Savanna-Fire Model: Combined effects of tree-tree establishment competition and spatially explicit fire on the spatial pattern of trees in savannas

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- What is a savanna.
- Robust coexistence vs exclusion
- The savanna problem
- Tree-tree competition and fire in savannas
- Savanna-Fire Models
- Some results
- Conclusions

Savanna is a grassland with widely spaced trees.

Grasslands are generally open and continuous, fairly flat areas of grass.

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Savannas cover 10-20% of the global land surface and about half the area of Africa.

Savannas provide natural resources (livestock, firewood, ecosystem services) for hundreds of millions of people.

Risk of overuse, degradation, desertification, … need to understand the processes shaping them

Darwin (1859), The Origin of the Species, Chapter VI:

``In looking at species as they are now distributed over a wide area, we generally find them tolerably numerous over a large territory, then becoming somewhat abruptly rarer and rarer on the confines, and finally disappearing. Hence the neutral territory between two representative species is generally narrow in comparison with the territory proper to each. We see the same fact in ascending mountains, and sometimes it is quite remarkable how abruptly, as Alph. de Candolle has observed, a common alpine species disappears. The same fact has been noticed by E. Forbes in sounding the depths of the sea with the dredge. ´´

Explanation: the struggle for life (**ecological competition**)

Many ecological observations suggest

The principle of competitive exclusion:

(Gause, 1934; Hardin, 1960)

Two species competing for the same resource will not coexist: one will become extinct or displaced

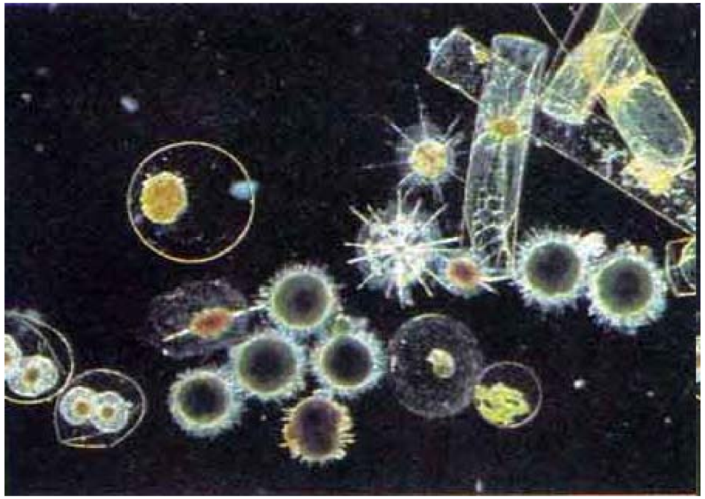
This is supported by several particular models, in particular Lotka-Volterra competition models with net growth depending on *n* resources:

$$\dot{N}_i = N_i f_i(R_1(N),\dots,R_n(N))$$

i=1,…,m species

There is no steady state coexistence of m species > n, number of resources.

But sometimes coexistence of similar species occurs !!!



(e.g. the Plankton paradox,

Hutchinson, Am. Nat. 1961)

Mechanisms allowing robust coexistence of similar species

Non-steady dynamics

Temporal **external disturbances**

Predation, **self-competition**

Spatial inhomogeneities

Fluid-flow effects

Non-competitive interactions …

The savanna question: ``What is special about the savanna environment that allows trees and grasses to coexist, as opposed to the general pattern in other areas of the world where either one or the other functional type is dominant?´´(Sarmiento 1984)

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Why not either woodland or grassland????

MECHANISMS FOR ROBUST COEXISTENCE OF TREES AND GRASS

What regulates the tree/grass balance in savannas?

- Historical focus on **tree-grass** competition for water (Walter hypothesis)
- Many savanna models have ignored **tree-tree interactions** (and those including it are too complex to understand).
- Strong emphasis on **disturbance** (fire, herbivory, rainfall variability)

Sankaran et al. 2004, Menaut et al. 1990, Jeltsch et al. 1996, Meyer et al. 2007, 2008, Moustakas et al. 2008

In mesic savannas (intermediate humidity), in addition to **tree-grass competition** there is evidence of the importance of

- **Tree-tree interactions**
- **Fire**

for supporting tree-grass coexistence in a robust manner

Tree-tree competition and fire

Vol 449|13 September 2007|**doi:10.1038/nature06060**

nature

LETTERS

Positive feedbacks promote power-law clustering of Kalahari vegetation

Todd M. Scanlon[1], Kelly K. Caylor[2], Simon A. Levin[3] & Ignacio Rodriguez-Iturbe[4]

TREE-TREE NEGATIVE INTERACTIONS (self-competition)

Competition for water, nutrients, light

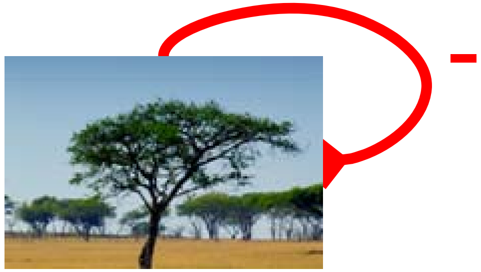
In arid savannas, competition for water may be long-range

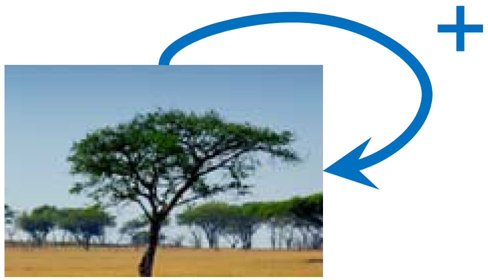
TREE-TREE POSITIVE INTERACTIONS (facilitation)

Water infiltration, retention

Shading, …

Local dispersion (seeds give rise to new trees close to existing ones).



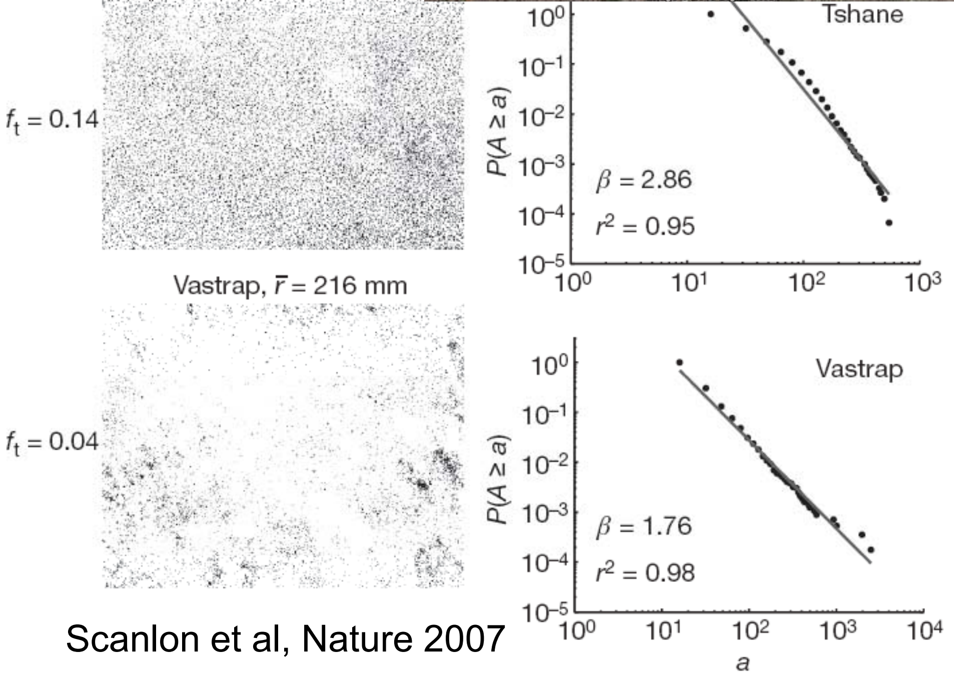


NIGER

MALI

Rietkerk, M., and J. van de Koppel, TREE 2008

Kalahari



Scanlon et al, Nature 2007

South Africa, Photograph by J. S. Levine, NASA

Photo of Cedar Creek Ecosystem Science reserve

Frequent fires (spontaneous or man-made): every few years

They only affect grass and small trees

South Africa,
Photograph by J. S. Levine, NASA

Could fire interact with competition?

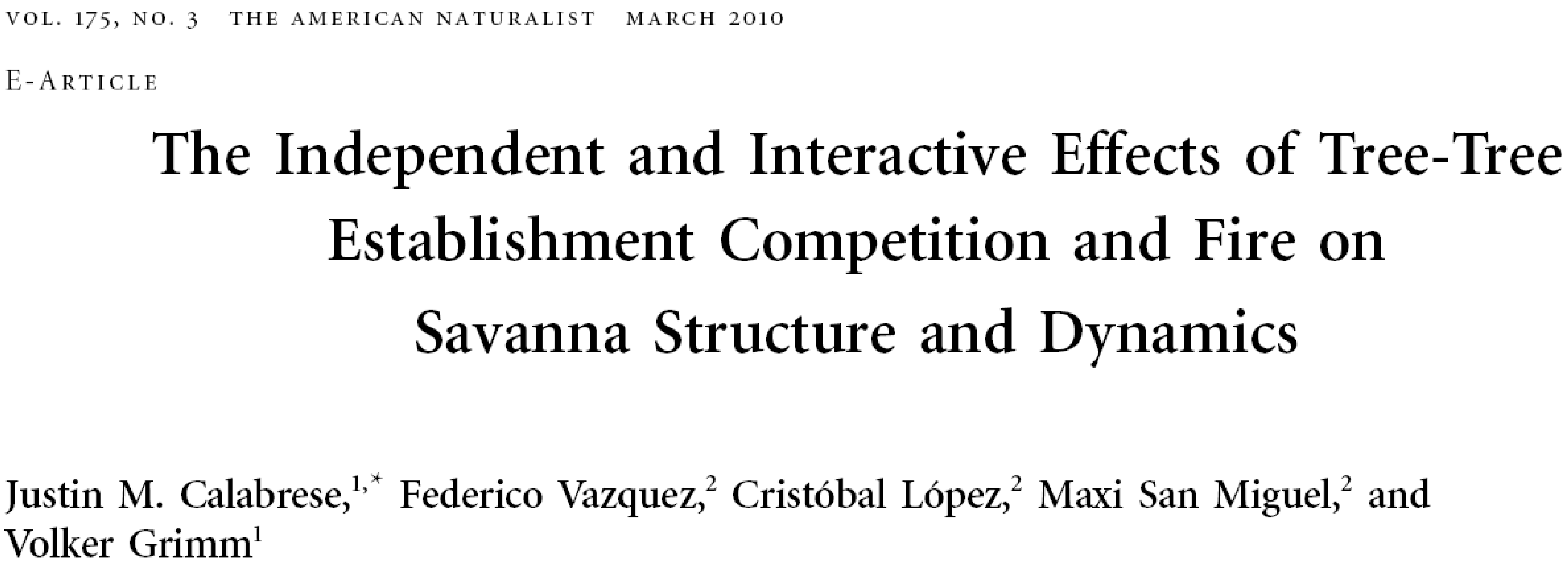
- Because of faster recovery times, fire gives indirect competitive advantage to grass over juvenile trees after both have burned. Since grass is the main fire fuel, this leads to a positive feedback favoring grass.
- Surrounding adult trees may protect juveniles from fire (facilitation).

Jeltsch et al. 1999, Caylor et al 2003, Meyer et al. 2007, Scanlon et al. 2007, Moustakas et al. 2008


South Africa,
Photograph by J. S.
Levine, NASA

Questions

1. What are the individual and combined effects of competition and fire on tree density?
2. Which are the different kinds of tree spatial patterns promoted by competition & fire ?



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E-ARTICLE

The Independent and Interactive Effects of Tree-Tree Establishment Competition and Fire on Savanna Structure and Dynamics

Justin M. Calabrese,[1,*] Federico Vazquez,[2] Cristóbal López,[2] Maxi San Miguel,[2] and Volker Grimm[1]

South Africa, Photograph by J. S. Levine, NASA

Calabrese et al.(2010) model

Two states:

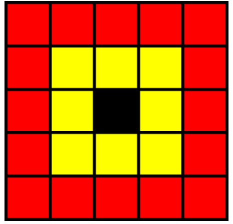
Grass occupied (G)

Tree occupied (T)

Moore Neighbourhood

🟨 Near

🟥 Far



Rules:

Death (T → G); with probability **α**

Birth/Dispersal; T sends out offspring to the near and far neighborhood at constant rate **b**.

Establishment: $P_e = P_c P_f$ — *C:* # near neighbors

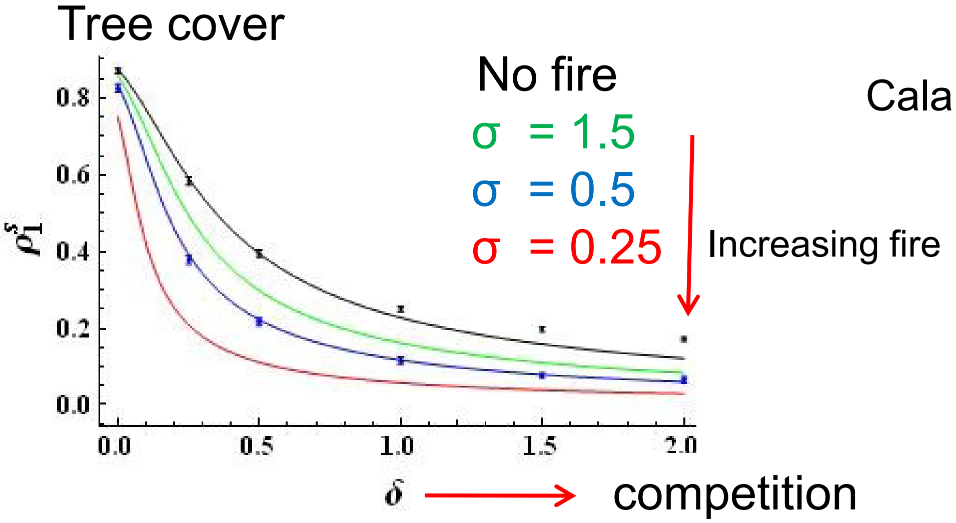
competition $P_c = e^{-\delta C}$ — **δ** competition coefficient

Survival to fire $P_f = \frac{\sigma}{\sigma + G}$

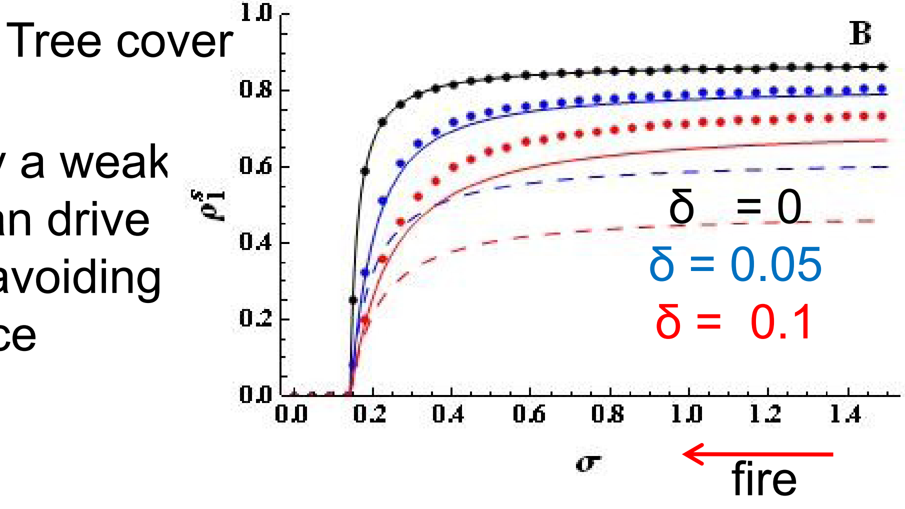
σ : grass biomass at which the probability of surviving to fire reaches half its maximum value

South Africa, Photograph by J. S. Levine, NASA

Calabrese et al, 2010



Competition has strong negative effect on tree cover



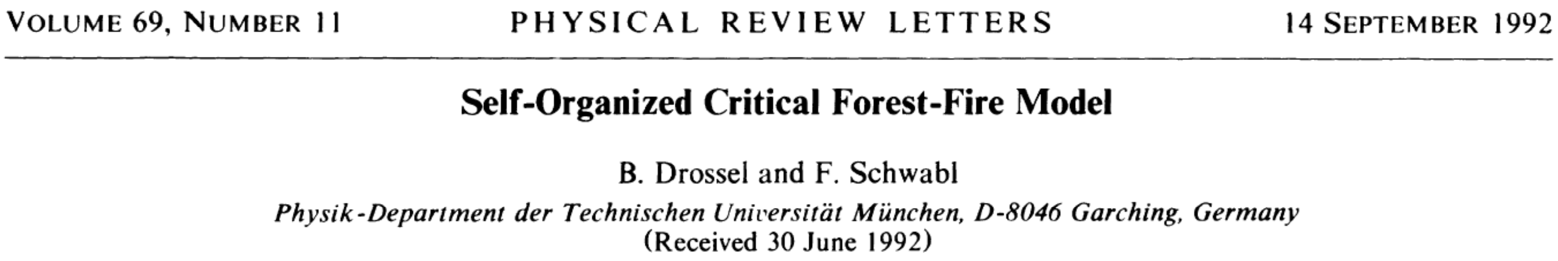
Fire has typically a weak influence but can drive tree extinction, avoiding coexistence

The Calabrese et al model includes the negative interaction of grass on trees, originated by fire.

But it is not able to consider the protection-against-fire effect of surrounding adult trees on juveniles, nor the mixed effects of both interactions.

Need to include explicitly the spatiotemporal dynamics of fire

Drossel-Schwabl ~~Forest~~ Grass Fire Model



VOLUME 69, NUMBER 11 PHYSICAL REVIEW LETTERS 14 SEPTEMBER 1992

Self-Organized Critical Forest-Fire Model

B. Drossel and F. Schwabl
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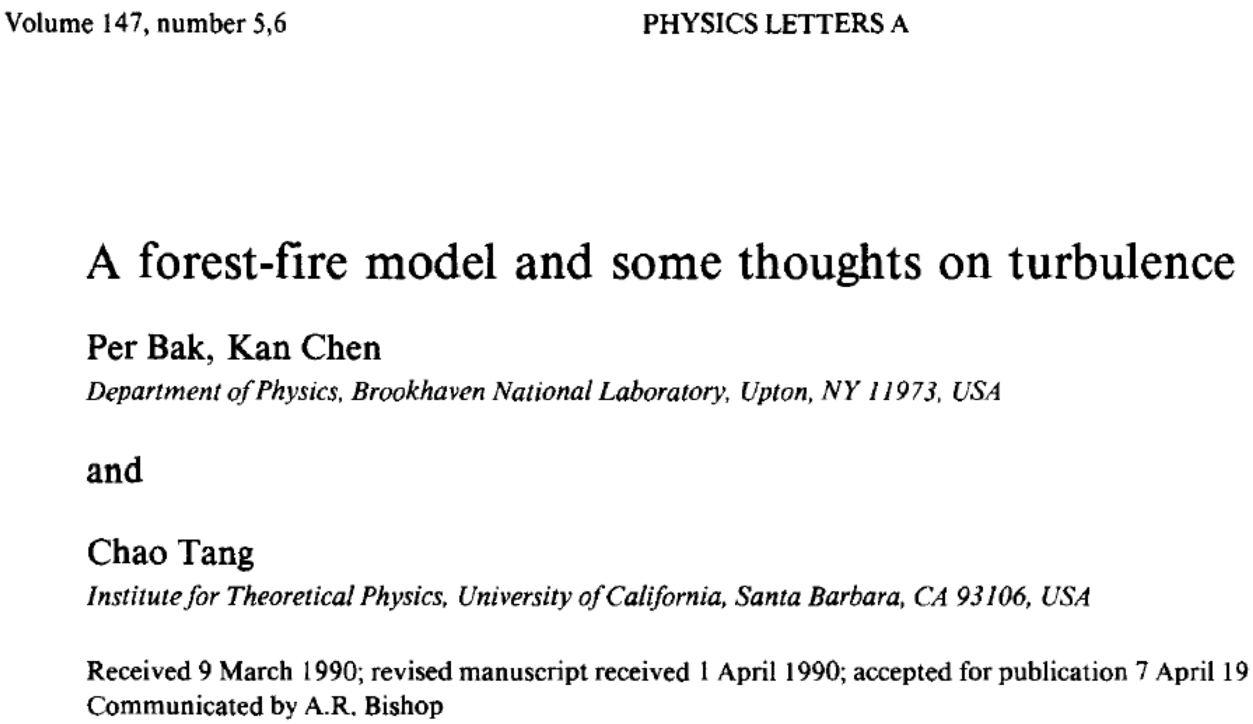
(Received 30 June 1992)



Volume 147, number 5,6 PHYSICS LETTERS A 16 July 1990

A forest-fire model and some thoughts on turbulence

Per Bak, Kan Chen
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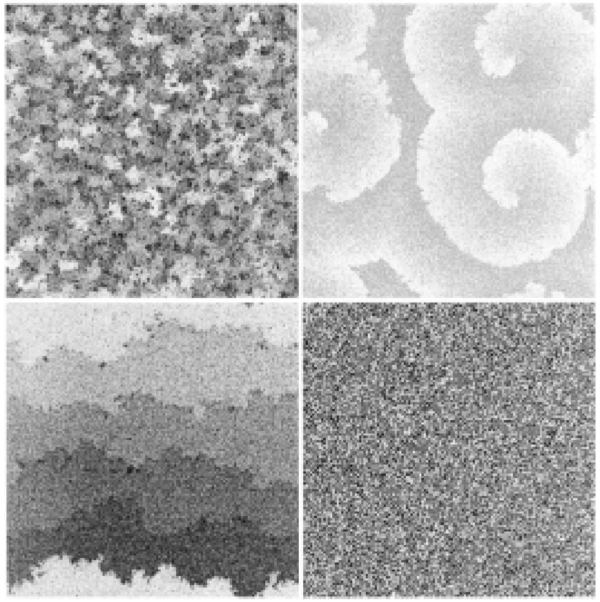
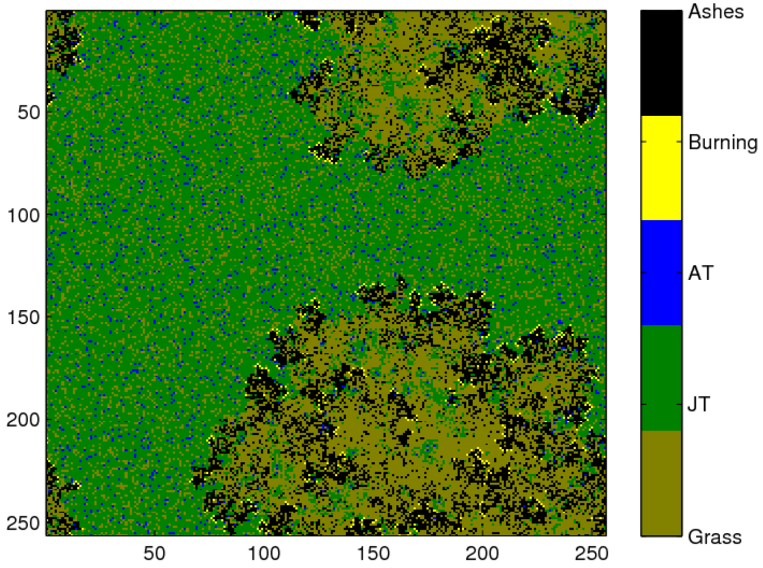
Received 9 March 1990; revised manuscript received 1 April 1990; accepted for publication 7 April 19
Communicated by A.R. Bishop



Combined model: Savanna-Fire Model

South Africa, Photograph by J. S. Levine, NASA



States:

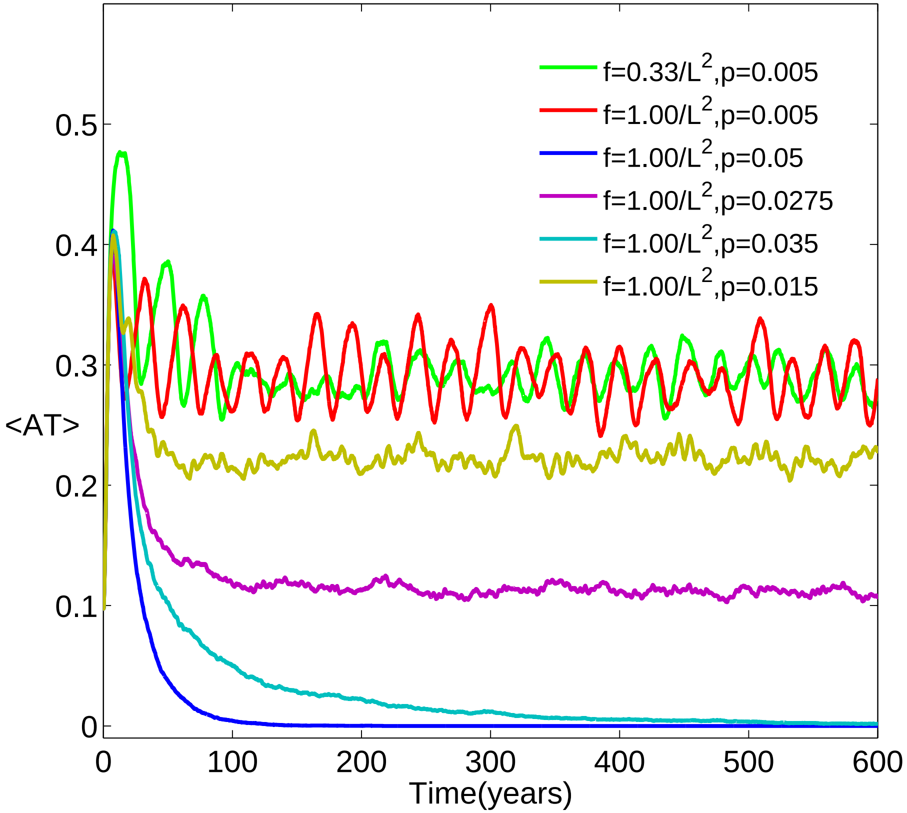
Grass (G)
Juvenile Tree (JT)
Adult Tree (AT)
Burning (B)
Ashes (A)

Rules:

Death (AT → G); **α** rate
Growth (JT →AT); **g** rate
Competition (JT → G); $P_c = e^{-\delta C}$; *C:* # near neighbors
Ashes (B → A)
Birth (G →JT);
Dispersal: near and far neighborhood at **β** rate;
Recovery (A → G); With probability **p**
Burn (G and JT → B); (at a faster time scale)
With probability **(1-lm),** if at least one nearest neighbor is burning;
With probability **f**, if no nearest neighbor is burning.

Density of trees versus time


South Africa, Photograph by J. S. Levine, NASA



$\alpha = 0.2$

$b = 8$

$\delta = 0.05$

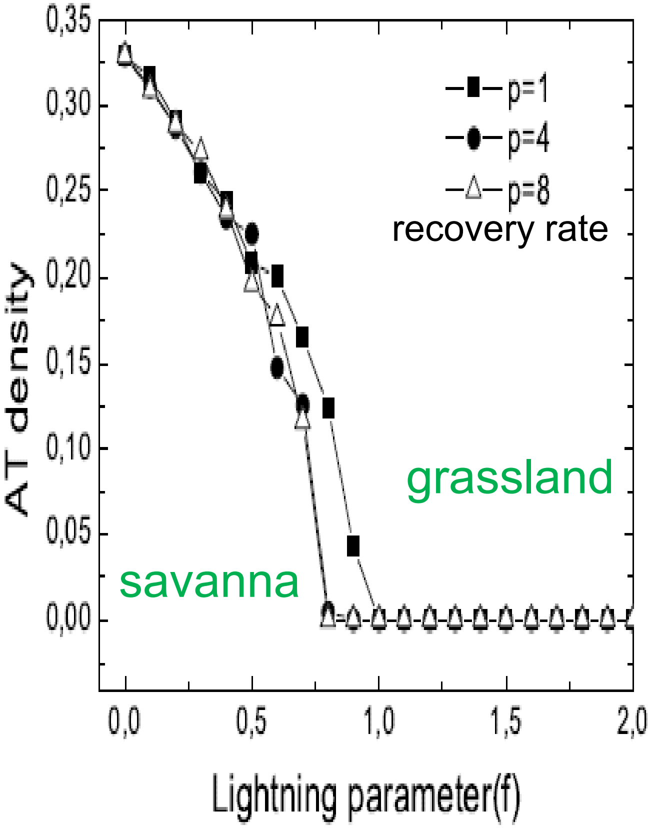
$f = \frac{1.0}{L^2}$

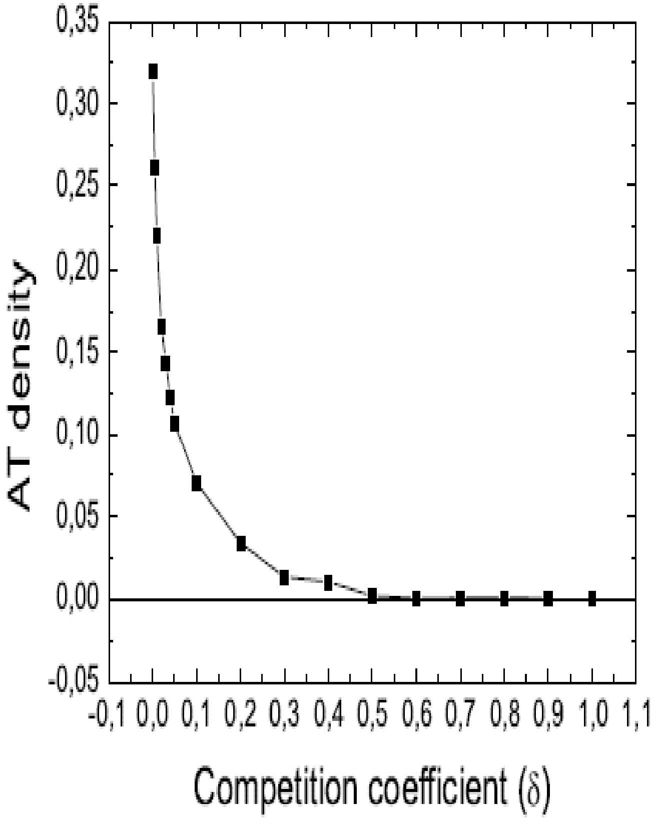
$g = 0.2$

$\mathrm{Im} = 0.0$

South Africa,
Photograph by J. S. Levine, NASA

Savanna – grassland transition

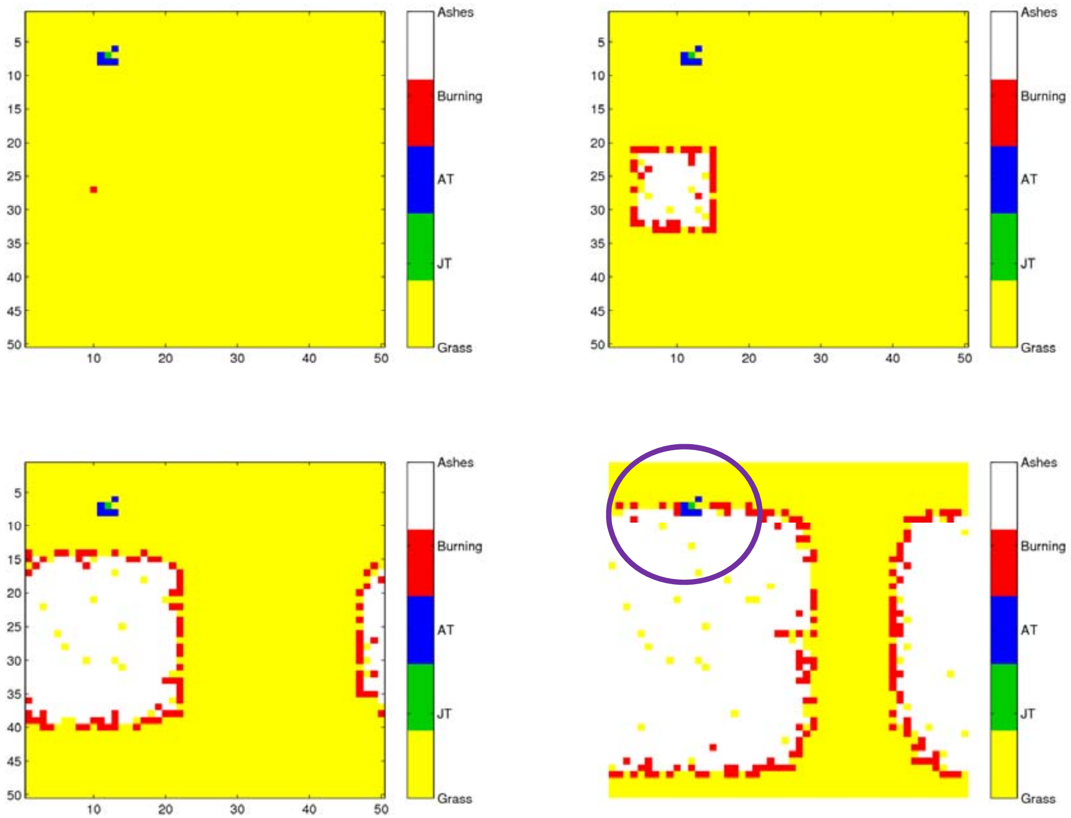




The indirect negative effect of fire on adult trees arises from the explicit modeling of fire.

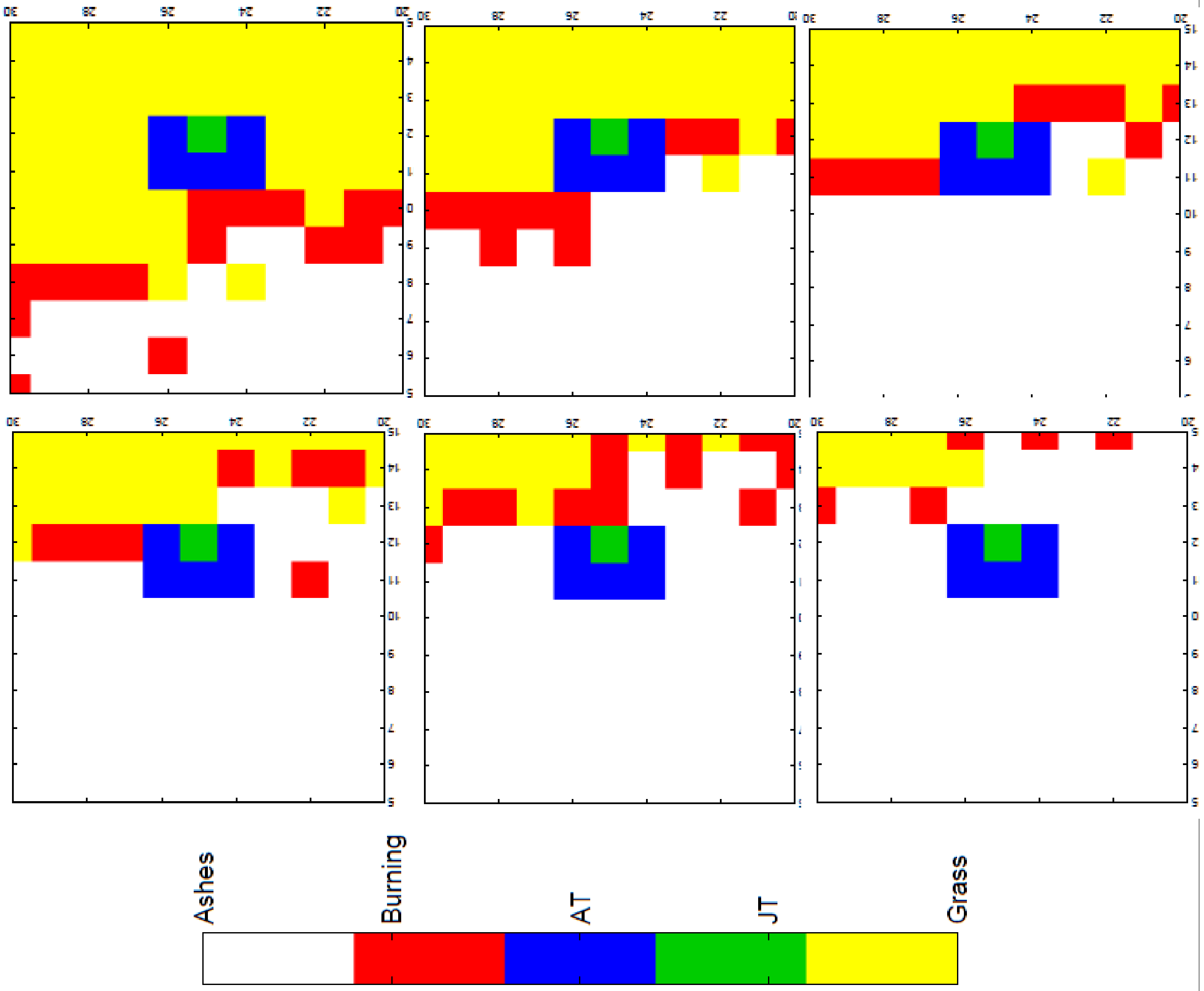
The model contains the protection effect

South Africa, Photograph by J. S. Levine, NASA



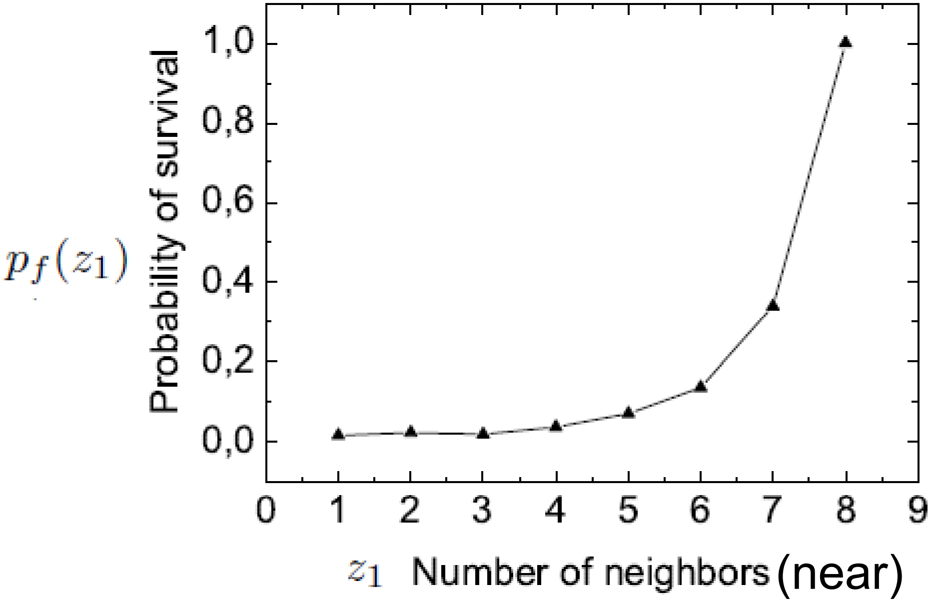
The model contains the protection effect

South Africa,
Photograph by J. S.
Levine, NASA

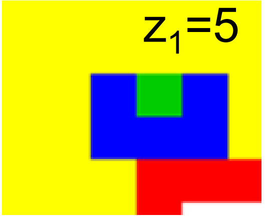


South Africa, Photograph by J. S. Levine, NASA

Quantifying the protection effect



Im=0.3



Combining positive and negative effects of surrounding adult trees on the recruiting probability of juveniles

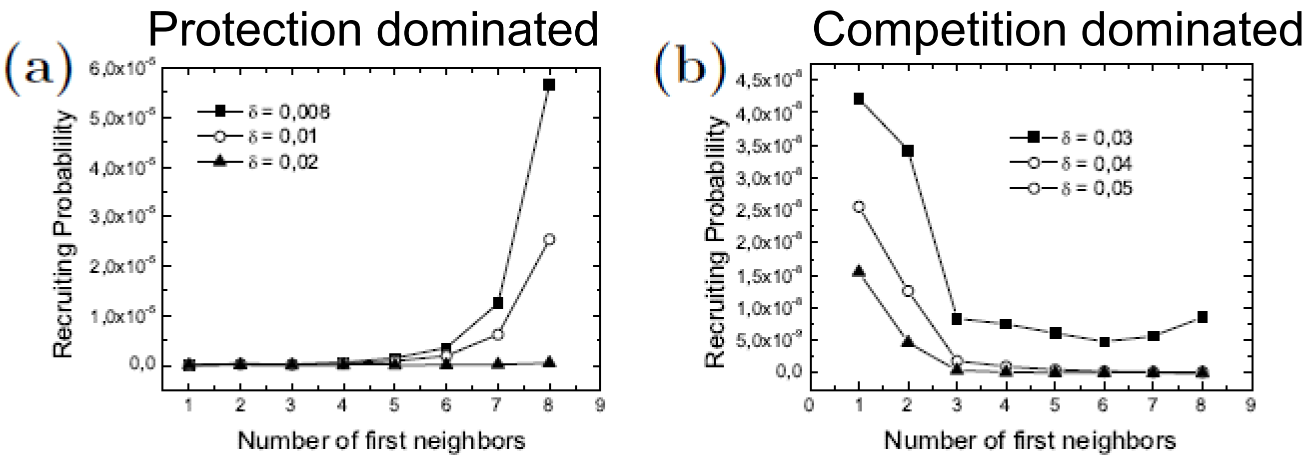
South Africa,
Photograph by J. S. Levine, NASA

competition

$$P_r(z_1) \approx [1-(1-\frac{\beta\Delta t}{24})^{z_1}]e^{-\frac{\delta z_1}{a\Delta t}}p_f(z_1)^{\frac{f}{a}}$$

Birth by seed dispersal

protection



(a) Protection dominated

(b) Competition dominated

z_1

$I = 0.3,\ f = 0.33/year$

Characterizing tree-cover spatial pattern

South Africa, Photograph by J. S. Levine, NASA

Pair Correlation function

how particles are packed together :

$$g(r) = \frac{\rho_{11}}{\rho_1^{\;2}}$$

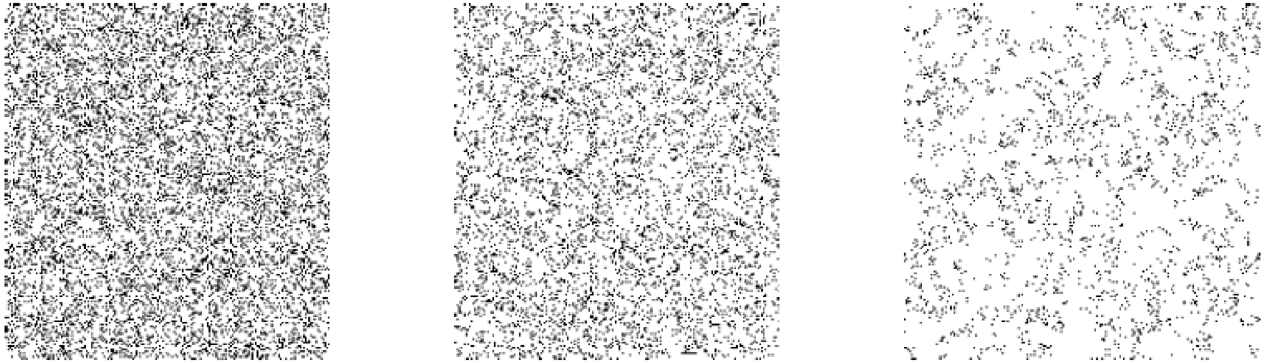
ρ_{11} : proportion of pairs of trees at distance r.

ρ_1 : density of trees

g(r) > 1: more trees at that distance than randomly expected
g(r) < 1: less trees at that distance than randomly expected

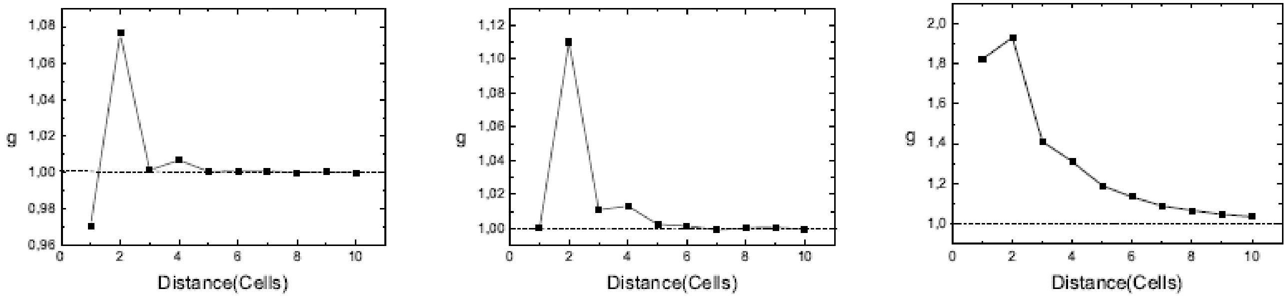
Scale-dependent spatial pattern

South Africa,
Photograph by J. S. Levine, NASA



Regular

Clumped



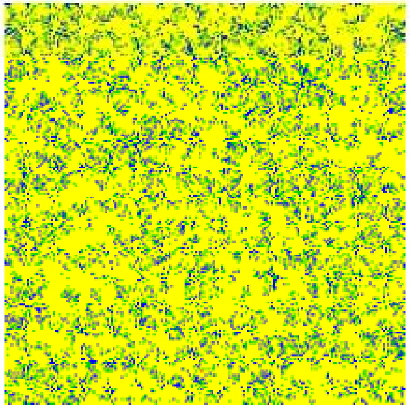
Increasing fire (*f*) →

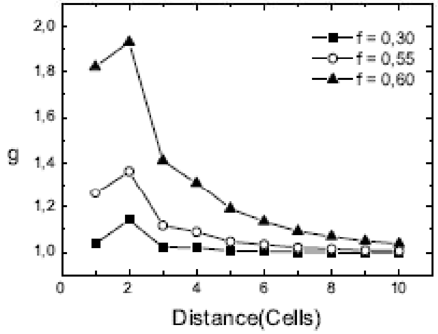
Spaced trees (regular state) are typical of strong competition situations

Protection effect reduces effective competition: **clumping**

Two types of clumped clusters

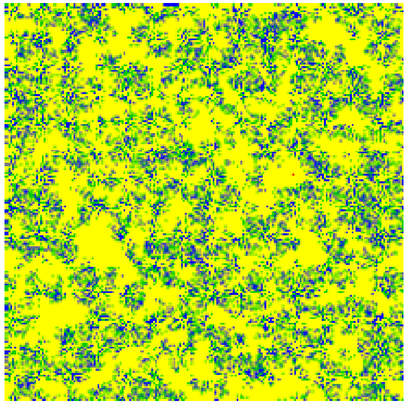
(only the first one in the Calabrese et al model)

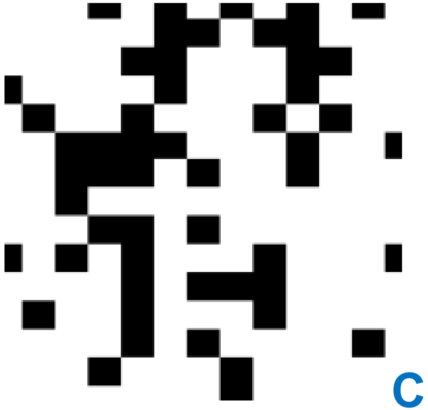


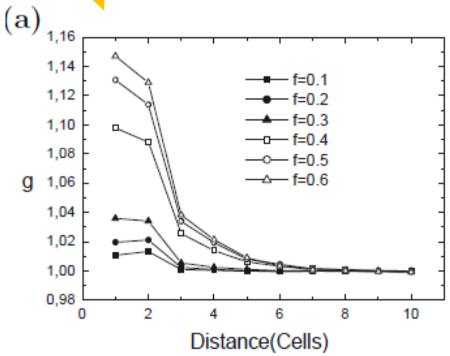


Open clusters

Decreasing competition or increasing fire





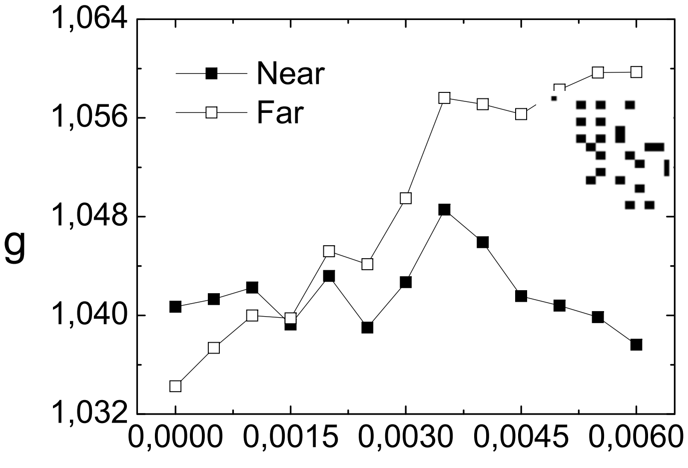


Closed clusters

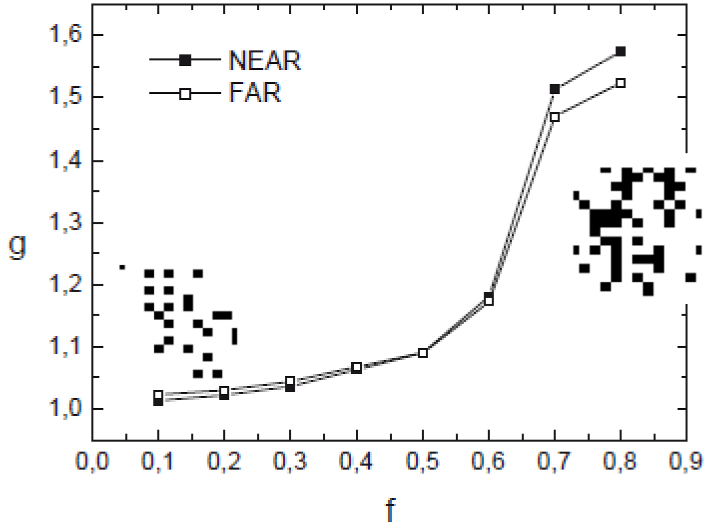
South Africa,
Photograph by J. S
Levine, NASA

Pair correlation function for the near and far neighborhood

South Africa,
Photograph by J. S.
Levine, NASA



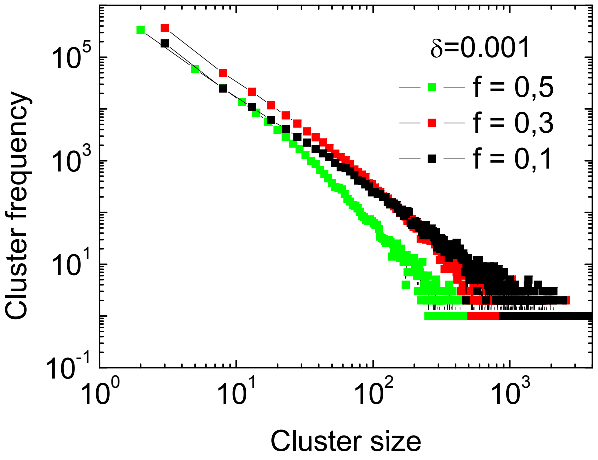
Change of dominance:
transition open-closed
clumped clusters

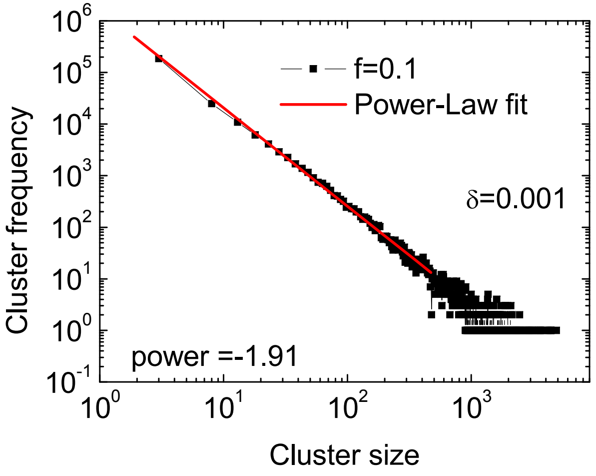


South Africa, Photograph by J. S. Levine, NASA

Tree-cluster size distributions.

Power-law clustering close to the percolation transition of the tree canopy (the canopy percolates when decreasing fire or competition).





Searching for robust power-laws
(Roy, Pascual & Franc, *Broad scaling region in spatial ecological system*, Complexity, 2003)

South Africa, Photograph by J. S. Levine, NASA

Conclusions

- Tree-tree competition can be a major constraint on tree density, thus facilitating the robust coexistence grass-trees characterizing savannas.
- Fire has several indirect effects on tree-grass and tree-tree competition, introducing both positive and negative effects on tree density. They can be studied in a model with explicit spatial fire.
- Regular, clumped open, and clumped closed cluster configurations arise when increasing fire or decreasing competition. The last one does not appear in the model without explicit fire.
- The tree canopy undergoes a percolation transition, with power-law cluster sizes, when decreasing fire or competition.