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1 A two layer model

1.1 Equations and assumptions

The equations for the upper and lower canopies are:

$$\frac{dG_u}{dt} = r_u S^\beta G_u \big(1 - \frac{G_u}{k_u}\big) \tag{1}$$

$$\frac{dG_l}{dt} = r_l S^\beta G_l \big(1 - \frac{G_l}{k_l}\big) - \alpha G_u G_l, \tag{2}$$

where subscripts indicate the canopy level, G is the biomass density, r is the growth rate, k is the carrying capacity, and α is a competition parameter, which effects the lower canopy only.

A vegetation growth limiting factor, S^β, slows the biomass growth rates as soil moisture decreases; this effect increases with increasing β.

Assume that fires occur with fixed return interval ξ and severity ϕ_S. The biomass immediately before each fire ($G_{u,max}$) and immediately after (G_{uo}) are related as:

$$\frac{G_{u,max}}{G_{uo}} = \frac{1}{\phi_R} \tag{3}$$

where ϕ_R is the proportion of biomass that remains after each fire. Defining fire severity as $\phi_S = 1-\phi_R$:

$$\frac{G_{u,max}}{G_{uo}} = 1 - \frac{1}{\phi_S} \tag{4}$$

1.2 Analytic solution for the upper canopy

Equation 1 is the logistic equation, and has an analytic solution:

$$G_u = \frac{k_u G_{uo}}{G_{uo} + (k_u - G_{uo})e^{-r'_u t}} \tag{5}$$

where G_{uo} is the initial biomass, and $r'_u = r_u S^\beta$ combines the growth rate and growth-limiting factor into an ‘effective‘ growth rate.

If time is measured as the time since the previous fire, then $G_u(t = 0) = G_{uo}$ and $G_u(t = \xi) = G_{u,max}$ (once the system is in a dynamic steady state):

$$\frac{G_{u,max}}{G_{uo}} = \frac{1}{\phi_R} = \frac{k_u}{G_{uo} + (k_u - G_{uo})e^{-r'_u \xi}} \tag{6}$$

Solving for G_{uo}:

$$G_{uo} = k_u \; \frac{\phi_R - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \tag{7}$$

Or, in terms of severity:

$$G_{uo} = k_u \; \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \tag{8}$$

Mean upper canopy biomass

Integrate Equation 5 to get average G_u:

$$\int_{G_{uo}}^{G_{u,max}} G_u dt = \int_0^\xi \frac{k_u G_{uo}}{G_{uo} + (k_u - G_{uo})e^{-r'_u t}} dt$$

$$= \frac{k_u}{r'_u} \log\left(|G_{uo} - G_{uo}e^{r'_u \xi} - k_u|\right) - \frac{k_u}{r'_u} \log\left(|-k_u|\right),$$

which simplifies to:

$$\int_{G_{uo}}^{G_{u,max}} G_u dt = \frac{k_u}{r'_u} \log\big(1 + \frac{G_{uo}}{k_u}(e^{r'_u\xi} - 1)\big)$$

Once the system is in dynamic equilibrium, the mean upper canopy biomass $\hat{G}_u$ is:

$$\hat{G}_u = \frac{k_u}{r'_u\xi} \log\left(1 + \frac{G_{uo}}{k_u}(e^{r'_u\xi} - 1)\right) \tag{9}$$

Substitute Equation 8 and simplify:

$$\hat{G}_u = \frac{k_u}{r'_u\xi} \log\big(1 + \frac{1 - \phi_S - e^{-r'_u\xi}}{1 - e^{-r'_u\xi}}(1 - e^{-r'_u\xi})\big) \tag{10}$$

$$\hat{G}_u = k_u\big(1 + \frac{1}{r'_u\xi}\log(1 - \phi_S)\big) \tag{11}$$

1.3 A modified logistic equation for the lower canopy

The equation for the lower canopy is:

$$\frac{dG_l}{dt} = r_l S^\beta G_l\left(1 - \frac{G_l}{k_l}\right) - \alpha G_u G_l \tag{12}$$

Since we have an analytic solution for $\hat{G}_u$, we can modify the logistic equation to solve for $\hat{G}_l$. Rewrite G_l in logistic equation form:

$$\frac{dG_l}{dt} = r'_l\left(1 - \frac{G_l}{k'_l}\right) \tag{13}$$

where $r'_l = r_l S^\beta - \alpha\hat{G}_u$ and $k'_l = k_l r'_l / r_l S^\beta$.

The analytic solution for G_{uo} (Equation 8) can then be used to estimate G_l after the fire:

$$G_{lo} = k'_l\ \frac{1 - \phi_S - e^{-r'_l\xi}}{1 - e^{-r'_l\xi}} \tag{14}$$

Similarly, the analytic solution for the mean biomass (Equation 11) can be used to estimate $\hat{G}_l$:

$$\hat{G}_l = k'_l\left(1 + \frac{1}{r'_l\xi}\log(1 - \phi_S)\right) \tag{15}$$

Substitute $\hat{G}_u$ (Equation 11) into $r'_l = r_l S^\beta - \alpha\hat{G}_u$ to get the modified growth rate:

$$r_l' = r_l S^\beta - \alpha k_u\big(1 + \frac{1}{r_u'\xi}\log(1-\phi_S)\big) \tag{16}$$

And similarly for $k_l' = k_l r_l'/r_l S^\beta$:

$$k_l' = \frac{k_l}{r_l S^\beta}\Big[r_l S^\beta - \alpha k_u\big(1 + \frac{1}{r_u'\xi}\log(1-\phi_S)\big)\Big] \tag{17}$$

Which simplifies to:

$$k_l' = k_l\Big[1 - \frac{\alpha k_u}{r_l S^\beta}\big(1 + \frac{1}{r_u'\xi}\log(1-\phi_S)\big)\Big] \tag{18}$$

2 Stability

2.1 Stability: conditions to sustain upper canopy biomass

Requiring that $\hat{G}_u > 0$ in Equation 11 yields:

$$\phi_S < 1 - e^{-r_u S^\beta \xi} \tag{19}$$

In terms of return time:

$$\xi > -\frac{1}{r_u S^\beta}\log(1-\phi_S) \tag{20}$$

For lower growth rates, a longer return interval is needed to sustain biomass. Increasing β and/or decreasing S lowers the effective upper canopy growth rate

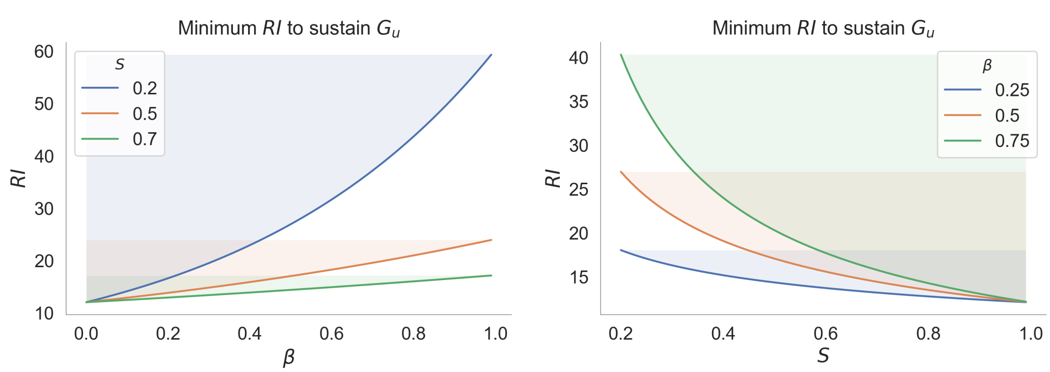

Figure 1: As β increases (left) or S decreases (right), the effective growth rate r_u' decreases, and so the minimum RI to sustain biomass increases.

If $\beta > 0$, a longer return time is needed for lower soil moisture conditions:

Rearranging to find the minimum soil moisture to sustain the upper canopy:

$$S > \Big(-\frac{1}{r_u \xi} \log(1-\phi_S) \Big)^{1/\beta} \tag{21}$$

$$\hat{G}_u = \begin{cases} k_u \big(1 + \frac{1}{r'_u \xi} \log(1-\phi_S)\big) & \text{if } S > \big(-\frac{1}{r_u \xi}\log(1-\phi_S)\big)^{1/\beta} \\ 0 & \text{otherwise} \end{cases} \tag{22}$$

2.2 Stability: Relating return interval and severity for the upper canopy

Suppose $\hat{G}_u = \gamma k_u$, where $\gamma < 1$. From Equation 11:

$$\gamma = 1 + \frac{1}{r'_u \xi} \log(1-\phi_S) \tag{23}$$

$$\xi = -\frac{1}{r'_u(1-\gamma)} \log(1-\phi_S) \tag{24}$$

Rearranging for ϕ_S:

$$\phi_S = 1 - e^{-\xi r'_u (1-\gamma)} \tag{25}$$

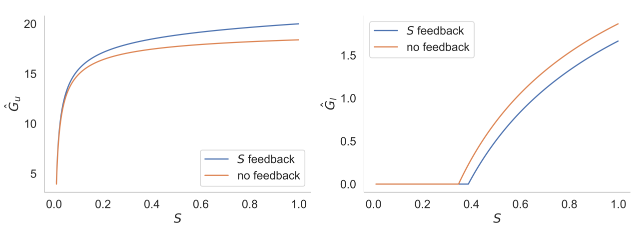

Figure 2: The relationship between $\hat{G}_u$ and k_u constrains that between RI and severity, and vice versa.

2.3 Stability: maximum return interval for a lower canopy

Equation 15 can be used to estimate the conditions for which $\hat{G}_l > 0$:

$$\hat{G}_l = k'_l \big(1 + \frac{1}{r'_l \xi} \log(1-\phi_S)\big) > 0 \tag{26}$$

$$\frac{1}{r'_l \xi} \log(1-\phi_S) > -1 \tag{27}$$

With some math:

$$\xi > -\frac{\log(1-\phi_S)}{r_u S^\beta} \frac{\alpha k_u - r_u S^\beta}{\alpha k_u - r_l S^\beta} \tag{28}$$

In cases where $\alpha k_u - r_l S^\beta < 0$, there is no maximum ξ to sustain G_l. Figure 3 shows example stability curves for $\hat{G}_l$ with varying β.

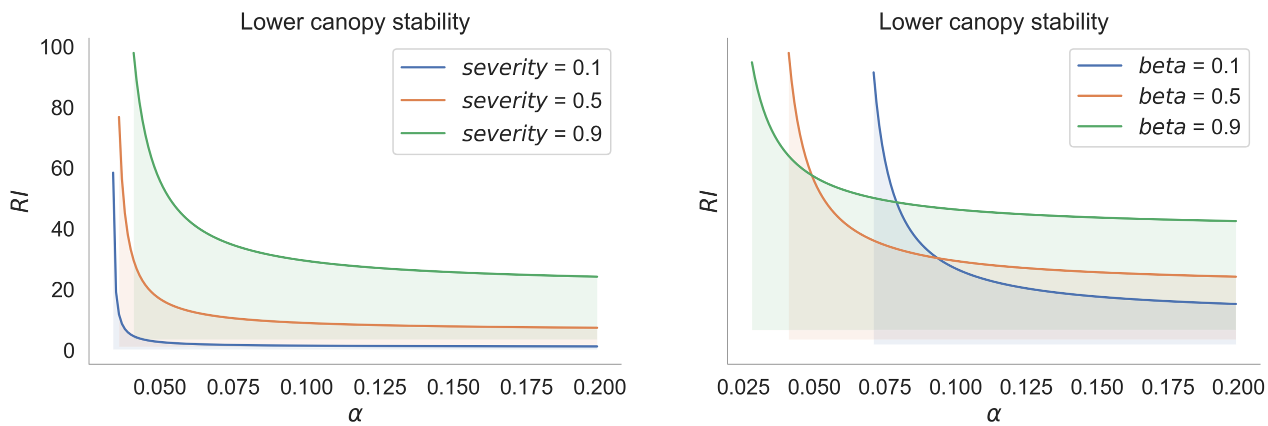

Figure 3: The maximum return interval for which a lower canopy is observed is complicated. (A) The lower canopy is more stable for higher severity fires; (B): If α is small, $\hat{G}_u$ is stability for small beta; the opposite is observed for large α

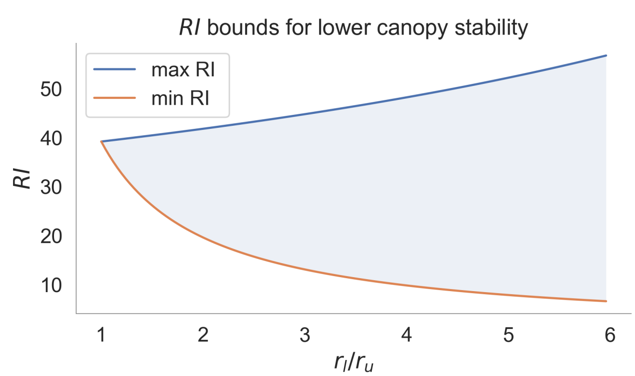

Figure 4: The lower canopy stability is sensitive to r_l. As lower canopy growth rate decreases, so does the range of values for which $\hat{G}_l > 0$,

2.4 $\hat{G}_l$ along the $\xi - \phi_S$ curves of constant $\hat{G}_u$

Does G_l vary along the $\xi - \phi_S$ curves of constant upper canopy $\hat{G}_u$? Specifying that $\hat{G}_u = \gamma k_u$ implies the relation between ϕ_S and ξ:

$$\phi_S = 1 - e^{-\xi r'_u (1-\gamma)}$$

Rearranging:

$$\frac{\log(1-\phi_S)}{r'_u \xi} = -(1-\gamma) \tag{29}$$

Substituting this constraint into the equations for r'_l and k'_l:

$$r'_l = r_l S^\beta - \alpha k_u \gamma \tag{30}$$

$$k'_l = k_l \left(1 - \frac{\alpha k_u \gamma}{r_l S^\beta}\right) \tag{31}$$

Substituting r'_l and k'_l into the equation for $\hat{G}_l$:

$$\hat{G}_l = k'_l \big(1 - \frac{(1-\gamma) r'_u}{r'_l})\big) \tag{32}$$

$$\hat{G}_l = k_l \left(1 - \frac{\alpha k_u \gamma}{r_l S^\beta}\right)\left(1 - \frac{(1-\gamma) r_u S^\beta}{(r_l S^\beta - \alpha k_u \gamma)}\right) \tag{33}$$

$$\hat{G}_l = k_l \left(1 - \frac{\alpha k_u \gamma - (1-\gamma) r_u S^\beta}{r_l S^\beta}\right) \tag{34}$$

Above, by specifying that $\hat{G}_u = \gamma k_u$, $\hat{G}_l$ does not depend on return interval or severity.

3 Potential feedbacks

3.1 Modify ignition probability to decrease with increasing S

Suppose the probability of ignition is: $p = \frac{1-S}{\xi}$.

The effective return time will be: $\xi' = \frac{\xi}{1-S}$, and the equation for $\hat{G}_u$ becomes:

$$\hat{G}_u = k_u \big(1 + \frac{(1-S)}{r_u S^\beta \xi} \log(1-\phi_S)\big) \tag{35}$$

4 Soil moisture

4.1 How does biomass change with decreasing soil moisture?

The derivative of $\hat{G}_u$ with respect to soil moisture is:

$$\frac{d\hat{G}_u}{dS} = \begin{cases} \frac{-\beta k_u}{r_u \xi} \log(1-\phi_S) S^{-(1+\beta)} & \text{if } S > \left(-\frac{1}{r_u \xi}\log(1-\phi_S)\right)^{1/\beta} \\ 0 & \text{otherwise} \end{cases} \tag{36}$$

For the lower canopy, the derivative is:

$$\frac{d\hat{G}_l}{dS} = \begin{cases} \frac{\beta k_l}{r_l r_u} S^{-2\beta-1}\left(r_u S^\beta(\alpha k_u - Z) + 2Z\alpha k_u\right) & \text{if } S > \left(-\frac{1}{r_l \xi}\log(1-\phi_S)\right)^{1/\beta} \\ \frac{-\beta k_l}{r_l \xi} \log(1-\phi_S) S^{-1-\beta} & \text{otherwise} \end{cases} \tag{37}$$

where

$$Z = \frac{\log(1-\phi_S)}{\xi} \tag{38}$$

$\hat{G}_l$ has a minimum value where:

$$\left(r_u S^\beta(\alpha k_u - Z) + 2Z\alpha k_u\right) = 0 \tag{39}$$

Rearranging:

$$S^\beta = \frac{-2Z\alpha k_u}{r_u(\alpha k_u - Z)} \tag{40}$$

Using the definition of Z:

$$S^\beta = \frac{-2\log(1-\phi_S)\alpha k_u}{r_u(\alpha k_u \xi - \log(1-\phi_S))} \tag{41}$$

The numerator and denominator are both always positive (because $\log(1-\phi_S) < 0$), so we expect a minima in $\hat{G}_l$ for $\alpha > 0$.

$\frac{d\hat{G}_l}{dS}$ has a discontinuity at $S = \left(-\frac{1}{r_l \xi}\log(1-\phi_S)\right)^{1/\beta}$, where G_l has a maximum value.

5 Estimating parameters

5.1 Estimating growth rates from timescales

Estimate the growth rates from the times for an isolated canopy to grow from ak_u to bk_u, where a and b are constants less than 1. Substituting into the logistic equation solution (with $G_uo = ak_u$):

$$bk_u = \frac{k_u a k_u}{ak_u + (k_u - ak_u)e^{-r_u \tau}} \tag{42}$$

where τ is the timescale to mature.

$$b(ak_u + (k_u - ak_u)e^{-r_u\tau}) = ak_u \tag{43}$$

$$b(a + (1-a)e^{-r'_u t}) = a \tag{44}$$

$$r_u = -1/\tau \log\big(\frac{a(1-b)}{(1-a)}\big) \tag{45}$$

With $a = 0.1$ and $b = 0.9$, then $r_u \approx 4.5/\tau$.

Estimate, growth rates from timescale to mature:

- conifer : $\tau = 30$, $r = 0.15$
- shrubs : $\tau = 10$, $r = 0.45$
- meadow : $\tau = 3$, $r = 1.50$
- grassland : $\tau = 3$, $r = 1.50$

6 Non-dimensionalize

The equations for the upper and lower canopies:

$$\frac{dG_u}{dt} = r_u S^\beta G_u \left(1 - \frac{G_u}{k_u}\right)$$

$$\frac{dG_l}{dt} = r_l S^\beta G_l \left(1 - \frac{G_l}{k_l}\right) - \alpha G_l G_u$$

Non-dimensionalize the upper canopy:

$$\frac{dG_u}{dt} = \frac{r_u S^\beta}{r_u S^\beta}\frac{G_u}{dt} = r_u S^\beta \frac{G_u}{d(r_u S^\beta t)} = r_u S^\beta \frac{G_u}{d\tau}$$

where $\tau = r_u S^\beta t$. Simplifying:

$$\frac{dG_u}{d\tau} = G_u\left(1 - \frac{G_u}{k_u}\right)$$

Let $g_u = G_u/k_u$, or $G_u = k_u g_u$. Then:

$$\frac{dg_u}{d\tau} = g_u\left(1 - g_u\right)$$

Moving on to the lower canopy. Substituting τ for t:

$$r_u S^\beta \frac{dG_l}{d\tau} = r_l S^\beta G_l\left(1 - \frac{G_l}{k_l}\right) - \alpha G_l G_u$$

Let $g_l = G_l/k_l$, or $G_l = k_l g_l$. Then:

$$r_u S^\beta \frac{dg_l}{d\tau} = r_l S^\beta k_l g_l\big(1 - g_l\big) - \alpha g_l k_l g_u k_u$$

$$\frac{dg_l}{d\tau} = \frac{r_l}{r_u} g_l\big(1 - g_l\big) - \frac{\alpha k_u}{r_u S^\beta} g_l g_u$$

So the dimensionless groups are r_l/r_u and $\alpha k_u/S_\beta r_u$, which are a generalized growth rate and competition, respectively. The rescaled time also need to be factored in: $\tau = r_u S^\beta t$

We have several fixed parameters: $k_u = 20$, $r_u = 0.25$, $S = 0.21$.

α ranges from 0 (no competition) to 0.1, β ranges from 0 (no soil moisture feedback) to 1, S^β ranges from 1 to 0.21

let $r = r_l/r_u$ and $\phi = \alpha k_u/S_\beta r_u$,

if r_l ranges from 0.25 to 2.5, r ranges from 1 to 10.

7 How close does G_u get to k_u ?

7.1 G_u approaches k_u leading up to each fire. How close does it get?

The pre-fire biomass is:

$$G_{u,max} = \frac{k_u}{1 - \phi_S} \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \tag{46}$$

Expanding:

$$G_{u,max} = k_u \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - \phi_S - e^{-r'_u \xi} + \phi_S e^{-r'_u \xi}} \tag{47}$$

Define x as:

$$x = \frac{\phi_S e^{-r'_u \xi}}{1 - \phi_S - e^{-r'_u \xi}} \tag{48}$$

so $G_{u,max} = k_u/(1 + x)$:

$$G_{u,max} = k_u \frac{1}{1 + \frac{\phi_S e^{-r'_u \xi}}{1 - \phi_S - e^{-r'_u \xi}}} \tag{49}$$

$G_{u,max} \sim k_u$ when x is very small. Suppose $G_{u,max} = \gamma k_u$, where γ is close to but less than one. Then:

$$k_u/(1 + x) = \gamma k_u \tag{50}$$

Rewriting as $x = 1/\gamma - 1 = C$ (where $C > 0$):

$$\frac{\phi_S e^{-r'_u \xi}}{1 - \phi_S - e^{-r'_u \xi}} = 1/\gamma - 1 = C \tag{51}$$

$$\phi_S e^{-r'_u \xi} = C(1 - \phi_S - e^{-r'_u \xi}) \tag{52}$$

Rearranging gives:

$$\phi_S = \frac{C(1 - e^{-r'_u \xi})}{C - e^{-r'_u \xi}} \tag{53}$$

This is an expression for the severity ϕ_S at which $G_u = \gamma k_u$.

Rearranging, the expression for ξ is:

$$\xi = \frac{1}{r'_u} \log \frac{C + \phi_S}{C(1 - \phi_S)} \tag{54}$$

In the limit that $G_u = k_u$, $C = 0$; Equation 53 yields $\phi_S = 0$, and Equation 54 yields $\xi \to \text{inf}$.

Lower canopy equilibrium

As an alternative approach, what if the lower canopy is in dynamic equilibrium with the upper canopy?

The lower canopy biomass is constant ($\frac{dG_l}{dt} = 0$) if:

$$r_l S^\beta G_l \left(1 - \frac{G_l}{k_l}\right) = \alpha G_{u,max} G_l \tag{55}$$

Solving for G_l:

$$G_{l,eq} = k_l \left(1 - \frac{\alpha G_{u,max}}{r_l S^\beta}\right) \tag{56}$$

where $G_{l,eq}$ denotes the equilibrium value for G_l.

From Equation 8:

$$G_{u,max} = \frac{k_u}{(1-\phi_S)} \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \tag{57}$$

Substituting, the equation is messy:

$$G_{l,eq} = k_l \left(1 - \frac{\alpha k_u}{r_l S^\beta} \frac{(1 - \phi_S - e^{-r'_u \xi})}{(1-\phi_S)(1 - e^{-r'_u \xi})}\right) \tag{58}$$

If $G_{l,eq} > 0$, we expect the lower canopy biomass to approach this value in advance of each fire. However, if $G_{l,eq} = 0$, lower canopy biomass may still be present because the system is out of equilibrium!

Estimate a stability boundary as:

$$\frac{\alpha G_{u,max}}{r_l S^\beta} < 1 \tag{59}$$

Substituting for $G_{u,max}$:

$$\frac{\alpha}{r_l S^\beta} \frac{k_u}{(1-\phi_S)} \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} < 1 \tag{60}$$

And solving for severity as a function for ξ:

$$\phi_S < 1 - \frac{\alpha k_u e^{-r'_u \xi}}{\alpha k_u - r_l S^\beta (1 - e^{-r'_u \xi})} \tag{61}$$