Mathematical modeling of a random dispersal in heterogeneous environments

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Abstract. The randomness is well-understood in homogeneous environments only. Brownian motion in a spatially constant temperature is an example. However, the randomness in heterogeneous environment is not well-understood and its understanding may give us a key to open many mysteries of real world phenomena. In this talk we will discuss how to model such heterogeneous randomness mathematically and then how to apply it to dispersals of biological organisms. Starvation driven dispersal will be introduced in the context.

Key words. random walk, starvation driven diffusion, Brownian motion, thermal diffusion

Derivation of a diffusion equation with a non-uniform randomness

Consider a random walk system with a walk length Δx and a traveling time Δt. Let $0 < \gamma(x_i) \le 1$ be the probability for a particle to depart a grid point x_i at each jumping time. (For a usual random walk system every particle departs at each jumping time and hence $\gamma = 1$.) Each particle moves to one of two adjacent grid points, x_{i+1} or x_{i-1}, randomly. Let $U(x_i)$ be the number of particles placed at the grid point x_i. Then, the particle density is $u = U/\Delta x$. Hence the net flux that crosses a middle point $x_{i+1/2} := \frac{x_i + x_{i+1}}{2}$ is

$$
\begin{aligned}
J\Big|_{x_{i+1/2}} &= \frac{\gamma(x_i)|\Delta x|u(x_i)}{2|\Delta t|} - \frac{\gamma(x_{i+1})|\Delta x|u(x_{i+1})}{2|\Delta t|} \\
&\cong -\frac{|\Delta x|}{2}\Big(\frac{|\Delta x|}{\Delta t}\gamma u\Big)_x\Big|_{x_{i+1/2}} \qquad (1) \\
&\cong -\frac{|\Delta x|^2}{2\Delta t}(\gamma u)_x\Big|_{x_{i+1/2}}. \qquad (2)
\end{aligned}
$$

Notice that, if Δx and Δt are non-constant, one should stop at (1). The approximation (2) is valid only if Δx and Δt are constant.

Applications of non-uniform random dispersal

Non-uniform random dispersal is found in many places.

1. *Homogeneous diffusion.* Brownian motion in a spatially constant temperature is an example. In the case Δx and Δt can be assumed constant. For the Brownian motions, $\gamma = 1$. Then, the corresponding diffusion equation comes from the conservation law $u_t == \nabla \cdot (J)$, i.e.,
$$u_t = du_{xx}, \quad d := \frac{1}{2}\frac{|\Delta x|^2}{\Delta t}. \tag{3}$$
2. *Heterogeneous diffusion.* Brownian motion in a spatially non-constant temperature is an example. Then, Δx and Δt cannot be assumed constant. The corresponding diffusion equation is
$$u_t = \frac{|\Delta x|}{2}\Big(\frac{|\Delta x|}{\Delta t}u\Big)_{xx}. \tag{4}$$
3. *Is the movement of a gas particle random?* Consider a room with gas particles of single kind where the room temperature is not constant. Color one of them with red. Then the movement of the colored particle is chaotic and brownian motion like. Then, is it a random movement? It seems that it couldn't. The probability density distribution does not satisfy (4) since the probability density should follow the gas density, which is probably
$$u_t = \Big(\frac{\Delta x}{2\Delta t}(\Delta x\, u)_x\Big)_x.$$
However, in this case, Δx is the mean free path in algebraic mean. On the other hand, the previous case is in root mean square sense. The thermal diffusion seems between these two cases. Understanding the relation between these two seems important in statistical physics.
4. *Dispersal strategy of biological organisms.* One may imagine several levels of dispersal strategies of biological organisms.
   (a) The species has no control of any kind and moves just randomly. Then, the equation (3) is the corresponding model.
   (b) The species may feel gradient of environment and move toward or against the gradient. Then, the model is
   $$u_t = (du_x + \alpha u\, m_x)_x. \tag{5}$$
   (c) The species does not know such a gradient, but has an ability to stay at a favorable place and to leave a unfavorable one. In the case we may use the model
   $$u_t = (\gamma u)_{xx}. \tag{6}$$
   This is the case of our interest and the detail of this case in the next section.

(d) The species do not know a gradient of environment. However, they may remember good places and bad places and move along mostly good places with possible erratic behavior. It seems human behavior is like this.

A more realistic case is not necessarily mathematically more meaningful. The linear model (a) has been intensively studied mathematically and physically. The case (b) is actually confusing since we can model the advection only phenomenologically. However, since the case (a) could not give any advection effect, (b) also has been studied a lot. The physical meaning of (c) is relatively simple and realistic. Furthermore, it gives advection effect. The case (d) or more detailed ones are can be useful in simulations. However, their mathematically meaning is doubtful.

Derivation of a starvation driven diffusion

If Δx and Δt are constant, after a time rescaling, we obtain

$$u_t = (\gamma u)_{xx}.$$

Notice that this derivation is valid since the probability γ depends only on the point x_i that the particle departs. For a more discussion including other cases, see Okubo and Levin [1, §5.4].

It is reasonable to believe that biological organisms will increase the departing rate if they are starved. Individuals will be starved if there is no food or if are are many organisms. Hence, if m is the amount of food available and u is the population, it is reasonable to assume that $\gamma = \gamma(m, u)$ and

$$\gamma_m \leq 0 \quad \text{and} \quad \gamma_u \geq 0.$$

The process with these properties can be called a starvation driven diffusion since the diffusion is increased on starvation.

If we set $s = \frac{m}{u}$, then s is the amount of food that each individuals may obtain on average. We may consider a case that γ is a decreasing function of s, i.e., $\gamma(m, u) = \gamma(\frac{m}{u})$ with $\gamma'(s) < 0$. Then, clearly,

$$\gamma_m = \gamma'(s)\frac{1}{u} \leq 0 \quad \text{and} \quad \gamma_u = -\gamma'(s)\frac{m}{u^2} \geq 0.$$

See [2] for a detailed discussion of the starvation driven diffusion. Also see [3–5] for its applications and analyses.

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