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ORIGINAL ARTICLE

Fractional Reproduction-Dispersal Equations and Heavy Tail Dispersal Kernels

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Abstract Reproduction-Dispersal equations, called reaction-diffusion equations in the physics literature, model the growth and spreading of biological species. Integro-Difference equations were introduced to address the shortcomings of this model, since the dispersal of invasive species is often more widespread than what the classical RD model predicts. In this paper, we extend the RD model, replacing the classical second derivative dispersal term by a fractional derivative of order $1 < \alpha \leq 2$. Fractional derivative models are used in physics to model anomalous super-diffusion, where a cloud of particles spreads faster than the classical diffusion model predicts. This paper also establishes a connection between the new RD model and a corresponding ID equation with a heavy tail dispersal kernel. The general theory developed here accommodates a wide variety of infinitely divisible dispersal kernels that adapt to any scale. Each one corresponds to a generalised RD model with a different dispersal operator. The connection established here between RD and ID equations can also be exploited to generate convergent numerical solutions of RD equations along with explicit error bounds.

Keywords Reproduction-dispersal equation · Integro-difference equation · Fractional derivative · Anomalous diffusion · Operator splitting

1. Introduction

The classical reproduction-dispersal (RD) equation

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2} \tag{1}$$

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for the growth and dispersal of biological species (Fisher, 1937; Kolmogorov et al., 1937) can underestimate the speed of invasion. This has lead to the consideration of the integro-difference (ID) equation

$$u(x, t+\tau) = \int_{-\infty}^{\infty} k^{\tau}(x, y) g_{\tau}\bigl(u(y, t)\bigr)\, dy \tag{2}$$

that replaces the classical second derivative dispersal term by a convolution with a dispersal kernel (Kot et al., 1996; Murray, 2002; Neubert and Caswell, 2000). In both models, the population density is $u(x, t)$ at location x and time t. In the physics literature, (1) is called the reaction-diffusion equation. The ID model with a Gaussian dispersal kernel is essentially equivalent to the classical RD model, in a sense that will be made precise in this paper. Alternative dispersal kernels with heavier tails model the faster and wider spreading observed in many field studies (Bullock and Clarke, 2000; Clark et al., 1999, 2001; Katul et al., 2005; Klein et al., 2006; Paradis et al., 2002). This paper proposes a new fractional RD equation

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^{\alpha} u}{\partial |x|^{\alpha}} \tag{3}$$

with $1 < \alpha \leq 2$, extending the classical approach. Fractional derivatives are used in physics to model anomalous diffusion, where a cloud of particles spreads farther and faster than the classical diffusion model predicts (Barkai et al., 2000; Blumen et al., 1989; Bouchaud and Georges, 1990; Klafter et al., 1987; Meerschaert et al., 1999, 2001, 2002a, 2002b; Metzler and Klafter, 2000, 2004; Saichev and Zaslavsky, 1997; Zaslavsky, 1994). Fractional derivative models have also been proposed in finance (Gorenflo et al., 2001; Raberto et al., 2002; Sabatelli et al., 2002; Scalas et al., 2000, 2005; Scalas, 2006) to model price volatility, and in hydrology (Baeumer et al., 2001, Benson et al., 2000a, 2000b, 2001; Schumer et al., 2001, 2003) to model fast spreading of pollutants. In each case, the fractional derivative term substitutes for the classical second derivative term, resulting in a wider and faster spread. Fractional derivatives are a natural analogue of their integer-order cousins (Miller and Ross, 1993; Samko et al., 1993). They were invented by Leibnitz, but their utility in modelling practical situations has only recently been recognised. In this paper, we develop a general theory of RD equations including the classical and fractional versions. We also prove an explicit connection between RD and ID models with infinitely divisible dispersal kernels that adapt to any scale. The dispersal kernels that correspond to the fractional RD model are stable probability densities (Samorodnitsky and Taqqu, 1994) that occur in the generalised central limit theorem of statistics (Feller, 1966; Gnedenko and Kolmogorov, 1968). The connection between ID and generalised RD models also yields numerical solutions with explicit error bounds, based on operator splitting.

2. The general reproduction-dispersal equation

The classical reproduction-dispersal equation (1) and its fractional analogue (3) are both special cases of a general form

$$\frac{\partial}{\partial t}u(x, t) = A\, u(x, t) + f\bigl(u(x, t)\bigr), \qquad u(x, 0) = u_0(x), \tag{4}$$

where A is a pseudo-differential operator (Jacob, 1996) that appears as the generator of some continuous convolution semi-group (Arendt et al., 2001; Pazy, 1983). Our goal in this section is to explore the connection between this continuous time evolution equation and its discrete time analogue, the integro-difference equation

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k^{\tau}(x, y) g_{\tau}\big(u_n(y)\big)\, dy, \tag{5}$$

where $u_n(x) = u(x, n\tau)$ with some $\tau > 0$ fixed. Our general approach is based operator theory for abstract differential equations (Arendt et al., 2001; Engel and Nagel, 2000; Pazy, 1983) and infinitely divisible probability distributions (Feller, 1966; Meerschaert and Scheffler, 2001).

Let X be a Banach space of functions $h : \mathbb{R} \to \mathbb{R}$ with associated norm $\|h\|$, and rewrite the RD equation (4) in operator theory notation as

$$\dot{u}(t) = Au(t) + f\big(u(t)\big), \quad t > 0, \qquad u(0) = u_0, \tag{6}$$

where $u : [0, \infty) \to X$ and A is the generator of a strongly continuous semi-group $T(t)$ on X. If $f : X \to X$ is Lipschitz continuous, then (6) has a unique global mild solution $u(t) := W(t)u_0$ for all $u_0 \in X$ (Pazy, 1983, Section 6.1), i.e., u is continuous and satisfies the corresponding integral equation

$$u(t) = T(t)u_0 + \int_0^t T(t - s) f\big(u(s)\big)\, ds. \tag{7}$$

The growth or reproduction equation $\dot{u} = f(u)$ is a special case of (6) with $A = 0$. Denote its unique mild solution by $u(t) := S(t)u_0$. Then u is also a strong solution (see, e.g., Hille and Phillips, 1974, p. 67) and the nonlinear operators $S(t)$ form a semi-group called the flow of the abstract differential equation $\dot{u} = f(u)$. The solution operator $W(t)u_0$ to the abstract RD equation (6) can then be computed using the Trotter product formula (Brézis and Pazy, 1972; Cliff et al., 2004; Miyadera and Ôharu, 1970)

$$W(t)u_0 = \lim_{n\to\infty} \big[T\big(\tfrac{t}{n}\big)S\big(\tfrac{t}{n}\big)\big]^n u_0 = \lim_{n\to\infty} \big[S\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0, \quad u_0 \in X. \tag{8}$$

This operator splitting expresses solutions in terms of the two sub-problems, since $T(t)u_0$ solves the dispersion equation $\dot{u} = Au$ and $S(t)u_0$ solves the growth equation $\dot{u} = f(u)$.

Assume that X is an *ordered Banach space*, i.e., a real Banach space endowed with a partial ordering $\leq$ such that

(1) $u \leq v$ implies $u + w \leq v + w$ for all $u, v, w \in X$.
(2) $u \geq 0$ implies $\lambda u \geq 0$ for all $u \in X$ and $\lambda \geq 0$.
(3) $0 \leq u \leq v$ implies $\|u\| \leq \|v\|$ for all $u, v \in X$.
(4) The positive cone $X_+ := \{u \in X : u \geq 0\}$ is closed.

A typical example of an ordered Banach space is $C_0(\mathbb{R})$, the space of continuous functions $u : \mathbb{R} \to \mathbb{R}$ such that $u(x) \to 0$ as $|x| \to \infty$, endowed with the supremum norm $\|u\| = \sup\{|u(x)| : x \in \mathbb{R}\}$, and endowed with the partial ordering $u \leq v$ whenever $u(x) \leq v(x)$ for all $x \in \mathbb{R}$. An operator A on an ordered Banach space is positive if $0 \leq u \leq v$ implies $0 \leq Au \leq Av$. We also write $B \leq A$ if $0 \leq Bu \leq Au$ for any $u \geq 0$.

The following result will be used to associate each abstract RD equation with an associated ID (integro-difference) equation.

Proposition 2.1. *Let X be an ordered Banach space, and assume that the strongly continuous semi-group $T(\cdot)$ generated by the linear operator A and the nonlinear semi-group $S(\cdot)$ generated by the Lipschitz continuous function f are positive. If*

$$T(t)S(t)u_0 \leq S(t)T(t)u_0 \tag{9}$$

holds for all $t \in [0,T]$ and $u_0 \geq 0$, then the unique mild solution $W(t)u_0$ of the abstract reaction-diffusion equation (6) is given by (8) and satisfies

$$\begin{aligned}\left[T\left(\tfrac{t}{n}\right)S\left(\tfrac{t}{n}\right)\right]^n u_0 &\leq \left[T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)\right]^{2n} u_0 \leq W(t)u_0\\ &\leq \left[S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)\right]^{2n} u_0 \leq \left[S\left(\tfrac{t}{n}\right)T\left(\tfrac{t}{n}\right)\right]^n u_0\end{aligned} \tag{10}$$

for all $u_0 \geq 0$, $n \in \mathbb{N}$ and $t \in [0,T]$.

Proof: We follow (Cliff et al., 2004, Theorem 15). It follows from our assumption that $W(t)u_0$ is given by (8). Next we show that

$$\begin{aligned}\left[T\left(\tfrac{t}{n}\right)S\left(\tfrac{t}{n}\right)\right]^n u_0 &\leq \left[T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)\right]^{2n} u_0\\ &\leq \left[S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)\right]^{2n} u_0 \leq \left[S\left(\tfrac{t}{n}\right)T\left(\tfrac{t}{n}\right)\right]^n u_0,\end{aligned} \tag{11}$$

$u_0 \geq 0$, $n \in \mathbb{N}$ and $t \in [0,T]$. For $u_0 \geq 0$ using (9) repeatedly we have

$$\begin{aligned}T\left(\tfrac{t}{n}\right)S\left(\tfrac{t}{n}\right)u_0 &= T\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)u_0\\ &\leq T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)u_0 \leq S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)u_0\\ &\leq S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)u_0 \leq S\left(\tfrac{t}{2n}\right)S\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)T\left(\tfrac{t}{2n}\right)u_0\\ &= S\left(\tfrac{t}{n}\right)T\left(\tfrac{t}{n}\right)u_0.\end{aligned}$$

For any operators $A, B : X \to X$, it is not hard to check that the inequality $0 \leq B \leq A$ implies $0 \leq B^n \leq A^n$ ($n \in \mathbb{N}$) which finishes the proof of (11). Fix $n \in \mathbb{N}$ and let

$$u_k := \left[T\left(\tfrac{t}{n2^k}\right)S\left(\tfrac{t}{n2^k}\right)\right]^{n2^k} u_0.$$

By (11), $u_0 \leq u_1 \leq \cdots \leq u_k \leq \cdots$ and $u_k \to W(t)u_0$ as $k \to \infty$ by (8). Therefore, it follows from the closedness of the positive cone X_+ that $u_k \leq W(t)u_0$ for all $k = 0, 1, \ldots$. This shows the second inequality in (10). A similar argument yields the third inequality and the proof is complete. ☐

For a detailed and exhaustive introduction to positive semi-groups we refer to (Arendt et al., 1986). One useful class of positive strongly continuous semigroups are the infinitely divisible semi-groups, which are associated with certain families of probability densities. Suppose that Y is a random variable on $\mathbb{R}$ with probability density $k(y)$ and Fourier transform $\hat{k}(\lambda) = \int e^{-i\lambda y} k(y)\,dy$. Let $k^n = k * \cdots * k$ denote the *n-fold convolution* of k with itself. We say that Y (or k) is *infinitely divisible* if for each $n = 1, 2, 3, \ldots$ there exist independent random variables $Y_{n1}, \ldots, Y_{nn}$ with the same density k_n such that $Y_{n1} + \cdots + Y_{nn}$ is identically distributed with Y. The normal, Cauchy, double-Gamma, Laplace, α-stable, and Student-t densities are all infinitely divisible. The *Lévy representation* (see, e.g., Theorem 3.1.11 in Meerschaert and Scheffler, 2001) states that if k is infinitely divisible then $\hat{k}(\lambda) = e^{\psi(\lambda)}$ where

$$\psi(\lambda) = -i\lambda a \; - \frac{1}{2}\lambda^2 b^2 + \int_{y\neq 0}\left(e^{-i\lambda y} - 1 + \frac{i\lambda y}{1+y^2}\right)\phi(y)\,dy, \tag{12}$$

where $a \in \mathbb{R}$, $b \geq 0$, and the *jump intensity* ϕ satisfies

$$\int_{y\neq 0} \min\{1, y^2\}\phi(y)\,dy < \infty.$$

The unique triple $[a, b, \phi]$ is called the Lévy representation of the infinitely divisible density k. It follows that we can define the convolution power k^t to be the infinitely divisible density with Lévy representation $[ta, tb, t\phi]$, so that k^t has Fourier transform $e^{t\psi(k)}$ for any $t \geq 0$. This simple fact will allow us to define appropriate dispersal kernels at any scale.

Any infinitely divisible density is associated (Jacob, 1996, Example 4.1.3) with a strongly continuous semi-group on $C_0(\mathbb{R})$ defined by

$$\big[T(t)u\big](x) := \int_{-\infty}^{\infty} k^t(x-y)u(y)\,dy. \tag{13}$$

Every function $u \in C_0(\mathbb{R})$ with u', $u'' \in C_0(\mathbb{R})$ belongs to the domain of the generator A of the semi-group (13), and for such functions we have (Sato, 1999, Theorem 31.5)

$$\begin{aligned} Au(x) &= -au'(x) + \tfrac{1}{2}b^2u''(x) \\ &\quad + \int_{y\neq 0}\left(u(x-y) - u(x) + \frac{u'(x)y}{1+y^2}\right)\phi(y)\,dy. \end{aligned} \tag{14}$$

We show now that in case of Fisher's equation, where the nonlinearity f is not globally Lipschitz, the solution of the discrete ID equation still yields bounds on the solution of the continuous RD equation and the solution of the ID equation converge to the unique solution of the RD equation as the time step tends to zero.

Theorem 2.2. *Let k be infinitely divisible and let A denote the generator of the associated strongly continuous convolution semi-group $T(t)$ defined by (13) on $X := C_0(\mathbb{R})$. Let $f(u) = ru(1-u/K)$. Then (6) with initial condition $u_0 \geq 0$ has a unique mild solution $u(t) = W(t)u_0$ for all $u_0 \geq 0$ in X given by the Trotter product formula*

$$W(t)u_0 = \lim_{n\to\infty}\big[T\big(\tfrac{t}{n}\big)S\big(\tfrac{t}{n}\big)\big]^n u_0 = \lim_{n\to\infty}\big[S\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0. \tag{15}$$

Moreover,

$$\begin{aligned} \big[T\big(\tfrac{t}{n}\big)S\big(\tfrac{t}{n}\big)\big]^n u_0 &\leq \big[T\big(\tfrac{t}{2n}\big)S\big(\tfrac{t}{2n}\big)\big]^{2n} u_0 \leq W(t)u_0 \\ &\leq \big[S\big(\tfrac{t}{2n}\big)T\big(\tfrac{t}{2n}\big)\big]^{2n} u_0 \leq \big[S\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0 \end{aligned} \tag{16}$$

for all $n \in \mathbb{N}$, *where*

$$S(t)u_0 = \frac{K u_0 \exp(rt)}{K + (\exp(rt) - 1)u_0}. \tag{17}$$

Proof: As the growth function in Fisher's equation is not Lipschitz, we introduce a cut off function (which is Lipschitz) via the function $\tilde{f}_N : \mathbb{R} \to \mathbb{R}$ as

$$\big[f_N(u)\big](x) = \tilde{f}_N\big(u(x)\big) := \begin{cases} 0, & \text{if } u(x) < 0, \\ ru(x)\left(1 - \dfrac{u(x)}{K}\right), & \text{if } 0 \le u(x) \le NK, \\ rNK(1 - N), & \text{if } u(x) > NK. \end{cases} \tag{18}$$

Choose $N \ge 2$ such that

$$0 \le u_0(x) \le NK \quad \text{for all } x \in \mathbb{R}. \tag{19}$$

Note that the initial population density $u_0(x)$ may exceed the carrying capacity. We are going to show that the solution to (6) is the same as the solution to the abstract reproduction-dispersal equation

$$\dot{u}(t) = Au(t) + f_N\big(u(t)\big), \qquad u(0) = u_0 \ge 0, \tag{20}$$

if N is chosen according to (19). As f_N is Lipschitz, the unique mild solution $u_N(t) = W_N(t)u_0$ of (20) is again given by the Trotter product formula

$$u_N(t) = W_N(t)u_0 = \lim_{n\to\infty}\big[T\big(\tfrac{t}{n}\big)S_N\big(\tfrac{t}{n}\big)\big]^n u_0 = \lim_{n\to\infty}\big[S_N\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0, \tag{21}$$

where $S_N(\cdot)$ is the nonlinear positive semi-group generated by f_N. The positivity of $S_N(\cdot)$ follows from the uniqueness of solutions of $\dot{u} = f_N(u)$, $u(0) = u_0$, and the fact that $\tilde{f}_N(0) = 0$.

Since k^t is a probability density function, the semi-group $T(\cdot)$ applied to u_0, with $0 \le u_0(x) \le NK$ for all x, satisfies

$$0 \le \big[T(t)u_0\big](x) \le NK \int_{-\infty}^{\infty} k^t(x - y)\, dy = NK. \tag{22}$$

Furthermore, (Baeumer et al., 2007, Proposition 4.2) shows that

$$0 \le \big[S_N(t)u_0\big](x) = \big[S(t)u_0\big](x) \le NK, \quad x \in \mathbb{R}$$

provided (19) holds. Hence,

$$0 \le \big[T\big(\tfrac{t}{n}\big)S_N\big(\tfrac{t}{n}\big)\big]^n u_0(x) = \big[T\big(\tfrac{t}{n}\big)S\big(\tfrac{t}{n}\big)\big]^n u_0(x) \le NK \tag{23}$$

for all $x \in \mathbb{R}$ and

$$0 \le \big[S_N\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0(x) = \big[S\big(\tfrac{t}{n}\big)T\big(\tfrac{t}{n}\big)\big]^n u_0(x) \le NK \tag{24}$$

for all $x \in \mathbb{R}$. This also shows that $0 \le [u_N(t)](x) \le NK$ for all $x \in \mathbb{R}$ in view of (21). Since $f_N(u(x)) = f(u(x))$ for $0 \le u(x) \le NK$, $u_N(t)$ is a mild solution of (6) as well.

Since f is locally Lipschitz, a well known result (Pazy, 1983, Chapter 6, Theorem 1.4) implies that (6) has a unique local mild solution and since $u_N(t)$ is defined for all $t > 0$ it follows that $u_N(t)$ is the unique global mild solution of (6) and is given by the Trotter product formula (15).

Finally, an easy computation shows that the function

$$y \mapsto \big[\tilde{S}(t)\big](y) := \frac{K y \exp(rt)}{K + (\exp(rt) - 1)y}$$

is concave down on $y > 0$ for any $t > 0$ and $[S(t)u_0](x) = [\tilde{S}(t)](u_0(x))$. Therefore, by Jensen's inequality (Feller, 1966, pp. 153–154),

$$\begin{aligned}\big[S(t)T(t)u_0\big](x) &= \tilde{S}(t)\left[\int_{-\infty}^{\infty} k^t(y)u_0(x-y)\,dy\right]\\ &\geq \int_{-\infty}^{\infty} k^t(y)\tilde{S}(t)\big[u_0(x-y)\big]\,dy\\ &= \int_{-\infty}^{\infty} k^t(y)\big[S(t)u_0\big](x-y)\,dy = \big[T(t)S(t)u_0\big](x).\end{aligned}$$

Thus,

$$S_N(t)T(t)u_0 = S(t)T(t)u_0 \geq T(t)S(t)u_0 = T(t)S_N(t)u_0,$$

which finishes the proof by Proposition 2.1, (23) and (24). ☐

Corollary 2.3. *Under the assumptions of Theorem 2.2, if u_0 and its first two derivatives in x exist and belong to $C_0(\mathbb{R})$, then (6) has a unique strong solution $u(t) = W(t)u_0$ for all $u_0 \geq 0$ in X given by the Trotter product formula (15).*

Proof: In this case u_0 is in the domain of the operator A, and since the function $f(u) = ru(1 - u/K)$ as a function $X \to X$ is continuously differentiable, u is also a strong solution by (Pazy, 1983, Chapter 6, Theorem 1.5). ☐

Proposition 2.1 and Theorem 2.2 show that the abstract RD equation (6) can be solved by operator splitting in terms of the two component equations, the reproduction or growth equation $\dot{u} = f(u)$ and the dispersal equation $\dot{u} = Au$. This also establishes a mathematical connection between RD and ID equations. For any abstract RD equation (1), there is a corresponding ID equation (2) at any time scale $\tau > 0$ where $g_\tau(u) = S(\tau)u$ represents population growth over a time period of length τ, and the dispersal kernel k^τ from the infinitely divisible semi-group (13) spreads the population over the same time step. The results in this section show that solutions to this ID equation converge to the RD equation solution as the time step shrinks to zero. Hence ID equations with any infinitely divisible dispersal kernel correspond precisely to the analogous RD equation. Gaussian dispersal kernels relate to the classical equation (1) with a Laplacian dispersal term. In the next section, we show in detail how the fractional RD equation (3) is linked to the ID equation with a stable probability density as the dispersal kernel.

3. Fractional reproduction-dispersal equations

The classical diffusion equation is closely connected to the central limit theorem of statistics, since the sum of a large number of independent and statistically identical random movements converges to a normal density (Feller, 1966; Meerschaert and Scheffler, 2001). The fractional diffusion equation relates to another central limit theorem. The classical result assumes that the individual random jump has a finite standard deviation. If instead we assume that the random movements X have power-law probability tails $P(|X| > r) \approx r^{-\alpha}$ for some $0 < \alpha < 2$, then the standard deviation is infinite, and the sum converges to a stable density (Feller, 1966; Samorodnitsky and Taqqu, 1994). The generalised central limit theorem is completely generic, in the sense that any convergence must approach one of these forms (Feller, 1966). The stable probability density functions cannot be written in closed form, except in a few special cases, so it is common to describe these distributions in terms of their Fourier transforms $\hat{k}^t(\lambda) = e^{t\psi(\lambda)}$ where

$$\psi(\lambda) = \begin{cases} -ia\lambda - \sigma^\alpha|\lambda|^\alpha\left(1 - i\beta(\operatorname{sign}\lambda)\tan\dfrac{\pi\alpha}{2}\right) & \text{for } \alpha \neq 1, \\ -ia\lambda - \sigma|\lambda|\left(1 + i\beta\dfrac{2}{\pi}(\operatorname{sign}\lambda)\ln\lambda\right) & \text{for } \alpha = 1. \end{cases}$$

The parameter $a \in \mathbb{R}$ centers the distribution, while $\sigma \geq 0$ provides a length scale. The stable index α and the parameter β that controls the skewness satisfy $0 < \alpha \leq 2$ and $-1 \leq \beta \leq 1$, (Samorodnitsky and Taqqu, 1994). This formula comes from computing the integral (12) with jump intensity $\phi\{x : |x| > r\} = Cr^{-\alpha}$ (Meerschaert and Scheffler, 2001, Section 7.3). This jump intensity comes from a regular variation argument, and reflects the power-law jumps in the limit theorem (Meerschaert and Scheffler, 2001, Section 8.2).

Stable densities are universal dispersal kernels, since any dispersal kernel converges to one of the stable densities (including the Gaussian, the special case $\alpha = 2$) after a number of convolutions. The stochastic process with stable transition densities k^t is called a Lévy motion, a generalised form of Brownian motion that allows for occasional large jumps. A random path in this model is a fractal of dimension α (Taylor, 1986). The stable densities possess a pleasant scaling property $k^t(x) = t^{-1/\alpha}k(xt^{-1/\alpha})$. Since the parameter α codes the scaling, the order of the derivative, and the fractal dimension, there are several possibilities for model fitting (Aban and Meerschaert, 2001, 2004; Aban et al., 2006; Benson et al., 2000a, 2001; Hill, 1975; Nolan, 1997).

The fractional diffusion equation models anomalous dispersion, the accumulation of random movements with power law probability tails (Chaves, 1998; Meerschaert et al., 2002a). Solutions to the fractional dispersion equation are stable probability densities (Meerschaert et al., 1999; Sokolov and Klafter, 2005). Using the convention $(re^{i\theta})^\alpha = r^\alpha e^{i\alpha\theta}$ for $-\pi < \theta \leq \pi$, we have

$$|\lambda|^\alpha\left(1 - i\beta(\operatorname{sign}\lambda)\tan\frac{\pi\alpha}{2}\right) = \frac{1}{\cos(\pi\alpha/2)}\left(\frac{1+\beta}{2}(i\lambda)^\alpha + \frac{1-\beta}{2}(-i\lambda)^\alpha\right).$$

Hence we can also write

$$\begin{aligned}\hat{k}^t(\lambda) &= \exp\left[t\left(-ai\lambda - \frac{\sigma^\alpha}{\cos(\pi\alpha/2)}\left(\frac{1+\beta}{2}(i\lambda)^\alpha + \frac{1-\beta}{2}(-i\lambda)^\alpha\right)\right)\right] \\ &= \exp\left[-vt(i\lambda) + pDt(i\lambda)^\alpha + qDt(-i\lambda)^\alpha\right], \end{aligned} \tag{25}$$

where $v = a$, $\sigma^\alpha = -D\cos(\pi\alpha/2)$, and $p - q = \beta$. Then the Fourier transform $\hat{k}^t$ solves the ordinary differential equation

$$\frac{d}{dt}\hat{k}^t(\lambda) = \left[-v(i\lambda) + pD(i\lambda)^\alpha + qD(-i\lambda)^\alpha\right]\hat{k}^t(\lambda). \tag{26}$$

Recall that $(i\lambda)^n \hat{f}(\lambda)$ is the Fourier transform of $d^n f(x)/dx^n$. Similarly, we define the fractional derivative $d^\alpha f(x)/dx^\alpha$ as the function whose Fourier transform is $(i\lambda)^\alpha \hat{f}(\lambda)$. We also define $d^\alpha f(x)/d(-x)^\alpha$ as the function whose Fourier transform is $(-i\lambda)^\alpha \hat{f}(\lambda)$. Now inverting (26) yields the fractional dispersion/diffusion equation

$$\frac{\partial k^t(x)}{\partial t} = -v\frac{\partial k^t(x)}{\partial x} + pD\frac{\partial^\alpha k^t(x)}{\partial x^\alpha} + qD\frac{\partial^\alpha k^t(x)}{\partial(-x)^\alpha}. \tag{27}$$

As a stochastic model for population movements, this fractional dispersion equation differs from the classical diffusion/dispersion equation by allowing for occasional large movements many times larger than average. The resulting population density curves retain the power law tails of the individual jump distributions, and super-dispersive spreading like $t^{1/\alpha}$ makes this a useful model for populations that grow and spread faster and farther than the classical equation predicts. In the limit theorem, the weights p, q are the probability of large jumps in the positive or negative direction, respectively. Hence, the special case $\partial k^t(x)/\partial t = D\partial^\alpha k^t(x)/\partial x^\alpha$ corresponds to zero drift $v = 0$ and only positive jumps $p = 1 - q = 0$. For symmetric jumps $p = q = 1/2$ we get a symmetric dispersal kernel that solves the (Riesz) fractional dispersion equation

$$\frac{\partial k^t(x)}{\partial t} = -v\frac{\partial k^t(x)}{\partial x} + \sigma^\alpha\frac{\partial^\alpha k^t(x)}{\partial|x|^\alpha}, \tag{28}$$

where $d^\alpha f(x)/d|x|^\alpha$ is defined as the function whose Fourier transform is $-|k|^\alpha \hat{f}(\lambda)$. This derivative operator is a classical fractional power of the second derivative or Laplacian (Arendt et al., 2001).

Solving the fractional dispersion equation with drift (27) in the constant coefficient case is equivalent to computing the stable densities. Although the stable Fourier transform cannot be inverted in closed form, probabilists have developed fast numerical methods for computing them, based on analytical expressions obtained from the Fourier inversion formula (Nolan, 1997). Figure 1 illustrates the numerical calculation of the stable density using Nolan's method. Stable densities are similar to the Gaussian end-member, but can incorporate both skewness and heavy tails.

For fractional dispersion equations with variable coefficients, efficient finite difference schemes (Deng et al., 2004; Lynch et al., 2003; Tadjeran et al., 2006; Tadjeran and

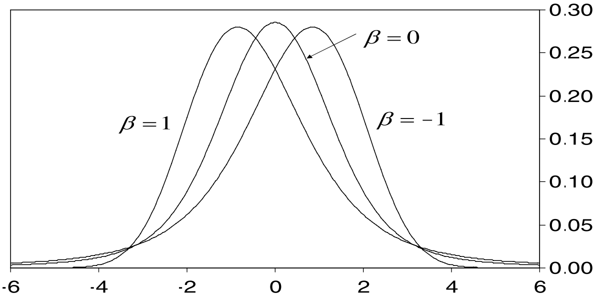

Fig. 1 Standard stable dispersal kernels with $\alpha = 1.6$ illustrating the bell shape and skewness.

Meerschaert, 2007) and particle tracking codes (Zhang et al., 2006) have recently become available. Finite difference schemes are based on the Grünwald formula

$$\frac{d^\alpha f(x)}{dx^\alpha} = \lim_{h \to 0} \frac{1}{h^\alpha} \sum_{k=0}^{\infty} \frac{\Gamma(k-\alpha)}{k!\Gamma(-\alpha)} f(x-kh). \tag{29}$$

This limit is a Riemann–Liouville fractional derivative (Podlubny, 1999; Samko et al., 1993)

$$\frac{d^\alpha f(x)}{dx^\alpha} = \frac{1}{\Gamma(n-\alpha)} \frac{d^n}{dx^n} \int_0^x \frac{f(y)}{(x-y)^{\alpha+1-n}}\, dy, \tag{30}$$

where $n-1 < \alpha \leq n$. If α is an integer, then the above definitions give the standard integer derivatives. For $0 < \alpha < 1$, integration by parts in (30) yields

$$\frac{d^\alpha f(x)}{dx^\alpha} = \frac{\alpha}{\Gamma(1-\alpha)} \int_0^\infty \frac{f(x) - f(x-y)}{y}\, y^{-\alpha}\, dy \tag{31}$$

a weighted average of difference quotients, with power law weights deriving from the underlying jump intensity or Lévy measure.

Now we consider the fractional Fisher's equation

$$\frac{\partial u}{\partial t}(x,t) = ru(x,t)\left(1 - \frac{u(x,t)}{K}\right) + \sigma^\alpha \frac{\partial^\alpha u}{\partial |x|^\alpha}(x,t); \qquad u(x,0) = u_0(x). \tag{32}$$

To apply the sequential operator splitting procedure from the previous section, we note that the fractional diffusion equation

$$\frac{\partial u}{\partial t}(x,t) = \sigma^\alpha \frac{\partial^\alpha u}{\partial |x|^\alpha}(x,t); \qquad u(x,0) = u_0(x) \tag{33}$$

has the unique solution

$$u(x,t) = \big[T(t)u_0\big](x) = \int_{-\infty}^{\infty} k^t(x-y)u_0(y)\, dy, \tag{34}$$

where $k^t(x)$ is a stable density with parameters $1 < \alpha \le 2$, $\beta = 0$, $a = 0$, and $\sigma^\alpha > 0$. Next consider the growth equation

$$\frac{\partial u}{\partial t}(x,t) = ru(x,t)\left(1 - \frac{u(x,t)}{K}\right); \qquad u(x,0) = u_0(x)$$

with solution (17). Define an iteration based on the sequential splitting by

$$\begin{aligned} u_{n+1}(x) &= \big[T(\tau)S(\tau)u_n\big](x) \\ &= \int_{-\infty}^{\infty} k^\tau(x-y)K\left(1 - \frac{K - u_n(y)}{K + u_n(y)(\exp(r\tau) - 1)}\right)dy. \end{aligned} \tag{35}$$

This is a discrete time ID equation of the form (5), an approximate solution $u(x, n\tau)$ of the fractional RD equation (32). Similarly, if we model first dispersion and then growth, we obtain the alternative sequential splitting

$$\begin{aligned} u_{n+1}(x) &:= \big[S(\tau)T(\tau)u_n\big](x) \\ &= K\left(1 - \frac{K - \big(\int_{-\infty}^{\infty} k^\tau(x-y)u_n(y)\,dy\big)}{K + \big(\int_{-\infty}^{\infty} k^\tau(x-y)u_n(y)\,dy\big)(\exp(r\tau) - 1)}\right). \end{aligned} \tag{36}$$

Theorem 2.2 and Corollary 2.3 imply that the fractional Fisher's equation (32) in continuous time can be solved numerically by computing solutions to one of its discrete time counterparts (35) or (36) with $\tau = t/n$. The approximate solutions $u_n(x,t)$ converge to the unique solution $u(x,t)$ of the fractional Fisher's equation at any time $t > 0$ for any smooth initial population density $u_0(x)$ as $n \to \infty$. This result links the continuous time partial differential equation model with the corresponding discrete time integro-difference equation model. Furthermore, the approximation (35) gives a lower bound to the exact solution while the approximation (36) gives an upper bound. Hence these two approximation can be compared to yield exact error bounds. See Section 4 for an illustration.

Theorem 2.2 and Corollary 2.3 extend immediately to any abstract RD equation of the form (6) as long as $u \mapsto [\tilde{S}(t)](u)$ is concave down on some interval $u \in [0, M]$ for each $t > 0$, and solutions to the differential equation $\dot{u} = f(u)$ remain in this interval for all time whenever $u(0) \in [0, M]$. They also extend to the case where $f(u, x)$ depends on the point x in space, and/or the multidimensional case $x \in \mathbb{R}^d$, since all the proofs are pointwise. The results of this paper also extend to model patchy populations in d-dimensional space, where the growth rate and carrying capacity vary with spatial location (Baeumer et al., 2007).

A wide variety of alternative models can be obtained by considering different infinitely divisible densities k as the dispersal kernel. The infinitely divisible densities are convenient because one can define the integro-difference equation (5) at any time scale τ based on the convolution power k^τ. The results of this paper also yield the corresponding RD model with a diffusion operator A exhibiting as the generator of the corresponding infinitely divisible semigroup. Lockwood et al. (2002) employ a Laplace (double exponential), or more generally, a double Gamma family of dispersion kernels, which are infinitely divisible with Lévy representation $[a, 0, \phi]$ with jump intensity $\phi(y) = |y|^{-1}e^{-c|y|}$. In this case the last term in the integral (14) converges, and hence we can choose a so that

$$Au(x) = \int_{-\infty}^{\infty} \frac{u(x-y) - u(x)}{|y|} e^{-c|y|}\, dy \tag{37}$$

an *exponentially weighted derivative*, which is similar to the fractional derivative formula (31) but with different weights (Kozubowski et al., 2006). For an exponential or Gamma dispersal kernel, the generator formula is the same as (37) except that the integral is taken over $y > 0$. Clarke et al. (1999, 2001) employ the Student-t dispersal kernel, which is infinitely divisible with Lévy representation as specified in (Heyde and Leonenko, 2005, Remark 2.3) in terms of Bessel functions. Substituting into (14) yields the corresponding generator, connecting the integro-difference equation (5) with a Student-t dispersal kernel to the analogous reaction-diffusion equation (4).

The fractional diffusion equation is a mathematical abstraction of the real situation in which a power law dispersal kernel pertains at some scale. Realistically, the power law probability density should not extend to infinity, since this would imply an unbounded velocity distribution. Of course, the same observation holds for the Gaussian, or any other dispersal kernel that extends to infinity. In the Gaussian case, the central limit theorem implies that the additive effect of a number of independent movements will approach a Gaussian form. For power law kernels, the extended central limit theorem implies an approach to a stable kernel. Truncated Lévy flights (Mantegna and Stanley, 1994; Shlesinger, 1995) and the corresponding fractional diffusion equation (Sokolov et al., 2004) provide a more realistic model that imposes a cutoff on the power-law tail. While the asymptotics are Gaussian at a sufficiently long time scale, the stable fit excels at the field scale (Mantegna and Stanley, 1997, 1998; Viswanathan et al., 1996), and thus provides the simplest useful approximation.

4. Numerical experiments

Consider a fractional Fisher's equation and a symmetric (Riesz) fractional diffusion term of order $1 \le \alpha \le 2$:

$$\frac{\partial u}{\partial t}(x,t) = \sigma^{\alpha} \frac{\partial^{\alpha} u}{\partial |x|^{\alpha}}(x,t) + ru(x,t)\left(1 - \frac{u(x,t)}{K}\right), \qquad u(x,0) = u_0(x). \tag{38}$$

Solutions to this equation can be computed using the results of Theorem 2.2, using the integro-difference model (5) as an approximation where the dispersal kernel $k^{\tau}(y)$ is a symmetric α-stable probability density function with index α, skewness $\beta = 0$, centre $a = 0$, and scale $\tau\sigma$. Note that in case $\alpha = 1$, k^{τ} is the density of a Cauchy distribution as used for example in (Kot et al., 1996; Shaw, 1995).

Numerical simulations were performed with $K = 1$, $c = 0.25$ and $\sigma^{\alpha} = 0.1$ and a smooth step-like initial function u_0 which takes the constant value $u = 0.8$ around the origin and rapidly decays to 0 away from the origin. $S(\tau)$ was computed analytically at each time step using the explicit analytical solution (17) and $T(\tau)u_n$ was computed by numerically convolving u_n against the symmetric α-stable dispersal kernel k^{τ}, which was computed numerically using the method of Nolan (1997). Note that the dispersal kernel

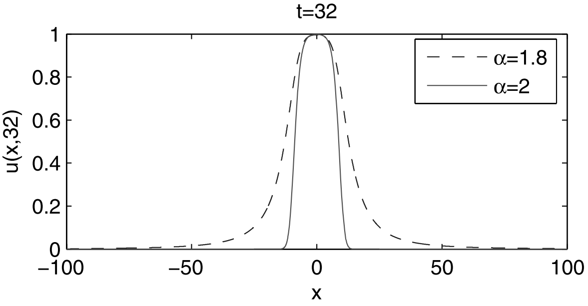

Fig. 2 Solution of the fractional Fisher's equation (38) with $\alpha = 1.8$ versus $\alpha = 2$ at $t = 32$ with $K = 1$, $r = 0.25$ and $\sigma^\alpha = 0.1$ showing heavier tails and faster spreading in the fractional case $\alpha < 2$.

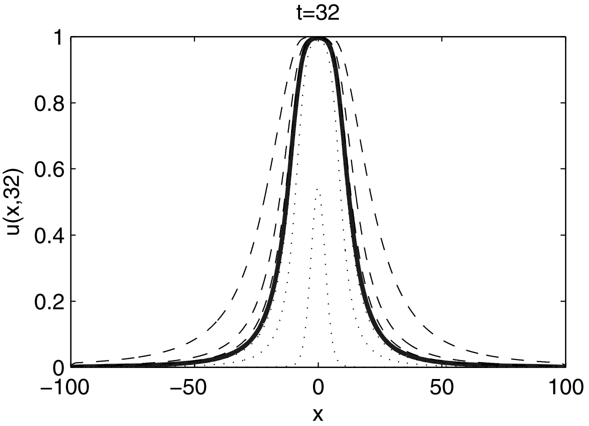

Fig. 3 Sequential splitting approximations of the solution of the fractional Fisher's equation (38) with $\alpha = 1.8$, $K = 1$, $r = 0.25$ and $\sigma^\alpha = 0.1$. Dashed lines are computed from (36) with time step $\tau = 32, 8, 2$ and dotted lines are computed from (35) at the same time steps to show monotone convergence to the exact (solid line) solution.

can be computed for any time scale τ, and that it only has to be computed once for each time scale. Figure 2 shows that the use of the conventional diffusion term $\alpha = 2$ in (38) produces a rapidly decaying solution away from the origin. However, if one replaces the diffusion term by a fractional one, even with an order α which is close to 2, then the solution picks up heavy tails and is spreading faster, similar to the results reported in del Castillo-Negrete et al. (2003) for the one-sided fractional RD equation (3).

Figure 3 visualises the conclusions of Theorem 2.2; that is, the sequential splitting approximations (35) and (36) converge in a pointwise monotone increasing and decreasing fashion, respectively, to the solution of (38).

Figure 4 shows evidence of an accelerating front. The selected population density level $u = c$ has spread a distance $x_c(t)$ by time $t > 0$, and since the graph of $x_c(t)$ versus t for various c closely resembles a straight line on the semi-log plot, we conclude that the

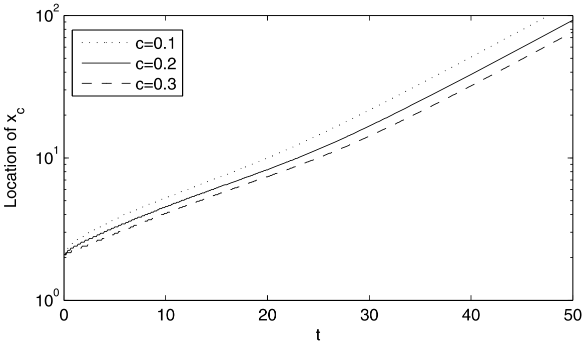

Fig. 4 Exponential spreading front for the fractional Fisher's equation (38) with $\alpha = 1.8$, $K = 1$, $r = 0.25$ and $\sigma^\alpha = 0.1$. The farthest distance to which a population density of c has spread by time t is plotted on a semi-log scale to illustrate the (nearly) exponential front growth over time.

front expands exponentially with time, in agreement with results reported by del Castillo-Negrete et al. (2003) for the one-sided model (3).

5. Conclusions

We showed how any integro-difference equation with an infinitely divisible dispersal kernel can be approximated by an integro-differential equation. Amongst the many infinitely divisible kernels there are only a few that are densities of stable probability distributions. They are the scaling limit of sums of independent identically distributed random variables and keep their shape at any time scale; the most popular being the Gaussian distribution. The classical central limit theorem implies that the Gaussian is the scaling limit of any distribution that does not have a power law tail. In case the dispersal kernels are power law of index $\alpha < 2$, the limit will be a stable distribution of index α. These stable distributions in general have no closed form description in real space (only Cauchy, Levy, and Gaussian), but are easily described in Fourier space. In the same way a Gaussian kernel gives rise to a Laplace operator in the differential equation, stable kernels give rise to fractional derivative operators and hence similarly parsimonious models. We investigated these fractional models, showed that solutions can be well approximated numerically and that they give rise to an accelerating invasion front.

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