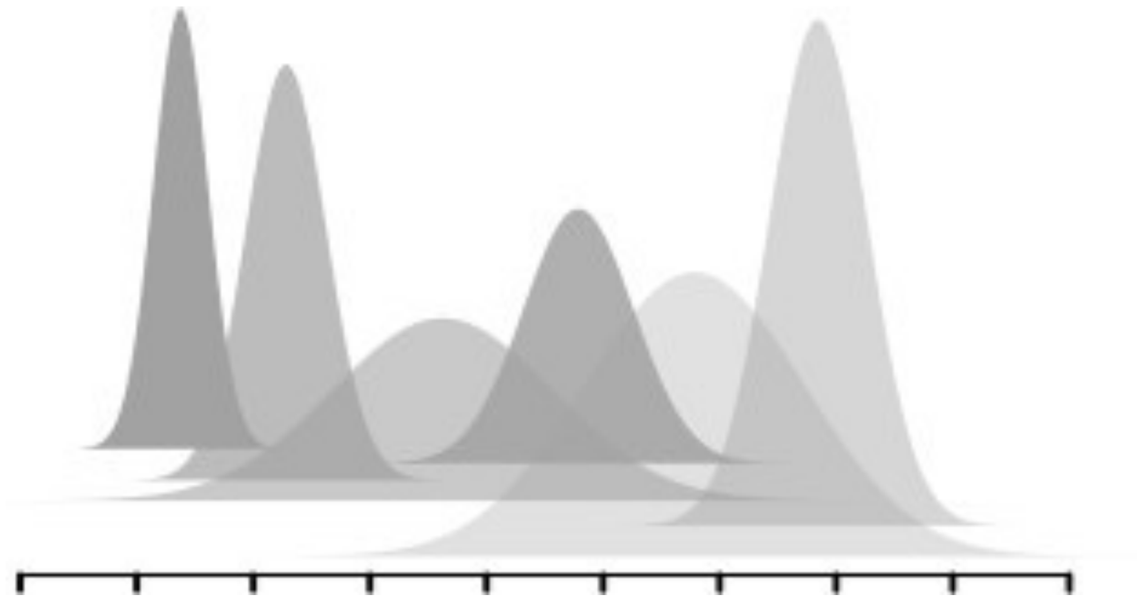
2.1 Survey of Ecological Models – Part 1



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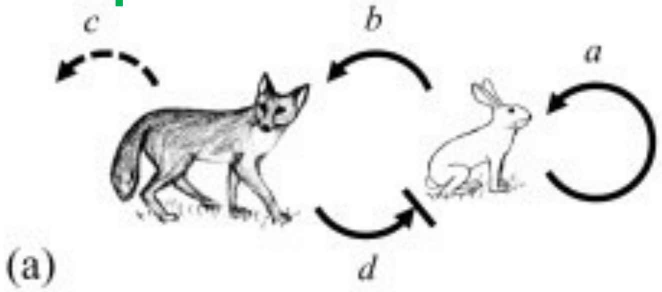
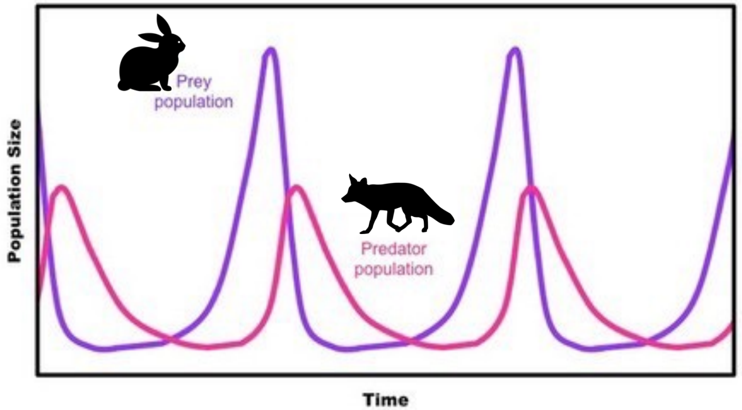
What is a model?

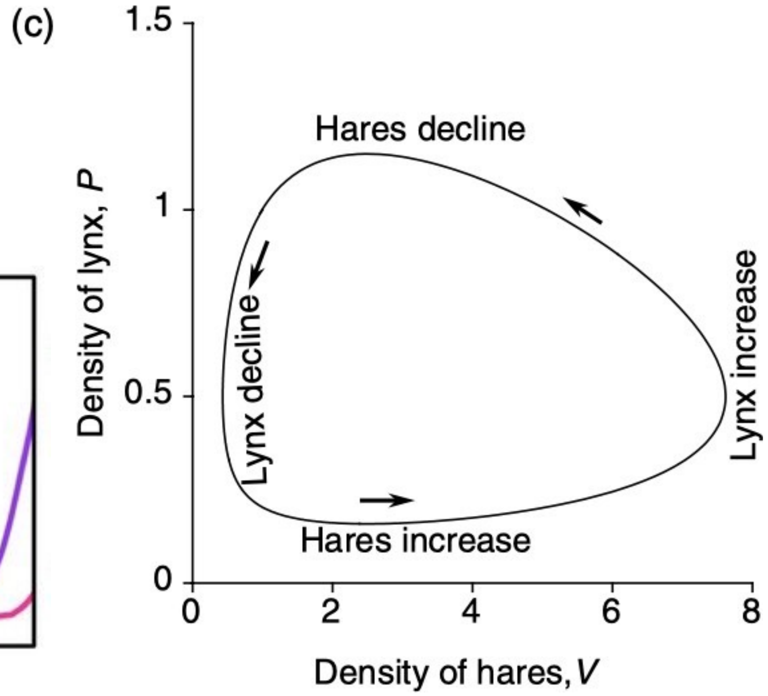
"A *model* is a representation of a particular thing, idea, or condition."

"The *modeling process* is the series of steps taken to convert an idea first into a conceptual model and then into a quantitative model"

Step 1. Formulate a conceptual model







Step 2. Formulate a quantitative model

$$\frac{\mathrm{d}V}{\mathrm{d}t} = aV - bVP$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -cP + dVP$$

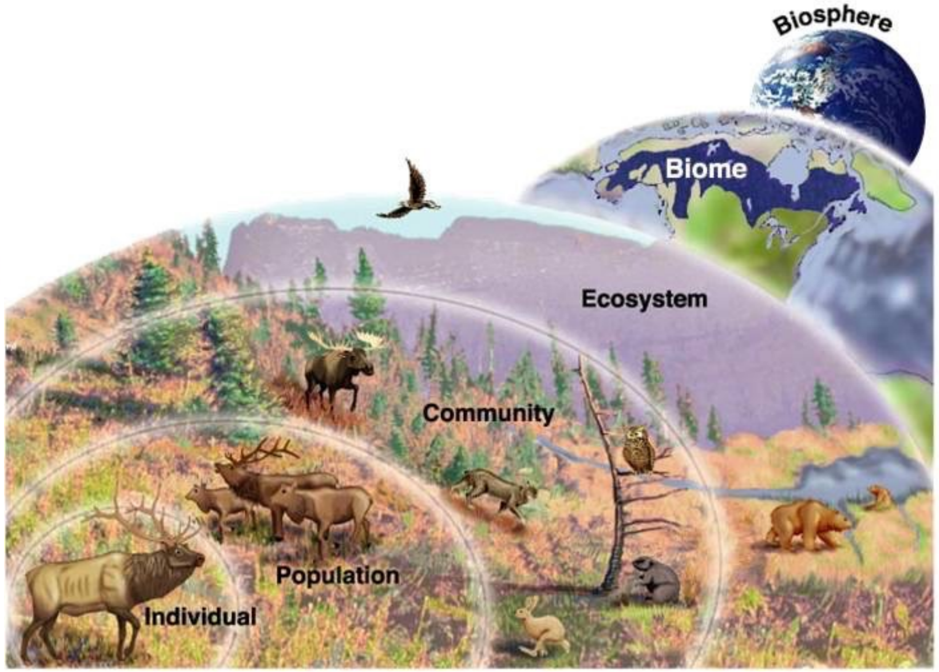
Step 3. Learn about study system through analysis of model behavior

Kinoshita, 2013, Intro to Nonequilibrium Phenomena

What is ecology?

The study of interactions between organisms and their environment, and with one another

The science that investigates the abundance and distribution of organisms



Step 3. Learn about study system through analysis of model behavior

Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Graphical techniques: develop a feeling for your model

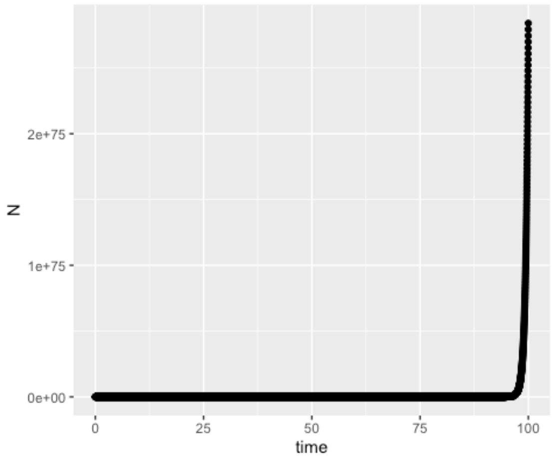
Expected dynamics → depends on r and n_0 (initial population size)

When $r > 0$?

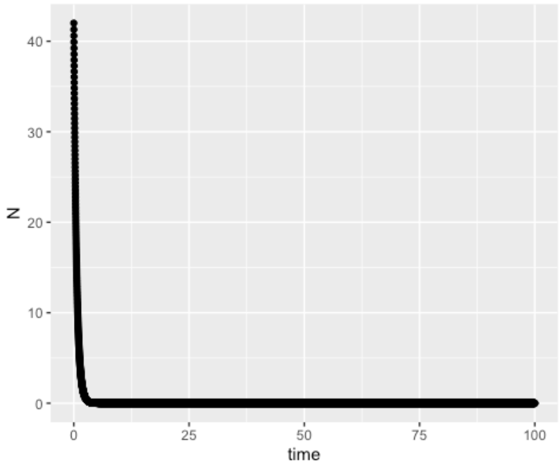
When $r < 0$?

When $r = 0$?

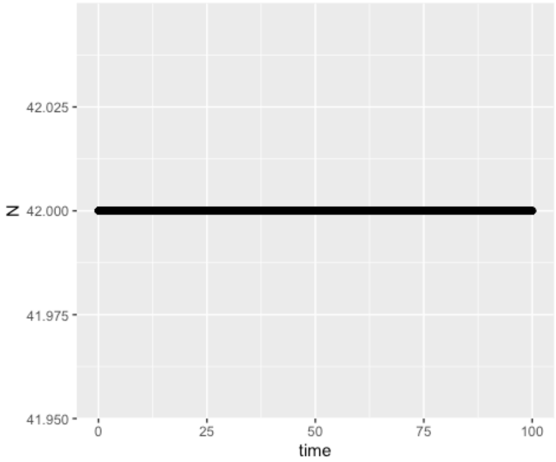
r = 1.7



r = -1.7



r = 0



parameter	
r	population growth rate

Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

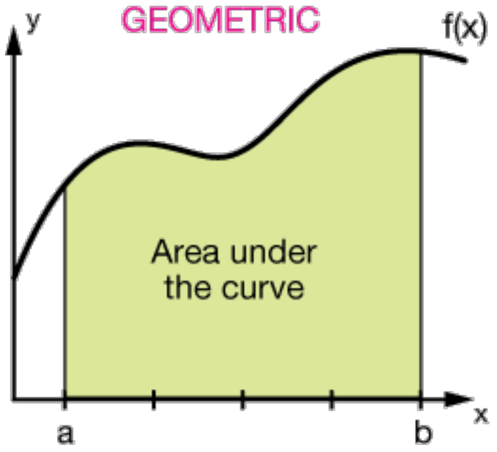
Graphical techniques: develop a feeling for your model

How did I develop a graph of population size over time for this equation?

I solved for values of n(t) at different points in time.

Let's solve the equation to get a formula for this: we'll need to integrate the formula

$$\frac{dn}{dt} = rn \rightarrow \frac{dn}{n} = rdt \rightarrow \int_{n_0}^{n(t)} \frac{dn}{n} = r\int_0^t dt \rightarrow ln\frac{n(t)}{n_0} = rt \rightarrow n(t) = n_0 e^{rt}$$



ANALYTIC

$$A = \int_a^b f(x)\, dx$$

The definite integral of f(x) between x=a & x=b

Table of Integrals

BASIC FORMS

(1) $\int x^n dx = \frac{1}{n+1} x^{n+1}$

(2) $\int \frac{1}{x} dx = \ln x$

(3) $\int u dv = uv - \int v du$

(4) $\int u(x)v'(x)dx = u(x)v(x) - \int v(x)u'(x)dx$

RATIONAL FUNCTIONS

(5) $\int \frac{1}{ax+b} dx = \frac{1}{a}\ln(ax+b)$

(6) $\int \frac{1}{(x+a)^2} dx = \frac{-1}{x+a}$

INTEGRALS WITH ROOTS

(18) $\int \sqrt{x-a}\, dx = \frac{2}{3}(x-a)^{3/2}$

(19) $\int \frac{1}{\sqrt{x \pm a}} dx = 2\sqrt{x \pm a}$

(20) $\int \frac{1}{\sqrt{a-x}} dx = 2\sqrt{a-x}$

(21) $\int x\sqrt{x-a}\, dx = \frac{2}{3}a(x-a)^{3/2} + \frac{2}{5}(x-a)^{5/2}$

(22) $\int \sqrt{ax+b}\, dx = \left(\frac{2b}{3a} + \frac{2x}{3}\right)\sqrt{b+ax}$

(23) $\int (ax+b)^{3/2} dx = \sqrt{b+ax}\left(\frac{2b^2}{5a} + \frac{4bx}{5} + \frac{2ax^2}{5}\right)$

Step 3. Learn about study system through analysis of model behavior

Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

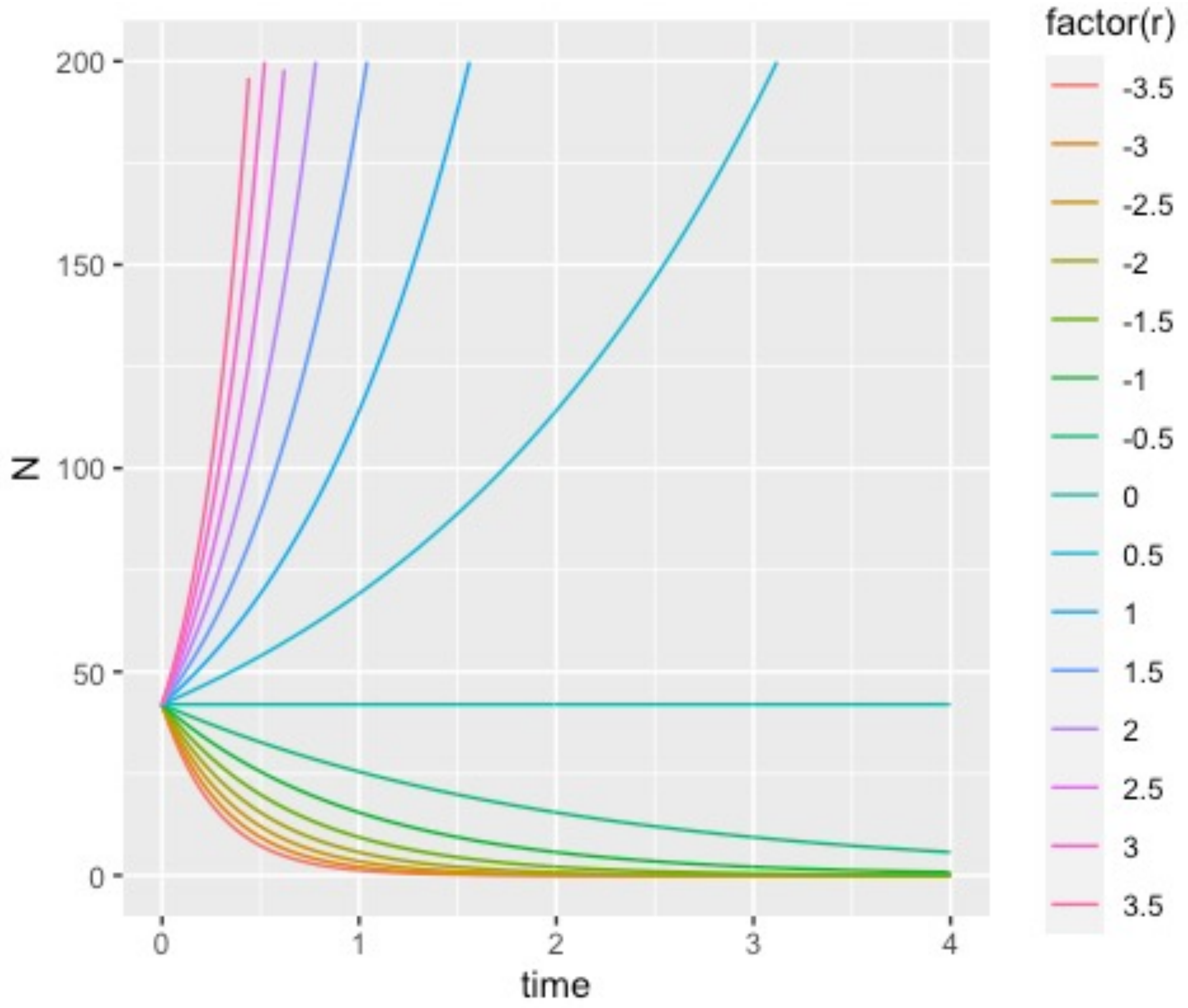
Graphical techniques: develop a feeling for your model

Expected dynamics

When r > 0?

When r < 0?

When r = 0?



parameter	
r	population growth rate

Step 3. Learn about study system through analysis of model behavior

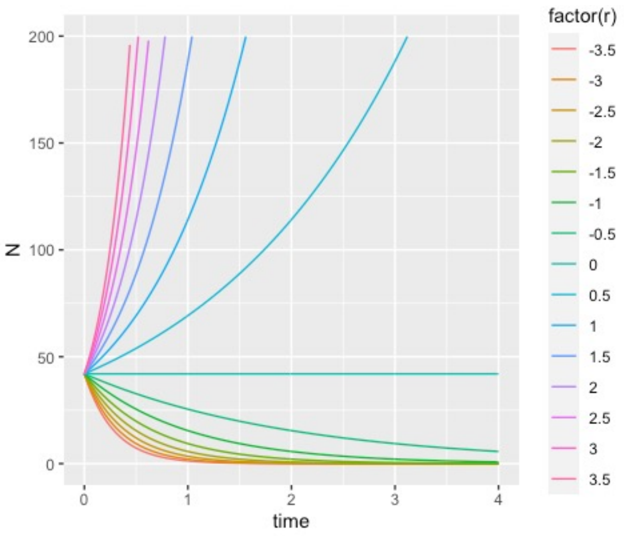
Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Graphical techniques: develop a feeling for your model

Expected dynamics



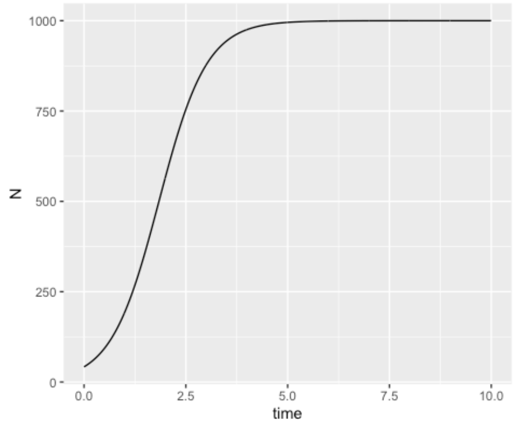
parameter	
r	population growth rate

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

Expected dynamics

r = 1.7



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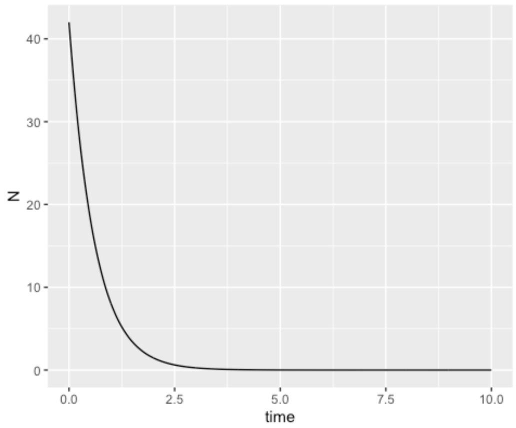
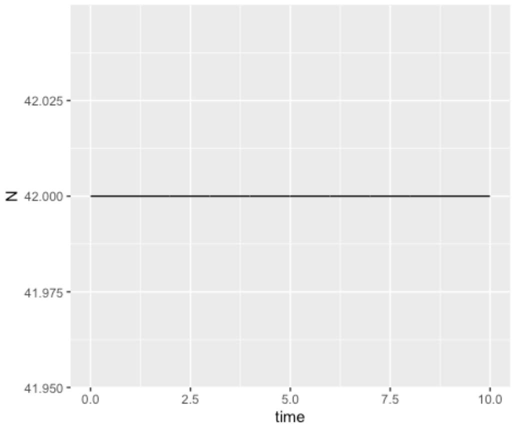


r = 0



parameter	
r	population growth rate
K	Carrying capacity

Step 3. Learn about study system through analysis of model behavior

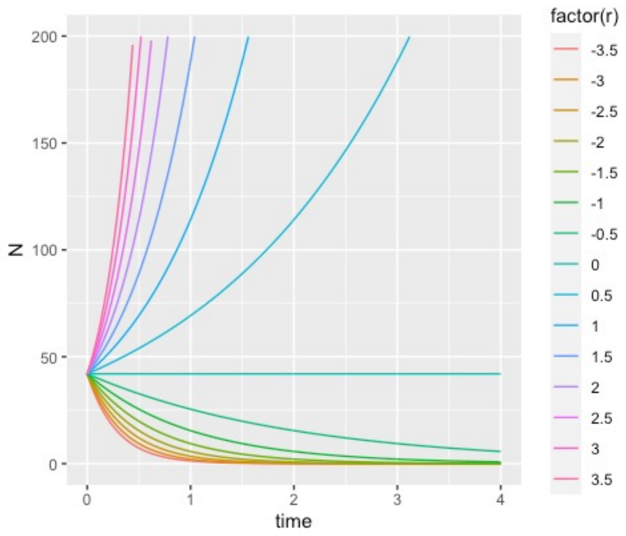
Population ecology

Exponential growth

$$\frac{dn}{dt} = rn \longrightarrow n(t) = n_0 e^{rt}$$

Graphical techniques: develop a feeling for your model

Expected dynamics

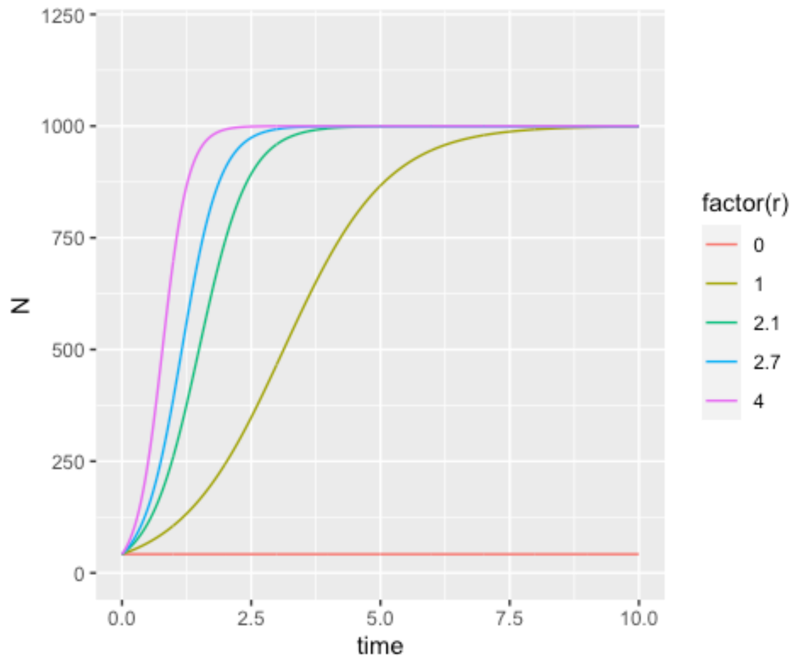


parameter	
r	population growth rate

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) \longrightarrow n(t) = \frac{K}{1 + n_0 e^{-rt}}$$

Expected dynamics



parameter	
r	population growth rate
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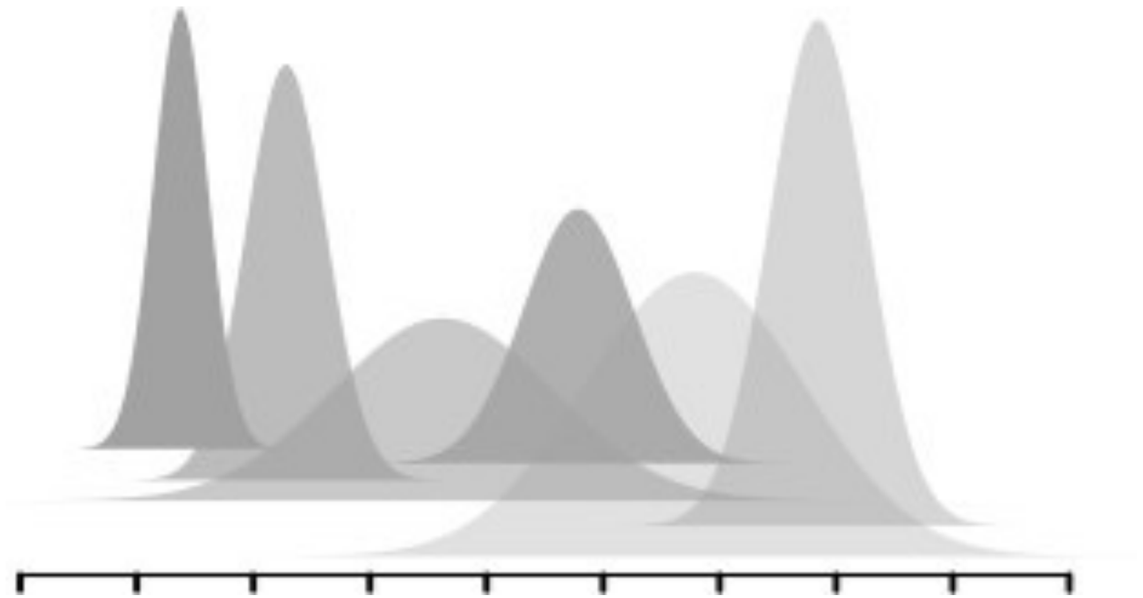
2.1 Survey of Ecological Models – Part 2



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Step 3. Learn about study system through analysis of model behavior

Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

Graphical techniques: develop a feeling for your model

Equilibria and stability analyses

Equilibrium

- a system at *equilibrium* does not change over time
- A particular value of a variable is called an *equilibrium value* if, when the variable is *started* at this value, the system never changes
- At equilibrium in a continuous-time model, dn/dt must equal 0 for each variable

How to solve for equilibrium values

- Replace desired value with «the equilibrium value»

$$\frac{dn}{dt} = rn \longrightarrow \frac{dn}{dt} = rn^*$$

- We would like to know n*, «the value of n at which the population size is no longer changing»

$$\frac{dn}{dt} = 0 \longrightarrow 0 = rn^*$$

- Solve for the equilibrium value of n (n*)

$$0 = rn^* \longrightarrow \frac{0}{r} = \frac{n^*}{r} \longrightarrow 0 = n^*$$

- The system is at equilibrium (n is not changing, dn/dt = 0) when n* = 0

Population ecology

Exponential growth

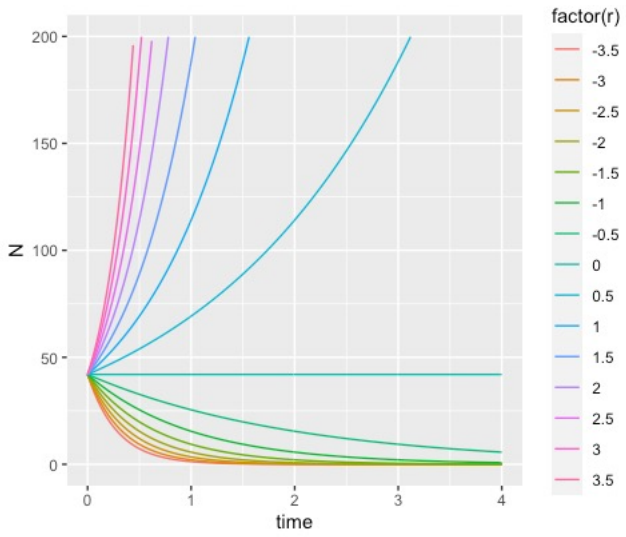
$$\frac{dn}{dt} = rn$$

Graphical techniques: develop a feeling for your model

Equilibria and stability analyses

Equilibrium

$$\frac{dn}{dt} = 0 \longrightarrow n_t^* = 0$$



Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

$$0 = rn\left(1 - \frac{n}{K}\right) \longrightarrow n^* = 0$$

$$\left(1 - \frac{n^*}{K}\right) = 0 \longrightarrow 1 = \frac{n^*}{K} \longrightarrow K = n^*$$

Step 3. Learn about study system through analysis of model behavior

Population ecology

Exponential growth

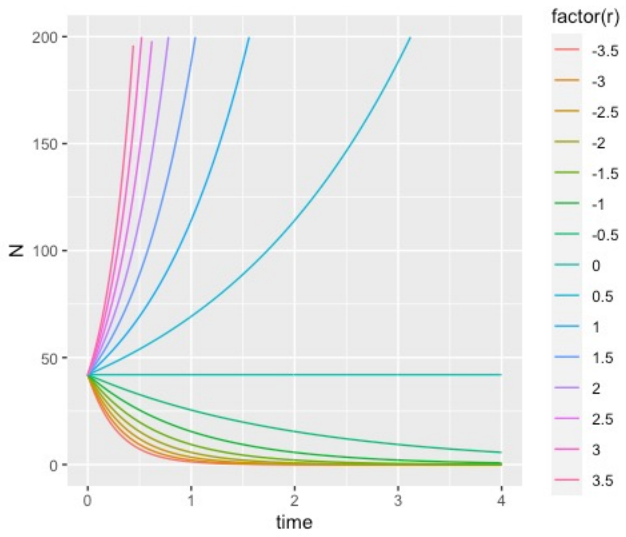
$$\frac{dn}{dt} = rn$$

Graphical techniques: develop a feeling for your model

Equilibria and stability analyses

Equilibrium

$$\frac{dn}{dt} = 0 \longrightarrow n_t^* = 0$$



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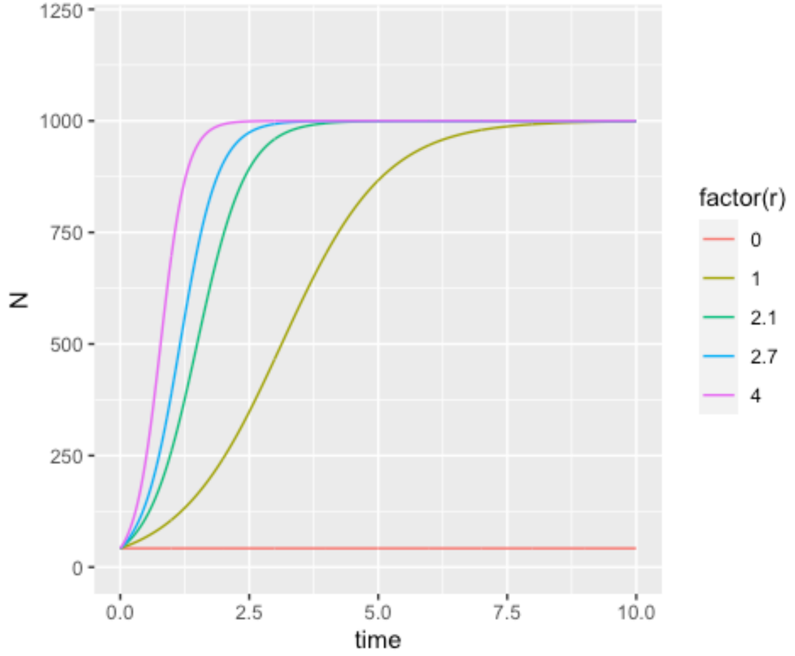
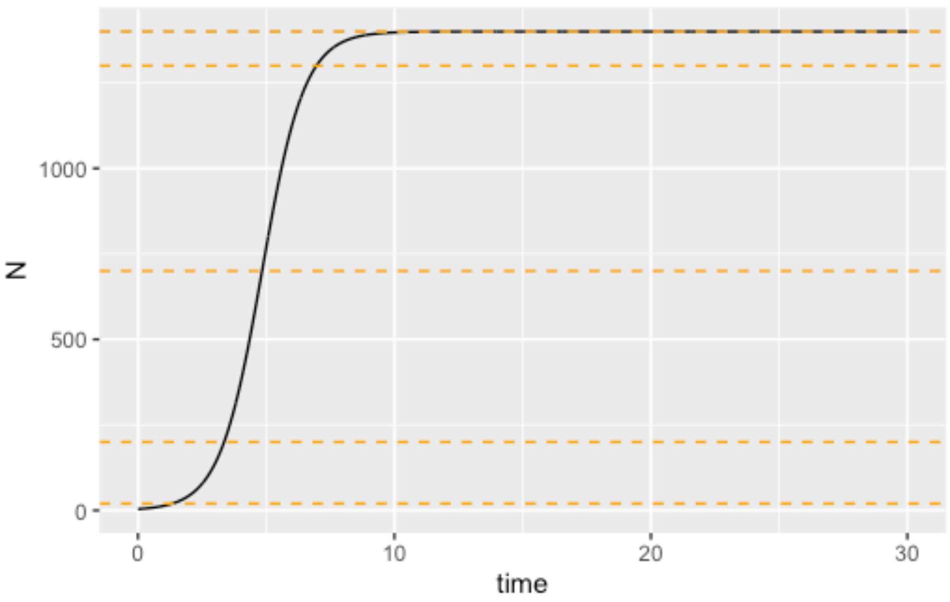


Step 3. Learn about study system through analysis of model behavior

Population ecology

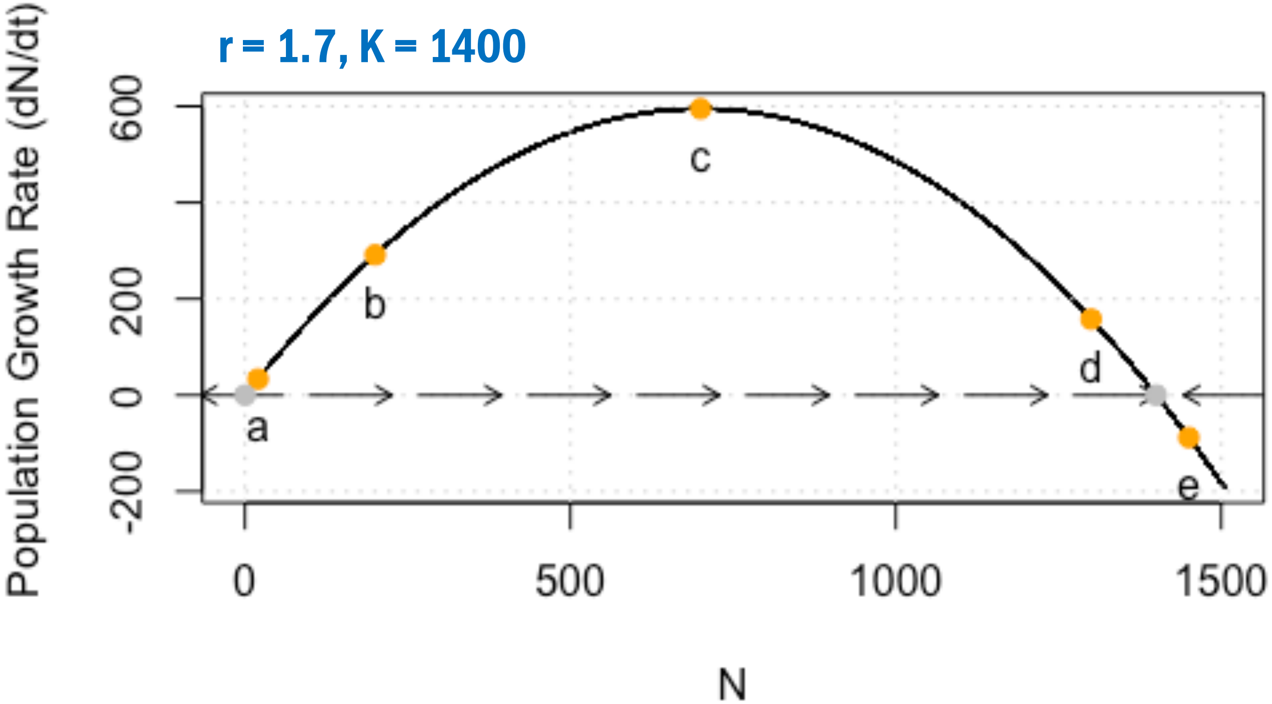
Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$



Graphical techniques: develop a feeling for your model
Equilibria, Stability, Phase plane diagram

How does the growth rate of the system (dn/dt) change for different values of *n*?



Step 3. Learn about study system through analysis of model behavior

Population ecology

Logistic growth

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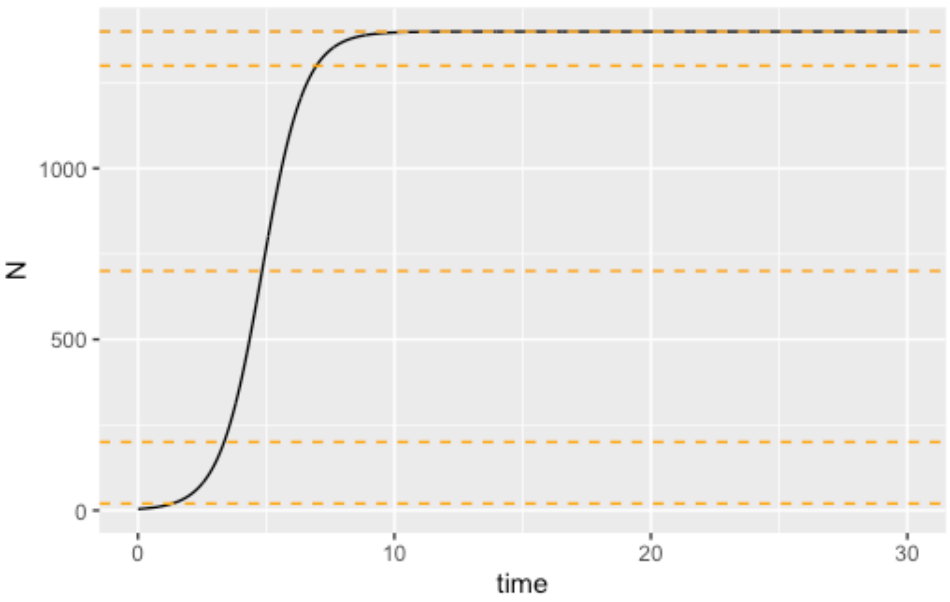
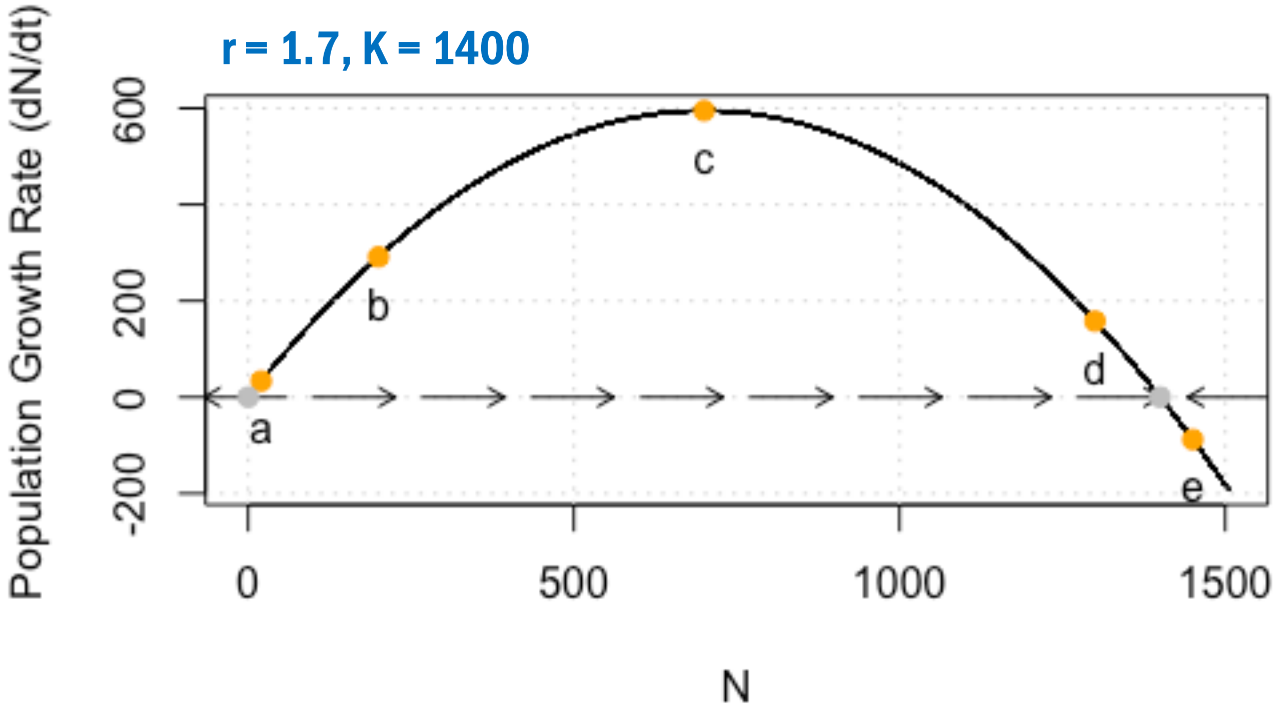


Graphical techniques: develop a feeling for your model
Equilibria, Stability, Phase plane diagram

How does the growth rate of the system (dn/dt) change for different values of *n*?

- **Note the equilibria N^* values (N=0,K) – where dn/dt = 0**

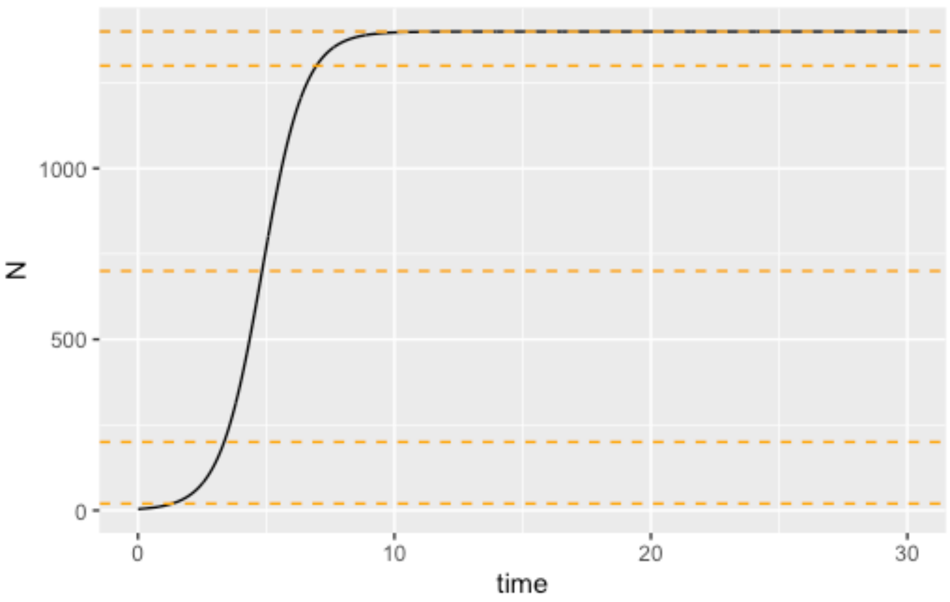
r = 1.7, K = 1400



Population ecology

Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$

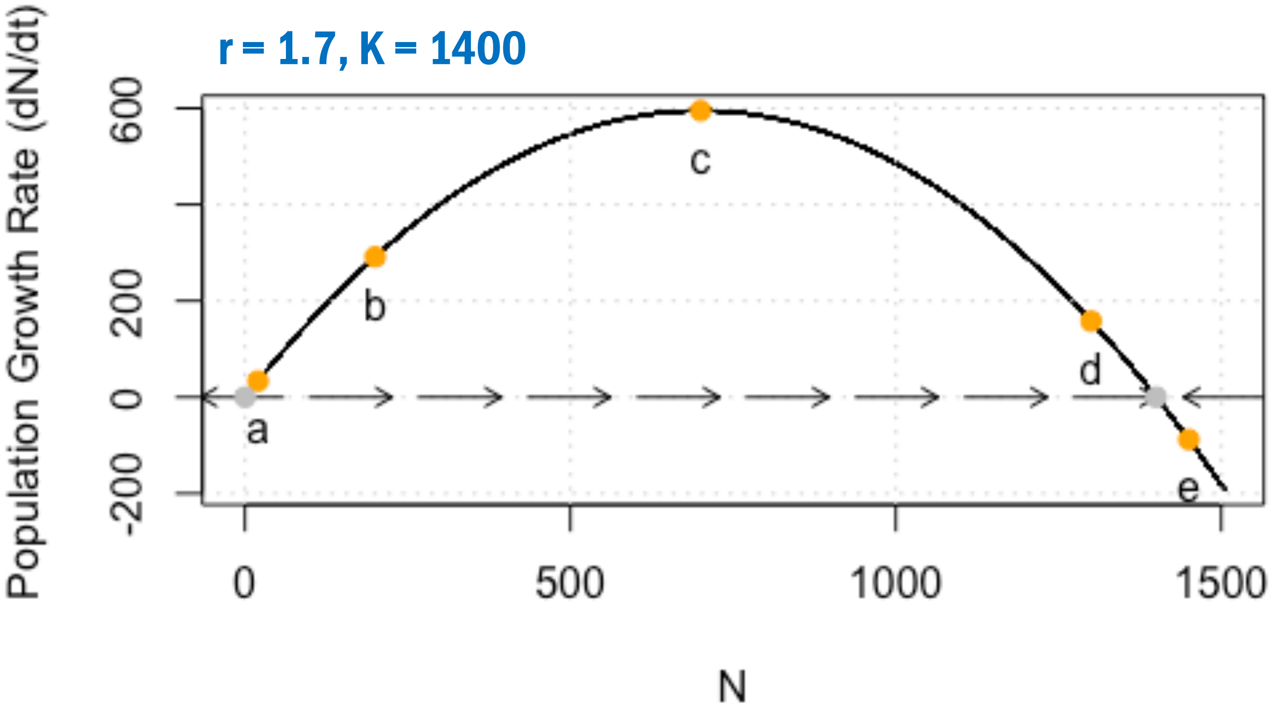


Graphical techniques: develop a feeling for your model
Equilibria, Stability, Phase plane diagram

How does the growth rate of the system (dn/dt) change for different values of *n*?

- **Note the equilibria N^* values (N=0,K) – where dn/dt = 0**
- **Note the changes in the growth rate of the system (dn/dt)**
  - **a (N=20), b (n=200), c (n=700), d (n = 1350)**

r = 1.7, K = 1400

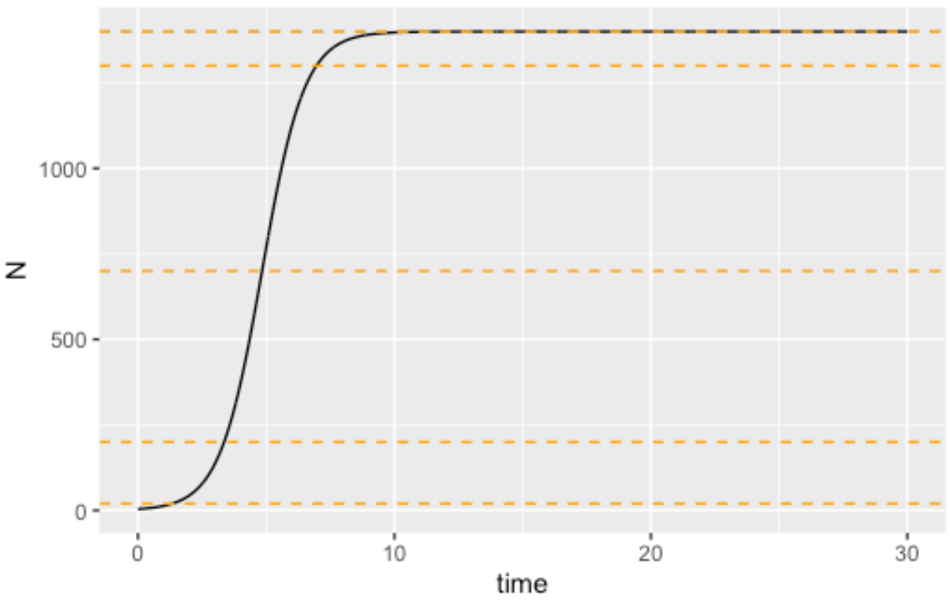


Step 3. Learn about study system through analysis of model behavior

Population ecology

Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$



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Equilibria, Stability, Phase plane diagram

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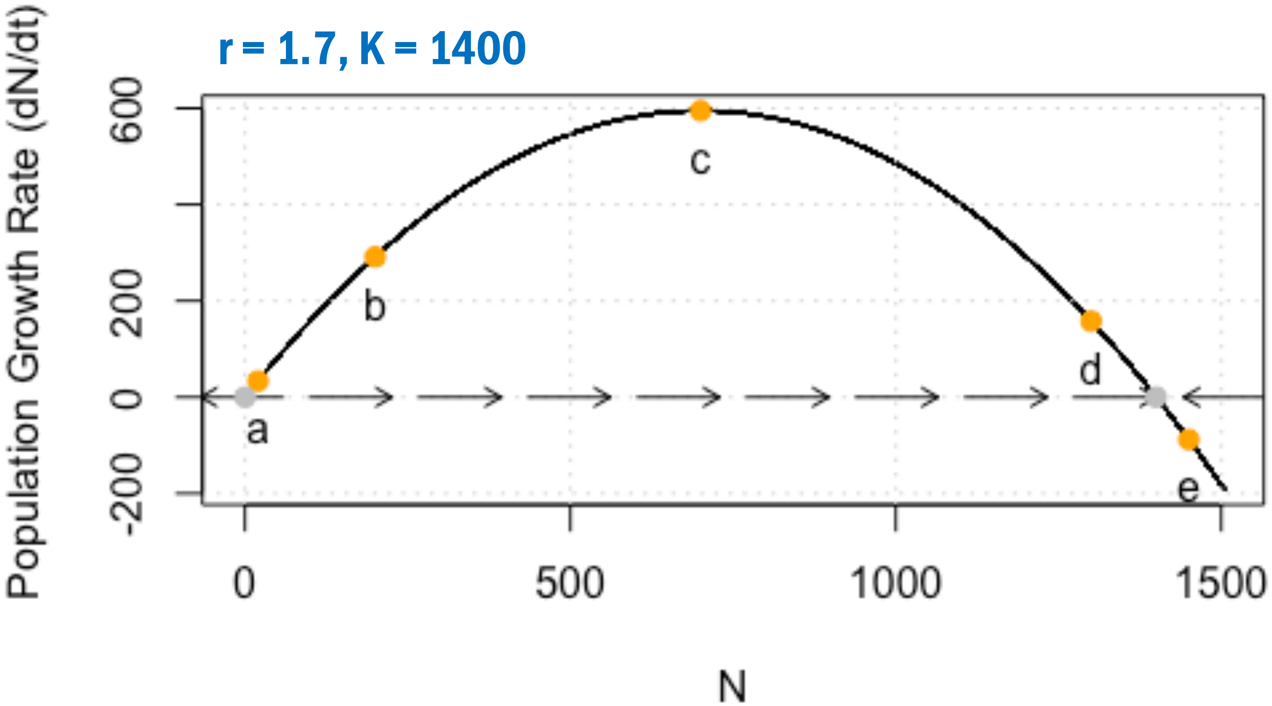
- Note the changes in the growth rate of the system (dn/dt)
  - a (N=20), b (n=200), c (n=700), d (n = 1350)
- Note the direction of the arrows along the axis of N (the state variable) – equilibrium analysis asks – what equilibria does the system move towards when N is moved *away* from one of these
  - This is *perturbation analysis*
  - If N > 0, N=K is the stable equilibrium

r = 1.7, K = 1400



Step 3. Learn about study system through analysis of model behavior

Population ecology

Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$

Graphical techniques: develop a feeling for your model
Equilibria, Stability, Phase plane diagram

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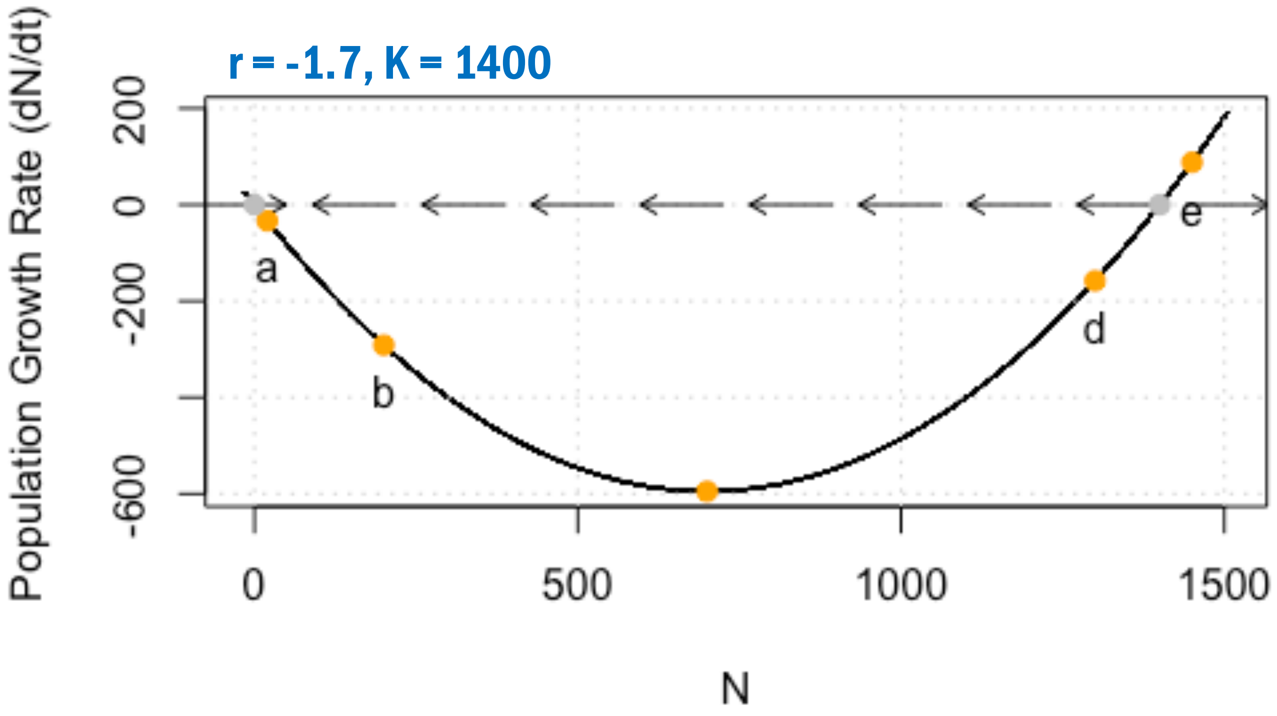
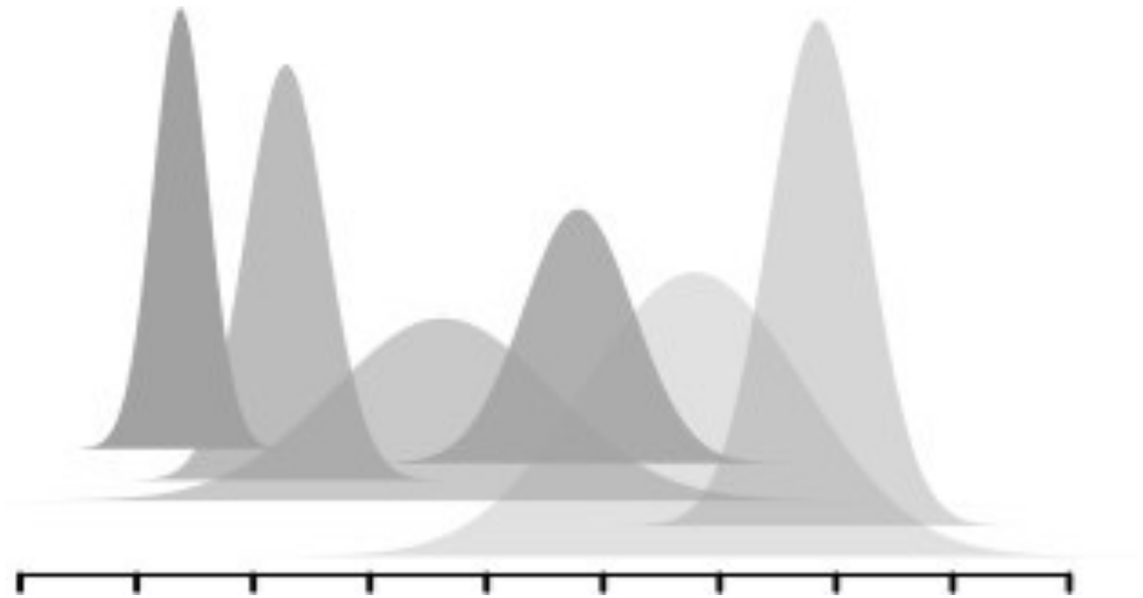
  - This is *perturbation analysis*
  - If N < K, N=0 is the stable equilibrium



2.3 Survey of Ecological Models – Part 3



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Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

parameter	
r	population growth rate
K	Carrying capacity
α_{ij}	Interaction coefficient

The *per capita* impact of Species j on Species i – negative for competition (positive for mutualism)

Community ecology

Lotka Volterra competition model

$$\frac{dn_i}{dt} = rn_i\left(1 - \frac{n_i + \alpha_{ij}n_j}{K_i}\right) \qquad \frac{dn_j}{dt} = rn_j\left(1 - \frac{n_j + \alpha_{ji}n_i}{K_j}\right)$$

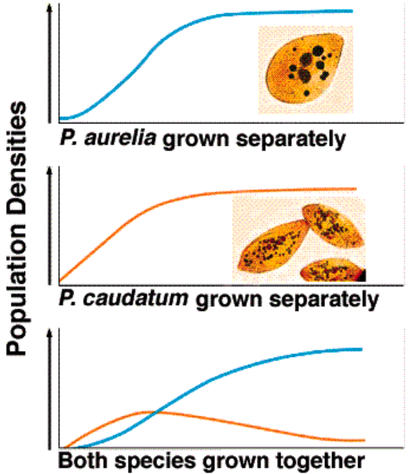
Alfred J. Lotka (1880-1949)
Chemist, ecologist, mathematician
Ukrainian immigrant to the USA

Vito Volterra (1860-1940)
Mathematical Physicist
Italian, refugee of fascist Italy

Testing the consequences of species interactions: Georgii Frantsevich Gause (b. 1910)

Paramecium caudatum

Paramecium aurelia



Population ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

parameter	
r	population growth rate
c	Encounter rate
a	Probability of successfully using / capturing prey
ε	Conversion efficiency (of consumed prey to predator population)
δ	Mortality rate

Community ecology

Lotka Volterra competition model

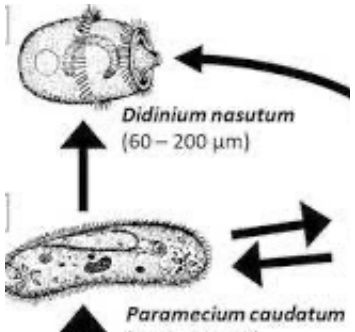
$$\frac{dn_i}{dt} = rn_i\left(1 - \frac{n_i + \alpha_{ij}n_j}{K_i}\right) \qquad \frac{dn_j}{dt} = rn_j\left(1 - \frac{n_j + \alpha_{ji}n_i}{K_j}\right)$$

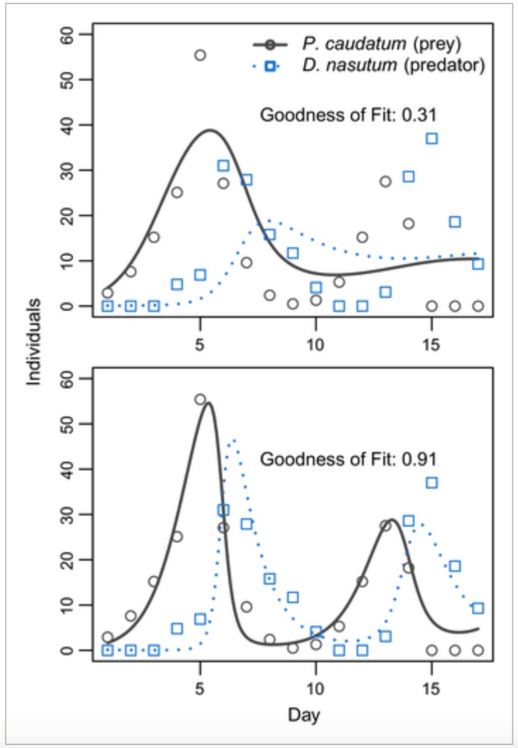
Lotka Volterra predator-prey model

prey
$$\frac{dn_i}{dt} = rn_i - acn_in_j$$

predator
$$\frac{dn_j}{dt} = \varepsilon acn_in_j - \delta n_j$$

Testing the consequences of species interactions: Georgii Frantsevich Gause (b. 1910)





Population ecology

Community ecology

Exponential growth

$$\frac{dn}{dt} = rn$$

Logistic growth

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right)$$

Lotka Volterra model

$$\frac{dn_i}{dt} = rn_i\left(1 - \frac{n_i + \alpha_{ij}n_j}{K_i}\right) \qquad \frac{dn_j}{dt} = rn_j\left(1 - \frac{n_j + \alpha_{ji}n_i}{K_j}\right)$$

Lotka Volterra predator-prey model

$$\frac{dn_i}{dt} = rn_i - acn_in_j \qquad \frac{dn_j}{dt} = \varepsilon acn_in_k - \delta n_j$$

What drives the dynamics of populations? – demographic rates

Birth rates, death rates (δ) → population growth rates (r)
Interaction and consumption rates (α, a, c)
Energy use rates (ε)

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Birth rates, death rates (δ) → population growth rates (r)
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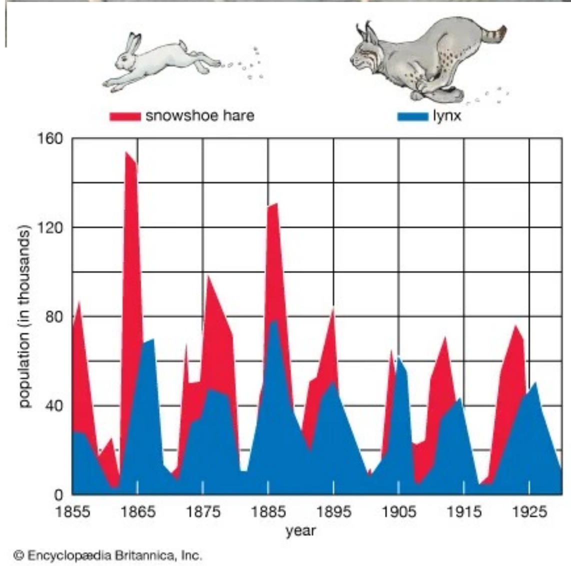
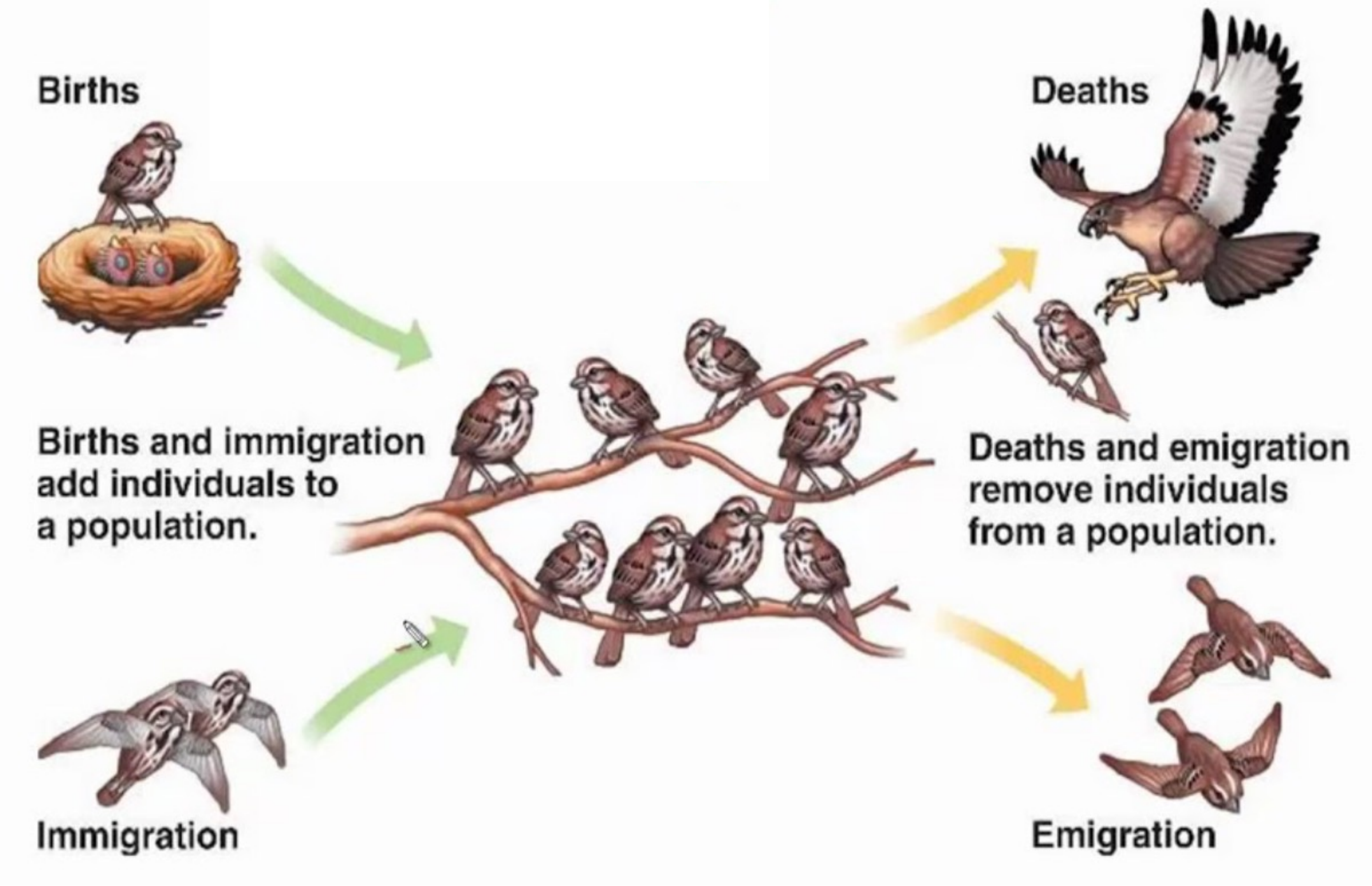




Population ecology

Exponential growth

$$\frac{dn}{dt} = rn_t$$

Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$

Community ecology

Lotka Volterra model

$$\frac{dn_i}{dt} = rn_i\left(1 - \frac{n_i + \alpha_{ij}n_j}{K_i}\right) \qquad \frac{dn_j}{dt} = rn_j\left(1 - \frac{n_j + \alpha_{ji}n_i}{K_j}\right)$$

Lotka Volterra predator-prey model

$$\frac{dn_i}{dt} = rn_i - acn_in_j \qquad \frac{dn_j}{dt} = \varepsilon acn_in_k - \delta n_j$$

What drives the dynamics of populations? – demographic rates

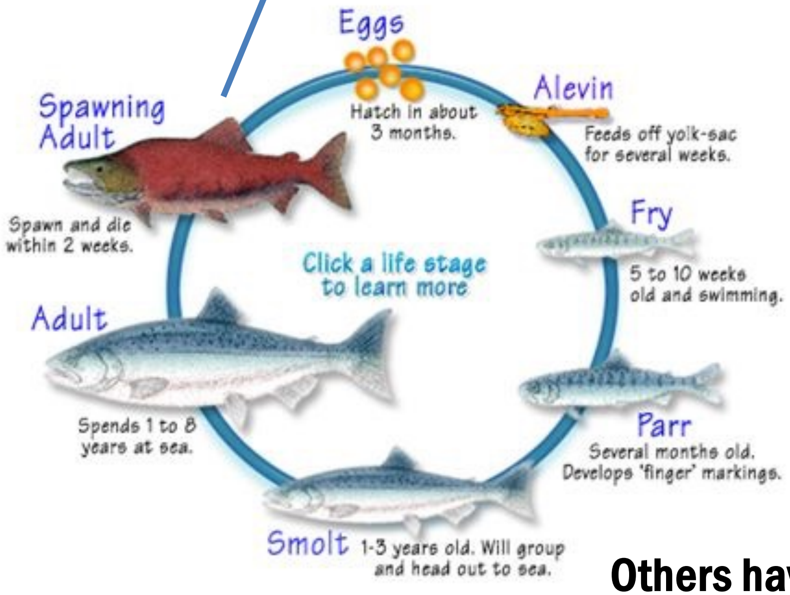
Birth rates, death rates (δ) → population growth rates (r)
Interaction and consumption rates (α, a, c)
Energy use rates (ε)

Notice how there is a single rate to describe the population

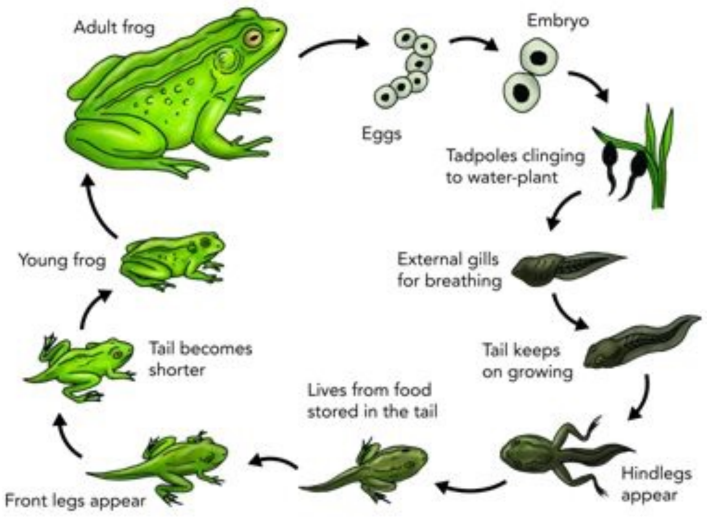
r = 1.3, α = 0.45, etc

Demographic rates can differ depending on age or life stage

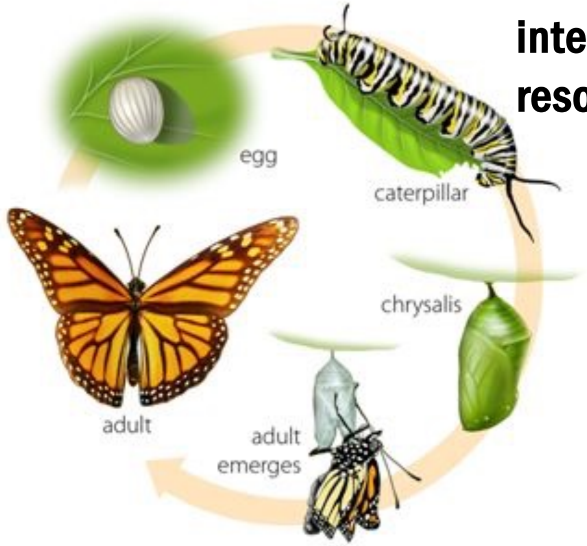
Only adults in this stage actually reproduce



Perhaps some stages have higher mortality / death rate than others



Others have different interaction rates with resources (or resource use)



Population ecology

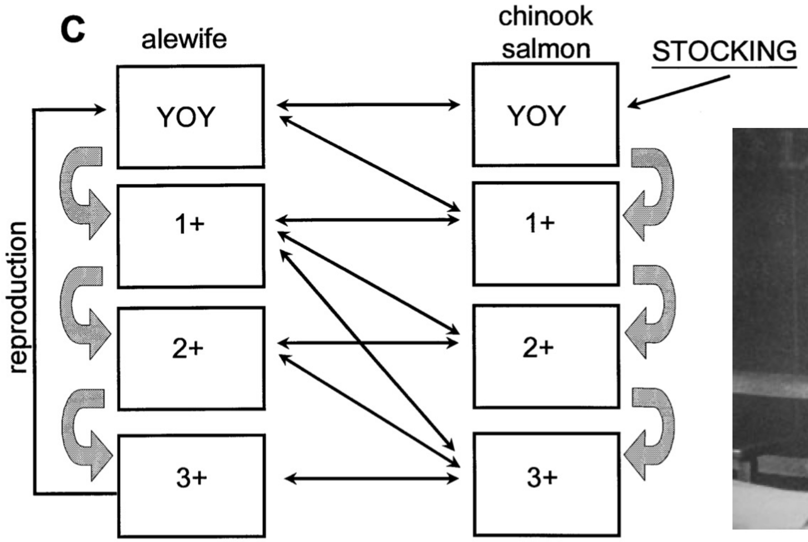
Exponential growth

$$\frac{dn}{dt} = rn_t$$

Logistic growth

$$\frac{dn}{dt} = rn_t\left(1 - \frac{n_t}{K}\right)$$

Stage-structured model



Jackson et al. 2000

Patrick H. Leslie

On the use of Matrices in Certain Population Mathematics, Biometrika , Vol. 32., pp. 183-212

Community ecology

Lotka Volterra model

$$\frac{dn_i}{dt} = rn_i\left(1 - \frac{n_i + \alpha_{ij}n_j}{K_i}\right) \qquad \frac{dn_j}{dt} = rn_j\left(1 - \frac{n_j + \alpha_{ji}n_i}{K_j}\right)$$

Lotka Volterra predator-prey model

$$\frac{dn_i}{dt} = rn_i - acn_in_j \qquad \frac{dn_j}{dt} = \varepsilon acn_in_k - \delta n_j$$

N is now a vector of abundances (for 2 stages)

$N_{t+1} = rN_t$ **A is now a *transition matrix***

$$N_{t+1} = AN_t$$

$$\begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_{t+1} = \begin{bmatrix} F_1 & F_2 \\ P_{1\to 2} & P_{2\to 2} \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \end{bmatrix}_t$$

F_1, F_2 – *fecundity* of stage 1 and stage 2 (per-capita number of offspring produced)

$P_{1\to 2}$, $P_{2\to 2}$ – *survivorship*: Stage 1 must become Stage 2 (or die). Stage 2 stays at Stage 2 (or dies)

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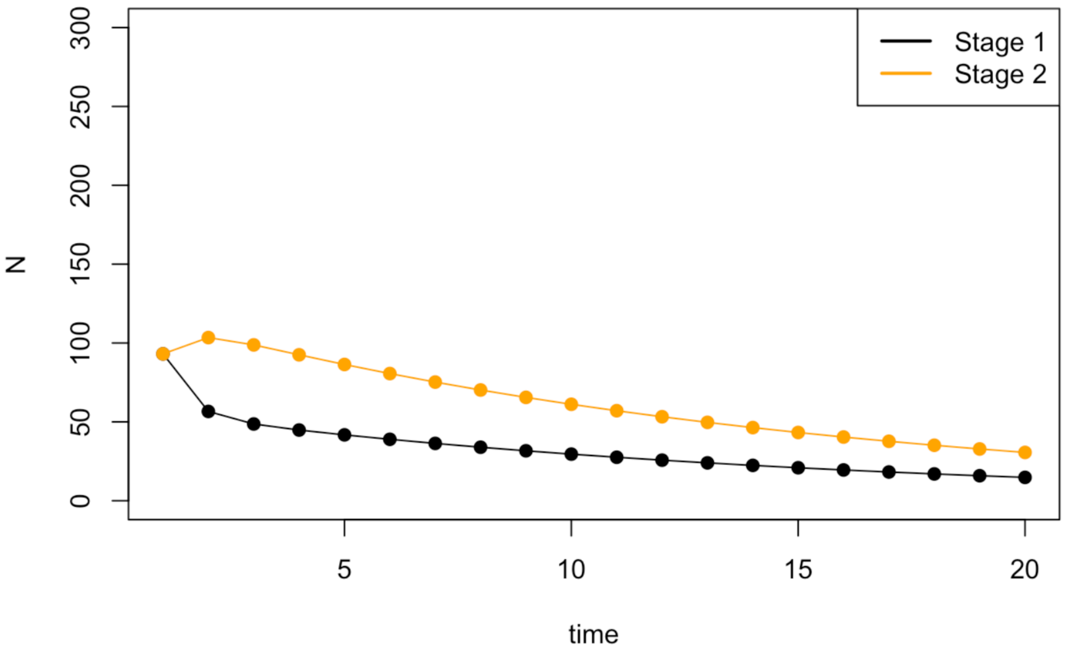
56.6	0.304	0.304	93.1	
103.43	0.344	0.767	93.1	



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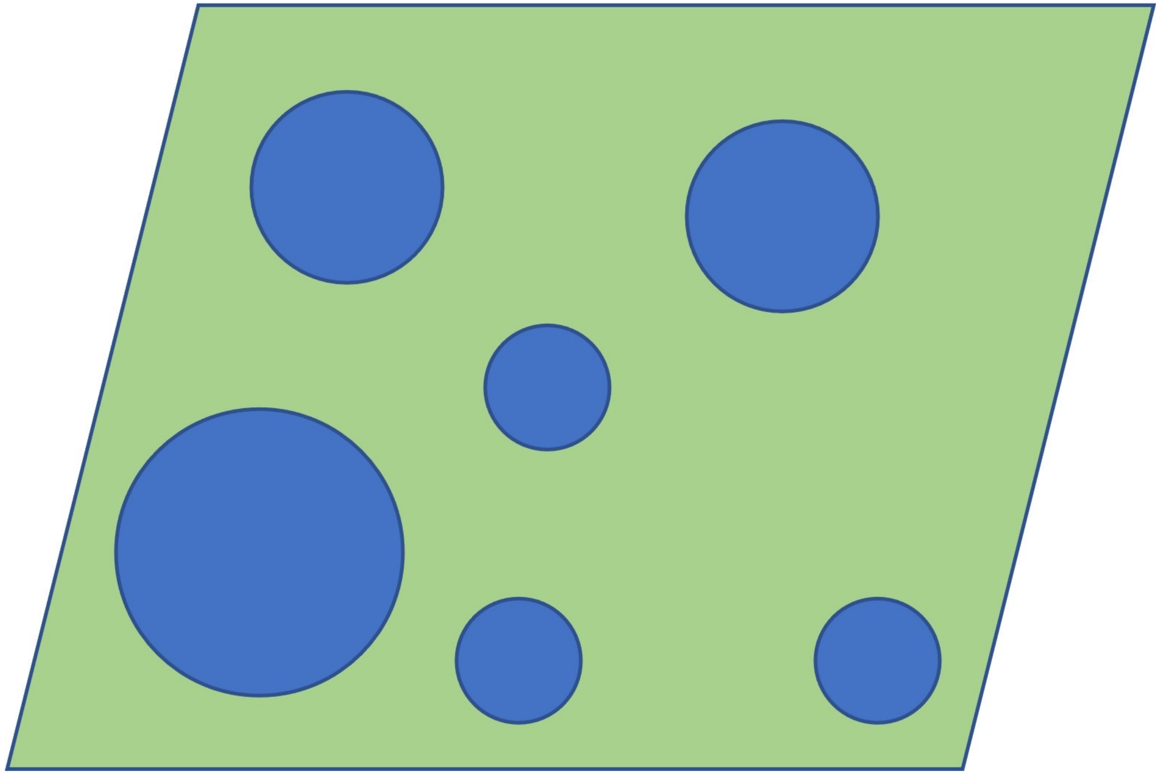
Metapopulation model



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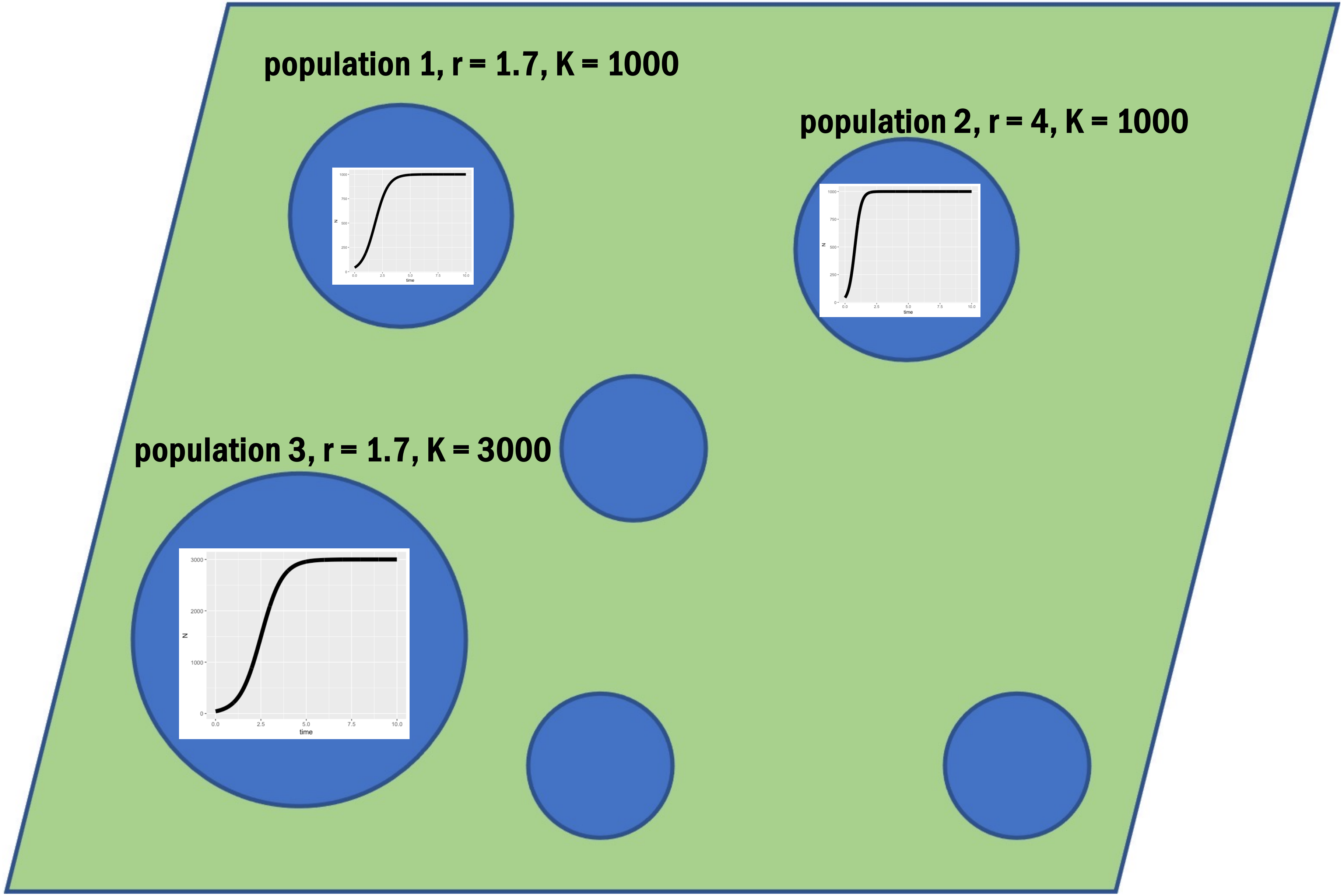
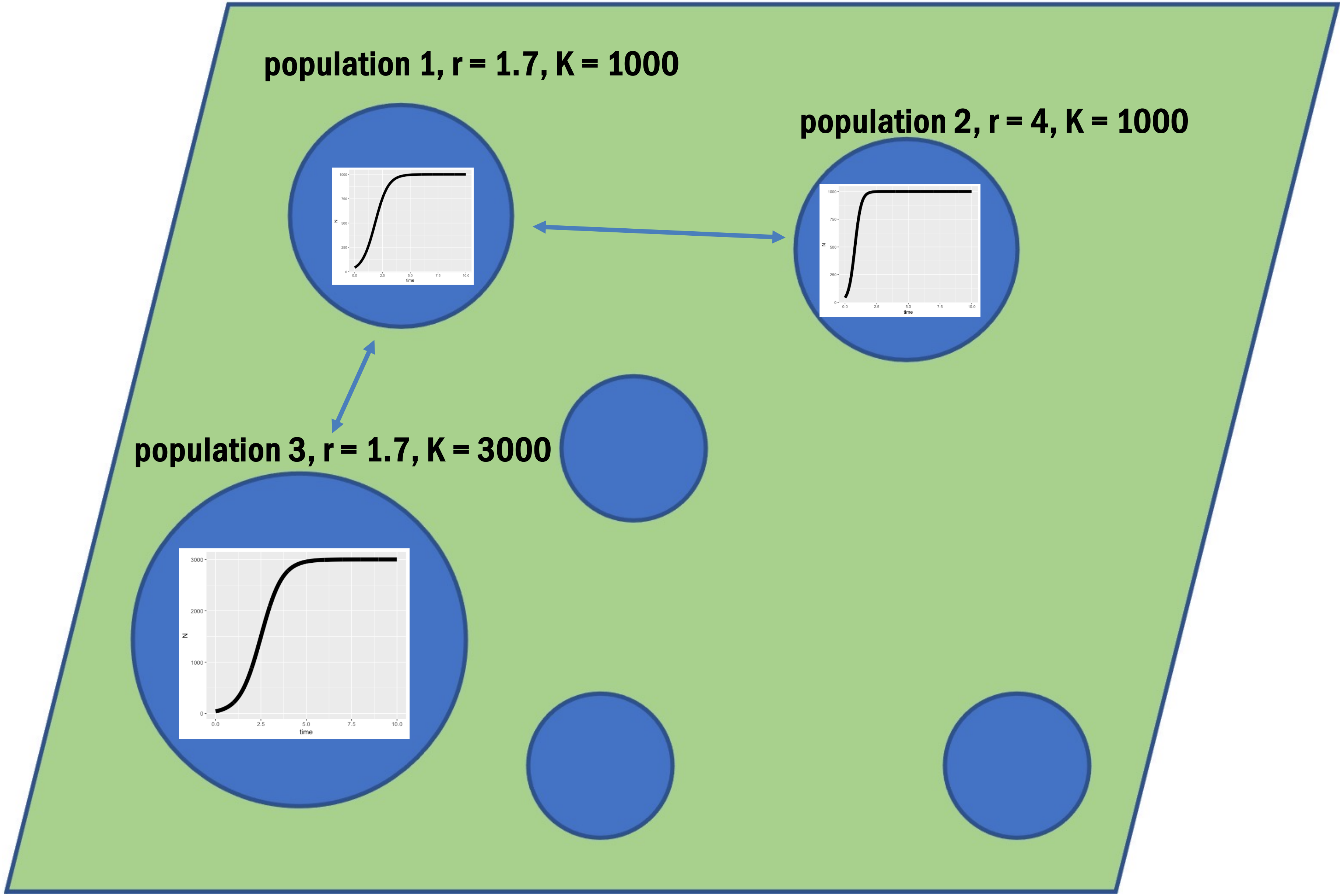
Population model

Assumes all population dynamics are independent



Metapopulation model

Assumes population dynamics are linked, as species can move among patches



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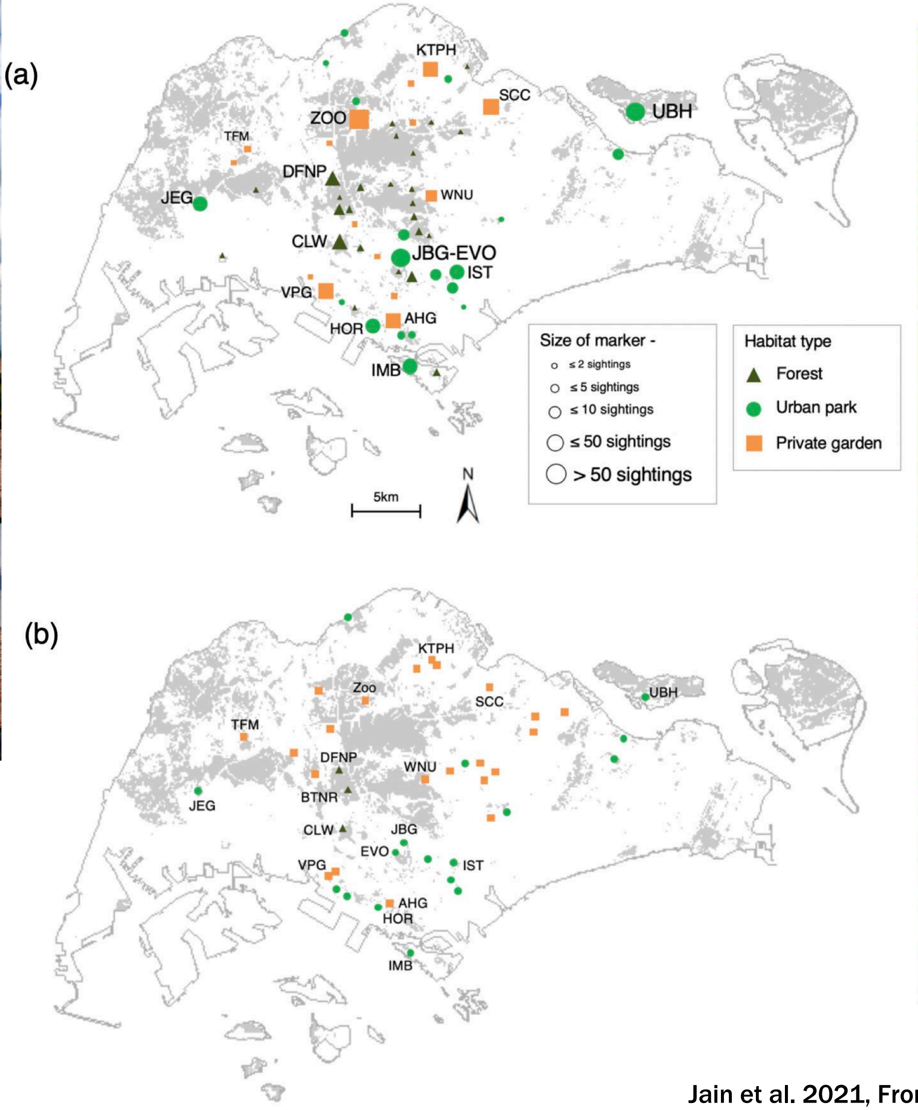

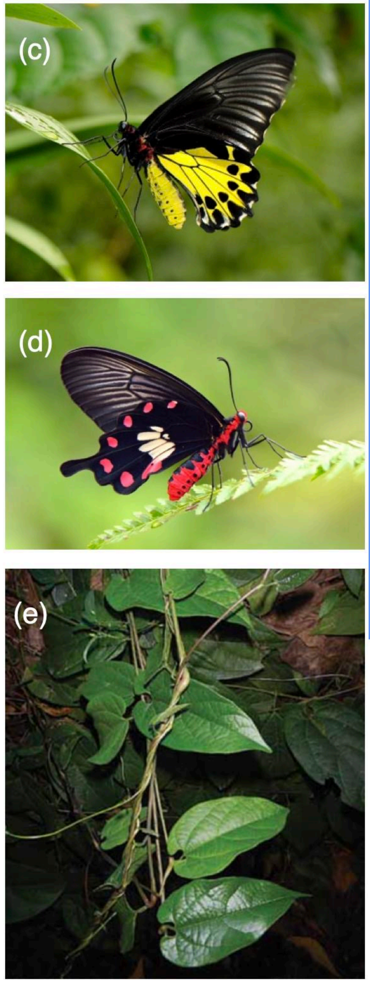

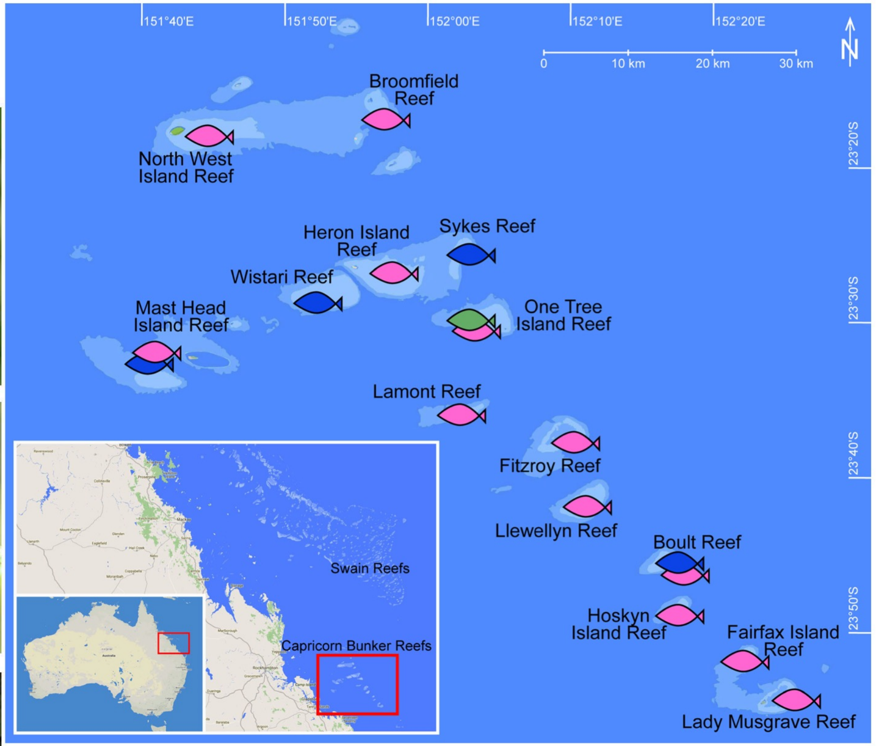

Gerlach et al. 2021, Coral Reefs 40: 999-1011

Jain et al. 2021, Frontiers in Ecology & Evolution

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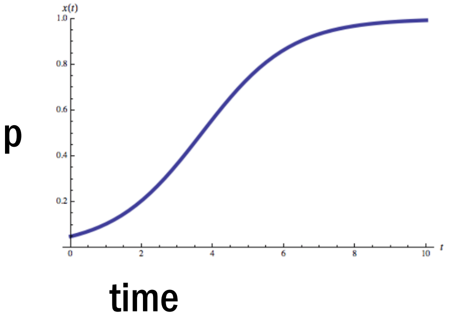
Metapopulation model

$$\frac{dp}{dt} = cp(1-p) - ep$$

Change in the proportion of occupied sites (p) over time (t)



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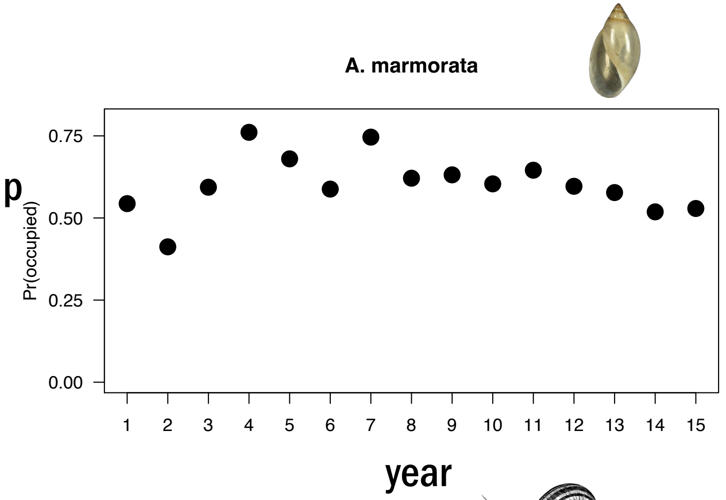
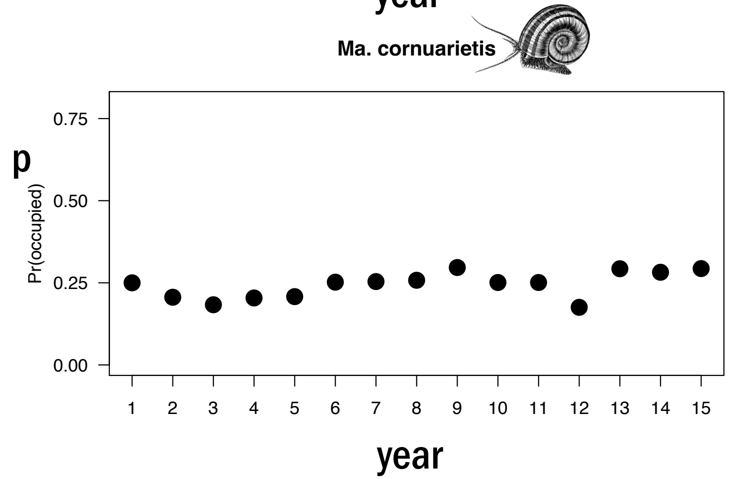




Metapopulation model

$$\frac{dp}{dt} = cp(1 - p) - ep$$

Change in the proportion of occupied sites (p) over time (t)

colonization rate (probability a site is colonized)

extinction rate (probability a site becomes extinct)

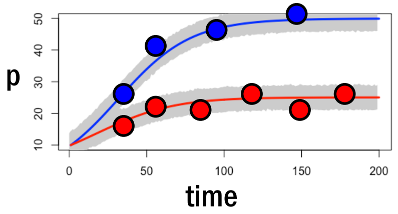
Metapopulation model

$$\frac{dp}{dt} = \underbrace{cp(1-p)}_{\text{Probability that an unoccupied site (1-p) becomes colonized by a population from an occupied site (cp)}} - ep$$

Change in the proportion of occupied sites (p) over time (t)

Equilibrium

time



$$\frac{dp}{dt} = cp^*(1-p^*) - ep^*$$

$$0 = cp^*(1-p^*) - ep^* \longrightarrow 0 = cp^* - cp^{*2} - ep^* \longrightarrow 0 = p(c - cp^* - e)$$

$$\frac{0}{p} = \frac{p(c-cp^*-e)}{p} \longrightarrow 0 = c - cp^* - e \longrightarrow cp^* = c - e$$

$$\frac{cp^*}{c} = \frac{c-e}{c} \longrightarrow p^* = 1 - \frac{e}{c}$$

When will the metapopulation become extinct (p* ≤ 0) ? → e > c

When will the metapopulation persist (p* > 0) ? → c > e

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