

Clustering of diffusing organisms

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Recently, a “Brownian bugs” model has been proposed as a possible explanation for the clustering of organisms such as planktons [W.R. Young, A.J. Roberts, and G. Stuhne, *Nature (London)* **412**, 328 (2001)]. In this model, diffusing organisms die and give birth with equal probabilities and are independent of each other. The clustering phenomenon is due to the discreteness of birth and death events and cannot be explained in the framework of the continuous model of population dynamics. We show by exact calculation that at dimensions smaller than or equal to 2, this simple mechanism is enough to provoke aggregations of the organisms. At dimensions higher than 2, the clustering phenomenon disappears, but reproductive fluctuations can still be large compared to diffusive ones.

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I. INTRODUCTION

Many processes in nature such as kinetic reactions or the fate of living organisms are inherently discrete. Very often, these systems are described in terms of the evolution of the *average* of the quantity of interest by means of continuum differential equations. In a kinetic reaction for example, the time evolution of different agents *concentrations* is computed. For living organisms, the discrete population size N is often replaced by a continuous quantity X , assuming that the relative variation of the population size $\Delta N/N$ in a short time interval is sufficiently small for the process to be considered as continuous. The fundamental assumption behind such modeling is that fluctuations are small compared to averages (typically of the order of the square root of averages) and can be neglected. There are cases however, where this assumption is violated and fluctuations can become arbitrary large. In these cases, the continuous description of the stochastic phenomenon fails completely, and numerical simulations of the discrete processes display behaviors strikingly different from the continuous approximation.

An example, which will be the subject of this paper, has been proposed by Young *et al.* [1] as a possible mechanism for clustering of organisms such as planktons. Clustering of organisms can be due to many causes such as social and (or) nonlinear interactions between one or more species which spontaneously break the translational symmetry and give rise to patterns. By numerical simulations, these authors show however that a population of independent diffusing “Brownian bugs” without any interaction, and submitted only to random division and death (of equal rate) can generate extremely heterogenous patterns of concentration and organize into clusters. The continuous equation, governing the evolution of such a population reads

$$\partial_t c = (\alpha - \mu)c + D\nabla^2 c, \quad (1)$$

where c is the local concentration of the organism, α and μ are the birth and death rates, respectively, and D is the dif-

fusion coefficient. When $\alpha = \mu$, there is no net creation or destruction of organisms, and the solution tends toward a homogeneous concentration. One may expect that when discrete individuals are simulated, even if random birth and death induce some (large) fluctuations, the local temporal cluster should disappear and be smoothed by diffusion. This is not the case: Fig. 1 shows a numerical simulation of the evolution of the $1d$ concentration profile of individual diffusing organisms, subject to random and equal birth and death events. The concentration does not tend toward a uniform one, but becomes extremely rough and its local fluctuation diverges as a function of time.

Ecologists generally think of population distribution as “niche oriented,” i.e., organisms tend to aggregate in areas where they are best adapted to the local ecosystem. Hubbell has recently proposed a neutral theory [2] where all species have equal fitness. Numerical simulations [3] show that this model displays a striking similarity with the pattern of spe-

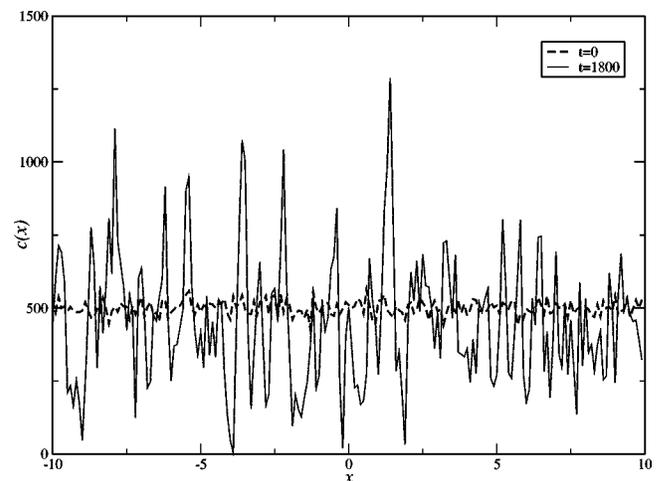


FIG. 1. Numerical simulation of 10^5 individual organisms, over a circular space of $L=20$. At $t=0$, particles are spread uniformly in space. $\alpha=0.1$, diffusion step=0.01. Concentrations are computed by counting the number of particles in a cell of size $\ell=0.1$ at position x . At each time step, individuals die or give birth according to α . Each remaining particle then moves by choosing randomly its direction and amplitude. Particle positions are continuous.

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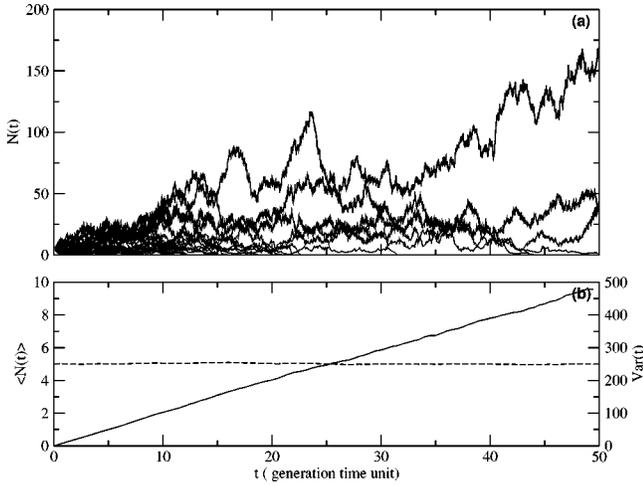


FIG. 2. Numerical simulation of a stochastic birth-death process, for equal birth and death rates; initial population 5. (a) Population size versus time for 50 different realizations; (b) average (left scale, dotted curve) and variance (right scale, black curve) as a function of time computed for 50 000 realizations.

cies distributions. The model we study below belongs to this class of models and we are able to derive exact analytical results for the aggregation phenomena.

In the following, we analyze, by exact computation of the master equation, the role of competition between smoothing by diffusion and clustering by random discrete birth (death). We will first recall the problem of a population at zero dimension ($d=0$) which contains the essential ingredients of fluctuation divergence. We will then introduce the diffusion for a spatially extended system. We will show that for $d \leq 2$, concentration fluctuations always diverge as a function of time. For higher dimensions, fluctuations remain finite. There is no phase transition from a diverging phase to a finite one at any dimension. Because for many organisms, life is at two dimensions, this mechanism may play an important role in aggregation and clustering phenomena.

II. MASTER EQUATION AT $d=0$

In this section, we will recall the main results of population size evolution at $d=0$ [4], which will be important when we introduce diffusion. Suppose that we begin at time $t=0$ with a population of n_0 individuals which can die or give birth to a new organism. In what follows, we will always suppose $\alpha=\mu$, i.e., equal probabilities for birth and death events. If the size of the population at time t is n , the probability for the population to lose or gain one individual during an infinitesimal time dt is $W(n \rightarrow n+1) = W(n \rightarrow n-1) = \alpha n dt$. Figure 2(a) shows 50 realizations of this stochastic process. As can be observed, the majority of the realizations disappear as time flows, but very few are able to escape and reach very high values. The ensemble average, however, remains constant, i.e., some of the few escapees can reach large values and compensate for the disappearance of the majority. Enrichment of the state $n=0$ and conservation of the ensemble average imply that the variance grows as a

function of time. The probability $P(n,t)$ of having n individuals at time t obeys

$$\partial_t P(n) = (n-1)P(n-1) + (n+1)P(n+1) - 2nP(n), \quad (2)$$

where time is written in $1/\alpha$ (generation) units and the initial condition is $P(n,0) = \delta_{n,n_0}$. The characteristic function, $\phi(s,t) = \sum_n P(n,t) \exp(isn)$, is given by

$$\phi(s,t) = \left[\frac{(t-1)e^{is} - t}{te^{is} - (t+1)} \right]^{n_0}. \quad (3)$$

Various moments are computed by the successive derivation of ϕ ,

$$\langle n(t) \rangle = i \partial_s \phi|_{s=0} = n_0, \quad (4)$$

$$\langle n^2(t) \rangle = -\partial_s^2 \phi|_{s=0} = n_0^2 + 2n_0 t, \quad (5)$$

$$\sigma^2(t) = 2n_0 t. \quad (6)$$

The variance of the population diverges linearly in time but the average is kept constant. $P(0,t)$, the fraction of realizations which have disappeared at time t , reads

$$P(0,t) = (t/(1+t))^{n_0}, \quad (7)$$

and tends toward 1 as $1 - n_0/t$. Large states n have nonzero amplitude. For $n_0=1$,

$$P(n,t) = t^{n-1}/(1+t)^{n+1}.$$

The above results for the moments can also be obtained by multiplying the master equation by n or n^2 and summing over n 's [5]:

$$d\langle n \rangle / dt = 0, \quad (8)$$

$$d\langle n^2 \rangle / dt = 2\langle n \rangle, \quad (9)$$

which are identical to Eqs. (4) and (5).

III. SPATIALLY EXTENDED SYSTEM

At zero dimensions, fluctuations due to random and equal birth and death rates diverge linearly in time. If we dispose an array of N noncommunicating petri dishes with n_0 organisms in each of them at $t=0$, after large enough time, we would observe that many of them are empty and few contain large quantities of the organism, hence the clustering phenomenon. Allowing the petri dishes to communicate will somehow diminish this clustering. We will investigate in this section the effect of diffusion by considering a d -dimensional lattice of cell size ℓ . We suppose homogeneous initial conditions, i.e., n_0 particles per lattice site.

We call $P(\mathbf{n};t) = P(\dots, n_i, \dots; t)$ the probability to have n_i particles at lattice site i at time t . The master equation reads

$$\begin{aligned} \frac{\partial P(\mathbf{n})}{\partial t} = & \beta \sum_{i,j} \{(n_i+1)P(n_i+1, n_j-1, \hat{\mathbf{n}}) - n_i P(\mathbf{n})\} \\ & + \alpha \sum_i \{(n_i-1)P(n_i-1, \hat{\mathbf{n}}) + (n_i+1)P(n_i+1, \hat{\mathbf{n}}) \\ & - 2n_i P(n_i, \hat{\mathbf{n}})\}, \end{aligned} \quad (10)$$

where β is the hopping rate to a neighbor site, α is, as before, the death (birth) rate, and $\hat{\mathbf{n}}$ designates all explicitly unwritten variables. The index j in the above equation designates neighbors of cell i . The first term in the right hand of Eq. (10) is the diffusion term, the second term is the source term, i.e., the local creation or annihilation of particles.

A. One dimensional systems

Let us first investigate the 1d case for ease of notation. By multiplying Eq. (10) by n_i and summing over \mathbf{n} , we obtain the evolution equation for the average values

$$d\langle n_i \rangle / dt = \beta (\langle n_{i-1} \rangle - 2\langle n_i \rangle + \langle n_{i+1} \rangle), \quad (11)$$

which is the usual diffusion equation. The source term, as in Eq. (8), makes no contribution. Initial conditions impose the trivial solution $\langle n_i(t) \rangle = n_0$.

For the correlations $\langle n_i n_{i+k} \rangle$, by multiplying Eq. (10) by $n_i n_{i+k}$ and summing over \mathbf{n} , we obtain

$$du_0 / dt = 2\beta(u_{-1} - 2u_0 + u_1) + \alpha n_0, \quad (12)$$

$$du_i / dt = 2\beta(u_{i-1} - 2u_i + u_{i+1}), \quad (13)$$

where $u_0 = \langle n_k^2 \rangle - n_0^2 - n_0$ and $u_i = \langle n_k n_{k+i} \rangle - n_0^2$ (note that $u_{-i} = u_i$). Because of the translational symmetry, $\langle n_k n_{k+i} \rangle$ depends only on the relative distance between two sites, i . The solution of linear equations (12) and (13) reads

$$u_n(t) = -n_0 e^{-4\beta t} I_n(4\beta t) + (\alpha n_0 / 4\beta) L_n(4\beta t), \quad (14)$$

where $I_n(z)$ is the modified Bessel function of order n and

$$L_n(\tau) = \int_0^\tau e^{-z} I_n(z) dz. \quad (15)$$

The first term in Eq. (14) is the relaxation of initial conditions, and the second term is the forcing term due to birth (death) source. As for large z , $e^{-z} I_n(z) = 1/\sqrt{2\pi z} + O(z^{-3/2})$, all correlations $u_n(t)$ diverge, for large t , as $\alpha n_0 \sqrt{t/4\beta}$. Thus, for a one dimensional system, we retrieve basically the same phenomenon as at $d=0$: fluctuations become arbitrarily large while the averages remain constant, hence the clustering of organisms for a particular realization of the discrete system.

At $d=1$, the solutions can be written explicitly,

$$L_0(z) = ze^{-z}[I_0(z) + I_1(z)], \quad (16)$$

and by using the derivative formula for Bessel functions, for $n \geq 1$,

$$L_n(z) = L_0(z) - n[1 - e^{-z} I_0(z)] + 2e^{-z} \sum_{k=1}^{n-1} (n-k) I_k(z) \quad (17)$$

$$= ze^{-z}(I_{n-1}(z) + I_n(z)) - 2e^{-z} \sum_{k=n}^{\infty} I_k(z). \quad (18)$$

For $z \gg 4n^2$, $L_n(z) = L_0(z) - n + O(z^{-1/2})$ and thus correlations decrease *linearly* in n . For small z , $L_n(z) \sim (z/2)^n / n!$.

B. Higher dimensions

The above equations for $d=1$ generalize without difficulty to higher dimensions. At any dimension, the averages $\langle n_i \rangle$ obey a simple diffusion equation, and because of homogeneous initial conditions of n_0 particles per cell, they remain constant: $\langle n_i(t) \rangle = n_0$. For the general case of d dimensions, the correlations read

$$\begin{aligned} u_{k, \dots, n} = & -n_0 e^{-d4\beta t} I_k(4\beta t) \dots I_n(4\beta t) \\ & + (\alpha n_0 / 4\beta) L_{k, \dots, n}(4\beta t), \end{aligned}$$

where

$$L_{k, \dots, n}(\tau) = \int_0^\tau e^{-dz} I_k(z) \dots I_n(z) dz,$$

and $u_{0, \dots, 0} = \langle n_{i_1, \dots, j_1} n_{i_2, \dots, j_2} \rangle - n_0^2 - n_0$ and $u_{k, \dots, n} = \langle n_{i_1+k_1, \dots, j_1+n_1, i_2, \dots, j_2} \rangle - n_0^2$.

For large z , the integrand $\sim z^{-d/2}$. For $d=2$, correlations diverge as $(\alpha n_0 / 4\beta) \ln(4\beta t)$: at two dimensions, diffusion is more efficient than at one but still not enough to inhibit fluctuation divergence.

For $d > 2$, $L_k(\tau)$ remains finite when $\tau \rightarrow \infty$. For large t , fluctuations are given by

$$\langle n^2 \rangle - n_0^2 = (1 + C\alpha/4\beta)n_0, \quad (19)$$

where C is a numerical constant. The second term in the right hand side of Eq. (19) is the reproductive fluctuations due to the source term. This last result is what is obtained from the mean field approximation of the master equation.

Even though at $d \geq 3$, fluctuations do not diverge in time, they can become arbitrarily large (compared to diffusion without the source term) if $\alpha \gg \beta$. As $\beta = D/\ell^2$ (D : diffusion coefficient), one can always consider large enough cells in order for the reproductive fluctuations to be noticeably larger than the diffusive ones. No clustering could however happen at $d > 2$, regardless of the lattice size: clustering can only happen if fluctuations are of the order of averages, i.e., if $\langle n^2 \rangle - n_0^2 > n_0^2$. This means that the added fluctuations due to birth (death) events, $\alpha/4\beta$, have to be of the order of the average number of particles per site, n_0 . The first term grows as ℓ^2 , and the second one as ℓ^d , so the condition is never satisfied as $\ell \rightarrow \infty$ for $d > 2$.

IV. CONCLUSION

The problem of clustering by birth (death) and diffusion processes was first investigated by Zhang *et al.* [5] and was further developed by Meyer *et al.* [6]. The first authors solved the problem at $d=0$ for equal birth and death rates. To solve the diffusive process, however, they introduced a global constraint which keeps constant the size of the population: each time an individual duplicates, another one, chosen at random in the whole population, dies. They then estimated the size of clusters and the diffusion of the center of the gravity of the whole population. The second authors also considered the case where less than one individual dies when one duplicates. The global constraint, however, removes all divergences from the correlation functions and their results are thus qualitatively different from ours. In general, we find it more attractive to consider the environment as affecting individuals' birth (death) rates, which in turn regulates the population size and not vice versa.

The problem we have investigated belongs to the class of nonequilibrium models where detailed balance is violated. A closely related problem, the branching and annihilating random walk (BARW) has received wide attention [7,8]. There, the reaction $A+A\rightarrow\emptyset$ and $A\rightarrow mA$ is considered and it is shown that there is a phase transition from an inactive phase (concentrations decaying as a function of time) to an active one (nonzero concentrations) at some critical dimension which depends on m .

The problem we have investigated could be relevant for living organisms. Due to limited resources, the condition of equal birth and death rates is satisfied for most organisms

evolving in their natural environment. However, local growth of an organism will deplete the local resources and hence inhibit cluster formations, and this situation is best studied in the framework of BARW processes, where the number of particles per site is not restricted to 0 or 1 [9]. If the local limiting resource can be considered as independent of the density of the organism, our treatment of clustering is valid. This is the case, for example, if the limiting resource is the available light, or if it is a small molecule diffusing much faster than the organism (such as Fe for phytoplankton). Using RG techniques, Schnerb *et al.* [10] have analyzed the problem of diffusing resources (catalyst) and have shown the existence of an active phase in some conditions.

To summarize, we have considered here the evolution of a population of Brownian particles, submitted to random and equally probable birth and death events: $A\rightarrow\emptyset$ and $A\rightarrow 2A$. We have shown that, even though the average concentration remains constant, fluctuations can become large. At $d\leq 2$, fluctuations diverge as a function of time, thus giving rise, for a particular realization, to the clustering phenomenon. At $d>2$, fluctuations remain finite, but concentration fluctuations can become arbitrarily large compared to ones due to diffusion, without inducing the formation of clusters.

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- [1] W.R. Young, A.J. Roberts, and G. Stuhne, *Nature* (London) **412**, 328 (2001).
 - [2] S.P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton University Press, Princeton, 2001).
 - [3] G. Bell, *Science* **293**, 2413 (2001).
 - [4] T.E. Harris, *The Theory of Branching Processes* (Springer-Verlag, Berlin, 1963).
 - [5] Y.C. Zhang, M. Serva, and M. Polikarpov, *J. Stat. Phys.* **58**, 849 (1990).
 - [6] M. Meyer, S. Havlin, and A. Bunde, *Phys. Rev. E* **54**, 5567 (1996).
 - [7] H. Takasuya and A.Y. Tretyakov, *Phys. Rev. Lett.* **68**, 3060 (1992).
 - [8] E. Carlon, M. Henkel, and U. Schollwok, *Phys. Rev. E* **63**, 036101 (2001).
 - [9] M.J. Howard and U.C. Tauber, *J. Phys. A* **30**, 7721 (1997).
 - [10] N.M. Shnerb, Y. Louzoun, E. Bettelheim, and S. Solomon, *Proc. Natl. Acad. Sci. USA* **97**, 10322 (2000).