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Birth, death and diffusion of interacting particles

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Abstract

Individual-entity-based models of chemical or biological dynamics usually consider individual entities diffusing in space and performing a birth–death-type dynamics. In this work we study the properties of a model in this class where the birth dynamics is mediated by the local, within a given distance, density of particles. Groups of individuals are formed in the system and in this paper we concentrate on the study of the properties of these clusters (lifetime, size, and collective diffusion). In particular, in the limit of the interaction distance approaching the system size, a unique cluster appears which helps us to understand and characterize the clustering dynamics of the model.

1. Introduction

Interacting particle systems are models in which the individual elements or *particles*, representing molecules, biological entities, or social agents, evolve in time following *microscopic* rules, from which collective macroscopic behaviour may emerge. This modelling approach has been used with success in physical, chemical, social, and biological dynamics [1–4]. Macroscopic diffusion in such systems usually arises from the random walk motion of the individuals.

An important subclass among these models is formed by those in which birth and death processes occur. Usually they have a biological inspiration, but they are also found in chemical or physical contexts. The combination of this number-changing dynamics with the diffusive motion which is usually assumed for the particles has profound consequences, one of the most striking being the formation of clusters and the apparent attraction among individuals that are actually noninteracting [5–7]. In addition, and most recently, interactions among individuals that are reflected in changes in their birth or death rates have also been considered, and have also given rise to a complex collective behaviour. In a recent paper [8] we explored the consequences for the dynamics of diffusing individuals induced by the introduction of a finite spatial extent for the range of such interactions. In particular we considered the case of a birth rate which becomes reduced proportionally to the number of particles at a distance smaller

than a range R . In a biological setting this dependence models in a natural way competition for resources, but it can also be a consequence of other phenomena such as toxin production. The most notable effect of the interaction was the appearance of a clustering instability organizing the distribution of individuals into clusters separated by a typical distance.

In this paper we address further characteristics of the model by focusing on such coherent objects, the clusters: we analyse here their diffusive motion, their size, and some aspects of their dynamics and interactions. These are characteristics that lie outside the capabilities of descriptions in terms of a continuous density of particles evolving deterministically [8–10], that have been sometimes used instead of the ones in terms of stochastic particles. The situation in which the range of interaction is of the order of the system size, so that any individual interacts with all the others in the system, allow us to focus on the dynamics of a single cluster: under these conditions a permanent unique cluster emerges in the system and the studies of the cluster properties are substantially facilitated. It will also be shown that a coarse-grained deterministic description of the system cannot explain the appearance of the cluster in this limit of global interaction of particles, placing emphasis on the importance of the fluctuations (discrete nature of the particles) in the model. Although the model was originally introduced in two spatial dimensions, we restrict consideration here to the one-dimensional case, since it contains the essentials of the phenomenology.

The paper is organized as follows. In the next section the model is presented. In section 3 we explain the clustering instability of the system through the introduction of a spatiotemporal field related to a net growth rate. In section 4 we study the properties of the system in the limit of global coupling, focusing on the dynamics of cluster competition, cluster size, and diffusion properties of the cluster. Section 5 presents our conclusions.

2. A model of interacting random walkers

Ensembles of particles performing Brownian motion and with a birth–death-type dynamics have long been used in the modelling of biological populations. A natural way of introducing an effective interaction among the organisms when there is a competition for the sources is to consider that birth and death rates of any individual are altered by the local density in its neighbourhood. With this in mind, the authors recently introduced a model where the birth rate for a given particle is decreased with the number of other particles that are within a finite distance R . In more detail, the system consists initially of a set of N particles randomly located at positions x_1, x_2, \dots, x_N in a one-dimensional segment of length L with periodic boundary conditions. The number N and the positions of the particles evolve according to the following algorithm. First, one of the particles is chosen at random (let us call it the i th particle, at position x_i). Second, the basic ingredients of the model, the probabilities λ_i and β_i of reproduction and death respectively, which depend on the environment surrounding i , are calculated as described later. Third, with the birth probability λ_i a new particle is introduced in the system exactly at the location of the mother particle i , or rather, with the death probability β_i , the particle i disappears from the system. With probability $r_i = 1 - \lambda_i - \beta_i$, no changes are made. These three steps leading to the trial of a particle and its fate are repeated a number N times, after which the number of particles N in the system is updated. We choose this lapse of N trials to be the unit of time, so that λ_i and β_i are also, at least at the beginning of each time unit, birth and death probabilities per particle and per unit of time. After this, each particle is moved a random distance drawn from a Gaussian distribution of variance σ^2 . This Brownian motion leads to macroscopic diffusion with diffusion coefficient $D = \sigma^2/2$. Then the process repeats for the following time units.

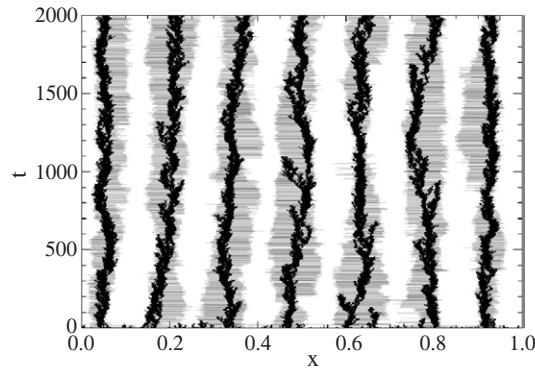


Figure 1. Spatiotemporal representation (space on the horizontal axis, and time on the vertical) of the patterns of our stochastic model. $R = 0.1$, $N_s = 50$, $\lambda_0 = 0.8$, $\beta_0 = 0.2$, $D = 5 \times 10^{-7}$. Positions of the particles are plotted in black. They cluster in seven groups during most of the simulation. The background grey level field displays the local net growth $\mu(x, t)$. White denotes the most negative value $\mu(x, t) = -\beta_0$, whereas the darkest shades of grey denote values fluctuating around zero.

The defining characteristic of the model is that the birth and death probabilities λ_i and β_i may depend on the number of other particles N_R^i within a distance R of the chosen one i (i.e. within an interval of size $2R$ centred on particle i). To compare with previous works we include the dependence only on the birth rate:

$$\lambda_i = \max\left(\lambda_0 - \frac{N_R^i}{N_s}, 0\right) \quad (1)$$

$$\beta_i = \beta_0. \quad (2)$$

The max function is introduced to avoid negative values for the probability. N_s is a saturation constant. In addition we choose $\lambda_0 + \beta_0 = 1$, so that the independent model parameters are D , R , N_s and β_0 (and the system size L). Instead of β_0 one can characterize the system with the maximum growth rate $\mu_0 \equiv \lambda_0 - \beta_0 = 1 - 2\beta_0$.

3. The clustering instability

A simple mean field argument would predict that, assuming a steady homogeneous density of particles ρ_0 , the expected number of particles at distance smaller than R from a given one would be $N_R^i \approx 2R\rho_0$, and thus the effective birth rate will be given by $\lambda_0 - 2R\rho_0/N_s$. In a statistically steady state this should equate to the death rate β_0 , so that $\rho_0 \approx \mu_0 N_s / 2R$. A typical evolution of the system when the diffusion coefficient is small and μ_0 positive and not too close to zero is shown in figure 1. The salient feature is the grouping of the particles in a number of fluctuating clusters. The first hypothesis in the mean field argument, namely the existence of a homogeneous density, is clearly inappropriate. In fact the total number of particles is larger than the $\rho_0 L$ predicted by the argument. One can understand the observed pattern from the following reasoning: if, after starting with a random distribution of particles, there is a fluctuation in the particle positions such that the local density increases at two relatively narrow locations (the cluster seeds) separated by a distance between R and $2R$, particles left close to the middle point between these locations will count the population of the two clusters among their neighbours, whereas particles in each cluster will count as neighbours only the particles

in their own clusters. As a consequence the birth rate in the cluster seeds will be larger than the one in the region in between, and the difference between the particle densities in the two regions will increase, leading to an instability that will finally concentrate all the particles in big clusters at a separation fR , intermediate between R and $2R$. In figure 1 the separation is fR with $f \approx 1.4$. Within this reasoning, all particles in a cluster feel essentially the same λ_i and β_i , and do not interact with particles in the other clusters if the cluster positions do not approach too much. Then the number of particles in each cluster N_c will stop growing when it reaches a level such that $\lambda_i \approx \beta_i$, i.e. $N_c \approx \mu N_s$. This gives $N_c \approx 30$ for each cluster in figure 1, whereas in the simulation this number fluctuates around 29. It is a curious and counterintuitive effect that, since $f < 2$, the mean number of particles in the system $\mu_0 N_s L / fR$ is larger than that in the homogeneous situation $\mu_0 N_s L / 2R$, despite the fact that grouping particles into clusters seems at first sight to increase N_R^i and thus to decrease the birth rate.

To give further support to the arguments above we plot in figure 1 a net growth rate field $\mu(x, t)$ defined as

$$\mu(x, t) = \max \left(-\beta_0, \lambda_0 - \beta_0 - \frac{1}{N_s} \int_{x-R}^{x+R} du \hat{\rho}(u, t) \right) \quad (3)$$

where $\hat{\rho}(x, t) \equiv \sum_{k=1}^{N(t)} \delta(x - x_k(t))$ is the microscopic density of particles. The integral in this expression counts the number of particles in the neighbourhood of a point x , so that the field $\mu(x, t)$ would give essentially the net particle number growth rate when evaluated at the particle positions ($\mu(x = x_i, t) \approx \lambda_i - \beta_i$) except for the extra counting of the particle i which is negligible in situations with many particles. The integral acts as a low pass filter of the microscopic density, so that typical features in $\mu(x, t)$ will have sizes of order R and above. Figure 1 displays this field and confirms that its value is $-\beta_0$ in most of the intercluster region, so that only death can occur there, and that it is slowly varying spatially (and temporally fluctuating close to zero) in regions of size close to R , which we call the *niches*, around the places where the particles are. The particles are in fact so concentrated inside the niches that there are no important differences among the values of $\mu(x, t)$ that they feel at most of the times t . The introduction of the field $\mu(x, t)$ is a convenient tool for representing the interactions at a distance between the particles in terms of the local interaction of each particle with the field $\mu(x, t)$ at its location.

The above heuristic calculations fail in at least two situations. First, they are qualitative arguments involving average quantities; thus they will give wrong results when statistical fluctuations are strong. This happens when the number of particles in the clusters is small, which occurs when decreasing μ_0 . It was shown in [8–10] that fluctuations lead to full extinction for μ_0 below a μ_c that for R, N_s , and D as in figure 1, is given by $\mu_c \approx 0.34$, which is far above the value $\mu_c \approx 0$ that one would estimate if fluctuations were neglected. This is so because the state with zero particles is an *absorbing state* [11] from which no recovery is possible. This irreversibility biases the statistics so that extinction occurs as soon as the average particle number becomes of the order of its fluctuations, despite them acting both to increase and decrease the number of particles. Close to μ_c the expected number of particles in any cluster is smaller than implied by the above estimations, in the same way as shown in [9, 10] for expected densities. This absorbing character of the empty state also has the consequence that a intercluster spacing between R and $2R$ is the expected outcome only from an initial condition of particles filling up the whole system. Initial conditions in which particles are already clustered into groups more distant than $2R$ will also be stable, despite the fact that a niche will develop in the empty space in between. This is so because of the impossibility of spontaneous creation of particles in that empty niche, and of the difficulties of particles in neighbouring niches colonizing the empty one due to the presence of *zones of*

death around it, and of the strong correlations in the motion of all the particles inside a cluster that will be discussed in section 4.3.

A more subtle failure occurs even at sufficiently large μ . The arguments above rely on the assumption that the clusters remain sufficiently narrower than R . In fact this is what happens in the situation of figure 1 and always for sufficiently small D . But the mechanism that keeps the cluster at this width without spreading over all the niche is by no means obvious, and will be discussed in section 4.2. It is natural to think, and it will be confirmed later, that increasing the diffusion coefficient D , a quantity that has not yet appeared in our argumentations, will increase the cluster size. For sufficiently large D , configurations will become homogenized and clustering will not be observed.

Another hypothesis in our reasoning, confirmed by the simulations, is that there is a single cluster in each niche. Therefore, it seems that it is essential for the understanding of the full dynamics to understand the behaviour—size, motion, stability, . . .—of single clusters. We address that in the following section, but after noting that the simplest situation that one can consider is that in which the range of interaction R reaches the full system size (i.e., $R = L/2$) since then there is a single niche in the system. This case should represent the dynamics of particles inside any of the niches (thus being noninteracting with the other clusters) in most of the situations, except when the cluster approaches the niche boundaries, that would produce an enhanced mortality at the exposed side.

4. Dynamics with global coupling

The case $R = L/2$ is the simpler one since then all the birth rates λ_i become completely independent of the position x_i of the particles, and $\mu(x, t)$ fluctuates only in time, not in space, adapting to the total number of particles in the system: $\mu(x, t) = \mu(t) = \mu_0 - N(t)/N_s$, if $N(t) < \lambda_0 N_s$, and $\mu(t) = -\beta_0$ for larger $N(t)$. We expect $N(t)$ to fluctuate around $N_c = \mu_0 N_s$. Next, we first explain why there is still a single cluster in the system, despite the large extent of the niche, and then estimate its width and diffusive behaviour.

4.1. Cluster competition and lifetime

In principle, since in this limit $R \rightarrow L/2$ the interactions among the particles are independent of their positions, and if we forget about stochastic effects, the system can be organized in a single cluster with N_c particles, or in two with $N_c/2$ particles each, or in fact in any configuration such that the total number of particles remains in average close to $N_c = \mu_0 N_s$. But not all these configurations are equally stable against stochastic particle number fluctuations. Clusters with a small number of particles will disappear quite fast because of the high probability of a number fluctuation of the order of its size, and the irreversibility of cluster extinction. This effect will be further on facilitated by the negative correlations between particle number fluctuations of different clusters (a positive fluctuation in one cluster will reduce λ_i for all particles, so that birth will be less frequent in the following steps). We expect that multiple cluster configurations will decay into the most stable state, the one consisting of a single cluster that will be the one observed for most of the time, independently of the extent of the niche.

Figure 2 shows the evolution of initial conditions containing several clusters under global coupling. The initial part of the evolution was generated with small values of R so that the system organizes in a number of clusters separated by distances fR . R is increased to $R = L/2$ at $t_i = 3500$. As expected, all the clusters except one disappear in a very short time. Figure 3 shows the evolution of the number of particles in each cluster in the case of two competing ones. Immediately after the change in R the total number of particles in the system decreases,

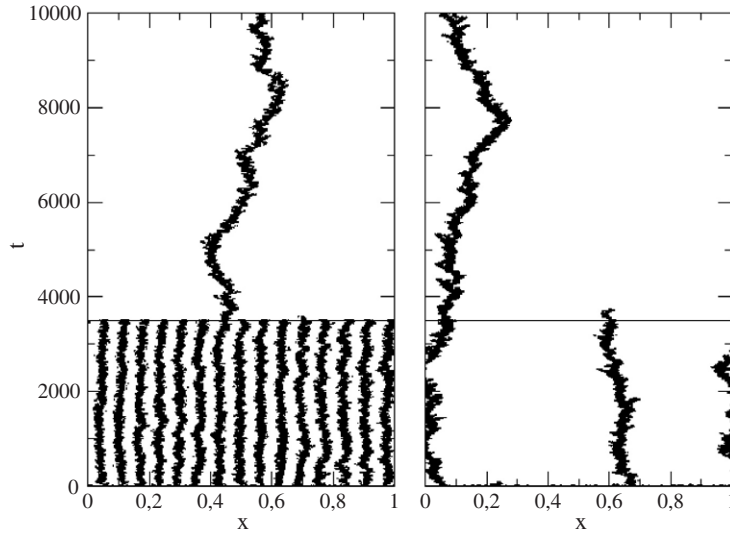


Figure 2. Left panel: evolution of a set of 15 clusters prepared under $R = 0.05$ before we change R to global coupling $R = L/2$ at time $t_i = 3500$ (indicated by the horizontal line). A short time afterwards, a single cluster survives. Right panel: analogous simulation but with only two clusters (prepared under $R = 0.324$) before switching to global coupling at $t_i = 3500$. The rest of parameters take the values $\beta_0 = 0.25$, $D = 10^{-6}$, and $N_s = 50$.

since the initial N is twice what it should be at the end, N_c . Once the total number of particles is close to N_c the real competition starts. One of the clusters becomes smaller by chance and disappears after some time, a victim of stronger relative fluctuations. Then, the survivor cluster adjusts its population to fluctuate close to the expected final value $N_c = \mu_0 N_s$ (which in figure 3 is $N_c = 25$ because $\beta_0 = 0.25$ and $N_s = 50$). The tendency of the single cluster to maintain this number of particles will make it much longer lived. On general grounds we expect the time of extinction of a single cluster to increase exponentially with its number of particles N_c so that for practical purposes single clusters remain forever when they have more than a few particles.

We can estimate the fluctuations in the particle numbers of competing clusters and their lifetimes by adapting some arguments from [7]. We can compare with the models in that paper if we introduce two approximations. First, we estimate that the total number of particles is exactly $N = N_c = \mu_0 N_s$ instead of fluctuating around this number. Second, we perform the calculations by thinking that all the N particles are checked for reproduction or death exactly once every unit of time, instead of being checked once *on average*. With these approximations, the number of particles in one of the clusters, say cluster 1, is given by

$$N_1(t) = N_1(t=0) + \sum_{\tau=1}^t \Delta N_1(\tau) \quad (4)$$

where $\Delta N_1(\tau)$ is the increment in particle number in that cluster occurring during step τ . This quantity is given by

$$\Delta N_1(\tau) = \sum_{i=1}^{N_1(\tau)} \alpha_i(\tau). \quad (5)$$

$\alpha_i(\tau)$ is the increment or decrease in particle number occurring when particle i is checked at time τ , i.e. $+1$ with probability $\lambda_0 - N(\tau)/N_s \approx \beta_0$, -1 with probability β_0 , and 0 with

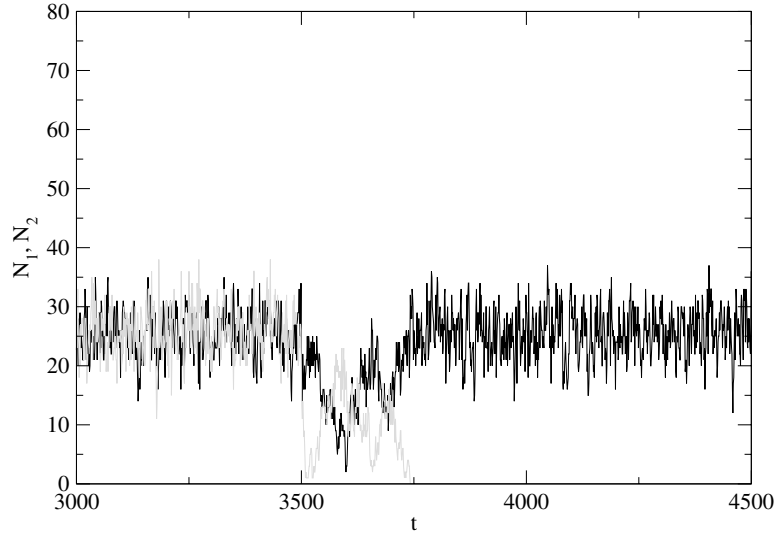


Figure 3. Time evolution of the number of particles of the two clusters in the right panel of figure 2 just before and after the time ($t_i = 3500$) at which R is switched to global coupling. In black, data for the surviving one; in grey, data for the one disappearing at $t \approx 3750$.

probability $1 - 2\beta_0$. We have used the assumption that the total number of particles in all the clusters $N(\tau)$ has a constant and nonfluctuating value: $\mu_0 N_s$ and, despite this constraint, we still assume that the $\{\alpha_i(\tau)\}$ are independent variables for each i and τ . These approximations will be more consistent when $N_1 \ll N$. From them we get

$$\langle \alpha_i(\tau) \rangle = 0, \quad \langle \alpha_i(\tau) \alpha_j(\tau') \rangle = \delta_{ij} \delta_{\tau\tau'} \langle \alpha_i(\tau)^2 \rangle, \quad \langle \alpha_i(\tau)^2 \rangle = 2\beta_0 \quad (6)$$

from which $\langle N_1(\tau) \rangle = N_1(0)$ and

$$\begin{aligned} \langle \Delta N_1(\tau) \rangle &= 0, & \langle \Delta N_1(\tau) \Delta N_1(\tau') \rangle &= \delta_{\tau\tau'} \langle \Delta N_1(\tau)^2 \rangle, \\ \langle \Delta N_1(\tau)^2 \rangle &= 2\beta_0 N_1(0). \end{aligned} \quad (7)$$

Thus we see that the expected number of particles in each cluster is a constant, but the variance increases without limit as follows from (4) and (7):

$$\langle N_1(t)^2 \rangle - \langle N_1(t) \rangle^2 \approx 2\beta_0 t N_1(0). \quad (8)$$

A natural identification of the time of extinction of the cluster is the time t_m for which the variance equates to the square of the mean value of N_1 . This happens when

$$t_m \approx \frac{N_1(0)}{2\beta_0}. \quad (9)$$

Clearly, this expression cannot be applied to the lifetime of a single cluster, since then one cannot neglect the fluctuations in N , or the correlations among N and the reproduction rates.

Figure 4 shows the average time for disappearance of one of the two clusters evolving in situations such as that in the right panel of figure 2 or 3. We plot this time versus N_s (the controllable parameter of the model) which approximates $N_1(0)$ via $N_1(0) \approx \mu_0 N_s$. In the figure, $\beta_0 = 0.25$, so that the slope of the curve should be 1. The slope of a linear fitting through the numerical data is 1.2. It is remarkable that despite the severe approximations introduced to obtain (9) the general trend is correct and quantitatively close to the numerically observed lifetimes.

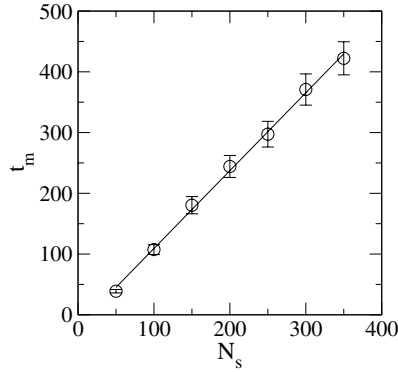


Figure 4. The average time (over 500 realizations) as a function of N_s for extinction of one of the two competing clusters evolving under global coupling. $D = 10^{-5}$ and $\beta_0 = 0.25$. The initial number of particles in the cluster $N_1(0)$ is approximately equal to $\mu_0 N_s$. The line is the best linear fit to the data, with slope 1.2.

4.2. Cluster spatial size

After justifying that a single cluster in a niche is the natural state of the evolving particle system, we can estimate the spatial extent of this cluster. Since particles do not attract nor repel, they will experience pure diffusive motion throughout their lifetimes. The only factor impeding the unbounded diffusive spreading of the cluster is the finiteness of the lifetime. One is tempted to guess that the size of the cluster would be $\sqrt{2D/\beta_0}$, since this is the diffusive displacement of a particle during its average lifetime β_0^{-1} (we define cluster size as the standard deviation of the particle positions: $S_c \equiv (\langle x_i^2 \rangle - \langle x_i \rangle^2)^{1/2}$; an alternative definition as the root mean square of the distance between two randomly chosen particles is larger by an extra factor $\sqrt{2}$). That guess of the size is incorrect because the cluster width will continue to grow after the initially chosen particle has died if its descendants (its *family*) are still alive and diffusing (we can say that the descendants continue the diffusion process of the mothers, since they are born at the mothers' locations). The width of the cluster will be determined from the diffusive spread among the members of the longest lived families. We cannot apply the arguments for lifetimes of the previous subsection to a whole cluster, but they can be applied to subsets inside a cluster (in the case of global coupling there is no difference between the interactions among particles in different and in the same cluster), for example a family. The longest lived families would be the ones reaching a size close to the total one N_c . From the estimation of the previous section, the typical lifetime of a family is of the order of $t_m = \mu_0 N_s / 2\beta_0$. The standard deviation reached by the particle positions after that time will be $\sqrt{2Dt_m}$. The typical cluster size is thus given by

$$S_c \approx \sqrt{\frac{DN_s(1 - 2\beta_0)}{\beta_0}}. \quad (10)$$

Figure 5 shows that this expression, obtained under several approximations, is surprisingly accurate.

4.3. Cluster diffusion

In figures 1 or 2 we see that each cluster as a whole undergoes a kind of random walk (in figure 1 only until the clusters touch the limit of the niche, the moment at which some particles interact

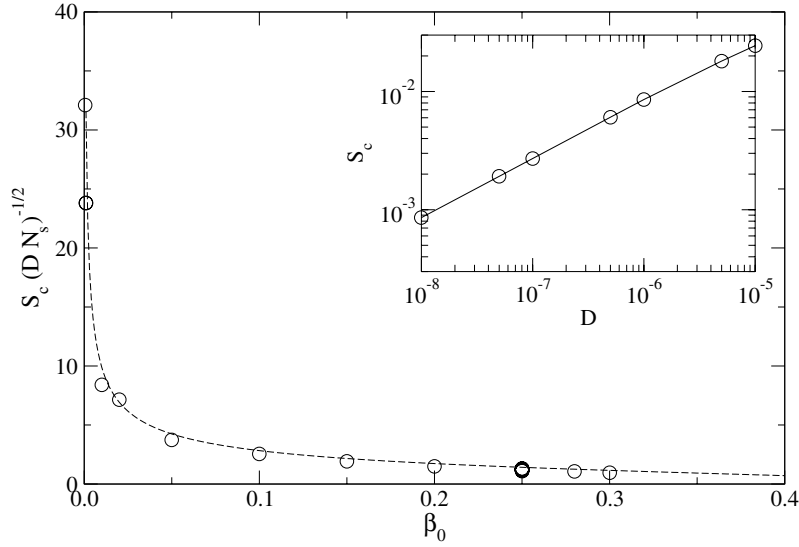


Figure 5. Cluster size, estimated as the mean square dispersion of the particles, and averaged over time, as a function of β_0 . The parameter values are $D = 10^{-7}$, $N_s = 50$, and $R = 0.5$ (global coupling). The vertical axis is scaled with $\sqrt{DN_s}$, and the solid line is the function $\sqrt{(1-2\beta_0)/\beta_0}$ predicted by (10). For $\beta_0 = 0.25$, and always $R = 0.5$, other values of the parameters have also been plotted (collapsing almost to the same point): $D = 10^{-7}$ and $N_s = 40, 50, 60, 70, 80, 90, 100, 150, 200, 250, 300$; $N_s = 50$ and $D = 10^{-9}, 10^{-8}, 10^{-6}, 10^{-5}$. The inset, for $\beta_0 = 0.25$ and $N_s = 50$, shows the clear diffusive dependence $S_c \sim D^{1/2}$ of the cluster size.

with the neighbouring niche, some of them die, and the remaining ones are the ones returning to the interior of the niche). If naively one forgets the correlations among the diffusing particles, one would guess that the diffusion coefficient (estimated from the displacement of the centre of mass) should be D/N_c . Figure 6 shows that in fact the diffusion coefficient is D , the same as that for the individual particles. The particles in the cluster move so coherently that they behave collectively as a single particle. We can understand this result again by modifying a discussion from [7].

We begin by splitting the expression for the centre of mass X_{cm} at time $t - 1$ as follows:

$$\begin{aligned} X_{cm}(t-1) &\equiv \frac{1}{N} \sum_{i=1}^N x_i(t-1) \\ &= \frac{1}{N} \sum_{i \in F} x_i(t-1) + \frac{1}{N} \sum_{i \in B} x_i(t-1) + \frac{1}{N} \sum_{i \in M} x_i(t-1). \end{aligned} \quad (11)$$

B is the set of particles that will give birth during the next time step, M is the set of particles that will die, and F is the remaining set. As before, we assume that the number of particles N is constant and equal to $N_c = \mu_0 N_s$. After one time step the birth, death, and diffusion process will change the above expression into

$$\begin{aligned} X_{cm}(t) &\equiv \frac{1}{N} \sum_{i=1}^N x_i(t) = \frac{1}{N} \sum_{i \in F} (x_i(t-1) + \sigma g_i^F(t)) \\ &\quad + \frac{1}{N} \sum_{i \in B} (x_i(t-1) + \sigma g_i^B(t)) + \frac{1}{N} \sum_{i \in M} (x_i(t-1) + \sigma h_i^M(t)). \end{aligned} \quad (12)$$

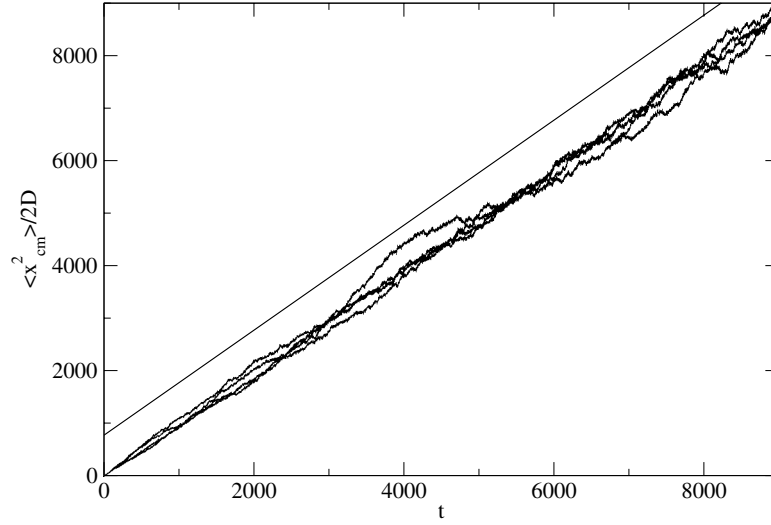


Figure 6. Position (average over 200 realizations) of the centre of mass of one cluster, $\langle X_{\text{cm}}^2 \rangle$, scaled with $2D$, versus time, and for different values of D , β_0 , and N_s . The slope of the straight line is 1, confirming that the centre of mass diffuses with coefficient D . Four different curves are plotted, that almost collapse onto a single one. They correspond to the following parameter sets: (a) $D = 10^{-6}$, $\beta_0 = 0.20$, $N_s = 50$; (b) $D = 10^{-6}$, $\beta_0 = 0.25$, $N_s = 80$; (c) $D = 10^{-7}$, $\beta_0 = 0.25$, $N_s = 50$; (d) $D = 10^{-5}$, $\beta_0 = 0.25$, $N_s = 50$.

The particles in M have disappeared, and there are two copies of the particles in B . $g_i^F(t)$, $g_i^B(t)$, and $h_i^B(t)$ are normalized and independent Gaussian random numbers, and $\sigma = \sqrt{2D}$. Subtraction of (12) and (11) gives (remember that we are assuming a constant total number of particles)

$$X_{\text{cm}}(t) - X_{\text{cm}}(t-1) = \frac{1}{N} \sum_{i \in B} x_i(t-1) - \frac{1}{N} \sum_{i \in M} x_i(t-1) + \frac{\sigma}{\sqrt{N}} g(t). \quad (13)$$

We see that, in addition to the standard diffusive motion given by the term containing the normalized Gaussian number $g(t)$, the displacement of the centre of mass is also controlled by the removal of the particles in M and the replication of particles in B . To explicitly estimate this contribution we approximate the number of particles in B and M by its expected value $n \equiv N\beta_0$. Thus the first two terms in the right-hand side of (13) can be written, after renaming the particle labels, as

$$\frac{1}{N} \sum_{i=1}^n (x_i(t-1) - x_{i+n}(t-1)). \quad (14)$$

The term in parenthesis is the distance between two randomly selected particles inside the cluster. Its typical (root mean square) value is $\sqrt{2}S_c$. If n is large enough we can invoke the law of the large numbers and find

$$\langle (X_{\text{cm}}(t) - X_{\text{cm}}(t-1))^2 \rangle \approx \frac{2D}{N} + \frac{n}{N^2} 2S_c^2 \approx \frac{2D}{N} + 2D. \quad (15)$$

In large clusters the first term, coming directly from the uncorrelated particle motion, becomes negligible, and the second, coming from the reproductive correlations, i.e. correlations introduced in the system when new particles are born at the mothers' positions, dominates. This demonstrates that the diffusion coefficient of big clusters approaches D , the diffusion

coefficient of a single particle. Reproductive correlations transform individual random walks into fully coherent motion of the particles inside a diffusing cluster.

5. Conclusions

We have described results for the behaviour of an interacting particle system evolving under diffusion, birth, and death processes. Because of its simplicity, and of the ubiquity of the interactions considered (essentially competition for resources), we expect this behaviour to represent features of real systems, in particular biological ones. The essential building blocks of the dynamics are particle clusters that spontaneously form in the parameter range considered here. They live in niches where birth and death rates equilibrate. Previous work [8] described the appearance and spacing of the clusters in terms of a deterministic equation for a continuous density, but it failed to reproduce many important properties of the model. Here we have noted the adequacy of the global interaction limit for representing the dynamics inside a single niche, and thus concentrated on that limit for understanding features not well described by the deterministic continuous description. It is worth mentioning that a deterministic continuous description is particularly inaccurate in this limit: the integrodifferential equation in [8] for an expected density of particles $\rho(x, t)$ becomes

$$\partial_t \rho(x, t) = \left(\mu_0 - \frac{N(t)}{N_s} \right) \rho(x, t) + D \partial_x^2 \rho \quad (16)$$

where the dynamics of the total number of particles is decoupled from the spatial distribution:

$$\dot{N}(t) = \mu_0 N(t) - \frac{1}{N_s} N(t)^2. \quad (17)$$

Equations (16) and (17) can be solved exactly. At long times $N(t) \rightarrow \mu_0 N_s$, in agreement with the calculations in this paper, but then (16) becomes a diffusion equation, predicting a homogeneous particle distribution at long times. This is in contrast with the grouping of all the particles in a single cluster that is observed in simulations of the stochastic particle model and understood using the previous calculations. The situation is very similar to the one described in [5]. Reproductive correlations, the phenomena produced by the fact that newborns appear at the mother location whereas death can occur anywhere, are responsible for shaping the clusters and their motions, despite a continuous equation that neglects them possibly giving the correct spacing. It was emphasized in [5] that an equation for an expected density is just the first step in the hierarchy describing particle distributions and that additional quantities—correlation functions—are needed to fully capture the clustering behaviour. In a remarkable recent paper [12], Birch and Young describe that hierarchy in general terms and they are even able to solve it in the case of global coupling for a model of interactions in which the death rate is neighbourhood dependent, and for which the death probability vanishes when there is a single particle in the system, so that complete extinction is impossible. It would be very interesting to understand the relationship between the results for their model and the ones presented here. Without using the power of that general framework, we have obtained here expressions for lifetimes, sizes, and collective diffusion that agree very well with numerical simulations.

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