Ruby An | 2024-04-10

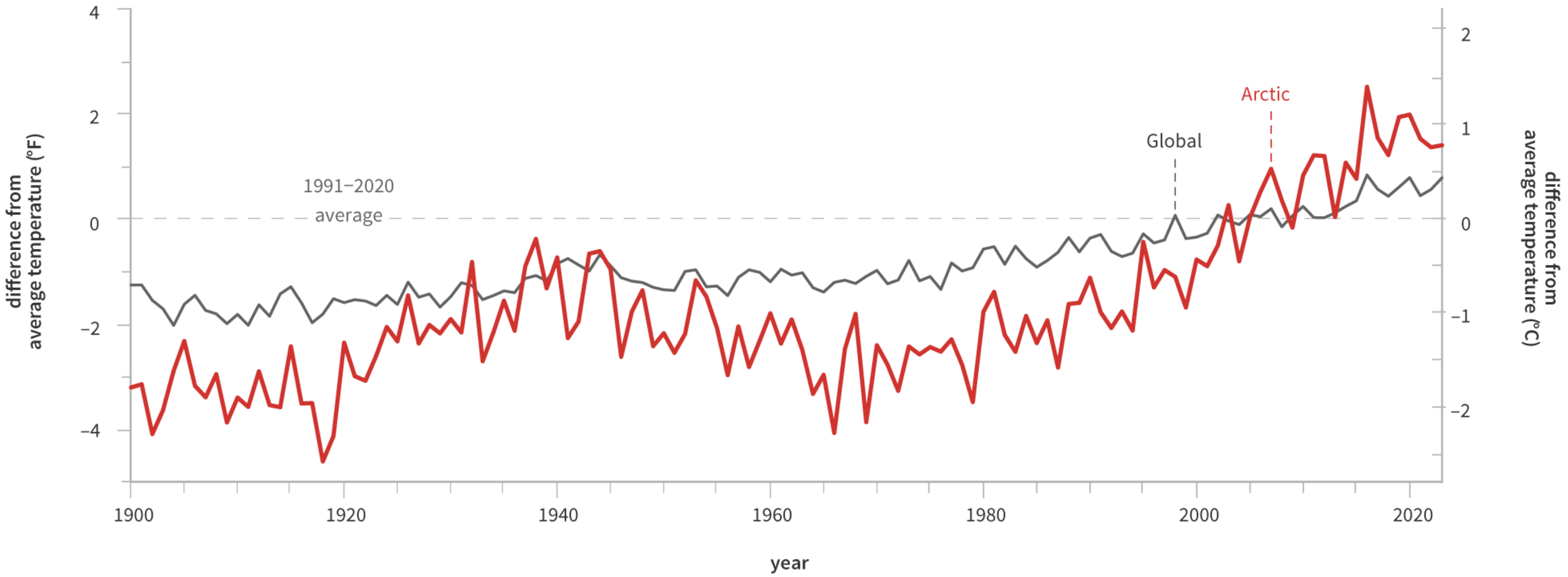
Theory Tea

Mechanistic models of Arctic Shrubification

Talk Outline

- Motivation
- How did I build the model?
  - Story, Equations, Equation Continuum
- Preliminary Results
  - Light requirement & max height, Implicit EQ solution, Simulations
- Next Steps
- Discussion

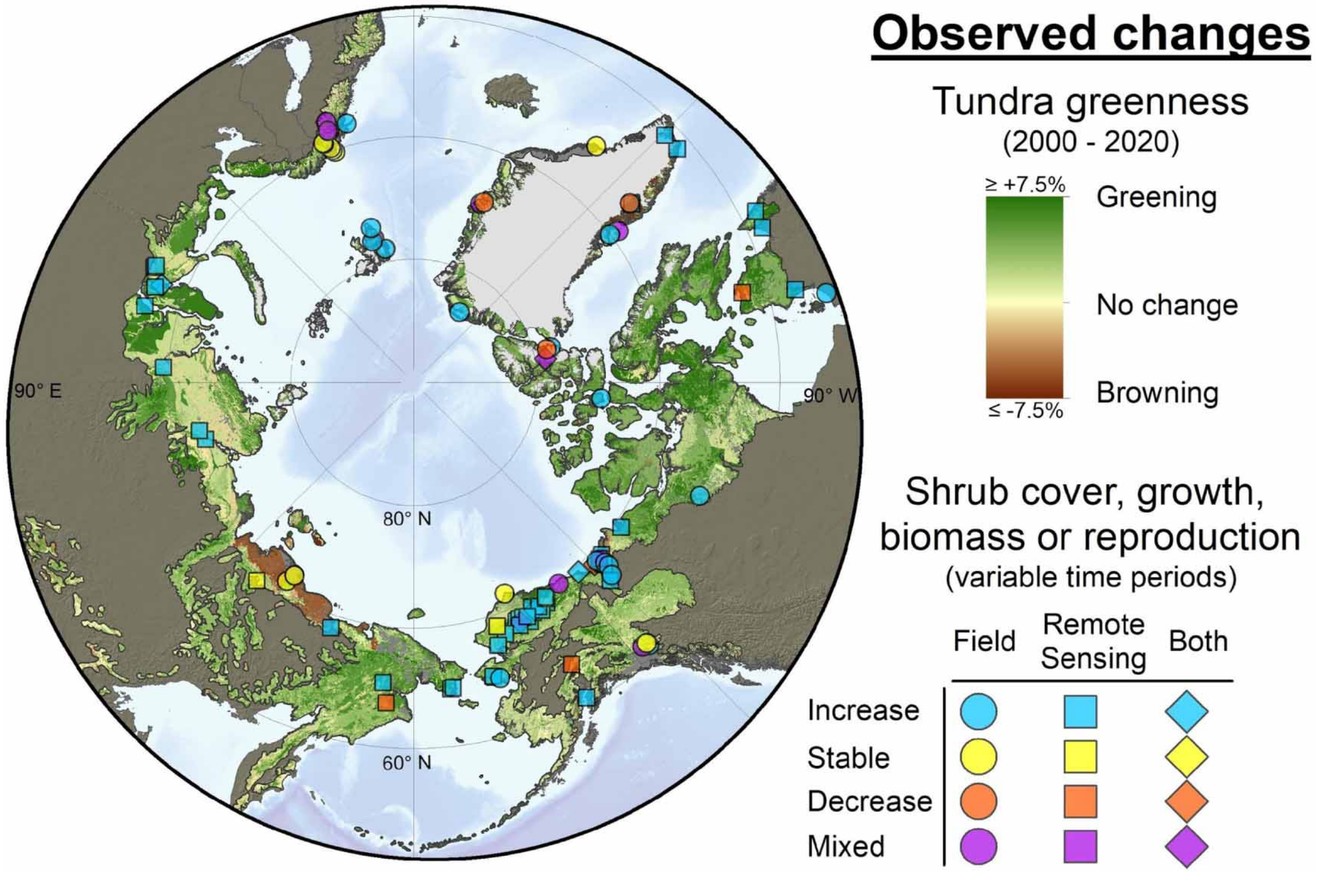
The Arctic is warming 3-4x the global average…
with ecological consequences

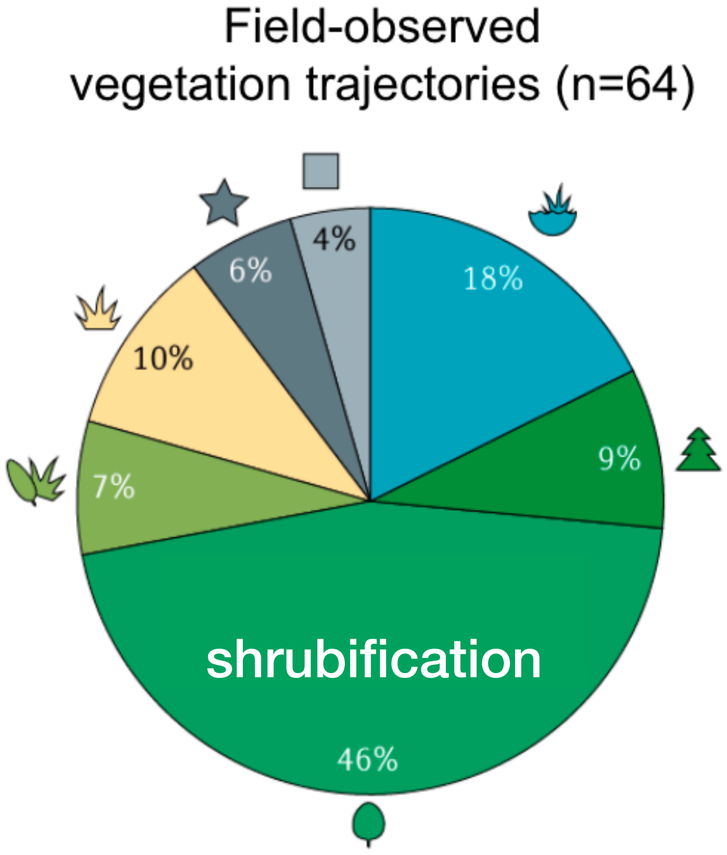


annual (Oct-Sep) temperatures compared to 1991-2020 average

NOAA Climate.gov
Data: ARC 2023

Patterns of Arctic “shrubification” are clear.





Heijmans et al. 2022

willows
Salix sp.

alder
Alnus viridus

dwarf birch
Betula nana

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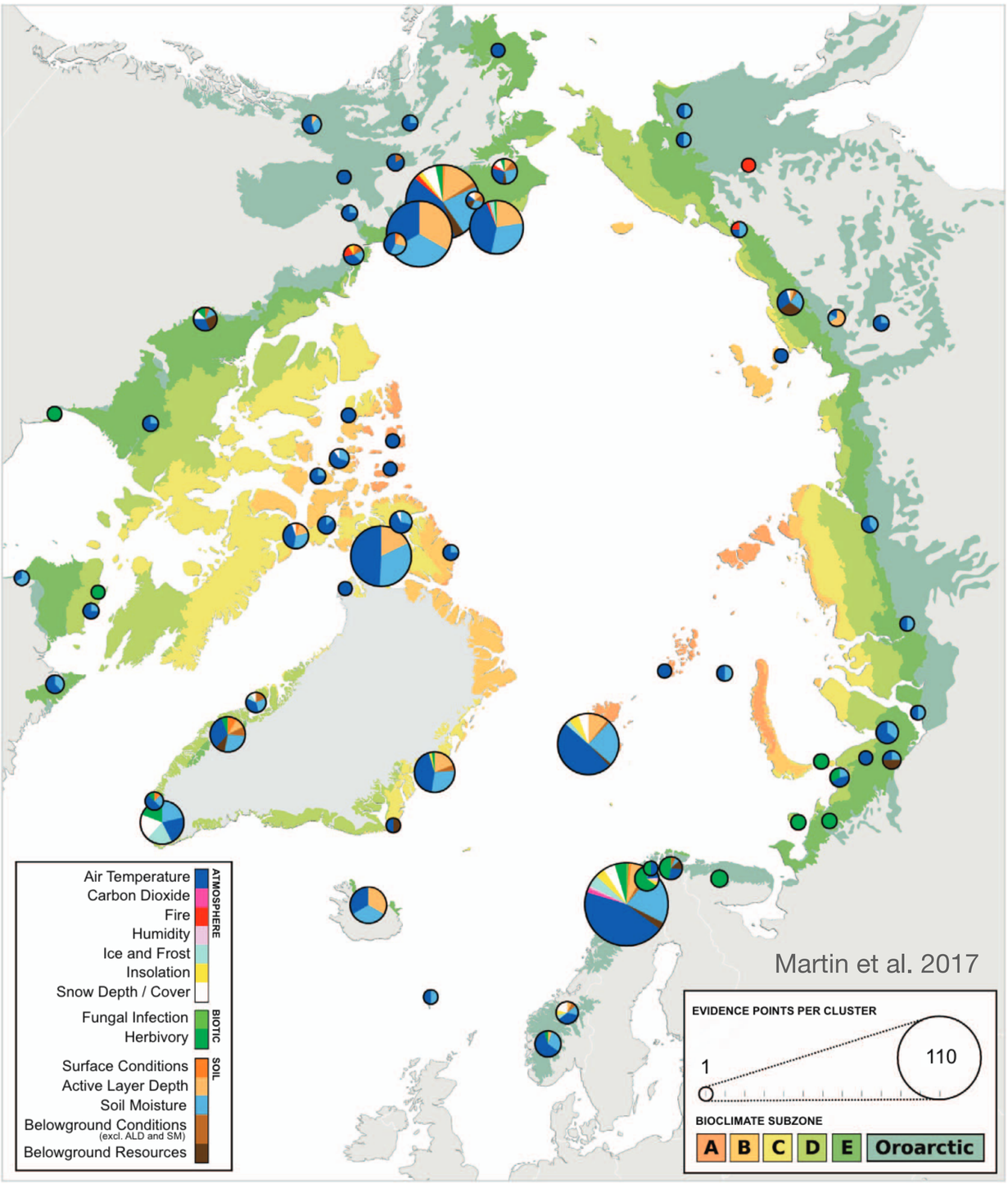
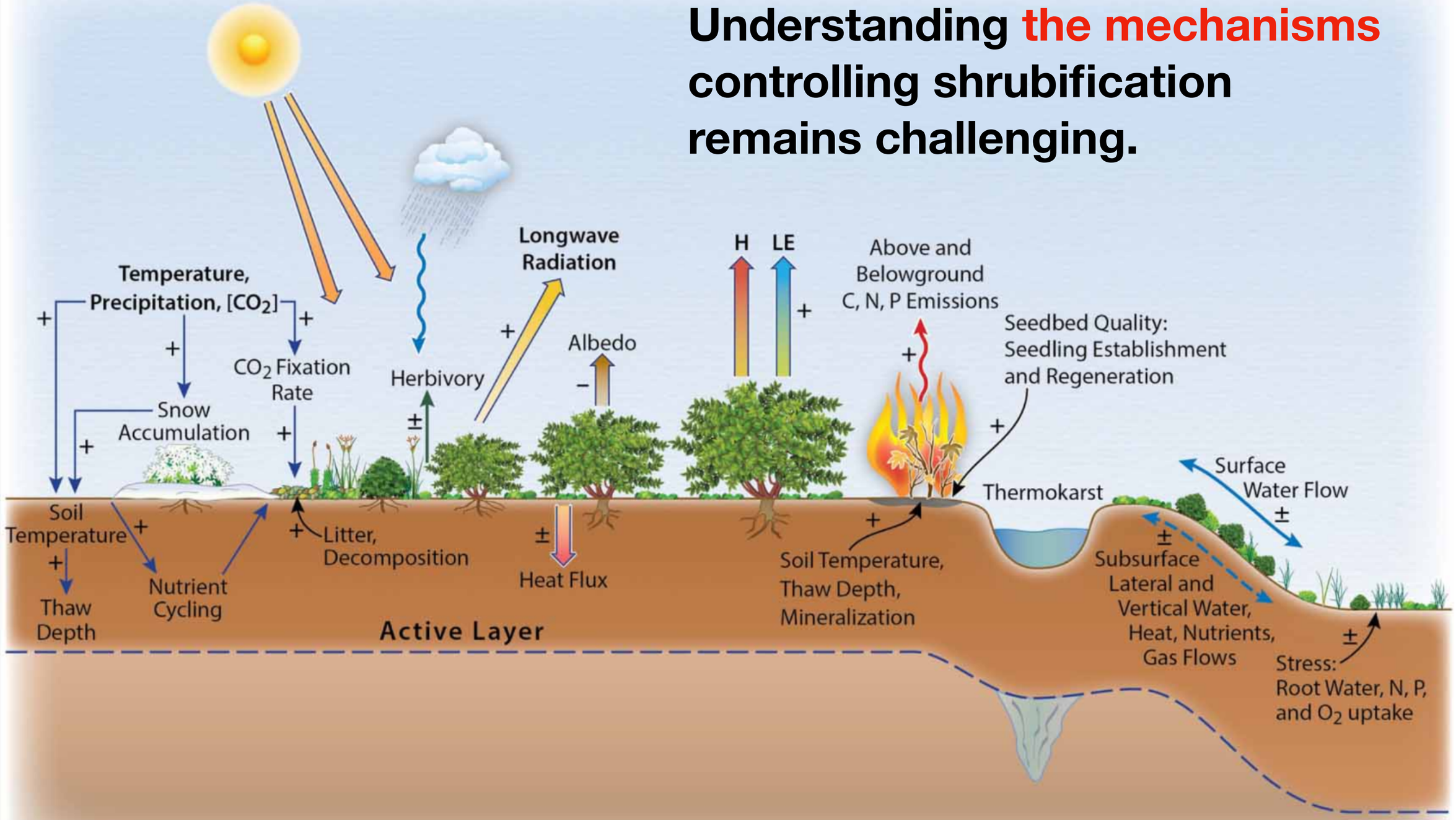
Model Outcome Wishlist



Understanding the mechanisms controlling shrubification remains challenging.

"Insufficient evidence."
-Martin et al. 2017

Understanding the mechanisms controlling shrubification remains challenging.



Mekonnen et al. 2021

“Mechanisms” of Arctic Shrubification

mechanism 1:

Photosynthetic Advantage

(Fig. 1, arrow B)

mechanism 2:

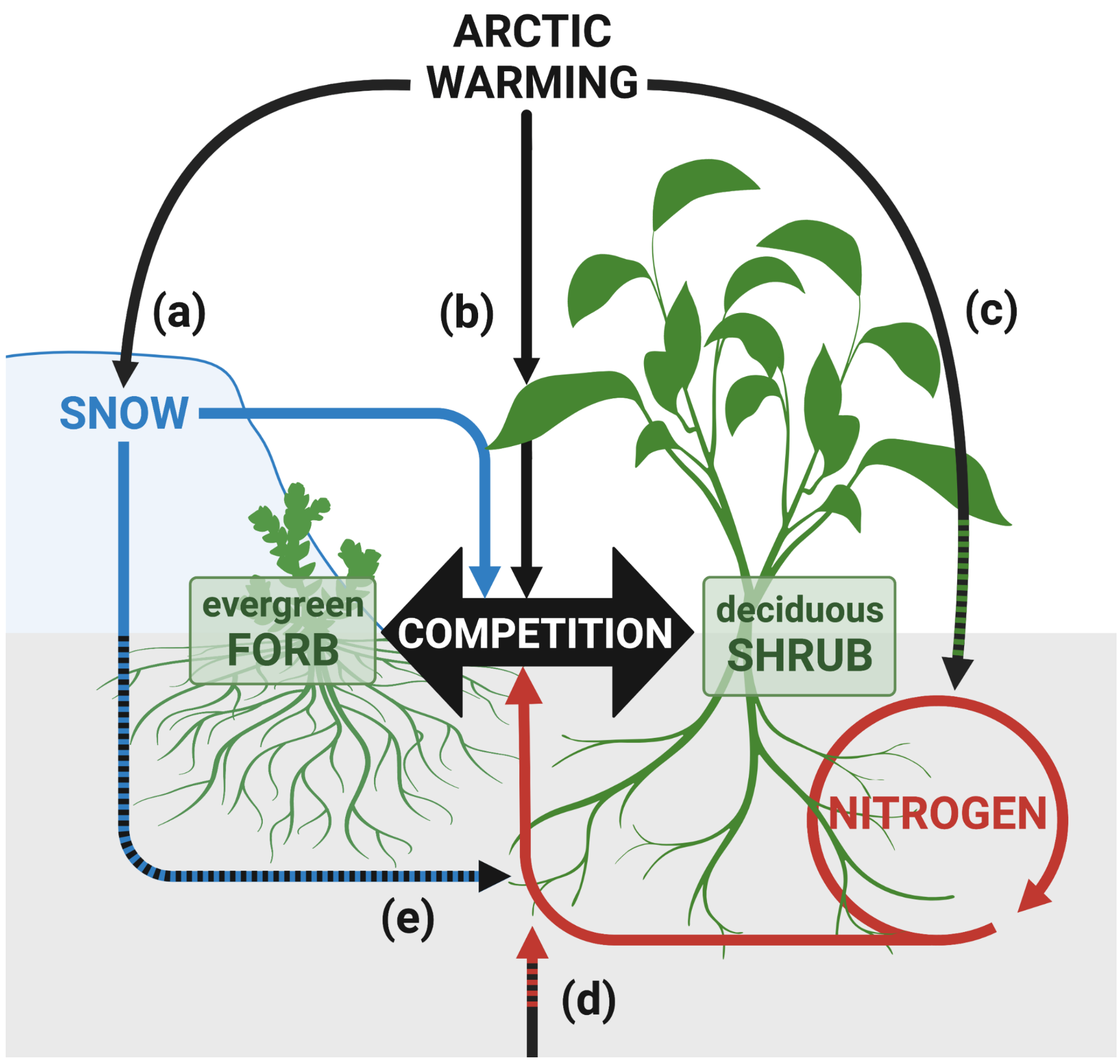
Nutrient-mediated Dominance

(Fig. 1, arrow C, D)

mechanism 3:

More Time to Win

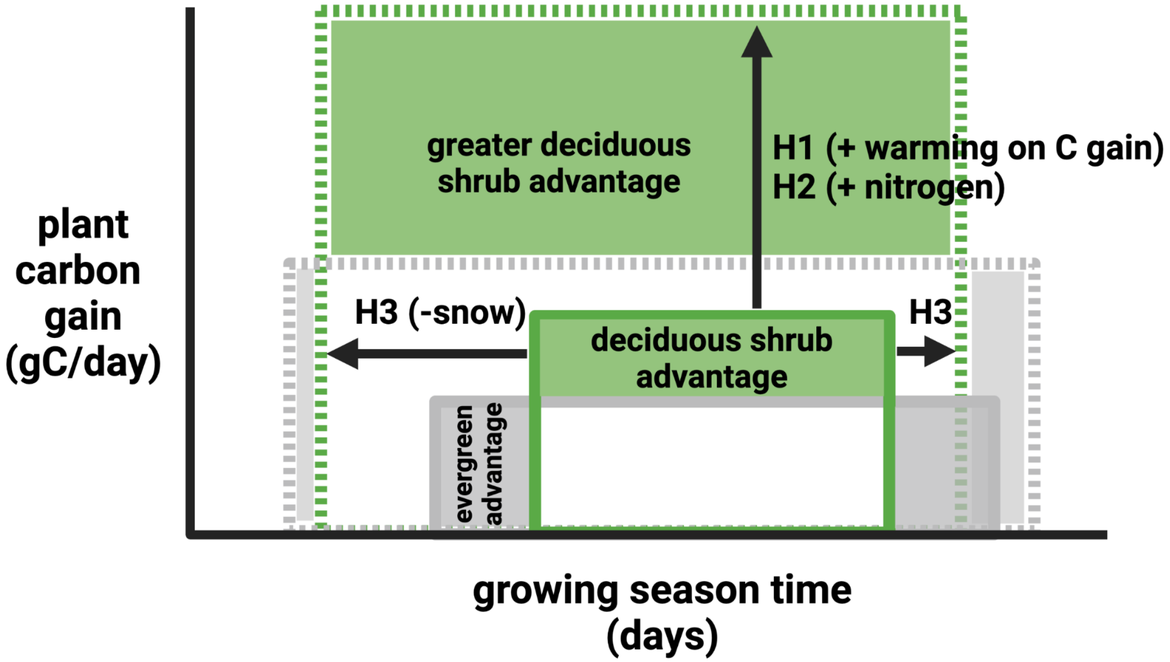
(Fig. 1, arrow A)



Arctic warming acts through **multiple pathways** to structure plant competition in Arctic ecosystems.

Necessary Model Ingredients

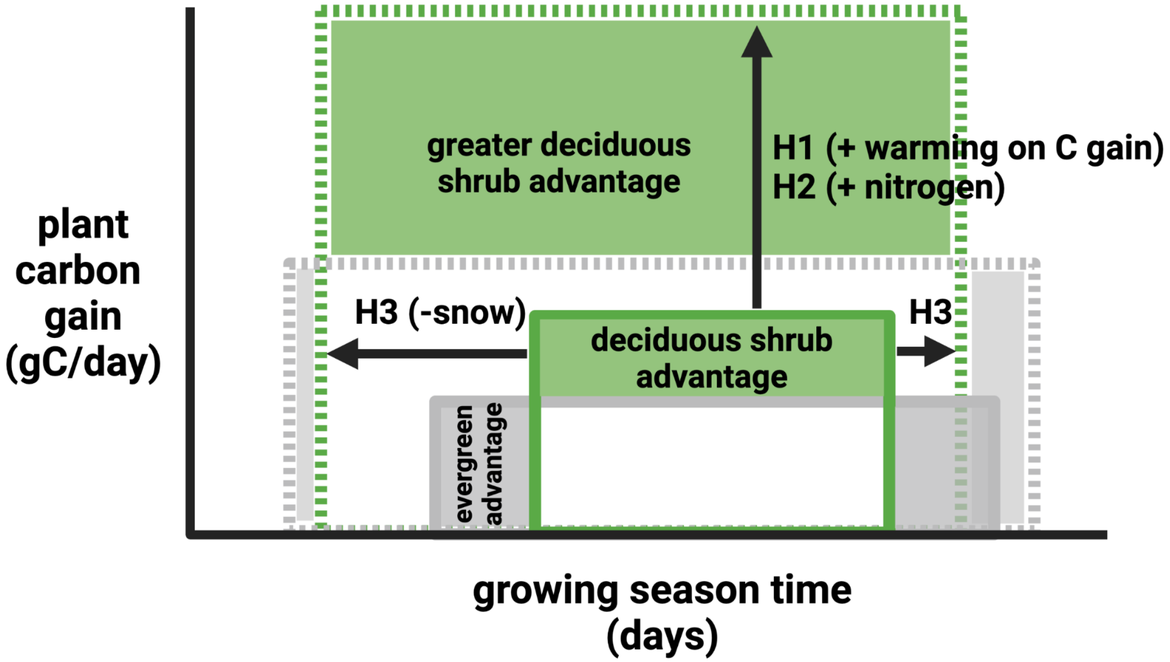
to build model that can test shrubification mechanisms



Differences in plant traits, related to

1. Temperature dependence of photosynthesis
2. Competition for nitrogen
3. Seasonality = period of time favorable for growth

Model Outcome Wishlist



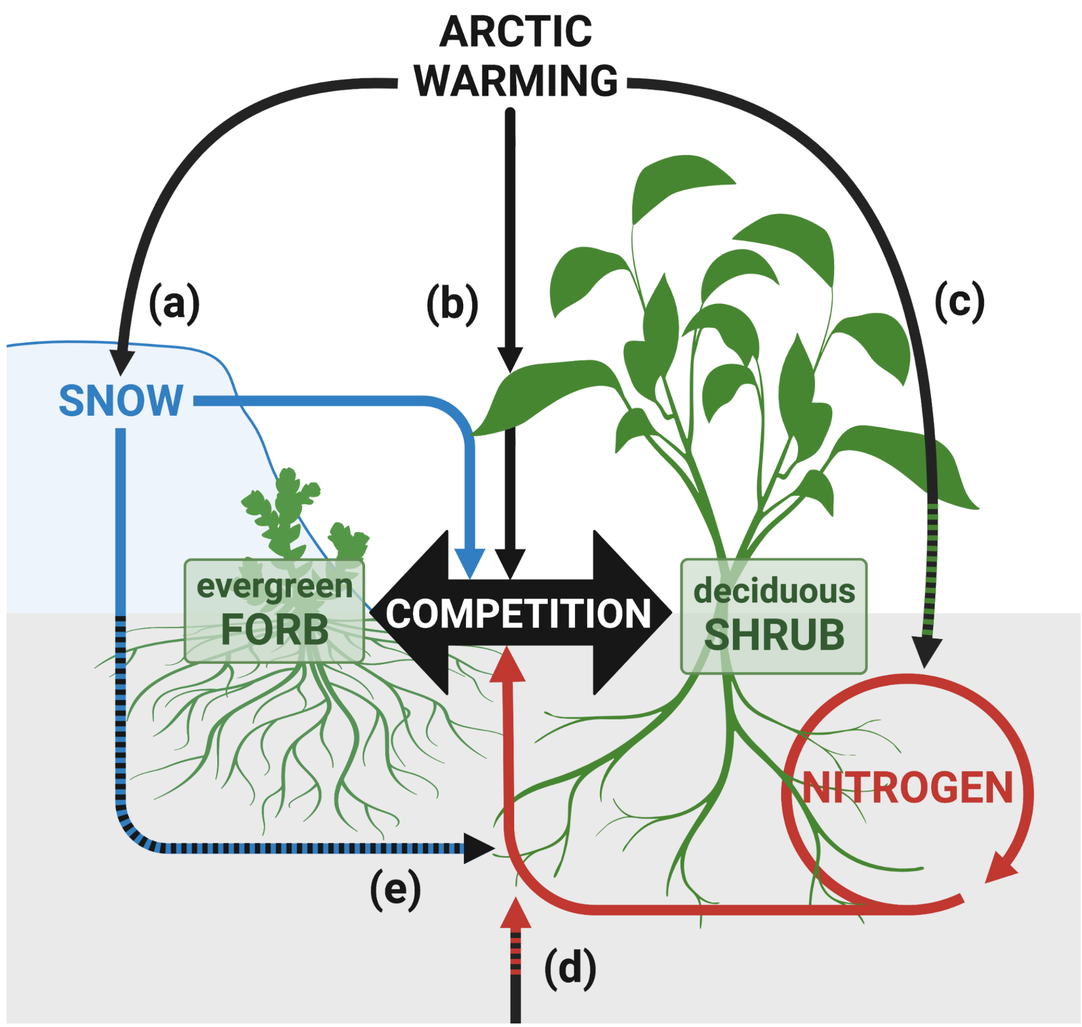
- via Analytical Results:
  - Expressions for predicting competitive outcome
  - Gain insight into relationship between traits & shifts in competitive outcome
- via Simulation:
  - Outcome of competition across simulations under different environmental conditions
  - Test varying the strength of mechanisms
  - Test against long-term data, locations across the Arctic

How did I build the model?

What limits Arctic plant growth?

- Light
- Soil resources
- Time above freezing

Mechanisms of Shrubification



Climate drivers act through **multiple pathways** to **<u>structure plant competition</u>** in Arctic ecosystems.

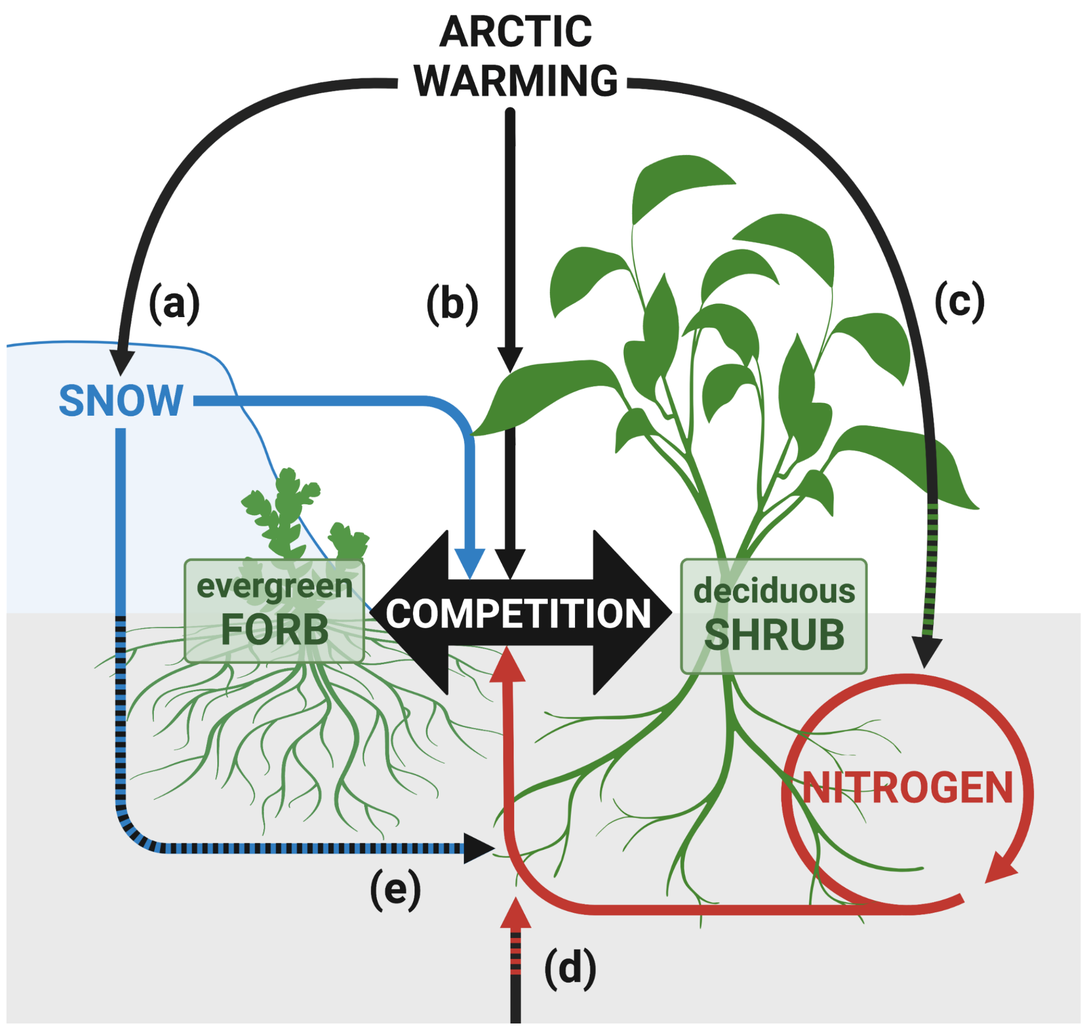
What limits Arctic plant growth?

- Light
- Soil resources
- Time above freezing

How do tundra species differ?

- Height (woody/non-woody)
- Leaf Habit (deciduous/evergreen)

Mechanisms of Shrubification



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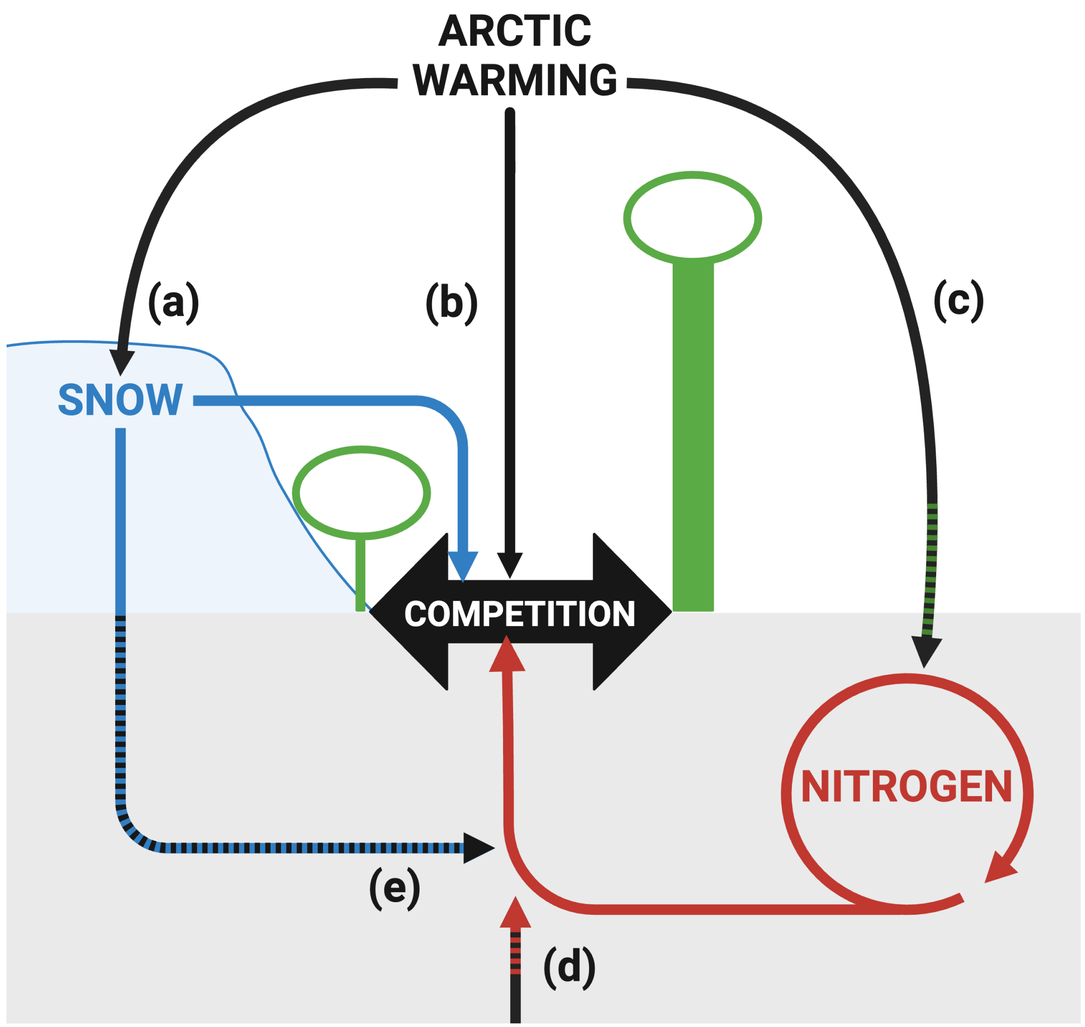
Model Questions

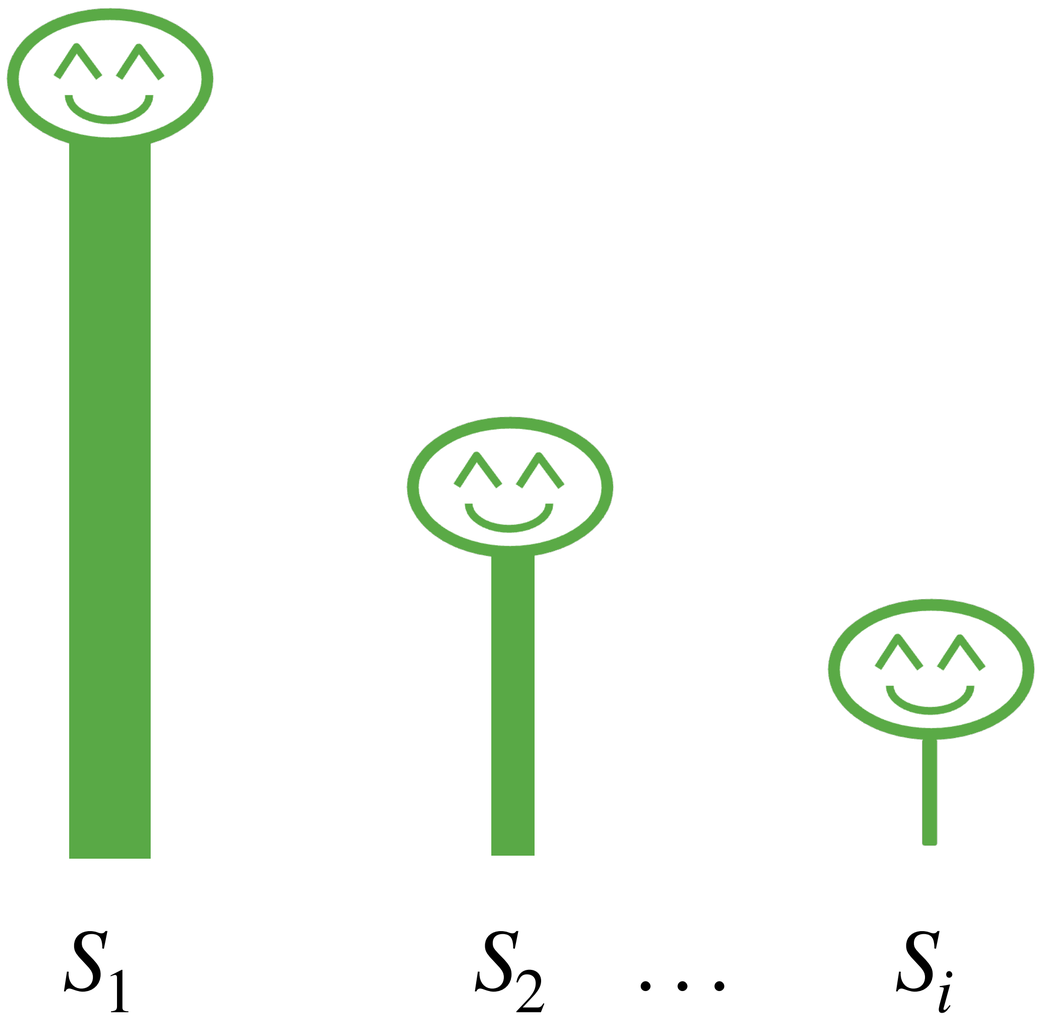
1. Under what conditions can a species persist?
2. Can multiple species coexist?
3. <u>What mechanism favors tall species with warming?</u>

mechanistic model



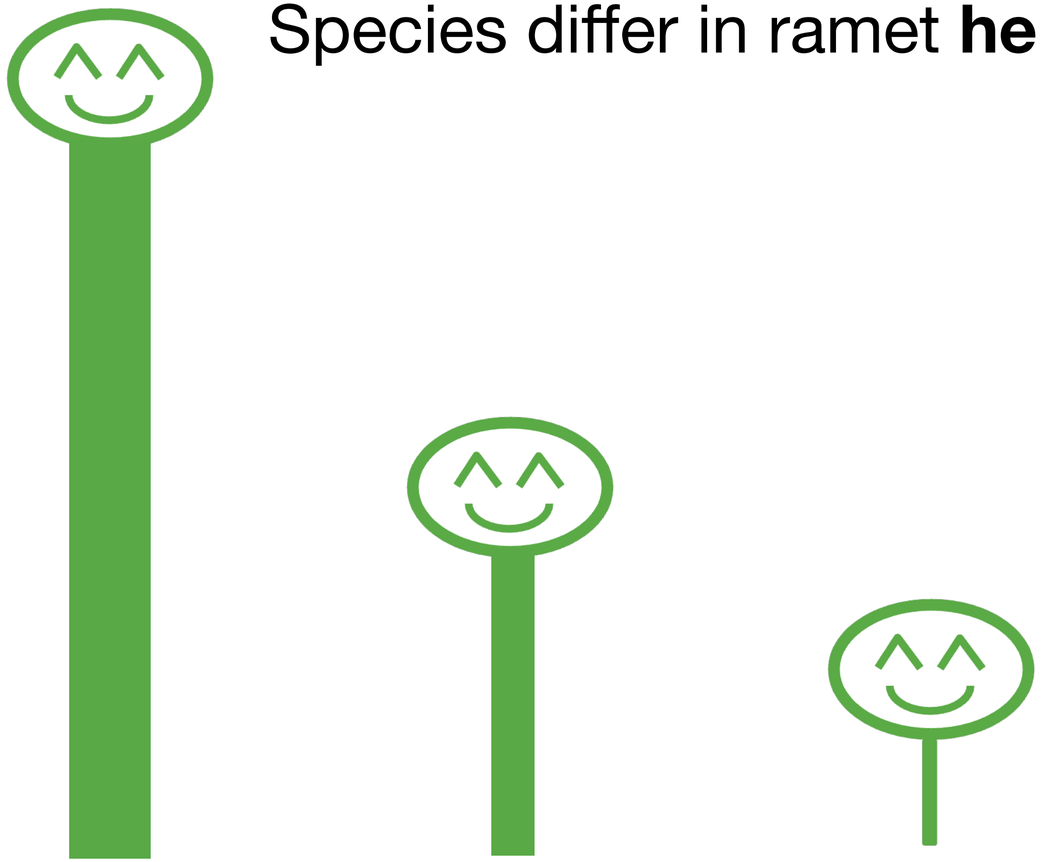
tundra ramet world

model | building tundra “plants”



model | tundra ramet world

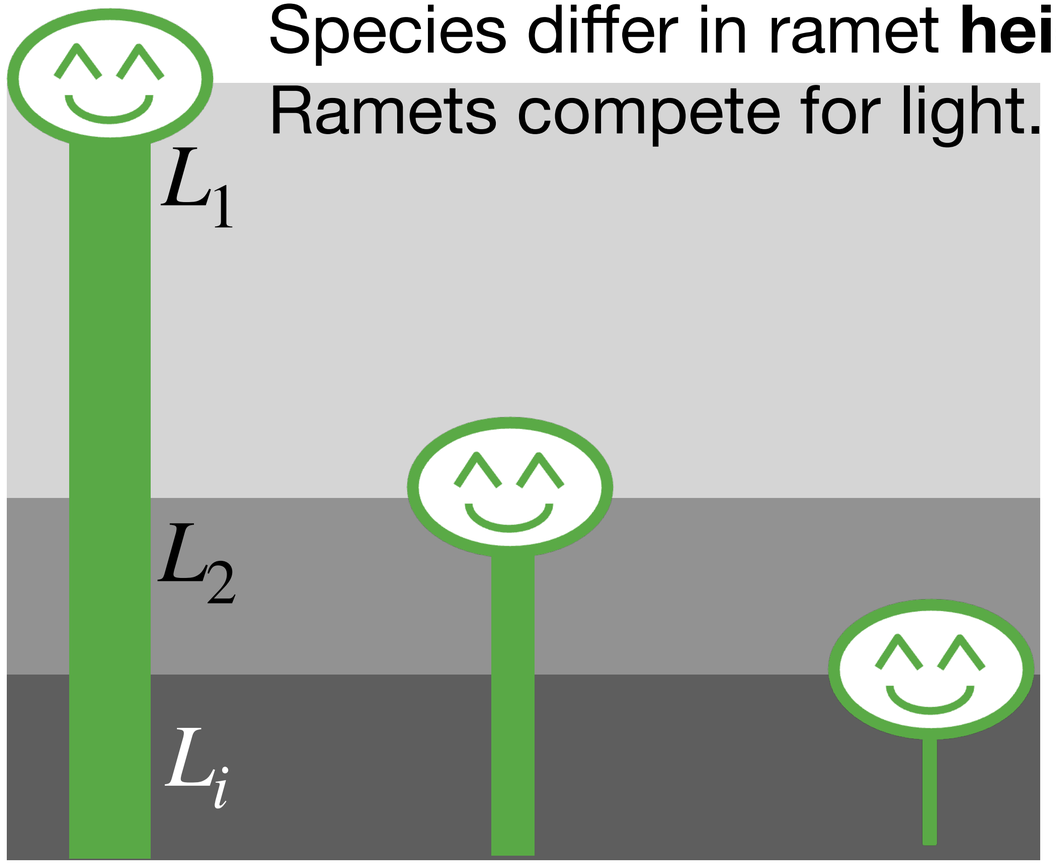
Species differ in ramet **height.**



$$H_1 > H_2 > \ldots H_i$$

model | tundra ramet world

Species differ in ramet **height.**
Ramets compete for light.



$$H_1 \quad > \quad H_2 \quad > \ldots H_i$$

LIGHT COMPETITION in a clonal ramet tundra world

Verbally, each species occupies one height H_i in the canopy

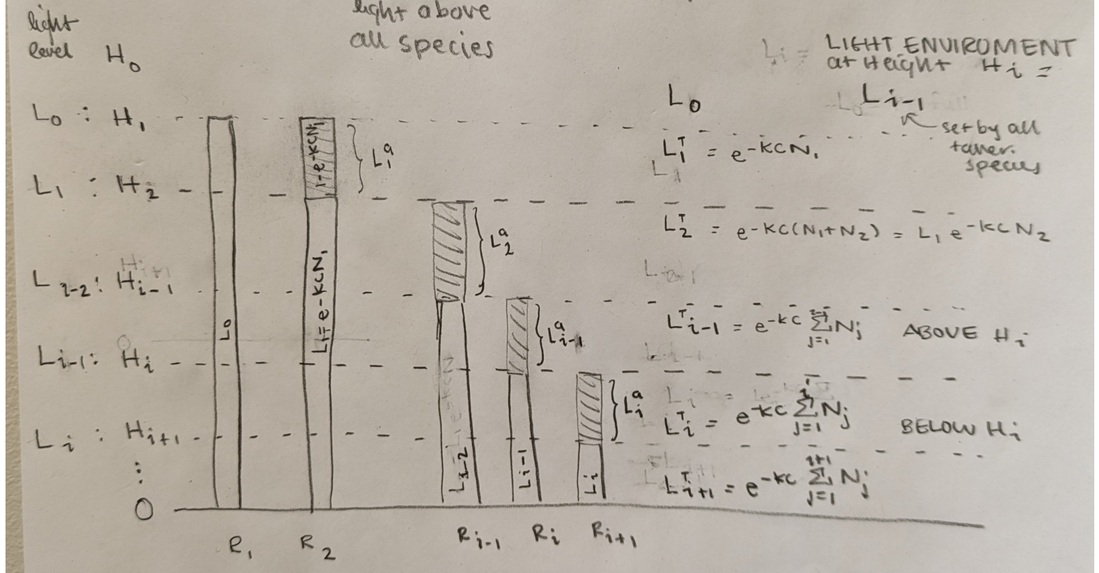
At the canopy height of species i, light is set by the number of ramets of taller species.

Light available decays through the canopy based on Beer's law

$$L(h) = L_0 e^{-k}$$ (layers of leaf light must get through)

L_0: light above all species

k: extinction coefficient



LIGHT ENVIROMENT at Height H_i = L_{i-1} ← set by all taller species

$L_1^T = e^{-kcN_1}$

$L_2^T = e^{-kc(N_1+N_2)} = L_1 e^{-kcN_2}$

$L_{i-1}^T = e^{-kc\sum_{j=1}^{i-1} N_j}$ ABOVE H_i

$L_i^T = e^{-kc\sum_{j=1}^{i} N_j}$ BELOW H_i

$L_{i+1}^T = e^{-kc\sum_{j=1}^{i+1} N_j}$

Def$^{\underline{ns}}$:

L_i^T is the light available directly BENEATH the canopy of sp. i

It is the value you would measure with a radiometer or light wand.

L_{i-1} is the light available AT THE TOP OF CANOPY i, i.e. the light level that is available to sp. i

$L_i^a = L_{i-1} - L_i$ = the light ABSORBED by CANOPY i

$= e^{-kc\sum_{j=1}^{i-1} N_j} - e^{-kc\sum_{j=1}^{i} N_j} = e^{-kc\sum_{j=1}^{i-1} N_j}(1 - e^{-kcN_i})$

L_{R_i} = the light experienced by ramet of sp i

• light available per ramet L_i^R of species i

The light that each ramet of sp i gets depends on

1) the light that reaches canopy i, L_{i-1}

2) the size of canopy i, how much light all the ramets of species i catch $(1 - e^{-kcN_i})$

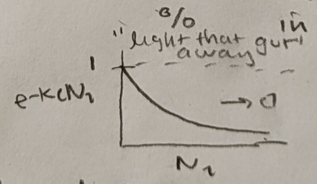
3) how i.e. are there big gaps in the canopy?

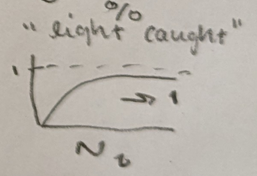
3) how many ways the ramets need to share the captured light N_i

$$L_i^R = \frac{L_i^a}{N_i} = \frac{L_{i-1}(1 - \overbrace{e^{-kcN_i}}^{\text{"the light that got away"}})}{N_i}$$

L_i^a: light absorbed by canopy i divided among the ramets equally

N_i: negative density dependence through "self-shading" which is more like "self-sharing" in this case

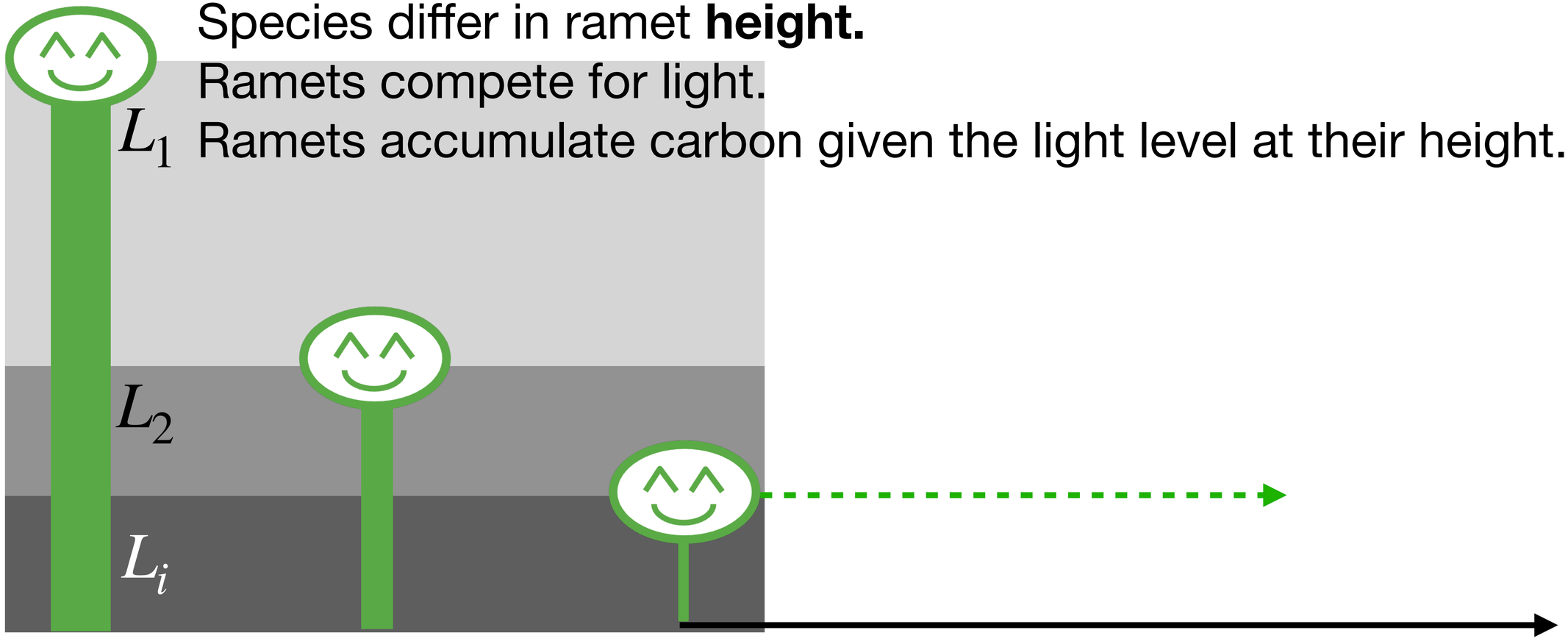




The light pool is shared among ramets, which are connected. They each get a "piece of the light", s.t. larger total leaf area cN_i is GOOD as more light is caught but N_i increasing also subdivides the pool more

model | tundra ramet world

Species differ in ramet **height.**
Ramets compete for light.
Ramets accumulate carbon given the light level at their height.



$$H_1 > H_2 > \ldots H_i$$

model | tundra ramet world

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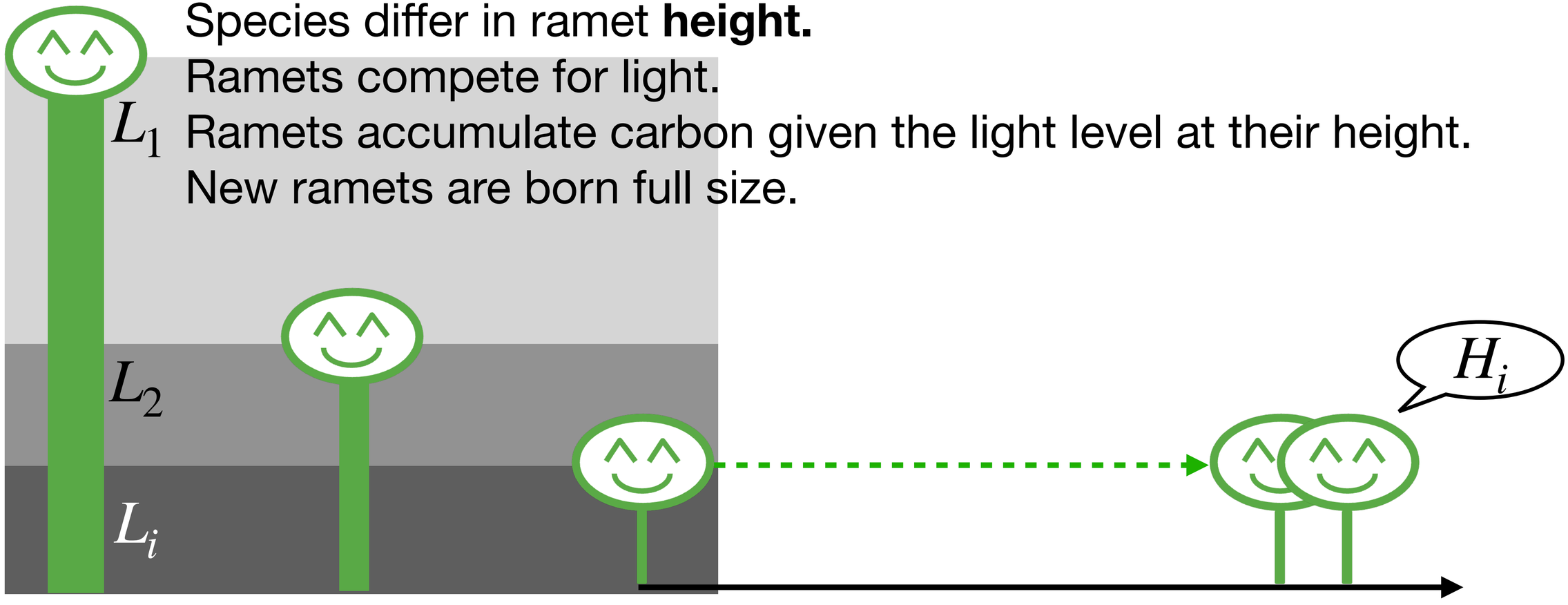
New ramets are born full size.



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Species differ in ramet **height.**
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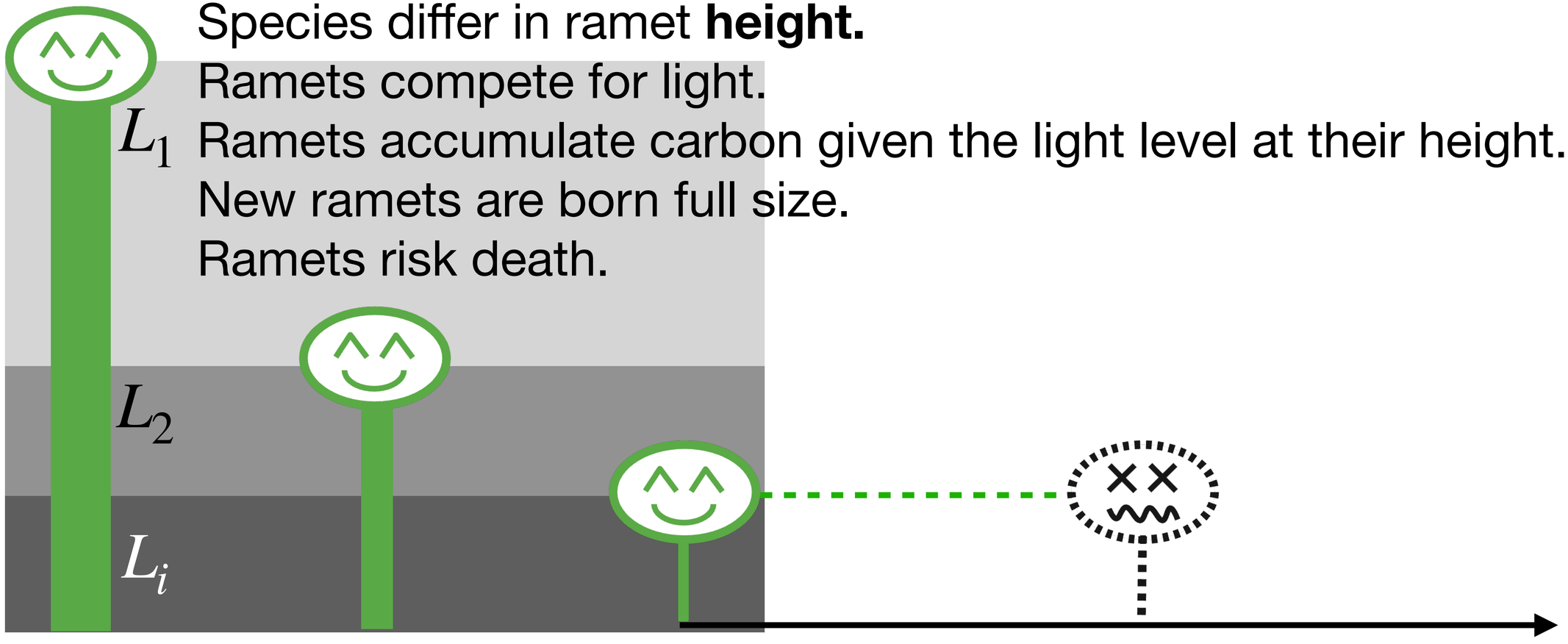
New ramets are born full size.
Ramets risk death.



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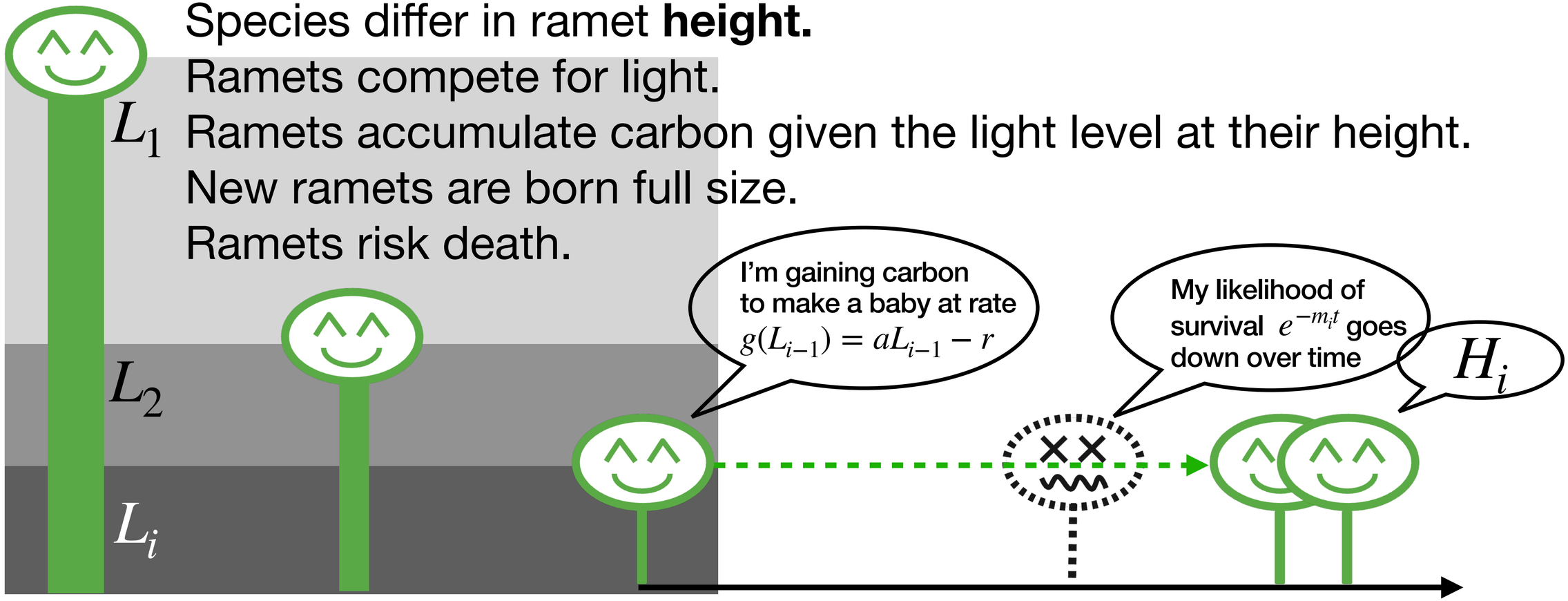


$$H_1 > H_2 > \ldots H_i$$

Model Description

State Variables x_i, density of species i

Species Description $H_1 > H_2 > \cdots > H_j > \cdots > H_Q$, $i = 1,...,Q$

Individual Allometry $B_i = bH_i^{\beta}$, $C_i = C_j = c \forall i, j,$

Individual Physiology $g_i(L_{R_i}) = A(L_{R_i}) - r,$ for now $A(L) = aL$

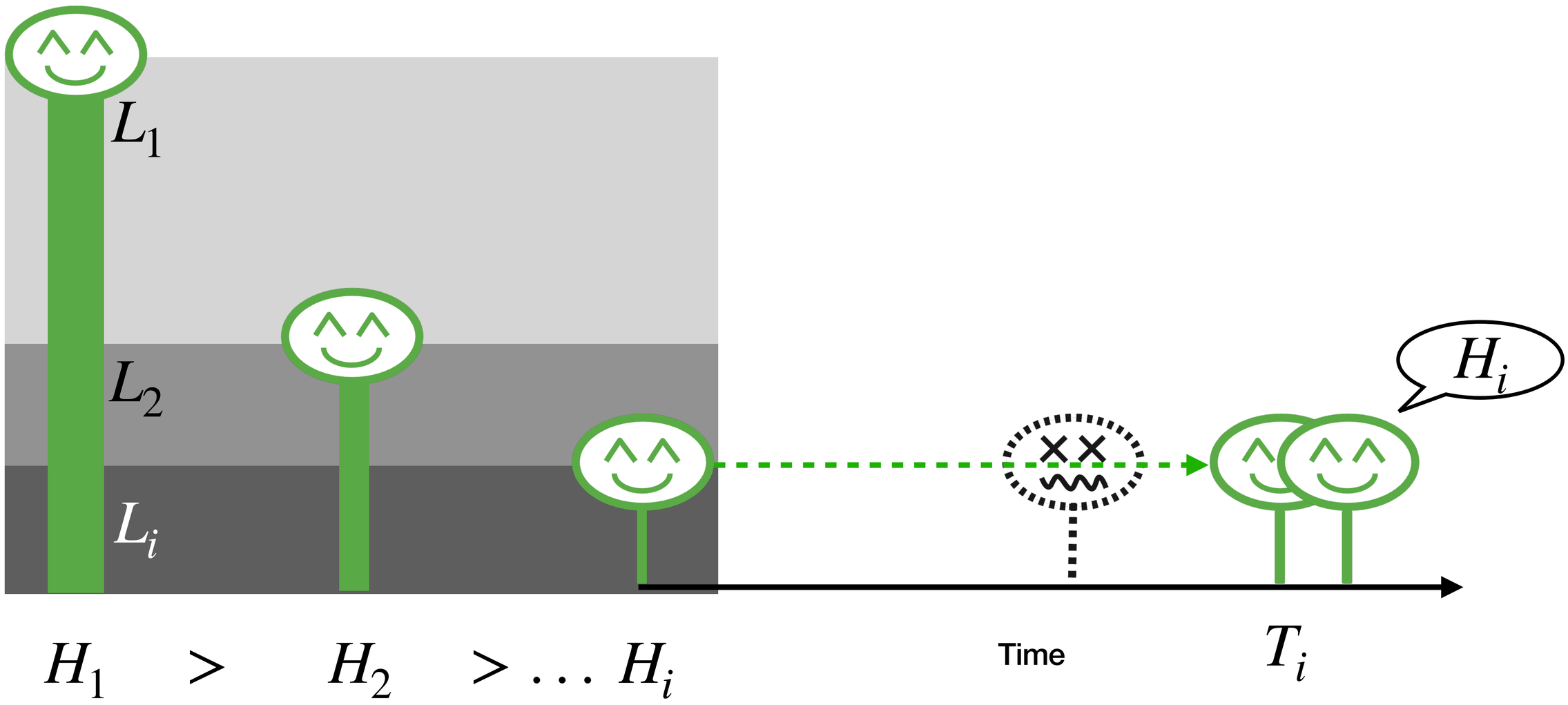
Light Competition $$L_{R_i} = \frac{L_0 e^{-kc\sum_{j=1}^{i-1} x_j}(1 - e^{-kcx_i})}{x_i}$$

Population* Demography $$f_i = \frac{g_i(L_{R_i})}{B_i}, m_i = m_j = m \forall i, j$$

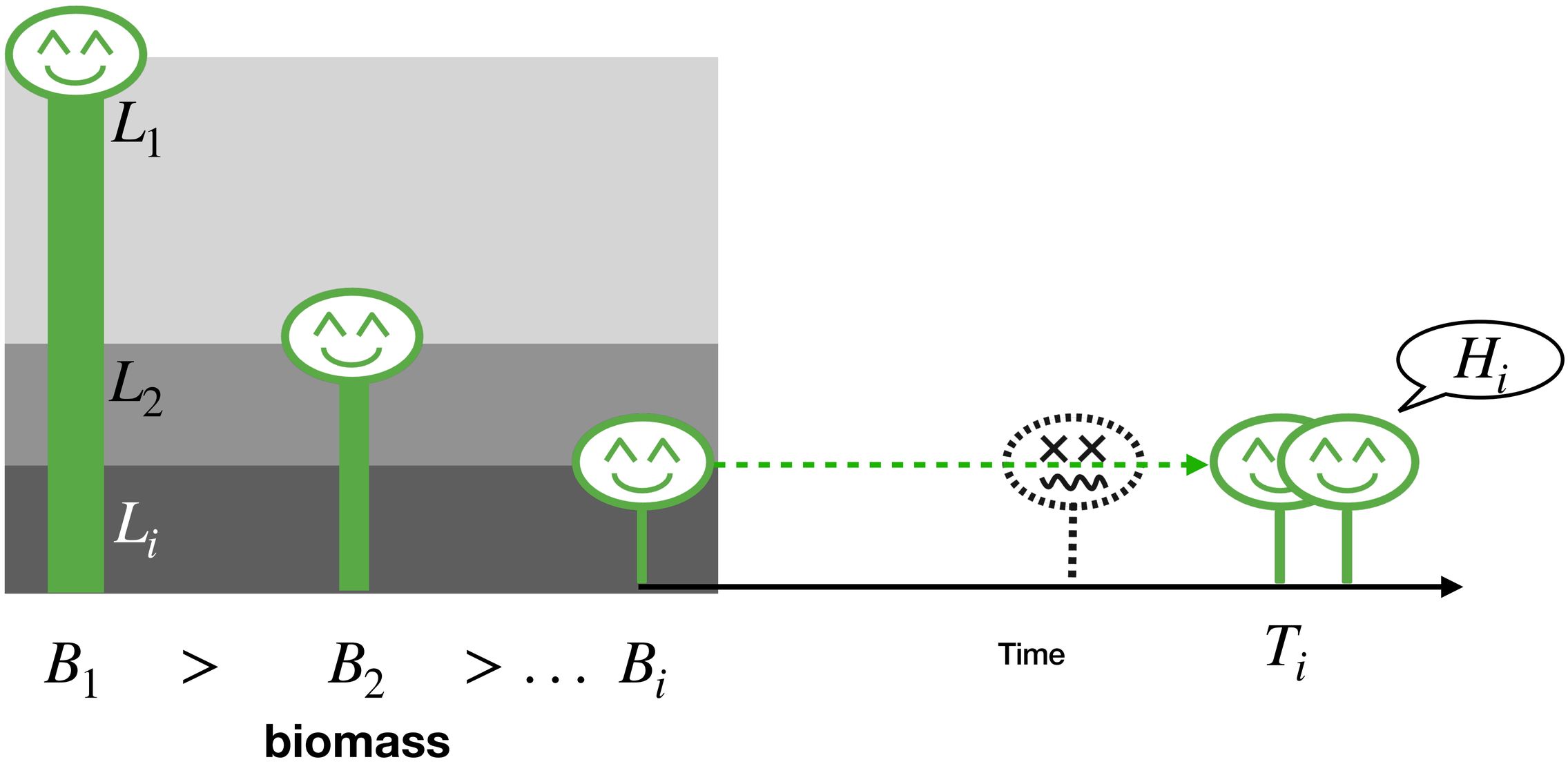
Population Dynamics $$\frac{dx_i}{dt} = f_i x_i - m x_i = (f_i - m)x_i$$

Preliminary Results

model | 1. Under what conditions can a species persist?



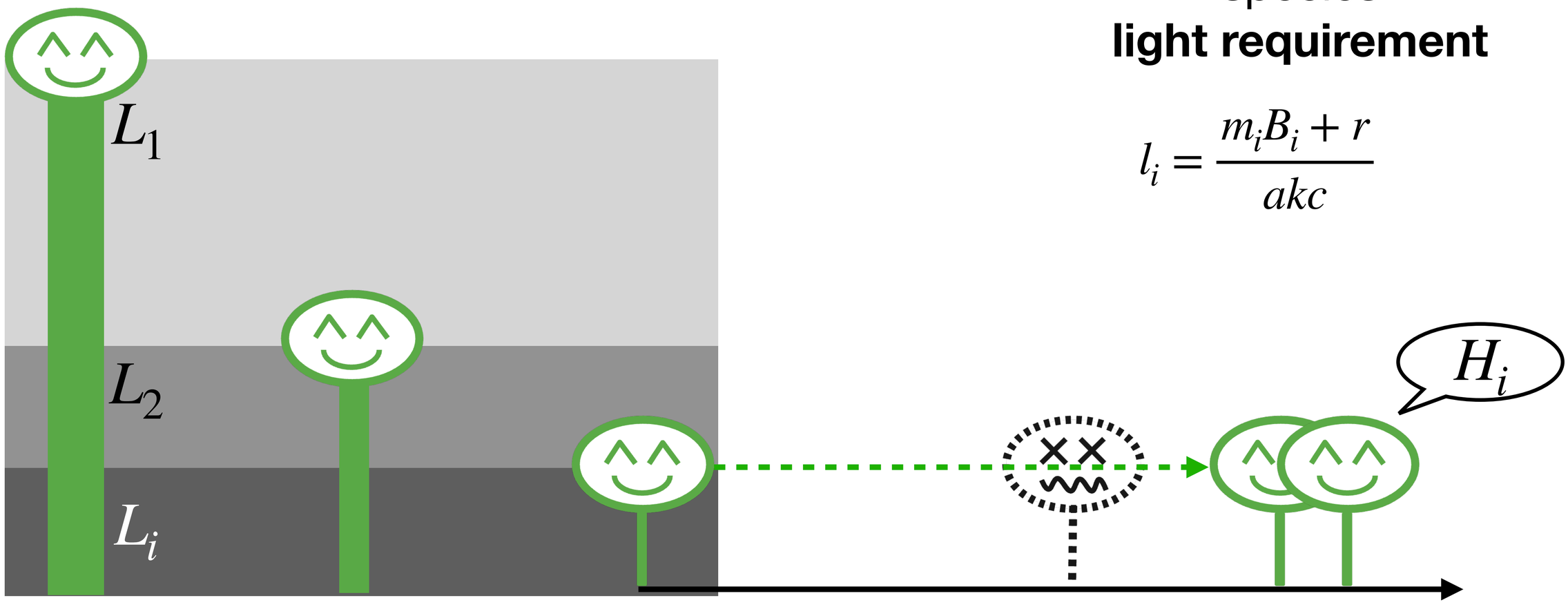
model | 1. Under what conditions can a species persist?



model | 1. Under what conditions can a species persist?

species
light requirement

$$l_i = \frac{m_i B_i + r}{akc}$$



$l_1 > l_2 > \ldots l_i$

light requirement

model | 1. Under what conditions can a species persist?

species
light received

$$L_{i-1} = e^{-kc \sum_{j \le i-1} X_j}$$

species
light requirement

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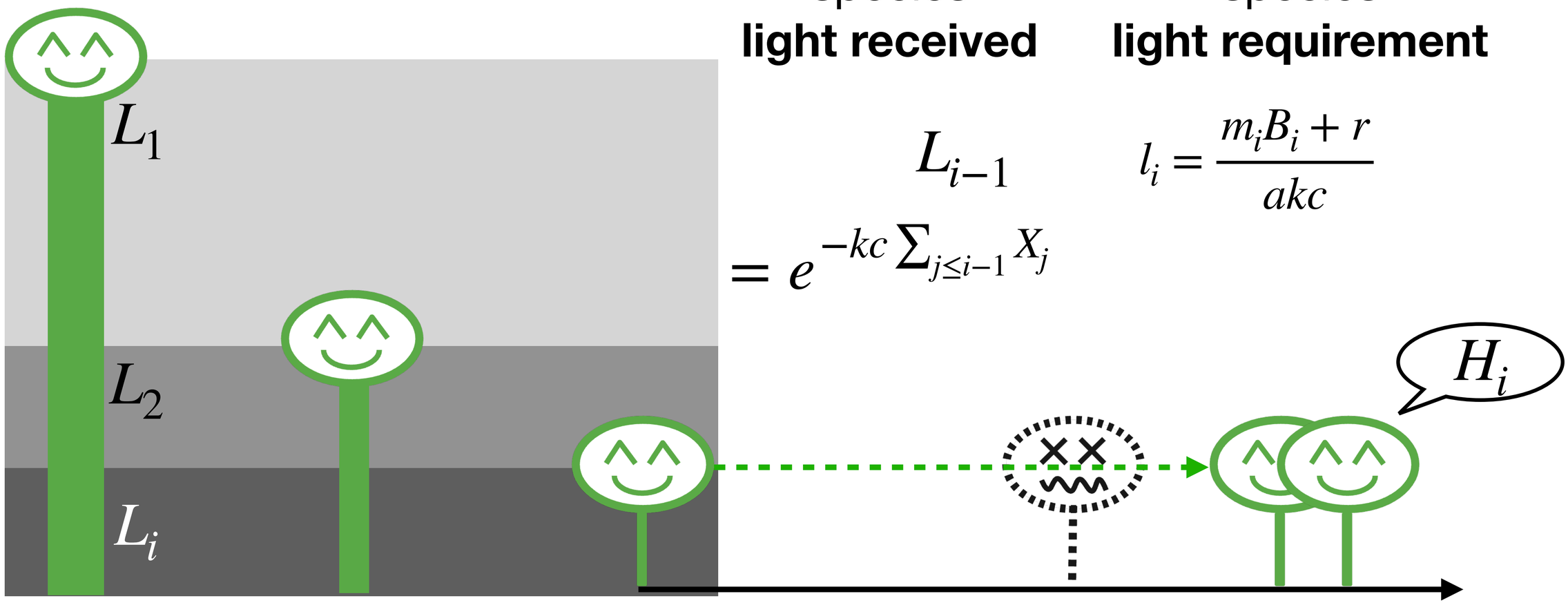


$$l_1 > l_2 > \ldots l_i$$

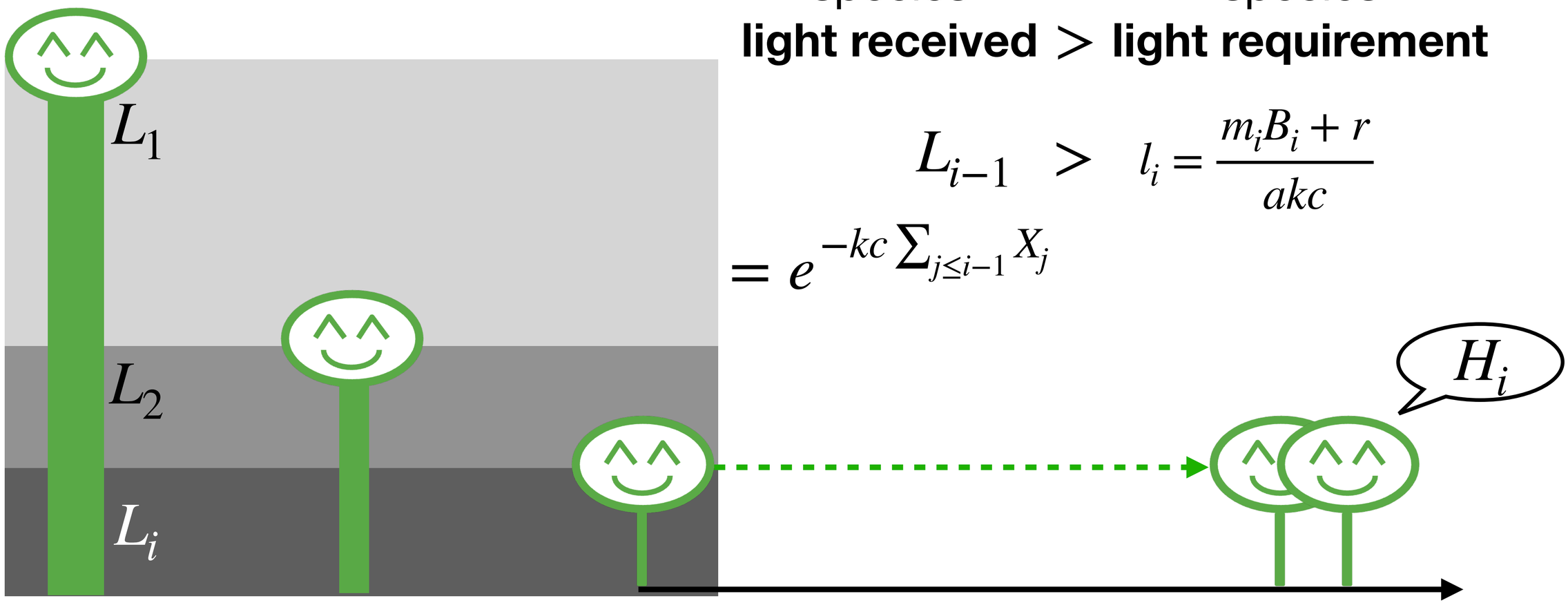
light requirement

model | 1. Under what conditions can a species persist?

species **light received** > species **light requirement**

$$L_{i-1} \quad > \quad l_i = \frac{m_i B_i + r}{akc}$$

$$= e^{-kc \sum_{j \le i-1} X_j}$$

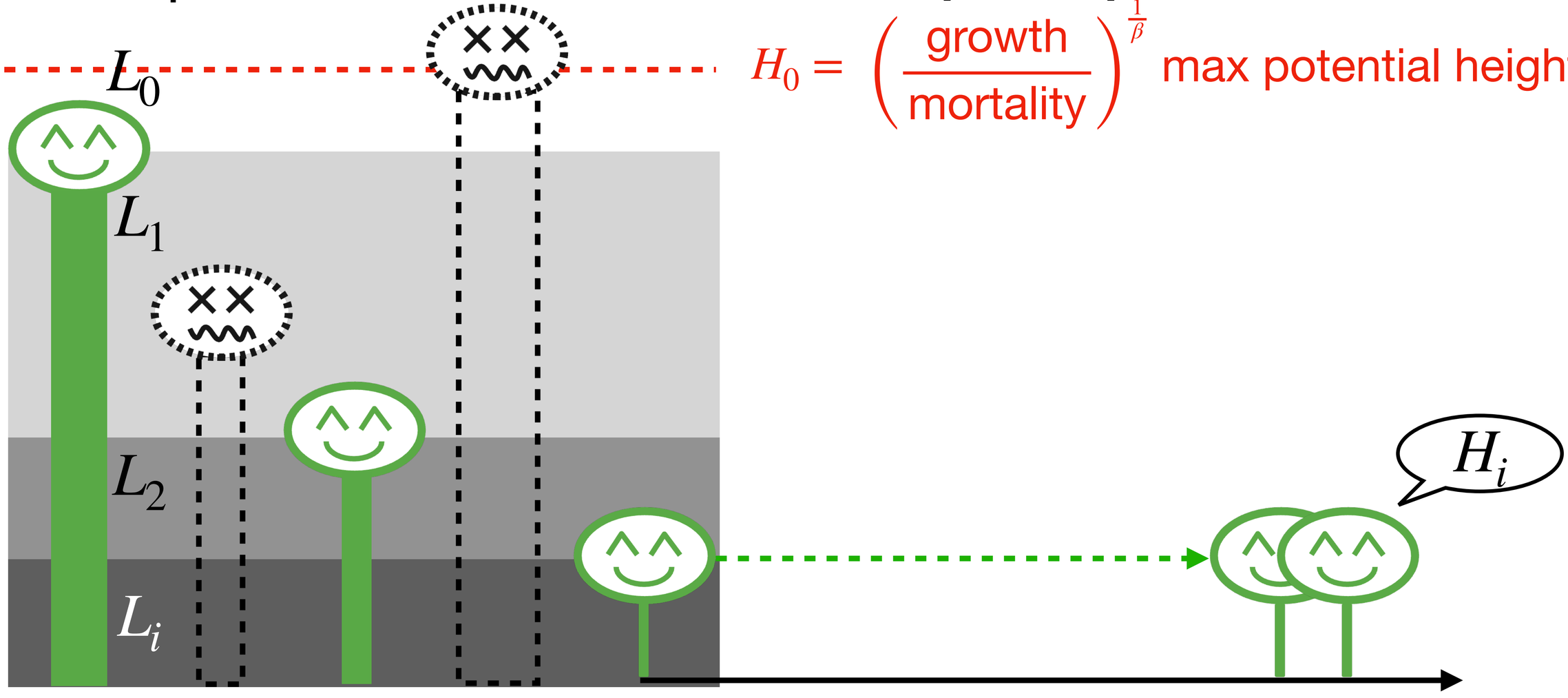


$$l_1 \quad > \quad l_2 \quad > \ldots \quad l_i$$

light requirement

model | 1. Under what conditions can a species persist?

$$H_0 = \left(\frac{\text{growth}}{\text{mortality}}\right)^{\frac{1}{\beta}}$$ max potential height



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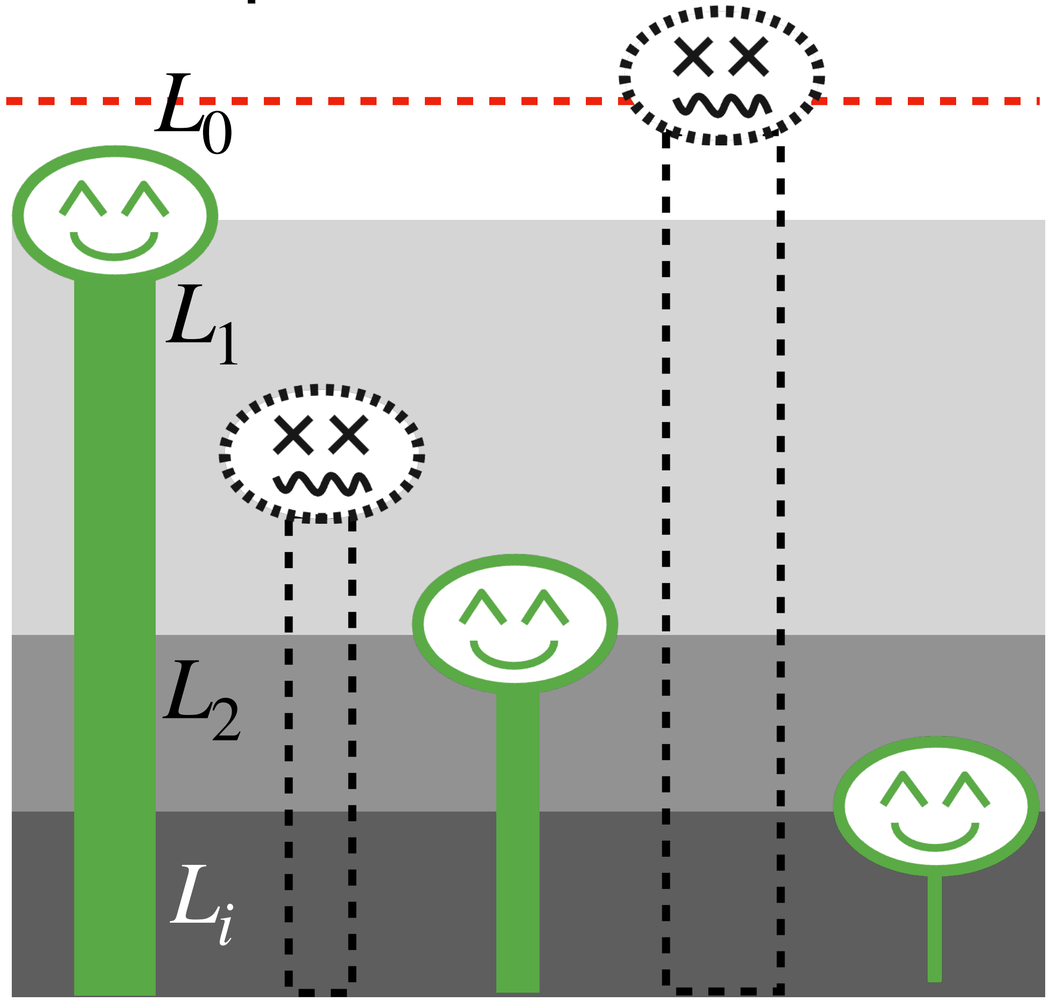

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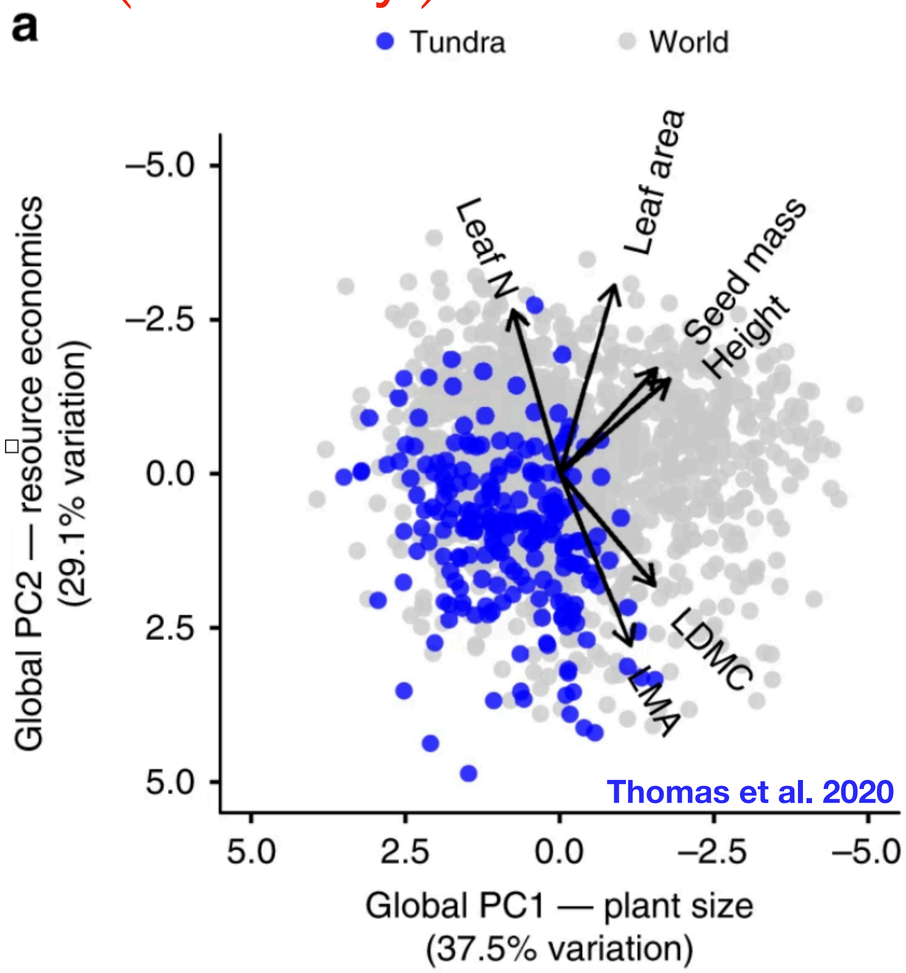
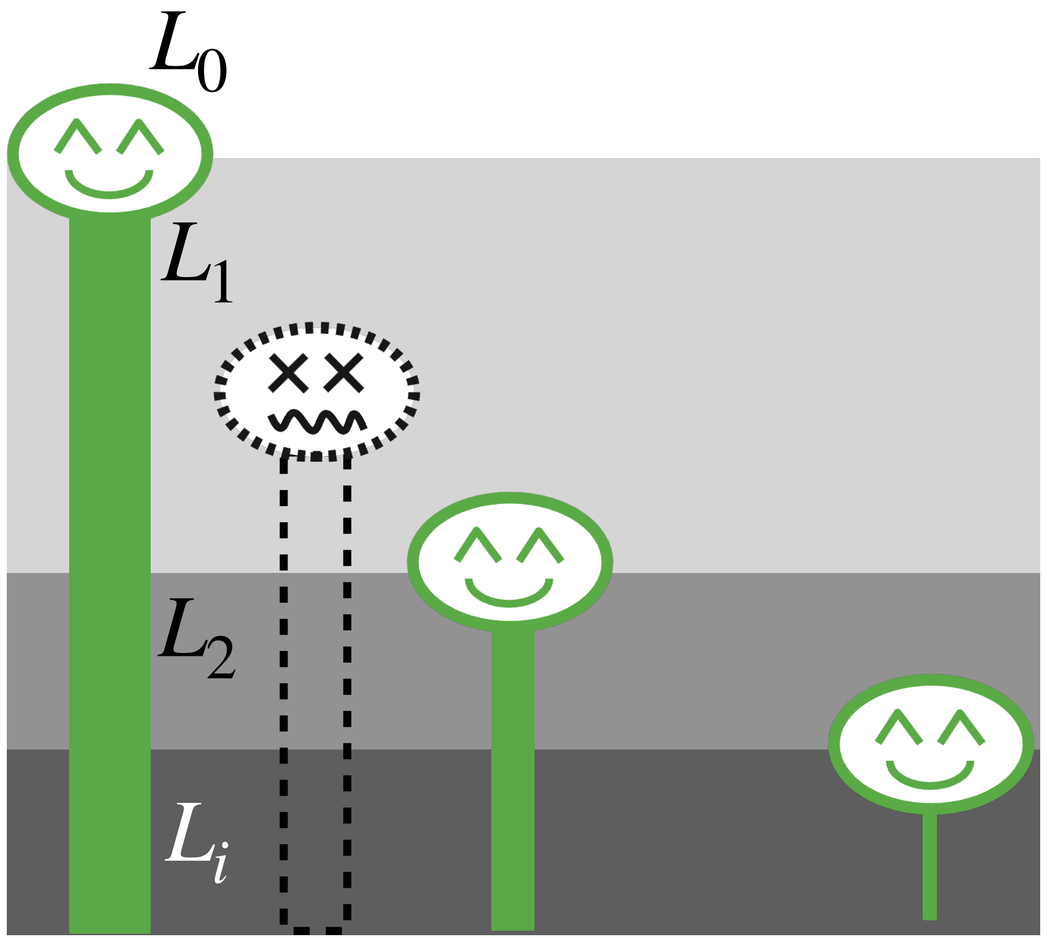


model | 2. can multiple species coexist?



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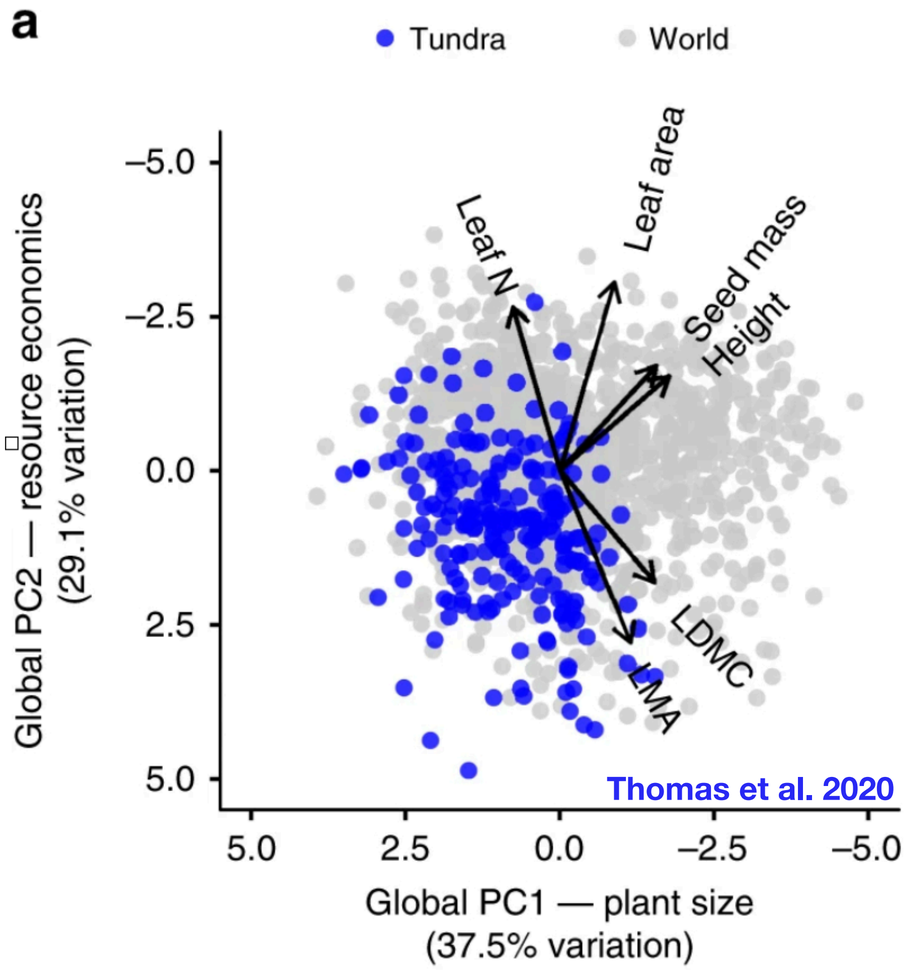


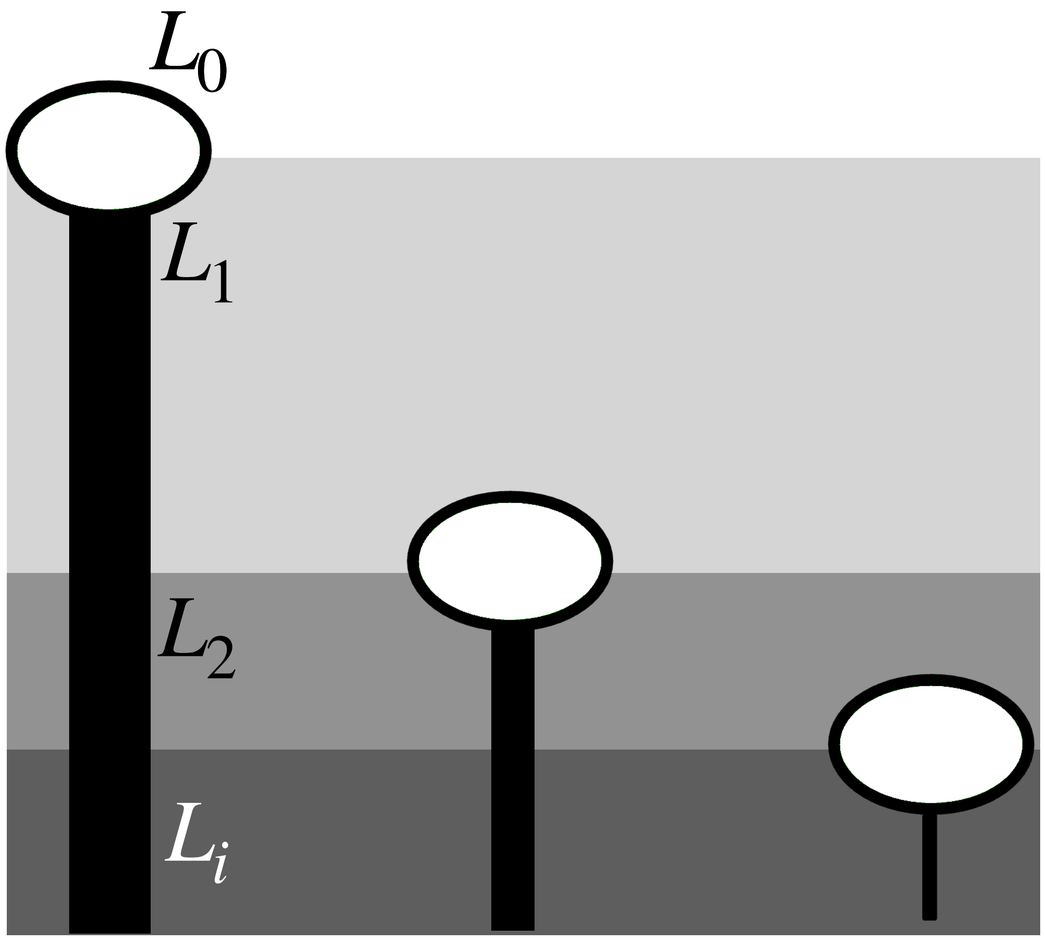
Implicit Equilibrium Solution (LRS = 1)

$$L_{i-1}(1 - e^{-k\hat{x}_i}) - kl_i\hat{x}_i = 0$$

Numerical Solutions

1. Select traits $\{l_1, l_2, \ldots, l_i\}$
2. Solve first species eq. density. $\hat{x}_1$
3. Set light level below species 1. $L_1 = L_0 e^{-k\hat{x}_1}$
4. Solve second species eq. density $\hat{x}_2 = f(L_1, \hat{x}_2)$
5. Set light level below species 2, $L_2 = L_0 e^{-k(\hat{x}_1 + \hat{x}_2)}$
6. etc.

model | 2. can multiple species coexist?



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light requirement

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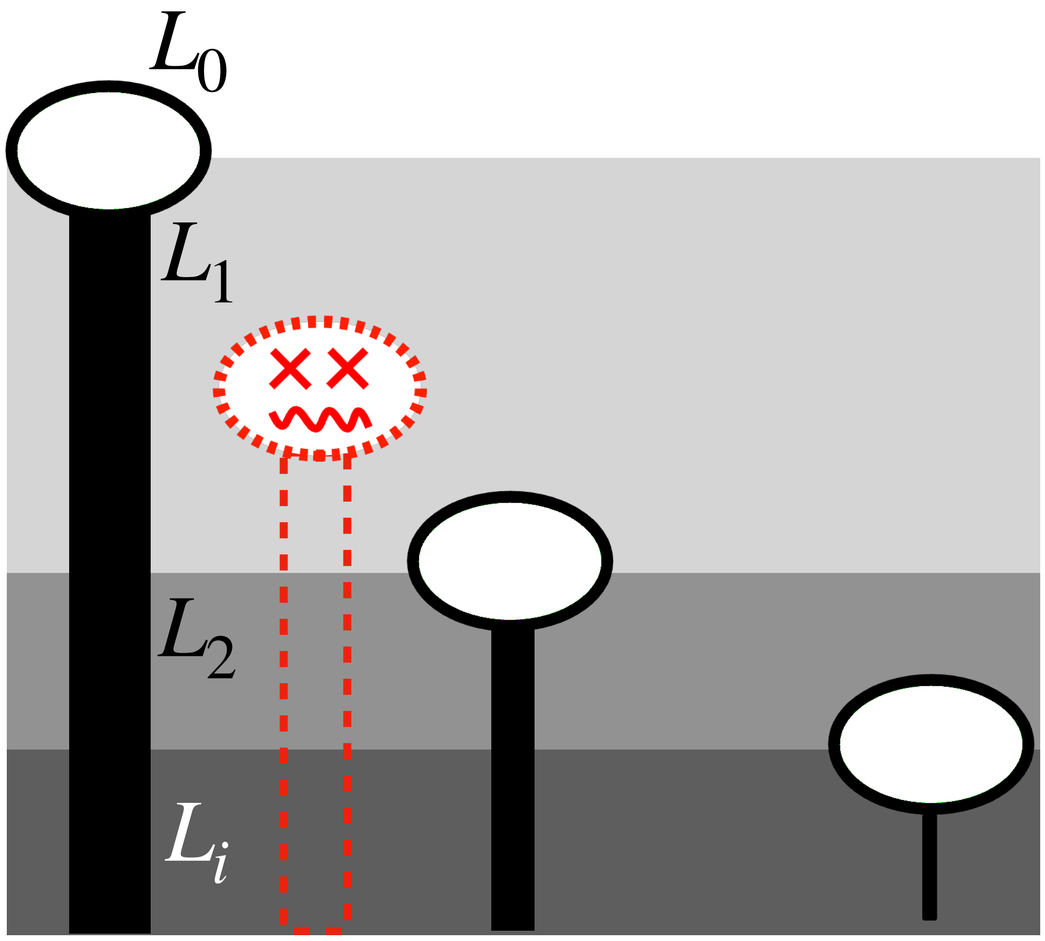

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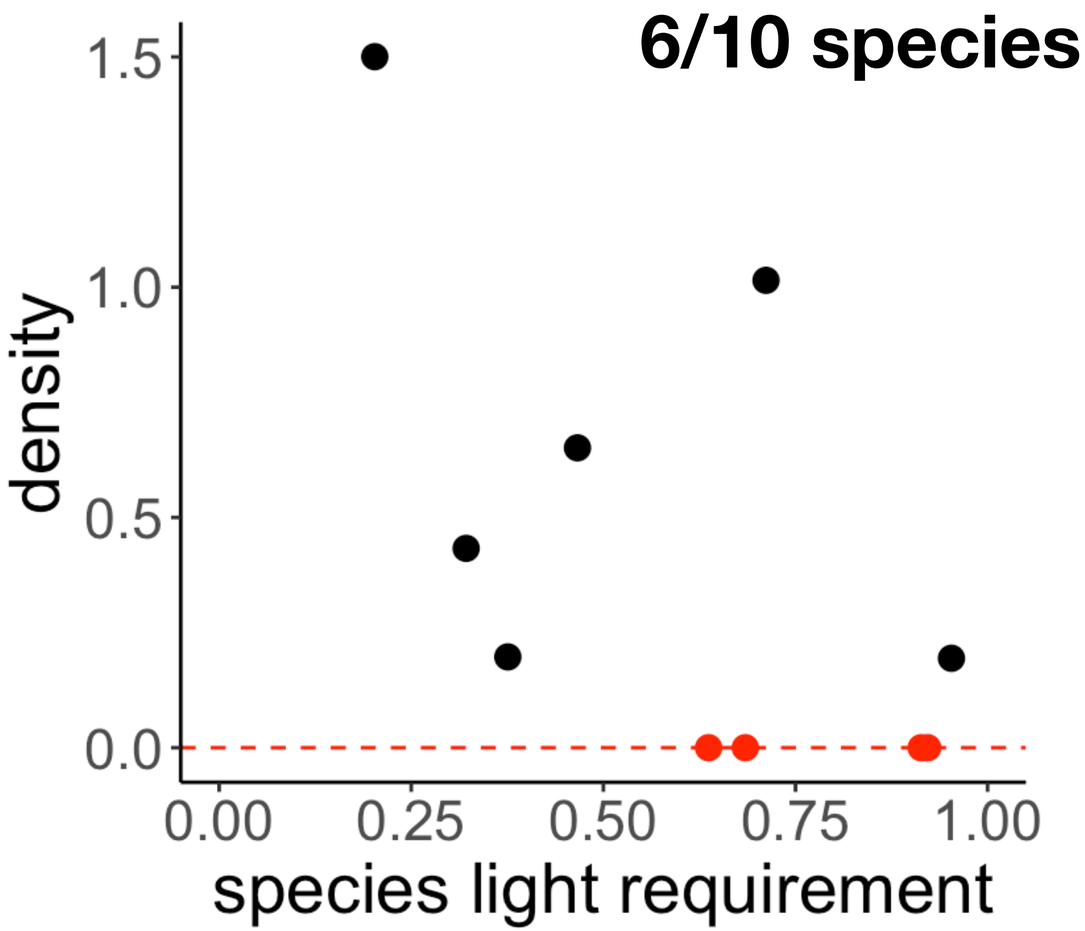

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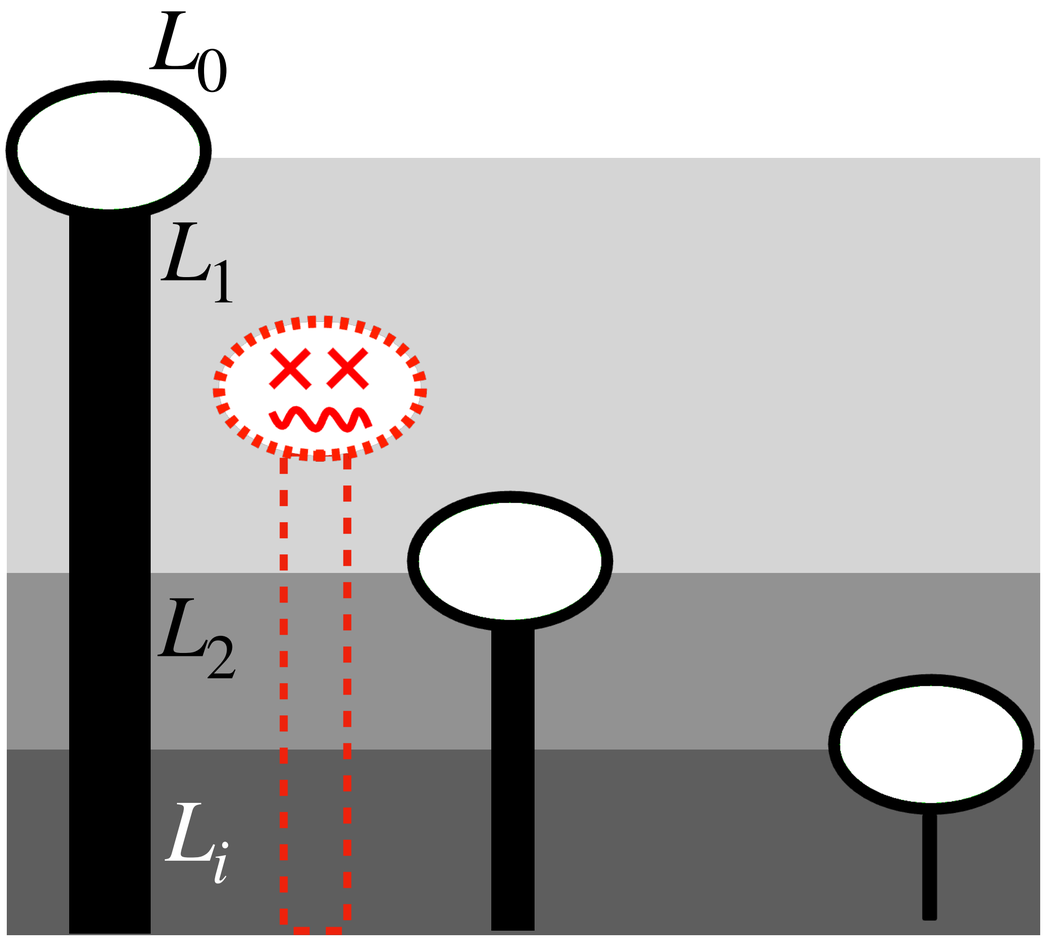

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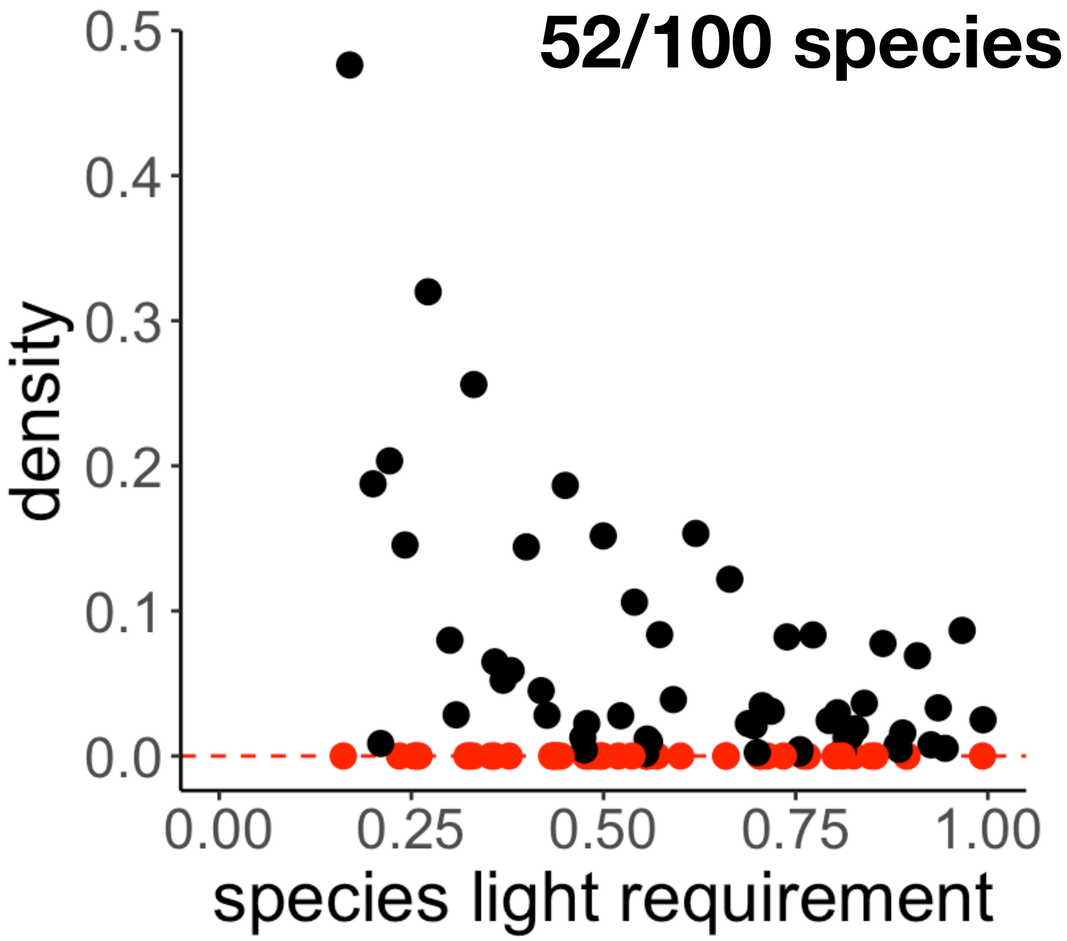
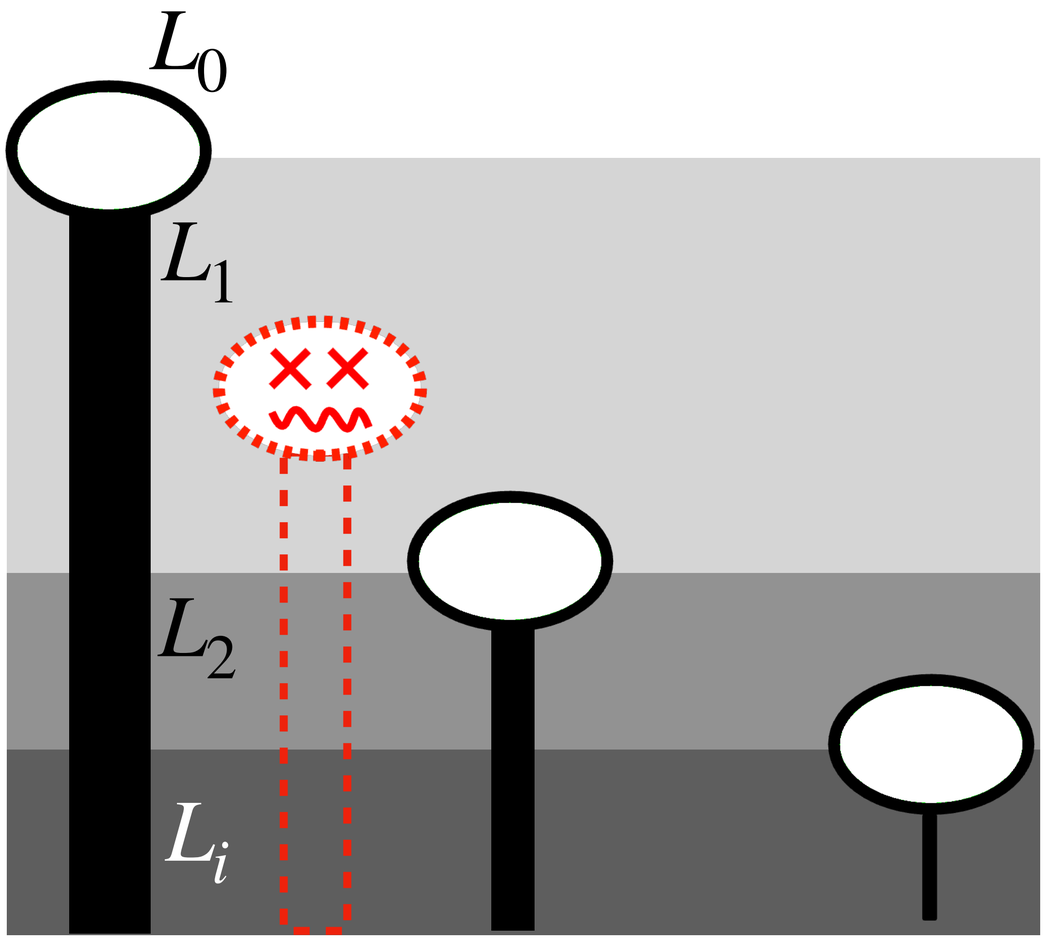


model | 3. what mechanism favors tall species with warming?



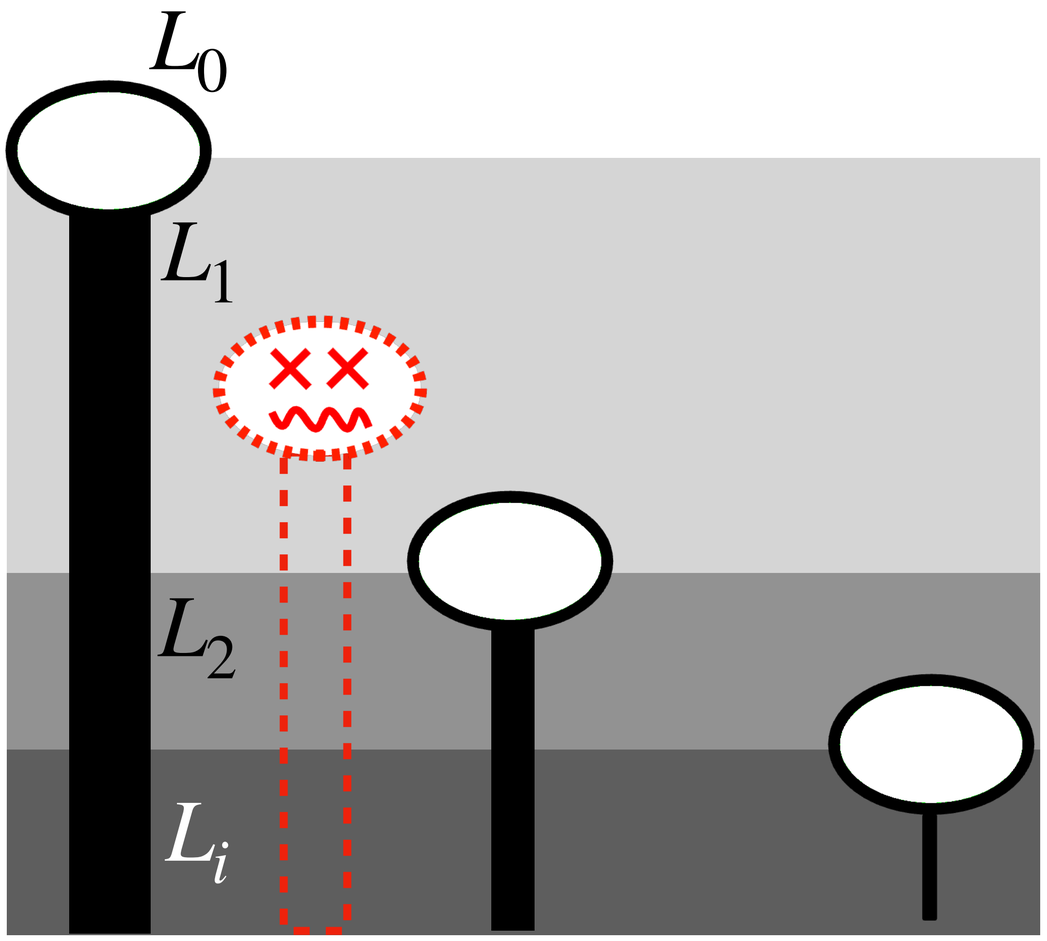
$l_1 > l_2 > \ldots l_i$

light requirement

max height: $\uparrow H_0 = \left(\frac{\text{growth}\uparrow}{\text{mortality}} \right)^{\frac{1}{\beta}}$

eq. density: $\uparrow X_i \approx \frac{2(L_{i-1} - l_i)\downarrow}{kL_{i-1}}$

model | 3. what mechanism favors tall species with warming?



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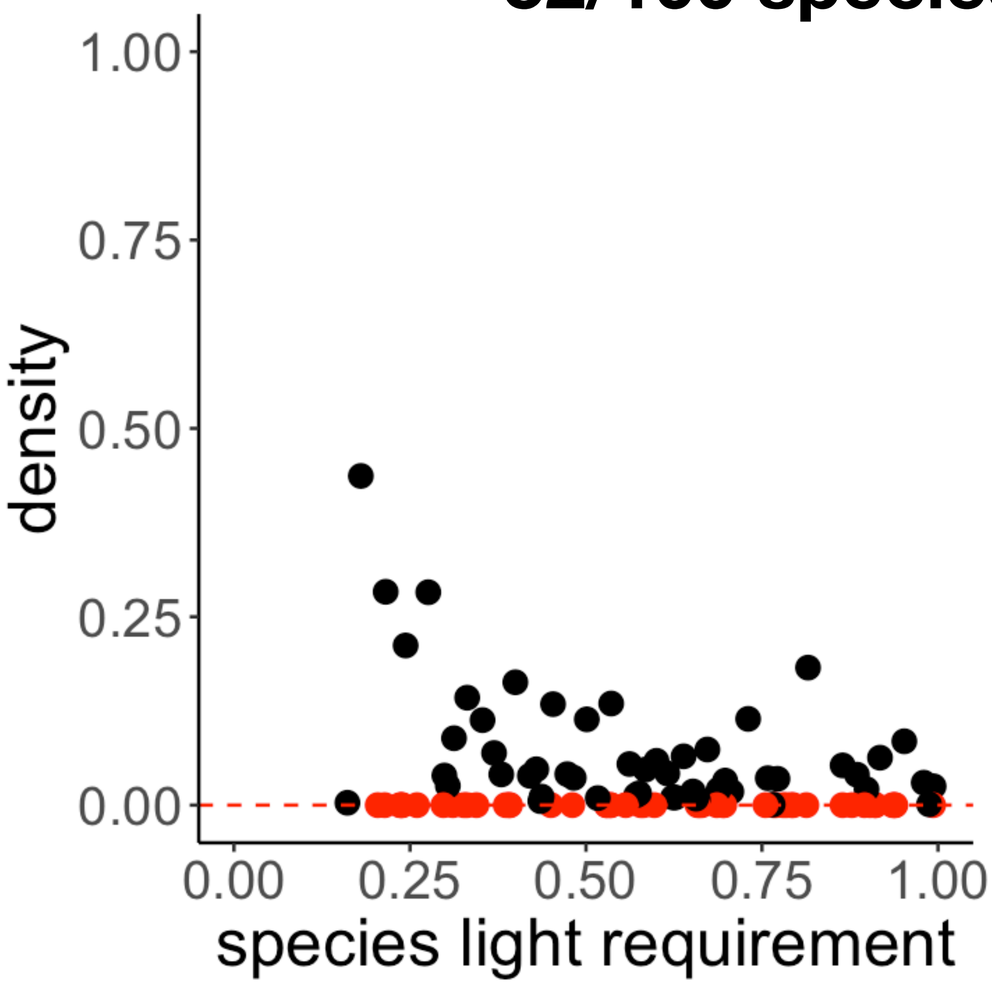
light requirement

52/100 species



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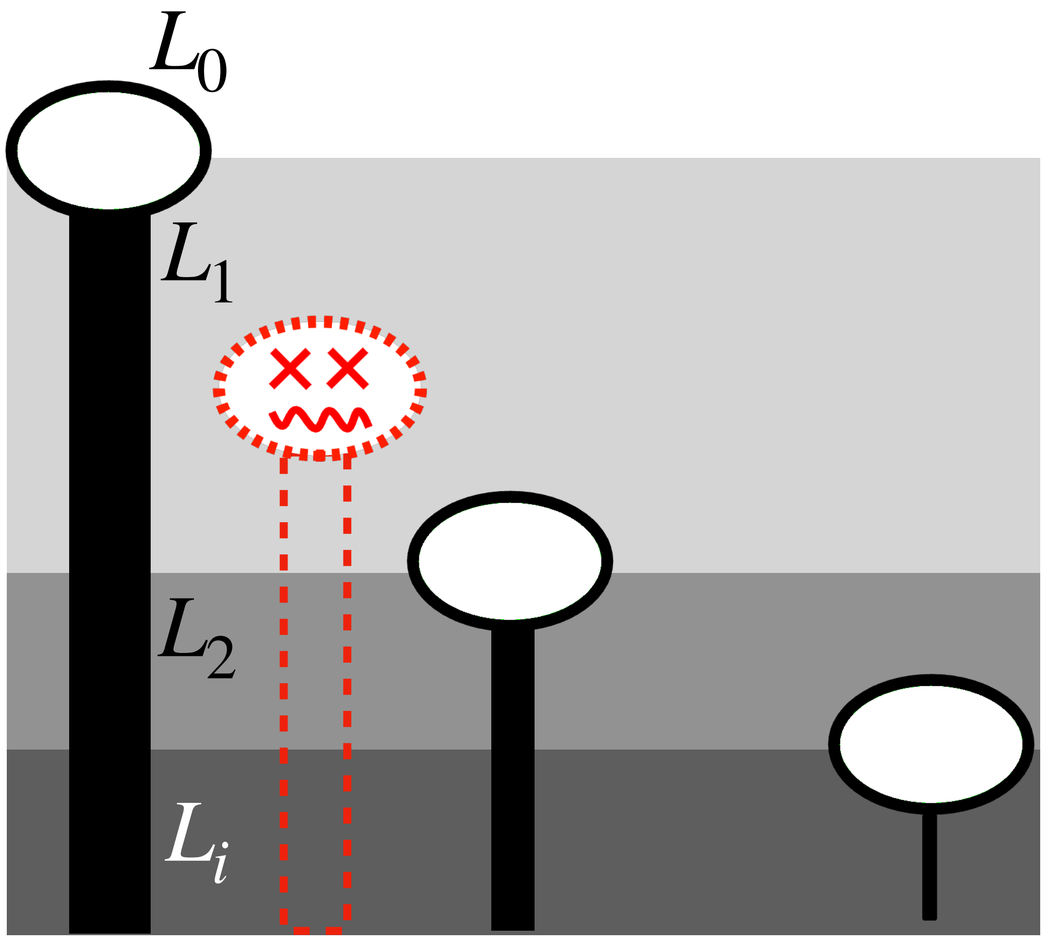

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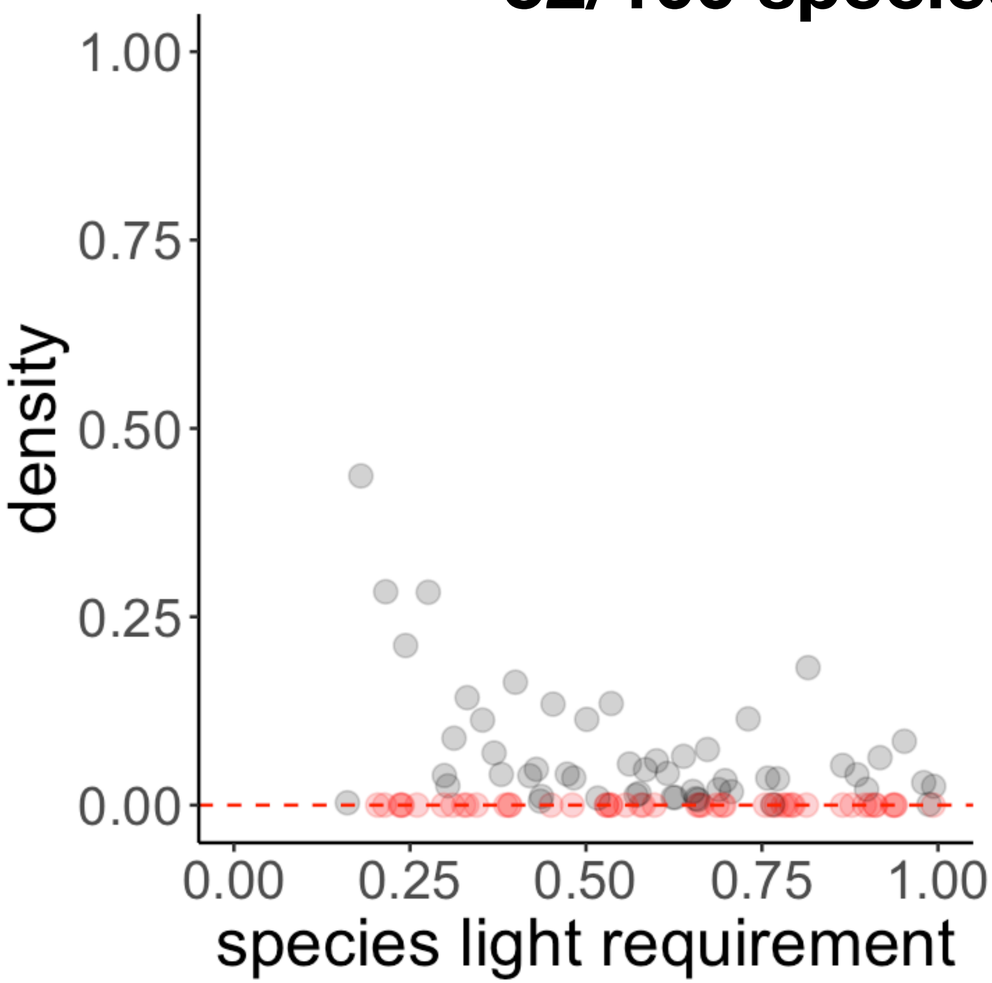

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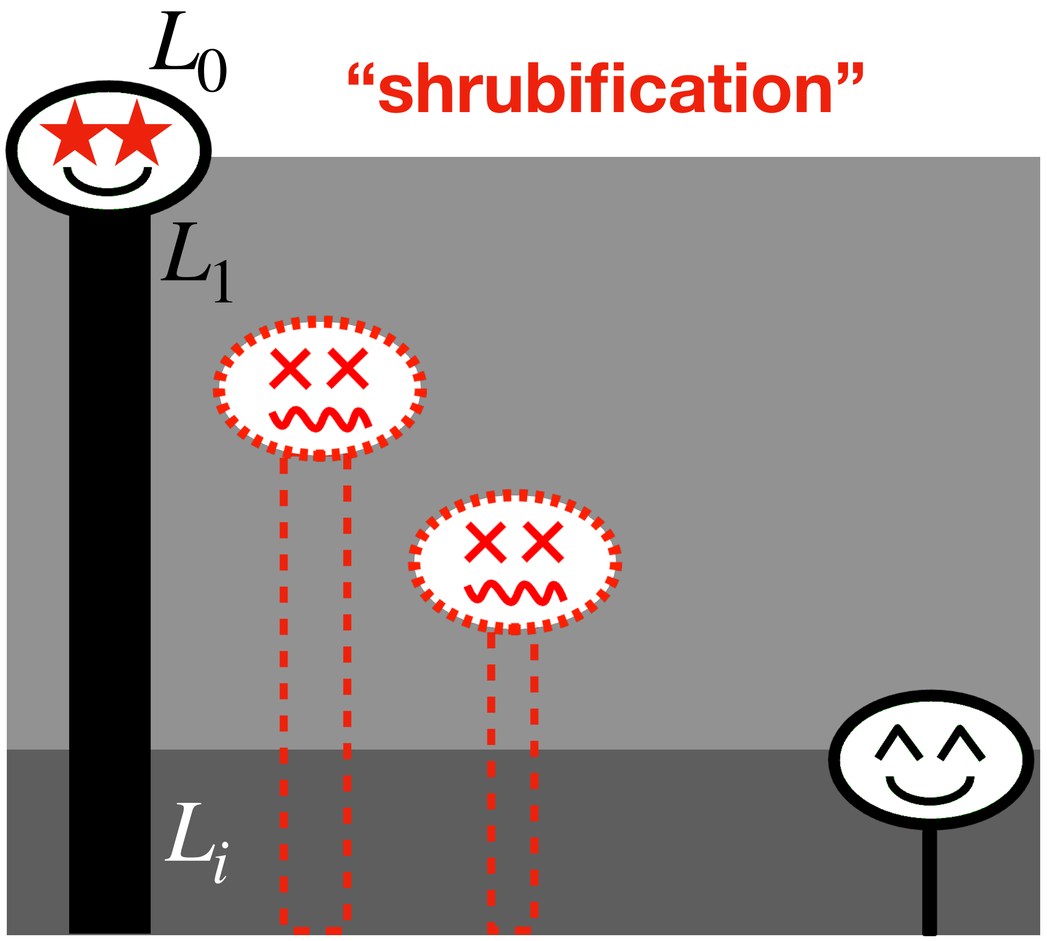
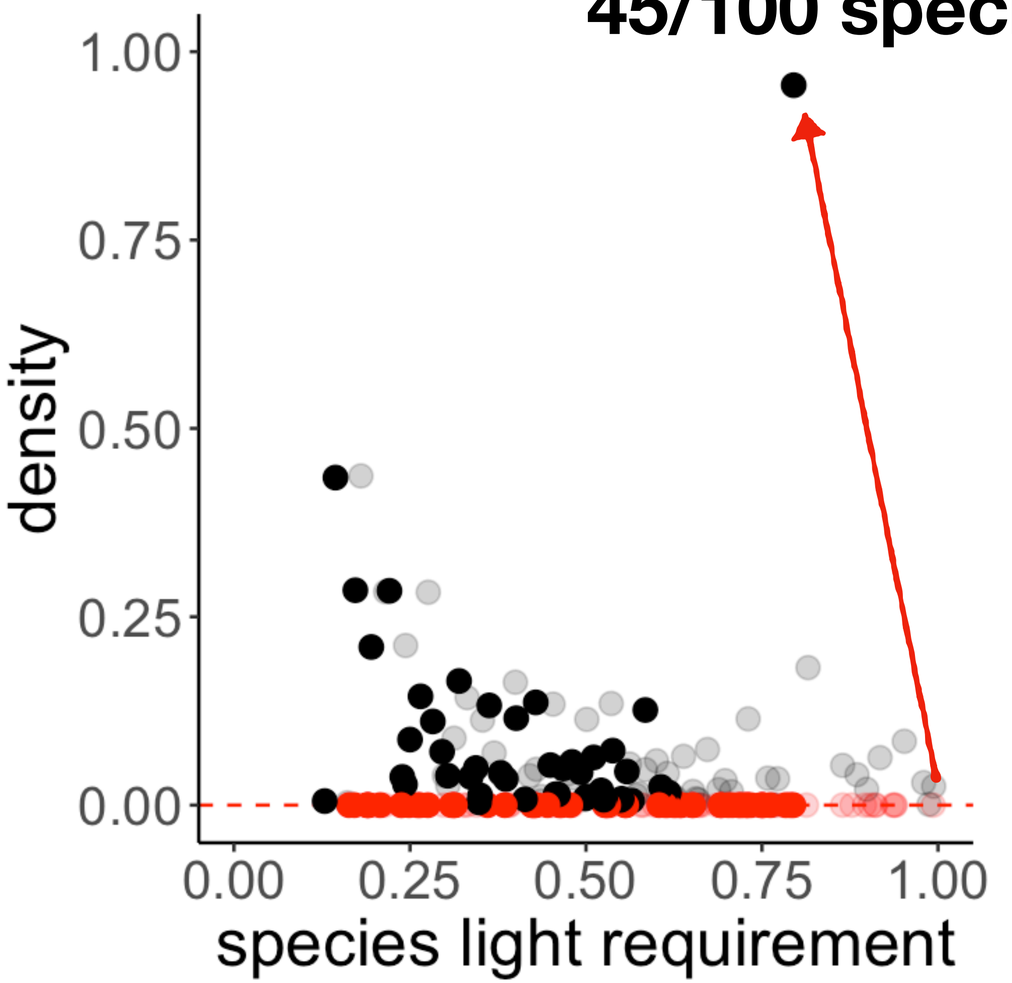


"shrubification"

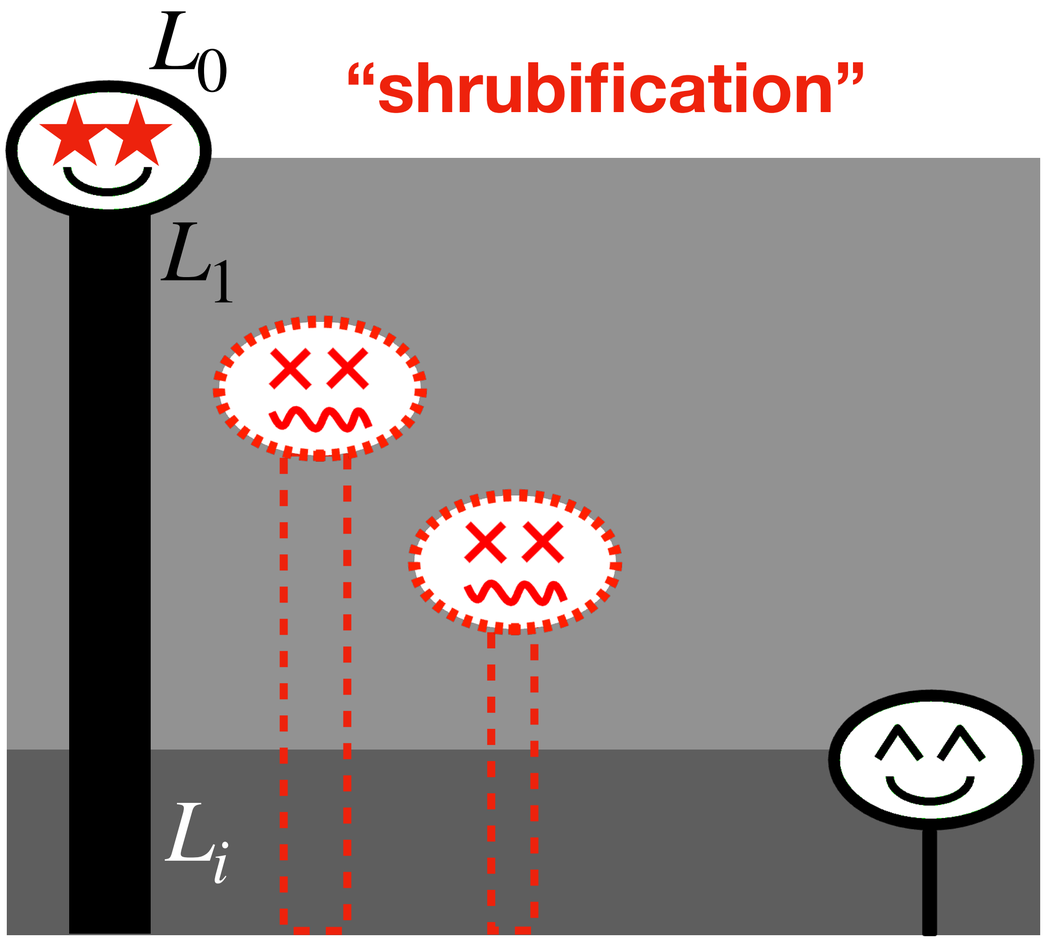
$l_1 > l_2 > \ldots l_i$

light requirement

45/100 species



model | tundra ramet world | summary



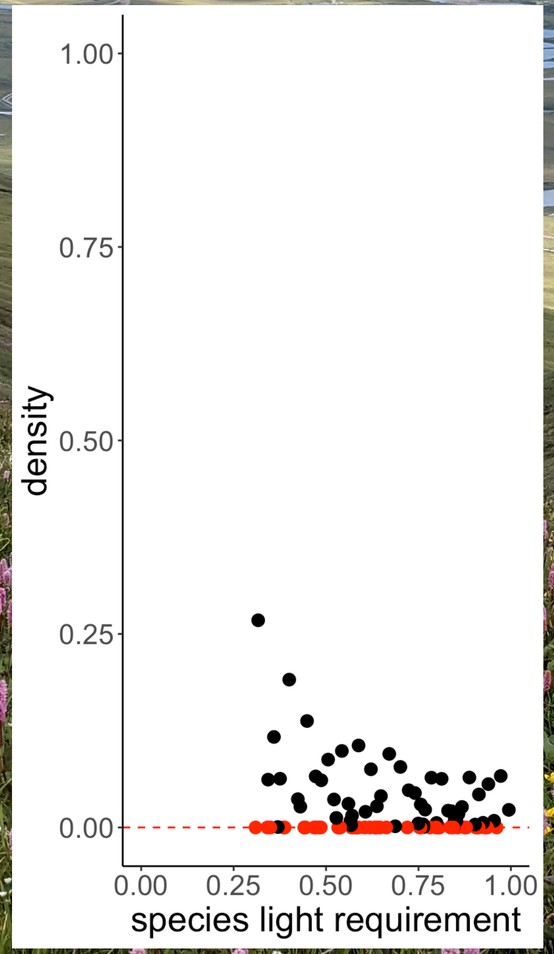
$$H_1 > H_2 > \ldots H_i$$

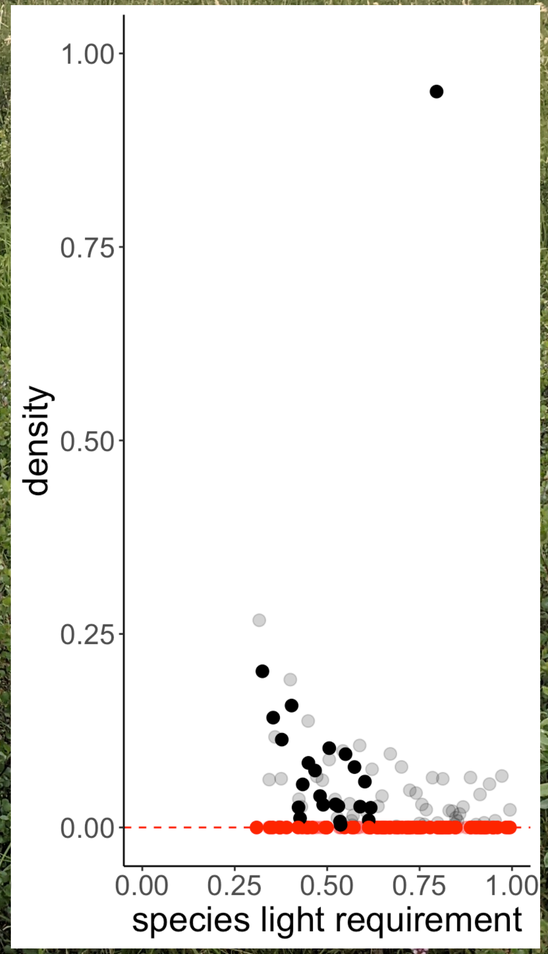
height

Competition for light between species that vary in height creates a world where **any increase in productivity will**:

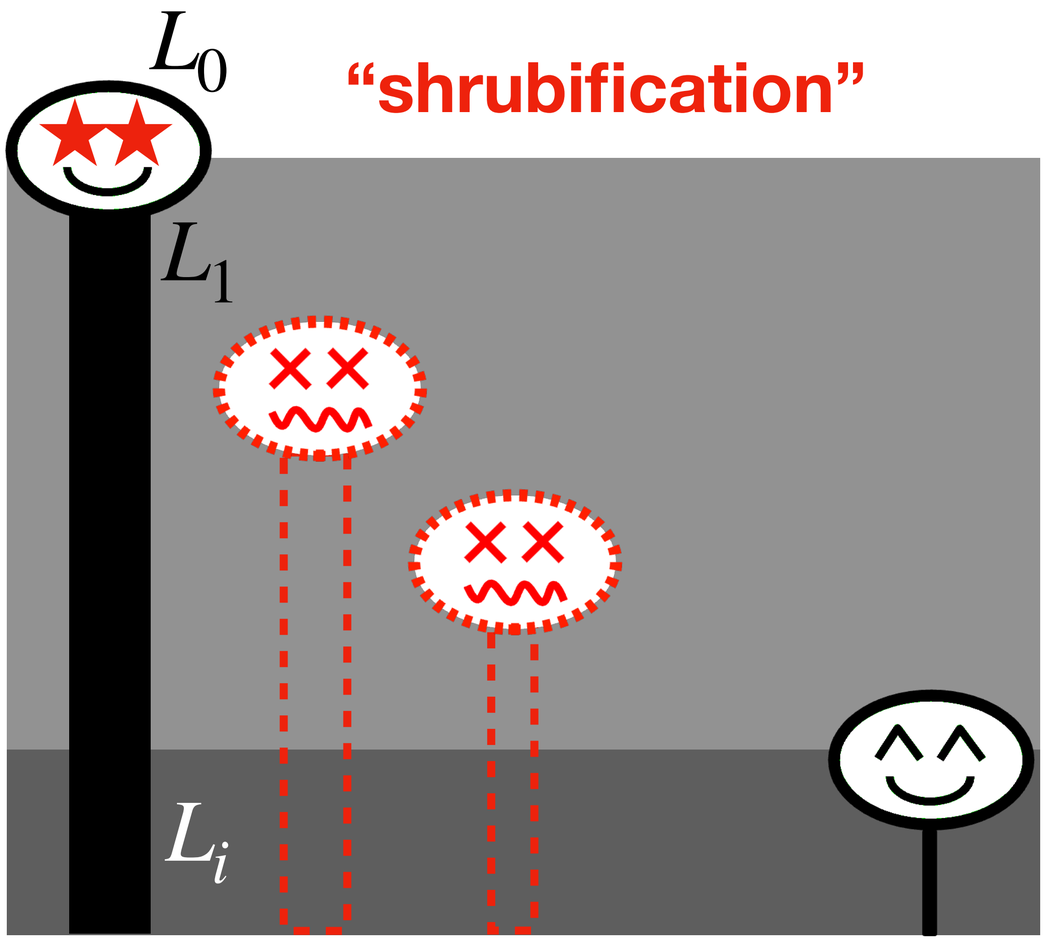
1. **allow taller species to persist**
2. **favor taller species**
3. **potentially cause extinction cascades**

Model Outcome Wishlist

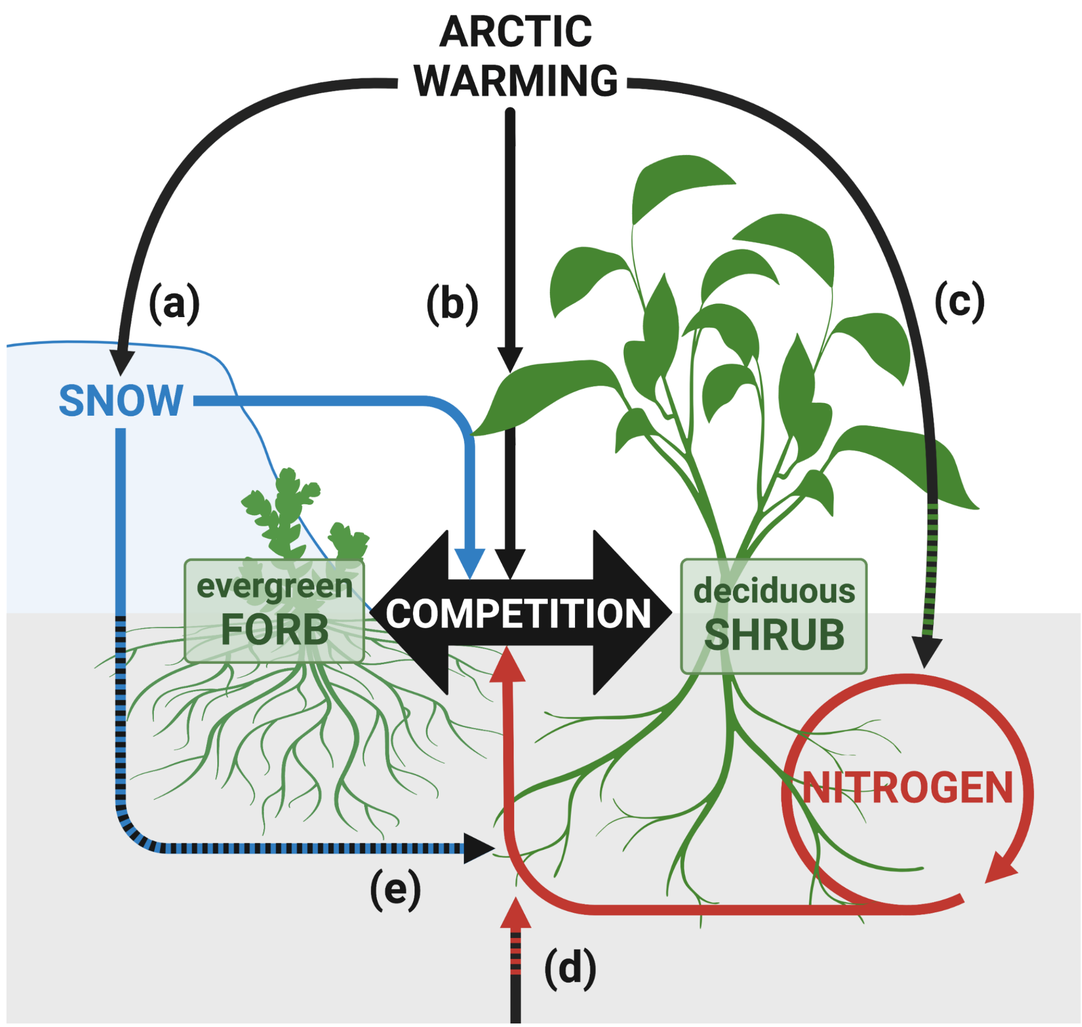




model | tundra ramet world | mechanisms of shrubification



$$H_1 > H_2 > \ldots H_i$$
$$F_1 < F_2 < \ldots F_i$$



Climate drivers act through **multiple pathways** to **increase productivity** in Arctic ecosystems.

Dynamical System - “plant” parameterization

Species 1

$$\frac{dx_1}{dt} = \frac{1}{B_1}(a\frac{L_0(1 - e^{-kcx_1})}{x_1} - r)x_1 - mx_1$$

Species 2

$$\frac{dx_2}{dt} = \frac{1}{B_2}(a\frac{L_0 e^{-kcx_1}(1 - e^{-kcx_2})}{x_2} - r)x_2 - mx_2$$

...

Species i

$$\frac{dx_i}{dt} = \frac{1}{B_i}(aL_0 e^{-kc\sum_{j=1}^{j=i-1} x_j}(1 - e^{-kcx_i}) - rx_i) - mx_i$$

“Simplified” System of Equations

Species 1

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

Species 2

$$\frac{dx_2}{dt} = f_2(e^{-kx_1} - e^{-k(x_1+x_2)}) - mx_2$$

…

Species i

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

collecting parameters $f_i = \frac{aL_0}{B_i}, m = (r + m), k = kc$

“Simplified” System of Equations

is analagous to "competition-colonization" model

$$f_1 < f_2 < \cdots < f_i$$

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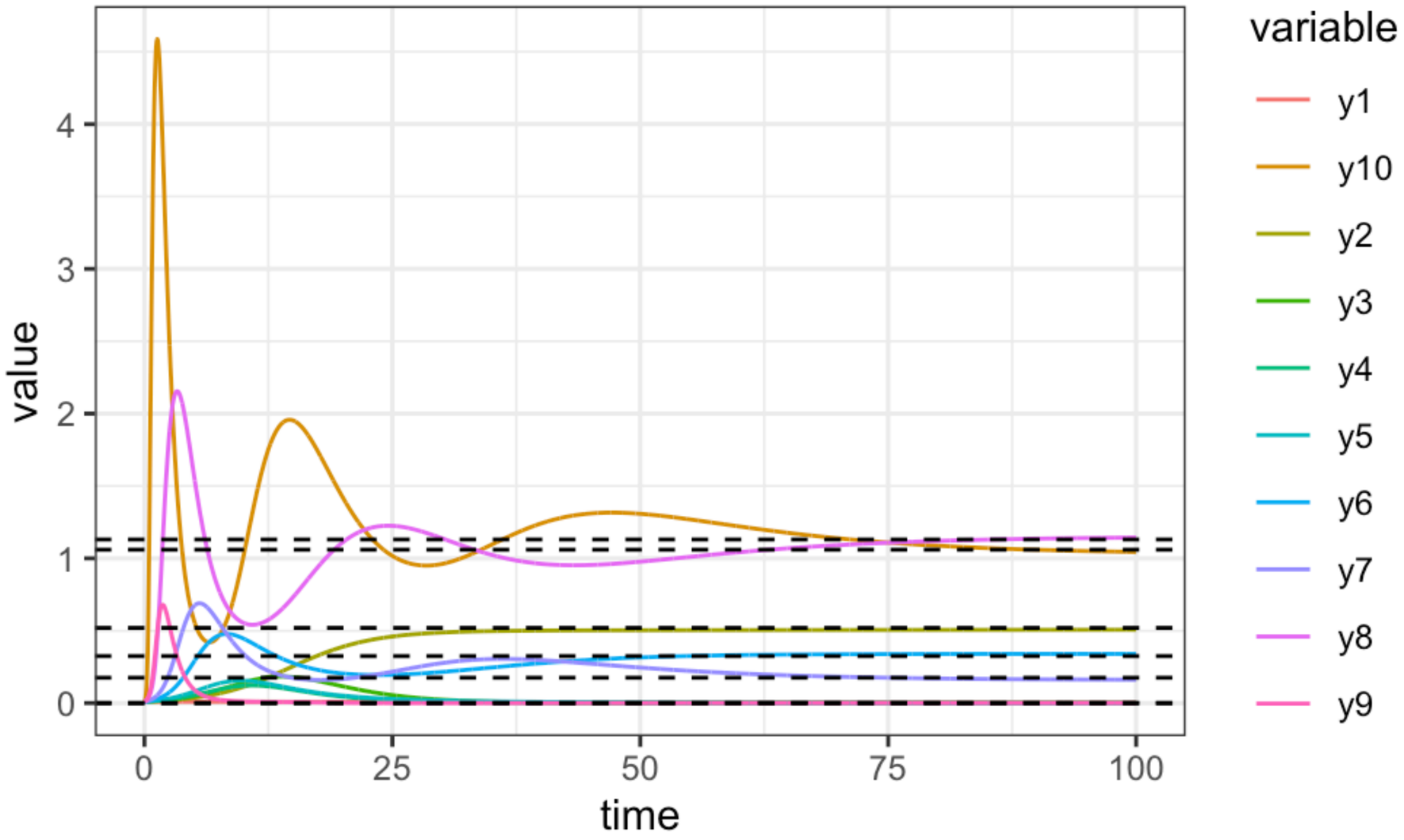
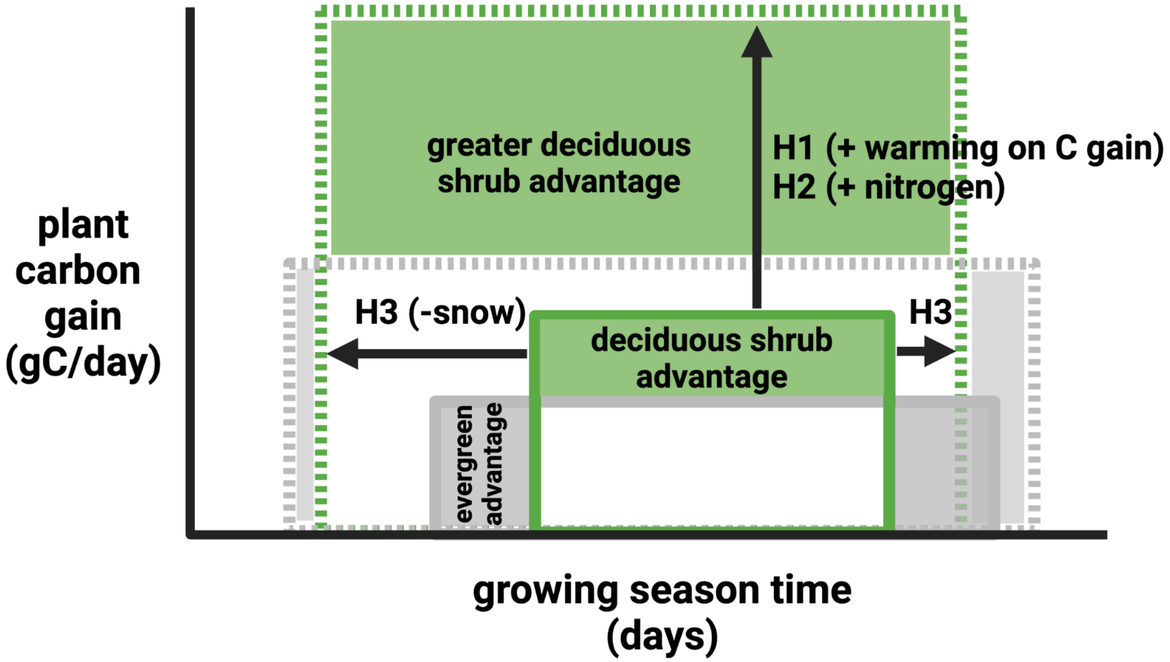
Simulations, to be continued…



Next Steps

Model Outcome Wishlist



- via Analytical Results:
  - Expressions for predicting competitive outcome (numerical solution)
  - Gain insight into relationship between traits & shifts in competitive outcome (some)
- via Simulation: (for simple light model!)
  - Outcome of competition across simulations under different environmental conditions
  - Test varying the strength of mechanisms
  - Test against long-term data, locations across the Arctic

1. Parameterize for tundra plants

- Physiological rates (photosynthesis, respiration)
- Allometry
- Mortality

2. Perturbation Simulations to “test mechanisms”

- Temperature increase
- Nutrient availability increase
- Longer growing seasons

2b. Model Structure + nitrogen

State Variables x_i, density of species i

Species Description $H_1 > H_2 > \cdots > H_j > \cdots > H_Q,\ i = 1,\ldots,Q$

Individual Allometry $B_i = bH_i^{\beta}\ ,\ C_i = C_j = c\,\forall i, j,$

Individual Physiology $g_i(L_{R_i}, N_S) = \dfrac{A(L_{R_i}) - r}{1 + \eta_C + \eta_N},$ for now $\eta_N(N_S) = n$ OR $\dfrac{1}{nN_S}$

Light + Nitrogen Competition $L_{R_i} = \dfrac{L_0(e^{-kc\sum_{j=1}^{i-1} x_j} - e^{-kc\sum_{j=1}^{i} x_j})}{x_i},$ $N_S = N_0 - \sum_{j=1}^{\infty} nB_i x_i$

Light Requirement $l_i(N_S) = \dfrac{1}{ack}\left(\dfrac{mB_i}{c}\left(1 + \dfrac{1}{nN_s}\right) + r\right)$

Nitrogen Requirement $n_i(L_{R_i}) = \dfrac{mB_i}{(aL_{R_i} - r) - mB_i}$

2c. Model Structure + seasonality

State Variables x_i, density of species i

Species Description $H_1 > H_2 > \cdots > H_j > \cdots > H_Q,\ i = 1,\ldots,Q$

Individual Allometry $B_i = bH_i^{\beta}\ ,\ C_i = C_j = c\,\forall i,j,$

Individual Physiology $g_i(L_{R_i}) = A(L_{R_i}) - r,$ for now $A(L) = aL$

Light Competition

$$L_{R_i} = \frac{L_0(e^{-kc\sum_{j=1}^{i-1} x_j} - e^{-kc\sum_{j=1}^{i} x_j})}{x_i}$$

Population* Demography

$$f_i = \frac{g_i(L_{R_i})}{B_i}, m_i = m_j \forall i,j$$

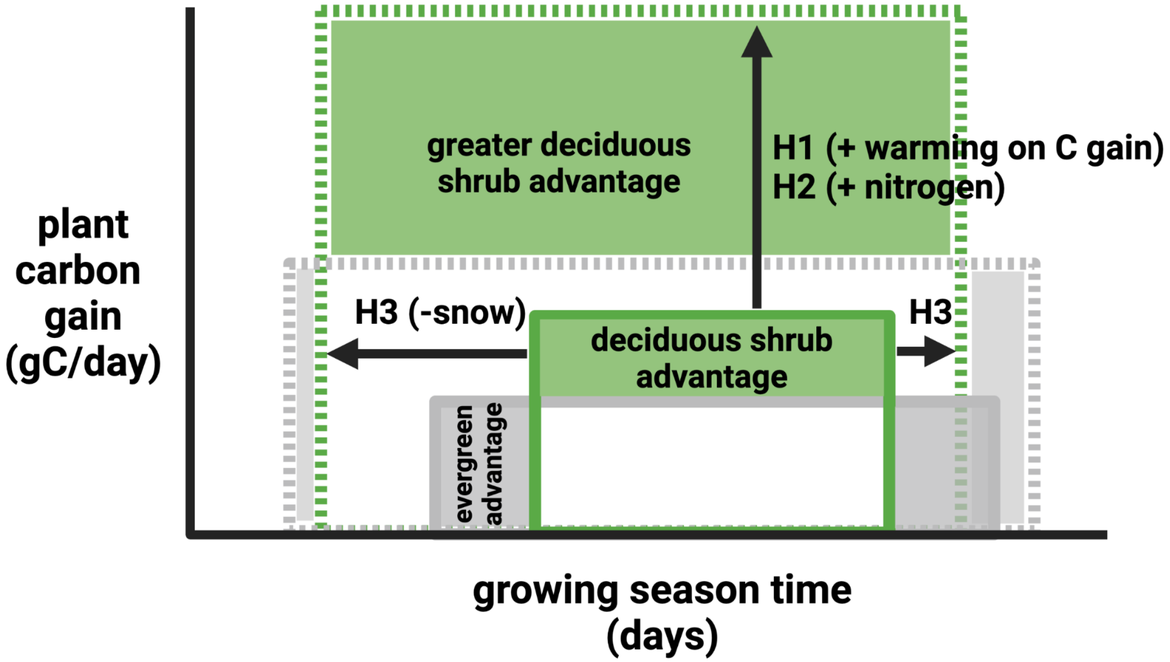
Population Dynamics

$$\frac{dx_i}{dt} = f_i x_i - m x_i = (f_i - m)x_i$$ **rewrite in discrete time**

3. Projects on deck

- Nutrient Competition Functions (Steve Pacala)
  1. Pay for what you get (infinite pool)
  2. Split finite N pool (pay fixed price per unit N)
  3. Litter feedback with N mineralization rate (microbial quasi-equilibria)
- Growing Season Length (Helen Brush)
  - Build discrete time version of model w/clonal (& seed?) reproduction
- Intra versus interspecific competition formulation (Chuliang Song)
  - Can these “mechanistic” approaches inform “realistic” constraints on “phenomenological” models of competition?

Model Outcomes Wishlist?



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  - Outcome of competition across simulations under different environmental conditions
  - Test varying the strength of mechanisms
  - Test against long-term data, locations across the Arctic
  - …
  - …

My Questions

+ your questions?

- How does nutrient competition change the story, if so? (i.e. hierarchical ammensalism + scramble competition)
- Separation of timescale between plant growth processes and litter feedbacks?
- What about true competition-colonization trade-offs?
  - Are the mechanisms constraining shrub density within the range the same as shrub expansion into new regions?

Discussion

+ advice

- Simple model vs. “stacking the deck”?
- The competition-colonization model is… weird?
- Connections back to consumer-resource theory?
- How to choose level of model complexity for different sets of questions?

all of you!

Thank you!

Matteo Detto
Steve Pacala
Jonathan Levine

Extra Slides

+ more limiting resources

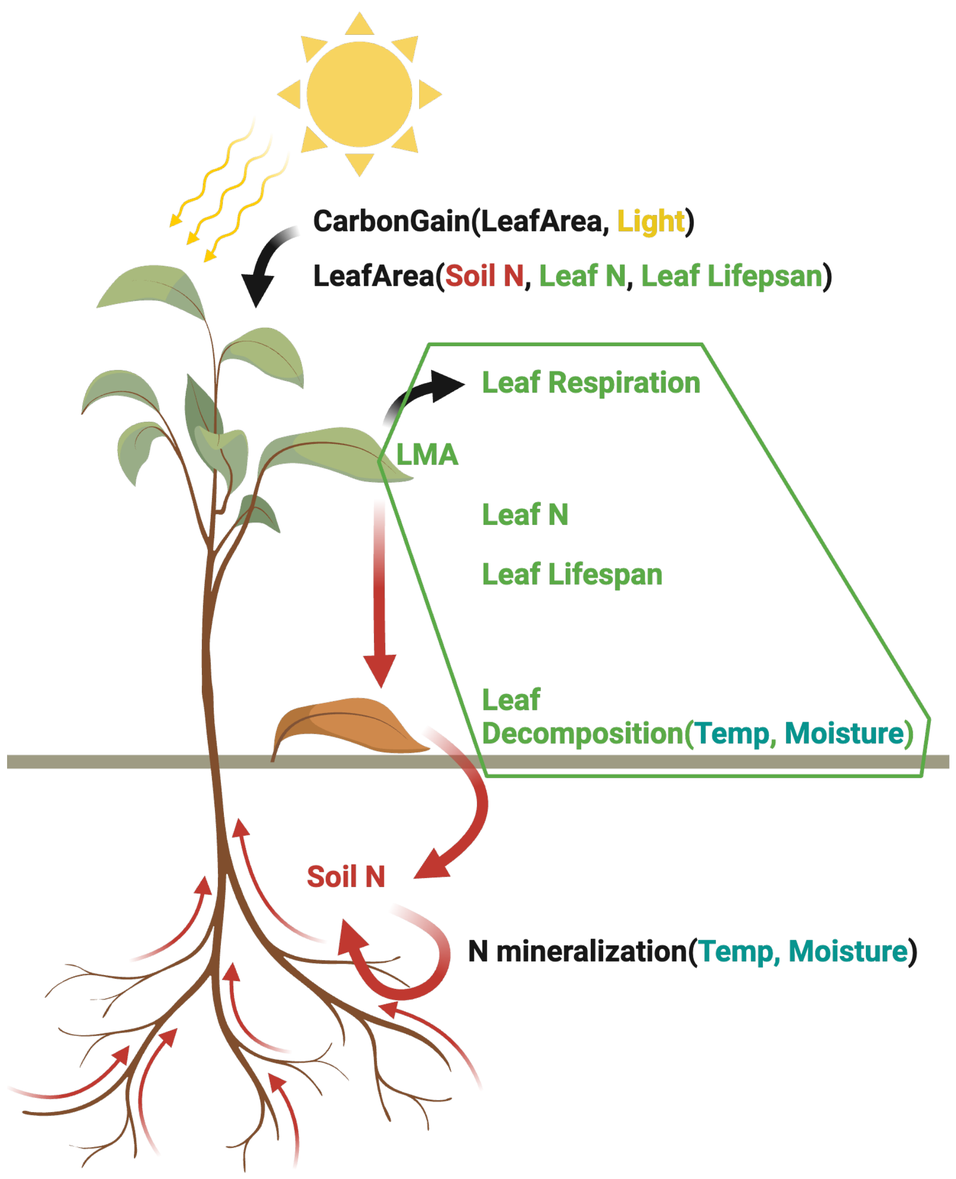
- Light
- Soil resources
- Time above freezing

+ more dimensions of trait diversity

- Height (woody/non-woody)
- Leaf Habit (deciduous/evergreen)

= same questions, different answers?

1. Under what conditions can a species persist?
2. Can multiple species coexist?
3. <u>What mechanism favors tall species with warming?</u>



biogeochemical feedbacks

Check assumptions in the field

- Light
- Soil resources
- Time above freezing

Productivity increases given:

- Temperature dependence of photosynthesis with warming

- Competition for nitrogen alleviated

- Seasonality = period of time favorable for growth is longer

Do different productivity drivers result in different dynamics?

model meets reality

“Plant Parameter” System of Equations

Species 1

$$\frac{dx_1}{dt} = \frac{1}{B_1}(a\frac{L_0(1 - e^{-kcx_1})}{x_1} - r)x_1 - mx_1$$

Species 2

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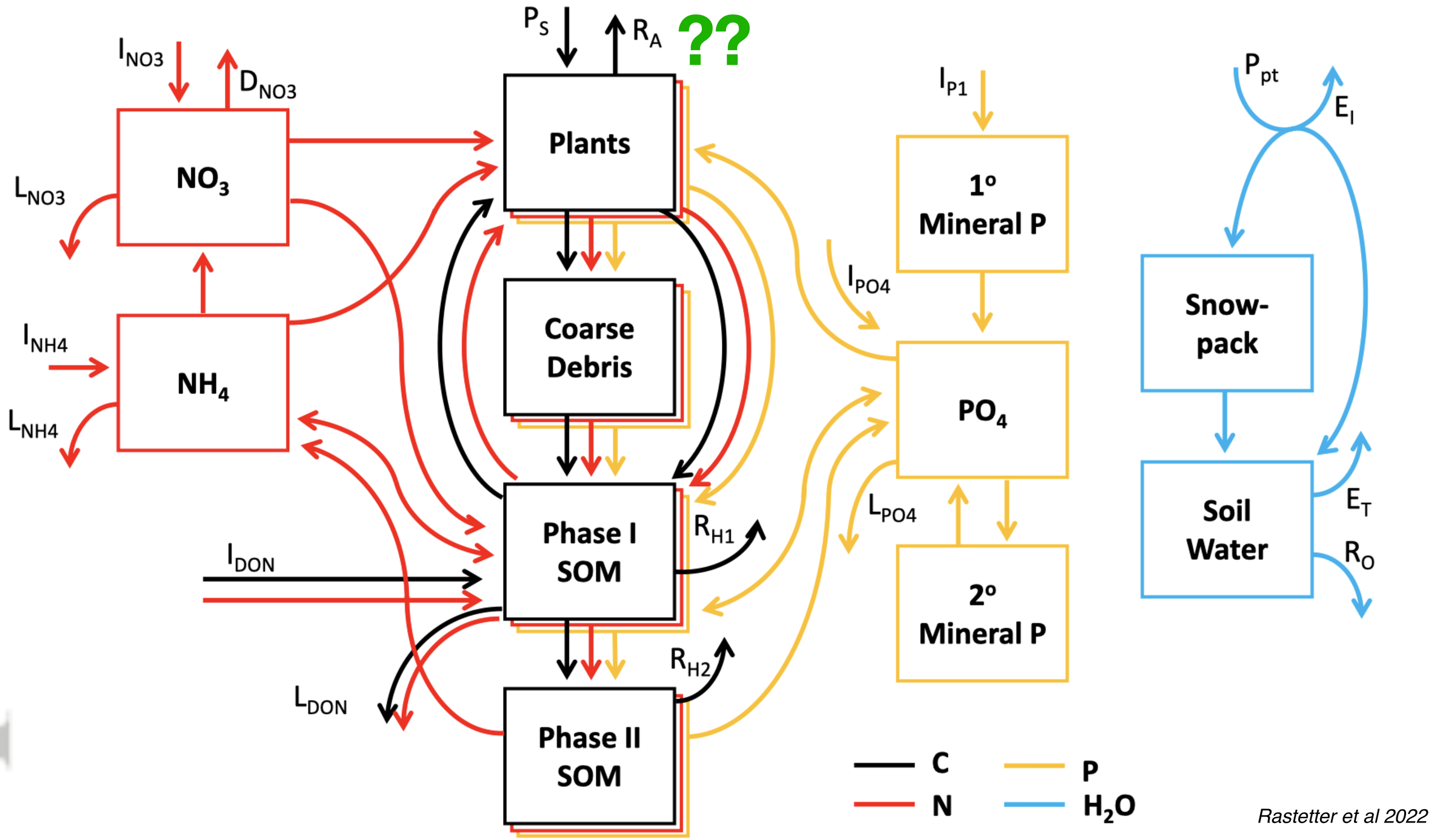
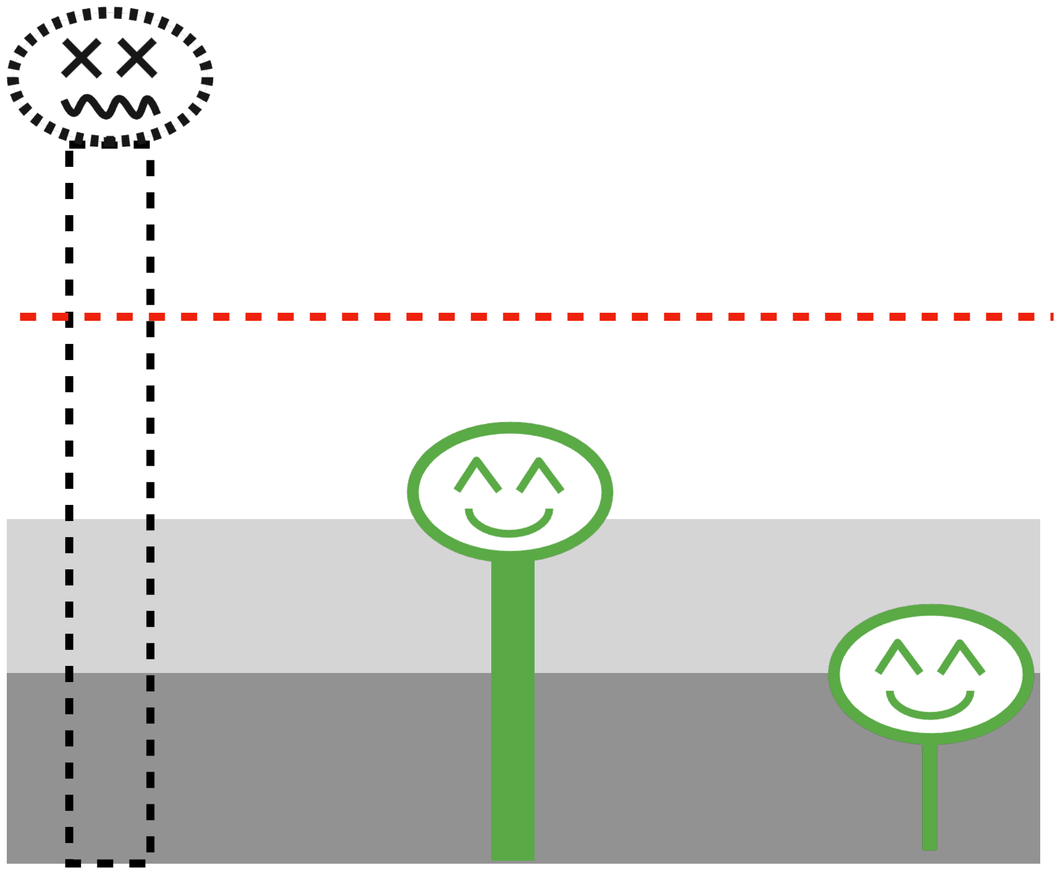


Rastetter et al 2022

Are the mechanisms constraining shrub density within the range the same as shrub expansion into new regions?

model | tundra ramet world | where can species survive?



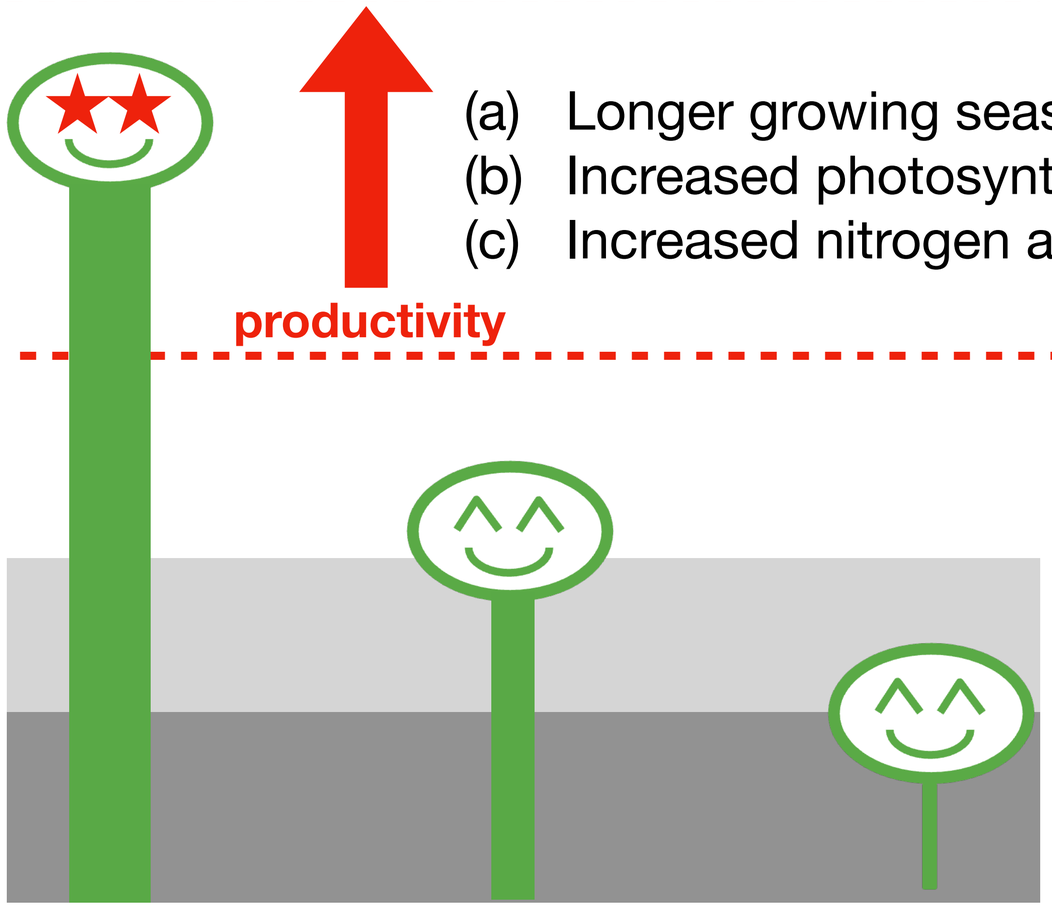
max height: $\uparrow H_0 = \left(\frac{\text{growth}\uparrow}{\text{mortality}} \right)^{\frac{1}{\beta}}$

$H_1 \quad > \quad H_2 \quad > \ldots H_i$

height

model | tundra ramet world | can shrubs expand northward?

max height in a warmer arctic?



(a) Longer growing seasons
(b) Increased photosynthesis
(c) Increased nitrogen availability

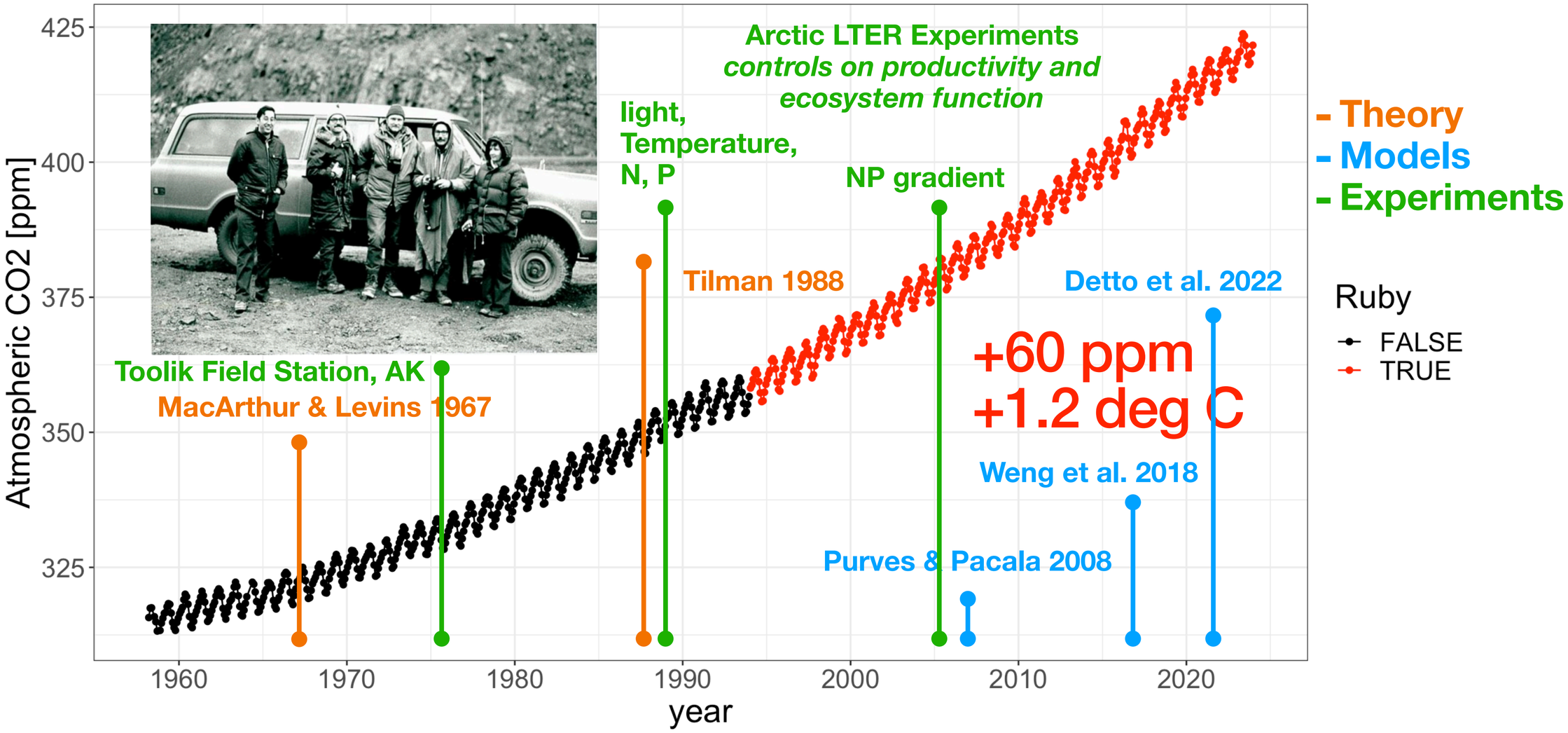
max height: $\uparrow H_0 = \left(\frac{\text{growth}\uparrow}{\text{mortality}} \right)^{\frac{1}{\beta}}$

can shrubs expand northward?

$$H_1 > H_2 > \ldots H_i$$

height

Mechanisms of Shrubification in a warming Arctic



Keeling, Ralph F; Keeling, Charles D. (2017). Atmospheric Monthly In Situ CO2 Data - Mauna Loa Observatory, Hawaii

Questions?

1. What functional trait differences underlie mechanisms of Arctic shrubification?

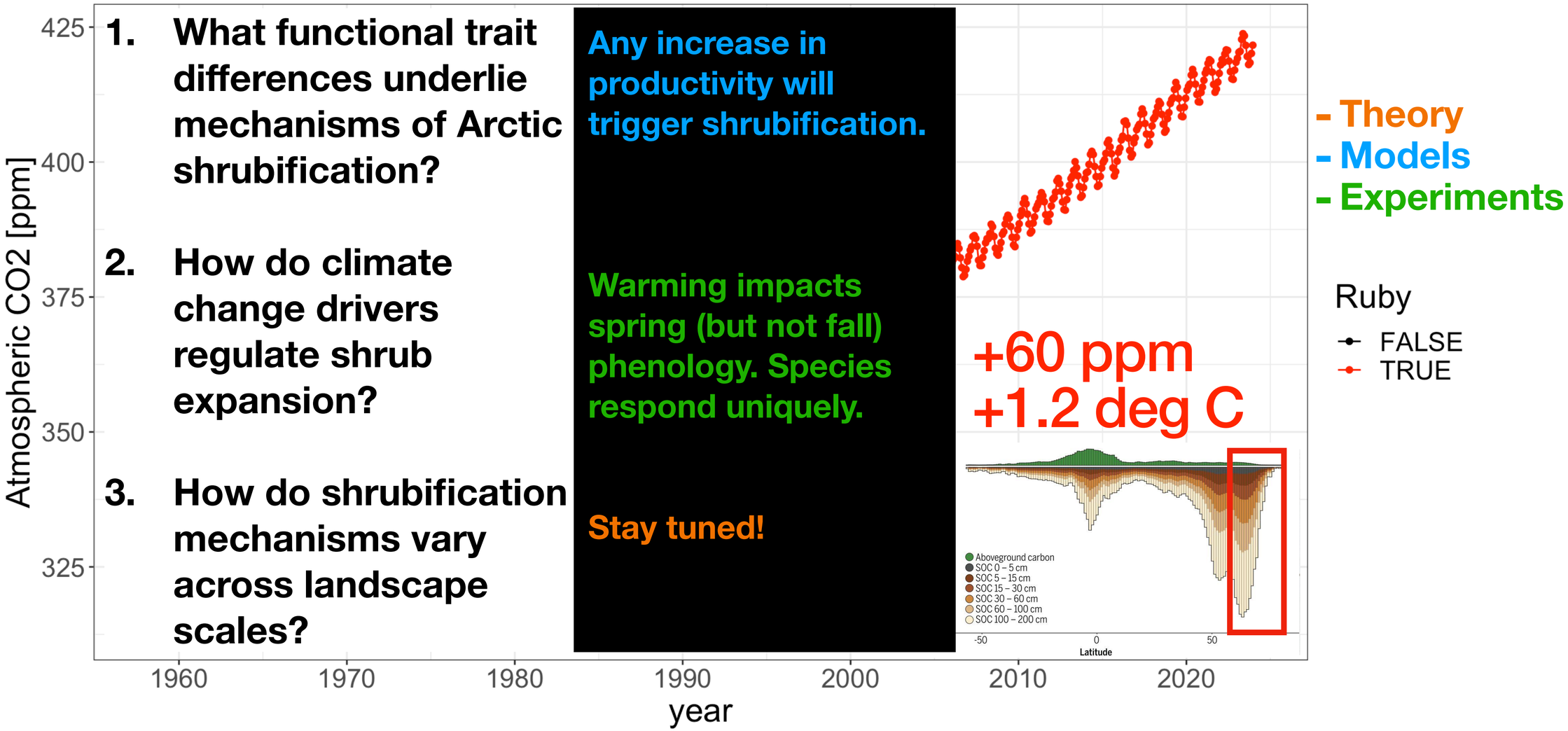
2. How do climate change drivers regulate shrub expansion?

3. How do shrubification mechanisms vary across landscape scales?

Any increase in productivity will trigger shrubification.

Warming impacts spring (but not fall) phenology. Species respond uniquely.

Stay tuned!



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What limits Arctic plant growth?

- Light
- Soil resources
- Time above freezing

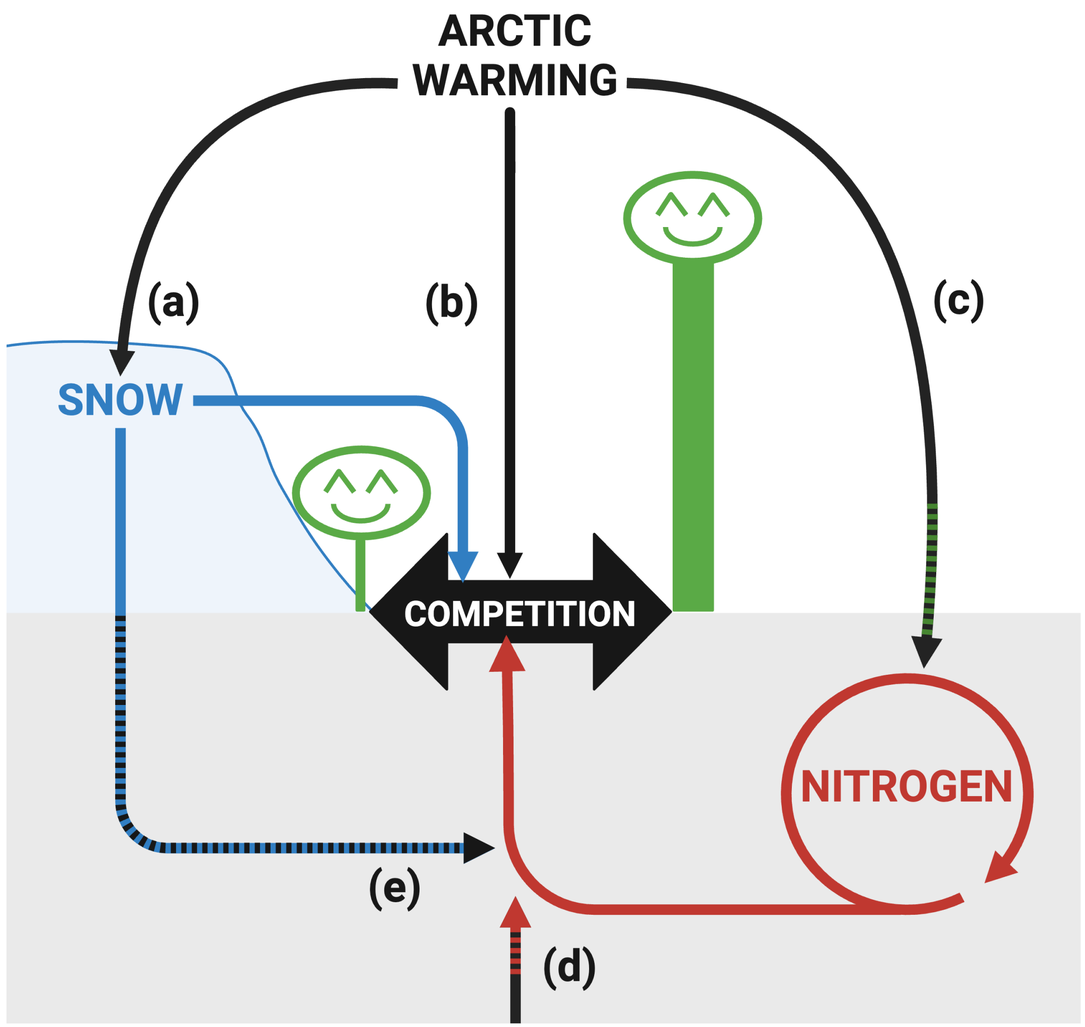
How do tundra species differ?

- Height (woody/non-woody)
- Leaf Habit (deciduous/evergreen)

Model Questions

1. When can a species survive?
2. Can multiple species coexist?
3. What happens to the community in response to warming?

model | tundra ramet world



welcome to tundra ramet world!

future results | northern shruburbia

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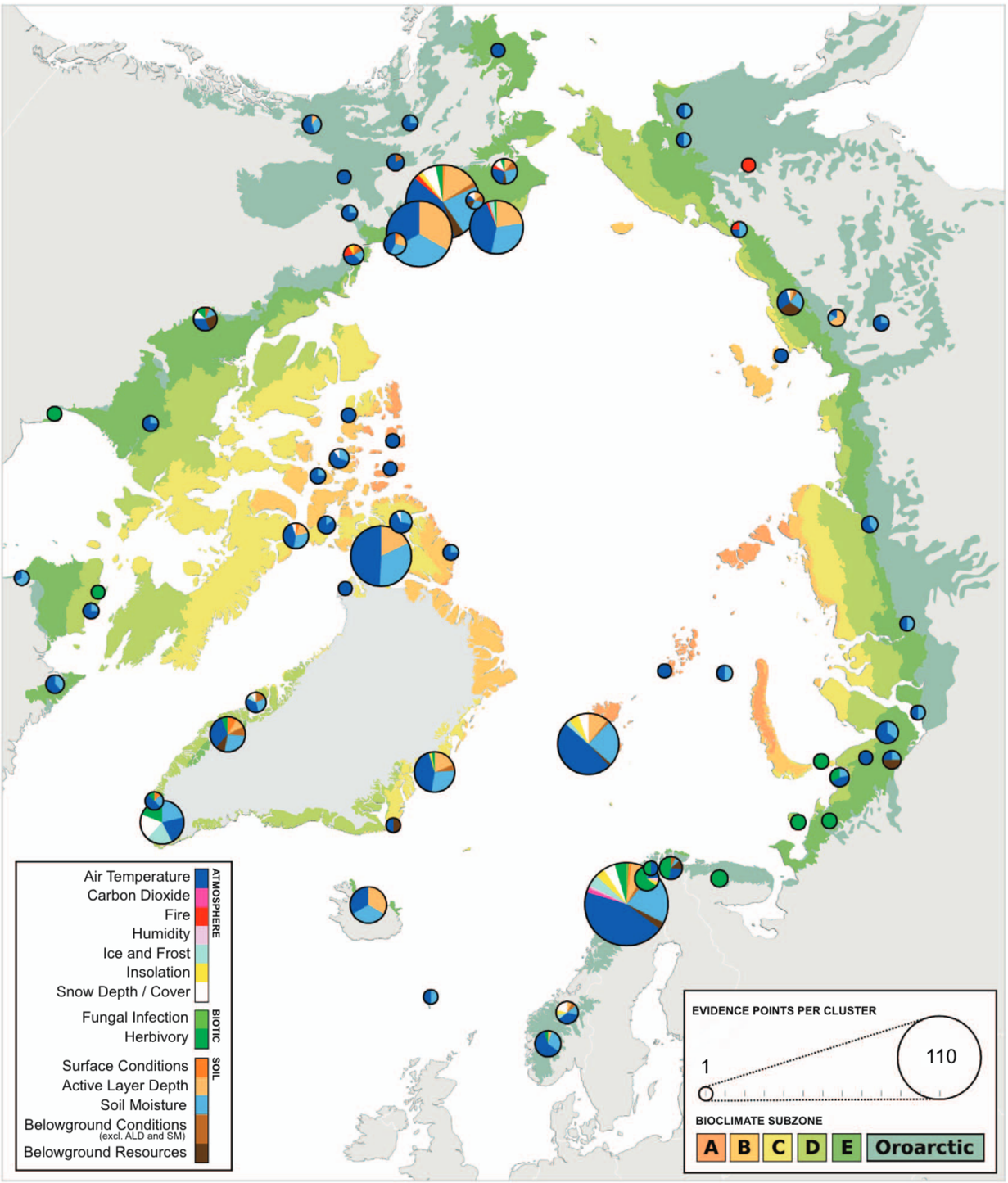
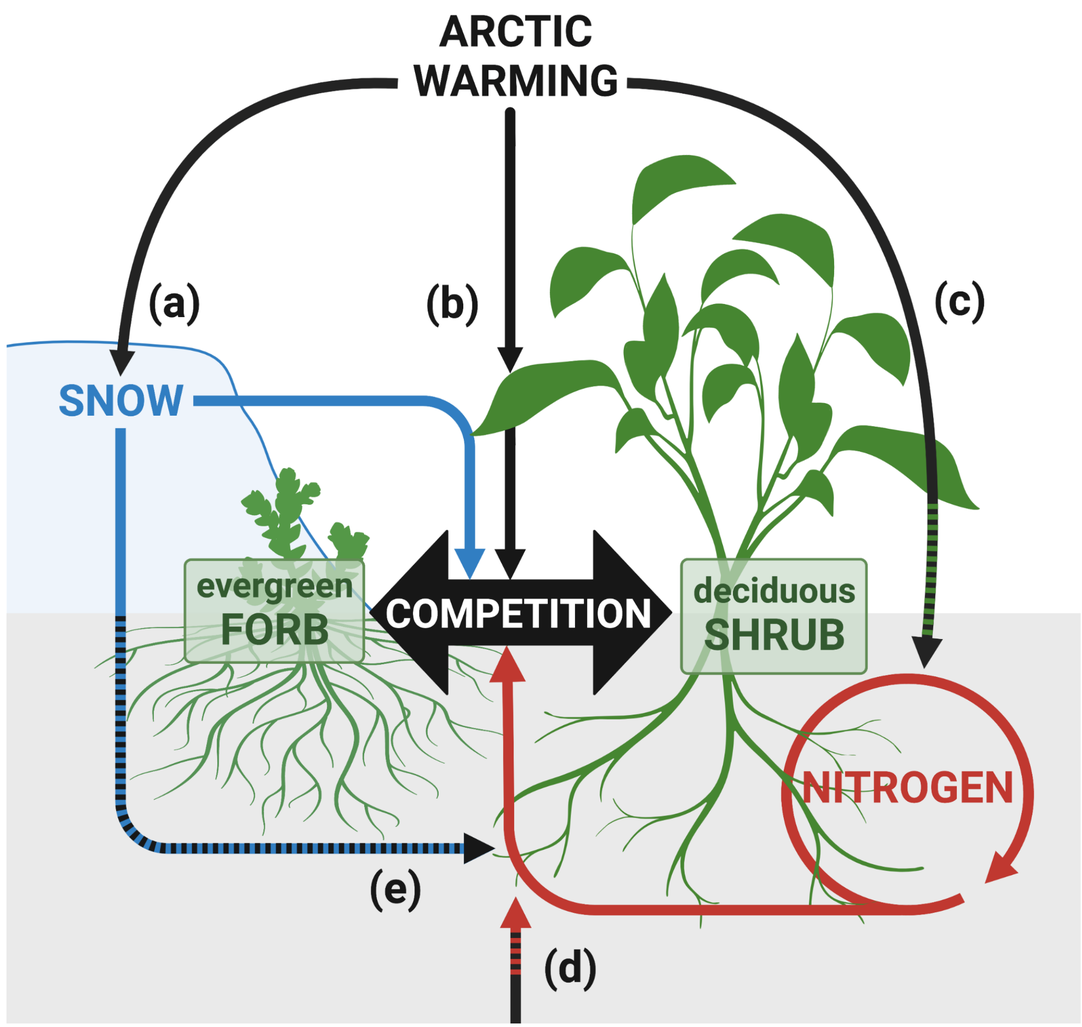
mechanistic model

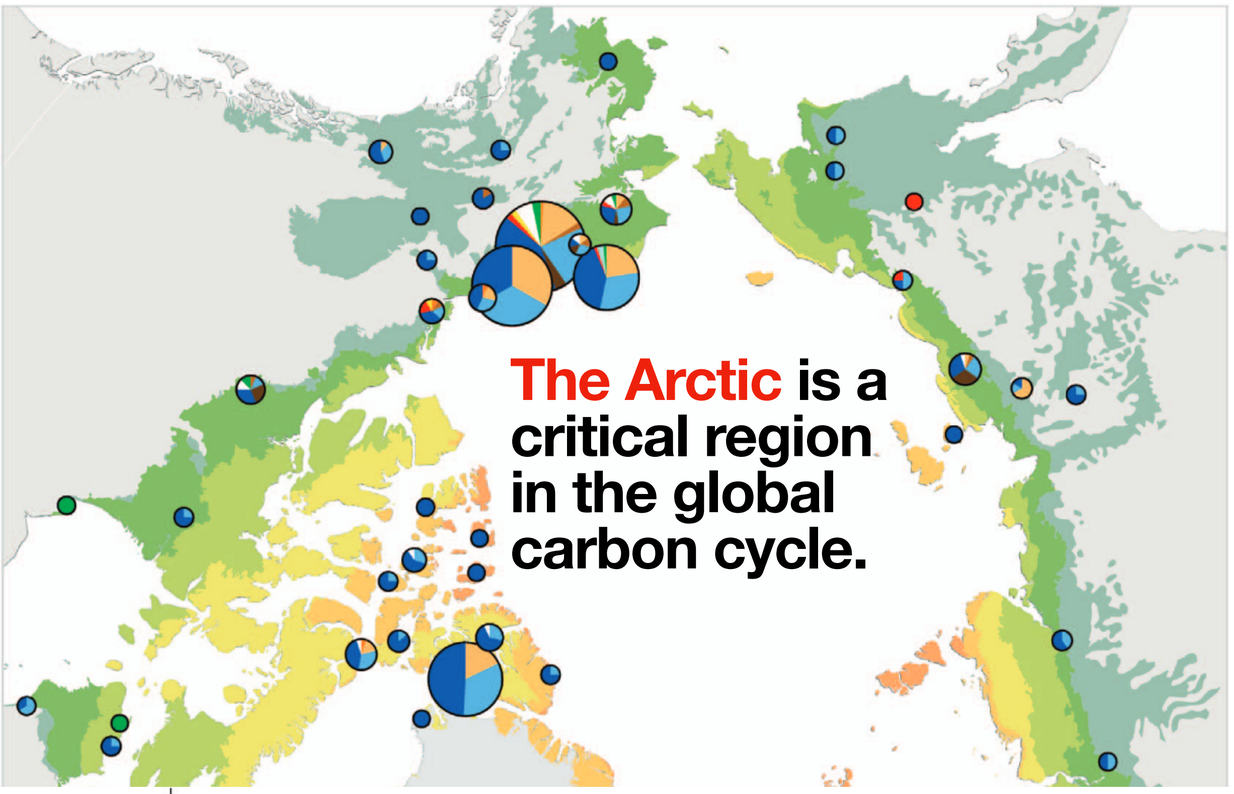
tundra ramet world

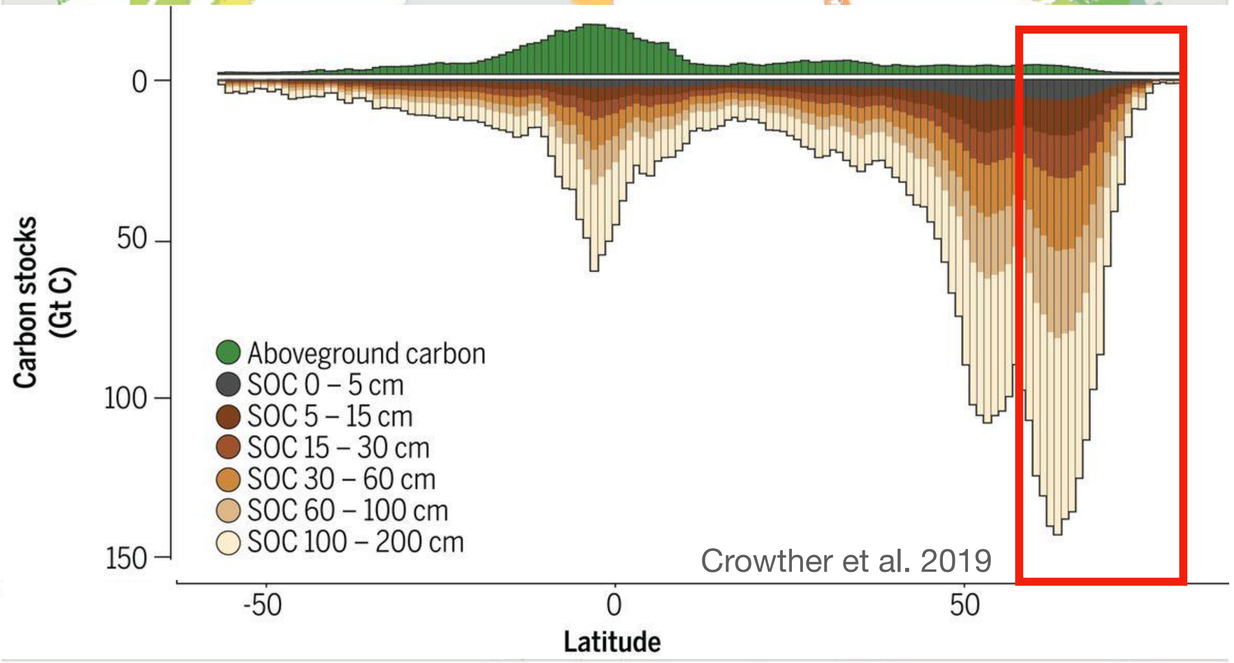


Mechanisms of Shrubification



Climate drivers act through **multiple pathways** to structure plant competition in Arctic ecosystems.





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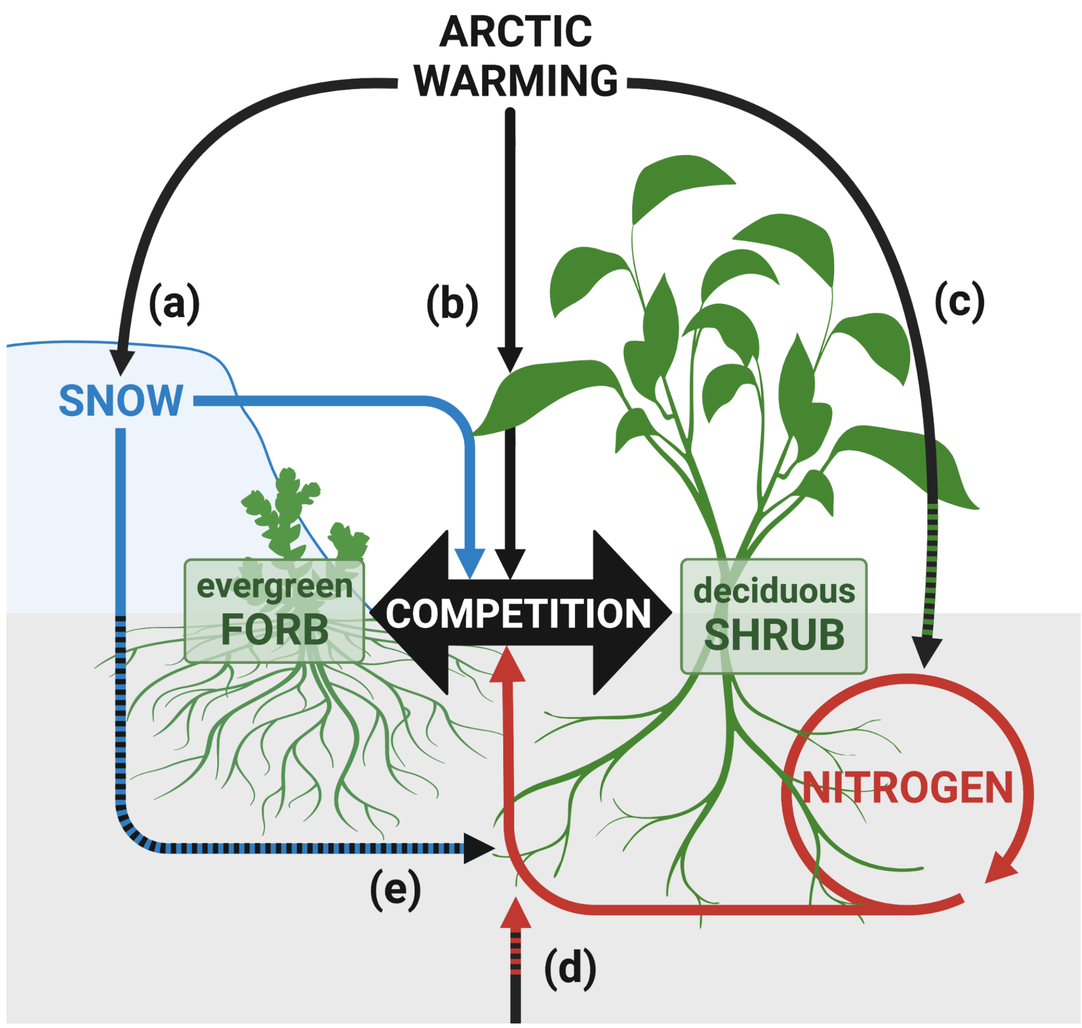

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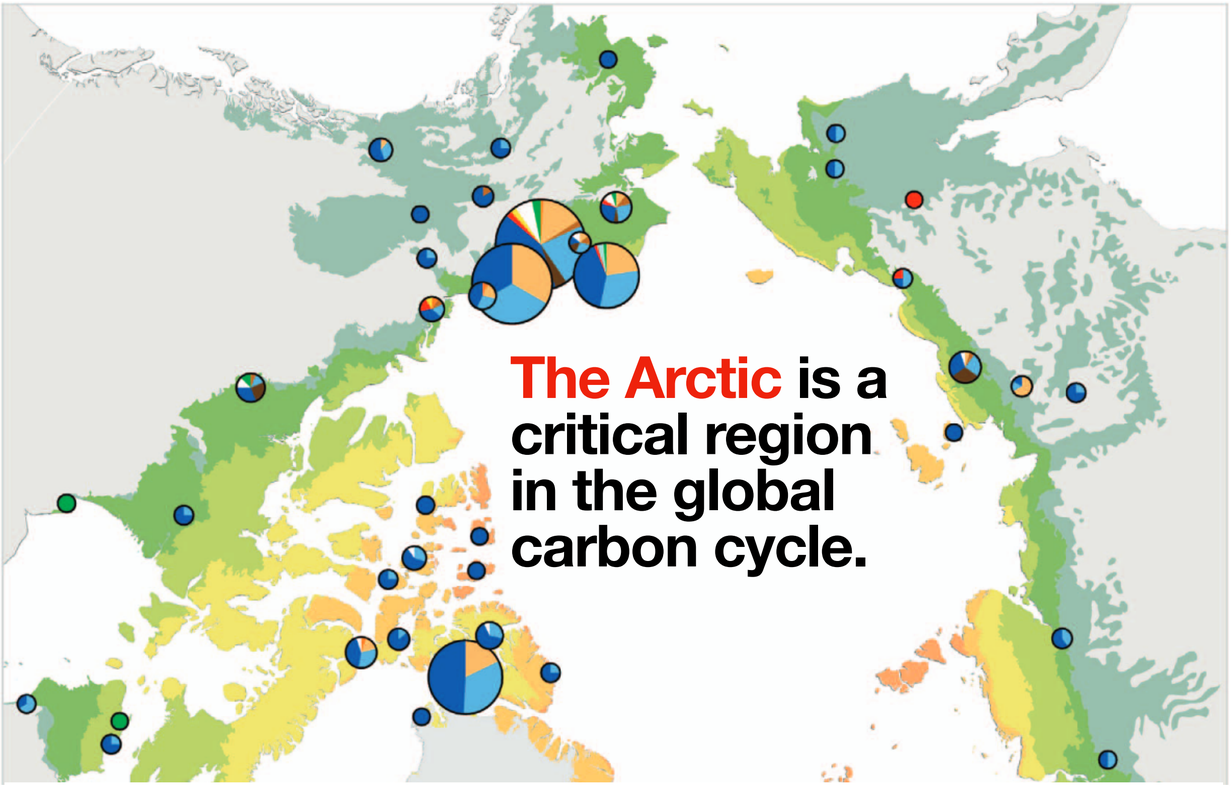
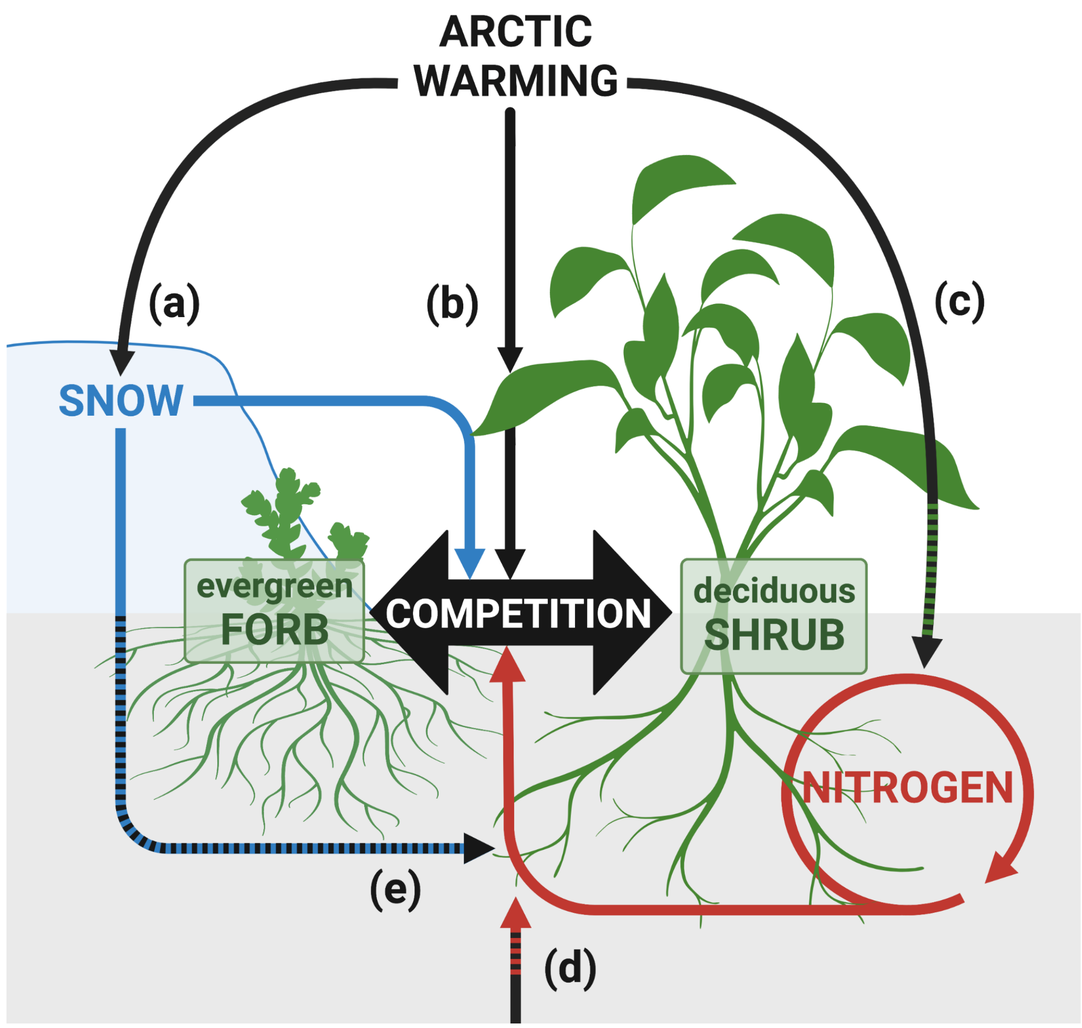


Understanding the mechanisms controlling shrubification remains challenging.

Mechanisms of Shrubification



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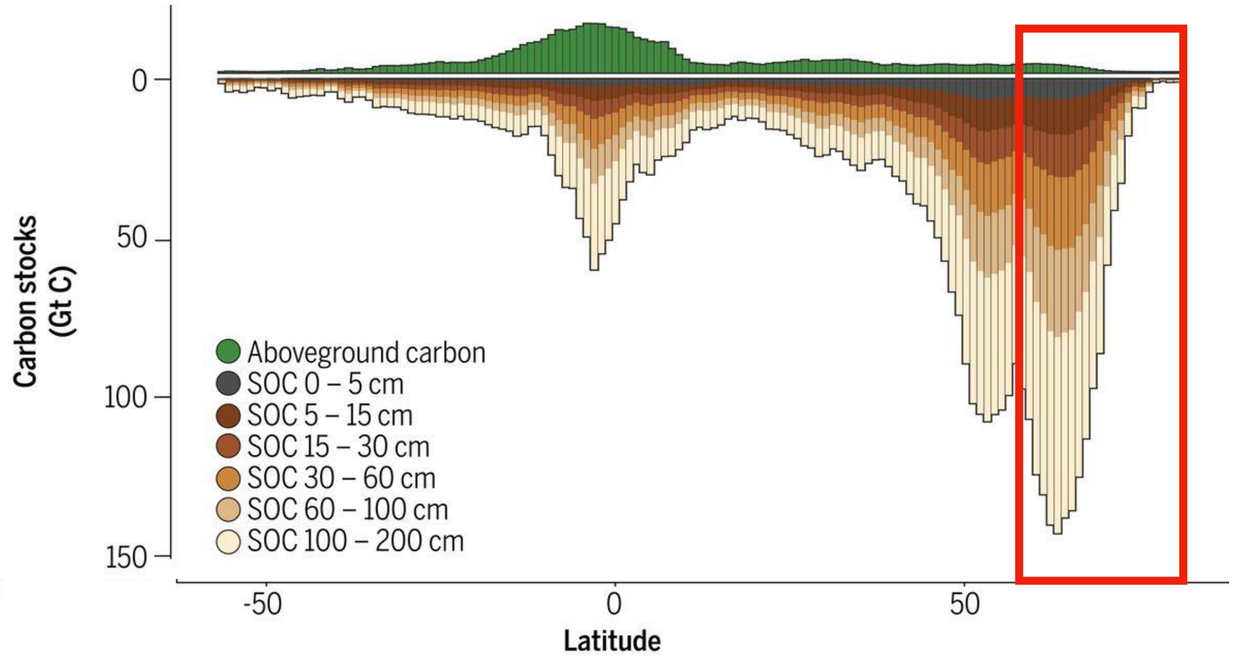
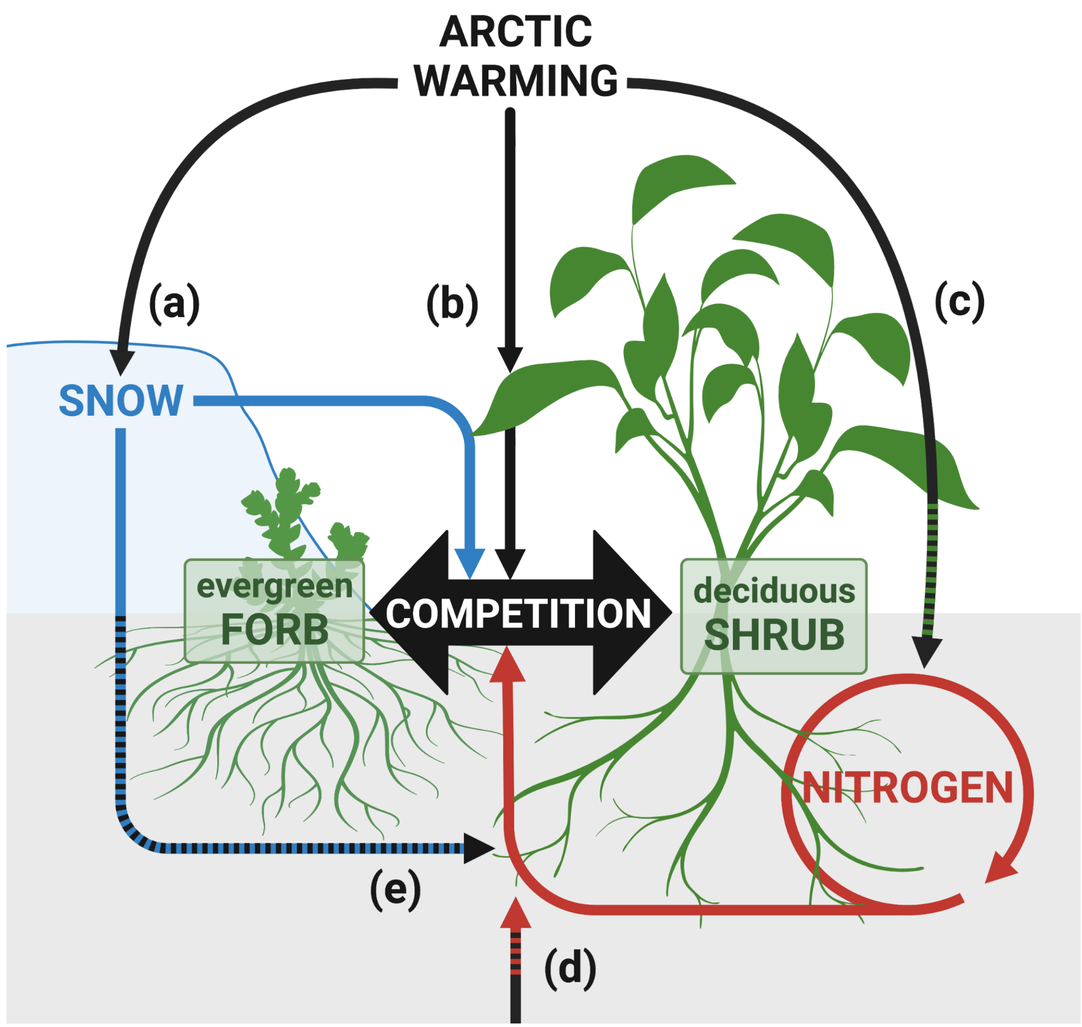
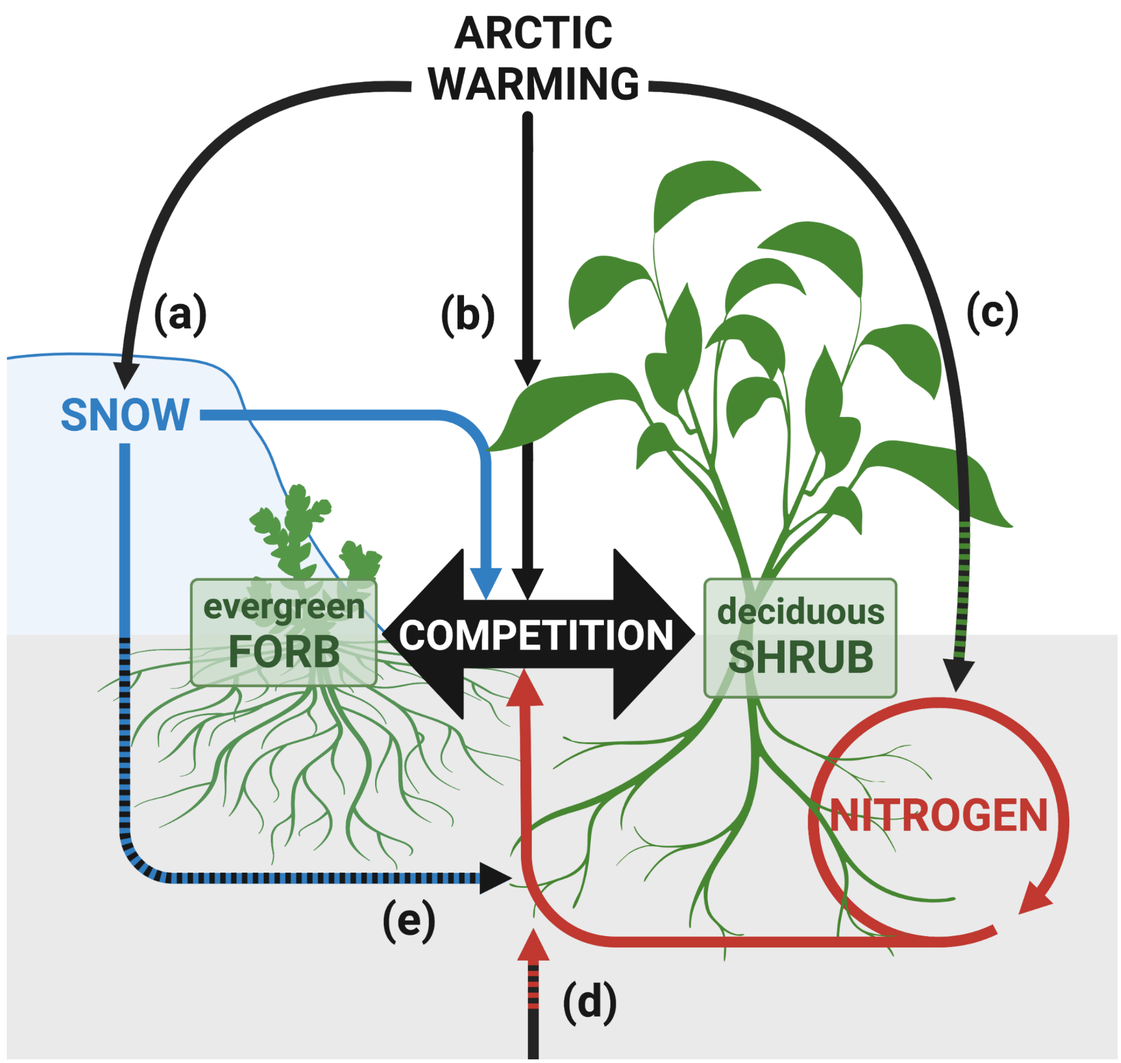


Mechanisms of Shrubification



Climate drivers act through **multiple pathways** to **<u>structure plant competition</u>** in Arctic ecosystems.

Mechanisms of Arctic Shrubification (?)



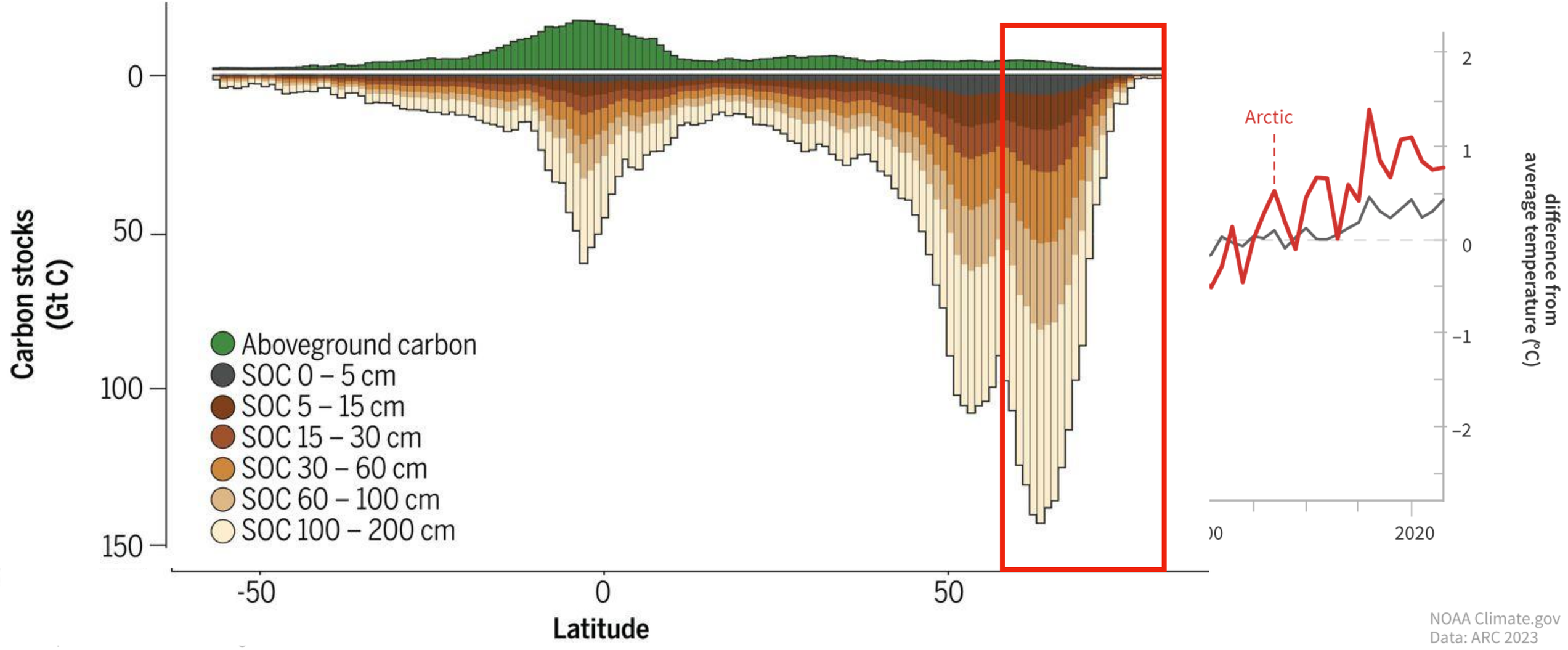
Arctic warming acts through **multiple pathways** to structure plant competition in Arctic ecosystems.

Hypothesis 1 (Photosynthetic Advantage): *Warming temperatures grant shrubs a disproportionate photosynthetic advantage over other tundra species (Fig. 1, arrow B)*

Hypothesis 2 (Nutrient-mediated Dominance): *Increasing nutrient availability resulting from Arctic warming disproportionately benefits nitrogen-demanding shrubs (Fig. 1, arrow C, D).*

Hypothesis 3 (More Time to Win): *Earlier snowmelt favors shrub expansion by extending the period over which deciduous shrubs outperform their competitors (Fig. 1, arrow A).*

The Arctic is warming 3-4x the global average…
with ecological consequences



NOAA Climate.gov
Data: ARC 2023