A STOCHASTIC MODEL FOR THE EVOLUTION OF SPECIES WITH
RANDOM FITNESS

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Abstract. We generalize the evolution model introduced by Guiol, Machado and Schinazi (2010).
In our model at odd times a random number $X$ of species is created. Each species is endowed with
a random fitness with arbitrary distribution on $[0,1]$. At even times a random number $Y$ of species
is removed, killing the species with lower fitness. We show that there is a critical fitness $f_c$ below
which the number of species hits zero i.o. and above of which this number goes to infinity. We
prove uniform convergence for the distribution of surviving species and describe the phenomena
which could not be observed in previous works with uniformly distributed fitness.

Keywords: birth and death process, branching process, survival, fitness, queuing process, shape
distribution.

AMS subject classification: 60J20, 60J80, 60J15.

1. Introduction

During the history of our planet, species have emerged and have become extinct, some have lasted
a relatively brief period, others are still present in a more or less unchanged form after millions of
years. It is widely accepted that the driving engine of evolution is natural selection or “survival of
the fittest”. It is therefore interesting to provide mathematical models for the evolution of species.

Guiol, Machado and Schinazi [6] proposed a model where creation and deletion of species is driven
by chance in the sense that at each step with probability $p$ one new species is created and its fitness
is chosen uniformly in $[0,1]$, while with probability $1-p$ the least fit species (if there are species alive
at that time) is removed. One motivation for the study of this model is that its long-term behaviour
is similar to the one which simulations show for the Bak-Sneppen model: there is a critical value
for the fitness and species with smaller fitness disappear, while species with a larger fitness persist
indefinitely. Bak and Sneppen [1] modelled a simple ecosystem where the population size is constant
and at each step not only the least fit is removed, but also its neighbours are replaced by new species
(proximity may be seen as representing ecological links between species). It has proven difficult to
obtain rigorous results for this model (see for instance [8]) and this motivates the search for similar,
more tractable models.

Several papers have studied the GMS model: [3] gives a law of the iterated logarithm and a
central limit theorem for number of species with supercritical fitness which go extinct (this number
is negligible with respect to $n$); [5] studies the maximal fitness ever appeared in the subcritical case.

The model has been generalized in [9] and [2]: there is still a toss of a coin to decide for creation
or deletion, but instead of adding/removing one species at a time, increments are arbitrary random
variables. Even with these assumptions, the same cut-off phenomenon of [6] appears.

In the original GMS, the lengths of subsequent births and deaths are geometrically distributed
random variables (with parameters which sum up to 1) and in [2,9] they are geometrical convolutions
of certain laws (where the parameters of these geometrically distributed number of convolutions,
again, sum up to 1). In our model we group all subsequent creations and deletions: the length of
subsequent creations $\{X_n\}_{n \in \mathbb{N}}$ and the length of subsequent annihilations $\{Y_n\}_{n \in \mathbb{N}}$ are such that
$\{(X_n,Y_n)\}_{n \in \mathbb{N}}$ is an i.i.d. sequence with arbitrary distribution. Whence our results apply to the
models in [2,6,9] (see Section 2.1). Besides, in the older papers the fitness is assigned uniformly
while we use a general distribution $\mu$. If $\mu$ has atoms, a new phenomenon appears: there might be a
fitness which acts as a barrier eventually protecting all species with higher fitness (see Corollary 2.4 and the subsequent discussion for details).

Here is the outline of the paper. In Section 2 we give the formal construction of the process and the necessary definitions. We state our main result, Theorem 2.2 which describe the asymptotic expression of the proportion of species in a generic (Borel) range of fitness. The asymptotic behavior of a single fitness is described by Theorem 2.3. Corollary 2.4 and the subsequent discussion gives some details on the number of species which are killed. Section 2.1 is devoted to a detailed comparison with previous works; we explain why our work is a generalization of the previous models and which new phenomena arise.

In Section 3 we study some examples: the original GMS with an atomic measure \( \mu \) (see Section 3.1), a Markov model which cannot be treated by using previously known results (see Section 3.2) and a model which is related to Branching Processes (see Section 3.3). We also give a counterexample to be compared with Theorem 2.2(2).

All the proofs are in Section 4 which contains a couple of results which are worth mentioning: a Law of Large Numbers (Proposition 4.2) and Proposition 4.1 which identifies the set of fitness which become empty i.o. (and the total amount of time they are empty).

2. THE PROCESS AND ITS ASYMPTOTIC BEHAVIOUR

We start by giving a formal description of the process.

Let \( \{X_n, Y_n, f_{n,i}\}_{n,i \in \mathbb{N}} \) be a family of nonnegative random variables and, for all \( n \in \mathbb{N} \), denote by \( f_n \) the sequence \( \{f_{n,i}\}_{i \in \mathbb{N}} \). Suppose that

1. for every \( n \in \mathbb{N} \), \( (X_n, Y_n) \) and \( f_n \) are independent,
2. \( \{(X_n, Y_n, f_n)\}_{n \in \mathbb{N}} \) are i.i.d.
3. all \( f_{n,i} \) are distributed according to a measure \( \mu \) on \( \mathbb{R} \).

Roughly speaking, \( X_n \) counts the new species at time \( n \), \( Y_n \) counts the deaths and \( f_{n,i} \) the fitness of a newly created species. In order to avoid trivial cases we suppose that \( \mathbb{E}[X_k] \) and \( \mathbb{E}[Y_k] \) are both in \( (0, +\infty) \); moreover we assume that at least one of these two expected values is finite. Note that in this case \( \{X_n\}_{n \in \mathbb{N}}, \{Y_n\}_{n \in \mathbb{N}} \) and \( \{X_n - Y_n\}_{n \in \mathbb{N}} \) are all i.i.d. families, but \( X_i \) and \( Y_i \) might be dependent. From now on, we will denote by \((X, Y)\) a couple with the same law as \((X_1, Y_1)\). For every fixed \( n \in \mathbb{N} \) also \( \{f_{n,i}\}_{i \in \mathbb{N}} \) might be dependent (for instance they can be generated by a Markov Chain or \( f_{n,i} = f_{n,j} \) for all \( i \in \mathbb{N} \)).

We will assume that \( \mu([0, 1]) = 1 \); there is no loss of generality, since any measure on \( \mathbb{R} \) can be mapped to a measure supported in \([0, 1] \). We denote its cumulative distribution function by \( F = F_\mu \) and we define \( F_f(\cdot) := \lim_{a \to f^-} F(a) \).

Let \( Z_n \) be the number of species alive at time \( n \). We start at time 0 with \( Z_0 = 0 \) (\( Z_0 \) could be a random variable with an arbitrary distribution on \( \mathbb{N} \)).

At time 1, \( X_1 \) species are generated and to each of them we assign a random fitness with law \( \mu \). More precisely the fitness of the \( i \)-th created species is \( f_{1,i} \) for all \( 1 \leq i \leq X_1 \). Thus \( Z_1 = Z_0 + X_1 \). The procedure is repeated at any odd time: \( Z_{2k+1} = Z_{2k} + X_{k+1} \), meaning that \( X_{k+1} \) species are created and their fitness \( f_{k+1,1}, \ldots, f_{k+1,X_{k+1}} \) are assigned. For any set \( A \subseteq [0, 1] \) we denote by \( Z_n(A) \) the total number of species alive at time \( n \) and with fitness in \( A \). The fitness of a species does not change during its entire lifetime, and species may disappear only at even times.

At time \( 2k+2 \), a number \( Y_{k+1} \wedge Z_{2k+1} \) of species are removed and removal starts from the least fit. This means that \( Z_{2k+2} = 0 \lor (Z_{2k+1} - Y_{k+1}) \). Thus if \( Y_{k+1} \geq Z_{2k+1} \) then \( Z_{2k+2}(A) = 0 \) for all \( A \subseteq [0, 1] \). Otherwise, let \( x_- := \max\{x \in [0, 1] : Z_{2k+1}([0, x]) \leq Y_{k+1}\} \) and \( x_+ := \min\{x \in [0, 1] : Z_{2k+1}([0, x]) \geq Y_{k+1}\} \). All species with fitness not larger than \( x_- \) are removed and \( Z_{2k+2}(A) = 0 \) for all \( A \subseteq [0, x_+] \). A number \( M_{k+1} := Y_{k+1} - Z_{2k+1}([0, x_-]) \) of species is removed from the set of species with fitness equal to \( x_+ := Z_{2k+2}([x_+]) = Z_{2k+2}((x_+)) - M_{k+1} \) and \( Z_{2k+2}(A) = Z_{2k+1}(A) \) for all \( A \subseteq (x_+, 1] \).
Given a Borel set $A \subseteq [0,1]$ such that $\mu(A) > 0$, we define the number of species created in $A$ as

$$\tilde{X}_n = \sum_{i=1}^{X_n} \mathbb{1}_A(f_{n,i}).$$

(2.1)

By our assumptions, for any $A$, we have that $\{(\tilde{X}_n, Y_n)\}_{n \in \mathbb{N}}$ are i.i.d. and $\mathbb{E}[\tilde{X}_n] = \mu(A)\mathbb{E}[X_n]$ (where $a \cdot (+\infty) = +\infty$, if $a > 0$ and $0 \cdot +\infty = 0$). Henceforth, an interval $I \subseteq [0,1]$ (either closed or not) such that $0 \in I$ is called a left interval. We note that, for a left interval $I$ such that $\mu(I) > 0$, $\{Z_{2n(I)}\}_{n \in \mathbb{N}}$ is the queuing process (see [4, Chapter VI.9]) associated to the i.i.d. increments $\{\tilde{X}_n - Y_n\}_{n \in \mathbb{N}}$ (see Section [4] for details).

We will often make use of the expected value $\mathbb{E}[\alpha X - Y]$ where $\alpha \in [0,1]$. If $\mathbb{E}[X] = +\infty > \mathbb{E}[Y]$ and $\alpha > 0$ then $\mathbb{E}[\alpha X - Y] := +\infty$; if $\mathbb{E}[Y] = +\infty > \mathbb{E}[X]$ then $\mathbb{E}[\alpha X - Y] := -\infty$ for all $\alpha \in [0,1]$.

We define the critical parameter:

$$f_c := \inf\{f \in \mathbb{R}: F(f) > \mathbb{E}[Y]/\mathbb{E}[X]\}$$

(2.2)

Note that when $\mathbb{E}[Y] \geq \mathbb{E}[X]$ then $f_c = +\infty$, otherwise $f_c$ is the only solution of $F(f_c) = \mathbb{E}[Y]/\mathbb{E}[X] \geq F(f_c)$, where both inequalities turn into equalities if and only if $\mu(\{f_c\}) = 0$.

When $\mathbb{E}[Y] < \mathbb{E}[X] < +\infty$, we define the following probability measure (on Borel sets $A \subseteq [0,1]$) and its cumulative distribution function

$$\mathbb{P}_\infty(A) := \frac{\mu(A \cap (f_c, 1])\mathbb{E}[X] + \mathbb{1}_A(f_c)\mathbb{E}[\mu([0,f_c))X - Y]}{\mathbb{E}[X - Y]}.$$

(2.3)

$$F_\infty(f) := \begin{cases} 0 & f < f_c, \\ \frac{\mathbb{E}[f(X - Y)]}{\mathbb{E}[X - Y]} & f \geq f_c. \end{cases}$$

Definition 2.1. Let $A \subseteq [0,1]$. We say that

(i) there is extinction in $A$ if and only if $Z_n(A) = 0$ infinitely often a.s.;

(ii) there is survival in $A$ if and only if for all $n \in \mathbb{N}$ such that $\mathbb{P}(Z_n(A) > 0) > 0$ we have $\mathbb{P}(Z_n(A) > 0, \forall m \geq n | Z_n(A) > 0) > 0$.

When $A = \{f\}$ we speak of extinction and survival of the fitness $f$.

It is a consequence of the following theorem that, when $A \subseteq [0,1]$ is a Borel set, either there is extinction in $A$ or there is survival. Indeed, if there is no extinction in $A$ then $\mathbb{P}_\infty(A) > 0$, thus $Z_n(A) \to +\infty$ almost surely. By a standard argument this implies survival.

Theorem 2.2 (Shape Theorem).

1. For all sets $A \subseteq [0,1]$ such that $\mu(A \setminus [0,f_c]) = 0$, there is extinction in $A$ and $Z_n(A)/n^{n+\infty} \to 0$ uniformly with respect to $A$ almost surely. If $F(f_c) = \mathbb{E}[Y]/\mathbb{E}[X]$ then the same holds for all $A \subseteq [0,1]$ such that $\mu(A \setminus [0,f_c]) = 0$.

2. If, for every $n$, $\{f_{n,i}\}_{i \in \mathbb{N}}$ are i.i.d and $\mathbb{E}[X] = +\infty > \mathbb{E}[Y]$ then we have that $Z_n/n^{n+\infty} \to 0$ and $Z_n(A)/Z_n^{n+\infty} \mu(A)$ a.s. (for Borel sets $A$ such that $\mu(A) > 0$).

3. If $\mathbb{E}[X - Y] \in (0, +\infty)$ then $Z_n/n^{n+\infty} \mathbb{E}[X - Y]/2$ a.s. and

$$\mathbb{P}\left(\frac{Z_n(A)}{Z_n} n^{n+\infty} \mathbb{P}_\infty(A), \forall \text{ every Borel set } A \subseteq [0,1]\right) = 1.$$ (2.4)

Moreover

$$\sup_{f \in [0,1]} \left| \frac{Z_n([0,f])}{Z_n} - F_\infty(f) \right| \to 0, \quad \text{as } n \to +\infty, \text{ a.s.}$$

It is worth noting that, as a consequence of Theorem 2.2(1), whenever $\mathbb{E}[\mu(I)X - Y] \in [-\infty, 0]$ for some left interval $I$, then $Z_{2n(I)} = 0$ infinitely often a.s.; nevertheless $Z_{2n(I)}$ has a non-trivial limit in
law (see Proposition 4.13 for details). This implies that when \( \mathbb{E}[X] < +\infty \) and \( \mathbb{E}[X] \leq \mathbb{E}[Y] \leq +\infty \) then all fitness go extinct.

The example given in Section 3.4 shows that, if \( \{f_{n,i}\}_{i \in \mathbb{N}} \) are just dependent, then the conclusion in Theorem 2.2 might be false.

The following theorem describes the long-term behaviour of a fixed fitness. Note that all \( f > f_c \) belong to case (1), while all \( f < f_c \) belong to (2). If \( f = f_c \), then case (2) applies if and only if \( F(f_c) = \mathbb{E}[Y]/\mathbb{E}[X] \).

**Theorem 2.3 (Extinction and survival).** Let \( f \in [0,1] \).

1. If \( \mathbb{E}[F(f)X - Y] \in (0, +\infty) \) then there is survival in \([0,f]\) and the fitness \( f \) survives. Moreover, \( \lim_{n \to \infty} Z_n([0,f]) = \infty \) a.s. and, if, \( \mu(\{f\}) > 0 \) then \( \lim_{n \to \infty} Z_n(\{f\}) = \infty \) almost surely.

2. If \( \mathbb{E}[F(f)X - Y] \in [-\infty,0) \) then there is extinction in \([0,f]\).

Denote by \( K_n(A) \) the number of species killed in \( A \) up to time \( n \) and by \( \tau_n(A) \) the total number of epochs that there are no species in \( A \) up to time \( n \). From Theorem 2.2 if \( \mathbb{E}[X - Y] > 0 \) then, as \( n \to +\infty \),

\[
K_n(A) = \frac{\sum_{i=1}^{[n/2]} \bar{X}_i - Z_n(A)}{n} \sim \frac{1}{2} \mu(A) \mathbb{E}[X] - \frac{1}{2} \mathbb{E}[A(f_c)\mathbb{E}[\mu([0,f_c])X - Y]] \quad \text{a.s.} \tag{2.5}
\]

where \( \bar{X}_n \) is the number of species created in the Borel set \( A \) (see equation (2.1)).

**Corollary 2.4.** If \( \mathbb{E}[X - Y] > 0 \) then

1. \( \lim_{n \to +\infty} K_n((f_c,1])/n = 0 \) a.s.;

2. \( K_n([f_c,1]) \to +\infty \) a.s.;

3. If \( F(f_c) > \mathbb{E}[Y]/\mathbb{E}[X] \) then \( \sup_{n \in \mathbb{N}} K_n((f_c,1]) < +\infty \) a.s., otherwise \( \lim_{n \to +\infty} K_n((f_c,1]) = +\infty \) a.s.;

4. If \( F(f_c) < \mathbb{E}[Y]/\mathbb{E}[X] \) then \( \lim_{n \to +\infty} K_n((f_c,1])/n > 0 \) a.s., otherwise \( \lim_{n \to +\infty} K_n((f_c,1])/n = 0 \) a.s.;

5. If \( f > f_c \) then \( \sup_{n \in \mathbb{N}} K_n([f,1]) < +\infty \) almost surely.

Here is a more explicit description. First of all, by (5) a.s. there are no more species killed in \([f,1]\) eventually as \( n \to +\infty \) but by (2) the number of species killed in \([f_c,1]\) diverges almost surely. If \( \mu(\{f_c\}) = 0 \) then \( F(f_c) = \mathbb{E}[Y]/\mathbb{E}[X] = F(f_c) \), so that by (4) \( K_n((f_c,1])/n \) goes to zero a.s. and \( \tau_n([0,f_c])/n \to 0 \) almost surely as \( n \to +\infty \) (see Proposition 4.1.2)).

If \( \mu(\{f_c\}) > 0 \) then we have the following possibilities:

- \( F(f_c) > \mathbb{E}[Y]/\mathbb{E}[X] = F(f_c^-) \) then by (4) \( K_n([f_c,1])/n \) goes to zero almost surely. Moreover, by Theorem 2.3.4 we have \( Z_n(\{f_c\}) \to +\infty \) almost surely as \( n \to +\infty \), implying that the species killed in \([f_c,1]\) eventually will have fitness \( f_c \) almost surely. Even though the number of species of fitness \( f_c \) which are killed diverges, by equation 4.10 the fraction of species alive with fitness \( f_c \) converges to \( (F(f_c) - \mathbb{E}[Y]/\mathbb{E}[X]) \cdot \mathbb{E}[X]/2 > 0 \). Also, \( \tau_n([0,f_c])/n \to 0 \) (see again Proposition 4.1.2)).

- \( F(f_c) > \mathbb{E}[Y]/\mathbb{E}[X] > F(f_c^-) \) then, just as before, a.s. the species killed in \([f_c,1]\) eventually will have fitness \( f_c \) and the fraction of species alive with fitness \( f_c \) converges to the same positive limit. This time \( K_n([f_c,1])/n \) has a positive limit: \(-\mathbb{E}[F(f_c^-)X - Y]/2 \) and \( \tau_n([0,f_c])/n \) converges to a positive limit almost surely as \( n \to +\infty \) (see Proposition 4.1.3)).

- \( F(f_c) = \mathbb{E}[Y]/\mathbb{E}[X] > F(f_c^-) \) then, by Theorem 2.2, every species with fitness \( f_c \) is eventually killed a.s. and \( K_n([f_c,1])/n \) converges to \(-\mathbb{E}[F(f_c^-)X - Y]/2 \). But \( K_n([f_c,1])/n \) tends to 0, a.s., thus outside a negligible proportion, the killed species all have fitness \( f_c \), whence \( K_n([f_c,1])/n \) has the same positive limit as before. Finally, \( \tau_n([0,f_c])/n \to 0 \) almost surely as \( n \to +\infty \) (see Proposition 4.1.2)).
2.1. Comparison with previous works. Our process extends those appeared in [2, 6, 9]. Aside from our general choice for the fitness law, the birth-and-death mechanism that we study is more general than those adopted in these papers.

One way to see the original GMS (see [9]) as a particular case of our process is by observing that the random sequences of consecutive births $X_k$ and consecutive deaths $Y_k$ have right-shifted Geometric distribution with parameter $1 - p$ and $p$ respectively.

In general, consider a process $\{Z_n\}_{n \in \mathbb{N}}$ where at each step either a species is created (along with its fitness) or the least-fit species, if any, is removed. Denote by $X_1 > 0$ the length of the first stretch of “creations”, followed by a stretch of “annihilations” of length $Y_1 > 0$, then another stretch of “creations” of length $X_2$ followed by a stretch of $Y_2$ “annihilations” and so on. Suppose that $\{X_n\}_{n \in \mathbb{N}}$ and $\{Y_n\}_{n \in \mathbb{N}}$ are two i.i.d. sequences. It is clear that there is a connection between our process and this one, namely for every set $A$, $Z_n(A) = Z_{N_n}(A)$ where $N_n = \sum_{i=0}^{\lfloor n/2 \rfloor} X_i + \sum_{i=1}^{\lfloor n/2 \rfloor} Y_i$.

In particular if $n$ is even and $k \in (N_n, N_{n+1})$, then $Z_k(A)$ is nondecreasing, while if $k \in (N_{n+1}, N_{n+2})$, then $Z_k(A)$ is nonincreasing. Proposition 4.2 shows that for every left interval $I$

$$
\frac{Z_n(I)}{n} = \frac{Z_{N_n}(I)}{n} \rightarrow \frac{\mathbb{E}[\mu(I) X - Y]}{2}, \quad \text{a.s.}
$$

When $\mathbb{E}[X + Y] < \infty$, then the monotonicity of $Z_k$ between $N_n$ and $N_{n+1}$, implies

$$
\frac{Z_n(I)}{n} \rightarrow \frac{\mathbb{E}[\mu(I) X - Y]}{2} = \frac{\mathbb{E}[\mu(I) X - Y]}{\mathbb{E}[X + Y]}, \quad \text{a.s.}
$$

Therefore, the long-term behaviour of $\{Z_n(I)\}_{n \in \mathbb{N}}$ can be derived simply by studying $\{Z_n(I)\}_{n \in \mathbb{N}}$.

Our work can also be considered as a generalization of [2] and [9] whose models are essentially equivalent. Indeed, in [2], a single family of $\mathbb{Z}$-valued variables $\{U_n\}_{n \in \mathbb{N}}$ is considered. In this process, $U_n > 0$ means that $U_n$ species are created, while $U_n < 0$ means that $-U_n$ species are killed. In this case the laws of length of a “creation” stretch $X_i$ and “annihilation” stretch $Y_i$ are necessarily geometric random variables. Moreover, the sum of the parameters of these geometric convolutions must be $1 - \mathbb{P}(U_i = 0)$. Therefore, a model constructed from the variables $\{U_n\}_{n \in \mathbb{N}}$ can be considered as a particular case of our model: take for instance $X_n := U_n \mathbb{1}_{U_n > 0}$, $Y_n := -U_n \mathbb{1}_{U_n < 0}$ and consider the process $\{Z_{2n}(A)\}_{n \in \mathbb{N}}$. In Section 5.2 we consider a particular case of our process which cannot be obtained with a single family of variables describing simultaneously creations and annihilations.

Observe that in Theorem 4.4 we used $Z_n$ as a normalizing factor for $Z_n(A)$ but there are two other natural choices: $n$ (to compare with [2, 9]) and $N_n$ (to compare with [3, 6]).

If $\mathbb{E}[X_i + Y_i] < +\infty$ then, by the Strong Law of Large Numbers (SLLN), $N_n \sim n \mathbb{E}[X + Y]/2$ almost surely as $n \rightarrow +\infty$. If, in addition, $\mathbb{E}[X - Y] \in (0, +\infty)$ then by Proposition 4.2 we have

$$
\frac{Z_n}{n} \sim \mathbb{E}[X - Y]/2 \sim \frac{N_n}{\mathbb{E}[X + Y]} \quad \text{a.s.}
$$

as $n \rightarrow +\infty$. Hence Theorem 2.2(3) can be equivalently written in terms of the timescale $n$ or $N_n$ (in this last case we obtain a generalization of Proposition 4.2(1) to Borel sets).

If $\mathbb{E}[X] = +\infty > \mathbb{E}[Y]$ then $Z_n \sim N_n$ almost surely as $n \rightarrow +\infty$. Indeed one can use the same kind of arguments used in the proof of Theorem 2.2(2), to prove that $Z_n$ and $\sum_{i=1}^{\lfloor n/2 \rfloor} X_i$ are asymptotic and the remaining terms are negligible. Roughly speaking, changing timescale turns out to be just a linear rescaling.

We note that for the GMS model and its generalizations, with $\mu \sim \mathcal{U}([0, 1])$ (where $\mathcal{U}(I)$ is the uniform distribution on $I$), the fraction of surviving species in any $I \subseteq [f_c, 1]$ is proportional to $\mu(I)$. This is still true in our case when $I \subseteq (f_c, 1]$, but it does not hold for instance if $I = [f_c, b]$ and $F(f_c) < \mathbb{E}[Y]/\mathbb{E}[X]$. Moreover if $\mu \sim \mathcal{U}([0, 1])$ then $K_n([f_c, 1])/n \rightarrow 0$ (the exact rate of convergence for the GMS is studied in [3]), while again this needs not to be true if $f_c$ is an atom for $\mu$. 

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3. Examples and counterexamples

3.1. The original GMS model. The original GMS process can be seen as the particular case where $X$ has a geometric law $\mathcal{G}(1-p)$ while $Y$ has a geometric law $\mathcal{G}(p)$. Thus $\mathbb{E}[X_i] = 1/(1-p)$, $\mathbb{E}[Y_i] = 1/p$ and $\mathbb{E}[Y_i]/\mathbb{E}[X_i] = (1-p)/p$ is the relevant term for computing $f_c$ according to equation (2.2).

In this example we choose $\mu := \alpha \delta_{1/2} + (1-\alpha)\nu$ (where $\nu \sim \mathcal{U}([0,1])$); the case $\alpha = 0$ is discussed in [6]. Roughly speaking, every time a new species is born we toss a (possibly biased) coin: with probability $\alpha$ we assign to the new species a fitness $1/2$ and with probability $1-\alpha$ the fitness is drawn uniformly and independently in $[0,1]$. Clearly

$$F(f) = \begin{cases} (1-\alpha)f & f \in [0,1/2) \\ (1-\alpha)f + \alpha & f \in [1/2,1]. \end{cases}$$

(3.6)

For every Borel set $A \subseteq [0,1]$, $\mathbb{E}[\mu(A)X - Y] = \mu(A)/(1-p) - 1/p$ and, according to equation (2.4),

$$\lim_{n \to +\infty} \frac{Z_n(A)}{Z_n} = \mu(A \cap (f_c, 1]) + \mathbb{1}_A(f_c) \frac{\mu([0,f_c])p - (1-p)}{2p-1},$$

where $f_c$ is given by equation (2.2) and it is the unique solution in $[0,1]$ of $F(f_c) \geq \mathbb{E}[Y]/\mathbb{E}[X] = (1-p)/p \geq F(f_c^-)$. More interesting is the cumulative limit distribution (see equation (2.3))

$$\lim_{n \to +\infty} \frac{Z_n([0,f])}{Z_n} = \begin{cases} 0 & f \in [0,f_c) \\ F(f) \frac{p}{2p-1} - \frac{1-p}{2p-1} & f \in [f_c,1]. \end{cases}$$

To avoid useless complications, we discuss just the “fair coin” case $\alpha = 1/2$. In this case we have

$$f_c = \begin{cases} 2(1-p)/p & p \in (4/5,1] \\ 1/2 & p \in [4/7,4/5] \\ (2-3p)/p & p \in (1/2,4/7). \end{cases}$$

There are five typical situations that we can explore and they are represented by the following table where we choose $(1-p)/p = 7/8, 3/4, 1/2, 1/4, 1/8$.

| $p$ | $f_c$ | $F(f_c)$ | $\mathbb{E}[F(f_c)X - Y]$ | $\mathbb{E}[F(f_c^-)X - Y]$ | $\lim_{n \to +\infty} \frac{Z_n([0,f])}{Z_n}$ | c.d.f. | Law |
|-----|-------|---------|-----------------|-----------------|-----------------------------------|------|-----|
| 8/15 | 3/4   | 7/8     | 0               | 0               | $(4f-3)\mathbb{1}_{[3/4,1]}(f)$ | $U([3/4,1])$ |
| 4/7  | 1/2   | 3/4     | 1/4             | 0               | $(2f-1)\mathbb{1}_{[1/2,1]}(f)$ | $U([1/2,1])$ |
| 2/3  | 1/2   | 3/4     | 1/4             | 3/4             | $f\mathbb{1}_{[1/2,1]}(f)$ | $\frac{\delta_{1/2}}{2} + \frac{\delta_{1/2} + 1}{2}U([1/2,1])$ |
| 4/5  | 1/2   | 3/4     | 1/4             | 5/2             | $\frac{f}{2f+1} \mathbb{1}_{[1/2,1]}(f)$ | $\frac{\delta_{1/2}}{2} + \frac{\delta_{1/2} + 1}{2}U([1/2,1])$ |
| 8/9  | 1/4   | 1/8     | 0               | 0               | $\frac{2f-1}{f} \mathbb{1}_{[1/4,1]}(f) + \frac{\delta_{1/2}}{2} U([1/4,1])$ | $\frac{\delta_{1/2}}{2} + \frac{\delta_{1/2} + 1}{2}U([1/4,1])$ |

3.2. The Markov case. Let the birth-death process be now a Markov chain with transition matrix

$$
\begin{pmatrix}
1 - p & p \\
q & 1 - q
\end{pmatrix}
$$

(3.7)

starting from a birth. Thus the probability of a birth after the birth $P_{++} = p$, the probability of death after the birth is $P_{-+} = 1 - p$ and so on. This can be seen as a particular case of our process where $X$ has a geometric law $\mathcal{G}(1-p)$ while $Y$ has a geometric law $\mathcal{G}(1-q)$. We assume that $p > q$; clearly $\mathbb{E}[Y]/\mathbb{E}[X] = (1-p)/(1-q)$.

As before we choose $\mu := \alpha \delta_{1/2} + (1-\alpha)\nu$ (where $\nu \sim \mathcal{U}([0,1])$); thus the cumulative distribution function is still given by equation (3.4).

Now $\mathbb{E}[\mu(X)Y - Y] = \mu(f)/(1-p) - 1/(1-q)$ and, according to equation (2.3),

$$\lim_{n \to +\infty} \frac{Z_n([0,f])}{Z_n} = \begin{cases} 0 & f \in [0,f_c) \\ F(f) \frac{p-q}{p-q} - \frac{1-p}{p-q} & f \in [f_c,1]. \end{cases}$$
where \(f_c\) is the unique solution in \([0, 1]\) of \(F(f_c) \geq (1 - p)/(1 - q) \geq F(f_c^-)\).

As before, we discuss just the “fair coin” case \(\alpha = 1/2\). In this case we have

\[
f_c = \begin{cases} 
(2(1 - p))/(1 - q) & (q + 3)/4 < p \\
1/2 & (1 + 3q)/4 \leq p \leq (3 + q)/4 \\
(1 + q - 2p)/(1 - q) & q < p < (1 + 3q)/4.
\end{cases}
\]

We retrieve the same typical cases as before by choosing \((1 - p)/(1 - q) = 7/8, 3/4, 1/2, 1/4, 1/8.\)

3.3. The Branching Process case. In this example we consider the case where \(\mathbb{P}(Y_n = 1) = 1\) while \(X_k\) has a generic discrete distribution on \(N\). In order to avoid a trivial situation we assume that \(\mathbb{P}(X_k = 1) < 1\). In the following, we make use of the generating function of the variables \(\{X_n\}_{n \in \mathbb{N}}\), that is, \(\Phi(z) := \sum_{n=0}^{\infty} \mathbb{P}(X_0 = n) z^n\) for all \(z \in [0, 1]\). Similarly, the generating function of the random number of species whose fitness belongs to \([0, f]\) (resp. \([f, 1]\)) is \(\bar{X}_n\), is \(\Psi_f(z) = \Phi(zF(1) + 1 - F(f))\) (resp. \(\Psi_f^-(z) = \Phi(zF(f) + 1 - F(f^-))\)); see Lemma 1[3] for details. In this case, clearly,

\[
f_c := \inf\{f \in \mathbb{R}: F(f) \Phi'(1) > 1\}
\]

The peculiarity of this case is the fact that the process can studied by means of a branching process and the probability of survival of a fitness can be computed in terms of the probability of survival of the branching process.

Proposition 3.1. Let \(f \in [0, 1]\) and consider the process \(\{Z_n([0, f])\}_{n \in \mathbb{N}}\). Denote by \(\bar{q}_f\) the smallest fixed point in \([0, 1]\) of the generating function \(\Psi_f = \Phi(zF(1) + 1 - F(f))\). Then

\[
\mathbb{P}(3k \geq n: Z_{j+2k}([0, f]) = 0|Z_{2n+1}([0, f]) = i) = \begin{cases} 
\bar{q}_f & \text{if } j = 1 \\
\bar{q}_f^{-1} & \text{if } j = 2
\end{cases} \quad (3.8)
\]

for \(i \geq 1\); moreover \(\bar{q}_f^+ = 1\) if and only if \(F(1) \leq 1/\Phi'(1)\). In particular, if \(f < f_c\), then there is extinction in \([0, f]\) and if \(f > f_c\), then there is survival in \([0, f]\). If \(f = f_c\), then there is extinction in \([0, f_c]\) if and only if \(F(f_c) = 1/\Phi'(1)\).

The same holds for the process \(\{Z_n([0, f])\}_{n \in \mathbb{N}}\) by using \([0, f]\) and \(\Psi_f^-=\Phi(zF(f^-) + 1 - F(f^-))\) instead of \([0, f]\) and \(\Psi_f\) respectively. In particular there is extinction in \([0, f_c]\).

3.4. Counterexample of Theorem 2.2(2) for dependent \(\{f_{n,i}\}_{i \in \mathbb{N}}\). We define \(Y_n := 1\) a.s. and \(f_{n,i} := f_{n-1}\) for all \(i \geq 1\) and \(n \in \mathbb{N}\) (where \(f_{n,1}\) is an i.i.d. sequence distributed according to \(\mu\)). We construct the sequence \(\{X_n\}_{n \in \mathbb{N}}\) as \(X_n := g(H_n)\), for a suitable choice of an i.i.d. sequence \(\{H_n\}_{n \in \mathbb{N}}\) and a function \(g\).

Let \(\{H_n\}_{n \in \mathbb{N}}\) be an i.i.d. sequence such that \(\mathbb{P}(H_n = i) := 1/2^i\) for all \(i \in \mathbb{N}\). We define \(n_i := i(i + 1)/2\) for all \(i \in \mathbb{N}\), hence \(\mathbb{P}(H_n \leq n_{i+1}|H_n > n_i) = 1 - 1/2^{1+i+1}\) for all \(i \in \mathbb{N}\).

Let us define \(T_k := \min\{i: H_i > n_k\}\) for all \(k \in \mathbb{N}\) (clearly \(T_0 = 1\)): note that \(T_k \sim G(1/2^{n_k})\). Since \(\lim_{n \to +\infty} \mathbb{P}(T_k < m, H_{T_k} \leq n_{k+1}) = \mathbb{P}(H_{T_k} \leq n_{k+1}) = 1 - 1/2^{k+1}\) then there exists \(\tau_k \in \mathbb{N}\) such that \(\mathbb{P}(T_k \leq \tau_k, H_{T_k} < n_{k+1}) \geq 1 - 1/2^k\). The sequence \(\{\tau_k\}_{k \geq 1}\) can always be constructed iteratively as a nondecreasing sequence. It is not difficult to prove, by using the Borel-Cantelli Lemma, that the event \(\Omega_0 := \bigcap_{k \in \mathbb{N}}\{H_{T_k} \leq n_{k+1}, T_k \leq \tau_k\}\) has positive probability.
We are now ready to define $g(i) := (k + 1)! \prod_{j=0}^{k} \tau_j$ for all $i = n_k + 1, \ldots, n_{k+1}$ (for all $k \in \mathbb{N}$); $X_n := g(H_n)$ for all $n \in \mathbb{N}$. On $\Omega_0$ we have

$$\frac{X_{T_k}}{\sum_{i=1}^{T_k} X_i} \geq \frac{X_{T_k}}{(T_k - 1)g(n_k) + X_{T_k}} \geq \tau_k \frac{(k + 1)! \prod_{j=0}^{k} \tau_j}{k! \prod_{j=0}^{k-1} \tau_j + (k + 1)! \prod_{j=0}^{k} \tau_j} \geq \frac{k + 1}{k + 2}.$$ 

Roughly speaking, this means that, on $\Omega_0$, for every $\varepsilon > 0$ infinitely often the last generation represents at least a fraction $1 - \varepsilon$ of the entire population. Hence due to our choice of $\{f_{n,i}\}_{i \in \mathbb{N}}$, on $\Omega_0$, for every Borel set $A \subseteq [0, 1]$ such that $\mu(A) > 0$ and for every $\varepsilon > 0$, we have $Z_n(A)/Z_n \geq 1 - \varepsilon$ infinitely often.

4. Proofs

We note that, for any fixed left interval $I$, $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ is a random walk on $\mathbb{N}$ (with increments depending on the position). More precisely it is the queuing process associated to the i.i.d. increments $\{\tilde{X}_n - Y_n\}_{n \in \mathbb{N}}$, as defined by equation (2.1): indeed

$$Z_{2n+2}(I) - Z_{2n}(I) = \max(-Z_{2n}(I), \tilde{X}_{n+1} - Y_{n+1}).$$

We denote by $\{S_n(I)\}_{n \in \mathbb{N}}$ the random walk with independent increments, where $S_n(I) := \sum_{i=1}^{n} (\tilde{X}_i - Y_i)$. The drift of this random walk is $E[\tilde{X}_i - Y_i] = E[\mu(I)X_i - Y_i]$ which is independent of $i$.

At time 0 we have $S_0 = Z_0(I) = 0$ and for all $n$

$$Z_{2n}(I) = S_{2n}(I) - \min_{i \leq n} S_i(I) = \max_{i \leq n} \sum_{k=i+1}^{n} (\tilde{X}_k - Y_k), \quad \forall n \in \mathbb{N}. \tag{4.9}$$

By the Duality Principle, $Z_{2n}(I)$ and $\max_{k \leq n} S_k(I)$ have the same law. Since $S_0(I) = 0$ then $\min_{i \leq n} S_i(I) \leq 0$, hence $Z_{2n}(I) \geq S_n(I)$ for all $n \in \mathbb{N}$.

Define $d := \gcd(n \in \mathbb{Z} : \mathbb{P}(\tilde{X} - Y > n) > 0)$; by elementary number theory it is easy to show that, since $E[X]E[Y] > 0$, when $\mu(I) > 0$ the random walk $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ (resp. $\{S_n(I)\}_{n \in \mathbb{N}}$) is irreducible on the set $\{dn : n \in \mathbb{N}\}$ (resp. $\{dn : n \in \mathbb{Z}\}$).

We start with the classification of the random walk $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$.

**Proposition 4.1 (Recurrence and transience).** Let $I$ be a left interval such that $\mathbb{P}(\tilde{X} \neq Y) > 0$. Denote by $\tau_n$ the time spent at 0 by the random walk $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ up to time $n$. The random walk is

1. **transient if and only if** $\mathbb{E}[\mu(I)X - Y] \in (0, +\infty)$, in this case $\mathbb{P}(\sup_{n \in \mathbb{N}} \tau_n < +\infty) = 1$;
2. **null recurrent if and only if** $\mathbb{E}[\mu(I)X - Y] = 0$, in this case $\mathbb{P}(\lim_{n \to +\infty} \tau_n/n = 0) = 1$;
3. **positive recurrent if and only if** $\mathbb{E}[\mu(I)X - Y] \in [-\infty, 0)$, in this case $\mathbb{P}(\lim_{n \to +\infty} \tau_n/n > 0) = 1$. Moreover, as $n \to +\infty$

$$Z_{2n}(I) \overset{\text{dist}}{\to} S_\infty(I), \quad \text{a.s., where } S_\infty(I) := \sup_{n \geq 0} S_n(I) < \infty, \quad \text{a.s.}$$

Note that the case where $\mathbb{P}(\tilde{X} = Y) = 1$ is trivial, since it means that $\mu(I) = 1$ and $X = Y = c \in (0, +\infty)$ a.s.; thus, $Z_n(I)$ equals $c$ when $n$ is odd and 0 when $n$ is even.

**Proof.** Recall the relation between the random walks $\{S_n(I)\}_{n \in \mathbb{N}}$ and $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ given by equation (4.9). In particular the return times to 0 of the second process are the weak descending ladder times of the first one, that is, the times $n$ such that $S_n(I) \leq S_i(I)$ for all $i \leq n$. We denote by $\{T_i\}_{i \in \mathbb{N}}$ the sequence of intervals between two consecutive weak descending ladder times of $\{S_n(I)\}_{n \in \mathbb{N}}$ (that is, the times between two consecutive returns at 0 of $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$). Note that $\{T_i\}_{i \in \mathbb{N}}$ are i.i.d random variables and $T_1 = \min\{n \geq 1 : S_n \leq 0\}$.

1. If $\mathbb{E}[\mu(I)X - Y] > 0$ (either finite or infinite) then, by the SLLN, $S_n(I) \to +\infty$ a.s., hence the same happens to the process $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ since $Z_{2n}(I) \geq S_n(I)$ for all $n \in \mathbb{N}$ (see equation (4.9) and the remark afterwards). This implies that $\inf_{n \geq 0} S_n(I) = S_{\infty} > -\infty$
a.s. and the Markov chain \(\{Z_{2n}(I)\}_{n\in\mathbb{N}}\) is transient. As a consequence \(\mathbb{P}(\sup_{n\in\mathbb{N}}\tau_n < +\infty) = 1\).

(2) When the distribution of \(X_n - Y_n\) is not degenerate (that is, it is not \(\delta_0\)) then according to [4 Theorem 4, Ch.VI.10] \(\{S_n(I)\}_{n\in\mathbb{N}}\) is a recurrent random walk on the set \(\{dn: n \in \mathbb{Z}\}\). Since there are infinitely many reachable states on the left (as well as on the right) of the origin, we have \(\mathbb{P}(T_1 < +\infty) = 1\) so that \(\{Z_{2n}(I)\}_{n\in\mathbb{N}}\) is recurrent. Moreover \(\mathbb{E}[T_1] = +\infty\) (see [4 Theorem 2(ii), Ch.XII.2]) and this implies the null recurrence of \(\{Z_{2n}(I)\}_{n\in\mathbb{N}}\). It is well known that, for a recurrent random walk \(\mathbb{P}(\lim_{n\to+\infty}\tau_n/n = 1/\mathbb{E}[T_1]) = 1\) where, in this case, \(1/\mathbb{E}[T_1] = 0\).

(3) We apply again the SLLN to \(\{S_n(I)\}_{n\in\mathbb{N}}\) to deduce that \(S_n(I) \to -\infty\) a.s., hence \(\sup_{n\geq 0} S_n(I) =: S_\infty(I) < +\infty\) and \(\mathbb{E}[T_1]\) is finite (see [4 Theorem 2(ii), Ch.XII.2]). Thus, \(\{Z_{2n}(I)\}_{n\in\mathbb{N}}\) is positive recurrent. As before \(\mathbb{P}(\lim_{n\to+\infty}\tau_n/n = 1/\mathbb{E}[T_1]) = 1\) where, in this case, \(1/\mathbb{E}[T_1] > 0\).

It is clear that \(\max_{i\leq n} S_n(I) \uparrow S_\infty(I)\) a.s. and the conclusion follows by equation (4.9) (see also [4 Ch.VI.9]).

The next proposition deals with the a.s. convergence of \(Z_n(I)/n\) as \(n \to \infty\).

**Proposition 4.2 (Law of large numbers).** (1) For every interval \(I \subseteq [0,1]\),

\[
Z_n(I)/n \to \frac{1}{2}\left(\mu(I \cap [f_c,1])\mathbb{E}[X] + \mathbb{I}_I(f_c)\mathbb{E}[\mu([0,f_c])[X-Y]\right), \quad \text{a.s.} \tag{4.10}
\]

(2) If \(\mathbb{E}[X-Y] \in [-\infty,0]\) then, for all sets \(A \subseteq [0,1]\), \(Z_n(A)/n \to 0\) almost surely as \(n \to +\infty\).

(3) Let \(I\) be a left interval and \(J \subseteq [0,1]\) be such that \(I \cap J = \emptyset\) and \(\mu(J) > 0\). Suppose that \(\mathbb{E}[\mu(I)(X-Y)] \in (0, +\infty]\). Then, a.s., \(Z_n(J)\) is nondecreasing eventually as \(n \to +\infty\) and \(Z_n(J)/n \to \mu(J)\mathbb{E}[X]/2\).

**Proof.**

(1) **Left interval I.** For a left interval \(I\) equation (4.10) becomes

\[
Z_n(I)/n \to \frac{1}{2}\mathbb{E}[\mu(I)X-Y] \uparrow 0, \quad \text{a.s.} \tag{4.11}
\]

Let \(\Delta := \mathbb{E}[\mu(I)X-Y] \in [-\infty, +\infty]\); by the SLLN we have that (a) \(S_n(I)/n \to \Delta\) a.s. We separate two cases.

- If \(\Delta \in [-\infty,0]\). Since \(\liminf_n S_n(I) = -\infty\), then (b) for every \(n_0\) there is a larger weak descending ladder time, i.e. \(n \geq n_0\) such that \(S_n(I) \leq S_k(I)\) for all \(k \leq n\). Hence almost every trajectory satisfies both (a) and (b): let us consider such a trajectory.

  When \(0 \geq \Delta > -\infty\) then for every \(\varepsilon > 0\) there exists \(n_0\) such that for every \(n \geq n_0\) we have \(|S_n(I)/n - \Delta| < \varepsilon/2\). Consider a weak descending ladder time \(n_1 \geq n_0\); it is clear that, for every \(n \geq n_1\) then \(\min_{k \leq n} S_k(I) = S_{k_n}(I)\) for some \(k_n\) such that \(n \geq k_n \geq n_1 \geq n_0\).

  When \(\Delta = 0\), then for every \(n \geq n_1\) we have, by equation (4.9),

\[
\frac{|Z_n(I)|}{n} = \frac{|S_n(I)|}{n} - \frac{\min_{k \leq n} S_k(I)}{n} = \frac{|S_n(I)|}{n} - \frac{S_{k_n}(I)}{n} \leq \frac{|S_n(I)|}{n} + \frac{S_{k_n}(I)}{n} \leq \frac{k_n}{n} < \varepsilon
\]

since \(n \geq n_0\) and \(k_n \geq n_0\).

  When \(-\infty < \Delta < 0\), take \(\varepsilon \in (0,-2\Delta)\). For every \(n \geq n_1\) we have

\[
\Delta + \varepsilon/2 \geq S_n(I)/n \geq S_{k_n}(I)/n \geq \frac{S_{k_n}(I)}{k_n} \geq \Delta - \varepsilon/2
\]

since \(S_{k_n}(I) \leq n(\Delta + \varepsilon) < 0\) for all \(n > 0\) and \(n \geq k_n \geq n_0\). From the above chain of inequalities we obtain \(|S_{k_n}(I)/n - \Delta| \leq \varepsilon/2\). Using again equation (4.9) we have

\[
\frac{|Z_n(I)|}{n} \leq \frac{|S_n(I)|}{n} - \Delta + \frac{|S_{k_n}(I) - \Delta|}{n} < \varepsilon.
\]
If $\Delta = -\infty$, consider the process $\{\tilde{Z}_{2n}\}_{n \in \mathbb{N}}$ constructed by using $Y_k \wedge M$ instead of $Y_k$ in such a way that $\mathbb{E}[\mu(I)X - Y \wedge M] \in (-\infty, 0)$. We have $0 \leq Z_{2n}(I)/n \leq Z_{2n}(I)/n \to 0$ almost surely as $n \to \infty$.

We are left to prove that
\[ \frac{Z_{2n+1}(I)}{n} \to 0, \quad \text{a.s.} \tag{4.12} \]
Remember that, for all $\varepsilon > 0$, $\mathbb{E}[X] < \infty$ if $\sum_{n \in \mathbb{N}} \mathbb{P}(X > \varepsilon n) < \infty$; thus, by the Borel-Cantelli's Lemma, $\mathbb{E}[X] < \infty$ implies $\mathbb{P}(\lim \inf_n \{X_n \leq \varepsilon n\}) = 1$. Thus
\[ \frac{|Z_{2n+1}(I) - Z_n(I)|}{n} \leq \frac{X_{n+1}}{n} \to 0, \quad \text{a.s.} \tag{4.13} \]
so that from $Z_{2n}/n \to 0$, a.s., the convergence (4.12) follows.

\*\*\* $\Delta \in (0, +\infty]$. By the SLLN, $S_n(I) \to +\infty$ a.s. and $\inf_{n \geq 0} S_n(I) =: S_{-\infty} > -\infty$, almost surely. By (a), using equation (4.9), we have $Z_{2n}(I) = S_n(I) - S_{-\infty}$ eventually a.s., which implies $Z_{2n}(I)/n \to \mathbb{E}[\mu(I)X - Y]$, almost surely.

As before we are left to show
\[ \frac{Z_{2n+1}(I)}{n} \to \mathbb{E}[\mu(I)X - Y], \quad \text{a.s.} \tag{4.14} \]
If $\mathbb{E}[X] < \infty$ then we use (4.13) to obtain (4.14).

If $\mathbb{E}[X] = \infty$, note that $Z_{2n+1}(I) \geq Z_2n(I)$, thus $Z_{2n+1}(I)/n \to +\infty$ almost surely.

**Generic interval** $I$. Consider the the two left intervals $I_1 := \{x \in [0, 1]: \exists y \in I, x < y\}$ and $I_2 := \{x \in [0, 1]: x < y, \forall y \in I\}$. Clearly $I_2 \subseteq I_1$, $I_1 \setminus I_2 = I$, whence $Z_n(I) = Z_n(I_1) - Z_n(I_2)$. For $I_1$ and $I_2$, the convergence in equation (4.11) holds.

If $f_c \in I$, then $I_2 \subseteq [0, f_c)$ so that $E[\mu(I_2)X - Y] \leq 0$ and by the result for left intervals, $Z_n(I_1)/n \to 0$ almost surely. Therefore,
\[ \lim_{n} \frac{Z_n(I)}{n} = \lim_{n} \frac{Z_n(I_1)}{n} = \frac{E[\mu(I_1)X - Y]}{2} = \frac{E[\mu(I \cap [0, f_c)]X - Y]}{2}, \quad \text{a.s.} \]

Suppose $f_c \not\in I$. If $I \subseteq [0, f_c)$, then $E[\mu(I_1)X - Y] \leq 0$ and $Z_n(I)/n \to 0$ almost surely.

If, $I \subseteq (f_c, 1]$, then by equation (4.11) we have
\[ \frac{Z_n(I)}{n} \to \frac{E[\mu(I)X - Y]}{2} = \frac{E[\mu(I \cap [f_c, 1])X - Y]}{2}, \quad \text{a.s.} \]
and the statement now follows.

(2) In this case $f_c = +\infty$. Whence $Z_n/n \to 0$ a.s., thus the same holds for $Z_n(A)$ for every $A \subseteq [0, 1]$.

(3) The result follows from the fact that $\lim_{n \to +\infty} Z_n(I) = +\infty$ almost surely. Since $Z_n(I) \to +\infty$, a.s. then no species with fitness from $[0, 1] \setminus I$ are removed, eventually. By the SLLN, the number of births in $J$ (up to time $n$) divided by $n$ goes to its expectation almost surely as $n \to +\infty$ and this yields the claim.

---

**Proof of Theorem 2.3**

(1) Take $I = [0, f]$ and suppose that $Z_{2n_0}(I) > 0$. Since $Z_{2n+1}(I) \geq Z_{2n}(I)$ for all $n$, in order to check whether the process hits the origin or not, it is enough to consider the process $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$. By Proposition 1.11 \{\{Z_{2n}(I)\}_{n \in \mathbb{N}} is transient and $\mathbb{P}(Z_{2n}(I) > 0, \forall n > n_0)Z_{2n_0} = i > 0$ (and this probability does not depend on $n_0$), for all $i \geq 1$ such that $\mathbb{P}(Z_{2n_0} = i) > 0$. Therefore we have survival. Moreover $Z_{2n}(I) \to +\infty$ a.s., thus from $Z_{2n+1}(I) \geq Z_{2n}(I)$ we have $Z_n(I) \to +\infty$ almost surely.

Suppose now that there are species with fitness $f$ alive at time $n_0$. If $Z_n(I)$ is never empty for $n \geq n_0$, then the fitness $f$ survives. Thus the probability of survival of $f$ equals to the probability that $Z_n(I)$ is always positive.

We now show that $Z_n(\{f\}) \to \infty$. If $Z_{2n}(\{f\}) > Z_{2n+2}(\{f\}$ then
\[ Z_{2n}(I) \geq Z_{2n}(\{f\}) > Z_{2n+2}(\{f\}) = Z_{2n+2}(I). \]
For all $M > 0$ let $n(M)$ be a random integer such that $Z_{2n}(I) \geq M$ for all $n \geq n(M)$. For every $n \geq n(M)$ either $Z_{2n}(\{f\}) \leq Z_{2n+2}(\{f\})$ or $Z_{2n+2}(\{f\}) \geq M$. In particular, if $Z_{2n_1}(\{f\}) \geq M$ for some $n_1 > n(M)$, then it is true for all $n \geq n_1$. Consider the first (random) time $n_1 \geq n(M)$ when $Z_{2n_1}([0, f]) = 0$. If $n_1 = \infty$ then, from time $n(M)$ on, $Z_n(\{f\})$ is non decreasing and strictly increasing infinitely many times a.s. (since $\mu(\{f\}) > 0$) and these species will be never removed after time $n(M)$ (since $Z_{2n}([0, f]) > 0$ for every $n \geq n(M)$). If, on the other hand, $n_1 < \infty$ then $Z_{2n}(\{f\}) \geq M$ for all $n \geq n_1$ and the result follows.

(2) By Proposition 4.1 applied to $I = [0, f]$, the process $\{Z_{2n}(I)\}_{n \in \mathbb{N}}$ is recurrent and so $Z_n(I) = 0$ infinitely often, almost surely. \qed

Proof of Corollary 2.4. The statement (1) follows from the equation (2.5). For every left interval $I$ such that $\mathbb{E}[\mu(I)X - Y] > 0$ by equation (4.11) we have $Z_n(I) \rightarrow +\infty$ a.s. and there are no more particles killed in $I$ eventually as $n \rightarrow +\infty$. This implies the first statement of (3) and the statement (5). Conversely, if $\mathbb{E}[\mu(I)X - Y] \leq 0$ then by equation (2.5) we have $K_n(I^c) \sim -\frac{1}{2}\mathbb{E}[\mu(I)X - Y]$ almost surely as $n \rightarrow +\infty$. This implies (4). Finally, if $\mathbb{E}[\mu(I)X - Y] = 0$ then $Z_n(I) = 0$ i.o. almost surely, whence by $\mathbb{E}[X - Y] > 0$ it follows that $K_n(I^c) \rightarrow +\infty$ as $n \rightarrow +\infty$ almost surely. This implies the second statement of (3) (applied to the case $F_{n}X - \mathbb{E}[X] - \mathbb{E}[Y] = 0$) and the statement (2) (applied to the case $F_{n}X - \mathbb{E}[X] - \mathbb{E}[Y] = 0$).

Proof of Theorem 2.2. (1) It is enough to consider $A \subseteq [0, 1] \cap [0, f_{\infty})$ since there are no births in $A \setminus ([0, 1] \cap [0, f_{\infty}))$ almost surely. It follows immediately from Proposition 1.2(1); the uniform convergence comes from the inequality $Z_n(A) \leq Z_n(I)$ for all $A \subseteq I$ and $n \in \mathbb{N}$.

(2) By Proposition 1.2(1) we have that $Z_n/n \rightarrow +\infty$ almost surely. Recall that $f_{n, 1}, f_{n, 2}, \ldots$ are i.i.d. We start by noting that

\[
\sum_{i=1}^{\left\lfloor (n+1)/2 \right\rfloor} (\bar{X}_i - Y_i) \leq Z_n(A) \leq \sum_{i=1}^{\left\lfloor (n+1)/2 \right\rfloor} \bar{X}_i,
\]

whence

\[
\sum_{i=1}^{\left\lfloor (n+1)/2 \right\rfloor} (\bar{X}_i - Y_i) \leq \frac{Z_n(A)}{Z_n} \leq \frac{\sum_{i=1}^{\left\lfloor (n+1)/2 \right\rfloor} \bar{X}_i}{\sum_{i=1}^{\left\lfloor (n+1)/2 \right\rfloor} (X_i - Y_i)}.
\]

Moreover, since a.s.

\[
\sum_{i=1}^{k} \frac{Y_i}{X_i} \rightarrow 0,
\]

it suffices to prove that a.s.

\[
\sum_{i=1}^{k} \frac{\bar{X}_i}{X_i} \rightarrow \mu(A).
\]

We recall that $\bar{X}_i$ is a sum of $X_i$ Bernoulli random variables of parameter $\mu(A)$ and that the family of these Bernoulli variables is independent of the family $\{X_n\}_{n \in \mathbb{N}}$. Thus

\[
\frac{\sum_{i=1}^{k} \bar{X}_i}{\sum_{i=1}^{k} X_i} = \frac{\mathbb{B}([\sum_{i=1}^{k} X_i, \mu(A)])}{\sum_{i=1}^{k} X_i},
\]

and we are therefore left to prove that a.s.

\[
\sum_{i=1}^{N_n} W_i \rightarrow \mu(A),
\]

whenever $\{N_n\}_{n \in \mathbb{N}}$ is a sequence of random variables such that $N_n \rightarrow \infty$ a.s. $\{W_n\}_{n \in \mathbb{N}}$ is a sequence of independent Bernoulli random variables of parameter $\mu(A)$ and the two sequences are independent.
Let $\Phi$ be the set of atoms on $\mathbb{R}$, let $P$ be the distribution function of a subprobability measure, so the pointwise convergence implies uniform convergence of the corresponding convolution $\sum_{i=1}^{\infty} P_i\delta_{x_i}$. Let, for every $i$, $P_i^n = P_i(\{x_i\})$, be distribution of the probability measure $\sum_{i=1}^{\infty} P_i\delta_{x_i}$. Since $P_i^n(\{x_1, x_2, \ldots\}) \to P(\{x_1, x_2, \ldots\})$, from Scheffé’s theorem, it follows that $\|H_n - H\|_\infty \to 0$. Since for every $t$, $H_n(t) \to F(t)$, we have that $(F_n(t) - H_n(t)) \to (F(t) - H(t))$ for every $t$. The function $F(t) - H(t)$ is a continuous distribution function of a subprobability measure, so the pointwise convergence implies uniform convergence. So, $\|F_n - F\|_\infty \leq \|H_n - H\|_\infty + \|(F_n - H_n) - (F - H)\|_\infty \to 0$.

The following Lemma is well known and we include it for the sake of completeness.

**Lemma 4.3.** Consider two $\mathbb{N}$-valued random variables $X$ and $Y$ on $\mathbb{N}$ with laws $\rho_X$ and $\rho_Y$ respectively; let $\Phi_X(z) = \mathbb{E}[z^X] = \sum_{i=0}^{\infty} \rho_X(i)z^i$ and $\Phi_Y(z) = \mathbb{E}[z^Y] = \sum_{i=0}^{\infty} \rho_Y(i)z^i$ the corresponding generating functions. Let $\{X_i\}_{i \in \mathbb{N}}$ be a i.i.d. sequence of random variables with law $\rho_X$. Finally let $\{Z_i\}_{i \in \mathbb{N}}$ be a generic sequence of $\mathbb{N}$-valued random variables with laws $\rho_{Z_i}$ and generating functions $\Phi_{Z_i}$.

1. If $Z = \sum_{i=1}^{\infty} \mathbb{1}_{\{X=i\}} Z_i$ then its law is $\rho_Z = \sum_{i \in \mathbb{N}} \rho_X(i)\rho_{Z_i}$ and the generating function is $\Phi_Z = \sum_{i \in \mathbb{N}} \rho_X(i)\Phi_{Z_i}$.
2. If $Z = \sum_{i=1}^{\infty} Z_i$, where $\{Z_1, \ldots, Z_n\}$ are independent, then $\rho_Z = \rho_{Z_1} \ast \cdots \ast \rho_{Z_n}$ (where $\ast$ denotes the usual convolution) and $\Phi_Z = \prod_{i=1}^{n} \Phi_{Z_i}$. 

(3) The a.s. convergence $Z_n/n \to \mathbb{E}[X - Y]/2$ as $n \to +\infty$ comes from Proposition 4.2.

As for the second part, if $A$ is an interval then the claim follows trivially by applying Proposition 4.2 to $Z_n(I)$ and $Z_n$. Let

$$\mathcal{B} := \{\bigcup_{i=1}^{k} [a_i, b_i] : a_1 < b_1 < a_2 < b_2 < \cdots < b_k, a_i, b_i \in \mathbb{Q}, \ k = 1, 2, \ldots\}.$$ 

Since there are countable many intervals with rational endpoints,

$$\mathbb{P}\left(\frac{Z_n(B)}{Z_n} \to P(B), \ \forall B \in \mathcal{B}\right) = 1. \quad (4.16)$$

By the regularity of probability measures, it is easy to see that for every Borel set $A$, for every $\varepsilon > 0$ there exists sets $B_1, B_2 \subset A$, both depending on $\varepsilon$ such that $B_1 \subset A \subset B_2$ and $P(B_2 \setminus B_1) \leq \varepsilon$. Thus, if $Z_n(B)/Z_n \to P(B)$ for every $B \in \mathcal{B}$, then for every $\varepsilon > 0$

$$\limsup_n \frac{Z_n(A)}{Z_n} \leq \limsup_n \frac{Z_n(B_2)}{Z_n} = P(B_2) \leq P(A) + \varepsilon,$$

$$\liminf_n \frac{Z_n(A)}{Z_n} \geq \liminf_n \frac{Z_n(B_1)}{Z_n} = P(B_1) \geq P(A) - \varepsilon,$$

so that equation (4.16) implies equation (2.4).

By the above arguments, it suffices to show the following: if $P_n$, $P$ are probability measures on $\mathbb{R}$, so that for every Borel set $A$, $P_n(A) \to P(A)$, then $\sup_n |F_n(t) - F(t)| =: \|F_n - F\|_\infty \to 0$, where $F_n$ and $F$ are the corresponding distribution functions. Let $\{x_i\}$ be the set of atoms on $P$, let $\{p_i\}$ be their masses and let $H(t) = \sum_{i=1}^{\infty} p_i I_{\{\infty, t\}}(x_i)$ be the distribution function of the subprobability measure $\sum_{i=1}^{\infty} p_i \delta_{x_i}$. Let, for every $i$, $p_i^n = \rho_{Z_i}(\{x_i\})$, be distribution of the subprobability measure $\sum_{i=1}^{\infty} p_i^n \delta_{x_i}$. Since $\rho_{Z_i}(\{x_1, x_2, \ldots\}) \to P(\{x_1, x_2, \ldots\})$, from Scheffé’s theorem, it follows that $\|H_n - H\|_\infty \to 0$. Since for every $t$, $F_n(t) \to F(t)$, we have that $(F_n(t) - H_n(t)) \to (F(t) - H(t))$ for every $t$. The function $F(t) - H(t)$ is a continuous distribution function of a subprobability measure, so the pointwise convergence implies uniform convergence. So, $\|F_n - F\|_\infty \leq \|H_n - H\|_\infty + \|(F_n - H_n) - (F - H)\|_\infty \to 0$. 

The following Lemma is well known and we include it for the sake of completeness.
(3) If \( Z = \sum_{i=0}^{Y} X_i \) then the law of \( Z \) is \( \rho_Z = \sum_{i \in \mathbb{N}} \rho_Y(i) \ast \rho_X \) (where \( \ast \) is the convolution of \( i \) copies of \( \rho_X \)) and \( \Phi_Z = \Phi_Y \circ \Phi_X \).

**Proof.**

(1) It is straightforward.

(2) The explicit expression of the law is trivial and \( \rho_Z = \mathbb{E}[z^{\sum_{i=1}^{n} Z_i}] = \mathbb{E}\left[ \prod_{i=1}^{n} z^{Z_i} \right] = \prod_{i=1}^{n} \mathbb{E}[z^{Z_i}] \) where the last equality comes from the independence.

(3) The explicit expression of the law follows by conditioning \( Z \) on \( Y \). Then (1) and (2) yield the conclusion.

\( \square \)

**Proof of Proposition 3.1.** Suppose that \( Z_{2n+k}(0, f) = 0 \) for some \( k \geq 0 \) then \( k_0 := \min\{k: Z_{2n+k}(0, f) = 0\} < +\infty \) and \( k_0 \) must be even. Hence there are no species in \([0, f]\) at some even time larger than \( 2n + 1 \) if and only if there is just one species at some odd time in \([0, f]\) (larger than \( 2n + 1 \)). The probability of having just one species at some odd time (larger than \( 2n + 1 \)) provided there are \( i \) species at time \( 2n + 1 \) equals the probability of having no species at some even time (larger than \( 2n + 1 \)) provided there are \( i - 1 \) species at time \( 2n + 1 \); thus the case \( j = 2 \) follows from the case \( j = 1 \).

Let us take \( j = 2 \) and consider the process \( \{ Z_{n+1}(0, f) \}_{n \in \mathbb{N}} \). Until all species in \([0, f]\) are gone, each time a species is removed it is replaced by a random number of species (in \([0, f]\)) with generating function \( \Psi_n \). This is equivalent to a branching process with generating function \( \Psi_n \). Equation (3.8) follows from standard results in Branching Process theory. The equivalence \( \tilde{q}_{f} < 1 \iff F(f) \leq 1/\Phi'(1) \) follows from the assumption \( P(X_1 = 1) < 1 \) and from the equality \( \Phi'(1) = F(a)\Phi'(1) \).

It is straightforward to prove that there is almost sure (temporary) extinction in \([0, f]\) if and only if \( F(f_c) \leq 1/\Phi'(1) \).

The case of the process \( \{ Z_n(0, f) \}_{n \in \mathbb{N}} \) is completely analogous. In this case we just need to note that \( F(f_c)\Phi'(1) \leq 1 \).

\( \square \)

**Acknowledgements**

The authors are grateful to Mauro Ghidelli for carefully reading the manuscript and for useful remarks. The first and last authors acknowledge support by INdAM and Prin 2015. The second author is supported by the Estonian institutional research funding IUT34-5.

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