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1 A two layer model

1.1 Equations and assumptions

The equations for the upper and lower canopies are:

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

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

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:

$$\frac{G_{u,max}}{G_{uo}} = \frac{1}{\phi_R} \quad (3)$$

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

$$\frac{G_{u,max}}{G_{uo}} = 1 - \frac{1}{\phi_S} \quad (4)$$

1.2 Analytic solution for the upper canopy

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

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

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):

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

Solving for G_{uo} :

$$G_{uo} = k_u \frac{\phi_R - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \quad (7)$$

Or, in terms of severity:

$$G_{uo} = k_u \frac{1 - \phi_S - e^{-r'_u \xi}}{1 - e^{-r'_u \xi}} \quad (8)$$

Mean upper canopy biomass

Integrate Equation 5 to get average G_u :

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

which simplifies to:

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

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

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

Substitute Equation 8 and simplify:

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

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

1.3 A modified logistic equation for the lower canopy

The equation for the lower canopy is:

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

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:

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

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:

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

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

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

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

$$r'_l = r_l S^\beta - \alpha k_u \left(1 + \frac{1}{r'_u \xi} \log(1 - \phi_S)\right) \quad (16)$$

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

$$k'_l = \frac{k_l}{r_l S^\beta} \left[r_l S^\beta - \alpha k_u \left(1 + \frac{1}{r'_u \xi} \log(1 - \phi_S)\right) \right] \quad (17)$$

Which simplifies to:

$$k'_l = k_l \left[1 - \frac{\alpha k_u}{r_l S^\beta} \left(1 + \frac{1}{r'_u \xi} \log(1 - \phi_S)\right) \right] \quad (18)$$

2 Stability

2.1 Stability: conditions to sustain upper canopy biomass

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

$$\phi_S < 1 - e^{-r_u S^\beta \xi} \quad (19)$$

In terms of return time:

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

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

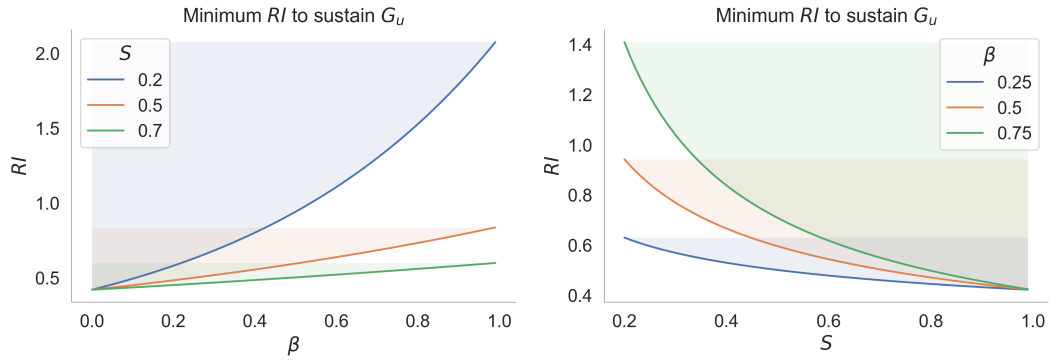


Figure 1: As β increases (left) or S decreases (right), the effective growth rate r'_u decreases, and so the minimum RI to sustain biomass increases.

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:

$$S > \left(-\frac{1}{r_u \xi} \log(1 - \phi_S) \right)^{1/\beta} \quad (21)$$

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

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:

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

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

Rearranging for ϕ_S :

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

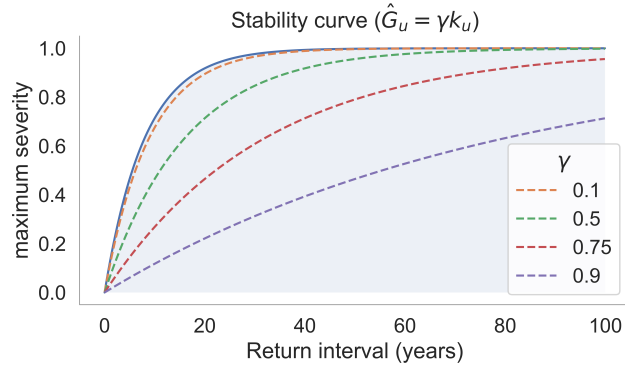


Figure 2: The relationship between \hat{G}_u and k_u constrains that between RI and severity, and vice versa.

2.3 Stability: maximum return interval for a lower canopy

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

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

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

With some math:

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

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 .

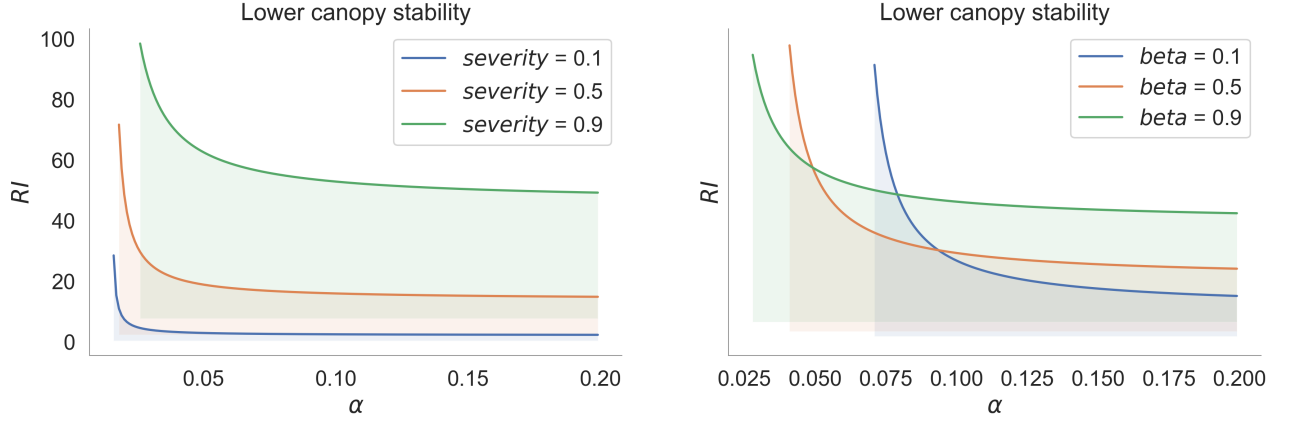


Figure 3: The maximum return interval for which a lower canopy is observed is complicated. (A) The lower canopy is more stable for higher severity fires; (B): If α is small, \hat{G}_u is stability for small beta; the opposite is observed for large α

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:

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

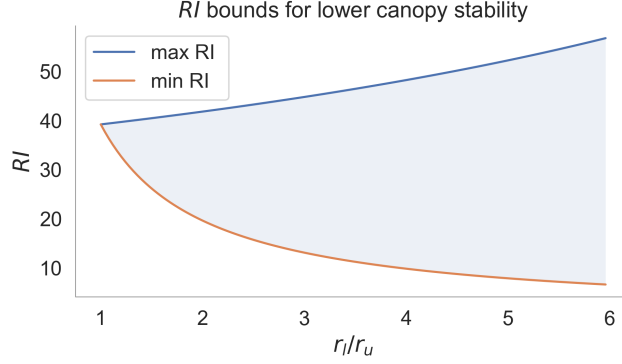


Figure 4: The lower canopy stability is sensitive to r_l . As lower canopy growth rate decreases, so does the range of values for which $\hat{G}_l > 0$,

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

$$r'_l = r_l S^\beta - \alpha k_u \gamma \quad (30)$$

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

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

$$\hat{G}_l = k'_l \left(1 - \frac{(1-\gamma)r'_u}{r'_l} \right) \quad (32)$$

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

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

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:

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

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:

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

For the lower canopy, the derivative is:

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

where

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

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

$$(r_u S^\beta (\alpha k_u - Z) + 2Z\alpha k_u) = 0 \quad (39)$$

Rearranging:

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

Using the definition of Z :

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

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 $G_u o = ak_u$):

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

where τ is the timescale to mature.

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

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

$$r_u = -1/\tau \log \left(\frac{a(1 - b)}{(1 - a)} \right) \quad (45)$$

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:

$$\begin{aligned} \frac{dG_u}{dt} &= r_u S^\beta G_u \left(1 - \frac{G_u}{k_u} \right) \\ \frac{dG_l}{dt} &= r_l S^\beta G_l \left(1 - \frac{G_l}{k_l} \right) - \alpha G_l G_u \end{aligned}$$

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:

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

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:

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

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

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:

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

Expanding:

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

Define x as:

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

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

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

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

$$k_u/(1+x) = \gamma k_u \quad (50)$$

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

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

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

Rearranging gives:

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

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

Rearranging, the expression for ξ is:

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

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

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:

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

Solving for G_l :

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

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

From Equation 8:

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

Substituting, the equation is messy:

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

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:

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

Substituting for $G_{u,max}$:

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

And solving for severity as a function for ξ :

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