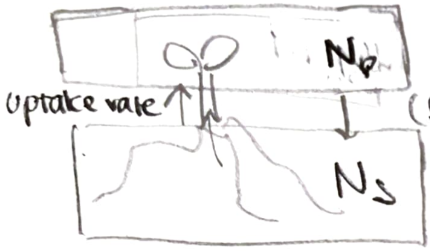
Nitrogen Environment

N_p = N in leaves of all species

N_s = N available in the environment in the soil
closed pool (for now)

$N_{TOT} = N_p + N_s$



$$N_p = \sum_i x_i N_i$$

N_i ← N content of ramet of sp. i

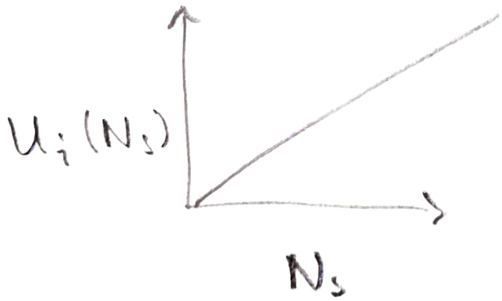
x_i ↑ density of ramets of species i

$$\frac{dN_s}{dt} = \left(\frac{1}{\text{leaf lifespan} + \text{litter decomp}}\right) N_p - U(N_s, x_1, x_2, \ldots x_i)$$

↗ Resource Replenishment

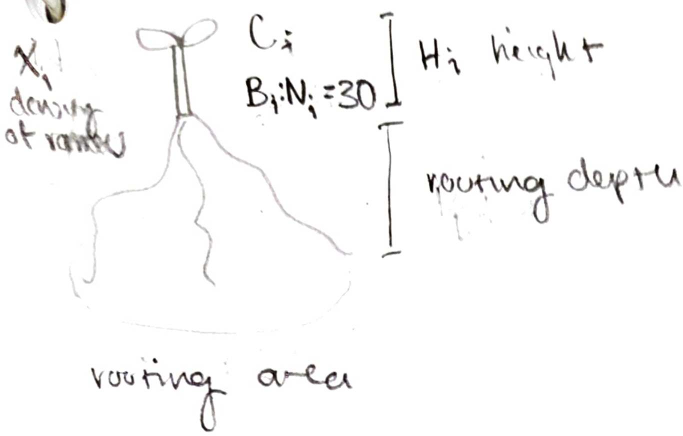
↑ uptake of N by all species

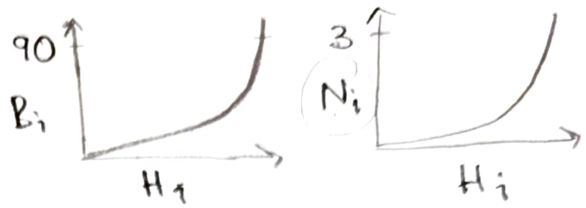
$$U(N_s) = \sum_{i=1}^{Q} U_i(N_s)$$



linear for now
$u_i N_s$

ALLOCATION
RAMET MORPHOLOGY





N acquisition depends on investment in roots

D_i = root mass of ramet

Nitrogen Gain function (N economy)

net gain in Nitrogen

$$g_N(N_s) = \left[\text{depends on } N_s\right] u_i - \left(\frac{1}{\text{leaf lifespan}}\right)$$

set by competition

$(N_0 - N_1)$

some uptake rate that's species specific or function

- each ramet must acquire N_i nitrogen before it can reproduce.

Nitrogen Requirement

$N_C + N_B$: nitrogen in biomass (wood) = N_i

nitrogen in crown (leaves)

$$n_c C_i + n_B B_i = N_i$$

amount of nitrogen in a ramet of sp. i

$n_c \rightarrow \frac{1}{10}$ $\quad$ $n_B \rightarrow \frac{1}{30}$

Nitrogen requirement options:

1. Each ramet contains a set amount of nitrogen, N_i

OR

2. The amount of N a species can gain sets it's crown area C_i, thus growth rate

$$g_i = [A(L_{R_i}) - r]\, C_i(t)$$

of

$$C_i = \underset{\uparrow}{u} N_{R_i}$$

$\left[\frac{\text{leaf area}}{g\,N}\right]$

N_{R_i} is the amount of N the ramet can turn into leaves

all the N locked in ramets

$$N_{TOT} = N_S - \sum_{i=1}^{\infty} x_i N_{R_i}$$

N in a given unit area

N available in soil of unit area

density of ramets of sp. i

establishment

$$l_2 (N_0 - N_1^*) < L_1 (N_0 N_1^*)$$

1 sp eq. N in plant sp. 1

coexistence (persistence)

$$l_1 (N_0 - N_2^*) < 1$$

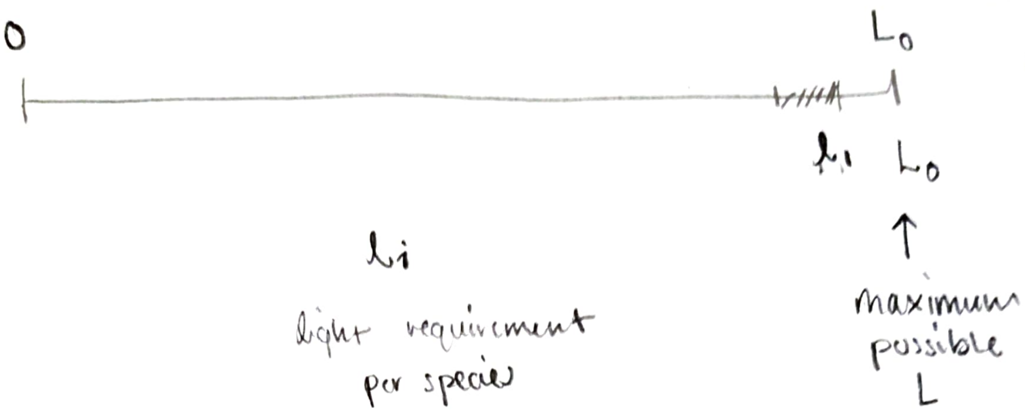
establishment

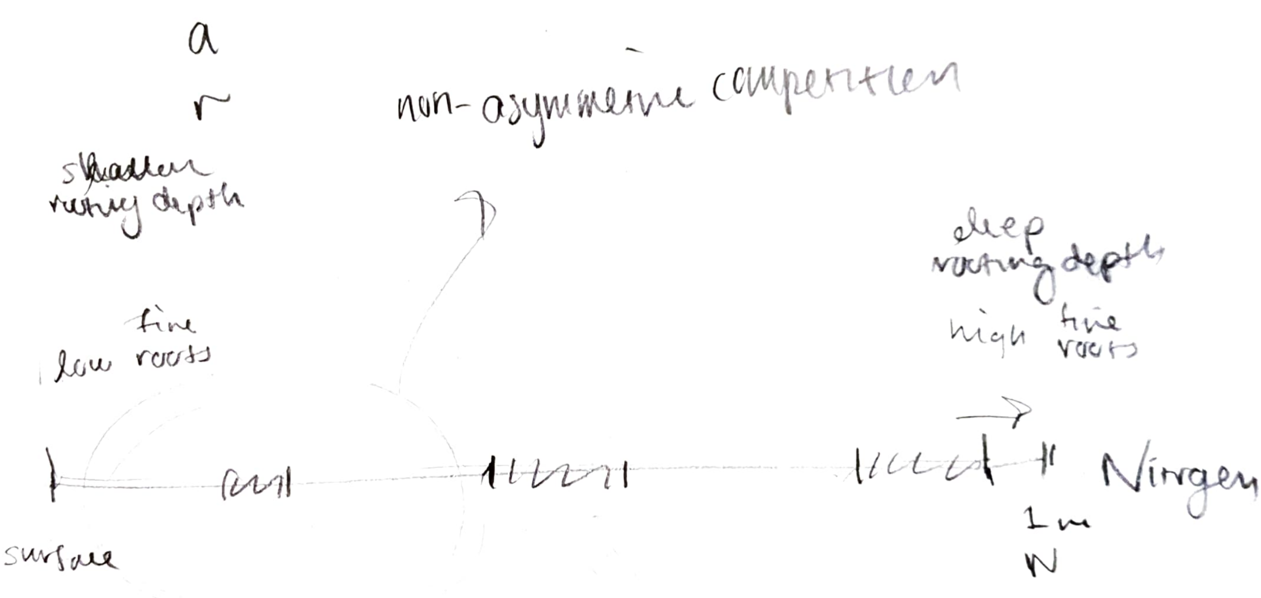
$$l_i \left(N_0 - \sum_{j=1}^{i-1}\right) < L^*_{i-1}$$

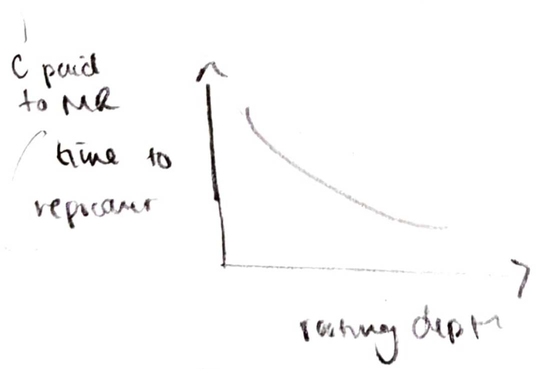
set of conditions for changing densities based on N availability by pushing into shadow

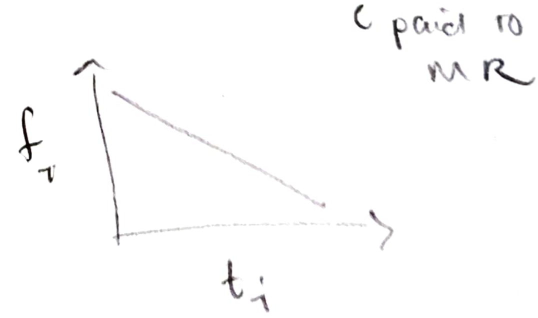
N_i

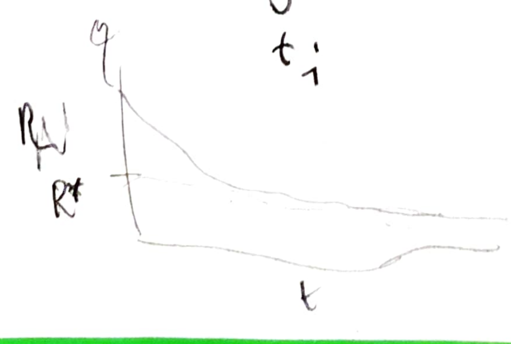
Scratch

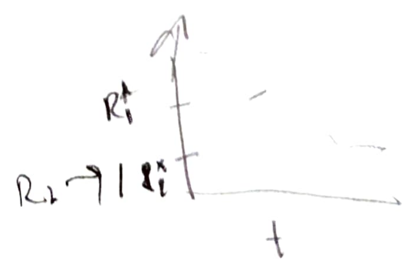

0
L_0
Light
l_i L_0
l_i
light requirement per species
maximum possible L

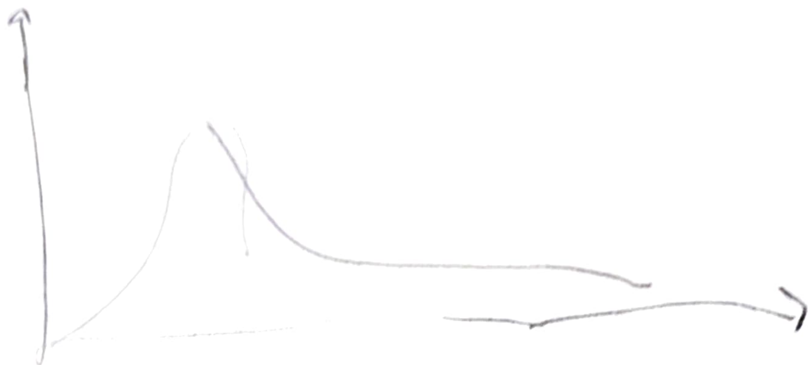

a
r
non-asymmetric competition
shallow rooting depth
deep rooting depth
low fine roots
high fine roots
Nitrogen
1 m
N
surface


C paid to MR
time to reproduce
rooting depth
t_i


C paid to MR
f_r
t_i


R_i
R^*
t


R_i^*
R_i
t



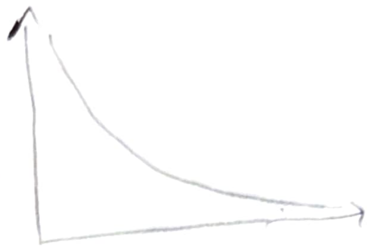
Break up

* mechanism that breaks R*

Matteo
2024-01-31

Fisher 2010

What is the biological cost to get nitrogen INTO the roots?



↑
cost

$$\left(1+\eta_c\right)\frac{dB}{dt} = \left(A(L) - R\right)C - \ell(N_0 - N_1)\frac{dB}{dt}$$

cost of carbon

cost of nitrogen

leaf respirat + tissue turnover

$r \quad + \frac{(1+\eta_c+\eta_N)}{\tau}$

cost of

light demanding is

$\frac{dB}{dt} \rightarrow B^* \rightarrow T_1^*$

$\ell_2(N_0 - N_1) < L_1$

$\ell_1(N_0 - \hat{N}_1 - \hat{N}_2) > 1$

$\ell_1(N_0) \rightarrow \hat{\ell}_1(\hat{N})$

$$(1+\eta_C+\eta_N)NPP = (A_N - R)\,a_L \qquad (A_N - R)\,\underline{a_L}$$

canopy "area" leaf

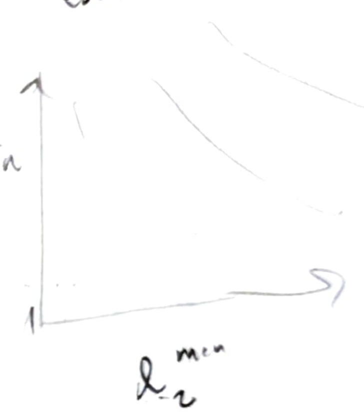
parameter

$$T_i = \left(\frac{B_i}{(A_N - R)\,a_L}\right)\left(\frac{1}{1+\eta_C^i+\eta_N}\right)$$

$$T = \frac{B_S + a_L \cdot LMA + a_R \cdot MRA}{NPP}$$

T_i

invade from rare establishment



$$\eta_N = c_N(N_S)\left(\frac{1}{C/N}\right)$$

$$\frac{1}{m_i} = T = \frac{B(1+\eta_C+\eta_N^B) + a_L LMA(1+\eta_C+\eta_N^L)}{NPP} \rightarrow N^{min},\ L^{min}$$

$$NPP = \left[A_N(L) - r - \left(\frac{1+\eta_C+\eta_N^T}{T}\right)^{(1-\lambda)}\right] C^{-a_L}$$

assume $\eta_N^B = \eta_N^L = \eta_N^T$

$$1 = \frac{B + a_L LMA}{\left(\frac{T(A_N(L)-r)}{1+\eta_C+\eta_N} - 1\right) C^{-a_L}} \qquad \begin{array}{l} \rightarrow N^{min}(L) \\ \rightarrow L^{min}(N_S) \end{array}$$

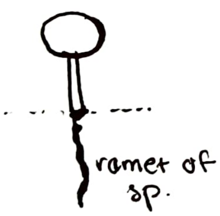
Case 1. There is a set amount of N in the soil + plant ecosystem

$$N_{TOT} = N_s + N_p$$

- All plants are equal competitors for nitrogen.
- They will split the amount of available N in the soil equally, in terms of uptake of N per unit time
- All plants (species) have equivalent nitrogen requirements
  i.e. or e.g. N sets crown area, which is equal.
  $n_i = n_j \ \forall i,j$ since $C_i = C_j$
- If there is no available N in the soil, no new plants/ramets can grow.
- Plants will <u>not</u> take up more Nitrogen than they need.

1 sp. community

L_0



N_0

total N in the system

leaf area *

carbon gain = (photosynthesis - respiration) - structural growth + maintenance costs

options for N limitation

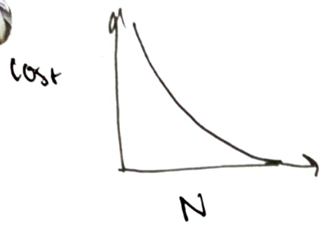
1. Add carbon cost for acquiring N. that is a function of N in soil.

   Then as $N_s \to 0$, cost increases and $g(N_s, L) \to 0$

2. Make uptake function for N, that sets sp. canopy area C_i

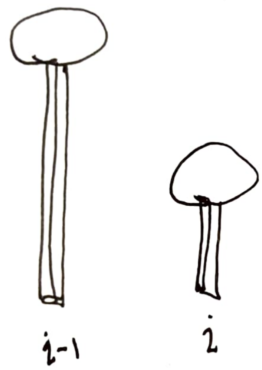
3. Add nitrogen cost to constructing biomass, so reproduction is contingent on available N and uptake ?

Adding Nitrogen to system



n-requirement per species

Nitrogen in system - all plants contain some nitrogen



N_i : nitrogen in the tissues of cohort of sp. i

$N_i = n B_i$

$$N_p = \sum_{i=1}^{\infty} x_i N_i$$

plant uptake ↑ N_p ↓ litter decomposition + leaf fall + mineralization

N_s

current growth model (carbon accumulation)

plants split N equally ?

$$T_i = \frac{B_i}{g_i(L,N)} = \frac{\ln(2)}{m_i}$$

$$N_s = N_T - N_p = N_T - \sum_{i=1}^{\infty} x_i N_i$$

needs to be some value $\Rightarrow g_i(L,N) = \dfrac{1}{m_i B_i}$

plants pay carbon to get nitrogen

they can always pay more C to get more N

but the lower the N, the more/higher the carbon cost

TASK LIST

- ☐ write out the modified growth eq^n w/ N costs
- ☐ write empirical sol^n to N_i needed at L

$l_i(N)$, $N_i(L)$

1. Add N limitation (as carbon cost) to biomass accumulation

$$\frac{dB}{dt} = \text{"net primary productivity" per ramet} = g(N_s, L)$$

N_s ↑ nitrogen in soil

L ↑ light

$$= A_N(L) - r -$$

A_N ↑ rate of photosynthesis depends on N in leaves?

r ↑ leaf respiration

$$\text{Time to reproduction} = \frac{\text{structural biomass} + \text{canopy biomass} + \text{root biomass}}{g(N_s, L)}$$

$$= \frac{B_i(1 + \eta_c + \eta_N^w) + C_i\,LMA_i(1 + \eta_c^L + \eta_N^L)}{g(N_s, L)}$$

assume growth costs are the same ?

carbon cost of nitrogen required per unit biomass accumulation:

$$\eta_N(N_s) = \frac{\cancel{\text{costs}}\ C}{\text{mass } N} \cdot [gN \text{ required}] = \eta f(N_s)$$

$\eta_N(N_s)$ ↑ soil Nitrogen

$\frac{C}{\text{mass } N}$ ↑ ~~C:N ratio of tissue~~ carbon cost of gN acquirement

$[gN \text{ required}]$ ↑ $[C \text{ required}] \cdot \frac{N \text{ in tissue}}{C \text{ in tissue}}$

$f(N_s)$ ← carbon cost / unit N

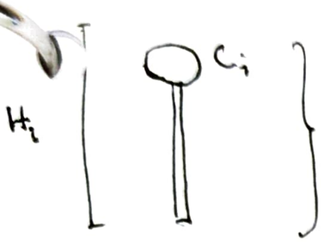
η ↑ ~~nitrogen~~ units / unit biomass

$\cancel{B_i}$

$$n = \left[\frac{gN}{gC} \text{ of biomass}\right]$$

$$f(N_s) \cdot n\,\cancel{B}_i : \quad f(N_s) = \frac{1}{N_s}$$

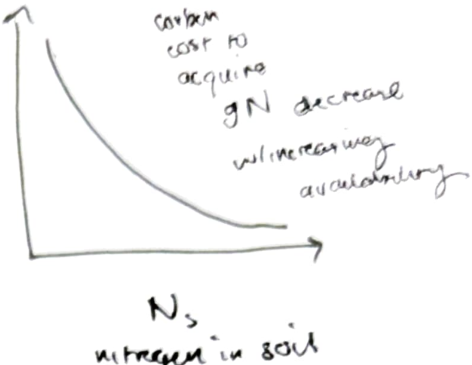
X_i : density



B_i biomass

L_i : light available to sp. i ~~[illegible]~~

N_i = nitrogen available to sp. i $\eta_N(N_s)$



carbon economy of 1 ramet:

$$(1 + n_c + n_N)\frac{dB_i}{dt} = [A(L_i) - R]C_i - \cancel{C}(N_i)\frac{dB_i}{dt}$$

$\eta_N(N_s)$

1: carbon cost of carbon — could be 30% to grow more structural material

n_c: carbon cost of nitrogen

can collect terms on the left

$A(L_i)$: light

R: leaf respiration + tissue turnover

$$r + \frac{(1 + n_c + n_{N_i})}{T}$$

T: leaf lifespan

$$g(L_i, N_i) = \frac{[A(L_i) - R]C_i}{1 + \eta_c + \eta_N(N_s)} = \frac{[A(L_i) - R]C_i}{1 + \eta_N(N_s)} = \frac{[aL_{R_i} - R]C_i}{1 + n\left(\frac{1}{N_s}\right)}$$

$g(L_i, N_i)$: carbon gain per ramet per unit time

i.e. $\frac{dB_i}{dt}$

$\underbrace{1 + \eta_c}$: consolidate for now, e.g. sp. B_i greater for equivalent mass

$\eta_N(N_s)$: carbon cost of acquiring nitrogen required per unit biomass gain

$$\eta_N = n f(N_s)$$

n: $\frac{1}{\quad}$ C:N ratio of tissue

Calculating Time to Reproduction:

it will be longer with low N_s

$$T_i = f(N_s, L_i) = \frac{B_i}{g(N_s, L_i)}$$

(leave out special canopy pars for now)

N_i = soil nutrients level available to ALL ramets of sp. i

$$g(N_s, L_i) = \frac{\left[a\frac{L_i}{X_i} - R\right]C_i}{1 + \frac{n}{N_0 - \sum_{i=1}^{\infty} nB_iX_i}}$$

to start, assume sp. are equal competitors so

$$N_i = N_j \quad \forall i, j$$

$$T_i = \frac{B_i\left(1 + \frac{n}{N_0 - \sum_{i=1}^{n} nB_iX_i}\right)}{\left(a\frac{L_i}{X_i} - R\right)C_i}$$

$$\underset{\text{Total}}{N_0} = \underset{\text{Soil}}{N_s} + \sum_{i=1}^{\infty} \underset{\text{nitrogen in each ramet}}{nB_i}X_i$$

X_i ← density of ramets of sp. i

$$N_s = N_0 - \sum_{i=1}^{\infty} nB_iX_i$$

$$= \frac{B_i + \frac{nB_i}{N_0 - \sum_{i=1}^{\infty} nB_iX_i}}{\left(a\frac{L_i}{X_i} - R\right)C_i}$$

$$T_i = \frac{B_i + \frac{B_i}{\frac{N_0}{n} - \sum_{i=1}^{\infty} B_iX_i}}{\left(a\frac{L_i}{X_i} - R\right)C_i} = \frac{1}{m_i} \quad \text{at } \underline{EQ}$$

$$B_i\left(1 + \frac{1}{\frac{N_0}{n} - \sum_{i=1}^{\infty} B_iX_i}\right) = \frac{C_i}{m_i}\left(a\frac{L_i}{X_i} - R\right)$$

implicit expression for $\hat{X}_i$

$$B_i\left(1+\frac{1}{N_s}\right)=\frac{C_i}{m_i}\left(a\frac{L_i}{X_i}-R\right)$$

$$\frac{m_iB_i}{C_i}\left(1+\frac{1}{N_s}\right)=\left(a\ \overbrace{\boxed{\frac{L_i}{X_i}}}^{L_{R_i}}-R\right)$$

$$X_iN_s\left(\frac{m_iB_i}{C_i}\right)+\frac{m_iB_i}{C_i}X_i=N_s(aL_i-R)$$

$$X_i(N_s+1)-N_s(aL_i-R)=\frac{C_i}{m_iB_i}$$

$\uparrow$ depends on $X_j\ \forall j$ ... seems not good for simplicity

In the light model alone, we had the implicit expression

$$\hat{X}_i=\frac{L_{i-1}(1-e^{-k\hat{X}_i})}{k\,l_i}\qquad l_i=\frac{m_iB_i+R}{aC_iK}$$

We can also find the condition l_i s.t. $LRS(R_i|X_1=0)>1$

$$LRS(R_i)=\frac{e^{-m_iT_i}}{1-e^{-m_iT_i}}\Rightarrow\text{ we must have } T_i\leq\frac{\ln(2)}{m_i}$$

$\downarrow$

light required for this to be true

or some function $f(N_s)$ cost

$$L_{R_i,N_s}=\frac{1}{a}\left[\frac{m_iB_i}{C_i}\left(1+\frac{1}{N_s}\right)+R\right]$$

light required by ramet R_i @ EQ depends on N_s

if $N_s\uparrow$, then $L_{R_i}\downarrow$ and vice versa

invasion condition for sp. i

$$cKL_{i-1}\geq L_{R_i,N_s}\Rightarrow\boxed{l_i(N_s)=\frac{1}{acK}\left[\frac{m_iB_i}{c_i}\left(1+\frac{1}{N_s}\right)+R\right]}$$

Nitrogen in soil required as a function of light available per variety

$$\frac{m_i B_i}{C_i}\left(1+\frac{1}{N_s}\right) = a L_{R_i} - R$$

$$\left(1+\frac{1}{N_s}\right) = \left(a L_{R_i} - R\right)\frac{C_i}{m_i B_i}$$

$$N_s = N_s\left[a L_{R_i} - R\right]\frac{C_i}{m_i B_i} - 1$$

$$N_s\left(1 - \left[a L_{R_i} - R\right]\frac{C_i}{m_i B_i}\right) = -1$$

$$N_s(L_{R_i}) = \frac{1}{(a L_{R_i} - R)\frac{C_i}{m_i B_i} - 1} = \frac{m_i B_i}{(a L_{R_i} - R) C_i - m_i B_i}$$

$$\boxed{N_s(L_{R_i}) = u_i(L_{R_i}) = \frac{m_i B_i}{(a L_{R_i} - R) C_i - m_i B_i}}$$

$$\boxed{\begin{array}{c} l_i(N_s) \\ u_i(L_{R_i}) \end{array}}$$

1

Steve chat 2024-02-28

simplest world

→ "plants can get as much N as they want"

, it just costs them C

1/2 is labile fast (recent)

1/2 recalcitrant (slow)

→ but what limits the microbes

- carbon limited?
- space limited?

sell all for expensive price

- eventually leaks carbon
- mycorrhizae actually
- ecto's sheath

$f(N_s)$ = cost per unit Nitrogen

- leak @ set rate

MZ grab + sell at constant price to plants

N → C microbial system

C & N min. rates equilibrate bc microbial biomass equilibrates

what's limiting the microbes?

- M are at EQ abundance limited by C
- get some extra they can sell for the plants

↳ quasi EQ

N_{min} → constant EQ?

Steve chat ~ N addition schemes

- price of N is fixed

microbial priming:

$\boxed{1}$ squirting eq. + leak

proper symbiosis

~~Algebr~~ quasi-eq.

$\frac{\text{microbe}}{\text{detritus}}$, less the microbe is getting

ectotropic paraite

$\boxed{2.}$ collusion of microbes

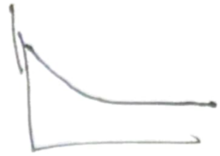
grab + sell "symbiosis"

$\boxed{3.}$ fungus can be paid to be saprophage to get recalcitrant

symbiosis prom paid to rhizobia Frankia

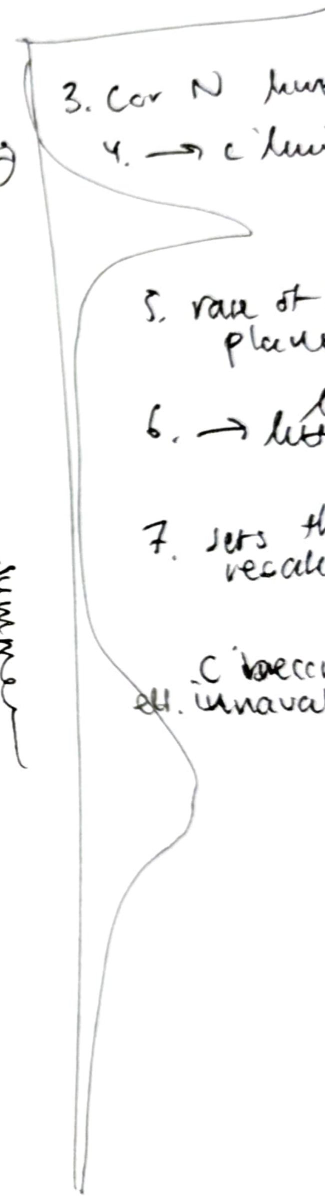
1. $\frac{dM}{dt}$ = collision to detritus

harvest rate / microbe



N O 3   M / D

2. litter stoichiometry



summer

3. C or N limitation
4. → C limited
5. rate of N → plants
6. → leaf litter
7. sets the recalcitrant

ex. C becomes unavailable

Next Session

graminoides: why tall except light

- plants can pay MZ to
  microbes dependent on

- plants productivity controlling microbe abundance

fine roots → plants pick up enough N

roots ← $\boxed{N_e \mid N_r}$ → microbes

plant buys up to the amount it needs
collision btw roots + NO_3

Menge

- ecosystem development

- quasi-eq.

everything shifts to <u>deciduous</u>

<u>park</u>

- evergreen / deciduous for now

- add N in different ways – look @ Menge → shift to deciduous
  - * Mingzhou w/ microrhizae

You don't need symbionts to make it work

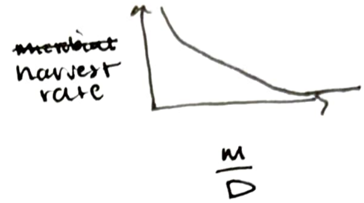
↓ microbes
pee nitrogen
@ some point

N addition schemes —

$\boxed{1.}$ squirt to leak ~ add microbial eq$\underline{^{n}}$s

step 1. D: detritus

M: microbial biomass



? figure out reasonable functional form

* michaelis menten situation

$$\frac{dM}{dt} = f(\text{\# of microbial collisions w/ detritus})$$

step 2. litter stoichiometry: what enters larder? microbial quasi-EQ

per unit harvest, microbes get some amount of C and some amount of N

which depends on the litter stoichiometry

- At first, microbes are N limited
  eventually, they eat enough D to get the N required to start experiencing density dependence due to competition for space (on the litter)
- microbes then become C limited, which is where plants come in

step 3. trade

Now C limited, the microbes have excess N from the detritus they are able to break down

They can trade this to plants, who will give them C in return.

In this way, when plants are present they can set the microbial biomass possible to

step 4. feedback

2024-02-27

Questions about the Model

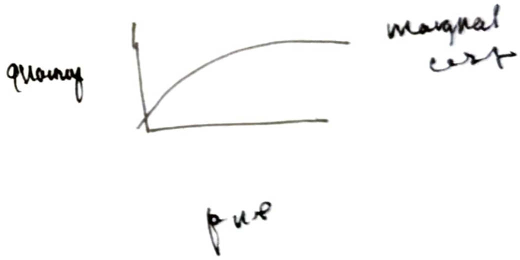
[1]

model choice
parameters
↓
parameterize for tundra

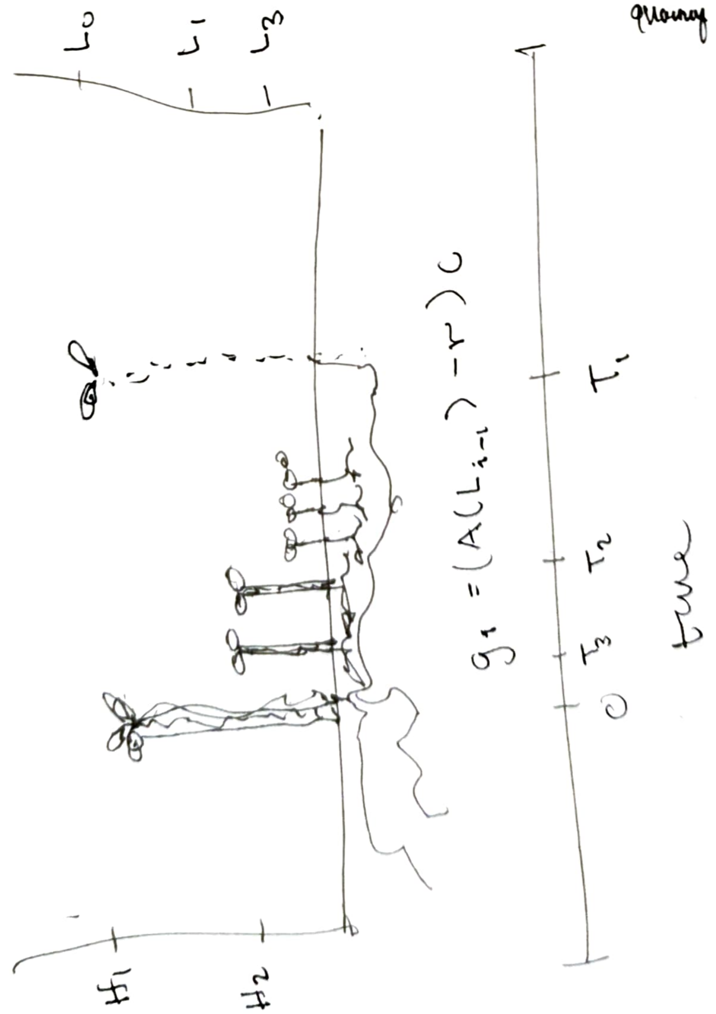
[2]

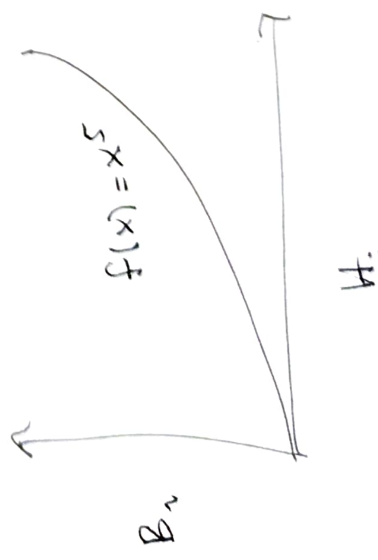
validating for system
↓
other
multiple
overlapping resource axes

simp



Model Structure





Tundra Plant Simulator - Construction steps

1. Start with one species + Define key traits

Height
Allometry → biomass
Crown area
Amax
C:N ratio

2. Define state variables

3. Set reproduction, mortality, etc. i.e. DEMOGRAPHY

4. Define environmental variables: light, N, seasonality

5. Write demographic rates as function of environment

    5a carbon economy of light

    5b Nutrient dynamics

6. Run simulations of 1 sp.

7. Add multiple species

8. Check EQ solutions

9. Run global change scenarios

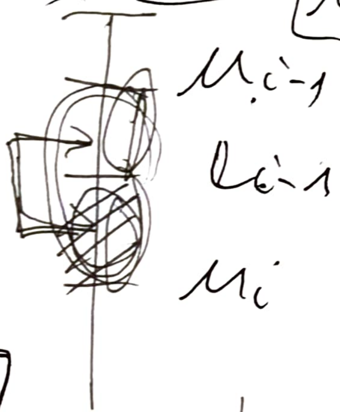
STRATEGY

- start w/ light only
- start w/ 1 species

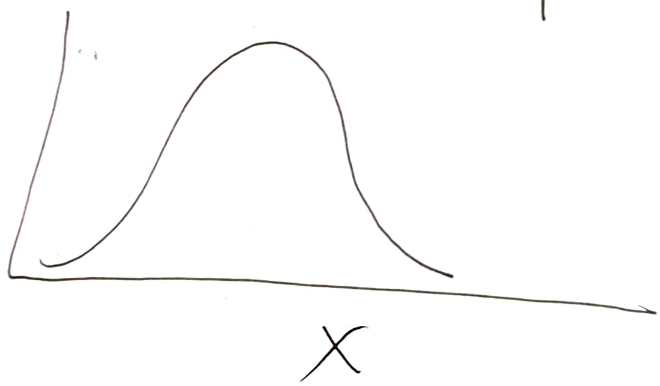
$$\boxed{F\left(e^{-rX_1} - e^{-r(X_1+X_2)}\right) = m}$$

$$m \sim L_{i-1} - L_i = \boxed{L_{i-1} - M}$$

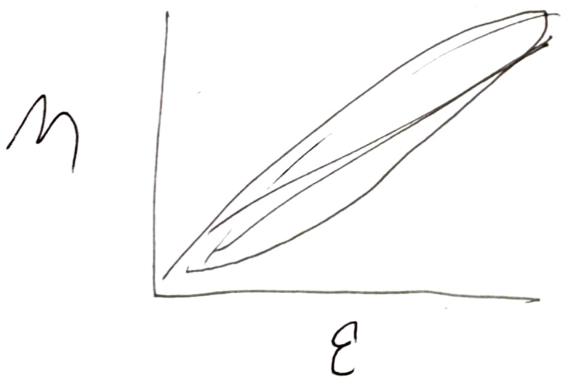
$[M, M, L_i$

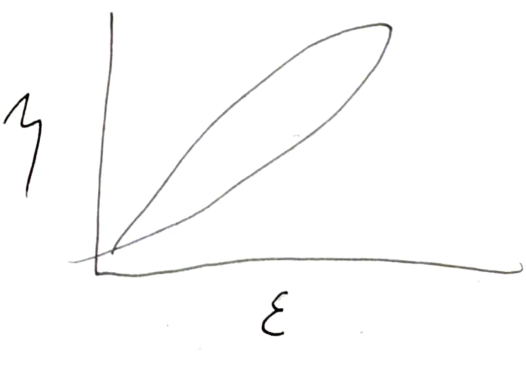


$P(X)$?

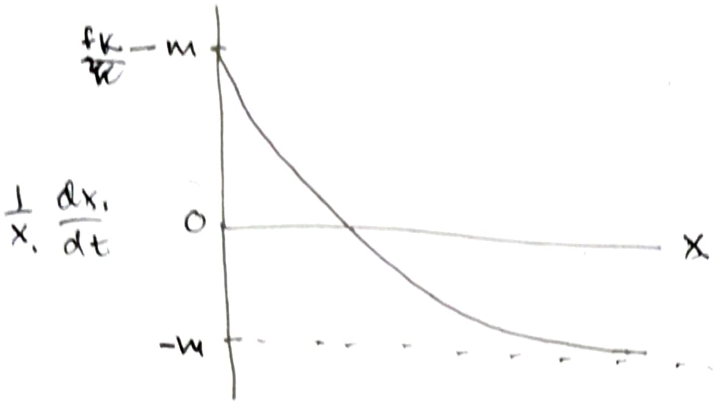


$$\varepsilon_i = L_{i-1} - M_i \sim m \qquad \eta_i = M_i - L_i$$





Per capita growth rate



$$\frac{1}{x_1}\frac{dx_1}{dt} = \frac{f_1(1-e^{-kx_1})}{x_1} - m$$

$$\boxed{\frac{1}{x_i}\frac{dx_i}{dt}} = f_i e^{-k(x_1+\dots+x_{i-1})}\frac{(1-e^{-kx_i})}{x_i} - m$$

L above

$$\boxed{m \sim \Delta t}$$

u

$$w_i = \sum_{j=1}^{i} x_j$$

$fk - m$

$x \approx$

$$\frac{m}{uk}k - m = \frac{m}{u} - m$$

$$\lambda_i = fk \underbrace{e^{-k\sum_{j=1}^{i} x_j}} - m$$

$E[\lambda]$

$\int E(\lambda|w)P(w)dw$

$$\lambda_1 = fk - m \quad \lim s \to \infty$$

$$\lambda_s = \cancel{f} - m \quad \lim s \to \infty$$

$$f_0 k e^{-w} - m$$

Smple model OBserver invariance : x_1, x_2, x_3

$x_0 = x_1 + x_3$, $\quad f_1 = f_3 = f_0$. out of order $\quad$ x_0 is the tallest ? $> x_2$ $\quad$ x_0 is shorter than x_2?

$$\frac{dx_1}{dt} + \frac{dx_3}{dt} = \underbrace{f_1(1-e^{-kx_1}) - mx_1}_{x_1} + f_3(e^{-k(x_1+x_2)} - e^{-k(x_1+x_2+x_3)}) - mx_3$$

$$= f(1 - e^{-kx_1} + e^{-k(x_1+x_2)} - e^{-k(x_1+x_2+x_3)}) - m(x_1+x_3)$$

$x_0 = x_2 + x_3 \quad f_2 = f_3 = f$ is the 2nd tallest sp.

$$\frac{dx_2}{dt} + \frac{dx_3}{dt} = f(e^{-kx_1} - e^{-k(x_1+x_2)}) - mx_2 + f(e^{-k(x_1+x_2)} - e^{-k(x_1+x_2+x_3)}) - mx_3$$

$$\frac{d(x_2+x_3)}{dt} = f(e^{-kx_1} - \cancel{e^{-k(x_1+x_2)}} + \cancel{e^{-k(x_1+x_2)}} - e^{-k(x_1+\underbrace{x_2+x_3}_{x_0})}) - m\underbrace{(x_2+x_3)}_{x_0}$$

$$F_1(x_1) = \frac{dx_1}{dt} = f_1(1-e^{-kx_1}) - mx_1$$

$$F_2(x_1, x_2) = \frac{dx_2}{dt} = f_1(e^{-kx_1} - e^{-k(x_1+x_2)}) - mx_2$$

$$F_3(x_1, x_2, x_3) = \frac{dx_3}{dt} = f_3(e^{-k(x_1+x_2)} - e^{-k(x_1+x_2+x_3)}) - mx_3$$

$\vdots$

$$F_i(\vec{x}) = \frac{dx_i}{dt} = f_i(e^{-k\sum_{j=1}^{i-1} x_j} - e^{-k\sum_{j=1}^{i} x_j}) - mx_i$$

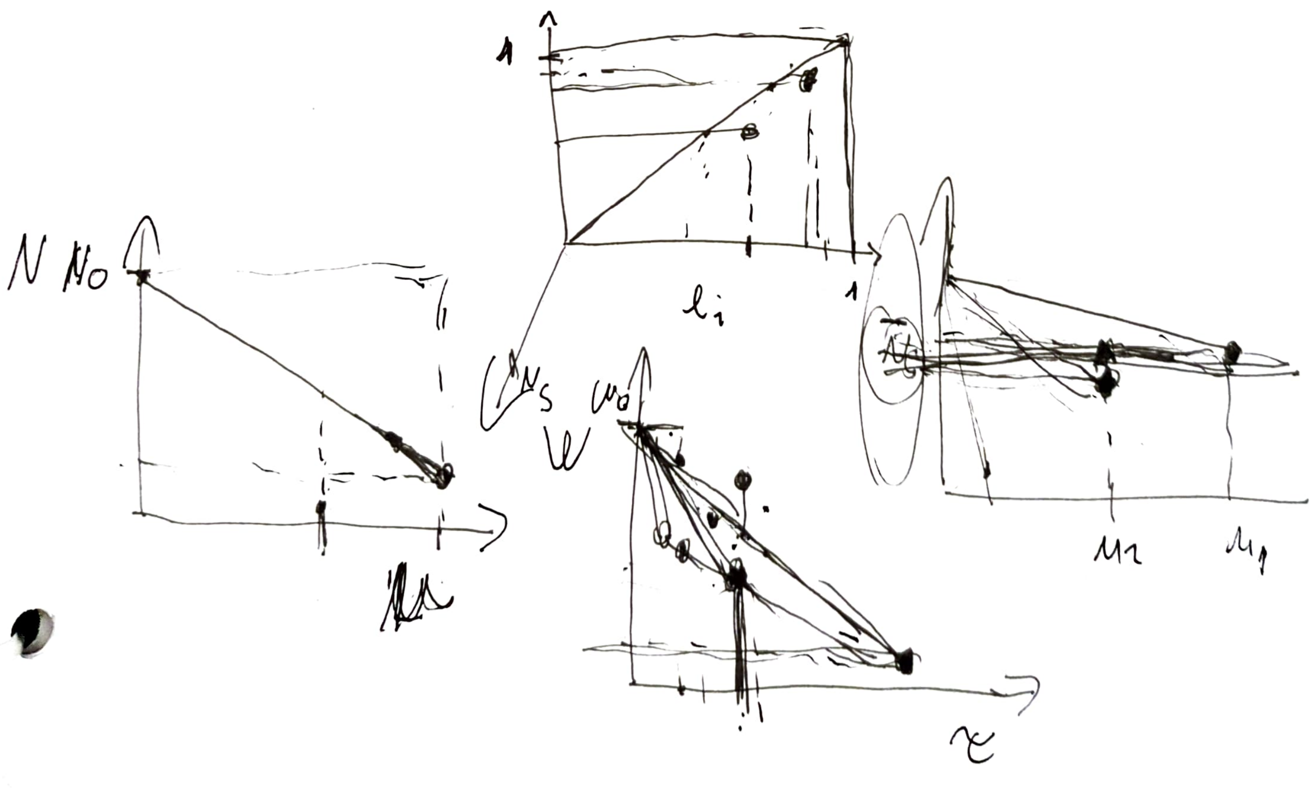
Matteo chat

March 2nd

- ~~finish slides~~
  - ~~results~~
  - ~~methods~~
- ~~seminar talks~~
- ~~practice talk~~
- ~~look @ papers~~

→ Soil depth - parameters of heterogeneity
- Mackenzie delta water flow - longer active layer - hydrological gradients
- deeper thaw - microtopography

→ nitrogen - light : 2 species case, mutual invasion
Tradeoff comes from Biomass dependence
correlated light and nutrient dependence
→ stochastic simulation → use light to characterize the species



2024-03-21

System of sp. w/ Beer's law light extinction

LIGHT ENVIRONMENT

$L_0 = 1 =$ light at top of canopy

$L_1 =$ light below sp. 1

$L_2 =$ light below sp. 2

$\vdots$

$L_i =$ light below sp. i

Beer's law leaves decay

$L_0 = 1$

$L_1 = L_0 e^{-kx_1}$

$L_2 = L_0 e^{-k(x_1+x_2)}$

$\vdots$

$L_i = L_0 e^{-k\sum_{j=1}^{i} x_j}$

LIGHT ~~ABSORBED~~ INTERCEPTED per SPECIES i (all leaves in that height layer) → INTERCEPTED

$I_1 = L_0 - L_1 = L_0 - L_0 e^{-kx_1}$

$I_2 = L_1 - L_2 = L_0 e^{-kx_1} - L_0 e^{-k(x_1+x_2)} = L_0 e^{-kx_1}(1-e^{-kx_2})$

$\vdots$

$I_i = L_{i-1} - L_i$ light above canopy i − light below canopy i $= L_0 e^{-k\sum_{j<i} x_j}(1-e^{-kx_i})$

$I_i = L_0 e^{-k\sum_{j=1}^{i-1} x_j} - L_0 e^{-k\sum_{j=1}^{i} x_j}$

LIGHT PER INDIVIDUAL RAMET of SPECIES i

$R_1 = \dfrac{I_1}{x_1} = \dfrac{L_0(1-e^{-kx_1})}{x_1}$

x_1 ← # of ramets of sp. 1

$R_2 = \dfrac{I_2}{x_2} = \dfrac{L_0 e^{-kx_1}(1-e^{-kx_2})}{x_2}$

$\vdots$

$R_i = \dfrac{I_i}{x_i} = \dfrac{L_0 e^{-k\sum_{j=1}^{i-1}}(1-e^{-kx_i})}{x_i}$

GROWTH PER INDIVIDUAL RAMET of SP. i (per capita)

$g_1(x_1) = aR_1 - r = a\dfrac{I_1}{x_1} - r = a\dfrac{L_0(1-e^{-kx_1})}{x_1} - r$

$g_2(x_1, x_2) = aR_2 - r = \dfrac{aL_0 e^{-kx_1}(1-e^{-kx_2})}{x_2} - r$

$\vdots$

$g_i(x_1, \ldots x_i) = aR_i - r$

GROWTH OF POPULATION of SPECIES i

$$G_1(x_1) = g_1(x_1)\,x_1 = aL_0(1-e^{-kx_1}) - rx_1$$
$$= (aR_1 - r)x_1$$
$$G_2(x_1,x_2) = (aR_2 - r)x_2 = aL_0e^{-kx_1}(1-e^{-kx_2}) - rx_2$$
$$\vdots$$
$$G_i(\vec{x}) = (aR_i - r)x_i = aL_0e^{-k\sum_{j=1}^{i-1}x_j}(1-e^{-kx_i}) - rx_i$$

POPULATION DYNAMICS for SPECIES $1, \ldots, i$

$$F_1(\vec{x}) = \frac{dx_1}{dt} = \frac{G_1(x_1)}{B_1} - mx_1 = \frac{1}{B_1}\left[aL_0(1-e^{-kx_1}) - rx_1\right] - mx_1$$
$$= \frac{aL_0}{B_1}(1-e^{-kx_1}) - \frac{r}{B_1}x_1 - mx_1$$
$$F_2(\vec{x}) = \frac{dx_2}{dt} = \left(\frac{1}{B_2}\right)\left[aL_0e^{-kx_1}(1-e^{-kx_2}) - rx_2\right] - mx_2$$
$$\vdots$$
$$F_i(\vec{x}) = \frac{dx_i}{dt} = \left(\frac{1}{B_i}\right)\left[aL_0e^{-k\sum_{j=1}^{i-1}x_j}(1-e^{-kx_i}) - rx_i\right] - mx_i$$

OBSERVER INVARIANCE CHECK, let $B_1 = B_2 = B$, $x_0 = x_1 + x_2$

$$\frac{dx_1}{dt} + \frac{dx_2}{dt} = \underbrace{\left(\frac{1}{B}\right)\left[aL_0(1-e^{-kx_1}) - rx_1\right] - mx_1}_{} + \left(\frac{1}{B}\right)\left[aL_0e^{-kx_1}(1-e^{-kx_2}) - rx_2\right] - mx_2$$
$$= \left(\frac{1}{B}\right)\left[aL_0 - \cancel{aL_0e^{-kx_1}} + \cancel{aL_0e^{-kx_1}} - aL_0e^{-k(x_1+x_2)} - rx_1 - rx_2\right] - mx_1 - mx_2$$
$$= \left(\frac{1}{B}\right)\left[aL_0(1 - e^{-k(x_1+x_2)}) - r(x_1+x_2)\right] - m(x_1+x_2)$$
$$= F_1(x_1+x_2)$$

fine for 1st two species

Statement: • asymmetric competition (for light) maintains coexistence of multispecies communities

Jacobian for 2 sp.

$$\vec{J} - \lambda I = \begin{bmatrix} \frac{\partial F_1}{\partial x_1} - \lambda & \frac{\partial F_1}{\partial x_2} \\ \frac{\partial F_2}{\partial x_1} & \frac{\partial F_2}{\partial x_2} - \lambda \end{bmatrix}$$

• in these models, increasing diversity ($s \to \infty$) increases stability ($Re(\lambda) \to -\infty$) [need to check this]

• this model exhibits stable coexistence when sp. fall "outside the shadow" of limiting similarity

$$\vec{J} = \begin{bmatrix} \left(\frac{1}{B_1}\right)(a L_0 k) e^{-kx_1} - \frac{r}{B_1} - m & \\ \frac{a L_0}{B_2} k e^{-k(x_1+x_2)} - \frac{a L_0 k e^{-kx_1}}{B_2} & \frac{a L_0}{B_2} k e^{-k(x_1+x_2)} - \frac{r}{B_2} - m \end{bmatrix}$$

→ numerical sol^n for $\vec{x}^*$

→ find eigenvalues for $\vec{J}$

→ simulate for $S = 10 \longrightarrow 1000$ sp × 1000 reps
choose uniform

↓

calculate $Re(\lambda)$ & plot w/ respect to S

$$\frac{\partial F_i}{\partial x_i} = f_i k e^{-k(x_1 + \cdots x_i)} - m$$

Simple Model Jacobian

$$\vec{J} = \begin{matrix} \dfrac{\partial F_1}{\partial x_1} & \cancel{\dfrac{\partial F_1}{\partial x_2}} \approx 0 & \cdots & \cancel{\dfrac{\partial F_1}{\partial x_i}} \approx 0 \\ \dfrac{\partial F_2}{\partial x_1} & \dfrac{\partial F_2}{\partial x_2} & \cdots & \cancel{\dfrac{\partial F_2}{\partial x_i}} \approx 0 \\ \vdots & & & \\ \dfrac{\partial F_i}{\partial x_1} & \dfrac{\partial F_2}{\partial x_2} & \cdots & \dfrac{\partial F_i}{\partial x_i} \end{matrix}$$

eigenvalues

$\lambda_i = f_i k e^{-k(\hat{x}_1 + \cdots \hat{x}_i)} - m$

$\lambda < 0$?

$f_i k e^{-k(x_1 + \cdots x_i)} < m$

$e^{-k(x_1 + \cdots + x_i)} < \dfrac{m}{f_i k}$

$-k(x_1 + \cdots + x_i) < \log\left(\dfrac{m}{f_i k}\right)$

$x_1 + \cdots + x_i > \dfrac{-\log\left(\frac{m}{f_i k}\right)}{k}$

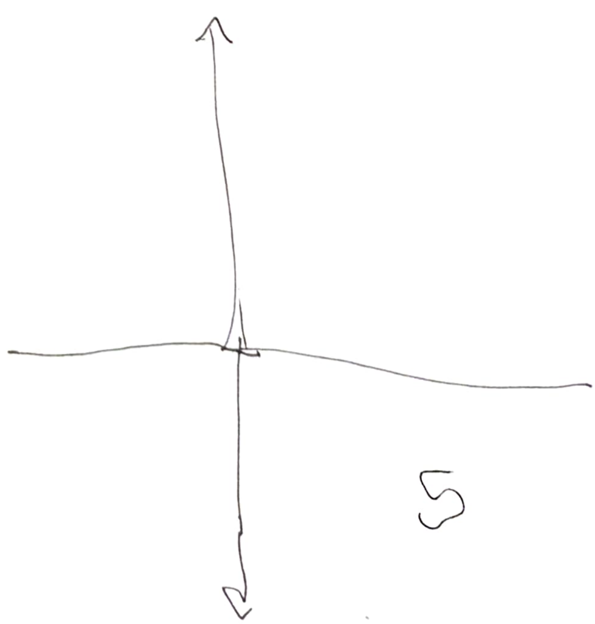
$x_1 + \cdots x_i > \log\left[\left(\dfrac{f_i k}{m}\right)^{\frac{1}{k}}\right]$

$x_1 + \cdots + x_i > \dfrac{\log\left(\frac{f_i k}{m}\right)}{k}$

system $=$

$$\begin{cases} F_1(x_1) = f_1(1 - e^{-kx_1}) - m x_1 \\ F_2(x_1, x_2) = f_2(e^{-kx_1} - e^{-k(x_1+x_2)}) - m x_2 \\ F_3(x_1, x_2, x_3) = f_3(e^{-k(x_1+x_2)} - e^{-k(x_1+x_2+x_3)}) - m x_3 \\ \vdots \\ F_i(\vec{x}) = f_i\left(e^{-k\sum_{j=1}^{i-1} x_j} - e^{-k\sum_{j=1}^{i} x_j}\right) - m x_i \end{cases}$$

$$\left.\begin{aligned} \frac{\partial F_1}{\partial x_1} &= f_1 k e^{-kx_1} - m \\ \frac{\partial F_2}{\partial x_2} &= f_2 k e^{-k(x_1+x_2)} - m \\ \frac{\partial F_3}{\partial x_3} &= f_3 k e^{-k(x_1+x_2+x_3)} - m \\ &\vdots \\ \frac{\partial F_i}{\partial x_i} &= f_i k e^{-k\sum_{j=1}^{i} x_j} - m \end{aligned}\right\}$$



Simple form of the model

$$\frac{dx_1}{dt} = f_1 g(x_1) x_1 - m x_1 = f_1 (1 - e^{-kx_1}) - m x_1$$

$$g(x_1) = \frac{1 - e^{-kx_1}}{x_1}$$

$$\frac{dx_2}{dt} = f_2 g(x_1, x_2) x_2 - m x_2 = f_1 ($$

$$g(x_1, x_2) = e^{-kx_1} - e^{-k(x_1 + x_2)}$$

$$\frac{dx_3}{dt} = f_3 \, g(x_1, x_2, x_3) x_3 - m x_3$$

$$= f_3 \left[e^{-k(x_1 + x_2)} - e^{-k(x_1 + x_2 + x_3)} \right] - m x_3$$

$$\frac{dx_3}{dt} = f_3 \left[e^{-k(x_1 + x_2)} \right] (1 - e^{-kx_3}) - m x_3$$

$\vdots$

$$\frac{dx_i}{dt} = f_i \, g(\vec{x}) x_i - m x_i = f_i \, L_{above} (1 - e^{-kx_i}) - m x_i$$

$$= f_i \left[e^{-k(x_1 + \cdots + x_{i-1})} - e^{-k(x_1 + \cdots x_i)} \right] - m x_i$$

~~numerical~~ simulations

$$\frac{1}{x_1} \frac{dx_i}{dt} = f_i \frac{L_{above}(1 - e^{-kx_i})}{x_i} - m > 0$$

~~analytical~~ invasion condition

$$l_i = \frac{m}{f_i k} < L_{above} \lim_{x_i \to 0}$$

$$L_{above} > \frac{m x_i}{f_i (1 - e^{-kx_i})}$$

~~implicit~~ expression for EQ

$$f_i L_{above} (1 - e^{-kx_i^*}) - m x_i = 0$$

plot this

$$L_{above} > \frac{m}{f_i k} = l_i$$

leaf area per variant × light × fraction

Light + Nitrogen Competition model

Step 1 : Flesh out / Write up Light Version of Model

- Finish writing up the light model (R studio)

- Further questions:
    - Would adding realistic growth in height change the story?

    - [SIMULATION]

    ↳ start w/ alternative version - cts reproduction

Step 2 : Bring model to the TUNDRA

- parameterize w/ tundra traits

    → do plants grow at all ???

- [SIMULATION]

Step 3 : Add N cost to light model ⇐

- Read Jacob paper
- Graphical method same or different, if so why?

Theory Tea
2024-04-10

Anne Kinzig —

CO_2 enrichment → photosynthetic efficiency

↳ taller

↳ N-fixation

Allometry

- mortality - allometry increases
- mortality snow

Competition - colonization

Seasonality

- sinusoidal
-

Extinction cascades

plot changes →

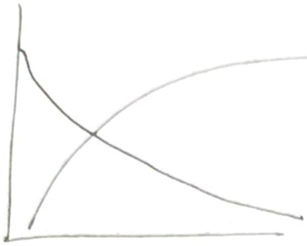
+X °C

When sp drop out and where?

Shrubification

- sp. loss in shrubs preferentially
- one shrub does well

grasses + forbs do okay



$e^{-kx_1} + e^{-k(x_1+x_2)}$

$$\frac{dg_2}{dx_2} = \frac{ke^{-k(x_1+x_2)}\cancel{x_2} - e^{-kx_1}(1-e^{-kx_2})}{x_2^2}$$

$\alpha_{22} < \alpha_{21}$

$$= \frac{ke^{-kx_1}}{x_2}\left(\frac{e^{-kx_2}x_2 - \frac{1+e^{-kx_2}}{k}}{x_2}\right)$$

$$\frac{dg_2}{dx_1} = \frac{ke^{-kx_1}}{x_2}\left(1-e^{-kx_2}\right) = \alpha_{21}$$

$\frac{1}{k}$

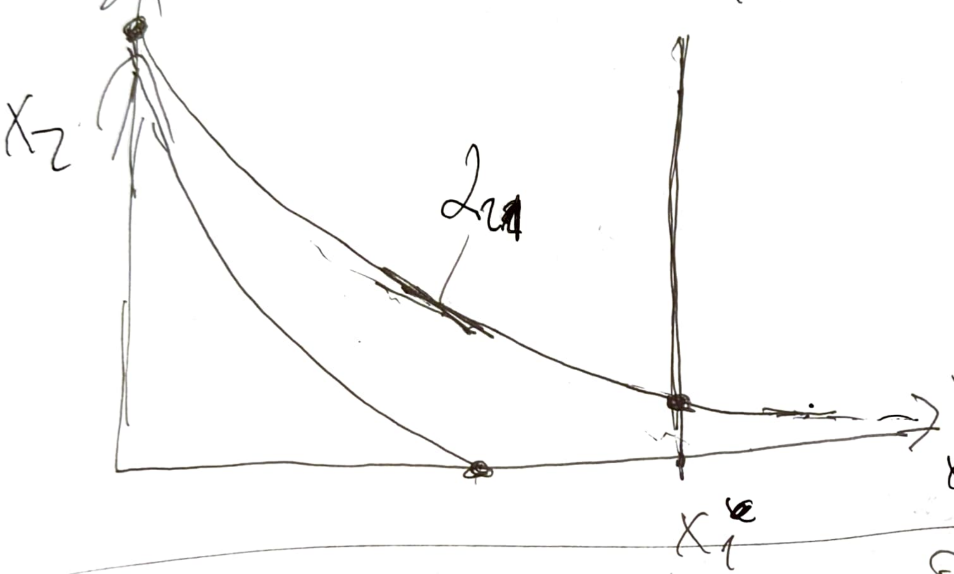
$$\frac{dg_2}{dx_2} = \frac{-ke^{-kx_1}}{x_2}\left(\frac{\frac{1+e^{-kx_2}}{k} - e^{-kx_2}x_2}{x_2}\right) = \alpha_{22}$$

$x=0$ $\quad x \to \infty$ $\quad [0,1]$

$$\left(\frac{1-e^{-kx_2}}{kx_2} - e^{-kx_2}\right)$$

$(0-1)$ $\quad (0-1)$

$\alpha_{21} \gtrless \alpha_{22}$



$\alpha_{11} = \bar{\alpha}_{11}$ $\qquad$ $\alpha_{22} \gtrless \alpha_{21}$

$\alpha_{12} = 0$

$\alpha_{22} > \alpha_{12}$

$\alpha_{11} > \alpha_{21}$

$\frac{dx_1}{dt} = r x_1 - \alpha_{11} x_1^2 - \cancel{\alpha x_2^2}$

$\frac{dx_2}{dt} = r x_2 - \alpha_{21} x_1 x_2 - \alpha_{22} x_2^2$

$\alpha_{11} > \alpha_{21}$

Matteo Chat