Spatial Model

- Rates are very slow---not sure why Tilman chose these. You may alter these as long as you explain what you are doing.
- Remember that the solution to the Levins model is based on continuous rates. You know how to change those to discrete rates.
- Two programming approaches are possible.
  - Cycle over 2- dimensional array (or sheet)
  - User defined data type for plants with locations

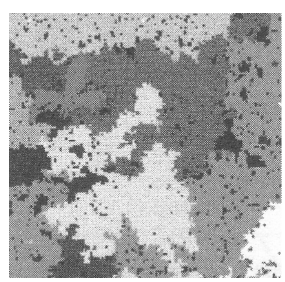
```
Option Explicit
Sub population()
Type Plant
   x As Double
   y As Double
End Type
Dim population(10000) As Plant
For j = 1 To 10000 step 1
   Plant(j).x = etc
   Plant(j).y = etc
etc.
Next j
End Sub
```

Grazing Model

- You specify U over a range of levels
- Initial conditions
  - NPP = 600
  - G = 0

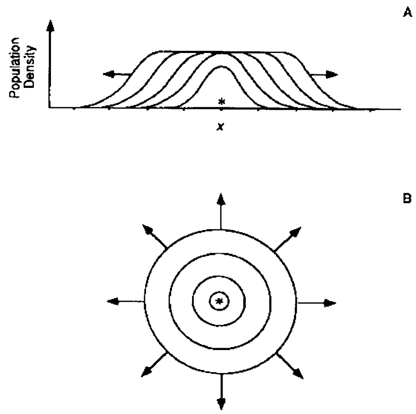
Types of Spatial Models

- Spatially Implicit
  - single state variable
  - multiple state variables
- Spatially Explicit
  - grid based
    - categorical
    - continuous
  - individual based
  - reaction diffusion



$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) + ru\left(1 - \frac{u}{K}\right)$$

Partial Differential Equation Models in Ecology



$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) + ru\left(1 - \frac{u}{K}\right)$$

Sources

- Turchin , P. 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinuear, Sunderland, Mass. USA.
- Holmes, E. E., M. A. Lewis, J. E. Banks, and R. R. Veit. 1994. Partial differential equations in ecology: Spatial interactions and population dynamics. Ecology **75**:17-29.
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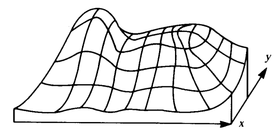
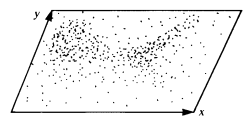
- Taubes, C. H. 2001. Modeling Differential Equations in Biology. Prentice Hall, Upper Saddle River, N.J., USA.
- Dieckmann, U., R. Law, and J. A. J. Metz. 2000. The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge, U. K.

Functions of 2 Variables



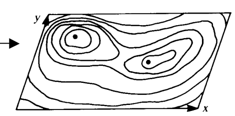
(a)

$u = f(x,y)$



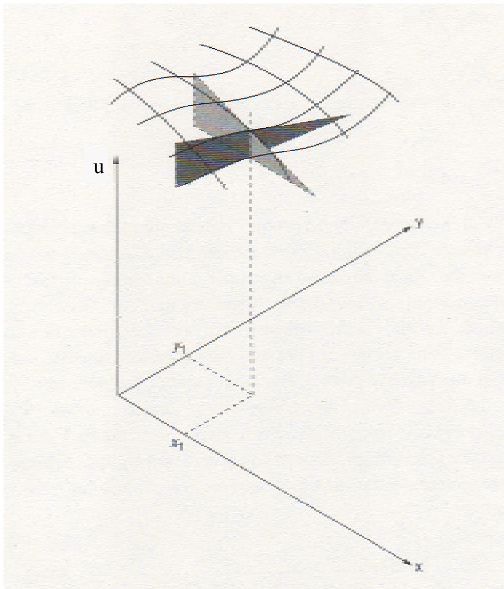
(c)

Special case $f(x,y) = k$, a constant



Partial Derivatives

- Partial derivatives have application in non-linear optimization and confidence intervals on model parameters.
- *Derivatives* apply to functions with 1 independent variable.
- *Partial derivatives* apply to functions with >1 independent variables.
- For each variable, take derivative as if it were the only independent variable. Treat others as constants.



Partial Derivatives

What are partial derivatives at point (x_1,y_1)?

Diagram from Gillman, M., and R. Hails. 1997. An Introduction to Ecological Modelling : Putting Practice Into Theory (Methods in Ecology Series). Blackwell Science, London.

First Principles Definition of Partial Derivative

Given a function $u = f(x, y)$

The partial derivative of f with respect to x:

$$\frac{\partial f}{\partial x} = \lim_{\Delta x \to 0} \frac{f(x + \Delta x, y) - f(x, y)}{\Delta x}$$

The partial derivative of f with respect to y:

$$\frac{\partial f}{\partial y} = \lim_{\Delta x \to 0} \frac{f(x, y + \Delta y) - f(x, y)}{\Delta y}$$

Partial derivative example

$$z = ax^2 + bxy + cy^2 + dx + ey + f$$

$$\frac{\partial z}{\partial x} = 2ax + by + d$$

$$\frac{\partial z}{\partial y} = bx + 2cy + e$$

Second Partial Derivatives

$$u(x, y) = x^2 y^3 + y^3 x - 7$$

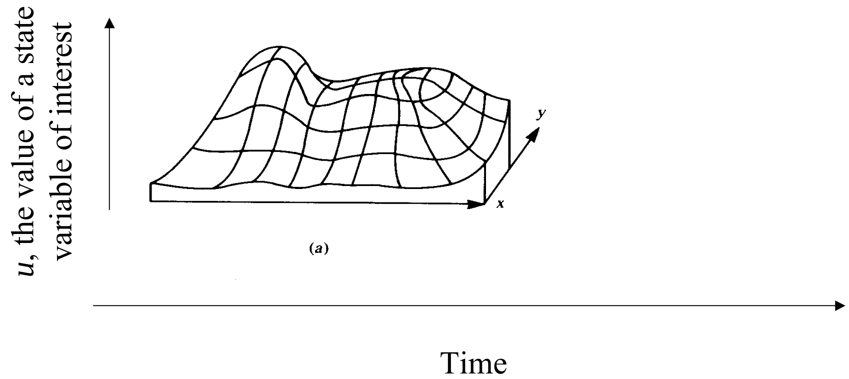
$$\frac{\partial u}{\partial x} = 2xy^3 + y^3$$

$$\frac{\partial}{\partial x}\left(\frac{\partial u}{\partial x}\right) = 2y^3$$

This is the common notation

$$\frac{\partial}{\partial x}\left(\frac{\partial u}{\partial x}\right) = \frac{\partial^2 u}{\partial x^2} = 2y^3$$

Partial Differential Equations



As before, we have an equation for the rate of change and we want to understand how the state changes. But now we want to know how the state changes over *x*, *y*, and *t*.

Partial Differential Equations to Model Change in Position with Time

Basic form of diffusion model: $\frac{\partial u(x,y,t)}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right)$

where D is the diffusion rate with units $\frac{\text{distance}^2}{\text{time}}$.

$u(x,y,t)$ is the mass, number, or density of a quantity of interest at location (x,y) at time t.

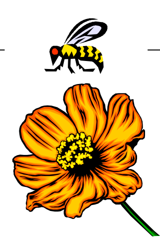
$$\frac{\partial u(x,y,t)}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right)$$

is usually written as

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right)$$

Derivation of Diffusion from Random Walk

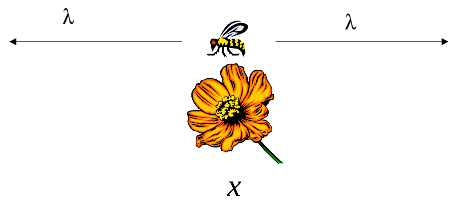
λ ← → λ



x

λ is the distance moved in one time step.

probability of move to left = probability of move to right = 1/2



Given that a bee starts at position $x = 0$ at time $t = 0$, what it the probability of finding the bee at any position x at a later time $t + \Delta t$, that is, $p(x,t + \Delta t)$? Let $\Delta t = \tau$.

Define an update rule for the bee's position:

$$p(x, t + \tau) = \frac{1}{2} p(x - \lambda, t) + \frac{1}{2} p(x + \lambda, t)$$

$$p(x, t + \tau) = \frac{1}{2} p(x - \lambda, t) + \frac{1}{2} p(x + \lambda, t)$$

- Subtract $p(x,t)$ from both sides
- Divide both sides by τ
- Divide both sides by λ^2

$$\begin{aligned} p(x, t + \tau) - p(x, t) &= \frac{1}{2} \left[p(x + \lambda, t) - 2p(x, t) + p(x - \lambda, t) \right] \\ \frac{p(x, t + \tau) - p(x, t)}{\tau} &= \frac{\lambda^2}{2\tau} \left[\frac{p(x + \lambda, t) - 2p(x, t) + p(x - \lambda, t)}{\lambda^2} \right] \end{aligned}$$

1) $$\frac{p(x,t+\tau)-p(x,t)}{\tau} = \frac{\lambda^2}{2\tau}\left[\frac{p(x+\lambda,t)-2p(x,t)+p(x-\lambda,t)}{\lambda^2}\right]$$

The next step may be easier to understand if we rearrange the quantity in the square brackets:

$$\frac{p(x+\lambda,t)-2p(x,t)+p(x-\lambda,t)}{\lambda^2} = \frac{\frac{p(x+\lambda,t)-p(x,t)}{\lambda} - \frac{p(x,t)-p(x-\lambda,t)}{\lambda}}{\lambda}$$

Change in the rate of change per unit distance

1) $$\frac{p(x,t+\tau)-p(x,t)}{\tau} = \frac{\lambda^2}{2\tau}\left[\frac{p(x+\lambda,t)-2p(x,t)+p(x-\lambda,t)}{\lambda^2}\right]$$

If τ is small relative to the time scale we observe the bee and if λ is small relative to the spatial extent over which the bee forages:

$$\text{lhs}(1) \approx \frac{\partial p(x,t)}{\partial t}$$

$$\text{rhs}(1) \approx \frac{\lambda^2}{2\tau}\frac{\partial^2 p(x,t)}{\partial x^2}$$

$$\text{lhs}(1) \approx \frac{\partial p(x,t)}{\partial t}$$

$$\text{rhs}(1) \approx \frac{\lambda^2}{2\tau}\frac{\partial^2 p(x,t)}{\partial x^2}$$

Allowing $\frac{\lambda^2}{2\tau} = D$, the diffusion coefficient,

and definfing $p \equiv p(x,t)$, we have

$$\frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2},$$

which is the one dimension equation for passive diffusion.

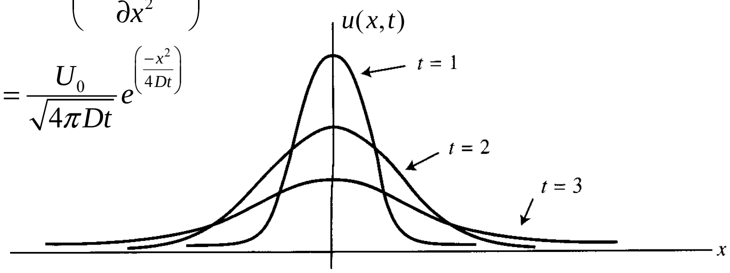
Interpretation

Given that p(x,t) is the probability of observing an individual bee at point x at time t, we can extend to many bees (*N*) by seeing that *p(x,t)N* = number of bees at bees at point *x* at time *t*, i.e., the spatial distribution of a population leaving a point at time *t=0.*

Solutions for Simple Diffusion Models

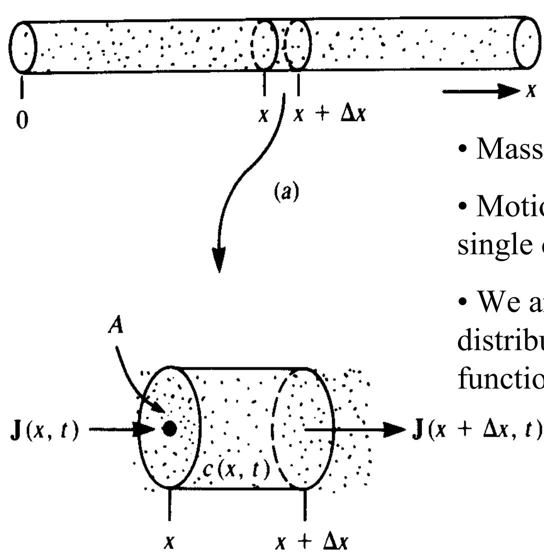
$$\frac{\partial u(x,t)}{\partial t} = D\left(\frac{\partial^2 u(x,t)}{\partial x^2}\right)$$

$$u(x,t) = \frac{U_0}{\sqrt{4\pi Dt}} e^{\left(\frac{-x^2}{4Dt}\right)}$$



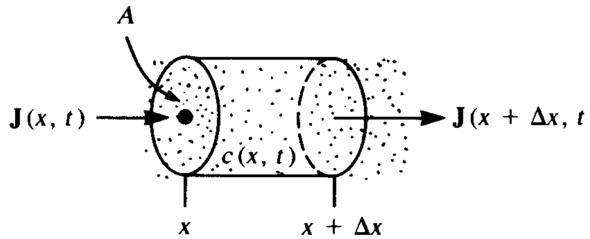
Normal distribution with variance proportional to time

Derivation of Diffusion from Fluxes



- Mass or number of particles
- Motion takes place in a single dimension
- We are interested in spatial distribution of particles as function of time

Derivation of Diffusion from Fluxes



$c(x,t)$ = concentration of particles at (x,t)

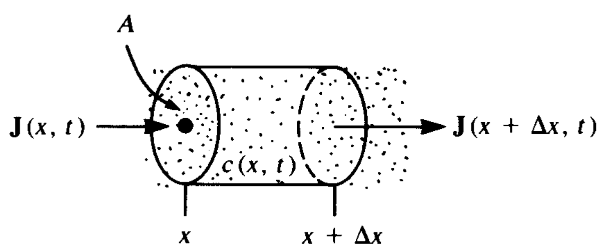
$\mathbf{J}(x,t)$ = flux of particles at (x,t) = number of particles crossing a unit area x in the positive direction per unit time

$\gamma(x,t)$ = rate of creation or elimination per unit volume at (x,t)

A = cross sectional area of tube

ΔV = volume of length element (Δx), i.e. $\Delta V = A\Delta x$

Derivation of Diffusion from Fluxes



$$\begin{pmatrix}\text{rate of change}\\ \text{of particle}\\ \text{population in}\\ (x, x+\Delta x)\\ \text{per unit time}\end{pmatrix} = \begin{pmatrix}\text{rate of entry}\\ \text{into } (x, x+\Delta x)\\ \text{per unit time}\end{pmatrix} - \begin{pmatrix}\text{rate of}\\ \text{departure}\\ \text{from}\\ (x, x+\Delta x)\\ \text{per unit time}\end{pmatrix} \pm \begin{pmatrix}\text{rate of}\\ \text{local degra-}\\ \text{dation or}\\ \text{creation per}\\ \text{unit time}\end{pmatrix}$$

$$\frac{\partial c(x,t)A\Delta x}{\partial t} = \mathbf{J}(x,t)A - \mathbf{J}(x+\Delta x,t)A \pm \gamma(x,t)A\Delta x$$

Derivation of Diffusion from Fluxes

$$\frac{\partial c(x,t)A\Delta x}{\partial t} = \mathbf{J}(x,t)A - \mathbf{J}(x+\Delta x,t)A \pm \gamma(x,t)A\Delta x$$

Dividing by $A\Delta x$:

$$\frac{\partial c(x,t)}{\partial t} = \frac{\mathbf{J}(x,t) - \mathbf{J}(x+\Delta x,t)}{\Delta x} \pm \gamma(x,t)$$

Taking the limit as $\Delta x \to 0$:

$$\frac{\partial c(x,t)}{\partial t} = -\frac{\partial \mathbf{J}(x,t)}{\partial x} \pm \gamma(x,t)$$ ← *One dimensional balance equation*

Derivation of Diffusion from Fluxes

$$\frac{\partial c(x,t)}{\partial t} = -\frac{\partial \mathbf{J}(x,t)}{\partial x} \pm \gamma(x,t)$$ ← *One dimensional balance equation*

$$\mathbf{J} = -D\frac{\partial c(x,t)}{\partial x}$$ ← Flick's law: flux due to random motion of particles is approximately proportionate to the local gradient in particle concentration.

Substituting:

$$\frac{\partial c(x,t)}{\partial t} = -\frac{\partial}{\partial x}\left(-D\frac{\partial c(x,t)}{\partial x}\right) \pm \gamma(x,t)$$

$$\frac{\partial c(x,t)}{\partial t} = D\frac{\partial^2 c(x,t)}{\partial x^2} \pm \gamma(x,t)$$

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2} \pm \gamma(x,t)$$

One-dimensional *reaction-diffusion* equation

Reaction Diffusion Models

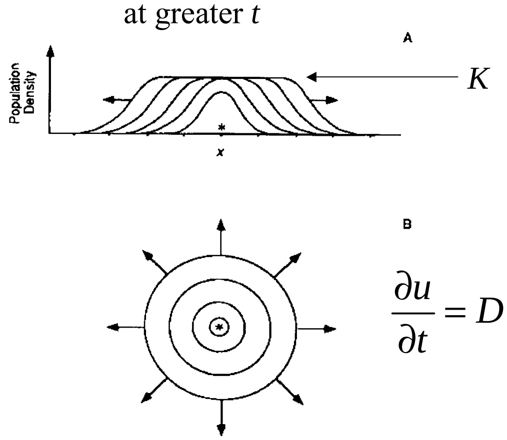
$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[D(u)\frac{\partial}{\partial x} \right] + \frac{\partial}{\partial y}\left[D(u)\frac{\partial}{\partial y} \right] + f(u)$$

or, if the diffuusion coefficient is constant,

$$\frac{\partial u}{\partial t} = \underbrace{D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right)}_{\text{diffusive movement}} + f(u)$$

$f(u)$: reaction term, describes growth dynamics

traveling wave, each curve at greater *t*



Logistic population growth plus random dispersal often used to model invasion.

$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + ru\left(1 - \frac{u}{K} \right)$$

Rate of Spread

For a wide range of fucntions [$f(u)$] for population growth, the asymptotic rate of spread is $\sqrt{4f'(0)D}$. This expression holds whenever population growth rate is positive at $u < K$ and when per capita growth rate is maximum when population is small.

Many Applications of PDE's

- Invasion
- Interspecific competition
- Predator-prey
- Disease dynamics
- Critical patch sizes
- Pattern formation
- See Holmes et al. 1994 for review

Limitations of PDE's

- Does not apply to discrete time, space--matrix or grid models more appropriate.
- Represents disturbance poorly—questions of biodiversity and coexistence better illustrated with alternative approaches (Tillman 1994, Ecology 75:2-16).

But, do thing in nature move randomly?

- Assumed randomness is a way to simplify movement processes that would otherwise be excessively detailed.
- Possible to explicitly include primary influences on movement (environmental heterogeneity, behavioral attraction, physical forces) while subsuming secondary influences into diffusion term.

For example:

$$\frac{\partial u}{dt} = \frac{\partial}{dx}\left(u \frac{\partial}{\partial x} \alpha(E) \right)$$

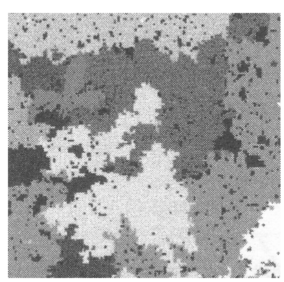
E is the environmental potential that increases as habitat quality decreases. The function a(E) describes how E alters behavior. This leads to distribution of organisms where E is lowest and habitat quality is greatest.

$$\frac{\partial u}{dt} = \frac{\partial}{dx}\left(D(E) \frac{\partial u}{\partial x} \right)$$

Represents organisms that move according to the average quality between their current location and neighboring sites. Produces homogeneous distribution.

Types of Spatial Models

- Spatially Implicit
  - single state variable
  - multiple state variables
- Spatially Explicit
  - grid based
    - categorical
    - continuous
  - individual based
  - reaction diffusion



$$\frac{\partial u}{\partial t} = D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + ru\left(1 - \frac{u}{K} \right)$$