}. \]

The amended birth-death process \( X(t) \) is a continuous time branching process, as shown in Section III.5 of \[ V \]

Given this, a standard renewal theorem (Theorem 4.4.5 of \[ W \]) implies that the solution to this renewal equation is given by 
\[ \sum_{k=0}^{\infty} s^k P(X(t) = k | X(0) = 1) \]

With these facts established we begin the proof of part (a) of Theorem 3. Let \( F(t) = P(R_1 \leq t) \), and let 
\[ U = \sum P^{(s^n)} \]

be the corresponding renewal function, \( U(t) = \sum_0^n P(R_n \leq t) \). Fix \( v \in (0, 1) \) and define 
\[ h_v(t) = P(\phi_t \leq v, R_1 > t) \text{ and } H_v(t) = P(\phi_t \leq v). \]

By decomposing the event defining \( H_v(t) \) according to the value of \( R_1 \), and using (3.2), we have 
\[ H_v(t) = h_v(t) + P(\phi_t \leq v, R_1 \leq t) = h_v(t) + \int_0^t H_v(t - s) F(ds). \] (3.4)

It follows from Theorem 4.4.4 of [4] that the solution to this renewal equation is given by 
\[ H_v(t) = \int_0^t h_v(t - s) U(ds). \] (3.5)

We claim that 
\[ h_v(t) \]

is directly Riemann integrable if \( \lambda < 1 \). (3.6)

Given this, a standard renewal theorem (Theorem 4.4.5 of [4]) implies that 
\[ H_v(t) \to \frac{1}{\mu} \int_0^\infty h_v(s) ds \text{ as } t \to \infty \] (3.7)

or 
\[ \lim_{t \to \infty} P(\phi_t \leq v) = \frac{1}{\mu} \int_0^\infty P(\phi_s \leq v, R_1 > s) ds \] (3.8)

(recall that \( \mu = E(R_1) \)). For \( \lambda = 1 \) we still have (3.5), but not (3.7) since this depends on \( \mu < \infty \).

In view of the fact that \( P(R_1 > t) \) decays exponentially fast, to prove (3.6) it suffices to prove that \( h_v(t) \) is a continuous function of \( t \). For \( s < t \) let \( \Gamma_{s,t} \) be the event that the birth-death process makes no transitions in the time interval \([s,t] \). On \( \Gamma_{s,t} \), \( \phi \) cannot change, and \( R_1 > s \) if and only if \( R_1 > t \), so that 
\[ P(\{ \phi_s \leq v, R_1 > s \} \cap \Gamma_{s,t}) = P(\{ \phi_t \leq v, R_1 > t \} \cap \Gamma_{s,t}) \]

It follows that 
\[ |h_v(s) - h_v(t)| \leq P(\Gamma_{s,t}^c) \]
\[ = \sum_{k=1}^{\infty} P(X(s) = k)(1 - e^{-k(\lambda+1)(t-s)}) \]
\[ \leq \sum_{k=1}^{\infty} P(X(s) = k)k(\lambda+1)(t-s) \]
\[ = (t-s)(\lambda+1)E(X(s)). \]
For $\lambda < 1$, $\sup_s E(X(s)) < \infty$, so we have proved that $h_v$ is continuous and directly Riemann integrable.

For Theorem 3(a), we suppose first that $a_0$ is exponential with parameter $2(\lambda + 1)$, so that (3.3) holds. Now we follow the previous argument. Fix $x > 0$ and define

$$g_x(t) = P(a_t \leq x, R_1 > t) \quad \text{and} \quad G_x(t) = P(a_t \leq x)$$

As in the argument for Theorem 2(b), for $\lambda \leq 1$ we have

$$G_x(t) = g_x(t) + \int_0^t G_x(t - s)F(ds) = \int_0^t g_x(t - s)U(ds). \quad (3.9)$$

For $\lambda < 1$, an argument similar to the one for $h_v(t)$ shows that $g_x(t)$ is directly Riemann integrable, and by the renewal theorem

$$G_x(t) \to \frac{1}{\mu} \int_0^\infty g_x(s)ds \quad \text{as} \quad t \to \infty \quad (3.10)$$

or

$$\lim_{t \to \infty} P(a_t \leq x) = \frac{1}{\mu} \int_0^\infty P(a_s \leq x, R_1 > s) \, ds. \quad (3.11)$$

Given any $a_0 \geq 0$, by using the same birth-death process and sequence of uniform random variables, we may construct an age process $\tilde{a}_t$ with the property that

$$\tilde{a}_t = a_t \quad \text{if} \quad t \geq R_1. \quad (3.12)$$

This is because at time $R_1 = T_k$ for some $k$, the most fit type is the uniform random variable created at time $T_k + \xi_k$, and has age $\eta_k = a_{R_1} = \tilde{a}_{R_1}$. After time $R_1$ the two age processes are identical. By (3.12), $P(a_t \neq \tilde{a}_t) \to 0$ as $t \to \infty$, and therefore for any $a_0$,

$$\lim_{t \to \infty} P(\tilde{a}_t \leq x) = \frac{1}{\mu} \int_0^\infty \tilde{g}_x(s)ds. \quad (3.13)$$

Finally, it is not hard to see that the right-hand side of (3.8) is strictly increasing in $v$, and the right-hand side of (3.11) is strictly increasing in $x$, so the limit distributions are nondegenerate.

## 4 Proof of Theorem 4.

We start with the case $r = 1$. In this case, conditional on $X_t = k$, the set of fitnesses has the same law as that of $k$ uniform $(0, 1)$ random variables, and hence

$$P(\phi^1_t \leq u | X_t = k) = u^k, \quad 0 < u < 1. \quad (4.1)$$

This is because (i) the sequence of uniforms created when $X_t$ jumps is independent of $X_t$, (ii) when $r = 1$, the type that is killed is independent of the types that are present, and (iii) $k$ uniforms chosen randomly from $n \geq k$ iid uniforms has the law of $k$ iid uniforms. For $\lambda \geq 1$, $P(X_t \leq K) \to 0$ as $t \to \infty$ for any $K < \infty$. Applying (4.1) we obtain

$$\phi^1_t \to_p 1 \quad \text{as} \quad t \to \infty. \quad (4.2)$$

To handle $\phi^r_t$ for $0 < r < 1$ we argue that $\phi^r_t$ is stochastically larger than $\phi^1_t$. To do this we will use a coupling that is based on the following definition and elementary lemma. For positive integers $k$ and sets $A, B \subset (0, 1)$ such that $|A| = |B| = k$, write $A \preceq B$ if $A$ has elements $a_1 < \cdots < a_k$ and $B$ has elements $b_1 < \cdots < b_k$ and

$$a_i \leq b_i \quad \text{for} \quad 1 \leq i \leq k. \quad (4.3)$$

**Lemma 4.** Let $A, B \subset (0, 1)$ each have $k$ elements, and suppose $A \preceq B$. Then $A' \preceq B'$ in each of the two cases:
(a) $A' = A \cup \{w\}$ and $B' = B \cup \{w\}$, where $w \in (0, 1)$ and $w \notin A \cup B$.

(b) $k \geq 2$, $A'$ is obtained by deleting any element of $A$ and $B'$ is obtained by deleting the smallest element of $B$.

In particular, $\max(B') \geq \max(A')$.

Proof. For (a), put $a_0 = b_0 = 0$ and $a_{k+1} = b_{k+1} = 1$. Then for some $0 \leq i \leq k$ and $0 \leq j \leq k$, $w \in (a_i, a_{i+1}) \cap (b_j, b_{j+1})$, where necessarily $j \leq i$. Then

$$a'_\ell = \begin{cases} a_\ell & \text{if } \ell \leq i, \\ w & \text{if } \ell = i + 1, \\ b'_\ell - 1 & \text{if } \ell \geq i + 2, \end{cases}$$

$$b'_\ell = \begin{cases} b_\ell & \text{if } \ell \leq j, \\ w & \text{if } \ell = j + 1, \\ a_{\ell - 1} & \text{if } \ell \geq j + 2. \end{cases}$$

It is easy to check that $a'_\ell \leq b'_\ell$ for all $\ell$.

For (b), if $a_i$ is the element deleted from $A$, then $a'_\ell = a_\ell$ if $\ell < i$ and $a'_\ell = a_{\ell + 1}$ if $\ell > i$, while $b'_\ell = b_{\ell + 1}$ for $\ell \geq 2$. Again, it is easy to check that $a'_\ell \leq b'_\ell$ for each $\ell$. \qed

Fix $0 < r < 1$. To be very clear about the coupling we need we note that our system can be constructed from (i) the birth-death process $X_t$, $t \geq 0$, (ii) an iid sequence of uniform $(0, 1)$ random variables $v_n$, $n \geq 0$, (iii) a sequence of iid mean $r$ Bernoulli random variables $\varepsilon_n$, $n \geq 0$, and (iv) independent random variables $W^n_k$, $n, k \geq 1$, $P(W^n_k = j) = 1/k$ for $1 \leq j \leq k$. When $X_t$ makes its $n$th transition up the uniform variable $v_n$ is added to the current set of types. If $X_t$ makes it’s $n$th transition down, and there are $k$ types before the transition, the least fit type is deleted if $\varepsilon_n = 0$ while if $\varepsilon_n = 1$ and $W^n_k = j$ then the $j$th largest type is deleted. This gives a construction of a set of types at time $t, F^r(t) = \{f_1(t), \ldots, f_{X_t(t)}(t)\}$, with $\phi'_t = \max(F^r(t))$.

Using the same collection of variables we may construct a second set of types $F^1(t) = \{f^1_1(t), \ldots, f^1_{X_t(t)}(t)\}$ as follows. Put $F^1(0) = F^r(0)$, so certainly $F^1(0) \leq F^r(0)$. Now suppose $F^1(t) \leq F^r(t)$ and the elements of each set are put in increasing order. If a jump up occurs for the birth process, and $w$ is the value of the uniform random variable added to $F^r(t)$ is also added to $F^1(t)$, preserving the $\leq$ relationship by Lemma 4. If a jump down occurs, and the appropriate $\varepsilon_n = 1$ and $W^n_k = j$, the $j$th largest element of each set is deleted. If $\varepsilon_n = 0$, the $j$ largest element of $F^1(t)$ is still deleted, while the smallest element of $F^r(t)$ is deleted. Again by Lemma 4, the $\leq$ relationship is preserved. Furthermore, this gives a construction of the fitness process when $r = 1$, i.e., the law of $\max\{F^1(t)\}, t \geq 0$ is the same as that of $\phi'_t, t \geq 0$.

This gives a construction with $\phi'_t \geq \phi^1_t, t \geq 0$. In view of (4.2) this proves $\phi'_t \to_p 1$ as $t \to \infty$.

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