Percolation models in fire ecology.

Emmanuel Schertzer (Laboratoire de Probabilités et Modèles Aléatoires,
Collège de France).
Joint work with **A.C. Staver** (Yale U.) and **S.A. Levin** (Princeton U.)

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Oultine

We use fire spread model to investigate a model from ecology and a model in evolution.

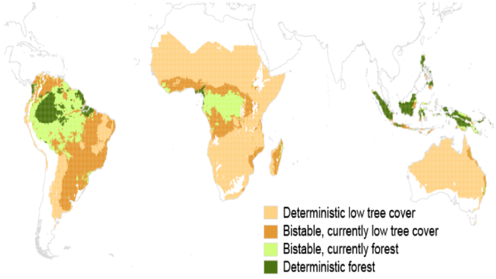
- Part 1 (ecology) Bistability of savanna and forests.
- Part 2 (evolution) Evolution of flammability in C4 grass species.

PART 1: Dynamics of fire spread and the bistability of savanna and forest.

(Joint work with C. Staver and S. Levin. Journal of Mathematical Biology 2014)

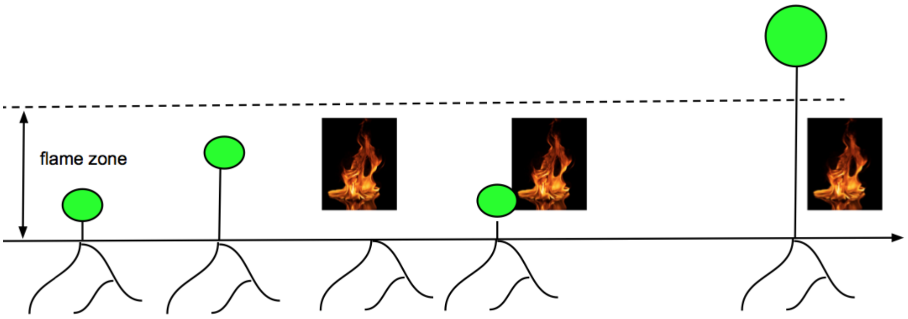
The Savanna Problem.

- Savannas are characterized by the coexistence of grass and tress, with low tree cover.
- Under the same environmental constraints (precipitation, soil composition), savannas and closed canopy forest are two alternative stable biomes.
- At the same location, fossils records have shown evidences of rapid transition from one state to the other.
- Fire hypothesis: fire gives a competitive advantage to grass.
    - at low tree density, fire propagates and tends to exclude trees.
    - at high tree density, fire is not able to propagate, and trees are favored.



Fire and vegetation feedbacks

- Fire readily propagates in savannas, but is blocked beyond a certain tree cover threshold.
- The effect of fire on tree mortality is negligeable. Fire mainly impacts demography.
    - Adult trees have thick bark, and their leaves are high enough to escape the flame zone.
    - Savanna saplings lie within the flame zone, but they are very robust resprouters after a fire, thanks to a sophisticated root system.



    - Saplings can be trapped in the flame zone.
- Fire primarily affects tree cover via its effects on tree establishment (demographic bottleneck).

A model for describing vegetation/fire feedbacks

- Simple model describing the local interaction between fire and vegetation.
- Analytically tractable.
- Provide insights on the physical/ecological processes affecting coexistence and bi-stability.

Individual based model

Individual based model on the square lattice $\mathbb{Z}^2$. Model with two interacting components:

- Ecology: each site can be either Sapling (S), adult tree (T) or grass (G).
- Fire spread.

Fire spread

- Tree patches act as barriers to fire spread.
- Partition the landscape into two parts: (1) fuel (S+G), and (2) non flammable (T).
- An ignition event at a flammable cell z will only be able to propagate to cells within the same flammable cluster. Fire frequency should be higher at sites belonging to a large flammable cluster.
- $F(z)$=density of the connected Flammable component containing z.
- survival probability of z (i.e., probability of not burning):

$$\Omega(F(z))$$

where Ω is a decreasing function.

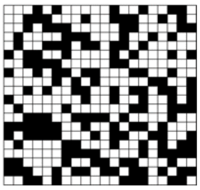
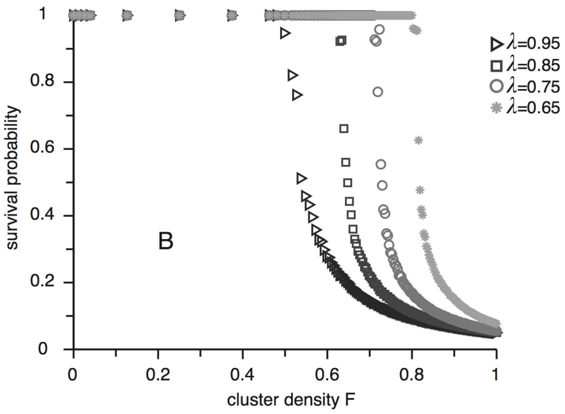


Figure : White = flammable, Black = non flammable

More on Ω

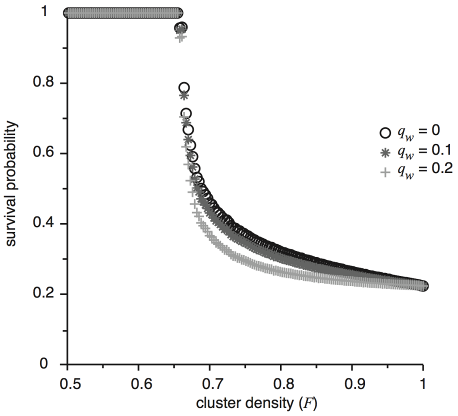
- fire propagates by a nearest neighbor infection process, i.e. if a site is on fire, the fire invades each of its neighboring flammable sites with a given probability λ.
- The survival probability is characterized by
  - A threshold θ_c, under which fire does not propagate through the cluster.
  - A convexity parameter α.



- Threshold $\theta_c \downarrow$ as infection probability $\lambda \uparrow$.

Fire stochasticity

- The interannual stochasticity of the infection rate λ impacts the convexity survival probability.



Fire spread model

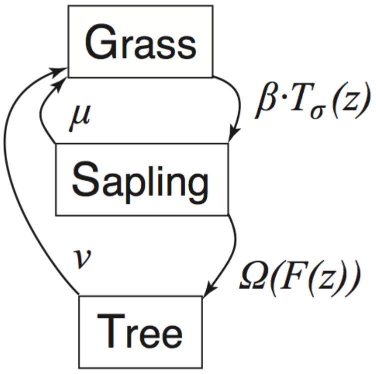
We choose Ω of the form

$$\Omega(F) = \Omega_{\max} - (\Omega_{\max} - \Omega_{\min}) \frac{\max\left((F - \theta_c), 0\right)^{\alpha}}{(1 - \theta_c)^{\alpha}}, \tag{1}$$

- θ_c is a macroscopic expression of the infection probability λ.
- The convexity parameter α encapsulates fire stochasticity.
- Simple enough to make the model analytically tractable, but capture the main features of fire spread (modeled as an infection process).

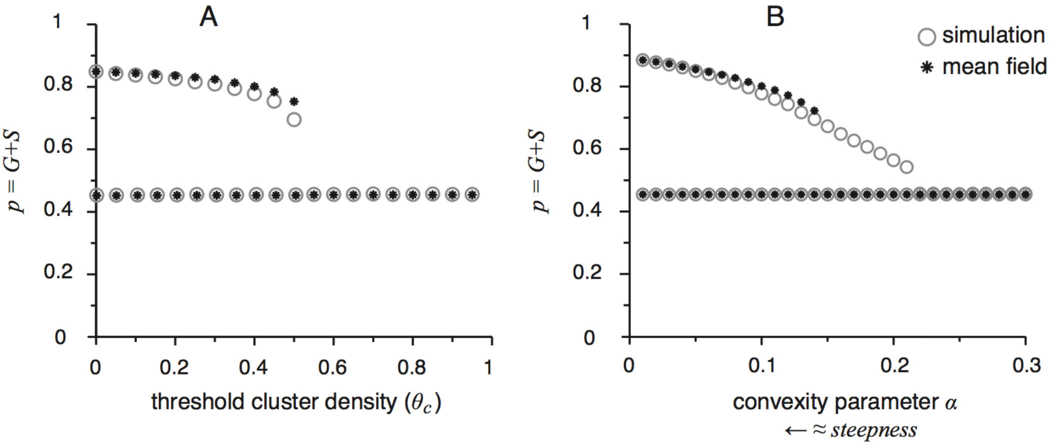
The ecology

- Individual based model on the square lattice on $\mathbb{Z}^2$. Each site can be either Sapling (S), adult Tree (T) or grass (G).



- Fire does not impact tree mortality : death rates ν and μ are constant.
- Saplings invasion rate is proportional to local tree density
  - $T_\sigma(z)$ = local density of tree in a neighborhood of radius $1/\sigma$.
- Adult tree recruitments increases with survival probability.
  - Fire primarily affects tree cover via its effects on tree establishment.

Results



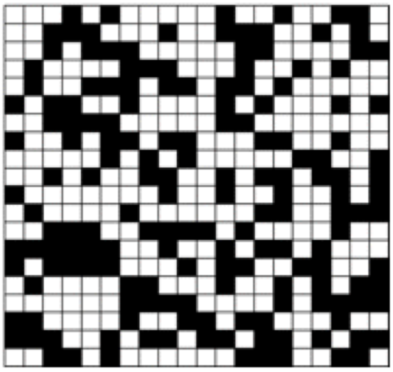
- There is always a "forest equilibrium" (low fuel density, high tree cover).
- High flammability (low θ_c) and high stochasticity (high α) tend to promote a second "savanna" equilibrium (at high fuel density).
- Consistent with the hypothesis that fire stochasticity can promote tree-grass coexistence via the storage effect
- Mild variation in θ_c can trigger a discontinuous transition from a savanna equilibrium to a forest equilibrium. Hysteresis effect.

Analytical results based on percolation theory

- The previous observations can be justified by heuristics arguments based on percolation theory.

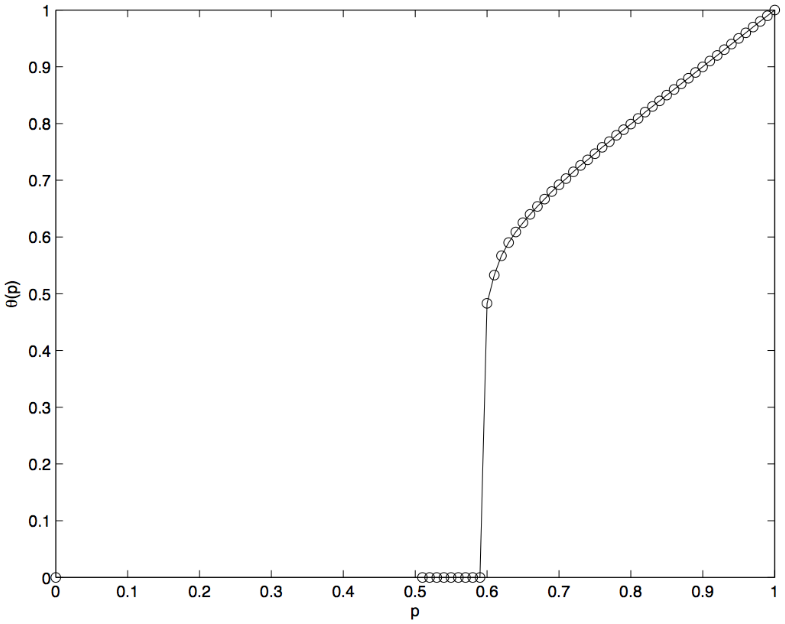
Analytical results based on percolation theory

- Let $p \in [0, 1]$.
- On $\mathbb{Z}^2$, color independently each square in white (resp., in black) with probability p (resp., $1 - p$). There exists $p_c \in (0, 1)$ such that
    - If $p \leq p_c$, there are only finite white clusters.
    - If $p > p_c$, there exists a unique infinite white cluster, whose density is deterministic and is denoted by $\theta(p)$.



Analytical results based on percolation theory

- $\theta(p)$ = density of the infinite cluster as a function of the percolation parameter p.



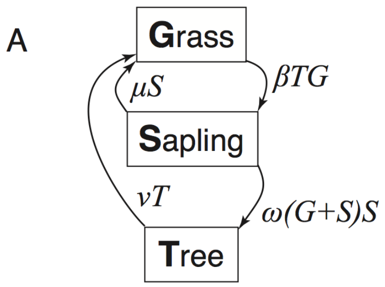
Mean field theory

- Simplifying assumption: The density of S,G and T can evolve in the landscape but spatial aggregation between types does not, i.e. the arrangement of trees and grasses in the landscape remains uncorrelated throughout.
- Assume that the density of fuel (G+S) at time t is given by p_t. Above the percolation threshold p_c:
  - a unique infinite inflammable cluster of density $\theta(p_t)$.
  - the remaining fraction of fuel sites (density $p_t - \theta(p_t)$) belongs to finite clusters (density 0).

Population dynamics

$$\omega(p) \;=\; [\frac{\theta(p)}{p}\Omega(\theta(p)) \;+\; (1-\frac{\theta(p)}{p})\Omega(0)]$$

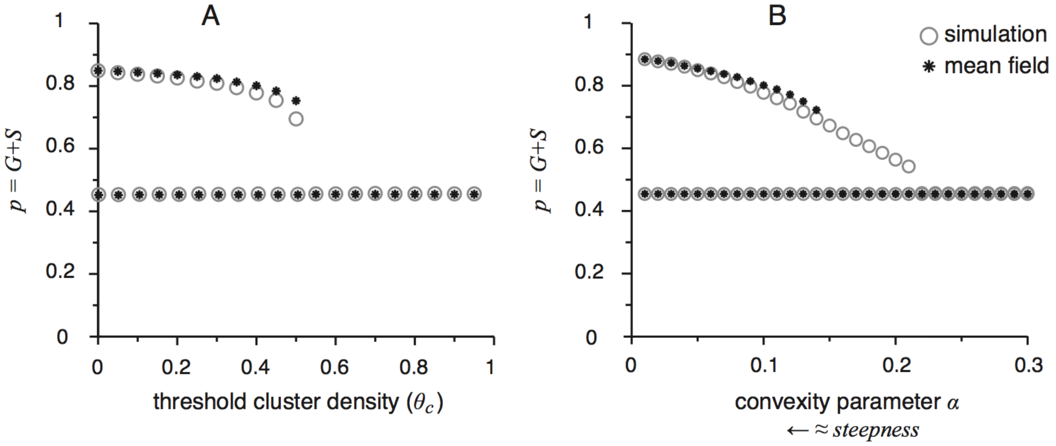
Population-level model:



$$\frac{dG_t}{dt} = \nu T_t - \beta T_t G_t + \mu S_t$$
$$\frac{dS_t}{dt} = \beta T_t G_t - \mu S_t - \omega(p_t) S_t$$
$$\frac{dT_t}{dt} = \omega(p_t) S_t - \nu T_t$$

e.g., during a time interval dt, the fraction of saplings establishing as adult trees is given by $S\;\omega(p)\;dt$

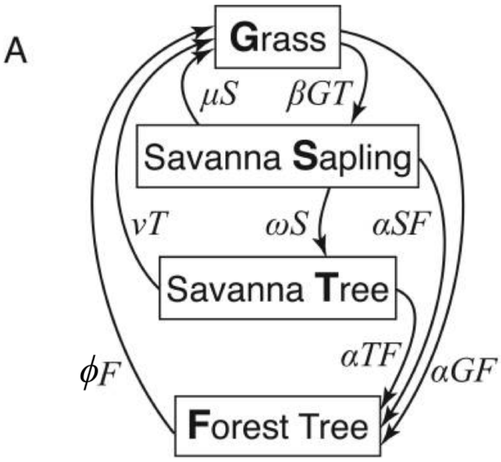
Population dynamics vs IBM



- Population dynamics predict a lower range of parameters under which bistability occurs.
- This shows that taking spatial aggregation into account can be important

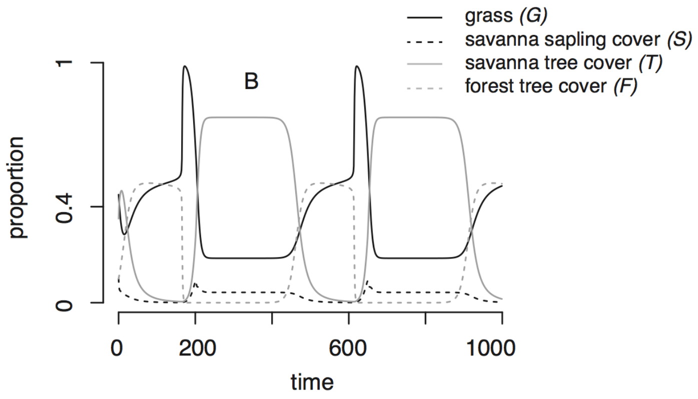
Extension of the population dynamics

- Staver et al ('12) studied an extension of the previous model where Savanna Trees compete with Grass and Forest trees.
- Fire trees more competitive in a fire-free regime.



Extension of the population dynamics

- Existence of heteroclinical cycles in a region of the parameter space.
- Question: can we estimate the parameters to evaluate whether the simulated non-linear oscillations belong to a realistic domain of the parameter space.



PART 2: A model for the evolution of C4 grasses.

(Joint work with C. Staver. Work in progress)

Adaptation of plants in fire prone systems

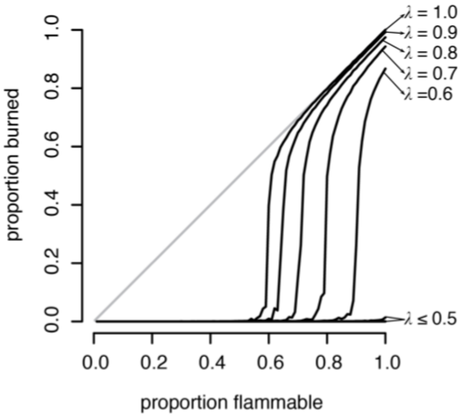
- Plants in fire prone ecosystem are well adapted to their environment.
- Thick bark, investment in root systems allowing savannah trees to re-grow after fire, pines etc ...

Mutch hypothesis (’70)

- “Fire dependent communities burn more readily than non-fire-dependent communities because natural selection has favored development of characteristics that make them more flammable”.
- Species have developed reproductive and anatomic mechanisms to survive fire. “Then” plants might also have evolved traits to enhance the occurrence of fire.

Controversial topic.

- Converse: if plants have developed flammability traits – whether or not as a by-product of selection for other traits – then there must exist some selective pressure for fire-resistant characteristics.
- Main criticism : fire is a collective phenomenon.



Group selection

- Fire occurrences are typically the result of few ignitions resulting in large fires.
- Evolution acts on individuals, not on groups.
- How can one single flammable mutant invade a whole non flammable landscape ?
- Even if it is advantageous from the group point of view, what is the evolutionary force driving individuals to evolve flammability.
- Group selection issue.

Grass evolution

- In savannah, fire prevents tree invasion and gives grass (as a group) a competitive advantage.
- First C4 dominated habitats coincide with the presence charcoal in the fossil records
- This indicates that fire may have played a role in making C4 ecologically dominant.

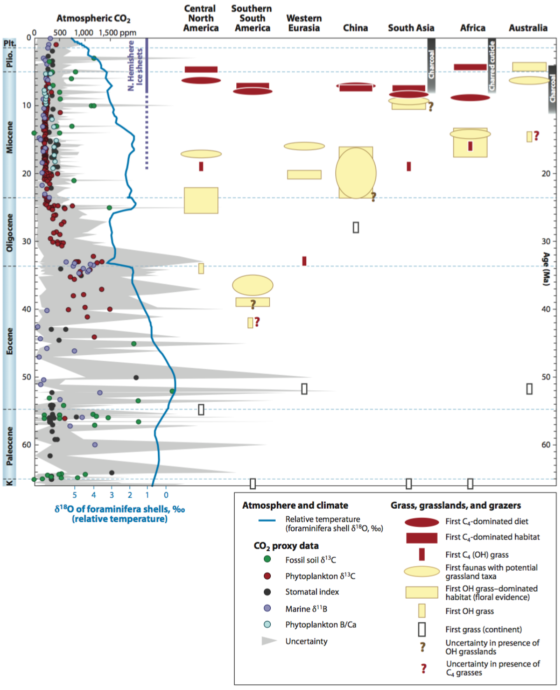


Figure : Strömberg 2011

A grass model

- Did flammability evolve ? or is it the by-product of favorable environmental conditions (high O_2 concentration, arid climate etc.)
- We propose a model for the evolution of grass, and show that the truth may lie in between:
  - Arid conditions may have favored the evolution of flammability.
  - Once flammability has evolved, there exists evolutionary forces maintaining, and promoting flammability in milder environments.

Decomposition strategies

- We assume that grasses are perennial and seasonal. Their fitness is determined by how well they grow over multiple years.
- Decomposition is key: Grasses that do not decompose, shade themselves. This prevents them from continuing to grow.
- Decomposition also plays an essential role in nutrients recycling (DeBano et al. ('98))
- Two alternative strategies
  (1) bacterial decomposition / moisture friendly,
  (2) fire / moisture adverse.

  More efficient to burn, but also more risky.

Costs

- Grasses come close to having a single, relatively simple trade-off axis:
    - m: moisture allocation
- Costs are built in. Let $p(z)$ the probability for z to burn:
    - Biomass loss from burning: $p(z) \times \pi_F$.
    - Biomass loss from decomposition : $(1 - p(z)) \times \pi_{NF}(m(z))$,
    - fitness:

$$p(z) \times \pi_F + (1 - p(z)) \times \pi_{NF}(m(z))$$

        - ★ π_{NF} is increasing in m.
        - ★ $p(z)$ is decreasing in m

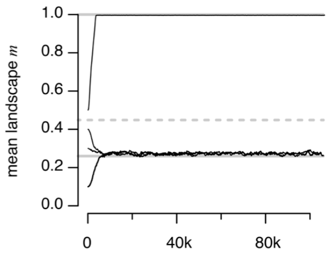
$p(z)$ depends on the moisture trait $m(z)$, but also on the ability of the whole population to spread fire !

Adaptive dynamics framework

- Decompose the landscape into units – grass tuft – of variable flammability $\{\lambda(z) : z \in \mathbb{Z}^2\}$.
- Infection probability
$$\lambda(z) \ = \ 1 - m(z).$$
- m is an heritable trait.
- For each individual, introduce small and rare mutations in m.

Equilibria

- $m = 1$ ($\lambda = 0$) is is always a (non flammable) stable equilibrium of the system.



- If π_F is large enough, there exists a second flammable stable equilibrium.
- Flammability can be maintained and even enhanced in a flammable landscape.
- Dependence of the initial conditions: flammability can not evolve in a non-flammable environment.
- Back to the original question: How did flammable C4 grass succeeded in invading non-flammable environment ?

moisture vs realized moisture

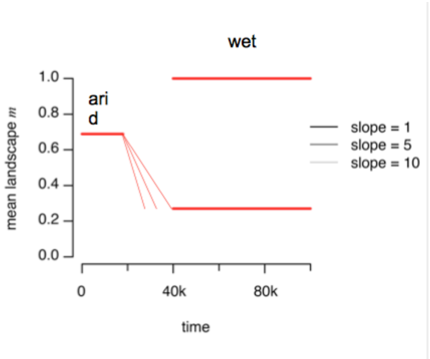
- Moisture was modeled as a trait, whose value was independent of the environment.
- We now assume that m is an heritable trait, but that the "realized moisture" also depends on environmental conditions

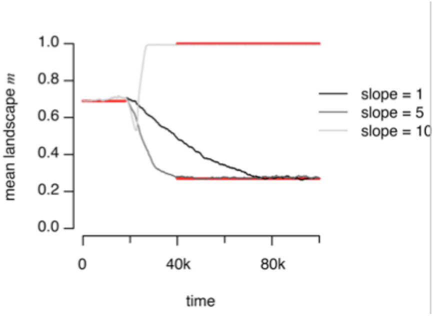
$$m_{real} = (m_{\max} - m_{\min})m + m_{\min}$$

- *dry*: low m_{max}, high m_{min}
- *wet*: high m_{max}, low m_{min}
- m_{min} and m_{max} can both depend on space and time (fluctuations of climatic conditions).
- Depending on the environment,
  - One flammable equilibrium (arid)
  - One flammable and one non-flammable equilibrium (wet)
  - One non-flammable equilibrium (very wet).

Temporal fluctuations

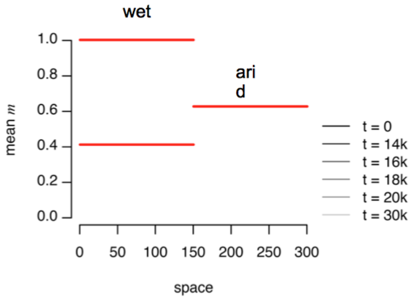
- Arid: only one flammable equilibrium
- Wet: two stable equilibria (flammable and non-flammable)

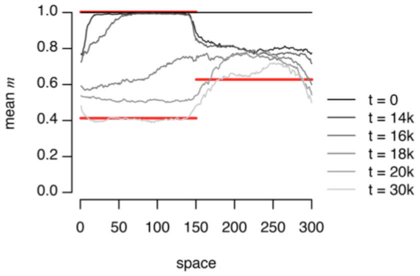




Flammability can evolve under an arid climatic regime. If aridity decreases slowly enough, evolution of the flammability trait m can maintain flammability.

Spatial fluctuations





Flammability can invade an area with a wet climate from a neighboring area with a dry climate, where flammability is the only stable strategy.

Conclusion

- Previous results suggest that the conditions for the evolution of flammability are not very restrictive
- The flammability trait can temporally persist or spatially invade into climates where flammability could not have evolved spontaneously.
- Necessary ingredient: spatially localized arid conditions in the past.