Forcing anomalous scaling on demographic fluctuations

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We discuss the conditions under which a population of anomalously diffusing individuals can be characterized by demographic fluctuations that are anomalously scaling themselves. Two examples are provided in the case of individuals migrating by Gaussian diffusion, and by a sequence of Lévy flights.

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I. INTRODUCTION

Simple birth-death models, with individual migration described by a diffusion process, provide a simple illustration of how demographic stochasticity at the microscopic level translates into the phenomenon of spatial clustering [1, 2]. The original setting of the model involved Brownian walkers ("Brownian bugs", in the terminology of [3]), but the generalization to the case of anomalously diffusing individuals was considered as well [4, 5]. Contrary to what could have been expected, clustering did not appear to be sensitive to the character of the diffusion process. What appeared to be effective in modifying the population dynamics, instead, was the possibility that memory of the trajectories be transferred from individuals to their descendants [5].

At least in the case of a migration dynamics of the continuous time random walk (CTRW) type [6, 7], memory transfer between generations was insufficient to produce any scaling dependence on the Hurst exponent of the diffusion in the population dynamics [5]. What was observed, was collapse on a Galton-Watson like behavior [8]. The question remained open on whether different models would lead to the same result.

What we intend to analyze in the present report is precisely under what conditions a dependence between the scaling of the local population fluctuations, and that of the diffusion process, can exist. We shall consider two cases: that of anomalous diffusion produced by a Gaussian process, and that of diffusion produced by a sequence of Lévy flights [9, 10]. These are situation of importance both conceptually and from the point of view of applications. Physically relevant examples of anomalous Gaussian diffusion include particles migrating with a velocity that is solution of a generalized Langevin equation (GLE) [11], and, of course, the fractional Brownian motion (FBM) [12]. Lévy flights constitute an important ingredient in modelling the spreading of epidemics [13], biologic searching strategies [14], as well as bacteria dynamics [15].

In the case of Gaussian diffusion, we shall see that "anomalous" scaling of the population fluctuation can indeed be produced, and it is the result of a delicate interplay between Gaussian statistics, memory transfer between generations, and the non-Markovian nature of the process. In the case of Lévy flights, the Markovian nature of the diffusion process makes any memory transfer between generations irrelevant to the dynamics, and the scaling of the local population fluctuations will appear to be determined automatically by the stable law of the Lévy process.

II. GAUSSIAN DIFFUSION

Let us consider the simple situation of a population of non-interacting individuals, with identical birth and death rates $\Gamma_B = \Gamma_D = \Gamma$ (one offspring for each birth event) to insure stationarity. We assume births and deaths to be Markovian and focus on the effect that anomalous diffusion of the individuals may have at the population level. Let us limit the analysis, for the moment, to a one-dimensional situation.

We consider first the case of a Gaussian, anomalous diffusion process. Contrary to the case of normal diffusion, in which the condition of linear scaling of the mean square displacement (assuming Gaussian statistics) determines uniquely the process, full knowledge of the displacement correlation is necessary in the anomalous case.

Let us consider a population that initially is uniformly distributed in space, with $\rho_1(x,0) = n_0$. Equality of the birth and death rates guarantees that the population remains on the average uniformly distributed, with the same population density $\rho_1(x,t) = \langle \tilde{n}(x,t) \rangle = n_0$ [we have indicated with $\tilde{n}(x,t)$ the instantaneous value of the population density, including fluctuations]. To study fluctuations, we must consider the higher moments of $\tilde{n}(x,t)$, in particular the two-bug correlation

$$\rho_2(x_1,x_2;t) = \langle \tilde{n}(x_1,t)\tilde{n}(x_2,t) \rangle,$$

or, more precisely, its connected part $\rho_{2c}(x_1,x_2;t) = \rho_2(x_1,x_2;t) - n_0^2$.

A representation of the population dynamics is obtained considering the family trees of its members, as illustrated in Fig. 1. A quantity such as the correlation $\rho_2(x_1,x_2;t)$ is obtained therefore by summing over the tree branches passing through $(x_1,t)$ and $(x_2,t)$ and averaging over the family tree configurations. The family trees responsible for the connected component $\rho_{2c}(x_1,x_2;t)$ are those represented in case a of Fig. 1,
We can read Eq. (2) from the family tree in which the individuals at \((x_{1,2}, t)\) share a common ancestor. Clearly, cutting the family tree of case \(a\) above the branching at \((z, \tau)\) and neglecting all the previous history, would lead to a disconnected tree identical to the one represented in \(b\). It is easy to be convinced that the same result would be obtained by reinitializing from scratch the migration strategies of the individuals at the branching. A complete reinitialization of migration at each birth event, would lead in fact to Markovianization.

Branching. A complete reinitialization of migration at each birth event, would lead in fact to Markovianization of the population dynamics at times longer than the individual lifetime \(\Gamma^{-1}\), with the displacements of different individuals over a lifetime becoming independent. (In the case of migration by a CTRW, this lead to a clustering dynamics in the population identical to that of Brownian bugs [16].)

In order to obtain a non-trivial dynamics, the newborn individuals must preserve some memory of the trajectories followed by their parents. We shall consider the situation in which individuals along the same family line have full memory of the trajectory followed by their ancestors.

Let us indicate by \(G(x - z, t - \tau) \equiv \rho_1(x, t|z, \tau)\) the mean population density at \((x, t)\) given presence of an ancestor at \((z, \tau)\), with \(\tau < t\), and with \(\rho_1(x, t|z, \tau; w, 0)\), the same quantity conditioned to presence of a common ancestor at \((w, 0)\). From equality of the birth and death rates, the total number of individuals accounted for by \(\rho_1(x, t|.)\) is one and these functions are normalized to one and coincide with the conditional PDF’s (probability density functions) for the position a single walker in the absence of birth and death effects. We can write:

\[
\rho_2c(x_1, x_2; t) = 2\Gamma \int_0^t \int_dz \int dw \, \rho_1(x_1, t|z, \tau; w, 0) \times \rho_1(x_2, t|z, \tau; w, 0)G(z - w, \tau) \times \rho_1(w, 0).
\]

We can read Eq. (2) from the family tree \(a\) in Fig. 1:

- The factor \(G(z - w, \tau)\rho_1(w, 0)\) is the individual density at \((z, \tau)\), originating from an ancestor at \((w, 0)\), that is available to generate offspring.

Gaussian statistics makes determination of the conditional PDF’s \(\rho_1(x, t|.)\) straightforward [19]:

\[
G(z - w, \tau) = \frac{1}{(2\pi)^{1/2}\sigma(\tau)} \exp\left(-\frac{|z - w|^2}{2\sigma^2(\tau)}\right)
\]

and

\[
\rho_1(x, t|z, \tau; w, 0) = \frac{1}{(2\pi)^{1/2}\sigma(t|\tau; z - w)} \times \exp\left(-\frac{|x - \mu(t|\tau, z - w)|^2}{2\sigma^2(t|\tau; z - w)}\right).
\]

where the conditional mean and mean square displacements \(\mu(t|.)\) and \(\sigma^2(t|.)\) are given by

\[
\mu(t|\tau, z - w) = w + \langle x(t|x(\tau)) \rangle - \langle x^2(\tau) \rangle (z - w)
\]

and

\[
\sigma^2(t|\tau; z - w) = \sigma^2(t) = \sigma^2(t) - \frac{\langle y(t)y(\tau) \rangle^2}{\sigma^2(\tau)}
\]

with \(y(t) = x(t) - x(0)\) and \(\sigma^2(t) = \langle y^2(t) \rangle\).

Substituting Eqs. (3-6) into Eq. (2), and using \(\rho_1(x, 0) = n_0\), we obtain the result

\[
\rho_2c(x_1, x_2; t) = \frac{\Gamma n_0}{2\sqrt\pi} \int_0^t \int \frac{\exp\left(-\frac{(x_1 - x_2)^2}{4\sigma^2(t, \tau)}\right)}{\sigma(t, \tau)} \, d\tau \, dt.
\]

For \(t \gg \tau\) we see that \(\sigma(t, \tau) \rightarrow \sigma(t)\). The Markovian case is obtained substituting \(\sigma(t, \tau) \rightarrow \sigma(t)\), for \(t, \tau\) generic, in Eq. (7), that becomes in this way the solution of a heat equation with constant Dirac delta forcing at \(x_1 = x_2\) [16].

The scaling of the square amplitude fluctuation \(\rho_2c(x, x; t)\) can be calculated explicitly if the correlation profile entering Eq. (6) is known. In the case of an FBM [12]:

\[
\langle y(t)y(\tau) \rangle = (\kappa_H/2)(t^2H + \tau^2H - |t - \tau|^{2H})
\]

and we get

\[
\rho_2c(x, x; t) = C n_0 \kappa_H^{1/2} t^{1-H},
\]

with

\[
C = \frac{1}{2\sqrt\pi} \int_0^1 \frac{u^H du}{u^{2H} - [1 + u^{2H} - (1 - u)^{2H}]^2/2}.
\]
The general condition \( \sigma(t; \tau) \rightarrow \sigma(t) \) for \( t/\tau \) large, leads us to expect that the same scaling of Eq. (8) be recovered also for other Gaussian, anomalous diffusion processes. An example is illustrated in Fig. 2, in the case of a superdiffusive process generated with the algorithm described in [17], in which the velocity of the individuals is obtained as a superposition of Ornstein-Uhlenbeck processes.

From Eq. (7) we could also obtain the scaling of the correlation length of the fluctuations, \( \lambda_c: \lambda_c^2 = \int dy \rho_{2c}(x,y;t)^{-1} \int dy (x-y)^2 \rho_{2c}(x,y;t) \). We obtain:

\[
\lambda_c(t) \sim \kappa_H^{1/2} t^H.
\]

We thus see that the slow-down of the fluctuation build-up in Eq. (9), with respect to a case without migration: \( \rho_{2c}(x,x;t) = 2n_0 \Gamma t \) (Galton-Watson dynamics [8]), is precisely the smearing of the fluctuations that is produced by anomalous diffusion. We notice that clustering is possible (in one dimension) only as long as \( H < 1 \); thus superdiffusive processes that are faster than ballistic are excluded.

\[
\rho_{2c}(x_1,x_2;t + \Delta t) = \int dy_1 \int dy_2 G(x_1 - y_1, \Delta t) G(x_2 - y_2, \Delta t) \rho_{2c}(y_1,y_2;t) + 2\Gamma n_0 \Delta \delta(x_1 - x_2).
\]

Fourier transforming in \( x_{1,2} \) and defining \( \rho_{2c,k_1,k_2}(t) = 2\pi \delta(k_1 + k_2) C_{k_1}(t) \), we obtain

\[
C_{k}(t + \Delta t) = G_{2k}^2(\Delta t) C_{k}(t) + 2\Gamma n_0 \Delta t.
\]

For \( t \gg \Delta t \), the space scale contributing in Eq. (16) are those corresponding to the asymptotics in Eq. (11). We can thus use Eq. (12), and Eq. (16) becomes, taking the continuous limit:

\[
\dot{C}_k + 2c|k|^\beta C_k = 2\Gamma n_0,
\]

which can be seen as a form of forced fractional heat equation [18]. Solution by Laplace transform in time gives

FIG. 2: Fluctuation build-up in the case the individuals migrate by Gaussian diffusion (heavy line) and by Lévy flights (thin line). The slope \( t^{1-H} \), for \( H = 1/\beta = 0.75 \), is shown for reference. In both cases \( N = 10^5 \) individuals in a periodic domain were considered. In the time units considered: the fastest mode in the FBM has relaxation time one; the discretization of the Lévy flights is \( \Delta t = 0.25 \); \( \Gamma = 0.1 \).

III. LÉVY FLIGHTS

In this case we do not have to bother with memory transfer among generations, as the process is Markovian. The process can be obtained as the continuous limit of a dynamics in which the individuals, at time intervals \( \Delta t \), carry on independent jumps distributed with a PDF characterized by power-law tails:

\[
G(y, \Delta t) \sim |y|^{-1-\beta}, \quad 0 < \beta < 2
\]

(Lévy flights). In Fourier space, this corresponds to the asymptotic behavior for small wavenumbers:

\[
G_k(\Delta t) \simeq 1 - c|k|^\beta \Delta t,
\]

where \( c \sim (\Delta x)^\beta /\Delta t \), and \( \Delta x \) is a microscale below which the scaling in Eq. (11) ceases to hold. The slow decay in \( y \) of the PDF, Eq. (11), implies divergence of the second moment of the displacement \( \langle |y(t)|^2 \rangle = \infty \) even for a single jump, and the PDF \( G(y,t) \) can be shown to tend to a Lévy distribution; in Fourier space [6]:

\[
G_k(t) = \exp(-c|k|^\beta t).
\]

Equation (13) tells us that, although \( G(y,t) \) does not have a second moment, we can identify a characteristic scale:

\[
y(t) = x(t) - x(0) \sim (\ell t)^{1/\beta},
\]

with the exponent \( 1/\beta \) playing a role analogous to that of the Hurst exponent for a diffusive process (more precisely, for a superdiffusive process, as \( 1/\beta > 1/2 \)).

As in the previous section, let us assume that the individuals undergo processes of birth and death with equal rate \( \Gamma \), and that the individuals are distributed at time \( t = 0 \) with uniform density \( n_0 \). As in the previous case, it is easy to see that the mean density remains constant \( \rho_1(x,t) = n_0 \), but fluctuations of increasing amplitude, accounted for by the connected correlation \( \rho_{2c}(x_1,x_2;t) \), are generated.

The Markovian nature of the process allows us to derive a version of the evolution equation for \( \rho_{2c} \), Eq. (2), that is local in time:
us:

\[
C_{kz} = \frac{2\Gamma n_0}{z(2 + 2z k^2 \rho)}. \tag{18}
\]

Inverse Fourier transform at zero space separation gives then the result

\[
C_z(0) = \int \frac{dk}{2\pi} C_{kz} = B\Gamma n_0 e^{-\frac{1}{2\rho z}} z^{1/\beta - 2},
\]

where \( B = \int_0^{+\infty} (1 + 2h)^{-1/\beta - 1} dh \), and this corresponds to the long-time asymptotics

\[
\rho(x, x; t) \sim \Gamma n_0 e^{-\frac{1}{\beta} t^{1/\beta}}. \tag{19}
\]

A realization of such a process is shown in Fig. 2. Again, fast processes for which \( \beta < 1 \) do not lead to clustering.

In spite of the fact that the dynamics considered in this and the previous section are completely different, as clear from Eqs. (9) and (19), the fluctuation build-up occurs in the two cases in the same way. Looking at Eq. (18) and comparing with Eqs. (7) and (10), we find in fact the same mechanism of smearing of fluctuations at scale \( x(t) \propto t^{1/\beta} \) [Eq. (14), Lévy flights] or \( \lambda_c(t) \propto t^{H} \) [Eq. (10), Gaussian diffusion].

IV. CONCLUSION

We have provided two separate examples of how the scaling in the build-up of demographic fluctuations in a birth-death model, can be made dependent on the kind of diffusion utilized for migration. We have seen that the basic ingredient for such dependence is the smearing of the fluctuations by the diffusion process, provided the inclusion of demography does not affect migration at population scale. With this we intend the fact that the dispersion of a group of individuals has the same scaling in the build-up of demographic fluctuations in a

- Gaussian anomalous diffusion (FBM, individuals moving with velocity that is solution of a GLE, and others): if offsprings share memory of the trajectories with their parents, demographic fluctuations will scale anomalously, as described by Eq. (9). Otherwise, the case of Brownian bugs is recovered.
- Lévy flights: demographic fluctuations scale anomalously, as described by Eq. (19).
- CTRW: in the absence of memory transfer between generations, the case of Brownian bugs is recovered. If the offsprings share their escape time (the only thing that they can share) with their parents, the dynamics falls back on that of a Galton-Watson process.
- A spatial assembly of random traps: the same behavior of the CTRW with memory transfer between generation is obtained; the dynamics falls back on that of a Galton-Watson process.

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[19] Recall that \( \rho_1(x, t_2 | z, t_1; w, 0) = \rho_{y(t_2), y(t_1)}(x - w, z - w)/G(z - w, t_1) \), where \( \rho_{y(t_2), y(t_1)} \) is the joint PDF of the individual displacement at times \( t_{1,2} \), that is a Gaussian.