

Generalized fractional diffusion equations for subdiffusion in arbitrarily growing domains

C. N. Angstmann,^{*} B. I. Henry,[†] and A. V. McGann[‡]*School of Mathematics and Statistics, University of New South Wales, Sydney, New South Wales 2052, Australia*

(Received 20 June 2017; published 26 October 2017)

The ubiquity of subdiffusive transport in physical and biological systems has led to intensive efforts to provide robust theoretical models for this phenomena. These models often involve fractional derivatives. The important physical extension of this work to processes occurring in growing materials has proven highly nontrivial. Here we derive evolution equations for modeling subdiffusive transport in a growing medium. The derivation is based on a continuous-time random walk. The concise formulation of these evolution equations requires the introduction of a new, comoving, fractional derivative. The implementation of the evolution equation is illustrated with a simple model of subdiffusing proteins in a growing membrane.

DOI: [10.1103/PhysRevE.96.042153](https://doi.org/10.1103/PhysRevE.96.042153)

A wide range of important physical phenomena involves transport in expanding, as well as contracting, domains. Fundamental examples include the diffusion of proteins within growing cells, the interactions of cells in a growing organism, and diffusion in an expanding universe. The governing equations for reaction diffusion on growing domains and related studies of pattern formation have been considered in a series of publications; see, for example, [1–8]. Domain growth has been shown to be fundamentally important to the development of patterns [9]. Here we consider the problem of subdiffusive transport in a growing domain by constructing a continuous-time random walk (CTRW) and limiting to a fractional-order partial differential equation (PDE).

Subdiffusion, which is characterized by a sublinear power-law scaling in time of the mean squared displacement, is common in biological systems with traps and obstacles [10], such as diffusion of molecules in spiny nerve cells [11], diffusion across potassium channels in membranes [12,13], and diffusion of HIV virions in cervical mucous [14]. Subdiffusion is also present in other physical systems such as cosmic rays [15], porous media [16], and volcanic earthquakes [17]. The generalization of canonical mathematical diffusion models to incorporate subdiffusive transport, such as reaction-diffusion PDEs [18–22] and Fokker-Planck PDEs [22–25], has proven nontrivial. In the work below we show that this is also true for subdiffusion in a growing domain.

There are different theoretical approaches that have been used to model subdiffusive transport. One of the more rigorous approaches is to derive the governing equations from the stochastic process of a CTRW [26]. The CTRW describes transport of particles on a mesoscopic scale in which particles wait for a time, governed by waiting time probability density, before randomly jumping, governed by a jump length probability density, to another location. If the jump length density is symmetric with a finite variance and the expected waiting time is convergent, then the CTRW limits to the standard diffusion PDE [27,28]. If the waiting time density is replaced with a heavy tailed power-law waiting time density,

such as a Mittag-Leffler density [27], then the CTRW limits to a time fractional subdiffusion PDE [27,28].

In the following we start with the underlying stochastic process of a CTRW to derive master equations for subdiffusive transport in a growing domain. In our derivation we first consider a mapping between a given position x on the domain at time $t = 0$ and the position that it evolves to, y , on the growing domain at a later time t . With this mapping we then transform the CTRW from the coordinates on the growing domain to a nongrowing fixed domain. An auxiliary master equation for the evolution of the density on the fixed domain is derived. The auxiliary master equation is constructed so that the value of the density at a given x and t equates to the probability density on the growing domain for y and t . The diffusion limit of the master equation is taken to produce a fractional diffusion equations on both the fixed and the growing domains.

Our approach enables us to model subdiffusive transport of particles on arbitrarily growing domains, and the solution of the auxiliary master equation on the fixed domain could be used as the basis for numerical simulations of subdiffusive transport on growing domains. The equations we derive on the growing domain can be interpreted phenomenologically as a reaction subdiffusion process with an additional advective term. In this context, the reaction represents the dilution of the concentration due to the growing domain.

We wish to construct a mapping between a location on the initial fixed domain, $x \in [0, L_0]$, to the corresponding location at some later time t , on the growing domain $y \in [0, L(t)]$. To characterize how the domain is changing in time, we begin by partitioning the domain $[0, L_0]$ into m cells of width $\delta x = \frac{L_0}{m}$. The i th partition begins at position $x_i = i\delta x$. As the domain grows, the width of the partitions, now denoted by $\delta y_i(t)$, will have grown with the domain and formed a partition of $[0, L(t)]$. Note that while the initial cell widths were constant, this is no longer the case in the growing domain; i.e., δy_i is a function of both the initial position x_i and time. The mapping is defined through a growth function, $\mu(x_i, t)$, via

$$\frac{1}{\delta y_i} \frac{d\delta y_i}{dt} = \mu(x_i, t). \quad (1)$$

Explicitly, it can be shown that the mapping $g(x, t)$ from a position in the fixed domain, x , to a corresponding position on

^{*}c.angstmann@unsw.edu.au[†]b.henry@unsw.edu.au[‡]a.mcgann@unsw.edu.au

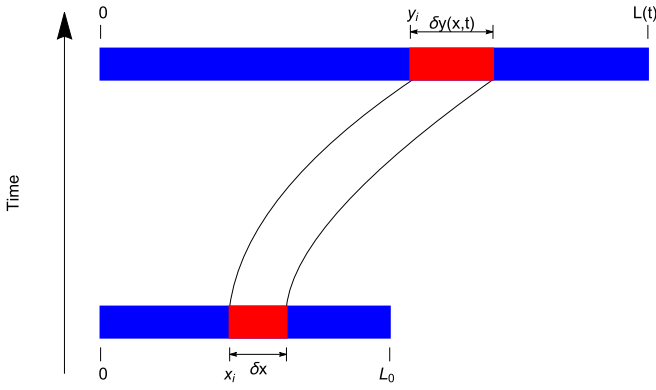


FIG. 1. Schematic representation of the growth of the domain and the mapping of an interval in the initial domain to a corresponding interval at some later time t .

the growing domain, y , is given by

$$y = \lim_{n \rightarrow \infty} \sum_{i=1}^n \delta y_i = \int_0^x \exp \left[\int_0^t \mu(z,s) ds \right] dz = g(x,t). \tag{2}$$

This is illustrated schematically in Fig. 1. Note that $g(0,t) = 0$ and the initial condition, $y = g(x,0) = x$ for all $x \in [0, L_0]$, place a physical restriction on the mapping between y and x . For future notational convenience we will denote the spatial derivative of $g(x,t)$ as $v^*(x,t)$, so that

$$v^*(x,t) = \frac{\partial g(x,t)}{\partial x} = e^{\int_0^t \mu(x,s) ds}, \tag{3}$$

and the time derivative as

$$\eta^*(x,t) = \frac{\partial g(x,t)}{\partial t} = \int_0^x \mu(z,t) e^{\int_0^t \mu(z,s) ds} dz. \tag{4}$$

As the mapping is invertible, so that $x = g^{-1}(y,t)$, these can be expressed on the growing domain, giving

$$v(y,t) = v^*(g^{-1}(y,t),t), \tag{5}$$

and

$$\eta(y,t) = \eta^*(g^{-1}(y,t),t). \tag{6}$$

It should also be noted that if we consider the growth of a small interval in the initial domain $(x, x + \delta x)$, then the width of the interval at some later time, in the limit of small δx , can be written as

$$\delta y(x,t) = e^{\int_0^t \mu(x,s) ds} \delta x. \tag{7}$$

We now consider a CTRW on a growing domain, such that a particle will jump to a location, wait for some time, and then jump to a new location. We will assume that the waiting time and jump length densities are independent. The waiting time probability density for a particle that arrived at a location at time t' to jump at time t will be denoted by $\psi(t-t')$, where $t-t'$ is the amount of time that the particle waited. The jump length density for a particle that is at a location z' to jump to location z at time t is denoted by $\lambda(z|z',t)$. In the following we consider a CTRW on the growing domain $z = y$ and an auxiliary CTRW on the fixed domain $z = x$. In taking the

diffusion limit we will restrict ourselves to fixed-length jumps on the growing domain, Δy , where the particle may jump either left or right. The corresponding jumps in the auxiliary CTRW on the initial fixed domain will therefore have lengths that change in both time and space as the domain grows.

For a particle undergoing a CTRW on the growing domain, we let $\rho(y,t)\delta y(x,t)$ denote the probability of finding the particle in the region $(y, y + \delta y(x,t))$, in the time $(t, t + \delta t)$ for a small $\delta y(x,t)$. Thus, $\rho(y,t)$ is the probability density of finding the particle, which we can express as

$$\rho(g(x,t),t)\delta y(x,t) = \int_0^t \Phi(t-t')q(g(x,t'),t')\delta y(x,t')dt', \tag{8}$$

where $\Phi(t-t')$ is the survival function associated with the waiting time density $\psi(t-t')$. The inbound flux, $q(g(x,t),t)$, is defined such that the probability of the particle entering the region $(y, y + \delta y(x,t))$ in the time $(t, t + \delta t)$, given $y = g(x,t)$, is $q(g(x,t),t)\delta y(x,t)\delta t$. This equation states that for a particle to be in the region, it must have previously arrived in the region and not jumped away.

Equation (8) can be simplified by using Eq. (7),

$$\begin{aligned} \rho(g(x,t),t)e^{\int_0^t \mu(x,s) ds} \\ = \int_0^t \Phi(t-t')q(g(x,t'),t')e^{\int_0^{t'} \mu(x,s) ds} dt'. \end{aligned} \tag{9}$$

To transform the evolution equation to a master equation, it is necessary to replace the explicit dependence on $q(g(x,t),t)$ with a dependence on $\rho(g(x,t),t)$. The growth of the domain requires us to utilize nonstandard techniques to achieve this. As the region is moving and growing this is most easily expressed by mapping the required functions back to the fixed x domain. The formulation of the CTRW on the fixed domain will be referred to as an auxiliary CTRW.

To formulate the auxiliary CTRW on the fixed domain, we relate the associated densities to densities on the growing domain, such that

$$\rho(y,t) = \rho(g(x,t),t) = \rho^*(x,t), \quad q(g(x,t),t) = q^*(x,t). \tag{10}$$

Here we use an asterisk to denote a function associated with the auxiliary process on the fixed domain. Hence, we can write the auxiliary form of Eq. (9) as

$$\rho^*(x,t)e^{\int_0^t \mu(x,s) ds} = \int_0^t \Phi(t-t')q^*(x,t')e^{\int_0^{t'} \mu(x,s) ds} dt'. \tag{11}$$

Note that this left-hand side, $\rho^*(x,t)e^{\int_0^t \mu(x,s) ds}$, is a conserved probability density. Differentiating Eq. (11) with respect to time and simplifying, we arrive at an evolution equation for the probability density,

$$\begin{aligned} \frac{\partial \rho^*(x,t)}{\partial t} = q^*(x,t) - \int_0^t \psi(t-t')e^{-\int_{t'}^t \mu(x,s) ds} q^*(x,t')dt' \\ - \mu(x,t)\rho^*(x,t). \end{aligned} \tag{12}$$

In this equation the second term on the right-hand side is the flux out of the neighborhood around x in the time interval around t , while the third term is the reduction in concentration

of particles, around x around t , due to the growth of the domain. Explicitly, we define the flux out as

$$i^*(x, t) = \int_0^t \psi(t - t') q^*(x, t') e^{-\int_{t'}^t \mu(x, s) ds} dt'. \quad (13)$$

In this equation the incoming flux, $q^*(x, t)$, can itself be expressed in terms of the flux out, resulting in the relation

$$q^*(x, t) = \int_0^{L(0)} \lambda(x|x', t) i^*(x', t) dx', \quad (14)$$

where $\lambda(x|x', t)$ is the jump probability density, where a particle at x' jumps to x , at time t .

Using Eq. (14), noting the semi-group property of the exponential function, we can rewrite Eq. (12) and, using Laplace transform methods, we can express the evolution equation for the auxiliary CTRW as the auxiliary master equation,

$$\frac{\partial \rho^*(x, t)}{\partial t} = \int_0^{L(0)} \lambda(x|x', t) \int_0^t K(t - t') \rho^*(x', t') e^{-\int_{t'}^t \mu(x', s) ds} dt' dx' - \int_0^t K(t - t') \rho^*(x, t') e^{-\int_{t'}^t \mu(x, s) ds} dt' - \mu(x, t) \rho^*(x, t). \quad (15)$$

In this equation, the memory kernel, $K(t)$, is defined by

$$\mathcal{L}_t\{K(t)\} = \frac{\mathcal{L}_t\{\psi(t)\}}{\mathcal{L}_t\{\Phi(t)\}}, \quad (16)$$

where \mathcal{L}_t denotes a Laplace transform with respect to time.

The master equation, Eq. (15), has been derived for arbitrary waiting time and jump densities. To obtain a diffusion limit of the master equation, we will require specific forms for these densities. We wish to consider the case of a fixed jump length on the growing domain, where the particle will jump either right or left with equal probability. In this case the jump length for the auxiliary master equation will change with both space and time. The jump probability density can therefore be written as

$$\lambda(x|x', t) = \frac{1}{2}[\delta(x - x' - \epsilon^+) + \delta(x - x' + \epsilon^-)], \quad (17)$$

where $\delta(x)$ is the Dirac δ function and ϵ^+ and ϵ^- are time and space dependent. To relate the ϵ 's to the fixed jump length, Δy , we note that from Eq. (2) we have

$$\Delta y = \int_{x-\epsilon^+}^x e^{\int_0^t \mu(z, s) ds} dz, \quad (18)$$

$$\Delta y = \int_x^{x+\epsilon^-} e^{\int_0^t \mu(z, s) ds} dz. \quad (19)$$

Using the relations from Eqs. (18) and (19), we perform a Taylor expansion of Eq. (15) with the jump distribution given by Eq. (17) around $\Delta y = 0$ to arrive at

$$\frac{\partial \rho^*(x, t)}{\partial t} = \frac{\Delta y^2 e^{-2 \int_0^t \mu(x, s) ds}}{2} \left\{ \left[\frac{\partial^2}{\partial x^2} \int_0^t K(t - t') \rho^*(x, t') e^{-\int_{t'}^t \mu(x, s) ds} dt' \right] - \left[\int_0^t \frac{\partial \mu(x, s)}{\partial x} ds \right] \left[\frac{\partial}{\partial x} \int_0^t K(t - t') \rho^*(x, t') e^{-\int_{t'}^t \mu(x, s) ds} dt' \right] \right\} - \mu(x, t) \rho^*(x, t) + O(\Delta y^3). \quad (20)$$

To consider subdiffusion on a growing domain, we now take a heavy tailed Mittag-Leffler waiting time density, given by

$$\psi(t) = \frac{t^{\alpha-1}}{\tau^\alpha} E_{\alpha, \alpha} \left[-\left(\frac{t}{\tau}\right)^\alpha \right], \quad (21)$$

with $0 < \alpha < 1$ and $\tau > 0$ [27], where $E_{\alpha, \beta}$ is a two-parameter Mittag-Leffler function defined by

$$E_{\alpha, \beta}(z) = \sum_{k=0}^{\infty} \frac{z^k}{\Gamma(\alpha k + \beta)}. \quad (22)$$

The Mittag-Leffler probability density is heavy tailed, which is asymptotically $\psi(t) \sim t^{-1-\alpha}$ for long times. The memory kernel of a Mittag-Leffler probability density can be calculated from the inverse Laplace transform of Eq. (16),

$$K(t) = \mathcal{L}_s^{-1} \left\{ \frac{s^{1-\alpha}}{\tau^\alpha} \right\}. \quad (23)$$

The Riemann-Liouville fractional derivative of order $1 - \alpha$ is defined as

$${}_0\mathcal{D}_t^{1-\alpha}[f(t)] = \frac{1}{\Gamma(\alpha)} \frac{d}{dt} \int_0^t f(t')(t - t')^{\alpha-1} dt'. \quad (24)$$

As we are considering smooth real-valued functions, the initial condition term in the Laplace transform of the Riemann-Liouville fractional derivative will be zero [29], so that

$$\mathcal{L}_t \{ {}_0\mathcal{D}_t^{1-\alpha} [f(t)] \} = s^{1-\alpha} \mathcal{L}_t \{ f(t) \}. \tag{25}$$

Using Mittag-Leffler distributed waiting times, the auxiliary master equation on the fixed domain, Eq. (20), becomes

$$\begin{aligned} \frac{\partial \rho^*(x,t)}{\partial t} &= \frac{\Delta y^2 e^{-2 \int_0^t \mu(x,s) ds}}{2\tau^\alpha} \left(\frac{\partial^2}{\partial x^2} \left\{ \frac{{}_0\mathcal{D}_t^{1-\alpha} [\rho^*(x,t) e^{\int_0^t \mu(x,s) ds}]}{e^{\int_0^t \mu(x,s) ds}} \right\} - \left[\int_0^t \frac{\partial \mu(x,s)}{\partial x} ds \right] \right. \\ &\quad \left. \times \frac{\partial}{\partial x} \left\{ \frac{{}_0\mathcal{D}_t^{1-\alpha} [\rho^*(x,t) e^{\int_0^t \mu(x,s) ds}]}{e^{\int_0^t \mu(x,s) ds}} \right\} \right) - \mu(x,t) \rho^*(x,t) + \mathcal{O}(\Delta y^3). \end{aligned} \tag{26}$$

The fractional diffusion limit is one in which the length and time scales are taken to zero, such that

$$D_\alpha = \lim_{\Delta y, \tau \rightarrow 0} \frac{\Delta y^2}{2\tau^\alpha} \tag{27}$$

exists. The fractional diffusion limit of Eq. (26) is

$$\begin{aligned} \frac{\partial \rho^*(x,t)}{\partial t} &= D_\alpha e^{-2 \int_0^t \mu(x,s) ds} \left(\frac{\partial^2}{\partial x^2} \left\{ \frac{{}_0\mathcal{D}_t^{1-\alpha} [\rho^*(x,t) e^{\int_0^t \mu(x,s) ds}]}{e^{\int_0^t \mu(x,s) ds}} \right\} - \left[\int_0^t \frac{\partial \mu(x,s)}{\partial x} ds \right] \right. \\ &\quad \left. \times \frac{\partial}{\partial x} \left\{ \frac{{}_0\mathcal{D}_t^{1-\alpha} [\rho^*(x,t) e^{\int_0^t \mu(x,s) ds}]}{e^{\int_0^t \mu(x,s) ds}} \right\} \right) - \mu(x,t) \rho^*(x,t). \end{aligned} \tag{28}$$

This is the auxiliary fractional diffusion equation defined on the fixed domain. Note that, apart from the advective type term, this is the same form as a fractional reaction subdiffusion equation [22], with the additional feature of a space and time-dependent diffusivity. In writing the equation in terms of the growing domain coordinates, the diffusivity will be constant.

Boundary conditions may be implemented by considering different jump length densities near the boundary. Explicitly, a zero flux boundary will be implemented by taking

$$\lambda(x|x',t) = \delta(x - x' + \epsilon^-), \tag{29}$$

for $x \in [L(0) - \epsilon^-, L(0)]$ and

$$\lambda(x|x',t) = \delta(x - x' - \epsilon^+), \tag{30}$$

for $x \in [0, \epsilon^+]$. This jump density guarantees that there is no flux across the boundary, and in the diffusive limit the master equation at the boundary point will be consistent with the master equation in the bulk.

Using the jump length density for the left boundary, Eq. (30), and taking a Taylor expansion around $\Delta y = 0$, the master equation, Eq. (15), becomes

$$\begin{aligned} \frac{\partial \rho^*(x,t)}{\partial t} &= \Delta y e^{-\int_0^t \mu(x,s) ds} \frac{\partial}{\partial x} \left[\int_0^t K(t-t') \rho^*(x,t') e^{-\int_{t'}^t \mu(x,s) ds} dt' \right] \\ &\quad + \frac{\Delta y^2 e^{-2 \int_0^t \mu(x,s) ds}}{2} \left\{ \left[\frac{\partial^2}{\partial x^2} \int_0^t K(t-t') \rho^*(x,t') e^{-\int_{t'}^t \mu(x,s) ds} dt' \right] \right. \\ &\quad \left. - \left[\int_0^t \frac{\partial \mu(x,s)}{\partial x} ds \right] \left[\frac{\partial}{\partial x} \int_0^t K(t-t') \rho^*(x,t') e^{-\int_{t'}^t \mu(x,s) ds} dt' \right] \right\} - \mu(x,t) \rho^*(x,t) + \mathcal{O}(\Delta y^3) \end{aligned} \tag{31}$$

for $x \in [0, \epsilon^+]$. The difference between this equation and the bulk result is the occurrence of a first-order spatial derivative. With the Mittag-Leffler waiting time density in order for the diffusion limit, Eq. (27), to exist, we require the first-order spatial derivative term to be

$$\frac{\partial}{\partial x} \left\{ \frac{{}_0\mathcal{D}_t^{1-\alpha} [\rho^*(x,t) e^{\int_0^t \mu(x,s) ds}]}{e^{\int_0^t \mu(x,s) ds}} \right\} \Big|_{x=0} = 0. \tag{32}$$

Only holding at the boundary point as $\Delta y \rightarrow 0$. This zero flux boundary condition is equivalent to the zero flux boundary derived for fractional reaction subdiffusion equations [30].

The derivation for the right-hand side of the boundary results in an equivalent condition.

The fractional diffusion equation can be found by mapping the auxiliary equation, Eq. (28), to the growing domain. Using the mapping $y = g(x,t)$ with Eqs. (5) and (6), we perform a change of variables and find

$$\begin{aligned} \frac{\partial \rho(y,t)}{\partial t} &= D_\alpha \frac{\partial^2}{\partial y^2} \left[\frac{1}{v(y,t)} {}_0\mathcal{C}_t^{1-\alpha} (\rho(y,t) v(y,t)) \right] - \eta(y,t) \\ &\quad \times \frac{\partial \rho(y,t)}{\partial y} - \left[\frac{\partial v(y,t)}{\partial t} \right] \frac{1}{v(y,t)} \rho(y,t). \end{aligned} \tag{33}$$

Here we have defined a new comoving fractional derivative, ${}^g_0\mathcal{C}_t^{1-\alpha}$, which operates along the curve, $y = g(x,t)$, for a fixed x . Formally, this is defined as

$${}^g_0\mathcal{C}_t^{1-\alpha} f(y,t) = \frac{1}{\Gamma(\alpha)} \frac{\partial}{\partial t} \int_0^t f(g(g^{-1}(y,t),t'),t')(t-t')^{\alpha-1} dt'. \quad (34)$$

Informally, the history of the function is not integrated over a fixed value of y but rather along the trajectory of the point in the domain as it grows. As with the Riemann-Liouville fractional derivative, the comoving fractional derivative becomes the identity operator in the limit as $\alpha \rightarrow 1$. We note that

$${}^g_0\mathcal{C}_t^{1-\alpha}(\rho(y,t)v(y,t)) = {}_0\mathcal{D}_t^{1-\alpha}(\rho^*(x,t)v^*(x,t)). \quad (35)$$

The physical understanding of Eq. (33) is that the third term on the right-hand side is a dilution factor due to the growing domain, the second term is an advection factor due to the growing domain, and the first term is a fractional diffusion term modified to take into account both the growth and dilution. The boundary condition, Eq. (32), on the growing domain is

$$\frac{\partial}{\partial y} \left[\frac{{}^g_0\mathcal{C}_t^{1-\alpha}(\rho(y,t)v(y,t))}{v(y,t)} \right] \Big|_{y=0,L(t)} = 0. \quad (36)$$

We note that when $\alpha \rightarrow 1$ this boundary condition is independent of the rate of the domain growth and is simplified to

$$\frac{\partial \rho(y,t)}{\partial y} \Big|_{y=0,L(t)} = 0 \quad (37)$$

on the growing domain.

It should also be noted that

$$\frac{d}{dt} \int_0^{L(t)} \rho(y,t) dy = 0. \quad (38)$$

This can be seen by integrating Eq. (33) over the growing domain and using the boundary conditions given by Eq. (36).

As a specific example, we consider a constant growth rate in which the mapping between the original and the growing

domain is defined by Eq. (2),

$$\mu(x,t) = r, \quad \text{and} \quad g(x,t) = xe^{rt}, \quad (39)$$

where $r \in \mathbb{R}$. Using this we can simplify the master equation on the growing domain, Eq. (33), and it becomes

$$\frac{\partial \rho(y,t)}{\partial t} = D_\alpha \frac{\partial^2}{\partial y^2} [e^{-rt} {}^g_0\mathcal{C}_t^{1-\alpha}(\rho(y,t)e^{rt})] - ry \frac{\partial \rho(y,t)}{\partial y} - r\rho(y,t), \quad (40)$$

with boundary conditions given by Eq. (36). This can be considered a simple model for diffusion of transmembrane proteins, such as potassium channels [12], that are anomalously diffusing in the plasma membrane of a uniformly growing cell, for example, during the G1 phase of growth of budding yeast [31]. In the case as $\alpha \rightarrow 1$, we recover the expected equation for diffusion on a uniformly growing domain; see Murray [2].

In this work we have derived evolution equations that describe subdiffusive transport on a growing domain. Equation (28) describes the transport on a rescaled fixed domain while Eq. (33) describes the same process on the growing domain. The evolution equation on the growing domain required the definition of a new fractional-order differential operator that follows the domain growth, Eq. (34). Our work provides the essential first step for modeling physical applications involving subdiffusion on growing domains. This work can be extended in numerous ways: including reactions through birth and death processes, including forces using biased CTRWs, and generalizing to higher dimensions using a multidimensional growth function and multidimensional CTRWs.

Note added in proof. We recently became aware of another formulation of subdiffusion on a growing domain [32].

ACKNOWLEDGMENTS

This work was supported by the Australian Commonwealth Government (Grant No. ARC DP140101193). We gratefully acknowledge useful discussions with S. B. Yuste.

[1] E. J. Crampin, E. A. Gaffney, and P. K. Maini, Reaction and diffusion on growing domains: Scenarios for robust pattern formation, *Bull. Math. Biol.* **61**, 1093 (1999).

[2] J. D. Murray, *Mathematical Biology. II. Spatial Models and Biomedical Applications Interdisciplinary Applied Mathematics* (Springer-Verlag, New York, 2001), Vol. 18.

[3] E. Crampin and P. Maini, Modelling biological pattern formation: The role of domain growth, *Comments Theor. Biol.* **6**, 229 (2001).

[4] R. E. Baker, C. A. Yates, and R. Erban, From microscopic to macroscopic descriptions of cell migration on growing domains, *Bull. Math. Biol.* **72**, 719 (2010).

[5] T. E. Woolley, R. E. Baker, E. A. Gaffney, and P. K. Maini, Stochastic reaction and diffusion on growing domains: Understanding the breakdown of robust pattern formation, *Phys. Rev. E* **84**, 046216 (2011).

[6] C. A. Yates, R. E. Baker, and R. Erban, P. K. Maini, Going from microscopic to macroscopic on nonuniform growing domains, *Phys. Rev. E* **86**, 021921 (2012).

[7] M. J. Simpson, J. A. Sharp, L. C. Morrow, and R. E. Baker, Exact solutions of coupled multispecies linear reaction-diffusion equations on a uniformly growing domain, *PLoS One* **10**, e0138894 (2015).

[8] S. Yuste, E. Abad, and C. Escudero, Diffusion in an expanding medium: Fokker-Planck equation, Green's function, and first-passage properties, *Phys. Rev. E* **94**, 032118 (2016).

[9] S. Kondo and R. Asai, A reaction-diffusion wave on the skin of the marine angelfish *Pomacanthus*, *Nature (London)* **376**, 765 (1995).

[10] M. J. Saxton, A biological interpretation of transient anomalous subdiffusion. I. Qualitative model, *Biophys. J.* **92**, 1178 (2007).

- [11] F. Santamaria, S. Wils, E. De Schutter, and G. J. Augustine, Anomalous diffusion in purkinje cell dendrites caused by spines, *Neuron* **52**, 635 (2006).
- [12] G. I. Mashanov, M. Nobles, S. C. Harmer, J. E. Molloy, and A. Tinker, Direct observation of individual KCNQ1 potassium channels reveals their distinctive diffusive behavior, *J. Biol. Chem.* **285**, 3664 (2010).
- [13] A. V. Weigel, B. Simon, M. M. Tamkun, and D. Krapf, Ergodic and nonergodic processes coexist in the plasma membrane as observed by single-molecule tracking, *Proc. Natl. Acad. Sci. USA* **108**, 6438 (2011).
- [14] S. A. Shukair, S. A. Allen, G. C. Cianci, D. J. Stieh, M. R. Anderson, S. M. Baig, C. J. Gioia, E. J. Sponberg, S. M. Kauffman, M. D. McRaven *et al.*, Human cervicovaginal mucus contains an activity that hinders HIV-1 movement, *Mucosal Immunol.* **6**, 427 (2013).
- [15] A. Shalchi, Time-dependent transport and subdiffusion of cosmic rays, *J. Geophys. Res.: Space Phys.* **110**, a09103 (2005).
- [16] M. Levy and B. Berkowitz, Measurement and analysis of non-Fickian dispersion in heterogeneous porous media, *J. Contam. Hydrol.* **64**, 203 (2003).
- [17] S. Abe and N. Suzuki, Subdiffusion of volcanic earthquakes, *Acta Geophys.* **65**, 491 (2017).
- [18] B. I. Henry, T. A. M. Langlands, and S. L. Wearne, Anomalous diffusion with linear reaction dynamics: From continuous time random walks to fractional reaction-diffusion equations, *Phys. Rev. E* **74**, 031116 (2006).
- [19] I. M. Sokolov, M. G. W. Schmidt, and F. Sagués, Reaction-subdiffusion equations, *Phys. Rev. E* **73**, 031102 (2006).
- [20] S. Fedotov, Non-Markovian random walks and nonlinear reactions: Subdiffusion and propagating fronts, *Phys. Rev. E* **81**, 011117 (2010).
- [21] E. Abad, S. Yuste, and K. Lindenberg, Reaction-subdiffusion and reaction-superdiffusion equations for evanescent particles performing continuous-time random walks, *Phys. Rev. E* **81**, 031115 (2010).
- [22] C. N. Angstmann, I. C. Donnelly, and B. I. Henry, Continuous time random walks with reactions forcing and trapping, *Math. Model. Nat. Phenom.* **8**, 17 (2013).
- [23] E. Barkai, R. Metzler, and J. Klafter, From continuous time random walks to the fractional Fokker-Planck equation, *Phys. Rev. E* **61**, 132 (2000).
- [24] I. M. Sokolov and J. Klafter, Field-Induced Dispersion in Subdiffusion, *Phys. Rev. Lett.* **97**, 140602 (2006).
- [25] B. I. Henry, T. A. M. Langlands, and P. Straka, Fractional Fokker-Planck Equations for Subdiffusion with Space- and Time-Dependent Forces, *Phys. Rev. Lett.* **105**, 170602 (2010).
- [26] E. Montroll and G. Weiss, Random walks on lattices II, *J. Math. Phys.* **6**, 167 (1965).
- [27] R. Hilfer and L. Anton, Fractional master equations and fractal time random walks, *Phys. Rev. E* **51**, R848 (1995).
- [28] R. Metzler and J. Klafter, The random walk's guide to anomalous diffusion: A fractional dynamics approach, *Phys. Rep.* **339**, 1 (2000).
- [29] C. Li and W. Deng, Remarks on fractional derivatives, *Appl. Math. Comput.* **187**, 777 (2007).
- [30] C. N. Angstmann, I. C. Donnelly, B. I. Henry, B. Jacobs, T. A. Langlands, and J. A. Nichols, From stochastic processes to numerical methods: A new scheme for solving reaction subdiffusion fractional partial differential equations, *J. Comput. Phys.* **307**, 508 (2016).
- [31] D. McCusker and D. R. Kellogg, Plasma membrane growth during the cell cycle: Unsolved mysteries and recent progress, *Curr. Opin. Cell Biol.* **24**, 845 (2012).
- [32] F. Le Vot, E. Abad, and S. B. Yuste, Continuous-time random-walk model for anomalous diffusion in expanding media, *Phys. Rev. E* **96**, 032117 (2017).