

# Asymptotically Optimal Amplifiers for the Moran Process<sup>\*</sup>

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## Abstract

We study the Moran process as adapted by Lieberman, Hauert and Nowak. This is a model of an evolving population on a graph or digraph where certain individuals, called “mutants” have fitness  $r$  and other individuals, called “non-mutants” have fitness 1. We focus on the situation where the mutation is advantageous, in the sense that  $r > 1$ . A family of digraphs is said to be strongly amplifying if the extinction probability tends to 0 when the Moran process is run on digraphs in this family. The most-amplifying known family of digraphs is the family of megastars of Galanis et al. We show that this family is optimal, up to logarithmic factors, since every strongly-connected  $n$ -vertex digraph has extinction probability  $\Omega(n^{-1/2})$ . Next, we show that there is an infinite family of undirected graphs, called dense incubators, whose extinction probability is  $O(n^{-1/3})$ . We show that this is optimal, up to constant factors. Finally, we introduce sparse incubators, for varying edge density, and show that the extinction probability of these graphs is  $O(n/m)$ , where  $m$  is the number of edges. Again, we show that this is optimal, up to constant factors.

## 1 Introduction

We study the Moran process [17] as adapted by Lieberman, Hauert and Nowak [13, 18]. This is a model of an evolving population. There are two kinds of individuals — “mutants” and “non-mutants”. The model has a parameter  $r$ , which is a positive real number, and is the fitness of the mutants. All non-mutants have fitness 1. The individuals reside at the vertices of a digraph  $G$  – each vertex contains exactly one individual, and it is either a mutant or a non-mutant. In the initial state, one vertex (chosen uniformly at random) contains a mutant. All of the other vertices contain non-mutants. The process evolves in discrete time. At each step, a vertex is selected at random, with probability proportional to its fitness. Suppose that this is vertex  $v$ . Next, an out-neighbour  $w$  of  $v$  is selected uniformly at random. Finally, the state of vertex  $v$  (mutant or non-mutant) is copied to vertex  $w$ .

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If  $G$  is finite and strongly connected then with probability 1, the process will either reach the state where there are only mutants (known as *fixation*) or it will reach the state where there are only non-mutants (*extinction*). If  $G$  is not strongly connected then the process may continue changing forever — thus, it makes sense to restrict attention to strongly-connected digraphs  $G$ . We do so for the rest of the paper.

Given a strongly-connected digraph  $G$ , we use the notation  $\rho_r(G)$  to denote the probability that the Moran process (starting from a uniformly-chosen initial mutant) reaches fixation and we use the notation  $\ell_r(G)$  to denote the probability that it reaches extinction. If  $\mathcal{G}$  is a set of digraphs then we use  $\ell_{r,\mathcal{G}}(n)$  to denote  $\max\{\ell_r(G) \mid G \in \mathcal{G} \text{ and } G \text{ has } n \text{ vertices}\}$ . (To avoid trivialities, we take the maximum of the empty set to be 0.) The function  $\ell_{r,\mathcal{G}}$  is called the “extinction limit” of the family  $\mathcal{G}$ . Lieberman et al. [13] raised the question of whether there exists an infinite family  $\mathcal{G}$  of digraphs for which  $\limsup_{n \rightarrow \infty} \ell_{r,\mathcal{G}}(n) = 0$ . We say in this case that  $\mathcal{G}$  is *strongly amplifying*. They defined two infinite families of strongly-connected digraphs — superstars and metafunnels — which turn out to be strongly amplifying. The most amplifying infinite family of strongly-connected digraphs that is known (in the sense that the extinction limit grows as slowly as possible, as a function of  $n$ ) is the family  $\Upsilon$  of *megastars* from [10]. Galanis et al. show [10, Theorem 6] that, for every  $r > 1$  there is an  $n_0$  (depending on  $r$ ) so that, for all  $n \geq n_0$  and for every  $n$ -vertex digraph  $G \in \Upsilon$ ,  $\ell_r(G) \leq (\log n)^{23}/n^{1/2}$ .

The first question addressed by this paper is whether the family of megastars is optimal in the sense that the extinction limit grows as slowly as possible (as a function of  $n$ ). We show that this is the case, up to logarithmic factors.

**Theorem 1.** *For all  $r > 1$ , any strongly-connected  $n$ -vertex digraph  $G$  with  $n \geq 2$  satisfies  $\ell_r(G) > 1/(5rn^{1/2})$ .*

For undirected graphs, the most amplifying graphs previously known were stars, whose extinction probability tends to  $1/r^2$  (as the size of the star grows). In particular, no strongly-amplifying family of undirected graphs was known. In our next result we show that such families do exist, and that they can have extinction probability  $\ell_r(G) = O(n^{-1/3})$ .<sup>1</sup> Note that throughout the paper, we write “graph” exclusively to refer to undirected graphs, which we view as a special case of digraphs.

**Theorem 2.** *For all  $r > 1$ , there exists an infinite family  $\mathcal{D}_r$  of connected graphs with the following property. If  $G \in \mathcal{D}_r$  has  $n$  vertices, then  $\ell_r(G) \leq 71/(r(r-1)^2n)^{1/3}$ .*

The graphs in the family  $\mathcal{D}_r$  are called *dense incubators*. Each such graph is parameterised by a number  $k$ , which is the square of an integer. Taking  $\beta$  to be an integer constant depending on  $r$ , the graph consists of  $k$  stars, each with  $\lceil r\sqrt{\beta k} \rceil$  leaves, together with a clique of size  $\beta k$ . Every centre of every star is connected to every node in the clique. More details are given in Definition 5 (this definition also defines sparse incubators, which we will discuss shortly).

It is known [5, Corollary 7] that extinction probabilities are monotonic in  $r$  in the sense that if  $0 < r \leq r'$  then, for any digraph  $G$ ,  $\ell_{r'}(G) \leq \ell_r(G)$ . Thus, Theorem 2 guarantees that, for every  $r' > r$  and every  $n$ -vertex graph in  $\mathcal{D}_r$ , we also have  $\ell_{r'}(G) \leq 71/(r(r-1)^2n)^{1/3}$ .

The next question that we address is whether the family  $\mathcal{D}_r$  is optimal (again, in the sense that the extinction limit grows as slowly as possible). We show that this is the case, up to constant factors (depending on  $r$ ).

<sup>1</sup>See Section 1.1 for a discussion of simultaneous independent work that also resolves this question.

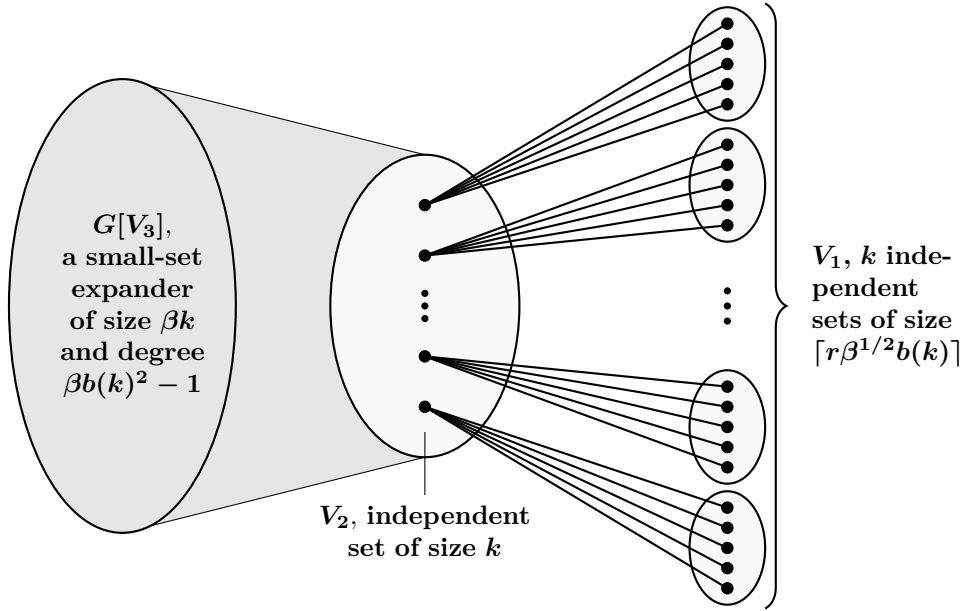


Figure 1: The family of  $\mathcal{I}_{r,b}$  incubators. As  $G[V_2, V_3]$  is a biregular graph with  $\beta k b(k)^2$  edges, each vertex in  $V_2$  sends  $\beta b(k)^2$  edges to  $V_3$  and each vertex in  $V_3$  sends  $b(k)^2$  edges to  $V_2$ .

**Theorem 3.** *Let  $r > 1$ . Consider any connected  $n$ -vertex graph  $G$  with  $n \geq 2$ . Then  $\ell_r(G) > 1/(42r^{4/3}n^{1/3})$ .*

The reason that dense incubators are called “dense” is that an  $n$ -vertex dense incubator has  $\omega(n)$  edges (more specifically, it has  $\Theta(n^{4/3})$  edges). The final question that we address is whether there are sparse families of graphs that are strongly amplifying. Once again, the answer is yes.

Before we present the relevant theorems (Theorems 6 and 7) we define a (parameterised) family of incubators, where the additional parameter controls the edge density. In order to define these, we need some definitions. Given a graph  $G = (V, E)$  and subsets  $S$  and  $T$  of  $V$ ,  $E(S, T)$  denotes the set of edges in  $E$  with one endpoint in  $S$  and the other in  $T$ . We also use the following standard definition.

**Definition 4.** Let  $G = (V, E)$  be a  $d$ -regular graph with  $n$  vertices.  $G$  is a *small-set expander* if

$$\min_{\substack{\emptyset \subset S \subseteq V, \\ |S| \leq n^{1/3}}} \frac{|E(S, V \setminus S)|}{|S|} \geq \frac{d}{4}.$$

Let  $\mathbb{Z}_{\geq 1}$  denote the set of positive integers. Given a graph  $G = (V, E)$  and disjoint subsets  $S$  and  $T$  of  $V$  we use  $G[S]$  to denote the subgraph of  $G$  induced by  $S$  and we use  $G[S, T]$  to denote the graph with vertex set  $S \cup T$  and edge set  $E[S, T]$ . This graph is said to be *biregular* if all vertices in  $S$  have the same degree and also all vertices in  $T$  have the same degree. Using Definition 4, we can now define families of incubators (see Figure 1).

**Definition 5.** Let  $r > 1$  and let  $\beta = 26\lceil r^2/(r-1) \rceil$ . Let  $b : \mathbb{Z}_{\geq 1} \rightarrow \mathbb{Z}_{\geq 1}$  be any function that satisfies  $b(k) \leq \sqrt{k}$  for all  $k$ . Then a graph  $G = (V, E)$  is a member of the family  $\mathcal{I}_{r,b}$

of *incubators with branching factor  $b$*  if and only if there exists a positive integer  $k$  and a partition  $V_1, V_2, V_3$  of  $V$  such that the following properties hold.

- (i)  $|V_1| = k\lceil r\sqrt{\beta}b(k) \rceil$ ,  $|V_2| = k$ , and  $|V_3| = \beta k$ .
- (ii)  $G[V_1, V_2]$  is biregular with  $k\lceil r\sqrt{\beta}b(k) \rceil$  edges.
- (iii)  $G[V_2, V_3]$  is biregular with  $\beta kb(k)^2$  edges.
- (iv)  $G[V_1]$ ,  $G[V_2]$ , and  $G[V_1, V_3]$  are empty.
- (v)  $G[V_3]$  is a small-set expander with degree  $\beta b(k)^2 - 1$ .

We will see at the end of this section how the branching factor  $b$  allows substantial control over the edge density of incubators. We will also see in Section 3 (Theorem 11) that, as long as  $b(k)$  is eventually sufficiently large, then the set  $\mathcal{I}_{r,b}$  is infinitely large. First, we present the relevant theorems.

**Theorem 6.** *Let  $r > 1$ . There is a constant  $b_0$  depending only on  $r$  such that the following holds. Let  $b : \mathbb{Z}_{\geq 1} \rightarrow \mathbb{Z}_{\geq 1}$  be any function that satisfies  $b(k) \leq \sqrt{k}$  for all  $k$ . Consider a graph  $G \in \mathcal{I}_{r,b}$  with branching factor  $b(k) \geq b_0$ . Let  $n$  be the number of vertices of  $G$  and  $m$  be the number of edges of  $G$ . Then  $\ell_r(G) \leq 2^{14}rn/((r-1)^2m)$ .*

As in the dense case, it turns out that the family  $\mathcal{I}_{r,b}$  is optimal in the sense that (up to constant factors) the extinction limit grows as slowly as possible.

**Theorem 7.** *Let  $r > 1$ . Consider any connected graph  $G$  with  $n \geq 2$  vertices and  $m$  edges. Then  $\ell_r(G) \geq n/(288r^2m)$ .*

Theorem 2 is closely related to a special case of Theorem 6. To see this, consider the function  $b(k)$  defined by  $b(k) = \lfloor \sqrt{k} \rfloor$ . Consider any  $r > 1$ , and let  $b_0$  be the constant (depending on  $r$ ) in Theorem 6. Let

$$\mathcal{D}_r = \{G \in \mathcal{I}_{r,b} \mid \text{The parameter, } k, \text{ of } G \text{ is the square of an integer and } b(k) \geq b_0\}.$$

Using these definitions, a slightly weaker version of Theorem 2 may be obtained directly from the statement of Theorem 6. We give the proof of the stronger version in Section 4.

Let us now consider sparse incubators. In order to appreciate how the branching factor  $b$  controls the edge density of incubators, it is useful to calculate the number of vertices and edges of a parameter- $k$  incubator in  $\mathcal{I}_{r,b}$ .

**Observation 8.** Consider  $G = (V, E) \in \mathcal{I}_{r,b}$  with  $|V_2| = k$ ,  $|V| = n$  and  $|E| = m$ . If  $b(k) \geq \beta/r$  then

- (i)  $kr\beta^{1/2}b(k) \leq n \leq 2kr\beta^{1/2}b(k)$ ,
- (ii)  $\beta^2 kb(k)^2/2 \leq m \leq \beta^2 kb(k)^2$ , and
- (iii)  $\beta^{3/2}b(k)/(4r) \leq m/n \leq \beta^{3/2}b(k)/r$ .

*Proof.* By the definition of  $\mathcal{I}_{r,b}$ , we have  $n = k\lceil r\beta^{1/2}b(k) \rceil + k + \beta k$  and  $m = k\lceil r\beta^{1/2}b(k) \rceil + \beta kb(k)^2 + \frac{k\beta(\beta b(k)^2 - 1)}{2}$ . The lower bounds on  $n$  and  $m$  follow immediately, and the upper bounds follow since  $\beta \geq 26\lceil r \rceil$ . Putting these together gives the bounds on  $m/n$ .  $\square$

Observation 8 makes it easy to see that the function  $b(k)$  can be tuned to achieve a variety of edge densities.

## 1.1 Related work

The Moran process is somewhat similar to a discrete version of directed percolation known as the contact process. There has been a lot of work (e.g., [1, 6, 7, 14, 19]) on the contact process and other related infection processes such as the voter model and SIS epidemic models. We refer the reader to [10, Section 1.4] for a discussion of how these models differ from the Moran process.

Lieberman, Hauert and Nowak [13, 18] introduced the version of the Moran process that we study. They raised the question of strong amplification and defined two infinite families of strongly-connected digraphs — superstars and metafunnels — which turn out to be strongly amplifying. Many papers contributed to determining the fixation probability of these digraphs [13, 3, 12] — see [10, Section 1.4] for a discussion. The first rigorous proof that there is an infinite family of strongly-amplifying digraphs is in [10]. This is the family of megastars discussed in the introduction. The paper also gives lower bounds on the extinction probability of superstars and metafunnels.

The best-known lower bounds on the extinction probability of connected undirected graphs are in [15, 16]. Theorem 1 of [16] shows that there is a constant  $c_0(r)$  such that for every  $\varepsilon > 0$  the extinction probability is at least  $c_0(r)/n^{3/4+\varepsilon}$ .

While this manuscript was under preparation, George Giakkoupis posted simultaneous, independent work [11] also showing that strong undirected amplifiers exist. In the remainder of this section, we discuss this work.

First, consider the model of Lieberman, Hauert and Nowak [13, 18] which we study. Our Theorem 2 shows that there is an infinite family of connected graphs  $G$  with  $\ell_r(G) \leq 71/(r(r-1)^2n)^{1/3}$ . Theorem 1 of [11] is similar, but weaker by a logarithmic factor — that paper constructs a (similar) family with extinction probability  $\ell_r(G) = O(\log(n)/((r-1)n^{1/3}))$ . Our Theorem 3 shows that any connected  $n$ -vertex graph (with  $n \geq 3$ ) has  $\ell_r(G) > 1/(42r^{4/3}n^{1/3})$ . Theorem 2 of [11] is similar, but weaker by a  $(\log n)^{4/3}$  factor — that paper shows that the extinction probability  $\ell_r(G)$  is  $\Omega(1/(r^{5/3}n^{1/3}(\log n)^{4/3}))$ .

Our paper is otherwise incomparable to [11]. We give a lower bound on the extinction probability of amplifying *digraphs* (Theorem 1) but [11] does not consider digraphs. We also construct sparse families of incubators (Theorem 6) which go all the way down to constant density and are optimally-amplifying up to constant factors (Theorem 7) but [11] does not consider sparse graphs. On the other hand, [11, Theorem 3] constructs a family of *suppressors* with extinction probability at least  $1 - O(r^2 \log n / n^{1/4})$ , which is something that we do not study here. Finally, Sood et al. [20] have introduced a variant of the model in which the fitness of a mutant is taken to be a function of the number of vertices of the underlying digraph (so as the number of vertices in the digraph grows, the fitness of each individual mutant decreases). The results of [11] extend to this model where  $r = 1 + o(1)$ , as a function of  $n$ . We are not aware of any applications of this model, and we don't consider it.

## 1.2 Organisation of the paper

In Section 2, we define some notation that we will use throughout the paper. In Section 3, we show that, as long as  $b(k)$  is eventually sufficiently large, then the set  $\mathcal{I}_{r,b}$  is infinitely large. In Section 4 we prove Theorems 2 and 6, which give upper bounds on extinction probability. In Section 5, we prove Theorems 1, 3 and 7 which give lower bounds on extinction probability.

## 2 Preliminaries

We write  $\mathbb{Z}_{\geq 1} = \{1, 2, \dots\}$ . For all  $n \in \mathbb{Z}_{\geq 1}$ , we write  $[n] = \{1, \dots, n\}$ . We write  $\log$  for the base- $e$  logarithm and  $\lg$  for the base-2 logarithm.

When  $G = (V, E)$  is a digraph and  $v \in V$ , we write  $N_{\text{in}}(v) = \{w \mid (w, v) \in E\}$ ,  $d_{\text{in}}(v) = |N_{\text{in}}(v)|$ ,  $N_{\text{out}}(v) = \{w \mid (v, w) \in E\}$ , and  $d_{\text{out}}(v) = |N_{\text{out}}(v)|$ . We view undirected graphs (or simply “graphs”) as digraphs such that for all  $u, v \in V$ ,  $(u, v) \in E$  if and only if  $(v, u) \in E$ . Of course, we use standard conventions when counting edges in undirected graphs. That is, an undirected edge  $\{u, v\}$  is only counted as one edge. If  $G$  is undirected, we write  $N(v) = N_{\text{out}}(v) = N_{\text{in}}(v)$  and  $d(v) = d_{\text{out}}(v) = d_{\text{in}}(v)$ . If  $S \subseteq V$ , we write  $N(S) = \bigcup_{v \in S} N(v)$ .

Recall that the initial configuration of the Moran process is the configuration in which one vertex is chosen uniformly at random to be a mutant, and the rest of the vertices are non-mutants. We have already defined  $\ell_r(G)$ , which is the probability that this process reaches extinction. When  $G = (V, E)$  is known from the context and  $v$  is a vertex of  $G$ , it will also be useful to define  $\ell_r(v)$  to be the extinction probability, conditioned on the fact that the initial mutant is  $v$ . In this case,  $\ell_r(G) = \frac{1}{n} \sum_{v \in V} \ell_r(v)$ . More generally, when  $G$  is known from the context and  $U$  is a subset of  $V(G)$ , we define  $\ell_r(U)$  to be the extinction probability, when the process is run starting from the state in which vertices in  $U$  are mutants and vertices in  $V \setminus U$  are non-mutants.

## 3 Infinite sets of incubators

The main result of this Section is Theorem 11, which shows that, as long as  $b(k)$  is eventually sufficiently large, then the set  $\mathcal{I}_{r,b}$  is infinitely large.

If a graph  $G$  has adjacency matrix  $A$  with eigenvalues  $\lambda_1 \geq \dots \geq \lambda_n$ , we let  $\lambda(G) = \max\{\lambda_2, -\lambda_n\}$ . We use two existing results which, between them, imply that a sparse random regular graph is likely to be a small-set expander.

**Theorem 9.** ([2, Theorem 1.1]) Let  $C_0, K > 0$ , and let  $\alpha = 459652 + 229452K + \max\{30C_0^{3/2}, 768\}$ . Let  $n, d \in \mathbb{Z}_{\geq 1}$ , and suppose  $d \leq C_0 n^{2/3}$  and  $n \geq 7 + K^2$ . Let  $G$  be a uniformly random  $d$ -regular graph on  $n$  vertices. Then  $\mathbb{P}(\lambda(G) \leq \alpha\sqrt{d}) \geq 1 - n^{-K}$ .  $\square$

The following theorem is well-known, and follows from, e.g., [21, Theorem 8.6.30].

**Theorem 10.** If  $G = (V, E)$  is a  $d$ -regular  $n$ -vertex graph, and  $S$  is a non-empty proper subset of  $V$ , then  $|E(S, V \setminus S)| \geq (d - \lambda(G)) |S| |V \setminus S| / n$ .  $\square$

**Theorem 11.** Let  $b : \mathbb{Z}_{\geq 1} \rightarrow \mathbb{Z}_{\geq 1}$ . Suppose that for all  $k \in \mathbb{Z}_{\geq 1}$ ,  $b(k) \leq \sqrt{k}$ . Suppose in addition that there are infinitely many  $k$  such that  $b(k) \geq 10^7$ . Then  $\mathcal{I}_{r,b}$  contains infinitely many graphs.

*Proof.* It suffices to prove that for all  $k$  such that  $b(k) \geq 10^7$ , there exists a small-set expander  $H_k$  on  $\beta k$  vertices with degree  $D = \beta b(k)^2 - 1$ . Since  $b(k) \leq \sqrt{k}$ , we have  $0 \leq D \leq \beta k - 1$ . Since  $\beta$  is even, it follows that there exists a regular graph with degree  $D$  on  $\beta k$  vertices. Let  $H$  be a uniformly random such graph, and suppose that  $\emptyset \subset S \subseteq V(H)$  satisfies  $|S| \leq (k\beta)^{1/3}$ .

**Case 1.** If  $D \geq 2(k\beta)^{1/3}$ , then we have

$$|E(S, V(H) \setminus S)| \geq \sum_{v \in S} (d(v) - |S|) \geq D|S| - (k\beta)^{1/3}|S| > D|S|/4.$$

Thus we may take  $H_k = H$  with certainty.

**Case 2.** Suppose instead that  $D \leq 2(k\beta)^{1/3}$ . Now apply Theorem 9 with  $n = \beta k$ ,  $d = D$ ,  $C_0 = 2$  and  $K = 1$ . This shows that  $\mathbb{P}(\lambda(H) \leq \alpha\sqrt{d}) \geq 1 - 1/(\beta k)$ . If  $\lambda(H) \leq \alpha\sqrt{d}$  then using Theorem 10,

$$|E(S, V \setminus S)| \geq (D - \alpha\sqrt{D}) \frac{|S|(k\beta - |S|)}{k\beta} \geq (D - \alpha\sqrt{D}) \frac{|S|}{2}.$$

To show that  $H$  is a small-set expander, we need only show that  $\alpha\sqrt{D} \leq D/2$ . This follows from the definitions of  $\alpha$  and  $D$  using  $\beta \geq 26$  and  $b(k) \geq 10^7$ . Since  $H$  is a small-set expander with non-zero probability, there exists a small-set expander on  $\beta k$  vertices with degree  $D$ , as required.  $\square$

Theorem 11 shows that the set  $\mathcal{I}_{r,b}$  is infinitely large, as long as there are infinitely many  $k$  such that  $b(k) \geq 10^7$ . This is sufficient for our purposes, since our goal is to show that there are infinitely-many incubators, even with constant density. However, the condition that  $b(k) \geq 10^7$  is not necessary. The lower bound could be weakened substantially by replacing the use of Theorem 9 with the result of Friedman [9] when  $b(k) < 10^7$ .

## 4 Upper bounding the extinction probability of incubators

In this section, we prove Theorems 2 and 6. For this, it will be useful to have a more formal definition of the Moran process, which defines some notation that we will use.

**Definition 12.** Let  $G = (V, E)$  be an  $n$ -vertex digraph, let  $r > 1$ , and let  $x_0 \in V$ . We define the *Moran process*  $(X_t)_{t \geq 0}$  on  $G$  with fitness  $r$  and initial mutant  $x_0$  inductively as follows, where all random choices are made independently. Let  $X_0 = \{x_0\}$ . For all  $S \subseteq V$ , let  $W(S) = n + (r - 1)|S|$ . Given  $X_t$  for some  $t \geq 0$ , we define  $X_{t+1}$  as follows. Randomly choose a vertex  $v_t \in V$  with distribution

$$\mathbb{P}(v_t = v) = \begin{cases} r/W(X_t) & \text{if } v \in X_t; \\ 1/W(X_t) & \text{if } v \in V \setminus X_t. \end{cases}$$

If  $d_{\text{out}}(v_t) = 0$ , then  $X_{t+1} = X_t$ . Otherwise, choose  $w_t \in N_{\text{out}}(v_t)$  uniformly at random. If  $v_t \in X_t$ , then  $X_{t+1} = X_t \cup \{w_t\}$ , and we say  $v_t$  *spawns a mutant onto*  $w_t$  *at time*  $t + 1$ . Otherwise,  $X_{t+1} = X_t \setminus \{w_t\}$ , and we say  $v_t$  *spawns a non-mutant onto*  $w_t$  *at time*  $t + 1$ .

If there exists  $t$  such that  $X_t = \emptyset$ , we say the process *goes extinct* at time  $t$ , and if there exists  $t$  such that  $X_t = V$ , we say the process *fixates* at time  $t$ . In either case, we say the process *absorbs* at time  $t$ .

Note that Moran processes are discrete-time Markov chains, and that nothing happens if (e.g.) a mutant is spawned onto a mutant. The notation  $v_1, v_2, \dots$  and  $w_1, w_2, \dots$  is not used outside Definition 12.

Incubators are defined in Definition 5 on page 3. Whenever we discuss a specific graph  $G = (V, E) \in \mathcal{I}_{r,b}$ , we will use the notation  $V_1, V_2, V_3, k$  and  $\beta$  from Definition 5 without explicitly redefining it. We use  $b$  as shorthand for  $b(k)$ . Because the final theorem assumes  $b \geq b_0$  for a constant  $b_0$ , depending on  $r$ , it will do no harm to assume that  $b$  is sufficiently large. To avoid cluttering the notation, we assume  $b \geq 6r$  everywhere, and we mention it explicitly only if we use a stronger bound. For all  $v \in V_1$ , we write  $c(v)$  for the (necessarily) unique neighbour of  $v$  in  $V_2$ .

#### 4.1 Going from a mutant in $V_1$ to many mutants in $V_3$

Our goal in this subsection is to prove Lemma 26, which says that if the initial mutant is in  $V_1$ , then with probability at least roughly  $1 - 1/b$  the process will eventually obtain  $\lfloor b^{1/3} \rfloor$  mutants in  $V_3$ . To prove this lemma, we will couple the evolution of mutants in  $V_3$  with the following Markov chain.

**Definition 13.** Throughout the rest of the section, let  $\gamma = \lfloor (k\beta)^{1/3} \rfloor$  and  $r' = (1 + r)/2$ . Define  $(Y_t)_{t \geq 0}$  to be a discrete-time Markov chain with state space  $\mathcal{S}_Y = \{F, 0, 1, \dots, \gamma + 1\}$ , initial state 0, and the following transition matrix:

$$\begin{aligned} p_{F,F} &= 1, \\ p_{0,F} &= \frac{6}{r\beta^{1/2}b}, \quad p_{0,0} = \left(1 - \frac{6}{r\beta^{1/2}b}\right) \frac{1}{1+r'}, \quad p_{0,1} = \left(1 - \frac{6}{r\beta^{1/2}b}\right) \frac{r'}{1+r'}, \\ \text{for all } 1 \leq i \leq \gamma, \quad p_{i,F} &= \frac{10}{r\beta b^2}, \quad p_{i,i-1} = \left(1 - \frac{10}{r\beta b^2}\right) \frac{1}{1+r'}, \quad p_{i,i+1} = \left(1 - \frac{10}{r\beta b^2}\right) \frac{r'}{1+r'}, \\ p_{\gamma+1,\gamma+1} &= 1, \end{aligned}$$

and  $p_{i,j} = 0$  for all other  $i, j \in \mathcal{S}_Y$ .

Our coupling is defined formally in Lemma 21 and will have the property that for all  $i \geq 0$ , if  $Y_i \neq F$ , then there exists  $t \geq 0$  such that  $|X_t \cap V_3| \geq Y_i$ . The “failure state”  $F$  in the state space of  $Y$  is used in the coupling to capture the possibility that the initial mutant (in  $V_1$ ) dies before the  $\lfloor b^{1/3} \rfloor$  mutants are obtained in  $V_3$ . Using the coupling, we prove Lemma 26 by using standard techniques to show that  $Y$  is likely to reach  $\lfloor b^{1/3} \rfloor$  before reaching the failure state  $F$ . We next define some stopping times which will be important to the coupling.

**Definition 14.** Let

$$T_{\text{end}} = \min\{t \geq 0 \mid X_t \cap V_1 = \emptyset \text{ or } |X_t \cap V_3| = \gamma + 1\}.$$

Note that  $T_{\text{end}}$  is finite with probability 1. Define  $T_0, T_1, \dots$  recursively by  $T_0 = 0$  and

$$T_i = \min(\{T_{\text{end}}\} \cup \{t > T_{i-1} \mid X_t \cap V_3 \neq X_{t-1} \cap V_3\}).$$

If  $T_{\text{end}} = 0$  then  $T_0, T_1, \dots$  are all 0. Otherwise, with probability 1, there is a  $j$  such that  $T_0 < \dots < T_j$  and, for all  $i \geq j$ ,  $T_j = T_{\text{end}}$ . The  $T_j$ 's will be used as update times in our coupling, and  $T_{\text{end}}$  will be used as a decoupling time; if  $T_j < T_{\text{end}}$ , then  $Y_{j+1}$  will depend on  $X_{T_{j+1}}$ , and otherwise the two processes will evolve independently. Thus in order to construct the coupling, we will need assorted bounds on the behaviour of  $X_{T_j}$  subject to  $T_j < T_{\text{end}}$ .

We first deal with the case where  $V_3$  contains at least one mutant at time  $T_j < T_{\text{end}}$ . We require an upper bound on the probability that  $X_{T_{j+1}} \cap V_1 = \emptyset$ , and on the probability that  $|X_{T_{j+1}} \cap V_3| = |X_{T_j} \cap V_3| - 1$ . These bounds are given in Lemma 17. Proving them will require that  $|X_{T_j} \cap V_3| \leq \gamma$ , which is true since  $T_j < T_{\text{end}}$ . To simplify the presentation, we first do the relevant calculations in the following two technical lemmas.

**Lemma 15.** Let  $t \geq 0$ , let  $M \subseteq V$ , and suppose  $1 \leq |M \cap V_3| \leq \gamma$ . Then we have

$$\begin{aligned} \mathbb{P}(|X_{t+1} \cap V_3| = |X_t \cap V_3| + 1 \mid X_t = M) &\geq \frac{r|E(V_3 \cap M, V_3 \setminus M)|}{W(M)(\beta b^2 + b^2 - 1)}, \\ \mathbb{P}(|X_{t+1} \cap V_3| = |X_t \cap V_3| - 1 \mid X_t = M) &\leq \left(1 + \frac{5}{\beta}\right) \frac{|E(V_3 \cap M, V_3 \setminus M)|}{W(M)(\beta b^2 + b^2 - 1)}. \end{aligned}$$



Moreover, if  $M \cap V_1 \neq \emptyset$ , then

$$\mathbb{P}(X_{t+1} \cap V_1 = \emptyset \mid X_t = M) \leq \frac{1}{W(M)\beta b^2}.$$

*Proof.* For brevity, write  $M' = M \cap V_3$ . For the first equation, note that  $|X_t \cap V_3|$  increases whenever a vertex in  $M'$  spawns a mutant onto a vertex in  $V_3 \setminus M'$ . We therefore have

$$\begin{aligned} \mathbb{P}(|X_{t+1} \cap V_3| = |X_t \cap V_3| + 1 \mid X_t = M) &\geq \sum_{v \in M'} \frac{r}{W(M)} \cdot \frac{|N(v) \cap (V_3 \setminus M')|}{d(v)} \\ &= \frac{r|E(M', V_3 \setminus M')|}{W(M)(\beta b^2 + b^2 - 1)}, \end{aligned}$$

as required.

For the second equation, note that  $|X_t \cap V_3|$  decreases precisely when a vertex in  $(V_2 \cup V_3) \setminus M$  spawns a non-mutant onto a vertex in  $M'$ . It follows that

$$\begin{aligned} \mathbb{P}(|X_{t+1} \cap V_3| = |X_t \cap V_3| - 1 \mid X_t = M) &= \sum_{v \in (V_2 \cup V_3) \setminus M} \frac{1}{W(M)} \cdot \frac{|N(v) \cap M'|}{d(v)} \\ &\leq \frac{|E(V_2, M')|}{W(M)(\beta b^2 + \lceil r\beta^{1/2}b \rceil)} + \frac{|E(M', V_3 \setminus M')|}{W(M)(\beta b^2 + b^2 - 1)}. \end{aligned}$$

Recall from Definition 5(v) that  $G[V_3]$  is a small-set expander, and  $1 \leq |M'| \leq \gamma \leq |V_3|^{1/3}$  by hypothesis, so since  $\beta \geq 26$  we have

$$\frac{|E(M', V_3 \setminus M')|}{\beta b^2 + b^2 - 1} \geq \frac{(\beta b^2 - 1)|M'|}{4(\beta b^2 + b^2 - 1)} \geq \frac{|M'|}{5}.$$

Moreover, since every vertex in  $V_3$  has degree  $b^2$  into  $V_2$ ,

$$\frac{|E(V_2, M')|}{\beta b^2 + \lceil r\beta^{1/2}b \rceil} \leq \frac{b^2|M'|}{\beta b^2} = \frac{|M'|}{\beta}.$$

It follows that

$$\mathbb{P}(|X_{t+1} \cap V_3| = |X_t \cap V_3| - 1 \mid X_t = M) \leq \left(1 + \frac{5}{\beta}\right) \frac{|E(M', V_3 \setminus M')|}{W(M)(\beta b^2 + b^2 - 1)},$$

as required.

For the third equation, recall that, by hypothesis,  $M \cap V_1 \neq \emptyset$ . For brevity, write  $p = \mathbb{P}(X_{t+1} \cap V_1 = \emptyset \mid X_t = M)$ . Note that if  $|M \cap V_1| > 1$  then  $p = 0$ . Suppose instead that  $M \cap V_1 = \{v_0\}$  for some  $v_0 \in V$ . Note that  $v_0$  can only become a non-mutant if its unique neighbour  $c(v_0)$  spawns a non-mutant onto it. Thus, if  $c(v_0) \in M$ ,  $p = 0$ . If  $c(v_0) \notin M$ , we have

$$p = \frac{1}{W(M)} \cdot \frac{1}{\lceil r\beta^{1/2}b \rceil + \beta b^2} \leq \frac{1}{W(M)\beta b^2}.$$

The desired inequality therefore holds in all cases.  $\square$

**Lemma 16.**

$$\frac{1 + 5/\beta}{r + 1 + 5/\beta} \leq \frac{1}{1 + r'} - \frac{10}{r\beta b^2}.$$

*Proof.*

$$\frac{1 + 5/\beta}{r + 1 + 5/\beta} \leq \frac{1 + 5(r-1)/(26r^2)}{1+r} \leq \frac{1}{1+r} + \frac{r-1}{5r^2(r+1)}.$$

Moreover, since  $r' = (r+1)/2$  and  $b \geq 6$  we have

$$\begin{aligned} \frac{1}{1+r'} - \frac{1}{1+r} - \frac{10}{r\beta b^2} &\geq \frac{2}{3+r} - \frac{1}{1+r} - \frac{10(r-1)}{900r^3} \geq \frac{r-1}{(r+1)(r+3)} - \frac{r-1}{90r^2} \\ &\geq \frac{r-1}{(r+1)(r+3)} - \frac{4(r-1)}{45(r+1)(r+3)} \\ &= \frac{41(r-1)}{45(r+1)(r+3)} \geq \frac{41(r-1)}{180r^2(r+1)} > \frac{r-1}{5r^2(r+1)}. \end{aligned}$$

□

**Lemma 17.** *Let  $t \geq 0$ , let  $j \geq 0$ , let  $M \subseteq V$ , and suppose  $1 \leq |M \cap V_3| \leq \gamma$  and  $M \cap V_1 \neq \emptyset$ . Then we have*

$$\begin{aligned} \mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid X_t = M, T_j = t \neq T_{\text{end}}) &\leq p_{1,F}, \text{ and} \\ \mathbb{P}(|X_{T_{j+1}} \cap V_3| = |X_{T_j} \cap V_3| - 1 \mid X_t = M, T_j = t \neq T_{\text{end}}) &\leq p_{1,0}. \end{aligned}$$

*Proof.* Write  $\mathcal{F}$  for the event that  $X_t = M$  and  $T_j = t \neq T_{\text{end}}$ . Throughout, suppose that  $\mathcal{F}$  occurs. First note that this implies

$$T_{j+1} = \min\{t' > t \mid X_{t'} \cap V_3 \neq X_t \cap V_3 \text{ or } X_{t'} \cap V_1 = \emptyset\}. \quad (1)$$

Now consider some non-negative integer  $i$ . For  $M' \subseteq V$ , let

$$q_i^{M'} = \mathbb{P}(T_{j+1} = t + i + 1 \text{ and } X_{t+i} = M' \mid \mathcal{F}).$$

Let  $\mathcal{M}_i = \{M' \subseteq V \mid q_i^{M'} \neq 0\}$ . For all  $M' \in \mathcal{M}_i$ , let

$$\begin{aligned} p_{\text{down},i}^{M'} &= \mathbb{P}(|X_{t+i+1} \cap V_3| = |X_{t+i} \cap V_3| - 1 \mid X_{t+i} = M', T_{j+1} = t + i + 1, \mathcal{F}), \\ p_{\text{fail},i}^{M'} &= \mathbb{P}(X_{t+i+1} \cap V_1 = \emptyset \mid X_{t+i} = M', T_{j+1} = t + i + 1, \mathcal{F}). \end{aligned}$$

Note that if  $M' \in \mathcal{M}_i$ , then  $M' \cap V_1 \neq \emptyset$ . Also,  $M' \cap V_3 = M \cap V_3$ , so  $1 \leq |M' \cap V_3| \leq \gamma$ . If  $X_{t+i} = M'$ , then the three events  $|X_{t+i+1} \cap V_3| = |M' \cap V_3| + 1$ ,  $|X_{t+i+1} \cap V_3| = |M' \cap V_3| - 1$  and  $X_{t+i+1} \cap V_1 = \emptyset$  are disjoint, and (by (1)) conditioning on  $T_{j+1} = t + i + 1$  is precisely equivalent to conditioning on one of the three events occurring. For brevity, write  $x(M') = |E(V_3 \cap M', V_3 \setminus M')|$  and  $y = \beta b^2 + b^2 - 1$ . It follows by Lemma 15 (with Lemma 15's  $t$  equal to our  $t + i$  and Lemma 15's  $M$  equal to our  $M'$ ) that for all  $M' \in \mathcal{M}_i$ ,

$$p_{\text{fail},i}^{M'} \leq \frac{1/(W(M')\beta b^2)}{rx(M')/(W(M')y)} = \frac{y}{rx(M')\beta b^2}.$$

Recall that  $G[V_3]$  is a small-set expander and, for  $M' \subseteq \mathcal{M}_i$ ,  $|M' \cap V_3| = |M \cap V_3| \leq \gamma \leq |V_3|^{1/3}$ , and so

$$x(M') \geq (\beta b^2 - 1)|M' \cap V_3|/4 \geq \beta b^2|M \cap V_3|/5 \geq \beta b^2/5.$$

Moreover,  $y \leq 2\beta b^2$ . It follows that

$$p_{\text{fail},i}^{M'} \leq \frac{10}{r\beta b^2} = p_{1,\text{F}}. \quad (2)$$

Similarly, it follows by Lemma 15 and Lemma 16 that

$$\begin{aligned} p_{\text{down},i}^{M'} &\leq \frac{(1 + 5/\beta)x(M')/(W(M')y)}{rx(M')/(W(M')y) + (1 + 5/\beta)x(M')/(W(M')y)} \\ &= \frac{1 + 5/\beta}{r + 1 + 5/\beta} \leq \left(1 - \frac{10}{r\beta b^2}\right) \frac{1}{1 + r'} = p_{1,0}. \end{aligned} \quad (3)$$

Now, by the law of total probability and (2), we have

$$\mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid \mathcal{F}) = \sum_{i \geq 0} \sum_{M' \in \mathcal{M}_i} p_{\text{fail},i}^{M'} q_i^{M'} \leq p_{1,\text{F}} \sum_{i \geq 0} \sum_{M' \in \mathcal{M}_i} q_i^{M'} = p_{1,\text{F}},$$

and so the first equation of the lemma statement follows. Similarly, the second equation follows from (3).  $\square$

In Lemma 17, we gave the necessary bounds to ensure that our coupling works when  $V_3$  contains at least one mutant at time  $T_j < T_{\text{end}}$ . We now do the same when  $V_3$  contains no mutants. Since in this case  $T_{j+1}$  is the first time after  $T_j$  at which  $V_3$  contains a mutant or  $V_1$  contains no mutants, we must show that  $V_3$  is likely to gain a mutant after  $T_j$ . For this we will need the fact that  $X_{T_j} \cap V_1 \neq \emptyset$ , which holds because  $T_j < T_{\text{end}}$ . We first prove the following ancillary lemma.

**Lemma 18.** *Let  $t \geq 0$ , let  $M \subseteq V$ , and suppose  $M \cap V_1 \neq \emptyset$ . Then there exists a stopping time  $T^{++} > t$  such that the following hold:*

- (i)  $\mathbb{P}(T^{++} < \infty \mid X_t = M) = 1$ ;
- (ii)  $\mathbb{P}(X_{t'} \cap V_1 = \emptyset \text{ for some } t < t' \leq T^{++} \mid X_t = M) \leq 1/(r\beta b^2)$ ;
- (iii)  $\mathbb{P}(|X_{T^{++}} \cap V_3| \geq 1 \mid X_t = M) \geq 1/(6\beta^{1/2}b)$ .

*Proof.* Let  $v_0 \in V_1 \cap M$  be arbitrary, and recall that  $c(v_0)$  is the unique neighbour of  $v_0$ . Let  $T^+$  be the minimum  $t' > t$  such that at time  $t'$ , either  $v_0$  spawns or  $c(v_0)$  spawns a non-mutant onto  $v_0$ . Let  $T^{++}$  be the minimum  $t' > T^+$  such that at time  $t'$ , either  $c(v_0)$  spawns onto some vertex in  $V_3$  or a neighbour of  $c(v_0)$  spawns a non-mutant onto  $c(v_0)$ . Note that since each vertex in  $V$  spawns infinitely often with probability 1, (i) holds.

For all  $i \geq 0$  and all  $M_i \subseteq V$  with  $v_0 \in M_i$ , we have

$$\begin{aligned} \mathbb{P}(v_0 \text{ spawns at } t + i + 1 \mid X_{t+i} = M_i) &= r/W(M_i), \\ \mathbb{P}(c(v_0) \text{ spawns a non-mutant onto } v_0 \text{ at } t + i + 1 \mid X_{t+i} = M_i) &\leq 1/(\beta b^2 W(M_i)). \end{aligned}$$

Write  $p_i^{M'} = \mathbb{P}(T^+ = t + i + 1, X_{t+i} = M' \mid X_t = M)$ . Then since  $v_0 \in V_1 \cap M$  and  $v_0$  remains a mutant throughout  $\{t, t + 1, \dots, T^+ - 1\}$ , it follows by the law of total probability applied

to  $T^+$  that

$$\begin{aligned}
\mathbb{P}(v_0 \in X_{T^+} \text{ and } v_0 \text{ spawns at } T^+ \mid X_t = M) &= \mathbb{P}(v_0 \text{ spawns at } X_{T^+} \mid X_t = M) \\
&\geq \sum_{i \geq 0} \sum_{\substack{M' \subseteq V \\ v_0 \in M'}} \frac{r/W(M')}{r/W(M') + 1/(\beta b^2 W(M'))} \cdot p_i^{M'} \\
&= \frac{r}{r + 1/(\beta b^2)} \geq 1 - \frac{1}{r\beta b^2}. \tag{4}
\end{aligned}$$

If  $v_0 \in X_{T^+}$  and  $v_0$  spawns at  $T^+$ , it follows that  $c(v_0) \in X_{T^+}$ . By the definition of  $T^{++}$ , it therefore follows that  $c(v_0) \in X_{t'}$  for all  $T^+ \leq t' \leq T^{++} - 1$ , and so  $c(v_0)$  does not spawn a non-mutant onto  $v_0$  at any time in  $\{T^+ + 1, \dots, T^{++}\}$ . Hence, (ii) follows from (4).

Now, for all  $i \geq 0$  and all  $M_i \subseteq V$  with  $c(v_0) \in M_i$ , since  $\beta \geq 26r$  and  $b \geq 6r$  we have

$$\mathbb{P}(c(v_0) \text{ spawns into } V_3 \text{ at } t+i+1 \mid X_{t+i} = M_i) \geq \frac{r}{W(M_i)} \cdot \frac{\beta b^2}{\beta b^2 + \lceil r\beta^{1/2}b \rceil} \geq \frac{r}{2W(M_i)}.$$

Moreover, writing  $\mathcal{E}$  for the event that some  $v \in V \setminus X_{t+i}$  spawns onto  $c(v_0)$  at time  $t+i+1$ , we have

$$\mathbb{P}(\mathcal{E} \mid X_{t+i} = M_i) \leq \frac{\lceil r\beta^{1/2}b \rceil}{W(M_i)} + \frac{\beta b^2}{W(M_i)} \cdot \frac{1}{\beta b^2 + b^2 - 1} \leq \frac{r\beta^{1/2}b + 1}{W(M_i)} + \frac{1}{W(M_i)} \leq \frac{2r\beta^{1/2}b}{W(M_i)}.$$

Now, suppose that  $M^+ \subseteq V$  and  $t^+ > t$  are such that  $\mathbb{P}(X_{t^+} = M^+ \text{ and } T^+ = t^+ \mid X_t = M) \neq 0$  and  $c(v_0) \in M^+$ . Write

$$q_i^{M^{++}} = \mathbb{P}(T^{++} = t^+ + i + 1, X_{t^++} = M^{++} \mid T^+ = t^+, X_{t^+} = M^+).$$

Since when  $X_{t^+} = M^+$  and  $T^+ = t^+$ ,  $c(v_0)$  remains a mutant throughout  $\{T^+, \dots, T^{++} - 1\}$ , by the law of total probability applied to  $T^{++}$  it follows that

$$\begin{aligned}
\mathbb{P}(X_{T^{++}} \cap V_3 \neq \emptyset \mid T^+ = t^+, X_{t^+} = M^+) &\geq \sum_{i \geq 0} \sum_{\substack{M^{++} \subseteq V \\ c(v_0) \in M^{++}}} \frac{r/(2W(M^{++}))}{r/(2W(M^{++})) + 2r\beta^{1/2}b/W(M^{++})} q_i^{M^{++}} \\
&= \frac{1}{1 + 4\beta^{1/2}b} \geq \frac{1}{5\beta^{1/2}b}.
\end{aligned}$$

It therefore follows from the law of total probability applied to  $T^+$  and (4) that

$$\begin{aligned}
\mathbb{P}(X_{T^{++}} \cap V_3 \neq \emptyset \mid X_t = M) &\geq \sum_{t^+ > t} \sum_{\substack{M^+ \subseteq V \\ v_0 \in M^+}} \mathbb{P}(X_{T^{++}} \cap V_3 \neq \emptyset, T^+ = t^+, X_{t^+} = M^+ \mid X_t = M) \\
&\geq \frac{1}{5\beta^{1/2}b} \mathbb{P}(v_0 \in X_{T^+} \mid X_t = M) \geq \frac{1}{5\beta^{1/2}b} - \frac{1}{r\beta b^2} \geq \frac{1}{6\beta^{1/2}b}.
\end{aligned}$$

Hence (iii) follows.  $\square$

Lemma 19 is then proved by repeatedly applying Lemma 18.

**Lemma 19.** *Let  $t \geq 0$ , let  $j \geq 0$ , let  $M \subseteq V$ , and suppose  $M \cap V_1 \neq \emptyset$  and  $M \cap V_3 = \emptyset$ . Then  $\mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid X_t = M, T_j = t \neq T_{\text{end}}) \leq p_{0,F}$ .*

*Proof.* Write  $\mathcal{F}$  for the event that  $X_t = M$  and that  $T_j = t \neq T_{\text{end}}$ , and suppose throughout that  $\mathcal{F}$  occurs. Thus, by definition,  $T_{j+1}$  is precisely the earliest time  $t' > t$  such that  $X_{t'} \cap V_3 \neq \emptyset$  or  $X_{t'} \cap V_1 = \emptyset$ .

Define stopping times  $\tau_0, \tau_1, \dots$  inductively as follows. Let  $\tau_0 = t$ . If  $\tau_i < T_{j+1}$ , then we must have  $X_{\tau_i} \cap V_1 \neq \emptyset$ , so we define  $\tau_{i+1}$  to be the stopping time  $T^{++}$  obtained by applying Lemma 18 with  $t = \tau_i$  and  $M = X_{\tau_i}$ . Note that in this case  $\tau_{i+1} > \tau_i$ . If  $\tau_i \geq T_{j+1}$ , we set  $\tau_{i+1} = \tau_i$ .

For every  $i \geq 0$ , every  $M_i \subseteq V$  with  $M_i \cap V_1 \neq \emptyset$  and  $M_i \cap V_3 = \emptyset$ , and every  $t' \geq t$ , write  $\mathcal{F}_{i,M_i,t'}$  for the event that  $\tau_i = t'$ ,  $X_{t'} = M_i$ ,  $t' < T_{j+1}$  and  $\mathcal{F}$  occurs. By Lemma 18, we have

$$\mathbb{P}(T_{j+1} \in (\tau_i, \tau_{i+1}] \mid \mathcal{F}_{i,M_i,t'}) \geq \mathbb{P}(|X_{\tau_{i+1}} \cap V_3| \geq 1 \mid \mathcal{F}_{i,M_i,t'}) \geq 1/(6\beta^{1/2}b),$$

and

$$\mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \text{ and } T_{j+1} \in (\tau_i, \tau_{i+1}] \mid \mathcal{F}_{i,M_i,t'}) \leq 1/(r\beta b^2).$$

It follows that

$$\mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid \mathcal{F}_{i,M_i,t'} \text{ and } T_{j+1} \in (\tau_i, \tau_{i+1}]) \leq \frac{1/(r\beta b^2)}{1/(6\beta^{1/2}b)} = p_{0,\mathbf{F}}.$$

Thus, writing  $\mathcal{F}'_{i,M_i,t'}$  for the event that  $\mathcal{F}_{i,M_i,t'}$  occurs and  $T_{j+1} \in (\tau_i, \tau_{i+1}]$ , we have

$$\mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid \mathcal{F}) = \sum_{i,M_i,t'} \mathbb{P}(X_{T_{j+1}} \cap V_1 = \emptyset \mid \mathcal{F}'_{i,M_i,t'}) \mathbb{P}(\mathcal{F}'_{i,M_i,t'} \mid \mathcal{F}) \leq p_{0,\mathbf{F}}$$

which proves the lemma.  $\square$

We now collect the bounds of Lemmas 17 and 19 into a single lemma.

**Lemma 20.** *Let  $i \geq 0$ ,  $t_i \geq 0$ ,  $M \subseteq V$  and  $y \geq 0$ . Suppose that  $y \leq |M \cap V_3| \leq \gamma$  and  $M \cap V_1 \neq \emptyset$ . Write  $\mathcal{F}$  for the event that  $X_{t_i} = M$  and  $T_i = t_i \neq T_{\text{end}}$ . Then, we have  $\mathbb{P}(X_{T_{i+1}} \cap V_1 = \emptyset \mid \mathcal{F}) \leq p_{y,\mathbf{F}}$  and*

$$\mathbb{P}(X_{T_{i+1}} \cap V_1 = \emptyset \mid \mathcal{F}) + \mathbb{P}(|X_{T_{i+1}} \cap V_3| = |X_{T_i} \cap V_3| - 1 \mid \mathcal{F}) \leq 1 - p_{y,y+1}.$$

*Proof.* If  $y > 0$ , so that  $M \cap V_3 \neq \emptyset$ , then the result follows by Lemma 17. If instead  $y = 0$  and  $M \cap V_3 = \emptyset$ , then the result follows by Lemma 19 (using the observation that  $\mathbb{P}(|X_{T_{i+1}} \cap V_3| = |X_{T_i} \cap V_3| - 1 \mid \mathcal{F}) = 0$  and  $p_{0,\mathbf{F}} \leq 1 - p_{0,1}$ ). Finally, suppose  $y = 0$  and  $M \cap V_3 \neq \emptyset$ . Then by Lemma 17, we have  $\mathbb{P}(X_{T_{i+1}} \cap V_1 = \emptyset \mid \mathcal{F}) \leq p_{1,\mathbf{F}} < p_{0,\mathbf{F}}$ , and

$$\mathbb{P}(X_{T_{i+1}} \cap V_1 = \emptyset \mid \mathcal{F}) + \mathbb{P}(|X_{T_{i+1}} \cap V_3| = |X_{T_i} \cap V_3| - 1 \mid \mathcal{F}) \leq p_{1,\mathbf{F}} + p_{1,0} = 1 - p_{1,2} < 1 - p_{0,1}.$$

Thus, the result follows in all cases.  $\square$

We are now finally in a position to define our coupling.

**Lemma 21.** *Suppose  $X_0 \cap V_1 \neq \emptyset$ . Then, there exists a coupling  $\Phi(X, Y)$  between  $(X_t)_{t \geq 0}$  and  $(Y_t)_{t \geq 0}$  such that for all  $i \geq 0$  with  $Y_i \neq \mathbf{F}$ , there exists  $t \leq T_i$  such that  $|X_t \cap V_3| \geq Y_i$ .*

*Proof.* We will construct a coupling  $\Phi(X, Y)$  such that the following properties hold for every non-negative integer  $j$ .

1. If  $T_j < T_{\text{end}}$ , then either  $Y_j = \text{F}$  or  $|X_{T_j} \cap V_3| \geq Y_j$ .
2. If  $T_j = T_{\text{end}}$  and  $j = \min\{s \geq 0 \mid T_s = T_{\text{end}}\}$  and  $|X_{T_j} \cap V_3| = \gamma + 1$ , then either  $Y_j = \text{F}$  or  $|X_{T_j} \cap V_3| \geq Y_j$ .
3. If  $T_j = T_{\text{end}}$  and  $j = \min\{s \geq 0 \mid T_s = T_{\text{end}}\}$  and  $X_{T_j} \cap V_1 = \emptyset$ , then  $Y_j = \text{F}$ .

First, we observe that a coupling satisfying Properties 1–3 would satisfy the condition in the statement of the lemma. To see this, consider some non-negative integer  $i$  for which we want to establish the condition in the statement of the lemma (that  $Y_i = \text{F}$  or there exists  $t \leq T_i$  such that  $|X_t \cap V_3| \geq Y_i$ ). If  $T_i < T_{\text{end}}$  then this follows from Property 1 with  $j = i$  and  $t = T_i$ . If  $T_i = T_{\text{end}}$  and  $i = \min\{s \geq 0 \mid T_s = T_{\text{end}}\}$ , then it follows from Properties 2 and 3 with  $j = i$  and  $t = T_i$ . Otherwise, there is a non-negative integer  $j < i$  such that  $T_j = T_{\text{end}}$  and  $j = \min\{s \geq 0 \mid T_s = T_{\text{end}}\}$ . Properties 2 and 3 guarantee that  $Y_j = \text{F}$  (in which case the definition of  $Y$  ensures that  $Y_i = \text{F}$  so the condition is satisfied) or  $|X_{T_j} \cap V_3| = \gamma + 1$  so (by the definition of  $Y$ )  $Y_i \leq |X_{T_j} \cap V_3|$  and taking  $t = T_j$  satisfies the condition.

In order to construct the coupling, it will be useful to have some notation. Given a coupling  $\Phi(X, Y)$  and a non-negative integer  $j$ , let  $\Phi^j$  denote the initial sequence  $(X_0, \dots, X_{T_j}, Y_0, \dots, Y_j)$ . We will construct  $\Phi(X, Y)$  by induction on  $j$ , using  $\Phi^j$  (and some randomness) to construct  $\Phi^{j+1}$ . To do this, we have to ensure that Properties 1–3 are satisfied, and also that the coupling is valid, in the sense that

- The marginal distribution of  $X_{T_j+1}, \dots, X_{T_{j+1}}$  is correct, given  $X_{T_j}$  and given whether or not  $T_j < T_{\text{end}}$  (which can be deduced from  $X_0, \dots, X_{T_j}$ ), and
- The marginal distribution of  $Y_{j+1}$  is correct, given  $Y_j$ .

Note that  $\Phi^0 = (X_0, 0)$  satisfies Properties 1–3 (for Property 3 it is important that  $X_0 \cap V_1 \neq \emptyset$  and this is guaranteed in the statement of the lemma) so we now show how to construct  $\Phi^{j+1}$ , given  $\Phi^j$ . In fact, if  $T_{\text{end}} \leq T_j$  then any coupling  $\Phi(X, Y)$  which is consistent with  $\Phi^j$  and satisfies the two marginal distributions is fine (since the three properties are irrelevant for  $T_i$  with  $i > j$ ). So we will not consider this case. However, if  $T_j < T_{\text{end}}$  we will show how to construct  $\Phi^{j+1}$ .

- **If  $Y_j = \text{F}$ :** The definition of  $Y$  guarantees that  $Y_{j+1} = \text{F}$ . This satisfies all three properties, so let  $X_{T_j+1}, \dots, X_{T_{j+1}}$  evolve independently of  $Y_{j+1}$  according to its correct marginal distribution, given  $X_{T_j}$  and given the fact that  $T_j < T_{\text{end}}$ .
- **If  $Y_j \neq \text{F}$ :** Let  $\mathcal{E}_{\text{F}}$  be the event that  $X_{T_{j+1}} \cap V_1 = \emptyset$  and let  $p_{\text{F}}$  denote the probability that  $\mathcal{E}_{\text{F}}$  occurs in the correct marginal distribution (which depends only on  $X_{T_j}$ , noting that  $T_j < T_{\text{end}}$ ). Let  $\mathcal{E}_{\text{down}}$  be the event that  $|X_{T_{j+1}} \cap V_3| = |X_{T_j} \cap V_3| - 1$  and let  $p_{\text{down}}$  be the probability that  $\mathcal{E}_{\text{down}}$  occurs in the same marginal distribution. Note that  $\mathcal{E}_{\text{F}}$  and  $\mathcal{E}_{\text{down}}$  are disjoint, since  $T_j < T_{\text{end}}$ . Let  $\mathcal{E}_{\text{up}}$  be the event that  $|X_{T_{j+1}} \cap V_3| = |X_{T_j} \cap V_3| + 1$ . In the marginal distribution, this occurs with probability  $1 - p_{\text{F}} - p_{\text{down}}$ . By Property 1 and the definition of  $T_{\text{end}}$ , we have  $0 \leq Y_j \leq |X_{T_j} \cap V_3| \leq \gamma$ . Now Lemma 20 (with  $i = j$ ,  $t_i = T_j$ ,  $M = X_{T_j}$  and  $y = Y_j$ ) shows that  $p_{\text{F}} \leq p_{Y_j, \text{F}}$  and  $p_{\text{F}} + p_{\text{down}} \leq 1 - p_{Y_j, Y_{j+1}}$ . The quantity  $1 - p_{Y_j, Y_{j+1}}$  is either  $p_{Y_j, \text{F}} + p_{Y_j, Y_{j-1}}$ , if  $Y_j > 0$ , or  $p_{Y_j, \text{F}} + p_{Y_j, Y_j}$ , if  $Y_j = 0$ . To unify these cases, let  $p_{Y_j, \text{down}}$  be  $p_{Y_j, Y_{j-1}}$  if  $Y_j > 0$  and  $p_{Y_j, Y_j}$  if  $Y_j = 0$ . Then we have

$$p_{\text{F}} \leq p_{Y_j, \text{F}} \text{ and } p_{\text{F}} + p_{\text{down}} \leq p_{Y_j, \text{F}} + p_{Y_j, \text{down}}. \quad (5)$$

The coupling is as follows: Choose  $X_{T_j+1}, \dots, X_{T_{j+1}}$  according to the correct marginal distribution.

- $\mathcal{E}_F$  happens with probability  $p_F \leq p_{Y_j, F}$ . When this happens, set  $Y_{j+1} = F$ .
- $\mathcal{E}_{up}$  happens with probability  $p_{up} \geq p_{Y_j, Y_{j+1}}$ . When this happens, with probability  $p_{Y_j, Y_{j+1}}/p_{up}$ , set  $Y_{j+1} = Y_j + 1$ . Let  $\xi = p_{up} - p_{Y_j, Y_{j+1}}$  and  $\rho = \min\{p_{Y_j, down}, \xi\}$ . With probability  $\rho/p_{up}$ , set  $Y_{j+1} = \max\{Y_j - 1, 0\}$  and with probability  $(\xi - \rho)/p_{up}$  set  $Y_{j+1} = F$ .
- $\mathcal{E}_{down}$  happens with probability  $p_{down}$ . When this happens, let  $\sigma = p_{Y_j, down} - \rho$ . Let  $Y_{j+1} = \max\{Y_j - 1, 0\}$  with probability  $\sigma/p_{down}$  and  $Y_{j+1} = F$ , with probability  $1 - \sigma/p_{down}$ .

It is now easy to check that  $Y_{j+1} = Y_j + 1$  and  $Y_{j+1} = \max\{Y_j - 1, 0\}$  both happen with the correct marginal distribution (so  $Y_{j+1} = F$  does as well). Also, equation (5) guarantees that the probabilities are all well-defined (and non-negative!). Finally, the coupling itself guarantees Properties 1–3.

□

Given our coupling, we want to analyse  $(Y_t)_{t \geq 0}$ , and this is easy, since it is very similar to the classical gambler's ruin problem. For completeness, we give details below.

**Definition 22.** Write  $\mathcal{S}_Z = \{0, 1, \dots, \gamma\}$ , and suppose  $z \in \mathcal{S}_Z$ . Then we define  $(Z_t^z)_{t \geq 0}$  to be a discrete-time Markov chain with state space  $\mathcal{S}_Z$ , initial state  $z$ , and the following transition matrix:

$$\begin{aligned} p'_{0,0} &= 1/(1+r'), & p'_{0,1} &= r'/(1+r'), \\ \text{for all } i \in [\gamma-1], & p'_{i,i-1} &= 1/(1+r'), & p'_{i,i+1} &= r'/(1+r'), \\ p'_{\gamma,\gamma-1} &= 1, \end{aligned}$$

and  $p'_{i,j} = 0$  for all other  $i, j \in \mathcal{S}_Z$ .

The following analysis of the classical gambler's ruin problem is well-known. See, for example, [8, Chapter XIV].

**Lemma 23.** *Consider a random walk on  $\mathbb{Z}_{\geq 0}$  that absorbs at 0 and  $a$  (for some positive integer  $a$ ), starts at  $z \in \{0, \dots, a\}$ , and from each state in  $\{1, \dots, a-1\}$  has probability  $p \neq 1/2$  of increasing (by 1) and probability  $q = 1 - p$  of decreasing (by 1). Then, the probability of reaching state  $a$  is*

$$\frac{1 - (q/p)^z}{1 - (q/p)^a}.$$

Moreover, if  $p > 1/2$ , then the expected number of transitions before absorption is at most

$$\frac{a}{p-q} \cdot \frac{1 - (q/p)^z}{1 - (q/p)^a}.$$

□

**Lemma 24.** Suppose  $b \geq ((1/\lg r') + 1)^3$ , and write  $T^Z = \min\{i \mid Z_i^0 = \lfloor b^{1/3} \rfloor\}$ . Then

$$\mathbb{E}(|\{0 \leq i < T^Z \mid Z_i^0 = 0\}|) \leq 2r'/(r' - 1), \text{ and}$$

$$\mathbb{E}(T^Z) \leq 6\lfloor b^{1/3} \rfloor r'/(r' - 1).$$

*Proof.* By Lemma 23, the probability of reaching  $\lfloor b^{1/3} \rfloor$  before 0 in  $Z^1$  is

$$\frac{1 - 1/r'}{1 - (1/r')^{\lfloor b^{1/3} \rfloor}} \geq \frac{r' - 1}{r'}.$$

Thus in  $Z^0$ , the probability of reaching  $\lfloor b^{1/3} \rfloor$  before returning to 0 is at least  $p'_{0,1}(r' - 1)/r' = (r' - 1)/(r' + 1)$ . Thus, the number of steps  $Z^0$  spends at 0 before reaching  $\lfloor b^{1/3} \rfloor$  is dominated from above by a geometric variable with parameter  $(r' - 1)/(r' + 1)$ , and so

$$\mathbb{E}(|\{0 \leq i < T^Z \mid Z_i^0 = 0\}|) \leq \frac{r' + 1}{r' - 1} \leq \frac{2r'}{r' - 1},$$

as required.

Now, by Lemma 23, the expected number of transitions that it takes for  $Z^1$  to reach either 0 or  $\lfloor b^{1/3} \rfloor$  is at most

$$\frac{\lfloor b^{1/3} \rfloor (r' + 1)}{r' - 1} \cdot \frac{1 - 1/r'}{1 - (1/r')^{\lfloor b^{1/3} \rfloor}} \leq \frac{\lfloor b^{1/3} \rfloor (r' + 1)}{r' - 1} \cdot 2(1 - 1/r') = \frac{2\lfloor b^{1/3} \rfloor (r' + 1)}{r'}.$$

So the expected number of transitions that it takes  $Z^0$  to return to 0 or reach  $\lfloor b^{1/3} \rfloor$  is at most

$$1 + p'_{0,1} \cdot \frac{2\lfloor b^{1/3} \rfloor (r' + 1)}{r'} = 1 + 2\lfloor b^{1/3} \rfloor \leq 3\lfloor b^{1/3} \rfloor.$$

By Wald's equation, it follows that

$$\mathbb{E}(T^Z) \leq \left( \frac{2r'}{r' - 1} \right) 3\lfloor b^{1/3} \rfloor,$$

and so the result follows.  $\square$

**Lemma 25.** Suppose  $b \geq \max\{((1/\lg r') + 1)^3, 120\}$ . Then the probability that  $Y$  reaches state  $\lfloor b^{1/3} \rfloor$  is at least  $1 - 25/(\beta^{1/2}b(r - 1))$ .

*Proof.* Let  $T^Z = \min\{i \mid Z_i^0 = \lfloor b^{1/3} \rfloor\}$  and let  $T^Y = \min\{i \geq 0 \mid Y_i \in \{\lfloor b^{1/3} \rfloor, F\}\}$ . Then we have

$$\begin{aligned} \mathbb{P}(Y_{T^Y} = F) &= \sum_{i=0}^{\infty} \sum_{x=0}^{\lfloor b^{1/3} \rfloor - 1} \mathbb{P}(Y_i = x \text{ and } T^Y > i) p_{x,F} \\ &= p_{0,F} \sum_{i=0}^{\infty} \mathbb{P}(Y_i = 0 \text{ and } T^Y > i) + p_{1,F} \sum_{i=0}^{\infty} \sum_{x=1}^{\lfloor b^{1/3} \rfloor - 1} \mathbb{P}(Y_i = x \text{ and } T^Y > i). \end{aligned}$$

Since  $\lfloor b^{1/3} \rfloor \leq \gamma$ , the definitions of  $Y$  and  $Z^0$  show that the following are equivalent.

- $(y_0, \dots, y_i)$  is a possible value of  $(Y_0, \dots, Y_i)$  which implies  $Y_i = x$  and  $T^Y > i$ .



- $(y_0, \dots, y_i)$  is a possible value of  $(Z_0^0, \dots, Z_i^0)$  which implies  $Z_i^0 = x$  and  $T^Z > i$ .

Moreover, for all  $0 \leq i \leq \lfloor b^{1/3} \rfloor - 1$  and all  $0 \leq j \leq \lfloor b^{1/3} \rfloor$  we have  $p_{i,j} \leq p'_{i,j}$ . It follows that

$$\begin{aligned} \mathbb{P}(Y_{T^Y} = F) &\leq p_{0,F} \sum_{i=0}^{\infty} \mathbb{P}(Z_i^0 = 0 \text{ and } T^Z > i) + p_{1,F} \sum_{i=0}^{\infty} \sum_{x=1}^{\lfloor b^{1/3} \rfloor - 1} \mathbb{P}(Z_i^0 = x \text{ and } T^Z > i) \\ &\leq p_{0,F} \cdot \mathbb{E}(|\{0 \leq i < T^Z \mid Z_i^0 = 0\}|) + p_{1,F} \cdot \mathbb{E}(T^Z). \end{aligned}$$

It follows by Lemma 24 and the fact that  $b \geq 120$  (and hence  $b^{2/3} \geq 120/5$ ) that

$$\begin{aligned} \mathbb{P}(Y_{T^Y} = F) &\leq \frac{6}{r\beta^{1/2}b} \cdot \frac{2r'}{r'-1} + \frac{10}{r\beta b^2} \cdot \frac{6\lfloor b^{1/3} \rfloor r'}{r'-1} \leq \frac{r'}{r(r'-1)\beta^{1/2}b} \left( 12 + \frac{60}{b^{2/3}\beta^{1/2}} \right) \\ &\leq \frac{2}{(r-1)\beta^{1/2}b} \left( 12 + \frac{1}{2} \right) \leq \frac{25}{\beta^{1/2}b(r-1)}, \end{aligned}$$

as required.  $\square$

The goal of the subsection, Lemma 26, now follows easily from Lemmas 21 and 25.

**Lemma 26.** *Suppose  $b \geq \max\{((1/\lg r') + 1)^3, 120\}$  and  $X_0 \cap V_1 \neq \emptyset$ . Then with probability at least  $1 - 25/(\beta^{1/2}b(r-1))$ , there exists  $t \geq 0$  such that  $|X_t \cap V_3| \geq \lfloor b^{1/3} \rfloor$ .*

*Proof.* By Lemma 25, the probability that  $Y$  reaches state  $\lfloor b^{1/3} \rfloor$  is at least  $1 - 25/(\beta^{1/2}b(r-1))$ . The result therefore follows from Lemma 21.  $\square$

## 4.2 Going from mutants in $V_3$ to fixation

Our goal in this subsection is to prove Lemmas 30 and 31, which give lower bounds on fixation probability conditioned on  $X_0 \subseteq V_1$  and  $X_0 \subseteq V_3$  respectively. Both arguments rely heavily on Lemma 29 below, which says that fixation is very likely if  $V_3$  contains at least  $\lfloor b^{1/3} \rfloor$  mutants. (Indeed, Lemma 30 is immediate from this combined with Lemma 26.) To prove Lemma 29, as in the previous section, we will need to couple the evolution of mutants in  $V_3$  with a gambler's ruin. However, this time we will need the coupling to last until the gambler's ruin absorbs — we cannot afford a chance of failure at every transition.

**Lemma 27.** *Suppose  $t \geq 0$  and  $M \subseteq V$ . Let  $z \geq 1$ , and suppose  $z \leq \min\{|M \cap V_3|, \gamma\}$ . Let  $I = \min\{i \mid Z_i^z = 0\}$ . Then, conditioned on  $X_t = M$ , there exists a coupling  $\Psi(X, Z^z)$  between  $(X_{t'})_{t' \geq t}$  and  $(Z_{t'}^z)_{t' \geq 0}$  such that, for all  $i < I$ , there is a  $t' \geq t + i - 1$  such that  $|X_{t'} \cap V_3| \geq Z_{t'}^z$ .*

*Proof.* Following Definition 14, let  $\mathcal{T}_{\text{end}} = \min\{\tilde{t} \geq t \mid X_{\tilde{t}} \cap V_3 = \emptyset \text{ or } X_{\tilde{t}} = V\}$ . Note that  $\mathcal{T}_{\text{end}}$  is finite with probability 1. Define  $\mathcal{T}_0, \mathcal{T}_1, \dots$  recursively by  $\mathcal{T}_0 = t$  and

$$\mathcal{T}_i = \min(\{\mathcal{T}_{\text{end}}\} \cup \{\tilde{t} > \mathcal{T}_{i-1} \mid X_{\tilde{t}} \cap V_3 \neq X_{\tilde{t}-1} \cap V_3\}).$$

Consider any  $t_i \geq t$  and  $M_i \subseteq V$  with  $1 \leq |M_i \cap V_3| \leq \gamma$ . Write  $\mathcal{F}_i$  for the event that  $\mathcal{T}_i = t_i \neq \mathcal{T}_{\text{end}}$ ,  $X_{t_i} = M_i$ , and  $X_t = M$ . For  $t'_i \geq t_i$  and  $M'_i \subseteq V$ , write

$$p_{t'_i}^{M'_i} = \mathbb{P}(X_{t'_i} = M'_i \text{ and } \mathcal{T}_{i+1} = t'_i + 1 \mid \mathcal{F}_i).$$

Then we have

$$\begin{aligned} & \mathbb{P}(|X_{\mathcal{T}_{i+1}} \cap V_3| = |X_{\mathcal{T}_i} \cap V_3| - 1 \mid \mathcal{F}_i) \\ &= \sum_{t'_i \geq t_i} \sum_{\substack{M'_i \subseteq V \\ M'_i \cap V_3 = M_i \cap V_3}} \mathbb{P}(|X_{t'_i+1} \cap V_3| = |X_{t'_i} \cap V_3| - 1 \mid X_{t'_i} = M'_i, \mathcal{T}_{i+1} = t'_i + 1, \mathcal{F}_i) \cdot p_{t'_i}^{M'_i}. \end{aligned}$$

Note that since  $1 \leq |M'_i \cap V_3| \leq \gamma \leq |V_3| - 1$ , the conditioning on  $\mathcal{T}_{i+1} = t'_i + 1$  in the above expression is precisely equivalent to conditioning on  $|X_{t'_i+1} \cap V_3| = |X_{t'_i} \cap V_3| \pm 1$ . Moreover, by Lemma 15, writing  $\kappa = |E(V_3 \cap M'_i, V_3 \setminus M'_i)| / (W(M'_i)(\beta b^2 + b^2 - 1))$ , when  $M'_i \cap V_3 = M_i \cap V_3$  we have

$$\begin{aligned} \mathbb{P}(|X_{t'_i+1} \cap V_3| = |X_{t'_i} \cap V_3| + 1 \mid X_{t'_i} = M'_i, \mathcal{F}_i) &\geq r\kappa, \\ \mathbb{P}(|X_{t'_i+1} \cap V_3| = |X_{t'_i} \cap V_3| - 1 \mid X_{t'_i} = M'_i, \mathcal{F}_i) &\leq (1 + 5/\beta)\kappa. \end{aligned}$$

It therefore follows from Lemma 16 that

$$\mathbb{P}(|X_{\mathcal{T}_{i+1}} \cap V_3| = |X_{\mathcal{T}_i} \cap V_3| - 1 \mid \mathcal{F}_i) \leq \frac{1 + 5/\beta}{1 + 5/\beta + r} \sum_{t'_i \geq t_i} \sum_{\substack{M'_i \subseteq V \\ M'_i \cap V_3 = M_i \cap V_3}} p_{t'_i}^{M'_i} \leq \frac{1}{1 + r'}. \quad (6)$$

Let  $I' = \min\{i \mid \mathcal{T}_i = \mathcal{T}_{\text{end}}\}$ . We are now in a position to define a coupling  $\Psi(X, Z^z)$  such that

$$\text{for all } j \leq I', |X_{\mathcal{T}_j} \cap V_3| \geq Z_j^z. \quad (7)$$

We first observe that such a coupling would satisfy the condition in the statement of the lemma. Consider  $i < I'$ . We wish to show that there is a  $t' \geq t + i - 1$  such that  $|X_{t'} \cap V_3| \geq Z_i^z$ . There are two cases to consider.

- If  $i < I'$ , then, since  $\mathcal{T}_i < \mathcal{T}_{\text{end}}$ , we have  $t + i - 1 < \mathcal{T}_i$ . But from (7),  $|X_{\mathcal{T}_i} \cap V_3| \geq Z_i^z$ . So we can take  $t' = \mathcal{T}_i$ .
- Suppose instead that  $i \geq I'$ . From the definition of  $I'$ ,  $\mathcal{T}_{I'} = \mathcal{T}_{\text{end}}$ , so from (7), we have  $|X_{\mathcal{T}_{\text{end}}} \cap V_3| \geq Z_{I'}^z$ . But since  $I' \leq i < I$ ,  $Z_{I'}^z > 0$ , so since  $X_{\mathcal{T}_{\text{end}}} \cap V_3$  is non-empty, the definition of  $\mathcal{T}_{\text{end}}$  implies that the process fixates by time  $\mathcal{T}_{\text{end}}$ . Thus, for any  $t' \geq \mathcal{T}_{\text{end}}$ , we have  $|X_{t'} \cap V_3| = |V_3|$ , and this is at least  $Z_j^z$  for any  $j$  (since the state space of  $Z^z$  only goes up to  $\gamma$ ) so it suffices to take any  $t' \geq \max\{\mathcal{T}_{\text{end}}, t + i - 1\}$ .

Given a coupling  $\Psi(X, Z^z)$  and a non-negative integer  $j$ , let  $\Psi^j$  denote the initial sequence  $(X_0, \dots, X_{\mathcal{T}_j}, Z_0^z, \dots, Z_j^z)$ . We will first construct the sequence  $\Psi^0, \Psi^1, \dots$  by induction on  $j$ , using  $\Psi^j$  (and some randomness) to construct  $\Psi^{j+1}$ . We will continue this process until, for some  $j > 0$ , we obtain a  $\Psi^j$  which implies  $\mathcal{T}_j = \mathcal{T}_{\text{end}}$ . (Note that  $\mathbb{P}(I' < \infty \mid X_t = M) = 1$ .) We will then complete the coupling by allowing  $X_{\mathcal{T}_{\text{end}}+1}, X_{\mathcal{T}_{\text{end}}+2}, \dots$  and  $Z_{I'+1}^z, Z_{I'+2}^z, \dots$  to evolve independently according to their marginal distributions (which will vacuously satisfy (7)). Note that  $\Psi^0 = (M, z)$  satisfies (7) since  $z \leq |M \cap V_3|$ . Suppose we are given  $\Psi^j$  satisfying (7) with  $\mathcal{T}_j < \mathcal{T}_{\text{end}}$ . We will now construct  $\Psi^{j+1}$ .

- **If  $|X_{\mathcal{T}_j} \cap V_3| \geq \gamma + 1$ :** We let  $X_{\mathcal{T}_j+1}, \dots, X_{\mathcal{T}_j+1}$  and  $Z_{j+1}^z$  evolve independently according to their correct marginal distributions. Note that  $|X_{\mathcal{T}_j+1} \cap V_3| \geq |X_{\mathcal{T}_j} \cap V_3| - 1 \geq \gamma \geq Z_{j+1}^z$ , so (7) is satisfied for  $j + 1$ .

- **If  $Z_j^z = \gamma$ :** We let  $X_{\mathcal{T}_j+1}, \dots, X_{\mathcal{T}_{j+1}}$  and  $Z_{j+1}^z$  evolve independently according to their correct marginal distributions. Note that by (7),  $|X_{\mathcal{T}_{j+1}} \cap V_3| \geq |X_{\mathcal{T}_j} \cap V_3| - 1 \geq Z_j^z - 1 = Z_{j+1}^z$ , so (7) is again satisfied for  $j+1$ .
- **If  $|X_{\mathcal{T}_j} \cap V_3| \leq \gamma$  and  $Z_j^z < \gamma$ :** Note that since  $\mathcal{T}_j < \mathcal{T}_{\text{end}}$ , in this case we also have  $|X_{\mathcal{T}_j} \cap V_3| \geq 1$ . Let  $\mathcal{E}_{\text{down}}$  be the event that  $|X_{\mathcal{T}_{j+1}} \cap V_3| = |X_{\mathcal{T}_j} \cap V_3| - 1$ , and let  $p_{\text{down}}$  be the probability that  $\mathcal{E}_{\text{down}}$  occurs in the correct marginal distribution (which depends only on  $X_{\mathcal{T}_j}$ ). Let  $\mathcal{E}_{\text{up}}$  be the event that  $|X_{\mathcal{T}_{j+1}} \cap V_3| = |X_{\mathcal{T}_j} \cap V_3| + 1$ , and let  $p_{\text{up}} = 1 - p_{\text{down}}$ . Then (6) shows that  $p_{\text{down}} \leq 1/(1+r')$ . The coupling is as follows.
  - Choose  $X_{\mathcal{T}_j+1}, \dots, X_{\mathcal{T}_{j+1}}$  according to the correct marginal distribution.
  - $\mathcal{E}_{\text{down}}$  occurs with probability  $p_{\text{down}} \leq 1/(1+r')$ . When this happens, set  $Z_{j+1}^z = \max\{Z_j^z - 1, 0\}$ .
  - $\mathcal{E}_{\text{up}}$  occurs with probability  $p_{\text{up}} \geq r'/(1+r')$ . When this happens, set  $Z_{j+1}^z = Z_j^z + 1$  with probability  $r'/(p_{\text{up}}(1+r'))$ , and set  $Z_{j+1}^z = \max\{Z_j^z - 1, 0\}$  with probability  $1 - r'/(p_{\text{up}}(1+r'))$ .

It is now easy to check that  $Z_{j+1}^z = Z_j^z + 1$  and  $Z_{j+1}^z = \max\{Z_j^z - 1, 0\}$  both happen with the correct marginal distribution. Moreover, the coupling itself guarantees that  $|X_{\mathcal{T}_{j+1}} \cap V_3| \geq Z_{j+1}^z$ , so (7) is satisfied for  $j+1$ .

□

We will use the following Lemma from [4, Theorem 9] (which applies to all graphs).

**Lemma 28.** *For all  $M \subseteq V$ , the expected absorption time of  $X$  from state  $M$  is at most  $r|V|^4/(r-1)$ .* □

Lemma 28 implies that, in order to prove that the Moran process is likely to fixate, it suffices to show that it runs for a long time without going extinct. We will use this in the proof of Lemma 29.

**Lemma 29.** *There exists  $b_0$  depending only on  $r$  such that the following holds whenever  $b \geq b_0$ . Suppose  $t \geq 0$  and  $M \subseteq V$  with  $|M \cap V_3| \geq \lfloor b^{1/3} \rfloor$ . Then we have*

$$\mathbb{P}(X \text{ fixates} \mid X_t = M) \geq 1 - 1/(\beta^{1/2}b(r-1)).$$

*Proof.* Recall that  $\gamma = \lfloor (k\beta)^{1/3} \rfloor$ . Let  $\xi = \lfloor b^{1/3} \rfloor$  and  $T = \lfloor (r')^{(\gamma-1)/2} \rfloor$ , and let  $b_0$  be such that  $b_0 \geq \max\{\beta/r, 120, ((1/\lg r') + 1)^3\}$  and, for all  $b \geq b_0$ ,

$$\frac{1}{(r')^\xi} + \frac{T}{(r')^{\gamma-1}} + \frac{16r^5k^4\beta^2b^4}{(r-1)(T-1)} \leq \frac{1}{\beta^{1/2}b(r-1)}. \quad (8)$$

(Note that  $b \geq b_0$  implicitly gives a lower bound on  $k$  since  $b = b(k) \leq \sqrt{k}$ .)

By Lemma 23, the probability that  $Z^\xi$  reaches  $\gamma$  before zero is

$$\frac{1 - (1/r')^\xi}{1 - (1/r')^\gamma} \geq 1 - \frac{1}{(r')^\xi}.$$

Moreover, Lemma 23 also shows that the probability that  $Z^\xi$  reaches 0 on any given sojourn from  $\gamma$  is at most

$$1 - \frac{1 - (\frac{1}{r'})^{\gamma-1}}{1 - (\frac{1}{r'})^\gamma} = \frac{r' - 1}{(r')^\gamma - 1} \leq \frac{1}{(r')^{\gamma-1}}.$$

Thus the probability that  $Z^\xi$  never reaches zero when it makes  $T$  transitions from state  $\gamma$  is at least

$$\left(1 - \frac{1}{(r')^{\gamma-1}}\right)^T \geq 1 - \frac{T}{(r')^{\gamma-1}}$$

Thus the probability that  $Z^\xi$  reaches zero from state  $\xi$  within  $T$  transitions is at most

$$\frac{1}{(r')^\xi} + \frac{T}{(r')^{\gamma-1}}.$$

If  $Z^\xi$  does not reach zero within  $T$  transitions and we couple it with  $X$  according to Lemma 27, noting that  $T < I$ , then there is a  $t' \geq t + T - 1$  such that  $X_{t'}$  is non-empty. Thus,

$$\mathbb{P}(X_{t+T-1} = \emptyset \mid X_t = M) \leq \frac{1}{(r')^\xi} + \frac{T}{(r')^{\gamma-1}}. \quad (9)$$

Now, by Lemma 28 combined with Markov's inequality, we have

$$\mathbb{P}(X_{t+T-1} \notin \{\emptyset, V\} \mid X_t = M) \leq \frac{r|V|^4}{(r-1)(T-1)} \leq \frac{r(2kr\beta^{1/2}b)^4}{(r-1)(T-1)} = \frac{16r^5k^4\beta^2b^4}{(r-1)(T-1)}.$$

(Here the upper bound on  $|V|$  follows from Observation 8.) Hence by (9) and a union bound, it follows that

$$\mathbb{P}(X_{t+T-1} \neq V \mid X_t = M) \leq \frac{1}{(r')^\xi} + \frac{T}{(r')^{\gamma-1}} + \frac{16r^5k^4\beta^2b^4}{(r-1)(T-1)}.$$

The result therefore follows from (8).  $\square$

**Lemma 30.** *There exists  $b_0$  depending only on  $r$  such that the following holds whenever  $b \geq b_0$ . If  $X_0 \cap V_1 \neq \emptyset$ , then  $(X_t)_{t \geq 0}$  fixates with probability at least  $1 - 26/(\beta^{1/2}b(r-1))$ .*

*Proof.* By Lemma 26 and Lemma 29, when  $b$  is sufficiently large we have

$$\mathbb{P}(X \text{ fixates} \mid X_0 \cap V_1 \neq \emptyset) \geq 1 - \frac{25}{\beta^{1/2}b(r-1)} - \frac{1}{\beta^{1/2}b(r-1)},$$

so the result follows.  $\square$

**Lemma 31.** *There exists  $b_0$  depending only on  $r$  such that, whenever  $b \geq b_0$ , for all  $x_0 \in V_3$ ,*

$$\mathbb{P}(X \text{ fixates} \mid X_0 = \{x_0\}) \geq 1 - 2/r.$$

*Proof.* Let  $T = \min\{t > 0 \mid |X_t \cap V_3| = \gamma\}$ . By Lemma 23, the probability that  $Z^1$  reaches  $\gamma$  before 0 is at least  $1 - 1/r'$ . Thus by Lemma 27, we have

$$\mathbb{P}(T < \infty \mid X_0 = \{x_0\}) \geq 1 - 1/r'. \quad (10)$$

Moreover, by Lemma 29, when  $b$  is sufficiently large, for all  $t > 0$  and all  $M \subseteq V$  with  $|M \cap V_3| \geq \gamma$ , we have

$$\mathbb{P}(X \text{ fixates} \mid T = t, X_t = M, X_0 = \{x_0\}) \geq 1 - \frac{1}{\beta^{1/2}b(r-1)}.$$

Summing over all possible values of  $t$  and  $M$ , we obtain

$$\mathbb{P}(X \text{ fixates} \mid T < \infty, X_0 = \{x_0\}) \geq 1 - \frac{1}{\beta^{1/2}b(r-1)}.$$

Thus by (10), taking  $b_0 \geq (r+1)/\sqrt{r-1}$ , it follows that

$$\mathbb{P}(X \text{ fixates} \mid X_0 = \{x_0\}) \geq 1 - \frac{1}{r'} - \frac{1}{\beta^{1/2}b(r-1)} \geq 1 - \frac{2}{r+1} - \frac{1}{5r(r+1)} \geq 1 - \frac{2}{r}.$$

□

### 4.3 Putting it all together

We can now prove Theorem 6, which we restate for convenience.

**Theorem 6.** Let  $r > 1$ . There is a constant  $b_0$  depending only on  $r$  such that the following holds. Let  $b : \mathbb{Z}_{\geq 1} \rightarrow \mathbb{Z}_{\geq 1}$  be any function that satisfies  $b(k) \leq \sqrt{k}$  for all  $k$ . Consider a graph  $G \in \mathcal{I}_{r,b}$  with branching factor  $b(k) \geq b_0$ . Let  $n$  be the number of vertices of  $G$  and  $m$  be the number of edges of  $G$ . Then  $\ell_r(G) \leq 2^{14}rn/((r-1)^2m)$ .

*Proof.* By Lemmas 30 and 31, when  $b(k)$  is sufficiently large we have

$$\ell_r(G) \leq \frac{|V_3|}{n} \cdot \frac{2}{r} + \frac{|V_2|}{n} + \frac{|V_1|}{n} \left( \frac{26}{\beta^{1/2}b(k)(r-1)} \right) \leq \frac{3\beta k}{rn} + \frac{26}{\beta^{1/2}b(k)(r-1)}.$$

Since Observation 8 implies that  $n \geq kr\beta^{1/2}b(k)$ , it follows that

$$\ell_r(G) \leq \frac{3\beta^{1/2}}{r^2b(k)} + \frac{26}{\beta^{1/2}b(k)(r-1)} \leq \frac{4\beta^{1/2}}{r^2b(k)}. \quad (11)$$

Since Observation 8 implies that  $m/n \leq \beta^{3/2}b(k)/r$ , it follows that

$$\ell_r(G) \leq \frac{\beta^{3/2}b(k)n}{rm} \cdot \frac{4\beta^{1/2}}{r^2b(k)} = \frac{4\beta^2n}{r^3m}.$$

Since  $r^2/(r-1) > 1$ , we have  $\beta \leq 52r^2/(r-1)$  and hence

$$\ell_r(G) \leq \frac{2^{14}rn}{(r-1)^2m},$$

as required. □

Finally, we prove Theorem 2.

**Theorem 2.** For all  $r > 1$ , there exists an infinite family  $\mathcal{D}_r$  of connected graphs with the following property. If  $G \in \mathcal{D}_r$  has  $n$  vertices, then  $\ell_r(G) \leq 71/(r(r-1)^2n)^{1/3}$ .

*Proof.* Let  $b(k) = \lfloor \sqrt{k} \rfloor$ . Consider any  $r > 1$  and let the constant  $b_0$  (depending on  $r$ ) be the one from the statement of Theorem 6. Define

$$\mathcal{D}_r = \{G \in \mathcal{I}_{r,b} \mid \text{The parameter, } k, \text{ of } G \text{ is the square of an integer and } b(k) \geq b_0\}.$$

Note that in the definition of  $\mathcal{I}_{r,b}$  (Definition 5), when  $k$  is a square integer,  $G[V_2, V_3]$  is a complete bipartite graph and  $G[V_3]$  is a clique. Thus  $\mathcal{D}_r$  is an infinite family.

Consider any  $G \in \mathcal{D}_r$ . Note that by Observation 8,  $n \leq 2k^{3/2}r\beta^{1/2}$ , and hence  $k^{1/2} \geq (n/(2r\beta^{1/2}))^{1/3}$ . Moreover, as in (11), we have  $\ell_r(G) \leq 4\beta^{1/2}/(r^2b(k))$ . It follows that

$$\ell_r(G) \leq \frac{4\beta^{1/2}}{r^2} \cdot \frac{2^{1/3}r^{1/3}\beta^{1/6}}{n^{1/3}} = \frac{2^{7/3}\beta^{2/3}}{r^{5/3}n^{1/3}} \leq \frac{71}{r^{1/3}(r-1)^{2/3}n^{1/3}},$$

and so the result follows. (The final inequality uses  $\beta \leq 52r^2/(r-1)$  as in the proof of Theorem 6.)  $\square$

## 5 Lower bounds on extinction probability

In this section, we prove Theorems 1, 3 and 7 which give lower bounds on extinction probability. The proofs of our theorems rely on the following quantity, which has also been studied in the undirected case in [15, 16].

**Definition 32.** Given a digraph  $G = (V, E)$ , we define the *danger* of any vertex  $v$  as

$$Q_v = \sum_{u \in N_{\text{in}}(v)} \frac{1}{d_{\text{out}}(u)}.$$

Note that the danger of  $v$  is essentially the rate at which  $v$  dies when all of its in-neighbours are non-mutants. The following observation is immediate, since  $Q_u/(r+Q_u)$  is the probability that  $u$  dies before spawning a mutant when the Moran process is run from state  $\{u\}$ .

**Observation 33.** Let  $G = (V, E)$  be a digraph with a vertex  $u \in V$ . Then

$$\ell_r(u) \geq Q_u/(r+Q_u).$$

The following lemma gives a lower bound on  $\ell_r(\{u, v\})$ , the extinction probability when the Moran process is run from state  $\{u, v\}$ . The lower bound is based on crudely ignoring every situation except the one in which the first state change is the death of the mutant at  $v$ . Though this is crude, it turns out to suffice for our purposes. For other situations in which such arguments have been used, see Theorem 1 of [15].

**Lemma 34.** Suppose  $r \geq 1$ . Let  $G = (V, E)$  be a digraph with a vertex  $u \in V$  satisfying  $\ell_r(u) \leq 1/2$  and a vertex  $v \in N_{\text{out}}(u)$ . Then

$$\ell_r(\{u, v\}) \geq \left(1 - \frac{3r}{2r + Q_v}\right) \ell_r(u).$$

*Proof.* Let  $W = n + 2(r-1)$ ,

$$\bar{Q}_u = \sum_{w \in N_{\text{in}}(u) \setminus \{v\}} \frac{1}{d_{\text{out}}(w)}, \quad \text{and} \quad \bar{Q}_v = \sum_{w \in N_{\text{in}}(v) \setminus \{u\}} \frac{1}{d_{\text{out}}(w)}.$$

We consider four events which may occur when the Moran process is run, starting from state  $\{u, v\}$ :

- Vertex  $u$  reproduces (probability  $r/W$ ),
- Vertex  $v$  reproduces (probability  $r/W$ ),
- Some vertex in  $N_{\text{in}}(u) \setminus \{v\}$  reproduces onto  $u$  (probability  $\bar{Q}_u/W$ ),
- Some vertex in  $N_{\text{in}}(v) \setminus \{u\}$  reproduces onto  $v$  (probability  $\bar{Q}_v/W$ ),

Note that any other event leaves the state unchanged. Thus,  $\ell_r(\{u, v\})$  is at least the probability that the last of these happens first, before the others, multiplied by  $\ell_r(u)$ , which is the extinction probability from the resulting state (which is  $\{u\}$ ). Thus,

$$\ell_r(\{u, v\}) \geq \frac{\bar{Q}_v}{2r + \bar{Q}_u + \bar{Q}_v} \ell_r(u).$$

Note that  $\bar{Q}_u \leq r$  (clearly  $\bar{Q}_u \leq Q_u$  and Observation 33, together with  $\ell_r(u) \leq 1/2$ , implies  $Q_u \leq r$ ). Also,  $\bar{Q}_v = Q_v - 1/d_{\text{out}}(v) \geq Q_v - r$ . Hence

$$\ell_r(\{u, v\}) \geq \frac{\bar{Q}_v}{3r + \bar{Q}_v} \ell_r(u) = \left(1 - \frac{3r}{3r + \bar{Q}_v}\right) \ell_r(u) \geq \left(1 - \frac{3r}{2r + Q_v}\right) \ell_r(u),$$

as required.  $\square$

We next use Lemma 34 to derive an upper bound on the danger of a vertex.

**Lemma 35.** *Suppose  $r \geq 1$ . Let  $G = (V, E)$  be a strongly-connected digraph with  $|V| \geq 2$ , and suppose that  $u \in V$  satisfies  $\ell_r(u) \leq 1/4$ . Then*

$$Q_u \leq \frac{4r\ell_r(u)}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \frac{r}{2r + Q_v}.$$

*Proof.* From the definition of the Moran process,

$$\ell_r(u) = \frac{Q_u}{r + Q_u} + \frac{r}{r + Q_u} \cdot \frac{1}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \ell_r(\{u, v\}).$$

It then follows from Lemma 34 that

$$\begin{aligned} \ell_r(u) &\geq \frac{Q_u}{r + Q_u} + \frac{r}{r + Q_u} \cdot \frac{1}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \left(1 - \frac{3r}{2r + Q_v}\right) \ell_r(u) \\ &= \frac{Q_u}{r + Q_u} + \frac{r}{r + Q_u} \ell_r(u) - \frac{r}{r + Q_u} \cdot \frac{1}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \frac{3r}{2r + Q_v} \ell_r(u). \end{aligned}$$

Multiplying by  $r + Q_u$  and rearranging, we obtain

$$\frac{r}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \frac{3r}{2r + Q_v} \ell_r(u) \geq (1 - \ell_r(u))Q_u.$$

Since  $\ell_r(u) \leq 1/4$ , we have  $3/(1 - \ell_r(u)) \leq 4$ , so

$$Q_u \leq \frac{4r\ell_r(u)}{d_{\text{out}}(u)} \sum_{v \in N_{\text{out}}(u)} \frac{r}{2r + Q_v},$$

as required.  $\square$

The following lemma gives an upper bound on the total danger of a set of vertices with low extinction probability. Throughout the rest of the section, this lemma will be the main point of interaction between our arguments and the definition of the Moran process — the remainder of our arguments will focus on how vertex dangers and extinction probabilities can be distributed.

**Lemma 36.** *Let  $G$  be a strongly-connected  $n$ -vertex digraph with  $n \geq 2$ . Consider the Moran process on  $G$  with fitness  $r \geq 1$ . Let  $S \subseteq V(G)$ . Suppose that, for some  $\alpha \leq 1/4$ , every vertex  $v \in S$  has  $\ell_r(v) \leq \alpha$ . Then  $\sum_{v \in S} Q_v \leq 4r^2\alpha|N_{\text{out}}(S)|$  and  $\sum_{v \in S} Q_v \leq 4r^2n\alpha\ell_r(G)$ .*

*Proof.* By applying Lemma 35 to all  $v \in S$ ,

$$\begin{aligned} \sum_{v \in S} Q_v &\leq \sum_{v \in S} \frac{4r\alpha}{d_{\text{out}}(v)} \sum_{w \in N_{\text{out}}(v)} \frac{r}{2r + Q_w} = \sum_{w \in N_{\text{out}}(S)} \frac{4r^2\alpha}{2r + Q_w} \sum_{v \in N_{\text{in}}(w) \cap S} \frac{1}{d_{\text{out}}(v)} \\ &\leq \sum_{w \in N_{\text{out}}(S)} \frac{4r^2\alpha Q_w}{2r + Q_w} \leq 4r^2\alpha \sum_{w \in N_{\text{out}}(S)} \ell_r(w), \end{aligned}$$

where the final inequality follows by Observation 33. The first part of the result follows by bounding  $\ell_r(w) \leq 1$ , and the second part of the result follows since

$$\sum_{w \in N_{\text{out}}(S)} \ell_r(w) \leq \sum_{w \in V} \ell_r(w) = n\ell_r(G).$$

□

We can now prove Theorem 1, which we restate here for convenience. Note that when  $r = 1$ , we have  $\ell_r(G) = 1 - 1/n$  for all strongly-connected  $n$ -vertex digraphs  $G$  (see Lemma 1 of [4]). So from now on, we will take  $r > 1$ .

**Theorem 1.** For all  $r > 1$ , any strongly-connected  $n$ -vertex digraph  $G$  with  $n \geq 2$  satisfies  $\ell_r(G) > 1/(5rn^{1/2})$ .

*Proof.* Let  $V$  be the vertex set of  $G$ . If  $n = 2$ , then  $\ell_r(G) = 1/(1 + r) \geq 1/(5r)$  and we are done. If  $n \geq 3$  and  $\ell_r(G) \geq 1/8$ , then likewise we are done. Therefore, suppose  $n \geq 3$  and  $\ell_r(G) < 1/8$ . Note that  $Q_v \geq 1/n$  for all  $v \in V$ . Let  $A = \{v \in V \mid \ell_r(v) \leq 2\ell_r(G)\}$ , and note that  $\ell_r(G) > (|V \setminus A|/n) \cdot 2\ell_r(G)$  and hence  $|A| > n/2$ . Applying Lemma 36 to  $A$  with  $\alpha = 2\ell_r(G) \leq 1/4$  yields

$$\frac{1}{2} < \sum_{v \in A} Q_v \leq 8r^2n\ell_r(G)^2,$$

from which the result follows. □

In the proof of Theorem 1, we used the fact that, in an  $n$ -vertex digraph, every vertex  $v$  with “low” extinction probability has  $Q_v \geq 1/n$ . For undirected graphs, where we want to prove a stronger result, this bound is too loose. Instead we must account for the vertices with low extinction probability that have high danger. We next show that any undirected graph with low extinction probability must contain a set of vertices with both high total degree and high minimum degree. We will use this to prove Theorem 7 and Theorem 3.



**Lemma 37.** *Let  $r > 1$ . Consider any connected  $n$ -vertex graph  $G = (V, E)$  with  $n \geq 2$  and  $\ell_r(G) \leq 1/8$ . Then there exists a non-empty subset  $B$  of  $V$  such that  $\sum_{v \in B} d(v) \geq n/(144r^2\ell_r(G))$  and, for all  $v \in B$ ,  $d(v) \geq 1/(32r^2\ell_r(G)^2)$ .*

*Proof.* Let  $A = \{v \in V \mid \ell_r(v) \leq 2\ell_r(G)\}$ ,  $A' = \{v \in A \mid Q_v < 32r^2\ell_r(G)^2\}$  and  $B = N(A')$ .

We first show the third claim in the statement of the lemma, that  $d(v) \geq 1/(32r^2\ell_r(G)^2)$  for all  $v \in B$ . This claim follows from the fact that every  $v \in B$  is adjacent to some  $w \in A'$ , so  $1/d(v) \leq Q_w < 32r^2\ell_r(G)^2$ .

We next show that  $B$  is non-empty. Since  $G$  is connected and  $n > 1$ , this follows from the fact that  $A'$  is non-empty. Instead of showing directly that  $A'$  is non-empty, we will show the stronger claim that  $|A'| \geq n/4$  — we will use this later. As in the proof of Theorem 1, note that  $|A| > n/2$ . Next, apply Lemma 36 with  $S = A$  and  $\alpha = 2\ell_r(G) \leq 1/4$ . This shows that  $\sum_{v \in A} Q_v \leq 8r^2n\ell_r(G)^2$ . Then, from the definition of  $A'$ ,

$$32r^2\ell_r(G)^2|A \setminus A'| \leq \sum_{v \in A \setminus A'} Q_v \leq \sum_{v \in A} Q_v \leq 8r^2n\ell_r(G)^2,$$

so  $|A \setminus A'| \leq n/4$  and  $|A'| \geq |A| - |A \setminus A'| \geq n/2 - n/4 = n/4$ .

In the rest of the proof, the goal is to show the first claim in the statement of the lemma, namely

$$\sum_{v \in B} d(v) \geq n/(144r^2\ell_r(G)). \quad (12)$$

To do this, we partition  $A'$ . For every positive integer  $i$ , let  $Q_i = 3^{i-1}/n$  and let  $A_i = \{v \in A' \mid Q_i \leq Q_v < Q_{i+1}\}$ . Every vertex  $v \in A'$  has  $Q_v \geq Q_1 = 1/n$  so  $A'$  is the union of the disjoint sets  $A_1, A_2, \dots$

For every positive integer  $i$ , let  $B_i = N(A_i)$ . It is clear that  $B = \bigcup_{i \geq 1} B_i$ , but the sets  $B_i$  may not be disjoint. Since every vertex  $v \in N(A_i)$  is joined to some vertex  $w \in A_i$ , we have  $1/d(v) \leq Q_w < Q_{i+1}$  and hence

$$\text{for all } i \geq 1, \text{ for all } v \in B_i, d(v) > 1/Q_{i+1}. \quad (13)$$

For  $v \in B$ , define  $\varphi(v)$  to be the smallest  $i$  such that  $v \in B_i$ . Then, by (13),

$$\sum_{v \in B} d(v) \geq \sum_{v \in B} \frac{1}{Q_{\varphi(v)+1}}. \quad (14)$$

For each  $v \in B$  we can use the definition of  $Q_i$  to obtain the following.

$$\sum_{i > \varphi(v)} \frac{1}{Q_{i+1}} = \frac{1}{Q_{\varphi(v)+1}} \sum_{j \geq 1} \frac{1}{3^j} = \frac{1}{2Q_{\varphi(v)+1}}. \quad (15)$$

For each  $v \in B$  we can omit indices  $i$  for which  $v \notin B_i$  to obtain the following.

$$\sum_{i > \varphi(v)} \frac{1}{Q_{i+1}} \geq \sum_{i > \varphi(v): v \in B_i} \frac{1}{Q_{i+1}} = \left( \sum_{i: v \in B_i} \frac{1}{Q_{i+1}} \right) - \frac{1}{Q_{\varphi(v)+1}}. \quad (16)$$

Putting together equations (15) and (16), we get

$$\frac{1}{Q_{\varphi(v)+1}} \geq \left( \frac{2}{3} \right) \sum_{i: v \in B_i} \frac{1}{Q_{i+1}}.$$

Substituting this into (14), we get

$$\sum_{v \in B} d(v) \geq \left(\frac{2}{3}\right) \sum_{v \in B} \sum_{i: v \in B_i} \frac{1}{Q_{i+1}}. \quad (17)$$

We now apply Lemma 36 with  $S = A_i$  and  $\alpha = 2\ell_r(G) \leq 1/4$  to show that  $\sum_{v \in A_i} Q_v \leq 4r^2\alpha|N(A_i)| = 8r^2\ell_r(G)|B_i|$ . Since, by the definition of  $A_i$ , we have  $Q_i|A_i| \leq \sum_{v \in A_i} Q_v$ , we conclude that  $|B_i| \geq Q_i|A_i|/(8r^2\ell_r(G))$ .

Equation (12) now follows from (17) together with the bound

$$\sum_{i \geq 1} \sum_{v \in B_i} \frac{1}{Q_{i+1}} \geq \sum_{i \geq 1} \frac{Q_i|A_i|}{8r^2Q_{i+1}\ell_r(G)} = \frac{1}{24r^2\ell_r(G)} \sum_{i \geq 1} |A_i| = \frac{|A'|}{24r^2\ell_r(G)} \geq \frac{n}{96r^2\ell_r(G)}.$$

□

We now use Lemma 37 to prove the remaining theorems.

**Theorem 7.** Let  $r > 1$ . Consider any connected graph  $G$  with  $n \geq 2$  vertices and  $m$  edges. Then  $\ell_r(G) \geq n/(288r^2m)$ .

*Proof.* Let  $G = (V, E)$ . Since  $G$  is connected and  $n \geq 2$ , we have  $m \geq n - 1 \geq n/2$ . Thus if  $\ell_r(G) \geq 1/8 > n/(288r^2m)$ , then the result holds. If not, we may apply Lemma 37 to  $G$  to obtain a subset  $B$  of  $V$ . We then have

$$|E| \geq \frac{1}{2} \sum_{v \in B} d(v) \geq \frac{n}{288r^2\ell_r(G)}.$$

The result follows. □

**Theorem 3.** Let  $r > 1$ . Consider any connected  $n$ -vertex graph  $G$  with  $n \geq 2$ . Then  $\ell_r(G) > 1/(42r^{4/3}n^{1/3})$ .

*Proof.* Let  $G = (V, E)$  be a connected  $n$ -vertex graph with  $n \geq 2$ . If  $\ell_r(G) > 1/(15r)$  then we are done. So suppose for the rest of the proof that  $\ell_r(G) \leq 1/(15r)$ .

By Lemma 37, factoring some of the constants to make the arithmetic easier below, there exists a non-empty subset  $B$  of  $V$  such that  $\sum_{v \in B} d(v) \geq n/(2^4 3^2 r^2 \ell_r(G))$  and, for all  $v \in B$ ,  $d(v) \geq 1/(2^5 r^2 \ell_r(G)^2)$ . For each positive integer  $i$ , let  $d_i = 4^{i-1}/(2^5 r^2 \ell_r(G)^2)$  and let  $B_i = \{v \in B \mid d_i \leq d(v) < d_{i+1}\}$ . Every vertex in  $B$  has degree at least  $d_1$ . Let  $\mathcal{I} = \{i \geq 1 \mid |B_i| > 0\}$ . Note that the sets in  $\{B_i \mid i \in \mathcal{I}\}$  are disjoint and they are a partition of  $B$ .

Let  $D = \sum_{i \in \mathcal{I}} d_i |B_i|$ . For every positive integer  $i$ , let  $\ell_i = d_i |B_i| / (2^6 3^2 r^2 4^{i-1} D)$ . The goal will be to show that  $B_i$  sends most of its edges to vertices  $v$  with  $\ell_r(v) > \ell_i$ , so plenty of these vertices exist. To do this, let  $X_i = \{v \in V \mid \ell_r(v) \leq \ell_i\}$ . We start by giving an upper bound on the number of edges from  $B_i$  to  $X_i$ . By Lemma 36 applied with  $S = X_i$  and  $\alpha = \ell_i \leq 1/(2^6 3^2 r^2) < 1/4$ , for all  $i \geq 1$  we have

$$\sum_{v \in X_i} Q_v \leq 4r^2 n \ell_i \ell_r(G) = \frac{d_i |B_i| n \ell_r(G)}{2^4 3^2 \cdot 4^{i-1} D} = \frac{|B_i| n}{2^9 3^2 r^2 \ell_r(G) D}. \quad (18)$$

Now, by the definitions of  $d_i$ ,  $B_i$  and  $B$ ,

$$D = \sum_{i \in \mathcal{I}} d_i |B_i| = \frac{1}{4} \sum_{i \in \mathcal{I}} d_{i+1} |B_i| \geq \frac{1}{4} \sum_{v \in B} d(v) \geq \frac{n}{2^6 3^2 r^2 \ell_r(G)}. \quad (19)$$

It follows from (18) and (19) that

$$\sum_{v \in X_i} Q_v \leq |B_i|/8. \quad (20)$$

On the other hand, using the definition of  $Q_v$  and then the definitions of  $B_i$  and  $d_i$ ,

$$\sum_{v \in X_i} Q_v \geq \sum_{v \in X_i} \sum_{w \in B_i \cap N(v)} \frac{1}{d(w)} = \sum_{w \in B_i} \frac{|N(w) \cap X_i|}{d(w)} \geq \sum_{w \in B_i} \frac{|N(w) \cap X_i|}{d_{i+1}} = \frac{1}{4d_i} \sum_{w \in B_i} |N(w) \cap X_i|.$$

Thus by (20),  $\sum_{w \in B_i} |N(w) \cap X_i| \leq d_i |B_i|/2$ . Now let  $C_i = N(B_i) \setminus X_i$ . It follows that

$$\sum_{w \in B_i} |N(w) \cap C_i| = \sum_{w \in B_i} d(w) - \sum_{w \in B_i} |N(w) \cap X_i| \geq d_i |B_i| - \frac{d_i |B_i|}{2} = \frac{d_i |B_i|}{2}. \quad (21)$$

Thus, we have succeeded in showing that most of the edges from  $B_i$  go to vertices  $v \in C_i$ , which have  $\ell_r(v) > \ell_i$ . For the rest of the proof, we show that the vertices in the sets  $C_i$  give a lower bound on  $\ell_r(G)$ .

When  $i \in \mathcal{I}$ ,  $B_i \neq \emptyset$  and so there is some vertex  $v \in B_i$  that sends at least as many edges into  $C_i$  as the average over  $B_i$ . Since the degree of every vertex is an integer, it follows from (21) that  $|C_i| \geq \lceil d_i/2 \rceil$ . Now, for all  $i \in \mathcal{I}$ , let  $C'_i$  be an arbitrary subset of  $C_i$  such that  $|C'_i| = \lceil d_i/2 \rceil$ . Note that since we have assumed  $\ell_r(G) \leq 1/(15r)$ , we have  $d_1 = 1/(2^5 r^2 \ell_r(G)^2) \geq 6$ . Thus for all  $i \in \mathcal{I}$ ,  $d_i \geq d_1 \geq 6$  and so

$$d_i/2 \leq |C'_i| \leq 2d_i/3. \quad (22)$$

Let  $C''_i = C'_i \setminus \bigcup_{j \in [i-1] \cap \mathcal{I}} C'_j$ . Then all sets  $C''_i$  are disjoint by construction, and by (22) we have

$$|C''_i| \geq \frac{d_i}{2} - \sum_{j \in [i-1] \cap \mathcal{I}} |C'_j| \geq \frac{d_i}{2} - \sum_{j \in [i-1]} \frac{2d_j}{3} = \frac{d_i}{2} - \frac{2}{3} \sum_{j \in [i-1]} \frac{d_i}{4^j} \geq d_i \left( \frac{1}{2} - \frac{2}{3} \sum_{j=1}^{\infty} 4^{-j} \right) > \frac{d_i}{4}.$$

Since  $C''_i \subseteq C'_i \subseteq C_i = N(B_i) \setminus X_i$ , we have  $C''_i \cap X_i = \emptyset$ . So by the definition of  $X_i$ , for all  $v \in C''_i$ , we have  $\ell_r(v) > \ell_i$ . It follows that

$$\begin{aligned} \ell_r(G) &= \frac{1}{n} \sum_{v \in V} \ell_r(v) \geq \frac{1}{n} \sum_{i \in \mathcal{I}} |C''_i| \ell_i \geq \frac{1}{n} \sum_{i \in \mathcal{I}} \frac{d_i}{4} \cdot \frac{d_i |B_i|}{2^6 3^2 r^2 4^{i-1} D} \\ &= \frac{1}{n} \sum_{i \in \mathcal{I}} \frac{4^{i-1}}{2^7 r^2 \ell_r(G)^2} \cdot \frac{d_i |B_i|}{2^6 3^2 r^2 4^{i-1} D} = \frac{\sum_{i \in \mathcal{I}} d_i |B_i|}{2^{13} 3^2 r^4 D n \ell_r(G)^2} = \frac{1}{2^{13} 3^2 r^4 n \ell_r(G)^2}. \end{aligned}$$

Rearranging yields  $\ell_r(G) \geq 1/(42r^{4/3}n^{1/3})$ , as required.  $\square$

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