# TUNDRA COEXISTENCE MODEL

community of species $i = 1, \ldots, Q$, defined by Height $H_i$

$$H_1 > H_2 > H_3 > \ldots > H_j > H_i$$

ramets are born at their full height, when parent ramet has accumulated enough carbon to produce it's biomass

- ramet biomass is related allometrically to height s.t

$B_i = bH_i^\beta$, thus by Biomass sp. are also ordered

$$B_1 > B_2 > B_3 > \ldots B_j > B_i$$

$b$: biomass conversion parameter, e.g. basal diameter * wood density * wood density

$\beta$ : using allometric eq^n's, $\Rightarrow \beta = 5$

$$H \sim D^{\frac{1}{2}}$$

$$B = \underset{\sim D^{\frac{1}{2}}}{\text{height}} * \underset{\sim D^2}{\text{basal diameter}} \sim D^{\frac{5}{2}}$$

$$\Rightarrow \beta = 5$$

- ramet crown area we fix to be equal for all species to start

i.e. $C_i = C_j \quad \forall i, j$

we also fix leaf area per unit crown area (LAI) to be $v$ for all species.

Thus $C_i v = C_j v$ = photosynthetically active leaf area per ramet is the same for all species

We will call this value $c$ = leaf area per ramet

- ramet carbon gain is the balance between photosynthesis gain and [respiration + maintenance cost] loses per unit leaf area

- ramet carbon economy:

$A(L)$ : photosynthesis rate per unit leaf area

$\uparrow$ light level experienced by unit of leaf area

$r$ : respiration and construction costs, essentially all carbon losses pooled

$$g_i = [A(L) - r]\, c$$ : rate of carbon accumulation per ramet

$c$: $\uparrow$

$$\left[\frac{\text{carbon}}{t \cdot \text{leaf area}}\right]\left[\frac{\text{leaf area}}{\text{individual}}\right] = \frac{\text{carbon}}{\text{indiv.} \cdot \text{time}}$$

this is the rate at which an individual ramet of sp. $i$ accumulates carbon, when exposed to light level $L$

once a ramet accumulates enough biomass to make a "baby" = full size ramet, i.e. $B_i$, it reproduces. The time until reproduction $T_i$ is thus dependent on both the

1) carbon accumulation rate $g(L)$, thus light

2) biomass. $B_i$, s.t.

$$g(L)\, T_i = B_i$$

$$\Rightarrow T_i = \frac{B_i}{g(L)}$$ } a function of ramet biomass $B_i$, light per ramet $L$

This time interval $T_i$ sets the rate of reproduction per ramet of species $i$.

After time $t$, a ramet will have produced $\left\lfloor \frac{t}{T_i} \right\rfloor$ offspring.
floor

• ramet demography

ramet fecundity is given by approximately $\frac{1}{T_i}$

ramet mortality is consant value per unit time

$m_i$ : species specific mortality rate

• ramet popⁿ dynamics.

we can track the number of individual ramets [per unit area], i.e. the density of species i

$\hat{N}_i(t)$ : $\frac{\text{\# individuals of sp } i}{\text{area}}$ over time

$$\frac{dN_i}{dt} = f_i N_i - m_i N_i = (f_i - m_i) N_i$$

$$\left[\frac{\text{\# indiv}}{\text{indiv}\cdot\text{time}} - \frac{\text{\# indiv}}{\text{indiv}\cdot\text{time}}\right]\left[\frac{\text{indiv}}{\text{area}}\right] = \left[\frac{\text{indiv}}{\text{area}\cdot\text{time}}\right]$$

↑ approximately

* This is a little more complicated due to the lag in reproduction since ramets are born FULL SIZE only

Our goal would be to define an expression for $\hat{N}_i$ when $\frac{dN_i}{dt} = 0$ ~ the system is at equilibrium

To get around ↑ we can use the fact that when $\frac{dN_i}{dt} = 0$, each ramet only exactly replaces itself in it's lifetime

i.e. the lifetime reproductive success (LRS) = 1 for all ramets of sp i

• ramet lifetime reproductive success

We can write ramet LRS as the $\infty$ sum of the number of times it accumulates enough carbon to make a baby.

$$LRS(R_i) = \sum_{w=0}^{\infty} \underbrace{e^{-m_i T_i w}}_{\text{Probability of survival until time } T_i w} ( \underbrace{b(w)}_{\text{\# offspring produced at age } w} ) = \sum_{w=1}^{\infty} e^{-m_i T_i w} (1)$$

$\to b(w) = 1 \; \forall w > 0$

ramet of sp. $i$

$w$: "age" in increments of $T_i$

$b(w) = \begin{cases} 0 & w = 0 \\ 1 & w > 0 \end{cases}$

We can solve for $\hat{T}_i$ at equilibrium with this expression by setting

$$LRS(R_i)\Big|_{eq} = 1 = \sum_{w=1}^{\infty} e^{-m_i \hat{T}_i w}$$

Recall the formula for the closed form of an infinite sum of a geometric series

$$\sum_{k=0}^{\infty} a r^k = \frac{a}{1-r} \quad \text{for } |r| < 1$$

In this format, let

$$a = 1$$
$$r = e^{-m_i T_i} \qquad \text{note this satisfies } |r| < 1$$
$$k = w$$

Then, we have

$$LRS(R_i) = \sum_{w=1}^{\infty} (e^{-m_i T_i})^w$$

$$= \sum_{w=0}^{\infty} e^{-m_i T_i w} - \underbrace{\left[e^{-m_i T_i (0)}\right]}_{\text{subtract term for } w=0}$$

$$= \frac{1}{1 - e^{-m_i T_i}} - 1$$

AT ANY POINT (even not EQ)

$$LRS(R_i) = \frac{e^{-m_i T_i}}{1 - e^{-m_i T_i}} = \text{function of } \begin{cases} B_i \\ L_{\text{light}} \end{cases}$$

per ramet determined by competition

• Equilibrium density $\hat{N}_i$ in clonal ramet world

Set $LRS(R_i) = 1 = \dfrac{e^{-m_i \hat{T}_i}}{1 - e^{-m_i \hat{T}_i}}$ then do some algebra

$$\Rightarrow (1 - e^{-m_i \hat{T}_i}) = e^{-m_i \hat{T}_i}$$

$$2e^{-m_i \hat{T}_i} = 1 \quad \text{rearranging}$$

$$e^{-m_i \hat{T}_i} = \frac{1}{2}$$

$$-m_i \hat{T}_i = \ln\left(\frac{1}{2}\right) = -\ln(2)$$

| at EQ $\hat{N}_i$ | $\hat{T}_i = \dfrac{\ln(2)}{m_i}$ |
|---|---|

by properties of logs

i.e. time to reproduction @ EQ must balance mortality rate

Recall, we have an expression for $T_i$ built from the physiological processes required to create a baby

$$\hat{T}_i = \frac{\ln(2)}{m_i} = \frac{B_i}{g(L_{R_i})} = \frac{B_i}{(a(L_{R_i}) - r)c}$$

Solving this for $\hat{L}_{R_i}$, the level of light per ramet, can tell us what this value must be at equilibrium.

$$a\hat{L}_{R_i} - r = \frac{m_i B_i}{\ln(2)\, c}$$

$$\hat{L}_{R_i} = \left(\frac{1}{a}\right)\left(\frac{m_i B_i}{\ln(2)\, c} + r\right)$$

light experienced by ramet $R_i$ at equilibrium

Based on our formulation of asymmetric light competition, $\hat{L}_{R_i}$ depends on the interspecific densities $\hat{N}_j$ for $j < i$ bigger sp. as well as intraspecific interference $\hat{N}_i$

By writing these formulations, we can get an expression for $\hat{N}_i$

$\hat{N}_i$ = clonal ramet model

$(R_i) + 1 = \frac{e^{-m_i \hat{T}_i}}{1 - e^{-m_i \hat{T}_i}}$ then do some algebra

$(1 - e^{-m_i \hat{T}_i}) = e^{-m_i \hat{T}_i}$ rearranging

$2e^{-m_i \hat{T}_i} = 1$

$e^{-m_i \hat{T}_i} = \frac{1}{2}$

$-m_i \hat{T}_i = \ln\left(\frac{1}{2}\right) = -\ln(2)$ by properties of logs

EQ $N_i$ | $\boxed{\hat{T}_i = \frac{\ln(2)}{m_i}}$

i.e. time to reproduction @ EQ must balance mortality rate

we have an expression for $T_i$ built from the physiological processes required to create a baby

$= \frac{\ln(2)}{m_i} = \frac{B_i}{g(L_{R_i})} = \frac{B_i}{(a(L_{R_i}) - r)c}$

for $\hat{L}_{R_i}$, the level of light per ramet, can what this value must be at equilibrium.

$a\hat{L}_{R_i} - r = \frac{m_i B_i}{\ln(2) c}$

$\hat{L}_{R_i} = \left(\frac{1}{a}\right)\left(\frac{m_i B_i}{\ln(2) c} + r\right)$ light experienced by ramet $R_i$ at equilibrium

on our formulation of ...

$\hat{L}_{R_i}$ depends ...

as well ...

...ring these ...

TAYLOR EXPANSION for APPROX. EXPRESSION of $\hat{N}_i$

an implicit expression for $\hat{N}_i$:

$$\hat{N}_i = \frac{L_{i-1}(1 - e^{-k\hat{N}_i})}{k l_i} = f(\hat{N}_i)$$

Then we can approximate around $\hat{N}_i = 0$,

$$\hat{N}_i = x \qquad f(x) \approx f(0) + f'(0)x + \frac{1}{2}f''(0)x^2$$

From above,

$$f'(x) = -\frac{L_{i-1}}{k l_i}(-k)e^{-kx} = \frac{L_{i-1}}{l_i}e^{-kx}$$

$$f''(x) = \frac{-k L_{i-1}}{l_i}e^{-kx}$$

So we have

$$f(x) = f(0) + f'(0)x + \tfrac{1}{2}f''(0)x^2$$

$$f(x) = 0 + \frac{L_{i-1}}{l_i}x + \frac{-kL_{i-1}}{2l_i}x^2$$

$$0 = \frac{-kL_{i-1}}{2l_i}x^2 + \left[\frac{L_{i-1}}{l_i} - 1\right]x$$

$$0 = \left(\frac{-kL_{i-1}}{2l_i}x + \left(\frac{L_{i-1}}{l_i} - 1\right)\right)x$$

$x = 0$ or

$$\hat{N}_i \approx \frac{2}{K}\left(1 - \frac{l_i}{L_{i-1}}\right)$$

$$\text{sol}^{\underset{\sim}{n}}\text{s} \begin{cases} x = \left[\dfrac{L_{i-1} - l_i}{\cancel{l_i}}\right]\left[\dfrac{2\cancel{l_i}}{kL_{i-1}}\right] = \dfrac{2(L_{i-1} - l_i)}{kL_{i-1}} = \dfrac{2L_{i-1}}{kL_{i-1}} - \dfrac{2l_i}{kL_{i-1}} = \dfrac{2}{K} - \dfrac{2l_i}{kL_{i-1}} \\ x = 0 \end{cases}$$

APPROXIMATE SOLⁿ for $\hat{N}_i$ :

2nd order taylor expansion around $\hat{N}_i = 0$

$$\hat{N}_i \approx \begin{cases} \hat{N}_i = 0 \\ \hat{N}_i = \frac{2}{K}\left(\frac{L_{i-1} - l_i}{L_{i-1}}\right) \end{cases}$$

$l_i$ cannot exceed $L_{i-1}$ for there to be a nonzero EQ solⁿ

the faster light decays in the canopy, the smaller EQ density possible

% of difference in available light ($L_{i-1}$) and light required for invasion ($l_i$)
the larger this % difference, the higher $\hat{N}_i$

CTS SOLⁿ for $n(l)$ · equilibrium density:

$$n(l) = \frac{1}{Kl} \qquad \text{when } \Delta l = l_{i-1} - l_i \to 0$$

APPROXIMATE SOL$^{\underline{N}}$ for $\hat{N}_1$:

2nd order taylor expansion around $\hat{N}_1 = 0$

$$\hat{N}_1 \approx \begin{cases} \hat{N}_i = 0 \\ \hat{N}_1 = \frac{2}{K}\left(\frac{L_{i-1} - l_i}{L_{i-1}}\right) \end{cases}$$

$l_i$ cannot exceed $L_{i-1}$ for there to be a nonzero EQ sol$^{\underline{n}}$

the faster light decays in the canopy, the smaller EQ density possible

% of difference in available light ($L_{i-1}$) and light required for invasion ($l_i$)
the larger this % difference, the higher $\hat{N}_i$

CTS SOL$^{\underline{n}}$ for $n(l)$: equilibrium density:

$$n(l) = \frac{1}{Kl} \quad \text{when } \Delta l = l_{i-1} - l_i \to 0$$

LIGHT COMPETITION in a clonal ramet tundra world

Verbally, each species occupies one height $H_i$ in the canopy

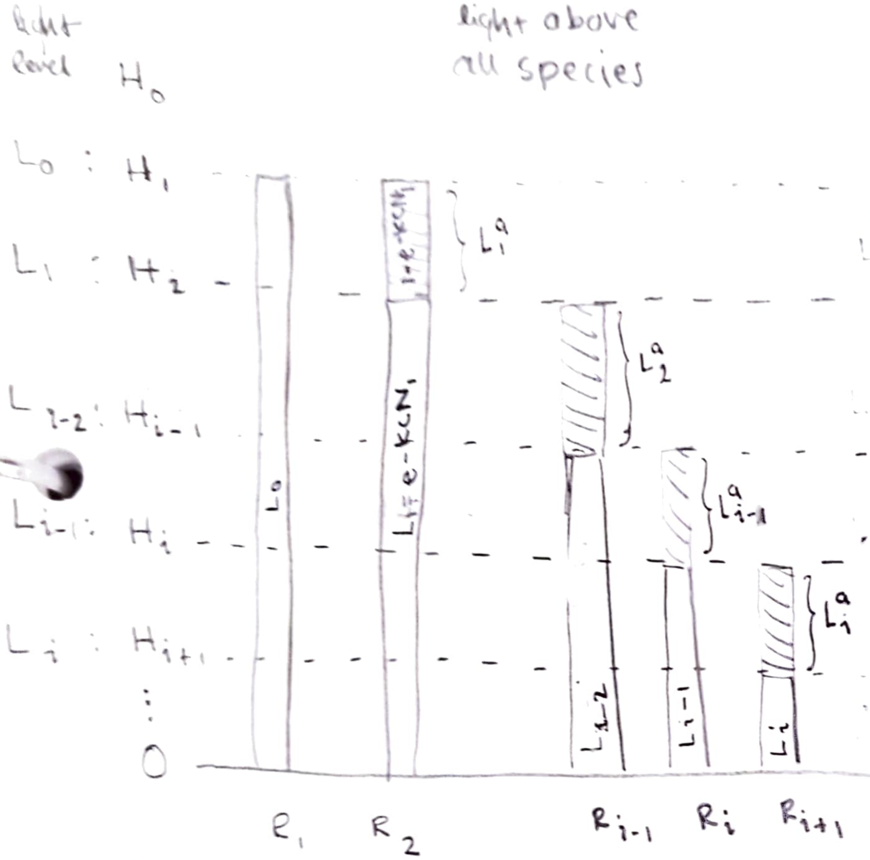
At the canopy height of species $i$, light is set by the number of ramets of taller species.

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

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

$L_0$ ↑ light above all species

$k$ ↑ extinction coefficient




LIGHT ENVIRONMENT at Height $H_i$ = $L_{i-1}$ ↖ set by all taller species

$L_0$

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

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

$L_{i-1}^T = e^{-kc\sum_{j=1}^{i-1} N_j}$ 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$\underline{^{n}}$s:

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

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

$L_{i-1}^T$ 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 $i$

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

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

• light available for 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 $(1 - e^{-kcN_i})$

i.e. are there big gaps in the canopy?

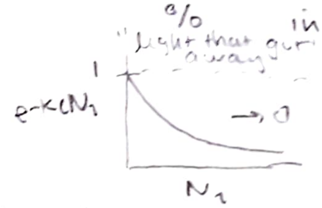
3) how many ways the ramets need to share the captured light $N_i$

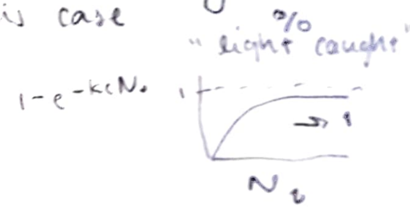
"the light that got away"

$$L_i^R \quad \frac{L_i^a}{N_i} = \frac{L_{i-1}(1 - e^{-kcN_i})}{N_i}$$

light absorbed by canopy i divided among the ramets equally

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

EQUILIBRIUM LIGHT LEVEL per Ramet of sp. i

This is the light level required for a ramet of sp. i to have a $LES(R_i) = 1$, i.e. for the system to be at EQUILIBRIUM

$$\frac{dN_i}{dt} = (f_i - m_i)\hat{N}_i = 0$$

from above, we know this must be

$$\hat{L}_{E_i} = \left(\frac{1}{a}\right)\left(\frac{m_i B_i}{\ln(2)\, c} + r\right)$$

we can condense some parameters for ease of calculation. specifically,

$$m_i' = \frac{m_i}{\ln(2)} \quad \text{and} \quad \begin{matrix} a' = ac \\ r' = rc \end{matrix} \longrightarrow \begin{matrix} m_i \\ a \\ r \end{matrix}$$

$$a\hat{L}_{E_i} - r = m_i B_i \Rightarrow$$

$$\hat{L}_{E_i} = \frac{m_i B_i + r}{a}$$ at equilibrium by def$^{\underline{n}}$

This gives us an implicit def$^{\underline{n}}$ of $\hat{N}_i$ as a function of

1) physiological, demographic, and allometric parameters for sp. i

2) light level at the top of the canopy, $L_{i-1}$

when we combine the above expression with our def$^{\underline{n}}$ of light competition -

$$\hat{L}_{E_i} = \underbrace{\frac{L_{i-1}(1 - e^{-kc\hat{N}_i})}{\hat{N}_i}}_{\text{light decay + competition}} = \underbrace{\frac{m_i B_i + r}{a}}_{\text{sp. traits}} \Rightarrow$$

EQ. expression $\underbrace{(m_i B_i + r)\hat{N}_i}_{\text{carbon loss}} = \underbrace{aL_{i-1}(1 - e^{-kc\hat{N}_i})}_{\text{carbon gain @ sp. level}}$

IMPLICIT DEF$^{\underline{N}}$ of $\hat{N}_i$

INVASION CONDITION for sp. $i$

For a species to invade from rare and persist, it must satisfy $LRS(R_i) \geq 1$ for $N_i \approx 0$.

Now, given the expression for light competition, we must take the limit as $N_i \to 0$.

$$\lim_{N_i \to 0} L_{R_i} = \lim_{N_i \to 0} \frac{L_i^a}{N_i} = \lim_{N_i \to 0} \frac{L_{i-1}(1-e^{-kcN_i})}{N_i}$$

$$L_{R_i}\Big|_{N_i \to 0} = ck L_{i-1}$$

We know that for species $i$

$$L_{R_i}\Big|_{N_i \to 0} = ck L_{i-1} \geq \frac{m_i B_i + r}{a} = \hat{L}_{R_i}$$

$\Rightarrow$ $L_{i-1} \geq \frac{\hat{L}_{R_i}}{ck} = l_i$ is the condition for invasion i.e. the light required by sp. $i$ to invade

we can then define sp. based on this light requirement ~ trait ~ that is independent of other sp in the community

$$l_i = \frac{m_i B_i + r}{ack}$$ light required for sp. $i$ to invade when rare

$$\hat{L}_{R_i} = \frac{m_i B_i + r}{a}$$ light required for a ramet to have $LRS(R_i) = 1$, i.e. be at EQ from demography

$$L_{R_i} = \frac{L_{i-1}(1-e^{-kcN_i})}{N_i}$$ light acquired per ramet from act^n of light competition

$l_i$ INVASION CONDITION INFORMED definition of EQ DENSITY $\hat{N}_1$

We can rewrite the expression for EQ in terms of $l_i$

$$(m_i B_i + r)\hat{N}_i = a L_{i-1}(1-e^{-kc\hat{N}_i})$$

Note that $l_1 = \frac{m_i B_i + r}{ack}$, so $\Rightarrow$

$$\frac{(m_i B_i + r)}{ack}\hat{N}_i = L_{i-1}(1-e^{-kc\hat{N}_1}) \Rightarrow$$

$$l_i \hat{N}_1 = \frac{L_{i-1}(1-e^{-kc\hat{N}_1})}{kc}$$

$\rightarrow$ we can consolidate $K = kc$

EQ expression implicitly defining $\hat{N}_1$ by sp. traits

$$l_i \hat{N}_1 = \frac{L_{i-1}(1-e^{-K\hat{N}_i})}{K}$$

EQ. DENSITY w/respect to $l$ cts def$^{\underline{n}}$ $n(l)$

$$\hat{N}_1 = \frac{L(l_{i-1}) - L(l_i)}{K l_i}$$

let $\Delta l = l_{i-1} - l_i$. then

$$n(l) = \lim_{\Delta l \to 0} \frac{\hat{N}_i}{\Delta l} = \frac{L(l_i + \Delta l) - L(l_i)}{K l_i \Delta l} = \left(\frac{1}{K l_i}\right)\frac{dL}{dl}$$ by def$^{\underline{n}}$ of derivative

$\uparrow$

density of indiv/area along cts trait axis $l$ = light requirement to invade from rare

$$n(l) = \left(\frac{1}{Kl}\right)\frac{dL}{dl}$$

## Continuous description of the light environment $L(l)$

Def$^n$: $L(l)$ is the light level measured under the canopy of the sp. that requires $l$ light per ... to maintain ...

Each $l$ will correspond to a specific biomass and height $h$, based on allometric, physiological and demographic parameters of each sp. and the light extinction coefficient $k$

$$l = \frac{mk + r}{\ldots} \Rightarrow$$

$$H^{\circ} \ldots h = \frac{l\,a\,k - r}{m}$$ for a given light requirement $l$

↑ height

We can define $L(l_i) = L_i$ by taking the limit of the sum of species taller and equal to the height of sp. $i$

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

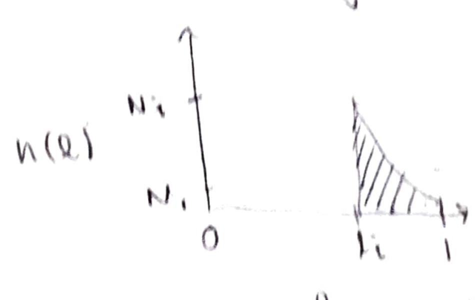
by def$^n$ of light decay according to Beer's law

↓

$$\log(L_i) = -k\sum_{j=1}^{i} N_j \Rightarrow$$

$$\left(-\frac{1}{k}\right)\log(L_i) = \sum_{j=1}^{i} N_j$$

now consider writing this as the integral




let $j = 1$, s.t. $1 - l_j \to 0$

sp. w/ light requirement $l_i - l_0 = 1$

$$\left(-\frac{1}{k}\right)\log(\underbrace{L(l_i)}) = \int_{l_i}^{1} n(l)\,dl$$

light under canopy of sp. $l_i$

sp. w/ light requirement $l_i$

LIGHT ENVIRONMENT cts density description

$$\left(-\frac{1}{K}\right) \log(L(\ell)) = \int_\ell^1 n(\ell')\, d\ell'$$

take the derivative w/ respect to $\ell$, $\frac{d}{d\ell}$

$$-\left(\frac{1}{K}\right) \frac{d}{d\ell} \log(L(\ell)) = \frac{d}{d\ell} \int_\ell^1 n(\ell')\, d\ell' = -\frac{d}{d\ell} \int_1^\ell n(\ell')\, d\ell'$$

$$-\left(\frac{1}{K}\right)\left(\frac{1}{L(\ell)}\right) \frac{dL}{d\ell} = -n(\ell)$$

$$\frac{dL}{d\ell} = K n(\ell) L(\ell)$$

amount of light under canopy $\ell$

EQ. ramet density

light extinction coefficient

change in light level under canopy $\ell$

from def$^{\underline{n}}$ of light competition and decay

DEF$^{\underline{N}}$ OF EQ RAMET DENSITY in cts trait space

$$n(\ell) = \left(\frac{1}{K\ell}\right) \frac{dL}{d\ell} \Rightarrow \ell K n(\ell) = \frac{dL}{d\ell}$$

Putting these two descriptions together, we get

$$K \cancel{n(\ell)} L(\ell) = K \ell \cancel{n(\ell)}$$

$$L(\ell) = \ell \qquad \Rightarrow \qquad \frac{dL}{d\ell} = 1$$

$$n(\ell) = \frac{1}{K\ell} = \frac{a}{m_\ell B_\ell + r}$$