Fixation Probability for Competing
Selective Sweeps

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Abstract: We consider a biological population in which a beneficial mutation is undergoing a selective sweep when a second beneficial mutation arises at a linked locus and we investigate the probability that both mutations will eventually fix in the population. Previous work has dealt with the case where the second mutation to arise confers a smaller benefit than the first. In that case population size plays almost no role. Here we consider the opposite case and observe that, by contrast, the probability of both mutations fixing can be heavily dependent on population size. Indeed the key parameter is $\rho N$, the product of the population size and the recombination rate between the two selected loci. If $\rho N$ is small, the probability that both mutations fix can be reduced through interference to almost zero while for large $\rho N$ the mutations barely influence one another. The main rigorous result is a method for calculating the fixation probability of a double mutant in the large population limit.

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1. Introduction

Natural populations incorporate beneficial mutations through a combination of chance and the action of natural selection. The process whereby a beneficial mutation arises (in what is generally assumed to be a large and otherwise neutral population) and eventually spreads to the entire population is called a selective sweep. When beneficial mutations are rare, we can make the simplifying assumption that selective sweeps do not overlap. A great deal is known about such isolated selective sweeps (see e.g. Chapter 5 of Ewens 1979). Haldane (1927) showed that under a discrete generation haploid model, the probability that a beneficial allele with selective advantage $\sigma$ eventually fixes in a population of size $2N$, i.e. its frequency increases from $1/(2N)$ to 1, is approximately $2\sigma$. Much less is understood when selective sweeps overlap, i.e. when further beneficial mutations arise at different loci during the timecourse of a sweep.

Our aim here is to investigate the impact of the resulting interference in the case when two sweeps overlap. In particular, we shall investigate the probability that both beneficial mutations eventually become fixed in the population. Because genes are organised on chromosomes and chromosomes are in turn grouped

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into individuals, different genetic loci do not evolve independently of one another. However, in a dioecious population (in which chromosomes are carried in pairs), nor are chromosomes passed down as intact units. A given chromosome is inherited from one of the two parents, but recombination or crossover events can result in the allelic types at two distinct loci being inherited one from each of the corresponding pair of chromosomes in the parent. We refer to these chromosomes as ‘individuals’.

Each individual in the population will have a type denoted $ij$ where $i, j \in \{0, 1\}$. We use the first and second digit, respectively, to indicate whether the individual carries the more recent or the older beneficial mutation, and assume that the fitness effects of these two mutations are additive. Suppose that a single advantageous allele with selective advantage $\sigma_1$ arises in an otherwise neutral (type 00) population of size $2N$, corresponding to a diploid population of size $N$. We use $X_{ij}$ to denote the proportion of individuals of type $ij$, then the frequency of the favoured allele, $X_{01}$, will be well-approximated by the solution to the stochastic differential equation

$$dX_{01} = \sigma_1 X_{01} (1 - X_{01}) \, ds + \sqrt{\frac{1}{2N} X_{01} (1 - X_{01})} \, dW(s), \quad (1.1)$$

where $s$ is the time variable, $\{W(s)\}_{s \geq 0}$ is a standard Wiener process, and $X_{01}(0) = 1/(2N)$ (Ethier & Kurtz 1986, Eq. 10.2.7). If the favoured allele reaches frequency $p$, then the probability that it ultimately fixes is

$$1 - e^{-2N \sigma_1 p},$$

If a sweep does take place then (conditioning on fixation) we obtain

$$d\tilde{X}_{01} = \sigma_1 \tilde{X}_{01} (1 - \tilde{X}_{01}) \coth(N \sigma_1 \tilde{X}_{01}) \, ds + \sqrt{\frac{1}{2N} \tilde{X}_{01} (1 - \tilde{X}_{01})} \, dW(s)$$

and from this it is easy to calculate the expected duration of the sweep. Writing $\tilde{T}_{fix} = \inf\{ s \geq 0 : \tilde{X}_{01}(s) = 1 \mid \tilde{X}_{01}(0) = 1/(2N)\}$, we have (see for example Etheridge et al. 2006)

$$E[\tilde{T}_{fix}] = \frac{2}{\sigma_1} \log(2N \sigma_1) + O\left(\frac{1}{\sigma_1}\right) \quad (1.2)$$

and the variance $\text{var}[\tilde{T}_{fix}]$ is $O(1/\sigma_1^2)$. More generally, an analogous Green function calculation to that leading to equation (1.2) gives that the expected time for the selected locus to reach frequency $\epsilon(N)$ is $\log(2N \epsilon(1) \sigma_1) + O(1/\sigma_1)$. This is the same as the expected time for $X_{01}$ to increase from $1 - \epsilon(N)$ to 1. On the other hand, for $\delta = O(1)$, the time for $X_{01}$ to increase from $\delta$ to $1 - \delta$ is $O(1/\sigma_1)$. As a result, for large populations, during almost all the timecourse of the sweep $\tilde{X}_{01}$ is either close to zero or close to one.

Now suppose that during the selective sweep of type 01 described by (1.1), more specifically, when $X_{01}$ reaches a level $U$, another beneficial mutation with
selection coefficient $\sigma_2$ occurs at a second linked locus in a randomly chosen individual, and the recombination rate between these two loci is $\rho$. If we assume that the arrival time of the second mutation is uniformly distributed over the timecourse of the sweep of the first mutation and that $N$ is large, then we can expect either $U$ or $1 - U$ to be close to 0 but $\gg 1/(2N)$. The new mutation can arise in a type 00 or 01 individual, forming a single type 10 individual in the former case, and a 11 individual in the latter case. If the second mutation arises during the first half (in terms of time) of the sweep of the first mutation, then $U$ is likely to be very small and it is more likely for a type 10 individual to be formed. Otherwise, the second mutation arises during the second half of the sweep and the formation of a type 11 individual is more likely.

The case of the second beneficial mutation forming a type 11 individual is relatively straightforward. Since type 11 is fitter than all other types, its fixation is almost certain once it becomes ‘established’ in the population, i.e. when the number of type 11 individuals is much larger than 1. If the population size is very large, then it only takes a short time to determine whether type 11 establishes itself, and we can assume the proportion of type 01 individuals remains roughly constant during this time. Hence the fixation probability of type 11 is essentially its establishment probability, which is approximately $2(\sigma_2 + \sigma_1 (1 - U))$, twice the ‘effective’ selective advantage of type 11 in a population consisting of $2NU$ type 01 and $2N(1 - U)$ type 00 individuals.

The case of the second beneficial mutation forming a type 10 individual is far more interesting. In order for both mutations to sweep through the population, recombination must produce an individual carrying both mutations. The relative strength of selection acting on the two loci now becomes important. The case of $\sigma_1 > \sigma_2$ has been dealt with in Barton (1995) and Otto & Barton (1997). Here, since type 01 is already present in significant numbers when the new mutation arises (and type 01 is fitter than type 10), the trajectory of $X_{01}$ is well approximated by the logistic growth curve $1/(1 + \exp(-\sigma_1 t))$ until $X_{11}$ reaches a level of $O(1)$. At that point, fixation of type 11 is all but certain. Barton (1995) then uses a branching process approximation to estimate the establishment probability of a type 11 individual produced by recombination. In particular, his approach is independent of population size. Not surprisingly, he finds that the fixation probability of the second mutation is reduced if it arises as a type 10 individual, but increased if it arises as a type 11 individual. Simulation studies performed in Otto & Barton (1997) confirm these findings in the case $\sigma_1 > \sigma_2$.

Gillespie (2001) considers the effects of repeated substitutions at a strongly selected locus on a completely linked (i.e. there is no recombination) weakly selected locus, extending his work in Gillespie (2000), where he considers a linked neutral locus. He too sees little dependence of his results on population size, leading him to suggest repeated genetic hitchhiking events as an explanation for the apparent insensitivity of the genetic diversity of a population to its size. Kim (2006) extends the work of Gillespie (2001) by considering the effect of repeated sweeps on a tightly (but not completely) linked locus. This whole body of work is concerned, in our terminology, with $\sigma_1 > \sigma_2$. 
The case of $\sigma_2 > \sigma_1$ brings quite a different picture. The analysis used in Barton (1995) breaks down for the following reason: because the second beneficial mutation is more competitive than the first, type 10 is destined to start a sweep itself if it gets established in the population. Once $X_{10}$ reaches $O(1)$, $X_{01}$ is no longer well approximated by a logistic growth curve and in fact will decrease to 0. The fixation probability of type 11 will then depend on the non-linear interaction of all four types, \{11, 10, 01, 00\}, and our analysis will show that it is heavily dependent on population size. See Figure 1 below.

\begin{figure}[h]
\centering
\includegraphics[width=0.5\textwidth]{fixation_probability}
\caption{Simulation results for fixation probability of type 11 for the following initial condition: the second mutation arises in a type 00 individual, when $(2N)^{0.7}$ individuals in the population has the first mutation (i.e. are of type 01). Vertical bars denote two standard deviations. Parameter values: $\sigma_1 = 0.012$, $\sigma_2 = 0.02$, $\rho = 4 \times 10^{-5}$ (recombination coefficient).}
\end{figure}

This paper is organized as follows. In §2.1 we set up a continuous time Moran model for the evolution of our population. In the biological literature, it would be more usual to consider a Wright-Fisher model, in which the population evolves in discrete, non-overlapping generations. The choice of a Moran model, in which generations overlap, is a matter of mathematical convenience. One expects similar results for a Wright-Fisher model. The choice of a discrete individual based model rather than a diffusion is forced upon us by our method of proof, but is anyway natural in a setting where population size plays a rôle in the results. A brief analysis of our model, for very large $N$, leads to our main rigorous result, Theorem 2.3, which provides a method to calculate the asymptotic ($N \to \infty$) fixation probability of type 11 when $\sigma_2 > \sigma_1$. We discuss the case of moderate $N$ in §2.3. The rest of the paper is devoted to proofs, with §3 containing the proof of Theorem 2.3 and §4 containing the proof of Proposition 3.1. Results in §4 rely on supporting lemmas of §5.
2. Main Results

2.1. A Moran Model for Two Competing Selective Sweeps

In this section we describe our model for the evolution of two competing selective sweeps. We use the notation from the introduction for the four possible types of individual in the population \( I = \{00, 10, 01, 11\} \), and assume that at the time when the second mutation arises, the number \( U \in \{0, 1, \ldots, 2N\} \) of type 01 individuals in the population is known. From now on we use \( t = 0 \) to denote the time when the second mutation arises. As explained in §1, we may assume that \( U \) is much larger than 1.

Let \( \sigma \in [0, 1] \) be the selective advantage of the second beneficial mutation and \( \sigma \gamma \) be the selective advantage of the first beneficial mutation (for some \( \gamma > 0 \)). The recombination rate between the two selected loci is denoted by \( \rho \) which we assume to be \( o(1) \). We use \( \{(\eta_n\zeta_n), n = 1, \ldots, 2N\} \) to denote the types of individuals in the population. At time \( t = 0 \), we assume that the population of \( 2N \) individuals consists of \( 2N - U - 1 \) type 00 individuals, \( U \) type 01 individuals and 1 type 10 individual. The dynamics of the model are as follows:

1. **Recombination:** Each ordered pair of individuals, \( (\eta_m\zeta_m) \) and \( (\eta_n\zeta_n) \in I \), is chosen at rate \( \rho/(2N) \). With probability \( 1/2 \), \( (\eta_m\zeta_m) \) replaces \( (\eta_n\zeta_n) \). Otherwise, \( (\eta_n\zeta_n) \) replaces \( (\eta_m\zeta_m) \).

2. **Resampling (and selection):** Each ordered pair of individuals, \( (\eta_m\zeta_m) \) and \( (\eta_n\zeta_n) \in I \), is chosen at rate \( 1/(2N) \). With probability \( p(\eta_m\zeta_m, \eta_n\zeta_n) \) given by

\[
p(ij, kl) := \frac{1}{2}(1 + \sigma(i - k) + \sigma\gamma(j - l)),
\]

a type \( (\eta_m\zeta_m) \) individual replaces \( (\eta_n\zeta_n) \). Otherwise a type \( (\eta_n\zeta_n) \) individual replaces \( (\eta_m\zeta_m) \).

**Remark 2.1.** Evidently we must assume \( \sigma(1 + \gamma) \leq 1 \) to ensure that all probabilities used in the definition of the model are in \([0, 1]\).

**Remark 2.2.** If \( \rho \) and \( \sigma \) are small, then decoupling recombination from the rest of the reproduction process does not affect the behaviour of the model a great deal and it will simplify analysis.

Let \( \mathbb{P} \) denote the law of this Moran particle system, and \( r_{10}^+ \) and \( r_{10}^- \) be the rates at which \( X_{1j} \) increases and decreases by \( 1/(2N) \), respectively, then

\[
\begin{align*}
\quad r_{10}^+ &= N\left(X_{10}(1 + \sigma)(1 - X_{10}) - (1 + \gamma)X_{11} - \sigma\gamma X_{01}\right) \\
&
+ \rho N\left(2X_{11}X_{00} + X_{10}X_{11} + X_{10}X_{00}\right)
\end{align*}
\]

\[
\begin{align*}
\quad r_{10}^- &= N\left(X_{10}(1 - \sigma)(1 - X_{10}) + (1 + \gamma)X_{11} + \sigma\gamma X_{01}\right) \\
&
+ \rho N\left(X_{10}(X_{00} + 2X_{01} + X_{11})\right)
\end{align*}
\]
\[ r_{01}^+ = NX_{01}[(1 + \sigma \gamma)(1 - X_{01}) - \sigma(1 + \gamma)X_{11} - \sigma X_{10}] + \rho N(X_{00}X_{01} + X_{11}X_{01} + 2X_{11}X_{00}) \]
\[ r_{01}^- = NX_{01}[(1 - \sigma \gamma)(1 - X_{01}) + \sigma(1 + \gamma)X_{11} + \sigma X_{10}] + \rho N(X_{01}X_{00} + 2X_{10} + X_{11}) \]
\[ r_{11}^+ = NX_{11}[(1 + \sigma(1 + \gamma))(1 - X_{11}) - \sigma X_{10} - \sigma \gamma X_{01}] + \rho N(2X_{10}X_{01} + X_{10}X_{11} + X_{01}X_{11}) \]
\[ r_{11}^- = NX_{11}[(1 - \sigma(1 + \gamma))(1 - X_{11}) + \sigma X_{10} + \sigma \gamma X_{01}] + \rho N(2X_{01}X_{00} + X_{01} + X_{10}) \]
\[ r_{00}^+ = NX_{00}[1 - X_{00} - \sigma(1 + \gamma)X_{11} - \sigma X_{10} - \sigma \gamma X_{01}] + \rho N(X_{01}X_{00} + X_{00}X_{10} + 2X_{01}X_{10}) \]
\[ r_{00}^- = NX_{00}[1 - X_{00} + \sigma(1 + \gamma)X_{11} + \sigma X_{10} + \sigma \gamma X_{01}] + \rho N X_{00}(X_{01} + 2X_{11} + X_{10}). \] (2.1)

2.2. Analysis and Results for Large N

We are concerned primarily with the case of very large population sizes, which is the regime where our main rigorous result, Theorem 2.3, operates. A non-rigorous analysis for moderate population sizes based on very similar ideas is also possible but will appear in Yu & Etheridge (2008).

To motivate our result, we present a heuristic analysis of the possible scenarios. The proof of our main result will fill in the necessary steps to make this rigorous. If the second beneficial mutation gives rise to a single type 10 individual, then the process whereby type 11 becomes fixed must proceed in three stages and our approach is to estimate the probability of each of these hurdles being overcome. First, following the appearance of the new mutant, \( X_{10} \) must ‘become established’, by which we mean achieve appreciable frequency in the population. Without this, there will be no chance of step two: recombination of a type 01 and a type 10 individual to produce a type 11. Finally, type 11 must become established (after which its ultimate fixation is essentially certain). Of course this may not happen the first time a new recombinant is produced. If type 11 becomes extinct and neither \( X_{01} \) nor \( X_{10} \) is one, then we can go back to step two.

We assume the first mutation has been undergoing a selective sweep prior to the arrival of the second mutation. Before the arrival of the second beneficial mutation (during which \( X_{10} \) and \( X_{11} \) are both 0), we can write

\[ X_{01}(s) = \frac{1}{2N} + M_{01}(s) + \int_0^s \sigma \gamma X_{01}(u)(1 - X_{01}(u)) \, du, \]

where \( M_{01} \) is a martingale with maximum jump size \( 1/(2N) \) and quadratic variation \( \langle M_{01} \rangle(s) = \frac{1}{2N^2} \int_0^s X_{01}(u)^2(1 - X_{01}(u)) \, du \). i.e. \( \langle M_{01} \rangle \) is the unique previsible process such that \( M_{01}(s)^2 - M_{01}(0)^2 - \langle M_{01} \rangle(s) \) is a martingale. See e.g. § II.3.9 of Ikeda & Watanabe (1981). We drop the martingale term \( M_{01} \) and
approximate the trajectory of $X_{01}$ using a logistic growth curve, i.e. $X_{01}(s) \approx 1/(1 + (2N - 1)\exp(-\sigma\gamma s))$ which solves $\frac{dX_{01}}{ds} = \sigma\gamma X_{01}(s)(1 - X_{01}(s))$ and $X_{01}(0) = 1/(2N)$. As discussed in §1, if we assume that the arrival time of the second mutation is uniformly distributed on the timecourse of the sweep of the first and $N$ is large, then $X_{01}$ spends most of the time near 0 or near 1.

We divide into two cases.

1. The second mutation arises during the first half of the sweep of the first mutation, i.e. when $X_{01} < 1/2$.
2. The second mutation arises during the second half of the sweep of the first mutation, i.e. when $X_{01} \geq 1/2$.

In Case 2, $X_{01}$ is close to 1 and it is most likely that the second mutation arises in a type 01 individual to form a single type 11 individual, in which case the fixation probability is roughly the same as the establishment probability of type 11 arising in a population consisting entirely of type 01 individuals, which in turn is roughly $2\sigma/(1 + \sigma)$.

From now on, we focus on the more interesting Case 1. In what follows, $t = 0$ will be the time of arrival of the second beneficial mutation. There it is most likely that the second mutation arises in a type 00 individual resulting in a single type 10 individual in the population. If we approximate the growth of $X_{01}$ by a logistic growth curve, then it reaches $1/2$ at time $\frac{1}{\sigma\gamma} \log(2N - 1) \approx \frac{1}{\sigma\gamma} \log(2N)$. Choosing the time of the introduction of the new mutation uniformly on $[0, \frac{1}{\sigma\gamma} \log(2N)]$ we see that at $t = 0$, $X_{01} \approx (2N)^{-\zeta}$, where $\zeta \sim Unif[0, 1]$.

The establishment probability for type 10 in this case is relatively easy to estimate. Since $\sigma_2 > \sigma_1$, type 10 either dies out becomes established before $X_{01}$ can grow to be a significant proportion of the population. Therefore the establishment probability of type 10 is almost the same as a type 10 arising in a population consisting entirely of type 00 individuals, roughly $2\sigma/(1 + \sigma)$.

We observe that if type 11 does get established, then since it has fitness advantage over all other types, the probability that it eventually fixes is very close 1 (this follows from Lemma 3.2). Therefore we can concentrate on the behaviour of $X$ before $X_{11}$ reaches say $(\log(2N))/(2N)$, which is still very small compared to 1. After type 10 is established and prior to type 11 being established, we approximate $X_{10}$ and $X_{01}$ deterministically. Until either $X_{10}$ or $X_{01}$ is $O(1)$, both grow roughly exponentially, so assuming that type 10 gets established, we have

$$X_{10}(t) \approx \frac{1}{2N} e^{\sigma t}, \quad X_{01}(t) \approx \frac{1}{(2N)^{\zeta}} e^{\sigma\gamma t}. \quad (2.2)$$

We divide Case 1 further into two sub-cases. See Figure 2 for an illustration.

Case 1a, $\zeta < \gamma$. The approximation (2.2) fails once either $X_{10}$ or $X_{01}$ reaches $O(1)$, which occurs at time $\frac{1}{\sigma\gamma} \log(2N) \land \frac{\zeta}{\sigma\gamma} \log(2N)$. If $\zeta < \gamma$, then $X_{01}$ reaches $O(1)$ before $X_{10}$, and will further increase to almost 1 (which takes time only $O(1)$) before $X_{10}$ reaches $O(1)$. At this time, which we denote $T_1$, the population
Case 1a: $\zeta = 0.3$, $\gamma = 0.6$. In Case 1a, $X_{01}$ reaches almost 1 before being displaced by $X_{10}$, but in Case 1b, $X_{01}$ never reaches $O(1)$.

Case 1b, $\zeta > \gamma$. In this case, $X_{10}$ reaches $O(1)$ at time roughly $\frac{1}{\gamma} \log(2N)$, before $X_{01}$ does, and $X_{01}$ is $O((2N)^{\gamma^{-\zeta}})$ at this time. Furthermore, the biggest $X_{01}$ can get is $O((2N)^{\gamma^{-\zeta}})$ since $X_{10}$ will very soon afterwards increase to almost 1, after which $X_{01}$ will exponentially decrease (since type 01 is less fit than type 10). Hence we expect $O(\rho N^{1+\gamma^{-\zeta}})$ recombination events between type 10 and type 01, and the 'correct' scaling for $\rho$ is $\rho = O(N^{\zeta-\gamma-1})$ in this case.

In case 1a, we take $\rho = O(1/N)$, then most of the recombination events between type 10 and type 01 individuals occur when type 10 islogistically displacing type 01, i.e. in the time interval $[T_1, T_2]$. During this time, we can approximate $X_{10}$ and $X_{01}$ by $Z_{10}$ and $1 - Z_{10}$, respectively, where $Z_{10}$ is deterministic and obeys the logistical growth equation with parameter $\sigma(1 - \gamma)$, twice the advantage of type 10 over type 01. We can further approximate $X_{11}$

Fig 2. Approximate trajectories of $X_{01}$ (solid line) and $X_{10}$ (dashed line) when $X_{11}$ is small: these curves are obtained assuming they undergo deterministic logistic growth with initial condition $X_{10}(0) = (2N)^{-1}$ and $X_{01}(0) = (2N)^{-\zeta}$. Parameter values: $\sigma = 0.02, (2N) = 10^8$. In Case 1a, $X_{01}$ reaches almost 1 before being displaced by $X_{10}$, but in Case 1b, $X_{01}$ never reaches $O(1)$. 
by a birth and death process \( Z_{11} \) with deterministic but time-varying rates that depend on \( Z_{10} \). Specifically, the rates of increase and decrease for \( Z_{11} \) are the same as \( r_{11}^{+} \) in (2.1), but with \( X_{10} \) replaced by \( Z_{10} \), \( X_{01} \) replaced by \( 1 - Z_{10} \) and \( X_{11} \) replaced by 0.

The probability that \( X_{11} \) gets established, i.e. reaches

\[
\delta_{11} = \frac{[\log(2N)]}{(2N)},
\]

is then approximated by the probability that the birth and death process \( Z_{11} \) reaches \( \delta_{11} \). The latter can be found by solving the forward equation for the process \( Z_{11} \), which can be found in (3.3). We define the fixation time of the Moran particle system of §2.1:

\[
T_{fix} = \inf\{ t \geq 0 : X_{ij}(t) = 1 \text{ for some } ij \in I \}.
\]

We observe that the Markov chain \( (X_{00}, X_{01}, X_{10}) \) has finitely many states and the recurrent states are \( R = \{(0,0,0),(0,0,1),(0,1,0),(1,0,0)\} \). Every other state is transient and there is positive probability of reaching \( R \) starting from any transient state in finite time. Therefore

\[
T_{fix} < \infty \text{ a.s.}
\]

Our main result, Theorem 2.3 below, concerns Case 1a, which is the most likely scenario if \( \gamma \) is close to 1.

**Theorem 2.3.** If \( \zeta < \gamma < 1 \) and \( \rho = \mathcal{O}(1/N) \), then there exists \( \delta > 0 \), whose value depends on \( \rho \), \( \sigma \), \( \gamma \), and \( \zeta \), such that

\[
\left| \text{P}(X_{11}(T_{fix}) = 1) - \frac{2\sigma}{1+\sigma}p_{\delta_{11}}^{(11)}(T_{\infty}) \right| \leq N^{-\delta}
\]

for sufficiently large \( N \), where \( p_{\delta_{11}}^{(11)}(t) \) solves the forward equation (3.3).

In the above, \( \frac{2\sigma}{1+\sigma} \) corresponds to the establishment probability of type 10, while \( p_{\delta_{11}}^{(11)}(T_{\infty}) \) approximates the establishment probability of type 11 conditioning on type 10 becoming established. Figure 3 compares fixation probabilities obtained from simulation, our non-rigorous calculation (which we briefly discuss in §2.3 below), and the large population limit of Theorem 2.3. In Figure 3(a) we hold \( \rho N \) constant in this simulation, and observe that the fixation probability of type 11 increases but does not change drastically as \( N \) becomes large. The reason for the drop in the fixation probability of type 11 when \( N \) is small may be because in this case, the early phase for \( X_{01} \) is very short and hence grows quickly to reduce the establishment probability of type 10. In Figure 3(a), we use a population size of \( 2N = 50,000 \) to approach the large population limit of Theorem 2.3. At \( 2N = 50,000 \), it takes roughly 12 hours on a PC to obtain one data point in Figure 3, which is run with 20,000 realisations. Apparently this population size still results in underestimates of the limiting large population limit.
exponential distribution with mean $1 + X$.

trajectory of large population limit of Theorem \ref{thm:large}, with $p(2N) = 0.2$.

We take $\sigma X = \frac{1}{2}(1 + \sigma + \rho)s^2 + \frac{1}{2}(1 - \sigma + \rho) - (1 + \rho)s$. Using Theorem III.8.3 of Athreya & Ney (1972), we can calculate $E[e^{-\gamma W}]$ for $W = \lim_{t \to \infty} e^{-\sigma t}Z(t)$ and conclude that $W$ is distributed according to $\frac{1 - \sigma + \rho}{1 + \sigma + \rho} \delta_0(x) + \exp(\frac{1 - \sigma + \rho}{1 + \sigma + \rho} x)$ for $x \geq 0$. Hence the conditional distribution function of $X_{10}(t_1) | X_{10}(t_1) > 0$ resembles $\text{Exp}(\frac{1 - \sigma + \rho}{2\sigma} (2N)^{-\epsilon})$, an exponential distribution with mean $\frac{1 + \sigma + \rho}{2\sigma} (2N)^{-\epsilon}$, as $N \to \infty$.

From time $t_1$ onwards, until either $X_{10}$ gets very close to 0 or $X_{10}$ becomes much smaller than $O((2N)^{(1-\epsilon)\gamma-\zeta})$, we can assume that the paths of $X_{10}$ and $X_{10}$ resemble those of $Z_{01}$ and $Z_{10}$, respectively, where

\begin{align*}
\frac{dZ_{10}}{dt} &= Z_{10}[(1 + \sigma)(1 - Z_{10}) - \sigma \gamma Z_{01}] dt \\
\frac{dZ_{01}}{dt} &= Z_{01}[(1 + \sigma \gamma)(1 - Z_{01}) - \sigma Z_{10}] dt
\end{align*}

with the initial condition $Z_{10}(t_1)$ drawn according to $\text{Exp}(\frac{1 + \sigma + \rho}{2\sigma} (2N)^{-\epsilon})$ and
3 PROOF OF THE MAIN THEOREM

As in Case 1a, we can then approximate $X_{11}$ by a birth and death process $Z_{11}$ with rates the same as $r_{11}^\pm$ from (2.1) but with $X_{10}$ replaced by $Z_{10}$ and $X_{01}$ replaced by $Z_{01}$. The probability that $Z_{11}$ reaches $\delta_{11}$ can then be found by solving the forward equation for $Z_{11}$. Finally, we integrate this probability against all initial conditions for $Z_{10}$, drawn according to $\text{Exp}(1 + \sigma + \rho (2N)^{-\epsilon})$. The proof of such a result is more tedious than that of Theorem 2.3 but makes use of similar ideas.

2.3. Brief Comment on Moderate $N$

For moderate population sizes, the observation in Case 1a of §2.2 that $X_{01}$ increases to close to 1 before $X_{10}$ reaches $O(1)$ breaks down. We can, however, compute the distribution function $f_{T_{10;\delta_{10}}}$ of the random time $T_{10;\delta_{10}}$ when $X_{10}$ hits a certain level $\delta_{10}$, assuming that $X_{01}$ grow logistically before $T_{10;\delta_{10}}$. From $T_{10;\delta_{10}}$ onwards and before $X_{11}$ hits $\delta_{11}$, $X_{10}$ grows roughly deterministically, displacing both type 10 and type 00, so we can approximate $X_{11}$ by $Z_{11}$, a birth and death process with time-varying jump rates in the form of $r_{11}^\pm$ in (2.1), but with $X_{10}$, $X_{01}$ and $X_{00}$ replaced by their deterministic approximations. Assuming $T_{10;\delta_{10}} = t$, we can numerically solve the forward equation for $Z_{11}$, which is directly analogous to (3.3), to find the probability that $Z_{11}$ eventually hits $\delta_{11}$, which we denote by $p_{\text{est}}^{(11)}(t)$. The dependence of $p_{\text{est}}^{(11)}$ on $t$ comes through the initial condition $X_{01}$ for the ODE system, which depends on $T_{10;\delta_{10}}$. The fixation probability of type 11 is then approximately $\int p_{\text{est}}^{(11)}(t)f_{T_{10}}(t)\,dt$. This is the algorithm we use to produce the solid line in Figure 3(a) and is given in its full detail in Yu & Etheridge (2008).

3. Proof of the Main Theorem

We first define some of the functions, events, and stochastic processes needed for the proof, then give some intuition, before we proceed with the proof of Theorem 2.3. We begin by describing a deterministic process $Y_{10}$ and a birth and death process $Y_{11}(t)$ which, up to a shift by a random time, are $Z_{10}$ and $Z_{11}$ described in §2.2, respectively. They approximate the trajectories of $X_{10}$ and $X_{11}$, respectively, after the establishment of type 10. To describe the (time-inhomogeneous) rates we need the solution

$$L(t; y_0, \theta) = \left[ 1 + \left( \frac{1}{y_0} - 1 \right) e^{-\theta t} \right]^{-1}$$

(3.1)

to the logistic growth equation $L(t; y_0, \theta) = y_0 + \theta \int_0^t L(s; y_0, \theta)(1 - L(s; y_0, \theta))\,ds$. In what follows, $a_0 = \zeta/(3\gamma)$ is a constant, $c_1$, $c_2$, $c_3$ are constants (slightly
smaller than $O(1)$) that we specify precisely in Proposition 3.1, and

$$ t_0 = \frac{a_0}{\sigma} \log(2N), \quad t_{\text{early}} = \frac{1.01 \log(2N)}{\sigma(1 - \gamma) - \rho}, \quad (3.2) $$

$$ t_{\text{mid}} = \frac{1}{\sigma(1 - \gamma)} \log \frac{1 - c_1}{c_1}, \quad t_{\text{late}} = \frac{1.02 \log(2N)}{\sigma \gamma}. $$

These deterministic times roughly correspond to the lengths of the ‘stochastic’, ‘early’ (an upper bound), ‘middle’, and ‘late’ phases of $X_{01}$, whose rôle is described in more detail in §4. During the time interval when $Y_{10}$ is between $c_1$ and $1 - c_1$, whose length is exactly $t_{\text{mid}}$, there are birth events of $Z_{11}$ corresponding roughly to recombination events between type 10 and 01 individuals. For $t \in [0, t_{\text{mid}})$, we define

$$ Y_{10}(t) = L(t; c_1, \sigma(1 - \gamma)) $$

$$ \beta^+(z, t) = Nz[(1 + \sigma(1 + \gamma))(1 - z) - (\sigma - \rho)Y_{10}(t) - (\sigma \gamma - \rho)(1 - Y_{10}(t))] $$

$$ + 2\rho NY_{10}(t)(1 - Y_{10}(t)) $$

$$ \beta^-(z, t) = Nz[(1 - \sigma(1 + \gamma) + 2\rho)(1 - z) + (\sigma - \rho)Y_{10}(t) $$

$$ + (\sigma \gamma - \rho)(1 - Y_{10}(t))], $$

and for $t \geq t_{\text{mid}}$, we define

$$ Y_{10}(t) = 1 $$

$$ \beta^+(z, t) = N(1 + \sigma \gamma + \rho)z(1 - z) $$

$$ \beta^-(z, t) = N(1 - \sigma \gamma + \rho)z(1 - z). $$

We then take $Y_{11}$ to be a birth and death process with birth and death rates $\beta^+(Y_{11}, t)$ and $\beta^-(Y_{11}, t)$, respectively (i.e. $Y_{11}$ jumps by $\pm 1/(2N)$ at rates $\beta^+(Y_{11}, t)$ and $\beta^+(Y_{11}, t)$, respectively), and initial condition $Y_{11}(0) = 0$. It is absorbed on hitting $\delta_{11}$.

It is convenient to write $k_- = k - 1/(2N)$ and $k_+ = k + 1/(2N)$. $Y_{11}$ is run until time $t_{\text{mid}} + t_{\text{late}}$. The probability that $Y_{11}$ hits $\delta_{11}$ before then can be found by solving a system of ODE’s. Let $p^{(11)}$ satisfy

$$ \frac{d}{dt}p_{k_{-}}^{(11)}(t) = \beta^+(k_-, t)p_{k_-}^{(11)}(t) + \beta^-(k_+, t)p_{k_+}^{(11)}(t) - (\beta^+(k, t) + \beta^-(k, t))p_{k}^{(11)}(t) $$

for $k = 1/(2N), \ldots, \delta_{11}_{-}$ where $\delta_{11}_{-} = \delta_{11} - 1/(2N)$, and

$$ \frac{d}{dt}p_{0}^{(11)}(t) = \beta^-(1/(2N), t)p_{1/(2N)}^{(11)}(t) - \beta^+(0, t)p_{0}^{(11)}(t) $$

$$ \frac{d}{dt}p_{\delta_{11}}^{(11)}(t) = \beta^+(\delta_{11}_{-}, t)p_{\delta_{11}_{-}}^{(11)}(t) - \beta^-(\delta_{11}, t)p_{\delta_{11}}^{(11)}(t) $$

(3.3)

with initial condition $p_{k}^{(11)}(0) = 1_{\{k = 0\}}$. Then

$$ \mathbb{P}(Y_{11} \text{ hits } \delta_{11} \text{ before } t_{\text{mid}} + t_{\text{late}}) = p_{\delta_{11}}^{(11)}(t_{\text{mid}} + t_{\text{late}}). $$

(3.4)
3 PROOF OF THE MAIN THEOREM

We use the following convention for stopping times:

\[ T_{ij,x} = \inf\{t \geq 0 : X_{ij} \geq x\}, \quad T_{Z:x} = \inf\{t \geq 0 : Z \geq x\} \quad (3.5) \]

\[ S_{Y,Z,diff} = \inf\{t \geq 0 : Y(t) \neq Z(t)\} \]

for any \( ij \in \{00, 01, 10, 11\} \) and processes \( Y \) and \( Z \), and define stopping times

\[ T_\infty = T_{10,c_1} + t_{mid} + t_{late}, \]

\[ S_{10,01,rec} = \inf\{t \geq 0 : \text{there is a recombination event between a type 10 and a type 01 individual before time } t\}. \]

We define events

\[ E_1 = \{X_{10}(t_0) > 0\} \]

\[ E_2 = \{T_{10,c_1} \leq T_{11;1/(2N)} \wedge (t_0 + t_{early})\} \cap \{X_{01}(T_{10,c_1}) \geq 1 - c_1 - c_2\} \]

\[ E_3 = \{|X_{10}(t) - Z_{10}(t)| \leq c_3 \text{ and } X_{00}(t) \leq \sqrt{c_1} \text{ for all } t \in [T_{10,c_1}, T_{10;1-c_1} \wedge T_{11;1}]\} \]

\[ E_4 = \{T_{10;1-c_1} \leq T_{11;\delta_{11}}\} \]

\[ E_5 = \{X_{11}(t) + X_{10}(t) > 1 - \sqrt{c_1} \text{ for all } t \geq T_{10;1-c_1}\} \]

\[ E_6 = \{X_{11}(T_\infty) + X_{10}(T_\infty) = 1\} \]

\[ E_7 = \{X_{11}(t) = Z_{11}(t) \text{ for all } t \in [T_{10,c_1}, T_\infty \wedge T_{11;\delta_{11}}]\} \]

\[ E_8 = \{T_{11;\delta_{11}} \leq T_\infty \text{ or } X_{11}(T_\infty) = Z_{11}(T_\infty) = 0\}. \]

We observe that \( T_{11;1/(2N)} \geq S_{10,01,rec} \). First we outline the intuition behind these definitions: \( t_0 \) is the length of the initial ‘stochastic’ phase for \( X_{10} \). At \( t_0 \), with high probability \( X_{10} \) either is \( O((2N)^{\alpha_0 - 1}) \) or has hit 0 (event \( E_1 \)). In the latter case, there is no need to approximate \( X_{10} \) any further. On the other hand, if \( E_3 \) occurs, then type 10 is very likely to be established by \( t_0 \) and, with high probability, grows almost deterministically to reach level \( c_1 \) (slightly smaller than \( O(1) \)) at time \( T_{10,c_1} \). Furthermore, as discussed in §1, in Case 1a, since \( \zeta < \gamma \), with high probability \( X_{01}(T_{10,c_1}) \) is close to 1. Hence conditional on \( E_1 \), the event \( E_2 \) is very likely.

For paths in \( E_2 \cap E_1 \), we define

\[ Z_{10}(T_{10,c_1} + t) = Y_{10}(t), \quad Z_{11}(T_{10,c_1} + t) = Y_{11}(t) \quad (3.6) \]

to be the approximations for the trajectories of \( X_{10} \) and \( X_{11} \), respectively, from time \( T_{10,c_1} \) onwards. For convenience, we define \( Z_{10}(t) = Z_{11}(t) = 0 \) for \( t \leq T_{10,c_1} \). With the convention of (3.5),

\[ T_{Z_{10;1-c_1}} = T_{10,c_1} + t_{mid}, \]

and we observe that \( Z_{10}(t) = 1 \) for \( t \geq T_{Z_{10;1-c_1}} \). Since \( X_{01}(T_{10,c_1}) \approx 1 \), \( X_{00}(T_{10,c_1}) \) is very small and is unlikely to recover because type 00 is the least fit type. During \( [T_{10,c_1}, T_{Z_{10;1-c_1}}] \), with high probability, type 10 grows logistically at rate \( \sigma(1 - \gamma) \), displacing type 01. Hence conditional on \( E_1 \cap E_2, E_3 \)
is very likely. During $[T_{10;c_1}, T_{10;1−c_1}]$, the definition of $Z_{11}$ takes into account recombination events between type 01 and 10 individuals that produce type 11 individuals at a rate of $\rho (2N)X_{01}X_{10}$, which in the definition of $X_{11}$, is approximated by $\rho (2N)Z_{10}(1 − Z_{10})$. Notice that we can approximate $X_{01}$ by $1 − Z_{10}$ since we assume throughout that $X_{11} ≤ \delta_{11}$, which is very small. Outside the time interval $[T_{10;c_1}, T_{10;1−c_1}]$, either $X_{10}$ is very small or very close to 1 (which means $X_{01}$ is very small), hence we ignore any recombination events. Because $Z_{11}$ closely approximates $X_{11}$, conditional on $E_3 \cap E_2 \cap E_1$, event $E_7$ has a high probability.

After $T_{Z_{10};1−c_1}$, $X_{11} + X_{10}$ is likely to remain close to 1 (event $E_5$) and hit 1 at time $T_\infty$ (event $E_6$). We ignore any more recombination events between type 10 and 01 and $Z_{11}$ is a time-changed branching process during this time. If $Z_{11}$ has not hit $\delta_{11}$ by time $T_{Z_{10};1−c_1}$ (event $E_4$), then we continue to keep track of $Z_{11}$ until $T_\infty$, at which time it most likely has already hit either $\delta_{11}$ or 0 (event $E_8$). In the latter case, we regard type 11 as having failed to establish and since $X_{10}$ is most likely to be 1 (event $E_6$) at $T_\infty$, the earlier mutation has gone extinct. If $X_{11}$ hits $\delta_{11}$ before $T_\infty$, we regard type 11 as having established and hence it will, with high probability, eventually sweep to fixation (Lemma 3.2).

Proposition 3.1 below estimates the probabilities of events $E_1$ through $E_8$. These are ‘good’ events, on which we can approximate the establishment probability of type 11 by the probability that $Z_{11}$ hits $\delta_{11}$ by time $T_\infty$. Proposition 3.1 is essential for the proof of Theorem 2.3, and will be proved in §4.

**Proposition 3.1.** There exist positive constants $\delta_{10,3}$ and $\delta_{10,4} > 0$ whose exact value depends on $\sigma$, $\gamma$ and $\zeta$, such that $c_1, c_2, c_3$ in the definition of $E_1, \ldots, E_8$ are all $\leq N^{-\delta_{10,3}}$ and for sufficiently large $N$,

\[
\begin{align*}
(a) & \quad P(E_1^c) - \frac{1 - \sigma + \rho}{1 + \sigma + \rho} \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}} \\
(b) & \quad P(E_2^c \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}} \\
(c) & \quad P(E_3^c \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}} \\
(d) & \quad P(E_4^c \cap E_2 \cap E_3 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}} \\
(e) & \quad P(E_5^c \cap E_2 \cap E_3 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}}.
\end{align*}
\]

Consequently, we have (f) $P(E_6^c \cap E_4 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,3}}$. Furthermore,

\[
\begin{align*}
(g) & \quad P(E_7^c \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma}(N^{-\delta_{10,3}} + N^{-\delta_{10,4}}) \\
(h) & \quad P(E_8^c \cap E_7 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma} N^{-\delta_{10,4}}.
\end{align*}
\]

**Lemma 3.2.** \(|P(X_{11}(T_{f_1}) \neq 1) − P(T_{11;\delta_{11}} < \infty)| \leq N^{\log \frac{1 - \sigma + 2\rho}{1 + \sigma + \rho}} .
\]

**Proof.** On $\{T_{11;\delta_{11}} < \infty\}$, $X_{11}$ dominates $\tilde{X}_{11}$, a birth and death process with initial condition $\tilde{X}_{11}(T_{11;\delta_{11}}) = \delta_{11} = [\log(2N)]/(2N)$, jump size $1/(2N)$, and the following jump rates

\[
\tilde{r}_{11}^+ = N(1 + \sigma \gamma)\tilde{X}_{11}(1 - \tilde{X}_{11}), \quad \tilde{r}_{11}^- = N(1 - \sigma \gamma + 2\rho)\tilde{X}_{11}(1 - \tilde{X}_{11}).
\]
3 PROOF OF THE MAIN THEOREM

Using standard Markov chain techniques, we may conclude
\[ \mathbb{P}(\{T_{X_{11}:1} > T_{X_{11}:0}, T_{11;\delta_{11}} < \infty\}) \leq (2N)^{\log \frac{1-a_0+2\rho}{1+\rho}} , \]
which implies \( \mathbb{P}(\{X_{11}(T_{fix}) \neq 1, T_{11;\delta_{11}} < \infty\}) \leq (2N)^{\log \frac{1-a_0+2\rho}{1+\rho}}. \) Since \( \{X_{11}(T_{fix}) = 1, T_{11;\delta_{11}} = \infty\} \) is a set with probability 0, we have the desired result. \( \square \)

Proof of Theorem 2.3. Recall from (3.2) that \( a_0 = \zeta/(3\gamma) \) and \( t_0 = \frac{a_0}{\rho} \log(2N) \).
We first show that we can safely ignore \( E_1 \). Let
\[ E_0 = \{X_{11}(t) = 0 \text{ for all } t \leq t_0\} . \]
Comparing with (2.1), we see that the jump process \( \hat{X}_{10} \) with initial condition \( \hat{X}_{10}(0) = 1/(2N) \), jump size 1/(2N), and the following jump rates
\[ \hat{r}_{10}^+ = N(1+\sigma)\hat{X}_{10} + 3\rho N, \hat{r}_{10}^- = N(1-\sigma)\hat{X}_{10} \]
dominates \( X_{10} \) for all time. Then
\[ d\hat{X}_{10} = dM + (\sigma\hat{X}_{10} + 1.5\rho) \, dt \]
where \( M \) is a martingale with maximum jump size 1/(2N) and quadratic variation \( \langle M \rangle \) satisfying \( d\langle M \rangle = \frac{1}{2N}(2\hat{X}_{10} + 3\rho) \, dt \). Hence
\[ E[\hat{X}_{10}(t)] = \left( \frac{1}{2N} + \frac{3\rho}{2\sigma} \right) e^{\sigma t} - \frac{3\rho}{2\sigma} \leq \left( \frac{1}{2N} + \frac{3\rho}{2\sigma} \right) e^{\sigma t} ; \]
We recall Burkholder’s inequality in the following form:
\[ E \left[ \sup_{s \leq t} |M(s)|^p \right] \leq C_p \mathbb{E} \left[ \langle M \rangle(t)^{p/2} + \sup_{s \leq t} |M(s) - M(s-)|^p \right] , \]
which may be derived from its discrete time version, Theorem 21.1 of Burkholder (1973).
We use this and Jensen’s inequality to obtain
\[ E \left[ \sup_{s \leq t} |M(s)| \right] \leq E \left[ \sup_{s \leq t} |M(s)|^2 \right]^{1/2} \leq \frac{C}{N} \left( 1 + N \int_0^{t_0} E[\hat{X}_{10}(s) + 1.5\rho] \, ds \right)^{1/2} \]
\[ \leq \frac{C}{N} + \frac{C\sigma}{\sqrt{N}} (\rho t_0 + (N^{-1} + \rho)e^{\sigma t_0})^{1/2} \leq C_{p,\sigma} N^{(a_0/2)-1} . \quad (3.7) \]
Therefore
\[ E \left[ \sup_{s \leq t} \hat{X}_{10}(s) \right] \leq E \left[ \sup_{s \leq t} |M(s)| \right] + 1.5\rho t_0 + \sigma \int_0^{t_0} E[\hat{X}_{10}(s)] \, ds \leq C_{p,\sigma} N^{a_0-1} . \]
Since \( \hat{X}_{10} \) dominates \( X_{10} \), we have
\[ \mathbb{P} \left( \sup_{s \leq t_0} X_{10}(s) \geq (2N)^{2a_0-1} \right) \leq C_{p,\sigma} N^{-a_0} . \]
On \( \{ \sup_{s \leq t_0} X_{10}(s) < (2N)^{2\alpha_0-1} \} \), the number of recombination events between type 10 and 01 during \([0, t_0] \) is at most \( \text{Poisson}(2\rho(2N)^{2\alpha_0-1}t_0) \), hence
\[
\mathbb{P}(E_8^c \cap E_1) \leq \mathbb{P}(E_0^c) \leq C_{\rho, \sigma}(N^{-\alpha_0} + N^{(2\alpha_0-1)/2})
\]
for sufficiently large \( N \). On \( E_0 \cap E_1^c \), type 10 has gone extinct by time \( t_0 \), before a single individual of type 11 has been born, hence type 11 will not get established, let alone fix. Therefore
\[
\mathbb{P}(\{ T_{11; \delta_{11}} < \infty \} \cap E_1) \leq \mathbb{P}(E_0^c \cap E_1^c) \leq C_{\rho, \sigma}(N^{-\alpha_0} + N^{(2\alpha_0-1)/2}). \tag{3.8}
\]

Now we concentrate on \( E_1 \) where type 10 has most likely established itself at time \( t_0 \). The nontrivial event here is \( E_8 \cap E_7 \cap E_2 \cap E_1 \). Let \( E_{81} = \{ T_{11; \delta_{11}} \leq T_\infty \} \) and \( E_{82} = \{ T_{11; \delta_{11}} > T_\infty, X_{11}(T_\infty) = Z_{11}(T_\infty) = 0 \} \), then \( E_8 = E_{81} \cup E_{82} \). The following events have small probabilities
\[
\mathbb{P}(E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma}N^{-\delta_{10.3}}, \\
\mathbb{P}(E_8 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma}(N^{-\delta_{10.3}} + N^{-\delta_{10.4}}), \\
\mathbb{P}(E_8 \cap E_7 \cap E_6 \cap E_2 \cap E_1) \leq C_{\rho, \gamma, \sigma}N^{-\delta_{10.3}}, \tag{3.9}
\]
by Prop 3.1(b), Prop 3.1(g-h), and Prop 3.1(f), respectively, where the last estimate above comes from the fact \( E_{82} \subset E_4 \). There are two events with significant probabilities: on \( E_{82} \cap E_7 \cap E_6 \cap E_2 \cap E_1 \), we have \( X_{11}(T_\infty) = 0, X_{10}(T_\infty) = 1 \) hence type 10 fixes by time \( T_\infty \), and on \( E_{81} \cap E_7 \cap E_2 \cap E_1 \), \( X_{11} = Z_{11} \) hits \( \delta_{11} \) and get established by time \( T_\infty \). On both these events, \( X_{11} = Z_{11} \) until at least \( T_\infty \cap T_{11; \delta_{11}} \). The union of these two events, \( E_{82} \cap E_7 \cap E_6 \cap E_2 \cap E_1 \) and \( E_{81} \cap E_7 \cap E_2 \cap E_1 \), and the three events in \( (3.9) \) is \( E_1 \). On \( E_1 \cap E_2 \), for exactly one of the two events \( \{ T_{11; \delta_{11}} < \infty \} \) and \( \{ T_{Z_{11}; \delta_{11}} \leq T_\infty \} \) to occur (i.e. either the former occurs but the latter does not, or the latter occurs and the former does not), one of the following three scenarios must occur:

1. \( X_{11} \) and \( Z_{11} \) disagree before \( T_\infty \), i.e. \( E_7^c \);
2. \( X_{11} \) and \( Z_{11} \) agree up to \( T_\infty \), but do not hit \( \{ 0, \delta_{11} \} \) before \( T_\infty \), i.e. \( E_8^c \);
3. \( X_{11} \) and \( Z_{11} \) agree up to \( T_\infty \) and \( X_{11}(T_\infty) = 1 \) thus allowing the possibility of type 11 being born due to recombination between type 10 and 01 individuals after \( T_\infty \), i.e. \( E_6^c \).

Hence
\[
\left| \mathbb{P}(\{ T_{11; \delta_{11}} < \infty \} \cap E_1) - \mathbb{P}(\{ T_{Z_{11}; \delta_{11}} \leq T_\infty \} \cap E_1) \right| \\
\leq \mathbb{P}(E_2^c \cap E_1) + \mathbb{P}(E_6^c \cap E_7^c \cap E_2 \cap E_1) + \mathbb{P}(E_{82} \cap E_7 \cap E_6 \cap E_2 \cap E_1) \\
\leq C_{\rho, \gamma, \sigma}(N^{-\delta_{10.3}} + N^{-\delta_{10.4}})
\]
by \( (3.9) \). From \( (3.8) \), we have
\[
\left| \mathbb{P}(T_{11; \delta_{11}} < \infty) - \mathbb{P}(\{ T_{11; \delta_{11}} < \infty \} \cap E_1) \right| \\
= \mathbb{P}(\{ T_{11; \delta_{11}} < \infty \} \cap E_1^c) \leq C_{\rho, \sigma}N^{-\alpha_0} + N^{(2\alpha_0-1)/2}
\]
4 PROOF OF PROPOSITION 3.1

But by Proposition 3.1(a),
\[ \left| \mathbb{P}(E_1) - \frac{2\sigma}{1 + \sigma} \right| \leq C_{\rho,\gamma,\sigma} N^{-\delta_{10.3}}. \]

We combine the three inequalities above to conclude
\[
\begin{align*}
&\left| \mathbb{P}(T_{11;\delta_{11}} < \infty) - \frac{2\sigma}{1 + \sigma} \mathbb{P}(T_{Z_{11};\delta_{11}} \leq T_{\infty}|E_1) \right| \\
&\leq \left| \mathbb{P}(T_{11;\delta_{11}} < \infty) - \mathbb{P}(T_{Z_{11};\delta_{11}} \leq T_{\infty}|E_1) \mathbb{P}(E_1) \right| + C_{\rho,\gamma,\sigma} N^{-\delta_{10.3}} \\
&= \left| \mathbb{P}(T_{11;\delta_{11}} < \infty) - \mathbb{P}(\{T_{Z_{11};\delta_{11}} \leq T_{\infty}\} \cap E_1) \right| + C_{\rho,\gamma,\sigma} N^{-\delta_{10.3}} \\
&\leq N^{-\delta}
\end{align*}
\]

for some \( \delta > 0 \), and then use Lemma 3.2, as well as (3.4) and (3.6) to obtain the desired conclusion. \( \square \)

4. Proof of Proposition 3.1

We divide the evolution of \( X_{10} \) and \( X_{01} \) roughly into 4 phases, ‘stochastic’, ‘early’, ‘middle’, and ‘late’, and use Lemmas 5.1, 5.2, and 5.3 for each of the last 3 phases, respectively. Lemma 4.1 deals with the early, middle, and late phases of \( X_{01} \). Because \( X_{01} \) starts at \( U = (2N)^{-\zeta} \gg 1/(2N) \) at \( t = 0 \), it has no stochastic phase. Its early phase is between \( t = 0 \) and the time when \( X_{01} \) reaches \( c_{10.1} \). Its middle phase is between \( c_{10.1} \) and \( 1 - c_{10.2} \), after which it enters the late phase.

For type 10, since \( X_{10}(0) = 1/(2N) \), whether it establishes itself is genuinely stochastic (i.e. its probability tends to a positive constant strictly less than 1 as \( N \to \infty \)). The stochastic phase lasts for time \( t_0 \), when, with high probability, either type 10 has established or it has gone extinct. If \( X_{10} \) reaches \( O((2N)^{a_{n-1}}) \) by time \( t_0 \), it enters the early phase, which is dealt with by Lemma 4.2. Part (b) of that lemma says that if \( \zeta < \gamma \) (as mentioned before, we only deal Case 1a of §1) then it does not reach \( c_{10.2} \) until \( X_{01} \) has entered its late phase, while part (c) says that it does reach \( c_{10.3} \) at some finite time. The proof of Proposition 3.1(a-b) reconciles various stopping times used in Lemmas 4.1 and 4.2, and prepares for part (c) of Proposition 3.1, which deals with the middle phase of \( X_{10} \) during which \( X_{10} \) increases from \( c_{10.3} \) to \( 1 - c_{10.3} \), displacing \( X_{01} \) in the process. The \( c_{ij,k} \)'s we use throughout the rest of this paper are small positive constants, all of \( O((2N)^{-b_{0,1}+}) \), whose exact values are specified immediately below (4.2).

Recall the definition of the logistic growth curve \( L(t; y_0, \theta) \) from (3.1). Throughout the rest of this section, We use \( L(t; (2N)^{-\zeta}, \sigma\gamma) \) to approximate the trajectory of \( X_{10} \) during its early phase and \( t_{01;x} \) to denote the time when this approximation hits \( x \), e.g. \( t_{01;x_{01.1}} \) below is when it hits \( c_{01.1} \). Furthermore, we use \( t_{01,x,y} \) to denote the time this approximation spends between \( x \) and \( y \). Thus
\[ L(t_{01;x}; (2N)^{-\zeta}, \sigma\gamma) = x \] and \[ L(t_{01,x,y}; x, \sigma\gamma) = y. \]
We also define

$$t'_{01;1-c_{01.2}} = t_{01;1-c_{01.1}} + t_{01.0.9c_{01.1},1-c_{01.2}}.$$ 

In the above, $t_{01.0.9c_{01.1},1-c_{01.2}}$ is the length of time for which we use the event $A_2$ in Lemma 4.1 below. On the event $A_1$ defined in that lemma, $X_{01}$ reaches 0.9$c_{01.1}$ at time $t_{01;1-c_{01.1}}$, after which event $A_2$ ensures $X_{01}$ grows to levels slightly smaller than 1 - $c_{01.2}$ after another time period of length $t_{01.0.9c_{01.1},1-c_{01.2}}$. Roughly speaking, the time when $L(\cdot; (2N)^{-\zeta}, \sigma\gamma)$ is between 0.9$c_{01.1}$ and $c_{01.1}$ is counted twice. We observe that

$$t_{01;1-c_{01.1}} = \frac{1}{\sigma\gamma} \log \left( \frac{(2N)^{\zeta} - 1}{c_{01.1}} - 1 \right)$$

$$t'_{01;1-c_{01.2}} = t_{01;1-c_{01.2}} + t_{01.0.9c_{01.1},1-c_{01.1}}$$

$$= \frac{1}{\sigma\gamma} \left\{ \log \left[ \left( (2N)^{\zeta} - 1 \right) \left( \frac{1}{c_{01.2}} - 1 \right) \right] + \log \frac{1}{c_{01.1}} - 1 \right\}. \tag{4.1}$$

We recall that $a_0 = \frac{\zeta}{\gamma}$ and define the constants required for the rest of the proof, as well as $c_1$, $c_2$, and $c_3$ as required by Proposition 3.1:

$$a_1 = \frac{\zeta}{4\gamma} \wedge \frac{1 - \zeta/\gamma}{4},$$

$$b_{10.0} = a_0 + a_1 - 1, \quad b_{10.2} = \frac{1 - \zeta/\gamma}{2}, \quad b_{10.3} = \frac{\gamma b_{10.2}}{90},$$

$$b_{01.0} = \frac{\zeta}{3}, \quad b_{01.1} = b_{01.2} = \frac{\gamma b_{10.2}}{3},$$

$$\delta_{01.1} = \frac{\gamma b_{10.2}}{9} \leq \frac{\gamma}{3} (b_{10.2} - b_{01.1} - b_{01.2}), \quad \delta_{10.2} = \frac{\delta_{01.1}}{60} = \frac{\gamma b_{10.2}}{540},$$

$$\delta_{10.0} = 2Nc_{10.0}(c_{10.0} + c_{01.0}), \quad \delta_{10.1} = (a_0 - a_1)/4, \quad c_1 = c_{10.3}, \quad c_2 = (2N)^{-\delta_{10.1}/2}, \quad c_3 = (2N)^{-\delta_{10.2}} \tag{4.2}$$

and $c_{ij,k} = (2N)^{-b_{ij,k}}$. These choices imply $a_1 + b_{10.2} + b_{01.2}/\gamma < 1 - \zeta/\gamma$, which in turn implies the following:

$$(1 - a_1) \log(2N) + \log c_{10.2} + \frac{1}{\gamma} \log c_{01.2} > \frac{1}{\gamma} \log((2N)^{\zeta} - 1),$$

$$\log((2N)^{1-a_1} - (2N)^{a_0}) - \log \left( \frac{1}{0.9c_{10.2}} - 1 \right) - \frac{1}{\gamma} \log \left( \frac{1}{c_{01.2}} - 1 \right)$$

$$> \frac{1}{\gamma} \log((2N)^{\zeta} - 1) + \frac{1}{\gamma} \log \frac{1}{0.9},$$

$$\log((2N)^{1-a_1} - (2N)^{a_0}) - \log \left( \frac{1}{0.9c_{10.2}} - 1 \right)$$

$$\geq \frac{1}{\gamma} \left\{ \log \left[ \left( (2N)^{\zeta} - 1 \right) \left( \frac{1}{c_{01.2}} - 1 \right) \right] + \log \frac{1}{0.9c_{01.1}} - 1 \right\} = \sigma t'_{01;1-c_{01.2}} \tag{4.3}$$

for sufficiently large $N$. This will be needed in Lemma 4.2.
Lemma 4.1. Let \( R_{01} = T_{11;1 /(2N)} \wedge T_{10;c_{10},2} \). We define

\[
\begin{align*}
A_1 & = \{ X_{01}(s) \leq 0.9L(s; (2N)^{-\zeta}, \sigma) \text{ for some } s \leq t_{01;c_{01},1} \wedge R_{01} \} \\
A_2 & = \{ X_{01}(s) < L(s - t_{01;c_{01},1}; 0.9c_{01,1}, \sigma) + (2N)^{-\delta_{01,1}} \text{ for some } s \in [t_{01;c_{01},1}, t_{01;c_{01},1} - \epsilon_{01,2} \wedge R_{01}] \} \\
A_3 & = \{ X_{10}(s) + X_{01}(s) \leq 1 - (2N)^{-\delta_{01,1}/2} \text{ for some } s \in [t'_{01;1-c_{01,2}}, S_{10,01,rec}] \}.
\end{align*}
\]

Then

\[
\begin{align*}
(a) & \quad \mathbb{P}(A_1) \leq C_{\rho, \gamma, \sigma} N^{-(1-\zeta)/4} \\
(b) & \quad \mathbb{P}(A_2 \cap \{ t'_{01;1-c_{01,1}} \leq R_{01} \}) \leq (2N)^{-\delta_{01,1}} \\
(c) & \quad \mathbb{P}(A_3 \cap A_2 \cap A_2 \cap \{ t'_{01;1-c_{01,2}} \leq R_{01} \}) \leq CN^{-1/2}.
\end{align*}
\]

Consequently,

\[
\mathbb{P}( (A_3 \cup A_2 \cup A_1) \cap \{ t'_{01;1-c_{01,2}} \leq R_{01} \} ) \leq C_{\rho, \gamma, \sigma} (2N)^{-\delta_{01,1}}.
\]

Proof. Early Phase. Before the stopping time \( R_{01} \), the jump rates of \( X_{01} \) satisfies

\[
\begin{align*}
r_{01}^+ & \geq NX_{01}[(1 + \sigma \gamma + \rho)(1 - X_{01}) - 1.1\sigma c_{10,2}], \\
r_{01}^- & \leq NX_{01}[(1 - \sigma \gamma + \rho)(1 - X_{01}) + 1.1\sigma c_{10,2}].
\end{align*}
\]

We take \( \xi = X_{01}, \alpha = 1 + \rho, \beta = \sigma \gamma, \delta_0 = 1.1\sigma c_{10,2}, \delta_1 = c_{01,1}, \delta_2 = (1 - \zeta)/4, \)
\( Y \) such that \( Y(t) = (2N)^{-\zeta} + \int_0^t Y(s)(\sigma \gamma(1 - Y(s)) - 1.1\sigma c_{10,2}) ds, \) and \( u_0 = \inf \{ t : Y(t) = \delta_1 \} > t_{01;c_{01},1} \) in Lemma 5.1 to obtain

\[
\mathbb{P}(X_{01}(s) < 0.99Y(s) \text{ for some } s \leq t_{01;c_{01},1} \wedge R_{01} \) \leq C_{\rho, \gamma, \sigma} N^{-(1-\zeta)/4}.
\]

Prior to \( u_0, Y \) is sandwiched between \( L(\cdot; (2N)^{-\zeta}, \sigma \gamma - 1.2\sigma c_{10,2}) \) and \( L(\cdot; (2N)^{-\zeta}, \sigma \gamma) \).

Since \( L(t; (2N)^{-\zeta}, \sigma \gamma) - L(t; (2N)^{-\zeta}, \sigma \gamma - v) \leq (1 - e^{-v})L(t; (2N)^{-\zeta}, \sigma \gamma) \) for \( v \leq \sigma \gamma, \) we have

\[
\begin{align*}
Y(t) & \geq L(t; (2N)^{-\zeta}, \sigma \gamma - 1.2\sigma c_{10,2}) \geq e^{-1.2\sigma c_{10,2}t}L(t; (2N)^{-\zeta}, \sigma \gamma) \\
& \geq 0.99L(t; (2N)^{-\zeta}, \sigma \gamma)
\end{align*}
\]

for \( t = O(\log N). \) Hence (a) follows.

Middle Phase. Before \( R_{01}, X_{11} = 0. \) Using the jump rates of \( X_{01} \) in (2.1), we can write

\[
X_{01}(t \wedge R_{01}) = b_0 + M_{01}(t \wedge R_{01}) \\
+ \int_{u_1}^{t \wedge R_{01}} X_{01}(s)[\sigma \gamma(1 - X_{01}(s)) - (\sigma + \rho)X_{10}(s)] ds,
\]

\[
X_{10}(s) + X_{01}(s) \leq 1 - (2N)^{-\delta_{01,1}/2} \text{ for some } s \in [t'_{01;1-c_{01,2}}, S_{10,01,rec}].
\]
where $M_{01}(\cdot \land R_{01})$ is a martingale with maximum jump size $1/(2N)$ and quadratic variation $\langle M_{01}(\cdot \land R_{01}) \rangle(t \land R_{01}) = \int_{0}^{t} \frac{1}{2} \rho_{1,1} \rho_{1,1} X_{01}(s)(1 - X_{01}(s)) \, ds$. We apply Lemma 5.2 with $b_0 = X_{01}(t_{01;c_{01,1}})$, $u_1 = t_{01;c_{01,1}}$, $u_2 = t_{01;1-c_{01,2}}$, $\delta_1 = b_{10,2}$, $\delta_2 = \infty$, $c_0 = b_{01,1}$, $c_1 = b_{01,2}$, $c_3(t) = c_4(t) = 0$, $T = R_{01}$ and $D_1 = A_{t}^{c}$. Then since $b_{10,2} > (b_{01,1} + b_{01,2}) \land \frac{1}{2}$, we have

$$\mathbb{P}(\{ |X_{01}(s) - L(s - t_{01;1-c_{01,1}}; X_{01}(t_{01;1-c_{01,1}}), \sigma \gamma) | > (2N)^{-\delta_{01,1}} \text{ for some} \quad s \in [t_{01;1-c_{01,2}} \land R_{01}] \cap A_{t}^{c} \cap \{ t_{01;1-c_{01,1}} \leq R_{01} \} ) \leq (2N)^{-\delta_{01,1}},$$

where $\delta_{01,1}$ is defined in (4.2). Now for paths in $A_{t}^{c} \cap \{ t_{01;1-c_{01,1}} \leq R_{01} \}$, we have $X_{01}(t_{01;1-c_{01,1}}) \geq 0.9c_{01,1}$ and hence

$$L(s - t_{01;1-c_{01,1}}; X_{01}(t_{01;1-c_{01,1}}), \sigma \gamma) \geq L(s - t_{01;1-c_{01,1}}; 0.9c_{01,1}, \sigma \gamma).$$

The desired conclusion in (b) follows. **Late Phase.** On $A_{t}^{c} \cap A_{t} \cap \{ t_{01;1-c_{01,2}} \leq R_{01} \}$, since $\delta_{01,1} \leq b_{01,2}$, we have

$$X_{01}(t_{01;1-c_{01,2}}) > L(t_{01;1-c_{01,2}} - t_{01;1-c_{01,1}}; 0.9c_{01,1}, \sigma \gamma) - (2N)^{-\delta_{01,1}} > 1 - c_{01,2} - (2N)^{-\delta_{01,1}}.$$

Therefore $X_{00}(t_{01;1-c_{01,2}}) < 2(2N)^{-\delta_{01,1}}$. Before $S_{10,0,1,c_{10,1}}$, $X_{11} = 0$, and the jump rates of $X_{00}$ satisfy

$$r_{00}^+ \leq N(1 - \sigma + \rho)X_{00}(1 - X_{00}), \quad r_{00}^- \geq N(1 + \sigma + \rho)X_{00}(1 - X_{00}).$$

By Lemma 5.3, $\mathbb{P}(\{ \sup_{t \geq t_{01;1-c_{01,2}}} X_{00}(t) \leq N^{-\delta_{01,1}/2} \} \cap A_{t}^{c} \cap A_{t} \cap \{ t_{01;1-c_{01,2}} \leq R_{01} \}) \leq CN^{-1/2}$, which implies the desired conclusion in (c). □

For the remainder of this section, we define the following events

$$A_{41} = \{ X_{10}(s) \geq (2N)^{a_0 + a_1 - 1} \text{ for some } s \leq t_0 \land T_{01;c_{01,0}} \land T_{11;1/(2N)} \},$$

$$A_{42} = \{ X_{10}(t_0) \in [1, (2N)^{a_0 - a_1 - 1}] \},$$

$$A_4 = A_{41} \cup A_{42} \cup E_{t}^{c},$$

$$B_4 = \{ t_0 \leq T_{01;c_{01,0}} \land T_{11;1/(2N)} \},$$

$$A_{51} = \{ X_{10}(s) \geq c_{01,2} \text{ for some } s \in [t_0, t_{01;1-c_{01,2}} \land T_{11;1/(2N)}] \},$$

$$A_{52} = \{ T_{10;c_{10,3}} \land T_{11;1/(2N)} \geq t_0 + t_{early} \}.$$

**Lemma 4.2.** Recall that $t_0 = \frac{a_0}{\rho} \log(2N)$, $\delta_{10,0} = 2Nc_{10,0}(c_{10,0} + c_{01,0})$, $\delta_{10,1} = (a_0 - a_1)/4$. We have

(a) $\mathbb{P}(A_{41}) \leq 2\delta_{10,0}t_0 + C_{\rho,\gamma,\sigma}N^{-a_1}$

$$\mathbb{P}(A_{42} \cap A_{51} \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-a_1} + 2\delta_{10,0}t_0$$

$$\left| \mathbb{P}(E_{t}^{c} \cap B_4) - \frac{1 - \sigma + \rho}{1 + \sigma + \rho} \right| \leq 6\delta_{10,0}t_0 + C_{\rho,\gamma,\sigma}N^{-a_1} + \mathbb{P}(B_{t}^{c})$$

(b) $\mathbb{P}(A_{51} \cap A_{52} \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}}$

(c) $\mathbb{P}(A_{52} \cap A_{52} \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}}$. 
Similarly, we can obtain the second statement of (a) and an additional error term. In particular,

\[
\eta \text{ implies the third statement in (a).}
\]

4 PROOF OF PROPOSITION 3.1

**Proof. Stochastic Phase.** We define \( R_{01,11} = T_{01; c_{01,0}} \land T_{11;1/(2N)} \). Before \( T_{11;1/(2N)} \), the jump rates of \( X_{10} \) are as follows:

\[
\begin{align*}
    r_{10}^+ &= NX_{10}(1 + \sigma + \rho)(1 - X_{10}) - (\sigma \gamma + \rho)X_{01}, \\
    r_{10}^- &= NX_{10}(1 - \sigma + \rho)(1 - X_{10}) + (\sigma \gamma + \rho)X_{01}.
\end{align*}
\]

We define \( \eta \) to be a jump process with \( \eta(0) = 1/(2N) \), jump size \( 1/(2N) \) and jump rates as follows:

\[
\begin{align*}
    r_{\eta,10}^+ &= N\eta(1 + \sigma + \rho), \\
    r_{\eta,10}^- &= N\eta(1 - \sigma + \rho).
\end{align*}
\]

then prior to \( S_{X_{10};\eta,\text{diff}} \land T_{10; c_{10,0}} \land R_{01,11} \), we have \( |r_{10}^+ - r_{\eta,10}^+| \leq \delta_{10,0} \) and \( |r_{10}^- - r_{\eta,10}^-| \leq \delta_{10,0} \). Therefore \( |X_{10} - \eta| \) is a jump process with initial value 0, jump size \( 1/(2N) \) and jump rates at most \( 2\delta_{10,0} \), and we can estimate the probability of \( |X_{10} - \eta| \) becoming nonzero before \( t_0 \):

\[
\mathbb{P}\left( S_{X_{10};\eta,\text{diff}} < t_0 \land T_{10; c_{10,0}} \land R_{01,11} \right) \leq 2\delta_{10,0}t_0. \tag{4.4}
\]

Since \( \eta \) is a branching process, Lemma 6.1(a) implies

\[
\begin{align*}
    \mathbb{P}\left( \sup_{s \leq t_0} \eta(s) \geq (2N)^{a_0 + a_1 - 1} \right) &\leq C_{\rho,\gamma,\sigma} N^{-a_1}, \\
    \mathbb{P}\left( 1 \leq \eta(t_0) \leq (2N)^{a_0 - a_1 - 1} \right) &\leq C_{\rho,\gamma,\sigma} N^{-a_1}, \\
    \left| \mathbb{P}(\eta(t_0) = 0) - \frac{1 - \sigma + \rho}{1 + \sigma + \rho} \right| &\leq \frac{1 - \sigma + \rho}{1 + \sigma + \rho} e^{-2\sigma t_0} \leq (2N)^{-a_0}.
\end{align*}
\]

Using (4.4), we can replace \( \eta \) in the above three estimates by \( X_{10} \) if we allow an additional error term. In particular,

\[
\begin{align*}
\mathbb{P}\left( \sup_{s \leq t_0 \land R_{01,11}} X_{10}(s) \geq c_{10,0} = (2N)^{a_0 + a_1 - 1} \right) &= \mathbb{P}\left( \sup_{s \leq t_0 \land R_{01,11}} X_{10}(s) \geq c_{10,0}, S_{X_{10};\eta,\text{diff}} < t_0 \land T_{10; c_{10,0}} \land R_{01,11} \right) \\
&\quad + \mathbb{P}\left( \sup_{s \leq t_0 \land R_{01,11}} X_{10}(s) \geq c_{10,0}, S_{X_{10};\eta,\text{diff}} \geq t_0 \land T_{10; c_{10,0}} \land R_{01,11} \right) \\
&\leq 2\delta_{10,0}t_0 + \mathbb{P}\left( \sup_{s \leq t_0 \land R_{01,11}} \eta(s) \geq c_{10,0} \right) \leq 2\delta_{10,0}t_0 + C_{\rho,\gamma,\sigma} N^{-a_1}.
\end{align*}
\]

Similarly, we can obtain the second statement of (a) and

\[
\left| \mathbb{P}(\{X_{10}(t_0) = 0\} \cap A_{41}^c \cap B_4) - \frac{1 - \sigma + \rho}{1 + \sigma + \rho} \right| \leq 2\delta_{10,0}t_0 + \mathbb{P}(A_{41}) + \mathbb{P}(B_4^c),
\]

which implies the third statement in (a).
Early Phase (Upper Bound). Before \( T_{11;1/(2N)} \), the jump rates of \( X_{10} \) satisfy
\[
\frac{r^+_1}{r^-_1} \leq N(1 + \sigma + \rho)X_{10}(1 - X_{10}), \quad \frac{r^-_1}{r^-_0} \geq N(1 - \sigma + \rho)X_{10}(1 - X_{10}).
\]
We take \( \hat{c} = X_{10}, \alpha = 1 + \rho, \theta = \delta, \delta_0 = 0, \delta_1 = 0.9c_{10,2}, \delta_2 = \delta_{10,1} = (a_0 - a_1)/4, Y(t) = L(t; X_{10}(t_0), 2\sigma) \), and \( u_0 = R_{10} = \inf\{t \geq 0 : L(t; X_{10}(t_0), 2\sigma) \geq \delta_1 \} \) in Lemma 5.1 to obtain
\[
\mathbb{P}(\{X_{10}(t_0 + s) \geq 1.01L(s; X_{10}(t_0), \sigma) \text{ for some } s \geq (R_{10} \wedge T_{11;1/(2N)}) - t_0\}) \cap A^c_1 \cap B_4 \leq C_{\rho,\gamma,\sigma}N^{-1-\zeta}/4.
\]
On \( A^c_1 \cap B_4 \subset \{X_{10}(t_0) \in ((2N)^{a_0-a_1-1}, (2N)^{a_0+a_1-1})\} \), we have
\[
 t_0 + R_{10} \geq \frac{1}{\sigma} \left[ a_0 \log(2N) + \log((2N)^{1-a_0-a_1} - 1) - \log \left( \frac{1}{0.9c_{10,2}} - 1 \right) \right] \\
\geq t'_{01;1-c_{01,2}}
\]
by (4.3) and the definition of \( t'_{01;1-c_{01,2}} \) in (4.1). Hence if
\[
X_{10}(t_0) \in ((2N)^{a_0-a_1-1}, (2N)^{a_0+a_1-1}),
\]
then \( L(t'_{01;1-c_{01,2}} - t_0; X_{10}(t_0), \sigma) \leq L(R_{10}; X_{10}(t_0), \sigma) = 0.9c_{10,2}, \) which implies (b).

Early Phase (Lower Bound). Before \( T_{11;1/(2N)} \), the jump rates of \( X_{10} \) satisfy
\[
\frac{r^-_1}{r^-_0} \geq N(1 + \sigma(1 - \gamma))X_{10}(1 - X_{10}), \quad \frac{r^-_1}{r^-_0} \leq N(1 - \sigma(1 - \gamma) + 2\rho)X_{10}(1 - X_{10}).
\]
We take \( \hat{c} = X_{10} \) shifted forward in time by \( t_0, \alpha = 1 + \rho, \theta = \sigma(1 - \gamma) - \rho, \delta_0 = 0, \delta_1 = 1.01c_{10,3}, \delta_2 = \delta_{10,1} = (a_0 - a_1)/4, Y(t) = L(t; N^{a_0-a_1-1}, \sigma(1 - \gamma) - \rho), \) and \( u_0 = \inf\{t : Y(t) = 1.01c_{10,3}\} \) in Lemma 5.1 to obtain
\[
\mathbb{P}(\{X_{10}(t_0 + s) < 1.005L(s; N^{a_0-a_1-1}, \sigma(1 - \gamma) - \rho) \text{ for some } s \leq u_0 \wedge (T_{11;1/(2N)} - t_0)\}) \cap A^c_1 \cap B_4 \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}}.
\]
Since \( u_0 \leq t_{early} = \frac{1.01}{\sigma(1 - \gamma) - \rho} \log(2N) \), the conclusion in (c) follows. \( \square \)

Proof of Proposition 3.1 (a-b). We define \( t_2 = t_0 + t_{early} \) and
\[
E_{21} = \left\{T_{10;1+c_{10,3}} \leq S_{10,01,rec} \wedge t_2 \right\}, \\
E_{22} = \left\{X_{01}(T_{10;1+c_{10,3}}) \geq 1 - c_{10,3} - (2N)^{-\delta_{10,1}/2} \right\}, \\
F_1 = \left\{S_{10,01,rec} \leq T_{10;1+c_{10,3}} \wedge (t_2 \vee t'_{01;1-c_{01,2}}) \right\},
\]
then \( E_{21} \cap E_{22} \subset E_2 \). Before \( T_{10;1+c_{10,3}} \wedge (t_2 \vee t'_{01;1-c_{01,2}}) \), the rate of recombination events between type 10 and 01 individuals is at most \( 4\rho N X_{10} X_{01} \leq 4\rho N N^{-b_{10,3}} \leq C_{\rho} N^{-b_{10,3}} \). Hence the total number of recombination events between type 10 and 01 individuals before \( T_{10;1+c_{10,3}} \wedge (t_2 \vee t'_{01;1-c_{01,2}}) \) is dominated by a Poisson random variable with mean \( C_{\rho,\gamma,\sigma}N^{-b_{10,3}} \log N \). Therefore
\[
\mathbb{P}(F_1) \leq C_{\rho,\gamma,\sigma}N^{-b_{10,3}/8}.
\]
4 PROOF OF PROPOSITION 3.1

On $F^c_1$, we have $S_{10,01} > T_{10; c_{10}, 3}$ or $S_{10,01} > t_2$. We observe that

$$E_2 \cap F^c_1 = \{T_{10; c_{10}, 3} > S_{10,01} \vee t_2\} \cap \{S_{10,01} > T_{10; c_{10}, 3} \vee t_2\} \subseteq \{S_{10,01} > t_2, T_{10; c_{10}, 3} > t_2\}. \quad (4.6)$$

Therefore Lemma 4.2(c) implies

$$\mathbb{P}(E_2 \cap F^c_1 \cap A^c_\delta \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}}. \quad (4.7)$$

Let $F_4 = \{T_{10; c_{10}, 2} \leq t'_{01;1-c_{01},2} \wedge T_{11;1/(2N)}\}$, then reasoning similar to that of (4.6) implies

$$F^c_2 \cap \{t'_{01;1-c_{01},2} \geq T_{11;1/(2N)} \vee T_{10; c_{10}, 2}\} \subseteq \{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)}\} \cap \{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)}\}.$$

which implies

$$\mathbb{P}(\{t'_{01;1-c_{01},2} \geq T_{11;1/(2N)} \vee T_{10; c_{10}, 2}\} \cap E_2 \cap F^c_1 \cap A^c_\delta \cap B_4) \leq \mathbb{P}(\{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)}\} \cap E_2 \cap F^c_1 \cap A^c_\delta \cap B_4) + \mathbb{P}(F_4 \cap A^c_\delta \cap B_4).$$

The first set on the right hand side satisfies

$$\{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)}\} \cap E_2 \cap F^c_1$$

$$\subseteq \{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)} \vee t_2\} \cap E_2$$

$$\subseteq \{T_{10; c_{10}, 2} \vee t'_{01;1-c_{01},2} \geq T_{11;1/(2N)} \} \cap t_2 \geq T_{10; c_{10}, 3}\} = \emptyset,$$

therefore

$$\mathbb{P}(\{t'_{01;1-c_{01},2} \geq T_{11;1/(2N)} \vee T_{10; c_{10}, 2}\} \cap E_2 \cap F^c_1 \cap A^c_\delta \cap B_4) \leq \mathbb{P}(F_4 \cap A^c_\delta \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}} \quad (4.8)$$

by Lemma 4.2(b). On $\{t'_{01;1-c_{01},2} < T_{11;1/(2N)} \vee T_{10; c_{10}, 2}\}$, we have $T_{10; c_{10}, 3} \geq T_{10; c_{10}, 2} \geq t'_{01;1-c_{01},2}$, therefore Lemma 4.1 implies

$$\mathbb{P}(\{X_{10}(T_{10; c_{10}, 3}) + X_{01}(T_{10; c_{10}, 3}) \leq 1 - (2N)^{-\delta_{11,1}/2}\} \cap \{t'_{01;1-c_{01},2} < T_{11;1/(2N)} \vee T_{10; c_{10}, 2}\} \cap E_2 \cap F^c_1 \cap A^c_\delta \cap B_4) \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,1}}. \quad (4.9)$$

Combining (4.5), (4.7), (4.8), and (4.9) yields

$$\mathbb{P}(E_{22} \cup E^c_{21}) \cap A^c_{41} \cap A^c_{42} \cap B_4 \cap E_1) \leq C_{\rho,\gamma,\sigma}(N^{-\delta_{11,1}} + N^{-\delta_{10,1}} + N^{-\delta_{10,3}/8})$$

where we also recall from Lemma 4.2 that $A^c_\delta = A^c_{41} \cap A^c_{42} \cap E_1$. We further combine the above estimate with the first two statements of Lemma 4.2(a) to obtain

$$\mathbb{P}(E_{22} \cup E^c_{21} \cap B_4 \cap E_1) \leq C_{\rho,\gamma,\sigma}(N^{-\delta_{11,1}} + N^{-\delta_{10,1}} + N^{-\delta_{10,3}/8} + \delta_{10,0} \rho + N^{-a_1}). \quad (4.10)$$
It remains to show that $B^c_2 = \{ t_0 > T_{10;c_{10},3} \lor T_{11;1/(2N)} \}$ has a small probability. Let $F_2 = \{ T_{10;c_{10},3} < t_0 \lor T_{11;1/(2N)} \}$. Before $T_{11;1/(2N)}$, the jump rates of $X_{10}$ satisfy

$$r^+_0 \leq N(1 + \sigma \gamma + \rho)X_{10}(1 - X_{10}), \quad r^-_0 \geq N(1 - \sigma \gamma + \rho)X_{10}(1 - X_{10}).$$

We take $\xi = X_{10}$, $\alpha = 1 + \rho$, $\theta = \sigma \gamma$, $\delta_0 = 0$, $\delta_1 = 0.9c_{10,3}$, $\delta_2 = (1 - 1/\gamma)/4$, and $Y(t) = L(t; (2N)^{-\gamma}, \sigma \gamma)$ in Lemma 5.1 to obtain

$$\mathbb{P}(X_{10}(s) \geq c_{10,0} \text{ for some } s \leq t_{10;0.9c_{10,0}} \land T_{11;1/(2N)}) \leq C_{\rho,\gamma,\sigma}N^{-1-1/\gamma}/4.$$ 

By the choice of $a_0$ in (4.2), $t_0 = \frac{\delta}{\delta_7} \log(2N) = \frac{\delta}{\delta_0} \log(2N)^{1/3} < t_{10;0.9(2N)^{-1/3} = t_{10;0.9c_{10,0}},}$ therefore

$$\mathbb{P}(F_2) \leq \mathbb{P}(T_{10;c_{10},3} \land T_{11;1/(2N)}) \leq C_{\rho,\gamma,\sigma}N^{-1-1/\gamma}/4.$$ 

We observe that $B^c_2 \cap F_2^c \subset \{ t_0 \land T_{10;c_{10},3} > T_{11;1/(2N)} \}$. By an argument similar to the one leading to (4.5), $\mathbb{P}(B^c_2 \cap F_2^c) \leq C_{\rho,\gamma,\sigma}N^{-1-1/\gamma}$, which implies

$$\mathbb{P}(B^c_2) \leq C_{\rho,\gamma,\sigma}(N^{-1-1/\gamma} + N^{-1-1/\gamma}). \quad (4.11)$$

Combining (4.10) and (4.11) yields the desired result in (b). For part (a), we combine the third statement of Lemma 4.2(a) and (4.11) to obtain the desired result.

**Proof of Proposition 3.1(c-e).** Recall that $Z_{10}(T_{10;c_{10},3} + t) = L(t; c_{10,3}, \sigma(1 - \gamma))$ for $t \in [T_{10;c_{10},3}, T_{20:c_{10},3}]$, and $T_{20:c_{10},3} = T_{10;c_{10},3} + \frac{1}{\sigma(1 - \gamma)} \log \frac{1 - c_{10,3}}{c_{10,3}}$. We work on $t \geq T_{10;c_{10},3}$ throughout this proof. On $E_2 \cap E_1$, we have $X_{10}(T_{10;c_{10},3}) \geq 1 - c_{10,3} - (2N)^{-\delta_{11}/2}, X_{10}(T_{10;c_{10},3}) = c_{10,3}$ and $X_{00}(T_{10;c_{10},3}) \leq (2N)^{-\delta_{11}/2}$. We can then write down the following equation using the jump rates of $X_{10}$ in (2.1):

$$X_{10}(t) = c_{10,3} + M_{10}(t) + \int_{T_{10;c_{10},3}}^{t} X_{10}(s)[\sigma(1 - \gamma)(1 - X_{10}(s)) - \sigma X_{11}(s) + \sigma \gamma X_{00}(s)] + \rho(X_{11}(s)X_{00}(s) - X_{10}(s)X_{01}(s)) \, ds,$$

where $M_{10}$ is a martingale with maximum jump size $1/(2N)$ and quadratic variation $\langle M_{10} \rangle(t) = \frac{1}{2N} \int_{T_{00;c_{10},3}}^{t} (1 + \rho)X_{10}(s)(1 - X_{10}(s)) + \rho X_{11}(s)X_{00}(s) \, ds$. We use Lemma 5.2 with $\theta = \sigma(1 - \gamma)$, $u_1 = 0$, $u_2 = \frac{1}{\sigma(1 - \gamma)} \log \frac{1 - c_{10,3}}{c_{10,3}}$, $\delta_1 = \delta_{11}/4$, $\delta_2 = \infty$, $e_0 = e_1 = b_{10,3} = \delta_{11}/10$, $T = T_{11;\delta_{11}} \land T_{00;2N} - \delta_1$, $\epsilon_2(t) = -\sigma X_{11}(t) + \sigma \gamma X_{00}(t)$, $\epsilon_3(t) = \rho(X_{11}(t)X_{00}(t) - X_{10}(t)X_{10}(t))$, $\epsilon_4(t) = X_{11}(t)X_{00}(t)$, $Y(t) = Z_{10}(T_{10;c_{10},3} + t)$, and $D_1 = E_2 \cap E_1$ to obtain

$$\mathbb{P}(|X_{10}(s, \omega) - Z_{10}(s, \omega)| > (2N)^{-\delta_{10}} \text{ for some } \omega \in E_2 \cap E_1, \quad (4.12)$$

such that

$$s \in [T_{10;c_{10},3}, T_{Z_{10;1-c_{10},3}} \land T_{11;\delta_{11}} \land T_{00;2N} - \delta_{11} - \delta_{10}/4] \leq (2N)^{-\delta_{10}}.$$
where $\delta_{10,2} = (\delta_1 - \epsilon_1 - \epsilon_2)/3 = \delta_{01,1}/60$, as defined in (4.2). The jump rates of $X_{00}$ satisfy
\[
\begin{align*}
r^{+}_{00} &\leq N[(1-\sigma\gamma+\rho)X_{00}(1-X_{00})+2\rho X_{01}X_{10}], \\
r^{-}_{00} &\geq N(1+\sigma\gamma+\rho)X_{00}(1-X_{00}).
\end{align*}
\]
On $E_2 \cap E_1$, we have $X_{00}(T_{10;c_{10,3}}) \leq (2N)^{-\delta_{01,1}/2}$. Therefore by Lemma 5.3,
\[
\mathbb{P} \left( \left\{ \sup_{s \in [T_{10;c_{10,3}},T_{10;\epsilon_1,c_{10,3}}]} X_{00}(s) \geq (2N)^{-\delta_{01,1}/4} \right\} \cap E_2 \cap E_1 \right) \leq CN^{-1/2}.
\]
We combine the above and (4.12) to arrive at the desired conclusion of (c).

For (d), we observe that the jump rates of $X_{11+10} = X_{11} + X_{10}$ satisfy
\[
\begin{align*}
r^{+}_{11+10} &= NX_{11}[(1+\sigma+\rho)X_{01} + (1+\sigma(1+\gamma)+2\rho)X_{00}] \\
&\quad + NX_{10}[(1+\sigma(1-\gamma)+2\rho)X_{01} + (1+\sigma+\rho)X_{00}] \\
r^{-}_{11+10} &= NX_{11}[(1-\sigma+\rho)X_{01} + (1-\sigma(1+\gamma)+\rho)X_{00}] \\
&\quad + NX_{10}[(1-\sigma(1-\gamma)+\rho)X_{01} + (1-\sigma+\rho)X_{00}],
\end{align*}
\]
where we drop the terms involving $X_{11}X_{10}$ in $r^{+}_{11}$ and $r^{+}_{11}$, which correspond to type 11 individuals replaced by type 10 individuals or vice versa. Therefore $X_{11+10}$ dominates $1-\eta$ where we define $\eta$ to be a jump process with initial condition $\eta(T_{10;c_{10,3}}) = 1 - X_{11+10}(T_{10;c_{10,3}})$ and jump rates of
\[
\begin{align*}
r^{+}_{\eta} &= N(1-\sigma(1-\gamma)+\rho)\eta(1-\eta), \\
r^{-}_{\eta} &= N(1+\sigma(1-\gamma)+\rho)\eta(1-\eta).
\end{align*}
\]
Since $\eta(T_{Z_{10;1-c_{10,3}}}) \leq 1 - X_{10}(T_{Z_{10;1-c_{10,3}}}) \leq c_{10,3}$ on $E_4 \cap E_3 \cap E_2 \cap E_1$, by Lemma 5.3,
\[
\mathbb{P} \left( \left\{ \eta(t) \geq \sqrt{c_{10,3}} \text{ for some } t \geq T_{Z_{10;1-c_{10,3}}} \right\} \cap E_4 \cap E_3 \cap E_2 \cap E_1 \right) \leq CN^{-1/2}.
\]
This implies the desired conclusion of (d).

Let $\tilde{\eta}$ be a time change of $\eta$ by $1-\eta$, then $2N\tilde{\eta}$ is a branching process and the clock for $\tilde{\eta}$ runs at the rate of at most 1.02 times that of $\eta$ on $\{\tilde{\eta}(t) < \sqrt{c_{10,3}} \text{ for all } t \geq T_{Z_{10;1-c_{10,3}}} \cap E_4 \cap E_3 \cap E_2 \cap E_1\}$. By Lemma 6.1(b),
\[
P(\{\eta(T_{Z_{10;1-c_{10,3}}+0.99{\text{late}}} > 0 \} \cap E_4 \cap E_3 \cap E_2 \cap E_1) \leq CN_{10,3}e^{-\log(2N)}.
\]
Hence $P(\{\eta(T_{Z_{10;1-c_{10,3}}+{\text{late}}} > 0 \} \cap E_4 \cap E_3 \cap E_2 \cap E_1) \leq C_{10,3}$, which implies (c) since $T_{Z_{10;1-c_{10,3}}+{\text{late}}} = T_\infty$. \hfill \square

Proof of Proposition 3.1 (g-h). We define $c_4$ and $\delta_{10,4}$ such that $c_4 = \max(\sqrt{c_1} + \delta_{11,1}, \epsilon_2, c_3) \leq N^{-2\delta_{10,4}}$ and we let
\[
S_{X;Z,\text{far}} = \inf \{ t \geq T_{10;\epsilon_1} : |X_{10}(t) - Z_{10}(t)| \vee X_{00}(t) > c_4 \}.
\]
By Proposition 3.1(c,d), there exists $\delta_{10,3} > 0$ such that
\[
\mathbb{P}(\{S_{X;Z,\text{far}} \leq T_{11;\delta_{1,1}} \} \cap E_2 \cap E_1) \\
\leq \mathbb{P}(\{E_{12}^1 \cup (E_{12}^5 \cap E_4 \cap E_3)) \cap E_2 \cap E_1\} \leq C_{\rho,\gamma,\sigma}N^{-\delta_{10,3}},
\]
(4.13)
where we have used that on $E_4 \cap E_3$, $S_{X,Z,\text{far}} \geq T_{Z_{10};1-c_1}$ and on $E_5$, $X_{10}(t) > 1 - \sqrt{c_1} - X_{11}(t) > 1 - \sqrt{c_1} - \delta_{11}$ and $X_{00}(t) \leq 1 - X_{10}(t) - X_{11}(t) < \sqrt{c_1}$ for $t \geq T_{Z_{10};1-c_1}$. Notice that on $E_2 \cap E_1$, $X_{11}(t) = 0 = Z_{11}(t)$ for all $t \leq T_{10;c_1}$. For $t < S_{X_{11},Z_{11},\text{diff}} \wedge S_{X,Z,\text{far}} \wedge T_{11;\delta_{11}}$, we have

$$|r_{Z_{11}} - r_{11}^+| \leq N\delta_{11}[(\sigma - \rho)3c_4 + \delta_{11}] + 2\rho N(3c_4 + \delta_{11}) \leq 4N\delta_{11}c_4$$

and similarly, $|r_{Z_{11}} - r_{11}^-| \leq 4N\delta_{11}c_4$. Thus the absolute difference between $X_{11}$ and $Z_{11}$ is bounded above by a Poisson process of rate $8N\delta_{11}c_4$, which stays 0 during $[T_{10;c_1}, T_{10;c_1} + t_{\text{mid}} + t_{\text{late}}]$ with probability at least $1 - c_4^{1/2}$, if $t_{\text{mid}} + t_{\text{late}} \leq c_4^{-1/4}$, which is satisfied by our choice of $t_{\text{mid}} + t_{\text{late}} = O(\log N)$. Hence

$$\mathbb{P}\{S_{X_{11},Z_{11},\text{diff}} \leq T_{\infty} \wedge S_{X,Z,\text{far}} \wedge T_{11;\delta_{11}} \cap E_2 \cap E_1\} \leq c_4^{1/2}.$$ 

We combine (4.13) and the above estimate to obtain

$$\mathbb{P}\{S_{X_{11},Z_{11},\text{diff}} \leq T_{\infty} \wedge T_{11;\delta_{11}} \cap E_2 \cap E_1\} \leq c_4^{1/2} + C_{\rho,\gamma,\sigma} N^{-\delta_{10.4}},$$

which implies (g).

Let $F_2 = \{T_{Z_{11};1-\delta_{11}} \geq T_{Z_{10};1-c_1}\}$. Starting from $T_{Z_{10};1-c_1}$, $Z_{11}$ is a time-changed branching process. We perform a time change of $1 - Z_{11}$ (from time $T_{Z_{10};1-c_1}$ onwards) to obtain a branching process $Z_{11}$, then the clock for $Z_{11}$ runs faster than that of $Z_{11}$ (at a rate of at most $1/(1 - \delta_{11})$ times before $Z_{11}$ reaches $\delta_{11}$). From time $T_{Z_{10};1-c_1}$ onwards, 0 and $\delta_{11}$ are absorption points for $Z_{11} \cdot (\wedge T_{Z_{11};\delta_{11}})$. We use Lemma 6.1(d) below to deduce that

$$\mathbb{P}\{|Z_{11}(T_{\infty} \wedge T_{Z_{11};\delta_{11}}) \in (0, \delta_{11})\} \cap F_3 \cap E_2 \cap E_1 \rangle$$

$$\leq \mathbb{P}\{|\tilde{Z}_{11}(s) \in (0, \delta_{11})\} \cap (1 - \delta_{11})\rangle \cap F_3 \cap E_2 \cap E_1 \rangle$$

$$\leq (2N\delta_{11})^2 C_{\rho,\gamma,\sigma} \exp(-0.99\sigma\gamma(T_{\infty} - T_{Z_{10};1-c_1})),$$

$$\leq C_{\rho,\gamma,\sigma}(\log^2 N) \exp(-0.99\sigma\gamma t_{\text{late}}) \leq C_{\rho,\gamma,\sigma} N^{-\delta_{10.4}},$$

if we choose a sufficiently small $\delta_{10.4}$. Therefore

$$\mathbb{P}\{|Z_{11}(T_{\infty}) \in (0, \delta_{11}), T_{Z_{11};\delta_{11}} \geq T_{\infty}\} \cap F_3 \cap E_2 \cap E_1 \rangle \leq C_{\rho,\gamma,\sigma} N^{-\delta_{10.4}}.$$ 

On $\{S_{X_{11},Z_{11},\text{diff}} > T_{\infty} \wedge T_{11;\delta_{11}}\}$, $X_{11}$ and $Z_{11}$ agree up to $T_{\infty} \wedge T_{11;\delta_{11}}$. Therefore

$$\mathbb{P}\{|S_{X_{11},Z_{11},\text{diff}} > T_{\infty}, T_{11;\delta_{11}} > T_{\infty}, X_{11}(T_{\infty}) = Z_{11}(T_{\infty}) \in (0, \delta_{11}), T_{11;\{0,\delta_{11}\}} = T_{Z_{10};1-c_1}\} \cap E_2 \cap E_1 \rangle \leq C_{\rho,\gamma,\sigma} N^{-\delta_{10.4}}.$$ 

We can drop the condition $T_{11;\{0,\delta_{11}\}} = T_{Z_{10};1-c_1}$, since on $\{S_{X_{11},Z_{11},\text{diff}} > T_{\infty}, T_{11;\delta_{11}} > T_{\infty}, T_{11;\{0,\delta_{11}\}} > T_{Z_{10};1-c_1}\}$, we have $X_{11}(T_{\infty}) = Z_{11}(T_{\infty}) = 0$. Hence

$$\mathbb{P}\{|T_{11;\delta_{11}} > T_{\infty}, X_{11}(T_{\infty}) = Z_{11}(T_{\infty}) \in (0, \delta_{11})\} \cap E_7 \cap E_2 \cap E_1 \rangle \leq C_{\rho,\gamma,\sigma} N^{-\delta_{10.4}},$$

which implies the desired result in (h).  

\[ \square \]
5. Supporting Lemmas

In this section, we establish Lemmas 5.1 to 5.3, one each for the early, middle, and late phase. They are used for the proof of Proposition 3.1 in §4. Lemma 5.1 deals with the early phase and approximates a 1-dimensional jump process undergoing selection by a deterministic function, where the error bound depends only on the initial condition of the process, as long as the process is stopped before it reaches \( O(1) \). Lemma 5.2 deals with the middle phase and uses the logistic growth as an approximation. The main difference between the early phase and the middle phase is the error bound: in Lemma 5.2, the error bound depends on both the initial and terminal conditions of the process. Lemma 5.3 deals with the late phase, for which we only need to show that the process does not stray too far away from 1 (or 0 for \( X_{00} \) once it gets close to 1 (or 0).

**Lemma 5.1.** Let \( \alpha \geq 1, \theta \in (0, 1), \delta_0 \in [0, 1/2] \) and \( x \in (0, 1) \) be constants. Let \( \xi \) be a jump process with initial value \( \xi(0) = (2N)^{-x} \geq (2N)^{-1} \), jump size \( 1/(2N) \), and jump rates

\[
\begin{align*}
  r^+ &= N\xi[(\alpha + \theta)(1 - \xi) - \delta_0], \\
  r^- &= N\xi[(\alpha - \theta)(1 - \xi) + \delta_0].
\end{align*}
\]

Suppose \( Y \) is a deterministic process that satisfies

\[
Y(t) = (2N)^{-x} + \int_0^t Y(s)(\theta(1 - Y(s)) - \delta_0) \, ds.
\]

If \( u_0 = \inf\{t : Y(t) = \delta_1\} \leq (\log 2)/(3\theta \delta_1 + \delta_0) \), then there exists \( \delta_2 \in (0, (1 - x)/4] \) such that

\[
P(\{\xi(s) - Y(s)\} > 4N^{-\delta_2}Y(s) \text{ for some } s \leq u_0) \leq C_{\alpha, \theta}N^{-\delta_2}.
\]

Moreover, if \( \xi \) and \( \hat{\xi} \) are jump processes such that \( \hat{\xi} \geq \xi \geq \hat{\xi} \) before a stopping time \( T \), then

\[
P(\{\hat{\xi}(s) < (1 - 4N^{-\delta_2})Y(s) \text{ for some } s \leq u_0 \land T\} \leq C_{\alpha, \theta}N^{-\delta_2}
\]

and

\[
P(\hat{\xi}(s) > (1 + 4N^{-\delta_2})Y(s) \text{ for some } s \leq u_0 \land T \leq C_{\alpha, \theta}N^{-\delta_2}.
\]

**Proof.** We can write

\[
d\xi = dM_\xi + \xi(\theta(1 - \xi) - \delta_0) \, dt, \quad d(M_\xi) = \frac{\alpha}{2N}\xi(1 - \xi) \, dt,
\]

and consequently,

\[
\begin{align*}
  d(e^{-\theta t}\xi(t)) &= d\hat{M}_\xi(t) - e^{-\theta t}(\theta\xi(t)^2 + \delta_0\xi(t)) \, dt, \\
  d(\hat{M}_\xi)(t) &= \frac{\alpha}{2N}e^{-2\theta t}\xi(t)(1 - \xi(t)) \, dt.
\end{align*}
\]

We define \( \tau = \inf\{t \leq u_0 : \xi(t) \geq 2\delta_1\} \), and take expectation on both sides of (5.1) to obtain

\[
E[e^{-\theta(t \land \tau)}\xi(t \land \tau)] = (2N)^{-x} - E\left[\int_0^{t \land \tau} e^{-\theta s}(\theta\xi(s)^2 + \delta_0\xi(s)) \, ds\right] \leq (2N)^{-x}.
\]
As in the steps leading to (3.7), we use Jensen’s and Burkholder’s inequalities to obtain

\[ E \left[ \sup_{s \leq t \wedge \tau} |\tilde{M}_{\xi}(s)| \right] \leq \frac{C}{N} + \frac{C\alpha}{N^{1/2}} \left( E \left[ \int_0^t e^{-2\theta s}(\xi(s)1_{\{s \leq \tau\}}) \, ds \right] \right)^{1/2} \]

\[ \leq \frac{C}{N} + \frac{C\alpha}{N^{1/2}} \left( \int_0^t e^{-\theta s}(2N)^{-x} \, ds \right)^{1/2} \leq C_{\alpha, \theta} N^{-(1+x)/2}. \quad (5.2) \]

Since \( de^{-\theta Y(t)} = -e^{-\theta t}(\theta Y(t)^2 + \delta_0 Y(t)) \, dt \), we use (5.2) in (5.1) to obtain

\[ E \left[ \sup_{s \leq t \wedge \tau} e^{-\theta s}|\xi(s) - Y(s)| \right] \leq C_{\alpha, \theta} N^{-(1+x)/2} e^{(3\delta_1 + \delta_0)t} \leq C_{\alpha, \theta} N^{-(1+x)/2}, \]

since \( \tau \leq u_0 \leq (\log 2)/(3\delta_1 + \delta_0) \). Let \( \delta_2 \in (0, (1-x)/4) \), then

\[ P \left( |\xi(s) - Y(s)| \geq N^{-\delta_2} e^{\theta s} \right) \text{ for some } s \leq u_0 \wedge \tau \leq C_{\alpha, \theta} N^{-\delta_2}. \]

We observe that for \( s \leq u_0 \), \( (2N)^{-x} e^{(\theta - \delta_1 - \delta_0)s} \leq Y(s) \), hence \( N^{-x} e^{\theta s}/Y(s) \leq 2^x e^{(\delta_1 + \delta_0)(\log 2)/(3\delta_1 + \delta_0)} \leq 4 \), i.e. \( N^{-x} e^{\theta s} \leq 4Y(s) \). Hence

\[ P \left( |\xi(s) - Y(s)| \geq 4N^{-\delta_2} Y(s) \right) \text{ for some } s \leq u_0 \wedge \tau \leq C_{\alpha, \theta} N^{-\delta_2}. \]

We can drop \( \tau \) in the event above, since \( |\xi(\tau) - Y(\tau)| \geq Y(\tau) \). The conclusion follows.

**Lemma 5.2.** Let \( \theta, \epsilon_1, \epsilon_2 \in (0, 1) \) and \( a_0, a_1 > 0 \) be constants. Suppose \( Y \) is a deterministic process defined from a stopping time \( u_1 \) onwards that has initial condition \( Y(u_1) = b_0 \geq a_0(2N)^{-\epsilon_0} \) and satisfies

\[ Y(t) = b_0 + \int_{u_1}^t \theta Y(s)(1 - Y(s)) \, ds. \]

Let \( u_2 = u_1 + \frac{\epsilon_0}{\log \frac{1}{b_0}} \log \frac{1}{b_0} \) such that \( Y(u_2) = 1 - b_1 \leq 1 - a_1(2N)^{-\epsilon_1} \). Suppose \( T \) is a stopping time and \( \xi \) is jump process that takes values in \([0, 1]\), has jump
size $1/(2N)$ and satisfies

$$
\xi(t \wedge T) = \xi(u_1) + M(t \wedge T) + \int_{u_1}^{t \wedge T} \xi(s)\theta(1 - \xi(s)) + \epsilon_2(s) + \epsilon_3(s) \, ds
$$

$$
\langle M \rangle(t \wedge T) = \frac{1 + \rho}{2N} \int_{u_1}^{t \wedge T} \xi(s)(1 - \xi(s)) + \epsilon_4(s) \, ds,
$$

where $|\epsilon_2(t)|, |\epsilon_3(t)| \leq (2N)^{-\delta_1}, \epsilon_4(t) \leq 1$ for $t \leq T$, and $M$ is a jump martingale with jump size $1/(2N)$. Furthermore, suppose on a set $D_1 \subset \mathcal{F}(u_1)$, we have $|\xi(u_1) - b_0| \leq (2N)^{-\delta_2}$. We define $D_2 = \{T \geq u_1\}$ and $\delta_3$ to be a constant $\leq ((\delta_1 \wedge \delta_2 \wedge \frac{1}{N}) - \epsilon_0 - \epsilon_1)/3$. If $\delta_3 > 0$, then

$$
P \left( \sup_{s \in [u_1, u_2 \wedge T]} |\xi(s, \omega) - Y(s, \omega)| > (2N)^{-\delta_3} \mid D_1 \cap D_2 \right) \leq (2N)^{-\delta_3}.
$$

Proof. Let $D = D_1 \cap D_2$. Notice that $D \in \mathcal{F}(u_1)$. Since

$$
|\xi(t)|\theta(1 - \xi(t)) + \epsilon_2(t) - \theta Y(t)(1 - Y(t))|1_{\{t \leq T\}}
$$

$$
\leq (2N)^{-\delta_1} + \theta|\xi(t) - Y(t)||1_{\{t \leq T\}}
$$

$$
\leq (2N)^{-\delta_1} + \theta|\xi(t) - Y(t)||1_{\{t \leq T\}},
$$

we have

$$
|\xi((u_1 + t) \wedge T) - Y((u_1 + t) \wedge T)|1_D \leq |\xi(u_1) - Y(u_1)|
$$

$$
+ |M((u_1 + t) \wedge T)1_D| + \int_{u_1}^{(u_1 + t) \wedge T} [(2N)^{-\delta_1} + \theta|\xi(s) - Y(s)||1_D \, ds.
$$

By Jensen’s and Burkholder’s inequalities,

$$
E \left[ \sup_{u_1 \leq s \leq u_1 + t} |M(s \wedge T)1_D| \right] \leq \frac{C}{N} + C\sqrt{\frac{t}{N}} \leq C\sqrt{\frac{t}{N}},
$$

therefore

$$
E \left[ \sup_{u_1 \leq s \leq u_1 + t} |\xi(s \wedge T) - Y(s \wedge T)|1_D \right] \leq C\sqrt{\frac{t}{N}} + E \left[ |\xi(u_1) - Y(u_1)|1_D \right]
$$

$$
+ 2(2N)^{-\delta_1}t + \int_{u_1}^{u_1 + t} \theta E[|\xi(s) - Y(s)||1_{\{s \leq T\}}1_D] \, ds.
$$

Since $E[|\xi(s) - Y(s)||1_{\{s \leq T\}}1_D] \leq E[|\xi(s \wedge T) - Y(s \wedge T)||1_D]$, and $|\xi(u_1) - Y(u_1)|1_D \leq (2N)^{-\delta_2}$, we have

$$
E \left[ \sup_{u_1 \leq s \leq u_1 + t} |\xi(s \wedge T) - Y(s \wedge T)|1_D \right] \leq C \left( \sqrt{\frac{t}{N}} + \frac{1}{(2N)^{\delta_2}} + \frac{t}{(2N)^{\delta_1}} \right) e^{\theta t}.
$$
by Gronwall’s inequality. We observe that \( u_2 - u_1 \leq \frac{1}{a} \log \frac{1}{a} \leq \frac{1}{a}[(\epsilon_0 + \epsilon_1) \log(2N) - \log(\alpha)] \), therefore the estimate above implies

\[
E \left[ \sup_{u_1 \leq s \leq u_2} |\xi(s \wedge T) - Y(s \wedge T)|1_D \right] \leq C(2N)^{\epsilon_0 + \epsilon_1} \log N \frac{\alpha}{\log(2N)} (2N)^{-\frac{1}{2} + \delta_1 + \delta_2 + \delta_3}.
\]

Since \( 0 < \delta_3 \leq (\delta_1 \wedge \delta_2 \wedge \delta_3) - (\epsilon_0 + \epsilon_1)/3 \), we have

\[
E \left[ \sup_{u_1 \leq s \leq u_2} |\xi(s \wedge T) - Y(s \wedge T)|1_D \right] \leq (2N)^{-2\delta_3},
\]

which implies the desired conclusion. \( \square \)

**Lemma 5.3.** Let \( \alpha \geq 1, \theta \in (0, 1), x \in (0, 1], c > 0 \) and \( \kappa \geq 0 \) be constants. Let \( \eta \leq \hat{\eta} \) be jump processes where \( \eta \) has initial value \( \eta(0) = 1 - c(2N)^{-x} \), jump size \( 1/(2N) \), jump rates

\[
r^+ = N(\alpha + \theta)\eta(1 - \eta), \quad r^- = N(\alpha - \theta)\eta(1 - \eta) + N\kappa,
\]

and absorbing boundary at \( 1/2 \). For \( t \leq c(2N)^{-x}/\kappa \) (if \( \kappa = 0 \), then \( t = \infty \)), we have

\[
P \left( \inf_{s \leq t} \hat{\eta}(s) > 1 - (2N)^{-x/2} \right) \geq P \left( \inf_{s \leq t} \eta(s) > 1 - (2N)^{-x/2} \right) \geq 1 - CN^{-1/2}.
\]

**Proof.** We take \( \xi = 1 - \eta \) and perform a time change of \( 1 - \xi \) on \( \xi \) to obtain a process \( \tilde{\xi} \) with jump rates

\[
\tilde{r}^+ = N(\alpha - \theta)\tilde{\xi} + N\kappa/(1 - \tilde{\xi}), \quad \tilde{r}^- = N(\alpha + \theta)\tilde{\xi}.
\]

Let \( \tilde{\xi}_{up} \) be a jump process with initial condition \( \tilde{\xi}_{up}(0) = \tilde{\xi}(0) = c(2N)^{-x} \), jump size \( 1/(2N) \) and jump rates

\[
\tilde{r}_{up}^+ = N(\alpha - \theta)\tilde{\xi}_{up} + 2N\kappa, \quad \tilde{r}_{up}^- = N(\alpha + \theta)\tilde{\xi}_{up}.
\]

Before the stopping time \( \tau = \inf\{t \geq 0 : \xi_{up} \geq 1/2\} \), \( \xi_{up} \) dominates \( \tilde{\xi} \). We can write

\[
d\tilde{\xi}_{up}(t) = dM_{\tilde{\xi}_{up}} + (\kappa - \theta)\tilde{\xi}_{up} dt, d(M_{\tilde{\xi}_{up}}) = \frac{1}{2N}(\kappa + \alpha\tilde{\xi}_{up}(t)) \, dt.
\]

Hence \( E[\tilde{\xi}_{up}(t)] = \frac{\theta}{\kappa} + (c(2N)^{-x} - \frac{\theta}{\kappa}) e^{-\theta t} \) and by Jensen’s and Burkholder’s inequalities,

\[
E \left[ \sup_{s \leq 2t} M_{\tilde{\xi}_{up}}(s) \right] \leq \frac{C}{N^2} + \frac{C}{\sqrt{N}} \left( \kappa t + \alpha \int_0^{2t} E[\xi_{up}(t)] \, ds \right)^{1/2}
\leq \frac{C_{\alpha, \theta}}{\sqrt{N}} \left( \kappa t + c(2N)^{-x} \right)^{1/2} \leq C_{\alpha, \theta} N^{-1+x/2}.
\]
if $kt \leq c(2N)^{-x}$, in which case

$$P \left( \sup_{s \leq 2t} \xi_{up}(s) \geq (2N)^{-x/2} \right) \leq P \left( \sup_{s \leq 2t} M_\xi(s) \geq (2N)^{-x/2} - c(2N)^{-x} - 4kt \right) \leq \frac{C_{\alpha,\theta}N^{-(x+1)/2}}{(2N)^{-x/2} - c(2N)^{-x} - 4kt} \leq C_{\alpha,\theta}N^{-1/2}. $$

On the set $\{ \sup_{s \leq 2t} \xi_{up}(s) \leq (2N)^{-x/2} \}$, $\xi_{up}$ certainly does not reach 1/2 before time 2t. Hence $\xi_{up}$ dominates $\xi$ before 2t for $\omega \in \{ \sup_{s \leq 2t} \xi_{up}(s) \leq (2N)^{-x/2} \}$, which implies $P \left( \sup_{s \leq 2t} \xi(s) < (2N)^{-x/2} \right) \geq 1 - C_{\alpha,\theta}N^{-1/2}$. Because $\xi$ is the process $\xi$ after a time change of $1-\xi$, the clock for $\xi$ runs faster than that of $\xi$, but at most twice as fast before $\xi$ reaches 1/2. Therefore the estimate above implies $P \left( \sup_{s \leq t} \xi(s) < (2N)^{-x/2} \right) \geq P \left( \sup_{s \leq 2t} \xi(s) < (2N)^{-x/2} \right) \geq 1 - C_{\alpha,\theta}N^{-1/2}$. The conclusion follows. \qed

6. Appendix: A Result on Branching Processes

**Lemma 6.1.** Let $\xi^{(k)}$ be a branching process with $\xi(0) = k$ and $u(s) = as^2 + b$ be the probability generating function of the offspring distribution. Then

$$G(s, t) = E(s^{\xi^{(k)}(t)}) = \left( \frac{b(s-1) - (as-b)e^{-(a-b)t}}{a(s-1) - (as-b)e^{-(a-b)t}} \right)^k. $$

(a) If $k = 1$ and $a > b$, then

1. $|P(\xi^{(1)}(t) = 0) - b/a| \leq be^{-(a-b)t}/a$.
2. $P(1 \leq \xi^{(1)}(t) \leq K) \leq C_{a,b}Ke^{-(a-b)t}K$ if $K \leq e^{(a-b)t}/6$.
3. $P \left( \sup_{s \leq 2t} \xi^{(1)}(s) \geq K \right) \leq C_{a,b}Ke^{(a-b)t}/K$.

(b) If $a < b$, then $P(\xi^{(k)}(t) > 0) \leq 1.2ke^{-(b-a)t}$.

(c) If $a > b$ and $k \in [1, K]$, then $P(\xi^{(k)}(t) \in [1, K]) \leq kC_{a,b}Ke^{-(a-b)t}$.

(d) If $a > b$ and $\xi$ is a branching process with an initial condition that has support on $[0, k]$, then $P(\xi(t) \in [1, K]) \leq kC_{a,b}Ke^{-(a-b)t}$. Consequently,

$$P(\xi(s) \in [1, K] \text{ for all } s \leq t) \leq kC_{a,b}Ke^{-(a-b)t}. $$

**Proof.** The formula for $G(s, t)$ comes from Chapter III.5 of Athreya & Ney (1972). From this formula, we deduce that

$$P(\xi^{(k)}(t) = 0) = G(0, t) = \left( \frac{b - be^{-(a-b)t}}{a - be^{-(a-b)t}} \right)^k. \quad (6.1)$$

For (a), we specialise to the case of $k = 1$ and $a > b$. We write $\xi = \xi^{(1)}$, then

$$\left| P(\xi(t) = 0) - \frac{b}{a} \right| = \frac{(a-b)be^{-(a-b)t}}{a(a-be^{-(a-b)t})} \leq \frac{b}{a}e^{-(a-b)t}. $$
Burkholder’s inequality implies
\[ P(1 \leq \xi(t) \leq K) \leq s^{-K} \sum_{i=1}^{\infty} P(\xi(t) = i)s^i = s^{-K}(G(s, t) - G(0, t)) \]
\[ = \frac{(a - b)^2 s}{(a - be^{-(a-b)t})(a e^{(a-b)t} s^K(1 - s) + s^{K+1}) - bs^K}. \]

where \( G(s, t) - G(0, t) \) can be computed from (6.1) using elementary algebra. The dominant term in the denominator of the above quantity is \( e^{(a-b)t} s^K(1 - s) \), which achieves the maximum
\[ \frac{e^{(a-b)t}}{K+1} \left( 1 - \frac{1}{K+1} \right)^K = e^{(a-b)t} \left( 1 - \frac{1}{K+1} \right)^{K+1} \]
at \( s = K/(K+1) \). For sufficiently large \( K \), this is at least \( e^{(a-b)t}/(3K) \). Therefore
\[ P(1 \leq \xi(t) \leq K) \leq \frac{(a - b)^2 K}{(a - be^{-(a-b)t})} \leq C_{a,b} \left( a e^{(a-b)t}/3K - b \right)^{-1}, \]
which implies the desired conclusion of (a.2), if \( K \leq e^{(a-b)t}/6. \)

For (a.3), we observe that \( M(t) = e^{-(a-b)t}\xi(t) \) is a martingale with maximum jump size 1 and quadratic variation \( \langle M \rangle(t) = \int_0^t e^{-2(a-b)s}(a + b)\xi(s) \) ds. Burkholder’s inequality implies
\[ E \left[ \sup_{s \leq t} M(s) \right] \leq C + C \int_0^t e^{-2(a-b)s}(a + b)E[\xi(s)] \]ds
\[ = C + C \int_0^t e^{-2(a-b)s}(a + b)e^{(a-b)s} \]ds \leq C_{a,b}. 

Therefore \( E \left[ \sup_{s \leq t} \xi(s) \right] \leq C_{a,b}e^{(a-b)t} \), which implies (a.3).

For (b), we observe that
\[ P(\xi^{(k)}(t) = 0) = \left( 1 - \frac{b - a}{be^{(b-a)t} - a} \right)^k. \]

For sufficiently large \( t \), we have
\[ \frac{be^{(b-a)t} - a}{b - a} = \frac{e^{(b-a)t} - a}{1 - \frac{a}{b}} \geq e^{(b-a)t} - \frac{a}{b} \geq \frac{1}{1.1} e^{(b-a)t}, \]
therefore
\[ P(\xi^{(k)}(t) = 0) \geq \left[ 1 - \frac{b - a}{be^{(b-a)t} - a} \right]^{k1.1e^{-(b-a)t}} \geq e^{-1.2ke^{-(b-a)t}} \]
\[ \geq 1 - 1.2ke^{-(b-a)t}. \]
if $t$ is sufficiently large and $ke^{-(b-a)t}$ is sufficiently small.

For (c), we observe that $\xi^{(k)} = \xi^{(1)}_1 + \xi^{(1)}_2 + \ldots + \xi^{(1)}_k$, where $\xi^{(1)}_i, i = 1, \ldots, k$ are independent copies of $\xi^{(1)}$. Therefore

$$P(\xi^{(k)}(t) \in [1, K]) \leq P(\xi^{(1)}_i \in [1, K] \text{ for some } i = 1, \ldots, k) \leq kC_{a,b}Ke^{-(a-b)t}$$

by part (a.2) of this lemma. Part (d) is a direct consequence of part (c). □

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