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Cite this article: Calabrese S, Porporato A, Laio F, D'Odorico P, Ridolfi L. 2017 Age distribution dynamics with stochastic jumps in mortality. *Proc. R. Soc. A* **473**: 20170451. http://dx.doi.org/10.1098/rspa.2017.0451

Received: 27 June 2017
Accepted: 20 September 2017

Subject Areas:
environmental engineering, applied mathematics, statistics

Keywords:
age distribution dynamics, stochastic mortality, Poisson jumps, M'Kendrick–von Foerster equation, stochastic soil salinity

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Age distribution dynamics with stochastic jumps in mortality

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While deterministic age distribution models have been extensively studied and applied in various disciplines, little work has been devoted to understanding the role of stochasticity in birth and mortality terms. In this paper, we analyse a stochastic M'Kendrick–von Foerster equation in which jumps in mortality represent intense losses of population due to external events. We present explicit solutions for the probability density functions of the age distribution and the total population and for the temporal dynamics of their moments. We also derive the dynamics of the mean age of the population and its harmonic mean. The framework is then used to calculate the age distribution of salt in the soil root zone, where the accumulation of salt by atmospheric deposition is counteracted by plant uptake and by jump losses due to percolation events.

1. Introduction

Estimating the residence time (or age) of a substance within a control volume has been of interest since early studies in chemical engineering [1,2]. The mathematical formalism, however, was mostly developed subsequently in the population dynamics context, where birth and death processes are expressed as explicit functions of age [3–5]. Many authors, interested in finding the age distribution of a substance within a system, then refined

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the theoretical framework in both its linear [6–9] and nonlinear [10–12] formulations. Such age distribution models have proved useful in different disciplines, e.g. to describe the age distributions of stars in galaxies [13,14], to determine water quality in surface and subsurface systems [15–19], as well as to model the dynamics of plant populations [20–22]. Further applications ranged from the interpretation of isotopic data to determine the age of continental crusts [23] and soils [24] to the analysis of cancer statistics [25].

While many of the systems where age distribution is important are subject to fluctuations originated by randomness in birth or death processes, little attention has been devoted to the effect of such random components on age distributions. On the one hand, birth may be characterized by random reproduction mechanisms, which are modelled by means of branching processes [26,27], or it may be given by a time-varying stochastic process independent of the age distribution (e.g. rainfall for a watershed in which the water age is being tracked) [28]. On the other hand, random mortality may arise as abrupt jump losses of population due to external events [29–32]. A few examples are the dynamics of soil formation affected by landslides [33], the growth of riparian vegetation disturbed by floods [34], the dynamics of soil salinity in which salt is flushed away by leaching events [35] and the growth of biomass in forested ecosystems hit by fires [36]. The existence and uniqueness of the solution for stochastic age distribution models applicable to problems previously listed have been proved [37], and some numerical schemes for their solutions introduced [38–41]. However, to our knowledge no work has been devoted to the derivation of analytical solutions that would allow one to identify explicitly the role of the stochastic mortality and the different parameters in the age distribution of the population.

Our goal is hence to analyse the age distribution dynamics with stochastic jumps in mortality. In particular, we consider the M'Kendrick–von Foerster equation [4,5] with the addition of a stochastic loss term in the form of Poisson jumps multiplied by the state of the system (i.e. age distribution). Having in mind systems in which the input is not due to reproduction mechanisms within the population, we assume that the input (birth) is a given function of time and independent of the age distribution. Our results include analytical transient solutions for the probability density function of age distribution and total population. We also analyse the dynamics of the moments of the age distribution, the total population and the mean age. The results are then extended to the case in which also the input is random. As an application, we calculate the age distribution of salt in the soil root zone. Over long time scales, the mass of salt contained in the root zone is the result of a balance between the input by atmospheric deposition, the uptake rate by plants and the random occurrence of percolation events which cause downward jumps of salt mass [35,42]. Here, we use the dynamics of salt in soils as a prototypical example, but similar dynamics apply to other soil nutrients and contaminants [43,44].

The remainder of the article proceeds as follows. Section 2 presents the differential equations governing the dynamics of the age distribution, the total population and the mean age, while §3 shows the corresponding analytical solutions. The work is then extended to the case of random input in §4. Lastly, in §5, we apply the theory to the salt dynamics in the root zone. We conclude in §6 by summarizing the results and by highlighting possible extensions of this work.

2. Mathematical framework

Given a system Ω, we define the age τ of each element as the time elapsed since it entered Ω. The population of Ω can be described in terms of the age distribution $n(t,\tau)$, such that $n(t,\tau)\,\mathrm{d}\tau$ is the number of elements having age between τ and $\tau+\mathrm{d}\tau$ at time t, and $\int_0^\infty n\,\mathrm{d}\tau = w$ is the total population. The temporal dynamics of n is governed by the M'Kendrick–von Foerster equation [4,5],

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial \tau}=-n_0, \tag{2.1}$$

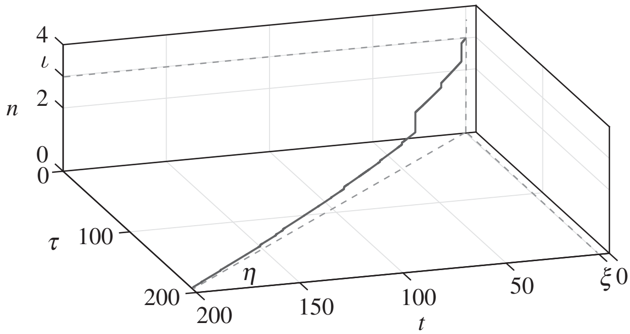

Figure 1. Time evolution of a population along the characteristic line η, according to equation (2.2). At time $t=\xi$, the population ι enters the system with age $\eta=0$ and starts decaying along η due to the deterministic and stochastic (jumps) mortality.

in which $n_0(t,\tau)$ represents the age distribution of the elements leaving Ω, and its integral with respect to τ yields the total output, $o(t)=\int_0^\infty n_0\,\mathrm{d}\tau$. The age distribution of the output can be expressed as $n_0=\mu n$, where μ is a specific output (mortality) rate μ, also called the loss function. In general, the latter can be a function of t, τ, w, n and so on; however, we limit our analysis to cases where the output rate is only a function of time and age, i.e. $\mu=\mu(t,\tau)$.

To introduce the stochasticity in the mortality term, we assume $\mu(t,\tau)$ to be composed of a deterministic term $\mu_\mathrm{d}(t,\tau)$ and a random term $\nu(t)$, $\mu(t,\tau)=\mu_\mathrm{d}(t,\tau)+\nu(t)$. In particular, we assume that $\nu(t)$ is a shot noise given by the time derivative of a marked Poisson process, $\nu(t)=\sum_{i=1}^{N_t} h_i\delta(t-t_i)$, in which h_i is the size of the i-th jump, t_i is its time of occurrence and N_t is the number of jumps that occurred up to time t [45]. The frequency of the jumps is λ, whereas their marks h_i are assumed to be exponentially distributed with mean γ^{-1}. With these assumptions, the M'Kendrick–von Foerster equation becomes a stochastic equation (capital letters indicate random variables),

$$\frac{\partial N}{\partial t}+\frac{\partial N}{\partial \tau}=-\mu_\mathrm{d}(t,\tau)N-\nu(t)\circ N, \tag{2.2}$$

in which the symbol $\circ$ indicates that the multiplication of the noise ν (white noise) by N, which is now a random function, is interpreted in the Stratonovich sense. This interpretation results from taking the zero limit of the time scale of the coloured noise term and has the advantage that the rules of calculus hold [46–49]. Equation (2.2) has initial condition $N(t=0,\tau)$ and boundary condition $N(t,\tau=0)=\iota(t)$, the input to Ω.

By introducing the variables $\eta=\tau$ and $\xi=t-\tau$, equation (2.2) reduces to an ordinary differential equation,

$$\frac{\mathrm{d}N}{\mathrm{d}\eta}=-\mu_\mathrm{d}(\xi+\eta,\eta)N-\nu(\xi+\eta)\circ N, \tag{2.3}$$

which for a single realization of the stochastic process can be solved in the Stratonovich prescription by classical integration. The solution in the original variables reads [6,7,50]

$$N(t,\tau)=\begin{cases} N(0,\tau-t)\,\mathrm{e}^{-\int_0^t(\mu_\mathrm{d}(u,\tau-t+u)+\nu(u))\,\mathrm{d}u} & t<\tau \\ \iota(t-\tau)\,\mathrm{e}^{-\int_0^\tau(\mu_\mathrm{d}(t-\tau+u,u)+\nu(t-\tau+u))\,\mathrm{d}u} & t>\tau. \end{cases} \tag{2.4}$$

Along the characteristic lines η, given by $\mathrm{d}t/\mathrm{d}\eta=1$ and $\mathrm{d}\tau/\mathrm{d}\eta=1$, the population evolves deterministically, according to an exponential decay at rate μ, and is perturbed by instantaneous jumps that cause abrupt losses of population. See figure 1 for an example of a realization of such a process.

To obtain the probabilistic description of the stochastic process, we need to consider the equation for the temporal dynamics of the single time, single age probability density function of N, $p_N(n;t,\tau)$. Differently from the case of additive noise in which the derivation of the master equation is unambiguous [51,52], for a multiplicative noise such as in equation (2.2) the master equation is formulated according to the prescription considered [48]. Remaining in the ξ and η variables for mathematical convenience, the master equation in the Stratonovich prescription for the evolution of $p_N(n;\xi+\eta,\eta)$, associated with equation (2.3), reads

$$\frac{\partial p_N(n)}{\partial \eta} = \frac{\partial(\mu_{\mathrm{d}} n p_N(n))}{\partial n} - \lambda p_N(n) + \lambda\gamma n^{\gamma-1}\int_n^\infty p_N(u)u^{-\gamma}\,\mathrm{d}u, \tag{2.5}$$

where the dependencies on ξ and η are dropped for the sake of conciseness. Once solved, it is straightforward to return to the original variables, $p_N(n;t,\tau)$. According to equation (2.5), the evolution of $p_N(n)$ is determined by a contribution given by the drift $\mu_{\mathrm{d}} n$, a loss of probability due to the instantaneous jumps away from n and a contribution due to the jumps to n.

The evolution equation for the total population, $W = \int_0^\infty N\,\mathrm{d}\tau$, can be derived by integrating equation (2.2) with respect to τ,

$$\frac{\mathrm{d}W}{\mathrm{d}t} = \iota(t) - o_d(t) - \nu(t)\circ W, \tag{2.6}$$

where $\iota(t) = -\int_0^\infty (\partial N/\partial\tau)\,\mathrm{d}\tau = N(t,\tau=0)$ is the input, $o_d = \int_0^\infty \mu_{\mathrm{d}} N\,\mathrm{d}\tau$ is the output due to the deterministic loss and the last term is the stochastic output due to instantaneous jumps. The Chapman–Kolmogorov forward equation governing the temporal evolution of the single time probability density function $p_W(w;t)$ is obtained as

$$\frac{\partial p_W(w)}{\partial t} = -\frac{\partial(\iota - o_d)p_W(w)}{\partial w} - \lambda p_W(w) + \lambda\gamma w^{\gamma-1}\int_w^\infty p_w(u)u^{-\gamma}\,\mathrm{d}u. \tag{2.7}$$

Again, the first term on the right-hand side determines the contribution of probability to $p_W(w)$ due to the deterministic drift $(\iota - o_{\mathrm{d}})$, while the last two terms represent the contribution by the jumps.

The mean age $\bar{T}$ for Ω is defined as $\bar{T} = M/W$, $M = \int_0^\infty \tau N\,\mathrm{d}\tau$ being the first moment of N. Multiplying (2.2) by τ and integrating with respect to τ, the temporal dynamics of M is obtained as

$$\frac{\mathrm{d}M}{\mathrm{d}t} = W(t) - \theta_{\mathrm{d}}(t) - \nu(t)\circ M, \tag{2.8}$$

where $\theta_{\mathrm{d}} = \int_0^\infty \tau\mu_{\mathrm{d}} N\,\mathrm{d}\tau$ can be interpreted as the first moment of $\mu_{\mathrm{d}} N$, which represents the age distribution of the deterministic output. In turn, by differentiating the definition of $\bar{T}$, the time evolution of the mean age reads

$$\frac{\mathrm{d}\bar{T}}{\mathrm{d}t} = 1 - \frac{1}{W}(\theta_{\mathrm{d}} + \bar{T}\iota - \bar{T}o_{\mathrm{d}}). \tag{2.9}$$

Note that, although the noise ν is not explicitly present in (2.9), $\bar{T}$ is still a random variable because the randomness enters through θ_{d} and W.

3. Solutions

To obtain an analytical solution to (2.5), it is convenient to divide equation (2.2) by N, so as to obtain an equation with additive noise for the variable $Y = \ln N$. The equation describing the temporal dynamics of $p_Y(y;\xi+\eta,\eta)$ is given by

$$\frac{\partial p_Y}{\partial \eta} = \frac{\partial(\mu_{\mathrm{d}} p_Y)}{\partial y} - \lambda p_Y + \lambda\gamma\int_y^\infty p_Y(u)\,\mathrm{e}^{-\gamma(u-y)}\,\mathrm{d}u. \tag{3.1}$$

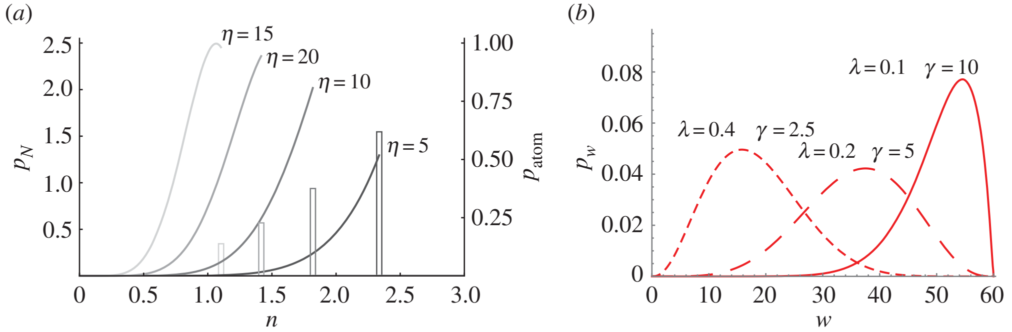

Figure 2. (*a*) Probability density function $p_N(n;\eta)$, from equation (A 5), plotted for different values of η. The probability density functions are plotted for input $\iota=3$, deterministic loss function $\mu_{\mathrm{d}}=0.05$, frequency of the jumps $\lambda=0.1$ and mean mark of the jumps $\gamma=10$ (dimensionless). (*b*) Probability density function $p_W(w)$, from equation (3.5), for different couples of parameters λ and γ (dimensionless), input $\iota=3$ and deterministic loss function $\mu_{\mathrm{d}}=0.05$. For the sake of generality, the units are not specified. (Online version in colour.)

Equation (3.1) can be analogously obtained by introducing $Y=\ln N$ directly in equation (2.5). From the solution of (3.1) (shown in appendix A), the probability density p_N (for $t>\tau$) can be obtained as

$$p_N(n;t,\tau)=\frac{1}{n}\,\mathrm{e}^{-\gamma\psi(t,\tau)-\tau\lambda}\left(\delta(\psi(t,\tau))+\frac{\sqrt{\gamma\tau\lambda}I_1(2\sqrt{\gamma\tau\lambda}\sqrt{\psi(t,\tau)})}{\sqrt{\psi(t,\tau)}}\right)\quad n\le\iota(t-\tau)\varphi(t,\tau),\tag{3.2}$$

in which $\varphi(t,\tau)=\mathrm{e}^{-\int_0^{\tau}\mu_{\mathrm{d}}(t-\tau+u,u)\,\mathrm{d}u}$, $\psi(t,\tau)=\ln(\varphi(t,\tau)\iota(t-\tau)/n)$ and $I_1(\cdot)$ is the modified Bessel function of the first kind of order 1.

The equation describing the temporal evolution of the moments of N can be obtained by applying the expectation operator $E[g(x)^k]=\int_0^{\infty}g(x)^k p_X(x)\,\mathrm{d}x$ to equation (2.5) (see appendix B),

$$\frac{\partial\bar{N}_k}{\partial t}+\frac{\partial\bar{N}_k}{\partial\tau}=-\mu_{\mathrm{d}}k\bar{N}_k-\lambda\bar{N}_k+\frac{\lambda\gamma}{\gamma+k}\bar{N}_k,\tag{3.3}$$

where $\bar{N}_k$ is the kth order moment of N, $\bar{N}_k=\int_0^{\infty}n^k p_N(n)\,\mathrm{d}n$. The solution of (3.3) is

$$\bar{N}_k(t,\tau)=\begin{cases}n(0,\tau-t)^k\,\mathrm{e}^{-k\int_0^t\mu_{\mathrm{d}}(u,\tau-t+u)\,\mathrm{d}u-\lambda t+(\lambda\gamma/(\gamma+k))t} & t<\tau\\ \iota(t-\tau)^k\,\mathrm{e}^{-k\int_0^{\tau}\mu_{\mathrm{d}}(t-\tau+u,u)\,\mathrm{d}u-\lambda\tau+(\lambda\gamma/(\gamma+k))\tau} & t>\tau.\end{cases}\tag{3.4}$$

The previous results, equations (3.2) and (3.4), are obtained for a time-dependent input $\iota(t)$ and a generic specific mortality rate $\mu(t,\tau)$. On the contrary, equation (2.7) for the total population W presents some analytical difficulties and we were able to find an explicit solution only for constant values of ι and μ_{d} and in steady state. Under these conditions, the solution (see appendix C for the derivation) reads

$$p_W(w)=\frac{\iota^{-\gamma-\lambda/\mu_{\mathrm{d}}}\mu_{\mathrm{d}}^{\gamma+1}}{B(\gamma+1,\lambda/\mu_{\mathrm{d}})}w^{\gamma}(\iota-\mu_{\mathrm{d}}w)^{\lambda/\mu_{\mathrm{d}}-1}\quad w\le\frac{\iota}{\mu_{\mathrm{d}}},\tag{3.5}$$

where $B(a,b)$ is the Beta function with shape parameters a and b. Note that (3.5) is defined on the interval $[0,\iota/\mu_{\mathrm{d}}]$, where the upper bound represents the value of w if there are no stochastic losses. The probability density $p_W(w)$ is plotted in figure 2*b* for different values of λ and γ. For low frequency and mean marks of the jumps, the distribution localizes on the upper side of the interval (close to the upper bound) and asymptotically becomes an atom at $w=\iota/\mu_{\mathrm{d}}$ for $\lambda/\gamma\to 0$. On the contrary, for higher frequency and mean mark of the jumps it spreads over lower values of W. By applying the expectation operator to equation (2.7), the equation for the temporal dynamics of the kth order moments of W is analogously obtained,

$$\frac{\mathrm{d}\bar{W}_k}{\mathrm{d}t} = \iota\mu_\mathrm{d}^{k-1}k\bar{W}_{k-1} - k\mu_\mathrm{d}^{k}\left(\frac{\gamma+\lambda/\mu_\mathrm{d}+k}{\gamma+k}\right)\bar{W}_k, \tag{3.6}$$

according to which the average population $\bar{W}_1$ satisfies

$$\frac{\mathrm{d}\bar{W}_1}{\mathrm{d}t} = \iota - \mu_\mathrm{d}\left(\frac{\gamma+\lambda/\mu_\mathrm{d}+1}{\gamma+1}\right)\bar{W}_1, \tag{3.7}$$

with explicit solution

$$\bar{W}_1 = \frac{\mathrm{e}^{-\alpha t\mu_\mathrm{d}}(\iota\,\mathrm{e}^{\alpha t\mu_\mathrm{d}} + \alpha W_0\mu_\mathrm{d} - \iota)}{\alpha\mu_\mathrm{d}}, \tag{3.8}$$

W_0 being the initial population and $\alpha = (\gamma + \lambda/\mu_d + 1)/(\gamma + 1)$.

Lastly, for conditions of statistical stationarity, an interesting result for the harmonic mean of $\bar{T}$, $\bar{T}_\mathrm{h}$, can be obtained by dividing equation (2.8) by M,

$$\frac{1}{\bar{T}} = \frac{\theta_\mathrm{d}}{M} + \nu(t), \tag{3.9}$$

and averaging,

$$\bar{T}_\mathrm{h} = \left(\overline{\frac{1}{\bar{T}}}\right)^{-1} = \left(\overline{\frac{\theta_\mathrm{d}}{M}} + \frac{\lambda}{\gamma}\right)^{-1}. \tag{3.10}$$

4. Age distribution with stochastic mortality and input

We have shown so far that a system driven by a time-dependent input ι and subject to both a deterministic and a stochastic loss, the latter in the form of a shot noise, has a single time, single age probability distribution of N given by (3.2). When, however, the input ι is also stochastic (i.e. I), the probability distribution function $p_N^*(n)$ (the asterisk indicates that there is stochasticity also in I) needs to account for both sources of randomness. As I represents a time-varying parameter, (3.2) remains valid for a given realization of I. On the other hand, given the single time probability density function of I, $p_I(\iota;t)$, from Bayes' theorem [53] it is straightforward to consider all the possible realizations of I as

$$p_N^*(n;t,\tau) = \int_0^\infty p_I(\iota;t-\tau)p_N(n;t,\tau,\iota)\,\mathrm{d}\iota. \tag{4.1}$$

As shown in equation (2.4), for $\tau > t$, the age distribution does not depend on ι and fluctuates only because of the loss term $\nu(t)$. Equation (4.1) thus yields

$$p_N^*(n;t,\tau) = p_N(n;t,\tau)\int_0^\infty p_I(\iota;t-\tau)\,\mathrm{d}\iota = p_N(n;t,\tau). \tag{4.2}$$

On the other hand, for $t > \tau$, the age distribution depends upon the value of ι, so that substituting (3.2) into (4.1) yields

$$p_N^*(n;t,\tau) = \int_0^\infty p_I(\iota;t-\tau)\frac{1}{n}\,\mathrm{e}^{-\gamma\psi(t,\tau)-\tau\lambda}\left(\delta(\psi(t,\tau)) + \frac{\sqrt{\gamma\tau\lambda}I_1(2\sqrt{\gamma\tau\lambda}\sqrt{\psi(t,\tau)})}{\sqrt{\psi(t,\tau)}}\right)\mathrm{d}\iota, \tag{4.3}$$

where the dependence on the parameter ι is contained in ψ. It then follows that the k-th order moment of the age distribution, $\bar{N}_k^*$, is given by

$$\bar{N}_k^* = \int_0^\infty p_I(\iota;t-\tau)\bar{N}_k\,\mathrm{d}\iota = \bar{\iota}(t-\tau)\,\mathrm{e}^{-k\int_0^\tau \mu_\mathrm{d}(t-\tau+u,u)\,\mathrm{d}u - \lambda\tau + \frac{\lambda\gamma}{\gamma+k}\tau}, \tag{4.4}$$

where equation (3.4) for $\bar{N}_k$ was used. Equations (4.3) and (4.4), interestingly, complete the previous work by Porporato & Calabrese [28], in which the randomness was accounted for ι but not in the mortality. An example of the above results is shown in figure 3.

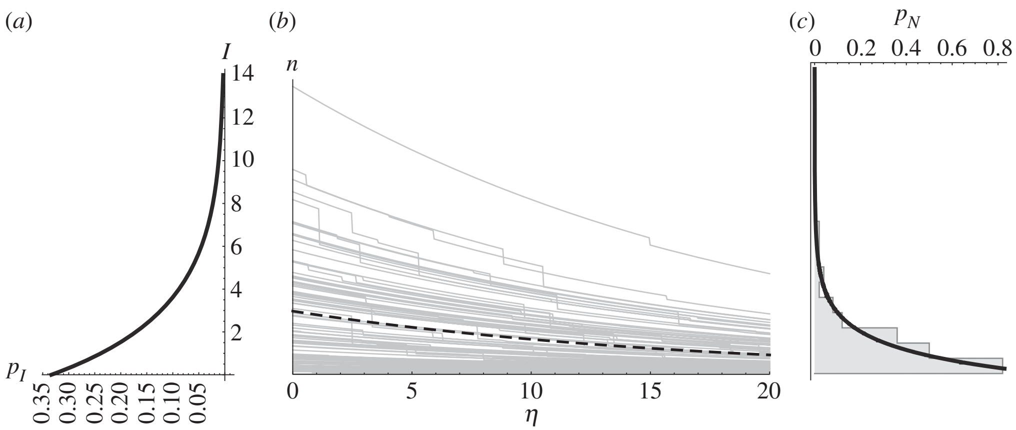

Figure 3. (*a*) Single time probability density function $p_I(\iota; t)$. The distribution is exponential with mean $\bar{\iota} = 3$. (*b*) Age distributions, shown along the characteristic line η, obtained from multiple realizations of the stochastic process described by (2.2) with random input ι distributed as in (*a*) (grey lines). Mean age distribution, $\bar{N}^*$, computed from equation (4.4) (dashed black line). (*c*) Probability density function $p_N^*(n; \eta)$, from equation (4.3), for $\eta = 20$. The plots are generated for mean input $\bar{\iota} = 3$, $\mu_d = 0.05$, $\lambda = 0.1$ and $\gamma = 10$ (dimensionless). For the sake of generality, the units are not specified.

5. Application to stochastic soil salinity

We apply the theory outlined above to compute the age distribution of salt in the soil root zone. Over long time scales, the dynamics of the mass of salt contained in the root zone W_{salt} per unit ground area is governed by Suweis *et al.* [42],

$$\frac{\mathrm{d}W_{\mathrm{salt}}}{\mathrm{d}t} = I_{\mathrm{d}} - \mu_{\mathrm{up}} W_{\mathrm{salt}} - \nu(t) \circ W_{\mathrm{salt}}, \tag{5.1}$$

where I_{d} is the atmospheric deposition, μ_{up} is the rate of uptake by plants and ν is the shot noise accounting for the flushing of the soil by percolation events. Frequency λ and mean mark γ^{-1} of the shot noise (percolation events) depend on rainfall characteristics, soil properties (e.g. porosity, root zone depth, soil field capacity) and withdrawal by plants via transpiration. Other soil nutrients, e.g. nitrates, or contaminants are subject to dynamics that are analogous to the one depicted in equation (5.1), so that the results can be easily extended to them. Examples of time evolutions of salt mass in the root zone calculated through equation (5.1) are shown in figure 4*a*, where we used the same values of the parameters as in [35,42].

In what follows, we first consider a constant plant uptake rate μ_{up} and then analyse the case in which the uptake is negligible, i.e. $\mu_{\mathrm{up}} = 0$. We also focus on large times ($t > \tau$), for which the system has no memory of the initial condition and has reached conditions of stochastic steady state (statistical stationarity), i.e. $t \to \infty$. The age distribution N_{salt} is still a function of time and age and fluctuates because of the stochastic term $\nu(t)$, whereas the probability density $p_{N_{\mathrm{salt}}}(n; \tau)$ is constant in time and varies only with respect to the parameter τ.

(a) Constant plant uptake rate

The M'Kendrick–von Foerster equation for the age distribution of salt N_{salt} in the root zone can be written as

$$\frac{\partial N_{\mathrm{salt}}}{\partial t} - \frac{\partial N_{\mathrm{salt}}}{\partial \tau} = -\mu_{\mathrm{up}} N_{\mathrm{salt}} - \nu(t) \circ N_{\mathrm{salt}}, \tag{5.2}$$

such that integration with respect to τ readily yields equation (5.1). In equation (5.2), μ_{up} and ν are not functions of age, meaning that, after deposition, salt is taken up by plants at constant rate μ_{up} and flushed away by percolation at rate ν regardless of its age [5,50,54].

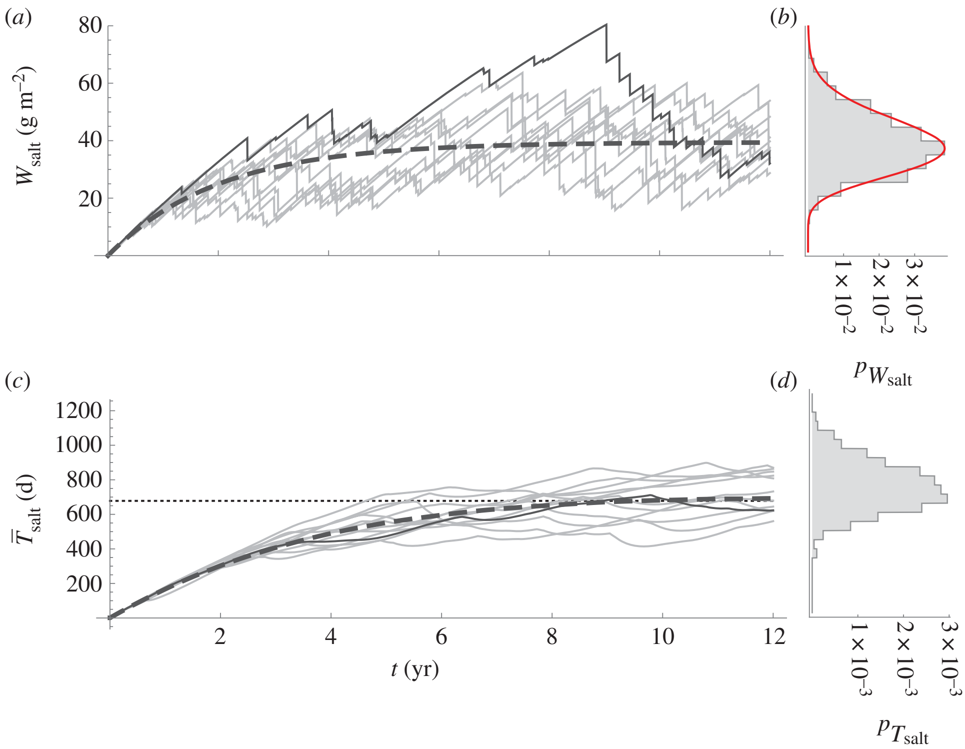

Figure 4. (*a*) Time evolution of total salt mass $W_{\mathrm{salt}}(t)$ in the root zone for different realizations of the shot noise ν (grey lines). Sample realization of $W_{\mathrm{salt}}(t)$ (black line). Time evolution of the mean total salt mass, described by equation (3.7) (dashed line). (*b*) Probability density function $p_{W_{\mathrm{salt}}}$ computed analytically (red line). Frequency histogram computed through numerical simulations (grey histogram). (*c*) Time evolution of mean age $\bar{T}_{\mathrm{salt}}(t)$ of salt in the root zone for different realizations of the shot noise ν (grey lines). Sample realization of $\bar{T}_{\mathrm{salt}}(t)$ (black line). Time evolution of the mean $\bar{T}_{\mathrm{salt}}(t)$ (dashed line). Harmonic mean of $\bar{T}_{\mathrm{salt}}(t)$, $\bar{T}_{\mathrm{h,salt}}$ (dotted line). (*d*) Frequency histogram for mean $\bar{T}_{\mathrm{salt}}(t)$ computed from numerical simulations. The plots are generated for input $\iota = 0.054$ g m^{-2} d^{-1}, $\mu_{\mathrm{d}} = 3 \times 10^{-4}$ d^{-1}, $\lambda = 0.018$ d^{-1} and $\gamma = 10$. (Online version in colour.)

From equation (2.4), for a single realization, the salt in the root zone has an age distribution

$$N_{\mathrm{salt}}(t,\tau) = I_{\mathrm{d}}\,\mathrm{e}^{-\mu_{\mathrm{up}}\tau - \int_0^\tau \nu(t-\tau+u)\,\mathrm{d}u}. \tag{5.3}$$

Introducing the survival function, $\varphi(\tau) = \mathrm{e}^{-\mu_{\mathrm{up}}\tau}$, (5.3) can also be written as

$$N_{\mathrm{salt}}(t,\tau) = I_{\mathrm{d}}\varphi(\tau)\,\mathrm{e}^{-\int_0^\tau \nu(t-\tau+u)\,\mathrm{d}u}, \tag{5.4}$$

where the deterministic, $I_{\mathrm{d}}\varphi(\tau)$, and the stochastic, $\mathrm{e}^{-\int_0^\tau \nu(t-\tau+u)\,\mathrm{d}u}$, components can be distinguished. From equation (A 5), the probability density function of the age distribution reduces to

$$p_{N_{\mathrm{salt}}}(n,\tau) = \frac{1}{n}\left(\frac{I_{\mathrm{d}}}{n}\right)^{-\gamma} \mathrm{e}^{-(\lambda-\gamma\mu_{\mathrm{up}})\tau} \times \left(\delta\left(\ln\left(\frac{I_{\mathrm{d}}\,\mathrm{e}^{-\mu_{\mathrm{up}}\tau}}{n}\right)\right) + \frac{\sqrt{\gamma\tau\lambda}\,I_1(2\sqrt{\gamma\tau\lambda}\sqrt{\ln((I_{\mathrm{d}}\,\mathrm{e}^{-\mu_{\mathrm{up}}\tau})/n)})}{\sqrt{\ln(I_{\mathrm{d}}\,\mathrm{e}^{-\mu_{\mathrm{up}}\tau}/n)}}\right) \quad n \le I_{\mathrm{d}}\varphi(\tau). \tag{5.5}$$

The average age distribution $\bar{N}_{\mathrm{salt},1}$, from (3.4), is given by

$$\bar{N}_{\mathrm{salt},1} = \iota\,\mathrm{e}^{(-\mu_{\mathrm{up}}-\lambda+\lambda\gamma/(\gamma+1))\tau}, \tag{5.6}$$

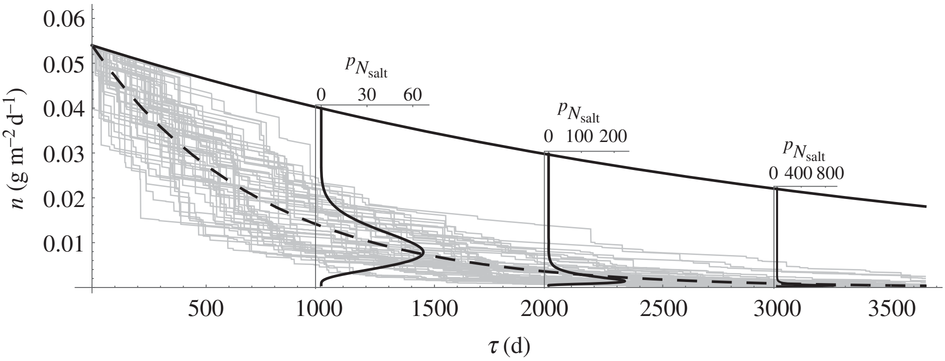

Figure 5. Age distributions obtained from multiple realizations of the stochastic dynamics as from equation (2.2) with constant μ_{up} (grey lines). Mean age distribution computed from the analytical solution (5.6) (dashed black line). Age distribution in the absence of jumps, given by $n = I_d\varphi(\tau)$ (solid back line). The insets show the probability density function p_N, from equation (5.5), for $\tau = 1000$, $\tau = 2000$, $\tau = 3000$ d. The plots are generated for input $\iota = 0.054\ \mathrm{g\ m^{-2}\ d^{-1}}$, $\mu_d = 3 \times 10^{-4}\ \mathrm{d^{-1}}$, $\lambda = 0.018\ \mathrm{d^{-1}}$ and $\gamma = 10$.

while, because $\theta_d = o_d = \mu_{up} W_{salt}$, the equation for the mean age reduces to

$$\frac{d\bar{T}_{salt}}{dt} = 1 - \frac{I_d}{W_{salt}} \circ \bar{T}_{salt}, \tag{5.7}$$

whereas the harmonic mean

$$\bar{T}_{h,salt} = \left(\mu_{up} + \frac{\lambda}{\gamma}\right)^{-1} = \frac{\gamma}{\gamma\mu_{up} + \lambda}. \tag{5.8}$$

The results are summarized in figure 5. In particular, the figure shows multiple realizations of N_{salt} along with the average distribution $\bar{N}_{salt,1}$ and the realization in which no jump occurs (black solid line), $n = I_d\varphi(\tau)$, which sets the upper bound for N_{salt}. The probability density function $p_{N_{salt}}$, which spreads over lower values of n as the age τ increases, is shown for three values of τ. The probability density function for the total population, $p_{W_{salt}}$, given by expression (3.5), is instead illustrated in figure 4*a*, while multiple realizations of the time evolution of $\bar{T}_{salt}$ are illustrated in figure 4*c*, showing how $\bar{T}_{salt}$ fluctuates around its mean value (dark grey dashed line) and its harmonic mean $\bar{T}_h$ (dark grey dotted line).

(b) No plant uptake

When plant uptake is negligible, equation (5.1) reduces to

$$\frac{dW_{salt}}{dt} = I_d - W_{salt} \circ \nu(t), \tag{5.9}$$

in which only the percolation events compensate for the accumulation by atmospheric deposition. The age distribution for such a system becomes

$$N_{salt}(t, \tau) = I_d\, e^{-\int_0^\tau \nu(t-\tau+u)\,du}. \tag{5.10}$$

In equation (5.10), the survivor function $\varphi = 1$, namely the upper bound, is now constant with respect to t and τ, and is simply given by I_d. The probability density function is obtained by setting $\mu_{up} = 0$ in equation (5.5),

$$p_{N_{salt}}(n, \tau) = \left(\frac{I_d}{n}\right)^{-\gamma} e^{-\lambda\tau} \left(\delta\left(\ln\left(\frac{I_d}{n}\right)\right) + \frac{\sqrt{\gamma\tau\lambda}\, I_1(2\sqrt{\gamma\tau\lambda}\sqrt{\ln(I_d/n)})}{\sqrt{\ln(I_d/n)}}\right) \quad n \le I_d, \tag{5.11}$$

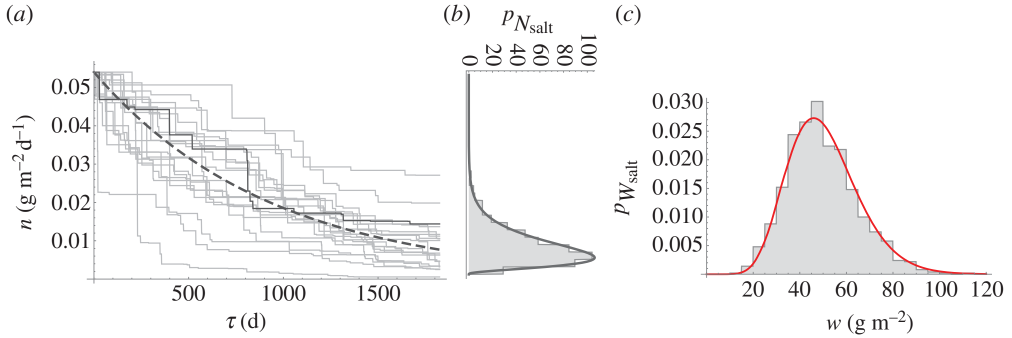

Figure 6. (*a*) Age distributions obtained from multiple realizations of the stochastic dynamics as from equation (2.2) with $\mu_{\mathrm{d}} = 0$ (grey lines). Mean age distribution computed from the analytical solution (5.6) (dashed black line). (*b*) Probability density function p_N, from equation (5.11), for $\tau = 2000$ d. (*c*) Probability density function $p_{W_{\mathrm{salt}}}$ computed from equation (3.5) (solid red line). Frequency histogram computed by generating multiple realizations of the stochastic dynamics (grey histogram). The plots are generated for input $\iota = 0.054$ g m^{-2} d^{-1}, $\lambda = 0.018$ d^{-1} and $\gamma = 10$. (Online version in colour.)

and the average age distribution simply reduces to

$$\bar{N}_{\mathrm{salt},1} = I_{\mathrm{d}}\,\mathrm{e}^{-\lambda\tau + (\lambda\gamma/(\gamma+1))\tau}. \tag{5.12}$$

With regard to the total mass of salt, evolving according to (5.9), its probability density can be obtained as a limiting case of expression (3.5) [42]. Specifically, by taking the limit of (3.5) for $\mu_{\mathrm{d}} \to 0$,

$$p_{W_{\mathrm{salt}}}(w) = \lim_{\mu_{\mathrm{up}}\to 0} \frac{I_{\mathrm{d}}^{-\gamma-\lambda/\mu_{\mathrm{up}}}\,\mu_{\mathrm{up}}^{\gamma+1}}{B(\gamma+1, \lambda/\mu_{\mathrm{up}})} w^{\gamma} (I_{\mathrm{d}} - \mu_{\mathrm{up}} w)^{\lambda/\mu_{\mathrm{up}}-1} = \frac{(\lambda/I_{\mathrm{d}})^{1+\gamma}}{\Gamma(1+\gamma)}\,\mathrm{e}^{-\lambda w/I_{\mathrm{d}}} w^{\gamma}, \tag{5.13}$$

which is a Gamma distribution, defined on $[0, \infty)$, with mean value $(I_{\mathrm{d}}/\lambda)(1+\gamma)$ that is in agreement with equation (3.7).

As $\theta_{\mathrm{d}} = o_{\mathrm{d}} = 0$, equation (2.9) for the mean age again reduces to

$$\frac{\mathrm{d}\bar{T}_{\mathrm{salt}}}{\mathrm{d}t} = 1 - \frac{I_{\mathrm{d}}}{W_{\mathrm{salt}}} \circ \bar{T}_{\mathrm{salt}}, \tag{5.14}$$

while the harmonic mean

$$\bar{T}_{\mathrm{h,salt}} = \frac{\gamma}{\lambda}. \tag{5.15}$$

Our findings are shown in figure 6. It can be seen that, for each realization, the age distribution with respect to τ is composed of horizontal segments separated by the downward jumps determined by the noise $\nu(t)$. The probability density functions $p_{N_{\mathrm{salt}}}$ and $p_{W_{\mathrm{salt}}}$ are shown in figure 6*b*,*c*, respectively.

6. Conclusion

We have analysed the role of stochastic jumps in the mortality rate in the age distribution dynamics. The master equations governing the evolution of the probability density function of the age distribution N and the total population W, together with the equation governing the time evolution of the mean age $\bar{T}$, are derived in §2. Their exact solutions are shown in §3, along with the differential equations for the temporal dynamics of the moments of N and W; see equations (3.2)–(3.6). We have also shown that, when the input is also a random variable, the probability density function of the age distribution can be obtained from Bayes' theorem (equation (4.1)). This complements the previous work on stochastic input [28]. The results have then been applied to the age distribution dynamics of salt in the root zone, in which the stochastic mortality is due to percolation events.

The framework can be further extended to explore the role of w- or n-dependencies in the mortality term μ_d or an age dependence in the shot noise ν. Lastly, stochastic mortality in the form of a renewal process (i.e. abrupt extinction) can also be included.

Data accessibility. This paper is a theoretical study and hence no data were used. The code is available at https://github.com/sasical91/CODES.
Authors' contributions. All the authors contributed equally to this work.
Competing interests. We have no competing interests.
Funding. A.P. and S.C. acknowledge support from the USDA Agricultural Research Service (cooperative agreement 58-6408-3-027), the National Science Foundation (NSF) (grant nos. CBET-1033467, EAR-1331846, FESD-1338694, EAR-1316258) and the Duke WISeNet (grant no. DGE-1068871). F.L. acknowledges financial support from the ERC Project CWASI (grant no. 647473).
Acknowledgements. The authors thank the anonymous reviewers for their comments.

Appendix A

We solve equation (3.1) for $p_Y(y)$. Introducing a new variable $z = y_0 - y$, where $y_0 = \ln(n(\xi, \eta = 0))$, equation (3.1) becomes

$$\frac{\partial p_Z}{\partial \eta} = -\frac{\partial(\mu_\mathrm{d} p_Z)}{\partial z} - \lambda p_Z + \lambda\gamma \int_0^z p_Z(u)\,\mathrm{e}^{-\gamma(z-u)}\,\mathrm{d}u, \tag{A 1}$$

and by applying a Laplace transform, $f^*(s) = \int_0^\infty \mathrm{e}^{-sx} f(x)\,\mathrm{d}x$, it reduces to

$$\frac{\partial p^*_{Z^*}}{\partial \eta} = -\mu_\mathrm{d} z^* p^*_{Z^*} - \lambda p^*_{Z^*} + \frac{\lambda\gamma}{z^* + \gamma} p^*_{Z^*}, \tag{A 2}$$

where we set $p_Z(0) = 0$. Integrating (A 2), one obtains

$$p^*_{Z^*}(z^*) = p^*_{0,Z^*}\,\mathrm{e}^{-z^* \int_0^\eta \mu_\mathrm{d}(\xi+u,u)\,\mathrm{d}u - \lambda\eta + \lambda\gamma\eta/(z^*+\gamma)}, \tag{A 3}$$

where p^*_{0,Z^*} represents the Laplace transform of the boundary condition $p_Z(z;\eta = 0)$. Specifically, as $y(\xi, \eta = 0) = y_0(\xi) = \ln(n(\xi, \eta = 0))$, we have $z_0 = z(\xi, \eta = 0) = 0$ and $p_Z(z;\eta = 0) = \delta(z)$, and thus $p^*_{0,Z^*} = \mathrm{e}^{-z_0 z^*} = 1$. By applying an inverse Laplace transform to (A 3) and substituting back $y = y_0 - z$, $p_Y(y)$ reads

$$\begin{aligned} p_Y(y) = \varphi(\xi+\eta,\eta)^{-\gamma} e^{\gamma(y - y_0(\xi)) - \eta\lambda} \Bigg(&\delta(-y + y_0(\xi) + \ln\varphi(\xi+\eta,\eta)) \\ &+ \frac{\sqrt{\gamma\eta\lambda} I_1(2\sqrt{\gamma\eta\lambda}\sqrt{-y + y_0(\xi) + \ln\varphi(\xi+\eta,\eta)})}{\sqrt{-y + y_0(\xi) + \ln\varphi(\xi+\eta,\eta)}}\Bigg) \end{aligned} \tag{A 4}$$

for $y \le y_0(\xi) - \int_0^\eta \mu_\mathrm{d}(\xi+u,u)\,\mathrm{d}u$, where $I_1(\cdot)$ is the modified Bessel function of the first kind of order 1, and $\varphi(\xi+\eta,\eta) = \mathrm{e}^{-\int_0^\eta \mu_\mathrm{d}(\xi+u,u)\,\mathrm{d}u}$ is the survivor function [36,54]. The probability density p_N can be obtained as

$$p_N(n;\eta) = \frac{1}{n}\,\mathrm{e}^{-\gamma\psi(\xi+\eta,\eta) - \eta\lambda}\left(\delta(\psi(\xi+\eta,\eta)) + \frac{\sqrt{\gamma\eta\lambda} I_1(2\sqrt{\gamma\eta\lambda}\sqrt{\psi(\xi+\eta,\eta)})}{\sqrt{\psi(\xi+\eta,\eta)}}\right) \quad n \le \iota(\xi)\varphi(\xi+\eta,\eta), \tag{A 5}$$

with $\varphi(\xi+\eta,\eta) = \mathrm{e}^{-\int_0^\eta \mu_\mathrm{d}(\xi+u,u)\,\mathrm{d}u}$ and $\psi(\xi+\eta,\eta) = \ln(\varphi(\xi+\eta,\eta)\iota(\xi)/n)$. In particular, the survivor function is the exceedance probability (i.e. the probability of surviving up to a time equal to η) for a cohort entering at $\eta = 0$ and subject exclusively to the deterministic decay. The product $\iota(\xi)\varphi(\xi+\eta,\eta)$ thus represents the value of N in the absence of jumps and sets the upper bound in (A 5). The probability density $p_N(n,\eta)$ in fact is a mixed distribution with an atom of probability along the deterministic path (no jumps), i.e. $n = \iota(\xi)\varphi(\xi+\eta,\eta)$, and a continuous part. As figure 2*a* shows, the probability that a cohort does not experience a jump decreases along the characteristic line η, as probability is transferred from the atom to the continuous part of the distribution. Substituting back $\xi = t - \tau$ and $\eta = \tau$ into (A 5) gives

$$p_N(n;t,\tau) = \frac{1}{n}\,\mathrm{e}^{-\gamma\psi(t,\tau)-\tau\lambda}\left(\delta(\psi(t,\tau)) + \frac{\sqrt{\gamma\tau\lambda}I_1(2\sqrt{\gamma\tau\lambda}\sqrt{\psi(t,\tau)})}{\sqrt{\psi(t,\tau)}}\right) \quad n \le \iota(t-\tau)\varphi(t,\tau), \tag{A 6}$$

where $\varphi(t,\tau) = \mathrm{e}^{-\int_0^\tau \mu_\mathrm{d}(t-\tau+u,u)\,\mathrm{d}u}$ and $\psi(t,\tau) = \ln(\varphi(t,\tau)\iota(t-\tau)/n)$.

Appendix B

We derive equation (3.3) for the kth order moment of N. By applying the expectation operator $E[g(x)^k] = \int_0^\infty g(x)^k p_X(x)\,\mathrm{d}x$ to equation (2.5), we obtain

$$\frac{\mathrm{d}\bar{N}_k}{\mathrm{d}\eta} = \mu_\mathrm{d}\int_0^\infty n^k\frac{\partial n p_N}{\partial n}\,\mathrm{d}n - \lambda\bar{N}_k + \lambda\gamma\int_0^\infty n^{\gamma-1+k}\int_n^\infty p_N(u)u^{-\gamma}\,\mathrm{d}u\,\mathrm{d}n. \tag{B 1}$$

The first integral on the right-hand side is solved by first expanding the derivative with respect to n and then integrating by parts,

$$\begin{aligned}\mu_\mathrm{d}\int_0^\infty n^k\frac{\partial p_N}{\partial n}\,\mathrm{d}n &= \mu_\mathrm{d}\int_0^\infty (n^k p + n^{k+1}\frac{\partial p_N}{\partial n})\,\mathrm{d}n = \mu_\mathrm{d}\bar{N}_k + \mu_\mathrm{d}\int_0^\infty n^{k+1}\frac{\partial p_N}{\partial n}\,\mathrm{d}n\\ &= \mu_\mathrm{d}\bar{N}_k - k\mu_\mathrm{d}\bar{N}_k - \mu_\mathrm{d}\bar{N}_k = -k\mu_\mathrm{d}\bar{N}_k.\end{aligned} \tag{B 2}$$

By using the product rule, the integrand in the last term can be expressed as

$$n^{\gamma-1+k}\int_n^\infty u^{-\gamma}p_N(u)\,\mathrm{d}u = \frac{1}{(\gamma+k)}\frac{\mathrm{d}}{\mathrm{d}n}\left(n^{\gamma+k}\int_n^\infty u^{-\gamma}p_N(u)\,\mathrm{d}u\right) + \frac{n^k p_N(n)}{(\gamma+k)}, \tag{B 3}$$

and, after integration with respect to n,

$$\int_0^\infty n^{\gamma-1+k}\int_n^\infty u^{-\gamma}p_N(u)\,\mathrm{d}u\,\mathrm{d}n = \frac{1}{\gamma+k}\bar{N}_k. \tag{B 4}$$

Substituting back into (B 1) yields

$$\frac{\mathrm{d}\bar{N}_k}{\mathrm{d}\eta} = -\mu_\mathrm{d}k\bar{N}_k - \lambda\bar{N}_k + \frac{\lambda\gamma}{\gamma+k}\bar{N}_k. \tag{B 5}$$

Returning to the original variables,

$$\frac{\partial\bar{N}_k}{\partial t} + \frac{\partial\bar{N}_k}{\partial\tau} = -\mu_\mathrm{d}k\bar{N}_k - \lambda\bar{N}_k + \frac{\lambda\gamma}{\gamma+k}\bar{N}_k. \tag{B 6}$$

Appendix C

We solve equation (2.7) in steady-state conditions for constant boundary condition, $n = \iota$, and constant deterministic loss function, μ_d. Introducing new variables [35], $W = \iota/\mu_\mathrm{d}\,\mathrm{e}^X$, $t = \bar{t}/\mu_\mathrm{d}$ and $\lambda = \bar{\lambda}\mu_\mathrm{d}$, equation (2.7) becomes

$$\frac{\mathrm{d}(1-e^{-X})p_X}{\mathrm{d}X} - \bar{\lambda}p_X + \bar{\lambda}\gamma\,\mathrm{e}^{\gamma X}\int_X^\infty p_X(u)\,\mathrm{e}^{-\gamma u}\,\mathrm{d}u = 0. \tag{C 1}$$

Multiplying (C 1) by $\mathrm{e}^{-\gamma X}$, differentiating with respect to X and then integrating once gives

$$X(e^{-X}-1)p_X + \frac{\mathrm{d}(1-e^{-X})p_X}{\mathrm{d}X} - \bar{\lambda}p_X = C, \tag{C 2}$$

where C is the integrating constant. As the left-hand side goes to zero as $X \to \infty$, C must be equal to zero. Finally, integrating again yields

$$p_X(X) = R\,\mathrm{e}^{X(\gamma+1)}(1-\mathrm{e}^X)^{\bar{\lambda}-1}, \tag{C 3}$$

where R is the normalization constant. Transforming back to the original variables gives equation (3.5) of the main text,

$$p_W(w) = R\iota^{-\gamma-\lambda/\mu_\mathrm{d}}\mu_\mathrm{d}^{\gamma+1}w^{\gamma}(\iota-\mu_\mathrm{d}w)^{\lambda/\mu_\mathrm{d}-1} \quad w \le \frac{\iota}{\mu_\mathrm{d}}, \tag{C 4}$$

where, by imposing the normalization condition, $R = 1/B(\gamma+1, \lambda/\mu_\mathrm{d})$, $B(a,b)$ being the Beta function with shape parameters a and b.

References

1. Langmuir I. 1908 The velocity of reactions in gases moving through heated vessels and the effect of convection and diffusion. *J. Am. Chem. Soc.* **30**, 1742–1754. (doi:10.1021/ja01953a011)
2. Danckwerts P. 1953 Continuous flow systems: distribution of residence times. *Chem. Eng. Sci.* **2**, 1–13. (doi:10.1016/0009-2509(53)80001-1)
3. Lotka AJ. 1956 *Elements of mathematical biology*. New York, NY: Dover Publications.
4. M'Kendrick A. 1925 Applications of mathematics to medical problems. *Proc. Edinburgh Math. Soc.* **44**, 98–130. (doi:10.1017/S0013091500034428)
5. von Foerster H. 1959 Some remarks on changing populations. In *The kinetics of cellular proliferation* (ed. JF Stohlman), pp. 382–407. New York, NY: Grune and Stratton.
6. Trucco E. 1965 Mathematical models for cellular systems the von Foerster equation. Part I. *Bull. Math. Biophys.* **27**, 285–304. (doi:10.1007/BF02478406)
7. Keyfitz BL, Keyfitz N. 1997 The McKendrick partial differential equation and its uses in epidemiology and population study. *Math. Comput. Model.* **26**, 1–9. (doi:10.1016/S0895-7177(97)00165-9)
8. Kot M. 2001 *Elements of mathematical ecology*. Cambridge, UK: Cambridge University Press.
9. Murray J. 2002 *Mathematical biology. I. An introduction*. Interdisciplinary Applied Mathematics, vol. 17. New York, NY: Springer.
10. Gurtin ME, MacCamy RC. 1974 Non-linear age-dependent population dynamics. *Arch. Ration. Mech. Anal.* **54**, 281–300. (doi:10.1007/BF00250793)
11. Gurtin ME, MacCamy RC. 1979 Some simple models for nonlinear age-dependent population dynamics. *Math. Biosci.* **43**, 199–211. (doi:10.1016/0025-5564(79)90049-X)
12. Webb GF. 1985 *Theory of nonlinear age-dependent population dynamics*. Boca Raton, FL: CRC Press.
13. Lineweaver CH, Fenner Y, Gibson BK. 2004 The galactic habitable zone and the age distribution of complex life in the milky way. *Science* **303**, 59–62. (doi:10.1126/science.1092322)
14. Fall SM, Chandar R, Whitmore BC. 2005 The age distribution of massive star clusters in the antennae galaxies. *Astrophys. J. Lett.* **631**, L133. (doi:10.1086/496878)
15. Ginn TR. 1999 On the distribution of multicomponent mixtures over generalized exposure time in subsurface flow and reactive transport: foundations, and formulations for groundwater age, chemical heterogeneity, and biodegradation. *Water Resour. Res.* **35**, 1395–1407. (doi:10.1029/1999WR900013)
16. Ginn TR, Haeri H, Massoudieh A, Foglia L. 2009 Notes on groundwater age in forward and inverse modeling. *Transp. Porous. Media* **79**, 117–134. (doi:10.1007/s11242-009-9406-1)
17. Duffy CJ. 2010 Dynamical modelling of concentration–age–discharge in watersheds. *Hydrol. Process.* **24**, 1711–1718. (doi:10.1002/hyp.7691)
18. Botter G, Bertuzzo E, Rinaldo A. 2011 Catchment residence and travel time distributions: the master equation. *Geophys. Res. Lett.* **38**, L11403. (doi:10.1029/2011GL047666)
19. Calabrese S, Porporato A. 2016 Multiple outflows, spatial components, and nonlinearities in age theory. *Water Resour. Res.* **53**, 110–126. (doi:10.1002/2016WR019227)
20. Wagner CEV. 1978 Age-class distribution and the forest fire cycle. *Canadian J. Forest Res.* **8**, 220–227. (doi:10.1139/x78-034)
21. Law R. 1983 A model for the dynamics of a plant population containing individuals classified by age and size. *Ecology* **64**, 224–230. (doi:10.2307/1937069)

22. Boychuk D, Perera AH, Ter-Mikaelian MT, Martell DL, Li C. 1997 Modelling the effect of spatial scale and correlated fire disturbances on forest age distribution. *Ecol. Model.* **95**, 145–164. (doi:10.1016/S0304-3800(96)00042-7)
23. DePaolo DJ, Linn AM, Schubert G. 1991 The continental crustal age distribution: methods of determining mantle separation ages from sm-nd isotopic data and application to the southwestern united states. *J. Geophys. Res.: Solid Earth* **96**, 2071–2088. (doi:10.1029/90JB02219)
24. Harlavan Y, Erel Y, Blum JD. 1998 Systematic changes in lead isotopic composition with soil age in glacial granitic terrains. *Geochim. Cosmochim. Acta.* **62**, 33–46. (doi:10.1016/S0016-7037(97)00328-1)
25. Parker SL, Tong T, Bolden S, Wingo PA. 1996 Cancer statistics, 1996. *CA Cancer J. Clin.* **46**, 5–27. (doi:10.3322/canjclin.46.1.5)
26. Jagers P. 1975 *Branching processes with biological applications*. New York, NY: Wiley.
27. Jagers P, Klebaner FC. 2000 Population-size-dependent and age-dependent branching processes. *Stoch. Process. Appl.* **87**, 235–254. (doi:10.1016/S0304-4149(99)00111-8)
28. Porporato A, Calabrese S. 2015 On the probabilistic structure of water age. *Water. Resour. Res.* **51**, 3588–3600. (doi:10.1002/2015WR017027)
29. Hanson FB, Tuckwell HC. 1981 Logistic growth with random density independent disasters. *Theor. Popul. Biol.* **19**, 1–18. (doi:10.1016/0040-5809(81)90032-0)
30. Lande R. 1993 Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142**, 911–927. (doi:10.1086/285580)
31. Hanson FB, Tuckwell HC. 1997 Population growth with randomly distributed jumps. *J. Math. Biol.* **36**, 169–187. (doi:10.1007/s002850050096)
32. Lande R, Engen S, Saether B-E. 2003 *Stochastic population dynamics in ecology and conservation*. Oxford, UK: Oxford University Press.
33. D'Odorico P. 2000 A possible bistable evolution of soil thickness. *J. Geophys. Res.: Solid Earth* **105**, 25 927–25 935. (doi:10.1029/2000JB900253)
34. Camporeale C, Ridolfi L. 2006 Riparian vegetation distribution induced by river flow variability: a stochastic approach. *Water. Resour. Res.* **42**, W10415. (doi:10.1029/2006WR004933)
35. Mau Y, Feng X, Porporato A. 2014 Multiplicative jump processes and applications to leaching of salt and contaminants in the soil. *Phys. Rev. E* **90**, 052128. (doi:10.1103/PhysRevE.90.052128)
36. Daly E, Porporato A. 2006 State-dependent fire models and related renewal processes. *Phys. Rev. E* **74**, 041112. (doi:10.1103/PhysRevE.74.041112)
37. Qi-Min Z, Wen-An L, Zan-Kan N. 2004 Existence, uniqueness and exponential stability for stochastic age-dependent population. *Appl. Math. Comput.* **154**, 183–201. (doi:10.1016/S0096-3003(03)00702-1)
38. Zhang Q-m, Han C-z. 2005 Numerical analysis for stochastic age-dependent population equations. *Appl. Math. Comput.* **169**, 278–294. (doi:10.1016/j.amc.2004.10.088)
39. Ovaskainen O, Meerson B. 2010 Stochastic models of population extinction. *Trends. Ecol. Evol. (Amst.)* **25**, 643–652. (doi:10.1016/j.tree.2010.07.009)
40. Wang L, Wang X. 2010 Convergence of the semi-implicit Euler method for stochastic age-dependent population equations with Poisson jumps. *Appl. Math. Model.* **34**, 2034–2043. (doi:10.1016/j.apm.2009.10.016)
41. Stukalin EB, Aifuwa I, Kim JS, Wirtz D, Sun SX. 2013 Age-dependent stochastic models for understanding population fluctuations in continuously cultured cells. *J. R. Soc. Interface* **10**, 20130325. (doi:10.1098/rsif.2013.0325)
42. Suweis S, Rinaldo A, Van der Zee S, Daly E, Maritan A, Porporato A. 2010 Stochastic modeling of soil salinity. *Geophys. Res. Lett.* **37**, L07404. (doi:10.1029/2010GL042495)
43. Rodríguez-Iturbe I, Porporato A. 2004 *Ecohydrology of water-controlled ecosystems: soil moisture and plant dynamics*. Cambridge, UK: Cambridge University Press.
44. Manzoni S, Molini A, Porporato A. 2011 Stochastic modelling of phytoremediation. *Proc. R. Soc. A* **467**, 3188–3205. (doi:10.1098/rspa.2011.0209)
45. Ridolfi L, D'Odorico P, Laio F. 2011 *Noise-induced phenomena in the environmental sciences*. Cambridge, UK: Cambridge University Press.
46. Stratonovich RL. 1967 *Topics in the theory of random noise*, vol. 2. Boca Raton, FL: CRC Press.
47. Gardiner C. 1985 *Handbook of stochastic processes*. Berlin, Germany: Springer.
48. Suweis S, Porporato A, Rinaldo A, Maritan A. 2011 Prescription-induced jump distributions in multiplicative Poisson processes. *Phys. Rev. E* **83**, 061119. (doi:10.1103/PhysRevE.83.061119)
49. Chechkin A, Pavlyukevich I. 2014 Marcus versus Stratonovich for systems with jump noise. *J. Phys. A: Math. Theor.* **47**, 342001. (doi:10.1088/1751-8113/47/34/342001)

50. Calabrese S, Porporato A. 2015 Linking age, survival, and transit time distributions. *Water. Resour. Res.* **51**, 8316–8330. (doi:10.1002/2015WR017785)
51. Cox DR, Miller HD. 1977 *The theory of stochastic processes*, vol. 134. Boca Raton, FL: CRC Press.
52. VanKampen N. 2007 *Stochastic processes in physics and chemistry*. Amsterdam, The Netherlands: North Holland.
53. Ross SM. 2014 *Introduction to probability models*. New York, NY: Academic Press.
54. Cox DR. 1962 *Renewal theory*. London, UK: Methuen.