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# Populations with interaction and environmental dependence: From few, (almost) independent, members into deterministic evolution of high densities

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## ABSTRACT

Many populations, e.g. not only of cells, bacteria, viruses, or replicating DNA molecules, but also of species invading a habitat, or physical systems of elements generating new elements, start small, from a few Individuals, and grow large into a noticeable fraction of the environmental carrying capacity  $K$  or some corresponding regulating or system scale unit. Typically, the elements of the initiating, sparse set will not be hampering each other and their number will grow from  $Z_0 = z_0$  in a branching process or Malthusian like, roughly exponential fashion,  $Z_t \sim a^t W$ , where  $Z_t$  is the size at discrete time  $t \rightarrow \infty$ ,  $a > 1$  is the offspring mean per individual (at the low starting density of elements, and large  $K$ ), and  $W$  a sum of  $z_0$  i.i.d. random variables. It will, thus, become detectable (i.e. of the same order as  $K$ ) only after around  $\log K$  generations, when its density  $X_t := Z_t/K$  will tend to be strictly positive. Typically, this entity will be random, even if the very beginning was not at all stochastic, as indicated by lower case  $z_0$ , due to variations during the early development. However, from that time onwards, law of large numbers effects will render the process deterministic, though initiated by the random density at time  $\log K$ , expressed through the variable  $W$ . Thus,  $W$  acts both as a random veil concealing the start and a stochastic initial value for later, deterministic population density development. We make such arguments precise, studying general density and also system-size dependent, processes, as  $K \rightarrow \infty$ . As an intrinsic size parameter,  $K$  may also be chosen to be the time unit. The fundamental ideas are to couple the initial system to a branching process and to show that late densities develop very much like iterates of a conditional expectation operator. The “random veil”, hiding the start, was first observed in the very concrete special case of finding the initial copy number in quantitative PCR under Michaelis-Menten enzyme kinetics, where the initial individual replication variance is nil if and only if the efficiency is one, i.e. all molecules replicate.

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## 1. Introduction: Replication with interaction and dependence

We consider sets of elements where, in principle, each element may generate new elements. For lucidity we regard time as discrete, labeling it by  $n = 0, 1, 2, \dots$ , referring to it also as generations, cycles or rounds, and call the system a ‘population’ of ‘individuals’, even though we have quite general such structures in mind. This is like in branching processes,<sup>[5,6]</sup> but without independence between individuals required. Here, we assume that the individual offspring generation (reproduction, replication or whatever) may be influenced by a system ‘carrying capacity’,  $K$ , which we think of as large, as compared to the population starting number  $Z_0$ , and also by the number of other individuals present. We say that replication is capacity and population size, or ‘density’ dependent, as in Refs. [1,2].

The process definition is patterned after the recursive scheme used to build up Galton–Watson processes: Let

$$\xi_{n,j}, n \in \mathbb{N}, j \in \mathbb{N},$$

be non-negative integer-valued random variables, where we think of  $\xi_{n,1}, \xi_{n,2}, \dots$  as the possible offspring numbers of various individuals in the  $n - 1$ :th generation. Thus, we define  $\{Z_n, n = 0, 1, 2, \dots\}$ , by the initial number  $Z_0$  and

$$Z_n = \sum_{j=1}^{Z_{n-1}} \xi_{n,j}. \quad (1.1)$$

The dependence structure is made precise in a basic assumption:

(A0) For each fixed  $n \in \mathbb{N}$ , the  $\xi_{n,j}, j = 1, 2, \dots$ , are *conditionally* independently and identically distributed, given the preceding,  $\mathcal{F}_{n-1} := \sigma(\{\xi_{k,j}, k < n, j \in \mathbb{N}\})$ . The process is Markovian in the sense that the conditional distribution should be determined by the couple  $K$  and  $X_{n-1} = Z_{n-1}/K$ , the *carrying capacity* and *population density*, in such a manner that the variables  $\xi_{k,j}$  increase in distribution with  $K$  and decrease with  $x = X_{n-1}$ , the limiting distribution, as  $K \rightarrow \infty$ , *the asymptotic reproduction*, being proper for each  $x \in \mathbb{R}_+$ .

Three entities pertaining to the density turn out to be crucial for the analysis of process start and late development. They are:

1. the conditional mean number of offspring per individual,

$$m^K(X_{n-1}) = \mathbb{E}[\xi_{n,i} | \mathcal{F}_{n-1}],$$

2. the corresponding variance,

$$\sigma_K^2(X_{n-1}) = \text{Var}[\xi_{n,i} | \mathcal{F}_{n-1}],$$

3. and the conditional expectation of the density process,

$$f^K(x) = \mathbb{E}[X_n | X_{n-1} = x] = xm^K(x),$$

where the dependence of variance and expectation operators upon  $K$  is implicit. From A0, it follows that the  $m^K$  form a non-decreasing sequence of non-increasing functions, and hence must have a non-increasing limit,  $m$ . The means and variances  $m^K$  and  $\sigma_K^2$  are supposed defined on all of  $\mathbb{R}_+$ .

We formulate boundedness and smoothness criteria for these functions, which will lead to classical Malthusian growth for  $Z_n$  in an early stage,  $n \leq n_K = c \log K, 0 < c < 1$ . Then, we make use of a law of large numbers for branching processes with a threshold and density dependence,<sup>[8]</sup> and a large initial value, in our case  $O(K^c)$ , at round  $n_K$ . All logarithms are with base  $a$ .

The assumptions beyond A0 are:

(A1) The limiting expected conditional reproduction given a population density  $x$ ,  $m(x)$  has a derivative which is uniformly continuous in a neighbourhood to the right of the origin, and  $a = m(0) > 1$ . As  $K \rightarrow \infty$ , the continuous non-increasing functions  $m^K$  converge uniformly to a bounded differentiable function  $m$ ,  $0 \leq m(x) - m^K(x) \leq Cx + o(x)$  for some  $C > 0$  and uniformly in  $K$ , as  $x \rightarrow 0$ .

(A2) The limiting conditional expected density  $f, f(x) = xm(x), x \geq 0$ , is strictly increasing.

(A3) As  $K \rightarrow \infty$ ,  $X_0$  converges in probability to some limit  $x_0 \geq 0$ . In particular, if there is a fixed starting number,  $x_0 = 0$ .

(A4) The conditional reproduction variance  $\sigma_K^2(x) = \text{Var}[\xi_{n,i} | X_{n-1} = x]$  is uniformly bounded and, as  $K \rightarrow \infty$ , converges to some  $\sigma^2(x)$  uniformly. The latter, hence, is also bounded.

(A5) There is a constant  $C > 0$  such that uniformly for all  $K$

$$a \geq m^K(x) = m^K(0) - Cx + o(x) \quad \text{as } x \rightarrow 0.$$

Further,  $0 \leq a - m^K(0) = O(1/\sqrt{K})$  and also  $\sup_{x \geq 0} |f^K(x) - f(x)| = O(1/\sqrt{K})$ .

These look like innocuous smoothness requirements, but A2 contains something more. For fixed  $K$  dependence upon the density is the same as dependence on population size, and it thus seems little of a restriction to ask that the next generation should tend to increase with density. It might however be argued that there could be a density above which for example no replication is possible. This in a sense, however, would introduce a sort of further carrying capacity, besides  $K$ .

## 2. In spite of interaction and capacity dependence, the beginning looks like branching, when the carrying capacity becomes large

An approximating process, at low density and high carrying capacity,  $\tilde{Z} = \{\tilde{Z}_n\}$ , is crucial in the analysis. It has the same starting number  $Z_0 = z_0$  as the original process, but then it continues as a classical Galton–Watson process,

$$\tilde{Z}_0 = z_0 \tag{2.1}$$

$$\tilde{Z}_n = \sum_{j=1}^{\tilde{Z}_{n-1}} \eta_{n,j}, \tag{2.2}$$

where the  $\eta$  variables are i.i.d. with the asymptotic reproduction distribution as  $K \rightarrow \infty$  for  $x=0$ . Thus,  $\mathbb{E}[\eta] = a = m(0) > 1$  and  $\text{Var}[\eta] = \sigma^2(0) < \infty$ . (Lower case  $z_0$  indicates an unknown but deterministic starting number.)

From classical branching process theory,  $W(z_0) := \lim_{n \rightarrow \infty} \tilde{Z}_n / a^n$  will have the distribution of  $z_0$  independent  $W$ -copies, each with expectation 1 and variance  $\sigma^2(0)/(a^2 - a)$ . In particular,

$$\tilde{Z}_{n_K} / K^c = \tilde{Z}_{n_K} / a^{n_K} \sim W(z_0).$$

By approximation, this extends to:

**Theorem 2.1.** *Under assumptions A0, A1, and A5,  $Z_{n_K} / a^{n_K} \rightarrow W(z_0)$  and thus  $X_{n_K} \sim W(z_0) K^{c-1}$ , in probability and  $L^1$ , as  $K \rightarrow \infty$ .*

*Proof.* Construct the replication processes  $Z$  and  $\tilde{Z}$ , as well as a third process  $Z^\gamma = \{Z_n^\gamma\}$ , on the same probability space by the following coupling. Let  $U_{n,j}$ ,  $n, j \in \mathbb{N}$  be independent uniformly distributed random variables on  $[0, 1]$ . For each  $K$  and  $x$  define  $t_{-1}^K(x) = t_{-1} = 0$  and  $0 \leq t_0^K(x) \leq t_1^K(x) \leq t_2^K(x) \leq \dots$  so that  $\mathbb{P}(t_{k-1}^K(x) < U_{n,j} \leq t_k^K(x)) = \mathbb{P}(\xi_{n,j} = k | X_{n-1} = x)$ ,  $k \in \mathbb{N}$ . Further, let  $0 \leq t_0 \leq t_1 \leq t_2 \leq \dots$  so that  $\mathbb{P}(t_{k-1} < U_{n,j} \leq t_k) = \mathbb{P}(\eta_{n,j} = k)$ ,  $k \in \mathbb{N}$ . We can then define the reproduction random variables  $\xi_{n,j}$  and population sizes  $Z_n, \tilde{Z}_n$ , as well as densities  $X_n$  inductively on the same probability space by,

$$\xi_{n,j} = k \iff t_{k-1}^K(X_{n-1}) < U_{n,j} \leq t_k^K(X_{n-1}) \text{ and } \eta_{n,j} = k \iff t_{k-1} < U_{n,j} \leq t_k.$$

and, as before, (1.1) and (2.1), using  $\xi_{n,j}$  and  $\eta_{n,j}$  respectively. Similarly, we write

$$\xi_{n,j}^\gamma := \sum_{k=0}^{\infty} k \mathbf{1}_{(t_{k-1}^{K(K^\gamma-1)}, t_k^{K(K^\gamma-1)})}(U_{n,j})$$

and  $Z_n^\gamma$  correspondingly.

By the distributional properties of  $\xi_{n,j}|X_{n-1} = x$  and  $\eta_{n,j}$  (Assumption A0),

$$t_k^K(x) = \mathbb{P}(\xi_{n,j} \leq k | X_{n-1} = x) \geq \mathbb{P}(\eta_{n,j} \leq k) = t_k$$

and

$$t_k^K(K^{\gamma-1}) \geq t_k^K(X_n),$$

the latter as long as  $n < \tau := \inf\{n; X_n > K^{\gamma-1}\}$ . Hence, by induction for the random entities realized with the help of the  $U_{n,j}, \tilde{Z}_n \geq Z_n, n \in \mathbb{N}$ , pointwise, and  $Z'_n \leq Z_n, n < \tau$ . Further,  $\tilde{Z}_n \geq Z'_n$  for all  $n$ . It follows that

$$0 \leq \tilde{Z}_n - Z_n \leq \tilde{Z}_n - Z'_n 1_{\{n < \tau\}} - Z_n 1_{\{n \geq \tau\}} \leq \tilde{Z}_n - Z'_n 1_{\{n < \tau\}} \leq \tilde{Z}_n - Z'_n + Z'_n 1_{\{n \geq \tau\}}.$$

Now, in order to show that

$$\lim_{K \rightarrow \infty} (\tilde{Z}_{n_K} - Z_{n_K}) K^{-c} = 0,$$

we choose  $1/2 < c < \gamma < 1$ . By this and A5,

$$a \geq m^K(K^{\gamma-1}) = a - (a - m^K(0)) - (m^K(0) - m^K(K^{\gamma-1})) \geq a - aAK^{-1/2} - aBK^{\gamma-1} + o(K^{\gamma-1}) = a(1 - BK^{\gamma-1} + o(K^{\gamma-1}))$$

for suitable constants  $A$  and  $B$ .

Hence,

$$\begin{aligned} \mathbb{E}(\tilde{Z}_{n_K} - Z'_{n_K}) &= z_0(a^{n_K} - m^K(K^{\gamma-1})^{n_K}) = \\ &= z_0 a^{c \log K} (1 - (1 - BK^{\gamma-1} + o(K^{\gamma-1}))^{c \log K}) = o(K^c). \end{aligned}$$

Thus,

$$\mathbb{E}[\tilde{X}_{n_K} - X'_{n_K}] = o(K^{c-1}).$$

For the remaining term, note that

$$\mathbb{E}[Z'_{n_K}; \tau \leq n_K] \leq \mathbb{E}[\tilde{Z}_{n_K}; \tau \leq n_K] \leq \left( \mathbb{E}[\tilde{Z}_{n_K}^2] \mathbb{P}(\tau \leq n_K) \right)^{1/2},$$

by the Cauchy-Schwartz inequality. Since  $Z_n \leq \tilde{Z}_n$  for all  $n$ , it takes longer for the former process to reach  $K^\gamma$  than for the latter, so that

$$\tau \geq \nu := \inf\{n : \tilde{Z}_n > K^\gamma\}$$

and

$$\begin{aligned} \mathbb{P}(\tau \leq n_K) &\leq \mathbb{P}(\nu \leq n_K) = \mathbb{P}\left(\sup_{n \leq n_K} \tilde{Z}_n > K^\gamma\right) = \\ &\mathbb{P}\left(a^{-n_K} \sup_{n \leq n_K} \tilde{Z}_n > K^\gamma a^{-n_K}\right) \leq \\ &\mathbb{P}\left(\sup_{n \leq n_K} \tilde{Z}_n a^{-n} > K^{\gamma-c}\right) \leq K^{c-\gamma}, \end{aligned}$$

where the last bound is Doob's inequality for the martingale  $\{\tilde{Z}_n a^{-n}\}$ . Since  $\mathbb{E}[\tilde{Z}_{n_K}^2] = O(K^{2c})$ , by the formula for expectation and variance of Galton–Watson processes,

$$\lim_{K \rightarrow \infty} K^{-c} \mathbb{E}[\tilde{Z}_{n_K}; \nu \leq n_K] = 0.$$

Recalling that  $\gamma > c$ , we conclude that

$$\lim_{K \rightarrow \infty} (\tilde{Z}_{n_K} - Z_{n_K}) K^{-c} = 0. \quad (2.3)$$

holds in  $L^1$ , and hence in probability. For the corresponding densities, division by  $K$  yields

$$\lim_{K \rightarrow \infty} (\tilde{X}_{n_K} - X_{n_K}) K^{1-c} = 0.$$

### 3. The branching like stage forms a random initial condition for later development

If the process does not die out, it will thus grow exponentially in  $n$ , at least as long as it does not approach  $K$  and for fixed  $K$  this holds for some  $n_K = c \log K$  generations. Then, law of large numbers type effects should stabilize the subsequent growth. We proceed to this, giving first a result on densities for fixed time,  $K \rightarrow \infty$ , and  $K$ -dependent but stabilizing starting density  $X_0$ :

**Theorem 3.1.** *Under the assumptions stated, for any time  $n$ ,*

$$\lim_{K \rightarrow \infty} X_n = x_n,$$

*in probability, where  $x_n$  is the  $n$ :th iterate of  $f$ ,  $x_n = f_n(x_0)$ . If  $X_0 \rightarrow x_0$  holds in  $L^1$ , the conclusion can actually be strengthened to mean square convergence.*

For a proof (under somewhat weaker conditions), see Ref. [10], or Theorem 1 of [8].

Now, in our framework the second, “post-branching”, stage starts at time  $n_K$  from  $W(z_0) a^{n_K} = W(z_0) K^c$  individuals. Hence, the starting density,  $W(z_0) K^{c-1} \rightarrow x_0 = 0$ . But this is a fixed point of  $f$ , and so Theorem 3.1 just yields convergence to zero. The remedy is to consider ever later time points.

**Lemma 3.2.** *If  $f$  increases strictly but  $m$  decreases and  $a = m(0) > 1$  (Assumptions A0, A1, and A2), then*

$$h(x) = \lim_{n \rightarrow \infty} f_n(x/a^n).$$

*is well defined, continuous, and strictly increasing. The convergence is uniform and  $h(0) = 0$ .*

*Proof.* Since  $f$  is increasing, so are all  $f_n$ . By definition,

$$f(x/a) = m(x/a)x/a \leq m(0)x/a = x,$$

for  $x \geq 0$ . Hence,

$$f_{n+1}(x/a^{n+1}) = f_n(f(x/a^{n+1})) \leq f_n(x/a^n).$$

The sequence  $h_n(x) := f_n(x/a^n)$  thus decreases in  $n$  for any positive  $x$ , and its limit  $h$ , as  $n \rightarrow \infty$ , must exist and be a non-decreasing function, like the  $f_n$ . By Dini's theorem, the convergence is uniform on any compact interval. Clearly,  $h(0) = h_n(0) = f_n(0) = 0$  for all  $n$ .

It remains to prove that the limit  $h$  increases strictly. However, there exist  $C > 0$  and  $\epsilon > 0$  such that

$$\begin{aligned} f'(x) &= m(x) + xm'(x) = m(0) + m(x) - m(0) \\ &+ xm'(x) \geq a - 2x \sup_{0 \leq u \leq x} |m'(u)| > a - Cx > 0, \end{aligned}$$

for  $0 < x < \epsilon$ . For any  $x < \min(\epsilon, 1/C)$ ,

$$\begin{aligned} h'_n(x) &= a^{-n} f'_n(x/a^n) = a^{-n} \prod_{j=0}^{n-1} f'(f_j(x/a^n)) \geq a^{-n} \prod_{j=0}^{n-1} (a - C f_j(x/a^n)) \geq \\ &a^{-n} \prod_{j=0}^{n-1} (a - C x a^{j-n}) \geq \prod_{j=0}^{n-1} (1 - a^{-j}) \geq e^{-a}, \quad \forall n \geq 0. \end{aligned}$$

Taking the limit  $n \rightarrow \infty$ , we see that  $h$  increases strictly in an open neighborhood of the origin. However, as  $f_{n+1}(x/a^{n+1}) = f(f_n((x/a)/a^n))$ , letting  $n \rightarrow \infty$ , shows that  $h$  solves Schröder's functional equation

$$h(x) = f(h(x/a)).$$

Therefore, if it were constant on an interval  $[x_1, x_2]$  with  $x_2 > x_1$ , then also  $h(x_1/a^k) = h(x_2/a^k)$ , for any integer  $k \geq 1$ , contradicting the fact that  $h$  increases strictly on some neighborhood of the origin. Thus,  $h$  must be strictly increasing on the positive half line. □

An immediate consequence of this will be of explicit use in the proof of our main Theorem 3.6 later:

**Corollary 3.3.**

$$\lim_{n \rightarrow \infty} f_n(x/a^n + o(a^{-n})) = h(x). \tag{3.1}$$

Now, for fixed  $K$ , the density process  $X$  satisfies the fundamental recursive equation (cf. <sup>[8]</sup>)

$$X_n = f^K(X_{n-1}) + \frac{1}{\sqrt{K}} \epsilon_n, \tag{3.2}$$

where

$$\varepsilon_n = \frac{1}{\sqrt{K}} \sum_{j=1}^{KX_{n-1}} (\xi_{n,j} - \mathbb{E}[\xi_{n,j} | \mathcal{F}_{n-1}])$$

a martingale difference sequence,  $\mathbb{E}[\varepsilon_n | \mathcal{F}_{n-1}] = 0$ , with

$$\mathbb{E}[\varepsilon_n^2 | \mathcal{F}_{n-1}] = \text{Var}[\varepsilon_n | \mathcal{F}_{n-1}] = \sigma_K^2(X_{n-1}).$$

The corresponding deterministic recursion, obtained by omitting the martingale difference term, is

$$x_n^K = f^K(x_{n-1}^K) = f_n^K(x_0).$$

From now on, what is needed of Assumptions A0-A5 is used freely. We take  $1/2 < c < 1$ , write  $\nu_K = \log K - n_K = (1-c) \log K$ , and interpret  $X$  subscripts as their integral parts.

**Lemma 3.4.**

$$X_{\log K} - f_{\nu_K}^K(X_{n_K}) \xrightarrow[K \rightarrow \infty]{L^1} 0.$$

*Proof.* Write

$$\Delta_n = X_n - f_{n-n_K}^K(X_{n_K}),$$

for  $n > n_K$ . Then,

$$\Delta_n = f^K(X_{n-1}) + \frac{1}{\sqrt{K}} \varepsilon_n - f^K \circ f_{n-1-n_K}^K(X_{n_K}).$$

Since for any  $x \geq 0$ ,  $0 \leq \frac{d}{dx} f^K(x) = m^K(x) + x \frac{d}{dx} m^K(x) \leq m^K(x) \leq a$  by assumption,

$$\begin{aligned} |\Delta_n| &\leq |f^K(X_{n-1}) - f^K \circ f_{n-1-n_K}^K(X_{n_K})| + \left| \frac{1}{\sqrt{K}} \varepsilon_n \right| \leq \\ &a |\Delta_{n-1}| + \left| \frac{1}{\sqrt{K}} \varepsilon_n \right| \leq \dots \leq \sum_{j=0}^{n-n_K-1} a^j \left| \frac{1}{\sqrt{K}} \varepsilon_{n-j} \right|. \end{aligned}$$

Adding to this that, for any natural  $k$ ,

$$\mathbb{E} \left[ |\varepsilon_k| \leq \sqrt{\mathbb{E}[\varepsilon_k^2]} = \sqrt{\mathbb{E}[\mathbb{E}[\varepsilon_k^2 | X_{k-1}]]} \right] \leq \sup_x \sigma_K(x) < \infty,$$

by A4, we can conclude that

$$\mathbb{E}[|\Delta_{\log K}|] \leq Ca^{\nu_K} \frac{1}{\sqrt{K}} \sup_x \sigma_K(x) = CK^{1/2-c} \sup_x \sigma_K(x) \rightarrow 0,$$

as  $K \rightarrow \infty$ . □

**Lemma 3.5.**

$$f_{\nu_K}^K(X_{n_K}) - f_{\nu_K}(X_{n_K}) \rightarrow 0.$$

*Proof.* By Assumption A5, for any  $0 \leq x \leq 1$  and some  $C > 0$ ,

$$\begin{aligned} |f_n^K(x) - f_n(x)| &\leq |f^K \circ f_{n-1}^K(x) - f \circ f_{n-1}^K(x)| + |f \circ f_{n-1}^K(x) - f \circ f_{n-1}(x)| \leq \\ &C/\sqrt{K} + a|f_{n-1}^K(x) - f_{n-1}(x)|. \end{aligned}$$

Hence, by induction, for any  $x$  and  $n$

$$|f_n^K(x) - f_n(x)| \leq \frac{C}{\sqrt{K}} \sum_{j=0}^{n-1} a^j \leq \frac{C}{(a-1)\sqrt{K}} a^n,$$

and

$$\sup_{0 \leq x} |f_{\nu_K}^K(x) - f_{\nu_K}(x)| = O\left(a^{\nu_K}/\sqrt{K}\right) = O(K^{1/2-c}) \rightarrow 0,$$

as  $K \rightarrow \infty$ . □

After these lemmas and the corollary, the proof of the main theorem below is direct.

**Theorem 3.6.** *Assume  $Z_0 = z_0$  given and all of Assumptions A0-A5 valid. Then  $X_{\log K}$  converges in distribution*

$$X_{\log K} \xrightarrow[K \rightarrow \infty]{D} h \circ W(z_0).$$

**Remark 3.7.** The limits increase strictly with  $n$ . Recall that logarithms are with base  $a$ .

**Corollary 3.8.** *For any fixed  $n$*

$$X_{\log K+n} \xrightarrow[K \rightarrow \infty]{D} f_n \circ h \circ W(z_0),$$

where  $f_n$  still denotes the  $n$ -th iterate of  $f$ . This extends to weak convergence of the sequences, regarded as random elements in  $\mathbb{R}^{\mathbb{Z}}$ :

$$\{X_{\log K+n}\}_{-\infty}^{\infty} \xrightarrow[K \rightarrow \infty]{D} \{f_n \circ h \circ W((z_0))\}_{-\infty}^{\infty}.$$

*Proof.* This follows by induction on  $n$  from the fundamental representation (3.2). For  $n=0$  it is the statement of the main result. For  $n=1$  take limits as  $K \rightarrow \infty$  in (3.2), and note that the stochastic term vanishes. Similarly, if

it holds true for  $n$ , it follows for  $n + 1$ . Functional convergence follows from finite dimensional convergence, cf. <sup>[3]</sup>, p. 19.  $\square$

**Corollary 3.9.** For any sequence  $\lambda_K = o(\log K)$ ,

$$X_{\lambda_K} \xrightarrow{K \rightarrow \infty} L^1 0.$$

*Proof.* This is direct from

$$\mathbb{E}[X_{\lambda_K}] \leq a^{\lambda_K - \log K} \rightarrow 0, \text{ as } K \rightarrow \infty. \quad \square$$

This means that there is a very particular scale,  $O(\log K)$ , at which an interesting weak limit is obtained, whereas slower or faster rates result in simpler convergences, as exhibited.

#### 4. Concluding remarks

Measuring population or set size in density rather than numbers, i.e. in capacity units, invites making the corresponding time change into an intrinsic scale also with unit  $K$ ,  $\bar{X}_t := X_{tK} = Z_{\lfloor tK \rfloor} / K, t \geq 0$ . For that process Theorem 3.6 yields that

$$\bar{X}_0 \leftarrow \bar{X}_{(\log K)/K} = X_{\log K} \xrightarrow{K \rightarrow \infty} D h \circ W(z_0).$$

Thus, the process in the intrinsic time scale seems to have started from a random number of first elements, unless the variance of  $W$  is zero. Only in that case, corresponding to a completely deterministic initial reproduction or replication process, can the the number  $z_0$  of ancestors or corresponding originators be recovered behind the random veil of history, by inversion of  $h$  <sup>[4]</sup>.

As mentioned, this article was sparked by the concrete problem of finding the number of original templates in PCR and answering questions about single- or multicell origin of cancers.<sup>[7]</sup> It is, however, tempting to suspect that similar patterns of late observed growth with unknown, seemingly random, origin may occur in many other contexts.<sup>[9]</sup>

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