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Modeling multiple anomalous diffusion behaviors on comb-like structures☆

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Abstract

In this work, a generalized comb model which includes the memory kernels and linear reactions with irreversible and reversible parts are introduced to describe complex anomalous diffusion behavior. The probability density function (PDF) and the mean squared displacement (MSD) are obtained by analytical methods. Three different physical models are studied according to different reaction processes. When no reactions take place, we extend the diffusion process in 1-D under stochastic resetting to the N-D comb-like structures with backbone resetting and global resetting by using physically derived memory kernels. We find that the two different resetting ways only affect the asymptotic behavior of MSD in the long time. For the irreversible reaction, we obtain memory kernels based on experimental evidence of the transport of inert particles in spiny dendrites and explore the front propagation of CaMKII along dendrites. The reversible reaction plays an important role in the intermediate time, but the asymptotic behavior of MSD is the same with that in case of no reaction terms. The proposed reaction-diffusion model on the comb structure provides a generalized method for further study of various anomalous diffusion problems.

Keywords: Comb model, Fractional dynamics, Physical mechanism,

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1. Introduction

Diffusion is an important natural phenomenon, and has attracted much attention in literature (see, e.g., [1, 2]). The comb-like structure is a classical model involved with many applications, such as diffusion problems in neurons [3], propagation of actin polymerization-reaction [4] and quantum nonlinear Schrödinger lattices [5]. Fig. 1 is a schematic diagram of a comb model, which consists of a one-dimensional backbone with branches.

The dynamic equation for the comb model is described as in [6]

$$\frac{\partial P}{\partial t} = D_x \frac{\partial^2 P}{\partial x^2}\delta(y) + D_y \frac{\partial^2 P}{\partial y^2} \tag{1}$$

where $P(t, x, y)$ **is the probability density function (PDF). The Dirac** $\delta(y)$ **function indicates that the diffusion in the** x **direction occurs only on the backbone.** This model is used to study tumor development and obtain solutions related to solid tumors and metastasis in the framework of the fractional Fokker-Planck equation [7]. Marin et al. [8] analyzed the diffusion of a system on a backbone structure by considering the presence of reaction terms. **Many theoretical and experimental results show that the fractional differential equation has become a powerful tool to solve problems in many fields. For recent related developments, we mention [9–13]. To describe more complex physical processes,** different memory kernels have been introduced into governing equations in recent years, for example, the generalized Langevin equation[14], diffusion equation [15] and diffusion-wave equation [16]. Naturally, the generalized diffusion equation with memory kernels is also used to describe the comb structure [17]. Rectenly, Liang et al. [18] explained the possibility of ultraslow diffusion on the comb structure by selecting the slowly varying logarithmic memory kernel and the inverse Mittag-Leffler (M-L) kernel.

The continuous time random walk (CTRW) model was proposed by Montroll and Weiss [19], and it has become a very useful tool to describe the complex anomalous diffusion problems. Sandev et al. [20] obtained a generalized diffusion equation modified from the CTRW theory and showed the analytical form of its mean square displacement (MSD) at different scales. Accordingly, we can analyze the CTRW process of the backbone (x direction) and branch (y direction) on comb structures, which ensures the nonnegativity of solutions.

In this work, we consider the effects of memory kernel and reaction terms on comb structures. **Our first motivation is to explore the form of the memory kernels which are obtained based on the specific physical problem rather than arbitrarily selected.** The first problem to be discussed is the stochastic resetting on comblike structures, studied recently in 3-D [21]. The governing equation of the 1-D diffusion process under the stochastic resetting can be transformed into a form with a memory kernel. Our motivation is to use the memory kernel obtained in 1-D to study the stochastic resetting on N-D comb structures without having to formulate the original governing equation. **In this way, the backbone resetting and global resetting problems of the high-dimensional comb structure are easily solved. This method may be used to deal with other types of stochastic resetting problems.** The second problem is to analyze the anomalous transport of inert particles along spiny dendrites and the linear dynamics of the calmodulin-dependent protein kinase II (CaMKII) diffusion-activation. It is worth mentioning that the diffusion of inert particles and the nonlinear reaction transport of CaMKII have been studied using theoretical and experimental methods [22–28]. This part of our work is to derive the memory kernels of the model from the perspective of the CTRW and the basic experimental results of inert particles, and then consider the spread of CaMKII. **The relationship between the propagation front speed and the spine density and reaction rate is obtained and shown graphically. Our second motivation is to investigate the behavior of particles with reversible reactions on the backbone under different memory kernels such as standard memory kernel, power-law memory kernel, distribution order kernel and logarithmic function kernel. We analyze the short and long term behavior of the diffusive particles,**

showing a variety of anomalous diffusion forms.

In order to verify that the memory kernels discussed are meaningful, we should ensure that the waiting time PDF is nonnegative. Fortunately, the nonnegativity of the solution of the generalized diffusion equations [29] and the Cattaneo equations [30] has been demonstrated by the completely monotonic functions (CMF) with the Bernstein theorem [31]. It is a powerful tool to test whether a memory kernel can be applied to this model.

The rest of this manuscript is organized as follows. In Sec. 2, we formulate the generalized equations coupled with linear reaction terms on the comb-like structure. The MSDs and waiting time PDFs are obtained by analytical methods. In Sec. 3, we extend the stochastic resetting problem of 1-D and 2-D comb to N-D comb structures. In Sec. 4, based on the model proposed and the experimental evidence, we study the translocation of dendritic CaMKII with linear reaction and obtain the propagation front velocity. The Linear reversible reaction diffusion under multiple memory kernels on comb models is investigated in Sec. 5. **Some conclusions and remarks are provided in Sec. 6.**

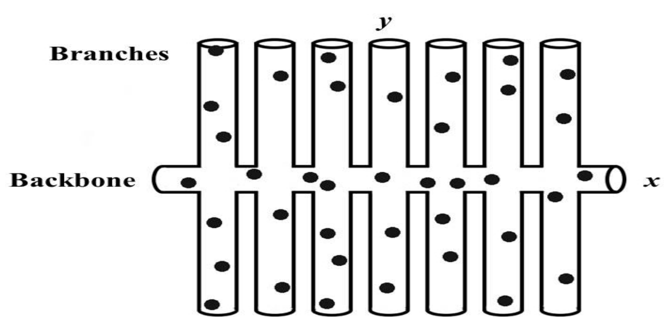

Figure 1: Schematic diagram of the comb-like structure consisting of a one-dimensional backbone with branches.

2. Comb model for the reaction diffusion process

We consider an anomalous transport on the comb structure, where a reversible reaction $A \rightleftharpoons B$ occurs on the backbone. The different fractional derivatives in front of spatial operators are used to describe the generalized comb models [32]

$$\frac{\partial P(t,x,y)}{\partial t} = D_x \delta(y) \frac{\partial}{\partial t} \int_0^t \xi_x(t-\tau) \left[\frac{\partial^2 P(\tau,x,y)}{\partial x^2} - \frac{\partial R(\tau,x,y)}{\partial \tau} \right] d\tau \\ + D_y \frac{\partial}{\partial t} \int_0^t \xi_y(t-\tau) \frac{\partial^2 P(\tau,x,y)}{\partial y^2} d\tau \tag{2}$$

and the reaction term $R(t,x,y)$ is linearly governed by

$$\frac{\partial R(t,x,y)}{\partial t} = C_f P(t,x,y) - C_b R(t,x,y). \tag{3}$$

Here Dirac delta function limits the diffusion in the x direction. C_f and C_b are the reaction rates connected with this process, and both are constants. They represent forward and backward reactions, respectively. In the spiny dendritic structure, the inert particles do not take place chemical reactions during the diffusion process, so in this case $R(t,x,y) = 0$. The spread of the CaMKII translocation mechanism with a linear irreversible reaction can also be described by taking $C_b = 0$. We set the diffusion coefficient $D_x = D_y = 1$ to simplify the calculation. $\xi_x(t)$ and $\xi_y(t)$ are the memory kernels and have the memory effect. The modified form of the equation has been used to generalize the 1-D diffusion equation [33] and Fokker-Planck equation [34]. The combination of experimental evidence and model, and consideration of the physical mechanisms of different kernels are the focus of our discussion. In the case of $\xi_x(t) = \xi_y(t) = 1$ and $C_f = C_b = 0$, this model returns to the classic comb structure, and its the MSD is $\langle x^2(t) \rangle \simeq t^{1/2}$ along the x direction, and $\langle y^2(t) \rangle \simeq t$ along the y direction [35].

The initial conditions are $P(0,x,y) = \delta(x)\delta(y)$ and $R(0,x,y)$=0, and the boundary conditions are $P(t,x,\pm\infty) = P(t,\pm\infty,0) = 0$ and $\frac{\partial}{\partial\{x,y\}} P(t,x,y) = 0$ for $\{x,y\} \to \pm\infty$.

Performing the Laplace transform in time on Eq. (2) and Eq. (3) can be combined as

$$sP(s,x,y) - \delta(x)\delta(y) = s\xi_x(s) \left[\frac{\partial^2 P(s,x,y)}{\partial x^2} - C(s)P(s,x,y) \right] \delta(y) \\ + s\xi_y(s) \frac{\partial^2 P(s,x,y)}{\partial y^2}, \tag{4}$$

where $C(s) = \frac{C_f s}{s+C_b}$. Applying the Fourier transform to space variables x and

y, the solution in frequency domains we obtain

$$\begin{aligned} P_x(s,k_x,k_y) = &\frac{2}{s\xi_x(s)[\xi_y(s)]^{1/2}} \times \frac{1}{2[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2} + C(s) + k_x^2} \\ &\times \frac{1}{[\xi_y(s)]^{-1} + k_y^2}. \end{aligned} \tag{5}$$

We can then obtain the Montroll-Weiss equation [19] along the x and y directions

$$P_x(s,k_x) = P(s,k_x,k_y=0) = \frac{2}{2s + sC(s)\xi_x(s)[\xi_y(s)]^{-1/2} + s\xi_x(s)[\xi_y(s)]^{-1/2}k_x^2}, \tag{6}$$

$$P_y(s,k_y) = P(s,k_x=0,k_y) = \frac{2}{2s\xi_y(s) + sC(s)\xi_x(s)[\xi_y(s)]^{1/2}} \times \frac{1}{[\xi_y(s)]^{-1} + k_y^2}. \tag{7}$$

Eqs. (6) and (7) can be rewritten as

$$\begin{aligned} sP_x(s,k_x) - 1 = &-\frac{1}{2}k_x^2 s\xi_x(s)[\xi_y(s)]^{-1/2}P_x(s,k_x) \\ &- \frac{1}{2}sC(s)\xi_x(s)[\xi_y(s)]^{-1/2}P_x(s,k_x), \end{aligned} \tag{8}$$

$$\begin{aligned} sP_y(s,k_y) - 1 = &-k_y^2 s\xi_y(s)P_y(s,k_y) - \frac{1}{2}k_y^2 sC(s)\xi_x(s)[\xi_y(s)]^{1/2}P_y(s,k_y) \\ &- \frac{1}{2}sC(s)\xi_x(s)[\xi_y(s)]^{-1/2}P_y(s,k_y). \end{aligned} \tag{9}$$

By inverse Fourier-Laplace transforms, the generalized reaction diffusion equations along the x and y directions are obtained respectively

$$\frac{\partial P_x(t,x)}{\partial t} = \frac{1}{2}\frac{\partial}{\partial t}\int_0^t \eta_1(t-\tau)\frac{\partial^2 P_x(\tau,x)}{\partial x^2}\,d\tau - \frac{1}{2}\frac{\partial}{\partial t}\int_0^t \eta_2(t-\tau)P_x(\tau,x)\,d\tau, \tag{10}$$

$$\frac{\partial P_y(t,y)}{\partial t} = \frac{\partial}{\partial t}\int_0^t \eta_3(t-\tau)\frac{\partial^2 P_y(\tau,y)}{\partial y^2}d\tau - \frac{1}{2}\frac{\partial}{\partial t}\int_0^t \eta_2(t-\tau)P_y(\tau,y)\,d\tau, \tag{11}$$

where $\eta_1(t) = L^{-1}\left[\xi_x(s)[\xi_y(s)]^{-1/2}\right]$, $\eta_2(t) = L^{-1}\left[C(s)\xi_x(s)[\xi_y(s)]^{-1/2}\right]$ and $\eta_3(t) = L^{-1}\left[\xi_y(s) - \frac{1}{2}C(s)\xi_x(s)[\xi_y(s)]^{1/2}\right]$. Eq. (11) is a generalized 1-D diffusion equation [20], which can be obtained directly from Eq. (2) by setting $y \neq 0$ and $R(t,x,y) = 0$.

The solutions in the Laplace domain are

$$
\begin{aligned}
P_x(s,x) = s^{-1}[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2}\left\{2[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2}+C(s)\right\}^{-1/2} \\
\times\, exp\left\{-\left[2[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2}+C(s)\right]^{1/2}|x|\right\},
\end{aligned} \tag{12}
$$

and

$$
P_y(s,y) = \left[2s[\xi_y(s)]^{1/2}+sC(s)\xi_x(s)\right]^{-1}\times exp\left[-[\xi_y(s)]^{-1/2}|y|\right]. \tag{13}
$$

From Eq. (6) or Eq. (12), we can calculate the MSD along the x direction

$$
\begin{aligned}
\langle x^2(t)\rangle = L^{-1}\left[-\frac{\partial^2 P_x(s,k_x)}{\partial k_x^2}\right]\Bigg|_{k_x=0} = \langle x^2 P_x(s,x)\rangle \\
= 4L^{-1}\left\{s^{-1}[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2}\left[2[\xi_x(s)]^{-1}[\xi_y(s)]^{1/2}+C(s)\right]^{-2}\right\},
\end{aligned} \tag{14}
$$

and along the y direction

$$
\begin{aligned}
\langle y^2(t)\rangle = L^{-1}\left[-\frac{\partial^2 P_y(s,k_y)}{\partial k_y^2}\right]\Bigg|_{k_y=0} = \langle y^2 P_y(s,y)\rangle \\
= 4L^{-1}\left\{[\xi_y(s)]^{3/2}\left[sC(s)\xi_x(s)+2s[\xi_y(s)]^{1/2}\right]^{-1}\right\}.
\end{aligned} \tag{15}
$$

To establish the relationship between the waiting time PDF $\psi(t)$ and the memory kernel from the perspective of the CTRW, by generalizing the classical Brownian motion, Ref. [20] provides a CTRW model that corresponds to Eqs. (10) and (11) with no reaction terms. This model may help us analyze the multiple effects of the waiting time PDF with different physical meanings on comb geometrical structures. For the x direction, the waiting time PDF is

$$
\psi_x(t) = L^{-1}\left[\frac{1}{1+\frac{1}{\eta_1(s)}}\right] = L^{-1}\left[\frac{1}{1+\frac{[\xi_y(s)]^{1/2}}{\xi_x(s)}}\right] \tag{16}
$$

where the kernel function has the property $\lim_{s\to 0}[\xi_y(s)]^{1/2}/\xi_x(s)=0$. For the y direction, the waiting time PDF is

$$
\psi_y(t) = L^{-1}\left[\frac{1}{1+\frac{1}{\xi_y(s)}}\right] \tag{17}
$$

where $\lim_{s\to 0} 1/\xi_y(s) = 0$.

3. Stochastic resetting memory kernel on comblike structures

First, we review the stochastic resetting of particles in the case of 1-D diffusion. For the particles stochastic resetting to the initial position with a constant rate r, the corresponding governing equation is proposed by Evans and Majumdar [36]

$$\frac{\partial P(t|0,x)}{\partial t} = D\frac{\partial^2 P(t|0,x)}{\partial x^2} - rP(t|0,x) + r\delta(x). \tag{18}$$

Here we set the initial position as the origin, and the initial condition is $P(0,x) = \delta(x)$. By applying the Fourier-Laplace transform, Eq. (18) can be written as a modified form as follows

$$\frac{\partial P(t|0,x)}{\partial t} = D\frac{\partial}{\partial t}\int_0^t \zeta(t-t^{'})\left[\frac{\partial^2 P(t^{'}|0,x)}{\partial x^2}\right] dt^{'}, \tag{19}$$

where $\zeta(t) = e^{-rt}$ and its Laplace transform is $\zeta(s) = (s+r)^{-1}$. Then, we use this concise result to study the stochastic resetting of particles on the comb structure from the perspective of the memory kernel. In this section, no reaction takes place ($R(t,x,y) = 0$).

3.1. Backbone resetting

On the 2-D comb model, we consider the particle on the branch reset to the backbone, that is the particle at position (x_0, y_0) is moved to its backbone position $(x_0, 0)$. This resetting process describes that the particle resetting only occurs on the branch and has no changes on the backbone, so we can take $\xi_x(t) = 1$ and $\xi_y(t) = e^{-rt}$. The MSDs along the x and y directions are

$$\langle x^2(t)\rangle = L^{-1}\left[\frac{s^{-2}}{(s+r)^{-1/2}}\right] = t^{1/2}E_{1,3/2}^{-1/2}(-rt) \sim \begin{cases} \frac{2}{\sqrt{\pi}}t^{1/2} & (t\to 0) \\ r^{1/2}t & (t\to\infty) \end{cases} \tag{20}$$

and

$$\langle y^2(t)\rangle = 2L^{-1}\left[\frac{s^{-1}}{(s+r)}\right] = 2tE_{1,2}(-rt) \sim \begin{cases} 2t & (t\to 0) \\ \frac{2}{r} & (t\to\infty) \end{cases}, \tag{21}$$

respectively, in accordance with the results in [21]. From Eq. (10), we obtain the dimensionless generalized diffusion equation along the x direction by substituting the memory kernel into the equation

$$\frac{\partial P(t|0,x)}{\partial t} = \frac{\partial}{\partial t}\int_0^t \gamma(t-\tau)\frac{\partial^2 P(\tau|0,x)}{\partial x^2}\,d\tau, \tag{22}$$

where $\gamma(t) = t^{-1/2}E_{1,1/2}^{-1/2}(-rt)$ (see Appendix A for this function).

Further, we extend Eq. (22) to the N-D comb structure, which is related to the mass transfer problem of living plants [37]. We modify $\gamma(t)$ to the form of truncated M-L memory kernel $\gamma_1(t) = t^{\alpha}E_{1,\alpha+1}^{\alpha}(-rt)$, where $\alpha = -\frac{2(N-1)-1}{2(N-1)}$. The Laplace transform of $\gamma_1(t)$ yields $\gamma_1(s) = [s(s+r)^{\alpha}]^{-1}$, the waiting time PDF becomes [20]

$$\psi_1(t) = L^{-1}\left[\frac{1}{1+\frac{1}{\gamma_1(s)}}\right] = L^{-1}\left[\frac{1}{1+s(s+r)^{\alpha}}\right], \tag{23}$$

where $s(s+r)^{\alpha}$ is a bernstein function (BF) [31]. Since the composition function of CMF and BF is a CMF, hence, $\psi_1(s)$ is CMF, and $\psi_1(t)$ is nonnegative.

Similar to Eq. (14), the MSD can be calculated

$$\langle x^2(t)\rangle = 2L^{-1}\left[\frac{s^{-2}}{(s+r)^{\alpha}}\right] = 2t^{\alpha+1}E_{1,\alpha+2}^{\alpha}(-rt) \sim \begin{cases} \frac{2}{\Gamma(\alpha+2)}t^{\alpha+1} & (t\to 0) \\ 2r^{-\alpha}t & (t\to\infty) \end{cases} \tag{24}$$

For $N = 3$, $\alpha = -3/4$, the result of MSD is consistent with that in section 3 of [21]. The MSD in the case of restting behave the same as no resetting in the short time, while in the long time limit, it returns to the normal diffusion. This resetting mechanism enhances the transport along the x direction, the form of its MSD is independent of the dimensionality of the comb structure in the long time. However, the coefficient is variable.

3.2. Global resetting

Global resetting process takes the particle to its initial position. Since the comb model has a special geometric structure, the particle can only be reset to the backbone and then to the initial position, that is, $(x_0, y_0) \to (x_0, 0) \to (0, 0)$.

We set $\xi_x(t) = e^{-rt}$ and $\xi_y(t) = e^{-rt}$. For the MSDs, we find

$$\langle x^2(t)\rangle = L^{-1}\left[\frac{s^{-1}}{(s+r)^{1/2}}\right] = t^{1/2}E^{1/2}_{1,3/2}(-rt) \sim \begin{cases} \frac{2}{\sqrt{\pi}}t^{1/2} & (t \to 0) \\ r^{-1/2} & (t \to \infty) \end{cases} \tag{25}$$

and

$$\langle y^2(t)\rangle = 2L^{-1}\left[\frac{s^{-1}}{(s+r)}\right] = 2tE_{1,2}(-rt) \sim \begin{cases} 2t & (t \to 0) \\ \frac{2}{r} & (t \to \infty) \end{cases}. \tag{26}$$

Similar to the previous section, we can also extend it to the global resetting of the N-D comb structure, the memory kernel $\gamma_2(t) = \frac{t^{\beta-1}}{\Gamma(\beta)}e^{-rt}$ which in the Laplace space is $\gamma_2(s) = (s+r)^{-\beta}$, and $\beta = \frac{1}{2(N-1)}$. The waiting time PDF reads

$$\psi_2(t) = L^{-1}\left[\frac{1}{1+(s+r)^{\beta}}\right] = e^{-rt}t^{\beta-1}E_{\beta,\beta}(-t^{\beta}). \tag{27}$$

The MSD yields the following general form

$$\langle x^2(t)\rangle = 2L^{-1}\left[\frac{s^{-1}}{(s+r)^{\beta}}\right] = 2t^{\beta}E^{\beta}_{1,\beta+1}(-rt) \sim \begin{cases} \frac{2}{\Gamma(\beta+1)}t^{\beta} & (t \to 0) \\ 2r^{-\beta} & (t \to \infty). \end{cases} \tag{28}$$

Different from the backbone resetting process, the MSD of the global resetting tends to be constant with time, that is, steady state.

4. Propagation of CaMKII with linear reaction

For the transport process of inert particles ($R(t,x,y) = 0$) in dendrites of cerebellar Purkinje cells, the experimental results show that the diffusion in the smooth dendrite is essentially linear, so we can set $\xi_x(t) = 1$ in our model to ensure that the particles maintain normal diffusion without spines. In spiny dendrites, some particles are trapped inside the spine for a random time τ_s, and after a random time, the particle is released to the dendrite. The PDF for the dwelling time τ_s is $\psi_y(\tau)$. According to the experimental evidence, the waiting time density $\psi_y(t) \sim t^{-1-\mu}$ as $t \to \infty$ [23], and in the Laplace space $\psi_y(s) \sim (1+s^{\mu})^{-1}$. Based on this information, we can easily obtain the power-law memory kernel $\xi_y(t) = \frac{t^{\mu-1}}{\Gamma(\mu)}$ in Eq. (17), the Laplace transform is $\xi_y(s) = s^{-\mu}$. In the x direction, the corresponding waiting time PDF is

$$\psi_x(t) = L^{-1}\left[\frac{1}{1+s^{1-\frac{\mu}{2}}}\right] = t^{-\frac{\mu}{2}} E_{1-\frac{\mu}{2},1-\frac{\mu}{2}}(-t^{1-\frac{\mu}{2}}), \tag{29}$$

where $E_{\alpha,\beta}(z) = \sum_{k=0}^{\infty} \frac{z^k}{\Gamma(\alpha k+\beta)}$ is the generalized M-L function. As $t \to \infty$, $\psi_x(t) \sim t^{-2+\frac{\mu}{2}}$.

For the diffusion of CaMKII along the dendrite, the primed CaMKII is activated and activated CaMKII both translocates into spines and diffuses into the dendrite where it activates primed CaMKII [38]. Based on the memory kernels we have obtained, in the governing equations, we can represent $P(t, x, y)$ as the PDF of the activated CaMKII, which keeps increasing. Here we assume a linear reaction, which is obviously irreversible and corresponding to the activation rate $C_f < 0$ and $C_b = 0$.

The PDFs behave as (for calculation details see Appendix B)

$$\begin{aligned} P_x(t,x) = &\frac{1}{|x|}\sum_{k=0}^{\infty}(-1)^k \frac{1}{k!}(\frac{1}{2}C_f)^k t^{(1-\frac{\mu}{2})k} \\ &\times H^{2,0}_{2,2}\left[\frac{2x^2}{t^{1-\frac{\mu}{2}}}\middle|\begin{matrix}(1-(\frac{\mu}{2}-1)k,1-\frac{\mu}{2}),(0,1)\\ \\(k,1),(-1,2)\end{matrix}\right], \end{aligned} \tag{30}$$

$$P_y(t,y) = \frac{1}{2}\sum_{k=0}^{\infty}(-1)^k \frac{1}{k!}|y|^k t^{-\frac{\mu}{2}(1+k)} E_{1-\frac{\mu}{2},1-\frac{\mu}{2}(1+k)}\left(-\frac{C_f}{2}t^{1-\frac{\mu}{2}}\right). \tag{31}$$

The results for the MSD are

$$\langle x^2(t)\rangle = L^{-1}\left[\frac{s^{-\frac{\mu}{2}}}{(s^{1-\frac{\mu}{2}}+\frac{C_f}{2})^2}\right] = t^{1-\frac{\mu}{2}} E^2_{1-\frac{\mu}{2},2-\frac{\mu}{2}}\left(-\frac{C_f}{2}t^{1-\frac{\mu}{2}}\right), \tag{32}$$

and

$$\langle y^2(t)\rangle = 2L^{-1}\left[\frac{s^{-\frac{3}{2}\mu}}{(s^{1-\frac{\mu}{2}}+\frac{C_f}{2})}\right] = 2t^{\mu} E_{1-\frac{\mu}{2},1+\mu}\left(-\frac{C_f}{2}t^{1-\frac{\mu}{2}}\right), \tag{33}$$

For a short time, $\langle x^2(t)\rangle \sim \frac{t^{1-\frac{\mu}{2}}}{\Gamma(2-\frac{\mu}{2})}$. For a long time, the MSD $\langle x^2(t)\rangle \sim te^{(-\frac{C_f}{2})^{\frac{2}{2-\mu}}t}$ since $E^{\delta}_{\alpha,\beta}(z) \sim z^{(\delta-\beta)/\alpha}e^{z^{1/\alpha}}$ as $z \to \infty$. For $C_f = 0$, the MSD reads $\langle x^2(t)\rangle \sim \frac{t^{1-\frac{\mu}{2}}}{\Gamma(2-\frac{\mu}{2})}$, which describes the diffusion of inert particles in spiny dendrites, and is consistent with the results obtained by applying the Riemann-Liouville fractional derivative [22].

The results of the memory kernel we obtained from the CTRW perspective. The MSD describes the transport of inert particles (tracer) in spiny dendrites of cerebellar Purkinje cells is subdiffusion behavior, which is consistent with the experimental results [25]. Then we consider the case of $C_f < 0$, it can show the linear dynamics of CaMKII. Fig. 2 shows the MSD change in the x direction, we use a numerical Laplace inversion algorithm in Matlab [39]. It can be observed that the growth form of the MSD is exponential and as μ increases, the density of dendritic spines increases, indicating that the diffusion of CaMKII along the dendrites becomes slower. When $t, x \gg 1$, the asymptotic behavior of $P_x(t,x)$ is obtained [24]

$$P_x(t,x) = exp\left[\left(\frac{-C_f}{2}\right)^{\frac{2}{2-\mu}} t - \frac{2^{\frac{2}{2-\mu}}(2-\mu)x^2}{8(-C_f)^{\frac{\mu}{2-\mu}} t}\right]. \tag{34}$$

To calculate the propagation front velocity, we apply the Hamilton-Jacobi method [24], yielding:

$$v = \frac{2^{\frac{3u-2}{2u-4}}(-C_f)^{\frac{2+u}{4-2u}}}{(2-u)^{1/2}} = const. \tag{35}$$

Fig. 3 shows the variation of propagation front velocity with the spine density being at various activation rates. We can see that the propagation front velocity slows down as the spine density increases and the activation rate decreases. Unlike the nonlinear reaction diffusion of CaMKII along the dendrites [24, 38], the failure of the front propagation is not observed in linear reaction.

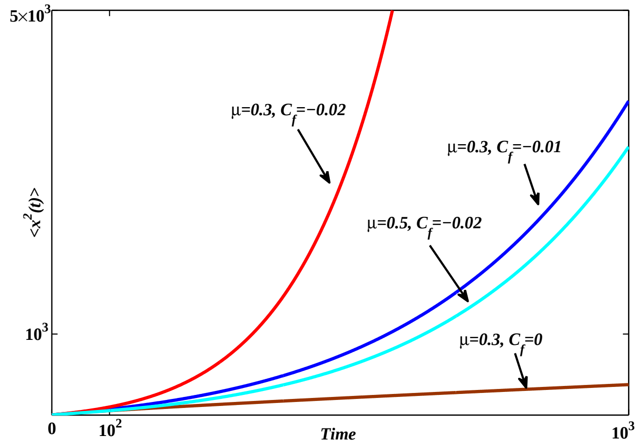

Figure 2: MSD $\langle x^2(t)\rangle$ versus time with the effects of different fractional parameter μ and activation rate C_f.

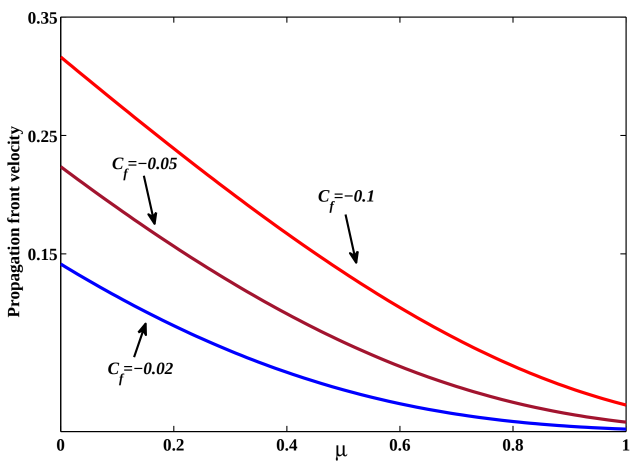

Figure 3: Propagation front velocity versus μ with various activation rates C_f.

5. Different diffusion regimes with reaction

In this section, we consider different forms of the memory kernels, including standard memory kernel, power-law memory kernel, distributed order memory kernel and structure function memory kernel in the framework of linear reaction on the backbone. The nonnegativity of the solutions are verified by analyzing the Laplace transform of the waiting time PDFs $\psi_x(s)$ and $\psi_y(s)$ in the CTRW model, that is, we need to prove that both $[\xi_y(s)]^{1/2}/\xi_x(s)$ and $1/\xi_y(s)$ are CBFs.

5.1. Standard memory kernel $\xi_x(t) = \xi_y(t) = 1$

The case with $\xi_x(t) = \xi_y(t) = 1$ corresponds to the classic comb model based on Fick's law. The waiting time PDF can be easily obtained from Eq. (16) and (17). Then we analyze the MSD along the x and y directions

$$\langle x^2(t)\rangle = 4L^{-1}\left\{\frac{s^{-1/2}}{[2s^{1/2}+\frac{sC_f}{s+C_b}]^2}\right\} \tag{36}$$

and

$$\langle y^2(t)\rangle = 4L^{-1}\left[\frac{s^{-3/2}}{2s^{1/2}+\frac{sC_f}{s+C_b}}\right]. \tag{37}$$

For $C_b = 0$ and $C_f > 0$, $\langle x^2(t)\rangle = t^{1/2}E^2_{1/2,3/2}\left(-\frac{C_f}{2}t^{1/2}\right)$ and $\langle y^2(t)\rangle = 2tE_{1/2,2}\left(-\frac{C_f}{2}t^{1/2}\right)$. For the short time limit $t\to 0$, $\langle x^2(t)\rangle \sim \frac{2}{\sqrt{\pi}}t^{1/2}$ and $\langle y^2(t)\rangle \sim 2t$. For the long time limit $t\to\infty$, $\langle x^2(t)\rangle \sim \frac{4}{\sqrt{\pi}C_f^2}t^{-1/2}$ and $\langle y^2(t)\rangle \sim \frac{8}{\sqrt{\pi}C_f}t^{1/2}$. When reversible reaction occurs on the backbone $C_b > 0$, we obtain (see Appendix C)

$$\langle x^2(t)\rangle = 4L^{-1}\left\{\frac{(s+C_b)^2}{[2s^{3/4}(s+C_b)+C_f s^{5/4}]^2}\right\} \sim \begin{cases} \frac{2}{\sqrt{\pi}}t^{1/2} & (t\to 0) \\ \frac{2}{\sqrt{\pi}}t^{1/2} & (t\to\infty), \end{cases} \tag{38}$$

$$\langle y^2(t)\rangle = 4L^{-1}\left\{\frac{s(s+C_b)}{2s^3(s+C_b)+C_f s^{7/2}}\right\} \sim \begin{cases} 2t & (t\to 0) \\ 2t & (t\to\infty). \end{cases} \tag{39}$$

To check the behavior of particles in irreversible and reversible reactions, Fig. 4 and Fig. 5 illustrate the MSD along the x and y directions for different backward reaction rates C_b with $C_f = 1$. As we analyzed above, for the reversible reaction process, the asymptotic behavior in a short and a long time is the same and is independent of reaction rates C_f and C_b, and its form is consistent with the results of the classical comb model. It is worth mentioning that with the increase of C_b, the transition time to the usual diffusion becomes shorter.

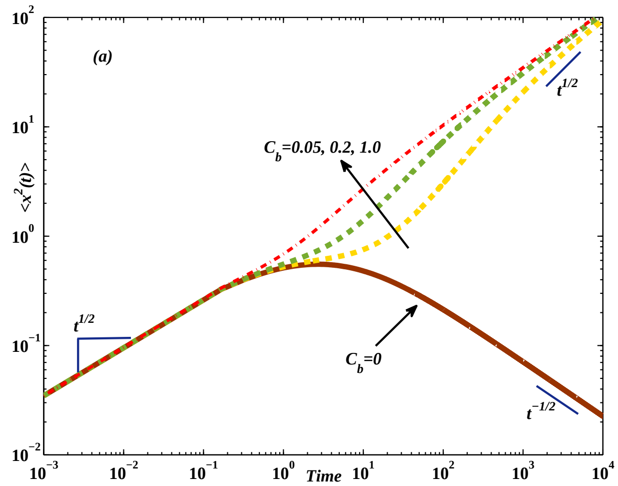

Figure 4: Behavior of Eq. (36) versus time for various backward reaction rates C_b with $C_f = 1$.

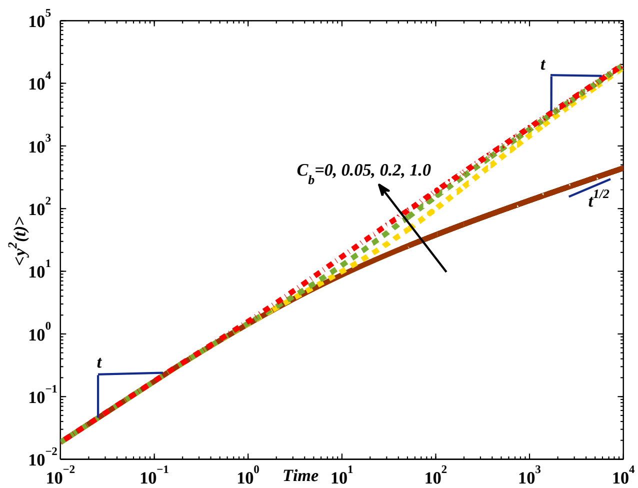

Figure 5: Behavior of Eq. (37) versus time for various backward reaction rates C_b with $C_f = 1$.

5.2. *Combination of power-law and distributed order memory kernel*

We set $\xi_x(t) = \frac{t^{v-1}}{\Gamma(v)}, \xi_y(t) = \int_0^1 p(\lambda)\frac{t^{\lambda-1}}{\Gamma(\lambda)}d\lambda$. In order to ensure the nonnegativity of the PDF, here $1/2 \le v \le 1$ and $0 \le \lambda \le 1$. $p(\lambda)$ is a weight function with $\int_0^1 p(\lambda)d\lambda = 1$. The Laplace transform is $\xi_y(s) = \int_0^1 p(\lambda)s^{-\lambda}d\lambda$.

The waiting time PDF to the y direction is $\psi_y(t) = L^{-1}\left\{\frac{1}{1+[\int_0^1 p(\lambda)s^{-\lambda}d\lambda]^{-1}}\right\}$ and the nonnegativity has been given in Ref. [20]. The waiting time PDF to the x direction is

$$\psi_x(t) = L^{-1}\left\{\frac{1}{1+s^v[\int_0^1 p(\lambda)s^{-\lambda}d\lambda]^{1/2}}\right\}. \tag{40}$$

Then we show that $s^v[\int_0^1 p(\lambda)s^{-\lambda}d\lambda]^{1/2} = s^{v-1/2}[\int_0^1 p(\lambda)s^{1-\lambda}d\lambda]^{1/2}$ is a CBF. In Ref. [29], it is shown that $\int_0^1 p(\lambda)s^{1-\lambda}d\lambda$ is a CBF. Thus, $s^{v-1/2}[\int_0^1 p(\lambda)s^{1-\lambda}d\lambda]^{1/2}$ is a CBF using the property that if $\alpha_1 + \alpha_2 \le 1$, then $m_1^{\alpha_1}m_2^{\alpha_2}$ is a CBF for all m_1 and m_2.

The uniformly distributed order memory kernel with $p(\lambda) = 1$ is a special case, and in this case $\xi_y(s) = \frac{s-1}{sIn(s)}$. By applying the Tauberian theorem [40], the long time limit of the waiting time PDFs become

$$\psi_x(t) = L^{-1}\left[\frac{1}{1+s^{v-1/2}\left(\frac{s-1}{In(s)}\right)^{1/2}}\right] \sim -\frac{d}{dt}\left[\frac{1}{\Gamma(\frac{3}{2}-u)}t^{1/2-v}In^{-1/2}(t)\right]$$
$$\sim \frac{u-\frac{1}{2}}{\Gamma(\frac{3}{2}-u)}t^{-1/2-u}In^{-1/2}(t), \tag{41}$$

and

$$\psi_y(t) = L^{-1}\left[\frac{1}{1+\frac{sIn(s)}{s-1}}\right] \sim t^{-2}. \tag{42}$$

For the MSD along the x and y directions, the case of no reaction term is considered first. Using Tauberian theorem again, we find

$$\langle x^2(t)\rangle = L^{-1}\left[s^{-(v+\frac{1}{2})}\left(\frac{In(s)}{s-1}\right)^{\frac{1}{2}}\right] \sim \begin{cases} \frac{1}{\Gamma(v+1)}t^{v}In^{\frac{1}{2}}(\frac{1}{t}) & (t\to 0) \\ \frac{1}{\Gamma(v+\frac{1}{2})}t^{v-\frac{1}{2}}In^{\frac{1}{2}}(t) & (t\to\infty), \end{cases} \tag{43}$$

and

$$\langle y^2(t)\rangle = 2L^{-1}\left[\frac{s-1}{s^2In(s)}\right] \sim \begin{cases} \frac{2}{In(\frac{1}{t})} & (t\to 0) \\ \frac{2t}{In(t)} & (t\to\infty). \end{cases} \tag{44}$$

When a reversible reaction takes place, we analyze the MSD along the x and y directions in a similar way and find that the behavior in either a short or a long time is not related to the reaction term. For irreversible reactions, the form of MSD along the x and y directions in a short time is the same as the case of no reaction terms. But in the long time limit

$$\langle x^2(t)\rangle = 4L^{-1}\left\{\frac{s^{v-\frac{3}{2}}(\frac{s-1}{In(s)})^{1/2}}{[2s^{v-\frac{1}{2}}(\frac{s-1}{In(s)})^{1/2}+C_f]^2}\right\} \sim \frac{4t^{\frac{1}{2}-v}}{\Gamma(\frac{3}{2}-v)C_f^2In^{\frac{1}{2}}(t)}, \tag{45}$$

and

$$\langle y^2(t)\rangle = 4L^{-1}\left[\frac{s^{-\frac{3}{2}}(\frac{s-1}{In(s)})^{3/2}}{2s^{\frac{1}{2}}(\frac{s-1}{In(s)})^{1/2}+s^{1-v}C_f}\right] \sim \frac{4t^{\frac{3}{2}-v}}{\Gamma(\frac{5}{2}-v)C_fIn^{\frac{3}{2}}(t)}, \tag{46}$$

The graphical representation of the MSD along the x and y directions is given in Fig. 6.

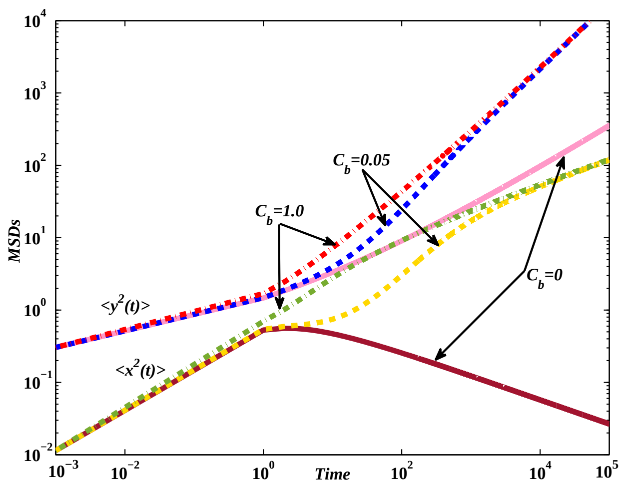

Figure 6: The MSD along the x and y directions versus time for various backward reaction rates C_b with $\mu = 0.8$ and $C_f = 1$.

5.3. Structure function memory kernel $\xi_x(t) = \xi_y(t) = In^q(t)$

Inspired by Ref. [18], we finally consider the case where both $\xi_x(t)$ and $\xi_y(t)$ are structural function memory kernels. In the long time limit, the Laplace transform of $In^q(t)$ is

$$\xi_x(t) = \xi_y(t) \sim \frac{In^q(1/s)}{s}, \tag{47}$$

where $q > 0$. The waiting time PDFs can be calculated using the same method as that for the Eq. (41).

For an irreversible reaction, we find the asymptotic behavior of the MSD

$$\langle x^2(t)\rangle = 4L^{-1}\left\{\frac{s^{-\frac{1}{2}}In^{-q/2}(1/s)}{[2s^{\frac{1}{2}}In^{-q/2}(1/s)+C_f]^2}\right\} \sim \frac{4t^{-\frac{1}{2}}In^{-q/2}(t)}{\sqrt{\pi}C_f^2} \tag{48}$$

along the x direction and

$$\langle y^2(t)\rangle = 4L^{-1}\left[\frac{s^{-\frac{3}{2}}In^{q/2}(1/s)}{2s^{\frac{1}{2}}In^{-q/2}(1/s)+C_f}\right] \sim \frac{8t^{\frac{1}{2}}In^{q/2}(t)}{\sqrt{\pi}C_f} \tag{49}$$

along the y direction.

For a reversible reaction, the asymptotic limit of the MSD is the same as that with no reaction terms, that is,

$$\langle x^2(t)\rangle = 4L^{-1}\left\{\frac{s^{-\frac{1}{2}}In^{-q/2}(1/s)}{[2s^{\frac{1}{2}}In^{-q/2}(1/s)+\frac{sC_f}{s+C_b}]^2}\right\} \sim \frac{2}{\sqrt{\pi}}t^{\frac{1}{2}}In^{q/2}(t) \tag{50}$$

and

$$\langle y^2(t)\rangle = 4L^{-1}\left[\frac{s^{-\frac{3}{2}}In^{q/2}(1/s)}{2s^{\frac{1}{2}}In^{-q/2}(1/s)+\frac{sC_f}{s+C_b}}\right] \sim 2tIn^{q}(t). \tag{51}$$

We can see that a structural function memory kernel is also suitable for this model. Fig. 7 illustrates the behavior of the MSD for a few different backward reaction rates C_b, and its limit behavior is consistent with the analysis.

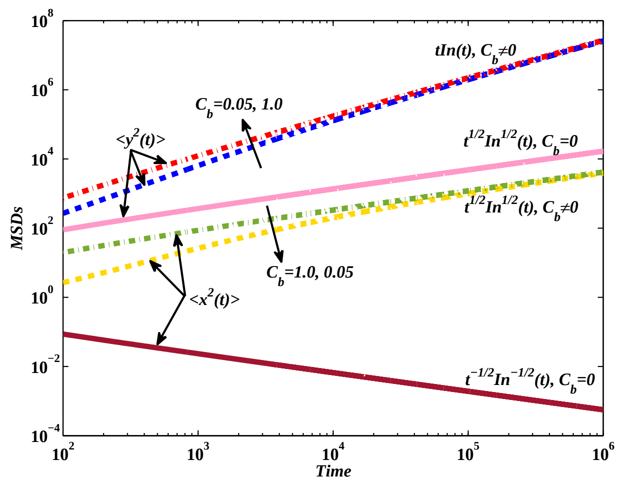

Figure 7: The MSD along the x and y directions versus time for various backward reaction rate C_b with $q = 1$ and $C_f = 1$.

6. Conclusions and remarks

In this paper, the generalized comb-like structure with memory kernels is investigated, with linear irreversible and reversible reactions being taken into consideration. The choice of memory kernels and reaction terms in the model are based on the actual physical background. First, we study the backbone resetting and global resetting in the 2-D comb structure from the perspective of the memory kernel, and generalize it to the N-D comb structure. The waiting time PDF and MSD on the backbone are obtained and analyzed. Then we continue to use the model to study the propagation of CaMKII with a linear reaction. The memory kernel in the x direction is obtained according to the experimental results, and the memory kernel in the y direction is obtained from the perspective of the random walk. The diffusion of inert particles and the linear reaction propagation of CaMKII are clearly described in this framework. Finally, the reversible reaction is discussed for various memory kernels, including standard memory kernels, distributed order memory kernels, and the recently proposed structural function memory kernels [18].

We suggest that this model can be used as a general model to describe the reaction-diffusion on comb structures. The form of the memory kernels need to be determined by the physical mechanism of specific problems. **It is noticed that with the development of numerical technology, more generalized variable-order fractional operators have been used to describe anomalous diffusion problems [41]. We shall work on these problems in future.**

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APPENDIX A: Mittag-Leffler (M-L) functions

$E^{\delta}_{\alpha,\beta}(z) = \sum_{k=0}^{\infty} \frac{\Gamma(\delta+k)}{\Gamma(\delta)\Gamma(\alpha k+\beta)} \frac{z^k}{k!}$ is the three parameter M-L function [42], and its Laplace transform is given by

$$L\left[t^{\beta-1}E^{\delta}_{\alpha,\beta}(\pm a t^{\alpha})\right] = \frac{s^{\alpha\delta-\beta}}{(s^{\alpha} \mp a)^{\delta}}, Re(s) > |a|^{1/\alpha}. \tag{A1}$$

The case $\delta = 1$ is the generalized M-L function. The asymptotic expansion for three parameter M-L function is

$$E^{\delta}_{\alpha,\beta}(-z) = \frac{z^{-\delta}}{\Gamma(\beta - \alpha\delta)} \quad (z \to \infty). \tag{A2}$$

APPENDIX B: Calculation of Eq. (30) and Eq. (31)

For Eq. (30), We use the variable change $r = \sqrt{2} s^{\frac{1}{2}-\frac{\mu}{4}}|x|$ and $z = \frac{1}{2}C_f s^{\frac{\mu}{2}-1} + 1$. We apply Merlin transform and then perform Taylor series expansion about $z = 1$:

$$\begin{aligned}
P(s,x) &= \frac{1}{2} M^{-1}\left[M\left[\frac{r}{|x|s} z^{-1/2} e^{-rz^{1/2}}\right](\xi)\right](s) \\
&= \frac{r}{2|x|s} M^{-1}\left[\int_0^t z^{\xi-\frac{3}{2}} e^{-rz^{1/2}}\, dz\right](s) \\
&= \frac{1}{s|x|} M^{-1}\left[\Gamma(2\xi-1) r^{-2\xi}\right](s) = \frac{1}{s|x|} H^{1,0}_{0,1}\left[r^2 z \middle|^{\text{---}}_{(-1,2)}\right] \\
&= \frac{1}{s|x|}\sum_{k=0}^{\infty} \frac{1}{k!}(z-1)^k \frac{d^k}{dz^k}\left\{H^{1,0}_{0,1}\left[r^2 z\middle|^{\text{---}}_{(-1,2)}\right]\right\}\Bigg|_{z=1} \\
&= \frac{1}{|x|}\sum_{k=0}^{\infty}\frac{(C_f)^k}{2^k k!} s^{(\frac{\mu}{2}-1)k-1} H^{1,1}_{1,2}\left[2s^{1-\frac{\mu}{2}}x^2\middle|^{(0,1)}_{(-1,2),(k,1)}\right],
\end{aligned} \tag{B1}$$

where $H^{m,n}_{p,q}\left[z\middle|^{(a_p,A_p)}_{(b_q,B_q)}\right]$ is the Fox H-function [43]. Eq. (B1) can be evaluated term by term using the inverse Laplace transform of the Fox H-function

$$\begin{aligned}
P(t,x) &= \frac{1}{|x|} L^{-1}\left\{\sum_{k=0}^{\infty}\frac{(C_f)^k}{2^k k!} s^{(\frac{\mu}{2}-1)k-1} H^{1,1}_{1,2}\left[2s^{1-\frac{\mu}{2}}x^2\middle|^{(0,1)}_{(-1,2),(k,1)}\right]\right\} \\
&= \frac{1}{|x|}\sum_{k=0}^{\infty}(-1)^k\frac{(C_f)^k}{2^k k!} t^{(1-\frac{\mu}{2})k} H^{2,0}_{2,2}\left[\frac{2x^2}{t^{1-\frac{\mu}{2}}}\middle|^{(1-(\frac{\mu}{2}-1)k,1-\frac{\mu}{2}),(0,1)}_{(k,1),(-1,2)}\right].
\end{aligned} \tag{B2}$$

For Eq. (31), Taylor series expansion and Eq. (A1) are used

$$\begin{aligned}
P_y(t,y) &= L^{-1}\left[\frac{e^{-s^{\frac{\mu}{2}}|y|}}{2s^{1-\frac{\mu}{2}} + C_f}\right] = \frac{1}{2}L^{-1}\left[\sum_{k=0}^{\infty}(-1)^k\frac{1}{k!}|y|^k\frac{s^{\frac{\mu}{2}k}}{s^{1-\frac{\mu}{2}}+\frac{C_f}{2}}\right] \\
&= \frac{1}{2}\sum_{k=0}^{\infty}(-1)^k\frac{1}{k!}|y|^k t^{-\frac{\mu}{2}(1+k)} E_{1-\frac{\mu}{2},1-\frac{\mu}{2}(1+k)}\left(-\frac{C_f}{2}t^{1-\frac{\mu}{2}}\right).
\end{aligned} \tag{B3}$$

APPENDIX C: The asymptotic behaviors of Eq. (38) and Eq. (39)

In order to analyze the behviors of the MSDs in the short time limit $t \to 0$ and the long time limit $t \to \infty$, a basic property of Laplace transform is used [44], that is, if $L\left[f(t)\right] = f(s)$, then

$$L\left[tf(t)\right] = -\frac{d}{ds}f(s). \tag{C1}$$

For Eq. (38), defining $f(t) = L^{-1}\left\{\frac{4(s+C_b)^2}{[2s^{3/4}(s+C_b)+C_f s^{5/4}]^2}\right\}$ and $g(t) = tf(t)$, Eq. (C1) is used

$$g(s) = L[tf(t)] = -\frac{d}{ds}f(s) \sim \begin{cases} \frac{3}{2}s^{-\frac{5}{2}} & t \to 0(s \to \infty) \\ \frac{3}{2}s^{-\frac{5}{2}} & t \to \infty(s \to 0). \end{cases} \tag{C2}$$

We therefore find

$$tf(t) = g(t) \sim \frac{2}{\sqrt{\pi}}t^{3/2} \longrightarrow f(t) \sim \frac{2}{\sqrt{\pi}}t^{1/2}(t \to 0, t \to \infty). \tag{C3}$$

Eq. (39) can be obtained by applying the same method.

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