Nonlinear dynamics and pattern formation with applications to ecology

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Part IV: Vegetation pattern formation

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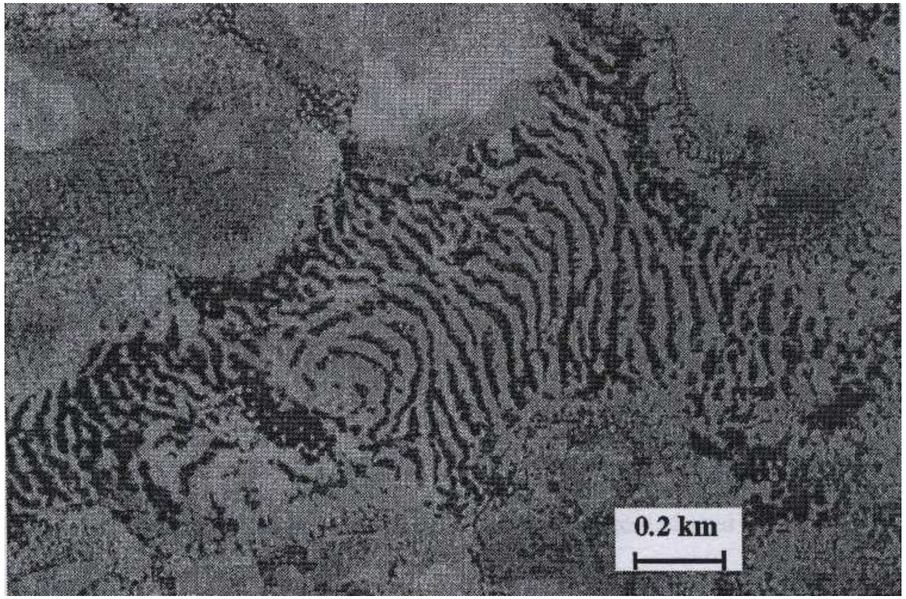
Outline of part IV

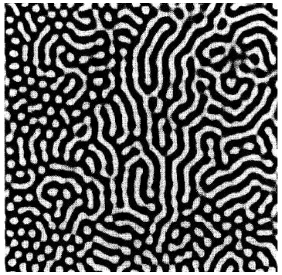
1. Background:
   Vegetation patterns, ecosystem engineers, inter-specific plant interactions along environmental gradients, vegetation-water feedbacks.
2. Population level:
   Introduction of a spatially explicit model for a plant population, applying it to pattern formation phenomena along environmental 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.

Background: Vegetation patterns

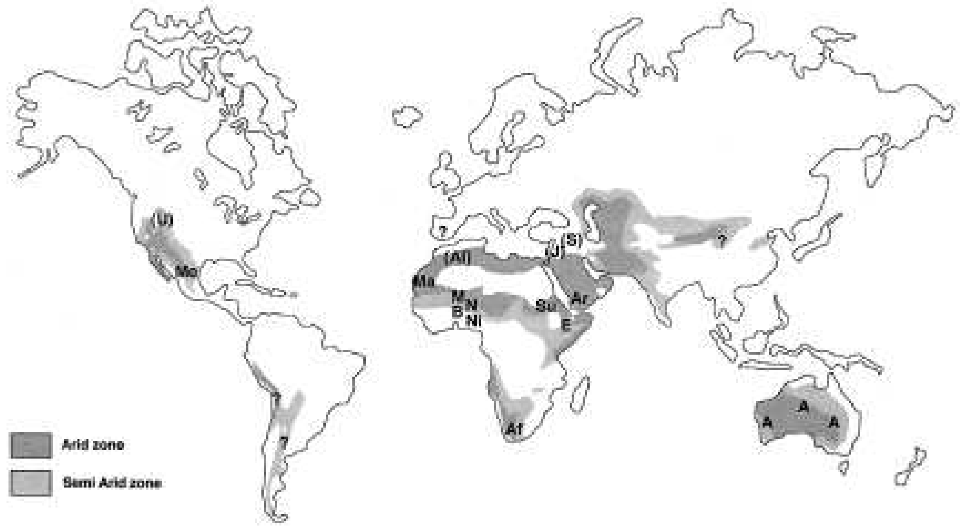
Aerial photograph of vegetation bands in Niger of 'tiger bush' patterns on hill slopes (Clos-Arceduc, 1956) →



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)

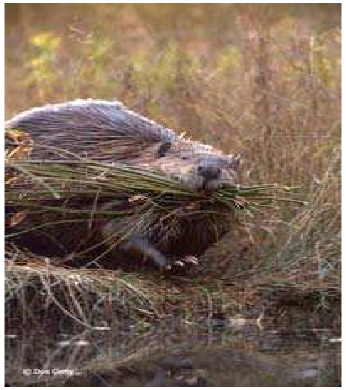


First requirement in modeling plant communities – produce patterns!

Background: Ecosystem engineers

Ecological communities consist in general of many species, but not all species are equally important in maintaining the community. One type of outstanding species in that respect is "ecosystem engineers". These are key species that modify the abiotic environment in ways that facilitate the growth of other species. Jones, Lawton & Shachak. 1994.

Example 1: Beavers in North-American forests that build dams.



Example 3: Plants in drylands that increase soil moisture (Holzapfel)

Second requirement in modeling plant communities – capture ecosystem engineering!

Background: Plant interactions along environmental gradients

Facilitative interactions among plant species, such as those induced by ecosystem engineers, have received much attention recently. Many studies have reported on transitions from plant competition (negative interaction) to plant facilitation (positive interaction) as environmental stresses increase.

(Pugnaire & Luque, Oikos 2001; (Callaway et al., Nature 2002; Maestre & Cortina, Proc. R. Soc. Lond. B 2004, and others)

This is in contrast to the traditional view of plant interactions as being competitive only through the consumption of common resources.

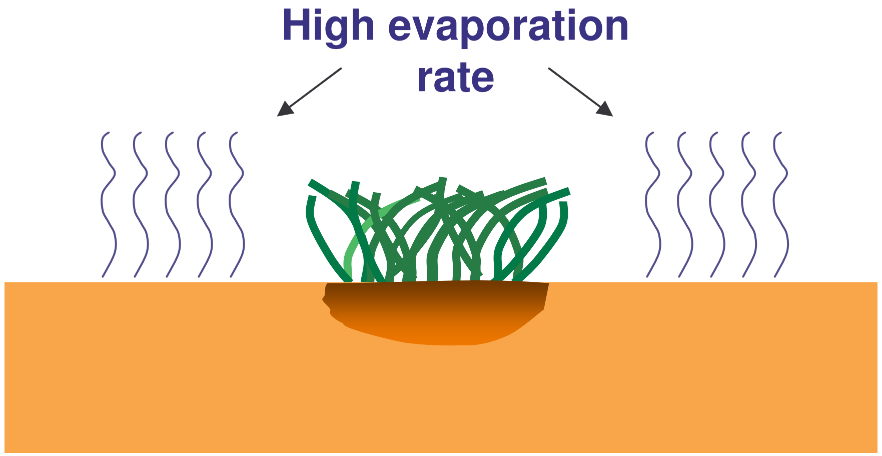
Third requirement in modeling plant communities – capture transitions from competition to facilitation along environmental gradients!

We want all three properties, pattern formation, ecosystem engineering and transitions from competition to facilitation, and other properties as well, to emerge as model solutions by modeling more basic principles.

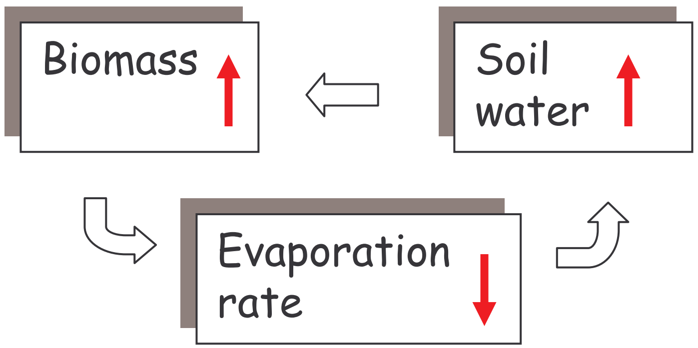
These basic principles are various feedbacks between biomass and water and between above-ground and below-ground biomass.

Background: Biomass-water feedbacks

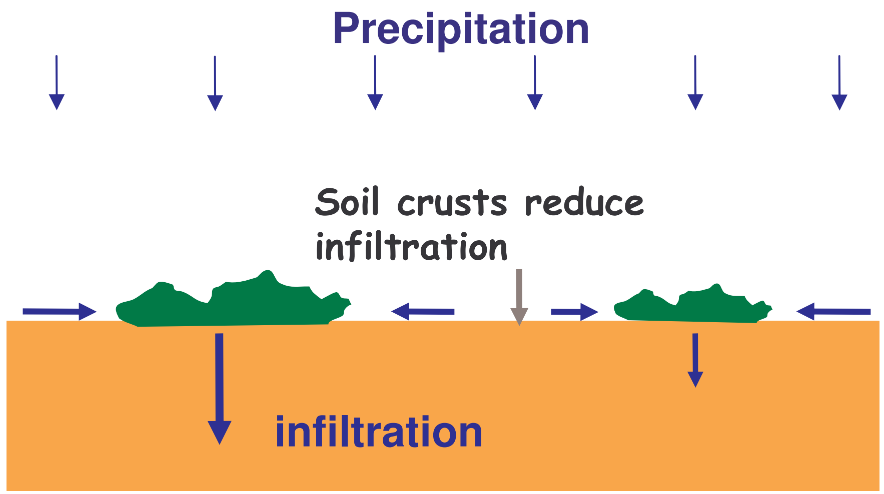
(1) Shading



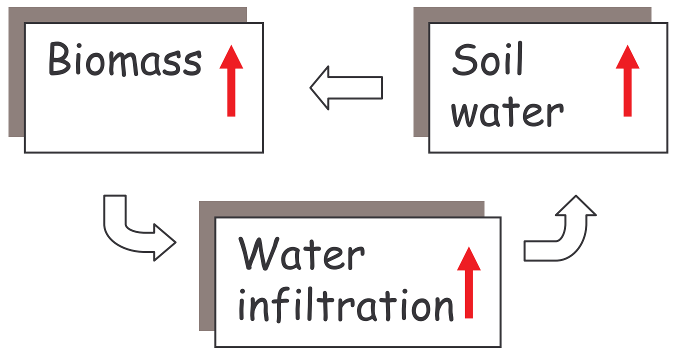
Positive feedback



(2) Increased infiltration



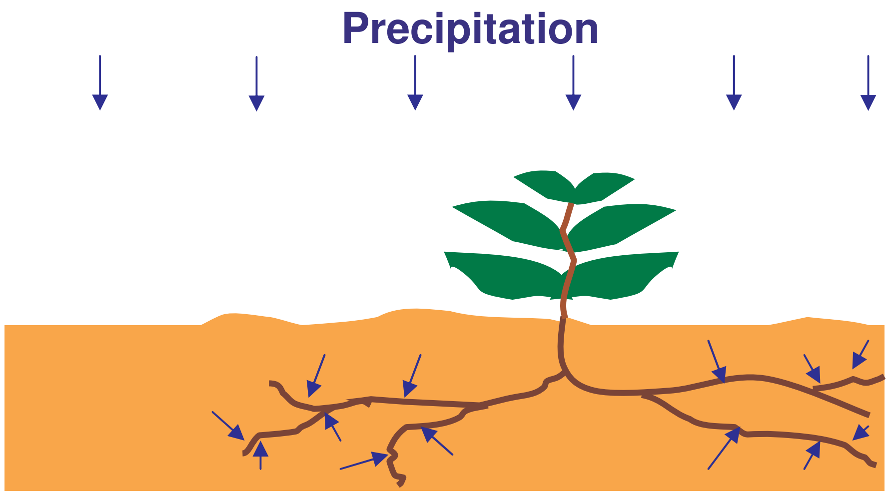
Positive feedback



Infiltration feedback involves water transport $\Rightarrow$ helps growth within the patch, but inhibits growth in the patch surroundings

Background: Biomass-water feedbacks

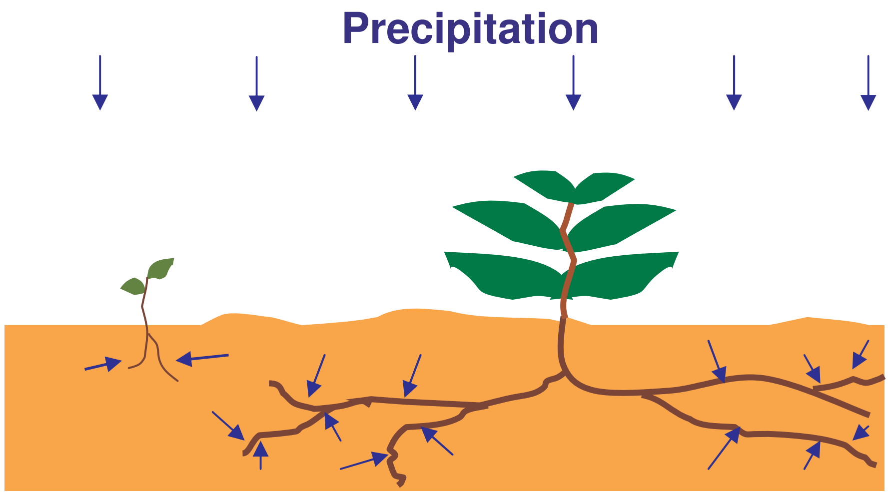
(3) Water uptake



Negative feedback

Biomass ↑ → Soil water ↓ → Biomass ↓

(4) Root augmentation



Positive feedback

Biomass ↑ → Root extension ↑ → Water uptake ↑ → Biomass ↑

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

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

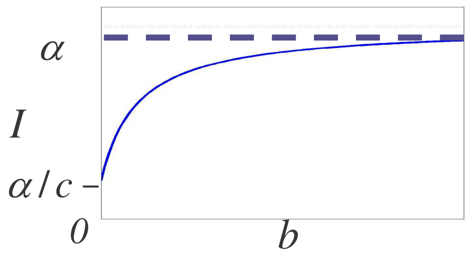
$$L = \frac{\nu}{1+\rho b}$$

Shading

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

Infiltration contrast

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



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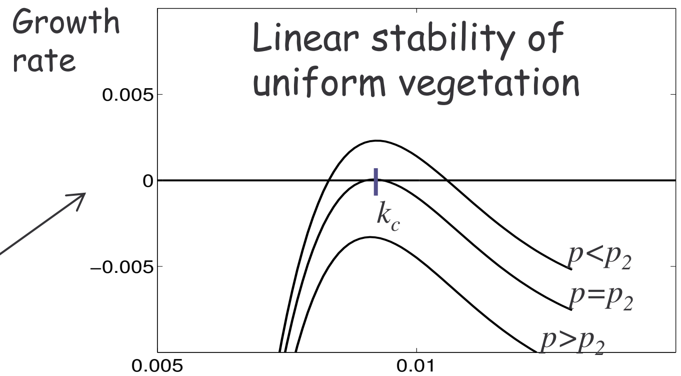
Population level: model solutions

Vegetation states along rainfall gradients

Bare state ($b = 0$):
Exists for all p values
Unstable for $p > p_c$ (dashed line)

Fully vegetated state ($b \neq 0$):
Exists for $p > p_1$
Unstable for $p_1 < p < p_2$ (dotted line): finite k instability at p_2

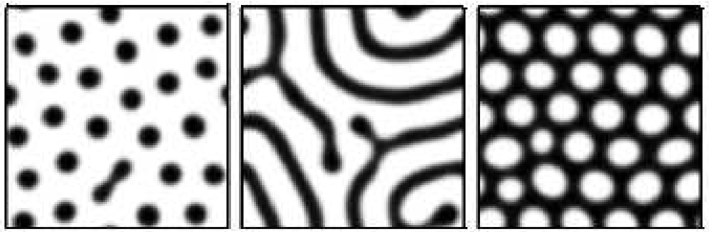


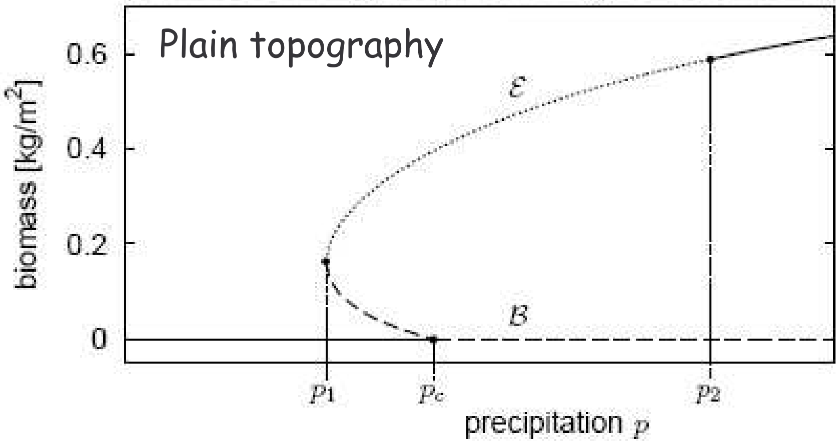
Pattern states:

Spots (hexagonal patterns)

Stripes (labyrinthine patterns)

Gaps (hexagonal patterns)





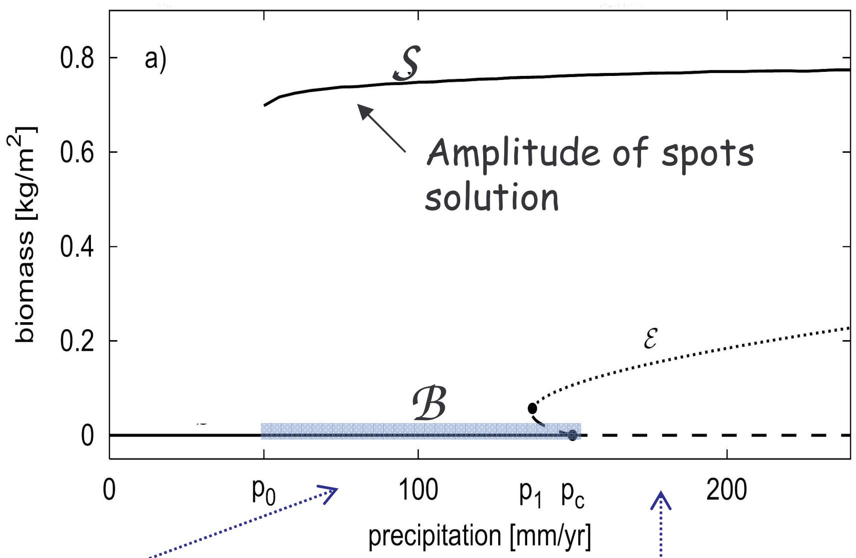
Induced by the feedbacks that involve water transport.

Population level: model solutions

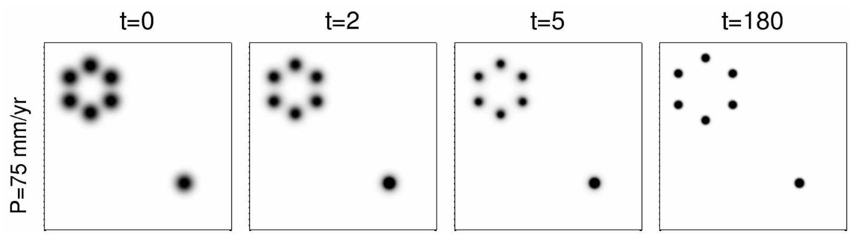
Coexistence of stable states:

Both bare-soil and spot-pattern solutions are stable in $p_0<p<p_c$

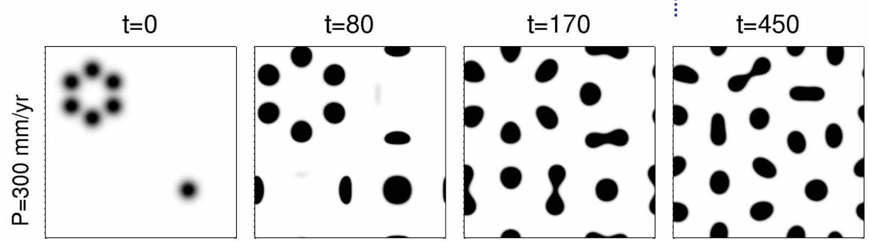
Holds for any consecutive pair of States: spots & stripes, stripes & gaps, gaps & uniform vegetation



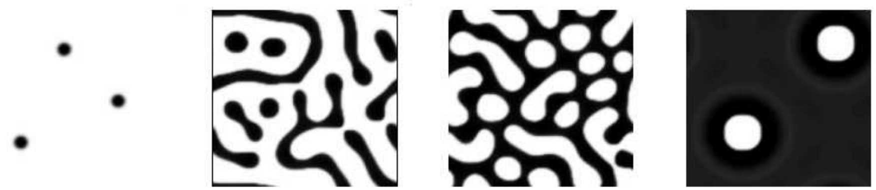
⇒ spatially mixed patterns



Spatial mixtures of bare soil & spots ↑



Monostability range of spots ↑



Bare-spots Spots-stripes Stripes-gaps Gaps-uniform

Multistability of states is a consequence of the biomass-water feedbacks

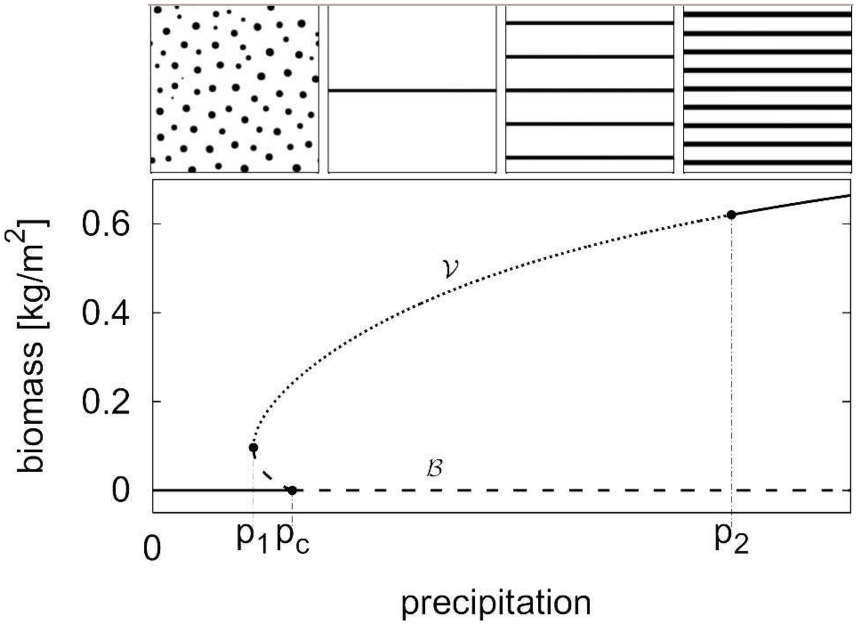
Population level: model solutions

Patterns on hill slopes:

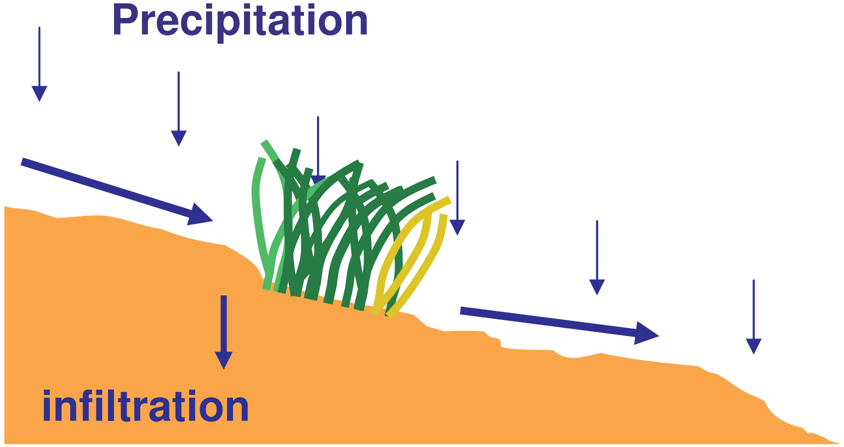
Same uniform states, bare soil and fully vegetation.

Stripe patterns:

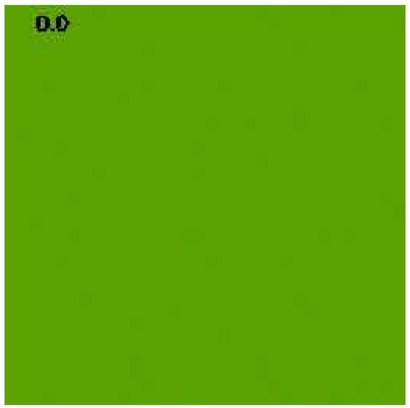
1. Reorient to form bands $\perp$ slope
2. Occupy wider p range
3. Multiple band patterns coexist
4. Migrate uphill



Mechanism of migration:



Model simulations ($\nabla\zeta$=Const.):

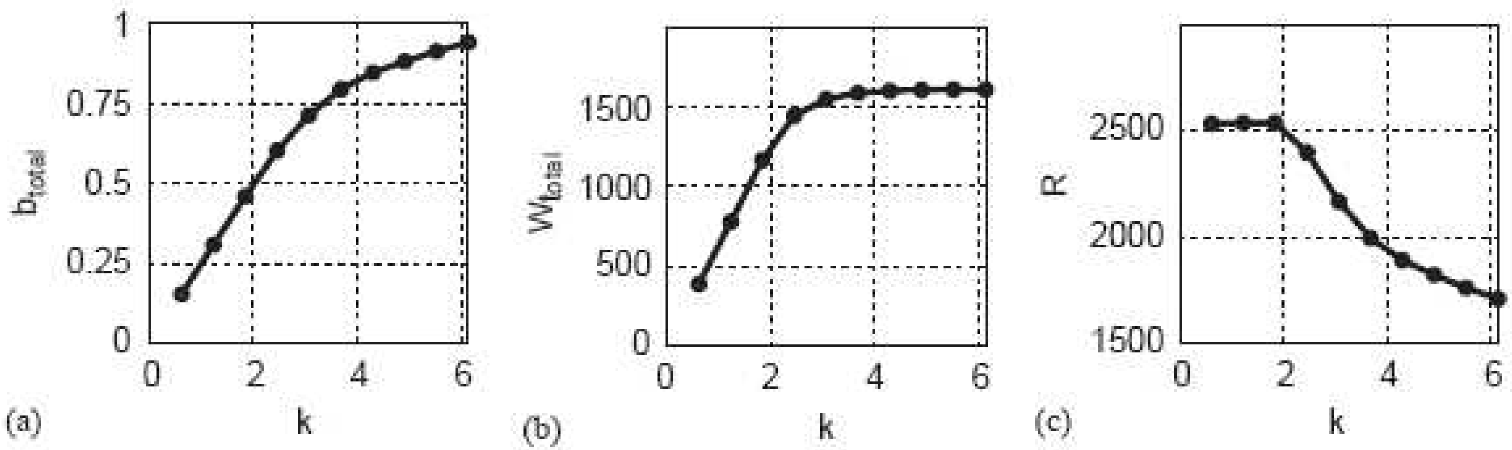


Down hill

Bands speed ~ 1 cm/year

Population level: model solutions

Dependence of biomass and water consumption on the wavenumebr of banded vegetation:



$$b_{total} = \int b d\vec{x} \qquad w_{total} = \int G_w w d\vec{x} \qquad R = \frac{w_{total}}{b_{total}}$$

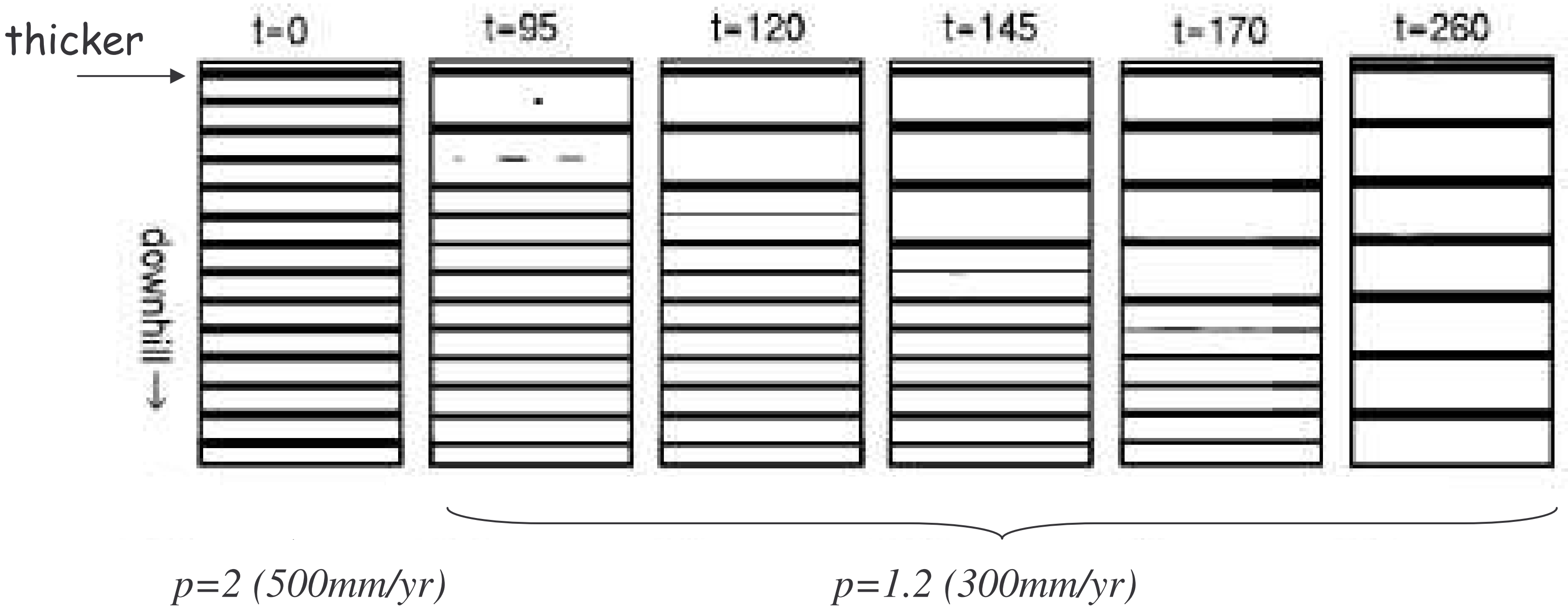
The water consumption per unit biomass decreases as the pattern's wavenumber increases.

$\Rightarrow$ higher wavenumber patterns increase the biological productivity.

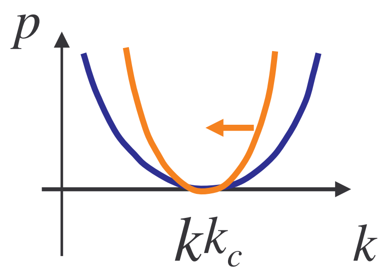
Population level: model solutions

Resilience of band states upon precipitation down shift:

Banded patterns with higher k produce more biomass but are less resilient to disturbances



A chain process by which a lower wavenumber pattern $k/2$ invades the initial higher wavenumber pattern k

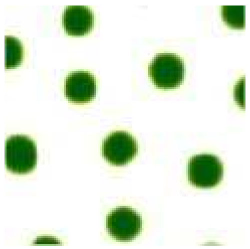


$\Rightarrow$ A tradeoff between productivity and resilience

Population level: Observations of vegetation patterns

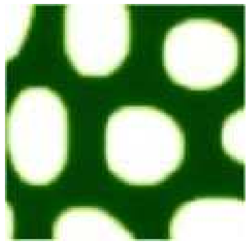
Stripes of *Paspalum vaginatum*

Spots

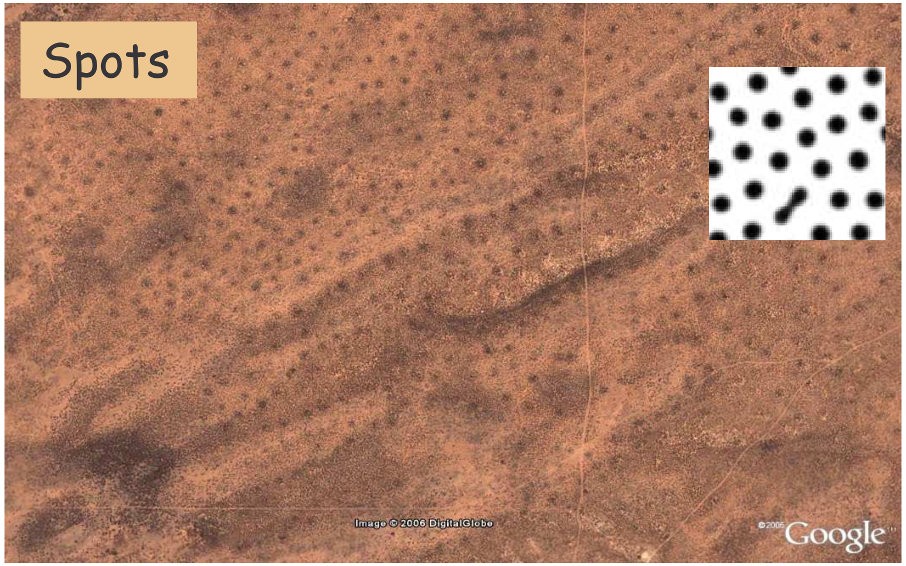


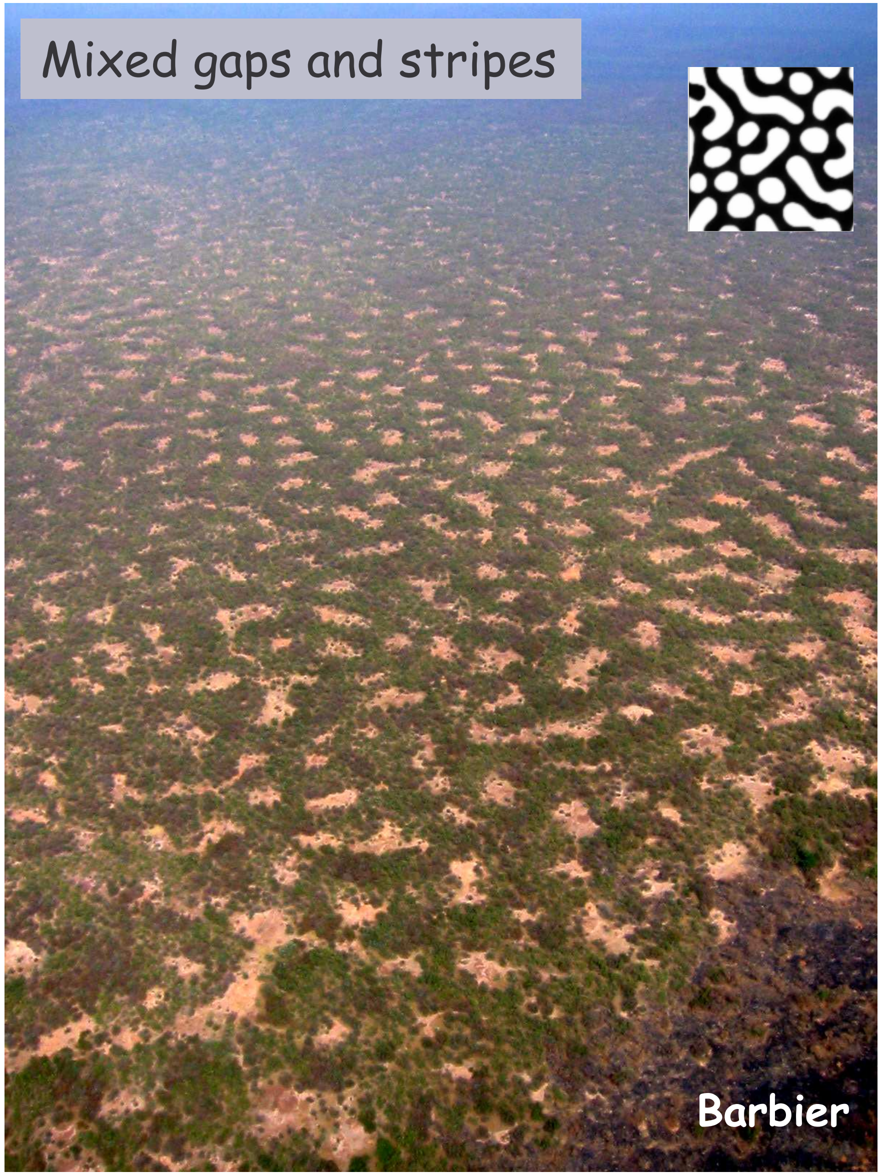
Stripes

Gaps



Population level: Observations of vegetation patterns





All patterns are pretty regular and have characteristic lengths !

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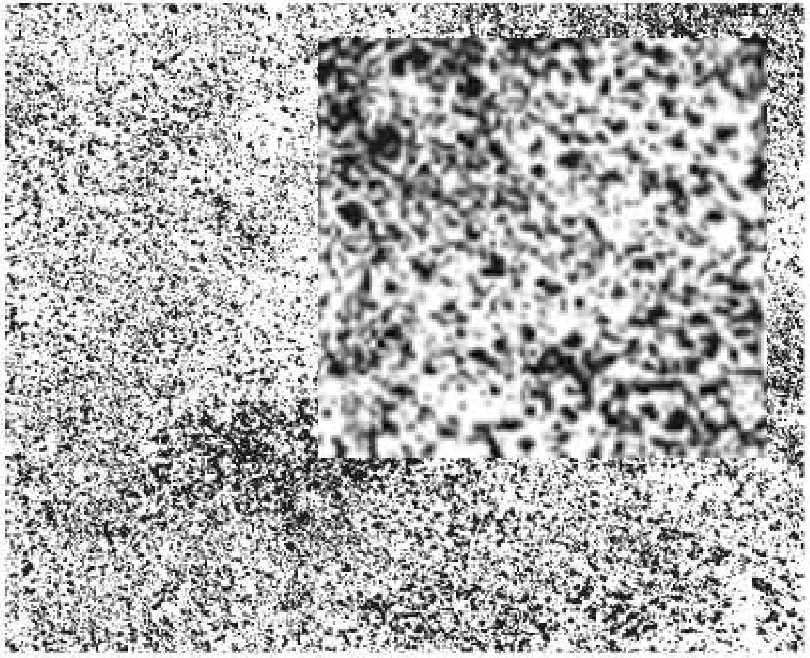
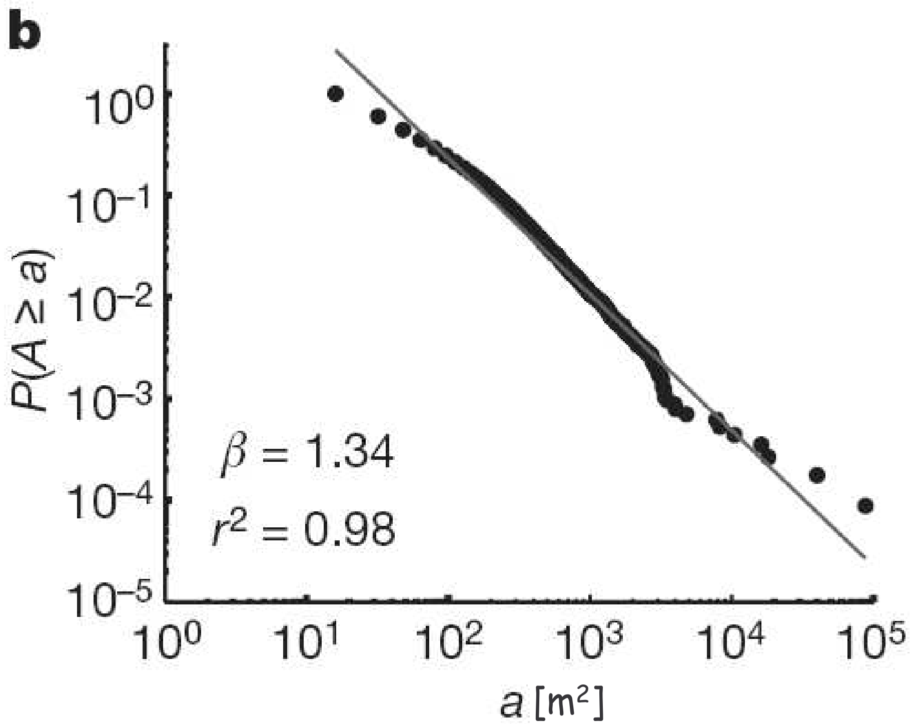
Population level: Scale-free vegetation patterns

Satellite image (Pandamatenga)



2x2 km^2, 4m resolution

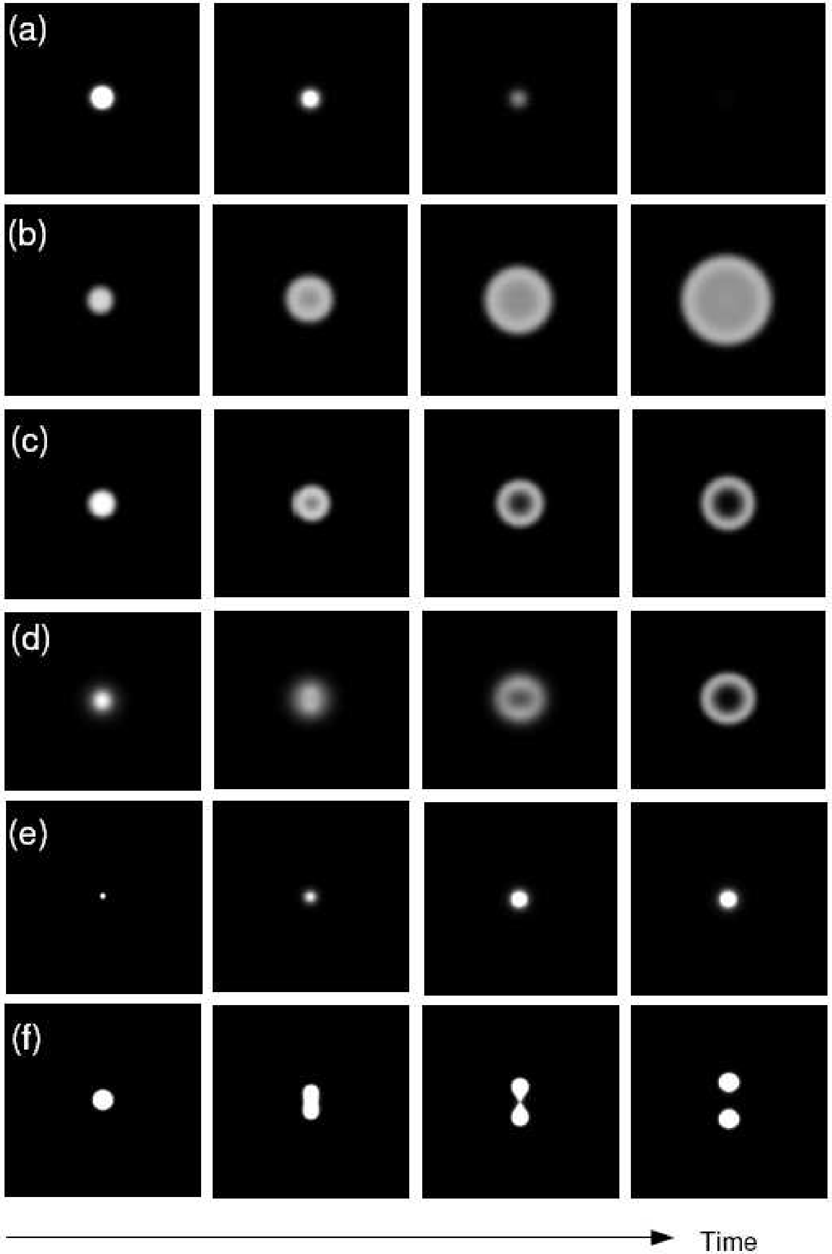
Scanlon et al., Nature 2007
Kefi et al., Nature 2007



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



$p < p_c$

$p > p_c$

Shading feedback only: $c=1,\ \eta=0.$ No inhibition processes to limit patch growth

$p > p_c$

Switching on the infiltration feedback: $c=10,\ \eta=0.$ Patch area limited by central dieback

$p > p_c$

$p < p_c$

Switching on moderate root-augmentation feedback: $c=1,\ \eta=1.$ Patch limited by central dieback ($p>p_c$) or does not expand ($p<p_c$)

$p > p_c$

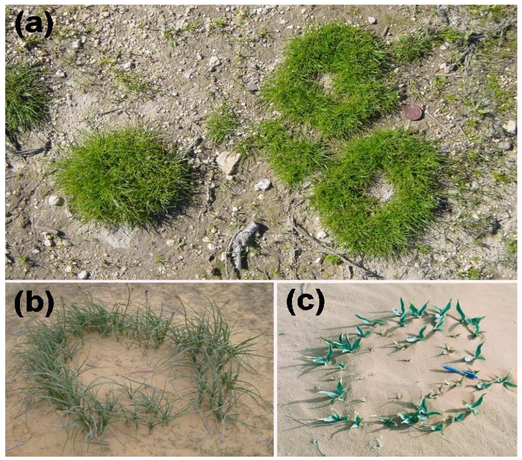
Switching on strong root-augmentation feedback: $c=1,\ \eta=4.$ Patch area limited by peripheral dieback

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)

Spots, rings, and crescents are widely observed in nature



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)

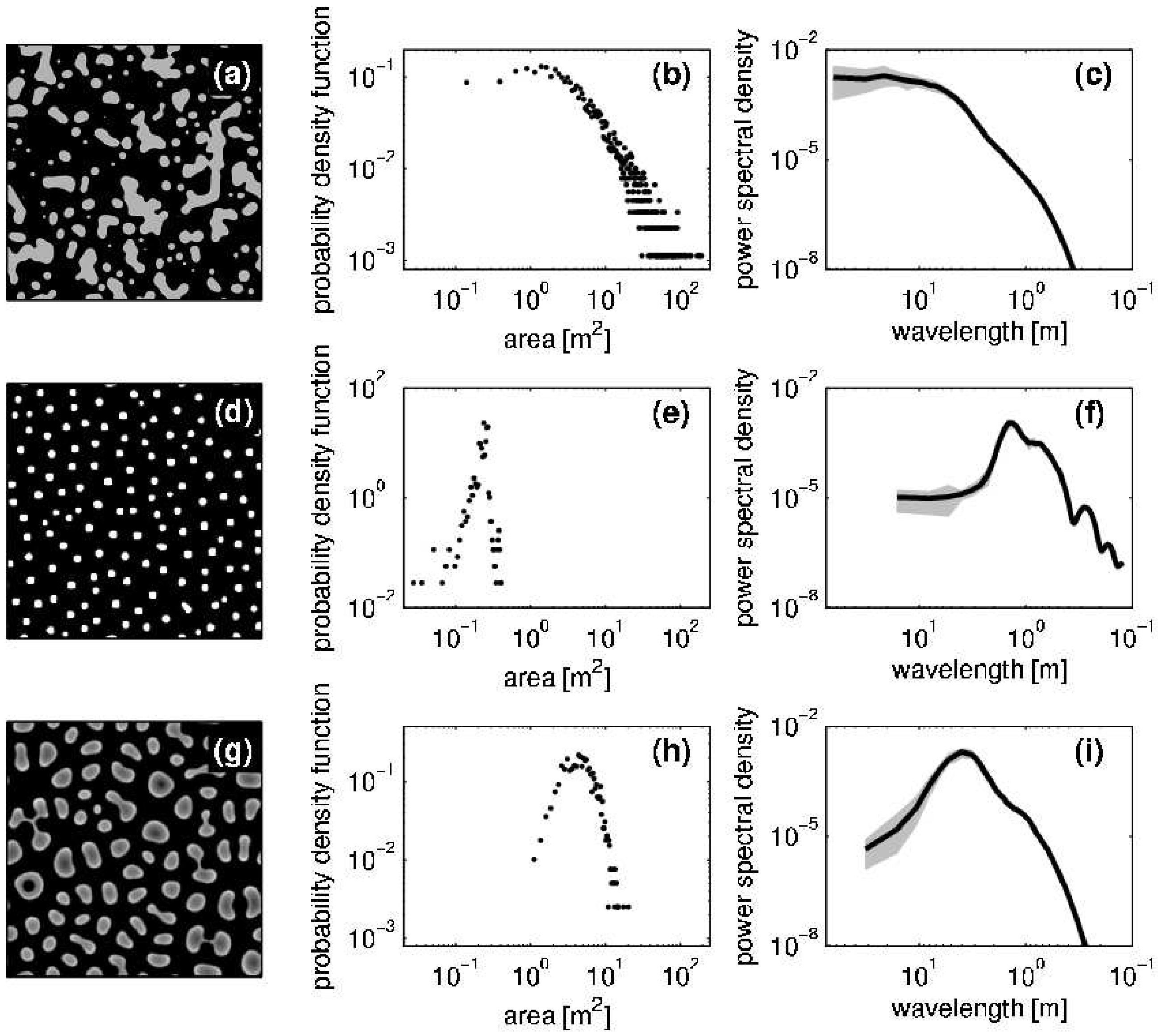
Population level: Scale-free vegetation patterns

Under these Conditions:

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

Switching on root augmentation $\eta > 0$

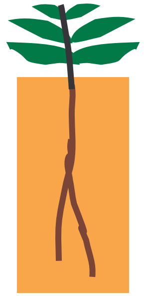
Decreasing τ_I , or increasing the infiltration rate

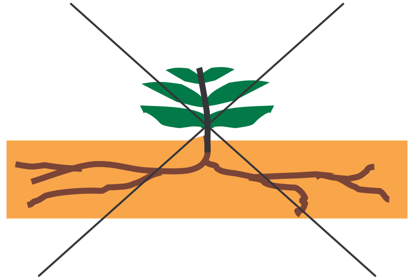


Population level: Scale-free vegetation patterns

Under what circumstances are these conditions realizable?

$\eta = 0 \Rightarrow$ no root augmentation in lateral dimensions – can be approached by plant species that grow roots vertically





$\tau_F / \tau_I << 1$ can be realized:

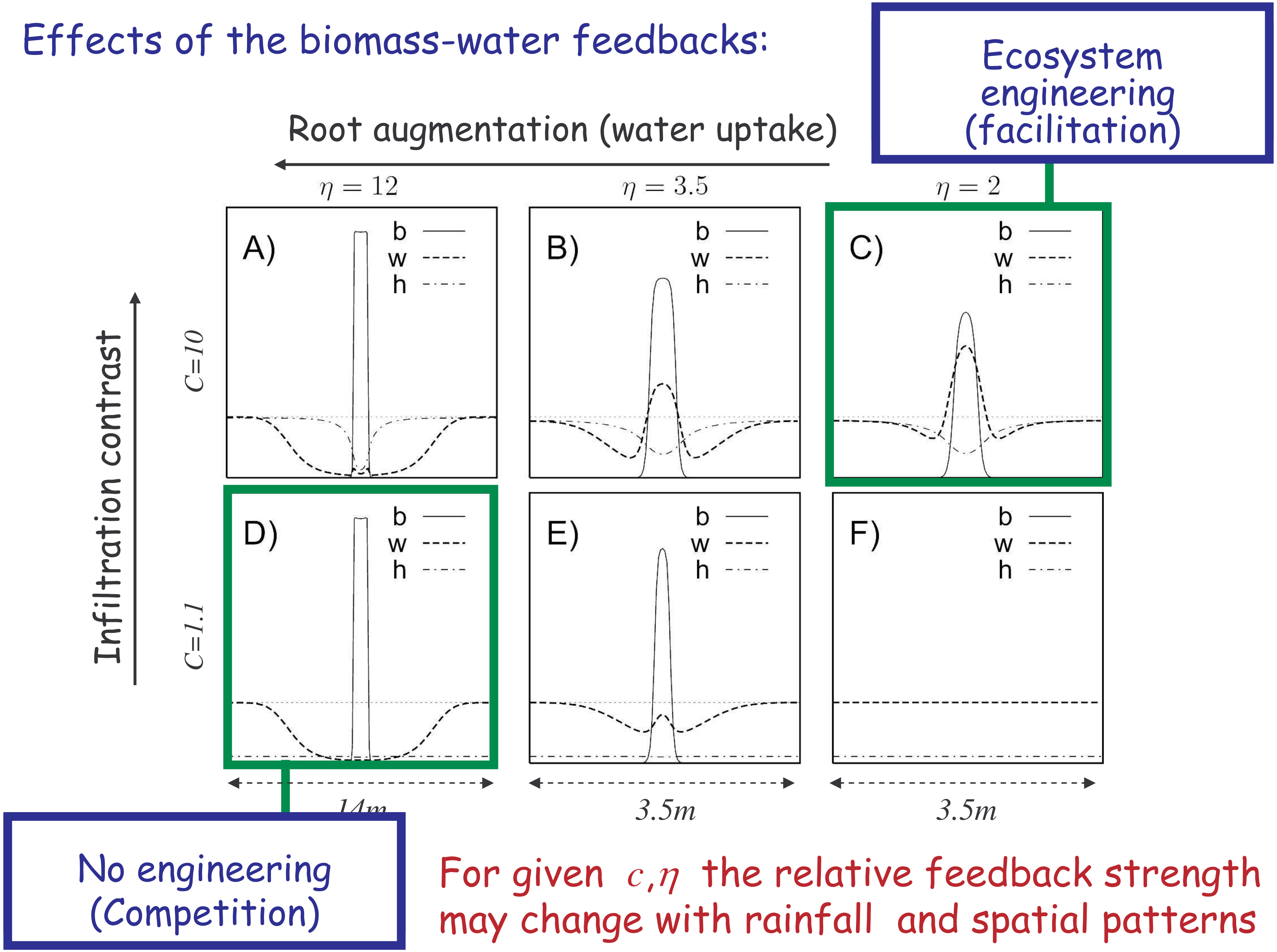
1. On slopes that accelerate water flow

2. With species whose patch sizes are relatively small

When these circumstances do not apply, exogenous environmental factors such as micro-topography are likely to be important.

Considerations of this kind can be used as criteria for assessing the relative importance of endogenous vs. exogenous factors in specific realizations of scale-free patterns.

Effects of the biomass-water feedbacks:



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

Community level: a model for several functional groups

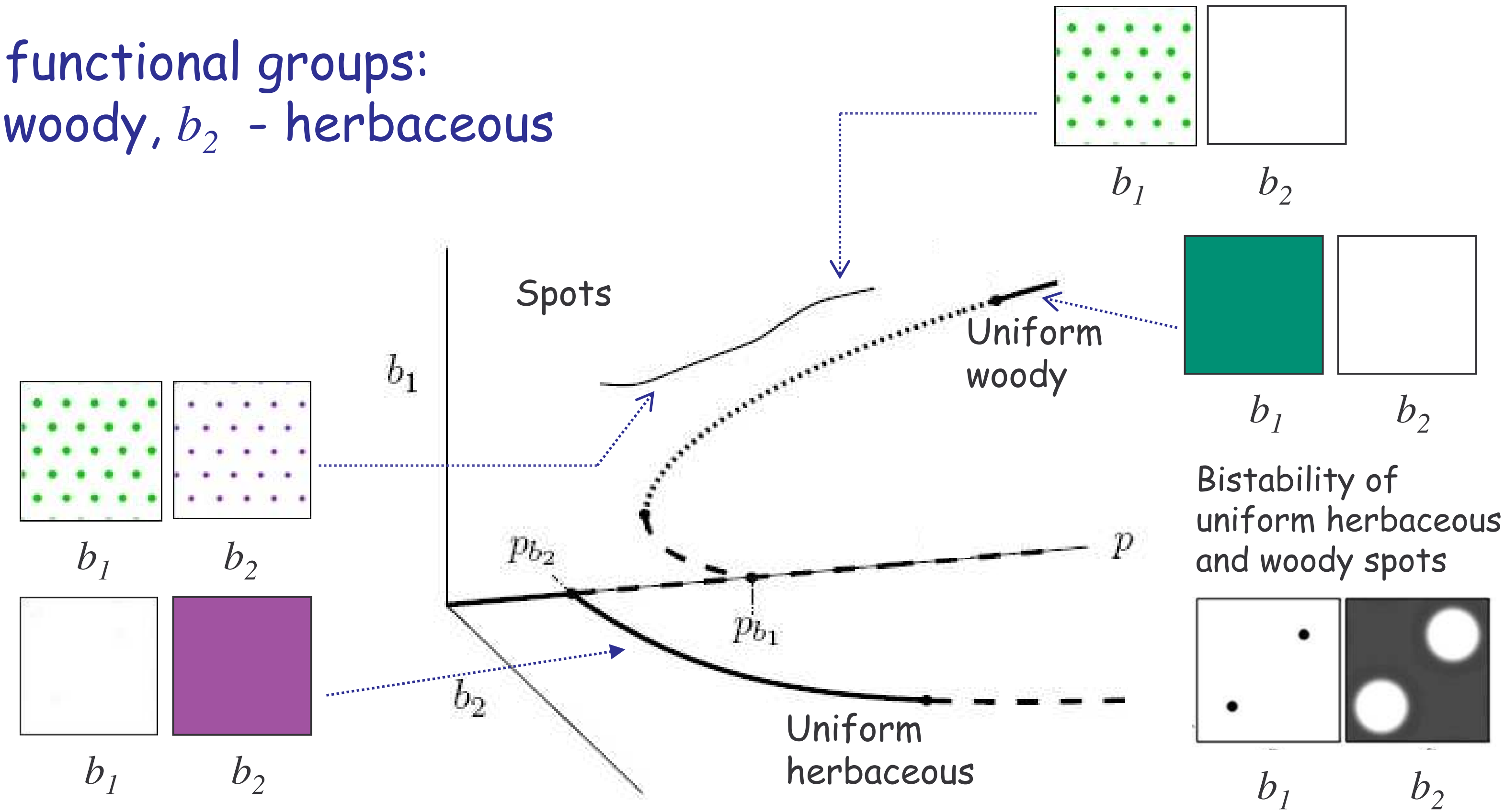
$$\frac{\partial b_i}{\partial t} = G_b^i b_i (1 - b_i) - \mu_i b_i + \delta_{b_i} \nabla^2 b \qquad i = 1, \ldots, n$$

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

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

# of functional groups (fg)

Two functional groups:
b_1 - woody, b_2 - herbaceous



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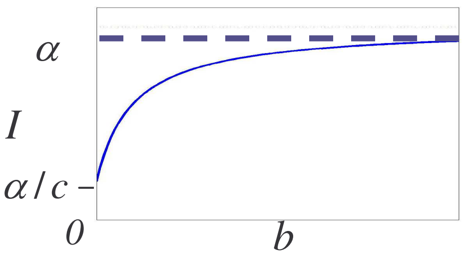
Community level: Competition vs. facilitation

Inter-specific interactions along a rainfall gradient:

Woody species alone:
Ameliorates its micro-environment as aridity increases.

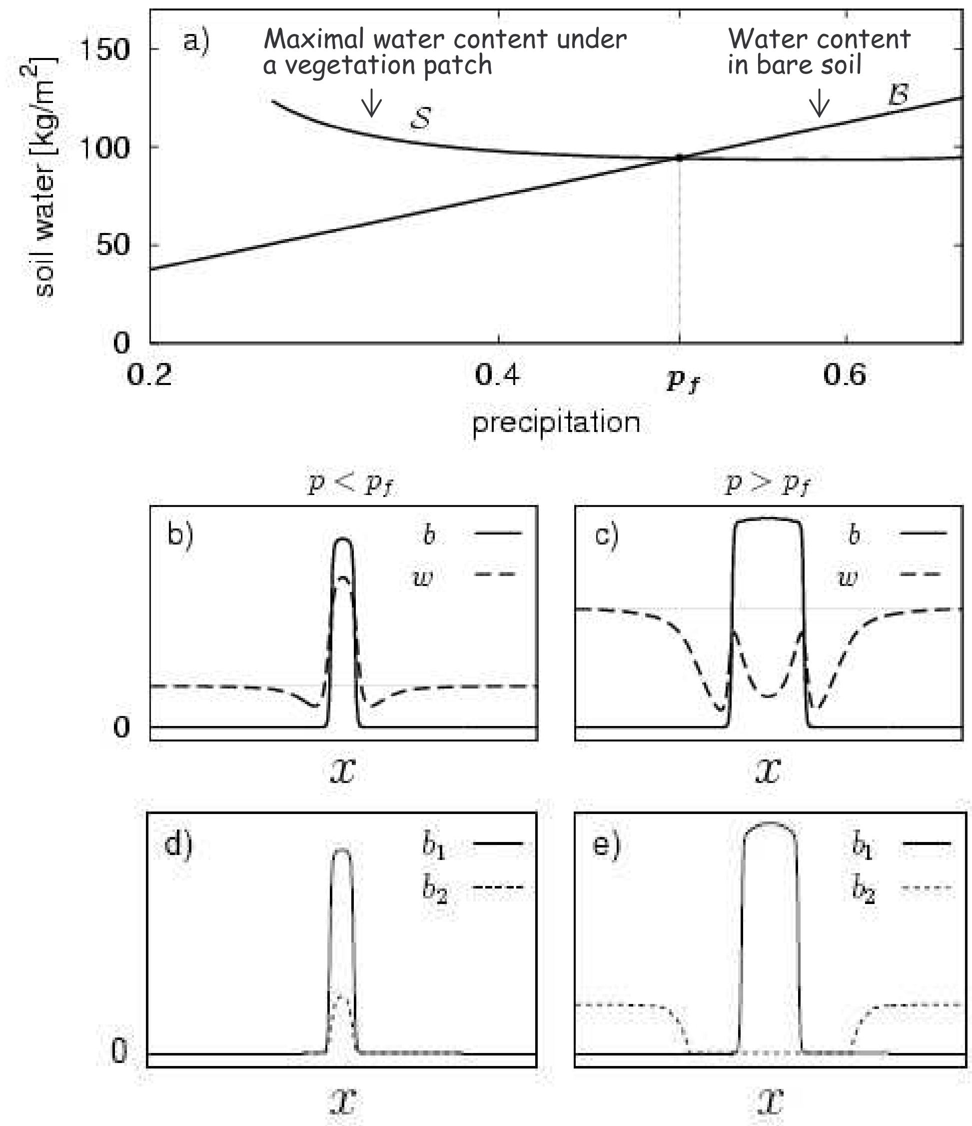
Mechanism:

Infiltration remains high, but uptake drops down because of smaller woody patch.



Woody-herbaceous system:

Competition → facilitation

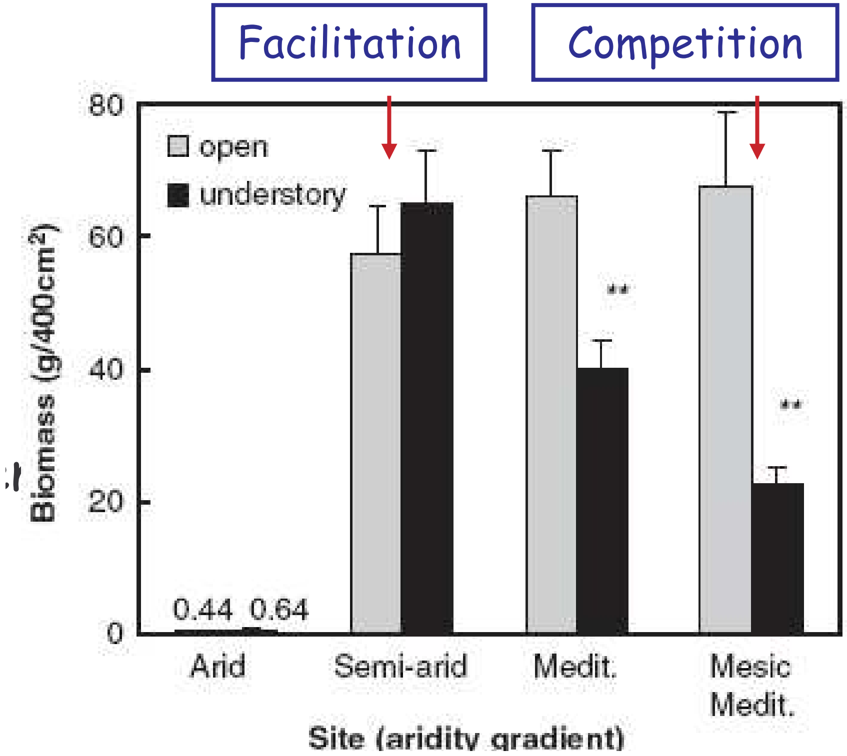


Community level: Competition vs. facilitation

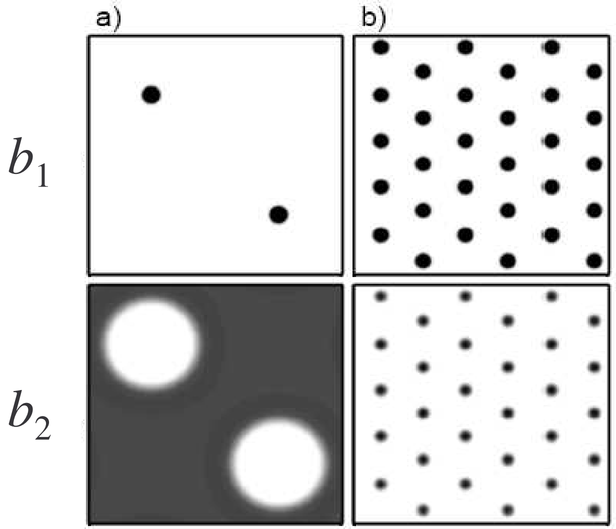
Consistent with field observations of annual plant-shrub interactions along an aridity gradient:

Holzapfel, Tielbörger, Parag, Kigel, Sternberg, 2006

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



Response to patch density at given environmental conditions:



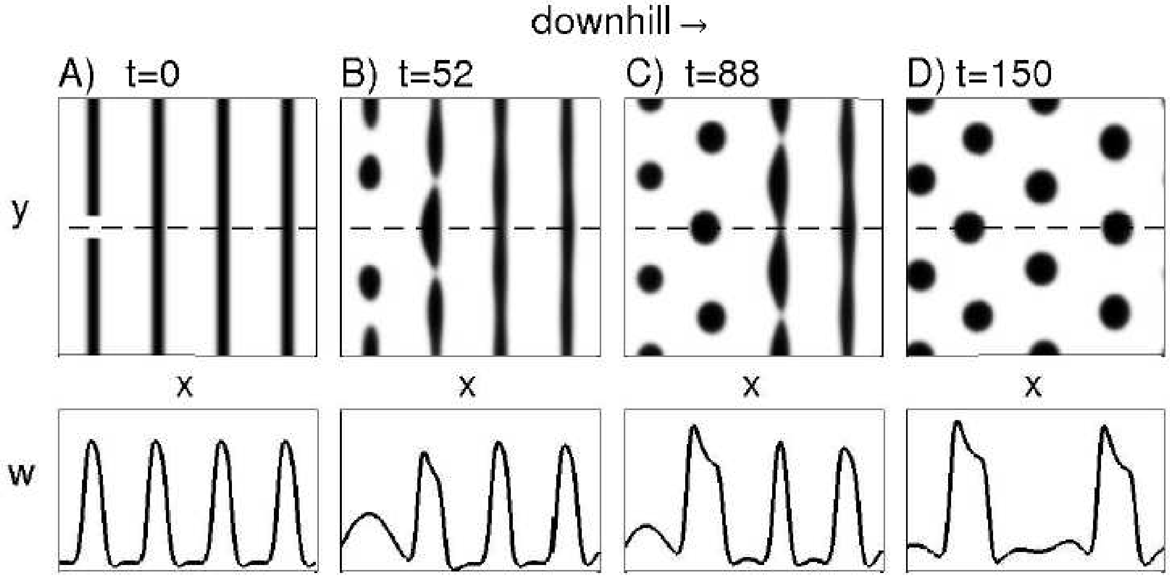
Competition $\Rightarrow$ facilitation as patch density increases.

Mechanism: Similar to facilitation as a result of decreasing rainfall rate, except that water deficiency is due patch competition over water.

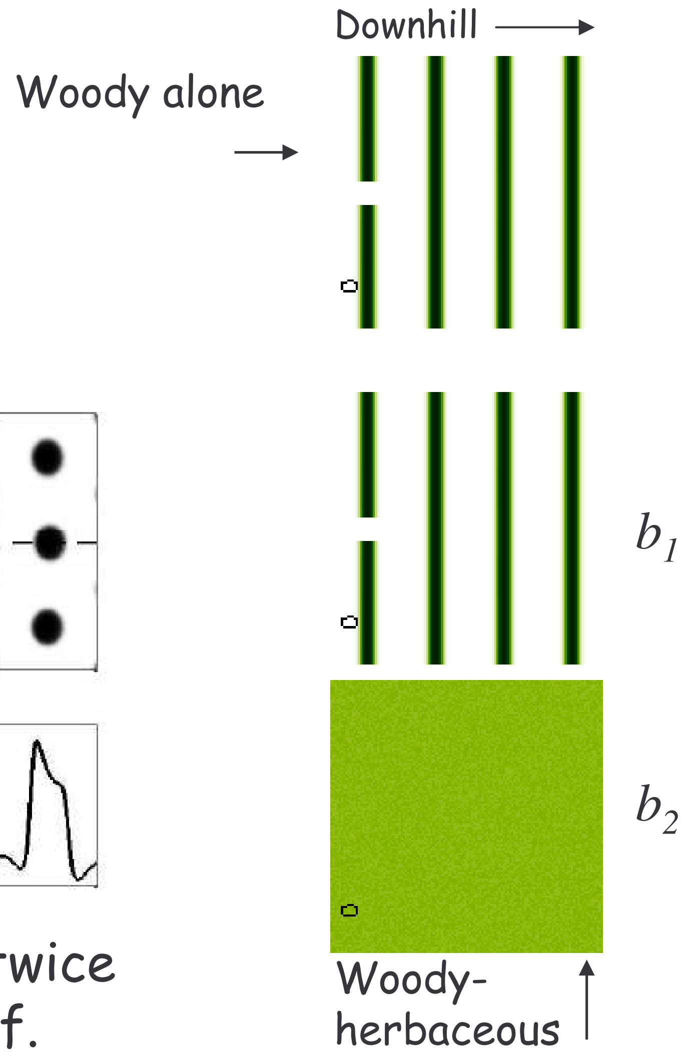
Community level: Competition vs. facilitation

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.

Conclusion

A platform of non-linear mathematical models have been developed for studying community-level properties of dryland vegetation on patch and landscape scales.

Solutions of these models capture vegetation pattern formation, ecosystem engineering and transitions from competition to facilitation along environmental gradients, and are consistent with field observations.

The models elucidate mechanisms of observed behaviors (e.g. pattern formation, ecosystem engineering) and predict behaviors that have not been observed yet such as the effects of global pattern transitions on local plant interactions.

Further developments of the models are needed, depending on the specific questions to be asked. These include adding a soil depth dimension, erosion, long distance seed dispersal, etc.

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References

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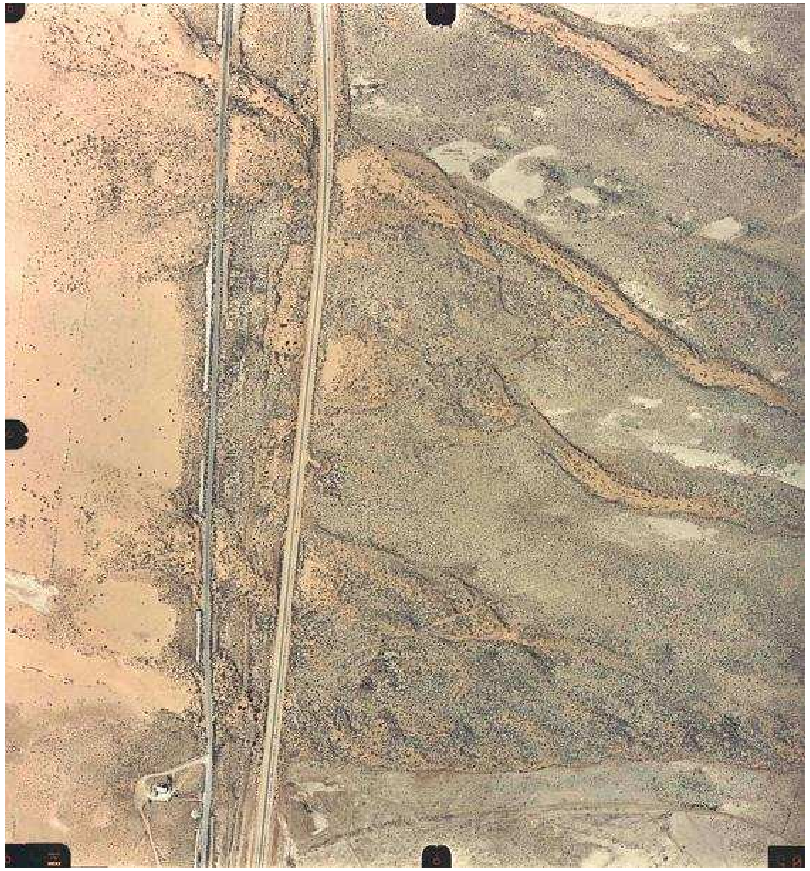
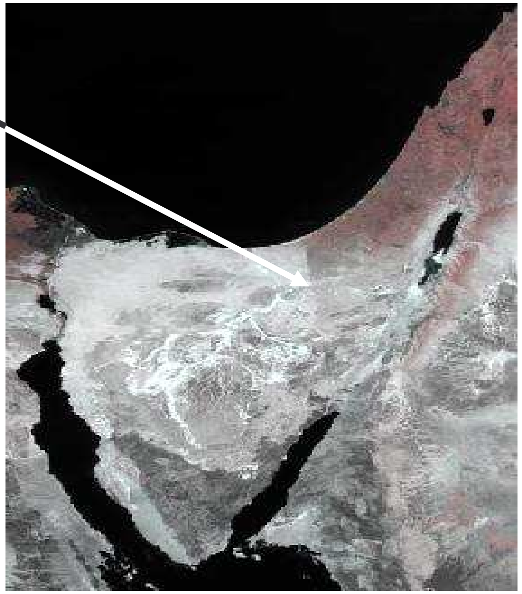
Biological soil crusts

Areal photographs
Egypt-Israel border



Soil crust



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