Population dynamics in the triplet annihilation model with a mutating reproduction rate

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Abstract

I study a population model in which the reproduction rate $\lambda$ is inherited with mutation, favoring fast reproducers in the short term, but conflicting with a process that eliminates agglomerations of individuals. The model is a variant of the triplet annihilation model introduced several decades ago [R. Dickman, Phys. Rev. B 40, 7005 (1989)] in which organisms (“particles”) reproduce and diffuse on a lattice, subject to annihilation when (and only when) occupying three consecutive sites. For diffusion rates below a certain value, the population possesses two “survival strategies”: (i) rare reproduction ($0 < \lambda < \lambda_{c,1}$), in which a low density of diffusing particles renders triplets exceedingly rare, and (ii) frequent reproduction ($\lambda > \lambda_{c,2}$). For $\lambda$ between $\lambda_{c,1}$ and $\lambda_{c,2}$ there is no active steady state. In the rare-reproduction regime, a mutating $\lambda$ leads to stochastic boom-and-bust cycles in which the reproduction rate fluctuates upward in certain regions, only to lead to extinction as the local value of $\lambda$ becomes excessive. The global population can nevertheless survive due to the presence of other regions, with reproduction rates that have yet to drift upward.

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I. INTRODUCTION

My regrettably few encounters with Dietrich Stauffer left an important imprint. He always impressed with his unconventional, even provocative attitude, his honesty, generosity, and sense of humor. I first met Prof. Dr. Stauffer at a Rutgers Meeting in the early ’80s. I’d been enumerating lattice animals as part of my PhD project on nucleation in lattice gases. When he asked what computer I used for the task, I simply gestured to indicate that this was hand enumeration. But a year later, having exhausted the possibilities of this approach (and/or my patience with filling notebooks with strange little diagrams), Stauffer’s question led me to develop Monte Carlo methods for counting lattice animals[1].

Toward the end of the 1980s, on a visit to Germany at the kind invitation of Prof. Kurt Binder, I met Stauffer at his lab in Jülich, and described my ongoing study of the triplet annihilation model, the subject of the present work. Hearing my explanation that particles could only be annihilated in groups of three, he turned and said, “Oh, you’re studying guerrilla warriors who spread out to evade detection from the air.” This colorful and somewhat poignant interpretation stuck with me, as did his advice (in reply to a letter sent shortly before defending my PhD, in which I confessed to having become “addicted” to Monte Carlo simulation), that I simply “enjoy my addiction.” And so I have. In a handful of encounters in Europe and Brazil, we chatted about science, politics and other matters. (I’m afraid my answers were sometimes disappointing: Seen any good movies recently? - My tastes were too art-house. Your favorite football team? - I had none.)

Dietrich Stauffer made major contributions to percolation theory, so it is fitting that the triplet annihilation model studied here belongs to the (rather broad) class of models with a directed percolation (DP)-like phase transition. In the stochastic particle systems of interest here, the directed spatial axis of DP corresponds to time; the (continuous) phase transition is between an active and an absorbing state. The simplest example is the contact process (CP) [2–6], in which each site of a lattice is either vacant or occupied by a single particle. The latter die at unit rate, and attempt to reproduce at rate $\lambda$, choosing a neighboring site at random and adding a particle if the chosen neighbor is vacant. In the infinite-size limit there is a transition between an active phase (for $\lambda > \lambda_c$) with a nonzero particle density and an absorbing phase (all sites vacant). To the CP dynamics, the triplet annihilation model [7, 8] adds diffusion (nearest-neighbor hopping) and a modified death process, in which only
groups of three particles are removed. The result is that (for not too rapid diffusion) an active phase exists for small \( \lambda \) (with a very low abundance of triplets) as well as for large \( \lambda \), but not for intermediate values. Here, I explore the effect of a reproduction rate, \( \lambda_i \) for each particle \( i \), that is inherited from its parent with some random variation. Depending on the degree of variability, this can lead to a population with minimal reproduction, to extinction, or to long-time survival punctuated by a series of local population explosions and collapses.

The remainder of this paper is organized as follows. In the next section I define the model and describe the simulation algorithm. Sec. III reports simulation results, followed by a summary and discussion in Sec. IV.

II. MODEL

A. Triplet annihilation model

The triplet annihilation model (TAM) is a stochastic particle system on a lattice, a ring of \( L \) sites in the present study. Each site can be either vacant or occupied by a (single) particle. Transitions between configurations occur through three basic processes:

- Creation: Each particle attempts independently, at rate \( 2\lambda \), to create a new particle at its nearest-neighbor to the left or right. The attempt is successful if the chosen neighbor is unoccupied.

- Hopping: Each particle attempts to hop, at rate \( 2d \), to its nearest-neighbor to the left or right. The attempt is successful if the chosen neighbor is unoccupied.

- Annihilation: If sites \( i-1, i, \) and \( i+1 \) are all occupied, we say there is a triplet centered at site \( i \). Triplets are annihilated a rate of unity. (All three particles are removed in this event.)

From this definition it is evident that the configuration with all sites vacant is absorbing. (The parameterization of the rates used here differs from that used in the earlier studies, although it has no qualitative effect on the phase diagram.)

Note that hopping tends to destroy triplets, whereas creation tends to generate them, raising the possibility of subtle interactions between these processes. The original motivation
for studying the model was to investigate what effect such conflicting tendencies might have on the phase diagram and critical behavior.\[10\]

The phase diagram, shown schematically in Fig. 1, is indeed intriguing. In simpler lattice birth-and-death models such as the contact process, sustained activity (i.e., a nonzero particle density, $\rho > 0$), requires a reproduction rate greater than some value $\lambda_c > 0$. The presence, in the TAM, of activity for arbitrarily small $\lambda$ is due, of course, to the death rate being proportional to the density of triplets, $\rho_3$, rather than of particles, $\rho$. In the presence of hopping ($d > 0$), there is an interval $(0, \lambda_-(d))$ of reproduction rates such that $\rho_3 \ll \rho$, permitting survival of activity. Of particular interest in the present work is the portion of the active phase bounded by $\lambda = 0$ and the small-$\lambda$ branch of the phase boundary, $\lambda_-(d)$, because in this region, paradoxically, increasing the reproduction rate leads to extinction, due to the increased abundance of triplets. An example of this behavior is shown in Fig. 2. The quasistationary particle density \[15\] peaks near $\lambda \simeq 0.005$ and falls rapidly for higher values. For this hopping rate ($d = 1.2346$), the upper critical reproduction rate, $\lambda_+ \simeq 1.17$, much larger than the values considered here; preliminary studies yield $\lambda_- \simeq 0.03$.

Although critical behavior is not the principal subject of the present study, it is worth noting that the entire phase boundary appears to be a line of critical points in the directed percolation universality class, and that the particle density $\rho \sim \lambda^{1/2}$ as $\lambda \to 0$. This property, as well as the qualitative form of the phase diagram, is captured by mean-field theory at the pair level \[7, 8\]. Several works have investigated the phase diagram and closely related models. Katori and Konno \[11\] established some general properties of systems like the TAM, while Poland \[12\] used time-series expansions to investigate population dynamics in the TAM and related models. A model with annihilation of quadruplets was analyzed by Ódor \[13, 14\].

B. TAM with mutating reproduction rate (MTAM)

In the present study, the reproduction rate is no longer a fixed parameter. Instead, each particle $i$ is assigned a value $\lambda_i$ when created, and carries this value during its lifetime, as it hops on the lattice. If particle $i$ creates a new particle $j$, then $\lambda_j$ is inherited from the parent with random variation:
FIG. 1: Schematic of the triplet annihilation model phase diagram in the reproduction rate-hopping rate ($\lambda - d$) plane. The phase boundary is a line of continuous phase transitions between the active and absorbing phases. For hopping rates $d > d^*$, there is activity for any $\lambda > 0$, while for $d < d^*$, the active phase exists for large $\lambda$, but also for very small $\lambda$. The present study focuses on the region bounded by $\lambda = 0$ and the small-$\lambda$ branch of the phase boundary, $\lambda_-(d)$.

\[
\lambda_j = \max \left[ \lambda_i + \Delta, \lambda_{\text{min}} \right],
\]

where $\Delta$ is a random variable with zero mean, and $\lambda_{\text{min}}$ is a small basal reproduction rate. I consider both additive and multiplicative schemes. In the former, $\Delta$ is simply chosen from a distribution uniform on $[-\gamma, \gamma]$. In the multiplicative case, $\Delta = \xi \lambda_i$, where $\xi$ is uniform on $[-\gamma, \gamma]$. Each realization of the process begins with all sites occupied, and $\lambda_i = \lambda_0$, $\forall i = 1, \ldots, L$. In what follows I refer to this as the mutating triplet annihilation model (MTAM).

C. Simulation algorithm

I developed an event-driven (rejection-free) Monte Carlo simulation algorithm for the present study. The basic requirements this type of simulation are lists of the possible transitions and pointers to facilitate updating the lists. In the TAM simulation one must maintain
FIG. 2: Quasistationary particle density $\rho$ versus reproduction rate $\lambda$ in the TAM, for hopping parameter $d = 1.2346$, system size $L = 10^4$. Error bars are smaller than the symbols. Inset: the same data plotted versus $\sqrt{\lambda}$.

a list of triplets and another list of nearest-neighbor particle-hole pairs (PHPs). One maintains, in addition, vectors carrying (i) the occupation status of each site; (ii) whether sites $i$ and $i+1$ belong to a PHP, and if so, the position on the PHP list, and which of the two sites is occupied; (iii) whether site $i$ is the central site of a triplet, and if so, the corresponding position on the triplet list. In the case of mutating reproduction rates, a fourth vector carries $\lambda_i$ associated with each occupied site $i$.

Given the numbers, $N_{trp}$ and $N_{php}$ of triplets and PHPs, respectively, the total transition rate out of the current configuration is,

$$R = N_{trp} + (d + \lambda)N_{php} \equiv R_{ann} + R_{hop} + R_{rep},$$ (2)

where in the second equality we define the total rates of annihilation, hopping and reproduction. The next transition is taken to be of type $j$ (annihilation, hopping or reproduction), with probability $P_j = R_j/R$. Then the specific event on the corresponding list is selected (with uniform probability over the list), the new configuration constructed, the lists updated,
and the time advanced so: $t \rightarrow t + 1/R$.

In the case of mutating reproduction rates, i.e., the MTAM, we must alter the expression for the total creation rate to $R_{rep} = \Lambda$, where

$$\Lambda = \sum_{i=1}^{N_{php}} \lambda_{j(i)},$$

where the sum is over PHPs and $j(i)$ denotes the occupied site in the $i$th PHP. In this case, of course, the PHP for creation must be chosen with a probability proportional to the associated $\lambda$ value. This is done by letting $\tilde{\Lambda} = \Lambda z$, where $z$ is a random number uniform on $[0, 1]$, and then evaluating the partial sums $\Lambda_k$, with $\Lambda_1 = \lambda_{j(1)}$ and,

$$\Lambda_k = \Lambda_{k-1} + \lambda_{j(k)},$$

until $\Lambda_k > \tilde{\Lambda}$, at which point creation is realized in the $k$th PHP. While more efficient methods for choosing the PHP exist, this approach is simple and unlikely to increase run times significantly since reproduction counts for only a small fraction of events and the number of PHPs is not very large in the regime of interest.

III. RESULTS

Given the sensitivity of the TAM to small changes in the reproduction rate, and the counterintuitive nature of the response, it is of interest to examine how a population evolves under a mutating rate.

In this section I report preliminary results for the time evolution and spatial structure of the MTAM. The fixed simulation parameters are $d = 1.2346$, initial creation rate $\lambda_0 = 0.005$, basal creation rate $\lambda_{\text{min}} = 0.001$, and system size $L = 2000$. Studies run to a maximum time of $10^6$ unless the absorbing state is attained prior to this time. (For these parameters, but without mutation, the probability of a realization surviving to time $10^6$ is about 0.86, and the quasistationary particle density is $\rho = 0.0331(1)$.)

To begin I consider the effect of multiplicative noise in the inherited reproduction rate, varying the noise intensity $\gamma$ between 0.005 and 0.25. Most realizations survive until the maximum time: For $\gamma = 0.025$, for example, the survival probability is about 0.87. Time
series for the particle density show significant fluctuations, with or without mutation, as shown in Fig. 3. This figure also shows the time series for $\bar{\lambda}(t)$, the instantaneous average of $\lambda$ over all particles, as well as the instantaneous maximum, $\lambda_{\text{max}}(t)$. These quantities exhibit a pattern of slow growth followed by a sudden crash. The mean reproduction rate remains “pinned” near its basal rate of $10^{-3}$ for long periods. The inset shows that the variations in the standard deviation of $\lambda$ mirror those of $\bar{\lambda}(t)$. The particle density also exhibits crashes (followed by recovery, at least in this example), but the relation between crashes in population and in $\lambda$ is unclear, since one may occur without the other. Similar examples of time series with mutating reproduction rates are shown in Figs. 4 and 5.

![Figure 3: Time series of the particle density $\rho(t)$ and reproduction rate in the TAM and MTAM with hopping parameter $d = 1.2346$, and system size $L = 2000$. Lower panel: $\lambda = 0.005$, without mutation (TAM). Middle panel: $\rho(t)$ for the MTAM with mutation parameter $\gamma = 0.1$ (multiplicative case). Upper panel: $\bar{\lambda}(t)$ (lower) and $\lambda_{\text{max}}(t)$ (upper) in the same realization as the middle panel. Inset: comparison of time series for $\bar{\lambda}(t)$ (upper curve) and the standard deviation of the set of $\lambda_i$ values at time $t$ (lower).](image)

For an initial reproduction rate $\lambda_0$ close to the upper phase boundary, $\lambda_+(d)$, mutations
FIG. 4: MTAM: Time series of the particle density $\rho(t)$ and reproduction rate as in Fig. 3 except $\gamma = 0.025$.

FIG. 5: MTAM: Time series of the particle density $\rho(t)$ and reproduction rate, parameters as in Fig. 4.

lead, as expected, to steady growth in $\bar{\lambda}$ and the particle density. An example is shown in Fig. 5 for $\lambda_0 = 1.15$, close to $\lambda_+ = 1.17$.

Time series for *additive* noise are generally similar to those for the multiplicative case,
FIG. 6: MTAM: Time series of the particle density $\rho(t)$ and mean reproduction rate in with multiplicative noise, hopping parameter $d = 1.2346$, initial reproduction rate $\lambda_0 = 1.15$, $\gamma = 5 \times 10^{-4}$, and system size $L = 2000$.

if we use noise intensities $\gamma$ about two orders of magnitude smaller. (Recall that in the multiplicative case, the noise term is scaled by $\lambda \sim 0.005$.) A typical example, for $\gamma = 5 \times 10^{-4}$, is shown in Fig. 7. “Pinning” of $\bar{\lambda}$ near $\lambda_{\text{min}}$ is not observed under additive noise, since the magnitude of mutations (i.e., of $\Delta \lambda$) is independent of $\lambda_i$. For $\gamma \geq 10^{-3}$ most realizations with additive noise do not survive until time $10^6$.

An example of a population that goes extinct rapidly is shown in Fig. 8. Inspection of the time series shows that even the exceptionally high values of $\bar{\lambda}$ for $t \simeq 1.7 \times 10^4$ do not lead to an immediate population crash. Partial extinction events near $t = 1.8$ and $2.1 \times 10^4$ appear to cull the rapidly reproducing subpopulations. The population and reproduction rate continue to fluctuate, until, at around $t = 2.8 \times 10^4$, the system attains a regime with small $\rho$ and small $\bar{\lambda}$. This combination makes appearance of individuals with larger $\lambda$ values unlikely, and the population goes extinct some time later. This example shows that although high reproduction rates play a role in extinction, they may not the direct or immediately cause. Further analyses will be required to assess the generality of this scenario.
FIG. 7: MTAM: Time series of the particle density $\rho(t)$ and reproduction rate, but with additive noise of intensity $\gamma = 5 \times 10^{-4}$. Other parameters as in Fig. 3.

FIG. 8: MTAM: Time series of the particle density $\rho(t)$ and reproduction rate, but with additive noise of intensity $\gamma = 0.005$. Other parameters as in Fig. 3. The population goes extinct at $t = 3.192 \times 10^4$.

A. Spatiotemporal evolution

An interesting aspect of the population dynamics is the appearance of localized subpopulations with a more or less uniform reproduction rate. The average reproduction rate within
such a group may fluctuate upward until it exceeds a “safe” value, and the group dies out due to overproduction or triplets. For parameter sets allowing long-time survival, it appears that when such a group goes extinct, there remain several other subpopulations, typically with small reproduction rates. An example of such an evolution is shown in Fig. 9 which covers the period $t = 4.0 - 4.8 \times 10^5$ shown in Fig. 5 during which the population grows and then crashes. Localized groups with restricted variations in $\lambda$ are evident; one does not find individuals with markedly different $\lambda$ values in the same region at the same time. In the region extending from $x \simeq 500 - 1000$, the mean value of $\lambda$ initially drifts upward. The region then becomes nearly empty, to be reoccupied at the final time shown, presumably by particles that have diffused in from nearby groups. By contrast, the region between $x = 1500$ and 200 (i.e., 2200 under the periodic boundary) exhibits only modest variations in density and reproduction rate. One may conjecture that this dynamic homogeneity is what allows for long-term survival in a population undergoing “boom-and-bust” cycles in localized regions. (Survival, one might say, lies in diversity.) Further studies, including the effect of varying system sizes, will be needed to test these ideas.

FIG. 9: MTAM: Spatiotemporal evolution during a period of population growth and decay. Each type of symbol (see legend) corresponds to a specific time in the time series of Fig. 5. Each symbol represents the position ($x$) and reproduction rate ($\lambda$) of a single particle.

IV. SUMMARY AND DISCUSSION

I study the population dynamics of the triplet annihilation model (TAM) in a regime in which only a narrow range of (quite small) reproduction rates assure survival. The mutating version, MTAM, individual reproduction rates are inherited with random mutation,
leading to complex spatiotemporal dynamics. Much remains to be analyzed following this preliminary study, including analytic approximations such as deterministic and/or stochastic partial differential equations.

There are further variations to be considered. In the present context, for example, individuals with an optimal reproduction rate (in the sense of Fig. 2) may be seen as cooperators, and rapid reproducers as cheaters or betrayers. This raises the possibility of introducing mechanisms that foster cooperation in an evolutionary-game context.

Stochastic particle systems offer fascinating challenges for physicists and mathematicians. Many of their interpretations, as models of populations, epidemics, social systems, or even guerrilla warriors, are imperfect, serving nevertheless as intuitively attractive metaphors for processes in the real world. I wonder what fanciful interpretation Dietrich Stauffer would have offered for the model considered here.
Acknowledgment

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A quasistationary mean is conditioned on long-term survival, or more formally, the limiting $(t \to \infty)$ value of a mean taken over the set of realizations that survive until time $t$ or longer. For models with an absorbing state, the quasistationary mean is the closest analog to the usual notion of a stationary mean.