

Calculating Biological Quantities

CSCI 2897

Prof. Daniel Larremore

2021, Lecture 7

daniel.larremore@colorado.edu

[@danlarremore](https://twitter.com/danlarremore)

Last time on CSCI 2897..

1. Haploid models of natural selection

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

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

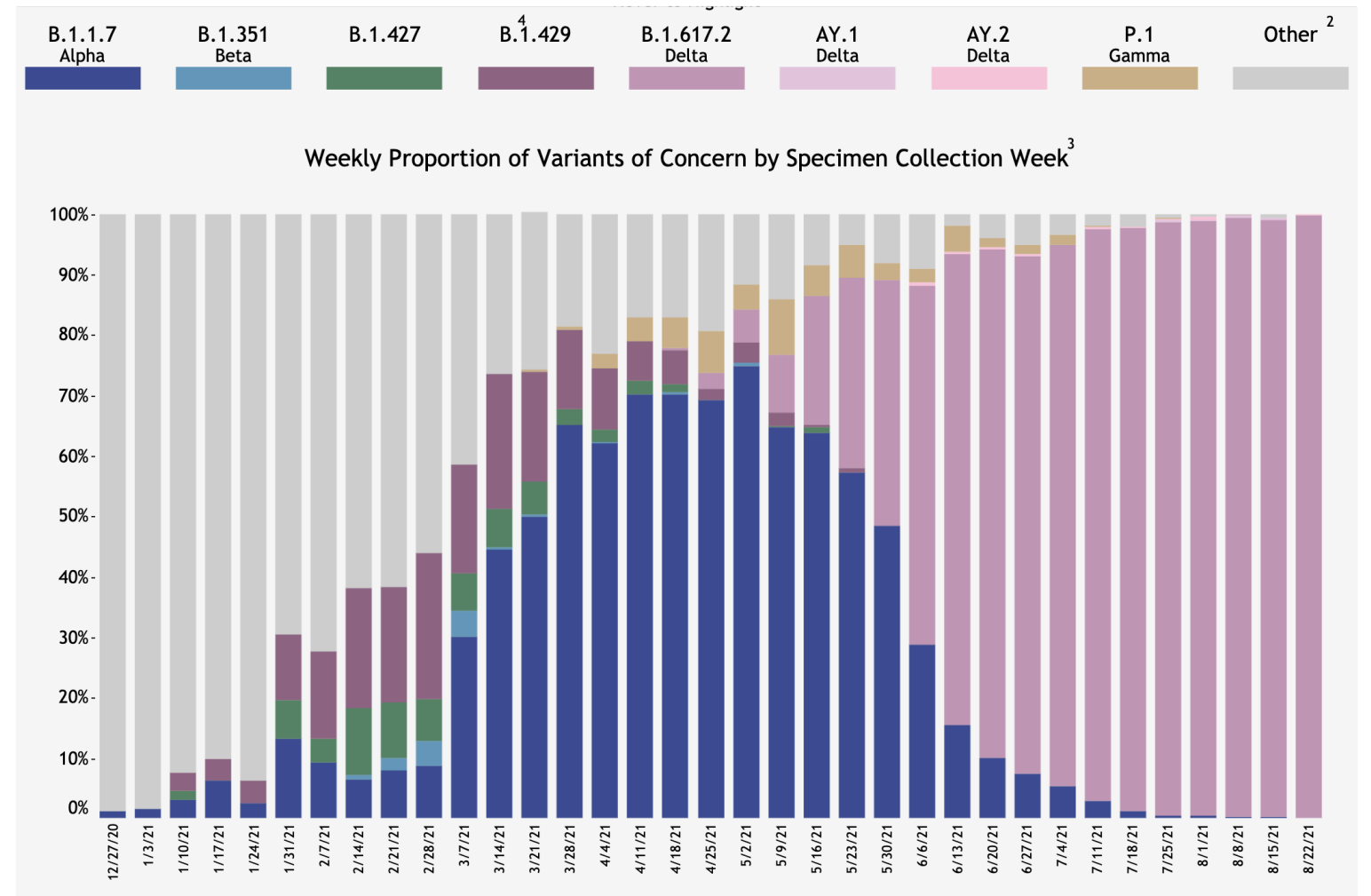
selection coeff. continuous

s_c positive A advantage
or
negative a advantage

thought experiment: $d_A = d_a = 0$

$$s_c = b_A - b_a$$

birth rate of A larger than birth rate of a, $s_c > 0$



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:

$$\Delta n = 0 \qquad n(t+1) - n(t) = 0 \quad \hookrightarrow \quad n(t+1) = n(t)$$

no change.

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

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

rate of change

Sometimes we call an equilibrium a **steady state**.

Equilibrium

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

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

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

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

② solve equation for variable.
(not for parameters.)

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

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



$$p = 0$$



$$p = 1$$

• If $p = 0$, $\frac{dp}{dt} = 0 \Rightarrow p$ will always $= 0$.

• If system is at equilibrium, it will always be there...
(unless something else happens)
perturbation.

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**.
*Suppose @ equilibrium.
→ jiggle/bump system. → go back to equilibrium.*

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**.

*Suppose @ equilibrium.
→ jiggle/bump system. → do not go back to equilibrium.*

Stability

ϵ epsilon = ϵ "really small"
 $\epsilon > 0$

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

$s_c > 0$

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

$p = 0$ Let $p = p_{\text{equil}} + \epsilon$

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

positive or negative?

$s_c > 0$
 $\Rightarrow \frac{dp}{dt} > 0$
 unstable.

$s_c < 0$
 $\Rightarrow \frac{dp}{dt} < 0$
 stable.

$p = 1$ Let $p = p_{\text{equil}} - \epsilon$

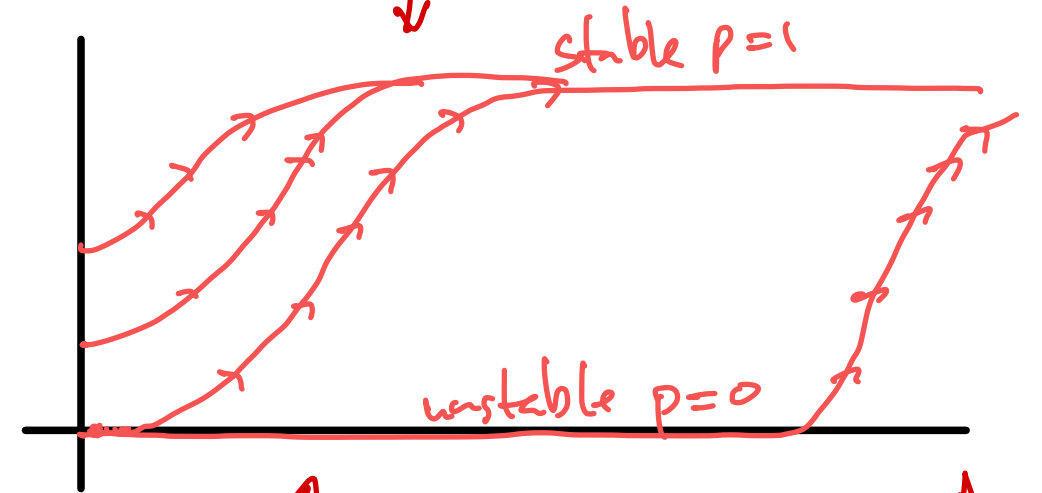
$$\frac{dp}{dt} = s_c(1 - \epsilon)(1 - (1 - \epsilon))$$

$$= s_c(1 - \epsilon)(\epsilon)$$

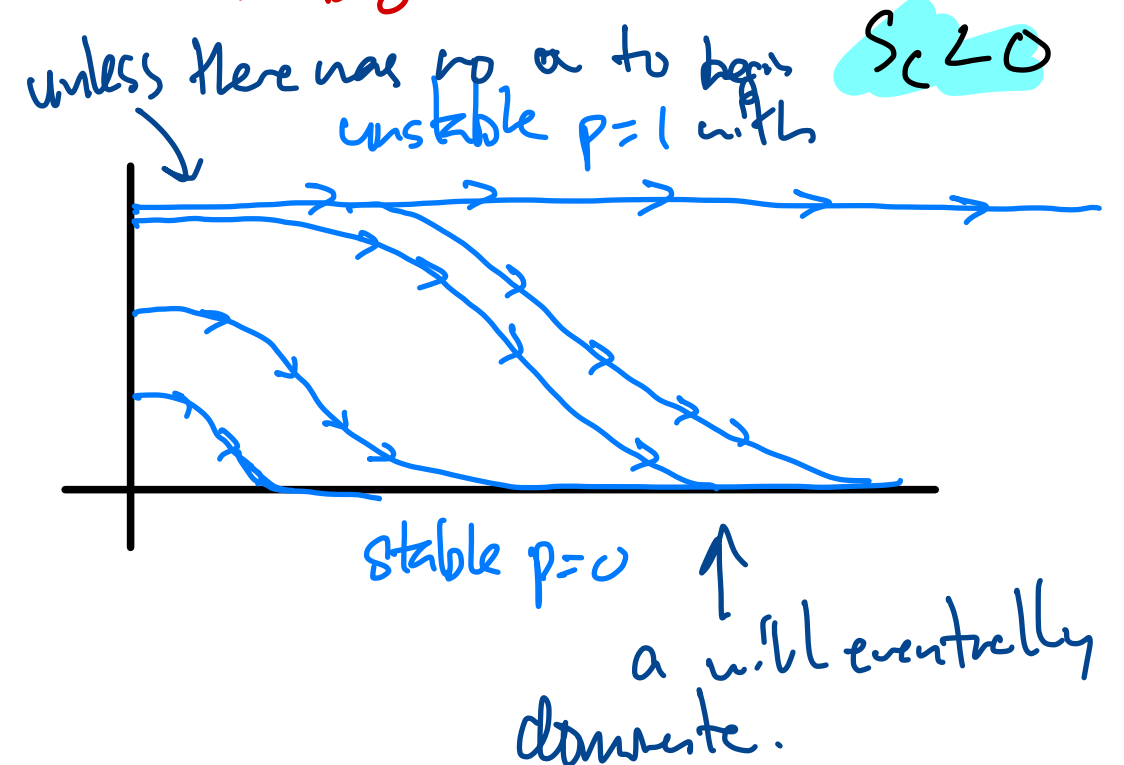
$\frac{dp}{dt} > 0$ when $s_c > 0$ stable

$\frac{dp}{dt} < 0$ when $s_c < 0$ unstable

A will eventually dominate!



unless there was never any A to begin with!



a will eventually dominate.

Bonus

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

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

$$r > 0$$

$$\dot{n} = 0$$

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

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

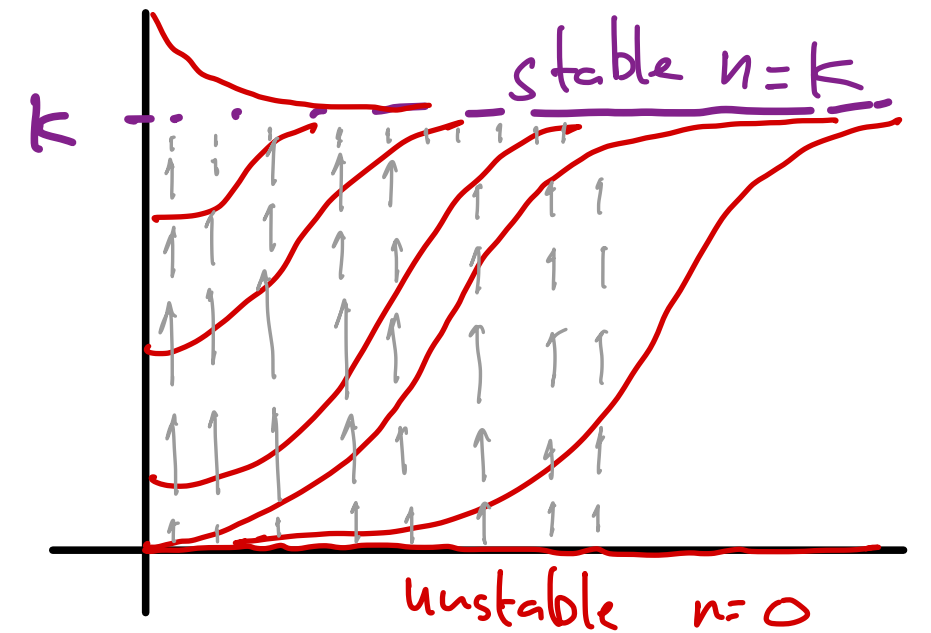
$$n = 0$$

$$n \neq 0$$

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

$$1 = \frac{n}{K}$$

$$K = n$$



learn from direction/vector
field arrows!

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).

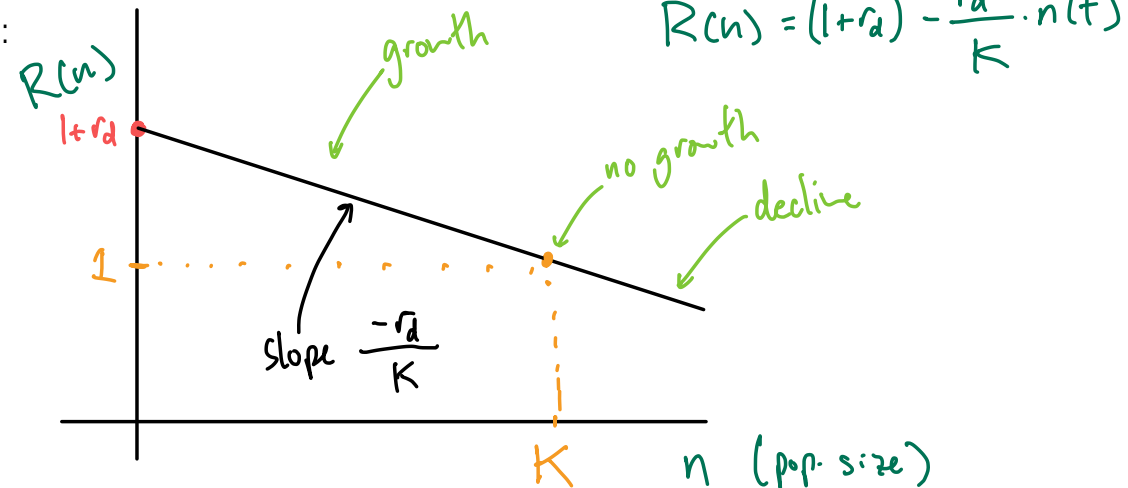
my pop feels like its size is $n_1(t) + \alpha_{12} n_2(t)$
(grows like)

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, $R(0) = 1 + r_d$.
 - 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 $n(t+1) = \underbrace{R(n)}_{\text{growth factor}} n(t)$, we now get $R(n) = (1+r_d) - \frac{r_d}{K} \cdot n(t)$
- $n(t+1) = \left[(1+r_d) - \frac{r_d}{K} n(t) \right] n(t)$

$$\underbrace{n(t+1)}_{\text{next}} = \underbrace{n(t)}_{\text{prev}} + \underbrace{r_d \left(1 - \frac{n(t)}{K} \right) n(t)}_{\text{change}}$$

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

Lotka-Volterra Competition

$$\text{Let } R_i = \underbrace{(1 + r_i)}_{\text{intrinsic}} + \underbrace{\left(\frac{-r_i}{K_i} \right)}_{\text{slope}} \underbrace{\left(n_i(t) + \alpha_{ij} n_j(t) \right)}_{\text{what I feel my population is.}}$$

my actual population.
how pop of n_2 gets experienced by n_1 .

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

"indexed by i "

$i=1,2$

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

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

influence of pop 2 on pop 1

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

influence of pop 1 on pop 2

Lotka-Volterra Competition

We can write similar equations in continuous time:

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

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

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

α_{12} and α_{21} need not be the same.

- α_{12} = impact that 1 feels due to 2
- α_{21} = impact that 2 feels due to 1.

Lotka-Volterra Competition

Quick check: if the species don't interact, then: $\alpha_{12} = 0$ $\alpha_{21} = 0$

which implies that...

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

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

Interpretation: If species don't interact \rightarrow Log. Growth

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

Lotka-Volterra...Competition?

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

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

$$\alpha_{12} = -1 \quad K = 10$$
$$r = 1$$

$$\frac{dn_1}{dt} \quad \text{when} \quad n_1 = 1 \quad n_2 = 1$$

$$\frac{dn_1}{dt} \quad \text{when} \quad n_1 = 1 \quad n_2 = 2$$

What if α_{12} is negative? How does an increase in n_2 affect $\frac{dn_1}{dt}$? \uparrow growth rate of n_1 !

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

$$\frac{dn_1}{dt} = 1 \cdot 1 \left(1 - \frac{1 + (-1) \cdot 2}{10} \right)$$
$$= \left(1 - \frac{1-2}{10} \right) = \left(1 - \frac{-1}{10} \right) = \frac{11}{10}$$

Lotka-Volterra...Competition? ↗

α_{12}	α_{21}	Relationship
0	0	none
+	+	competitive
+	-	parasitic
-	+	parasitic
-	-	mutualistic
-	0	commensal
0	-	comensa

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

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

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

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

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

notebook 3.

with initial conditions

$$n_1(0) = a$$

$$n_2(0) = b$$