Global signature of diffusion

Random walk
\[ x(t+1) = x(t) \pm 1 \]
\[ \Rightarrow x^2(t+1) = x^2(t) + 2x(t) + 1 \quad (1/2 \text{ of time}) \]
\[ = x^2(t) - 2x(t) + 1 \quad (1/2 \text{ of time}) \]

\[ <x^2(t+1)> = (1/2) * <x^2(t) + 2x(t) + 1> \]
\[ + (1/2) * <x^2(t) - 2x(t) + 1> \]
\[ = <x^2(t)> + 1 = <x^2(t-1)> + 2 \]

Iterating this gives: \[ <x^2(t+1)> = \text{Number of time steps} \sim t \]

\[ \Rightarrow |x| = \sqrt{x^2} = \sqrt{t} \]
Net Flow--Directional Forces

Net Flow = Flow In - Flow Out

\[ f(i,t+1) - f(i,t) = v(i-1)f(i-1,t) - v(i)f(i,t) \]

Continuum limit:

\[ \frac{df}{dt} = -\frac{d(vf)}{dx} \] (i.e., distance = velocity * time)

\[ f(i,t) \] is abundance or probability of being in bin \( i \) at time, \( t \).

\[ v(i) \] is speed of flow out of bin \( i \).
Net Flow--Nondirectional Forces

Net Flow = Flow In - Flow Out

= Flow from left (i-1 -> i) + Flow from right (i+1 -> i)
- Flow to right (i -> i-1) - Flow to left (i -> i+1)

-> f(i,t+1) - f(i,t) = D(i-1)f(i-1,t) + D(i+1)f(i+1,t) - 2*D(i)f(i,t)

D(i) is the diffusion rate

Continuum limit:
- > df/dt = d^2(Df)/dx^2 (Second derivative)

Local process and affects width of distribution, not mean
Combined Effects

Person trying to walk north (directional) through a busy intersection (nondirectional)

Net Flow = Directional Flow + Nondirectional Flow

Diffusion Equation
(Also known as Kolmogorov forward equation)

\[ \frac{\partial f}{\partial t} = - \frac{\partial (vf)}{\partial x} + \frac{\partial^2 (Df)}{\partial x^2} \]
Different derivation

\[ \Psi(p,t + dt \mid p_0) = \int \Psi(p - \varepsilon, t \mid p_0) g(p - \varepsilon, \varepsilon, dt) d\varepsilon \]

Probability density of having frequency \( p \) at time \( t + dt \)

Probability of moving from \( p - \varepsilon \) to \( p \)

Taylor expand in \( p \) around epsilon to get Kolmogorov forward equations

\[ \frac{\partial \Psi(p,t \mid p_0)}{\partial t} = - \frac{\partial}{\partial p} \left[ \Psi(p,t \mid p_0) M(p) \right] + \frac{1}{2} \frac{\partial^2}{\partial p^2} \left[ \Psi(p,t \mid p_0) V(p) \right] \]
Looking backward in time, as for coalescence, gives Kolmogorov backward equation

$$\frac{\partial \Psi(p,t | p_0)}{\partial t} = M(p_0) \frac{\partial \Psi(p,t | p_0)}{\partial p_0} + \frac{V(p_0)}{2} \frac{\partial^2 \Psi(p,t | p_0)}{\partial p_0^2}$$

Sign of directional term flips because now going backwards in time and is time reversible. Non-directional term does not flip sign because non-reversible.
Types of multidisciplinary influences

- Physical Process: Magnetotactic bacteria
- Conceptual and Mathematical Analogy: Evolution and Population Genetics
  -> Combine natural selection and genetic drift
We can also understand process of evolution by means of diffusion equation. Requires different sort of extension to biology. It’s not just understanding how biological organisms use and are constrained by physics, but it’s using analogies to mathematical physics to understand biological problems.
Selection--Directional Force

Let a population (wild type) suddenly have a few individuals with a mutation that forms a new allele.

If fitness (as measured by growth rate--number of offspring per individual per generation that survive to next generation) of wild type is normalized to 1, and mutants have fitness 1+s

\[ \ln(\text{Population Size}) \]

\[ \text{Wild type} \]

\[ \text{Mutant} \]

\[ \text{time} \]
Position space, $x$, is replaced by frequency space, $p$, for frequency of mutants.

Velocity of selection force is $\sim p(1-p)s$.
So, rate of spread of the width of distribution is $\sim p(1-p)/2N$.
Equation for Population Genetics

\[
\frac{\partial P(p,t \mid p_0)}{\partial t} = -p(1-p)s \frac{\partial P(p,t \mid p_0)}{\partial p} + \frac{p(1-p)}{4N} \frac{\partial^2 P(p,t \mid p_0)}{\partial p^2}
\]

\(p_0\) is initial frequency of mutants in the population.

Questions we can answer using this equation.
1. Is mutant population likely to go extinct or take over population (fixation)?
2. How long does it take before extinction or fixation occurs?
3. For a given \(N\) and \(s\), how large does \(p_0\) need to be before mutants are likely to take over.
Equilibrium Distribution of Kolmogorov backward equations

\[ P(x,t) = A \int_0^{x'} e^{-2 \int_0^{x'} \frac{M(x'')}{V(x'')}} \, dx'' \]
Probability of Fixation

Solve equation at $\frac{\partial P}{\partial t} = 0$ and impose boundary condition for $p_0=0$ and $p_0=1$.

Probability of Fixation of mutants

$$u(p_0) = \frac{1 - e^{-4Ns p_0}}{1 - e^{-4N_s}}$$
Investigate some limits

1. Large population, strong selection:
   \[ e^{-4Nsp_0} \ll 1 \rightarrow u(p_0) \sim 1 \text{ (guaranteed to fix)} \]

2. Under very weak selection (s->0):
   \[ e^{-4Nsp_0} \sim 1 - 4Nsp_0 \rightarrow u(p_0) \sim p_0, \]
   When one mutant, \( p_0 = 1/N \), and \( u(1/N) \sim 1/N \) (same as for pure drift)
Strong Analogy

1. Selection ↔ Gravity ↔ Pushed by marathon
2. Drift ↔ Brownian motion ↔ Crowd at intersection

3. Small organisms ↔ Small populations
   (Brownian>>Gravity)   (Drift>>Selection)
4. Large organisms ↔ Large populations
   (Gravity>>Brownian)   (Selection>>Drift)
Economics Black-Scholes model

Price of stock is like position space (physics) or frequency space (population genetics).

Directional force--general increase in worth of the market, represented by interest rate.

Nondirectional force--random forces in market.
Individual stocks or groups of stock will wander randomly in price. (major insight of this model!
Also, because it shows value of volatility and how to make money from it.)
Assumptions of Black-Scholes

1. Price follows Brownian motion
2. It is possible to short sell stock (options)
3. No arbitrage is possible (no asymmetry of which to take advantage)
4. Trading is continuous
5. No transaction costs or taxes
6. Stock’s price is continuous and can be arbitrarily small
7. Risk-free interest rate is constant
Results from Black-Scholes

Provides method for calculating fair cost of an option.

Provides method for hedging “bets” and getting “risk-free” investment that allows one to make money according to the overall growth of the market.
Black-Scholes PDE

$$\frac{\partial V}{\partial t} = -\frac{1}{2} \sigma^2 S^2 \frac{\partial^2 V}{\partial S^2} - rS \frac{\partial V}{\partial S} + rV$$

S-stock price
V-option cost
r-interest rate
\(\sigma\)-variance of random process
Impact of this work

One equation, similar concepts, applications to multiple fields with its own set of insights

1. Fourier developed the heat equation
2. Brownian motion, Einstein’s greatest achievement?
3. Applied in cosmology, particle physics, etc.
4. Big advance in population genetics, used to study molecular motors, and lots of intracellular processes
5. 1997 Nobel prize in economics for Black-Scholes
Conclusions

1. Diffusion equations describe directional and nondirectional forces. (Could also have forces on higher-order moments by extending this.)

2. Because of generality of 1, we can apply them to many different types of problems in many different fields. (Multidisciplinary)

3. Diffusion equations have already proved very useful in physics, biology, and economics.

4. Examples of two types of multidisciplinary science:
   a. Results from one field directly place constraints on or are utilized by agents in the other field.
   b. By the correct choice of analogy between fields, mathematical treatments and results can be used to draw new conclusions and insights within another field.