Growth and dispersal with inertia: Hyperbolic reaction-transport systems

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We investigate the behavior of five hyperbolic reaction-diffusion equations most commonly employed to describe systems of interacting organisms or reacting particles where dispersal displays inertia. We first discuss the macroscopic or mesoscopic foundation, or lack thereof, of these reaction-transport equations. This is followed by an analysis of the temporal evolution of spatially uniform states. In particular, we determine the uniform steady states of the reaction-transport systems and their stability properties. We then address the spatiotemporal behavior of pure death processes. We end with a unified treatment of the front speed for hyperbolic reaction-diffusion equations with Kolmogorov–Petrosvskii–Piskunov kinetics. In particular, we obtain an exact expression for the front speed of a general class of reaction correlated random walk systems. Our results establish that three out of the five hyperbolic reaction-transport equations provide physically acceptable models of biological and chemical systems.

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I. INTRODUCTION

The spatial dispersal of organisms or particles is frequently modeled by Brownian motion or diffusion. The inclusion of birth-and-death processes of organisms or reactions between particles leads to the reaction-diffusion equation, also called the reproduction-dispersal equation. Reaction-diffusion models are used to describe the spatiotemporal behavior of systems in a wide variety of fields, including biology [1,2], ecology [3,4], chemistry [5–8], physics [9], and materials science [10].

There exists, however, a range of applications where a description of spatial dispersal by Brownian motion or simple diffusive transport is not entirely satisfactory. It is well known that the diffusion equation possesses the undesirable feature that localized disturbances spread infinitely fast, although with heavy attenuation, through the system. This pathology of the diffusion equation stems from a lack of inertia of Brownian particles. Individuals move with infinite velocity along random paths, and their motion is unpredictable even at the smallest scales. Such behavior describes neither molecules nor organisms in a realistic way. Brownian motion should be replaced by a process that assigns finite speeds to individuals. This goal can be achieved, for example, by using velocity jump processes to model the dispersal of molecules and organisms [11]. The simplest such process is the persistent or correlated random walk (CRW) [12–14]. Individuals move ballistically on short timescales, which immediately introduces the idea of motion persistence, i.e., the tendency to resist changes in direction [15–18]. By explicitly including persistence and a fixed speed of movement, the problem of infinite propagation speed is avoided. However, the position of the individuals is no longer a Markov process [16–19]; the spatial transport process now possesses memory.

It has been observed empirically that the motion of most animals tends to show persistence. CRWs have been used to model animal paths in various contexts [16,20–22]. In addition, CRWs have also been found to describe the pattern of motion of various microorganisms [23–26]. In a physical context, turbulent diffusion is better modeled by a CRW than by Brownian motion, i.e., classical diffusion, see Ref. [27, Sect. 10.6]. Furthermore, correlation effects in the dispersal of molecules have been conjectured to be important in multicomponent reacting mixtures [28].

In addition to descriptions based on CRWs, other approaches that do not invoke directly the underlying random process for the dispersal of individuals have been employed to account for inertia in the transport process and to remedy the infinitely fast propagation of disturbances in reaction-diffusion equations. All these approaches rely on hyperbolic evolution equations and have been applied to various phenomena, such as the Neolithic transition and the spread of virus and epidemics; see for example Refs. [11,15,29–38]. Recently, the validity of one of these hyperbolic reaction-transport equations has been questioned and a modified version been introduced [39]. We have been motivated by this development to investigate in detail several aspects of hyperbolic reaction-transport systems. Inertia endows the transport process with memory, and dealing jointly with transport and growth in the presence of persistence (memory) effects is far from trivial. All approaches face the problem of how to incorporate properly the contributions from reactions and dispersal into the evolution equation. This is a subtle and delicate problem, since there may be unanticipated interactions between the two processes, if one or both involve memory. Various processes contribute additively to the evolution equation only if *all* processes are *memoryless* or, in other words, if the underlying random processes are Markovian [19,33]. In the following, we will present the five most commonly used hyperbolic reaction-transport systems and will explore their foundation, the dynamics of spatially uniform states, the dynamics of the pure death process, and the speed of propagating fronts. We employ the results of these studies to identify which of these widely used equations are physically acceptable to model transport with inertia in systems of interacting organisms or reacting particles.

The paper is organized as follows: In Sec. II we briefly present the five model evolution equations and formulate criteria of good modeling. We review the derivation and foundation of the five hyperbolic reaction-transport equations in Sec. III. Section IV deals with the dynamics of spatially uniform states and Sec. V with the behavior of the pure death

process. We present in Sec. VI a unified derivation of the propagation speed of a front corresponding to the invasion of an unstable stationary state by a stable stationary state. We summarize our findings and draw conclusions in Sec. VII.

II. FIVE HYPERBOLIC REACTION-TRANSPORT EQUATIONS

Five different hyperbolic evolution equations are commonly employed to overcome the infinitely fast propagation of disturbances in the reaction-diffusion equation. For the sake of simplicity, we write the following equations for one spatial dimension and one species. The usefulness of the various hyperbolic evolution equations can be assessed already in this simple setting, without the complexity of more dimensions or more species obscuring the salient points. The population density of organisms or the concentration of particles is denoted by ρ. The growth rate of the population or the reaction rate of the particles is given by the kinetic rate function $F(\rho)$. The transport process is characterized by the diffusion coefficient D and the persistence (inertial) time τ. We consider either an infinite system or a finite system of length L with no-flow boundary conditions.

(1) The hyperbolic reaction-diffusion equation (HRDE) [40–45]:

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}+F(\rho). \tag{2.1}$$

This type of equation is also encountered in other areas, such as nonlinear waves, nucleation theory, and phase-field models of phase transitions, where it is known as the damped nonlinear Klein–Gordon equation; see for example Refs. [46–48].

(2) The reaction-Cattaneo system (RCS) [33,49–57]:

$$\frac{\partial\rho}{\partial t}=-\frac{\partial J}{\partial x}+F(\rho), \tag{2.2a}$$

$$\tau\frac{\partial J}{\partial t}=-J-D\frac{\partial\rho}{\partial x}. \tag{2.2b}$$

Here J is the flux of the organisms or particles.

(3) The reaction-telegraph equation (RTE) [15,29,31–33,58,59]:

$$\tau\frac{\partial^2\rho}{\partial t^2}+[1-\tau F'(\rho)]\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}+F(\rho). \tag{2.3}$$

(4) The modified hyperbolic reaction-diffusion equation (mHRDE) [39,60–62]:

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}+F(\rho)+\tau F'(\rho)F(\rho). \tag{2.4}$$

(5) The reaction correlated random walk system (RCRW) [19,33,49,63–65]:

$$\frac{\partial\rho_+}{\partial t}+\gamma\frac{\partial\rho_+}{\partial x}=\mu(\rho_--\rho_+)+F_+(\rho_+,\rho_-), \tag{2.5a}$$

$$\frac{\partial\rho_-}{\partial t}-\gamma\frac{\partial\rho_-}{\partial x}=\mu(\rho_+-\rho_-)+F_-(\rho_+,\rho_-). \tag{2.5b}$$

Here $\rho_+(x,t)$ is the density of individuals traveling to the right, and $\rho_-(x,t)$ is the density of individuals traveling to the left. The speed of the individuals is γ and their turning frequency is μ. The kinetic terms for the two classes of particles are $F_+(\rho_+,\rho_-)$ and $F_-(\rho_+,\rho_-)$, respectively.

Evolution equations for systems of organism or molecules should possess one essential feature to be acceptable descriptions of reacting and dispersing systems. A density or concentration, ρ, cannot be negative, and evolution equations for densities should preserve positivity, i.e., $\rho(x,0)\geqslant 0$ for all x at time $t=0$ implies $\rho(x,t)\geqslant 0$ for all x for all times $t>0$. It is well known that the diffusion equation

$$\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2} \tag{2.6}$$

possesses this required feature. Principles of kinetics dictate that proper rate functions obey

$$F(0)\geqslant 0. \tag{2.7}$$

This property ensures that the rate equation for spatially unstructured populations or well-stirred reactors, which we will call lumped systems for the sake of brevity,

$$\frac{d\rho}{dt}=F(\rho), \tag{2.8}$$

and the reaction-diffusion equation

$$\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}+F(\rho) \tag{2.9}$$

preserve positivity. In general, hyperbolic evolution equations do not preserve positivity; the RCRW is an exception [33,66].

We suggest that three further features are desirable for models of systems of interacting and dispersing individuals to be physically acceptable. First, given the fact that dealing jointly with transport and growth in the presence of persistence (memory) effects is a far from trivial task, the reaction-transport equation should have a sound macroscopic or mesoscopic foundation. Second, if the state of the reaction-transport system is spatially uniform, the characteristics of the transport process should play no role in the evolution of the density. For $\rho(x,t)\equiv\rho(t)$, the reaction-transport equation should reduce to the rate equation of the lumped system (2.8). Third, if propagating fronts corresponding to the invasion of an unstable stationary state by a stable one can occur in the system, their propagation speed should approach the ballistic speed as the characteristic inertial time of the transport process increases and reach this value if the characteristic kinetic time is smaller than the inertial time (high reaction rate regime).

As mentioned above, hyperbolic reaction-transport equations generally do not preserve positivity, the RCRW being an exception. While preservation of positivity is certainly a very desirable feature in an evolution equation for densities, evolution equations that violate this property may still be acceptable for practical applications as long as the violation is small in a certain sense. This has to be determined for the case under consideration. We will therefore consider the specific case of a pure death process, i.e., first-order decay for the kinetic term in the hyperbolic evolution equations, and require as a minimal condition that the density $\rho(x,t)$ approaches zero as time goes to infinity. We provide a heuristic argument in Sec. V E that RCRWs preserve positivity if $F_+(0,\rho_-)\geqslant 0$ and $F_-(\rho_+,0)\geqslant 0$.

Guided by these considerations, we choose four criteria to assess the value of the five types of hyperbolic reaction-diffusion systems: (I) Does the reaction-transport equation have a sound macroscopic (thermodynamic) or mesoscopic foundation? (II) Does the reaction-transport equation reduce to the rate equation (2.8) for $\rho(x,t) \equiv \rho(t)$, i.e., for uniform densities? (III) Does the solution of the hyperbolic equation approach zero for large times in the case of a pure death process, i.e., $\rho(x,t) \to 0$ for $t \to \infty$? (IV) Does the reaction-transport equation yield speeds for propagating fronts that do not exceed the ballistic speed and reach the latter in the fast reaction regime?

III. DERIVATION OF REACTION-TRANSPORT EQUATIONS

We summarize briefly the derivation of the five hyperbolic reaction-transport equations for the convenience of the reader and to make the discussion of the foundation of each equation more comprehensible.

A. Hyperbolic reaction-diffusion equation

The HRDE

$$\tau \frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho) \tag{3.1}$$

can be derived in two ways. From a mathematical point of view, the origin of the infinitely fast spreading of local disturbances in the reaction-diffusion equation can be traced to its parabolic character. Adding a term $\tau \partial_{tt} \rho$ confers a hyperbolic character on the equation, which results in finite speeds for local disturbances. If τ is small, then the HRDE can be considered to be a singular perturbation of the reaction-diffusion equation (2.9). This is of course entirely an *ad hoc* manner of proceeding. The second way, which we discuss in greater detail below (see Sec. III E), consists of replacing Brownian motion, a simple random walk, by a persistent or correlated random walk, a velocity jump process, which results in replacing the diffusion equation by the telegraph equation [11,15,33,49]

$$\tau \frac{\partial^2 \rho}{\partial t^2} + \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2}. \tag{3.2}$$

The RDE (2.9) is obtained from the diffusion equation (2.6) by adding a kinetic term to the transport term. Similarly, the HRDE (3.1) can be obtained by adding a kinetic term to the telegraph equation (3.2). Adding contributions from birth-and-death processes or reactions to the contributions from transport processes to obtain the overall evolution of the density ρ is legitimate in the first case, but not in the second case. The contributions from different processes to the total evolution of a system are additive only if all processes are memoryless or Markovian [19,33]. While the rate equation (2.8) and the diffusion equation (2.6) describe processes without memory, this is not the case for the telegraph equation (3.2). The HRDE is entirely an *ad hoc* evolution equation; it lacks both a macroscopic and a mesoscopic foundation.

B. Reaction-Cattaneo system

The macroscopic foundation of the reaction-diffusion equation consists of the continuity equation

$$\frac{\partial \rho}{\partial t} = -\frac{\partial J}{\partial x} + F(\rho) \tag{3.3}$$

and Fick's first law as the constitutive equation,

$$J = -D \frac{\partial \rho}{\partial x}. \tag{3.4}$$

Cattaneo and others [67] suggest that Fick's first law is unphysical and that the flux should adjust to changes in the gradient of the density with a small, nonzero relaxation time τ,

$$\tau \frac{\partial J}{\partial t} = -J - D \frac{\partial \rho}{\partial x}. \tag{3.5}$$

Jou and coworkers derived the Cattaneo equation from extended irreversible thermodynamics [68]. Eu and Al-Ghoul derived the reaction-Cattaneo system from linear nonequilibrium thermodynamics and generalized hydrodynamic theory [50–52,54]. Hillen used an energy minimization principle to obtain the Cattaneo system from general transport equations [55]. Valenti and coworkers resorted to the framework of extended thermodynamics theory to derive reaction-Cattaneo equations for the hantavirus infection [56] and the dynamics of an epidemic with susceptible, infected, and removed individuals [57]. The reaction-Cattaneo system has a macroscopic foundation consisting either of the continuity equation and a constitutive equation or generalized thermodynamic theory.

C. Reaction-telegraph equation

Differentiating the first equation of the reaction-Cattaneo system, (3.3), with respect to t and the second equation of the reaction-Cattaneo system, (3.5), with respect to x, and eliminating the mixed second derivatives, we obtain the reaction-telegraph equation

$$\tau \frac{\partial^2 \rho}{\partial t^2} + [1 - \tau F'(\rho)] \frac{\partial \rho}{\partial t} = D \frac{\partial^2 \rho}{\partial x^2} + F(\rho). \tag{3.6}$$

Note that the RTE (3.6) differs from the *ad hoc* HRDE (3.1) by the term

$$-\tau F'(\rho) \frac{\partial \rho}{\partial t} \tag{3.7}$$

on the left-hand side [15]. This underlines our earlier statement that contributions from different processes cannot simply be added to obtain the total evolution of the density, if one or more processes display memory effects. The RTE is obtained from the RCS by differentiating and therefore has a sound macroscopic foundation.

D. Modified hyperbolic reaction-diffusion equation

Isern and Fort derive the mHRDE in the following way [39]: They consider systems where the individuals or particles experience a time delay T between successive dispersal events. The time delay is assumed to correspond to the length of one generation in most ecological applications. They write the

finite-time difference of the density as

$$\rho(x,t+T)-\rho(x,t)=[\rho(x,t+T)-\rho(x,t)]_g + [\rho(x,t+T)-\rho(x,t)]_m. \quad (3.8)$$

The subscript g denotes contributions from birth-and-death processes, i.e., it represents the kinetic term. The subscript m denotes contributions from migration or dispersal processes, i.e., it represents the transport term. The premise that the growth and dispersal processes remain uncoupled during a *finite* time interval and contribute simply additively to the total change of the density is questionable. As mentioned in Sec. I, dealing jointly with transport and growth in the presence of memory effects is by no means a trivial task.

Carrying out a Taylor expansion of the growth term up to second order,

$$[\rho(x,t+T)-\rho(x,t)]_g = T\left.\frac{\partial\rho}{\partial t}\right|_g + \frac{T}{2}\left.\frac{\partial^2\rho}{\partial t^2}\right|_g, \quad (3.9)$$

and identifying the rate function $F(\rho)$ as

$$\left.\frac{\partial\rho}{\partial t}\right|_g = F(\rho), \quad (3.10)$$

Isern and Fort obtain

$$\begin{aligned}[\rho(x,t+T)-\rho(x,t)]_g &= TF(\rho)+\frac{T}{2}\left.\frac{\partial F}{\partial t}\right|_g \\ &= TF(\rho)+\frac{T}{2}\left.\frac{dF}{d\rho}\frac{\partial\rho}{\partial t}\right|_g \\ &= TF(\rho)+\frac{T}{2}F'(\rho)F(\rho) \quad (3.11)\end{aligned}$$

for the kinetic contribution. They write the dispersal contribution as

$$[\rho(x,t+T)-\rho(x,t)]_m = \int \rho(x+\Delta_x,t)w(\Delta_x)d\Delta_x - \rho(x,t), \quad (3.12)$$

where $w(\Delta_x)$ is the dispersal kernel. Assuming that the kernel is symmetric, one obtains the diffusion approximation via a Taylor expansion in x up to second order,

$$[\rho(x,t+T)-\rho(x,t)]_m = \frac{\langle\Delta_x^2\rangle}{2}\frac{\partial^2\rho}{\partial x^2}. \quad (3.13)$$

Carrying out a Taylor expansion up to second order of the left-hand side of Eq. (3.9) and combining the kinetic contribution (3.11) and the transport contribution (3.13) according to Eq. (3.9), one obtains the mHRDE,

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t} = D\frac{\partial^2\rho}{\partial x^2}+F(\rho)+\tau F'(\rho)F(\rho), \quad (3.14)$$

where $D=\langle\Delta_x^2\rangle/(2T)$ and $\tau=T/2$.

The mHRDE lacks both a macroscopic and a mesoscopic foundation. Furthermore, it is obtained by a Taylor expansion, which will be justified only if T is small compared to the other timescales of the model; see below.

E. Reaction correlated random walk system

The persistent random walk, also called a correlated random walk, is the simplest velocity jump process that remedies the physically undesirable features of Brownian motion; namely, that Brownian particles move with arbitrarily large velocity and that the motion of dispersing individuals is uncorrelated even on the smallest timescales. The persistent random walk was introduced by Fürth [12] to model the motion of bacteria and further studied by Taylor [13] and Goldstein [14].

In the correlated or persistent random walk [19,69], an individual or particle takes steps of length Δx and duration Δt. The individual continues in its previous direction with probability $\alpha=1-\mu\Delta t$ and reverses direction with probability $\beta=\mu\Delta t$. In the continuum limit $\Delta x\to 0$ and $\Delta t\to 0$, such that

$$\lim_{\Delta x,\Delta t\to 0}\frac{\Delta x}{\Delta t}=\gamma=\text{constant}, \quad (3.15)$$

we obtain the following set of equations for the density of individuals moving to the right, $\rho_+(x,t)$, and the density of individuals moving to the left, $\rho_-(x,t)$:

$$\frac{\partial\rho_+}{\partial t}+\gamma\frac{\partial\rho_+}{\partial x}=\mu(\rho_- -\rho_+), \quad (3.16a)$$

$$\frac{\partial\rho_-}{\partial t}-\gamma\frac{\partial\rho_-}{\partial x}=\mu(\rho_+ -\rho_-). \quad (3.16b)$$

The particles travel with speed γ and turn with frequency μ.

The persistent random walk spans the whole range of dispersal, from ballistic motion, in the limit $\mu\to 0$, to diffusive motion, in the limit $\gamma\to\infty$, $\mu\to\infty$, such that

$$\lim_{\gamma,\mu\to\infty}\frac{\gamma^2}{2\mu}=D=\text{constant}. \quad (3.17)$$

The total density of the dispersing individuals is given by

$$\rho(x,t)=\rho_+(x,t)+\rho_-(x,t), \quad (3.18)$$

and the flux J of individuals is given by $J=\gamma j$, where the "flow" j is defined as

$$j(x,t)=\rho_+(x,t)-\rho_-(x,t). \quad (3.19)$$

Adding Eqs. (3.16a) and (3.16b), we obtain the continuity equation

$$\frac{\partial\rho}{\partial t}+\gamma\frac{\partial j}{\partial x}=0. \quad (3.20)$$

Subtracting Eq. (3.16b) from Eq. (3.16a), we recover the Cattaneo equation

$$\frac{\partial j}{\partial t}+\gamma\frac{\partial\rho}{\partial x}=-2\mu j. \quad (3.21)$$

Differentiating Eq. (3.20) with respect to t and Eq. (3.21) with respect to x and eliminating the mixed second derivatives, we obtain Eq. (3.2). The persistent random walk provides a mesoscopic foundation for the Cattaneo equation (3.5) and the telegraph equation (3.2) [59].

The persistent random walk is a Markov process, and it is legitimate to add kinetic rate terms to the transport

equation (3.16) for (ρ_+,ρ_-) to obtain the total evolution of the densities due to birth-and-death processes and dispersal:

$$\frac{\partial\rho_+}{\partial t}+\gamma\frac{\partial\rho_+}{\partial x}=\mu(\rho_- -\rho_+)+F_+(\rho_+,\rho_-), \tag{3.22a}$$

$$\frac{\partial\rho_-}{\partial t}-\gamma\frac{\partial\rho_-}{\partial x}=\mu(\rho_+ -\rho_-)+F_-(\rho_+,\rho_-). \tag{3.22b}$$

The RCRW has a sound mesoscopic foundation.

The question arises how the rate terms $F_+(\rho_+,\rho_-)$ and $F_-(\rho_+,\rho_-)$ are related to the rate term $F(\rho)$. The simplest model assumes that $F(\rho)$ is a source term for the individuals, that the interactions do not depend on the direction of motion, and that new individuals choose either direction with equal probability [15,33,49,63,70]. Then

$$F_+(\rho_+,\rho_-)=F_-(\rho_+,\rho_-)=\tfrac{1}{2}F(\rho), \tag{3.23}$$

which is the so-called isotropic reaction walk. With Eq. (3.23), we obtain from Eq. (3.22) the reaction-Cattaneo system,

$$\frac{\partial\rho}{\partial t}+\gamma\frac{\partial j}{\partial x}=F(\rho), \tag{3.24a}$$

$$\frac{\partial j}{\partial t}+\gamma\frac{\partial\rho}{\partial x}=-2\mu j. \tag{3.24b}$$

The isotropic reaction walk appears to provide a mesoscopic foundation for the reaction-Cattaneo system, and consequently for the reaction-telegraph equation. This is, however, not the case; isotropic reaction walks are unsound. They violate a basic principle of kinetics [33,64,65]; namely, the rate of loss or death of individuals of a given type must go to zero as the density of those individuals goes to zero. Otherwise, the population density can become negative, which is unphysical. There are various ways of arriving at RCRWs that obey the principles of kinetics. We will focus here on a class of RCRWs defined by the following assumptions [19,49,59,71]: (i) The individuals undergo a birth and death process with "fertilities" and "mortalities" that are independent of the direction of motion of the individuals. (ii) The direction of "daughters" is correlated with that of the "mother." The degree of correlation is given by $\kappa\in[0,1]$. The value $\kappa=1/2$ corresponds to no correlation, $\kappa=1$ to complete correlation, and $\kappa=0$ to complete anticorrelation. We write the rate term $F(\rho)$ in production-loss form, $F(\rho)=F^+(\rho)-F^-(\rho)$, with $F^+(\rho)\geqslant 0$, $F^-(\rho)\geqslant 0$, and $F^-(0)=0$, and define the per capita birth and death rates,

$$f^+(\rho)\equiv\frac{F^+(\rho)}{\rho},\quad f^-(\rho)\equiv\frac{F^-(\rho)}{\rho}. \tag{3.25}$$

Then the RCRW is given by Eq. (3.22) with

$$F_+(\rho_+,\rho_-)=[\kappa\rho_++(1-\kappa)\rho_-]f^+(\rho)-f^-(\rho)\rho_+, \tag{3.26a}$$

$$F_-(\rho_+,\rho_-)=[(1-\kappa)\rho_++\kappa\rho_-]f^+(\rho)-f^-(\rho)\rho_-. \tag{3.26b}$$

Adding Eqs. (3.22a) and (3.22b), we obtain

$$\frac{\partial\rho}{\partial t}+\gamma\frac{\partial j}{\partial x}=F(\rho). \tag{3.27}$$

Subtracting Eq. (3.22b) from Eq. (3.22a), we obtain

$$\frac{\partial j}{\partial t}+\gamma\frac{\partial\rho}{\partial x}=-[2\mu+(1-2\kappa)f^+(\rho)+f^-(\rho)]j. \tag{3.28}$$

For RCRWs with $\kappa=1/2$, which are called direction-independent reaction walks (DIRWs) [64,65], the last equation reduces to

$$\frac{\partial j}{\partial t}+\gamma\frac{\partial\rho}{\partial x}=-[2\mu+f^-(\rho)]j. \tag{3.29}$$

Note that Eqs. (3.27) and (3.28) do not form a RCS for any value of κ due to the contributions from the kinetics to the decay rate of the flow j.

IV. DYNAMICS OF SPATIALLY UNIFORM STATES

If the density is spatially uniform, then the dispersal process does not contribute to the evolution of the density. We expect therefore that the dynamics of spatially constant states should be described by the rate equation of the lumped system (2.8). In this section we consider finite systems, $x\in[0,L]$, with no-flow boundary conditions. We study the dynamics of spatially uniform states for the various hyperbolic reaction-transport equations and determine the instability thresholds of uniform steady states.

A. Hyperbolic reaction-diffusion equation

If the density of the system is uniform, then the HRDE (2.1) reduces to

$$\tau\frac{d^2\rho}{dt^2}+\frac{d\rho}{dt}=F(\rho), \tag{4.1}$$

which differs from the rate equation of the lumped system (2.8). The uniform steady states of the HRDE (2.1) are given by $\bar\rho(x)=\bar\rho$, where

$$F(\bar\rho)=0, \tag{4.2}$$

and coincide with the stationary states of the lumped system (2.8). The latter are stable if

$$F'(\bar\rho)<0. \tag{4.3}$$

We determine the stability of the uniform steady states of the HRDE (2.1) via a linear stability analysis. Let $\delta\rho(x,t)$ be a small perturbation of the uniform steady state $\bar\rho$,

$$\rho(x,t)=\bar\rho+\delta\rho(x,t). \tag{4.4}$$

The perturbations obey the linearized evolution equation

$$\tau\frac{\partial^2\delta\rho}{\partial t^2}+\frac{\partial\delta\rho}{\partial t}=D\frac{\partial^2\delta\rho}{\partial x^2}+F'(\rho)\delta\rho. \tag{4.5}$$

We write the small perturbation as

$$\delta\rho(x,t)=\sum_k a_k\psi_k(x)\exp(\lambda_k t), \tag{4.6}$$

where the spatial modes $\psi_k(x)$ satisfy

$$\frac{d^2\psi_k(x)}{dx^2}=-k^2\psi_k(x) \tag{4.7}$$

with no-flow boundary conditions. The growth rates λ_k of the spatial modes $\psi_k(x)$ are given by the characteristic equation

$$\lambda_k^2 + \frac{1}{\tau}\lambda_k + \frac{1}{\tau}[Dk^2 - F'(\bar{\rho})] = 0. \tag{4.8}$$

We write this equation as

$$\lambda_k^2 - T_k\lambda_k + \Delta_k = 0, \tag{4.9}$$

with

$$T_k = -\frac{1}{\tau}, \tag{4.10}$$

$$\Delta_k = \frac{1}{\tau}[Dk^2 - F'(\bar{\rho})]. \tag{4.11}$$

The roots of Eq. (4.9) are given by

$$\lambda_k = \tfrac{1}{2}\left[T_k \pm \sqrt{T_k^2 - 4\Delta_k}\right] \tag{4.12}$$

and have a negative real part if

$$T_k < 0, \tag{4.13a}$$

$$\Delta_k > 0. \tag{4.13b}$$

If the conditions (4.13) are satisfied for all k, then perturbations with any wave number decay and the uniform steady state $\bar{\rho}$ of the HRDE is stable. Since T_k is always negative, the stability is determined by Δ_k. If the stationary state of the lumped system (2.8) is stable, i.e., $F'(\bar{\rho}) < 0$, then Δ_k is positive. In other words, the uniform steady state $\bar{\rho}$ is stable against perturbations with any wave number k. If the stationary state of the lumped system (2.8) becomes unstable, i.e., $F'(\bar{\rho})$ goes through zero and becomes positive, then Δ_0 will go through zero and become negative. In other words, the uniform steady state $\bar{\rho}$ of the HRDE becomes unstable against uniform perturbations, $k = 0$. This implies not only that the uniform steady states of Eq. (2.1) coincide with those of the lumped system (2.8), but also that their instability thresholds are exactly the same. However, the temporal evolution of the uniform states of the HRDE differs from that given by the rate equation of the lumped system (2.8).

B. Reaction-Cattaneo system

For uniform states, $(\rho(x,t), J(x,t)) \equiv (\rho(t), J(t))$, Eqs. (3.3) and (3.5) of the RCS reduce to

$$\frac{d\rho}{dt} = F(\rho), \tag{4.14a}$$

$$\frac{dJ}{dt} = -\frac{1}{\tau}J. \tag{4.14b}$$

The evolution equations for the density and flow decouple for uniform states, and the flow relaxes to zero with the inertial time τ. Since we consider the system on a finite interval with no-flow boundary conditions, the flow vanishes for all times, $J(t) \equiv 0$. The temporal evolution of the density for a uniform RCS (4.14a) is identical with the one for the lumped system (2.8).

The uniform steady states of the RCS (2.2) are given by $(\bar{\rho}(x), \bar{J}(x)) = (\bar{\rho}, 0)$ with $F(\bar{\rho}) = 0$. Perturbations around the uniform steady state $(\bar{\rho}, 0)$ obey the linearized evolution equations

$$\frac{\partial\delta\rho}{\partial t} = -\frac{\partial\delta J}{\partial x} + F'(\rho)\delta\rho, \tag{4.15a}$$

$$\tau\frac{\partial\delta J}{\partial t} = -\delta J - D\frac{\partial\delta\rho}{\partial x}. \tag{4.15b}$$

For the spatial mode with wave number k, we find

$$\lambda_k\delta\rho_k = -\frac{d\delta J_k}{dx} + F'(\rho)\delta\rho_k, \tag{4.16a}$$

$$\tau\lambda_k\delta J_k = -\delta J_k - D\frac{d\delta\rho_k}{dx}. \tag{4.16b}$$

Differentiating the first equation with respect to x, using the second equation to eliminate $d\delta\rho_k/dx$, and using $d^2\delta J_k/dx^2 = -k^2\delta J_k$, we obtain the characteristic equation

$$\lambda_k^2 + \frac{1}{\tau}[1 - \tau F'(\bar{\rho})]\lambda_k + \frac{1}{\tau}[Dk^2 - F'(\bar{\rho})] = 0. \tag{4.17}$$

We read off that

$$T_k = \frac{1}{\tau}[\tau F'(\bar{\rho}) - 1], \tag{4.18}$$

$$\Delta_k = \frac{1}{\tau}[Dk^2 - F'(\bar{\rho})]. \tag{4.19}$$

If the stationary state $\bar{\rho}$ of the lumped system (2.8) is stable, $F'(\bar{\rho}) < 0$, then $T_k < 0$ and $\Delta_k > 0$ for all k. In other words, the uniform steady state $(\bar{\rho},0)$ of the RCS (2.2) is stable against perturbations with any wave number. If the stationary state of the lumped system (2.8) becomes unstable, i.e., $F'(\bar{\rho})$ goes through zero and becomes positive, then Δ_0 will go through zero and become negative. In other words, the uniform steady state $(\bar{\rho},0)$ of the RCS becomes unstable against uniform perturbations, $k = 0$.

In summary, the temporal evolution of the density for a uniform RCS is identical with the one of the lumped system (2.8). Also, the instability thresholds of the uniform steady states of the RCS, $(\bar{\rho},0)$, coincide with the instability thresholds of the stationary states of the lumped system (2.8).

C. Reaction-telegraph equation

If the density of the system is uniform, then the RTE reduces to

$$\tau\frac{d^2\rho}{dt^2} + [1 - \tau F'(\rho)]\frac{d\rho}{dt} = F(\rho). \tag{4.20}$$

We define a new variable,

$$\xi = \frac{d\rho}{dt} - F(\rho). \tag{4.21}$$

Differentiating $\xi(t)$ with respect to time, we obtain

$$\frac{d\xi}{dt} = \frac{d^2\rho}{dt^2} - F'(\rho)\frac{d\rho}{dt}, \tag{4.22}$$

which allows us to rewrite (4.20) in the form

$$\tau\frac{d\xi}{dt} + \xi = 0. \tag{4.23}$$

The solution of (4.23) is given by

$$\xi(t) = \xi(0)\exp(-t/\tau), \tag{4.24}$$

which in light of Eq. (4.21) implies

$$\frac{d\rho}{dt} = F(\rho) + \xi(0)\exp(-t/\tau). \tag{4.25}$$

In other words, the uniform RTE (4.20) relaxes to the rate equation of the lumped (2.8) with the characteristic inertial time of the flux. Except for an initial boundary layer, the temporal evolutions of Eqs. (4.20) and (2.8) are identical. The existence of the boundary layer $t \lessapprox \tau$ is due to the somewhat different notion of uniformity for RCSs and RTEs. For a RCS with no-flow boundary conditions, uniformity implies that $\rho(x,t) \equiv \rho(t)$ and $J(x,t) \equiv 0$. Since the flux has been eliminated as a variable in the RTE description, uniformity simply corresponds to $\rho(x,t) \equiv \rho(t)$; there is no control over the flux. As is clear from Eq. (3.5), any nonvanishing flux will decay with a characteristic time τ.

The uniform steady states of the RTE (2.3) are given by $\bar{\rho}(x) = \bar{\rho}$ with $F(\bar{\rho}) = 0$. The characteristic equation for the growth rates of spatial perturbations with wave number k coincides with Eq. (4.17). Consequently, not only do the uniform steady states of the RTE (2.3) coincide with those of the lumped system (2.8), but also their instability thresholds are exactly the same. Furthermore, the evolution equation for uniform densities reduces to the rate equation of the lumped system (2.8) after an initial boundary layer.

D. Modified hyperbolic reaction-diffusion equation

If the density of the system is uniform, then the mHRDE reduces to

$$\tau\frac{d^2\rho}{dt^2} + \frac{d\rho}{dt} = F(\rho) + \tau F'(\rho)F(\rho). \tag{4.26}$$

The temporal evolution for spatially uniform states differs from that of the lumped system (2.8). This is inconsistent with Eq. (3.10), used in the derivation of the mHRDE, which assumes that the contribution from growth processes is given by Eq. (2.8).

The uniform steady states of the mHRDE are given by

$$F(\bar{\rho}) + \tau F'(\bar{\rho})F(\bar{\rho}) = 0, \tag{4.27}$$

which implies that either

$$F(\bar{\rho}) = 0, \tag{4.28}$$

or

$$1 + \tau F'(\bar{\rho}) = 0. \tag{4.29}$$

The uniform steady states given by Eq. (4.28) coincide with the stationary states of the lumped system. However, Eq. (4.29) leads potentially to additional uniform steady states. Consider, for example, the case of logistic growth,

$$F(\rho) = r\rho\left(1 - \frac{\rho}{K}\right), \tag{4.30}$$

where r and K are positive parameters. Then the solutions of Eq. (4.28) are given by

$$\bar{\rho}_1 = 0, \tag{4.31}$$

$$\bar{\rho}_2 = K, \tag{4.32}$$

which are the usual steady states of logistic growth; namely, extinction and saturation at the carrying capacity K. For the mHRDE, Eq. (4.29) reads

$$1 + \tau r\left(1 - 2\frac{\bar{\rho}}{K}\right) = 0, \tag{4.33}$$

which leads to the extraneous uniform steady state

$$\bar{\rho}_3 = \frac{K(1+\tau r)}{2\tau r}. \tag{4.34}$$

Small perturbations to the uniform steady state of the mHRDE, $\bar{\rho}(x) = \bar{\rho}$, with $\bar{\rho}$ given either by Eq. (4.28) or by Eq. (4.29), obey the linearized evolution equation

$$\tau\frac{\partial^2\delta\rho}{\partial t^2} + \frac{\partial\delta\rho}{\partial t} = D\frac{\partial^2\delta\rho}{\partial x^2} + [F'(\bar{\rho}) + \tau F'(\bar{\rho})^2 + \tau F''(\bar{\rho})F(\bar{\rho})]\delta\rho. \tag{4.35}$$

The characteristic equation is given by

$$\lambda_k^2 + \frac{1}{\tau}\lambda_k - \frac{1}{\tau}\{F'(\bar{\rho})[1+\tau F'(\bar{\rho})] + \tau F''(\bar{\rho})F(\bar{\rho}) - Dk^2\} = 0. \tag{4.36}$$

We read off that

$$T_k = -\frac{1}{\tau}, \tag{4.37}$$

$$\Delta_k = -\frac{1}{\tau}\{F'(\bar{\rho})[1+\tau F'(\bar{\rho})] + \tau F''(\bar{\rho})F(\bar{\rho}) - Dk^2\}. \tag{4.38}$$

Since T_k is always negative, the stability is determined by Δ_k. For the uniform steady states given by Eq. (4.28), i.e., those that coincide with the steady states of the lumped system (2.8), we find

$$\Delta_k = -F'(\bar{\rho})\left[\frac{1}{\tau} + F'(\bar{\rho})\right] + \frac{1}{\tau}Dk^2. \tag{4.39}$$

If the steady state $\bar{\rho}$ of (2.8) is unstable, i.e., $F'(\bar{\rho}) > 0$, then Δ_0 is negative and $\bar{\rho}$ is also an unstable steady state of Eq. (2.4). If the steady state $\bar{\rho}$ of Eq. (2.8) is stable, i.e., $F'(\bar{\rho}) < 0$, then it is a stable steady state of Eq. (2.4) only if

$$-\frac{1}{\tau} < F'(\bar{\rho}) < 0, \tag{4.40}$$

i.e., only if the inertial time τ is smaller than the characteristic kinetic time $-1/F'(\bar{\rho})$. Otherwise, there exists a k_c such that Δ_k is negative for $k \leqslant k_c$. While $\bar{\rho}$ is a stable steady state of Eq. (2.8), it is an unstable steady state of Eq. (2.4). In other words, the instability thresholds of those steady states common to the lumped system and the mHRDE are not identical.

For the extraneous steady states given by Eq. (4.29) we find

$$\Delta_k = -F''(\bar{\rho})F(\bar{\rho}) + \frac{1}{\tau}Dk^2. \tag{4.41}$$

The extraneous steady states are stable, $\Delta_k > 0$ for all k, if $F(\bar{\rho})$ and $F''(\bar{\rho})$ have the opposite sign.

For logistic growth

$$F''(\rho) = -\frac{2r}{K}, \tag{4.42}$$

and the extraneous uniform steady state $\bar{\rho}_3$ is stable if $F(\bar{\rho}_3) > 0$, which is true if

$$\frac{1}{\tau} < r. \tag{4.43}$$

Since $F'(\bar{\rho}_2) = -r$, Eqs. (4.40) and (4.43) imply that the two steady states $\bar{\rho}_2$ and $\bar{\rho}_3$ exchange stability at $r_c = 1/\tau$. Note that, for $r > 1/\tau$, the stable nontrivial uniform steady state lies below the carrying capacity K.

The evolution equation for spatially uniform states of the mHRDE (2.4) differs from the rate equation (2.8) for lumped systems. Further, the instability thresholds of the steady states in common with those of the lumped system can differ, and there may be extraneous homogeneous steady states.

E. Reaction correlated random walk system

If the state of the system is uniform, $\rho_+(x,t) \equiv \rho_+(t)$ and $\rho_-(x,t) \equiv \rho_-(t)$, then the RCRW (2.5) reduces to

$$\frac{d\rho_+}{dt} = \mu(\rho_- - \rho_+) + F_+(\rho_+,\rho_-), \tag{4.44a}$$

$$\frac{d\rho_-}{dt} = \mu(\rho_+ - \rho_-) + F_-(\rho_+,\rho_-). \tag{4.44b}$$

According to Eqs. (3.27) and (3.28), the evolution of the total density ρ is given by the rate equation of the lumped system (2.8),

$$\frac{d\rho}{dt} = \rho f^+(\rho) - \rho f^-(\rho) = F(\rho), \tag{4.45}$$

and the evolution equation for the flow j is given by

$$\frac{dj}{dt} = -[2\mu + (1-2\kappa)f^+(\rho) + f^-(\rho)]j. \tag{4.46}$$

Note that the evolution equation for the flow is coupled to the density, in contrast to RCSs.

Equations (4.45) and (4.46) imply that the uniform steady states of the RCRW are given by $(\bar{\rho}(x), \bar{j}(x)) = (\bar{\rho},0)$ or $(\bar{\rho}_+(x), \bar{\rho}_-(x)) = (\bar{\rho}/2, \bar{\rho}/2)$, where $\bar{\rho}$ is determined by

$$F(\bar{\rho}) = F^+(\bar{\rho}) - F^-(\bar{\rho}) = \bar{\rho}[f^+(\bar{\rho}) - f^-(\bar{\rho})] = 0. \tag{4.47}$$

In other words, the total density of the uniform steady states of the RCRW coincides with the density of the stationary states of the lumped system (2.8).

Perturbations around the uniform steady state $(\bar{\rho},0)$ obey the linearized evolution equations

$$\frac{\partial \delta\rho}{\partial t} + \gamma\frac{\partial \delta j}{\partial x} = F'(\bar{\rho})\delta\rho, \tag{4.48a}$$

$$\frac{\partial \delta j}{\partial t} + \gamma\frac{\partial \delta\rho}{\partial x} = -[2\mu + (1-2\kappa)f^+(\bar{\rho}) + f^-(\bar{\rho})]\delta j. \tag{4.48b}$$

The corresponding characteristic equation is given by

$$0 = \lambda_k^2 + [2\mu + (1-2\kappa)f^+(\bar{\rho}) + f^-(\bar{\rho}) - F'(\bar{\rho})]\lambda_k + \gamma^2 k^2 - F'(\bar{\rho})[2\mu + (1-2\kappa)f^+(\bar{\rho}) + f^-(\bar{\rho})], \tag{4.49}$$

and

$$T_k = -\beta + F'(\bar{\rho}), \tag{4.50}$$

$$\Delta_k = \gamma^2 k^2 - F'(\bar{\rho})\beta, \tag{4.51}$$

with

$$\beta = 2\mu + (1-2\kappa)f^+(\bar{\rho}) + f^-(\bar{\rho}). \tag{4.52}$$

If $\bar{\rho}$ of the lumped system (2.8) is stable, $F'(\bar{\rho})$ is negative. Then T_k will be negative, if β is nonnegative. If $\kappa \leqslant 1/2$, all three terms of β are nonnegative, and T_k is negative. If $\kappa > 1/2$, the second term of β is negative, and T_k could become positive. Let κ_c be the value of κ where the sign of β changes from negative to positive:

$$\kappa_c = \frac{2\mu + f^+(\bar{\rho}) + f^-(\bar{\rho})}{2f^+(\bar{\rho})}. \tag{4.53}$$

If $\bar{\rho} \neq 0$, then $f^+(\bar{\rho}) = f^-(\bar{\rho})$, and

$$\kappa_c = \frac{\mu + f^+(\bar{\rho})}{f^+(\bar{\rho})} > 1. \tag{4.54}$$

Since κ must lie in the interval $[0,1]$, clearly β is always positive and T_k is always negative for stable nontrivial uniform steady states of the RCRW (2.5). If the kinetics have a trivial steady state, i.e., if $F^+(0) = 0$, then

$$\kappa_c = \frac{2\mu + f^+(0) + f^-(0)}{2f^+(0)}. \tag{4.55}$$

The trivial steady state is a stable steady state of the lumped system (2.8) if $F'(0) < 0$, which is equivalent to $f^-(0) > f^+(0)$. Consequently, if $F'(0) < 0$, then

$$\kappa_c = \frac{2\mu + f^+(0) + f^-(0)}{2f^+(0)} > \frac{2\mu + 2f^+(0)}{2f^+(0)} > 1. \tag{4.56}$$

In other words, β is always nonnegative and T_k is always negative for stable trivial uniform steady states of the RCRW (2.5). Consequently, the stability of the uniform steady states of the RCRW (2.5) is determined by Δ_k. If $F'(\bar{\rho}) < 0$, then Eq. (4.51) implies that Δ_k is positive for all k, i.e., the uniform steady state is stable against perturbations with any wave number. If the steady state of the lumped system is unstable, $F'(\bar{\rho}) > 0$, then Δ_0 is negative and the uniform steady state is unstable against spatially constant perturbations. In conclusion, the primary bifurcation threshold is determined by the sign change of $F'(\bar{\rho})$. The evolution equation for uniform densities of the RCRW (2.5) is identical with the rate equation of the lumped system (2.8). Furthermore, steady states of Eq. (2.8) and their instability threshold coincide exactly with those of the uniform steady states of the RCRW.

V. PURE DEATH PROCESS

If only a pure death process occurs in the system, i.e., the kinetic rate term corresponds to first-order decay, then extinction should be the final outcome. The density should go to zero for large times.

A. Hyperbolic reaction-diffusion equation

We consider a system with $F(\rho) = -r\rho$, where $r > 0$ is a constant death rate, on the interval $[0,L]$ with no-flow

boundary conditions,

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}-r\rho, \tag{5.1}$$

$$\left.\frac{\partial\rho}{\partial x}\right|_{x=0}=\left.\frac{\partial\rho}{\partial x}\right|_{x=L}=0. \tag{5.2}$$

The set

$$\psi_n(x)=\begin{cases}1/\sqrt{L} & \text{for } n=0\\ \sqrt{2/L}\cos(k_n x) & \text{for } n=1,2,3,\ldots,\end{cases} \tag{5.3}$$

with $x\in[0,L]$ and $k_n=n\pi/L$ forms a complete orthonormal set of eigenfunctions of the diffusion operator that obey no-flow boundary conditions. We write $\rho(x,t)$ as a Fourier series

$$\rho(x,t)=\sum_{n=0}^{\infty}c_n(t)\psi_n(x). \tag{5.4}$$

We have obtained the eigenvalues of the linear HRDE in the previous Sec. IV A; namely,

$$\lambda_n=\tfrac{1}{2}\left[T_{k_n}\pm\sqrt{T_{k_n}^2-4\Delta_{k_n}}\right], \tag{5.5}$$

with

$$T_{k_n}=-\frac{1}{\tau}, \tag{5.6}$$

$$\Delta_{k_n}=\frac{1}{\tau}\left[r+Dk_n^2\right], \tag{5.7}$$

for the HRDE of a pure death process. Thus the dispersion relation reads

$$\lambda_{n;1,2}=\frac{1}{2\tau}\left[-1\pm\sqrt{1-4\tau\left(r+Dk_n^2\right)}\right]. \tag{5.8}$$

The coefficients in the Fourier series are given by

$$c_n(t)=c_{n;1}\exp(\lambda_{n;1}t)+c_{n;2}\exp(\lambda_{n;2}t), \tag{5.9}$$

where $c_{n;1}$ and $c_{n;2}$ are determined by the initial conditions. The eigenvalues are real and negative for modes with

$$r+Dk_n^2<\frac{1}{4\tau}, \tag{5.10}$$

and are complex conjugate with a negative real part otherwise. Consequently, all coefficients $c_n(t)$ decay to zero and $\rho(x,t)\to 0$ for all $x\in[0,L]$ for $t\to\infty$. Long-wavelength modes decay monotonically, and short-wavelength modes decay in an oscillatory manner. Note that all modes decay monotonically in a standard reaction-diffusion system (2.9) with first-order decay. It is the inertia in the transport that gives rise to the oscillatory decay of short-wavelength modes.

B. Reaction-Cattaneo system

The RCS for the pure death process reads

$$\frac{\partial\rho}{\partial t}=-\frac{\partial J}{\partial x}-r\rho, \tag{5.11a}$$

$$\tau\frac{\partial J}{\partial t}=-J-D\frac{\partial\rho}{\partial x}, \tag{5.11b}$$

$$J(0,t)=J(L,t)=0. \tag{5.11c}$$

The set

$$\phi_n(x)=\sqrt{2/L}\sin(k_n x),\quad n=1,2,3,\ldots \tag{5.12}$$

with $x\in[0,L]$ and $k_n=n\pi/L$ forms a complete orthonormal set with $\phi_n(0)=\phi_n(L)=0$. Evaluating Eq. (5.11b) at $x=0$ and $x=L$, we find that

$$\left.\frac{\partial\rho}{\partial x}\right|_{x=0}=\left.\frac{\partial\rho}{\partial x}\right|_{x=L}=0, \tag{5.13}$$

and we can write $\rho(x,t)$ and $J(x,t)$ as the Fourier series

$$\rho(x,t)=\sum_{n=0}^{\infty}c_n(t)\psi_n(x), \tag{5.14}$$

$$J(x,t)=\sum_{n=1}^{\infty}b_n(t)\phi_n(x). \tag{5.15}$$

The eigenvalues of the linear RCS are given by Eq. (5.5), with

$$T_{k_n}=-\frac{1}{\tau}-r, \tag{5.16}$$

$$\Delta_{k_n}=\frac{1}{\tau}\left[r+Dk_n^2\right]; \tag{5.17}$$

see Sec. IV B. This results in the following dispersion relation for the RCS of a pure death process:

$$\lambda_{n;1,2}=\frac{1}{2\tau}\left[-1-r\tau\pm\sqrt{(1-r\tau)^2-4Dk_n^2\tau}\right]. \tag{5.18}$$

The eigenvalues are real and negative for modes with

$$Dk_n^2<\frac{(1-r\tau)^2}{4\tau}, \tag{5.19}$$

and complex conjugate with a negative real part otherwise. Consequently, all coefficients $c_n(t)$ and $b_n(t)$ decay to zero and $(\rho(x,t),J(x,t))\to(0,0)$ for all $x\in[0,L]$ for $t\to\infty$. Again, long-wavelength modes decay monotonically and short-wavelength modes display damped oscillations.

C. Reaction-telegraph equation

The RTE for a pure death process on the interval $[0,L]$ with no-flow boundary conditions reads

$$\tau\frac{\partial^2\rho}{\partial t^2}+[1+\tau r]\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}-r\rho, \tag{5.20}$$

$$\left.\frac{\partial\rho}{\partial x}\right|_{x=0}=\left.\frac{\partial\rho}{\partial x}\right|_{x=L}=0. \tag{5.21}$$

We write $\rho(x,t)$ again as the Fourier series (5.4). The dispersion relation is identical with Eq. (5.18) for the pure death RCS. Consequently, all coefficients $c_n(t)$ decay to zero and $\rho(x,t)\to 0$ for all $x\in[0,L]$ for $t\to\infty$.

D. Modified hyperbolic reaction-diffusion equation

The mHRDE for a pure death process on the interval $[0,L]$ with no-flow boundary conditions reads

$$\tau\frac{\partial^2\rho}{\partial t^2}+\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}-r[1-\tau r]\rho, \tag{5.22}$$

$$\left.\frac{\partial\rho}{\partial x}\right|_{x=0}=\left.\frac{\partial\rho}{\partial x}\right|_{x=L}=0. \tag{5.23}$$

We write $\rho(x,t)$ again as the Fourier series (5.4). The eigenvalues of the linear mHRDE are given by Eq. (5.5), with

$$T_{k_n} = -\frac{1}{\tau}, \tag{5.24}$$

$$\Delta_{k_n} = \frac{1}{\tau}\left[r(1-\tau r) + Dk_n^2\right]; \tag{5.25}$$

see Sec. IV D. This results in the following dispersion relation for the mHRDE of a pure death process:

$$\lambda_{n;1,2} = \frac{1}{2\tau}\left[-1 \pm \sqrt{1 - 4Dk_n^2\tau - 4r\tau + 4r^2\tau^2}\right]. \tag{5.26}$$

The Fourier coefficients are given by

$$c_n(t) = c_{n;1}\exp(\lambda_{n;1}t) + c_{n;2}\exp(\lambda_{n;2}t). \tag{5.27}$$

Let $c_{n0} = c_n(0)$ and $C_{n0} = \dot{c}_n(0)$. Then

$$c_n(0) = c_{n;1} + c_{n;2} = c_{n0}, \tag{5.28}$$

$$\dot{c}_n(0) = \lambda_{n;1}c_{n;1} + \lambda_{n;2}c_{n;2} = C_{n0}, \tag{5.29}$$

which implies

$$c_{n;2} = c_{n0} - c_{n;1}, \tag{5.30}$$

$$c_{n;1} = \frac{C_{n0} - \lambda_{n;2}c_{n0}}{\lambda_{n;1} - \lambda_{n;2}}. \tag{5.31}$$

Note that $\lambda_{n;1}$ goes through zero at

$$\tau_{c,n} = \frac{Dk_n^2 + r}{r^2} \tag{5.32}$$

and is positive for $\tau > \tau_{c,n}$. The nth mode becomes unstable if τ is too large. The first mode to go unstable is the homogeneous mode, $n = 0$, at $\tau = 1/r$. It follows from Eq. (5.31) that $\rho(x,t)$ will go to $\pm\infty$ unless $C_{n0} = \lambda_{n;2}c_{n0}$ for all n. In other words, the solution of the mHRDE either explodes for a pure death process or becomes negative for almost all initial conditions, unless τ is sufficiently small. Such a result is unphysical, and the pathological behavior of the mHRDE arises from the term $F'(\rho)F(\rho)$. It changes the nature of the total kinetic term $F(\rho) + \tau F'(\rho)F(\rho) = -r[1-\tau r]\rho$ from a net loss term for small τ to a net production term for $\tau > \tau_{c,0}$.

E. Reaction correlated random walk system

The RCRW for the pure death process reads

$$\frac{\partial\rho}{\partial t} + \gamma\frac{\partial j}{\partial x} = -r\rho, \tag{5.33a}$$

$$\tau\frac{\partial j}{\partial t} + \gamma\frac{\partial\rho}{\partial x} = -[2\mu + r]j, \tag{5.33b}$$

$$j(0,t) = j(L,t) = 0. \tag{5.33c}$$

Proceeding as in Sec. V B, we write $\rho(x,t)$ and $j(x,t)$ as the Fourier series

$$\rho(x,t) = \sum_{n=0}^{\infty} c_n(t)\psi_n(x), \tag{5.34}$$

$$j(x,t) = \sum_{n=1}^{\infty} b_n(t)\phi_n(x). \tag{5.35}$$

The eigenvalues of the linear RCRW are given by Eq. (5.5), with

$$T_{k_n} = -2(\mu + r), \tag{5.36}$$

$$\Delta_{k_n} = r(2\mu + r) + \gamma^2 k_n^2; \tag{5.37}$$

see Sec. IV E. This results in the following dispersion relation for the RCRW of a pure death process:

$$\lambda_{n;1,2} = -(\mu + r) \pm \sqrt{\mu^2 - \gamma^2 k_n^2}. \tag{5.38}$$

The eigenvalues are real and negative for modes with

$$\gamma^2 k_n^2 < \mu^2, \tag{5.39}$$

and complex conjugate with a negative real part otherwise. Consequently, all coefficients $c_n(t)$ and $b_n(t)$ decay to zero and $(\rho(x,t), j(x,t)) \to (0,0)$ for all $x \in [0,L]$ for $t \to \infty$.

While most hyperbolic evolution equations do not preserve positivity, the RCRW (2.5) does. This can be seen by the following heuristic argument. For a more detailed mathematical discussion, see Refs. [33,66]. Let $\rho_\pm(x,0) > 0$ and let $x_\pm$ be the point where the density first attains 0 at time $t_\pm$. Since the density $\rho_\pm(x,t)$ must be a continuous and differentiable function, it must have a minimum at that point, i.e.,

$$\left.\frac{\partial\rho_\pm(x,)}{\partial x}\right|_{x=x_\pm} = 0, \tag{5.40}$$

and consequently

$$\left.\frac{\partial\rho_+(x_+,t)}{\partial t}\right|_{t=t_+} = \mu\rho_- + F_+(0,\rho_-), \tag{5.41a}$$

$$\left.\frac{\partial\rho_-(x_-,t)}{\partial t}\right|_{t=t_-} = \mu\rho_+ + F_-(\rho_+,0). \tag{5.41b}$$

Therefore, RCRWs will preserve positivity, if the right-hand side of Eqs. (5.41a) and (5.41b) is nonnegative, which is guaranteed if the rate terms $F_\pm(\rho_+,\rho_-)$ are proper kinetic functions, i.e., in analogy to Eq. (2.7),

$$F_+(0,\rho_-) \geqslant 0, \quad F_-(\rho_+,0) \geqslant 0. \tag{5.42}$$

RCRWs with proper kinetic terms, such as DIRWs, for example, preserve positivity.

VI. FRONT SPEED

The propagation of a front corresponding to the invasion of an unstable stationary state by a stable stationary state has been investigated via various methods for reaction-transport equations. For HRDEs, front propagation has been studied analytically and numerically [40–45]. Abi Mansour and Al-Ghoul analyzed the propagation of reaction fronts for RCSs with reactions of the type $n\mathrm{A} + m\mathrm{B} \to k\mathrm{C}$ [72]. Front propagation in RTEs was investigated in Refs. [29,31,32,73–77], and traveling waves for isotropic reaction walks were studied in Refs. [15,70] and for DIRWs in Refs. [19,65].

We present a unified approach to front propagation in the five types of reaction-transport system (2.1)–(2.5). To determine the speed of invasion into the unstable state $\bar{\rho} = 0$, we employ hyperbolic scaling and large deviation theory to obtain the Hamilton–Jacobi equation for the front position.

Equations (2.1), (2.3), and (2.4) can be rewritten in more general form as

$$\tau\frac{\partial^2\rho}{\partial t^2}+\Phi(\rho)\frac{\partial\rho}{\partial t}=D\frac{\partial^2\rho}{\partial x^2}+\Psi(\rho). \tag{6.1}$$

Substituting the hyperbolic scaling $x\to x/\varepsilon$ and $t\to t/\varepsilon$ into Eq. (6.1) we obtain

$$\tau\varepsilon^2\frac{\partial^2\rho^\varepsilon}{\partial t^2}+\varepsilon\Phi(\rho^\varepsilon)\frac{\partial\rho^\varepsilon}{\partial t}=D\varepsilon^2\frac{\partial^2\rho^\varepsilon}{\partial x^2}+\Psi(\rho^\varepsilon), \tag{6.2}$$

where $\rho^\varepsilon(x,t)=\rho(x/\varepsilon,t/\varepsilon)$. Introducing in Eq. (6.2) the new field $G^\varepsilon(x,t)$, defined as in the Wenzel–Kramers–Brillouin (WKB) ansatz $\rho^\varepsilon(x,t)=\exp[-G^\varepsilon(x,t)/\varepsilon]$ with $G^\varepsilon(x,t)\geqslant 0$, and performing the asymptotic limit $\varepsilon\to 0$, we obtain the relativistic Hamilton–Jacobi equation

$$\tau\left(\frac{\partial G}{\partial t}\right)^2-\Phi(0)\frac{\partial G}{\partial t}=D\left(\frac{\partial G}{\partial x}\right)^2+\sigma. \tag{6.3}$$

This equation, with $\Phi(0)=1$ was already obtained in Ref. [78]. The limiting function $G(x,t)$ corresponds to $G(x,t)=\lim_{\varepsilon\to 0}G^\varepsilon(x,t)$ and $\rho^\varepsilon(x,t)=\exp[-G^\varepsilon(x,t)/\varepsilon]\to 0$ as $\varepsilon\to 0$. The constant σ is given by

$$\sigma=\lim_{\varepsilon\to 0}\frac{\Psi(\rho^\varepsilon)}{\rho^\varepsilon}=\Psi'(0), \tag{6.4}$$

where the prime denotes the derivative with respect to the argument. We assume the kinetic rate function to be of the Kolmogorov–Petrosvskii–Piskunov (KPP) type, i.e., $F\in C^1[0,\bar\rho]$, $F(0)=F(\bar\rho)=0$, $F'(0)>0$, $F'(\bar\rho)<0$, and $0<F(\rho)\leqslant F'(0)\rho$ for $\rho\in(0,\bar\rho)$. Then the parameter σ is a nonzero constant for all cases. Equation (6.3) for $G(x,t)$ can be regarded as a Hamilton–Jacobi equation, and its solution can be written as $G(x,t)=px-H(p)t$, where $p=\partial G/\partial x$ and $H=-\partial G/\partial t$. The location of the front is determined by the equation $G(x,t)=0$, so that

$$v=\frac{dx}{dt}=\min_H\frac{H}{p(H)}. \tag{6.5}$$

From Eqs. (6.3) and (6.5) the front speed is given by

$$v=\min_H\frac{H\sqrt{D}}{\sqrt{\tau H^2+\Phi(0)H-\Psi'(0)}}=\begin{cases}\frac{2\sqrt{\Psi'(0)D}}{\sqrt{4\tau\Psi'(0)+\Phi(0)^2}}, & \Phi(0)\geqslant 0\ \text{(diffusive regime)}\\ \sqrt{D/\tau}, & \Phi(0)\leqslant 0\ \text{(ballistic speed).}\end{cases} \tag{6.6}$$

For the following we define $r=F'(0)$.

A. Hyperbolic reaction-diffusion equation

For HRDEs we have $\Phi(0)=1$ and $\Psi(\rho)=F(\rho)$. Equation (6.6) implies for this case,

$$v_{\mathrm{HRDE}}=\frac{2\sqrt{rD}}{\sqrt{4\tau r+1}}<\sqrt{D/\tau}, \tag{6.7}$$

and the front speed never reaches the ballistic speed.

B. Reaction-telegraph equation

For RTEs we have $\Phi(0)=1-\tau r$ and $\Psi(\rho)=F(\rho)$. The front speed is given by Eq. (6.6),

$$v_{\mathrm{RTE}}=\begin{cases}\frac{2\sqrt{rD}}{1+r\tau}, & r\leqslant 1/\tau\ \text{(diffusive regime)}\\ \sqrt{D/\tau}, & r\geqslant 1/\tau\ \text{(ballistic speed).}\end{cases} \tag{6.8}$$

In this case the front can propagate with the ballistic speed if the inertial time τ is larger than or equal to the characteristic kinetic time $1/r$, due to the presence of the term (3.7), which is missing in the HRDE and mHRDE.

C. Modified hyperbolic reaction-diffusion equation

For mHRDEs we have $\Phi(0)=1$, $\Psi(\rho)=F(\rho)[1+\tau F'(\rho)]$ and the front speed is given by Eq. (6.6),

$$v_{\mathrm{mHRDE}}=\frac{2\sqrt{rD(1+\tau r)}}{1+2r\tau}<\sqrt{D/\tau}. \tag{6.9}$$

As for the HRDE, the front speed never reaches the ballistic speed.

D. Reaction-Cattaneo system

The front speed for the RCS (2.2a)–(2.2b) is the same as in Eq. (6.8). To see this, we introduce the hyperbolic scaling and the new fields $\rho^\varepsilon(x,t)=A_1\exp[-G^\varepsilon(x,t)/\varepsilon]$ and $J^\varepsilon(x,t)=A_2\exp[-G^\varepsilon(x,t)/\varepsilon]$ in Eqs. (2.2a)–(2.2b) and find the characteristic equation,

$$\begin{vmatrix}H-r & p\\ Dp & 1+H\tau\end{vmatrix}=(H-r)(1+H\tau)-Dp^2=0, \tag{6.10}$$

which corresponds to the Hamilton–Jacobi equation. By using Eq. (6.5), we obtain

$$v=\min_H\frac{H\sqrt{D}}{\sqrt{(H-r)(1+H\tau)}}=\begin{cases}\frac{2\sqrt{rD}}{1+r\tau}, & r\leqslant 1/\tau\ \text{(diffusive regime)}\\ \sqrt{D/\tau}, & r\geqslant 1/\tau\ \text{(ballistic speed),}\end{cases} \tag{6.11}$$

as in Eq. (6.8). As for the RTE, the front can propagate with the ballistic speed if the inertial time is larger than or equal to the characteristic kinetic time.

E. Reaction correlated random walk system

Finally, we determine the front speed for RCRWs given by the set of equations (3.22a) and (3.22b) with Eqs. (3.26a) and (3.26b). The front joins the unstable state $(\bar\rho_{+,0},\bar\rho_{-,0})=(0,0)$ to the stable state $(\bar\rho_{+,1},\bar\rho_{-,1})=(\bar\rho/2,\bar\rho/2)$, where $\bar\rho$ is such that $f^+(\bar\rho)=f^-(\bar\rho)$. The stationary state $(0,0)$ is unstable if $f^+(0)>f^-(0)$, and the stationary state $(\bar\rho/2,\bar\rho/2)$ is stable if $f'^+(\bar\rho)<f'^-(\bar\rho)$. By introducing the hyperbolic scaling and the new fields $\rho^\varepsilon_\pm(x,t)=A_\pm\exp[-G^\varepsilon(x,t)/\varepsilon]$,

we obtain the characteristic equation

$$\begin{vmatrix} H-\gamma p+\mu-\kappa f^{+}(0)+f^{-}(0) & -\mu-f^{+}(0)(1-\kappa) \\ -\mu-f^{+}(0)(1-\kappa) & H+\gamma p+\mu-\kappa f^{+}(0)+f^{-}(0) \end{vmatrix}=0. \tag{6.12}$$

In this case, the Hamilton–Jacobi equation coincides with the characteristic equation for the RCS if we make the substitutions

$$r\equiv f^{+}(0)-f^{-}(0),\quad \tau\equiv\frac{1}{2\mu+(1-2\kappa)f^{+}(0)+f^{-}(0)},\quad D\equiv\gamma^{2}\tau. \tag{6.13}$$

As shown in Eq. (4.56), $2\mu+(1-2\kappa)f^{+}(0)+f^{-}(0)>0$ for $\kappa\in[0,1]$, and the inertial time τ is well defined.

Then, from Eq. (6.11) the front speed is given by

$$v=\begin{cases}\gamma\sqrt{f^{+}(0)-f^{-}(0)}\,\frac{\sqrt{2\mu+(1-2\kappa)f^{+}(0)+f^{-}(0)}}{\mu+(1-\kappa)f^{+}(0)}, & \mu\geqslant\kappa f^{+}(0)+f^{-}(0)\ \text{(diffusive regime)}\\ \gamma, & \mu\leqslant\kappa f^{+}(0)+f^{-}(0)\ \text{(ballistic speed).}\end{cases} \tag{6.14}$$

The front propagates with the ballistic speed if the turning frequency is smaller than or equal to the reaction rate. In other words, as for the RTE and the RCS, the front can propagate with the ballistic speed if the inertial time is larger than or equal to the characteristic kinetic time.

VII. CONCLUSIONS

We analyzed the features of five hyperbolic reaction-diffusion systems in four main areas. As stressed in the introduction, accounting properly for the contributions of growth and transport in the total evolution of the density is not a trivial task if processes are not memoryless. It is therefore desirable for hyperbolic reaction-transport equations to have a sound macroscopic or mesoscopic foundation. RCSs rest on a solid foundation of thermodynamics or generalized hydrodynamic theory. RTEs are derived from RCSs and therefore also have a sound foundation. A mesoscopic approach provides an even more desirable foundation, since it ensures that the reaction-transport equation is mathematically and biologically or physically acceptable. RCRWs are based on a description of the transport by a persistent random walk. These three reaction-transport equations have a sound foundation and fulfill criterion (I). In contrast, both the HRDE and the mHRDE lack a macroscopic or mesoscopic foundation and do not meet criterion (I).

Transport should play no role in the evolution of spatially uniform states, and the reaction-transport equation should reduce to the kinetic rate equation of the lumped system. This is the case for RCSs and RCRWs, and for RTEs after an initial boundary layer determined by the characteristic time of the transport process, i.e., the inertial time τ. Furthermore, the uniform steady states and their instability thresholds coincide with those of the rate equation of the lumped system for all three of these reaction-transport equations. These three evolution equations fulfill criterion (II). The HRDE does not reduce to the kinetic rate equation of the lumped system for spatially uniform states, but the uniform steady states and their instability thresholds coincide with those of the lumped system. The mHRDE also does not reduce to the kinetic rate equation of the lumped system for uniform states. The instability thresholds of the uniform steady states do not always coincide with the instability thresholds of the lumped system. Furthermore, the mHRDE may give rise to extraneous uniform steady states that cannot occur in the lumped system. HRDEs and mHRDEs do not meet criterion (II).

Densities or concentrations cannot be negative, and evolution equations for such fields should preserve positivity. While hyperbolic evolution equations in general do not preserve positivity, RCRWs do so for proper kinetic rate functions. For the other four hyperbolic reaction-transport equations we have adopted as a minimal performance criterion that the density of a pure death process must go to zero at long times. This is the case for HRDEs, RCSs, and RTEs. The solution of the mHRDE with first-order kinetics is unbounded for almost all initial conditions, unless the inertial time τ is sufficiently small. HRDEs, RCSs, RTEs, and RCRWs fulfill criterion (III), while mHRDEs do not.

As a last area we investigated the speed with which a stable steady state invades an unstable steady state for systems with KPP kinetics. As the inertial time τ of the transport processes increases and approaches the characteristic time of the kinetic process, the front speed should approach the ballistic speed of the individuals or particles. We further expect the front to propagate with the ballistic speed, if the inertial character of the transport process dominates the evolution of the system. This corresponds to the high reaction rate regime, where the inertial time is larger than the characteristic kinetic time. This is exactly what we found for RCSs, RTEs, and RCRWs, i.e., these hyperbolic reaction-diffusion equations that have a sound foundation, either macroscopic or mesoscopic. These hyperbolic evolution equations fulfill criterion (IV). In contrast, the front speed of HRDEs and mHRDEs with KPP kinetics is always given by the diffusive expression and never reaches the ballistic speed. These two hyperbolic reaction-diffusion equations do not meet criterion (IV).

In conclusion, RCSs, RTEs, and RCRWs meet all four criteria and represent physically acceptable evolution equations for systems of individuals or particles that undergo interactions or reactions and dispersal with inertia. Among these three, RCRWs should be preferred. They are the only ones that have a mesoscopic foundation and are guaranteed to preserve positivity.

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