

An evolution model with event-based extinction*

Luiz Renato Fontes¹ , Carolina Grejo²  and Fábio Sternieri Marques¹

¹ USP - Instituto de Matemática e Estatística, Rua do Matão, 1010 Cidade Universitária Butantã, 05508090 - São Paulo, SP - Brasil, SP, Brazil

² UFSCar - Departamento de Estatística, Rodovia Washington Luiz, km 235, CEP 13565-905, So Carlos, SP, Brazil

E-mail: lfontes@usp.br, fmarques2015@gmail.com and carolina@ime.usp.br

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Abstract

We propose a variation of the Guiol–Machado–Schinazi (GMS) model of evolution of species. In our version, as in the GMS model, at each birth, the new species in the system is labeled with a random fitness, but in our variation, to each extinction event is associated a random threshold and all species with fitness below the threshold are removed from the system. We present necessary and sufficient criteria for the recurrence and transience of the empty configuration of species; we show the existence of a long time limit distribution of species in the system, and present necessary and sufficient criteria for the finiteness of the number of species in that distribution. There is a remarkable symmetry between both sets of criteria. We also highlight fundamental differences between ours and the GMS model, putting them in different *universality classes*.

Keywords: Poisson processes, records, evolution

1. Introduction

In a seminal paper, Bak and Sneppen [1] have proposed a simple model of evolution of species, which has inspired a wealth of studies in several areas of knowledge, including physics, biology and mathematics. In [1], species are identified with sites in a circular 1d grid, and their evolution are described through a dynamics on their fitnesses, which at each step replaces the current minimal fitness along with neighboring current fitnesses at the grid with fresh, independent fitnesses sampled from the standard uniform distribution.

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In the mathematics literature, there are few rigorous results concerning the long term behavior of the Bak–Sneppen system. Noteworthy are papers of Meester and Znamenski [2, 3], which derive information on the asymptotic fitness distribution of the model.

Guiol, Machado and Schinazi [4] proposed a different, if somewhat similar dynamics, describing the evolution (in discrete time, as in [1]) of species who independently appear at each time step with probability p , and are assigned a fitness sampled from the uniform distribution on $[0, 1]$. Extinction occurs at each time step, also independently and with probability $1 - p$, whenever there is at least one species present at the corresponding time, in which case the one with the least fitness is removed from the system. Note that the rule to ‘kill the least fit’ is a common feature with [1]; however, the local interactions of the Bak–Sneppen system are absent. In [4] it was proved that species fitnesses are asymptotically uniformly distributed in $(f_c, 1)$, where $f_c = (1 - p)/p$, a similar result to Meester and Znamenski’s.

Several extensions and generalizations of the GMS model were subsequently introduced and studied, as in Ben-Ari *et al* [5], Michael and Volkov [6], Bertacchi *et al* [7] and Grejo *et al* [8]. Further, Guiol *et al* [9] proposed a variation of the model, where the evolution is given in continuous time. See also Formentin and Swart [10] for a closely related model with a different motivation. We refer to this literature for further discussion of the models and results.

We consider here a variation of the GMS model [9] in which, as in that model, new species are born at a given rate, and at possibly another rate we have extinction of species. For each new species in the system, we associate a positive random number, chosen from a distribution F_* . We call this random number the *fitness* of the species. So far, the setting is the same as (or quite similar to the one) in [9].

Our variation is (more markedly) related with the extinction events. At the time of each such event, we have a positive threshold random variable, with distribution F_{\dagger} , and all species with fitness below this threshold at that time, if any, get extinct.

We believe this is a natural variation of the GMS model, when we consider extinction of species in the natural world produced by major events such as abrupt habitat change, where conceivably each species might be affected according to its own aptitude to face the new challenge, irrespective of other species.

The random fitnesses and the random thresholds are independent of each other and of everything else in the process. We assume F_* is continuous on $\mathbb{R}_+ = [0, \infty)$; so, in particular, we can and will identify each species with its fitness. We also assume, for simplicity, that F_* and F_{\dagger} have unbounded support.

Let Π_* and Π_{\dagger} be independent Poisson point processes in \mathbb{R} with rates λ_* and λ_{\dagger} , respectively. Define $\{T_i\}_{i \in \mathbb{Z}^*}$ as the set of birth time instants of a new species in the system, define $\{S_j\}_{j \in \mathbb{Z}^*}$ as the instants of time in which there is an extinction event. These sequences represent the points in the Poisson processes and are indexed in increasing order. At each time $T_i \in \Pi_*$ we assign to the newly appeared species the fitness X_i , drawn from F_* , and to each time $S_j \in \Pi_{\dagger}$ we associate the threshold Y_j from distribution F_{\dagger} .

Given a locally finite subset A of \mathbb{R}_+ , let $\eta_t = \{\eta_t(s), s \geq t\}$ denote our evolution model starting from A at time t . So, at initial time $t \in \mathbb{R}$, the process has initial configuration $\eta_t(t) = A$, and at time $s \in (t, \infty)$, the process has the configuration $\eta_t(s)$ which is composed of all species/fitnesses either of A or that have appeared in the time interval $(t, s]$, and that have survived the events of extinction in $[t, s]$, i.e. species whose fitnesses are greater than the highest threshold drawn in events of extinction in $[t, s]$ after their birth.

Notice that as long as A does not depend on t , neither does the distribution of η_t , so below we will often restrict to η_0 .

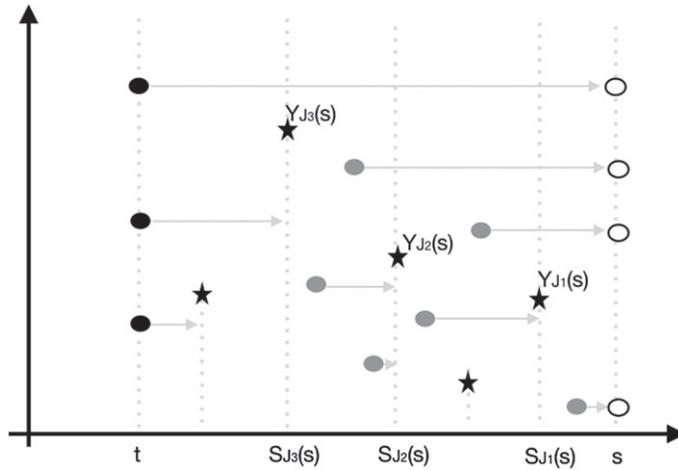


Figure 1. Possible configuration of process η_t in the time interval $[t, s]$.

Figure 1 simulates a realization of the process η_t in the time interval $[t, s]$. Each circle represents a species alive in the process and the gray arrow issuing from it represents its life time. Observe that the position of each species in relation to the vertical axis is given by its fitness. The three black circles represent the configuration of the process at time t . The six gray circles represent the species that were born in the time interval $[t, s]$; the positions that they occupy represent the respective instants of time they were born (horizontal axis) and the fitnesses that were drawn to them (vertical axis). The four white circles represent the species that survived the extinction events and are alive at the time s . Finally, each extinction threshold is represented in figure 1 by black stars.

1.1. Preliminary comparison to the GMS model

Before going to our results, let us briefly discuss preliminarily how our model compares with the GMS model (of [9]). One difference is that we have fitnesses in \mathbb{R}_+ rather than $[0, 1]$, but this is not important, or rather just a matter of changing the fitness scale. More importantly, our thresholds are also supported in \mathbb{R}_+ , and one might point out that the model makes sense for a bounded threshold distribution. In this case, we would allow for another feature missing from our model and present in the GMS model, namely, the eternal species. However, this would be a trivial phenomenon in our model (any species with fitness above the upper bound of the threshold distribution would automatically be eternal, and none below that upper bound). The most interesting comparison between the models would be thus our model in the above formulation (both fitnesses and extinction thresholds unboundedly supported) and the GMS model below the critical fitness value (for the occurrence of eternal species).

In terms of recurrence of the empty state and finiteness of the number of species in the limiting distribution of species fitnesses, the latter model is known to show recurrence and infinitely many species in the limit. As we will see below our model may show different behavior in both this respects, depending on F_* and F_{\dagger} , but there are choices, such as $F_* = F_{\dagger}$, for which both models behave the same in both these respects. It is then natural to ask whether our model with $F_* = F_{\dagger}$ behaves the same as the GMS model below the critical fitness value at other fundamental levels, thus putting them in a sense in the same *universality class*. But we find that

the models behave fundamentally differently, regarding a third issue, in this case as well; see remark 2.14 below.

One other distinguishing aspect, a more technical one, is that the GMS model may be described in terms of a spatial birth-and-death process. Ours cannot. In particular, the number of species present at time t , which performs an ordinary birth-and-death process on \mathbb{N} in the GMS model, with jumps only of size 1 in any direction, does not do so in our case, where there may be jumps larger than 1 towards 0, and is not even Markovian. The technical approach of analysis required in our case is thus quite different from the ones of the literature related to [9], as will become clear below.

1.2. Records.

Elaborating on the latter point above, our technical approach to treat our model relies substantially on classical record theory. This is a topic of much recent interest in theoretical physics, with an effort in modeling phenomena such as record temperatures in global warming, or record prices in the stock market, and other examples; see [11, 12], and references therein. Some of these phenomena depart from the classical i.i.d. setting in that the underlying sequence of random variables have a time trend, and are thus not identically distributed, or exhibit correlations; these are the settings analyzed in [11, 12] and other recent work.

The questions we ask about our model involve records as follows. As regards recurrence of the empty state, we have returns to that state whenever we find extinction points above the staircase formed by records of fitness of successive species, as they appear going forward in time. The other issue is finiteness of the limiting configuration of species fitnesses, and this is given by the fitnesses of the species appearing above the staircase of records of extinction thresholds, going backwards in time. We defer further details for the coming sections of this paper. The description of the record staircase in both cases follows from the classical theory, since we specify i.i.d. fitnesses and extinction thresholds, and Poisson point processes for the birth and extinction times. It makes sense however to consider time dependent and/or correlated specifications, as those of [11, 12], in the context of our model, which might yield interesting extensions of our results.

2. Results

We derive three kinds of results. First, criteria for recurrence and transience of the empty configuration in η_0 ; see theorem 2.1 below; they are obtained from the analysis of a Poisson process of records. Second, we derive the existence of a limit distribution for $\eta_0(s)$ as $s \rightarrow \infty$; see theorem 2.2 below. Finally, we derive criteria for finiteness and infiniteness of the number of species present in the limit distribution; see theorem 2.3 below; curiously, the Poisson process of records of the recurrence and transience issue appears here as well, but *in reverse*. The behavior of $\bar{F}_\dagger \circ \bar{F}_*^{-1}$ at the origin plays a determinant role in the first result, and thus, in reverse, so does that of $\bar{F}_* \circ \bar{F}_\dagger^{-1}$ in the third one; as usual, for $*$ = \star and \dagger , $\bar{F}_* = 1 - F_*$, and \bar{F}_*^{-1} indicates the (right-continuous) inverse of \bar{F}_* , namely

$$F_*^{-1}(t) = \inf\{s : F_*(s) > t\}, \quad 0 < t < 1.$$

For the latter result we need to assume that F_\dagger is continuous. Proofs are deferred to the last section.

Let us define the functions $R_*, R_\dagger : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ by

$$\begin{aligned} R_*(x) &= -\log \bar{F}_*(x), \\ R_\dagger(x) &= -\log \bar{F}_\dagger(x). \end{aligned}$$

For birth events denote by I_k the record indexes and by X_{I_k} the record values, as follows: $I_1 \doteq 1$; and for $k \geq 1$

$$I_{k+1} \doteq \min\{i > I_k : X_i > X_{I_k}\}.$$

Proposition 2.1 (Proposition 4.11.1, Resnick [13]). *The record values $(X_{I_k})_{k \geq 1}$ form a Poisson point process in \mathbb{R}_+ with intensity measure $\int_B R_*(dx)$, $B \in \mathcal{B}(\mathbb{R}_+)$.*

The next result refines the previous one.

Proposition 2.2 *Let T_k be the time of the k th record and denote by $\Delta T_k \doteq T_{k+1} - T_k$ the interval between two consecutive records. Then, $\{(X_{I_k}, \Delta T_k)_{k \geq 1}\}$ is a Poisson process in \mathbb{R}_+^2 with intensity measure*

$$\hat{\mu}_*(C) \doteq \iint_C \lambda_* \bar{F}_*(x) e^{-\lambda_* \bar{F}_*(x)s} ds R_*(dx), \quad C \in \mathcal{B}(\mathbb{R}_+^2).$$

Proposition 2.3 *The set of points $(S_j, Y_j)_{j \geq 1}$ is a Poisson process in \mathbb{R}_+^2 , denoted by $\hat{\Pi}_\dagger$, with intensity measure*

$$\mu_\dagger(C) \doteq \lambda_\dagger \int_C dF_\dagger(dx), \quad C \in \mathcal{B}(\mathbb{R}_+^2).$$

To study recurrence and transience, we will build a ladder of records using the process of births and the fitness associated to each species. Let us denote the random region above each step of the ladder by $\{D_k\}_{k \geq 1}$, and the region above the full ladder is denoted by D , namely, for $k \geq 1$

$$D_k \doteq [T_{I_k}, T_{I_{k+1}}) \times [X_{I_k}, \infty) \quad \text{and} \quad D \doteq \bigcup_{k \geq 1} D_k.$$

Let $\Lambda \doteq \mu_\dagger(D)$, $\mathcal{M} \doteq D \cap \hat{\Pi}_\dagger$, and $M = \#\mathcal{M}$. Observe that M counts the number of extinction events in D —as noted in Sub section 1.2, these extinction marks generate empty configurations, with no species present at and immediately after their corresponding times³. Given D , M has a Poisson distribution with mean Λ (because $\hat{\Pi}_\dagger$ is a Poisson process), so

$$\mathbb{E}[e^{-tM}] = \mathbb{E}[\mathbb{E}[e^{-tM} | \Lambda]] = \mathbb{E}\left[e^{-(1-e^{-t})\Lambda}\right]. \tag{1}$$

Here we allow $\Lambda = \infty$, in which case $M = \infty$ a.s. It may be checked, from ergodicity considerations, that $\{\Lambda = \infty\}$ is a trivial event, and, thus, so is $\{M = \infty\}$.

Remark 2.4. Define $h_\dagger : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$ by $h_\dagger(x, s) \doteq \lambda_\dagger s \bar{F}_\dagger(x)$. From the definition of μ_\dagger in proposition 2.3, we have

$$\Lambda = \mu_\dagger(D) = \sum_{k \geq 1} \mu_\dagger(D_k) = \sum_{k \geq 1} \lambda_\dagger \Delta T_k \bar{F}_\dagger(X_{I_k}) = \sum_{k \geq 1} h_\dagger(X_{I_k}, \Delta T_k). \tag{2}$$

³ But there may be, and indeed there a.s. are, extinction marks generating an empty configuration which appear below D .

Note that $\mathbb{E}[M] = \mathbb{E}[\mathbb{E}[M|\Lambda]] = \mathbb{E}[\Lambda]$ and we may use Campbell's formula (see proposition 2.7 in [14]) and (2) to find

$$\mathbb{E}[\Lambda] = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^{\infty} \frac{\bar{F}_{\dagger}(x)}{\bar{F}_{\star}(x)} R_{\star}(dx). \tag{3}$$

Proposition 2.5. *For $t > 0$*

$$\mathbb{E}[e^{-tM}] = \exp \left[- \int_0^{\infty} \frac{(1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + (1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)} R_{\star}(dx) \right].$$

2.1. Recurrence/transience of η_0

We start by discussing the a.s. finiteness of M . Define the functions $\phi : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ and $\psi : [0, 1] \rightarrow [0, 1]$ by

$$\phi(t) \doteq \int_0^{\infty} \frac{(1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + (1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)} R_{\star}(dx),$$

and

$$\psi(u) \doteq \bar{F}_{\dagger} \circ \bar{F}_{\star}^{-1}(u). \tag{4}$$

By monotone convergence, we have that

$$\phi(\infty) \doteq \lim_{t \rightarrow \infty} \phi(t) = \int_0^{\infty} \frac{\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + \lambda_{\dagger}\bar{F}_{\dagger}(x)} R_{\star}(dx).$$

Proposition 2.6. *The following statements are equivalent:*

- (a) $\phi(\infty) < \infty$;
- (b) $\mathbb{P}(M < \infty) = 1$;
- (c) $\mathbb{E}[M] < \infty$;
- (d) $\frac{\psi(u)}{u^2}$ is integrable at the origin;
- (e) $\psi(s^{-1})$ is integrable at infinity.

Definition 2.7. Let $\Upsilon = \{s \geq 0 : \eta_0(s) = \emptyset\}$ denote the set of times where the species configuration is empty; in other words, Υ is the set of times where there is no species in the system. Υ is readily seen to a.s. consist of a collection $\{[a_j, b_j], j \geq 1\}$, either finite or infinite, of disjoint finite intervals. Let $\Upsilon' = \{a_j, j \geq 1\}$ be the collection of left endpoints of such intervals, correspondings to the times where the species configuration freshly becomes empty. We have that $\mathcal{M}' \subset \Upsilon'$, where \mathcal{M}' is the projection of \mathcal{M} on the time axis. (However, as pointed out above, $\mathcal{M}' \neq \Upsilon'$ a.s.; see footnote on page 5.)

The process η_0 is said to be *transient* if Υ is a.s. a bounded set. On the other hand, if Υ is a.s. an unbounded set, then we say that η_0 is *recurrent*.

We point out that, since the set of fitness record times $\{T_{I_k}, k \geq 1\}$ is unbounded, we have that Υ/Υ' is bounded if and only if \mathcal{M}' is bounded.

Theorem 2.1. *The process η_0 is transient if*

$$\int_0^{\infty} \frac{\bar{F}_{\dagger}(x)}{\bar{F}_{\star}(x)} R_{\star}(dx) < \infty,$$

and recurrent otherwise.

Example 2.8. Suppose that (X_i) and (Y_j) are exponentially distributed with parameter α_\star and α_\dagger , respectively. Then,

$$\int_0^\infty \frac{\bar{F}_\dagger(x)}{\bar{F}_\star(x)} R_\star(dx) = \begin{cases} \frac{\alpha_\star}{\alpha_\dagger - \alpha_\star}, & \text{if } \alpha_\dagger > \alpha_\star \\ \infty, & \text{if } \alpha_\dagger \leq \alpha_\star. \end{cases}$$

By proposition 2.6, if $\alpha_\dagger \leq \alpha_\star$, then $M = \infty$ a.s., and from theorem 2.1, η_0 is recurrent. If $\alpha_\dagger > \alpha_\star$, then η_0 is transient. We may compute the distribution of Λ and M in this case (it will come in handy below), as follows: by 2, $\mathbb{E}[e^{-t\Lambda}] = \mathbb{E}\left[e^{-\sum_{k \geq 1} t \cdot h_\dagger(X_{I_k}, \Delta T_{I_k})}\right]$ and using the characterisation of a Poisson process via its Laplace functional (see theorem 3.9 on page 23 of [14])

$$\begin{aligned} \mathbb{E}\left[e^{-\sum_{k \geq 1} t \cdot h_\dagger(X_{I_k}, \Delta T_{I_k})}\right] &= \exp\left[-\int_{[0,+\infty)} \frac{t\lambda_\dagger \bar{F}_\dagger(x)}{\lambda_\star \bar{F}_\star(x) + t\lambda_\dagger \bar{F}_\dagger(x)} R_\star(dx)\right] \\ &= \left(\frac{\lambda_\star}{\lambda_\star + t\lambda_\dagger}\right)^{\frac{\alpha_\star}{\alpha_\dagger - \alpha_\star}} = (1 + t\beta^{-1})^{-r}. \end{aligned}$$

By proposition 2.5, $\mathbb{E}[e^{-tM}] = \left(\frac{1-p}{1-pe^{-t}}\right)^r$, where $r = \frac{\alpha_\star}{\alpha_\dagger - \alpha_\star}$, $\beta = \frac{\lambda_\star}{\lambda_\dagger}$ and $p = \frac{\lambda_\dagger}{\lambda_\star + \lambda_\dagger}$. Hence, Λ follows the gamma distribution with parameters r and β , and M follows the negative binomial distribution with parameters r and p .

2.2. Existence and in/finiteness of a long time limit distribution.

We now establish the existence of a limit distribution for $\eta_0(s)$ as $s \rightarrow \infty$. Remarkably, a ladder construction based on a record process comes up here as well, entirely parallel to that of subsection 2.1, with births and extinctions swapping roles. For that to hold we need however to assume that F_\dagger is continuous. The ladder construction then immediately yields necessary and sufficient criteria for the almost sure in/finiteness of the number of species present in the limit distribution, identical to those for transience/recurrence of η_0 , except that the symbols \star and \dagger swap roles.

As a preliminary, we will use the process of extinctions and the associated thresholds to build a ladder of records, much as in subsection 2.1. We define the k th record index J_k and the record value Y_{J_k} as follows: $J_1 \doteq -1$ and; for $k \geq 1$

$$J_{k+1} \doteq \max\{j < J_k : Y_j > Y_{J_k}\}$$

Again by proposition 4.11.1 in [13], we get that the $\{Y_{J_k}\}_{k \geq 1}$ form a Poisson point process in \mathbb{R}_+ with intensity measure $\int_B R_\dagger(dx)$, $B \in \mathcal{B}(\mathbb{R}_+)$.

Denote by $S_{J_k}(0)$ the time of the k th record, and by $\Delta S_{J_k} \doteq S_{J_k} - S_{J_{k+1}}$ the time span between two consecutive records. Similarly as in subsection 2.1, we have the following results.

Proposition 2.9. *The points $(Y_{J_k}, \Delta S_{J_k})_{k \geq 1}$ form a Poisson point process in \mathbb{R}_+^2 with intensity*

$$\hat{\mu}_\dagger(C) \doteq \iint_C \lambda_\dagger \bar{F}_\dagger(x) e^{-\lambda_\dagger \bar{F}_\dagger(x)s} ds R_\dagger(dx), \quad C \in \mathcal{B}(\mathbb{R}_+^2).$$

Proposition 2.10. *The points $\{(T_{-i}, X_{-i})\}_{i \geq 1}$ form a Poisson point process in $\mathbb{R}_- \times \mathbb{R}_+$, $\mathbb{R}_- = (-\infty, 0]$, denoted by $\hat{\Pi}_*$, with intensity*

$$\mu_*(C') \doteq \lambda_* \iint_{C'} dt F_*(dy), \quad C' \in \mathcal{B}(\mathbb{R}_- \times \mathbb{R}_+).$$

We thus have our ladder of thresholds; denote the region above each step by

$$E_0 \doteq [S_{J_1}, 0) \times \mathbb{R}_+;$$

$$E_k \doteq (S_{J_{k+1}}, S_{J_k}] \times (Y_{J_k}, \infty), k \geq 1; \quad E \doteq \bigcup_{k \geq 1} E_k.$$

We state our existence result.

Theorem 2.2. *$\eta_0(t)$ converges in distribution to $\hat{\eta}$ as $t \rightarrow \infty$, where*

$$\hat{\eta} \doteq \{X_i : T_i \in (S_{J_1}, 0]\} \cup \left(\bigcup_{k \geq 1} \{X_i > Y_{J_k} : T_i \in (S_{J_{k+1}}, S_{J_k}]\} \right).$$

Remark 2.11. The topology for weak convergence is the usual one in the context of point processes. Our proof indeed makes use of a coupling to a sequence of processes for which the convergence is a strong one, and follows by monotonicity.

Next, we address the issue of finiteness of the number of species in $\hat{\eta}$. For each $k \geq 0$, let

$$\Sigma_k \doteq \mu_*(E_k); \quad N_k \doteq \#\{E_k \cap \hat{\Pi}_*\}.$$

Let also $\Sigma \doteq \mu_*(E)$; $N \doteq \#\{E \cap \hat{\Pi}_*\}$. We may use Campbell's formula to find

$$\mathbb{E}[N] = \frac{\lambda_*}{\lambda_{\dagger}} \int_0^{\infty} \frac{\bar{F}_*(x)}{\bar{F}_{\dagger}(x)} R_{\dagger}(dx).$$

Note that N is the number of birth events above the threshold ladder. Also, note that E has a parallel structure to that of the D ladder of subsection 2.1; the random variables Σ and N are parallel to Λ and M in that same subsection. Thus, we get parallel results, once we exchange the roles of (λ_*, \bar{F}_*) and $(\lambda_{\dagger}, \bar{F}_{\dagger})$.

From theorem 2.2, the number of species present in the limit distribution $\hat{\eta}$, denoted by $\#\hat{\eta}$, is

$$\#\hat{\eta} = \sum_{k \geq 0} \#\{E_k \cap \hat{\Pi}_*\} = \sum_{k \geq 0} N_k = N_0 + N. \tag{5}$$

It is enough to consider the finiteness of N . From the parallel situation of subsection 2.1, we get the following results. For $t > 0$

$$\begin{aligned} \mathbb{E}[e^{-tN}] &= \mathbb{E}[e^{-(1-e^{-t})\Sigma}] \\ &= \exp \left[- \int_0^\infty \frac{(1-e^{-t})\lambda_* \bar{F}_*(x)}{\lambda_\dagger \bar{F}_\dagger(x) + (1-e^{-t})\lambda_* \bar{F}_*(x)} R_\dagger(dx) \right]. \end{aligned}$$

Setting

$$\bar{\phi}(t) \doteq \int_0^\infty \frac{(1-e^{-t})\lambda_* \bar{F}_*(x)}{\lambda_\dagger \bar{F}_\dagger(x) + (1-e^{-t})\lambda_* \bar{F}_*(x)} R_\dagger(dx), \quad t > 0,$$

and

$$\bar{\psi}(u) \doteq \bar{F}_* \circ \bar{F}_\dagger^{-1}(u), \quad u > 0,$$

we have

$$\bar{\phi}(\infty) \doteq \lim_{t \rightarrow \infty} \bar{\phi}(t) = \int_0^\infty \frac{\lambda_* \bar{F}_*(x)}{\lambda_\dagger \bar{F}_\dagger(x) + \lambda_* \bar{F}_*(x)} R_\dagger(dx).$$

Proposition 2.12. *The following statements are equivalent:*

- (a) $\bar{\phi}(\infty) < \infty$;
- (b) $\mathbb{P}(N < \infty) = 1$;
- (c) $\mathbb{E}[N] < \infty$.
- (d) $\frac{\bar{\psi}(u)}{u^2}$ is integrable at the origin;
- (e) $\bar{\psi}(s^{-1})$ is integrable at infinity.

Theorem 2.3. *The number of species in the limit distribution, $\#\hat{\eta}$, is finite if*

$$\int_0^\infty \frac{\bar{F}_*(x)}{\bar{F}_\dagger(x)} R_\dagger(dx) < \infty,$$

and infinite otherwise.

Example 2.13. Let (X_i) and (Y_j) be as in example 2.8. We have then

$$\int_0^\infty \frac{\bar{F}_*(x)}{\bar{F}_\dagger(x)} R_\dagger(dx) = \begin{cases} \frac{\alpha_\dagger}{\alpha_* - \alpha_\dagger}, & \text{if } \alpha_* > \alpha_\dagger \\ \infty, & \text{if } \alpha_* \leq \alpha_\dagger. \end{cases}$$

By the theorem 2.3, if $\alpha_* \leq \alpha_\dagger$, then $\#\hat{\eta} = \infty$ a.s. If $\alpha_* > \alpha_\dagger$, then $\#\hat{\eta} < \infty$ a.s.; let us find its distribution. We can show that, as in example 2.8, N follows the negative binomial distribution with parameters $\frac{\alpha_\dagger}{\alpha_* - \alpha_\dagger}$ and $\frac{\lambda_*}{\lambda_* + \lambda_\dagger}$. From the joint distribution of (N_0, Σ_0) , discussed in the proof of theorem 2.3 below, we have that N_0 follows the negative binomial distribution with parameters 1 and $\frac{\lambda_*}{\lambda_* + \lambda_\dagger}$. It may be checked that N_0 and N are independent, and we find from (5) that $\#\hat{\eta}$ follows the negative binomial distribution with parameters $\frac{\alpha_*}{\alpha_* - \alpha_\dagger}$ and $\frac{\lambda_*}{\lambda_* + \lambda_\dagger}$.

Remark 2.14. We might label the case of ∞ in both criteria in theorems 2.1 and 2.3 as *null recurrent*. This is of course the case when $F_* = F_\dagger$, which then becomes a natural candidate for comparison with the GMS model *below the critical point*, which also is recurrent and has infinitely many species in its limiting distribution, as anticipated in subsection 1.1, and is thus null recurrent in the same way. However, as we briefly discuss below—see remark 3.1—, in this case the models are different in another fundamental level, namely the behavior

of N^f , the number of species in the limiting distribution with fitness below f , as $f \rightarrow \infty$ (in our setting; in the setting of [9], the limit should be taken as $f \uparrow f_c$). While for the GMS model the suitably rescaled object converges in distribution as the scale parameter vanishes to a nontrivial distribution—see theorem 1.2 of [10]—, we have a law of large numbers type of convergence to a constant in our model. In the terms proposed in the latter reference, this puts the two models in different universality classes.

3. Proofs

Our proofs of propositions 2.2 and 2.3 use definition 5.3 (K-marking process), as well as theorem 5.6 (Marking theorem) in [14].

Proof of Proposition 2.2. Conditional on $\{(X_{I_k})_{k \geq 1} = (x_k)_{k \geq 1}\}$, the random variables ΔT_{I_k} are independent of each other and follow the exponential distribution of rate $\lambda_* \bar{F}_*(x_k)$. Denote by $K_*(x, B)$ the following probability kernel: for $x \geq 0$, and $B = (s_1, s_2] \subset [0, \infty)$, let $K_*(x, (s_1, s_2]) \doteq e^{-\lambda_* \bar{F}_*(x)s_1} - e^{-\lambda_* \bar{F}_*(x)s_2}$, and extend the definition for Borelians B in the usual way.

The points $(X_{I_k}, \Delta T_{I_k})_{k \geq 1}$ form a K_* -marking of the Poisson process of proposition 2.1. The result follows by the Marking Theorem (theorem 5.6 of [14]). \square

Proof of Proposition 2.3. The random variables $(Y_j)_{j \geq 1}$ are independent of each other and independent of $(S_j)_{j \geq 1}$. Then, the points $(S_j, Y_j)_{j \geq 1}$ form a \mathbb{Q}_\dagger -marking independent of $(S_j)_{j \geq 1}$, where \mathbb{Q}_\dagger is the measure induced by Y . The result follows again by the Marking theorem. \square

Proof of Proposition 2.5. From equations (1) and (2)

$$\begin{aligned} \mathbb{E}[e^{-tM}] &= \mathbb{E}[e^{-(1-e^{-t})\Lambda}] = \mathbb{E}\left[e^{-\sum_{k \geq 1} (1-e^{-t})h_\dagger(X_{I_k}, \Delta T_{I_k})} \right] \\ &= \exp\left[-\iint_{[0, \infty)^2} (1 - e^{-(1-e^{-t})h_\dagger(x,s)}) \hat{\mu}_*(dx, ds) \right] \end{aligned} \tag{6}$$

$$= \exp\left[-\iint_{[0, \infty)^2} (1 - e^{-(1-e^{-t})\lambda_\dagger s \bar{F}_\dagger(x)}) \lambda_* \bar{F}_*(x) e^{-\lambda_* \bar{F}_*(x)s} ds R_*(dx) \right]. \tag{7}$$

In (6) we used the characterisation of a Poisson process via its Laplace functional (see theorem 3.9 on page 23 of [14]), and (7) follows by proposition 2.2.

Integrating the above expression in s , we have

$$\begin{aligned} \mathbb{E}[e^{-tM}] &= \exp\left[-\int_0^\infty \left(1 - \frac{\lambda_* \bar{F}_*(x)}{\lambda_* \bar{F}_*(x) + (1 - e^{-t})\lambda_\dagger \bar{F}_\dagger(x)} \right) R_*(dx) \right] \\ &= \exp\left[-\int_0^\infty \frac{(1 - e^{-t})\lambda_\dagger \bar{F}_\dagger(x)}{\lambda_* \bar{F}_*(x) + (1 - e^{-t})\lambda_\dagger \bar{F}_\dagger(x)} R_*(dx) \right]. \end{aligned}$$

\square

Proof of Proposition 2.6. To prove (a) \Rightarrow (b) note that

$$0 \leq \frac{(1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + \lambda_{\dagger}\bar{F}_{\dagger}(x)} \leq \frac{(1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + (1 - e^{-t})\lambda_{\dagger}\bar{F}_{\dagger}(x)} \leq \frac{\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + \lambda_{\dagger}\bar{F}_{\dagger}(x)}. \tag{8}$$

Integrating (8) against $R_{\star}(dx)$ we get,

$$(1 - e^{-t})\phi(\infty) \leq \phi(t) \leq \phi(\infty). \tag{9}$$

If $\phi(\infty) < \infty$, by monotone convergence theorem, $\lim_{t \downarrow 0} \phi(t) = 0$. Then,

$$\lim_{t \downarrow 0} \mathbb{E}[e^{-tM}] = \lim_{t \downarrow 0} \exp[-\phi(t)] = \exp[-\lim_{t \downarrow 0} \phi(t)] = 1$$

and, on the other hand,

$$\begin{aligned} \lim_{t \downarrow 0} \mathbb{E}[e^{-tM}] &= \lim_{t \downarrow 0} \sum_{m \geq 0} e^{-tm} \mathbb{P}(M = m) + 0 \cdot \mathbb{P}(M = \infty) \\ &= \sum_{m \geq 0} \mathbb{P}(M = m) = \mathbb{P}(M < \infty) \end{aligned}$$

To prove (b) \Rightarrow (a) suppose $\phi(\infty) = \infty$. By (9), $\phi(t) = +\infty$ for each $t > 0$. Then,

$$\begin{aligned} \mathbb{E}[e^{-tM}] &= \exp[-\phi(t)] = 0 \quad \text{for each } t > 0 \\ \Rightarrow \mathbb{P}(e^{-tM} = 0) &= 1 \quad \text{for each } t > 0 \\ \Rightarrow \mathbb{P}(M = \infty) &= 1. \end{aligned}$$

By contradiction we get (b) \Rightarrow (a).

Since trivially (c) \Rightarrow (b), we have from the above that (c) \Rightarrow (a).

To show that (a) \Rightarrow (c), we will change variables. Let $y = R_{\star}(x) = -\log \bar{F}_{\star}(x)$, so $x = \bar{F}_{\star}^{-1}(e^{-y})$. From this and (4), $\bar{F}_{\dagger}(x) = \bar{F}_{\dagger} \circ \bar{F}_{\star}^{-1}(e^{-y}) = \psi(e^{-y})$. Making $u = e^{-y}$, we find that

$$\begin{aligned} \phi(\infty) &= \int_0^{\infty} \frac{\lambda_{\dagger}\bar{F}_{\dagger}(x)}{\lambda_{\star}\bar{F}_{\star}(x) + \lambda_{\dagger}\bar{F}_{\dagger}(x)} R_{\star}(dx) \\ &= \int_0^{\infty} \frac{\lambda_{\dagger}\psi(e^{-y})}{\lambda_{\star}e^{-y} + \lambda_{\dagger}\psi(e^{-y})} dy = \int_0^1 \frac{\lambda_{\dagger}\psi(u)}{\lambda_{\star}u + \lambda_{\dagger}\psi(u)} \frac{du}{u}, \end{aligned}$$

where the second equality is quite clear if F_{\star} is strictly increasing, but holds in general (see e.g. the [15] for a discussion and justification).

If $\phi(\infty) < \infty$, then dominated convergence yields

$$\lim_{\varepsilon \downarrow 0} \int_{\varepsilon}^{2\varepsilon} \frac{\lambda_{\dagger} \psi(u)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(u))u} du = \lim_{\varepsilon \downarrow 0} \int_0^1 \frac{\lambda_{\dagger} \psi(u)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(u))u} I_{(\varepsilon, 2\varepsilon)}(u) du = 0.$$

Since

$$0 \leq \int_{\varepsilon}^{2\varepsilon} \frac{\lambda_{\dagger} \psi(\varepsilon)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(\varepsilon))u} du \leq \int_{\varepsilon}^{2\varepsilon} \frac{\lambda_{\dagger} \psi(u)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(u))u} du,$$

we get that

$$\lim_{\varepsilon \downarrow 0} \int_{\varepsilon}^{2\varepsilon} \frac{\lambda_{\dagger} \psi(\varepsilon)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(\varepsilon))u} du = 0. \tag{10}$$

Solving the integral,

$$\int_{\varepsilon}^{2\varepsilon} \frac{\lambda_{\dagger} \psi(\varepsilon)}{(\lambda_{\star} u + \lambda_{\dagger} \psi(\varepsilon))u} du = \log \left(1 + \frac{\lambda_{\dagger} \psi(\varepsilon)}{\lambda_{\star} 2\varepsilon + \lambda_{\dagger} \psi(\varepsilon)} \right),$$

and from (10)

$$\lim_{\varepsilon \downarrow 0} \log \left(1 + \frac{\lambda_{\dagger} \psi(\varepsilon)}{\lambda_{\star} 2\varepsilon + \lambda_{\dagger} \psi(\varepsilon)} \right) = 0 \Rightarrow \lim_{\varepsilon \downarrow 0} \frac{\lambda_{\dagger} \psi(\varepsilon)}{\lambda_{\star} 2\varepsilon + \lambda_{\dagger} \psi(\varepsilon)} = 0 \Rightarrow \lim_{\varepsilon \downarrow 0} \frac{\lambda_{\dagger} \psi(\varepsilon)}{\lambda_{\star} \varepsilon} = 0.$$

We may thus find $\delta \in (0, 1)$ such that $\lambda_{\dagger} \psi(u) \leq \lambda_{\star} u$ for each $u \in (0, \delta)$. Thus,

$$\int_0^{\delta} \frac{\lambda_{\dagger} \psi(u)}{\lambda_{\star} u} \frac{du}{u} \leq 2 \int_0^{\delta} \frac{\lambda_{\dagger} \psi(u)}{\lambda_{\star} u + \lambda_{\dagger} \psi(u)} \frac{du}{u} \leq 2 \int_0^1 \frac{\lambda_{\dagger} \psi(u)}{\lambda_{\star} u + \lambda_{\dagger} \psi(u)} \frac{du}{u} < \infty.$$

Thus, since also $\psi(u) \leq 1$, we have

$$\frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^1 \frac{\psi(u)}{u^2} du = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^{\delta} \frac{\psi(u)}{u^2} du + \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_{\delta}^1 \frac{\psi(u)}{u^2} du < \infty.$$

Rewriting (3) in terms of ψ , we have

$$\mathbb{E}[M] = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^{\infty} \frac{\bar{F}_{\dagger}(x)}{\bar{F}_{\star}(x)} R_{\star}(dx) = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^{\infty} \frac{\psi(e^{-y})}{e^{-y}} dy = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_0^1 \frac{\psi(u)}{u^2} du, \tag{11}$$

and the finiteness of the latter expression establishes that (a) \Rightarrow (c).

(c) \Leftrightarrow (d) follows readily from (11). To prove (d) \Leftrightarrow (e) make the following substitution

$$s = u^{-1} \Rightarrow \frac{ds}{du} = -u^{-2} \Rightarrow ds = -\frac{du}{u^2}$$

and we can rewrite $\mathbb{E}[M]$ as

$$\mathbb{E}[M] = -\frac{\lambda_{\dagger}}{\lambda_{\star}} \int_{\infty}^1 \psi(s^{-1}) ds = \frac{\lambda_{\dagger}}{\lambda_{\star}} \int_1^{\infty} \psi(s^{-1}) ds.$$

Note that

$$\int_1^{\delta} \psi(s^{-1}) ds < \infty \quad \text{for each } \delta \in \mathbb{R}^+;$$

as a consequence

$$\mathbb{E}[M] < \infty \Leftrightarrow \int_{\delta}^{\infty} \psi(s^{-1})ds < \infty \quad \text{for some } \delta \in \mathbb{R}^+.$$

□

Proof of Theorem 2.1. By proposition 2.6, if $\int_0^{\infty} \frac{\bar{F}_+(x)}{\bar{F}_*(x)} R_*(dx) = \infty$, then $M = \infty$ a.s. Since $\mathcal{M}_k \doteq D_k \cap \hat{\Pi}_+$ is a.s. finite for every $k \geq 1$, we have that \mathcal{M} is a.s. unbounded, and thus so is Υ' and Υ .

If $\int_0^{\infty} \frac{\bar{F}_+(x)}{\bar{F}_*(x)} R_*(dx) < \infty$, then by proposition 2.6, we have that a.s. $M < \infty$, and thus \mathcal{M} is bounded, and thus so is Υ' and Υ , as follows from what has been pointed out at the end of definition 2.7 above. □

Proof of Theorem 2.2. By the homogeneity of the model, the process $\eta_t = \{\eta_t(t+s) : s \geq 0\}$ has the same distribution for each $t \in \mathbb{R}$. In particular,

$$\mathbb{P}(\eta_0(t) \in \cdot | \eta_0(0) = A) = \mathbb{P}(\eta_{-t}(0) \in \cdot | \eta_{-t}(-t) = A), \tag{12}$$

where A is a locally finite subset of $[0, \infty)$. Let $(t_l)_{l \geq 1}$ be an increasing sequence in \mathbb{R}^+ such that $t_l \rightarrow \infty$ as $l \rightarrow \infty$ and A as above; take a sequence of processes $(\eta_{-t_l})_{l \geq 1}$ such that $\eta_{-t_l}(-t_l) = A$, $l \geq 1$. Define the sequence $(\eta'_l)_{l \geq 1}$ by

$$\eta'_l \doteq \begin{cases} \{X_i : T_i \in (-t_l, 0]\}, & \text{if } \Pi_+ \cap (-t_l, 0) = \emptyset; \\ \{X_i : T_i \in (S_{J_1}, 0]\} \cup \left(\bigcup_{k=1}^{\hat{k}_l-1} \{X_i > Y_{J_k} : T_i \in (S_{J_{k+1}}, S_{J_k}]\} \right) \\ \cup \{X_i > Y_{J_{\hat{k}_l}} : T_i \in (-t_l, S_{J_{\hat{k}_l}}]\}, & \text{otherwise,} \end{cases}$$

where $\hat{k}_l \doteq \max\{k : S_{J_k} > -t_l\}$, and the union $\bigcup_{k=1}^{\hat{k}_l-1}$ above is empty if $\hat{k}_l = 1$. Note that $(\hat{k}_l)_{l \geq 1}$ is an increasing sequence with $\hat{k}_l \rightarrow \infty$ as $l \rightarrow \infty$. Thus, the sequence $(\eta'_l)_{l \geq 1}$ is increasing and $\lim_{l \rightarrow \infty} \eta'_l = \bigcup_{l \geq 1} \eta'_l = \hat{\eta}$, with

$$\hat{\eta} \doteq \{X_i : T_i \in (S_{J_1}, 0]\} \cup \left(\bigcup_{k \geq 1} \{X_i > Y_{J_k} : T_i \in (S_{J_{k+1}}, S_{J_k}]\} \right).$$

Define the sequence $(\eta''_l)_{l \geq 1}$ by

$$\eta''_l \doteq \begin{cases} A, & \text{if } \Pi_+ \cap (-t_l, 0) = \emptyset \\ A \cap (Y_{J_{\hat{k}_l}}, \infty), & \text{otherwise.} \end{cases}$$

By proposition 2.9, $Y_{J_k} \rightarrow \infty$ as $k \rightarrow \infty$, since $R_+(x) < \infty$ for every $x > 0$ and $R_+(x) \rightarrow \infty$ as $x \rightarrow \infty$. Thus, $(Y_{J_{\hat{k}_l}})_{l \geq 1}$ is an increasing sequence with $\lim_{l \rightarrow \infty} Y_{J_{\hat{k}_l}} = \infty$, since $\hat{k}_l \rightarrow \infty$ as $l \rightarrow \infty$. Therefore, $(\eta''_l)_{l \geq 1}$ is a decreasing sequence and $\lim_{l \rightarrow \infty} \eta''_l = \bigcap_{l \geq 1} \eta''_l = \emptyset$. Because $\eta_{-t_l}(0) = \eta'_l \cup \eta''_l$ for each $l \geq 1$, we have that $\lim_{l \rightarrow \infty} \eta_{-t_l}(0) = \lim_{l \rightarrow \infty} \eta'_l \cup \lim_{l \rightarrow \infty} \eta''_l = \hat{\eta}$, and notice that the limit does not depend on the choice of $(t_l)_{l \geq 1}$. Thus $\lim_{t \rightarrow \infty} \eta_{-t}(0) = \hat{\eta}$ a.s., and, by (12), $\eta_0(t) \rightarrow \hat{\eta}$ in distribution as $t \rightarrow \infty$. □

Proof of Proposition 2.12. The proof is analogous to that of proposition 2.6, using the same ideas, and changing the roles of (λ_*, \bar{F}_*) and (λ_+, \bar{F}_+) . □

Proof of Theorem 2.3. N_0 has a Poisson distribution with parameter Σ_0 . Since $\Sigma_0 = \mu_*(E_0) = \lambda_*(0 - S_{-1}) \sim \text{exponential}(\lambda_\dagger/\lambda_*)$, we have that $\mathbb{E}[N_0] = \mathbb{E}[\Sigma_0] = \lambda_*/\lambda_\dagger < \infty$, and thus $N_0 < \infty$ a.s.

By (5) and proposition 2.12, if $\int_0^\infty \frac{\bar{F}_*(x)}{\bar{F}_\dagger(x)} R_\dagger(dx) < \infty$, then $N < \infty$ a.s., and thus $\#\hat{\eta} < \infty$ a.s. Otherwise, $N = \infty$ a.s., and we have $\#\hat{\eta} = \infty$ a.s. \square

Remark 3.1. As a final remark, we argue in a few brief steps that, as pointed out in remark 2.14 above, when $F_* = F_\dagger = F$, then N^f , the number of species in the limiting distribution with fitness below f , when properly rescaled, converges (a.s.) to a nontrivial constant. First, by the above construction of the limiting distribution of species fitnesses, it is enough to consider the intensity measure of the region bounded by the ladder of records, the x -axis and the horizontal line through $(0, f)$. This in turn may be readily written as

$$\sum_{i=1}^{|\mathcal{P} \cap [0, f]|} \left(1 - \frac{\bar{F}(f)}{\bar{F}(X_i)}\right) \mathcal{E}_i = \sum_{i=1}^{|\mathcal{P} \cap [0, f]|} \mathcal{E}_i - \bar{F}(f) \sum_{i=1}^{|\mathcal{P} \cap [0, f]|} \frac{1}{\bar{F}(X_i)} \mathcal{E}_i \tag{13}$$

where $\mathcal{P} = \{X_1, X_2, \dots\}$ is a Poisson point process on \mathbb{R}_+ of intensity measure $\int_B R(dx)$, $B \in \mathcal{B}(\mathbb{R}_+)$, with $R(x) = -\log \bar{F}(x)$, and $\mathcal{E}_1, \mathcal{E}_2, \dots$ are i.i.d. standard exponential random variables. Clearly, the first term on the right hand side of (13), when scaled by $R(f)$, converges to 1 almost surely as $f \rightarrow \infty$, by the law of large numbers. We leave as an exercise to check, using well known properties of Poisson point processes such as \mathcal{P} , that the second term, when scaled by $R(f)$, vanishes almost surely as $f \rightarrow \infty$; indeed, *without scaling*, it is stochastically bounded uniformly by a non degenerate random variable; we immediately get convergence to 0 in probability of the scaled quantity, and a closer look reveals that this can be strengthened to a.s. convergence.

ORCID iDs

Luiz Renato Fontes  <https://orcid.org/0000-0002-2685-1845>
 Carolina Grejo  <https://orcid.org/0000-0001-8164-7874>

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