Patterns of biomass, resource and species diversity in dryland vegetation

Ehud Meron

Ben Gurion University

Assaf Kletter, Jonathan Nathan, Erez Gilad, Efrat Sheffer, Hezi Yizhaq,
Jost von Hardenberg, Antonello Provenzale, Moshe Shachak

Understanding the coupling between species diversity and pattern formation in different environments

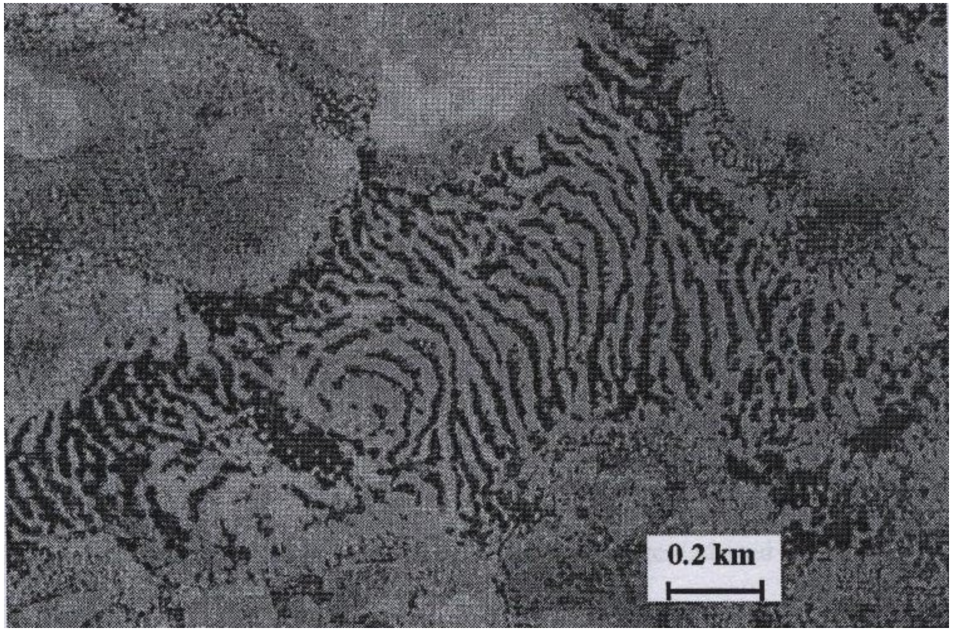
4th European PhD Complexity School, Hebrew University, Sept. 10-14, 2008

Outline

1. Background:
   Vegetation patterns, inter-specific plant interactions, vegetation-water feedbacks.
2. Population level:
   Introduction of a spatially explicit model for a plant population, applying it to pattern formation phenomena along environmental gradients.
3. Two-species communities:
   Extending the model to two populations representing species belonging to different functional groups – the woody-herbaceous system. Using it to study mechanisms affecting species diversity (not yet community level properties).
4. Many-species communities:
   Extending the model to include trait-space dynamics and using it to derive species assemblage properties such as species diversity.
5. Conclusions and prospects for future studies

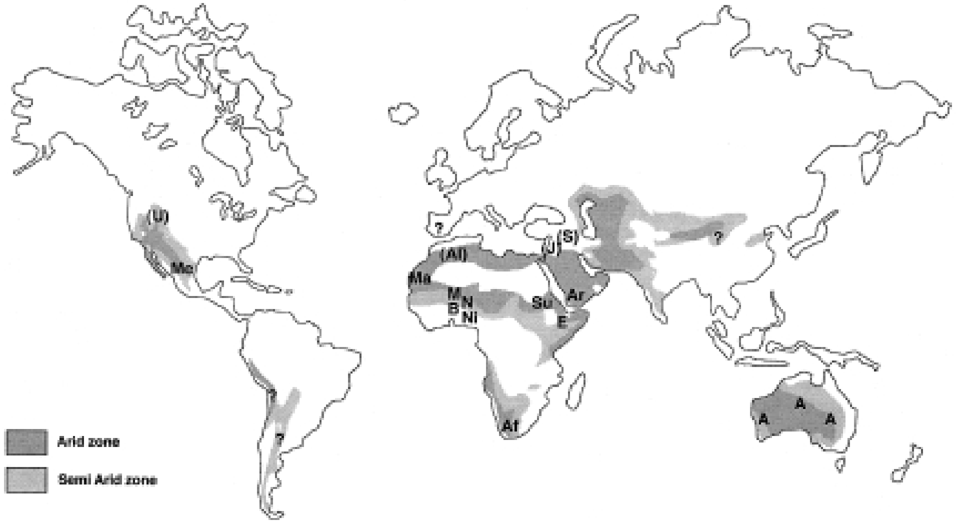
Background: Vegetation patterns

Aerial photograph of vegetation bands in Niger of 'tiger bush' patterns on hill slopes (Clos-Arceduc, 1956) →



Recent studies: Catena Vol. 37, 1999
Valentin et al. Catena 1999, Rietkerk et al. Science 2004

A worldwide phenomenon observed in arid and semi-arid regions, 50–750 mm rainfall (Valentin et al. 1999)



Background: Inter-specific plant interactions

Field observations:

Competition ⇒ facilitation as environmental stresses increase

1. Changes in plant interactions along a gradient of environmental stress (Pugnaire & Luque, Oikos 2001)
2. Positive interactions among alpine plants increase with stress (Callaway et al., Nature 2002)
3. Do positive interactions increase with abiotic stress? A test from a semiarid steppe (Maestre & Cortina, Proc. R. Soc. Lond. B 2004)

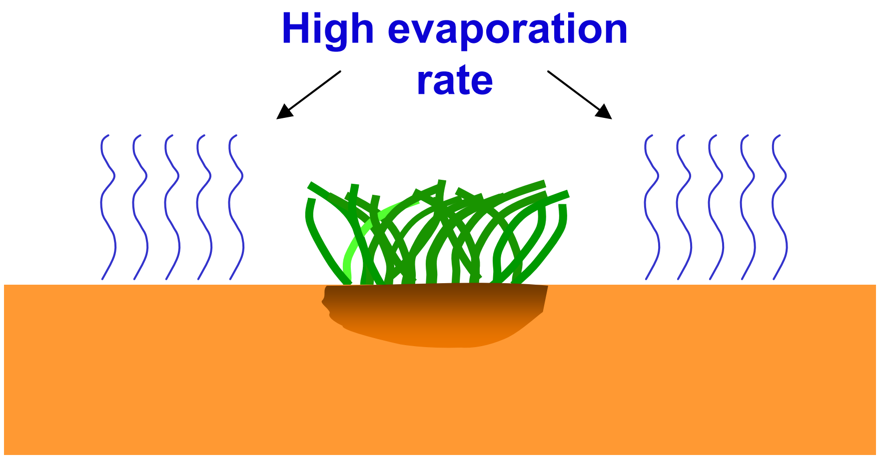
Theory is needed:

Inclusion of facilitation into ecological theory (Bruno, Stachowicz & Bertness TREE 2003)

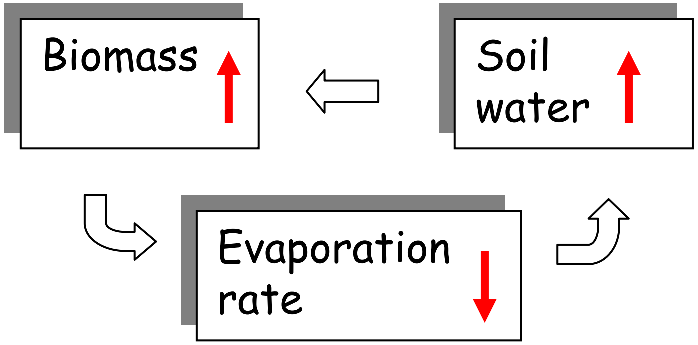
Let competition and/or facilitation emerge from the theory

Background: Biomass-water feedbacks

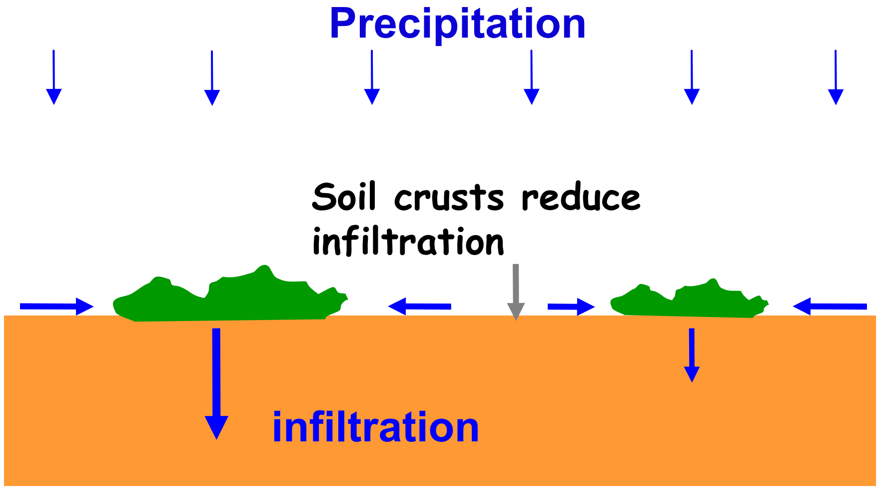
(1) Shading



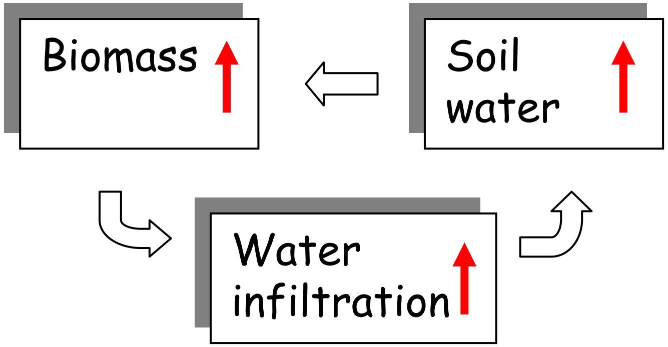
Positive feedback



(2) Increased infiltration



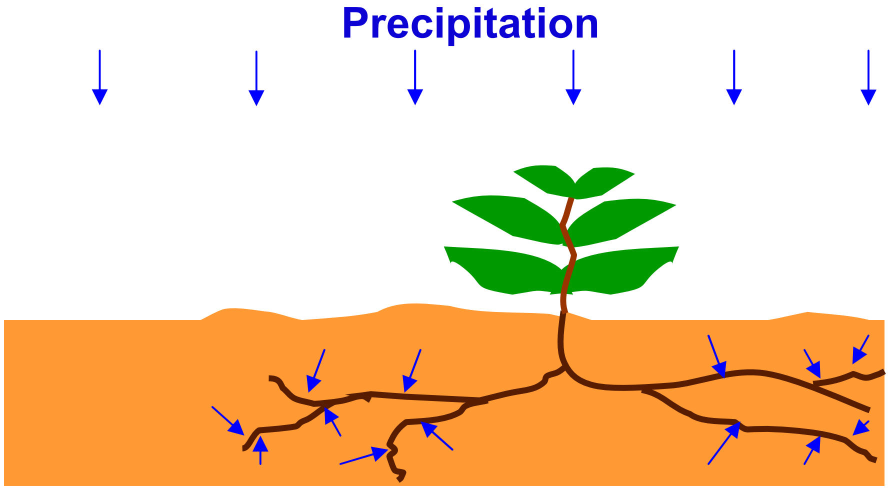
Positive feedback



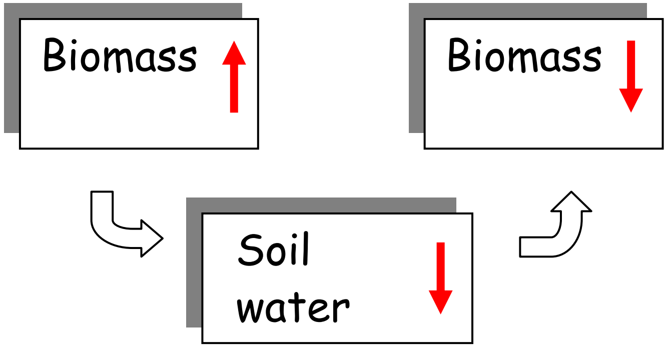
Infiltration feedback involves water transport ⇒ helps growth within the patch, but inhibits growth in the patch surroundings

Background: Biomass-water feedbacks

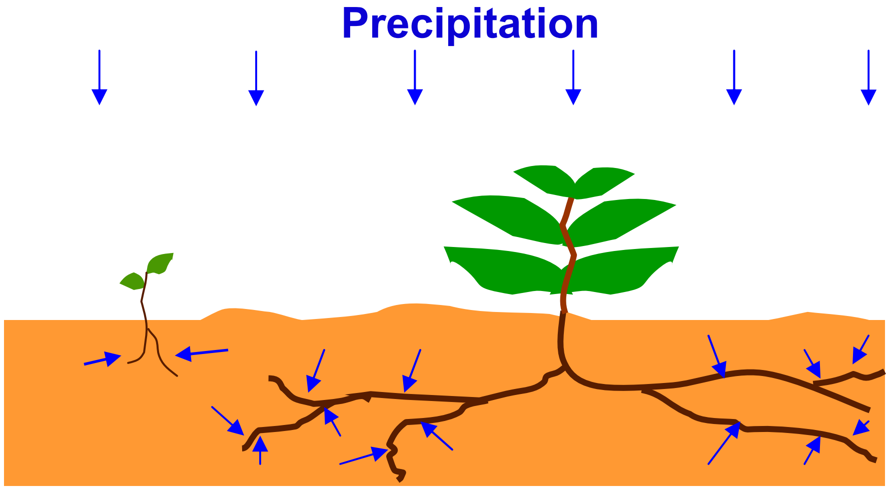
(3) Water uptake



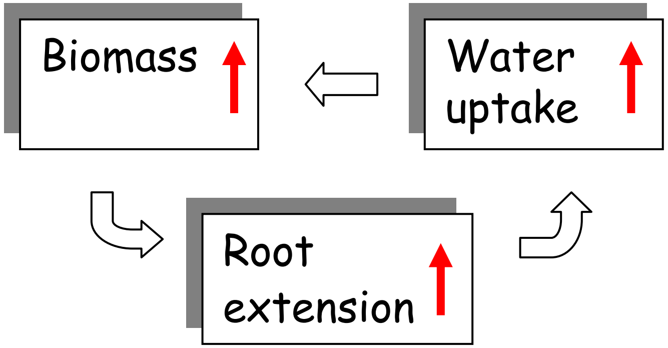
Negative feedback



(4) Root augmentation



Positive feedback



Root-augmentation feedback involves water transport ⇒ helps growth within the patch, but inhibits growth in the patch surroundings

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Population level: a spatially explicit model

Earlier models: Lefever & Lejeune (1997); Klausmeier, (1999); HilleRisLambers et al. (2000), Okayasu & Aizawa (2001); Von Hardenberg et al. (2001); Rietkerk et al. (2002); Lejeune et al. (2002); Shnerb et al. (2003).
Current model: Gilad et al. PRL 2004, JTB 2007.

$$\frac{\partial b}{\partial t} = G_b b(1-b) - \mu b + \delta_b \nabla^2 b$$

Biomass

$$\frac{\partial w}{\partial t} = Ih - Lw - wG_w + \delta_w \nabla^2 w$$

Soil-water content

$$\frac{\partial h}{\partial t} = p - Ih + \delta_h \nabla^2 h^2 + 2\delta_h \nabla h \cdot \nabla \zeta + 2\delta_h h \nabla^2 \zeta$$

Surface-water height

$$G_b(\vec{r},t) = \nu \int_\Omega g(\vec{r},\vec{r}\,',t) w(\vec{r}\,',t) d\vec{r}\,' \qquad G_w(\vec{r},t) = \gamma \int_\Omega g(\vec{r}\,',\vec{r},t) b(\vec{r}\,',t) d\vec{r}\,'$$

Water uptake

$$g(\vec{r},\vec{r}\,',t) = \frac{1}{2\pi} \exp\left\{ -\frac{|\vec{r}-\vec{r}\,'|^2}{2[1+\eta b(\vec{r},t)]^2} \right\}$$

Root augmentation

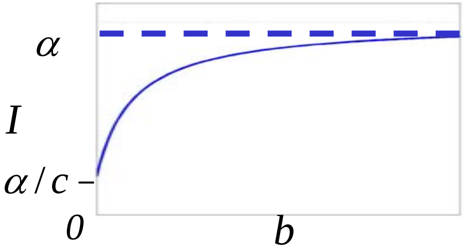
$$L = \frac{\nu}{1+\rho b}$$

Shading

$$I(\vec{r},t) = \alpha \frac{b(\vec{r},t) + q/c}{b(\vec{r},t) + q}$$

Infiltration contrast

c= *1* - no contrast
c>>*1* - high contrast

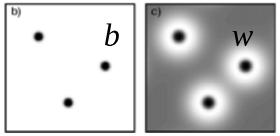


Population level: Vegetation states along a rainfall gradient

Uniform states:
Bare-soil state ($b = 0$)
Fully vegetated state ($b \neq 0$)

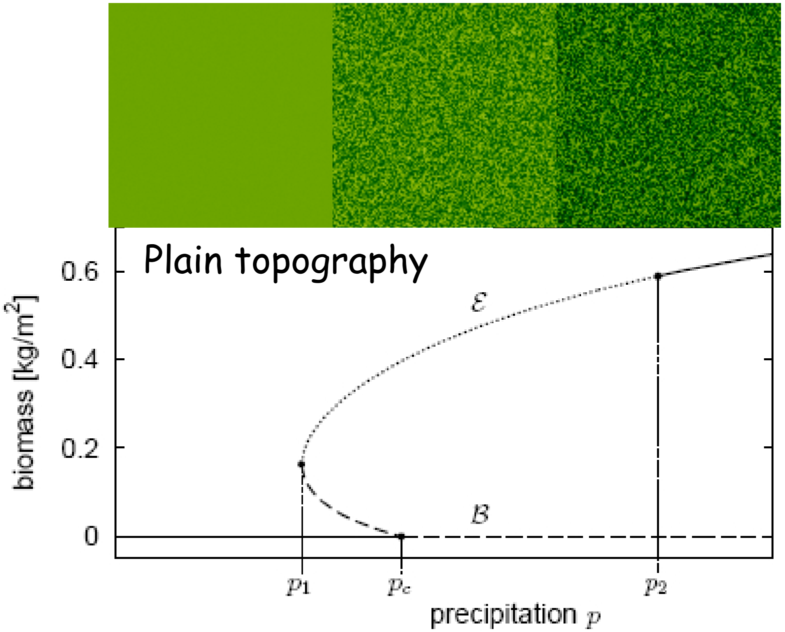
Pattern states: Spots, stripes, gaps

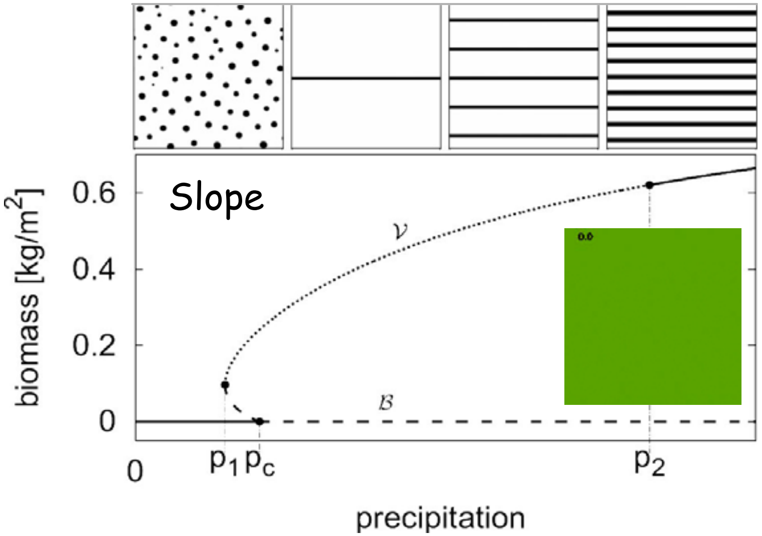
Multistability:
bare-soil & spots



Tlidi, Taki & Kolokolnikov, Chaos 17 (2007)

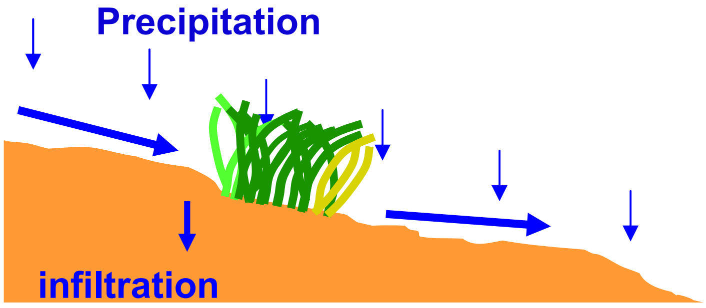
spots & stripes, stripes & gaps,
gaps & uniform vegetaqtion





~ 1 cm/yr

Mechanism of migration:

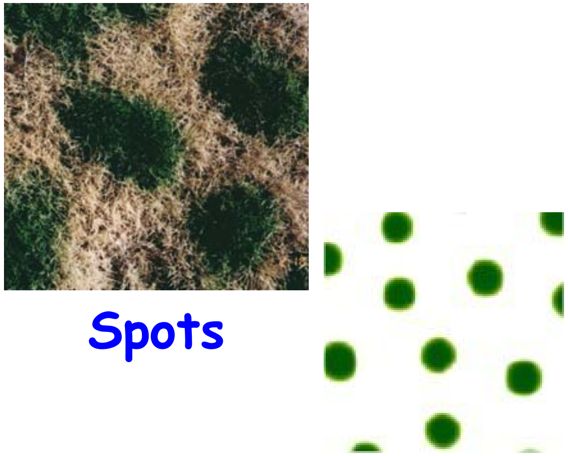


Precipitation

infiltration

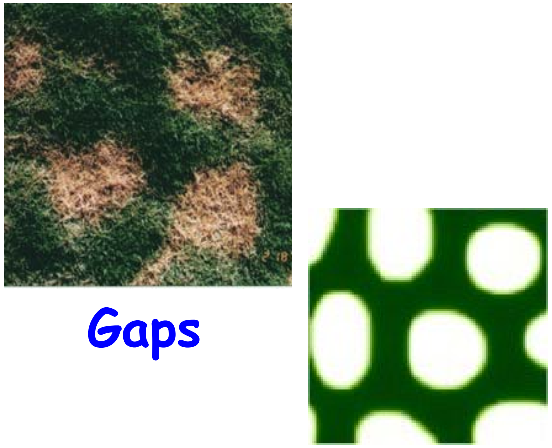
Population level: Observations of vegetation patterns

Stripes of *Paspalum vaginatum*



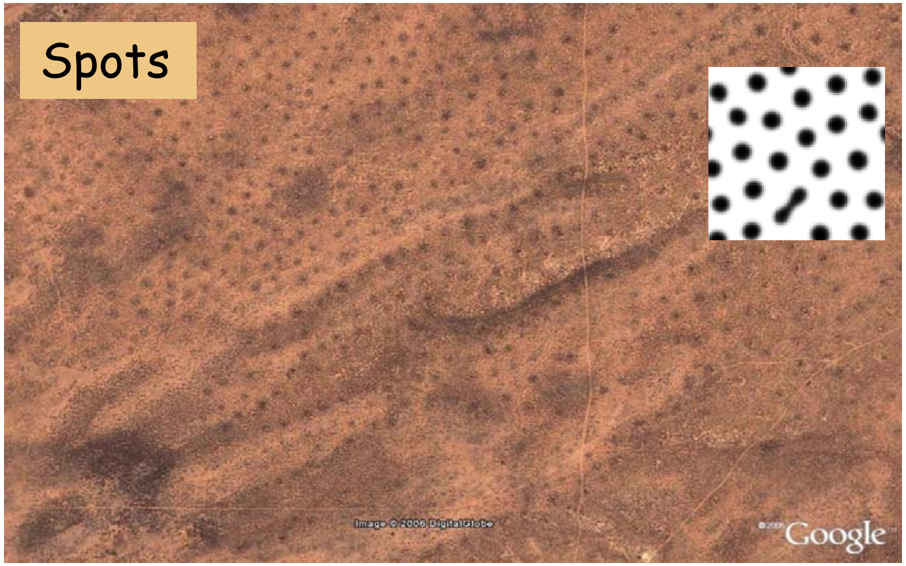
Spots

Stripes



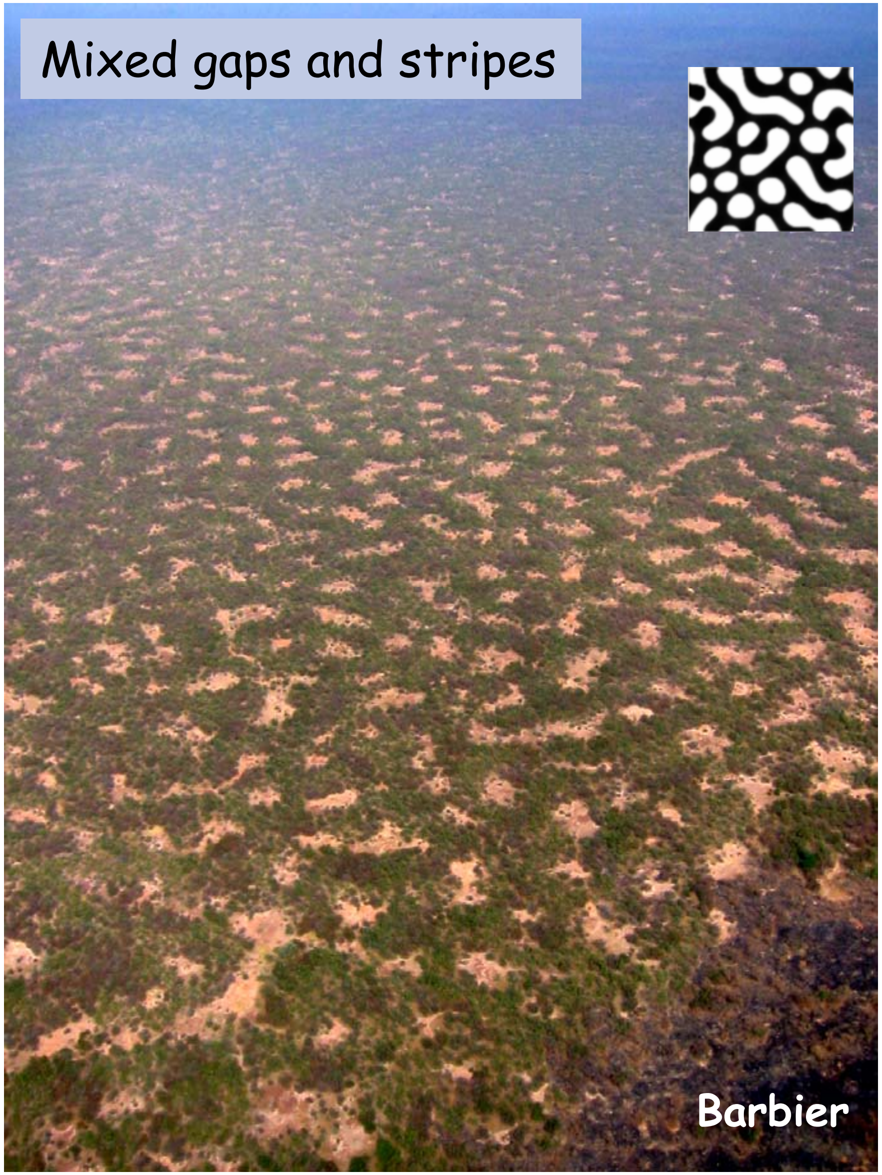
Gaps

Population level: Observations of vegetation patterns


Spots


Mixed spots and stripes

Rietkerk

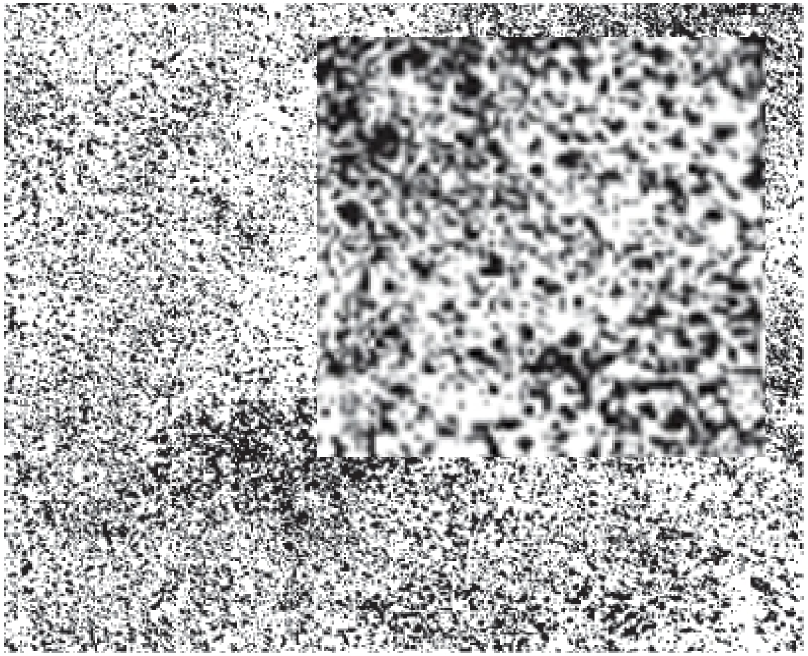

Mixed gaps and stripes

Barbier

All patterns are pretty regular and have characteristic lengths !

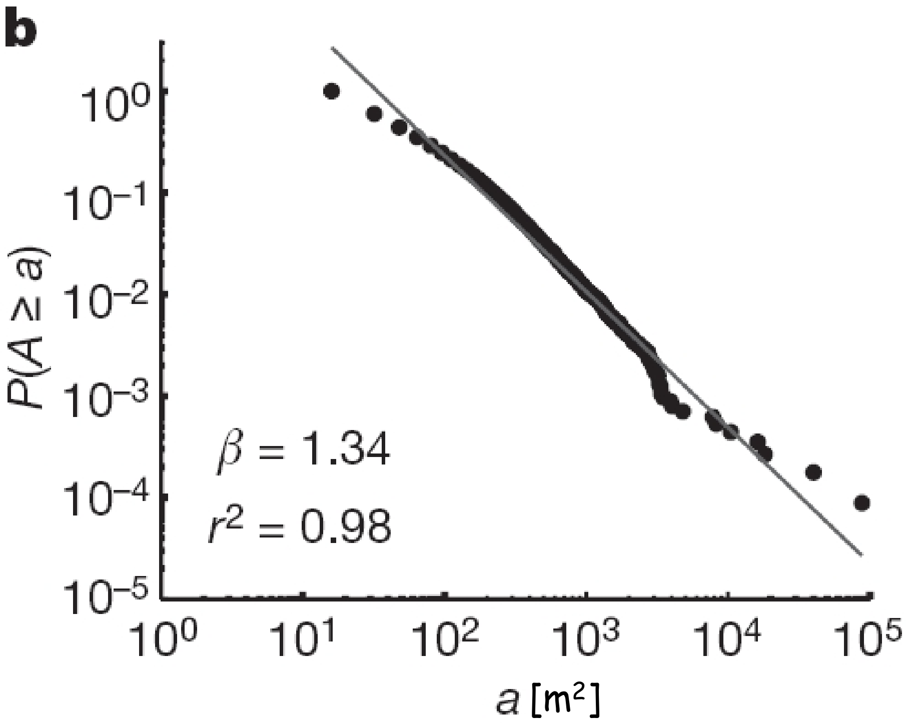
Population level: Scale-free vegetation patterns

Satellite image (Pandamatenga)



2x2 km^2, 4m resolution

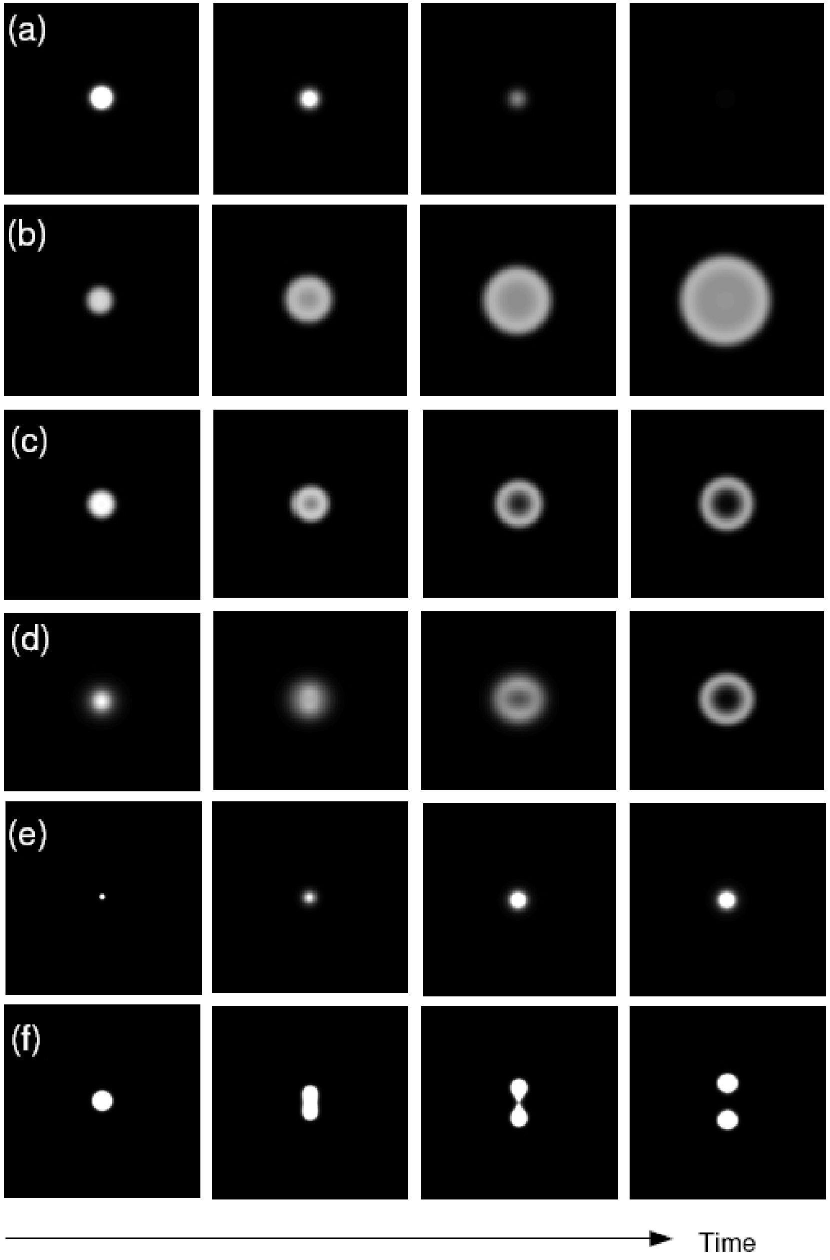
Scanlon et al., Nature 2007
Kefi et al., Nature 2007



Can scale-free patterns form as a self-organization process, or are they merely a result of exogenous factors such as microtopography, rocky soil, etc. ?

Can we resolve this dichotomy of vegetation patterns: Regular vs. scale-free patterns ? (Manor & Shnerb JTB 2008)

Population level: Scale-free vegetation patterns

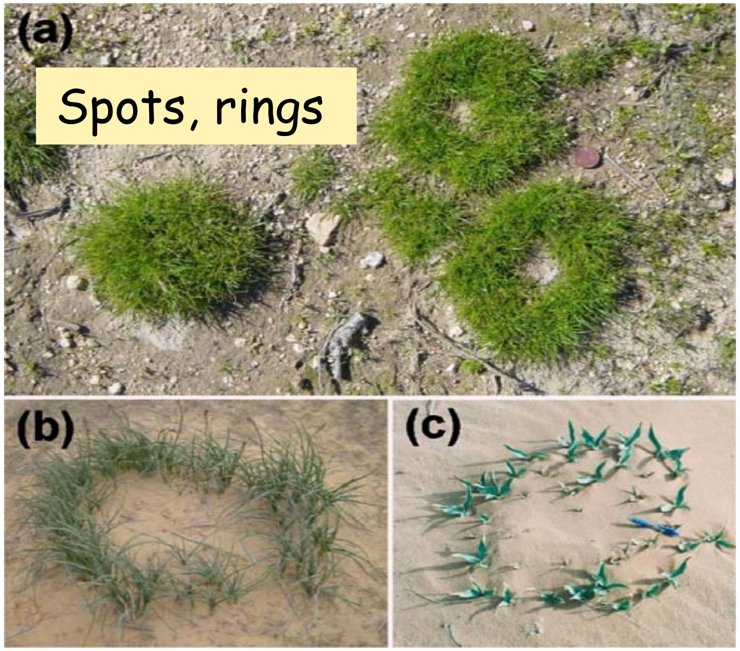


Summarizing,

The feedbacks that involve water transport (infiltration and root-augmentation) limit patch areas by:

1. Inhibiting the growth (spots)
2. Causing central dieback (rings)
3. Causing peripheral dieback (spot splitting)

Population level: Scale-free vegetation patterns



All patch forms have characteristic lengths: spot diameter, ring width, etc.

Population level: Scale-free vegetation patterns

How can we get scale-free patterns with wide patch-size distributions?

Eliminating both infiltration and the root-augmentation feedbacks
$\Rightarrow$ patches grow to uniform vegetation or shrink to bare soil.

Some form of inhibition must exist for patchy vegetation to persist.
The inhibition must be global !

1. Eliminate the root-augmentation feedback which induces short range inhibition (roots size).
2. Increase the inhibition range of the infiltration feedback:

Time-scale of surface-water flow $\tau_F \propto \delta_h^{-1}$ **<<** $\tau_I \propto \alpha^{-1}$ Infiltration time-scale

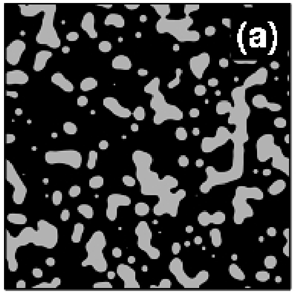
Large patches can survive because surface water reach any point before significant infiltration takes place.

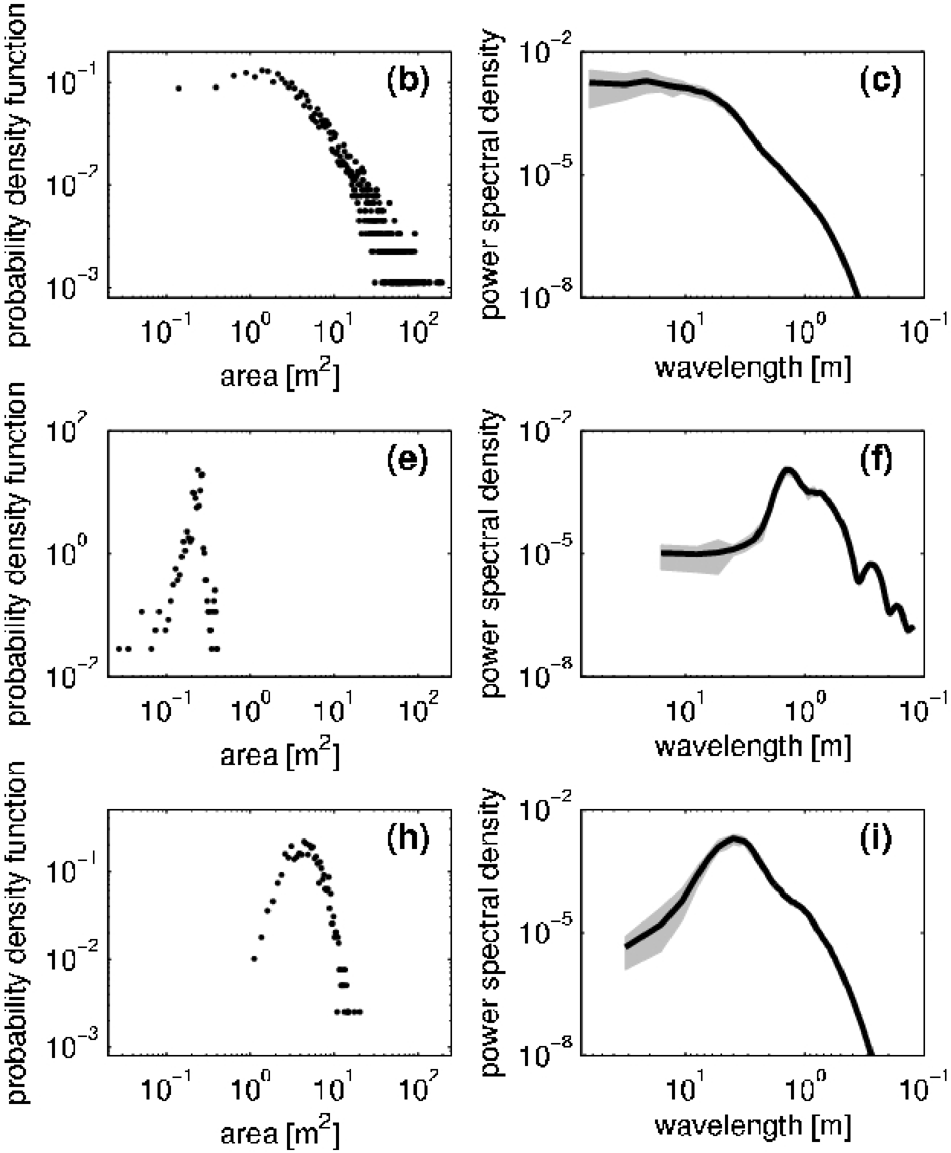
Small patches remain small if the water resource is already exhausted by all other patches (even remote ones)

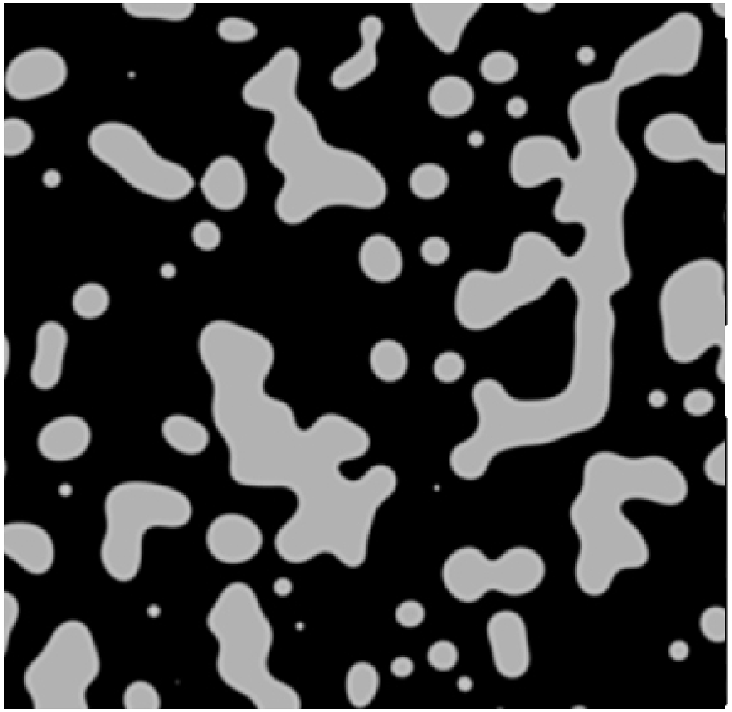
Population level: Scale-free vegetation patterns

Under these Conditions:

$\eta = 0, \quad \tau_F / \tau_I << 1$ $\longrightarrow$



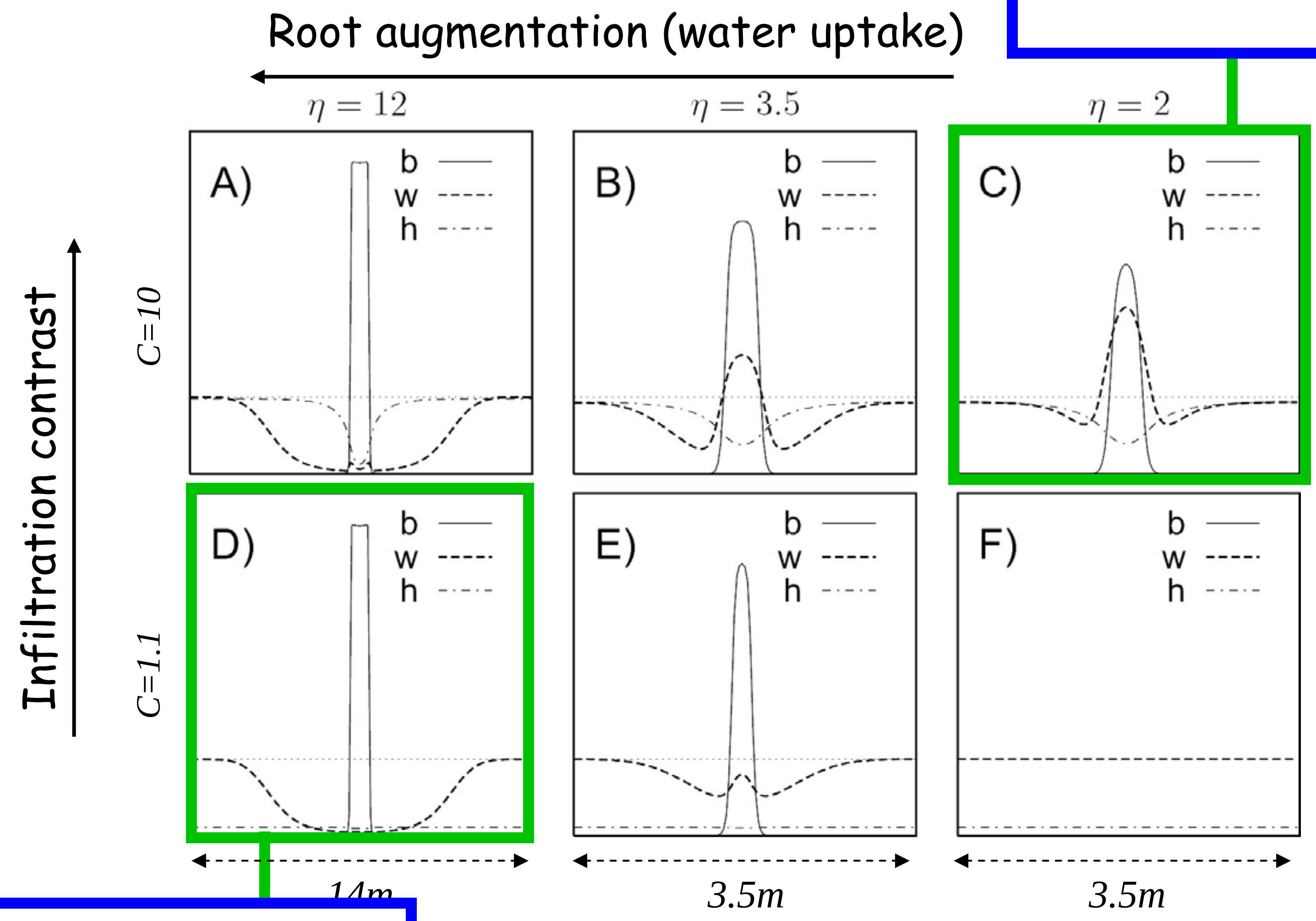




Population level: Soil-water patterns

Effects of the biomass-water feedbacks:

Facilitation



Competition

For given c, η the relative feedback strength may change with rainfall and spatial patterns

Community level: a model for several functional groups

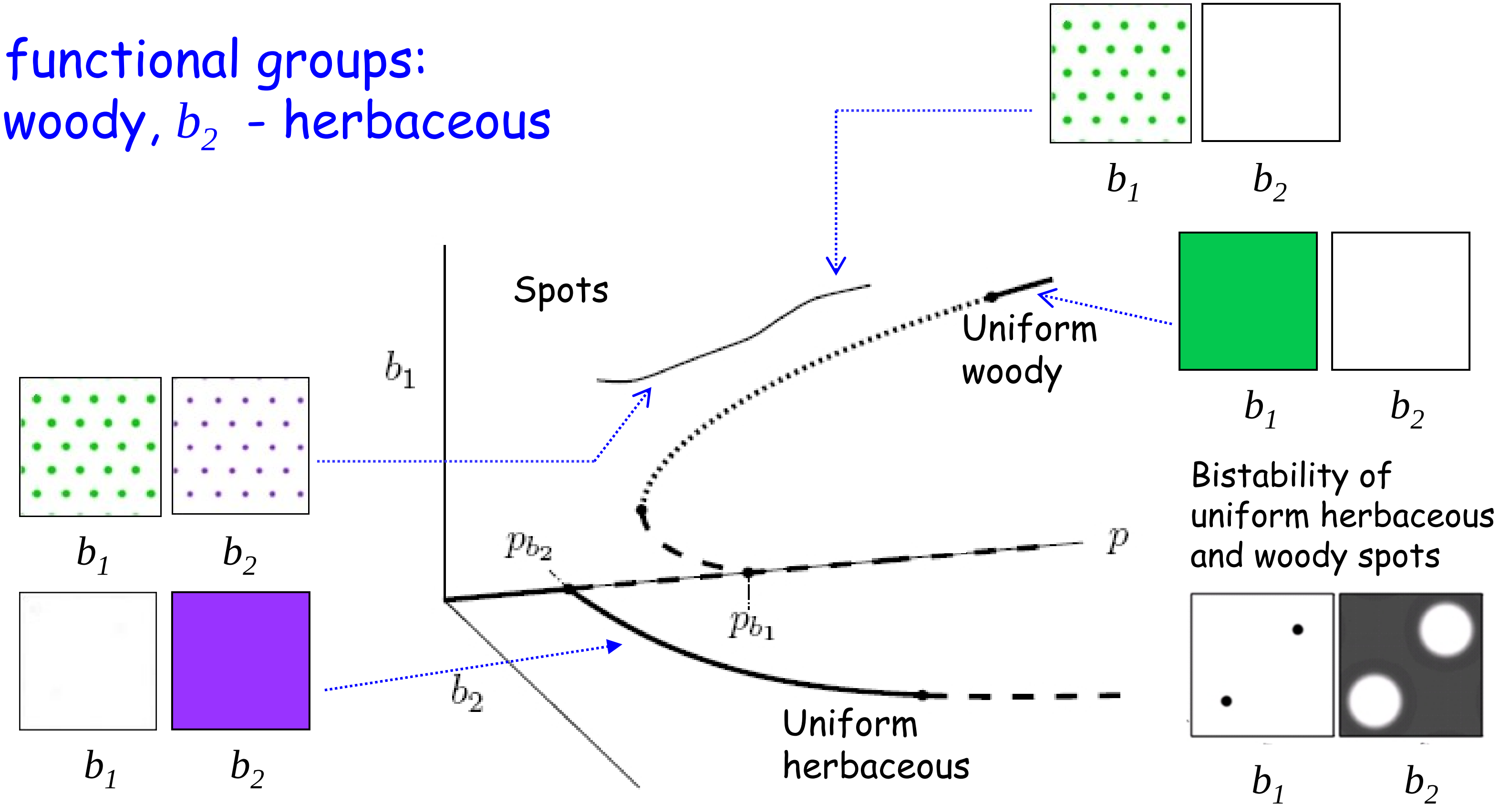
$$\frac{\partial b_i}{\partial t} = G_b^i b_i (1 - b_i) - \mu_i b_i + \delta_{b_i} \nabla^2 b \qquad i = 1, \ldots, n$$

$$\frac{\partial w}{\partial t} = Ih - Lw - w \sum_{i=1}^{n} G_w^i + \delta_w \nabla^2 w$$

$$\frac{\partial h}{\partial t} = p - Ih + \delta_h \nabla^2 h^2 + 2\delta_h \nabla h \cdot \nabla \zeta + 2\delta_h h \nabla^2 \zeta$$

# of functional groups (fg)

Two functional groups:
b_1 - woody, b_2 - herbaceous



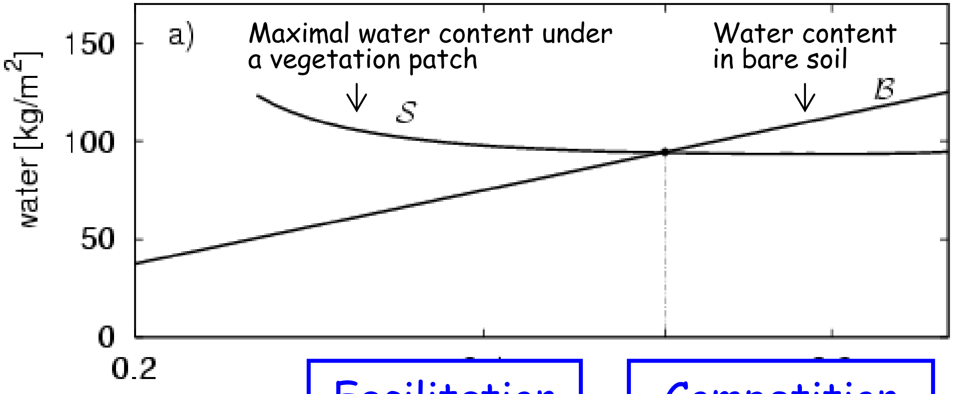
Bistability of uniform herbaceous and woody spots

Community level: Competition vs. facilitation

Inter-specific interactions along a rainfall gradient:

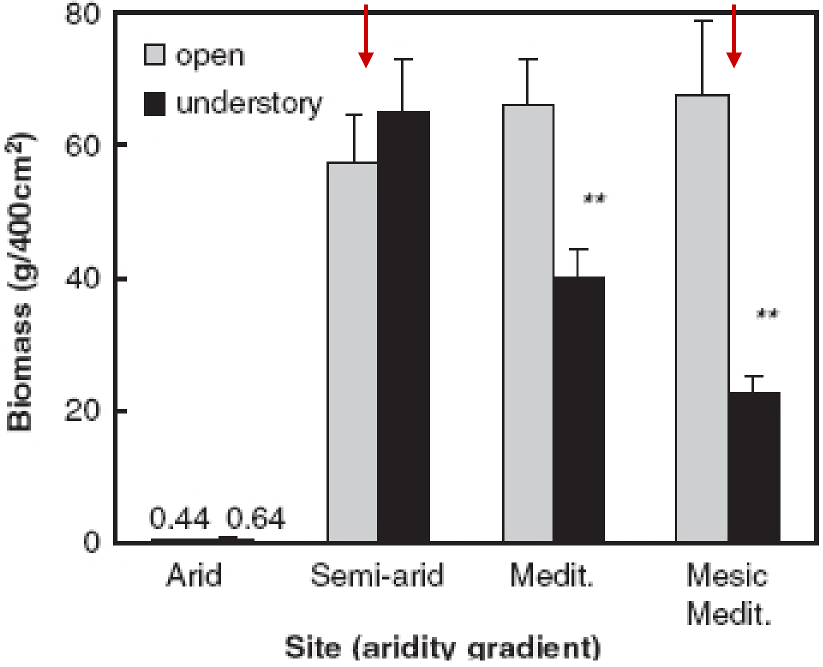
Woody species alone:

Ameliorates its micro-environment as aridity increases.



Facilitation

Competition



Consistent with field observations of annual plant–shrub interactions along an aridity gradient:

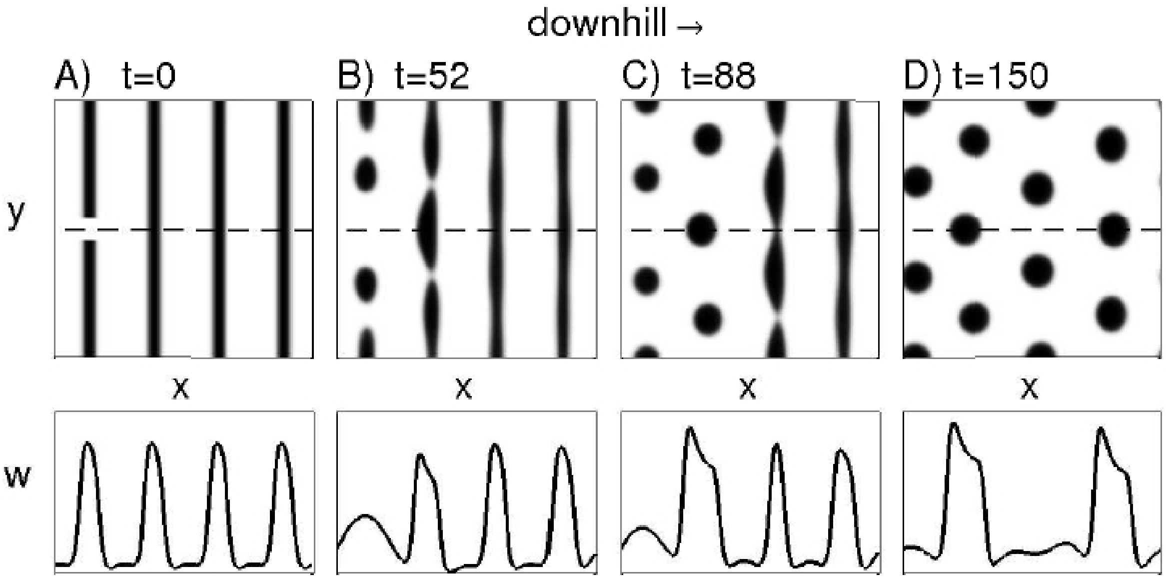
Holzapfel, Tielbörger, Parag, Kigel, Sternberg, 2006

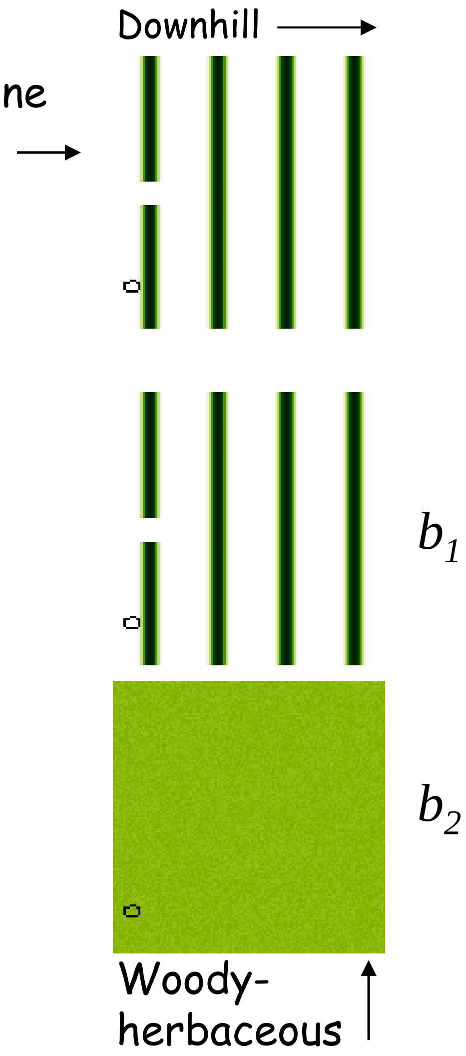
Facilitation in stressed environments:
Pugnaire & Luque, Oikos 2001,
Callaway and Walker 1997
Bruno et al. TREE 2003

Community level: Competition vs. facilitation

Inter-specific interactions and pattern transitions:

Clear cutting on a slope in a bistability range of spots and bands:





Mechanism: spots “see” bare areas uphill twice as long as bands and infiltrate more runoff.

Species coexistence and diversity are affected by global pattern transitions. Coexistence appears as a result of bands → spots transition.

Community level: Deriving community-level properties

Current form of model cannot provide information about species diversity $\Rightarrow$ extend the model to include trait-space dynamics

...

This study has not been published yet and therefore is not included here

Conclusion

Vegetation pattern formation and species diversity in dryland plant communities can be studied using a single platform of non-linear mathematical models that capture biomass-water feedbacks in a product space spanned by spatial axes and trait axes.

More complicated systems and questions:

Add physical space dependence:
How pattern formation affects species diversity and other community level properties?

Add another functional group:

1. How patches of a woody species affect the diversity of annuals along a rainfall gradient? (facilitation at low rainfall)
2. How pattern transitions of the woody species affect annuals diversity?

Stability and resilience:
How spatial organization of a species assemblage in a patch affects its resilience to climatic fluctuations and disturbances

Context-specific modeling vs. problem-specific modeling

References

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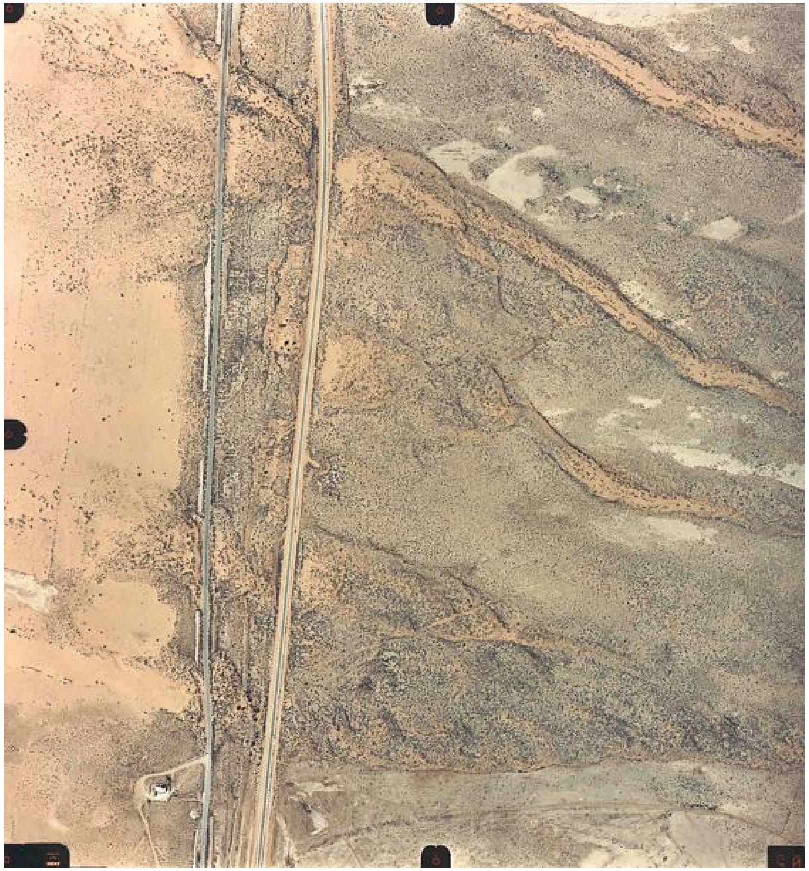
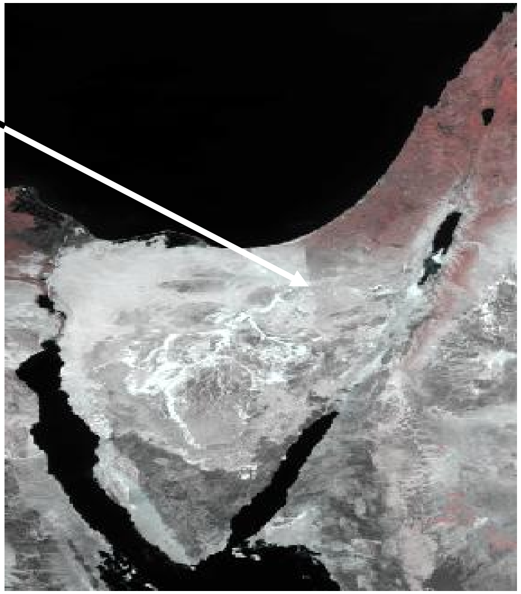
Biological soil crusts

Areal photographs →
Egypt-Israel border



Soil crust



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