Deterministic Models in Ecology

ESS 575 Models for Ecological Data

N. Thompson Hobbs

January 29, 2019

Announcements

- See email for temporary adjustment to Brian's office hours.
- Find revised course schedule in class repository.
- Mark calendars for extended lab on March 6: 10:00 - 2:00.

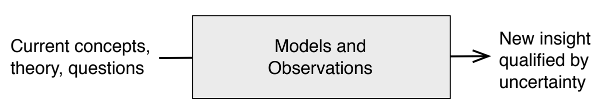
Art is a lie that makes us realize the truth.
Pablo Picasso

All models are wrong, but some are useful.
G.E.P. Box

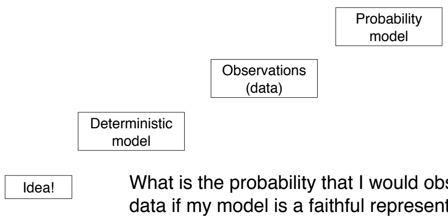
It is better to invent reality than to copy it.
G. Verdi

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

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?

Layout of next few lectures

- Today: a toolbox for deterministic models
- Thursday: basic laws of probability
- Next week: probability distributions
- Week after: Likelihood and Bayes' Theorem

Objectives of today's lecture

- Introduce first ideas about "support."
- Distinguish between purely empirical models and models symbolizing processes.
- Introduce a set of functional forms useful for composing deterministic models.
- 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.
  - The same functional form can be used to represent different processes.

Some other great sources

- Bolker, B. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, NJ USA.
- Otto, S. P., and T. Day. 2007. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution . Princeton University Press, Princeton, NJ USA.

Deterministic models

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

A deterministic model

$$\underbrace{\mu_i}_{\text{response}} = g(\underbrace{\boldsymbol{\theta}}_{\text{parameters}}, \overbrace{\mathbf{x}_i}^{\text{predictors}}) \qquad (2)$$

What makes it deterministic? Predictors also called predictor variables and covariates.

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

Any type of process

- Spread of avian influenza
- Decomposition in grassland soils
- Movement of elephants across landscapes
- Food web dynamics in streams
- Growth of waterfowl populations
- Influence of hydrologic regime on riparian plan communities
- Invasion of native plant communities by exotic species

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

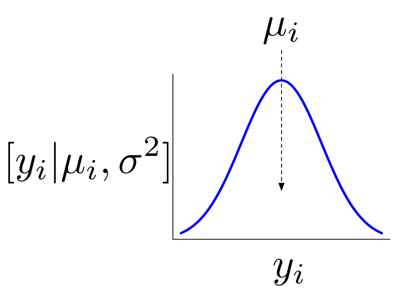
Any type of mathematical function

- linear models
- non-linear models
- systems of differential equations
- systems of difference equations
- integral-projection models
- state-transition models
- matrix models

Any equation or system of equations making a prediction that can be compared with an observation.

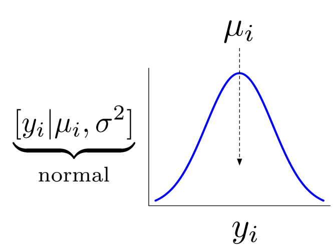
Linking models to data

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



For example,

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



This model is often a poor choice in biology. Why?

The concept of support (intuitively)

Support refers to the range of values that a variable can realize. A more formal definition will come soon. Describe the support for the following variables:

- Soil organic matter content (gm OM / gm dry matter)
- Observed survival of an individual
- Species richness
- Carbon flux
- Above ground biomass of grassland

Empirical vs Theoretical models

Board work on the disc equation

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

- Additive effects
- Asymptotic processes
- Power functions

Additive, nonlinear models

- Additive models contain linear functions of coefficients and predictor variables, e.g. $\beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i}$.......
- Often referred to as general linear models family because transforming the left hand side results in a linear model.
- Are usually empirical – very useful for modeling effects of predictors on responses.

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.

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

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

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

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

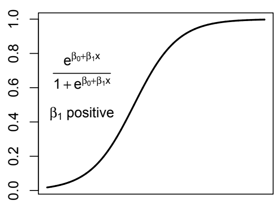
You will also see

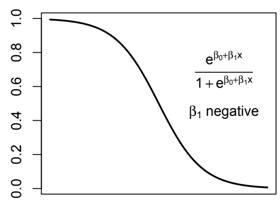
$$p = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 .... + \beta_n x_n)}}$$

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

Can include powers and products of the $x's$

Inverse logit function





What *not* to do!

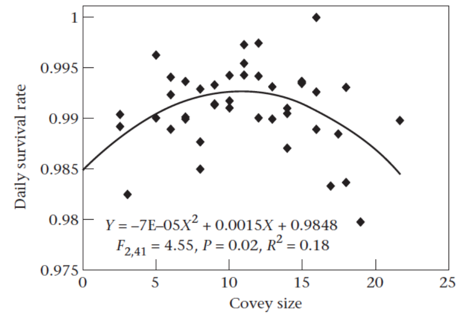


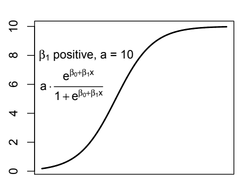
Figure 10. The influence of covey size on individual daily survival between 9 November and 31 January 1997–2000 in east-central Kansas.

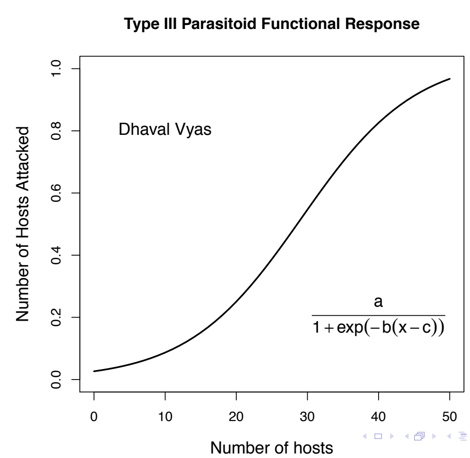
What if response is between 0 and a?

Multiply by a:

$$\frac{a\,e^{(\beta_0+\beta_1 x_i\ldots.+\beta_n x_n)}}{1+e^{(\beta_0+\beta_1 x_i\ldots.+\beta_n x_n)}} \tag{3}$$

Always non-negative and does not reach excessively large values





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:

$$
\begin{aligned}
N_{t+1} &= \lambda_t N_t && (4)\\
\lambda_t &= g(\boldsymbol{\beta}, \mathbf{x}_t) && (5)
\end{aligned}
$$

Other example responses that must be non-negative:

- biomass
- energy expenditure
- nitrogen mineralization
- population density
- species richness
- ground water flow

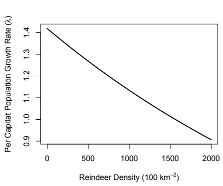
Exponential model

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

which is also written as

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

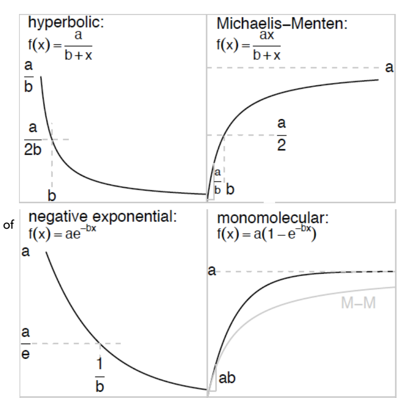
$$\lambda_{i,t} = e^{(B_0 + B_1 D_{i,t-1} + B_2 L_{i,t} + B_3 W_{i,t} + B_4 G_i + B_5 O_t)\Delta t}$$

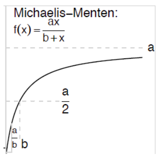


Hobbs, N. T., H. Andren, J. Persson, M. Aronsson, and G. Chapron. 2012. Native predators reduce harvest of reindeer by Sami pastoralists. Ecological Applications 22:1640-1654.

Asymptotic functions

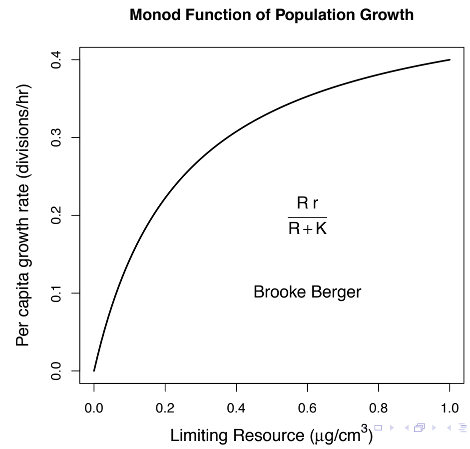
Figures courtesy of Bolker, B. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, N. J. USA.





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.



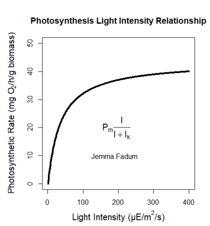
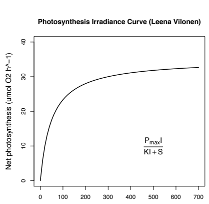
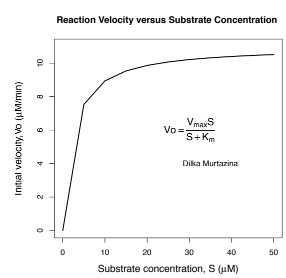
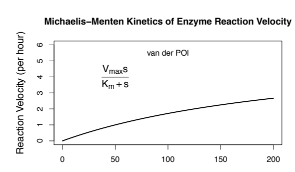
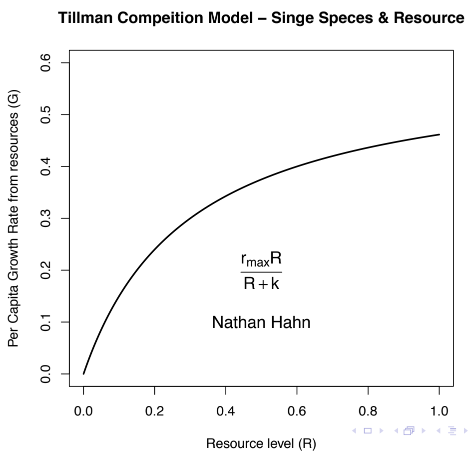


Figure 1: Model of the photosynthetic rate of individual algae conditional on light intensity.









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)

$$\mu = \frac{a\,(x-c)}{b+(x-c)} \tag{6}$$

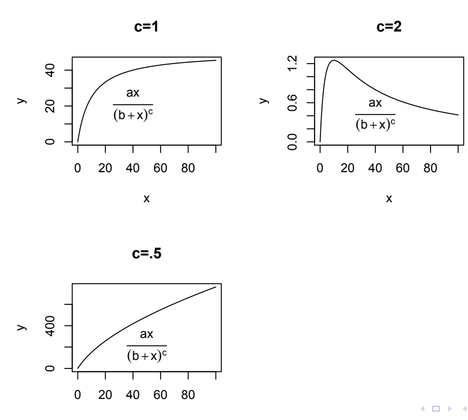
We can shift the curve up or down by adding or subtracting a constant to the right hand side. If we add d, the curve starts a y = d instead of 0 when x = c.

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

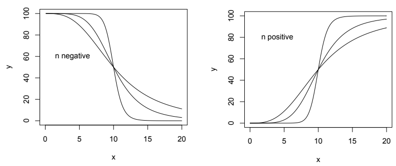
If it makes sense, we can give biological meaning to b by defining it as the ratio of a divided by dy/dx when x is "small" , i.e

$$b = \frac{a}{f}, f = \frac{dy}{dx}\,\text{when}\,x = 0\,\text{or}\,x = c \tag{8}$$

Using exponents

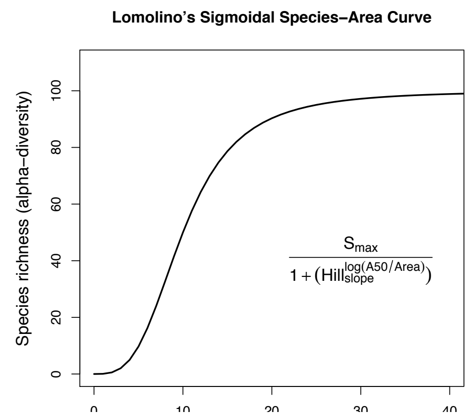


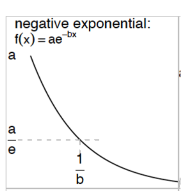
$y = \frac{V_{max} x^n}{h^n + x^n}$ Using exponents: Hill function



Steepness of slope increases as |n| increases

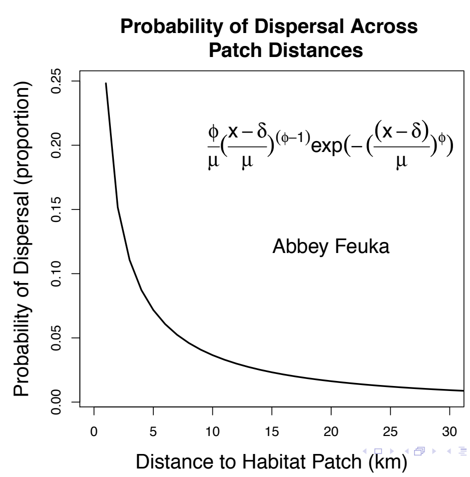
Hyperbolic with exponent



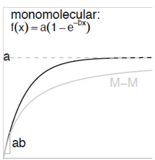


Solution to differential equation $\frac{dy}{dx} = -bx$

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

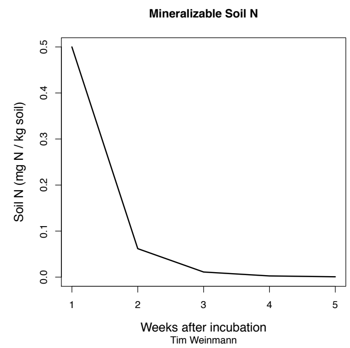


Examples of Mono-molecular

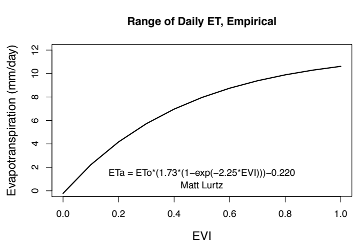


- the *catalytic curve* in infectious disease epidemiology, where it represents the change over time in the fraction of a cohort that has been exposed to disease (Anderson and May, 1991);
- the simplest form of the *von Bertalanffy* growth curve in organismal biology and fisheries, where it arises from 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).

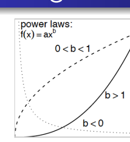
Bolker, B. 2008. Ecological Models and Data in R. Princeton University Press, Princeton, N. J USA.



$$N_t = N_{t-1}(1 - e^{-kt})$$



Scaling models, power functions



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

Can be log transformed to linear form:

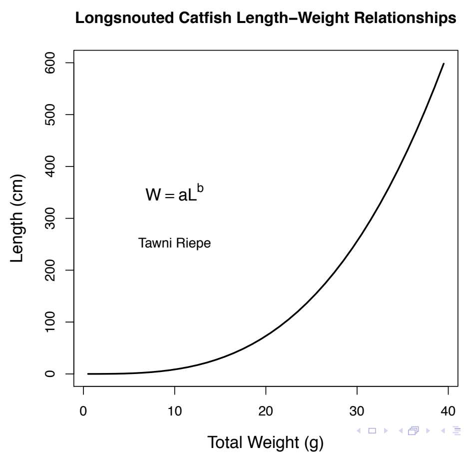
$$y = ax^b \quad (9)$$

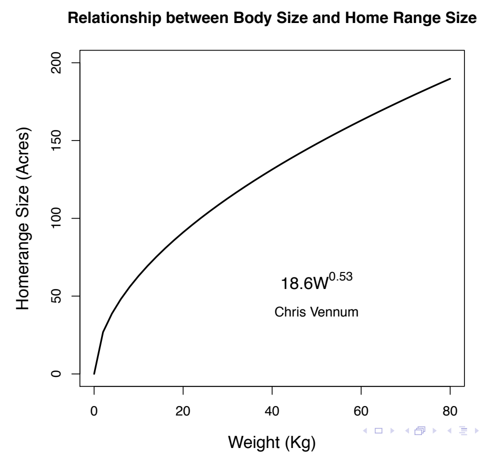
$$\log(y) = \log(a) + b\log(x) \quad (10)$$

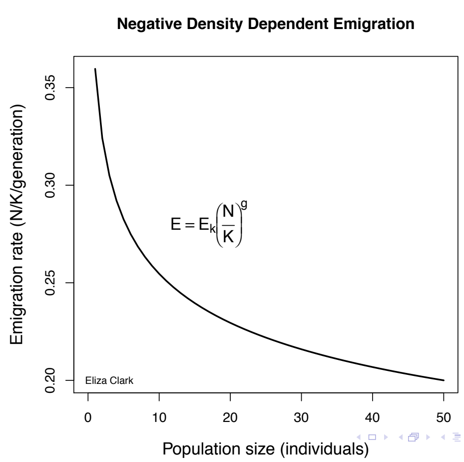
$$\beta_0 = \log(a) \quad (11)$$

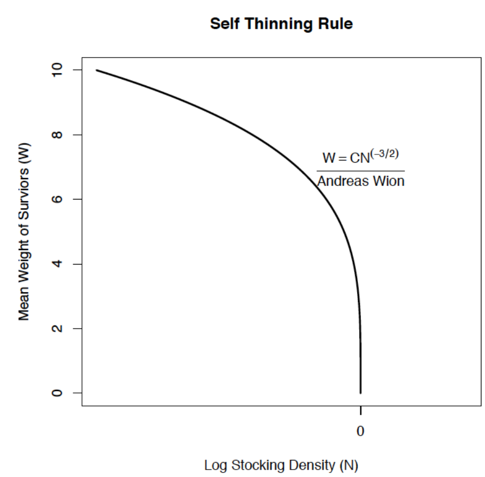
$$\beta_1 = b \quad (12)$$

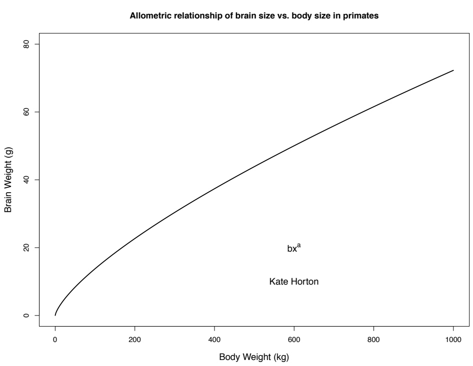
$$\log(y) = \beta_0 + \beta_1 \log(x) \quad (13)$$

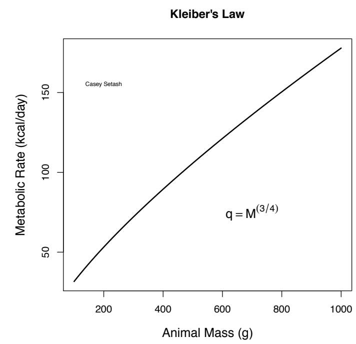

Longsnouted Catfish Length–Weight Relationships
Length (cm)
Total Weight (g)
0 100 200 300 400 500 600
0 10 20 30 40
W = aL^b
Tawni Riepe

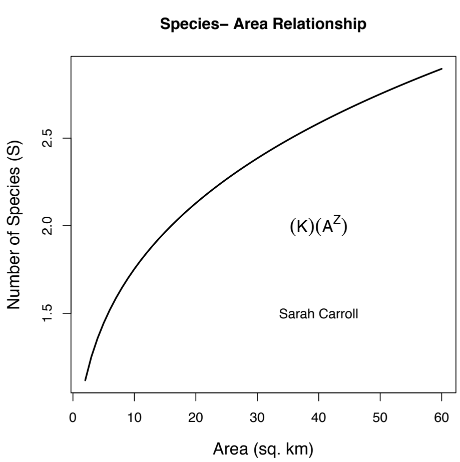

Relationship between Body Size and Home Range Size
Homerange Size (Acres)
Weight (Kg)
0 50 100 150 200
0 20 40 60 80
18.6W^0.53
Chris Vennum


Negative Density Dependent Emigration
Emigration rate (N/K/generation)
Population size (individuals)
0.20 0.25 0.30 0.35
0 10 20 30 40 50
E = E_k (N/K)^g
Eliza Clark


Self Thinning Rule
Mean Weight of Surviors (W)
Log Stocking Density (N)
0 2 4 6 8 10
0
W = CN^(−3/2)
Andreas Wion







Scaling models, power functions

Multiple predictor variables can be accommodated using

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

which you will see rewritten as

$$\log(y) = \log(\beta_0) + \beta_1 \log(x_1) + \beta_2 \log(x_2), + \ldots + \beta \log(x_n).$$

Droop Model

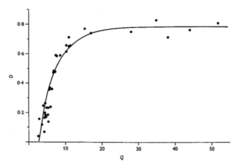


Figure 3. Chemostat steady states. Relation between dilution rate (D) and cell quota (Q). Reproduced from Droop 1968 with permission of the Journal of the Marine Biological Association UK.

$$D = D_{\max}\left(1 - \frac{k_q}{Q}\right)$$

- D = realized dilution rat
- $D_{\max}$ = maximum growth rate
- k_q= intercept (abscissa)
- Q = cell quota

Context
Toolbox
Additive
Asymptotic
Power

Combined feedbacks

Combined Feedbacks

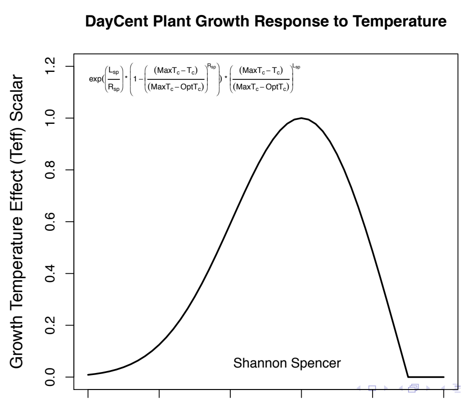
- Combination of positive and negative feedback, e.g., Allee effect, photoinhibition, plant water relations.
- Example:

$$\text{rate of photosynthesis} = \underbrace{P_{max}}_{\text{maximum rate g/time}}\overbrace{\left[\underbrace{(aI)}_{\text{facilitation}}\underbrace{\left(e^{1-aI}\right)}_{\text{inhibition}}\right]}^{\text{Between 0-1}}$$

I=light intensity, a = unitless shape parameter

Context
Toolbox
Additive
Asymptotic
Power

Droop + exponent



Context
Toolbox
Additive
Asymptotic
Power

Linking models to data

Probability model

Observations (data)

Deterministic model

Idea!

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?