I. Review: the General Lotka-Volterra (L-V) model

II. L-V details for case of competition & mutualism

III. Project context: Linking Plant ecology & biogeochemistry
\[ \frac{dx_1}{dt} = \alpha_1 x_1 + \beta_{12} x_1 x_2 - \gamma_1 x_1^2 \]
\[ \frac{dx_2}{dt} = \alpha_2 x_2 + \beta_{21} x_1 x_2 - \gamma_2 x_2^2 \]

\[ \lambda^2 + \lambda \left( \gamma_1 \bar{x}_1 + \gamma_2 \bar{x}_2 \right) + \left( \gamma_1 \gamma_2 - \beta_{12} \beta_{21} \right) \bar{x}_1 \bar{x}_2 = 0 \]

\[ \lambda = \frac{-b \pm \sqrt{b^2 - 4c}}{2} \]

Assume non-trivial sol'n: \( x_1, x_2 \neq 0 \)

\( \text{if } b = 0 \rightarrow \gamma_1, \gamma_2 = 0: \)
(i.e., No self-limitation)

\[ \lambda = \pm \sqrt{-4c} \]

\( \text{if } c > 0 \rightarrow \text{predator-prey neutral cycles} \)
\( \text{if } c < 0 \rightarrow \text{competition or mutualism} \)

\( \text{if } \text{Sign}(\beta_{12}) = -\text{Sign}(\beta_{21}) \rightarrow \text{pred.-prey neutral cycles} \)
\( \text{if } \text{Sign}(\beta_{12}) = \text{Sign}(\beta_{21}) \rightarrow \text{competition/mutualism} \)

\( \lambda = \pm (\text{imaginary \#}) \rightarrow \text{Saddle (unstable)} \)

\( \lambda = \pm (\text{real \#}) \rightarrow \text{stable or asymp-totically stable} \)

\( \text{if } b \neq 0 \rightarrow \gamma_1 \text{ or } \gamma_2 > 0: \)
\( \rightarrow b > 0 \)

\( \text{if } \text{Sign}(\beta_{12}) = \text{Sign}(\beta_{21}) \rightarrow \text{competition/mutualism} \)
\( \text{if } (\gamma_1 \gamma_2 > \beta_{12} \beta_{21}) \rightarrow c > 0 \rightarrow \text{Re(\lambda)} < 0 \rightarrow \text{stable} \)
\( \text{if } (\gamma_1 \gamma_2 < \beta_{12} \beta_{21}) \rightarrow c < 0 \rightarrow \text{Re(\lambda)} > 0 \rightarrow \text{saddle (unstable)} \)
\[
\begin{align*}
\frac{dx_1}{dt} &= \alpha_1 x_1 + \beta_{12} x_1 x_2 - \gamma_1 x_1^2 \\
\frac{dx_2}{dt} &= \alpha_2 x_2 + \beta_{21} x_1 x_2 - \gamma_2 x_2^2
\end{align*}
\]

Let \( \alpha \to r \)

\[
\begin{align*}
\frac{dx_1}{dt} &= r_i x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \\
\frac{dx_2}{dt} &= r_2 x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2}
\end{align*}
\]

\( r_i = \text{intrinsic growth rate} \)

\( K_i = \text{carrying capacity (in absence of interaction)} \)

\( \beta_{ij} = \text{interaction strength (effect of } j \text{ on } i \text{) } \to \beta_{ij} > 0: \text{ mutualism (positive effect)} \)

(assume same sign for this analysis) \( \to \beta_{ij} < 0: \text{ competition (negative "")} \)

**Step 1: Determine nullclines (lines where derivatives are zero)**

\[
\frac{dx_1}{dt} = 0: \quad r_i x_1 \left( 1 - \frac{x_1}{K_1} + \frac{\beta_{12}}{K_1} x_2 \right) = 0
\]

\( x_1 = 0 \)

\[
\frac{x_1}{K_1} = 1 + \frac{\beta_{12}}{K_1} x_2
\]

\( x_1 = K_1 + \beta_{12} x_2 \)

\[
1 - \frac{x_1}{K_1} + \frac{\beta_{12}}{K_1} x_2 = 0
\]

\( x_1 = K_1 + \beta_{12} x_2 \)
\[
\frac{dx_1}{dt} = \alpha_1 x_1 + \beta_{12} x_1 x_2 - \gamma_1 x_1^2 \\
\frac{dx_2}{dt} = \alpha_2 x_2 + \beta_{21} x_1 x_2 - \gamma_2 x_2^2
\]

Let \( \alpha \to r \)

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \\
\frac{dx_2}{dt} &= r x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2}
\end{align*}
\]

\( r_i \) = intrinsic growth rate

\( K_i \) = carrying capacity (in absence of interaction)

\( \beta_{ij} \) = interaction strength (effect of \( j \) on \( i \))

\( \rightarrow \beta_{ij} > 0 \): mutualism (positive effect)

\( \rightarrow \beta_{ij} < 0 \): competition (negative “”)

(assume same sign for this analysis)

**Step 1: Determine nullclines (lines where derivatives are zero)**

\[
\frac{dx_1}{dt} = 0: \quad r x_1 \left(1 - \frac{x_1}{K_1} + \frac{\beta_{12}}{K_1} x_2\right) = 0 \quad \overset{\leftarrow}{\rightarrow} \quad 1 - \frac{x_1}{K_1} + \frac{\beta_{12}}{K_1} x_2 = 0 \quad \rightarrow \quad x_1 = 0 \quad \rightarrow \quad x_1 = K_1 + \beta_{12} x_2
\]

\[
\frac{dx_2}{dt} = 0: \quad \overset{\rightarrow}{\rightarrow} \quad 1 - \frac{x_1}{K_1} + \frac{\beta_{12}}{K_1} x_2 = 0 \quad \rightarrow \quad x_2 = 0 \quad \rightarrow \quad x_2 = K_2 + \beta_{21} x_1
\]
\[ \frac{dx_1}{dt} = r_1 x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \]
\[ \frac{dx_2}{dt} = r_2 x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2} \]

where
- \( r_i \) = intrinsic growth rate
- \( K_i \) = carrying capacity (in absence of interaction)
- \( \beta_{ij} \) = interaction strength (effect of j on i)

(assume same sign for this analysis)

\( \beta_{ij} > 0 \): mutualism (positive effect)

\( \beta_{ij} < 0 \): competition (negative effect)

Equilibria are where \( x_1 \) and \( x_2 \) nullclines intercept

What directions do the arrows point?
\[
\frac{dx_1}{dt} = r_1x_1 \frac{K_1 - x_1 + \beta_{12}x_2}{K_1},
\]
\[
\frac{dx_2}{dt} = r_2x_2 \frac{K_2 - x_2 + \beta_{21}x_1}{K_2}.
\]

- \( r_i \) = intrinsic growth rate
- \( K_i \) = carrying capacity (in absence of interaction)
- \( \beta_{ij} \) = interaction strength (effect of j on i)

(assume same sign for this analysis)

→ \( \beta_{ij} > 0 \): mutualism (positive effect)

→ \( \beta_{ij} < 0 \): competition (negative effect)

\[
\frac{dx_2}{dt} = 0: \quad x_2 = 0
\]

if \( x_1 = 0 \):

\[
\frac{dx_2}{dt} = r_2x_2 \frac{K_2 - x_2}{K_2} > 0 \text{ (if } x_2 < K_2), < 0 \text{ (if } x_2 > K_2) \]

What directions do the arrows point?

Start by looking around equilibrium points:

\[
\frac{dx_1}{dt} = 0: \quad x_1 = 0
\]

if \( x_2 = 0 \):

\[
\frac{dx_1}{dt} = r_1x_1 \frac{K_1 - x_1}{K_1} > 0 \text{ (if } x_1 < K_1), < 0 \text{ (if } x_1 > K_1) \]
\[ \frac{dx_1}{dt} = r_1 x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \]

\[ \frac{dx_2}{dt} = r_2 x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2} \]

\[ \frac{dx_2}{dt} = 0 : \quad x_2 = K_2 + \beta_{21} x_1 \]

\( r_i = \) intrinsic growth rate  
\( K_i = \) carrying capacity (in absence of interaction)  
\( \beta_{ij} = \) interaction strength (effect of j on i)  
(assume same sign for this analysis)

\( \beta_{ij} > 0: \) mutualism (positive effect)

\( \beta_{ij} < 0: \) competition (negative effect)

Rules for direction vectors on nullclines (text, p. 180):
1. steady-states are intersections of \( x_1 \) and \( x_2 \) nullclines (i.e. where both derivatives=0)
2. Since there is no change in either \( x_1 \) or \( x_2 \) at steady states, direction vectors are zero length at steady states
3. Direction vectors vary smoothly along nullclines  
\( \rightarrow \) a change in orientation (e.g. from pointing up to down) can only take place passing through steady-states

\[ \frac{dx_1}{dt} = 0 : \quad x_1 = K_1 + \beta_{12} x_2 \]

\[ \frac{dx_2}{dt} = 0 : \quad x_2 = K_2 + \beta_{21} x_1 \]
\[ \frac{dx_1}{dt} = r_1 x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \]

\[ \frac{dx_2}{dt} = r_2 x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2} \]

\[ \frac{dx_2}{dt} = 0: \quad x_2 = 0 \]
\[ \quad x_2 = K_2 + \beta_{21} x_1 \]

\( r_i = \) intrinsic growth rate
\( K_i = \) carrying capacity (in absence of interaction)
\( \beta_{ij} = \) interaction strength (effect of j on i)

(assume same sign for this analysis)

\( \Rightarrow \beta_{ij} > 0: \) mutualism (positive effect)

\( \Rightarrow \beta_{ij} < 0: \) competition (negative effect)

Species 2 equilibria are unstable, and competition leads to “competitive exclusion” of species 2. Species 1 outcompetes species 2.

This is not the only possibility:

\[ \frac{dx_1}{dt} = 0: \]
\[ x_1 = 0 \]
\[ x_1 = K_1 + \beta_{12} x_2 \]

\[ \frac{K_1}{-\beta_{12}} < \text{or} > K_2 \]

\[ \frac{K_2}{-\beta_{21}} < \text{or} > K_1 \]

\( \Rightarrow 4 \) permutations
\[ \frac{dx_1}{dt} = r_1 x_1 \frac{K_1 - x_1 + \beta_{12} x_2}{K_1} \]
\[ \frac{dx_2}{dt} = r_2 x_2 \frac{K_2 - x_2 + \beta_{21} x_1}{K_2} \]

- \( r_i \) = intrinsic growth rate
- \( K_i \) = carrying capacity (in absence of interaction)
- \( \beta_{ij} \) = interaction strength (effect of j on i)

(assume same sign for this analysis)

- \( \beta_{ij} > 0 \): mutualism (positive effect)
- \( \beta_{ij} < 0 \): competition (negative effect)

\[ \rightarrow 4 \text{ permutations} \]

1. \( \frac{K_1}{-\beta_{12}} > K_2 \) and \( \frac{K_2}{-\beta_{21}} > K_1 \)
   - Spp 1 always wins

2. \( K_2 > \frac{K_1}{-\beta_{12}} \) and \( \frac{K_2}{-\beta_{21}} > K_1 \)
   - Spp 2 always wins

3. \( K_2 > \frac{K_1}{-\beta_{12}} \) and \( K_1 > \frac{K_2}{-\beta_{21}} \)
   - Spp 1 OR Spp2: depends on start-point

4. \( \frac{K_1}{-\beta_{12}} > K_2 \) and \( \frac{K_2}{-\beta_{21}} > K_1 \)
   - Stable coexistence
All possible outcomes for Competitive Interactions: $\beta_{ij} < 0$ (negative interactions)

- **Spp 1 always wins**
- **Spp 2 always wins**
- **Spp 1 OR Spp2: depends on start-point**
- **Stable coexistence**

- $Spp \ 1$ always wins
- $Spp \ 2$ always wins
- $Spp \ 1$ OR $Spp 2$: depends on start-point
- Stable coexistence

Where

- $K_1$ and $K_2$ represent the carrying capacities of species 1 and 2, respectively.
- $-\beta_{12}$ and $-\beta_{21}$ represent the negative interaction coefficients between species 1 and 2.

All possible outcomes for Competitive Interactions:

- $\beta_{ij} < 0$ (negative interactions)
Investigate the effects of the interaction terms, $\beta_{12} \beta_{21}$.

Consider simplified Cases where $K_1 = K_2 = K$, $r_1 = r_2 = r$, and $\beta_{12} = \beta_{21} = \beta$

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1 \frac{K - x_1 + \beta x_2}{K} \\
\frac{dx_2}{dt} &= r x_2 \frac{K - x_2 + \beta x_1}{K}
\end{align*}
\]

Non-trivial equilibrium (intersection of the two nullclines):

\[
\begin{align*}
\frac{dx_1}{dt} = 0: & \quad x_1 = 0 \\
& \quad x_1 = K + \beta x_2 \\
\frac{dx_2}{dt} = 0: & \quad x_2 = 0 \\
& \quad x_2 = K + \beta x_1 \\
& \quad x_1 = K + \beta (K + \beta x_1) \\
& \quad x_1 = K \frac{(1 + \beta)}{(1 - \beta^2)}
\end{align*}
\]

nullcline axis intersections

\[
\begin{align*}
& \quad x_1 = K; \quad x_2 = \frac{K}{-\beta} \\
& \quad x_2 = K; \quad x_1 = \frac{K}{-\beta}
\end{align*}
\]
Investigate the effects of the interaction terms, $\beta_{12} \beta_{21}$.

Consider simplified Cases where $K_1 = K_2 = K$, $r_1 = r_2 = r$, and $\beta_{12} = \beta_{21} = \beta$

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1 \frac{K - x_1 + \beta x_2}{K} \\
\frac{dx_2}{dt} &= r x_2 \frac{K - x_2 + \beta x_1}{K}
\end{align*}
\]

Non-trivial equilibrium (intersection of the two nullclines):

\[
\begin{align*}
\frac{dx_1}{dt} &= 0: & x_1 &= 0 \\
\frac{dx_2}{dt} &= 0: & x_2 &= 0 \\
& & x_1 &= K + \beta (K + \beta x_1) \\
& & x_1 &= K \frac{(1 + \beta)}{(1 + \beta)(1 - \beta)}
\end{align*}
\]

Nullclines:

\[
\begin{align*}
\frac{dx_1}{dt} &= 0: & x_1 &= 0 \\
\frac{dx_2}{dt} &= 0: & x_2 &= 0 \\
\end{align*}
\]

nullcline axis intersections

\[
\begin{align*}
& x_1 = K; \quad x_2 = \frac{K}{-\beta} \\
& x_2 = K; \quad x_1 = \frac{K}{-\beta}
\end{align*}
\]
Investigate the effects of the interaction terms, $\beta_{12} \beta_{21}$.

Consider simplified Cases where $K_1 = K_2 = K$, $r_1 = r_2 = r$, and $\beta_{12} = \beta_{21} = \beta$.

\[
\begin{align*}
\frac{dx_1}{dt} &= r x_1 \frac{K - x_1 + \beta x_2}{K} \\
\frac{dx_2}{dt} &= r x_2 \frac{K - x_2 + \beta x_1}{K}
\end{align*}
\]

Nullclines:
\[
\begin{align*}
\frac{dx_1}{dt} &= 0: \\
&\quad x_1 = 0 \\
&\quad x_1 = K + \beta x_2
\end{align*}
\]

nullcline axis intersections
\[
\begin{align*}
x_1 &= K; \\
x_2 &= K; \\
x_2 &= \frac{K}{-\beta}
\end{align*}
\]

Non-trivial equilibrium (intersection of the two nullclines):
\[
\begin{align*}
&\quad x_1 = K + \beta (K + \beta x_1) \\
&\quad x_1 = \frac{K}{1 - \beta}
\end{align*}
\]

By symmetry:
\[
\begin{align*}
&\quad x_2 = \frac{K}{1 - \beta}
\end{align*}
\]
\[ \beta \text{ Negative (competition)} \]

\[ \frac{K}{-\beta} \]

\[ \frac{K}{(1-\beta)} \]

\[ \frac{K}{(1-\beta)} \]

\[ \frac{K}{-\beta} \]

\[ \frac{K}{(1-\beta)} \]

\[ \beta \text{ Positive (mutualism)} \]

\[ \frac{K}{(1-\beta)} \]

\[ \frac{K}{(1-\beta)} \]

\[ \frac{K}{-\beta} \]

\[ \frac{K}{(1-\beta)} \]

\[ \beta \text{ Stable coexistence} \]

\[ \beta < K \]

\[ \beta > K \text{ (competition exclusion)} \]

\[ \beta > K \text{ (mutualism)} \]

\[ \beta > K \text{ (unstable)} \]

\[ \beta > K \text{ (unstable)} \]
See actual trajectories in numerical example using PPLANE java software at:

http://math.rice.edu/~dfield/dfpp.html
III. Project context: Linking Plant ecology & biogeochemistry

A. Ecology: Species coexistence vs. competitive exclusion
B. Biogeochemistry: carbon cycling and potential feedbacks to climate change
A. Ecology: Species coexistence vs. competitive exclusion

Longstanding question in ecology: When do species co-exist, when does one drive another to extinction?

(basic question driving classic Lotka-Volterra models for species competition, studied extensively by Gause, 1934)

Question goes back at least 100 years:

Grinnell (1904) posited that if two species were too similar (i.e. accessed the same resources in the same way), coexistence would be unstable, and one of them would inevitably drive the other to extinction.

In particular, the species that is able to tolerate the lowest resource density (in other words, the one with the highest carrying capacity $K$ for a given resource supply) would “win” any competition.

This is the “competitive exclusion” principle (also sometimes called Gause’s principle, because Gause showed how a L-V type model could explain it).
B. Biogeochemistry: Carbon cycling and potential feedbacks to climate change

Biogeochemistry = the study of how the cycling of elements through the earth system (water, atmosphere, living organisms, soil and rock) is governed by biological, physical, and chemical processes

Names

Vladimir Vernadsky (1863-1945): Russian scientists known as the “father of biogeochemistry”, invented the terms geosphere, biosphere, and “noosphere”

G. Evelyn Hutchinson (1903-1991): famous limnologist (considered to be founder of limnology) (also studies the question of how species coexist)

Our Focus here: biogeochemistry of carbon.

Carbon is important as the building block of life and, in the form of CO2, as an important greenhouse gas in the atmosphere.
Carbon Cycle and potential feedback to climate change:

(1) Reduced Photosynthesis

(3) Reduced Litterfall

(4) Average Soil Respiration maintained

(5) Reduced soil carbon (from reduced input)

atmospheric CO₂
Warming causes shift in species composition

Peak Above-ground biomass (1993)

- **Shrub**: *Artemisia tridentata* (sagebrush)
- **Forbs**: *Delphinium nuttallianum*, *Erigeron speciosus*, *Helianthella quinquenervis*
- **Grass**: *Festuca thurberi*, *Poa spp.*

Harte & Shaw (1995)
Experimental Warming reduces soil carbon storage in top 10 cm

Heated plot decline converts to:

~200 g C m$^{-2}$
(out of ~2300 total, 0-10 cm)
Project question: can we build and analyze a simple model that links climate-induced changes in plant species composition to changes in the carbon cycle?
A Simple Model of Soil Carbon-Vegetation dynamics

Plant Biomass, $B_i$ of productivity $P_i$:

- Shrub: $P_{\text{shrub}} \cdot B_{\text{shrub}}$
- Forb: $P_{\text{forb}} \cdot B_{\text{forb}}$
- Grass: $P_{\text{grass}} \cdot B_{\text{grass}}$

soil organic carbon, $SOC_i$ of decomposition rate, $k_i(T,M)$:

- Shrub: $k_{\text{shrub}} \cdot SOC_{\text{shrub}}$
- Forb: $k_{\text{forb}} \cdot SOC_{\text{forb}}$
- Grass: $k_{\text{grass}} \cdot SOC_{\text{grass}}$

Litter inputs
Decomposition losses
Two-Part Project

1. Coupled Differential Equation problem to investigate ecology-biogeochemistry links
2. Difference equation problem: Discrete-time logistic equation with time-varying carrying capacity $K$
   (specifically, varying periodically in time)

Will be posted later tonight or tomorrow.