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Muller's ratchet in a near-critical regime: Tournament versus fitness proportional selection

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ABSTRACT

Muller's ratchet, in its prototype version, models a haploid, asexual population whose size N is constant over the generations. Slightly deleterious mutations are acquired along the lineages at a constant rate, and individuals carrying less mutations have a selective advantage. The classical variant considers *fitness proportional* selection, but other fitness schemes are conceivable as well. Inspired by the work of Etheridge et al. (2009) we propose a parameter scaling which fits well to the "near-critical" regime that was in the focus of Etheridge et al. (2009) (and in which the mutation–selection ratio diverges logarithmically as $N \to \infty$). Using a Moran model, we investigate the"rule of thumb" given in Etheridge et al. (2009) for the click rate of the "classical ratchet" by putting it into the context of new results on the long-time evolution of the size of the best class of the ratchet with (binary) tournament selection. This variant of Muller's ratchet was introduced in González Casanova et al. (2023), and was analysed there in a subcritical parameter regime. Other than that of the classical ratchet, the size of the best class of the tournament ratchet follows an autonomous dynamics up to the time of its extinction. It turns out that, under a suitable correspondence of the model parameters, this dynamics coincides with the so called Poisson profile approximation of the dynamics of the best class of the classical ratchet.

1. Introduction

Muller's ratchet is a prototype model in population genetics. Originally it was conceived to explain the ubiquity of sexual reproduction among eukaryotes despite its many costs (Muller, 1964; Felsenstein, 1974). In its bare bones version, Muller's ratchet models a haploid, asexual population whose size N is constant over the generations. The neutral part of the random reproduction is given by a Wright–Fisher or a Moran dynamics. Slightly deleterious mutations are acquired along the lineages at a rate m, and individuals carrying less mutations have a selective advantage. The classical variant of Muller's ratchet considers *fitness proportional* selection, where the selective advantage of an individual carrying κ deleterious mutations over a contemporanean that carries a larger number κ' of deleterious mutations is $\frac{\mathfrak{s}}{N}(\kappa' - \kappa)$. Since the mutation mechanism is assumed to be unidirectional, every once in a while the type with the currently smallest number of mutations κ will disappear from the population. As Herbert Muller puts it in his pioneering paper (Muller, 1964), "*an irreversible ratchet mechanism exists in the non-recombining species ... that prevents selection, even if intensified, from reducing the mutational loads below the lightest ..., whereas, contrariwise, 'drift', and what might be called 'selective noise' must allow occasional slips of the lightest loads in the direction of increased weight.*"

It is these "slips of the lightest loads" which are called *clicks of the ratchet*. The question "How often does the ratchet click?" was asked by Etheridge, Pfaffelhuber and one of the present authors in Etheridge et al. (2009), and there it was found that

$$\gamma := \frac{m}{\mathfrak{s}\log(Nm)} \tag{1.1}$$

is "*an important factor in determining the rate of the ratchet*". Specifically, under the assumption $1 \ll Nm \ll N$, Etheridge et al. (2009) states the following *Rule of Thumb* for the classical ratchet:

(RTC) *The rate of the (classical) ratchet is of the order $N^{\gamma-1}m^{\gamma}$ for $\gamma \in (\frac{1}{2}, 1)$, whereas it is exponentially slow in $(Nm)^{1-\gamma}$ for $\gamma < \frac{1}{2}$.*

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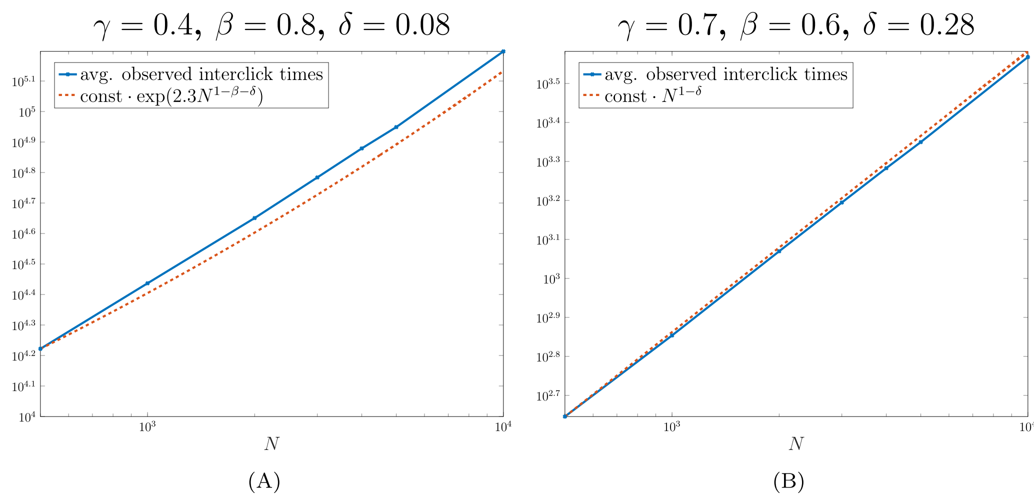

Fig. 1. This is an illustration of the *Rule of Thumb* (RTC) predicting the order of magnitude of the interclick times of the classical ratchet. Each data point was obtained by pooling the interclick times no. 50 to 150 from 100 simulations of the (classical) ratchet for the corresponding parameter configuration (N, β, δ) in the (β, δ)-scaling (1.2). In the exponential regime, (RTC) predicts an order of magnitude $\exp(c\,N^{1-\beta-\delta})$ for the interclick times. In panel (A), we see that the constant c is difficult to estimate from simulations up to $N = 10^4$, but $c = 2.3$ as chosen there gives a reasonable fit. For the polynomial regime, (RTC) predicts the order of magnitude $N^{1-\delta}$, which fits very well the data in the situation of panel (B).

With the *mutation–selection ratio*

$$\theta := \frac{m}{\mathfrak{s}},$$

(RTC) predicts the expected interclick time in the case $\gamma \in (\frac{1}{2}, 1)$ as

$$N(Nm)^{-\gamma} = Ne^{-\theta}.$$

As observed by John Haigh (Haigh, 1978), in the deterministic limit ($N \to \infty$ and $m, \mathfrak{s}$ not depending on N) the type frequency profile in equilibrium becomes Poisson with parameter θ. Consequently, for $\gamma \in (\frac{1}{2}, 1)$ the rule (RTC) goes along with Haigh's prediction that the rate of the ratchet should be proportional to the inverse of the size of the best class.

For a polynomial mutation rate $m = N^{-\beta}$, $0 < \beta < 1$, the condition that γ remains constant (or at least bounded away from 0 and ∞) as $N \to \infty$ amounts to the requirement that the mutation–selection ratio θ is of the order $\log N$ as $N \to \infty$.

For the purpose of illustration we will consider a family of parameter scalings for (m, θ) which we call the *(β, δ)-scaling of the classical ratchet*:

$$m = N^{-\beta}, \qquad \theta = \delta \log N. \tag{1.2}$$

This amounts to *moderate mutation–selection*, with the mutation–selection ratio θ diverging logarithmically in N. The factor δ in front of $\log N$ turns out to be critical for the click rate. Indeed, in the (β, δ)-scaling, (1.1) takes the form

$$\gamma(\beta, \delta) = \frac{\delta}{1-\beta}.$$

The condition $0 < \gamma < 1$ from (RTC) restricts the pair (β, δ) to the triangle

$$\Delta := \{(\beta, \delta) : 0 < \beta, 0 < \delta < 1 - \beta\}. \tag{1.3}$$

The *polynomial* and the *exponential regime* predicted by (RTC) correspond to

$$\mathcal{P} := \{\tfrac{1}{2} < \gamma(\beta, \delta) < 1\} = \{(\beta, \delta) \in \Delta : \tfrac{1}{2}(1-\beta) < \delta < 1 - \beta\},$$

$$\mathcal{E} := \{0 < \gamma(\beta, \delta) < \tfrac{1}{2}\} = \{(\beta, \delta) \in \Delta : 0 < \delta < \tfrac{1}{2}(1-\beta)\},$$

and the predictions for the orders of magnitude of the expected interclick times take the form

$$N(Nm)^{-\gamma} = N^{1-\delta} \qquad \text{for } \gamma \in (\tfrac{1}{2}, 1), \tag{1.4}$$

$$\exp\left(\text{const}(Nm)^{1-\gamma}\right) = \exp\left(\text{const}\, N^{1-\beta-\delta}\right) \quad \text{for } \gamma \in (0, \tfrac{1}{2}). \tag{1.5}$$

In view of the predicted transition from polynomial to exponential click rates we refer to $\mathcal{P} \cup \mathcal{E}$ as a *near-critical regime*. See Fig. 1 for an illustration of (RTC) via simulations.

The evidence for (RTC) that is given in Etheridge et al. (2009) is based on a diffusion approximation for the evolution of the relative size X_0 of the *best class* (which consists of the individuals that carry the least amount of mutations in the current population). Because of the fitness proportional selection, the drift coefficient in this diffusion approximation contains the first moment M of the type frequency configuration $(X_0, X_1, \ldots)$. In order to obtain an approximate autonomous dynamics for X_0, the empirical first moment M has to be predicted based on X_0. A classical way to do this uses the so-called *Poisson profile approximation*, which we will explain in some detail in Section 3.

In the present paper we will consider a variant of Muller's ratchet in which fitness proportional selection is replaced by *(binary) tournament selection*. This kind of selection has been studied in the context of evolutionary computation (Blickle and Thiele, 1996; Bäck et al., 2018) and has found attention also in the biological literature (Paixão et al., 2015). In the ratchet's context this means that selective advantage of an individual carrying κ deleterious mutations over a contemporanean that carries a larger number κ' of deleterious mutations is constant (say $\frac{s}{N}$ for some $s = s_N > 0$), irrespective of the value of the difference $\kappa' - \kappa$. For the Moran version of the tournament ratchet, which was introduced in González Casanova et al. (2023) and whose definition we recall in Section 2, this means that "pairwise selective fights" are always won by the fitter individual.

Other than in the classical ratchet, the size of the (m, s)-tournament ratchet's best class follows an autonomous dynamics *up to its time of extinction*; at this time the class which was so far the second-best becomes the best one. As we will see in Section 3, this dynamics is *equal* to that of the Poisson profile approximation of the size of the classical $(m, \mathfrak{s})$-ratchet's best class, provided that

$$\rho := \frac{m}{s} = 1 - \exp(-m/\mathfrak{s}) = 1 - e^{-\theta}. \tag{1.6}$$

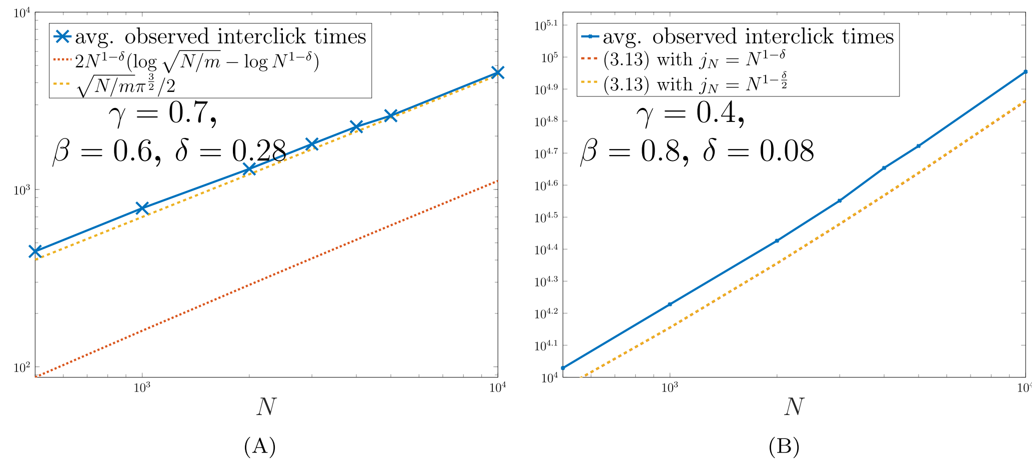

Fig. 2. This is an illustration of the *Rule of Thumb for the tournament ratchet* (RTT) in the light of Theorem 3.4. Each data point was obtained by pooling the interclick times no. 50 to 150 from 100 simulations of the tournament ratchet for the corresponding value of N. Here, in panel (A) $(\beta,\delta) = (0.6, 0.28)$, which belongs to the polynomial regime $\mathcal{P}$, and in panel (B) $(\beta,\delta) = (0.8, 0.08)$, which belongs to the exponential regime $\mathcal{E}$. Each panel shows two predictions based on the asymptotics of Theorem 3.4, using the initial values $\mathfrak{a} = N^{1-\delta}$ and $\mathfrak{b} = N^{1-\delta/2}$, respectively. In the exponential regime the predictions using $\mathfrak{a}$ and $\mathfrak{b}$, respectively, are virtually indistinguishable, while in the polynomial regime the prediction using $\mathfrak{b}$ is by far better than the one using $\mathfrak{a}$.

We now state a main finding of the present paper.

Rule of thumb for the near-critical tournament ratchet (RTT): *As $N \to \infty$, the expected time between clicks is*

$$\asymp \sqrt{\frac{N}{m}} \qquad \text{if } Nm(1-\rho)^2 \to 0, \tag{1.7}$$

$$\asymp \exp\left(Nm(1-\rho)^2\right) \qquad \text{if } Nm(1-\rho)^2 \to \infty. \tag{1.8}$$

Here and below, $\asymp$ stands for logarithmic equivalence, i.e. $a_N \asymp b_N$ means $\log a_N \sim \log b_N$, or equivalently $\frac{\log a_N}{\log b_N} \to 1$.

We will not give a complete proof of (RTT) in this work, but will present Theorem 3.4 which gives strong evidence for its validity. See Fig. 2 for an illustration of (RTT) in the light of Theorem 3.4. In Remark 3.5 we will discuss what are the ingredients missing to go from Theorem 3.4 to a proof of (RTT), and we will also indicate a different route to the proof of (RTT), using the technique developed in González Casanova et al. (2023).

We emphasise that, in view of the correspondence (1.6), Theorem 3.4 also is a result on the asymptotics of the Poisson profile approximation of the classical ratchet, here in terms of Moran processes with mutation and selection. A similar asymptotics was obtained in Etheridge et al. (2009) heuristically by passing right away to the diffusion approximation for logistic branching processes.

In view of (1.6) we define, in analogy to (1.2), the (β,δ)-scaling for the tournament ratchet as

$$m = N^{-\beta}, \qquad \rho = \frac{m}{s} = 1 - N^{-\delta}.$$

With this scaling, (RTT) takes the following form: *As $N \to \infty$, the expected time between clicks is*

$$\asymp N^{\frac{1+\beta}{2}} \qquad \text{if } (\beta,\delta) \in \mathcal{P}, \tag{1.9}$$

$$\asymp \exp\left(N^{1-\beta-2\delta}\right) \qquad \text{if } (\beta,\delta) \in \mathcal{E}. \tag{1.10}$$

While both (RTC) and (RTT) state the same boundary ($\gamma = \frac{1}{2}$) between the polynomial and the exponential regime, the exponents differ between (1.4) and (1.9) as well as between (1.5) and (1.10). Specifically, in the polynomial regime $\mathcal{P}$ the exponent $\frac{1+\beta}{2}$ for the tournament ratchet is larger than the exponent $1-\delta$ for the classical ratchet.

Here is an explanation for the polynomial regime. The centers of attraction of the equilibrium profile weights of the best and the second best class differ asymptotically by the factor $\sqrt{1-\rho} = N^{\frac{\delta}{2}}$ for the tournament ratchet (see (3.5)), while they are given by the Poisson weights $e^{-\theta}$ and $\theta e^{-\theta}$ for the classical ratchet and hence for the latter differ only by the factor $\theta = \delta \log N$ (and thus have the same polynomial order $N^{1-\delta}$). This latter factor is only logarithmic in N; therefore, when starting the "new best class" at the time of a click in its "old" center of attraction, the tournament ratchet has a longer way to go than the classical ratchet. The exponent $\frac{1+\beta}{2}$ in (1.7) will be obtained by a Green function analysis in the proof of Theorem 3.4. This analysis will also explain the exponent $1-\delta$ in (1.4), which corresponds to Haigh's prediction, saying that "the interclick times are of the order of the size of the best class". An intuitive explanation for the appearance of the exponent $1-\beta-2\delta$ in (1.8) will be given at the end of Section 3.2. The reason why this exponent is different from the one appearing in (1.5) is that Etheridge et al. (2009) work here not with the Poisson profile approximation, but with (a rescaling of the diffusion approximation of) the so-called *relaxed Poisson profile approximation*.

Similar as Etheridge et al. (2009), the papers Pfaffelhuber et al. (2012), Neher and Shraiman (2012), Audiffren and Pardoux (2013), Mariani et al. (2020), Bräutigam and Smerlak (2022) used a diffusion approximation for the classical ratchet and modifications thereof. Metzger and Eule (Metzger and Eule, 2013) consider, as a proxy to the classical ratchet, a two-type Moran model with selective advantage s of type 0 over type 1 and mutation rate m from type 0 to type 1. Their formula (8) corresponds to our formula (1.6) but their approximations for the classical ratchet concentrate on a regime in which θ remains bounded (see the discussion around (Metzger and Eule, 2013, (23)), and also Waxman and Loewe (2010, (7),(8))), whereas we focus here on a regime in which $\theta = \theta_N$ diverges logarithmically in N.

In González Casanova et al. (2023) it was discovered that the tournament ratchet has a dual which consists of a hierarchy of competing logistic processes. The main results of González Casanova et al. (2023) (on the click rate of the tournament ratchet and its type frequency profile between clicks) were obtained for the so-called subcritical regime (see Section 2.2) and were proved there via duality, with the help of recent results on logistic processes (see Lambert (2005), Sagitov and Shaimerdenova (2013), Chazottes et al. (2016)). This "backward in time" view, which comes on top of an Ancestral Selection Graph decorated with mutation events, opens a route for proving the above stated result (RTT) and for analysing the type frequency profile of the tournament ratchet also in the near-critical regime. This will be pursued in future work.

In González Casanova et al. (2023) the rate of the tournament ratchet was identified in the subcritical regime (i.e. for $\rho = m/s < 1$ and not depending on N) up to logarithmic equivalence. Thus our Theorem 3.4 (b), which is valid both for the near-critical *and* the subcritical regime, provides an essential step in sharpening the rate asymptotics of González Casanova et al. (2023) from logarithmic equivalence to asymptotic equivalence, see Remark 3.5(a).

2. Muller's ratchet as a Moran process with mutation and selection

2.1. Model and basic concepts

In the Moran version of Muller's ratchet, neutral resampling within any ordered pair of individuals happens at rate $\frac{1}{2N}$, and mutation from κ to $\kappa+1$ takes place at rate m/N along each individual lineage. Selective reproduction for an individual i of type $\kappa(i)$ happens at rate $\frac{1}{N}\sum_j \Phi(\kappa(j)-\kappa(i))$, where the sum is taken over all those individuals j whose type $\kappa(j)$ is larger (and therefore "worse") than $\kappa(i)$. Here Φ is the *fitness function*, with $\Phi(0) = 0$ and $\Phi(-d) = -\Phi(d)$ for $d \in \mathbb{N}$. For the classical case of *proportional selection*, one has $\Phi(\kappa'-\kappa) = \mathbf{s}(\kappa'-\kappa)$, while for the case of *(binary) tournament selection* one has $\Phi(\kappa'-\kappa) = \mathbf{s}(\mathbf{1}_{\{\kappa'>\kappa\}} - \mathbf{1}_{\{\kappa'<\kappa\}})$. In the sequel we will refer to these two Moran variants of Muller's ratchet briefly as the *classical ratchet* and the *tournament ratchet*. Both models have $(N, m, \mathbf{s})$ as their parameter triple, and in both models a crucial role is played by the *mutation–selection ratio* $\frac{m}{\mathbf{s}}$. In this section we reserve the symbol $\mathbf{s}$ for the selection parameter. Later, this will be specified as different parameters s and $\mathfrak{s}$ for the tournament and the classical ratchet, respectively. The following definition gives the rates for the type frequencies of the two ratchets.

Definition 2.1.

(a) Writing N_κ for the current number of individuals of type κ, the jump rates are specified as follows:
- Resampling: for $\kappa \neq \kappa'$,
  $(N_\kappa, N_{\kappa'})$ jumps to $(N_\kappa+1, N_{\kappa'}-1)$ at rate $\frac{1}{2N}N_\kappa N_{\kappa'}$
- Mutation: for κ,
  $(N_\kappa, N_{\kappa+1})$ jumps to $(N_\kappa-1, N_{\kappa+1}+1)$ at rate mN_κ
- Selection: for $\kappa < \kappa'$,
  $(N_\kappa, N_{\kappa'})$ jumps to $(N_\kappa+1, N_{\kappa'}-1)$ at rate
  $$\begin{cases} \frac{\mathbf{s}}{N}N_\kappa N_{\kappa'}(\kappa'-\kappa) & \text{for the classical ratchet} \\ \frac{\mathbf{s}}{N}N_\kappa N_{\kappa'} & \text{for the tournament ratchet} \end{cases}$$

(b) The currently best type is
$$K^*(t) := \min\left\{\kappa \in \mathbb{N}_0 : N_\kappa(t) > 0\right\}.$$

(c) The click times of the ratchet are the jump times of K^*, i.e. the times at which the currently best type is lost from the population. The type frequency profile seen from the currently best type has the (random) weights
$$X_k^{(N)}(t) := \frac{1}{N}N_{K^*(t)+k}(t), \qquad k = 0,1,2\dots \tag{2.1}$$

We say that a (non-random) type frequency profile $(p_k)_{k\in\mathbb{N}_0}$ obeys the mutation–selection equilibrium conditions (for the parameters m and $\mathbf{s}$) if
$$m(p_k - p_{k-1}) = \mathbf{s}\,p_k\left(\sum_{k'\in\mathbb{N}_0} p_{k'}\Phi(k'-k)\right), \quad k = 0,1,2\dots, \tag{2.2}$$
where we put $p_{-1} := 0$.

For the classical ratchet, (2.2) turns into
$$m(p_k - p_{k-1}) = \mathbf{s}\,p_k(\mu - k), \quad k = 0,1,2\dots, \tag{2.3}$$
where $\mu := \sum_\ell \ell p_\ell$ is the first moment of the profile. As already noticed by John Haigh (Haigh, 1978), (2.3) is solved by the *Poisson weights* with first moment $\mu = \frac{m}{\mathbf{s}}$. Indeed, this is the unique solution of (2.3) under the condition $p_0 > 0$.

For the tournament ratchet, (2.2) turns into
$$m\left(p_k - p_{k-1}\right) = \mathbf{s}\,p_k\left(\sum_{k'\in\mathbb{N}_0} p_{k'}\left(\mathbf{1}_{\{k'>k\}} - \mathbf{1}_{\{k'<k\}}\right)\right), \quad k = 0,1,2\dots \tag{2.4}$$
Here the condition $p_0 > 0$ leads to the requirement $m < \mathbf{s}$ and yields $p_0 = 1 - \frac{m}{\mathbf{s}}$. Various properties of the solution $(p_{k'})$ of (2.4) are stated in González Casanova et al. (2023) Theorem 2.4. The r.h.s. of (2.4) equals
$$\mathbf{s}\,p_k\left(1 - p_k - 2\sum_{k'=0}^{k-1} p_{k'}\right), \quad k = 0,1,2\dots \tag{2.5}$$
A formal analogy between (2.3) and (2.4) results because (2.5) is close to $2\mathbf{s}\,p_k(\frac{1}{2} - g(k))$, where g is the cumulative distribution function of $(p_{k'})$. In this sense the role played by the profile's first moment in (2.3) is taken by the profile's median in (2.4).

2.2. The subcritical regime of the tournament ratchet

We now report briefly on the main results of the recent paper (González Casanova et al., 2023). The parameters of the tournament ratchet will be denoted by (m, s) and its mutation–selection ratio by $\rho := \frac{m}{s}$. In González Casanova et al. (2023), as $N \to \infty$, the mutation–selection ratio $\rho = \frac{m}{s}$ is kept constant and smaller than 1, and it is assumed that $m \to 0$ and $mN \to \infty$. (For technical reasons, mN is assumed to be of larger order of $\log\log N$, which keeps the regime slightly away from that of weak mutation, in which mN would be of order one as $N \to \infty$.) We will refer to this regime as the *subcritical regime* of the tournament ratchet. Informally stated, the main results of González Casanova et al. (2023) are

• *In the subcritical regime the click rate of the tournament ratchet on the $\frac{1}{m}$-timescale is, as $N \to \infty$, logarithmically equivalent to*
$$e^{-2Nm\left(\frac{1}{\rho}-1+\log\rho\right)}. \tag{2.6}$$

• *In the subcritical regime and for N large, the empirical type frequency profile at generic time points between clicks of the tournament ratchet is with high probability close to the mutation–selection equilibrium system (p_k) given by (2.4) with $p_0 = 1 - \rho$.*

See Theorems 2.2 and 2.3 in González Casanova et al. (2023), which there are proved via a hierarchical duality. As discussed in Remark 3.5. (a), Theorem 3.4 (b) can be considered as a significant step in sharpening (2.6) to an asymptotic equivalence.

3. A synopsis of the classical and the tournament ratchet

3.1. The dynamics of the best classes

For $k = 0, 1, \dots$ let $Y_k^{\mathrm{C}}(t) = N_{K^*+k}^{\mathrm{C}}(t)$ and $Y_k^{\mathrm{T}}(t) = N_{K^*+k}^{\mathrm{T}}(t)$ be the sizes of the

$(k+1)^{\mathrm{st}}$-best class of the classical and the tournament ratchet, where $(N_\kappa^{\mathrm{C}})_{\kappa\in\mathbb{N}_0}$ and $(N_\kappa^{\mathrm{T}})_{\kappa\in\mathbb{N}_0}$ follow the dynamics specified in Definition 2.1. Here we assume that the mutation rate m is equal for both ratchets, but the selection coefficients are different:
$$\mathbf{s} = \begin{cases} \frac{m}{\theta} =: \mathfrak{s} & \text{for the classical ratchet} \\ \frac{m}{\rho} =: s & \text{for the tournament ratchet.} \end{cases}$$
The jump rates from n to $n-1$ are given for both Y_0^{C} and Y_0^{T} by
$$n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + m\right), \tag{3.1}$$
but the jump rates from n to $n+1$ are different: those of Y_0^{T} are
$$n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + \frac{m}{\rho}\left(1 - \frac{n}{N}\right)\right), \tag{3.2}$$

while those of Y_0^{C} are

$$n\left(\frac{1}{2}\left(1-\frac{n}{N}\right)+\frac{m}{\theta}\sum_{k=1}^{\infty}kX_k\right) \tag{3.3}$$

where $(X_k(t))_{k\in\mathbb{N}_0}$ is the type frequency profile as defined in (2.1), with (N_κ^{C}) in place of (N_κ). Writing

$$M(t) := \sum_{k=1}^{\infty} kX_k(t)$$

for the first moment of the type frequency profile (X_k), the upward jump rate (3.3) takes the form

$$n\left(\frac{1}{2}\left(1-\frac{n}{N}\right)+m\frac{M}{\theta}\right). \tag{3.4}$$

An inspection of the jump rates in Definition 2.1 reveals that for each $k\in\mathbb{N}$ the process $(Y_0^{\mathrm{T}},\dots,Y_k^{\mathrm{T}})$ obeys an autonomous dynamics up to the extinction time of Y_0^{T}; for $k=0$ this is evident from (3.1) and (3.2). For later reference we note here that $(Y_0^{\mathrm{T}},Y_1^{\mathrm{T}})$ has, asymptotically as $N\to\infty$, the center of attraction

$$(\mathfrak{a},\mathfrak{b}) := \left(N(1-\rho), N\sqrt{1-\rho}\right) \tag{3.5}$$

provided $Nm\to\infty$ and $\rho\to 1$. To see this, note that the dynamics of $(Y_0^{\mathrm{T}},Y_1^{\mathrm{T}})$ is autonomous up to the first hitting of $\{0\}\times\{0,\dots,N\}$, and that the states of $(Y_0^{\mathrm{T}},Y_1^{\mathrm{T}})$ for which the upward jump rates are asymptotically equal to the downward jump rates have the asymptotic (Np_0,Np_1), with (p_0,p_1) given by (2.4) and (2.5). In addition to $p_0=1-\rho$, this leads to the equation

$$p_1(1-p_1-2(1-\rho)) = \rho(p_1-(1-\rho)),$$

with the solution

$$p_1 = \sqrt{1-\rho}\left(\sqrt{\rho+\frac{1}{4}(1-\rho)}-\frac{1}{2}\sqrt{1-\rho}\right)\sim\sqrt{1-\rho} \text{ as } \rho\uparrow 1.$$

In contrast to the tournament ratchet, the rates (3.4) depend not only on the size of the best class but also on the profile $(X_k(t))_{k\geq 0}$ (via its first moment $M(t)$). There are various ways to predict $M(t)$ on the basis of $Y_0^{\mathrm{C}}(t)$, and thereby to replace (3.4) by a rate which is autonomous. One of them will be described in the remainder of this section, a second one will be addressed in Remark 3.2. As observed already by John Haigh (Haigh, 1978), such a strategy requires a regime in which "genetic drift", i.e. the fluctuations due to neutral reproduction, needs a time to take Y_0^{C} to extinction which is large compared to the time which the noiseless classical ratchet needs to "relax" towards its (new) equilibrium. The dynamics of the latter is

$$\mathrm{d}x_k(t) = \left(\mathfrak{s}\sum_{\ell}x_\ell(\ell-k)+m(x_{k-1}(t)-x_k(t))\right)\mathrm{d}t, \qquad k=0,1,\dots \tag{3.6}$$

(with $x_{-1}\equiv 0$). As already indicated after (2.3), the unique vector of probability weights on $\mathbb{N}_0$ which has a non-vanishing weight at 0 and is a stationary point of (3.6) is given by the *Poisson profile*

$$\pi_k = e^{-\theta}\frac{\theta^k}{k!}, \quad k\geq 0. \tag{3.7}$$

For the initial profile

$$x(0) := \tfrac{1}{1-\pi_0}(\pi_1,\pi_2,\dots),$$

the *relaxation time* τ which it takes for $x_0(t)$ to come down from $\frac{1}{1-\pi_0}\pi_1$ to $\frac{e}{e-1}\pi_0$ turns out to be

$$\tau = \frac{\log\theta}{\mathfrak{s}},$$

(see Etheridge et al. (2009, Remark 4.3)[1]). The time to extinction of a neutral Moran(N)-process starting in $N\pi_0 = Ne^{-\theta}$ is of the order $Ne^{-\theta}$. Haigh's requirement can thus be formulated as

$$Ne^{-\theta}\gg\frac{\log\theta}{\mathfrak{s}},$$

which in the (β,δ)-scaling (1.2) just means that $\beta+\delta<1$.

3.2. The Poisson profile approximation for the classical ratchet

Here the idea is to think of the profile $(X_k)_{k\geq 1}$ as (nearly) proportional to the Poisson profile (3.7), and as the mass π_0-X_0 being distributed proportionally upon this profile. This leads to the so-called *Poisson profile approximation* of $(X_k)_{k\geq 1}$ based on X_0, given by

$$\Pi(X_0) := \left(X_0, \frac{1-X_0}{1-\pi_0}(\pi_1,\pi_2,\dots)\right).$$

(cf Etheridge et al. (2009, (2.5))). The first moment of $\Pi(X_0)$ is

$$M(X_0) := (1-X_0)\frac{\theta}{1-\pi_0},$$

in accordance with Etheridge et al. (2009, (5.3a)). Plugging this into (3.4) in place of M leads to the following *Poisson profile approximation* of the upward jump rates (3.4):

$$n\left(\frac{1}{2}\left(1-\frac{n}{N}\right)+\frac{m}{1-e^{-\theta}}\left(1-\frac{n}{N}\right)\right). \tag{3.8}$$

We denote the birth-and death-process on $\mathbb{N}_0$ with downward jump rates (3.1) and upward jump rates (3.8) by Y_{PPA}; this process can be seen as an approximation of Y_0^{C}.

Remark 3.1. A crucial observation is that the upward jump rates (3.2) and (3.8) are equal if and only if $\rho=1-e^{-\theta}$. In other words, under the "dictionary" (1.6), the jump rates (3.1) and (3.2) of the size of the best class of the (m,s)-tournament ratchet are equal to the jump rates (3.1) and (3.8) of the Poisson profile approximation for the size of the best class of the classical $(m,\mathfrak{s})$-ratchet.

Remark 3.2. Not least to provide a systematic framework for previous approaches (Stephan et al., 1993; Gordo and Charlesworth, 2000) to the approximation of the size of the ratchet's best class, Etheridge et al. (2009) embedded the Poisson profile approximation (PPA) into a one-parameter family RPPA(A), $A\geq 0$, the so-called *relaxed Poisson profile approximations*. Roughly, the idea was to take some *delay* into account for the prediction of M based on X_0. For $A=1$, this results (see Etheridge et al. (2009, (5.3b))) in

$$M(X_0) := \theta+\frac{1}{e-1}\left(1-\frac{X_0}{\pi_0}\right), \tag{3.9}$$

which then is plugged into the upward jump rate (3.4) in place of M. In Fig. 6 we compare the quality of the PPA and RPPA(1) approximations for the rate of the classical ratchet in the light of simulations of our Moran model.

3.3. On the expected time to extinction of the best class

In this subsection we focus on the birth-and-death process $Y := Y_0^{\mathrm{T}}$ with jump rates (3.1) and (3.2). As observed in Remark 3.1, this process has the same dynamics as the process Y_{PPA} defined in Section 3.2, provided the mutation rates are equal and the selection coefficients are translated through the "dictionary" (1.6).

Remark 3.3. Before turning to a rigorous analysis, let us give a heuristics for the long-term behaviuor of Y, which also points towards (RTT) as well as part of (RTC). The rates (3.1) and (3.2) display 3 parts: the fluctuation terms $\pm\frac{n}{2}\left(1-\frac{n}{N}\right)$, the net linear birth rate $n\frac{m}{\rho}(1-\rho)$ and the quadratic death rate $\frac{m}{\rho}\frac{n^2}{N}$. The center of attraction of Y (which we encountered already in (3.5)) is that (asymptotic) value of n for which the net linear birth rate equals the quadratic death rate and thus

[1] In order to ease the look-up we use here and below the numbering of the arxiv version of Etheridge et al. (2009), which otherwise is identical in content with the version published in the LMS Lecture Note Series.

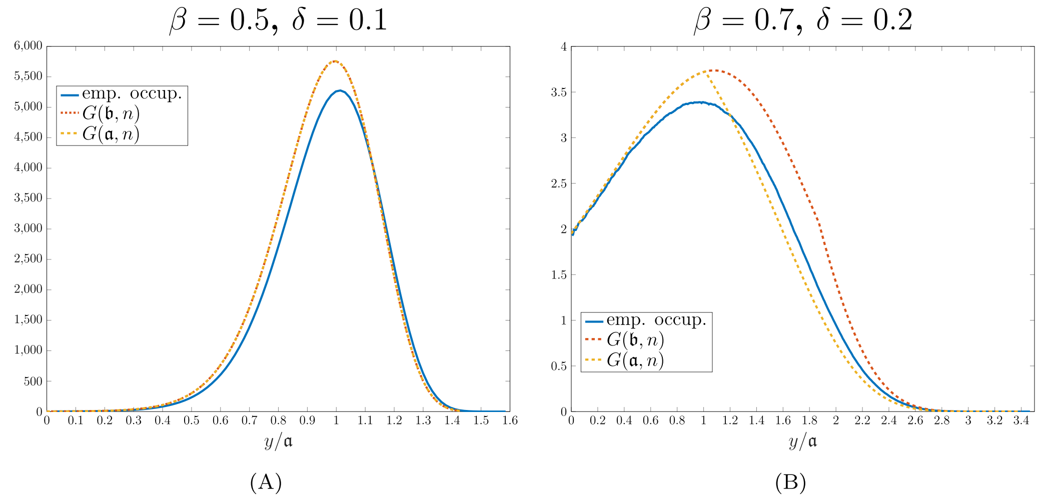

Fig. 3. The empirical occupation times of the size of the best class in a simulation of the tournament ratchet are compared to the Green functions $G(\mathfrak{a},\cdot)$, $G(\mathfrak{b},\cdot)$, which are computed numerically using formula (4.4). Panels (A) and (B) feature the exponential and the polynomial regime, respectively, with $\gamma = 0.2$ in panel (A) and $\gamma = \frac{2}{3}$ in panel (B). In panel (B) the population size is $N = 500$ and simulations were run up to the first $10^4 + 1$ clicks, where the first click was ignored. In (A), 101 clicks were observed and the first one ignored. Here the population size was $N = 100$. See Etheridge et al. (2009, Figure 5) for similar plots concerning the classical ratchet.

equals $\mathfrak{a} = N(1-\rho)$. As long as Y is below $\mathfrak{a}/2$, it is stochastically bounded from below by a binary Galton–Watson process Y^ℓ with supercriticality $m(1-\rho)/2$, and stochastically bounded from above by a binary Galton–Watson process Y^u with supercriticality $m(1-\rho)$. By Haldane's formula (which in this case coincides with the formula for the escape probability of a simple random walk with constant drift), the survival probability of the offspring of one individual in Y^ℓ (resp Y^u) is $\sim N^{-\beta-\delta}$ (resp. $\sim 2N^{-\beta-\delta}$). Hence the probability that Y when starting in $\mathfrak{a}/4$ hits 0 before reaching $\mathfrak{a}/2$, is asymptotically between $\left(1-2N^{-\beta-\delta}\right)^{N^{1-\delta}/4}$ and $\left(1-N^{-\beta-\delta}\right)^{N^{1-\delta}/4}$, which converge to 0 if and only if $1-\beta-2\delta > 0$, i.e. $\gamma > \frac{1}{2}$. In this case the number of excursions which Y makes from $\mathfrak{a}/4$ up to $\mathfrak{a}/2$ before going extinct is geometric with expectation asymptotically between $\exp\left(\frac{1}{4}N^{1-\beta-2\delta}\right)$ and $\exp\left(\frac{1}{2}N^{1-\beta-2\delta}\right)$. This gives an intuitive explanation why $\gamma = \frac{1}{2}$ is the bound between the exponential and the polynomial regime, and also sheds light on the result of Theorem 3.4

In the case $\gamma > \frac{1}{2}$, the center of attraction plays a negligible role. What becomes relevant then is that threshold for n above which the quadratic death rate $\frac{m}{\rho}\frac{n^2}{N}$ becomes large. Obviously, the order of magnitude of this threshold is $\sqrt{\frac{N}{m}} = N^{\frac{1+\beta}{2}}$. Above this threshold, Y is strongly pushed downwards, making the time spent above the threshold negligible. Below the threshold, Y behaves similar to a (driftless linear) birth-and-death process with upward and downward jump rates (3.1). This gives a qualitative explanation of the orders of magnitude of the expected times to extinction that are obtained in Theorem 3.4 also for the polynomial regime.

The proof of the following theorem is the content of Section 4. This proof relies on an asymptotic analysis of the Green function represented by formula (4.3). The fit of a numerical calculation of the Green function based on this formula with the empirical occupation times of the size of the best class of the tournament ratchet is displayed in Fig. 3. A heuristic explanation of the orders obtained in Theorem 3.4 has been given in Remark 3.3.

In the following we use the notation

$$f(N) \ll g(N) \iff \lim_{N\to\infty}\frac{f(N)}{g(N)} = 0. \tag{3.10}$$

Also, we will usually suppress the N-dependence in the notation, as for example in Y, m and ρ in the following theorem. Note that this theorem comprises a larger regime than the one described by the (β,δ)-scaling for $(\beta,\delta)\in\Delta$, see (1.3).

Theorem 3.4. *Let T_0 be the extinction time of the birth-and-death process Y with jump rates (3.1) and (3.2), let $1 \gg m \gg \frac{1}{N}$, and let ρ be a sequence in $[\rho_0, 1)$ for some fixed $\rho_0 \in (0,1)$.*

(a) [Polynomial regime] *Assume $Nm(1-\rho)^2 \to 0$ as $N\to\infty$. Let (j_N) be a sequence of natural numbers in $[N]$. If $j_N \ll \sqrt{\frac{N/m}{\log(N/m)}}$, then*

$$\mathbb{E}_{j_N}[T_0] \sim 2j_N\left(\log\sqrt{\frac{N}{m}} - \log j_N\right), \tag{3.11}$$

whereas if $j_N \gg \sqrt{\frac{N}{m}}$, then

$$\mathbb{E}_{j_N}[T_0] \sim \frac{\pi^{3/2}}{2}\sqrt{\frac{N}{m}}. \tag{3.12}$$

The expected number of returns of the process Y to $\lceil\mathfrak{a}\rceil$, when starting above $\mathfrak{a} = (1-\rho)N$, is asymptotically equivalent to $\frac{1}{m(1-\rho)}$ as $N\to\infty$.

(b) [Exponential regime] *Assume $Nm(1-\rho)^2 \to \infty$ and $1 \ll j_N \le N$ as $N\to\infty$. Then*

$$\mathbb{E}_{j_N}[T_0] \sim \left(1-\exp\left(-2m\left(\frac{1}{\rho}-1\right)j_N\right)\right)\sqrt{\frac{\pi}{mN}}\,v_N, \tag{3.13}$$

with

$$v_N := \frac{1}{m\left(\frac{1}{\rho}-1\right)}\exp\left(2Nm(1-\rho)^2\eta(m,\rho)\right), \tag{3.14}$$

$$\eta(m,\rho) := -\frac{1}{2m}\left[\frac{1}{1-\rho}\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{\ell=1}^{\infty}\left(1-\frac{1}{(1+2m)^\ell}\right)\frac{(1-\rho)^{\ell-1}}{\ell(\ell+1)}\right].$$

In particular, with

$$e_N := \frac{1}{1-\rho}\sqrt{\frac{\pi}{mN}}\,v_N \tag{3.15}$$

one has

$$\mathbb{E}_{j_N}[T_0] \sim \begin{cases} e_N & \text{if } j_N \gg \frac{1}{m(1-\rho)} \\ e_N(1-\exp(-2C/\rho)) & \text{if } j_N \sim \frac{C}{m(1-\rho)} \\ e_N\, 2j_N\, m(1/\rho-1) & \text{if } j_N \ll \frac{1}{m(1-\rho)}. \end{cases} \tag{3.16}$$

The expected number of returns of the process Y to $\lfloor\mathfrak{a}\rfloor$, when starting above $\mathfrak{a} = (1-\rho)N$, is asymptotically equivalent to (3.14) as $N\to\infty$.

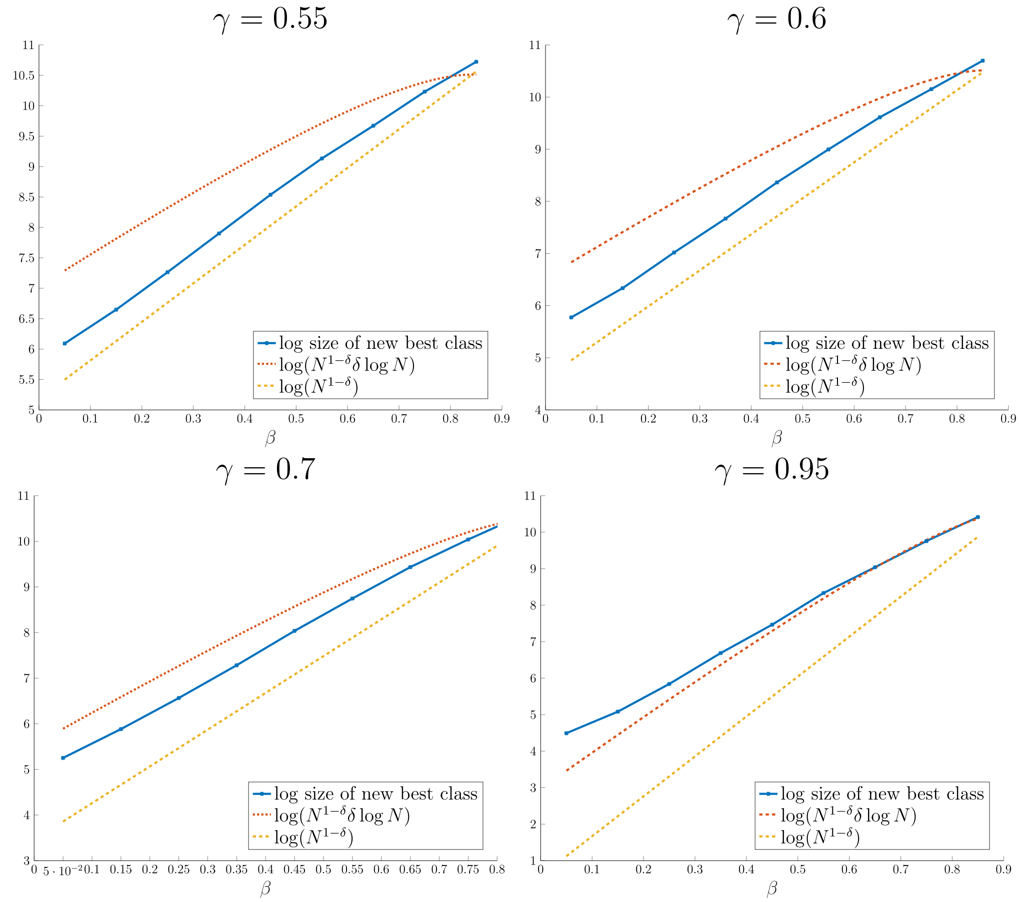

Fig. 4. For $N = 10^5$ we compare the size of the "new best class" of the classical ratchet immediately after a click (observed in simulations) with the two theoretical predictions $N\pi_0 = N^{1-\delta}$ and $N\pi_1 = N^{1-\delta}\delta \log N$, cf. Remark 3.6. (b). For various values of $\gamma = \delta/(1-\beta)$, we consider (the logarithms of) these observed and predicted quantities as functions of β. Each data point was obtained by pooling the interclick times no. 5 to 30 from 20 simulations of the classical ratchet for the corresponding parameter configuration. Roughly, the average of the observed logarithmic sizes of the new best class seems to wander away from $N\pi_0$ towards $N\pi_1$ (and beyond) as γ increases.

Remark 3.5.

(a) Theorem 3.4 constitutes an essential step on the way to a proof of the claim (RTT) formulated in (1.7) and (1.8). One way to complete this proof could lead via the analysis of the system (Y_0^N, Y_1^N) of the sizes of the best and the second-best class of the tournament ratchet; recall that this system is autonomous up to the time of extinction of its first component. Then, $Y_0^N(0)$ and $Y_1^N(0)$ stand for the (random) sizes of the *new* best and second best class at the time of a click. With T_0^N denoting the extinction time of Y_0^N, we conjecture that both in the polynomial and in the exponential regime $Y_1^N(T_0^N)$ will with high probability be $\gg \sqrt{\frac{N}{m}}$, provided that both $Y_0^N(0)$ and $Y_1^N(0)$ are $\gg \sqrt{\frac{N}{m}}$.

(b) While the present work focuses on a forward-in-time approach, an alternative route for proving (RTT) is provided by the backward-in-time approach that was developed in González Casanova et al. (2023) in terms of a hierarchical duality for the tournament ratchet. This requires the extension of the backward-in-time analysis from the subcritical to the near-critical regime, and will be a subject of future research.

Remark 3.6.

(a) Theorem 3.4(b) suggests the conjecture that not only in the exponential regime of the near-critical case $\rho \uparrow 1$, but also in the entire subcritical case $\rho < 1$ the rate of the tournament ratchet is asymptotically equivalent to (3.15). This would improve the logarithmic equivalence (2.6) obtained in González Casanova et al. (2023, Theorem 2.2) to an asymptotic equivalence. Here it is worth noticing that (as we will show at the end of Section 4.2) the exponents in (2.6) and (3.14) obey for all $\rho < 1$

$$(1-\rho)^2 \eta(m,\rho) \sim \frac{1}{\rho} - 1 + \log \rho \quad \text{as } m \to 0. \tag{3.17}$$

(b) In the light of Remark 3.1, Theorem 3.4 is relevant not only for the tournament ratchet, but also for the Poisson profile approximation of the classical ratchet. Prominent starting values for Y are
– with regard to the classical ratchet: $n_0^C := N\pi_1 = N\theta e^{-\theta}$, which in the (β,δ)-scaling equals $N^{1-\delta}\delta \log N$,
– with regard to the tournament ratchet: $n_0^T := N\sqrt{1-\rho}$, which according to (3.5) is the asymptotic center of attraction of the size of its second best class, and in the (β,δ)-scaling equals $N^{1-\delta/2}$.
Figs. 4 and 5 illustrate that these asymptotics of the starting values can indeed be seen in simulations of the classical and the tournament ratchet. The starting values n_0^C and n_0^T are used in Figs. 6 and 7.
For $(\beta,\delta) \in \mathcal{P}$ we have

$$1-\delta < \frac{1+\beta}{2} < 1 - \tfrac{\delta}{2}.$$

Hence Theorem 3.4(a) gives, in accordance with (1.4) and (1.7),

$$\mathbb{E}_{n_0^T}[T_0] \asymp N^{\frac{1+\beta}{2}} \qquad \text{and} \qquad \mathbb{E}_{n_0^C}[T_0] \asymp N^{1-\delta}.$$

(c) Recalling that $m = \rho s$ with $\rho < 1$ (and all these parameters depending on N), the difference of the upward and downward jump rates (3.1) and (3.2) is

$$\lambda_n - \mu_n = n\left(s - m - s\frac{n}{N}\right)$$

and their sum is $\lambda_n + \mu_n \sim n$ as long as $n \ll N$. Hence the dynamics of Y^N (although its state space is $\{0, 1, \dots, N\}$ rather than $\mathbb{N}_0$) bears similarities to that of a logistic branching process. Indeed, we conjecture that a logistic branching process $\widehat{Y}^N$ with upward and downward jump rates $\widehat{\lambda}_n$ and $\widehat{\mu}_n$ given by

$$\widehat{\lambda}_n = n\left(\frac{1}{2} + s\right), \qquad \widehat{\mu}_n = n\left(\frac{1}{2} + m + s\frac{n}{N}\right) \tag{3.18}$$

will exhibit very similar asymptotics of the expected times to extinction as those obtained for the process Y^N in Theorem 3.4. This would complement results of Sagitov and Shaimerdenova (2013) and Chazottes et al. (2016), both of which do not cover the parameter regime given by (3.18). The paper Sagitov and Shaimerdenova (2013) considers jump rates of the form $\widehat{\lambda}_n = ns$, $\widehat{\mu}_n = nm + n(n-1)\theta$ with constant s, m and small θ; this corresponds to (3.18) but without the fluctuation terms $\frac{1}{2}$ which are of dominant order in (3.18). (For conceptual clarification we point out that Sagitov and Shaimerdenova (2013) addresses the case of a constant ratio $s/m > 1$ as supercritical, while in our context this corresponds to a subcritical mutation–selection ratio.) The paper Chazottes et al. (2016) considers quasi-equilibria and extinction times of a class of birth-and-death processes that is more general than logistic branching processes, but imposes a scaling condition of the dynamics which is not fulfilled by (3.1) and (3.2). Still, both papers point to interesting routes which may offer alternatives to our way of proving Theorem 3.4.

4. Proof of Theorem 3.4

4.1. Green function

The proof is based on an asymptotic analysis of the Green function of $Y = Y^N$,

$$G(j,n) := G^N(j,n) = \mathbb{E}_j\left[\int_0^{T_0} I_{\{Y_t^N = n\}}\, dt\right], \quad 1 \le j, n \le N$$

as $N \to \infty$. By assumption the upward and downward jump rates of Y from n are given by

$$\lambda_n := n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + \frac{m}{\rho}\left(1 - \frac{n}{N}\right)\right), \tag{4.1}$$

$$\mu_n := n\left(\frac{1}{2}\left(1 - \frac{n}{N}\right) + m\right).$$

Recall that all quantities, including λ_n and μ_n, depend on N, even if we suppress this in the notation for the sake of readability. We express the Green function in terms of the *oddsratio products*

$$r_0 := 1, \quad r_k := \prod_{l=1}^{k} \frac{\mu_l}{\lambda_l}, \qquad k \in \{1, \dots, N-1\}. \tag{4.2}$$

The following lemma is well known, see e.g. Sagitov and Shaimerdenova (2013, (2.4)) for a proof of (4.5) via a decomposition with respect to excursions from j. For convenience we include a derivation of (4.3) in Section 4.5. See also Doering et al. (2005, (15)) for a similar representation of $G(j,n)$.

Lemma 4.1. *For $1 \le j, n \le N$,*

$$G(j,n) = \frac{1}{\mu_n} \sum_{l=0}^{j-1\wedge n-1} \prod_{k=l+1}^{n-1} \frac{\lambda_k}{\mu_k}. \tag{4.3}$$

In Fig. 3, formula (4.3) is compared to empirical occupation times from simulations of the process Y.

With

$$R_k := \sum_{i=0}^{k-1} r_i, \qquad k \in \{1, \dots, N\},$$

we obtain from (4.3):

$$G(j,n) = \begin{cases} \frac{R_{j\wedge n}}{\lambda_n r_n} & \text{if } n < N, \\ \frac{R_j}{\mu_N r_{N-1}} & \text{if } n = N. \end{cases} \tag{4.4}$$

Consequently,

$$\mathbb{E}_j[T_0] = \sum_{n=1}^{N} G(j,n) = \sum_{n=1}^{N-1} \frac{R_{n\wedge j}}{\lambda_n r_n} + \frac{R_j}{\mu_N r_{N-1}}. \tag{4.5}$$

Note that

$$U(j) := \log r_j \tag{4.6}$$

(sometimes also referred to as *potential*, cf. Doering et al. (2005, (16))) is an additive functional, and (4.3) translates into

$$G(j,n) = \frac{1}{\mu_n} \sum_{l=0}^{j-1\wedge n-1} e^{-(U(n-1) - U(\ell))}.$$

4.2. Asymptotics for the cumulated oddsratio products

In view of (4.5) we are going to find asymptotics for the terms r_k and R_k as $N \to \infty$.

Our analysis, see Lemmas 4.3 and 4.6, shows that, as j increases, r_j is essentially constant on a large interval, before it starts to decrease as j approaches the center of attraction $N(1-\rho)$. The asymptotics of the cumulated oddsratio products R_j and of the terms $G(j,n)$ will be analysed, depending on the order of magnitude of j, in Lemmas 4.3, 4.4 and 4.5 for the polynomial regime, and in Lemma 4.6 and Proposition 4.7 for the exponential regime.

We recall the notation $f(N) \ll g(N)$ from (3.10). Also, we recall that we usually suppress the N-dependence in the notation, as for example in m, ρ and j.

We can express $\log r_j$ as

$$\log r_j = \sum_{k=1}^{j} \log\left(\frac{\mu_k}{\lambda_k}\right) = j \log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{k=1}^{j} \log\left(\frac{1 - k/((1+2m)N)}{1 - k/N}\right). \tag{4.7}$$

This expression allows us the following asymptotic description which is key in what follows.

Lemma 4.2. *Let $\xi = \xi_N$ be a sequence converging to 0 so slowly that $\xi \gg m$. Then for N large enough and $j \le (1-\xi)N$*

$$0 \le \log r_j - j \log\left(\frac{1+2m}{1+2m/\rho}\right) - \sum_{l=1}^{\infty}\left(1 - \frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{j^{l+1}}{N^l} \le \text{const} \cdot \frac{m}{\xi}. \tag{4.8}$$

Lemma 4.3. *Let $K := K_N > 0$ either be constant or a diverging sequence. Then for all $k \le K\sqrt{N/m}$*

$$e^{k^2 m/((1+2m)N) - 4(1-\rho)K\sqrt{mN}} \le r_k \le e^{k^2 m/N + K^3/(\sqrt{mN} - K)} \tag{4.9}$$

and

$$e^{-4(1-\rho)K\sqrt{mN}} \int_0^{k-1} e^{x^2 m/((1+2m)N)} dx \le R_k \le e^{K^3/(\sqrt{mN}-K)} \int_1^k e^{x^2 m/N} dx. \tag{4.10}$$

Lemmas 4.2 and 4.3 will be proved in Section 4.5. We conclude this subsection by showing (3.17). To this end, note the two asymptotic equivalences

$$\log\left(\frac{1+2m}{1+2m/\rho}\right) = \log\left(1 + \frac{2m(\rho-1)}{\rho+2m}\right) \sim 2m\left(1 - \frac{1}{\rho}\right)$$

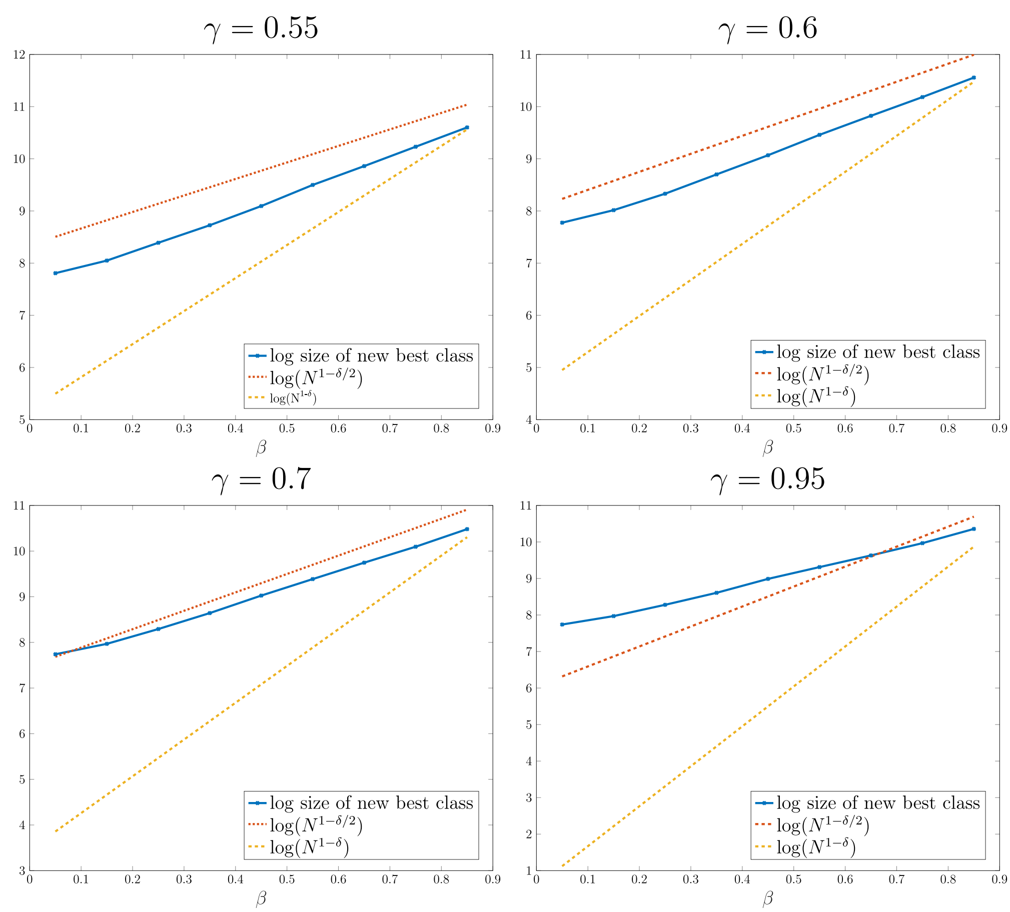

Fig. 5. For $N = 10^5$ we compare the size of the "new best class" of the tournament ratchet immediately after a click (as observed by simulations) with $\mathfrak{a} = N^{1-\delta}$ and $\mathfrak{b} = N^{1-\delta/2}$, which are the centers of attraction of the best and the second best class of the tournament ratchet(cf. Remark 3.6. (b)). For various values of $\gamma = \delta/(1-\beta)$, we consider (the logarithms of) these quantities as functions of β. Each data point was obtained by pooling the interclick times no. 5 to 30 from 20 simulations of the tournament ratchet for the corresponding parameter configuration. For a wide range of parameters with γ between 1/2 and 1, $\mathfrak{b}$ is a better fit for the size of the new best class than $\mathfrak{a}$.

and

$$\sum_{\ell=1}^{\infty}\left(1-\frac{1}{(1+2m)^{\ell}}\right)\frac{(1-\rho)^{\ell-1}}{\ell(\ell+1)} \sim 2m\sum_{\ell=1}^{\infty}\frac{(1-\rho)^{\ell-1}}{\ell+1},$$

which combine to

$$(1-\rho)^2\eta(m,\rho) \sim \frac{1}{\rho}-1-(1-\rho)-\sum_{\ell=2}^{\infty}\frac{(1-\rho)^{\ell}}{\ell} = \frac{1}{\rho}-1+\log\rho.$$

4.3. The polynomial regime: Proof of Theorem 3.4(a)

Throughout this subsection we assume $Nm(1-\rho)^2 \to 0$ as $N\to\infty$.

We start with the expected number of returns to $a := \lfloor N(1-\rho)\rfloor$ of the process Y when starting in a. (4.4) together with Lemma 4.3 gives

$$G(a,a) = \frac{R_a}{\lambda_a r_a} \sim \frac{\int_1^a e^{x^2\frac{m}{N}}\,\mathrm{d}x}{\lambda_a r_a}.$$

From Weisstein (2024, (1), (9)) we get

$$\int_1^a e^{x^2\frac{m}{N}}\,\mathrm{d}x \sim \frac{e^{a^2m/N}}{2\frac{m}{N}a},$$

and hence by using (4.9) as well as $\lambda_a \sim \frac{1}{2}\rho(1-\rho)N$ we get

$$G(a,a) \sim \frac{1}{m\rho(1-\rho)^2N} \qquad \text{as } N\to\infty,$$

which together with the asymptotics $\lambda_a+\mu_a \sim \rho(1-\rho)N$ gives

$$G(a,a)(\lambda_a+\mu_a) \sim \frac{1}{m(1-\rho)} \qquad \text{as } N\to\infty. \tag{4.11}$$

In order to prove the rest the following two lemmas will be proved in Section 4.6.

Lemma 4.4. *Let $\zeta := \zeta_N \to 0$ such that $\zeta \gg \left[N(1-\rho)^2m\right]^{1/4}$, and $K = K_N$ such that $K\to\infty$ and*

$$K\left((1-\rho)\sqrt{Nm}\vee(Nm)^{-1/6}\right)\to 0.$$

Then

$$\sum_{k=\zeta\sqrt{N/m}}^{K\sqrt{N/m}}\frac{R_k}{\lambda_k r_k} = \sqrt{\frac{N}{m}}\left(\frac{\pi^{3/2}}{2}+O(\zeta)+O\left(\frac{1}{K}\right)\right) \quad \textit{as } N\to\infty.$$

Here and below, we will omit the Gauss brackets in the summation bounds for better readability.

Lemma 4.5. *Let $K = K_N$ and $\xi = \xi_N$ be sequences with $K_N\to\infty$ and $1 \gg \xi \gg m$. Then there exists a constant $C>0$ such that for all k with*

$$K\sqrt{N/m} \le k \le N(1-\xi)$$

we have

$$\frac{R_k}{r_k} \le C\frac{Nm}{k}. \tag{4.12}$$

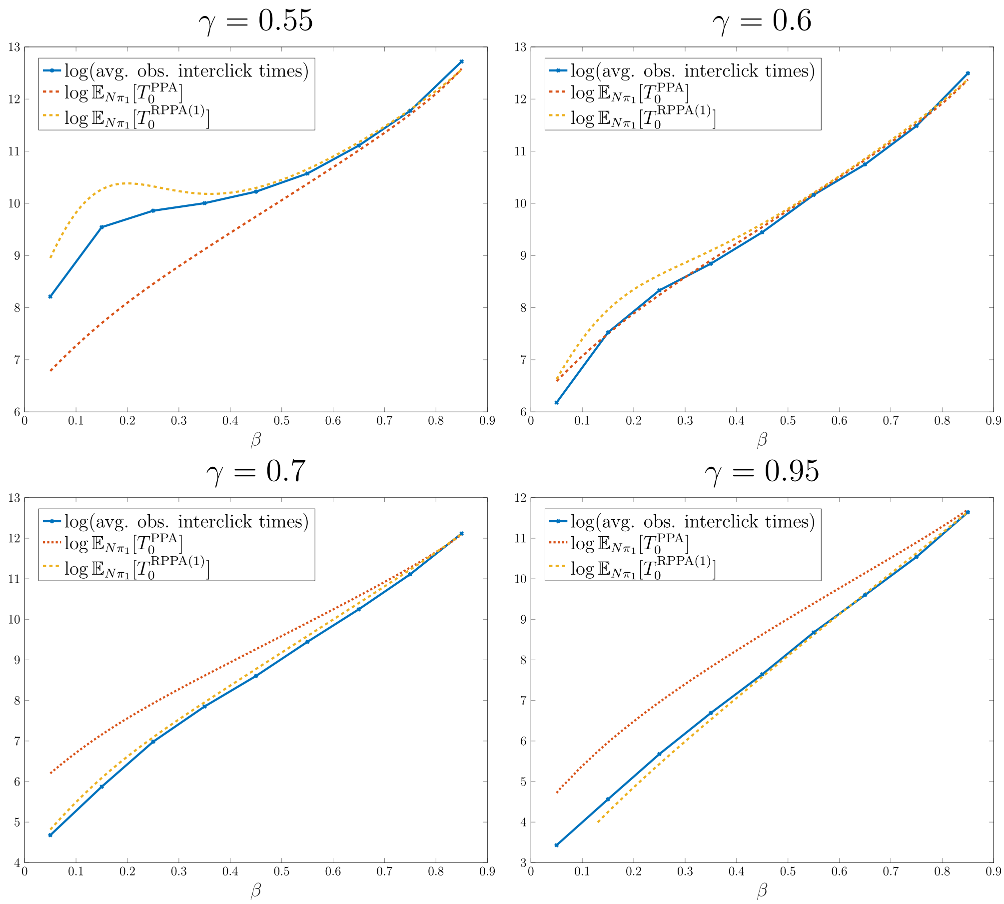

Fig. 6. For fixed population size $N = 10^5$ the predictions for the expected interclick time of the classical ratchet based on a numerical calculation of the Green function (i) of the PPA and (ii) of the RPPA(1) approximation are compared with simulations. Here, formula (4.3) is used (i) for the jump rates (3.1) and (3.2), and (ii) for the downward jump rate (3.1) and the upward jump rate resulting from (3.4) and (3.9). Each data point was obtained by pooling the interclick times no. 5 to 30 from 20 simulations of the tournament ratchet for the corresponding parameter configuration. Each plot shows this for one fixed value of γ with varying β.

With these three lemmas we have the tools for proving Theorem 3.4(a), which concerns the polynomial regime. We will distinguish between the cases $j \gg \sqrt{N/m}$ and $j \ll \sqrt{N/m}$, since the potential U (given by (4.6)) turns out to be essentially flat below $\sqrt{N/m}$.

4.3.1. *Proof of* (3.11)

Abbreviating $\gamma := \log(1/m)$ and recalling that we are in the case

$$j \ll \sqrt{\frac{N/m}{\log(N/m)}}, \tag{4.13}$$

we decompose the mean extinction time from state j given by (4.5) as follows

$$\begin{aligned}\mathbb{E}_j[T_0] &= \sum_{k=1}^{j-1} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=j}^{\gamma\sqrt{N/m}} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=\gamma\sqrt{N/m}+1}^{N} \frac{R_{k\wedge j}}{\lambda_k r_k} \\ &= \sum_{k=1}^{j-1} \frac{R_k}{\lambda_k r_k} + R_j \sum_{k=j}^{\gamma\sqrt{N/m}} \frac{1}{\lambda_k r_k} + R_j \sum_{k=\gamma\sqrt{N/m}+1}^{N} \frac{1}{\lambda_k r_k} \\ &=: E_1(j) + E_2(j) + E_3(j).\end{aligned} \tag{4.14}$$

In view of the asymptotics

$$R_k \sim k \quad \text{for } k \ll \sqrt{N/m}$$

and $\lambda_k \sim k/2$ for $k \ll N$, and because of the inequality $\lambda_k r_k = \mu_k r_{k-1} \geq mk r_{k-1}$ for any $k \leq N-1$, we have

$$E_1(j) + E_3(j) \leq 4 \sum_{k=1}^{j-1} \frac{k}{k} + \frac{2j}{m} \sum_{k=\gamma\sqrt{N/m}+1}^{N} \frac{1}{k r_{k-1}}.$$

For the sake of readability, let us introduce the function $f(k)$ via

$$\frac{m}{N} k^2 f(k) := k \log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^{\infty} \left(1 - \frac{1}{(1+2m)^l}\right) \frac{k^{l+1}}{l(l+1)N^l}. \tag{4.15}$$

We see that $f(k) \geq 1/2$ when $k \gg \sqrt{N/m}$. Hence there exists a finite constant C such that

$$\sum_{k=\gamma\sqrt{N/m}+1}^{N} \frac{1}{k r_{k-1}} \leq \sum_{k=\gamma\sqrt{N/m}}^{N} \frac{e^{-\frac{mk^2}{2N}}}{k} \leq \int_{\gamma}^{\infty} \frac{e^{-x^2/2}}{x} \mathrm{d}x \leq \frac{e^{-\gamma^2/2}}{\gamma^2}.$$

In order to see the first inequality we argue as follows: From Lemma 4.2 we get that for any k,

$$\begin{aligned}\log r_k &\geq k \log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^{\infty} \left(1 - \frac{1}{(1+2m)^l}\right) \frac{1}{l(l+1)} \frac{k^{l+1}}{N^l} \\ &\geq k \log\left(\frac{1+2m}{1+2m/\rho}\right) + \left(1 - \frac{1}{(1+2m)}\right) \frac{1}{2} \frac{k^2}{N}.\end{aligned}$$

From the observation that

$$\log\left(\frac{1+2m}{1+2m/\rho}\right) \sim -\frac{2m}{\rho}(1-\rho), \qquad \left(1 - \frac{1}{(1+2m)}\right) \frac{1}{2} \frac{k}{N} \sim m \frac{k}{N}$$

and

$$\frac{k}{N} \gg (1-\rho)$$

for k at least of order $\sqrt{N/m}$ we see that $r_{k-1} \geq e^{mk^2/(2N)}$. From this we get

$$E_1(j) + E_3(j) \leq 4j + 2j e^{\gamma} \frac{e^{-\gamma^2/2}}{\gamma^2},$$

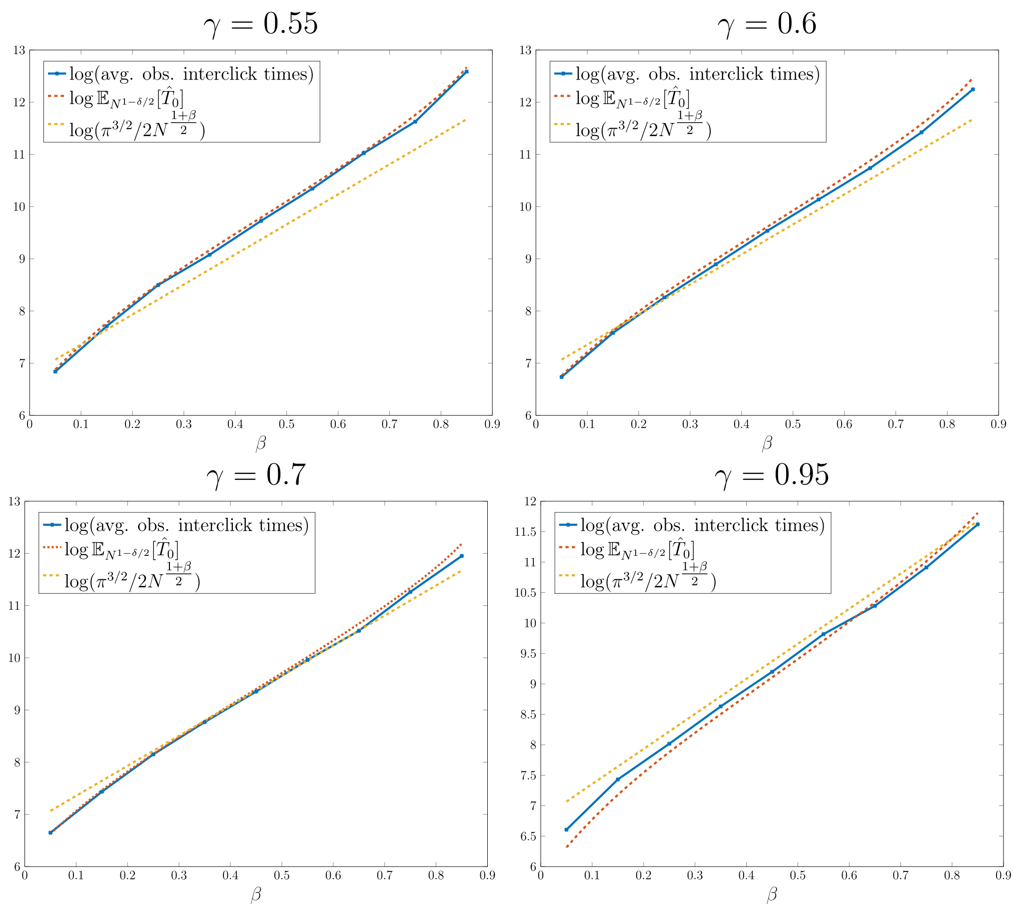

Fig. 7. For fixed population size $N = 10^5$ the predictions for the expected interclick time of the tournament ratchet based on (i) a numerical calculation of the Green function (using formula (4.3)) and (ii) the asymptotics provided by Theorem 3.4 are compared with simulations. Each data point was obtained by pooling the interclick times no. 5 to 30 from 20 simulations of the tournament ratchet for the corresponding parameter configuration. Each plot shows this for one fixed value of γ and for varying β.

which is of lower order than the r.h.s of (3.11). We will now analyse $E_2(j)$, which turns out to be the dominant term. First, as $j \ll \sqrt{N/m}$, it may be simplified as follows,

$$E_2(j) \sim 2j \sum_{k=j}^{\log(1/m)\sqrt{N/m}} \frac{1}{kr_k}.$$

By sandwiching arguments using (4.8) and (4.15) we conclude that

$$\sum_{k=j}^{\gamma\sqrt{N/m}} \frac{1}{kr_k} \sim \int_j^{\gamma\sqrt{N/m}} \frac{e^{-\frac{m}{N}x^2 f(x)}}{x} \mathrm{d}x.$$

Thanks to (4.13) there exists a sequence $\xi = \xi_N \to 0$ such that $\xi^2 \gg 1/\log\left(\sqrt{N/m}\right)$ and $j_N \le \xi_N\sqrt{N/m}$. From (4.9), if $k \le \xi\sqrt{N/m}$ and N is large enough, then $|(m/N)k^2 f(k)| \le 2\xi^2$. Hence

$$e^{-2\xi^2}\left(\log\left(\xi\sqrt{N/m}\right) - \log j\right) \le \int_j^{\xi\sqrt{N/m}} \frac{e^{-\frac{m}{N}x^2 f(x)}}{x}\mathrm{d}x \le e^{2\xi^2}\left(\log\left(\xi\sqrt{N/m}\right) - \log j\right).$$

Moreover, $f(k) \ge \xi^2/2$ for $k \ge \xi\sqrt{N/m}$. We deduce

$$\int_{\xi\sqrt{N/m}}^{\gamma\sqrt{N/m}} \frac{e^{-\frac{m}{N}x^2 f(x)}}{x}\mathrm{d}x \le \int_{\xi\sqrt{N/m}}^{\gamma\sqrt{N/m}} \frac{e^{-\frac{m}{N}x^2\xi^2/2}}{x}\mathrm{d}x \le \int_{\xi}^{\infty} \frac{e^{-y^2\xi^2/2}}{y}\mathrm{d}y.$$

By substituting $t = \xi y$ in the integral, the right hand side can be written as

$$\int_{\xi^2}^{\infty} \frac{e^{-t^2/2}}{t}\mathrm{d}t,$$

which is of order ξ^{-2}. Since this is of lower order than $\log\left(\sqrt{N/m}\right)$ we deduce that

$$E_2(j) \sim 2j\left(\log\left(\sqrt{N/m}\right) - \log j\right). \tag{4.16}$$

This ends the proof of (3.11). □

4.3.2. *Proof of* (3.12)

We recall that this concerns the case $j = j_N \gg \sqrt{N/m}$. Let $K = K_N$ be a sequence which converges to ∞ so slowly that $K\sqrt{N/m} \le j$ and that K satisfies the requirements of Lemma 4.3. Moreover, let $\xi = \xi_N$ be a sequence with $\xi \to 0$ and $\xi \gg m$. In the **first part of the proof** we impose the condition

$$j_N \le N(1 - \xi_N). \tag{4.17}$$

Let $\zeta = \zeta_N$ be a sequence converging to 0. Using again (4.5), we decompose the mean extinction time from state j as follows:

$$\begin{aligned}
&\mathbb{E}_j[T_0] \\
&= \sum_{k=1}^{\zeta\sqrt{N/m}} \frac{R_k}{\lambda_k r_k} + \sum_{k=\zeta\sqrt{N/m}+1}^{K\sqrt{N/m}} \frac{R_k}{\lambda_k r_k} + \sum_{k=K\sqrt{N/m}+1}^{N(1-\xi)} \frac{R_{k\wedge j}}{\lambda_k r_k} \\
&\quad + \sum_{k=N(1-\xi)+1}^{N-1} \frac{R_j}{\lambda_k r_k} + \frac{R_j}{\mu_N r_{N-1}} \\
&=: F_1 + F_2 + F_3(j) + F_4(j) + F_5(j).
\end{aligned}$$

The asymptotic of the second sum, F_2, has been derived in Lemma 4.4 and leads to the r.h.s. of (3.12). It thus suffices to show that $F_1 + F_3(j) +$

$F_4(j) + F_5(j) = o\left(\sqrt{N/m}\right)$. With $E_2(1)$ defined in (4.14), and because of (4.16) we obtain the estimate

$$F_1 \le E_2(1) \sim 2\log\left(\sqrt{Nm}\right) = o\left(\sqrt{N/m}\right).$$

The term $F_5(j)$ is bounded by $\frac{R_{N-1}}{\mu_N r_{N-1}}$. By (3.1) and (4.12) the latter is at most of order $1/m$, which is $o\left(\sqrt{N/m}\right)$ because of the standing assumption that $Nm \to \infty$.

Let us now turn to the analysis of $F_3(j)$. For this we have the upper bound

$$\sum_{k=K\sqrt{N/m}+1}^{N(1-\xi)} \frac{R_k}{\lambda_k r_k}. \tag{4.18}$$

By using

$$\lambda_k \sim \frac{k}{2}\left(1-\frac{k}{N}\right) = \frac{1}{2}\frac{k}{N}(k-N)$$

and the bound (4.12), the term (4.18) is asymptotically bounded from above by

$$2\sum_{k=K\sqrt{N/m}+1}^{N-1} \frac{N}{k(N-k)}\frac{N}{2mk} = \frac{N^2}{m}\sum_{k=K\sqrt{N/m}+1}^{N-1}\frac{1}{k^2(N-k)}.$$

We claim that this is $o\left(\sqrt{N/m}\right)$, which is equivalent to

$$\frac{N^2}{m}\sqrt{\frac{m}{N}}\sum_{k=K\sqrt{N/m}+1}^{N-1}\frac{1}{k^2(N-k)} \tag{4.19}$$

converging to zero. This term we approximate by an integral

$$\begin{aligned}
&\frac{N^2}{m}\sqrt{\frac{m}{N}}\sum_{k=K\sqrt{N/m}+1}^{N-1}\frac{1}{k^2(N-k)}\\
&= \frac{N^2}{m}\sqrt{\frac{m}{N}}\cdot\frac{1}{N^3}\cdot N\cdot\frac{1}{N}\sum_{k=K\sqrt{N/m}+1}^{N-1}\frac{1}{(k/N)^2(1-k/N)}\\
&\sim \frac{N^2}{m}\sqrt{\frac{m}{N}}\cdot\frac{1}{N^3}\cdot N\cdot\int_{K/\sqrt{mN}}^{1-\frac{1}{N}}\frac{1}{x^2(1-x)}\mathrm{d}x\\
&= \frac{1}{\sqrt{Nm}}\int_{K/\sqrt{mN}}^{1-\frac{1}{N}}\frac{1}{x^2(1-x)}\mathrm{d}x.
\end{aligned}$$

The integral is of order

$$\left(K/\sqrt{mN}\right)^{-1} \vee \log N = \left(\frac{1}{K}\sqrt{mN}\right) \vee \log N.$$

Thus (4.19) is of order $\frac{(\sqrt{Nm}/K)\vee\log N}{\sqrt{Nm}}$, which converges to zero as $N \to \infty$.

We are left with the analysis of

$$F_4(j) = \sum_{k=N(1-\xi)+1}^{N-1}\frac{R_{k\wedge j}}{\lambda_k r_k}.$$

This sum is bounded by

$$R_j\sum_{k=N(1-\xi)+1}^{N-1}\frac{1}{\lambda_k r_k}.$$

Since we assumed $j \le N - \xi N$ this is again bounded from above by

$$\frac{R_{N(1-\xi)}}{r_{N(1-\xi)}}\sum_{k=N(1-\xi)+1}^{N-1}\frac{r_{N(1-\xi)}}{\lambda_k r_k}.$$

Recall from (4.7) that for $j, \ell \in \mathbb{N}$,

$$\log r_{j+l} - \log r_j = \ell\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{k=j+1}^{j+\ell}\log\left(\frac{1-k/((1+2m)N)}{1-k/N}\right).$$

Noticing that the term

$$\log\left(\frac{1-k/((1+2m)N)}{1-k/N}\right)$$

is increasing with k, and performing a Taylor expansion, we obtain that for

$$k = N(1-\xi)+\ell$$

we have the inequality

$$\log r_k - \log_{N(1-\xi)} \ge \ell(1-\xi)m.$$

Together with Lemma 4.5 and the asymptotic $\lambda_k \sim k(1-k/N)$ we obtain

$$\begin{aligned}
&\frac{R_{N(1-\xi)}}{r_{N(1-\xi)}}\sum_{k=N(1-\xi)+1}^{N-1}\frac{r_{N(1-\xi)}}{\lambda_k r_k}\\
&\le \text{const}\cdot\frac{Nm}{N(1-\xi)}\sum_{k=N(1-\xi)+1}^{N-1}\frac{1}{k(1-k/N)}\exp\left(-m(1-\xi)\left[k-N(1-\xi)-1\right]\right)
\end{aligned}$$

By using

$$\frac{1}{k(1-k/N)} \le 2 \qquad \text{for } N(1-\xi) \le k \le N-1$$

this is bounded by

$$\text{const}\cdot\frac{m}{1-\xi}\sum_{k=N(1-\xi)+1}^{N-1}\exp\left(-m(1-\xi)\left[k-N(1-\xi)-1\right]\right),$$

which in turn can be bounded by

$$\begin{aligned}
&\text{const}\cdot\frac{m}{1-\xi}\int_{x=N(1-\xi)+1}^{N-1}\exp\left(-m(1-\xi)\left[x-N(1-\xi)-1\right]\right)\mathrm{d}x\\
&\le \frac{\text{const}\cdot m}{1-\xi}\int_0^{N(1-\xi)}\exp\left(-m(1-\xi)x\right)\mathrm{d}x.
\end{aligned}$$

The latter integral is of order $1/m$ as $N \to \infty$. Thus we obtain

$$F_4(j) = o\left(\sqrt{\frac{N}{m}}\right),$$

which finishes the proof of (3.12) in the case $j \le N(1-\xi)$.

In the **remaining part of the proof** we consider sequences which not necessarily satisfy the restriction (4.17). In view of the first part it suffices to show that the expected time which Y needs to come down from N to $N(1-\xi)$ is of lower order than $\sqrt{N/m}$. For this, we impose an additional condition on the sequence ξ, and will show the following claim: Let $\xi = \xi_N$ be a sequence converging to 0 and obeying $m \ll \xi \ll m(N/m)^{1/4}$ as $N \to \infty$. Then $\mathbb{E}_N[T_{N(1-\xi)}] = o(\sqrt{N/m})$.

To prove this claim, let $\mathcal{Y}$ be the time-discrete birth-and-death process corresponding to Y. By (3.1) and (3.2) the probability of $\mathcal{Y}$ to go down in the next step when starting in k is given by

$$\frac{\frac{1}{2}\left(1-\frac{k}{N}\right)+m}{\left(1-\frac{k}{N}\right)+m+\frac{m}{\rho}\left(1-\frac{k}{N}\right)}.$$

which for $N(1-\xi) \le k \le N$ is bounded from below by

$$q := \frac{1}{2}\frac{1+\frac{2m}{\xi}}{1+\frac{m}{\xi}+\frac{m}{\rho}}.$$

Let us put $p := 1-q$, and consider the (p,q)-random walk W on $\mathbb{Z}$ as well as the random walk $\widehat{W}$ on $\mathbb{Z} \cap \{\dots, N-2, N-1, N\}$ that is obtained by reflecting W at N, i.e. by putting $\mathbb{P}_N(\widehat{W}_1 = N) := p$, $\mathbb{P}_N(\widehat{W}_1 = N-1) := q$. A suitable coupling of $\mathcal{Y}$ and $\widehat{W}$ (both starting in N) shows that for $N(1-\xi) \le k \le N$ the expected number visits of $\mathcal{Y}$ to k before $\mathcal{Y}$ reaches $N(1-\xi)$ is not larger than the expected number of visits of $\widehat{W}$ to k before $\widehat{W}$ reaches $N(1-\xi)$. The expected number of visits of the transient random walk W to its starting point is $\frac{q}{q-p} \sim \frac{\xi}{m}$, and the same is true for $\widehat{W}$. The jump rates (3.1) and (3.2) from state $k \ge N(1-\xi)$ add up to

$$k\left[\frac{N-k}{N}+m+\frac{N-k}{N}\frac{m}{\rho}\right] \ge \frac{1}{2}Nm.$$

Altogether, we obtain the estimate

$$\mathbb{E}_N[T_{N(1-\xi)}] \le \frac{2}{Nm}\xi N \frac{q}{p-q} \sim \frac{2\xi^2}{m^2}, \tag{4.20}$$

whose r.h.s. is $o(\sqrt{N/m})$ due to our assumption on ξ.

This concludes the proof of Theorem 3.4(a). □

4.4. The exponential regime: Proof of Theorem 3.4(b)

Throughout this section we assume $Nm(1-\rho)^2 \to \infty$. In this regime the process Y should spend a long time around its center of attraction $(1-\rho)N$, which makes the following decomposition of (4.5) natural: for a small $\zeta > 0$ write

$$\mathbb{E}_j[T_0] = \sum_{k=1}^{(1-\zeta)(1-\rho)N} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=(1+\zeta)(1-\rho)N+1}^{N} \frac{R_{k\wedge j}}{\lambda_k r_k}$$
$$=: A(\zeta) + B(\zeta) + C(\zeta). \tag{4.21}$$

The assertion of Theorem 3.4.(b) will be derived at the end of this section from Proposition 4.7, whose proof, in turn, will rely on the following lemma. The proof of this lemma as well as that of Proposition 4.7 will be given in Section 4.7.

Lemma 4.6. *Let $j = j_N$ be a sequence of natural numbers converging to ∞, and let $\xi < 1/2$. Then*

- *If $j \le \xi(1-\rho)N$, then for sufficiently large N*
$$\frac{1-e^{-(1+2\xi)2m(1-\rho)j/\rho}}{(1+2\xi)2m(1-\rho)/\rho} \le R_j \le \frac{1-e^{-(1-2\xi)2m(1-\rho)j/\rho}}{(1+2\xi)2m(1-\rho)/\rho}.$$
- *If $1/(m(1-\rho)) \ll j \le (2-\xi)(1-\rho)N \wedge N(1-\sqrt{m})$, then, under the assumption $\xi \ge 2\log(mN(1-\rho)^2)/(mN(1-\rho)^2)$,*
$$R_j \sim \frac{\rho}{2m(1-\rho)} \quad \text{as } N \to \infty.$$
- *If $j = C(1-\rho)N \le N(1-\sqrt{m})$, with $\frac{1}{1-\rho} \ge C > 2/\rho$ (implying $\rho > \frac{2}{3}$), then*
$$R_j \sim \rho(1-C(1-\rho))\frac{\exp\left(-2m(1-\rho)^2 NH(C)\right)}{2m(C-1)(1-\rho)} \quad \text{as } N \to \infty,$$
where the function $H(.) = H((m,\rho),.)$ on $\mathbb{R}_+$ is defined by

$$H(y) := -\frac{y}{2m}\left[\frac{1}{1-\rho}\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{(1-\rho)^{l-1}y^l}{l(l+1)}\right]. \tag{4.22}$$

This is the central ingredient for the proof of the following proposition, which, in turn, will be key for the proof of Theorem 3.4(b).

Proposition 4.7. *Let $A(\zeta)$, $B(\zeta)$ and $C(\zeta)$ be defined by (4.21). Then for $\zeta = \zeta_N$ converging to 0 so slowly that $\zeta\sqrt{mN}(1-\rho) \to \infty$, we have*

$$B(\zeta) \sim \left(R_j \wedge \frac{\rho}{2m(1-\rho)}\right)\sqrt{\frac{\pi}{mN}}\frac{2}{1-\rho}\exp\left(2m(1-\rho)^2 NH(1)\right) \quad \text{as } N \to \infty, \tag{4.23}$$

and

$$A(\zeta) + C(\zeta) = o(B(\zeta)) \quad \text{as } N \to \infty.$$

The proof of this proposition will be given in Section 4.7.

Proof of Theorem 3.4(b). (i) For $j = j_N = O(1/(m(1-\rho)))$ and any sequence $\xi = \xi_N$ converging to zero we have

$$1 - \exp(-(1 \pm 2\xi)2m(1-\rho)j/\rho) \sim 1 - \exp(-2m(1-\rho)j/\rho).$$

Hence Proposition 4.7 together with the first bullet point of Lemma 4.6 gives

$$\mathbb{E}_j[T_0] \sim B(\zeta) \sim \frac{1-\exp(-2m(1-\rho)j/\rho)}{2m(1-\rho)}\sqrt{\frac{\pi}{mN}}\frac{2\rho}{1-\rho}\exp\left(2m(1-\rho)^2 NH(1)\right),$$

(ii) For $j \gg 1/(m(1-\rho))$ Proposition 4.7 together with the second bullet point of Lemma 4.6 gives

$$\mathbb{E}_j[T_0] \sim B(\zeta) \sim \frac{\rho}{m(1-\rho)^2}\sqrt{\frac{\pi}{mN}}\exp\left(2m(1-\rho)^2 NH(1)\right).$$

(iii) To conclude (3.13) from (i) and (ii) it suffices to observe that $\eta(m,\rho) = H(1)$, and that the assumption on j in (ii) implies the convergence $1 - \exp(-2m(1-\rho)j_N/\rho) \to 1$ as $N \to \infty$. The claimed asymptotics (3.16) is an immediate consequence of (3.13).

(iv) It remains to prove the claim on the expected number of excursions from $a := \lfloor \mathfrak{a} \rfloor$, with $\mathfrak{a} = (1-\rho)N$ being the asymptotic center of attraction of Y. In view of (4.4) this expected number equals

$$(\lambda_a + \mu_a)G(a,a) = (\lambda_a + \mu_a)\frac{R_a}{\lambda_a r_a}. \tag{4.24}$$

In order to estimate r_a we observe that (4.8), when expressed in terms of the function H (which was defined in (4.22)), gives the asymptotics

$$\frac{1}{r_a} \sim \exp\left(2m(1-\rho)^2 NH(1)\right) \quad \text{as } N \to \infty. \tag{4.25}$$

In addition, the second bullet point of Lemma 4.6 gives

$$R_a \sim \frac{\rho}{2m(1-\rho)} \quad \text{as } N \to \infty. \tag{4.26}$$

Since $\lambda_a \sim \mu_a$ as $N \to \infty$, the combination of (4.25) and (4.26) shows that (4.24) is asymptotically equivalent to (3.14). □

4.5. Proofs of Lemmas 4.1, 4.2 and 4.3

Proof of Lemma 4.1. We denote the time-discrete embedded process corresponding to Y by $\mathcal{Y}$, and write $\mathcal{G}(m,n)$ for the expected number of visits at n of $\mathcal{Y}$ when starting in m. Let us start with an analysis of $\mathcal{G}(n,n)$. By standard arguments we have

$$\mathcal{G}(n,n) = \frac{1}{\phi(n)}, \tag{4.27}$$

where $\phi(n)$ is the escape probability of $\mathcal{Y}$ from the state n, i.e.

$$\phi(n) = \frac{\mu_n}{\mu_n + \lambda_n}(1 - h^{(n)}(n-1)), \tag{4.28}$$

where $h^{(n)} : \{0,1,\dots,n\} \to [0,1]$ is $\mathcal{Y}$-harmonic on $\{1,\dots,n-1\}$ and satisfies the boundary conditions $h^{(n)}(0) = 0$, $h^{(n)}(n) = 1$. Hence

$$h^{(n)}(\ell) = \frac{\sum_{j=0}^{\ell-1} r_j}{\sum_{k=0}^{n-1} r_k}, \quad \ell = 0,\dots,n, \tag{4.29}$$

with the oddsratio product r_k as in (4.2). From (4.29) we obtain

$$1 - h^{(n)}(n-1) = \frac{r_{n-1}}{\sum_{k=0}^{n-1} r_k}. \tag{4.30}$$

For $G(n,n)$, the expected time spent by Y in n when starting in n, we thus obtain the relation

$$G(n,n) = \frac{\mathcal{G}(n,n)}{\lambda_n + \mu_n} = \frac{1}{\phi(n)} \cdot \frac{1}{\mu_n + \lambda_n}.$$

Combining this with (4.27), (4.28) and (4.30) we arrive at

$$G(n,n) = \frac{1}{\mu_n} \cdot \sum_{k=0}^{n-1} \frac{r_k}{r_{n-1}} = \frac{1}{\mu_n}\sum_{l=0}^{n-1}\prod_{k=l+1}^{n-1}\frac{\lambda_k}{\mu_k}. \tag{4.31}$$

For $j > n$ we have

$$G(j,n) = G(n,n), \tag{4.32}$$

while for $j < n$

$$G(j,n) = h^n(j)G(n,n) = \frac{\sum_{l=0}^{j-1} r_l}{\sum_{l=0}^{n} r_l} G(n,n).$$

Together with (4.31) this gives for $j < n$

$$G(j,n) = \frac{1}{\mu_n}\sum_{k=0}^{n-1}\frac{r_k}{r_{n-1}}\cdot\frac{\sum_{l=0}^{j-1} r_l}{\sum_{l=0}^{n-1} r_l} = \frac{1}{\mu_n}\sum_{l=0}^{j-1}\prod_{k=l+1}^{n-1}\frac{\lambda_k}{\mu_k}. \tag{4.33}$$

It remains to observe that the three cases $j > n$, $j = n$, $j < n$ (which are covered by (4.32), (4.31) (4.33)) combine to (4.3) □

Proof of Lemma 4.2. We have already seen

$$\log r_j = \sum_{k=1}^{j}\log\left(\frac{\mu_k}{\lambda_k}\right) = j\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{k=1}^{j}\log\left(\frac{1-k/(1+2m)N}{1-k/N}\right) = j\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{k=1}^{j}\sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l}\left(\frac{k}{N}\right)^l.$$

As $j \le N-1$, we may apply Fubini's theorem to write

$$\sum_{k=1}^{j}\sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l}\left(\frac{k}{N}\right)^l = \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l}\sum_{k=1}^{j}\left(\frac{k}{N}\right)^l.$$

Now sandwiching arguments yield

$$\frac{j^{l+1}}{(l+1)N^l} = \int_0^j\left(\frac{x}{N}\right)^l \mathrm{d}x \le \sum_{k=1}^{j}\left(\frac{k}{N}\right)^l \le \int_1^j\left(\frac{x}{N}\right)^l \mathrm{d}x + \left(\frac{j}{N}\right)^l = \frac{1}{(l+1)N^l}(j^{l+1}-1) + \left(\frac{j}{N}\right)^l.$$

This means that if we introduce

$$\Delta_j := \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l}\sum_{k=1}^{j}\left(\frac{k}{N}\right)^l - \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{j^{l+1}}{N^l},$$

we have

$$0 \le \Delta_j \le \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l}\left(\frac{j}{N}\right)^l$$

From the observation that

$$1-\frac{1}{(1+2m)^l} \le 2ml,$$

we get

$$0 \le \Delta_j \le 2m\sum_{l=1}^{\infty}\left(\frac{j}{N}\right)^l.$$

Now let $\xi \gg m$. Then $j \le (1-2\xi)N$ implies that for N marge enough, $j+1 \le (1-\xi)N$. Hence

$$\Delta_j \le 2m\sum_{l=1}^{\infty}(1-\xi)^l = 2m\frac{1-\xi}{\xi} = o(1).$$

This entails that there exists C such that for any $j \le (1-2\xi)N$ and N large enough,

$$0 \le \log r_j - j\log\left(\frac{1+2m}{1+2m/\rho}\right) - \sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{j^{l+1}}{N^l} \le \text{const}\cdot\frac{m}{\xi}. \quad \square \tag{4.34}$$

Proof of Lemma 4.3. We set out from (4.8). Notice that for any $x, y \ge 0$, $1-(1+x)^{-y} \le xy$. Hence, for $k \le K\sqrt{N/m}$,

$$\sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{k^{l+1}}{l(l+1)N^l} \le 2m\sum_{l=1}^{\infty}\frac{k^{l+1}}{(l+1)N^l} \le m\sum_{l=1}^{\infty}\frac{k^{l+1}}{N^l} = k^2m/N + mN\sum_{l=3}^{\infty}\frac{k^l}{N^l} = k^2m/N + mN\frac{k^3}{N^3}\frac{1}{1-k/N} \le k^2m/N + \frac{K^3}{\sqrt{mN}-K}.$$

Conversely we have

$$\sum_{l=1}^{\infty}\left(1-\frac{1}{(1+2m)^l}\right)\frac{k^{l+1}}{l(l+1)N^l} \ge \left(1-\frac{1}{(1+2m)}\right)\frac{k^2}{2N} \sim k^2m/N.$$

Finally, for $k \le K\sqrt{N/m}$ we also have

$$\left|k\log\left(\frac{1+2m}{1+2m/\rho}\right)\right| = k\left|\log\left(1-\frac{2m(1-\rho)}{\rho+2m}\right)\right| \sim 2mk(1-\rho) \le 2K\sqrt{m(1-\rho)^2N} = o(1).$$

This concludes the proof of (4.9). The estimate (4.10) then follows by approximating the sum $R_k := \sum_{l=0}^{k-1} r_l$ from below by an integral from 0 to $k-1$ and from above by an integral from 1 to k. □

4.6. Proofs of Lemmas 4.4 and 4.5

Proof of Lemma 4.4. Noting that our choices of K and ζ entail

$$\frac{k^2m}{(1+2m)N} \gg 4(1-\rho)\sqrt{mN} \qquad \forall k \ge \zeta\sqrt{N/m}$$

as well as

$$4(1-\rho)K\sqrt{mN} \to 0, \qquad \frac{K^3}{\sqrt{mN}-1} \to 0.$$

We can deduce

$$\sum_{k=\zeta\sqrt{N/m}}^{K\sqrt{N/m}}\frac{R_k}{kr_k} \sim \int_{y=\zeta\sqrt{N/m}}^{K\sqrt{N/m}} e^{-\frac{m}{N}y^2}\frac{\mathrm{d}y}{y}\int_{z=0}^{y} e^{\frac{m}{N}z^2}\mathrm{d}z =: I_N$$

from (4.9) and (4.10). We thus need to find an equivalent of I_N for large N. Three successive changes of variables entail the equalities:

$$I_N = \int_{y=\zeta\sqrt{N/m}}^{K\sqrt{N/m}}\frac{\mathrm{d}y}{y}\int_{z=0}^{y} e^{-\frac{m}{N}(y^2-z^2)}\mathrm{d}z = \int_{y=\zeta\sqrt{N/m}}^{K\sqrt{N/m}}\mathrm{d}y\int_{\lambda=0}^{1} e^{-\frac{m}{N}y^2(1-\lambda^2)}d\lambda = \sqrt{\frac{N}{m}}\int_{\lambda=0}^{1}d\lambda\int_{z=\zeta}^{K} e^{-z^2(1-\lambda^2)}\mathrm{d}z = \sqrt{\frac{N}{m}}\int_{\lambda=0}^{1}\frac{d\lambda}{\sqrt{1-\lambda^2}}\int_{w=\zeta\sqrt{1-\lambda^2}}^{K\sqrt{1-\lambda^2}} e^{-w^2}dw.$$

Hence

$$I_N \le \sqrt{\frac{N}{m}}\int_{\lambda=0}^{1}\frac{d\lambda}{\sqrt{1-\lambda^2}}\int_{w=0}^{\infty} e^{-w^2}dw = \sqrt{\frac{N}{m}}\frac{\pi}{2}\frac{\sqrt{\pi}}{2} = \sqrt{\frac{N}{m}}\frac{\pi^{3/2}}{4}.$$

For the lower estimate we proceed as follows:

$$\frac{\pi^{3/2}}{4} - I_N\sqrt{\frac{m}{N}} = \int_{\lambda=0}^{1}\frac{d\lambda}{\sqrt{1-\lambda^2}}\left(\int_{w=0}^{\zeta\sqrt{1-\lambda^2}} e^{-w^2}dw + \int_{w=K\sqrt{1-\lambda^2}}^{\infty} e^{-w^2}dw\right) \le \int_{\lambda=0}^{1}\frac{d\lambda}{\sqrt{1-\lambda^2}}\left(\zeta + \int_{w=K\sqrt{1-\lambda^2}}^{\infty} e^{-w^2}dw\right) \le \frac{\pi}{2}\zeta + \int_{\lambda=0}^{1}\frac{d\lambda}{\sqrt{1-\lambda^2}}\left(\int_{w=K\sqrt{1-\lambda^2}}^{\infty} e^{-w^2}dw\right).$$

We write the double integral on the r.h.s. as

$$\int_0^1\int_{z=K}^{\infty} e^{-z^2(1-\lambda^2)}\mathrm{d}z\mathrm{d}\lambda = \int_{z=K}^{\infty} e^{-z^2}\int_0^1 e^{z^2\lambda^2}\mathrm{d}\lambda\mathrm{d}z.$$

By substituting $x = \lambda z$ the inner integral is equal to

$$\frac{1}{z}\int_0^z e^{x^2}\mathrm{d}x,$$

which by Weisstein (2024, (1),(9)) is bounded from above by $\text{const}\cdot e^{z^2}/z^2$, such that in total is bounded from above by

$$\int_K^\infty e^{-z^2}\left(\text{const}\cdot\frac{e^{z^2}}{z^2}\right)\mathrm{d}z \le \text{const}\cdot\frac{1}{K},$$

so in total

$$\frac{\pi^{3/2}}{4} - I_N\sqrt{\frac{m}{N}} = O(\zeta) + O\left(\frac{1}{K}\right).$$

Hence, as $\lambda_k \sim k/2$ for $k \ll N$, we have proved that

$$\sum_{k=\zeta\sqrt{N/m}}^{K\sqrt{N/m}} \frac{R_k}{\lambda_k r_k} \sim \sum_{k=\zeta\sqrt{N/m}}^{K\sqrt{N/m}} 2\frac{R_k}{k r_k} = \sqrt{\frac{N}{m}}\left(\frac{\pi^{3/2}}{2} + O(\zeta) + O\left(\frac{1}{K}\right)\right). \qquad \square$$

Proof of Lemma 4.5. Lemma 4.2 enables us to write

$$r_j \sim \exp\left(\frac{m}{N}j^2 f(j)\right) \qquad \text{for } j \le N - \xi N.$$

So

$$\begin{aligned} R_j &= \sum_{l=1}^{j} r_l \sim \sum_{l=1}^{j}\exp\left(\frac{m}{N}l^2 f(l)\right) \\ &\le \text{const}\cdot\int_1^j \exp\left(\frac{m}{N}x^2 f(x)\right)\mathrm{d}x \end{aligned}$$

and

$$\begin{aligned} \frac{R_j}{r_j} &\le \text{const}\exp\left(-\frac{m}{N}j^2 f(j)\right)\cdot\int_1^j \exp\left(\frac{m}{N}x^2 f(x)\right)\mathrm{d}x \\ &= \text{const}\cdot\int_1^j \exp\left(\frac{m}{N}\left(x^2 f(x) - j^2 f(j)\right)\right)\mathrm{d}x. \end{aligned} \tag{4.35}$$

Since f is non-decreasing and $f(x) \ge \frac{1}{2}$ for $x \gg \sqrt{N/m}$, see the discussion after (4.15), we have $f(x) \le f(j)$ for $x \le j$ as well as $f(j) \ge \frac{1}{2}$. So since the exponent in the integral in (4.35) is negative, (4.35) is bounded from above by

$$\text{const}\exp\left(-\frac{m}{2N}j^2\right)\cdot\int_0^j \exp\left(\frac{m}{2N}x^2\right)\mathrm{d}x. \tag{4.36}$$

By substituting $z = \sqrt{\frac{m}{2N}}$ the integral is equal to

$$\sqrt{\frac{2N}{m}}\int_0^{\sqrt{\frac{m}{2N}}j} e^{z^2}\mathrm{d}z,$$

which by Weisstein (2024, (1),(9)) is bounded from above by

$$\text{const}\cdot\frac{e^{j^2\cdot\frac{m}{2N}}}{j}\cdot\frac{2N}{m}.$$

So (4.36) - and hence also (4.35) - is asymptotically bounded by $\text{const}\cdot\frac{N}{mj}$, which concludes the proof of the Lemma. $\square$

4.7. Proofs of Lemma 4.6 and Proposition 4.7

Proof of Lemma 4.6. We start by collecting a few properties of the function H defined in (4.22). The first two derivatives of H are

$$\begin{aligned} H'(y) &= -\frac{1}{2m}\left[\frac{1}{1-\rho}\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^\infty\left(1 - \frac{1}{(1+2m)^l}\right)\frac{(1-\rho)^{l-1}y^l}{l}\right] \\ &= -\frac{1}{2m(1-\rho)}\left[\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^\infty\left(1 - \frac{1}{(1+2m)^l}\right)\frac{(1-\rho)^l y^l}{l}\right] \\ &= -\frac{1}{2m(1-\rho)}\log\left(\frac{1+2m}{1+2m/\rho}\,\frac{1-(1-\rho)y/(1+2m)}{1-(1-\rho)y}\right) \\ &= -\frac{1}{2m(1-\rho)}\log\left(\frac{1+2m-(1-\rho)y}{(1+2m/\rho)(1-(1-\rho)y)}\right) \\ &= -\frac{1}{2m(1-\rho)}\log\left(1 + \frac{2m}{\rho}\,\frac{(1-\rho)(y-1)}{(1+2m/\rho)(1-(1-\rho)y)}\right). \end{aligned} \tag{4.37}$$

Since $\rho \ge \rho_0$ we have that for $y < \frac{1}{2}$ and N large enough

$$\left|\frac{2m}{\rho}\,\frac{(1-\rho)(y-1)}{(1+2m/\rho)(1-(1-\rho)y)}\right| \ge \frac{2m}{\rho}\,\frac{(1-\rho)\frac{1}{2}}{1+2m/\rho},$$

such that

$$\left|\log\left(1 + \frac{2m}{\rho}\,\frac{(1-\rho)(y-1)}{(1+2m/\rho)(1-(1-\rho)y)}\right)\right| \ge \frac{1}{2}\,\frac{2m(1-\rho)}{\rho(1+2m/\rho)},$$

which gives

$$H'(y) \ge \frac{1}{2m(1-\rho)}\,\frac{1}{2}\,\frac{2m(1-\rho)}{\rho(1+2m/\rho)} \ge \frac{1}{2\rho}\,\frac{1}{1+2m/\rho_0} \ge \frac{1}{4} \tag{4.38}$$

for $y \le \frac{1}{2}$ and N large enough. We continue with the analysis of H'' and obtain

$$\begin{aligned} H''(y) &= -\frac{1}{2m(1-\rho)}\left[-\frac{(1-\rho)}{1+2m-(1-\rho)y} + \frac{(1-\rho)}{1-(1-\rho)y}\right] \\ &= \frac{1}{2m}\left[\frac{1}{1+2m-(1-\rho)y} - \frac{1}{1-(1-\rho)y}\right] \le 0. \end{aligned}$$

Hence, $H(0) = 0$, H reaches its maximum at $y = 1$, and then decreases, and as $N \to \infty$

$$H(1) = -\frac{1}{2m}\left[\frac{1}{1-\rho}\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^\infty\left(1 - \frac{1}{(1+2m)^l}\right)\frac{(1-\rho)^{l-1}}{l(l+1)}\right],$$

and

$$H''(1) = \frac{1}{2\rho m}\left[\frac{1}{1+2m/\rho} - 1\right] \sim -\frac{1}{2\rho m}2m/\rho = -\frac{1}{\rho^2}, \qquad \text{as } N \to \infty.$$

Moreover, H is non-negative on $[0, y_0]$ and negative on (y_0, ∞), with y_0 satisfying

$$y_0 \sim \frac{2}{\rho} \qquad \text{as } N \to \infty.$$

For later use we also notice that from (4.37) we get for all $y \in \mathbb{R}\setminus\{1\}$

$$H'(y) \sim \frac{1-y}{\rho(1-(1-\rho)y)} \qquad \text{as } N \to \infty. \tag{4.39}$$

We now focus on the **second bullet point** of the lemma. So j is of the form

$$j = \frac{g(N)}{2m(1-\rho)} \tag{4.40}$$

with $g(N)$ satisfying

$$g(N) \to \infty \quad \text{and} \quad g(N) \le (2/\rho - \xi)2m(1-\rho)^2 N.$$

In particular, this means

$$\frac{1}{m(1-\rho)} \ll j \le (2/\rho - \xi)(1-\rho)N \wedge N(1-\sqrt{m}).$$

Using (4.7) we obtain by a sandwiching argument

$$\begin{aligned} R_j &\sim \int_0^j \exp\left(x\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^\infty\left(1 - \frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{x^{l+1}}{N^l}\right)\mathrm{d}x \\ &= j\int_0^1 \exp\left(jy\left[\log\left(\frac{1+2m}{1+2m/\rho}\right) + \sum_{l=1}^\infty\left(1 - \frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{(jy)^l}{N^l}\right]\right)\mathrm{d}y \\ &= j\int_0^1 \exp\left(-2m(1-\rho)^2 NH\left(\frac{jy}{N(1-\rho)}\right)\right)\mathrm{d}y \\ &= j\left(\int_0^\varepsilon \exp\left(-2m(1-\rho)^2 NH\left(\frac{jy}{N(1-\rho)}\right)\right)\mathrm{d}y \right.\\ &\qquad \left. + \int_\varepsilon^1 \exp\left(-2m(1-\rho)^2 NH\left(\frac{jy}{N(1-\rho)}\right)\right)\mathrm{d}y\right) \end{aligned}$$

where an adequate choice of ε (independent of N) will be made below. By (4.40) and the above stated properties of the function H we get that for all $y \in [\varepsilon, 1]$,

$$H\left(\frac{jy}{N(1-\rho)}\right) \ge H\left(\frac{g(N)\varepsilon}{2m(1-\rho)^2 N}\right) \wedge H(2/\rho - \xi). \tag{4.41}$$

Moreover, because

$$H'(0) \sim \frac{1}{\rho} \quad \text{and} \quad H'(2/\rho) \sim -\frac{1}{\rho} \quad \text{as } N \to \infty,$$

combining (4.38) and (4.41) and setting $\varepsilon = \frac{1}{4}$ we obtain for all $y \in [\varepsilon, 1]$ and N large enough,

$$H\left(\frac{jy}{N(1-\rho)}\right) \geq \inf_{0\leq u\leq \varepsilon} H'((2/\rho-\xi)u)\frac{g(N)\varepsilon}{2\rho m(1-\rho)^2 N} \wedge \inf_{0\leq u\leq y_0-2/\rho+\xi}|H'(u)|\xi$$
$$\geq \frac{g(N)\varepsilon}{8\rho m(1-\rho)^2 N} \wedge \frac{\xi}{4\rho}.$$

Hence

$$\int_\varepsilon^1 \exp\left(-2m(1-\rho)^2 N H\left(\frac{jy}{N(1-\rho)}\right)\right)\mathrm{d}y$$
$$\leq \exp\left(-2m(1-\rho)^2 N\left(\frac{g(N)\varepsilon}{8\rho m(1-\rho)^2 N} \wedge \frac{\xi}{4\rho}\right)\right)$$
$$= \exp\left(-\frac{g(N)\varepsilon}{4\rho}\right) \vee \exp\left(-\frac{1}{2}m(1-\rho)^2 N\xi/\rho\right).$$

The equivalence $H'(0) \sim 1/\rho$ also entails that

$$j\int_0^\varepsilon \exp\left(-2m(1-\rho)^2 N H\left(\frac{jy}{N(1-\rho)}\right)\right)\mathrm{d}y$$
$$\sim j\int_0^\varepsilon \exp\left(-2m(1-\rho)^2 N\frac{jy}{N\rho(1-\rho)}\right)\mathrm{d}y$$
$$= j\int_0^\varepsilon \exp(-2m(1-\rho)jy/\rho)\,\mathrm{d}y$$
$$\sim \frac{\rho}{2m(1-\rho)} = \frac{j\rho}{g(N)}.$$

In total, as

$$\exp\left(-\frac{g(N)\varepsilon}{4\rho}\right) = o\left(\frac{1}{g(N)}\right)$$

and

$$\exp\left(-\frac{1}{2}m(1-\rho)^2 N\xi/\rho\right) \leq \frac{2}{(Nm(1-\rho))^2} \leq \left(\frac{8}{\rho g(N)}\right)^2 = o\left(\frac{1}{g(N)}\right)$$

this gives $R_j \sim \rho/(2m(1-\rho))$ and thus proves the second bullet point of the lemma.

We now turn to the **third bullet point**. So j is of the form $j = C(1-\rho)N$ with $C > 2/\rho$ and $j \leq N(1-\sqrt{m})$ (Note that $C(1-\rho)N \leq N$ and $C > 2\rho$ imply $\rho > 2/3$.) Using (4.8) and sandwiching arguments yields

$$R_j \sim (1-\rho)N\int_0^C \exp\left(-2m(1-\rho)^2 N H(y)\right)\mathrm{d}y.$$

$H(y)$ is non-negative for $y \leq y_0$ with $y_0 \sim 2/\rho$, and negative for $y > y_0$. Moreover, $H'' < 0$. Consequently we get

$$R_j \sim (1-\rho)N\int_{y_0}^C \exp\left(-2m(1-\rho)^2 N H(y)\right)\mathrm{d}y.$$

By (4.39) there exists $\mathfrak{r} \geq 0$ such that

$$H'(y) \in [-\mathfrak{r}\xi - (C-1)/(\rho(1-C(1-\rho))), \mathfrak{r}\xi - (C-1)/(\rho(1-C(1-\rho)))],$$
$$\forall y \in [C-\xi, C+\xi].$$

This entails

$$\int_{C-\xi}^C e^{-2m(1-\rho)^2 N((C-1)/(\rho(1-C(1-\rho)))+\mathfrak{r}\xi)(C-y)}\mathrm{d}y$$
$$\leq \int_{C-\xi}^C e^{-2m(1-\rho)^2 N(H(y)-H(C))}\mathrm{d}y$$
$$\leq \int_{C-\xi}^C e^{-2m(1-\rho)^2 N((C-1)/(\rho(1-C(1-\rho)))-\mathfrak{r}\xi)(C-y)}\mathrm{d}y.$$

Moreover,

$$\int_{y_0}^{C-\xi} \exp\left(-2m(1-\rho)^2 N H(y)\right)\mathrm{d}y \leq C\exp\left(-2m(1-\rho)^2 N H(C-\xi)\right)$$
$$= o\left(\exp\left(-2m(1-\rho)^2 N H(C)\right)\right).$$

We deduce that

$$R_j \sim (1-\rho)N\frac{\rho(1-C(1-\rho))\exp\left(-2m(1-\rho)^2 N H(C)\right)}{2m(C-1)(1-\rho)^2 N}$$
$$= \frac{\rho(1-C(1-\rho))}{2m(C-1)(1-\rho)}\exp\left(-2m(1-\rho)^2 N H(C)\right),$$

which proves the third bullet point of the lemma.

Finally, we focus on the **first bullet point**. Let $j \leq \xi(1-\rho)N$ with $\xi \leq \frac{1}{2}$. From the observation that

$$1 - \frac{1}{(1+2m)^l} \leq 2ml$$

we get

$$\sum_{l=1}^\infty\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{j^l}{N^l} \leq 2m\sum_{l=1}^\infty \frac{1}{l+1}\frac{j^l}{N^l}$$
$$\leq m\sum_{l=1}^\infty \frac{j^l}{N^l}$$
$$\leq m\frac{\xi(1-\rho)}{1-\xi(1-\rho)} \leq \frac{m}{\rho}\xi(1-\rho).$$

As

$$\log\left(\frac{1+2m/\rho}{1+2m}\right) = \log\left(1+\frac{2m}{\rho}\frac{1-\rho}{1+2m}\right) \sim \frac{2m}{\rho}(1-\rho)$$

we deduce that

$$\sum_{l=1}^\infty\left(1-\frac{1}{(1+2m)^l}\right)\frac{1}{l(l+1)}\frac{j^l}{N^l} \leq \xi\log\left(\frac{1+2m/\rho}{1+2m}\right).$$

Hence for $j \leq \xi(1-\rho)N \leq (1-\rho)N$,

$$-(1+\xi)\frac{2m}{\rho}(1-\rho)j \leq j\log\left(\frac{1+2m}{1+2m/\rho}\right)$$
$$+\sum_{l=1}^\infty\left(1-\frac{1}{(1+2m)^l}\right)\frac{j^{l+1}}{l(l+1)N^l}$$
$$\leq -(1-\xi)\frac{2m}{\rho}(1-\rho)j.$$

Consequently,

$$\frac{1-e^{-(1+2\xi)(2m/\rho)(1-\rho)j}}{(1+2\xi)(2m/\rho)(1-\rho)} = \int_0^j e^{-(1+2\xi)(2m/\rho)(1-\rho)x}\mathrm{d}x$$
$$\leq R_j \leq \int_0^j e^{-(1-2\xi)(2m/\rho)(1-\rho)x}\mathrm{d}x$$
$$= \frac{1-e^{-(1-2\xi)(2m/\rho)(1-\rho)j}}{(1+2\xi)(2m/\rho)(1-\rho)}.$$

This ends the proof of Lemma 4.6. □

Proof of Proposition 4.7. Let us first study the asymptotics of $B(\zeta)$. Thanks to the second bullet point of Lemma 4.6 we know that for any $(1-\zeta)(1-\rho)N \leq k \leq (1+\zeta)(1-\rho)N$ one has $R_k \sim \rho/(2m(1-\rho))$. Hence

$$B(\zeta) \sim \left(R_j \wedge \frac{\rho}{2m(1-\rho)}\right)\sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N}\frac{1}{\lambda_k r_k}.$$

Moreover, for $k \in [(1-\zeta)(1-\rho)N, (1+\zeta)(1-\rho)N]$ we have $\lambda_k \sim \rho k/2$. Hence

$$\frac{2}{\rho(1+2\zeta)(1-\rho)N}\sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N}\frac{1}{r_k} \leq \sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N}\frac{1}{\lambda_k r_k}$$
$$\leq \frac{2}{\rho(1-2\zeta)(1-\rho)N}\sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N}\frac{1}{r_k}.$$

We are left with the study of

$$\sum_{k=(1-\zeta)(1-\rho)N+1}^{(1+\zeta)(1-\rho)N}\frac{1}{r_k} \sim N(1-\rho)\int_{1-\zeta}^{1+\zeta}\exp\left(2m(1-\rho)^2 N H(y)\right)\mathrm{d}y,$$

where the equivalence is a consequence of (4.8). (Note that the function H, see (4.22), appears in (4.8).) Since the function H reaches its maximum at 1 and $H''(1) \sim -1/\rho^2$, and since ζ satisfies

$$\zeta\sqrt{mN}(1-\rho) \to \infty \quad \text{as } N \to \infty,$$

an application of the Laplace method yields

$$\int_{1-\zeta}^{1+\zeta} \exp\left(2m(1-\rho)^2 N H(y)\right) \mathrm{d}y \sim \sqrt{\frac{2\pi\rho^2}{2m(1-\rho)^2 N}} \exp\left(2m(1-\rho)^2 N H(1)\right) = \sqrt{\frac{\pi}{mN}} \frac{\rho}{1-\rho} \exp\left(2m(1-\rho)^2 N H(1)\right).$$

Hence

$$B(\zeta) \sim \left(R_j \wedge \frac{\rho}{2m(1-\rho)}\right) \sqrt{\frac{\pi}{mN}} \frac{2}{1-\rho} \exp\left(2m(1-\rho)^2 N H(1)\right).$$

This completes the proof of (4.23).

To bound $A(\zeta)$, it is enough to notice that for any $k \le (1-\zeta)(1-\rho)N$,

$$\lambda_k \ge \frac{k}{2}(1-(1-\zeta)(1-\rho)), \quad r_k \ge \exp\left(-2m(1-\rho)^2 N H(1-\zeta/2)\right), \quad R_{k\wedge j} \le \frac{\rho}{2m(1-\rho)}.$$

The first inequality is a direct consequence of the definition of λ_k in (4.1), the second one stems from equality (4.7), and the last one is a consequence of Lemma 4.6. Altogether this yields that

$$A(\zeta) \le \frac{(1-\zeta)(1-\rho)\rho N}{2m(1-\rho)} \frac{2}{k(1-(1-\zeta)(1-\rho))} \exp\left(2m(1-\rho)^2 N H(1-\zeta/2)\right) = o\left(B(\zeta)\right).$$

The term $C(\zeta)$ is more delicate to bound and we have to decompose it into several terms. This decomposition depends on the value of ρ:

Let us begin with the simplest case, that is $\rho \le 2/3$. In this case $(2/\rho)(1-\rho) \ge 1$ and thus $(2/\rho)(1-\rho)N \ge N$. Recall that the positive root y_0 of H satisfies $y_0 \sim 2/\rho$. We may decompose $C(\zeta)$ as follows:

$$C(\zeta) = \sum_{k=(1+\zeta)(1-\rho)N+1}^{(y_0(1-\rho)\wedge 1)N(1-\sqrt{m})} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=(y_0(1-\rho)\wedge 1)N(1-\sqrt{m})+1}^{N} \frac{R_{k\wedge j}}{\lambda_k r_k} := C_\alpha(\zeta) + C_\beta(\zeta).$$

Using that H is non-negative and decreasing on $[1, y_0]$ and $y_0 \sim 2/\rho$ we obtain from equality (4.7) that for any $(1+\zeta)(1-\rho)N + 1 \le k \le (y_0(1-\rho)\wedge 1)N(1-\sqrt{m})$,

$$\lambda_k r_k = k q_k r_{k-1} \ge km \exp\left(-2m(1-\rho)^2 N H(1+\zeta/2)\right) \quad \text{and} \quad R_{k\wedge j} \le \frac{\rho}{2m(1-\rho)}.$$

Hence

$$C_\alpha(\zeta) \le \frac{\rho N}{2m(1-\rho)} \frac{1}{km} \exp\left(2m(1-\rho)^2 N H(1+\zeta/2)\right) = o\left(B(\zeta)\right).$$

To bound $C_\beta(\zeta)$ we apply (4.20) with $\xi \sim \sqrt{m}$ satisfying

$$(y_0(1-\rho)\wedge 1)N(1-\sqrt{m}) = N(1-\xi).$$

This shows that $C(\zeta) = o(B(\zeta))$ in the case $\rho \le 2/3$.

Let us now consider the case $\rho > 2/3$. We decompose $C(\zeta)$ into three terms as follows:

$$C(\zeta) = \sum_{k=(1+\zeta)(1-\rho)N+1}^{(2/\rho-\zeta)(1-\rho)N} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=(2/\rho-\zeta)(1-\rho)N+1}^{(2/\rho+\zeta)(1-\rho)N} \frac{R_{k\wedge j}}{\lambda_k r_k} + \sum_{k=(2/\rho+\zeta)(1-\rho)N+1}^{N} \frac{R_{k\wedge j}}{\lambda_k r_k} := C_1(\zeta) + C_2(\zeta) + C_3(\zeta).$$

$C_1(\zeta)$ may be bounded with similar arguments as for $A(\zeta)$: for any $(1+\zeta)(1-\rho)N \le k \le (2/\rho-\zeta)(1-\rho)N$,

$$\lambda_k r_k = k q_k r_{k-1} \ge km \exp\left(-2m(1-\rho)^2 N H(1+\zeta/2)\right) \quad \text{and} \quad R_{k\wedge j} \le \frac{\rho}{2m(1-\rho)}.$$

This entails

$$C_1(\zeta) \le \frac{(1-2\zeta)(1-\rho)N}{2m\rho(1-\rho)} \frac{1}{km} \exp\left(2m(1-\rho)^2 N H(1+\zeta/2)\right) = o\left(B(\zeta)\right).$$

Now, recalling the third bullet point of Lemma 4.6, that $R_.$ is increasing and that r_k is increasing with k when k is larger than $(1+\zeta)(1-\rho)N$, we get for $(2/\rho-\zeta)(1-\rho)N \le k \le (2/\rho+\zeta)(1-\rho)N$,

$$\lambda_k r_k = k q_k r_{k-1} \ge km \exp\left(-2m(1-\rho)^2 N H(2/\rho - 2\zeta)\right)$$

and

$$R_k \le R_{(2/\rho+\zeta)(1-\rho)N} \sim \rho(1-(2/\rho+\zeta)(1-\rho)) \frac{\exp\left(-2m(1-\rho)^2 N H(2+\zeta)\right)}{2m(2/\rho+\zeta-1)(1-\rho)}.$$

Using that $H'(2/\rho) \sim -1/\rho$, we deduce that there exists a constant $\mathfrak{K}$ such that

$$C_2(\zeta) \le \frac{\mathfrak{K}\zeta(1-\rho)N}{(1-\rho)^2 N m^2} \exp\left(2m(1-\rho)^2 N(H(2-2\zeta) - H(2+2\zeta))\right) \le \frac{\mathfrak{K}\zeta}{(1-\rho)m^2} \exp\left(\mathfrak{K}m(1-\rho)^2 N\zeta\right) = o\left(B(\zeta)\right).$$

Notice that for $k \ge (2/\rho+\zeta)(1-\rho)N - 1$, $r_k = \sup\{r_l,\ l \le k\}$. Hence, for any j,

$$C_3(\zeta) = \sum_{k=(2/\rho+\zeta)(1-\rho)N+1}^{N} \frac{R_{k\wedge j}}{k q_k r_{k-1}} \le \frac{1}{m} \sum_{k=(2/\rho+\zeta)(1-\rho)N+1}^{N} \frac{R_k}{k r_{k-1}} = \frac{1}{m} \sum_{k=(2/\rho+\zeta)(1-\rho)N+1}^{N} \frac{r_0 + \cdots + r_{k-2} + r_{k-1}}{k r_{k-1}} \le \frac{N}{m} = o\left(B(\zeta)\right).$$

This shows that $C(\zeta) = o(B(\zeta))$ in the case $\rho > 2/3$, and thus concludes the proof of Proposition 4.7. □

CRediT authorship contribution statement

J.L. Igelbrink: Visualization, Writing – original draft, Writing – review & editing. **A. González Casanova:** Visualization, Writing – original draft, Writing – review & editing. **C. Smadi:** Writing – original draft, Writing – review & editing, Visualization. **A. Wakolbinger:** Visualization, Writing – original draft, Writing – review & editing.

Data availability

No data was used for the research described in the article.

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References

Audiffren, J., Pardoux, E., 2013. Muller's ratchet clicks in finite time. Stochastic Process. Appl. 123 (6), 2370–2397. http://dx.doi.org/10.1016/j.spa.2013.02.008.

Bäck, T., Fogel, D.B., Michalewicz, Z., 2018. Evolutionary Computation 1: Basic Algorithms and Operators. CRC Press.

Blickle, T., Thiele, L., 1996. A comparison of selection schemes used in evolutionary algorithms. Evol. Comput. 4 (4), 361–394. http://dx.doi.org/10.1162/evco.1996.4.4.361.

Bräutigam, C., Smerlak, M., 2022. Diffusion approximations in population genetics and the rate of Muller's ratchet. J. Theoret. Biol. 550, 111236. http://dx.doi.org/10.1016/j.jtbi.2022.111236.

Chazottes, J.R., Collet, P., Méléard, S., 2016. Sharp asymptotics for the quasi-stationary distribution of birth-and-death processes. Probab. Theory Related Fields 164 (1), 285–332. http://dx.doi.org/10.1007/s00440-014-0612-6.

Doering, C.R., Sargsyan, K.V., Sander, L.M., 2005. Extinction times for birth-death processes: exact results, continuum asymptotics, and the failure of the Fokker–Planck approximation. Multiscale Model. Simul. 3 (2), 283–299. http://dx.doi.org/10.1137/030602800, 2122989.

Etheridge, A.M., Pfaffelhuber, P., Wakolbinger, A., 2009. How often does the ratchet click? Facts, heuristics, asymptotics. In: Blath, J., Mörters, P., Scheutzow, M. (Eds.), Trends in Stochastic Analysis. In: London Mathematical Society Lecture Note Series, Cambridge University Press, pp. 365–390. http://dx.doi.org/10.1017/CBO9781139107020.016, arXiv:0709.2775.

Felsenstein, J., 1974. The evolutionary advantage of recombination. Genetics 78 (2), 737–756. http://dx.doi.org/10.1093/genetics/78.2.737.

González Casanova, A., Smadi, C., Wakolbinger, A., 2023. Quasi-equilibria and click times for a variant of Muller's ratchet. Electron. J. Probab. 28, http://dx.doi.org/10.1214/23-ejp1055, Paper No. 159, 37.

Gordo, I., Charlesworth, B., 2000. The degeneration of asexual haploid populations and the speed of Muller's ratchet. Genetics 154 (3), 1379–1387. http://dx.doi.org/10.1093/genetics/154.3.1379.

Haigh, J., 1978. The accumulation of deleterious genes in a population—Muller's ratchet. Theor. Popul. Biol. 14 (2), 251–267. http://dx.doi.org/10.1016/0040-5809(78)90027-8.

Lambert, A., 2005. The branching process with logistic growth. Ann. Appl. Probab. 15 (2), 1506–1535. http://dx.doi.org/10.1214/105051605000000098.

Mariani, M., Pardoux, E., Velleret, A., 2020. Metastability between the clicks of the Muller ratchet. arXiv:2007.14715.

Metzger, J.J., Eule, S., 2013. Distribution of the fittest individuals and the rate of Muller's Ratchet in a model with overlapping generations. PLoS Comput. Biol. 9 (11), 1–10. http://dx.doi.org/10.1371/journal.pcbi.1003303.

Muller, H., 1964. The relation of recombination to mutational advance. Mutat. Res. Fund. Mol. Mech. Mut. 1 (1), 2–9. http://dx.doi.org/10.1016/0027-5107(64)90047-8.

Neher, R.A., Shraiman, B.I., 2012. Fluctuations of fitness distributions and the rate of Muller's ratchet. Genetics 191 (4), 1283–1293. http://dx.doi.org/10.1534/genetics.112.141325.

Paixão, T., Badkobeh, G., Barton, N., gan Çörüş, D., Dang, D.-C., Friedrich, T., Lehre, P.K., Sudholt, D., Sutton, A.M., Trubenová, B., 2015. Toward a unifying framework for evolutionary processes. J. Theoret. Biol. 383, 28–43. http://dx.doi.org/10.1016/j.jtbi.2015.07.011.

Pfaffelhuber, P., Staab, P.R., Wakolbinger, A., 2012. Muller's ratchet with compensatory mutations. Ann. Appl. Probab. 22 (5), 2108–2132. http://dx.doi.org/10.1214/11-AAP836.

Sagitov, S., Shaimerdenova, A., 2013. Extinction times for a birth–death process with weak competition. Lith. Math. J. 53 (2), 220–234. http://dx.doi.org/10.1007/s10986-013-9204-x.

Stephan, W., Chao, L., Smale, J.G., 1993. The advance of Muller's ratchet in a haploid asexual population: approximate solutions based on diffusion theory. Genet. Res. 61 (3), 225–231. http://dx.doi.org/10.1017/S0016672300031384.

Waxman, D., Loewe, L., 2010. A stochastic model for a single click of Muller's ratchet. J. Theoret. Biol. 264 (4), 1120–1132. http://dx.doi.org/10.1016/j.jtbi.2010.03.014.

Weisstein, E.W., 2024. Dawson's integral. URL https://mathworld.wolfram.com/DawsonsIntegral.html. (Visited on 21 February 2024).