

Deterministic Models in Ecology

ESS 575 Models for Ecological Data

N. Thompson Hobbs

January 24, 2017



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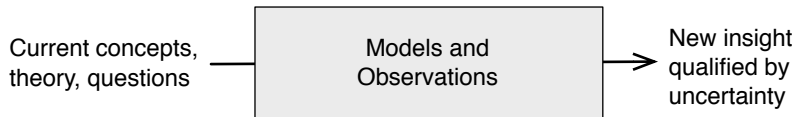
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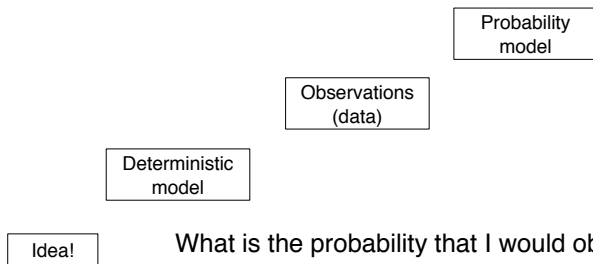
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Goal of course



Linking models to data



What is the probability that I would observe the data if my model is a faithful representation of the processes that gave rise to the data?

Deterministic models

$$\mu_i = g(\boldsymbol{\theta}, \mathbf{x}_i) \quad (1)$$

$$\underbrace{\mu_i}_{\text{response}} = g\left(\underbrace{\boldsymbol{\theta}}_{\text{parameters}}, \underbrace{\mathbf{x}_i}_{\text{predictors}}\right) \quad (2)$$

Also range and domain, dependent variable and independent variable. Predictors also called predictor variables and covariates.

$$g(\boldsymbol{\theta}, \mathbf{x}_i)$$

Any type of process

- ▶ Effects of soil properties on nitrogen mineralization
- ▶ Effects of elephant poaching on recruitment
- ▶ Responses of carnivore to energy development
- ▶ Food web dynamics of streams
- ▶ Hydrologic regime and riparian plant dynamics
- ▶ Controls on plant invasion in sagebrush steppe

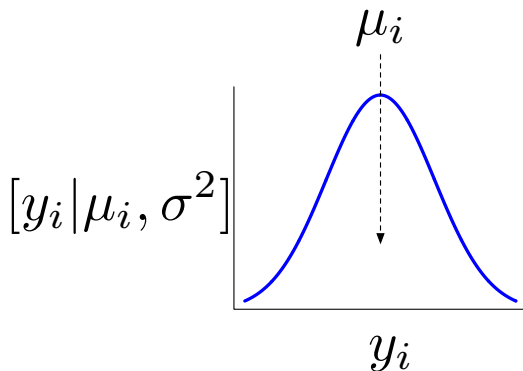
$$g(\boldsymbol{\theta}, \mathbf{x}_i)$$

Any type of mathematical function

- ▶ linear models
- ▶ non-linear models
- ▶ differential equations
- ▶ difference equations
- ▶ landscape transmission models

Linking models to data

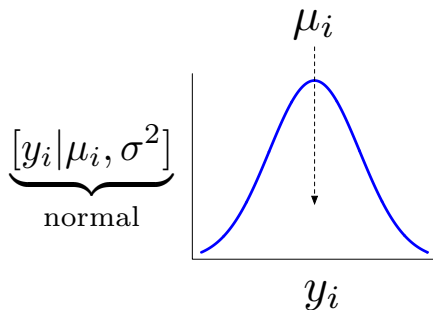
$$\mu_i = g(\boldsymbol{\theta}, x_i)$$



For example,

$$\boldsymbol{\theta} = (\beta_0, \beta_1)'$$

$$\mu_i = g(\boldsymbol{\theta}, x_i) = \beta_0 + \beta_1 x_i$$



Layout of next few lectures

- ▶ Today: a toolbox for $g(\boldsymbol{\theta}, \mathbf{x})$
- ▶ Thursday: basic laws of probability
- ▶ Next week: probability distributions
- ▶ Week after: Likelihood and Bayes' Theorem

Objectives of lecture(s)

- ▶ Introduce a set of functional forms useful for composing deterministic models
- ▶ Illustrate mechanistic approach to deriving models of ecological processes.
- ▶ Cross cutting themes
 - ▶ A relatively small set of functions can be used to describe a broad array of ecological processes .
 - ▶ The same process can be represented by different functional forms.

Some functional forms for $g(\boldsymbol{\theta}, \mathbf{x})$

- ▶ Functions for additive effects
- ▶ Asymptotic processes
- ▶ Biological scaling and other power functions
- ▶ Change points
- ▶ Competing controls, interactions, composites of functions

What if response is > 0 and < 1 ?

- ▶ Proportion of plots with invasive species
- ▶ Nitrogen content of soil (gN / g OM)
- ▶ Proportion of landscape burned
- ▶ Survival probability of juveniles
- ▶ Prevalence of a disease in a population

Inverse logit function

Let p = variable that can take on values between 0 and 1.

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) \text{ converts } p \text{ to } -\text{inf} \rightarrow +\text{inf}$$

$$\text{logit}(p) = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x_1 + \dots + \beta_n x_n$$

$$p = \text{inverse logit}(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n)$$

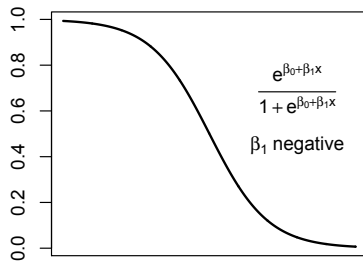
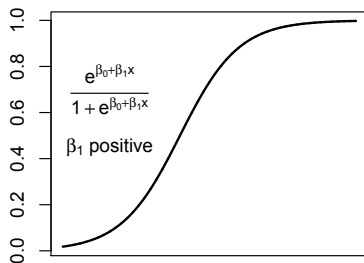
$$p = \frac{e^{\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n}}{1 + e^{\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n}}$$

You will also see

$$p = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n)}}$$

**BUT BE CAREFUL ABOUT THE MINUS
IN THE EXPONENT!!!**

Inverse logit function

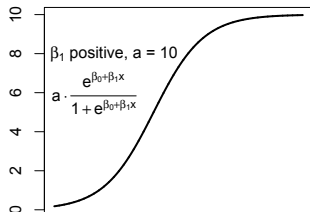


What if response is between 0 and a ?

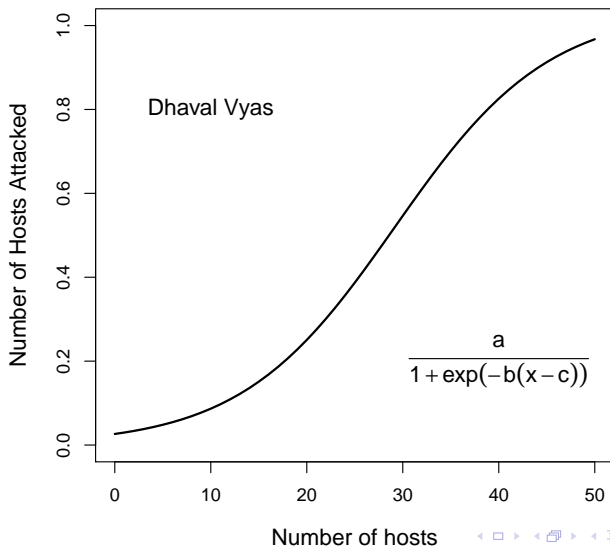
Multiply by a :

$$\frac{a e^{(\beta_0 + \beta_1 x_i + \dots + \beta_n x_n)}}{1 + e^{(\beta_0 + \beta_1 x_i + \dots + \beta_n x_n)}} \quad (3)$$

Always non-negative and does not reach excessively large values



Type III Parasitoid Functional Response



What if response must be ≥ 0 ?

What if the response must be ≥ 0 ?

For example we want to model λ_t as an additive function of covariates:

$$N_{t+1} = \lambda_t N_t \quad (4)$$

$$\lambda_t = g(\boldsymbol{\beta}, \mathbf{x}_t) \quad (5)$$

Other example responses that must be non-negative:

- ▶ biomass
- ▶ energy expenditure
- ▶ population density
- ▶ species richness

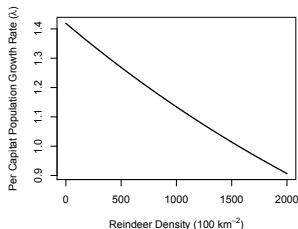
Exponential model

$$\mu_i = \exp(\beta_0 + \beta_1 x_{1,i}, \dots, + \beta_n x_{n,i}),$$

which is also written as

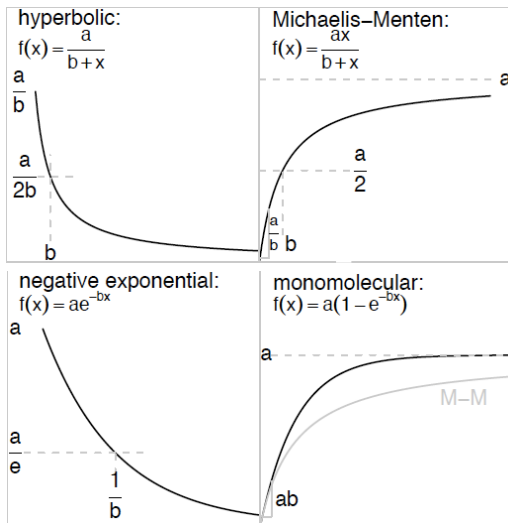
$$\log(\mu_i) = \beta_0 + \beta_1 x_{1,i}, \dots, + \beta_n x_{n,i}$$

$$\lambda_{i,t} = e^{(B_0 + B_1 D_{i,t-1} + B_2 L_{i,t} + B_3 W_{i,t} + B_4 G_i + B_5 O_t) \Delta t}$$

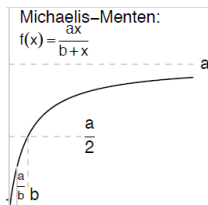


Hobbs, N. T., H. Andren, J. Persson, M. Aronsson, and G. Chapron. 2012. Native predators reduce harvest of reindeer by Sami pastoralists. *Ecological Applications* 22:1640-1654.

Asymptotic functions



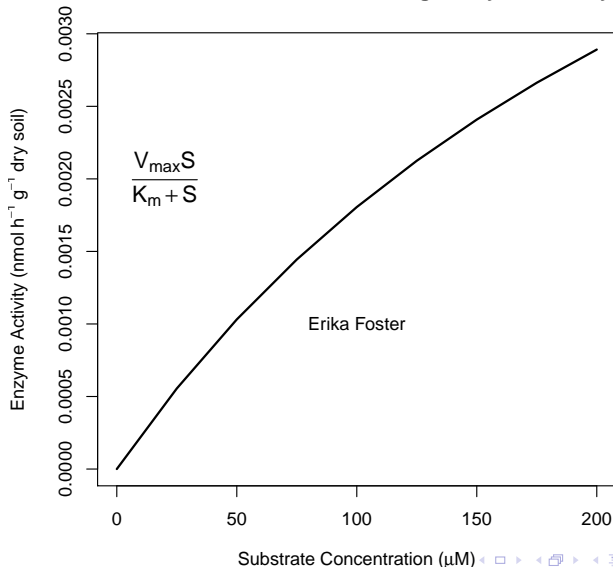
Figures courtesy of
Bolker, B. 2008.
Ecological Models and
Data in R. Princeton
University Press,
Princeton, N. J. USA.



Also written as $\frac{ax}{\frac{a}{b} + x}$

- ▶ Enzyme kinetics
- ▶ As Beverton-Holt equation, describes dynamics of populations, particularly fish.
- ▶ As Holling's disc equation and Spalinger-Hobbs model, portrays functional response
- ▶ As the "Monad equation" used to represent the limitation of soil nutrients on plant growth.

Michaelis–Menten Plot of Average Enzyme Activity



You will also see functions that look like:

$$\mu = \frac{\alpha x}{1 + \alpha \gamma x}$$

let $a = \frac{1}{\gamma}$, $b = \frac{1}{\alpha \gamma}$

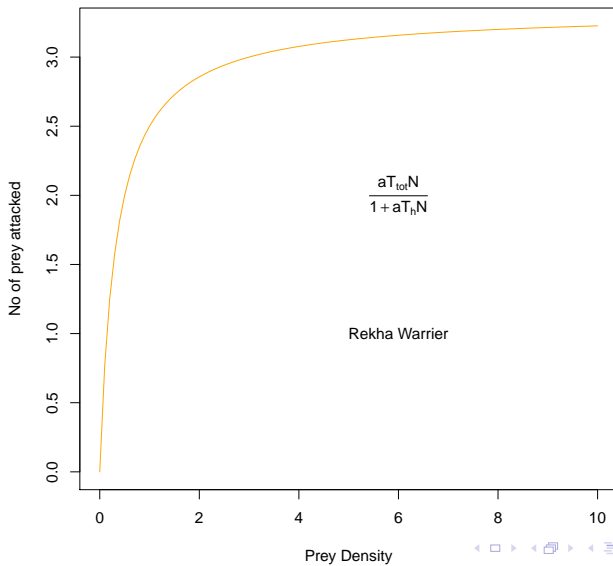
multiply numerator and denominator by $\frac{1}{\alpha \gamma}$

$$\mu = \frac{\frac{\alpha x}{\alpha \gamma}}{\frac{1}{\alpha \gamma} + \frac{\alpha \gamma x}{\alpha \gamma}} \quad (6)$$

simplify and substitute:

$$\mu = \frac{ax}{b+x}$$

Holling's Type 2 Functional Response



Some useful rescaling tricks

Applied to Michaelis-Menton but applicable to any function

$$\mu = \frac{x}{1+x}, \text{ simplest form of MM model}$$

asymptote at 1, half - maximum at 1

substitute $\frac{x}{b}$ for x multiply numerator and denominator by b

$$\mu = \frac{x}{b+x}$$

asymptote at 1, half - maximum at b

multiply rhs by a

$$\mu = \frac{ax}{b+x}$$

asymptote at a , half - maximum at b

More rescaling tricks

We can shift curve to right or left by adding or subtracting a constant from x . Useful when $y = 0$ is reached at positive x to represent lower threshold (see light limitation of trees example)

$$\mu = \frac{a(x - c)}{b + (x - c)} \quad (7)$$

We can shift the curve up or down by adding or subtracting a constant to the right hand side. If we add d , the curve starts at $y = d$ instead of 0 when $x = c$. What happens to the asymptote?

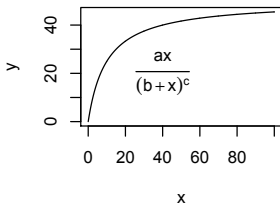
$$\mu = \frac{a(x - c)}{b + (x - c)} + d \quad (8)$$

If it makes sense, we can give biological meaning to b by defining it as the ratio of a divided by dy/dx when x is “small”, i.e

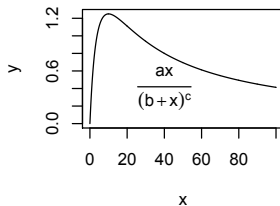
$$b = \frac{a}{f}, f = \frac{dy}{dx} \text{ when } x = 0 \text{ or } x = c \quad (9)$$

Using exponents

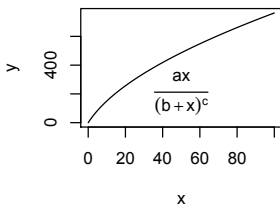
c=1

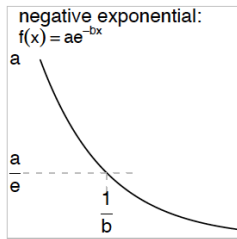


c=2



c=.5

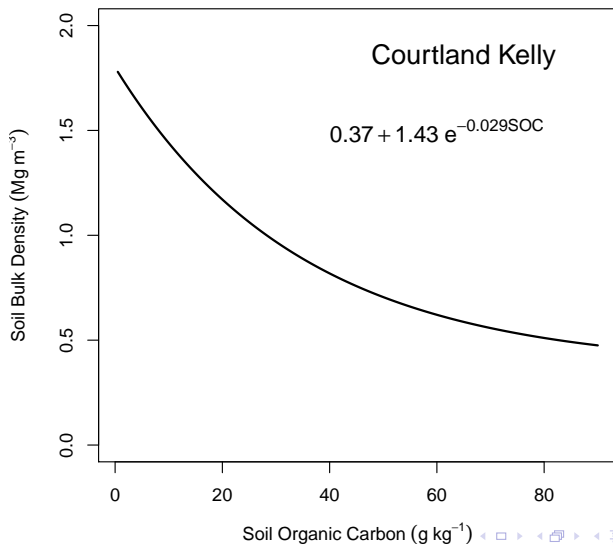


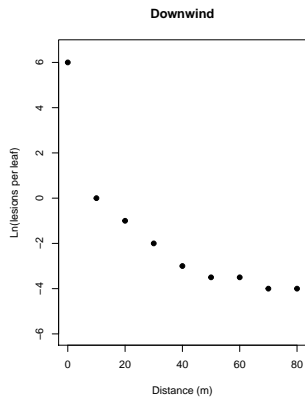


Solution to differential equation $\frac{dy}{dx} = -bx$

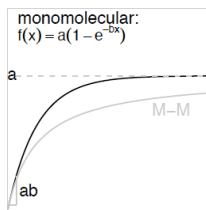
- ▶ Many applications in population ecology
- ▶ Detection functions in distance sampling
- ▶ Beer's law for light attenuation through plant canopy

Bulk Density and Soil Organic Carbon





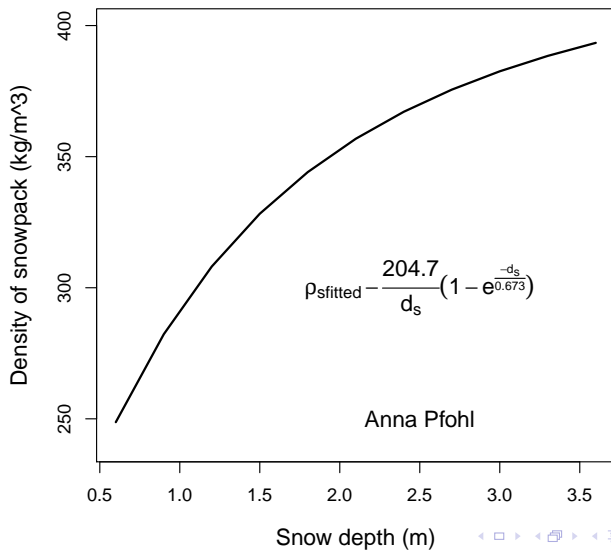
Examples of Mono-molecular



- the *catalytic curve* in infectious disease epidemiology, where it represents the change over time in the fraction of a cohort that has been exposed to disease (Anderson and May, 1991);
- the simplest form of the *von Bertalanffy* growth curve in organismal biology and fisheries, where it arises from the competing effects of changes in catabolic and metabolic rates with changes in size (Essington et al., 2001);
- the *Skellam model* in population ecology, giving the number of offspring in the next year as a function of the adult population size this year when competition has a particularly simple form (Skellam, 1951; Brännström and Sumpter, 2005).

Bolker, B. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, N. J. USA.

Snow density for a deep snowpack



Droop Model

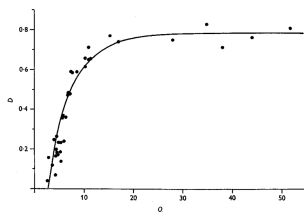
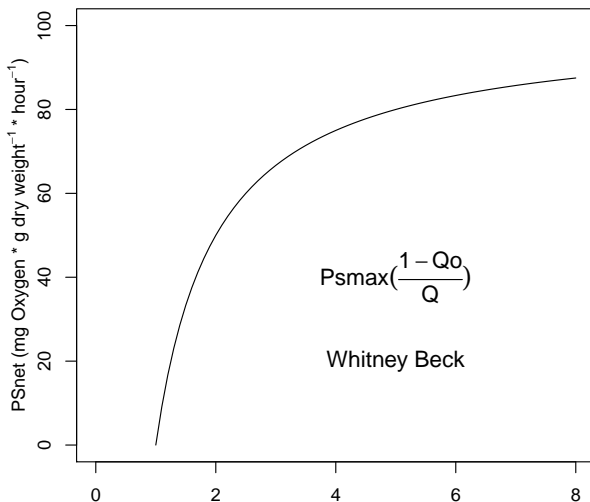


Figure 3. Chemostat steady states. Relation between dilution rate (D) and cell quota (Q). Reproduced from Droop 1968 with permission of the Journal of the Marine Biological Association UK.

$$\mu = \mu_{\max} \left(1 - \frac{k_q}{x} \right)$$

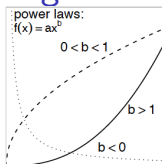
- ▶ μ = realized growth rate
- ▶ μ_{\max} = maximum growth rate
- ▶ k_q = intercept (abscissa)
- ▶ x = organism or population size

Droop Model of Algal Growth



Nitrogen Cell Quota (% Nitrogen)

Scaling models, power functions



- Species area curves
- Scaling physiological and ecological parameters to body mass
- Adjusting measurements taken at different spatial scales

Can be log transformed to linear form:

$$y = ax^b \quad (10)$$

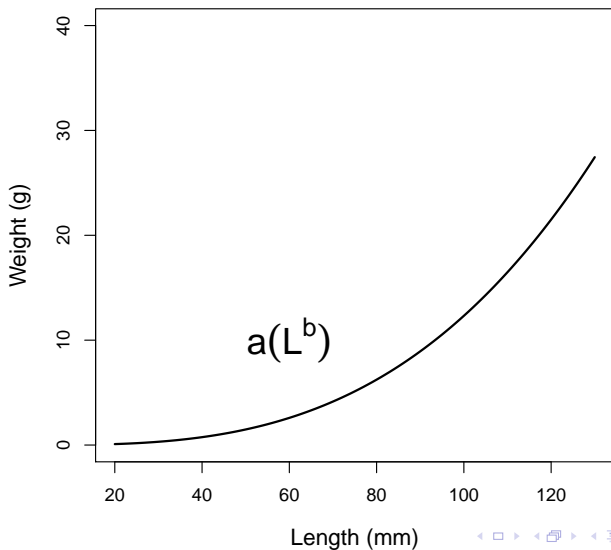
$$\log(y) = \log(a) + b \log(x) \quad (11)$$

$$\beta_0 = \log(a) \quad (12)$$

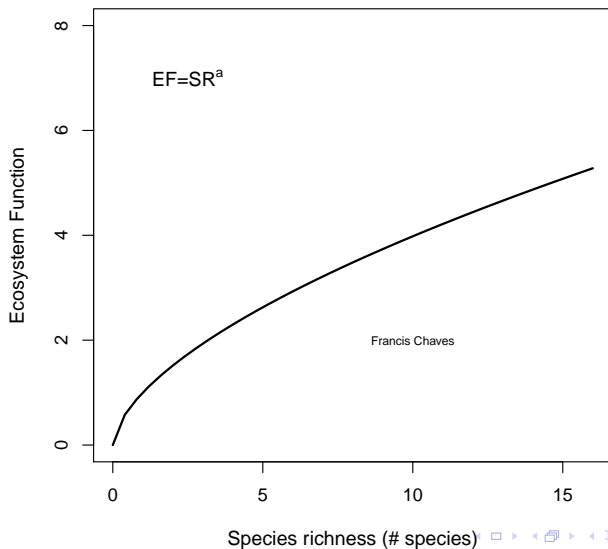
$$\beta_1 = b \quad (13)$$

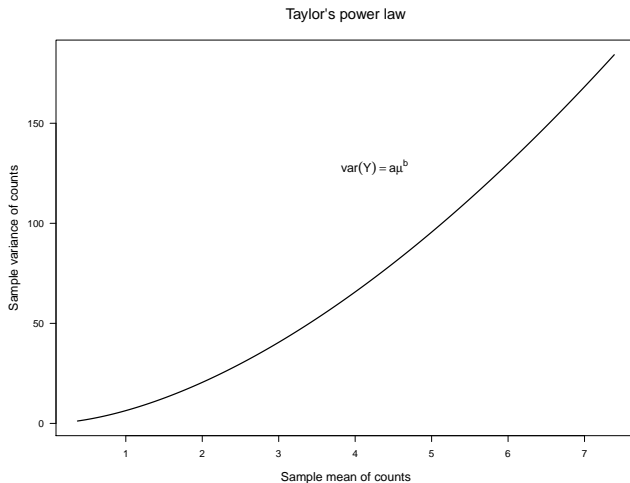
$$\log(y) = \beta_0 + \beta_1 \log(x) \quad (14)$$

Weight–Length Relationship for Mottled Sculpin (Brian Avila)

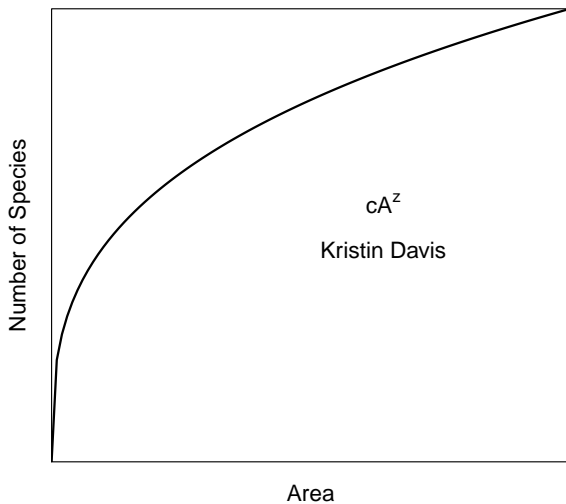


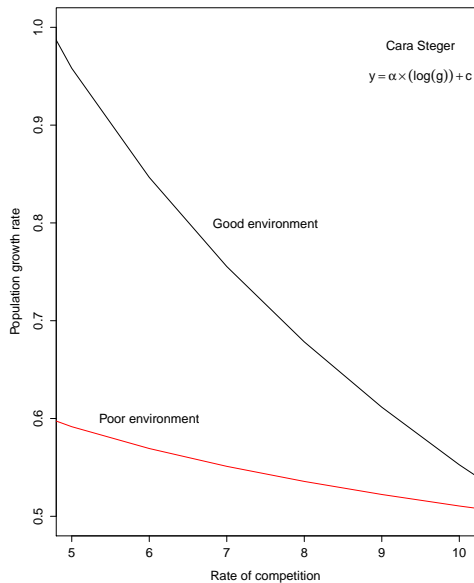
Biodiversity – Ecosystem Function Relationship





Species–Area Relationship



Sub-Additive Growth Mechanism of Coexistence

Scaling models, power functions

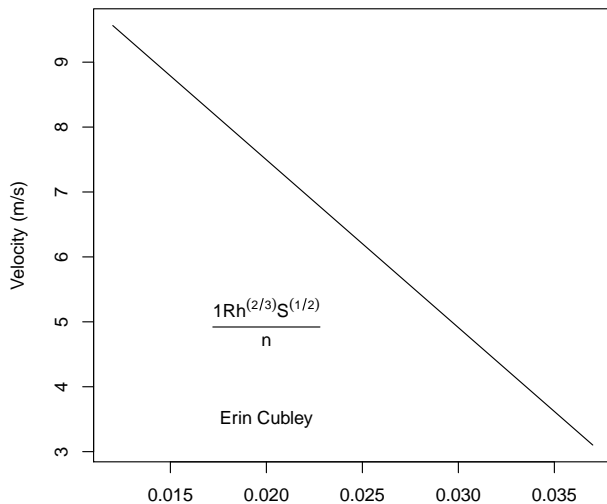
Multiple predictor variables can be accommodated using

$$g(\boldsymbol{\beta}, \mathbf{x}) = \beta_0 x_1^{\beta_1} x_2^{\beta_2} \dots x_n^{\beta_n}$$

which you will see rewritten as

$$\log(y) = \log(\beta_0) + \beta_1 \log(x_1) + \beta_2 \log(x_2) + \dots + \beta_n \log(x_n) .$$

Channel Velocity and Channel Roughness



Erin Cubley

Some change point possibilities

Bolker, B. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, N. J. USA.

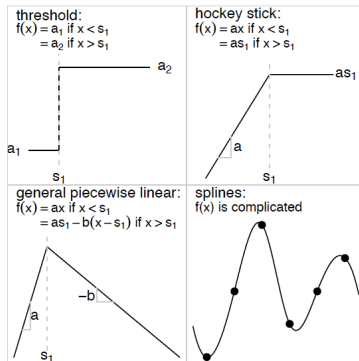
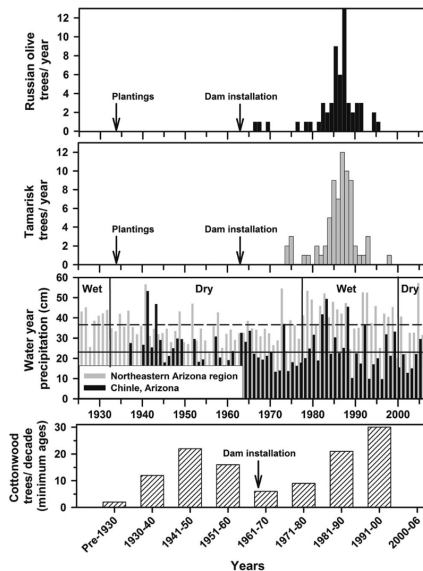


Figure 3.7 Piecewise polynomial functions: the first three (threshold, hockey stick, general piecewise linear) are all piecewise linear. Splines are piecewise cubic; equations are complicated and usually handled by software (see `?spline` or `?smooth.spline`).



Reynolds, L. V., D. J. Cooper, and N. T. Hobbs. 2014. Drivers of riparian tree invasion on a desert stream. *River Research and Applications* 30:60-70.

Combined Feedbacks

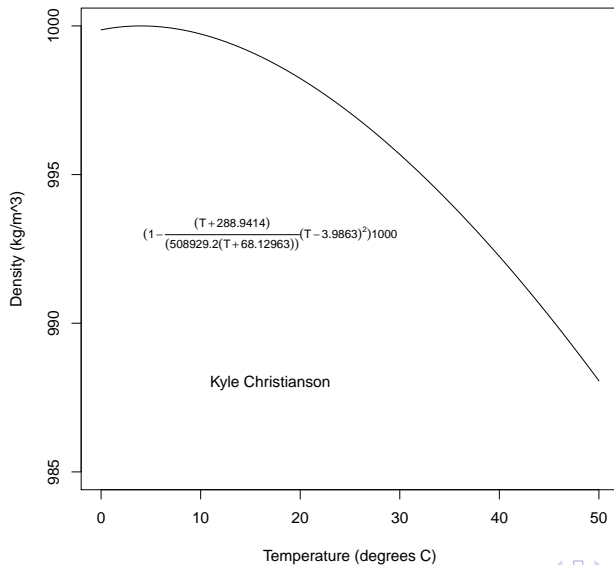
- Combination of positive and negative feedback, e.g., Allee effect, photoinhibition, plant water relations.
- Example:

$$\text{rate of photosynthesis} = P_{\max} \left[(aI) (e^{1-aI}) \right]$$

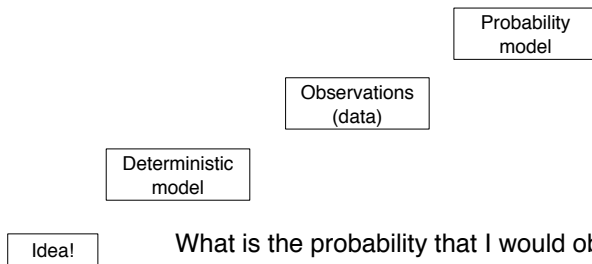
Between 0-1
 maximum rate g/time facilitation inhibition

I =light intensity, a = unitless shape parameter

Water Density by Temperature



Linking models to data



What is the probability that I would observe the data if my model is a faithful representation of the processes that gave rise to the data?