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# THE EXTINCTION PROBLEM FOR A CLASS OF DISTYLOUS PLANT POPULATIONS

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In this paper, the extinction problem for a class of distylous plant populations is considered within the framework of certain nonhomogeneous nearest-neighbor random walks in the positive quadrant. For the latter, extinction means absorption at one of the axes. Despite connections with some classical probabilistic models (standard two-type Galton-Watson process, two-urn model), exact formulae for the probabilities of absorption seem to be difficult to come by and one must therefore resort to good approximations. In order to meet this task, we develop potential-theoretic tools and provide various sub- and super-harmonic functions which, for large initial populations, provide bounds which in particular improve those that have appeared earlier in the literature.

**1. Introduction.** In distylous flowering plant populations, where each plant belongs to one of two classes, sporophytic self-incompatibility means that every plant produces pollen that can only fecundate the stigmata of plants from the opposite class but not from its own class. A general model for such populations was developed by Billiard and Tran [1], which allowed them to study different relationships between mate availability and fertilization success and to compare the dynamics of distylous species and self-fertile species. An important problem in this context is to find the probability of extinction for one of the styles or at least good approximations thereof. In [8] by Lafitte-Godillon et al., this is done under the following more specific assumptions which are also the basis of the present article:

- Each plant in the population is diploid and its style is characterized by the two alleles it carries at a particular locus.
- There are two allelic types, say A and B, the last one being dominant. Hence, the possible genotypes of the plants are AA, AB and BB, the

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resulting phenotypes, i.e., types of proteins carried by their pollen and stigmates, being A, B and B, respectively.

- Due to self-incompatibility, only pollen and stigmates with different proteins can give viable seeds, i.e., pollen of a plant of phenotype A can only fecundate stigmates of a plant of phenotype A and vice versa.

By the last assumption, seeds of type BB cannot be created. One may therefore consider, without loss of generality, populations made of individuals of genotypes AA and AB only. Each seed is then necessarily also of one of these two genotypes, with probability  $1/2$  each. It is assumed that ovules are produced in continuous time at rate  $r > 0$  and that there is no pollen limitation, that is, each ovule is fecundated to give a seed provided there exists compatible pollen in the population. The lifetime of each individual is supposed to follow an exponential distribution with mean  $1/d$ , where  $d > 0$ . Denoting by  $N_t^A$  and  $N_t^B$  the number of individuals of genotype AB (phenotype A) and BB (phenotype B) at time  $t \in \mathbb{R}_+$ , the process  $(N_t^A, N_t^B)_{t \geq 0}$  forms a Markov jump process on the quarter plane  $\mathbb{N}_0^2 := \{0, 1, 2, \dots\}^2$  with transition rates on  $\mathbb{N}^2 := \{1, 2, 3, \dots\}^2$  displayed in the left panel of Fig. 1. The associated jump chain  $(X_n, Y_n)_{n \geq 0}$ , also called embedded Markov chain and obtained by evaluation of  $(N_t^A, N_t^B)_{t \geq 0}$  at its jump epochs, then has transition probabilities (displayed in the right panel of Fig. 1)

$$(1) \quad \begin{aligned} p_{(x,y),(x+1,y)} &= p_{(x,y),(x,y+1)} = \frac{\bar{\lambda}}{2}, \\ p_{(x,y),(x-1,y)} &= \lambda \cdot \frac{x}{x+y}, \quad p_{(x,y),(x,y-1)} = \lambda \cdot \frac{y}{x+y} \end{aligned}$$

for  $x, y \in \mathbb{N}^2$ , where

$$\lambda := \frac{d}{d+r} \quad \text{and} \quad \bar{\lambda} := 1 - \lambda.$$

Note that it may also be viewed as a spatially nonhomogeneous nearest-neighbor random walk in the quarter plane. Self-incompatibility implies that reproduction becomes impossible and thus extinction occurs once one of the phenotypes disappears, i.e.,  $Z_t^B = 0$  or  $Z_t^A = 0$  for some  $t$ . Consequently, both introduced processes are absorbed when hitting one of the axes. Defining the extinction probabilities

$$(2) \quad q_{x,y} := \mathbb{P}_{x,y}(\tau < \infty),$$

where  $\mathbb{P}_{x,y} := \mathbb{P}(\cdot | X_0 = x, Y_0 = y)$  and

$$\tau := \inf\{n \geq 0 : X_n = 0 \text{ or } Y_n = 0\},$$

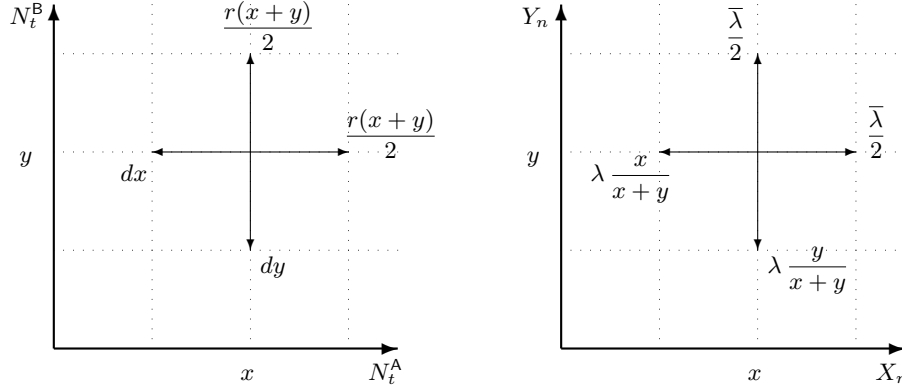


FIG 1. Transition rates at  $(x, y)$  for the population-size Markov jump process  $(N_t^A, N_t^B)_{t \geq 0}$  (left) and the transition probabilities for its associated embedded Markov chain  $(Z_n^A, Z_n^B)_{n \geq 0}$  (right).

it is of great interest to compute these probabilities or to find good approximations. Billiard and Tran [1, Prop. 9] used a coupling argument to show that

$$(3) \quad \mu^{x+y} \leq q_{x,y} \leq \mu^x + \mu^y - \mu^{x+y} = 1 - (1 - \mu^x)(1 - \mu^y)$$

for all  $x, y \in \mathbb{N}_0$  if

$$\mu := \frac{d}{r} < 1 \quad (\text{supercritical case}),$$

while  $q_{x,y} = 1$  for all  $x, y \in \mathbb{N}_0$  if  $\mu \geq 1$ .

From now on we will focus on the supercritical case and therefore make the standing assumption  $\mu < 1$ , equivalently  $\lambda = \frac{\mu}{1+\mu} < \frac{1}{2}$ , unless explicitly stated otherwise.

As usual, we put  $x \wedge y := \min\{x, y\}$  and  $x \vee y := \max\{x, y\}$ . If  $P$  denotes the transition operator of  $(X_n, Y_n)_{n \geq 0}$ , thus  $Pf(x, y) = f(x, y)$  if  $x \wedge y = 0$  and

$$(4) \quad Pf(x, y) = \lambda \left( \frac{x}{x+y} f(x-1, y) + \frac{y}{x+y} f(x, y-1) \right) + \frac{\bar{\lambda}}{2} \frac{f(x+1, y) + f(x, y+1)}{2}$$

for  $x, y \in \mathbb{N}$ , then  $q_{x,y}$  is  $P$ -harmonic, i.e.,  $Pq = q$  or, in explicit form,

$$(5) \quad q_{x,y} = \lambda \left( \frac{x}{x+y} q_{x-1,y} + \frac{y}{x+y} q_{x,y-1} \right) + \frac{\bar{\lambda}}{2} \frac{q_{x+1,y} + q_{x,y+1}}{2}$$

for all  $x, y \in \mathbb{N}_0$ . Hence  $q$  forms a solution to the Dirichlet problem

$$Pf(x, y) = f(x, y) \quad \text{and} \quad f(x, 0) = f(0, y) = 1 \quad \text{for all } x, y \in \mathbb{N}.$$

There are infinitely many positive solutions, for instance  $f \equiv 1$ , among which  $q$  constitutes the minimal one as has been shown in [8, Prop. 2.1] by a standard martingale argument. It is also shown there that in fact any specification of  $f(x, 1)$  for  $x \in \mathbb{N}$  uniquely determines a solution. By the symmetries of the model, any solution  $f$  must clearly satisfy  $f(x, y) = f(y, x)$  for all  $x, y \in \mathbb{N}_0$ .

As it seems impossible to find explicit formulae for  $q_{x,y}$ , which a priori might appear surprising, there is need for good approximations, lower and upper bounds, and asymptotic estimates as  $x$  and/or  $y$  tend to infinity. This is the main topic of the present article. Apart from inequality (3), which appears to be rather crude, the only further result, obtained in [8, Prop. 2.3 and Rem. 2.4], asserts that, for any fixed  $y \in \mathbb{N}$  and  $x \rightarrow \infty$ ,

$$(6) \quad q_{x,y} \simeq (2\mu)^y \frac{y!}{x^y}.$$

On the other hand, the behavior of  $q_{x,y}$  as  $x$  and  $y$  both get large (including the case of particular interest when  $x = y$ ) appears to be completely open. Already the determination of the lower and upper rate of exponential decay of  $q_{x,x}$ , viz.

$$(7) \quad \kappa_* := \liminf_{x \rightarrow \infty} q_{x,x}^{1/x} \quad \text{and} \quad \kappa^* := \limsup_{x \rightarrow \infty} q_{x,x}^{1/x},$$

including the question whether or not  $\kappa_* = \kappa^*$ , poses a very difficult problem. By inequality (3),

$$(8) \quad \mu^2 \leq \kappa_* \leq \kappa^* \leq \mu.$$

An improvement of (3) and (8) will be stated as Theorem 3.1 and derived in Section 4 by quite different, rather simple potential-theoretic arguments along with an interpretation of the bounds. It will also be shown in Section 8 that  $\mu^x + \mu^y - \mu^{x+y}$ , the upper bound in (3), equals exactly the extinction probability function for the two 2-type population models with transition probabilities shown in Fig. 2. In the first one (left panel), here called *independent branching with complete segregation (IBCS)*, the two subpopulations A and B evolve independently, meaning that, given current subpopulation sizes  $x$  and  $y$ , a birth or death “picks” an individual at random and thus with probabilities  $\frac{x}{x+y}$  and  $\frac{y}{x+y}$  from A and B, respectively. In the second model,

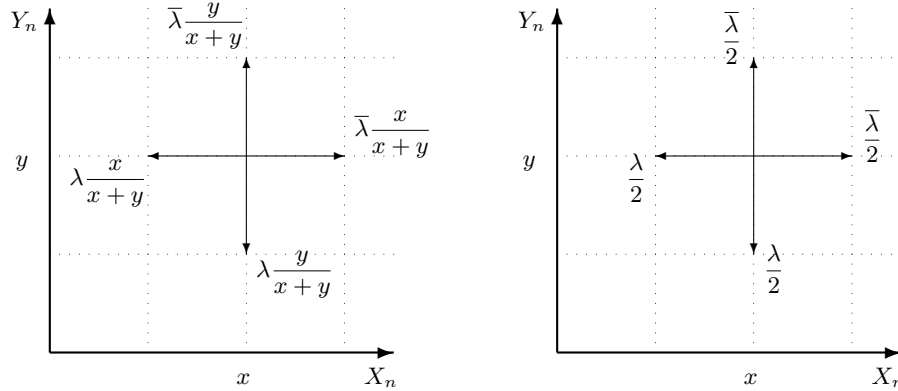


FIG 2. Transition probabilities at  $(x, y)$  for  $(X_n, Y_n)_{n \geq 0}$  in the branching model with complete segregation (left panel) and the model with fully symmetric type selection (right panel).

here called *branching with unbiased type selection (BUTS)*, it is the subpopulation (and thus the type) which is picked at random by a birth and death and thus with probability  $\frac{1}{2}$  each (before absorption). Obviously, the model studied in this work constitutes a hybrid of the two aforementioned ones and this may be taken as some evidence for the conjecture that the upper bound in (3) is also a good approximation for  $q_{x,y}$ , at least in the sense that it determines the asymptotic exponential decay of  $q_{x,x}$ , thus  $\kappa_* = \kappa^* = \mu$ . However, Theorem 3.3, one of our main results, will actually show that  $\kappa^*$  is *always* strictly less than  $\mu$ . For an explanation of this outcome we refer to Section 3.

We conclude this introduction by mentioning some related work. First, the probabilities of absorption at a given axis for the BUTS model are computed in [7, Thm. 13] in terms of integrals of Chebychev polynomials; applications of these results in finance (study of Markovian order books) can be found in [2], see in particular Prop. 3 there. For a generalization of the BUTS model with eight jump directions (see the right panel of Fig. 3), it is shown in [7, Prop. 9] (in the presence of a positive drift) that  $\frac{a_{x,y}}{2} \leq q_{x,y} \leq a_{x,y}$ , with

$$a_{x,y} = \left( \frac{p_{-1,-1} + p_{0,-1} + p_{1,-1}}{p_{-1,1} + p_{0,1} + p_{1,1}} \right)^x + \left( \frac{p_{-1,-1} + p_{-1,0} + p_{-1,1}}{p_{1,-1} + p_{1,0} + p_{1,1}} \right)^y.$$

Second, when restricting our model (with jumps as in Fig. 1) to the very particular case  $\lambda = 1$  (pure death model), i.e., with no jumps to the North and the East, the probabilities of absorption at a given axis are computed in [3], together with a proposed interpretation within the framework of a war-of-attrition problem. Finally, for a queueing model with South and West

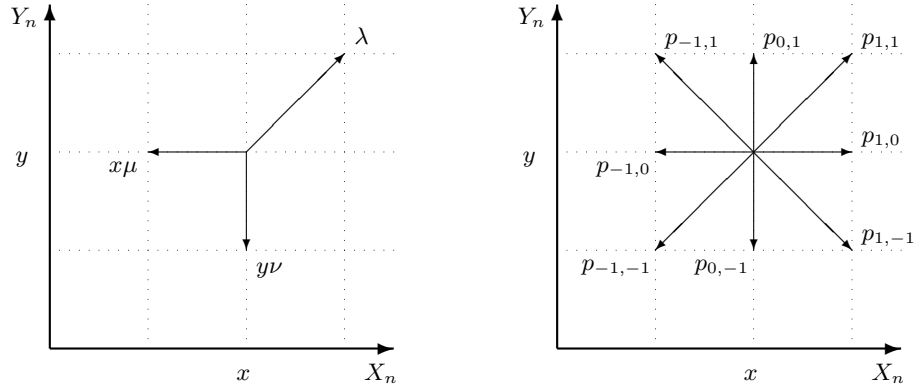


FIG 3. Transition probabilities at  $(x, y)$  for  $(X_n, Y_n)_{n \geq 0}$  in the  $M/M/\infty$  parallel queuing model with simultaneous arrivals of [5] (left panel) and for a generalization to eight neighbors of the unbiased type selection model (right panel).

rates as in Fig. 1, and one last homogeneous North-East rate (see Fig. 3), Foddy in her PhD thesis arrives at a closed-form expression for the generating function of the stationary distribution, see [5, Thm. 24].

**2. The random walk  $(X_n, Y_n)_{n \geq 0}$  in alternative contexts.** From a mathematical point of view, it is useful to see the random walk  $(X_n, Y_n)_{n \geq 0}$  appearing in various contexts, three of which we shortly describe hereafter. The last of these will be particularly interesting because it offers an extended framework by introducing a random environment. This will allow us to look at the behavior of  $(X_n, Y_n)_{n \geq 0}$  also on a quenched level and thus provide an additional leverage for the derivation of good bounds for the  $q_{x,y}$ .

*2.1. Standard 2-type binary splitting.* Consider a two-type binary splitting population model in continuous time, in which individuals act independently and any individual  $v$  has a type  $\sigma_v \in \{A, B\}$ , a standard exponential lifetime and a random number  $N_v^x$  of type- $x$  offspring for  $x \in \{A, B\}$  which is produced at the end of her life and independent of the lifetime. Furthermore,

$$\begin{aligned} \mathbb{P}((N_v^A, N_v^B) = (0, 0) | \sigma_v = A) &= \mathbb{P}((N_v^A, N_v^B) = (0, 0) | \sigma_v = B) = \frac{d}{d+r} = \lambda, \\ \mathbb{P}((N_v^A, N_v^B) = (1, 1) | \sigma_v = A) &= \mathbb{P}((N_v^A, N_v^B) = (2, 0) | \sigma_v = A) = \frac{\bar{\lambda}}{2}, \\ \mathbb{P}((N_v^A, N_v^B) = (1, 1) | \sigma_v = B) &= \mathbb{P}((N_v^A, N_v^B) = (0, 2) | \sigma_v = B) = \frac{\bar{\lambda}}{2} \end{aligned}$$

for parameters  $r, d > 0$  such that  $d < r$ . Denoting by  $Z_t^x$  the number of living individuals of type  $x$  at time  $t$ , the process  $(Z_t^A, Z_t^B)_{t \geq 0}$  is a supercritical

two-type Bellman-Harris branching process with mean reproduction matrix

$$\begin{pmatrix} m_{AA} & m_{AB} \\ m_{BA} & m_{BB} \end{pmatrix} = \begin{pmatrix} \frac{3r}{2(d+r)} & \frac{r}{2(d+r)} \\ \frac{r}{2(d+r)} & \frac{3r}{2(d+r)} \end{pmatrix},$$

where  $m_{xy} = \mathbb{E}(N_v^y | \sigma_v = x)$ . Due to the symmetric reproduction mechanism, the total population size  $Z_t = Z_t^A + Z_t^B$  at time  $t$  forms a supercritical binary splitting Bellman-Harris process with offspring mean

$$\mathbf{m} = m_{AA} + m_{AB} = m_{BA} + m_{BB} = 2\bar{\lambda} > 1.$$

As a consequence, the pertinent total generation-size sequence  $(Z_n)_{n \geq 0}$  is an ordinary binary splitting Galton-Watson process with offspring mean  $\mathbf{m}$ , offspring distribution

$$p_0 = \lambda = 1 - p_2$$

and extinction probability

$$q = \frac{d}{r} = \mu$$

when starting with one ancestor ( $Z_0 = 1$ ). Clearly,  $q$  is also the probability of extinction for  $(Z_t)_{t \geq 0}$ .

To make the connection with our original model, notice that  $(Z_t^A, Z_t^B)_{t \geq 0}$  also constitutes a continuous-time birth and death process on  $\mathbb{N}_0^2$  and has the same transition rates as  $(N_t^A, N_t^B)_{t \geq 0}$  on  $\mathbb{N}^2$ . Consequently,

$$(N_t^A, N_t^B)_{t \geq 0} \stackrel{d}{=} (Z_{t \wedge T}^A, Z_{t \wedge T}^B)_{t \geq 0} \quad \text{and} \quad (X_n, Y_n)_{n \geq 0} \stackrel{d}{=} (Z_{n \wedge \nu}^A, Z_{n \wedge \nu}^B)_{n \geq 0},$$

where  $(Z_n^A, Z_n^B)_{n \geq 0}$  denotes the associated jump chain of  $(Z_t^A, Z_t^B)_{t \geq 0}$ ,

$$T := \inf\{t \geq 0 : Z_t^A \wedge Z_t^B = 0\}, \quad \nu := \inf\{n \geq 0 : Z_n^A \wedge Z_n^B = 0\}$$

and  $\stackrel{d}{=}$  denotes equality in law. We thus see that our extinction problem may be rephrased as an extinction problem for a particular 2-type Galton-Watson process which, however, is nonstandard because for the latter process it means to find the probability for each of the types to disappear momentarily (by irreducibility, new individuals of that type may be produced afterwards as offspring from the other type).

*2.2. A two-urn model.* Another very simple way to obtain the sequence  $(X_n, Y_n)_{n \geq 0}$  is by considering the following nonterminating two-step procedure of adding or removing a ball, one per round, from one of two urns, say A and B. Initially, these urns contain  $\widehat{X}_0$  and  $\widehat{Y}_0$  balls, respectively. In the



first step of each round, we toss a coin so as to determine whether a ball is removed or added, which happens with respective probabilities  $0 < \lambda < 1/2$  and  $\bar{\lambda}$ . Then, if a ball is to be removed, we just pick one at random not regarding the urn in which it lies. But if a ball is to be added, then we pick the designated urn at random. Let  $\widehat{X}_n$  and  $\widehat{Y}_n$  be the number of balls in A and B after  $n$  rounds, respectively, and put

$$\nu := \inf\{n \geq 0 : \widehat{X}_n \wedge \widehat{Y}_n = 0\}.$$

Then  $(X_n, Y_n) := (\widehat{X}_{n \wedge \nu}, \widehat{Y}_{n \wedge \nu})$ ,  $n \in \mathbb{N}_0$ , is indeed a random walk on  $\mathbb{N}_0^2$  with transition probabilities and transition operator given by (1) and (4), respectively, and this time obtained from the nonhomogeneous random walk  $(\widehat{X}_n, \widehat{Y}_n)_{n \geq 0}$  on  $\mathbb{N}_0^2$  by killing the latter when it first hits one of the axes. Unfortunately, this nice alternative interpretation of our model does again not lead to any additional clue about how to solve our extinction problem.

*2.3. A Markov chain with iid random transition probabilities.* Rather than yet another alternative, our last model description should be seen as an extension of the one given in Subsection 2.1 by enlarging our perspective in some sense. Recall from there that  $(Z_n^A, Z_n^B)_{n \geq 0}$  denotes the jump chain of the 2-type Bellman-Harris process  $(Z_t^A, Z_t^B)_{t \geq 0}$  and that  $(Z_n^A + Z_n^B)_{n \geq 0}$  has iid increments  $e_1, e_2, \dots$  taking values  $-1$  and  $+1$  with respective probabilities  $\lambda$  and  $\bar{\lambda}$ . Obviously, the value of  $e_n$  determines whether the  $n$ th jump epoch marks a birth ( $+1$ ) or a death ( $-1$ ) in the population. Let us adopt the perspective of  $\mathbf{e} = (e_n)_{n \geq 1}$  being a random environment for the Markov chain  $(Z_n^A, Z_n^B)_{n \geq 0}$ . Then, given  $\mathbf{e}$ , this sequence is still Markovian but temporally nonhomogeneous, its transition operator at time  $n$  being  $\mathcal{P}_{e_n}$ , where

$$\mathcal{P}_1 f(x, y) := \frac{f(x+1, y) + f(x, y+1)}{2}$$

and

$$\mathcal{P}_{-1} f(x, y) := \frac{x}{x+y} f(x-1, y) + \frac{y}{x+y} f(x, y-1)$$

for  $x, y \in \mathbb{N}_0$ . In other words,

$$\mathbb{E}_{x,y}^{\mathbf{e}}(f(Z_n^A, Z_n^B) | Z_{n-1}^A, Z_{n-1}^B) = \mathcal{P}_{e_n} f(Z_{n-1}^A, Z_{n-1}^B) \quad \text{a.s.}$$

and

$$\mathbb{E}_{x,y}^{\mathbf{e}} f(Z_n^A, Z_n^B) = \mathcal{P}_{e_1} \mathcal{P}_{e_2} \cdots \mathcal{P}_{e_n} f(x, y) \quad \text{a.s.}$$

for all  $n \in \mathbb{N}$  and  $x, y \in \mathbb{N}_0$ , where  $\mathbb{E}_{x,y}^{\mathbf{e}} := \mathbb{E}_{x,y}(\cdot | \mathbf{e})$ . Freezing  $(Z_n^A, Z_n^B)_{n \geq 0}$  when it hits the axes leads to  $(X_n, Y_n)_{n \geq 0}$  which in turn implies that

$$\mathbb{E}_{x,y}^{\mathbf{e}}(f(X_n, Y_n) | X_{n-1}, Y_{n-1}) = P_{e_n} f(X_{n-1}, Y_{n-1}) \quad \text{a.s.}$$

and

$$\mathbb{E}_{x,y}^{\mathbf{e}} f(X_n, Y_n) = P_{e_1} P_{e_2} \cdots P_{e_n} f(x, y) \quad \text{a.s.}$$

for all  $n \in \mathbb{N}$  and  $x, y \in \mathbb{N}_0$ , where  $P_{\pm 1}$  equals the modification of  $\mathcal{P}_{\pm 1}$  which is absorbing on the axes, i.e.,  $P_{\pm 1}(x, y) = f(x, y)$  if  $x \wedge y = 0$ . So we see that, by introduction of  $\mathbf{e}$ ,  $(X_n, Y_n)_{n \geq 0}$  becomes a Markov chain with iid random transition probabilities, viz.

$$(9) \quad \begin{aligned} p_{(x,y),(x+1,y)}(e_n) &= p_{(x,y),(x,y+1)}(e_n) = \frac{1}{2} \mathbf{1}_{\{e_n=1\}}, \\ p_{(x,y),(x-1,y)}(e_n) &= \frac{x}{x+y} \mathbf{1}_{\{e_n=-1\}}, \\ p_{(x,y),(x,y-1)}(e_n) &= \frac{y}{x+y} \mathbf{1}_{\{e_n=-1\}} \end{aligned}$$

for  $x, y \in \mathbb{N}^2$  and  $p_{(x,0),(x,0)}(e_n) = p_{(0,y),(0,y)}(e_n) = 1$  for  $x, y \in \mathbb{N}_0^2$ . The associated quenched extinction probabilities are denoted by  $q_{x,y}(\mathbf{e})$ , so

$$q_{x,y}(\mathbf{e}) := \mathbb{P}_{x,y}^{\mathbf{e}}(\tau < \infty)$$

for  $x, y \in \mathbb{N}_0$ . Plainly,  $q_{x,0}(\mathbf{e}) = q_{0,y}(\mathbf{e}) = 1$ , and

$$q_{x,y} = \mathbb{E} q_{x,y}(\mathbf{e}).$$

**3. Results.** Let us define the following functions on  $\mathbb{N}_0^2$  that will appear in our results and frequently be used in our analysis, namely

$$(10) \quad f_0(x, y) := \mu^{x+y}, \quad f_1(x, y) := \mu^x + \mu^y$$

and

$$(11) \quad h(x, y) := \mu^x + \mu^y - \mu^{x+y} = f_1(x, y) - f_0(x, y).$$

The very same functions multiplied with  $\binom{x+y}{x}^{-1}$  are denoted as  $\widehat{f}_0$ ,  $\widehat{f}_1$  and  $\widehat{h}$ , respectively. Our first theorem restates inequalities (3) and (8) with improved lower bounds.

**THEOREM 3.1.** *For all  $x, y \in \mathbb{N}_0$ ,*

$$(12) \quad f_0(x, y) \vee \left[ \left( 1 + \frac{\mu}{2(1+\mu)} \right)^{x \wedge y} \widehat{f}_1(x, y) \right] \leq q_{x,y} \leq h(x, y)$$

As a consequence,

$$(13) \quad \mu^2 \vee \left[ \frac{\mu}{4} \left( 1 + \frac{\mu}{2(1+\mu)} \right) \right] \leq \kappa_* \leq \kappa^* \leq \mu.$$

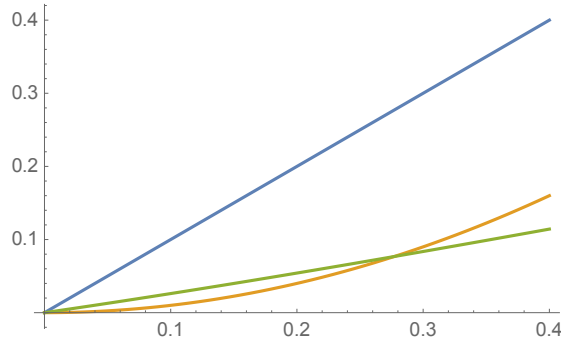


FIG 4. The curves  $\mu \mapsto \mu^2$  (orange) and  $\mu \mapsto \frac{\mu}{4} \left( 1 + \frac{\mu}{2(1+\mu)} \right)$  (green) for small values of  $\mu$ . The identity function is shown in blue.

It will be shown in Section 4 that the functions  $h$  and  $\widehat{h}$  are super- and subharmonic for  $P$ , respectively, with  $h(x, y) = \widehat{h}(x, y) = 1$  if  $x \wedge y = 0$ . This leads to

$$(14) \quad \widehat{h}(x, y) \leq q_{x,y} \leq h(x, y)$$

for all  $x, y \in \mathbb{N}_0$  as an almost direct consequence (use Lemma 4.1). But since

$$\widehat{h}(x, y) = \widehat{f}_1(x, y) - \widehat{f}_0(x, y) \leq \left( 1 + \frac{\mu}{2(1+\mu)} \right)^{x \wedge y} \widehat{f}_1(x, y),$$

we see that inequality (12) stated in our Theorem 3.1 is stronger. Its lower bound does indeed provide a strong improvement over that in (8) for small values of the parameter  $\mu$  (see Fig. 4). On the other hand, our conjecture, supported by Fig. 5, is that  $\kappa_* = \kappa^* = \kappa$  and

$$(15) \quad \kappa = \begin{cases} \frac{\mu}{2} & \text{if } \mu \in [0, \frac{1}{2}), \\ \mu^2 & \text{if } \mu \in [\frac{1}{2}, 1], \end{cases}$$

and that a phase transition occurs at  $\mu = \frac{1}{2}$ . Further evidence in support of (15) for  $\mu \in (\frac{1}{2}, 1]$  is provided by Fig. 6: for the random walk to reach the boundary, it has to traverse one of the regions confined by an axis and

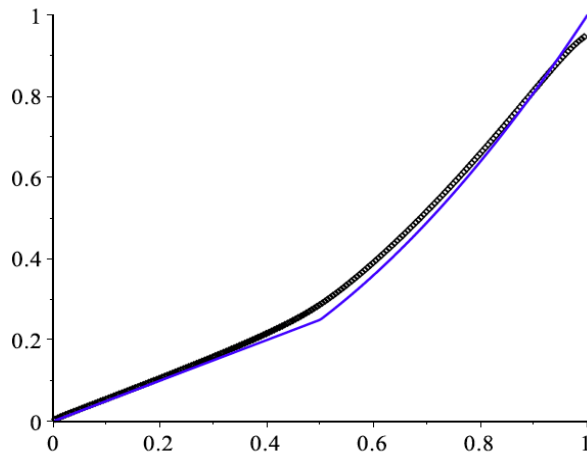


FIG 5. Simulations of the exponential decay  $\kappa$  in (7) (black) and comparison with the conjectured curve (15) (blue). The simulations were realized with  $R$ .

a neighboring red line, where the drift vector  $(\mathbb{E}_{x,y}X_1 - x, \mathbb{E}_{x,y}Y_1 - y)$  has a negative component which pushes the walk closer to the origin. In other words, in the event that the walk hits one of the axes, its nonzero component should not be too large either and thus become eventually absorbed as well. Equivalently, the probability of absorption at one of the axes for remote starting points  $(x, x)$  is essentially the same as the probability of absorption of  $X_n + Y_n$  at 0. But the latter equals  $\mu^{2x}$  and has therefore asymptotic exponential decay  $\mu^2$  as  $x \rightarrow \infty$ . Unfortunately, we have no intuitive explanation for the rate  $\frac{\mu}{2}$  in the case  $\mu \in [0, \frac{1}{2}]$ .

The following corollary is a straightforward consequence of (14), more precisely  $q_{x,y} \geq \widehat{h}(x, y)$ , when using the standard asymptotics for  $\binom{x+y}{x}$ .

COROLLARY 3.2. *For any fixed  $y \in \mathbb{N}$  and  $x \rightarrow \infty$ ,*

$$\liminf_{x \rightarrow \infty} x^y q_{x,y} \geq y! \mu^y.$$

The result should be compared with the exact asymptotics stated in (6), the only difference there being an extra term  $2^y$ .

As announced in the Introduction, it is one of our main results that the exponential decay of the extinction probability  $q_{x,x}$  is strictly less than  $\mu$ :

THEOREM 3.3. *If  $\mu < 1$ , then there exists  $\nu \in (0, \mu)$  such that*

$$q_{x,x} = o(\nu^x)$$

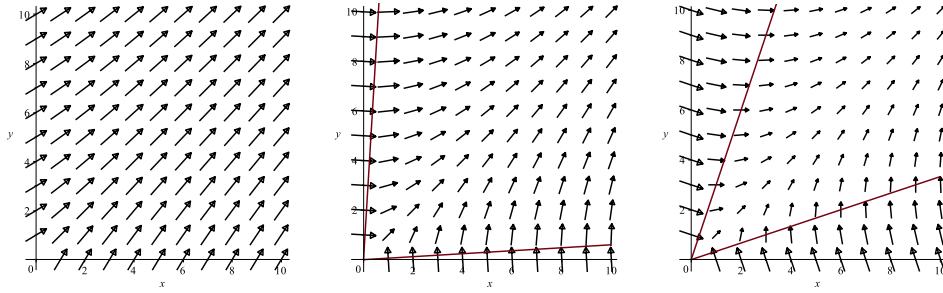


FIG 6. Drift vectors for  $\mu = 0.2$  (left),  $\mu = 0.53$  (middle), and  $\mu = 0.66$  (right). The red lines are  $y = (2\mu - 1)x$  and  $y = (2\mu - 1)^{-1}x$ . They are located in the positive quarter plane if, and only if,  $\mu \in [\frac{1}{2}, 1]$ . Within the cone delimited by these two lines, both drift coordinates are positive, while outside the cone one of them becomes negative.

as  $x \rightarrow \infty$ , thus  $\kappa^* < \mu$ .

It is intuitively appealing if not obvious that  $q_{x,y}$  decreases in both arguments. Although confirmed by our last theorem, the proof requires some care and will be based on a coupling argument.

**THEOREM 3.4.** *As a function of  $(x, y) \in \mathbb{N}^2$ ,  $q_{x,y}$  is nonincreasing in each argument, thus*

$$q_{x,1} \leq q_{x,2} \leq \dots \leq q_{x,x} \leq q_{x,x+1} \leq \dots$$

for all  $x \in \mathbb{N}$ .

In connection with the later use of  $P$ -sub- and  $P$ -superharmonic functions in order to prove Theorem 3.1, a required property of our random walk is the following *standard behavior*: If  $(X_n, Y_n)_{n \geq 0}$  is not absorbed at one of the axes ( $\tau = \infty$ ), then explosion not only of the total population size occurs, i.e.,  $X_n + Y_n \rightarrow \infty$  a.s., but actually of both subpopulation sizes as well, i.e.,  $X_n \wedge Y_n \rightarrow \infty$  a.s., see Lemma 4.1 for the result where this property enters. The property is stated in the subsequent proposition and proved at the end of Section 4.

**PROPOSITION 3.5.** *The random walk  $(X_n, Y_n)_{n \geq 0}$  on  $\mathbb{N}_0^2$  with transition probabilities defined by (1) on  $\mathbb{N}^2$  exhibits standard behavior in the sense that*

$$(16) \quad \lim_{n \rightarrow \infty} X_n \wedge Y_n = \infty \quad \mathbb{P}_{x,y}\text{-a.s. on } \{\tau = \infty\}$$

for all  $x, y \in \mathbb{N}$ .

Let us finally stipulate for the rest of this work that  $\mathbb{P}$  will be used for probabilities that are the same under any  $\mathbb{P}_{x,y}$ ,  $x, y \in \mathbb{N}_0$ .

**4. Annealed harmonic analysis and proof of Theorem 3.1.** The purpose of this section is to show that standard harmonic analysis for the transition operator  $P$  of  $(X_n, Y_n)_{n \geq 0}$ , see (4), provides the appropriate tool to rather easily derive bounds for  $q_{x,y}$  of the form stated in Theorem 3.1.

4.1. *Sub(super)harmonic functions and applications.* We begin with the statement of the following basic result, valid for any transition operator  $P$  on  $\mathbb{N}_0^2$  that is absorbing on the axes.

LEMMA 4.1. *Let  $f$  be any nonnegative sub[super]harmonic function for  $P$  such that  $f(x, y) = 1$  for  $x \wedge y = 0$  and  $\lim_{x \wedge y \rightarrow \infty} f(x, y) = 0$ . Then  $q_{x,y} \geq [\leq] f(x, y)$  for all  $x, y \in \mathbb{N}_0$ .*

PROOF. By the assumptions,  $(f(X_n, Y_n))_{n \geq 0}$  forms a nonnegative bounded sub[super]martingale satisfying  $f(X_\tau, Y_\tau) = 1$  on  $\{\tau < \infty\}$ . Moreover, by Proposition 3.5,  $f(X_n, Y_n) \rightarrow 0$  a.s. on  $\{\tau = \infty\}$  so that  $f(X_{\tau \wedge n}, Y_{\tau \wedge n})$  converges a.s. to  $\mathbf{1}_{\{\tau < \infty\}}$ . Now use the Optional Sampling Theorem to infer

$$f(x, y) \leq [\geq] \lim_{n \rightarrow \infty} \mathbb{E}_{x,y} f(X_{\tau \wedge n}, Y_{\tau \wedge n}) = \mathbb{P}_{x,y}(\tau < \infty) = q_{x,y}$$

for all  $x, y \in \mathbb{N}_0$ . □

Besides  $f_0$ ,  $f_1$  and  $h$  already defined at the beginning of Section 3, the following functions will also be useful hereafter:

$$(17) \quad \begin{aligned} f_\wedge(x, y) &:= \mu^{x \wedge y}, \\ f_\vee(x, y) &:= \mu^{x \vee y}, \\ f_2(x, y) &:= f_\wedge(x, y) - f_\vee(x, y) = \mu^{x \wedge y} - \mu^{x \vee y}. \end{aligned}$$

Their counterparts multiplied with  $\binom{x+y}{x}^{-1}$  are denoted  $\widehat{f}_\wedge$ ,  $\widehat{f}_\vee$  and  $\widehat{f}_2$ . In order to prove Theorem 3.1, we continue with a derivation of the  $P$ -harmonic properties of these functions. The results will particularly show that  $h$  is  $P$ -superharmonic (Lemma 4.5), and that  $\widehat{f}_1$  and  $\widehat{h}$  are  $P$ -subharmonic (Lemmata 4.6 and 4.8).

LEMMA 4.2. *The function  $f_0(x, y) = \mu^{x+y}$  is  $P$ -harmonic.*

PROOF. For all  $x, y \in \mathbb{N}$ , we have that

$$Pf_0(x, y) = \lambda\mu^{x+y-1} + \bar{\lambda}\mu^{x+y+1} = \bar{\lambda}\mu^{x+y} + \lambda\mu^{x+y} = \mu^{x+y},$$

which proves the assertion.  $\square$

The subsequent lemmata will provide formulae for  $Pf_\wedge$ ,  $Pf_\vee$ , etc.

LEMMA 4.3. *For  $x, y \in \mathbb{N}$ , the function  $f_\wedge(x, y)$  satisfies*

$$Pf_\wedge(x, y) = \begin{cases} 2\bar{\lambda}f_\wedge(x, y), & \text{if } x = y, \\ \left(1 - (1 - 2\lambda)\frac{|x - y|}{2(x + y)}\right) f_\wedge(x, y), & \text{if } x \neq y. \end{cases}$$

As a consequence,

$$Pf_\wedge(x, y) \begin{cases} \geq f_\wedge(x, y), & \text{if } x = y, \\ \leq f_\wedge(x, y), & \text{if } x \neq y. \end{cases}$$

PROOF. It suffices to consider  $x \leq y$ . Note that  $\lambda < 1 - \lambda$  implies  $\bar{\lambda}x + \lambda y \leq \frac{1}{2}(x + y)$ . Using this, we find for  $x < y$

$$\begin{aligned} Pf_\wedge(x, y) &= \lambda \left( \frac{x}{x + y} \mu^{x-1} + \frac{y}{x + y} \mu^x \right) + \bar{\lambda} \frac{\mu^{x+1} + \mu^x}{2} \\ &= \mu^x \left( \bar{\lambda} \frac{x}{x + y} + \lambda \frac{y}{x + y} + \frac{1}{2} \right) \\ &= \mu^x \left( 1 - (1 - 2\lambda) \frac{|x - y|}{2(x + y)} \right) \\ &\leq \mu^x = f_\wedge(x, y), \end{aligned}$$

whereas for  $x = y$ ,

$$Pf_\wedge(x, x) = \lambda\mu^{x-1} + \bar{\lambda}\mu^x = 2\bar{\lambda}\mu^x \geq \mu^x = f_\wedge(x, x)$$

holds true as claimed.  $\square$

LEMMA 4.4. *For  $x, y \in \mathbb{N}$ , the function  $f_\vee(x, y)$  satisfies*

$$Pf_\vee(x, y) = \begin{cases} 2\lambda f_\vee(x, y), & \text{if } x = y, \\ \left(1 + (1 - 2\lambda)\frac{|x - y|}{2(x + y)}\right) f_\vee(x, y), & \text{if } x \neq y. \end{cases}$$

As a consequence,

$$Pf_{\vee}(x, y) \begin{cases} \leq f_{\vee}(x, y), & \text{if } x = y, \\ \geq f_{\vee}(x, y), & \text{if } x \neq y. \end{cases}$$

PROOF. Again, it suffices to consider  $x \leq y$ . Note that  $\lambda < 1 - \lambda$  then implies  $\lambda x + \bar{\lambda}y \geq \frac{1}{2}(x + y)$ . For  $x < y$ , we obtain

$$\begin{aligned} Pf_{\vee}(x, y) &= \lambda \left( \frac{x}{x+y} \mu^y + \frac{y}{x+y} \mu^{y-1} \right) + \bar{\lambda} \frac{\mu^y + \mu^{y+1}}{2} \\ &= \mu^y \left( \lambda \frac{x}{x+y} + \bar{\lambda} \frac{y}{x+y} + \frac{1}{2} \right) \\ &= \mu^y \left( 1 + (1 - 2\lambda) \frac{|x - y|}{2(x + y)} \right) \\ &\geq \mu^y = f_{\vee}(x, y), \end{aligned}$$

where  $\lambda x + \bar{\lambda}y \geq \frac{1}{2}(x + y)$  has been utilized. If  $x = y$ , then

$$Pf_{\vee}(x, x) = \lambda \mu^x + \bar{\lambda} \mu^{x+1} = 2\lambda \mu^x \leq \mu^x = f_{\vee}(x, x),$$

which completes the proof.  $\square$

LEMMA 4.5. For  $x, y \in \mathbb{N}$ , the function  $h$  in (11) satisfies

$$(18) \quad Ph(x, y) = h(x, y) - (1 - 2\lambda) \frac{|x - y|}{2(x + y)} f_2(x, y) \leq h(x, y)$$

with  $f_2$  defined in (17), and is thus  $P$ -superharmonic. Furthermore, the same identity holds true for  $f_1 = h - f_0$ , and

$$(19) \quad Pf_2(x, y) = \begin{cases} (1 - 2\lambda) f_1(x, y), & \text{if } x = y, \\ f_2(x, y) - (1 - 2\lambda) \frac{|x - y|}{2(x + y)} f_1(x, y), & \text{if } x \neq y. \end{cases}$$

PROOF. It suffices to prove (18) for  $f_1$ , for  $f_0 = f_1 - h$  is harmonic by Lemma 4.2. With the help of Lemmata 4.3 and 4.4, we obtain for  $x < y$

$$\begin{aligned} Pf_1(x, y) &= Pf_{\wedge}(x, y) + Pf_{\vee}(x, y) \\ &= f_{\wedge}(x, y) + f_{\vee}(x, y) - (1 - 2\lambda) \frac{|x - y|}{2(x + y)} (f_{\wedge}(x, y) - f_{\vee}(x, y)) \\ &= f_1(x, y) - (1 - 2\lambda) \frac{y - x}{2(x + y)} f_2(x, y) \end{aligned}$$



$$\leq f_1(x, y),$$

and for  $x = y$  (note that obviously  $f_\wedge(x, x) = f_\vee(x, x)$ )

$$Pf_1(x, x) = (2\bar{\lambda} + 2\lambda)f_\wedge(x, x) = 2f_\wedge(x, x) = f_1(x, x),$$

which proves (18). Eq. (19) follows in a similar manner.  $\square$

Turning to the harmonic properties of  $\widehat{f}_0$ ,  $\widehat{f}_1$  and  $\widehat{h}$ , we first study  $\widehat{f}_1$ .

LEMMA 4.6. *The function  $\widehat{f}_1$  is subharmonic for  $P$ , in fact for  $x, y \in \mathbb{N}$*

$$Pf_1(x, y) - \widehat{f}_1(x, y) \begin{cases} = \frac{1}{2} \left( 1 + \frac{1}{x+y+1} \right) \widehat{f}_1(x, y), & \text{if } x = y \\ \geq \frac{\lambda}{2} \left( 1 + \frac{1}{x+y+1} \right) \widehat{f}_1(x, y), & \text{if } x \neq y \end{cases} \geq \frac{\lambda}{2} \widehat{f}_1(x, y).$$

PROOF. Using

$$\frac{x}{x+y} \binom{x+y-1}{x-1}^{-1} = \binom{x+y}{x}^{-1}$$

for  $x, y \in \mathbb{N}$ , we find

$$\begin{aligned} Pf_1(x, y) &= \lambda \left( \frac{x}{x+y} \widehat{f}_1(x-1, y) + \frac{y}{x+y} \widehat{f}_1(x, y-1) \right) \\ &\quad + \bar{\lambda} \left( \frac{\widehat{f}_1(x+1, y) + \widehat{f}_1(x, y+1)}{2} \right) \\ &= \widehat{f}_1(x, y) + \frac{1}{2} \binom{x+y}{x}^{-1} \mu^x \left( \lambda \frac{x+1}{x+y+1} + \bar{\lambda} \frac{y+1}{x+y+1} \right) \\ &\quad + \frac{1}{2} \binom{x+y}{x}^{-1} \mu^y \left( \bar{\lambda} \frac{x+1}{x+y+1} + \lambda \frac{y+1}{x+y+1} \right), \end{aligned}$$

and from this, the assertion is easily derived.  $\square$

LEMMA 4.7. *The functions  $\widehat{f}_0$  and  $\widehat{f}(x, y) := \binom{x+y}{x}^{-1} (2\mu)^{x+y} = 2^{x+y} \widehat{f}_0(x, y)$  are both  $P$ -subharmonic.*

PROOF. Regarding  $\widehat{f}_0$ , we obtain, for  $x, y \in \mathbb{N}$ ,

$$Pf_0(x, y) = 2\bar{\lambda} \widehat{f}_0(x, y) + \frac{\lambda}{2} \left( 1 + \frac{1}{x+y+1} \right) \widehat{f}_0(x, y)$$

$$\geq \bar{\lambda} \left(2 + \frac{\mu}{2}\right) \widehat{f}_0(x, y) \geq \widehat{f}_0(x, y)$$

and analogously

$$P\widehat{f}(x, y) = \bar{\lambda} \widehat{f}(x, y) + \lambda \left(1 + \frac{1}{x+y+1}\right) \widehat{f}(x, y) \geq \widehat{f}(x, y). \quad \square$$

LEMMA 4.8. *The function  $\widehat{h}$  is  $P$ -subharmonic.*

PROOF. Noting that  $\widehat{h} = \widehat{f}_1 - \widehat{f}_0$  and  $\frac{\lambda}{2} \widehat{f}_1(x, y) \geq \widehat{f}_0(x, y)$  for  $x, y \in \mathbb{N}$ , the previous calculations provide us with

$$\begin{aligned} P\widehat{h}(x, y) &= P\widehat{f}_1(x, y) - P\widehat{f}_0(x, y) \\ &\geq \widehat{f}_1(x, y) + \frac{x+y+2}{x+y+1} \widehat{f}_0(x, y) \\ &\quad - \left( \frac{2}{1+\mu} + \frac{\mu}{2(1+\mu)} \frac{x+y+2}{x+y+1} \right) \widehat{f}_0(x, y) \\ &\geq \widehat{h}(x, y) + \frac{x+y+2}{x+y+1} \widehat{f}_0(x, y) \\ &\quad - \left( \frac{1-\mu}{1+\mu} + \frac{\mu}{2(1+\mu)} \frac{x+y+2}{x+y+1} \right) \widehat{f}_0(x, y) \\ &\geq \widehat{h}(x, y) + \left(1 - \frac{2-\mu}{2(1+\mu)}\right) \frac{x+y+2}{x+y+1} \widehat{f}_0(x, y) \\ &= \widehat{h}(x, y) + \frac{\mu}{2(1+\mu)} \frac{x+y+2}{x+y+1} \widehat{f}_0(x, y) \\ &\geq \widehat{h}(x, y) \end{aligned}$$

for all  $x, y \in \mathbb{N}$  (including the case  $x = y$ ). □

#### 4.2. Proofs of Theorem 3.1 and of Proposition 3.5.

PROOF OF THEOREM 3.1. Since  $(X_n, Y_n)_{n \geq 0}$  exhibits standard behavior (Proposition 3.5) and, using Lemmata 4.4 and 4.8,  $h$  and  $\widehat{h}$  are obviously functions satisfying the conditions of Lemma 4.1, we directly infer  $\widehat{h}(x, y) \leq q_{x,y} \leq h(x, y)$  for all  $x, y \in \mathbb{N}_0$ . As for  $f_0$ , it does not meet the boundary conditions stated in Lemma 4.1, yet

$$\begin{aligned} f_0(x, y) &= \lim_{n \rightarrow \infty} \mathbb{E}_{x,y} \mu^{X_{\tau \wedge n} + Y_{\tau \wedge n}} \\ &= \int_{\{X_{\tau=0}\}} \mu^{Y_{\tau}} d\mathbb{P}_{x,y} + \int_{\{Y_{\tau=0}\}} \mu^{X_{\tau}} d\mathbb{P}_{x,y} \end{aligned}$$

$$\begin{aligned} &\leq \mathbb{P}_{x,y}(X_\tau = 0) + \mathbb{P}_{x,y}(Y_\tau = 0) \\ &= q_{x,y} \end{aligned}$$

for all  $x, y \in \mathbb{N}_0$  as asserted. Turning to the proof of (13), it suffices to note that

$$\lim_{x \rightarrow \infty} f_0(x, x)^{1/x} = \mu^2, \quad \lim_{x \rightarrow \infty} h(x, x)^{1/x} = \mu$$

and

$$\lim_{x \rightarrow \infty} \widehat{h}(x, x)^{1/x} = \lim_{x \rightarrow \infty} \left( \frac{2x}{x} \right)^{-1/x} h(x, x)^{1/x} = \frac{\mu}{4},$$

having used Stirling's formula for the last assertion.  $\square$

**PROOF OF PROPOSITION 3.5.** Recall from Subsection 2.1 that, on  $\{\tau = \infty\}$ ,  $X_n + Y_n$  can be viewed as the total population size of a 2-type Bellman-Harris process at its  $n$ th jump epoch. The extinction-explosion principle for such branching processes (see [6, Thm. (6.5.2)]) implies that  $X_n + Y_n \rightarrow \infty$   $\mathbb{P}_{x,y}$ -a.s. on  $\{\tau = \infty\}$  for all  $x, y \in \mathbb{N}$ . Now use that  $(h(X_n, Y_n))_{n \geq 0}$  forms a bounded supermartingale under any  $\mathbb{P}_{x,y}$  and thus converges a.s. Consider the event

$$E := \left\{ \tau = \infty, \lim_{n \rightarrow \infty} X_n = \infty, \limsup_{n \rightarrow \infty} Y_n < \infty \right\}$$

and write

$$h(X_n, Y_n) = 1 - (1 - \mu^{X_n})(1 - \mu^{Y_n}).$$

Then we see that the integer-valued  $Y_n$  must a.s. eventually stay constant on  $E$ . But this is impossible because at each birth epoch  $Y_n$  changes by +1 with probability  $\frac{1}{2}$ . So  $\mathbb{P}_{x,y}(E) = 0$ . Similarly, we find

$$\mathbb{P}(\tau = \infty, \lim_{n \rightarrow \infty} Y_n = \infty, \limsup_{n \rightarrow \infty} X_n < \infty) = 0$$

and so  $X_n \wedge Y_n \rightarrow \infty$  a.s. on  $\{\tau = \infty\}$  as claimed.  $\square$

**4.3. Construction of harmonic functions.** A central role in the present work is played by the use of harmonic and sub(super)harmonic functions. Indeed, the various functions that are provided in Subsection 4.1 are all of this kind and used to get bounds for the lower and upper exponential decay  $\kappa_*$  and  $\kappa^*$  of the extinction probability, respectively, which forms a crucial tool to establish our main results. An obvious key point is that the functions  $f_0, f_1, h$ , etc., and their counterparts  $\widehat{f}_0, \widehat{f}_1, \widehat{h}$ , etc., are explicit and rather simple. In this subsection, we would like to discuss some aspects of the construction of these functions.

Finding exact expressions for harmonic functions reveals intrinsic properties of the model at hand. For instance, harmonic functions can be used to define martingales, which in turn yield information on the pathwise behavior of the random walks. Of related interest, one may cite the constructive theory of Lyapunov functions for nonhomogeneous random walks, see [4, 9].

Our (sub,super)harmonic functions can be interpreted both combinatorially and probabilistically. From a combinatorial viewpoint, they are constructed from classical binomial coefficients  $\binom{x+y}{x}$  and power functions  $\mu^x$ ,  $\mu^{x+y}$ , etc. On the probabilistic side, they can be interpreted as absorption probabilities for related models (which later will appear in some coupling arguments):

- First,  $f_0(x, y)$  in (10) is the probability that the simple random walk on the nonnegative integers with probabilities  $\lambda$  and  $\bar{\lambda}$  for making a jump to the left and right, respectively, is eventually absorbed at the origin when starting from  $x + y$ .
- The quantity  $h(x, y)$  in (11) is the probability that a homogeneous random walk in the positive quadrant  $\mathbb{N}^2$  which jumps to the four nearest neighbors  $\rightarrow, \uparrow, \leftarrow$  and  $\downarrow$  with respective probabilities  $\frac{\lambda}{2}, \frac{\lambda}{2}, \frac{\bar{\lambda}}{2}$  and  $\frac{\bar{\lambda}}{2}$  (see right panel of Fig. 2) is eventually absorbed at the boundary when starting from  $(x, y)$ , see [7, 1].
- Finally, the binomial coefficient  $\binom{x+y}{x}^{-1}$  has a simple interpretation, since the probability of the path

$$(x, y) \rightarrow (x, y - 1) \rightarrow (x, y - 2) \rightarrow \cdots \rightarrow (x, 1) \rightarrow (x, 0)$$

is exactly  $\left(\frac{\mu}{1+\mu}\right)^y \binom{x+y}{x}^{-1}$ . This path is the shortest one for the random walk to get absorbed (if  $x < y$ ). Notice further that this binomial coefficient does respect the symmetry of the model, as obviously  $\binom{x+y}{x}^{-1} = \binom{x+y}{y}^{-1}$ .

**5. Quenched harmonic analysis.** Adopting the framework of Subsection 2.3, we will now turn to an analysis of the model given the iid random environment  $\mathbf{e} = (e_1, e_2, \dots)$ , i.e., under the probability measures  $\mathbb{P}_{x,y}^{\mathbf{e}}$ , where the value of  $e_n$  marks whether the  $n$ th jump is a birth (+1) or a death (-1). As we explained in this subsection, the sequence  $(X_n, Y_n)_{n \geq 0}$  then becomes a Markov chain with iid random transition probabilities  $p_{(x,y),(x \pm 1, y \pm 1)}(e_n)$  which are displayed in (9) for  $x, y \in \mathbb{N}$  and  $p_{(x,0),(x,0)}(e_n) = p_{(0,y),(0,y)}(e_n) = 1$  for  $x, y \in \mathbb{N}_0^2$ .

Put  $T_0 := 0$  and let  $T_1 + 1, T_2 + 2, \dots$  denote the successive epochs when

$e_n = -1$ , thus

$$T_n + n := \inf\{k > T_{n-1} + n - 1 : e_k = -1\}$$

for each  $n \geq 1$ . Notice that all  $T_n$  are measurable with respect to  $\mathbf{e}$  and thus constants under any  $\mathbb{P}_{x,y}^{\mathbf{e}}$ . Furthermore,  $(T_n)_{n \geq 0}$  has iid increments  $\chi_1, \chi_2, \dots$  under any  $\mathbb{P}_{x,y}$  with a geometric distribution on  $\mathbb{N}_0$ , more precisely

$$\mathbb{P}(\chi_1 = n) = \lambda \bar{\lambda}^n$$

for  $n \in \mathbb{N}_0$ . Its generating function  $\varphi(\theta) = \mathbb{E} \theta^{\chi_1}$  equals

$$\varphi(\theta) = \frac{\lambda}{1 - \lambda\theta}$$

for  $\theta < \bar{\lambda}^{-1}$ , giving in particular  $\varphi((2\bar{\lambda})^{-1}) = 2\lambda$ . As a direct consequence, to be used later on, we note that:

LEMMA 5.1. *Under each  $\mathbb{P}_{x,y}$ , the sequence*

$$\left( \frac{1}{(2\lambda)^n (2\bar{\lambda})^{T_n}} \right)_{n \geq 0}$$

*forms a product martingale with mean 1 and almost sure limit 0.*

Since absorption at the axes can clearly occur only at the  $T_n + n$ , we will study hereafter the behavior of the subsequence

$$(\widehat{X}_n, \widehat{Y}_n)_{n \geq 0} := (X_{T_n+n}, Y_{T_n+n})_{n \geq 0}$$

under  $\mathbb{P}_{x,y}^{\mathbf{e}}$ . Recall from Subsection 2.3 the definition of the transition operators  $P_1$  and  $P_{-1}$ .

LEMMA 5.2. *Put  $\widehat{P}_n := P_1^{\chi_n} P_{-1}$ . Then  $(\widehat{X}_n, \widehat{Y}_n)_{n \geq 0}$  is a nonhomogeneous Markov chain under  $\mathbb{P}_{x,y}^{\mathbf{e}}$  with transition operators  $\widehat{P}_1, \widehat{P}_2, \dots$ , thus*

$$(20) \quad \widehat{P}_1 \cdots \widehat{P}_n f(x, y) = \mathbb{E}_{x,y}^{\mathbf{e}} f(\widehat{X}_n, \widehat{Y}_n)$$

*for any  $x, y, n \in \mathbb{N}$  and any nonnegative function  $f$  on  $\mathbb{N}_0^2$ .*

PROOF. Recalling that  $\chi_1, \chi_2, \dots$  and thus the  $T_n$  are measurable with respect to  $\mathbf{e}$  and that  $(X_n, Y_n)_{n \geq 0}$  is Markovian under  $\mathbb{P}_{x,y}^{\mathbf{e}}$ , we obtain

$$\mathbb{E}_{x,y}^{\mathbf{e}} f(\widehat{X}_n, \widehat{Y}_n) = \mathbb{E}_{x,y}^{\mathbf{e}} \mathbb{E}_{x,y}^{\mathbf{e}} (f(\widehat{X}_n, \widehat{Y}_n) | \widehat{X}_{n-1}, \widehat{Y}_{n-1}) = \mathbb{E}_{x,y}^{\mathbf{e}} \widehat{P}_n f(\widehat{X}_{n-1}, \widehat{Y}_{n-1})$$

and then (20) upon successive conditioning.  $\square$

The following lemma provides the crucial information about the spectral properties of  $P_1$  and  $P_{-1}$  with respect to the functions  $f_0$  and  $f_1$  introduced in (10). Let us put

$$(21) \quad \gamma := \frac{1-\mu}{1+\mu} = \bar{\lambda} - \lambda = 1 - 2\lambda \in (0, 1).$$

LEMMA 5.3. *For all  $x, y \in \mathbb{N}$ , the following assertions hold true:*

$$(22) \quad P_1 f_0(x, y) = \mu f_0(x, y) \quad \text{and} \quad P_{-1} f_0(x, y) = \mu^{-1} f_0(x, y),$$

$$(23) \quad P_1 f_1(x, y) = \frac{1+\mu}{2} f_1(x, y) = \frac{1}{2\lambda} f_1(x, y),$$

$$(24) \quad \begin{aligned} P_{-1} f_1(x, y) &= \frac{1 - \delta_1(x, y)}{2} (\mu^{x-1} + \mu^x + \mu^y + \mu^{y-1}) \\ &= \frac{1 - \delta_1(x, y)}{2\lambda} f_1(x, y), \end{aligned}$$

where

$$\delta_1(x, y) = \gamma \frac{1 - \mu^{|x-y|}}{1 + \mu^{|x-y|}} \frac{|x-y|}{x+y}.$$

PROOF. We will only prove (24), for all other identities are readily checked. Let us start by noting that, if  $y = x + m$  for some  $m \in \mathbb{N}_0$ , then

$$\frac{1}{2} - \frac{x}{x+y} = \frac{y}{x+y} - \frac{1}{2} = \frac{m}{2(x+y)}$$

and therefore

$$\begin{aligned} \left( \frac{1}{2} - \frac{x}{x+y} \right) (\mu^{x-1} + \mu^y) + \left( \frac{1}{2} - \frac{y}{x+y} \right) (\mu^x + \mu^{y-1}) \\ = \frac{m}{2(x+y)} \mu^{x-1} (1 - \mu^m) (1 - \mu). \end{aligned}$$

It follows that

$$\begin{aligned} P_{-1} f_1(x, y) &= \frac{x}{x+y} (\mu^{x-1} + \mu^y) + \frac{y}{x+y} (\mu^x + \mu^{y-1}) \\ &= \frac{1}{2} \mu^{x-1} (1 + \mu^m) (1 + \mu) + \frac{m}{2(x+y)} \mu^{x-1} (1 - \mu^m) (1 - \mu), \end{aligned}$$

and with this at hand, it remains to assess for (24) that the last term in the previous line equals

$$\frac{\delta_1(x, y)}{2} (\mu^{x-1} + \mu^x + \mu^y + \mu^{y-1}) = \frac{\delta_1(x, y)}{2} \mu^{x-1} (1 + \mu^m) (1 + \mu)$$

and that  $m = y - x = |y - x|$ .  $\square$

Note that  $\delta_1(x, x) = 0$  and

$$(25) \quad \gamma^2 \frac{|x-y|}{x+y} \leq \delta_1(x, y) \leq \gamma \frac{|x-y|}{x+y}$$

for all  $x, y \in \mathbb{N}$ .

LEMMA 5.4. *For all  $n \in \mathbb{N}_0$  and  $x, y \in \mathbb{N}$  such that  $(x \wedge y) \wedge |y-x| \geq n$ ,*

$$(26) \quad \frac{1 - a_n(x, y)}{2\lambda(2\bar{\lambda})^n} f_1(x, y) \leq P_1^n P_{-1} f_1(x, y) \leq \frac{1 - \gamma a_n(x, y)}{2\lambda(2\bar{\lambda})^n} f_1(x, y),$$

where

$$a_n(x, y) := \gamma \frac{|x-y|}{x+y+n} + \gamma^2 \frac{n}{x+y+n}.$$

PROOF. We use induction over  $n \in \mathbb{N}_0$ . For  $n = 0$ , the result follows from (24) and (25). Put  $b_n^{(i)}(x, y) := 1 - \gamma^i a_n(x, y)$  for  $i \in \mathbb{N}_0$ . Assuming (26) be true for  $n$ , we obtain for  $x, y \in \mathbb{N}$ , w.l.o.g.  $x \leq y$ , such that  $x \wedge (y-x) \geq n+1$

$$\begin{aligned} 2\lambda(2\bar{\lambda})^n P_1^{n+1} P_{-1} f_1(x, y) &\geq P_1 \left[ b_n^{(0)}(x, y) f_1(x, y) \right] \\ &= \frac{1}{2} \left( b_n^{(0)}(x+1, y)(\mu^{x+1} + \mu^y) + b_n^{(0)}(x, y+1)(\mu^x + \mu^{y+1}) \right) \\ &= \frac{1}{2} \left( b_{n+1}^{(0)}(x, y) + \frac{\gamma^2}{x+y+n+1} \right) (\mu^{x+1} + \mu^y + \mu^x + \mu^{y+1}) \\ &\quad + \frac{1}{2} \left( \frac{\gamma}{x+y+n+1} \right) (\mu^{x+1} + \mu^y - \mu^x - \mu^{y+1}) \\ &= \frac{1+\mu}{2} \left( b_{n+1}^{(0)}(x, y) + \frac{\gamma^2}{x+y+n+1} \right) (\mu^x + \mu^y) \\ &\quad - \frac{1}{2} \left( \frac{\gamma}{x+y+n+1} \right) (\mu^x + \mu^y)(1-\mu) \\ &= \frac{1}{2\bar{\lambda}} b_{n+1}^{(0)}(x, y) f_1(x, y) \end{aligned}$$

and in exactly the same way

$$2\lambda(2\bar{\lambda})^n P_1^{n+1} P_{-1} f_1(x, y) \leq P_1 \left[ b_n^{(1)}(x, y) f_1(x, y) \right] = \frac{1}{2\bar{\lambda}} b_{n+1}^{(1)}(x, y) f_1(x, y)$$

which proves the assertion.  $\square$

**6. Proof of Theorem 3.3.** Given a sequence  $(Z_n)_{n \geq 0}$  of random variables, we stipulate for our convenience that its extension to the time domain  $[0, \infty)$  is defined by  $Z_t := Z_{\lfloor t \rfloor}$  for  $t \geq 0$ . For  $c \geq 0$ , let

$$\tau_c := \inf\{n \geq 0 : X_n \wedge Y_n \leq c\},$$

thus  $\tau_c = \tau_{\lfloor c \rfloor}$  and  $\tau = \tau_0$ .

The proof of Theorem 3.3 is furnished by a number of lemmata, but let us sketch its main arguments first. In order to hit one of the axes, the random walk  $(X_n, Y_n)_{n \geq 0}$ , when starting at  $(x, x)$ , must clearly first hit one of the halflines

$$\{(y, \lfloor \beta x \rfloor) : \mathbb{N} \ni y \geq \lfloor \beta x \rfloor\} \quad \text{or} \quad \{(\lfloor \beta x \rfloor, y) : \mathbb{N} \ni y \geq \lfloor \beta x \rfloor\}$$

for any  $\beta \in (0, 1)$  (see Fig. 7), and the probability for this to happen, that is for  $\tau_{\beta x}$  to be finite, can easily be bounded by  $2\mu^{(1-\beta)x}$ , see Lemma 6.1. On the other hand, it can further be shown for sufficiently large  $x$  that  $|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}|$  is not too small with very high probability, namely larger than  $\alpha x$  for some  $\alpha > 0$ , see Lemma 6.2. With the help of the strong Markov property and the obvious fact that  $(\tau_{\beta x}, X_{\tau_{\beta x}}) \stackrel{d}{=} (\tau_{\beta x}, Y_{\tau_{\beta x}})$  under  $\mathbb{P}_{x,x}$ , it then follows that

$$\begin{aligned} q_{x,x} &\leq 2 \int_{\{\tau_{\beta x} < \infty, X_{\tau_{\beta x}} = \lfloor \beta x \rfloor, Y_{\tau_{\beta x}} - X_{\tau_{\beta x}} > \alpha x\}} q_{\lfloor \beta x \rfloor, Y_{\tau_{\beta x}}} d\mathbb{P}_{x,x} + r(x) \\ &\leq \mathbb{P}_{x,x}(\tau_{\beta x} < \infty) \sup_{y \geq (1+\alpha)\lfloor \beta x \rfloor} q_{\lfloor \beta x \rfloor, y} + r(x) \\ &\leq 2\mu^{(1-\beta)x} \sup_{y \geq (1+\alpha)\lfloor \beta x \rfloor} q_{\lfloor \beta x \rfloor, y} + r(x) \end{aligned}$$

where  $r(x)$  is a remainder of order  $o(\mu^{(1+\varepsilon)x})$  for some  $\varepsilon > 0$ . The proof of the theorem is finally completed by showing that, for some  $\nu < \mu$ ,

$$\sup_{y \geq (1+\alpha)x} q_{x,y} = o(\nu^x)$$

as  $x \rightarrow \infty$ , see Lemma 6.5. This is actually accomplished by choosing  $\beta$  and then  $\alpha$  in an appropriate manner.

**LEMMA 6.1.** *For all  $x, y \in \mathbb{N}$  and  $c \in [0, x \wedge y)$ ,*

$$\mathbb{P}_{x,y}(\tau_c < \infty) \leq f_1(x-c, y-c) \leq 2\mu^{(x-c) \wedge (y-c)}.$$

*In particular*

$$(27) \quad \mathbb{P}_{x,y}(\tau_{\beta x} < \infty) \leq 2\mu^{(1-\beta)x}$$

*if  $x \leq y$  and  $\beta \in (0, 1)$ .*



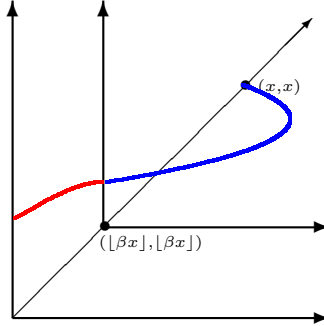


FIG 7. In the event of absorption at one of the axes, the walk  $(X_n, Y_n)_{n \geq 0}$ , when starting at  $(x, x)$ , must necessarily pass through one of the halflines emanating from  $(\lfloor \beta x \rfloor, \lfloor \beta x \rfloor)$  for  $\beta \in (0, 1)$ . A typical absorbed trajectory can thus be split in two parts: a first part prior to  $\tau_{\beta x}$  (in blue) and a final part (in red) which in fact may return to the inner cone before absorption.

PROOF. Let  $c$  be an integer. By Lemma 4.5,  $(h(X_{\tau_c \wedge n}, Y_{\tau_c \wedge n}))_{n \geq 0}$  forms a bounded nonnegative supermartingale, and it converges  $\mathbb{P}_{x,y}$ -a.s. to

$$h(c, Y_{\tau_c}) \mathbf{1}_{\{\tau_c < \infty, X_{\tau_c} = c\}} + h(X_{\tau_c}, c) \mathbf{1}_{\{\tau_c < \infty, Y_{\tau_c} = c\}} \geq \mu^c \mathbf{1}_{\{\tau_c < \infty\}}$$

because, by Proposition 3.5,  $X_n \wedge Y_n \rightarrow \infty$  a.s. on  $\{\tau_c = \infty\} \subset \{\tau = \infty\}$ . Consequently,

$$\mu^c \mathbb{P}_{x,y}(\tau_c < \infty) \leq \lim_{n \rightarrow \infty} \mathbb{E}_{x,y} h(X_{\tau_c \wedge n}, Y_{\tau_c \wedge n}) \leq h(x, y)$$

and therefore

$$\mathbb{P}_{x,y}(\tau_c < \infty) \leq \mu^{-c} h(x, y) \leq f_1(x - c, y - c) \leq 2\mu^{(x-c) \wedge (y-c)}$$

for all  $x, y \in \mathbb{N}$  and  $c \in [0, x \wedge y)$ , as claimed.  $\square$

LEMMA 6.2. Given any  $\beta \in (0, 1)$  and  $\alpha > 0$ ,

$$\mathbb{P}_{x,x}(|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| \leq \alpha x) \leq \mu^{(2-2\beta-\alpha)x}$$

for all  $x \in \mathbb{N}$ .

PROOF. The Optional Sampling Theorem provides us with

$$\mu^{2x} = \mathbb{E}_{x,x} \mu^{X_{\tau_{\beta x}} + Y_{\tau_{\beta x}}} \geq \mu^{2\beta x} \mathbb{E}_{x,x} \mu^{X_{\tau_{\beta x}} \vee Y_{\tau_{\beta x}} - X_{\tau_{\beta x}} \wedge Y_{\tau_{\beta x}}},$$

thus

$$\mu^{2(1-\beta)x} \geq \mathbb{E}_{x,x} \mu^{X_{\tau_{\beta x}} \vee Y_{\tau_{\beta x}} - X_{\tau_{\beta x}} \wedge Y_{\tau_{\beta x}}}$$

$$\begin{aligned}
 &\geq \mu^{\alpha x} \mathbb{P}_{x,x}(X_{\tau_{\beta x}} \vee Y_{\tau_{\beta x}} - X_{\tau_{\beta x}} \wedge Y_{\tau_{\beta x}} \leq \alpha x) \\
 &= \mu^{\alpha x} \mathbb{P}_{x,x}(|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| \leq \alpha x)
 \end{aligned}$$

which immediately implies the assertion.  $\square$

Recall that  $T_n + n$  denotes the epoch at which the  $n$ th death (downward step) occurs, so that  $T_n$  provides the number of births (upward steps) until then. Since any birth is equally likely to be of phenotype A (upward jump in the  $x$ -coordinate) and B (upward jump in the  $y$ -coordinate), the total number of A-type births until  $T_n + n$ , say  $S_n$ , has a binomial distribution with parameters  $T_n$  and  $\frac{1}{2}$  under any  $\mathbb{P}_{x,y}^e$ , and the increments  $S_k - S_{k-1}$  are independent and binomial with parameters  $\chi_k$  and  $\frac{1}{2}$ . Notice also that

$$\begin{aligned}
 (28) \quad \widehat{Y}_n - \widehat{X}_n &= Y_{T_n+n} - X_{T_n+n} \\
 &\geq y - x - n + T_n - 2S_n \geq y - x - n - T_n
 \end{aligned}$$

for all  $n \in \mathbb{N}$ , a fact to be used in the proof of the subsequent lemma.

LEMMA 6.3. *For any  $\beta > 0$ , there exists  $\xi > \mu^{-1}$  large enough such that*

$$(29) \quad \mathbb{P}(T_{\beta x} > \xi \beta x) = o(\mu^{(1+2\beta)x})$$

and, for any  $\alpha > (\xi + 2)\beta$ ,

$$(30) \quad \sup_{y \geq (1+\alpha)x} \mathbb{P}_{x,y} \left( \min_{1 \leq n \leq \beta x} (\widehat{Y}_n - \widehat{X}_n) \leq \beta x \right) = o(\mu^{(1+\beta)x})$$

as  $x \rightarrow \infty$ .

PROOF. Fix  $\beta > 0$ . Since, for each  $n \in \mathbb{N}$ ,  $T_n$  is the sum of  $n$  iid geometric random variables with parameter  $\lambda$  (thus mean  $\bar{\lambda}/\lambda = \mu^{-1}$ ) under any  $\mathbb{P}_{x,y}$ , Cramér's theorem implies that, for sufficiently large  $\xi > \mu^{-1}$  and  $n \rightarrow \infty$ ,

$$\mathbb{P} \left( \frac{T_n}{n} > \xi \right) = o(\mu^{(2+1/\beta)n})$$

and thus (29) holds true as  $x \rightarrow \infty$ . Now pick an arbitrary  $\alpha > (\xi + 2)\beta$ . Using (28), we then obtain for  $1 \leq n \leq \beta x$  and  $y \geq (1 + \alpha)x$

$$\begin{aligned}
 \mathbb{P}_{x,y} \left( \widehat{Y}_n - \widehat{X}_n \leq \beta x \right) &\leq \mathbb{P}(y - x - n - T_n \leq \beta x) \\
 &\leq \mathbb{P}(T_n \geq (\alpha - 2\beta)x) \\
 &\leq \mathbb{P}(T_{\beta x} \geq \xi \beta x)
 \end{aligned}$$

and thereupon with the help of (29)

$$\begin{aligned} \mathbb{P}_{x,y} \left( \min_{1 \leq n \leq \beta x} (\widehat{Y}_n - \widehat{X}_n) \leq \beta x \right) &\leq \sum_{1 \leq n \leq \beta x} \mathbb{P}_{x,y} (\widehat{Y}_n - \widehat{X}_n \leq \beta x) \\ &\leq \beta x \mathbb{P}(T_{\beta x} \geq \xi \beta x) = o(\mu^{(1+\beta)x}) \end{aligned}$$

as  $x \rightarrow \infty$ . □

LEMMA 6.4. *Let  $\beta \in (0, 1)$ ,  $\xi > 0$ ,  $\alpha > (\xi + 3)\beta$ ,  $y = (1 + \alpha)x$ ,  $\gamma$  defined in (21), and put  $n(x) := \lfloor \beta x \rfloor + 1$ . Then there exists  $\theta = \theta(\alpha, \beta, \gamma, \xi) \in (0, 1)$  such that, for all sufficiently large  $x$ ,*

$$\sup_{1 \leq n \leq n(x)} \frac{(2\lambda)^n (2\bar{\lambda})^{T_n}}{\theta^n} \widehat{P}_1 \cdots \widehat{P}_n f_1(x, y) \leq f_1(x, y) \quad \mathbb{P}_{x,y}^e\text{-a.s.}$$

on the event

$$E_{\beta, \xi} := \left\{ \min_{1 \leq n \leq n(x)} |\widehat{X}_n - \widehat{Y}_n| > \beta x, T_{n(x)} \leq \xi n(x) \right\},$$

in particular

$$\widehat{P}_1 \cdots \widehat{P}_{n(x)} f_1(x, y) \leq \frac{\theta^{\beta x}}{(2\lambda)^{n(x)} (2\bar{\lambda})^{T_{n(x)}}} f_1(x, y) \quad \mathbb{P}_{x,y}^e\text{-a.s.}$$

PROOF. Recall from Lemma 5.4 the definition of  $a_n(x, y)$  and observe that  $\mathbb{P}_{x,y}^e$ -a.s. on  $E_{\beta, \xi}$

$$\begin{aligned} a_{\chi_n}(\widehat{X}_{n-1}, \widehat{Y}_{n-1}) &\geq \gamma \frac{|\widehat{X}_{n-1} - \widehat{Y}_{n-1}|}{\widehat{X}_{n-1} + \widehat{Y}_{n-1} + \chi_n} \\ &= \gamma \frac{|\widehat{X}_{n-1} - \widehat{Y}_{n-1}|}{x + y + T_n + n - 1} \geq \frac{\gamma \beta}{2 + \alpha + \beta(1 + \xi)} \end{aligned}$$

for all  $n = 1, \dots, n(x) - 1$ . With this at hand, we use Lemmata 5.2 and 5.4 to infer for such  $n$

$$\begin{aligned} \widehat{P}_1 \cdots \widehat{P}_n f_1(x, y) &= \mathbb{E}_{x,y}^e \widehat{P}_n(\widehat{X}_{n-1}, \widehat{Y}_{n-1}) \\ &\leq \mathbb{E}_{x,y}^e \left[ \frac{1 - \gamma a_{\chi_n}(\widehat{X}_{n-1}, \widehat{Y}_{n-1})}{2\lambda(2\bar{\lambda})^{\chi_n}} f_1(\widehat{X}_{n-1}, \widehat{Y}_{n-1}) \right] \\ &\leq \frac{1}{2\lambda(2\bar{\lambda})^{\chi_n}} \left( 1 - \frac{\gamma^2 \beta}{2 + \alpha + \beta(1 + \xi)} \right) \mathbb{E}_{x,y}^e f_1(\widehat{X}_{n-1}, \widehat{Y}_{n-1}) \end{aligned}$$

$$= \frac{1}{2\lambda(2\bar{\lambda})\lambda^n} \left( 1 - \frac{\gamma^2\beta}{2 + \alpha + \beta(1 + \xi)} \right) \widehat{P}_1 \cdots \widehat{P}_{n-1} f_1(x, y) \quad \mathbb{P}_{x,y}^e\text{-a.s.}$$

Upon setting

$$(31) \quad \theta := 1 - \frac{\gamma^2\beta}{2 + \alpha + \beta(1 + \xi)}$$

and iteration, the assertions now easily follow.  $\square$

LEMMA 6.5. *Let  $E_{\beta,\xi}$  be the set defined in Lemma 6.4. Given any  $\beta > 0$ , let  $\xi > \mu^{-1}$  be such that, by Lemma 6.3,  $\mathbb{P}_{x,y}(E_{\beta,\xi}^c) = o(x^{(1+\beta)x})$  as  $x \rightarrow \infty$ . Then*

$$\sup_{y \geq (1+\alpha)x} q_{x,y} \leq \theta^{\beta x} \mu^x + o(\mu^{(1+\beta)x})$$

for  $\theta$  defined in (31),  $\alpha > (\xi + 2)\beta$  and all  $x \in \mathbb{N}$ .

PROOF. For  $\alpha, \beta, \xi$  as claimed and  $n(x) = \lfloor \beta x \rfloor + 1$ , we obtain with the help of the previous lemmata in combination with Lemma 5.1

$$\begin{aligned} q_{x,y} &\leq \mathbb{E}_{x,y} h(X_{T_{n(x)}+n(x)}, Y_{T_{n(x)}+n(x)}) = \mathbb{E}_{x,y} h(\widehat{X}_{n(x)}, \widehat{Y}_{n(x)}) \\ &\leq \mathbb{E}_{x,y} f_1(X_{T_{n(x)}+n(x)}, Y_{T_{n(x)}+n(x)}) = \widehat{P}_1 \cdots \widehat{P}_{n(x)} f_1(x, y) \\ &\leq \mathbb{E}_{x,y} \left( \frac{1}{(2\lambda)^{n(x)} (2\bar{\lambda})^{T_{n(x)}}} \right) \theta^{\beta x} f_1(x, y) + \mathbb{P}_{x,y}(E_{\beta,\xi}^c) \\ &\leq \theta^{\beta x} (\mu^x + \mu^{(1+\alpha)x}) + o(\mu^{(1+\beta)x}) \end{aligned}$$

for all  $x \in \mathbb{N}$  and  $y \geq (1 + \alpha)x$ .  $\square$

We are now in position to prove Theorem 3.3.

PROOF OF THEOREM 3.3. Fix  $\alpha > 0$  such that, by Lemma 6.5,  $q_{x,y} = o(\mu^{(1+\varepsilon)x})$  for all  $x \in \mathbb{N}$ ,  $y \geq (1 + \alpha)x$  and some  $\varepsilon > 0$ . Then pick  $\beta \in (0, 1)$  so small that  $(2 + \alpha)\beta < 1 - \varepsilon$ . Lemma 6.2 then provides us with

$$\mathbb{P}_{x,x}(|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| \leq \beta\alpha x) \leq \mu^{(2-\beta(2+\alpha))x} = o(\mu^{(1+\varepsilon)x}).$$

Note also that, by Lemma 6.1,

$$\mathbb{P}_{x,y}(\tau_{\beta x} < \infty) \leq 2\mu^{(1-\beta)x}$$

for all  $x \in \mathbb{N}$  and  $y \geq (1 + \alpha)x$ . By combining these facts and using the strong Markov property, we now obtain

$$q_{x,x} = \int_{\{\tau_{\beta x} < \infty\}} q_{X_{\tau_{\beta x}}, Y_{\tau_{\beta x}}} d\mathbb{P}_{x,x}$$

$$\begin{aligned}
&\leq \mathbb{P}_{x,x}(|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| \leq \beta \alpha x) \\
&\quad + \int_{\{|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| > \beta \alpha x, \tau_{\beta x} < \infty\}} q_{X_{\tau_{\beta x}}, Y_{\tau_{\beta x}}} d\mathbb{P}_{x,x} \\
&\leq \mathbb{P}_{x,x}(|X_{\tau_{\beta x}} - Y_{\tau_{\beta x}}| \leq \beta \alpha x) + q_{\beta x, (1+\alpha)\beta x} \mathbb{P}_{x,x}(\tau_{\beta x} < \infty) \\
&\leq o(\mu^{(1+\varepsilon)x}) + o(\mu^{(1+\varepsilon)\beta x}) 2\mu^{(1-\beta)x} = o(\mu^{(1+\varepsilon)\beta x})
\end{aligned}$$

and this proves our assertion.  $\square$

**7. Proof of Theorem 3.4.** Since  $q_{x,y} = q_{y,x}$ , it suffices to prove  $q_{x,y} \geq q_{x+1,y}$  for all  $x, y \in \mathbb{N}$ . Let  $(X_n, Y_n)_{n \geq 0}$  and  $(X'_n, Y'_n)_{n \geq 0}$  be two coupled Markov chains on a common probability space  $(\Omega, \mathfrak{A}, \mathbb{P})$  with increments  $(\zeta_n, \chi_n)$  and  $(\zeta'_n, \chi'_n)$ , respectively, and joint canonical filtration  $(\mathcal{G}_n)_{n \geq 0}$  such that the following conditions hold:

- (C1)  $(X_0, Y_0) = (x, y)$  and  $(X'_0, Y'_0) = (x+1, y)$ .
- (C2) Both chains have transition kernel  $P$ .
- (C3) The two ordinary random walks

$$(S_n)_{n \geq 0} := (X_n + Y_n)_{n \geq 0} \quad \text{and} \quad (S'_n)_{n \geq 0} := (X'_n + Y'_n)_{n \geq 0}$$

have the same increments  $\xi_1, \xi_2, \dots$ , but starting points  $S_0 = x + y$  and  $S'_0 = x + y + 1$ , thus  $S'_n - S_n = 1$  for all  $n \in \mathbb{N}_0$ .

- (C4) The conditional laws of  $(\zeta_n, \chi_n)$  and  $(\zeta'_n, \chi'_n)$  given  $\xi_n$  and  $\mathcal{G}_{n-1}$  are specified as follows: If  $(X_{n-1}, Y_{n-1}) = (x, y)$ ,  $(X'_{n-1}, Y'_{n-1}) = (x', y') \in \{(x, y+1), (x+1, y)\}$  and  $S_{n-1} = S'_{n-1} - 1 = x + y =: s$ , then

$$\begin{aligned}
\mathbb{P}((\zeta_n, \chi_n) = (\zeta'_n, \chi'_n) = (1, 0) | \xi_n = 1, \mathcal{G}_{n-1}) &= \frac{1}{2}, \\
\mathbb{P}((\zeta_n, \chi_n) = (\zeta'_n, \chi'_n) = (0, 1) | \xi_n = 1, \mathcal{G}_{n-1}) &= \frac{1}{2}, \\
\mathbb{P}((\zeta_n, \chi_n) = (\zeta'_n, \chi'_n) = (-1, 0) | \xi_n = -1, \mathcal{G}_{n-1}) &= \frac{x}{s} \wedge \frac{x'}{s+1}, \\
\mathbb{P}((\zeta_n, \chi_n) = (\zeta'_n, \chi'_n) = (0, -1) | \xi_n = -1, \mathcal{G}_{n-1}) &= \frac{y}{s} \wedge \frac{y'}{s+1}, \\
\mathbb{P}((\zeta_n, \chi_n) = (-1, 0), (\zeta'_n, \chi'_n) = (0, -1) | \xi_n = -1, \mathcal{G}_{n-1}) \\
&= \left( \frac{x}{s} - \frac{x'}{s+1} \right)^+ = \frac{x}{s(s+1)} \mathbf{1}_{x=x'}, \\
\mathbb{P}((\zeta_n, \chi_n) = (0, -1), (\zeta'_n, \chi'_n) = (-1, 0) | \xi_n = -1, \mathcal{G}_{n-1}) \\
&= \left( \frac{y}{s} - \frac{y'}{s+1} \right)^+ = \frac{y}{s(s+1)} \mathbf{1}_{y=y'}.
\end{aligned}$$

We claim that  $(X'_n, Y'_n)$  equals either  $(X_n + 1, Y_n)$  or  $(X_n, Y_n + 1)$  for all  $n \in \mathbb{N}_0$  and note that this is true for  $n = 0$  by (C1). Assuming it be true for all  $k = 0, \dots, n - 1$  (inductive hypothesis) and further  $(X_{n-1}, Y_{n-1}) = (x, y)$ ,  $(X'_{n-1}, Y'_{n-1}) = (x', y')$ , the claim must be checked for  $(X'_n, Y'_n)$  only in the case when  $\xi_n = -1$  and  $(\zeta_n, \chi_n)$  and  $(\zeta'_n, \chi'_n)$  take different values. But if this happens, then  $x = x'$  leads to  $(X_n, Y_n) = (x - 1, y)$  and  $(X'_n, Y'_n) = (x', y' - 1) = (x, y)$ , while  $y = y'$  leads to  $(X_n, Y_n) = (x, y - 1)$  and  $(X'_n, Y'_n) = (x' - 1, y') = (x, y)$ . This proves our claim. Finally, recalling that

$$\tau = \inf\{n \geq 0 : X_n = 0 \text{ or } Y_n = 0\}$$

and defining  $\tau'$  accordingly for the primed chain, we conclude  $\tau \leq \tau'$  and thus

$$q_{x,y} = \mathbb{P}(\tau < \infty) \geq \mathbb{P}(\tau' < \infty) = q_{x+1,y}. \quad \square$$

**8. The absorption probabilities for IBCS and BUTS.** As pointed out in the Introduction, our model constitutes a hybrid of the two homogeneous models IBCS (independent branching with complete segregation) and BUTS (branching with unbiased type selection) for which one-step transition probabilities of the associated random walk  $(X_n, Y_n)_{n \geq 0}$  are shown in Fig. 2. Homogeneity refers to the fact that these transition probabilities are the same regardless of whether a birth or a death of an individual has occurred.

LEMMA 8.1. *Let  $(X_n, Y_n)_{n \geq 0}$  be a random walk on  $\mathbb{N}_0^2$  which is absorbed at the axes and has transition probabilities*

$$(32) \quad \begin{aligned} p_{(x,y),(x+1,y)} &= \bar{\lambda} p_+(x, y), & p_{(x,y),(x,y+1)} &= \bar{\lambda} \bar{p}_+(x, y), \\ p_{(x,y),(x-1,y)} &= \lambda p_-(x, y), & p_{(x,y),(x,y-1)} &= \lambda \bar{p}_-(x, y) \end{aligned}$$

for  $(x, y) \in \mathbb{N}^2$  and arbitrary functions  $p_{\pm} : \mathbb{N}^2 \rightarrow (0, 1)$ . Then the function  $h$  in (11) is harmonic for the associated transition operator  $P$ .

The proof of this lemma is very easy and therefore omitted.

PROPOSITION 8.2. *Given any of the 2-type population models IBCS or BUTS, let  $(X_n, Y_n)_{n \geq 0}$  be the random walk describing the subpopulation sizes for the two types and, as usual,  $q_{x,y}$  the probability of absorption at one of the axes given  $X_0 = x$  and  $Y_0 = y$ . Then*

$$q_{x,y} = h(x, y)$$

for all  $x, y \in \mathbb{N}_0$ .

PROOF. By Lemma 8.1 in combination with Lemma 4.1, the assertion follows if we can verify that  $(X_n, Y_n)_{n \geq 0}$  is standard, i.e.,  $X_n \wedge Y_n \rightarrow \infty$  a.s. on  $\{\tau = \infty\}$ , where  $\tau$  denotes the absorption time. For the BUTS model, this follows in the same manner as for our hybrid model (see proof of Proposition 3.5), but for the IBCS model, we need an extra argument. To this end, observe that  $(X_n, Y_n)_{n \geq 0}$  may be obtained as the jump chain of a 2-type Bellman-Harris process  $(N_t^A, N_t^B)_{t \geq 0}$  with independent components, the latter being both single-type supercritical Bellman-Harris processes. Now, if neither  $X_n$  nor  $Y_n$  ever hits the axis, then the same must hold for  $N_t^A$  and  $N_t^B$ , giving

$$\lim_{n \rightarrow \infty} X_n \wedge Y_n = \lim_{t \rightarrow \infty} N_t^A \wedge N_t^B = \infty \quad \text{a.s.}$$

by the extinction-explosion principle.  $\square$

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