

# Calculating Biological Quantities

CSCI 2897

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# Last time on CSCI 2897..

## 1. Haploid & <sup>not yet</sup> diploid ~~models~~ models of natural selection

$$\frac{dp}{dt} = \overset{\text{const.}}{s_c} p(t) (1 - p(t))$$

$p(t)$  = fraction of population type/variant A (vs a)

$$s_c = (b_A - d_A) - (b_a - d_a)$$

↑   ↑   ↓   ↑  
birth death   a  
A

### CDC director warns Covid variants could reverse the recent drop in cases and hospitalizations

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#### KEY POINTS

- New variants are a “threat” to the U.S. and could reverse the recent declines in Covid-19 cases and hospitalizations, CDC Director Dr. Rochelle Walensky said Monday.
- “Please continue to wear a mask and stay 6 feet apart from people you don’t live with. Avoid travel, crowds and poorly ventilated spaces and get vaccinated when it’s available to you,” she added.



# Lecture 7 Plan

- 1. Equilibrium solutions**
- 2. Lotka-Volterra Model of Competition**

# Equilibrium

A system at **equilibrium** does not change over time. (Plural: **equilibria**.)

For a discrete time model, at equilibrium, it must be true that:

$$n(t+1) = n(t) \quad (\text{no change}) \quad \Delta n = 0$$

For a continuous time model, at equilibrium, it must be true that:

$$\frac{dn}{dt} = 0 \quad (\text{no change})$$

↑  
rate of change

# Equilibrium

$$c \cdot x(1-x) = 0 \quad \text{what is } x?$$

$c=0$        $x=0$        $x=1$

A system at **equilibrium** does not change over time. (Plural: **equilibria**.)

What is the equilibrium / what are the equilibria for our haploid frequency equation?

$$\frac{dp}{dt} = s_c p(t)(1 - p(t))$$

$$s_c p(t)(1 - p(t)) = 0$$

$p=0$        $p=1$

"steady state solutions"

① set  $\frac{dp}{dt} = 0$  (no change)

② solve the equation for the variables, but not for the parameters

not interested

- If the system is at  $p=0$ , it will always be at  $p=0$ .
- If the system is at equilibrium, it will always be at that eq.

Note: we're always solving for equilibrium values of the *variables*, not the *parameters*.

# Stability

An equilibrium is **locally stable** if a system near that equilibrium approaches it. This property is called **locally attracting**.

*If I jiggle/bump the system a little, does it come back to equil.? YES*

An equilibrium is **globally stable** if a system approaches that equilibrium *regardless* of its initial position.

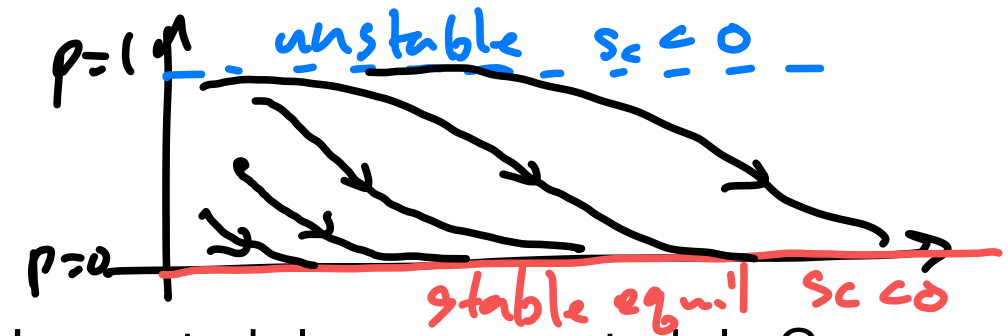
An equilibrium is **unstable** if a system near the equilibrium moves away from it. This property is called **repelling**.

*If I "bump" the system a little, does it come back to equil.? NO*

*Liz.  
Bradley.*

*bump = some perturbation  $\epsilon > 0$  e.g. 0.0000000000000001*

# Stability



Are the equilibria for our haploid allele frequency equation stable or unstable?

$$\frac{dp}{dt} = s_c p(t)(1 - p(t))$$

$$p = 0$$

Let  $p = p_{\text{equil}} + \varepsilon$   $\varepsilon > 0$ , but v. small

$$s_c = (b_A - d_A) - (b_a - d_a)$$

$$p = 1$$

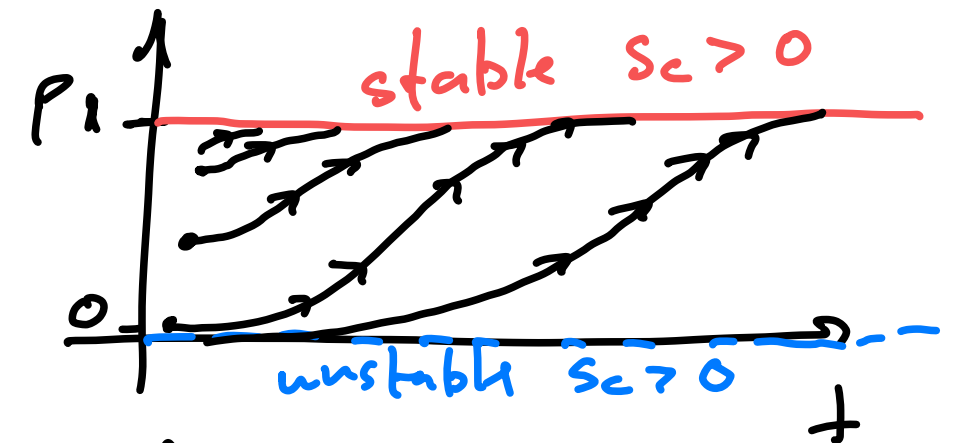
Let  $p = p_{\text{equil}} - \varepsilon$ ,  $\varepsilon > 0$  but v. small

$$\frac{dp}{dt} = s_c (\varepsilon)(1 - \varepsilon)$$

positive or negative?

when  $s_c > 0$

$s_c < 0$



• If  $s_c > 0$ ,  $p = 0$  is unstable.

• If  $s_c < 0$ ,  $p = 0$  is stable

• If  $s_c > 0 \Rightarrow p = 1$  stable

• If  $s_c < 0 \Rightarrow p = 1$  unstable

$= s_c (1 - \varepsilon)(\varepsilon)$   
positive when  $s_c > 0$ , negative when  $s_c < 0$

# Bonus

Identify the equilibrium/a of the logistic growth equation, and characterize stability.

$$\dot{n} = r n \left( 1 - \frac{n}{K} \right) = 0$$

$r > 0$   
 $n = 0$   
 $n = K$

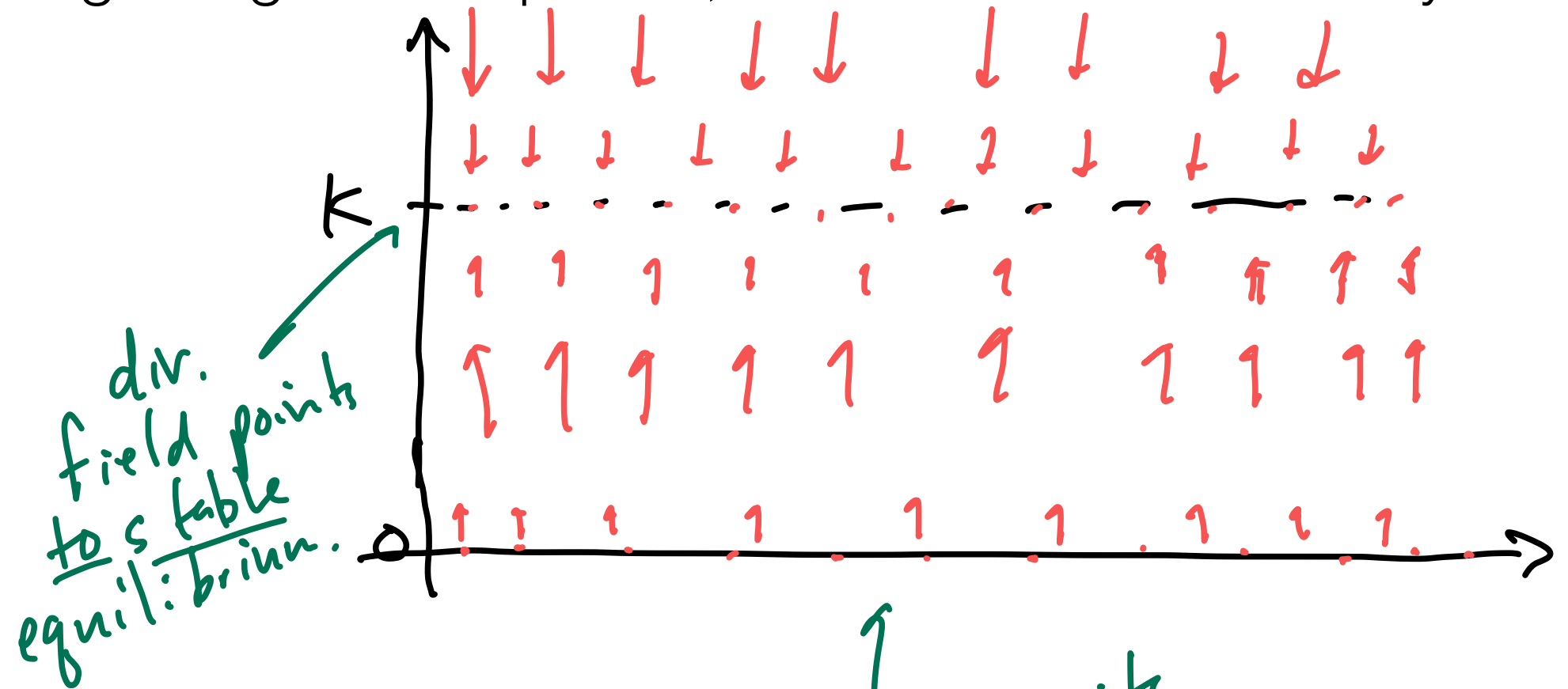
$n = 0$   
 $\text{pop} = 0$   
 $n = \varepsilon$

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

$\Rightarrow n = K$

pop = carrying capacity  $K$

$n = K + \varepsilon$      $n = K - \varepsilon$



div field points away from unstable equilibrium.



# Lotka-Volterra Competition

Imagine that there are two species, with population sizes  $n_1(t)$  and  $n_2(t)$ .

Let's imagine that each one has the property from Logistic Growth where its growth rate  $R$  depends on its population size  $n$ , so we have  $R_1(n_1)$  and  $R_2(n_2)$ .

What if one species' growth rate depended on the size of the other population?

Specifically, suppose that species  $i$  experiences competition *as if its own species had population*  $n_i(t) + \alpha_{ij} n_j(t)$ . (Here,  $i$  could be 1 or 2).

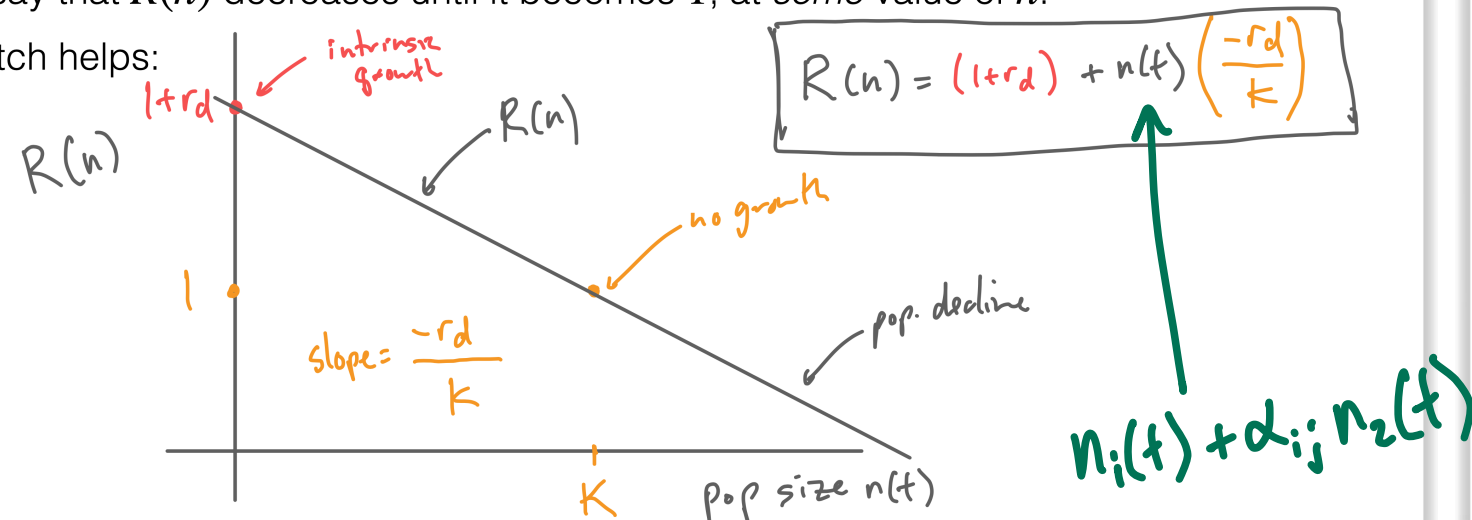
my pop.  
feels like  
its size  $\rightarrow (n_i(t) + \alpha_{i2} n_2(t))$

# Lotka-Volterra Competition

Remember when we derived the Logistic Growth equation?

## Logistic growth in discrete time

- Let's say that when the population size is zero,  $R(0) = 1 + r_d$ . *intercept.*
  - This is called the **intrinsic rate of growth**.
  - It's what happens when there aren't resource limitations (= prev. model).
- Let's say that  $R(n)$  decreases until it becomes 1, at some value of  $n$ .
- A sketch helps:



## Logistic growth in discrete time

- If we write  $n(t+1) = R(n) n(t)$ , we now get

$$n(t+1) = \left[ (1+r_d) - \frac{r_d}{K} n(t) \right] n(t)$$

$$n(t+1) = n(t) + r_d \left( 1 - \frac{n(t)}{K} \right) n(t)$$

We're now going to modify that equation for  $R(n)$ .

# Lotka-Volterra Competition

$$\text{Let } R_i = (1 + r_i) + \left( \frac{-r_i}{K_i} \right) \left( n_i(t) + \alpha_{ij} n_j(t) \right)$$

used to be  $n_i(t)$  for log. growth.

"index" species by  $i, j$ .

$i=1, j=2$

$i=2, j=1$

$$n(t+1) = R \cdot n(t)$$

Let's plug in this reproductive factor into *each* of our two update equations:

$$n_1(t+1) = \left[ (1 + r_1) + \left( \frac{-r_1}{K_1} \right) (n_1(t) + \alpha_{12} n_2(t)) \right] \cdot n_1(t)$$

$$n_2(t+1) = \left[ (1 + r_2) + \left( \frac{-r_2}{K_2} \right) (n_2(t) + \alpha_{21} n_1(t)) \right] \cdot n_2(t)$$

# Lotka-Volterra Competition

We can write similar equations in continuous time:

$$\frac{dn_1}{dt} = r_1 n_1(t) \left[ 1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right]$$

$$\frac{dn_2}{dt} = r_2 n_2(t) \left[ 1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right]$$

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

$\alpha_{12}$  and  $\alpha_{21}$   
need not be same.

- $\alpha_{12}$  = impact that species 1 feels from species 2.

- $\alpha_{21}$  = impact that 2 feels from 1.

# Lotka-Volterra Competition

Quick check: if the species don't interact, then:

$$\alpha_{12} = 0, \alpha_{21} = 0$$

which implies that...

$$\frac{dn_1}{dt} = r_1 n_1(t) \left( 1 - \frac{n_1(t) + \cancel{\alpha_{12} n_2(t)}}{K_1} \right) = r_1 n_1(t) \left( 1 - \frac{n_1(t)}{K_1} \right) \quad \text{Log. growth.}$$

$$\frac{dn_2}{dt} = r_2 n_2(t) \left( 1 - \frac{n_2(t) + \cancel{\alpha_{21} n_1(t)}}{K_2} \right) = r_2 n_2(t) \left( 1 - \frac{n_2(t)}{K_2} \right) \quad \text{Log. growth.}$$

Interpretation: If species don't interact  $\longrightarrow$  Log. growth.

Also note: this model is *symmetric* in that relabeling  $1 \leftrightarrow 2$  produces the same equations.

# Lotka-Volterra...Competition?

$$r_1 = 1, \quad n_1(t) = 1, \quad K_1 = 10 \\ n_2(t) = 2$$

$$\frac{dn_1}{dt} = r_1 n_1(t) \left( 1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right)$$

$$\frac{dn_2}{dt} = r_2 n_2(t) \left( 1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right)$$

$$\alpha_{12} = 0$$

$$\Rightarrow \frac{dn_1}{dt} = 1 \cdot 1 \left( 1 - \frac{1 + 0 \cdot 2}{10} \right) \\ = 1 \left( 1 - \frac{1}{10} \right) = \frac{9}{10}$$

What if  $\alpha_{12}$  is negative? How does an increase in  $n_2$  affect  $\frac{dn_1}{dt}$ ?

$$\alpha_{12} = -1 \quad \frac{dn_1}{dt} = 1 \cdot 1 \left( 1 - \frac{1 + (-1) \cdot 2}{10} \right)$$

$$= 1 \left( 1 - \frac{1-2}{10} \right) = \left( 1 - \frac{-1}{10} \right) = \frac{11}{10}$$

pop  $n_2$   
helps grow  $n_1$ !

# Lotka-Volterra...Competition?

$\alpha_{12}$	$\alpha_{21}$	Relationship
0	0	none
+	+	competitive
+	-	parasitic
-	+	parasitic
-	-	mutualistic
-	0	commensal
0	-	commensal

$$\frac{dn_1}{dt} = r_1 n_1(t) \left( 1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right)$$

$$\frac{dn_2}{dt} = r_2 n_2(t) \left( 1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right)$$

Let's code up the Lotka-Volterra model to explore!

$$\frac{dn_1}{dt} = r_1 n_1(t) \left( 1 - \frac{n_1(t) + \alpha_{12} n_2(t)}{K_1} \right)$$

$$\frac{dn_2}{dt} = r_2 n_2(t) \left( 1 - \frac{n_2(t) + \alpha_{21} n_1(t)}{K_2} \right)$$

with initial conditions

$$n_1(0) = a$$

$$n_2(0) = b$$