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A surprising Poisson process arising from a species competition model

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Abstract

Motivated by the work of Tilman (Ecology 75 (1994) 2) and May and Nowak (J. Theoret. Biol. 170 (1994) 95) we consider a process in which points are inserted randomly into the unit interval and a new point kills each point to its left independently and with probability a. Intuitively this dynamic will create a negative dependence between the number of points in adjacent intervals. However, we show that the ensemble of points converges to a Poisson process with intensity $1/(a(1-x))$, and the number of points at time t grows like $(\log t)/a$.
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1. Introduction

Tilman (1994) studied coexistence among a sequence of species in which species with lower numbers are superior competitors. Letting p_i to be the fraction of patches occupied by type i and taking the limit of an infinite number of patches, he arrived at the following ordinary differential equations:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \beta_i p_i \left(1 - \sum_{j=1}^{i} p_j\right) - \delta_i p_i - p_i \sum_{j=1}^{i-1} \beta_j p_j. \tag{1}$$

Here β_i and δ_i are the colonization and death rates for the ith species. The first term on the right-hand side represents births by type i onto sites that are vacant or occupied

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by inferior competitors. The second and third terms represent loss of sites of type i due to deaths or takeover by lower numbered species.

The first equation in (1) says $\mathrm{d}p_1/\mathrm{d}t = \beta_1 p_1(1-p_1) - \delta_1 p_1$, so in equilibrium we have $p_1^* = (\beta_1 - \delta_1)/\beta_1$. In general, the equation for each p_i^* only involves $p_1^*, \dots, p_i^*$, so the equations can be solved recursively for the equilibrium frequencies. The algebra of the exact solution is somewhat messy, but one can easily verify that an arbitrarily large number of species can coexist. If we take $\delta_i = 1$ for all i, and each β_i is in turn chosen large enough, then each $p_i^* > 0$.

Tilman's result shows that if we are allowed to design the competing species, then an arbitrarily large number can coexist. May and Nowak (1994) considered the problem of determining how many species will coexist if the system is subject to a sequence of random arrivals. They investigated two special cases of Tilman's model: constant mortality $\delta_i \equiv 1$ and constant fecundity $\beta_i \equiv 1$. The former is perhaps more realistic for competition of species, but for mathematical simplicity we will concentrate here on the "constant fecundity" case of the model which can be thought of as competition of different strains of a virus that are equally transmissible but differ in their levels of virulence. May and Nowak investigated the distribution of types in the following system. Each species (or type) is represented by its death rate which is a number in $(0,1)$. A *configuration* is a family of coexisting species represented by a subset of $(0,1)$ with their corresponding densities. May and Nowak devised a fairly complicated algorithm that took a given configuration as input and produced the corresponding "equilibrium configuration" as output. Assume for concretness that originally there are no species in the system. The original May end Nowak species competition model evolves according to the dynamics:

(i) introduce a new species with death rate δ chosen at random from $(0,1)$;
(ii) recompute the equilibrium configuration.

To make contact with Tilman's setup we suppose that species with higher death rates are superior competitors to those with lower death rates.

The long-term behavior of this process should reflect the behavior of a system where migrations into the system are rare, and the system has a chance to relax to equilibrium between migrations. The details of step (ii) are quite messy (we omit them here) so May and Nowak (1994) introduced a toy version of the model in which instead of (ii) we have:

(ii$'$) simultaneously with the insertion of the new species δ, each species $\delta_1 < \delta$, which was present in the previous time step is eliminated, independent of the past and other species, with probability a (α in their notation).

To analyze the original model, they used simulations to argue (see their p. 102) that it behaved like the toy model with $a = 0.114$, and they used physics-style calculations to analyze the toy model.

The purpose of this note is to give a rigorous analysis of the toy model. The first step is to show

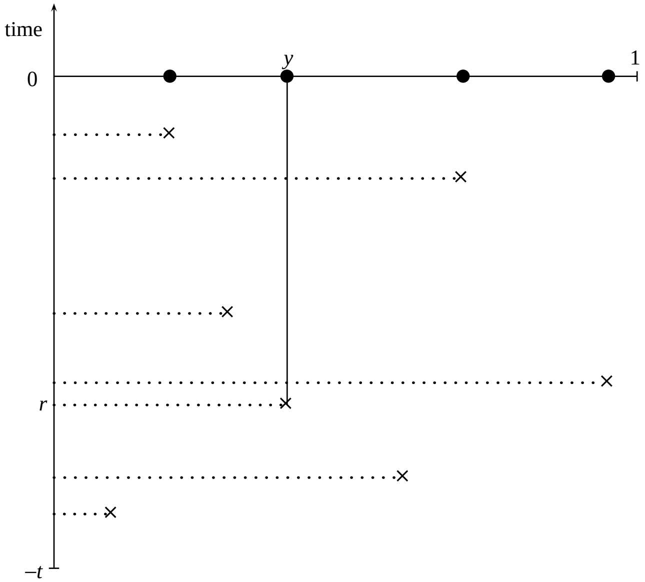

Fig. 1. Graphical construction.

Proposition 1. *Consider the model defined by* (i) *and* (ii′). *As time* $t \to \infty$ *the distribution of the current configuration converges to a stationary distribution* π^a.

Proof. For convenience we reformulate the model in continuous time so that points are added at rate 1, and shift the initial time to $-t$ for some $t > 0$. To construct the process at time 0 we use a Poisson process on $(0,1)\times[-t,0]$ with mean measure $\mathrm{d}x\,\mathrm{d}s$. Connect each point (x,s) of the Poisson process via a dotted line segment to $(0,s)$. To see if a species y that arrived at time r will show up in the configuration at time 0, we draw a line segment from (y,r) to $(y,0)$ and count the number of horizontal dotted segments it crosses. If this number is k then the probability there is a point at y at time 0 is $(1-a)^k$. See Fig. 1 for a picture. There a circle at $(x,0)$ indicates that the species x survives the thinning above and therefore remains in the configuration at time 0.

In Fig. 1, $k=2$ for y, and y does survive the thinning. It is clear that the resulting set of points at time 0 has the same distribution as the process with dynamics determined by (i) and (ii′) at time $N_t(0,1)$, where $N_t(0,1)$ is the total number of Poisson points in $[-t,0]\times(0,1)$. To complete the proof it remains to show that the set of points converges almost surely as $t\to\infty$. This is an immediate consequence of the fact that the set of points is increasing. □

Let $\mathscr{S}$ denote the set of distributions supported only on configurations that have finitely many points in each interval $[0,x]$, $x<1$. The graphical construction implies that if the system is started from any $\mu \in \mathscr{S}$, the statement of Proposition 1 remains to hold. Therefore, we have

Corollary 1. *π^a is the unique stationary distribution in $\mathscr{S}$.*

The graphical construction allows us to easily compute the mean measure of the resulting point process. Fix $x \in (0,1)$ and let $0 = -T_0 > -T_1 > -T_2 > -T_3 > \cdots$ be the heights of the successive points in the strip $(x,1) \times (-\infty, 0]$. Let $\delta > 0$ be a small number and consider a modified version of the process in which points inserted into $(x-\delta, x)$ do not eliminate other points in that interval. Let N_s^δ be the number of Poisson points in $(x-\delta,x) \times [-s,0]$ and $\hat{N}_s^\delta$ be the number of those points that survive the thinning. Elementary properties of the Poisson process imply that

$$P(N^\delta(T_k) - N^\delta(T_{k-1}) = m) = \left(\frac{\delta}{\delta + 1 - x}\right)^m \frac{1-x}{\delta + 1 - x},$$

$$P(\hat{N}^\delta(T_k) - \hat{N}^\delta(T_{k-1}) = m) = \left(\frac{(1-a)^{k-1}\delta}{(1-a)^{k-1}\delta + 1 - x}\right)^m \frac{1-x}{(1-a)^{k-1}\delta + 1 - x}.$$

In other words the increments $\hat{N}^\delta(T_k) - \hat{N}^\delta(T_{k-1})$ have a shifted geometric distribution with success probability $p = (1-x)/((1-a)^{k-1}\delta + 1 - x)$. The mean of the shifted geometric is $1/p - 1$ so the expected number of points in $(x-\delta,x)$ in equilibrium is

$$\sum_{k=1}^{\infty} \frac{\delta(1-a)^{k-1}}{1-x} = \frac{\delta}{a(1-x)}.$$

Letting $\delta \to 0$ and ignoring the simple detail of justifying that the modification we have made in the process does not matter, it follows that the mean measure of the limit process is $\mathrm{d}x/(a(1-x))$.

A closer look at the calculation above can mislead the reader into thinking that the limit process is not Poisson. To explain this, let $\mathscr{F}_x$ denote the σ-field generated by the Poisson points in $(x,1) \times (-\infty, 0]$. It is easy to see from the calculation above that the conditional intensity of the limiting point process given $\mathscr{F}_x$ is

$$\sum_{k=1}^{\infty} (1-a)^k (T_k - T_{k-1}),$$

which is a random variable. In contrast, if the limit is to be an inhomogeneous Poisson process, then the conditional intensity given $\mathscr{G}_x$, the σ-field generated by the positions of the points in $(x,1)$ that are retained, must be a constant. Of course there is nothing to prevent the conditional intensity given $\mathscr{G}_x$ from being constant when the intensity given $\mathscr{F}_x$ is not. Indeed, our main result is to show

Theorem 1. *The stationary distribution π^a is inhomogeneous Poisson with mean measure* $\mathrm{d}x/(a(1-x))$.

Originally we showed that the limiting point process has independent increments, via a discrete approximation that divided $(0,1)$ into subintervals $((m-1)/n, m/n)$ and modified the dynamics so that a new point does not kill any of the points in its own subinterval. Computation of all product moments showed that the equilibrium distribution of the discrete system has independent increments, and a passage to limit gave the result for the continuous space. In the next section, we give instead a shorter proof, suggested by Jim Pitman. This proof works directly in continuous space, and is based on thinning and superposition properties of standard Poisson processes.

It is interesting to note that the Poisson process π^a is closely related to Poisson–Dirichlet and GEM distributions, and appears as a stationary distribution in numerous species sampling models. Let $\theta = a^{-1}$. If $0 = X_0 < X_1 < X_2 < \cdots$ are the points of π^a, then the corresponding sequence of interval lengths $X_1 - X_0, X_2 - X_1, \ldots$ has the GEM (θ) distribution, and the sequence of ordered (by length) interval lengths has the Poisson–Dirichlet (θ) distribution (see Ignatov, 1982). Pitman (1996) gives a detailed account of the related species sampling literature.

Recent studies of the scale invariant Poisson processes, that have intensity measure θx^{-1} on $(0,\infty)$, and their connection to Poisson–Dirichlet distributions and various processes arising in applications were conducted by Arratia (1998) and Arratia et al. (1999).

Gnedin and Kerov (2000) discovered that GEM (θ) is a stationary distribution of a certain split-and-merge process. Mayer-Wolf et al. (2001) study related coagulation-fragmentation processes and show that, for appropriate a, Poisson–Dirichlet (θ) is the unique stationary law in a certain class of laws (see also Pitman, 2002). Even though the species sampling and related models above have qualitatively similar dynamics (the transitions involve splitting and merging of intervals of the point process), there seems to be no obvious close relation between them and the species competition toy model analyzed here. It seems that the closest model is an allele competition model studied by Sawyer and Hartl (1985). In this model a population is divided into subpopulations with different alleles, new favorable alleles are repeatedly introduced, and each new allele overtakes a (random) fraction of all preexisting subpopulations, the fraction being the same for all subpopulations. Sawyer and Hartl (1985) show that a Poisson–Dirichlet distribution is the equilibrium distribution of this process.

David Aldous has pointed out that time reversal of our process together with a transformation of (0,1) to $(0,\infty)$ by $x \to \ln(1-x)$ (cf. proof of Theorem 1) is an interesting branching Markov chain $(\mathscr{M}_t, t > 0)$ taking values in the space of countable subsets of $(0,\infty)$. Each point $x \in \mathscr{M}_t$ lives an exponential (rate e^{-x}) amount of time (independent of all other points) after which it dies and gives birth to a Poisson (rate 1) process of points on $(0,x)$, independent of the past. It follows from Theorem 1 that for each $a < 1$, the law of a Poisson (rate $1/a$) process on $(0,\infty)$ is a stationary law for $\mathscr{M}$.

With Theorem 1 established it is straightforward to prove

Theorem 2. *Let X_t be the number of points at time t. As $t \to \infty$, $X_t/\log t \to 1/a$ in probability.*

Proof (Sketch). Elementary extreme value theory shows that the distance from the right most point to 1 at time t is $O(1/t)$. The law of large numbers for the Poisson process implies that the number of points in equilibrium between 0 and $1-1/t$ is $\approx (\log t)/a$. To bridge the gap between equilibrium and time t, we will show in Section 2 that if $\varepsilon > 0$ then with high probability no points in $(0, 1-1/t^{1-\varepsilon}) \times (-\infty, -t]$ will survive. □

Our final topic is to investigate the extinction distribution. Suppose that the system is in equilibrium and let p_k be the probability, the next inserted species eliminates k of the current species. Motivated by Bak (1996) who argues that many systems self-organize themselves into a critical state, see also Solé et al. (1999), we ask: Does p_k follow a power law? To guess the answer to this question, one can observe that Theorem 1 implies that the number of points in $(0, x)$ has a Poisson distribution with mean $-(1/a)\log(1-x)$, so a species inserted at x will eliminate a Poisson number with mean $-\log(1-x)$. This suggests that to eliminate k or more species, a point should be inserted to the right of $1-\mathrm{e}^{-k}$, an event of probability of e^{-k}. The next result shows that this reasoning does not give the right constant but gives the right qualitative answer.

Theorem 3. $p_k = 1/2^{k+1}$.

Proof. By the reasoning above

$$p_k = \int_0^1 \mathrm{e}^{\log(1-x)} \frac{(-\log(1-x))^k}{k!}\,\mathrm{d}x.$$

So $p_0 = 1/2$ and integrating by parts shows

$$p_k = \int_0^1 \frac{(1-x)^2}{2} \frac{(-\log(1-x))^{k-1}}{(k-1)!} \frac{1}{1-x}\,\mathrm{d}x = \frac{p_{k-1}}{2}, \qquad k \geqslant 1.$$

Induction then implies $p_k = c/2^{k+1}$. □

Returning to the heuristic argument, we see that what it really shows is $\sum_{j\geqslant k} p_j \geqslant \mathrm{e}^{-k}$. The implied converse that we need to insert the point above $1-\mathrm{e}^{-k}$ to kill k points is false. If we insert the point above $1-\mathrm{e}^{-bk}$ with $b<1$, then the number of points killed, Z, will have a Poisson distribution with mean bk. Standard large deviations for the Poisson (see, e.g., Section 1.9 of Durrett, 1995) imply that

$$\frac{1}{k}\log P(Z \geqslant k) \to -(b-1-\ln b).$$

The probability that a point is inserted into $(1-\mathrm{e}^{-bk}, 1)$ and causes an avalanche of size at least k is $\geqslant \mathrm{e}^{-bk} P(Z \geqslant k)$. Taking $b = 1/2$ to maximize this, we end up with $\sum_{j\geqslant k} p_j \geqslant 2^{-k}$.

2. Proofs of Theorems 1 and 2

Proof of Theorem 1. Consider the process defined by (i) and (ii′). Due to Corollary 1, it suffices to show that the law ν^a of the Poisson process with mean measure $\mathrm{d}x/(a(1-x))$ is a stationary law.

Define $f:[0,1)\mapsto[0,\infty)$ by $f(x)=-\log(1-x)$ and observe the original system under the transformation f. Now each new species is introduced in the system with death rate $f(\delta)=-\log(1-\delta)$ having an exponential (rate 1) distribution, and the rule (ii′) is modified so that each species with type $f(\delta_1)<f(\delta)$ is removed independently, with probability a. Similarly, under the transformation f, the law ν^a becomes the law of the Poisson (rate $1/a$) process on $[0,\infty)$.

We now recall some well-known facts about Poisson processes. If $U_1<U_2<U_3<\cdots$ are the points of a Poisson (rate λ) process, $V_1<V_2<V_3<\cdots$ are the points of an independent Poisson (rate μ) process, and we define $UV_1<UV_2<UV_3<\cdots$ by $\{UV_1,UV_2,UV_3,\ldots\}=\{U_1,U_2,U_3,\ldots\}\cup\{V_1,V_2,V_3,\ldots\}$. Then $UV_k, k\geqslant 1$ are the points of a Poisson (rate $\lambda+\mu$) process. Moreover, conditionally on the position of the first point V_1 in the second process, $\{UV_1,UV_2,\ldots\}\cap[0,V_1)$ is a Poisson (rate λ) process on $[0,V_1)$, and $\{UV_1,UV_2,\ldots\}\cap(V_1,\infty)$ is an independent Poisson (rate $\lambda+\mu$) process on (V_1,∞). The first assertion in the last sentence is due to independence of the U and V processes, and the second one is a consequence of the memoryless property of exponential distribution.

Now assume that our transformed system on $[0,\infty)$ is started with the law of a Poisson (rate $1/a$) process. Denote its points by $X_1<X_2<X_3<\cdots$. It suffices to show that the law remains unchanged if a point is added independently at $X\overset{d}{=}$ exponential (rate 1), and each point $X_j<X$ is removed with probability a, independent of others and the past. Conditionally on X, due to independence we have that $\{X_1,X_2,\ldots\}\cap[0,X)$ is a Poisson (rate $1/a$) process on $[0,X)$, and that $\{X_1,X_2,\ldots\}\cap(X,\infty)$ is an independent Poisson (rate $1/a$) process on (X,∞). By performing independent removals with probability a (or equivalently, an independent $(1-a)$ thinning), we get a new point process $X_1^*<X_2^*<\cdots$ where, conditionally on X, $\{X_1^*,X_2^*,\ldots\}\cap[0,X)$ is a Poisson (rate $1/a-1$) process on $[0,X)$, and $\{X_1^*,X_2^*,\ldots\}\cap(X,\infty)=\{X_1,X_2,\ldots\}\cap(X,\infty)$ is an independent Poisson (rate $1/a$) process on (X,∞). Therefore, the distribution of the random object $(X,\{X_1^*,X_2^*,\ldots\}\cap[0,X),\{X_1^*,X_2^*,\ldots\}\cap(X,\infty))$ is the same as the distribution of $(V_1,\{UV_1,UV_2,\ldots\}\cap[0,V_1),\{UV_1,UV_2,\ldots\}\cap(V_1,\infty))$, where $\lambda=1/a-1$ and $\mu=1$. Hence, the set $\{X_1^*,X_2^*,\ldots\}\cup\{X\}$ has the same law as the set $\{UV_1,UV_2,\ldots\}$, namely the law of a Poisson (rate $1/a$) process. Together with the previous observations, this completes the proof of the theorem. □

Proof of Theorem 2. Recall the graphical construction in the proof of Proposition 1. Let $N_t(a,b)$ be the number of Poisson points in $(a,b)\times[-t,0]$ and let $M_t(a,b)$ be the number of Poisson points in $(a,b)\times[-t,0]$ that are not killed by the thinning. Let $s_\varepsilon=1-t^{-(1-\varepsilon)}$ and let $u_\varepsilon=1-t^{-(1+\varepsilon)}$. The upper bound is easy:

$$M_t(0,1)\leqslant N_t(u_\varepsilon,1)+M_\infty(0,u_\varepsilon).$$

To bound the first term we note

$$P(N_t(u_\varepsilon,1) > 0) \leqslant EN_t(u_\varepsilon,1) = t^{-\varepsilon} \tag{a}$$

For the second we use the law of large numbers for the Poisson process to conclude

$$P(M_\infty(0,u_\varepsilon) > (1+\varepsilon)^2(\log t)/a) \to 0. \tag{b}$$

For the lower bound we use

$$M_t(0,1) \geqslant M_t(0,s_\varepsilon) = M_\infty(0,s_\varepsilon) - \{M_\infty(0,s_\varepsilon) - M_t(0,s_\varepsilon)\}.$$

The law of large numbers for the Poisson process implies

$$P(M_\infty(0,s_\varepsilon) < (1-\varepsilon)^2(\log t)/a) \to 0. \tag{c}$$

To bound the other term we will use the following.

Lemma. *There is a* $\gamma > 0$ *with* $\mathrm{e}^{-\gamma} > 1-a$ *so that if* Z *is Poisson with mean* λ *then*

$$P(Z \leqslant \lambda/2) \leqslant \mathrm{e}^{-\gamma\lambda}.$$

Proof. $E\mathrm{e}^{-\zeta Z} = \exp(-\lambda(1-\mathrm{e}^{-\zeta}))$. Markov's inequality implies

$$\mathrm{e}^{-\zeta\lambda/2}P(Z \leqslant \lambda/2) \leqslant E\mathrm{e}^{-\zeta Z}.$$

Rearranging we have $P(Z \leqslant \lambda/2) \leqslant \exp(\lambda(\mathrm{e}^{-\zeta}-1+\zeta/2))$. As $\zeta \to 0$, $(\mathrm{e}^{-\zeta}-1)/\zeta \to -1$ so if we choose ζ small enough then $\gamma = \mathrm{e}^{-\zeta}-1+\zeta/2 > 0$. By choosing ζ even smaller we can guarantee $\mathrm{e}^{-\gamma} > 1-a$. □

By considering the value of $N_{kt}(s_\varepsilon,1)$ we have

$$\begin{aligned} E(M_{(k+1)t}(0,s_\varepsilon) - M_{kt}(0,s_\varepsilon)) &\leqslant tP(N_{kt}(s_\varepsilon,1) \leqslant kt^\varepsilon/2) + t(1-a)^{kt^\varepsilon/2} \\ &\leqslant 2t\mathrm{e}^{-\gamma kt^\varepsilon/2} \end{aligned}$$

by the lemma and our choice of γ. Summing we have

$$E(M_\infty(0,s_\varepsilon) - M_t(0,s_\varepsilon)) \leqslant 2t\sum_{k=1}^{\infty} \mathrm{e}^{-\gamma kt^\varepsilon/2} = \frac{2t\mathrm{e}^{-\gamma t^\varepsilon/2}}{1-\mathrm{e}^{-\gamma t^\varepsilon/2}}.$$

The right-hand side gives an upper bound on $P(M_\infty(0,s_\varepsilon) - M_t(0,s_\varepsilon) > 0)$ and converges to 0 as $t \to \infty$. With (c) this completes the proof. □

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