# Reflections on the extinction-explosion dichotomy 

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## A R T I C L E I N F O

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#### Abstract

A wide range of stochastic processes that model the growth and decline of populations exhibit a curious dichotomy: with certainty either the population goes extinct or its size tends to infinity. There is an elegant and classical theorem that explains why this dichotomy must hold under certain assumptions concerning the process. In this note, I explore how these assumptions might be relaxed further in order to obtain the same, or a similar conclusion, and obtain both positive and negative results.


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## 1. Introduction

The 'merciless dichotomy' (Section 5.2 of Haccou et al., 2005) concerning extinction refers to a very general property of stochastic processes that describes the long-term fate of populations. Roughly speaking, the result states that if there is always a strictly positive chance the population could become extinct in the future (depending, perhaps, on the current population size), then the population is guaranteed to either become extinct or to grow unboundedly large. More precisely, a formal version of this result, due to Jagers (Theorem 2 of Jagers, 1992), applies to any sequence $X_{1}, X_{2}, \ldots, X_{n} \ldots$ of non-negative real-valued random variables that are defined on some probability space and which is absorbing at 0 (i.e. $X_{n}=0 \Rightarrow X_{n+1}=0$ for all $n$ ). It states that, provided:
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{1}, X_{2}, \ldots, X_{n}\right) \geq \delta_{x}>0 \quad$ whenever $X_{n} \leq x$
holds for all positive integers $n$, then, with probability 1 , either $X_{n} \rightarrow \infty$ or a value of $n$ exists for which $X_{k}=0$ for all $k \geq n$ (notice that $\delta_{x}$ can tend towards 0 at any rate as $x$ grows). The proof in Jagers (1992) involves an elegant and short application of the martingale convergence theorem. It is important to stress that condition (1) does not assume or require that $X_{n}$ is a Markov process, and we make no such assumption either.

Jagers' theorem applies to a wide variety of stochastic processes arising in evolution and population biology (e.g. Yule birth-death models, branching processes, etc.). For example, the result is applicable to any Markovian process of population size where the probability of future extinction is bounded away from zero for any given population size. Galton-Watson branching processes

[^0]provide a well-known example: For any sub-critical or a (nondegenerate) critical process extinction is certain, while for a supercritical process, the population either becomes extinct or its size necessarily tends to infinity (Kimmel and Axelrod, 2002). Similarly, in evolutionary biology, phylogenetic trees of species are typically modelled using a continuous-time process where, in the simplest case, the rate of speciation $\lambda$ and rate of extinction $\mu$ is constant (Kendall, 1949; Yule, 1924). If one samples the number of species present at regular time intervals, we obtain a Markov chain $X_{n}$ which satisfies the condition of Jagers' theorem. Moreover, extinction is certain whenever $\lambda \leq \mu$, while for $\lambda>\mu$ the tree either dies out or the number of leaves tends to infinity. Allowing the speciation and extinction rates ( $\lambda$ and $\mu>0$ ) to depend on the number of species present at that time (density-dependent diversification) (Lambert and Stadler, 2013), leads to a process that is still Markovian and also satisfies (1). However if $\mu$ depends on time then (1) may or may not apply.

Extensions of these models can readily lead to non-Markovian processes. For example, introducing age-dependence into branching processes (a 'Bellman-Harris' process), or phylogenetic models that allow the speciation or extinction rate to depend on the 'age' of the species (i.e. the length of the branch leading to that species Lambert and Stadler, 2013) produces a stochastic sequence $X_{n}$ that can violate the Markov condition. Thus, it is of interest to consider whether any non-Markovian stochastic population model, in which a population of any given size always has some positive chance of eventual extinction, must invariably either become extinct or grow unboundedly. Could it be, for instance, that some such models could allow a population that is able to persist by oscillating within finite bounds for long enough to persist indefinitely within these bounds?

Although the processes considered in Jagers (1992) (and here) need not be Markovian, nevertheless, the lower-bound inequality
condition in (1) has a Markovian-like flavour in that it is required to hold for all values of $X_{1}, X_{2}, \ldots, X_{n-1}$ whenever $X_{n}$ is less than $x$. This raises the question of how much this uniform bounding across the previous history of the process might be relaxed without sacrificing the conclusion of certain extinction or explosion. In this short note, we consider possible extensions of Jagers' theorem by weakening the assumption in (1). Specifically, we will consider a lower bound that conditions just on the event that $0<X_{n} \leq x$, either alone or alongside another variable that is dependent on (but less complete than) the past history $X_{1}, \ldots, X_{n-1}$.

First, we consider what happens if the probability in the lower bound (1) were to condition just on $0<X_{n} \leq x$. In this case, we describe a positive result that delivers a slightly weaker conclusion than the original theorem of Jagers. We then show that the full conclusion cannot be obtained by lower bounds that condition solely on $0<X_{n} \leq x$ by exhibiting a specific counterexample. However, in the final section, we show that the full conclusion of Jagers' theorem can be obtained by conditioning on $0<X_{n} \leq x$, together with some partial information concerning the past history of the process.

## 2. A simple general lemma and its consequence for bounded populations

We first present an elementary but general limit result, stated within the usual notation of a probability space $(\Omega, \Sigma, \mathbb{P})$ consisting of a sigma-algebra $\Sigma$ of 'events' (subsets of the sample space $\Omega$ ) and a probability measure $\mathbb{P}$ (for background on probability theory, see Grimmett and Stirzaker, 2001).

Suppose that $E_{1}, E_{2}, \ldots$ are ascending (i.e. $E_{i} \subseteq E_{i+1}$ ) and $E=\bigcup_{n=1}^{\infty} E_{n}$. For example, suppose that $E_{n}$ is the event that some particular 'situation' (e.g. extinction of the population) has arisen on or before a given time step $n$ (e.g. day, year). These events are ascending and their union $E$ is the event that the 'situation' eventually arises. We are interested in when $\mathbb{P}(E)=1$. A sufficient condition to guarantee this is to impose any non-zero lower bound on the probability that the 'situation' arises at time step $n$ given that it has not done so already; in other words, to require that the conditional probability $\mathbb{P}\left(E_{n} \mid \overline{E_{n-1}}\right)$ is at least $\delta>0$ for all sufficiently large values of $n$ (throughout this paper an overline denotes the complementary event).

On the other hand, it is equally easy to check that if $p_{n}=$ $\mathbb{P}\left(E_{n} \mid \overline{E_{n-1}}\right)$ is allowed to converge to zero sufficiently quickly (so the probability of the 'situation' first arising on day $n$ goes to zero sufficiently fast that $\left.\sum_{n} p_{n}<\infty\right)$, then it is possible for $\mathbb{P}(E)<1$. For example, if accidents occur independently and the probability of a particular accident is reduced each year by $1 \%$ of its current value, then there is a positive probability that no accident will ever occur; but if the probability reduces at the rate $1, \frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \frac{1}{5}, \ldots$, then an accident is guaranteed to eventually occur (by the second Borel-Cantelli lemma).

Rather than placing some lower bound on the probability that the situation arises at time step $n$, we can, following Jagers (1992), make a weaker assumption that if the situation has not happened yet, there is always a non-vanishing chance that it will occur some time in the future (formally, requiring merely that $\mathbb{P}\left(E \mid \overline{E_{n}}\right)$ is uniformly bounded away from 0 ). For maximal generality, we also wish to avoid any Markovian or independence assumptions. The following lemma provides a sufficient condition for $\mathbb{P}(E)=1$ without any further assumptions, and uses an elementary argument that will be useful later.

Lemma 1. Suppose $E_{n}$ is an ascending sequence with limit $E$ and suppose that for some $\epsilon>0, \mathbb{P}\left(E \mid \overline{E_{n}}\right) \geq \epsilon$ holds for all $n \geq 1$. Then $\mathbb{P}(E)=1$.

Proof. Let $p_{n}=P\left(E_{n}\right)$. Then, by the law of total probability:
$\mathbb{P}(E)=\mathbb{P}\left(E \mid \overline{E_{n}}\right)\left(1-p_{n}\right)+\mathbb{P}\left(E \mid E_{n}\right) p_{n}$.
Now, $\mathbb{P}\left(E \mid E_{n}\right)=1$ and, by assumption, $\mathbb{P}\left(E \mid \overline{E_{n}}\right) \geq \epsilon$. Therefore:
$\mathbb{P}(E) \geq \epsilon\left(1-p_{n}\right)+p_{n}$.
Since the events $E_{n}$ are ascending, a well known and elementary result in probability theory ensures that $\mathbb{P}(E)=\lim _{n \rightarrow \infty} p_{n}$. So, letting $n \rightarrow \infty$ in the previous inequality gives:
$\mathbb{P}(E) \geq \epsilon(1-\mathbb{P}(E))+\mathbb{P}(E)$,
which implies that $\mathbb{P}(E)=1$, as claimed.
Example 1. Consider population of a species where $X_{n}$ denotes the size of the population at time step $n$. The event $E_{n}=\left\{X_{n}=0\right\}$ is the event that the population is extinct by time step $n$ and this ascending sequence has the limit $E$ equal to the event of eventual extinction. In this setting, Lemma 1 provides the following special case of Jagers' theorem.

Corollary 2. Suppose that $X_{1}, X_{2}, \ldots, X_{n}$ is a sequence of nonnegative real-valued random variables that are absorbing at 0 and are constrained to lie between 0 and $M$. Moreover, suppose that for some $\delta>0$ and all positive integers $n$ we have: $\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \neq\right.$ $0) \geq \delta$. Then, with probability 1 , a value $n$ exists for which $X_{k}=0$ for all $k \geq n$.

### 2.1. Remarks

(a) One might view Lemma 1 as a simple formulation of 'Murphy's Law' - the idea that if something bad can happen, it will at some point (a popular claim often made in jest that has an interesting history Wikipedia, 2014). In that context, $E_{n}$ is simply the event that the 'bad thing' has happened on or before day $n$.
(b) The proof of Lemma 1 shows that $\lim _{n \rightarrow \infty} \mathbb{P}\left(E \mid \overline{E_{n}}\right)>0 \Longrightarrow$ $\mathbb{P}(E)=1$. The converse also holds, provided that $\mathbb{P}\left(E_{n}\right)<1$ for all $n$; indeed under that restriction, a sharper limit can be stated: $\mathbb{P}(E)=1 \Longrightarrow \lim _{n \rightarrow \infty} \mathbb{P}\left(E \mid \overline{E_{n}}\right)=1$. With a view towards Borel-Cantelli type results, note also that one can have: $\sum_{n \geq 1} \mathbb{P}\left(E \mid \overline{E_{n}}\right)=\infty$ and $\mathbb{P}(E)<1$, if, for example, $\mathbb{P}\left(E_{n}\right)=q-\frac{1}{n}$, where $q<1$.
(c) A general characterisation for when $\mathbb{P}(E)=1$ is the following result from Bruss (1980).

Proposition 1. If $E_{n}$ is an ascending sequence of events with limit $E$, then $\mathbb{P}(E)=1$ if and only if either $\mathbb{P}\left(E_{1}\right)=1$ or $\mathbb{P}\left(E_{i} \mid \overline{E_{i-1}}\right)=1$ for some $i$, or $\sum_{i=1}^{\infty} \mathbb{P}\left(E_{t_{i}} \mid \overline{E_{t_{i-1}}}\right)=\infty$ for some strictly increasing sequence $t_{i}$.

## 3. A convergence in probability result for $\boldsymbol{X}_{\boldsymbol{n}}$

We now consider what happens if the population size is not bounded above by some maximal value $M$ as in Corollary 2. In this case, by weakening the conditioning in Inequality (1) to just $X_{n} \in(0, m]$, one can still derive a result concerning convergence in probability (rather than almost sure convergence) of the population size to 0 or infinity, as we now show.

Proposition 2. Suppose that $X_{1}, X_{2}, \ldots, X_{n}$ is a sequence of nonnegative real-valued random variables that are absorbing at 0 , and that for each positive integer $m$, there is a value $\delta_{m}>0$ for which the following holds for all values of $n$ :
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0, m]\right) \geq \delta_{m}$.
Then, for every $m \geq 1$, we have $\lim _{n \rightarrow \infty} \mathbb{P}\left(X_{n}=0 \cup X_{n}>m\right)=1$.

Proof. Throughout this proof we will let $E$ denote the event $\{\exists r$ : $\left.X_{r}=0\right\}$. The proof of Proposition 2 relies on the following result.

Claim. Both $\mathbb{P}\left(X_{n}=0 \mid X_{n} \leq m\right)$ and $\mathbb{P}\left(E \mid X_{n} \leq m\right)$ converge to 1 as $n \rightarrow \infty$.
Proposition 2 follows directly from this claim, since, for any $m \geq 1$ :

$$
\begin{aligned}
\mathbb{P}\left(X_{n}=0 \cup X_{n}>m\right)= & \mathbb{P}\left(X_{n}=0\right)+\mathbb{P}\left(X_{n}>m\right) \\
\geq & \mathbb{P}\left(X_{n}=0 \mid X_{n} \leq m\right) \mathbb{P}\left(X_{n} \leq m\right) \\
& +\mathbb{P}\left(X_{n}>m\right) .
\end{aligned}
$$

By the claim, $\mathbb{P}\left(X_{n}=0 \mid X_{n} \leq m\right)$ converges to 1 as $n$ grows, and so the previous inequality ensures that $\lim _{n \rightarrow \infty} \mathbb{P}\left(X_{n}=0 \cup X_{n}>\right.$ $m)=1$, as required. Thus it suffices to establish the claim.
Proof of Claim. Consider any subsequence $n(k)$ of positive integers for which the bounded sequence $\mathbb{P}\left(X_{n(k)} \leq m\right)$ has a limit. Such subsequences exist (by the Bolzano-Weierstrass theorem), and since $\lim \inf _{n \rightarrow \infty} \mathbb{P}\left(X_{n} \leq m\right)>0$ (by (2)) for all $m \geq 1$, the limit of $\mathbb{P}\left(X_{n(k)} \leq m\right)$ for any such subsequence is strictly positive (this latter observation also ensures that some conditional probabilities below are well defined for large enough values of $k$ ). By the law of total probability:

$$
\begin{aligned}
\mathbb{P}\left(E \mid X_{n(k)} \leq m\right)= & \mathbb{P}\left(E \mid X_{n(k)}=0\right) \mathbb{P}\left(X_{n(k)}=0 \mid X_{n(k)} \leq m\right) \\
& +\mathbb{P}\left(E \mid X_{n(k)} \in(0, m]\right) \\
& \times \mathbb{P}\left(X_{n(k)}>0 \mid X_{n(k)} \leq m\right)
\end{aligned}
$$

Thus if we let $p_{k}=\mathbb{P}\left(X_{n(k)}=0 \mid X_{n(k)} \leq m\right)$, then, by (2):
$\mathbb{P}\left(E \mid X_{n(k)} \leq m\right) \geq 1 \cdot p_{k}+\delta_{m}\left(1-p_{k}\right)$.
Now, $p_{k}=\mathbb{P}\left(X_{n(k)}=0\right) / \mathbb{P}\left(X_{n(k)} \leq m\right)$ and so $\lim _{k \rightarrow \infty} p_{k}=$ $\lim _{k \rightarrow \infty} \mathbb{P}\left(X_{n(k)}=0\right)$, since the numerator and denominator limits are non-zero. Moreover, we have $\mathbb{P}(E)=\lim _{k \rightarrow \infty} \mathbb{P}\left(X_{n(k)}=0\right)$ and so:
$\lim _{k \rightarrow \infty} p_{k}=\lim _{k \rightarrow \infty} \mathbb{P}\left(E \mid X_{n(k)} \leq m\right)$.
Let $p$ denote the shared limit in Eq. (4). Then, from Inequality (3) we have:
$p \geq p+\delta_{m}(1-p)$,
which implies that $p=1$. Thus, for all subsequences $n(k)$ of positive integers for which $\mathbb{P}\left(X_{n(k)} \leq m\right)$ has a limit, this limit takes the same value (namely 1). It follows from a well-known result in analysis (e.g. Theorem 11, p. 67 of Malik and Arora, 1992) that the full sequence $\mathbb{P}\left(X_{n} \leq m\right)$ also converges to 1 as $n \rightarrow \infty$, and, therefore, so do the sequences $\mathbb{P}\left(X_{n}=0 \mid X_{n} \leq m\right)$ and $\mathbb{P}\left(E \mid X_{n} \leq m\right)$. This establishes the two limit claims in the Claim, and so completes the proof of Proposition 2.

Notice that Proposition 2 also implies Corollary 2 by taking $m=M$ and $\delta_{m}=\delta$ in (2).
3.1. The conclusion of Proposition 2 cannot be strengthened to almost sure convergence

Suppose $X_{1}, X_{2}, \ldots, X_{n} \ldots$ is a sequence of non-negative realvalued random variables that satisfy the conditions described in Proposition 2. In this case, the proposition assures us that $X_{n}$ converges in probability either to 0 or to infinity. This is a weaker conclusion than the statement that, with probability 1, either $X_{n}=$ 0 for all sufficiently large $n$, or $X_{n} \rightarrow \infty$. We now show, by an explicit example, that such a stronger conclusion (which holds under the stronger condition (1) required for Jagers' theorem) need not hold under just the conditions described in Proposition 2. In other words, some additional conditioning on the past history of
the process is required in order to secure the stronger conclusion (we describe this further in the next section).

Example 2. Consider the following process. Let $X_{n}^{1}, n \geq 1$ be a sequence of independent random variables with:
$\mathbb{P}\left(X_{n}^{1}\right)= \begin{cases}1, & \text { with probability } \frac{1}{n} ; \\ n, & \text { otherwise. }\end{cases}$
For each $k \geq 2$, let $X_{n}^{k}, n \geq 1$ be the (deterministic) random variables defined by:
$\mathbb{P}\left(X_{n}^{k}\right)= \begin{cases}1, & \text { with probability } 1 \text { for all } n \in\left[1, \ldots, 2^{k}\right) ; \\ 0, & \text { with probability } 1 \text { for all } n \geq 2^{k} .\end{cases}$
Now, let $X_{n}$ be the stochastic process which selects $K=k$ with probability $\frac{1}{2^{k}}$ (for $k=1,2, \ldots$ ) and then takes $X_{n}$ to be the process $X_{n}^{K}$ for all $n \geq 1$.

Firstly, note that this mixture process is well defined, since $\sum_{k \geq 1} \mathbb{P}(K=k)=1$. Next, observe that since $X_{n}^{1}=1$ infinitely often (with probability 1 ) by the Borel-Cantelli Lemma (for independent random variables) and since there is a probability of $\frac{1}{2}$ that $X_{n}=X_{n}^{1}$ for all $n$, then, with probability $\frac{1}{2}, X_{n}$ does not converge to infinity or hit zero (note that $X_{n}^{1} \neq 0$ for any $n$, and $X_{n}^{1}$ returns to 1 infinitely often and so does not tend to infinity).

Thus, to establish the claim regarding our example it suffices to show that Inequality (2) applies. This can be verified, and the details are provided in the Appendix.

## 4. An extended extinction dichotomy theorem

The example in the previous section shows that in (2) we need to supplement the condition $X_{n} \in(0, m]$ with some further information concerning the past history of the process, in order to guarantee eventual extinction or $X_{n} \rightarrow \infty$. Here, we provide a mild extension of Theorem 2 of Jagers (1992) by conditioning on the number of times the process has dipped below each given value $m$ up to the present step of the process.

Theorem 3. Suppose $X_{1}, X_{2}, \ldots, X_{n} \ldots$ is a sequence of nonnegative real-valued random variables that are absorbing at 0 . For each positive integer $m \geq 1$, let $\kappa_{m}\left(X_{1}, \ldots, X_{n-1}\right)$ count the number of $X_{1}, X_{2}, \ldots, X_{n-1}$ that are less than or equal to $m$. Suppose that for each positive integer $m$, there exists $\delta_{m}>0$ for which the following holds for all $n$ :
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0, m], \kappa_{m}\left(X_{1}, \ldots, X_{n-1}\right)\right) \geq \delta_{m}$.
Then, with probability 1, either $X_{n} \rightarrow \infty$ or a value of $n$ exists for which $X_{k}=0$ for all $k \geq n$.
Proof. For any strictly positive integers $n$ and $m$, let $E_{n}$ be the event that $X_{n}=0$ and let $J_{m}$ be the event that $X_{k} \leq m$ for infinitely many values of $k$. Notice that $E_{n}$ and $J_{m}$ are both ascending sequences. Moreover, if we let $E=\bigcup_{n \geq 1} E_{n}, J=\bigcup_{m \geq 1} J_{m}$ and $\bar{J}=\bigcap_{m \geq 1} \overline{J_{m}}$, then $E$ is the event that some $k$ exists such that $X_{k}=0$ and $\bar{J}$ is the event that $X_{n} \rightarrow \infty$. We wish to show the following:
$\mathbb{P}(E \cup \bar{J})=1$.
Notice that:
$E \subseteq J_{m}$ for each $m \geq 1$.
Furthermore, $\mathbb{P}(E)>0$ by Inequality (5) applied to $n=1$, and any value of $m \geq 1$ for which $\mathbb{P}\left(X_{1} \leq m\right)>0$. Thus, from $(7), \mathbb{P}\left(J_{m}\right)>0$ (and so $\mathbb{P}(J)>0$ also), so the conditional probabilities $\mathbb{P}(E \mid J)$ and
$\mathbb{P}\left(E \mid J_{m}\right)$ are well defined, and for each $m \geq 1$, the inclusion (7) gives:
$\mathbb{P}(E)=\mathbb{P}\left(E \mid J_{m}\right) \mathbb{P}\left(J_{m}\right)$.
We will show that:
$\mathbb{P}\left(E \mid J_{m}\right)=1 \quad$ for each $m \geq 1$,
which, combined with Eq. (8), gives $\mathbb{P}(E)=\mathbb{P}\left(J_{m}\right)$ for each $m \geq 1$. Thus, since $\mathbb{P}(J)=\lim _{m \rightarrow \infty} \mathbb{P}\left(J_{m}\right)$ (recall $J_{m}$ are ascending), we have $\mathbb{P}(E)=\mathbb{P}(J)$, and consequently $\mathbb{P}(E)+\mathbb{P}(\bar{J})=1$, since $E$ and $\bar{J}$ are mutually exclusive. In this way we obtain the required identity (6) that establishes the theorem.

Thus it suffices to establish Eq. (9). For this we employ a coupling-style argument. For each positive integer $m$, we will associate to $X_{n}$ a second sequence of random variables $Y_{k}, k \geq 1$ as follows. Let $O_{m}=\left\{n \geq 1: X_{n} \leq m\right\}$, and for each $k \leq\left|\bar{O}_{m}\right|$, let $Y_{k}=X_{v(k)}$ where the random variable $v(k)$ is the $k$ th element of $O_{m}$ under the natural ordering of the positive integers. If $O_{m}$ is finite, then set $Y_{k}=0$ for all $k>\left|O_{m}\right|$ (notice that this will not occur when we condition on $J_{m}$ below).

We may assume that the joint probability $\mathbb{P}\left(Y_{k} \neq 0, J_{m}\right)$ is strictly positive; otherwise $\mathbb{P}\left(Y_{k}=0 \mid J_{m}\right)=1$ and so (9) holds, since $\mathbb{P}\left(Y_{k}=0 \mid J_{m}\right) \leq \mathbb{P}\left(E \mid J_{m}\right)$. Consequently, the conditional probabilities are well defined in the following equation:

$$
\begin{align*}
\mathbb{P}\left(E \mid Y_{k} \neq 0, J_{m}\right)= & \sum_{n \geq 1} \mathbb{P}\left(E \mid X_{n} \in(0, m], v(k)=n, J_{m}\right) \\
& \cdot \mathbb{P}\left(v(k)=n \mid Y_{k} \neq 0, J_{m}\right) . \tag{10}
\end{align*}
$$

From (7) and (5), we obtain the following equality and inequality, respectively:

$$
\begin{align*}
& \mathbb{P}\left(E \mid X_{n} \in(0, m], v(k)=n, J_{m}\right) \\
& \quad \geq \mathbb{P}\left(E \mid X_{n} \in(0, m], v(k)=n\right) \geq \delta_{m} \tag{11}
\end{align*}
$$

where the first inequality is from (7) and the second inequality is from (5), since conditioning on the conjunction $X_{n} \in$ ( $0, m], v(k)=n$ is equivalent to conditioning on the conjunction of $X_{n} \in(0, m]$ and $\kappa_{m}\left(X_{1}, \ldots, X_{n-1}\right)=k-1$. Substituting (11) into the right-hand side of $(10)$ gives $\mathbb{P}\left(E \mid Y_{k} \neq 0, J_{m}\right) \geq \delta_{m}$. Thus, we have:

$$
\begin{align*}
\mathbb{P}\left(E \mid J_{m}\right) & =\mathbb{P}\left(E \mid Y_{k} \neq 0, J_{m}\right) \mathbb{P}\left(Y_{k} \neq 0 \mid J_{m}\right)+1 \cdot \mathbb{P}\left(Y_{k}=0 \mid J_{m}\right) \\
& \geq \delta_{m}\left(1-p_{k}\right)+1 \cdot p_{k}, \tag{12}
\end{align*}
$$

where $p_{k}=\mathbb{P}\left(Y_{k}=0 \mid J_{m}\right)$, and where the factor 1 is because, conditional on $J_{m}$, the event $E$ occurs whenever $Y_{k}=0$. Now, $\left\{Y_{k}=\right.$ $0\}$ is an ascending sequence in $k$, so if we let $y:=\bigcup_{k \geq 1}\left\{Y_{k}=0\right\}$, then:
$p:=\lim _{k \rightarrow \infty} p_{k}=\mathbb{P}\left(y \mid J_{m}\right)$.
Moreover:
$\mathbb{P}\left(E \mid J_{m}\right)=\mathbb{P}\left(y \mid J_{m}\right)$.
Applying (13) and (14) into (12) gives: $p \geq \delta_{m}(1-p)+p$, which, in turn, implies that $p=1$ (since $\delta_{m}>0$ ). Thus, $\mathbb{P}\left(E \mid J_{m}\right)=p=1$, which establishes (9) and so completes the proof.

### 4.1. Remarks concerning Theorem 3

Notice that Theorem 3 implies Theorem 2 of Jagers (1992), since the lower bound (5) involves conditioning on aggregates of values for $X_{1}, \ldots, X_{n}$, so it holds automatically under the lower bound (1). Notice also that the proof of Theorem 3, though longer than the elegant martingale argument for Theorem 2 of Jagers (1992), requires merely elementary notions in probability.

It turns out that the collection of random variables $\kappa_{m}\left(X_{1}\right.$, $\ldots, X_{k}$ ) across all (real) values of $m$ and all integer values of $k$ between 1 and $n$ suffices to determine the sequence of random variables $X_{1}, \ldots, X_{n}$ (by induction on $k$ ), so it is not immediately clear that Theorem 3 really allows greater generality than Theorem 2 of Jagers (1992). Therefore we provide an example to show that this is indeed the case. Informally, the extra generality in Theorem 3, arises from imposing fewer inequalities: in (5) there are $n$ inequalities corresponding to the $n$ possible values that $\kappa_{m}\left(X_{1}, \ldots, X_{n-1}\right)$ can take, while in (1), there are potentially infinitely many, corresponding to all possible values for $X_{1}, \ldots, X_{n-1}$ (and for $X_{n} \leq x$ ).

Example 3. Roughly speaking, the stochastic process we will construct becomes extinct unless it oscillates regularly within a fixed range for an initial period, and the longer that it oscillates the greater the chance that it will escape to infinity rather than become extinct. We show that such a process satisfies (5) but not (1).

First, consider a simple Markov chain $Y_{n}$ on the three states 0 , 1,2 that starts in state 2 (i.e. $Y_{1}=2$ with probability 1 ) and with transition probabilities described as follows:

- 0 is an absorbing state;
- from state 1 or state 2 , the next state is chosen with equal probability $\left(\frac{1}{3}\right)$ from $0,1,2$.
Thus, with probability 1 , a value $n$ exists for which $Y_{k}=0$ for all $k \geq n$.

We will say that a sequence of values $y_{1}, y_{2}, y_{3}, \ldots, y_{k}$ from $\{1,2\}$ is a terminated flip sequence (of length $k$ ) if $y_{1}=2$ and $y_{i}=y_{i-1}$ only for $i=k$. For example ( $2,1,2,1,2,1,2,1,1$ ) and ( $2,1,2,1,2,2$ ) are terminated flip sequences of lengths nine and six respectively.

We use $Y_{n}$ to define our process $X_{n}$ which takes non-negative integer values as follows. If there is no value $N \geq 4$ for which $Y_{1}, Y_{2}, \ldots, Y_{N}$ is a terminated flip sequence, then set $X_{n}=Y_{n}$ for all $n$; in which case $X_{n}$ absorbs at 0 with probability 1 . On the other hand, if a value $N \geq 4$ exists for which $Y_{1}, Y_{2}, \ldots, Y_{N}$ is a terminated flip sequence, then, conditional on this value of $N$, $X_{n}=Y_{n}$ for all $n \leq N$, and for $n>N, X_{n}=Z_{n-N}^{N}$, where $Z_{1}^{N}, Z_{2}^{N}, \ldots$ is a second Markov chain on the state space $\{0\} \cup\{N-1, N, N+$ $1, N+2, \ldots$. This second chain has $Z_{1}=N-1$ (with probability 1), and has transitions from each state $i \geq N-1$ to 0 and to $i+1$ with probabilities of $2^{-i}$ and $1-2^{-i}$, respectively.

Notice that, although the process $X_{n}$ is absorbing at 0 , it fails to satisfy (1) since, for an terminated flip sequence ( $x_{1}, x_{2}, \ldots, x_{n}$ ), of length 4 or more, we have $x_{n} \leq 2$ and yet:
$\mathbb{P}\left(\exists r: X_{r}=0 \mid \wedge_{i=1}^{n}\left\{X_{i}=x_{i}\right\}\right)=\sum_{j=n-1}^{\infty} \frac{1}{2^{j}} \rightarrow 0, \quad$ as $n \rightarrow \infty$.
To show that $X_{n}$ satisfies (5), we consider the cases $m=1$, $m=2$ and $m>2$ separately. For $m=1$, (5) is equivalent to the following inequality holding for all $n \geq 1$ :
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n}=1, \kappa_{1}\left(X_{1}, \ldots, X_{n-1}\right)\right) \geq \delta_{1}>0$.
Now, if $\kappa_{1}\left(X_{1}, \ldots, X_{n-1}\right) \neq\lfloor(n-1) / 2\rfloor$ then $X_{1}, \ldots, X_{n}$ cannot be a terminated flip sequence, and so, with probability at least $\frac{1}{3}$, we have $X_{n+1}=0$. On the other hand, if $\kappa_{1}\left(X_{1}, \ldots, X_{n-1}\right)=\lfloor(n-$ 1) $/ 2$ 」 then the probability that $Y_{1}, Y_{2}, \ldots, Y_{n}$ is a terminated flip sequence of length 4 or more is bounded away from 1 as $n$ grows, and so the event $\left\{\exists r: X_{r}=0\right\}$ has a probability that is bounded away from 0 for all $n$ when we condition on $\kappa_{1}\left(X_{1}, \ldots, X_{n-1}\right)$ and $X_{n}=1$. Thus a value $\delta_{1}>0$ can be chosen to satisfy (15) for all $n \geq 1$.

For $m=2$, (5) is equivalent to the following inequality holding for all $n \geq 1$ :
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0,2]\right) \geq \delta_{2}>0$.
Notice that $\kappa_{2}$ has vanished, since $X_{n} \in(0,2]$ implies that $\kappa_{2}\left(X_{1}\right.$, $\left.\ldots, X_{n-1}\right)=n-1$ with probability 1 . Now, conditional on $X_{n} \in$ $(0,2]$, the probability that $Y_{1}, Y_{2}, \ldots, Y_{n}$ is a terminated flip sequence of length 4 or more is bounded away from 1 as $n$ grows, and so the event $\left\{\exists r: X_{r}=0\right\}$ has a probability that is bounded away from 0 for all $n$ when we condition on $X_{n} \in\{1,2\}$. Thus a value $\delta_{2}>0$ can be chosen to satisfy (16) for all $n \geq 1$.

Finally, for each $m>2$, for all $n \geq 1$ :
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0, m], \kappa_{m}\left(X_{1}, \ldots, X_{n-1}\right)\right) \geq 2^{-m}>0$,
so we can set $\delta_{m}=2^{-m}$ for all $m>2$. In summary, for all values of $m, X_{n}$ satisfies (5) for all $n$, as claimed.

## 5. Concluding comments

Our study of Jagers' theorem was motivated on two fronts. Firstly, it is of interest to explore why this general result holds, which assumptions are required for its conclusion to hold, and what machinery is needed for its proof. For instance, we have seen how a slightly weaker version conclusion is possible under less restrictive assumptions (Proposition 2) and this result follows easily from elementary probability theory. Also, a more general version of Jagers' theorem (requiring slightly weaker hypotheses) can be established (Theorem 3) also by elementary but more lengthy arguments. While elementary proofs are helpful, it may also be interesting to see whether this or other extensions of Jagers' theorem can be obtained by extending the martingale-type approach used in its original proof.

Secondly, for applications, Proposition 2 shows that any population in which the probability of eventual extinction, given the present population size, is bounded away from zero, must converge in probability to 0 or infinity. While this is obvious for Markovian processes, it is less so for non-Markovian ones discussed in the introduction (e.g. the Bellman-Harris branching processes and phylogenetic models with age-dependent extinction rates). But even for processes where this condition applies, this alone is not enough to ensure the almost sure convergence of the population to 0 or infinity, as Example 2 demonstrated. For this stronger convergence, one really needs an inequality on eventual extinction that conditions not just on the present population size but also, at least partly, on the prior history of the process. Yet, as Theorem 3 and Example 3 show, the entire history of the process is not required.

Finally, is useful to remember that although a population may be certain to become extinct eventually for certain models, in applications we are typically considering a population that is still extant. In other words, biologists will often consider such a process conditional on it not being extinct. This in turn can lead to interesting theory concerning the stochastic nature of populations, such as Yaglom's theorem for subcritical branching processes (Kimmel and Axelrod, 2002), or of phylogenetic trees, such as the critical branching model of Aldous and Popovic (2005). From this perspective, extinction is not the end of the story, but merely the beginning of a new one.

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## Appendix. Proof that Example 2 satisfies inequality (2)

Firstly, if $m<1$, then conditioning on $X_{n} \leq m$ is equivalent to conditioning on $K>1$ and so we can take any positive value for $\delta_{m}$ (even $=1$ ) and satisfy Inequality (2).

Next, suppose that $m \geq 1$, and, for any $n \geq 1$, write:
$n=2^{q}+r, \quad$ where $0 \leq r<2^{q}, q \geq 0$.
Since $\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0, m]\right)=\mathbb{P}\left(K>1 \mid X_{n} \in(0, m]\right)$ we have:
$\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in(0, m]\right)=\sum_{k \geq 2} \mathbb{P}\left(K=k \mid X_{n} \in(0, m]\right)$,
and, from Bayes' identity:
$\mathbb{P}\left(K=k \mid X_{n} \in(0, m]\right)=\frac{\mathbb{P}\left(X_{n} \in(0, m] \mid K=k\right) \mathbb{P}(K=k)}{\mathbb{P}\left(X_{n} \in(0, m]\right)}$.
Now, for any $k \geq 2$ (and still with $m>1$ ):
$\mathbb{P}\left(X_{n} \in(0, m] \mid K=k\right)= \begin{cases}1, & \text { provided } k \geq q+1 ; \\ 0, & \text { otherwise; }\end{cases}$
since $X_{n}^{k}=1$ with probability 1 for all $n \in\left[1, \ldots, 2^{k}\right)$. Consequently, the numerator of (19) equals $\frac{1}{2^{k}}(=\mathbb{P}(K=k))$ when $k \geq q+1$ and is zero otherwise.

Now, the denominator of (19), namely $\mathbb{P}\left(X_{n} \in(0, m]\right)$, can be written as:

$$
\begin{align*}
& {\left[\sum_{k \geq 2} \mathbb{P}\left(X_{n} \in(0, m] \mid K=k\right) \mathbb{P}(K=k)\right]} \\
& \quad+\mathbb{P}\left(X_{n} \in(0, m] \mid K=1\right) \mathbb{P}(K=1) \tag{21}
\end{align*}
$$

From (20), the first term in (21) is:
$\sum_{k \geq 2} \mathbb{P}\left(X_{n} \in(0, m] \mid K=k\right) \mathbb{P}(K=k)=\sum_{k \geq q+1} \frac{1}{2^{k}}=\frac{1}{2^{q}}$.
Regarding the second term in (21), observe that:
$\mathbb{P}\left(X_{n} \in(0, m] \mid K=1\right)= \begin{cases}\frac{1}{n}, & \text { provided } n>m ; \\ 1, & \text { if } n \leq m .\end{cases}$
Therefore, recalling (17), the second term in (21) is:
$\begin{cases}\frac{1}{n} \times \frac{1}{2}=\frac{1}{2^{q+1}+2 r} \leq \frac{1}{2^{q+1}}, & \text { provided } n>m ; \\ 1 \times \frac{1}{2}, & \text { when } n \leq m .\end{cases}$
Consequently, by combining (21)-(23) into (19) (and noting again that $\left.\sum_{k \geq q+1} \frac{1}{2^{k}}=\frac{1}{2^{q}}\right)$ we have that if $n>m$, then $\sum_{k \geq 2} \mathbb{P}(K=$ $\left.k \mid X_{n} \in(0, m]\right) \geq \frac{\frac{1}{2^{q}}}{\frac{1}{2 q}^{q}+\frac{1}{2^{q+1}}} \geq \frac{1}{2}$, while if $n \leq m$, then $\sum_{k \geq 2} \mathbb{P}(K=$ $\left.k \mid X_{n} \in(0, m]\right) \geq \frac{\frac{1}{2 q}}{\frac{1}{2 q}+\frac{1}{2}} \geq \frac{\frac{1}{2 q}}{1+\frac{1}{2}} \geq \frac{2}{3} \cdot \frac{1}{2 q} \geq \frac{2}{3 m}$, where the last inequality is from $m \geq n \geq 2^{q}$. Thus, if we take $\delta_{1}=\frac{1}{2}$ and $\delta_{m}=\frac{2}{3 m}$ for each $m \geq 2$, then, from (18), $\mathbb{P}\left(\exists r: X_{r}=0 \mid X_{n} \in\right.$ $(0, m]) \geq \delta_{m}$ for all $n, m$, as claimed.

## References

Aldous, D., Popovic, L., 2005. A critical branching process model for biodiversity. Adv. Appl. Probab. 37 (4), 1094-1115.
Bruss, F.T., 1980. A counterpart of the Borel-Cantelli Lemma. J. Appl. Probab. 17, 1094-1101
Grimmett, G.R., Stirzaker, D.R., 2001. Probability and Random Processes, third ed. Oxford University Press, New York, USA.
Haccou, P., Jagers, P., Vatutin, V.A., 2005. Branching Processes: Variation, Growth, and Extinction of Populations. In: Cambridge Studies in Adaptive Dynamics, Cambridge University Press, Cambridge UK.
Jagers, P., 1992. Stabilities and instabilities in population dynamics. J. Appl. Probab. 29 (4), 770-780.

Kendall, D.G., 1949. Stochastic processes and population growth. J. R. Stat. Soc. Ser. B 11, 230-264.
Kimmel, M., Axelrod, D.E., 2002. Branching Processes in Biology. Springer-Verlag, New York.
Lambert, A., Stadler, A., 2013. Birth-death models and coalescent point processes: the shape and probability of reconstructed phylogenies. Theor. Popul. Biol. 90, 113-128.
Malik, S.C., Arora, S., 1992. Mathematical Analysis. New Age International, New Delhi, India.
Wikipedia, 2014. http://en.wikipedia.org/wiki/Murphy'slaw (accessed 15.09.14.).
Yule, G.U., 1924. A mathematical theory of evolution, based on the conclusions of Dr J. C. Willis. Philos. Trans. R. Soc. Lond. B 213, 21-87.


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