Ecosystem Engineers, Landscape Diversity and Species Richness: A Pattern Formation Approach

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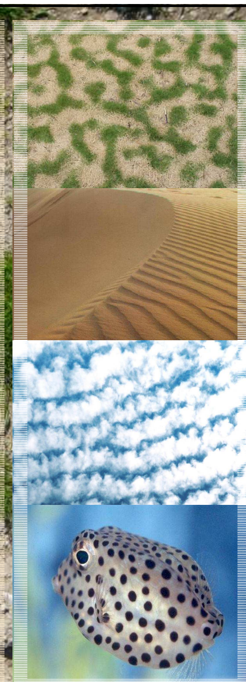
Outline

- Vegetation patterns – mechanisms
- Mathematical models of vegetation patterns
- Applying the models to "ecosystem engineers"
- Relating species richness to pattern formation
- Conclusion



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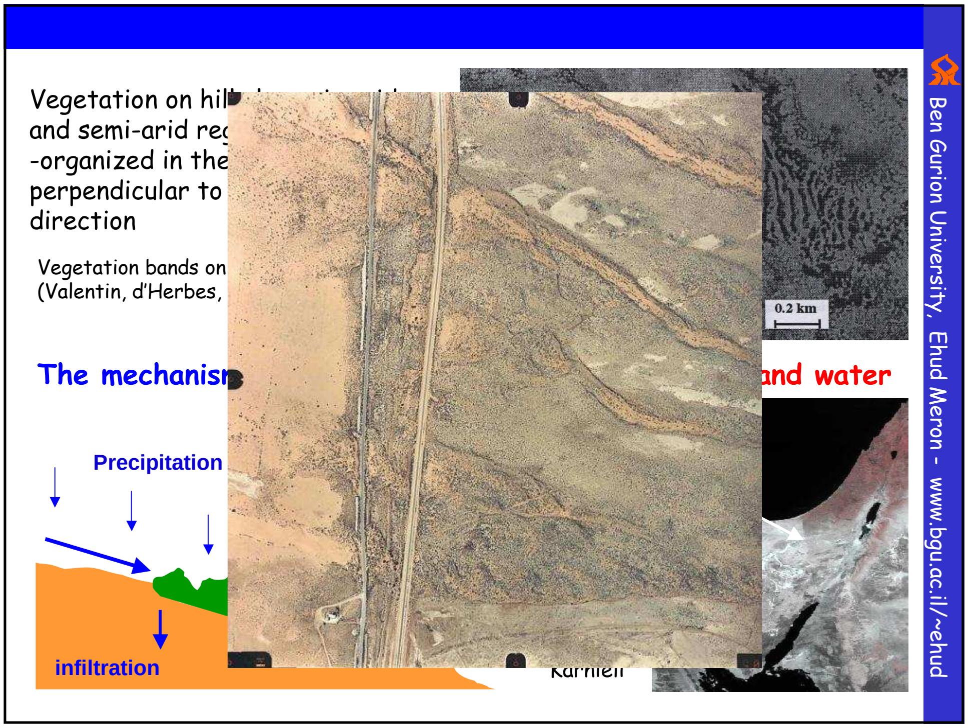
Vegetation on hil
and semi-arid reg
-organized in the
perpendicular to
direction
Vegetation bands on
(Valentin, d'Herbes,
0.2 km
The mechanism
and water
Precipitation
infiltration
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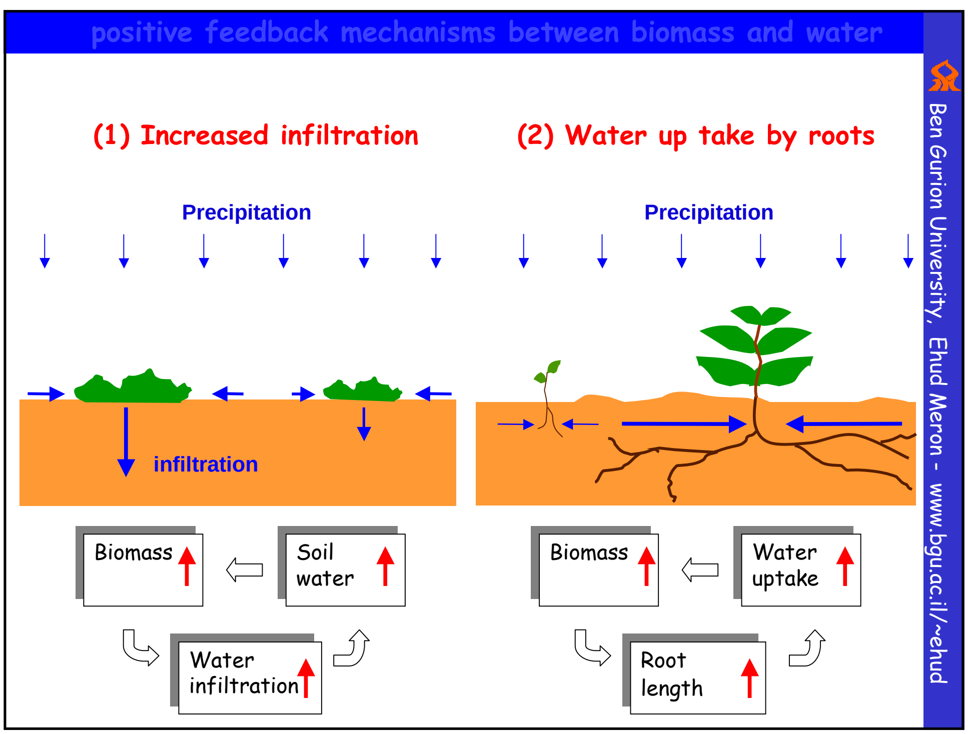
positive feedback mechanisms between biomass and water
(1) Increased infiltration
(2) Water up take by roots
Precipitation
infiltration
Precipitation
Biomass
Soil water
Water infiltration
Biomass
Water uptake
Root length
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Lefever and Lejeune (1997); Klausmeier, (1999); HilleRisLambers et al. (2000), Okayasu and Aizawa (2001); Rietkerk et al. (2002); Lejeune et al. (2002); Shnerb et al. (2003).

Reproduce observed behaviors

Make predictions

Shed new light on ecological processes

Hardenberg, Meron, Shachak, Zarmi, PRL (2001)

$n(x,t)$ - Plant biomass density

$w(x,t)$ - Soil water density

Positive feedback terms (boxed)

$$\frac{\partial n}{\partial t} = \frac{\gamma w}{1+\sigma w} n - n^2 - \mu n + \nabla^2 n$$

$$\frac{\partial w}{\partial t} = p - (1-\rho n) w - w^2 n + \delta_1 \nabla^2 w - \delta_2 \nabla^2 n$$

Biomass growth rate

Maximum standing biomass

Mortality, grazing

Seed dispersal

Precipitation

Evaporation

Biomass decrease water loss

Transpiration

Water transport (Darcy's law)

Water uptake by roots

Increased infiltration

Ecological & physical input - small scale

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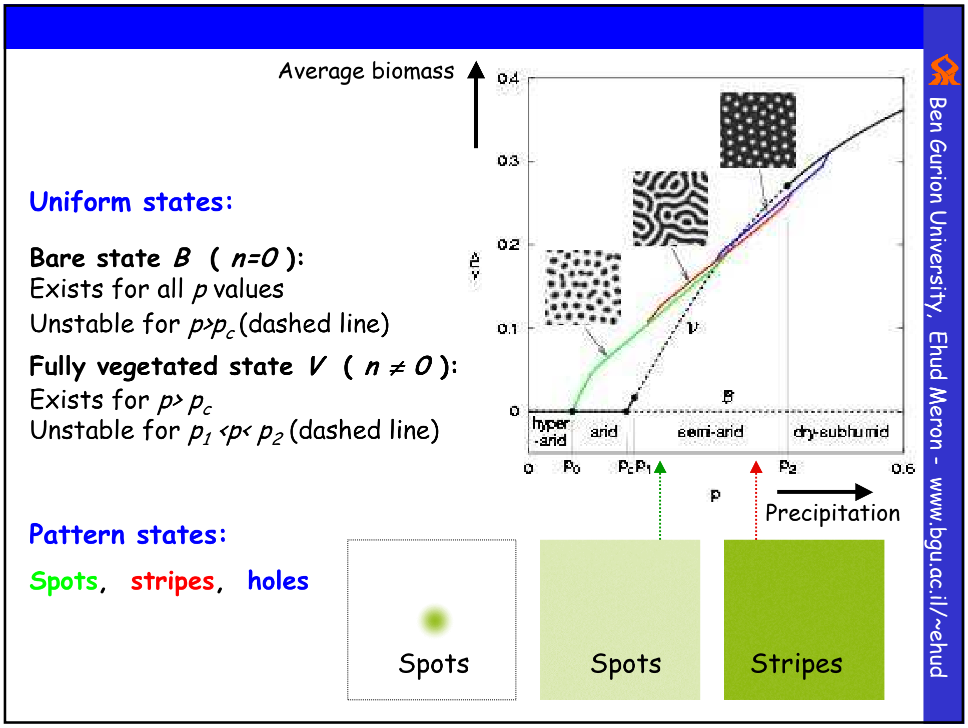

Uniform states:
Bare state B (n=0):
Exists for all p values
Unstable for p>p_c (dashed line)
Fully vegetated state V (n ≠ 0):
Exists for p> p_c
Unstable for p_1 <p< p_2 (dashed line)
Pattern states:
Spots, stripes, holes
Average biomass
<n>
0.4
0.3
0.2
0.1
0
V
B
hyper -arid
arid
semi-arid
dry-subhumid
0
P0
Pc P1
P2
0.6
p
Precipitation
Spots
Spots
Stripes
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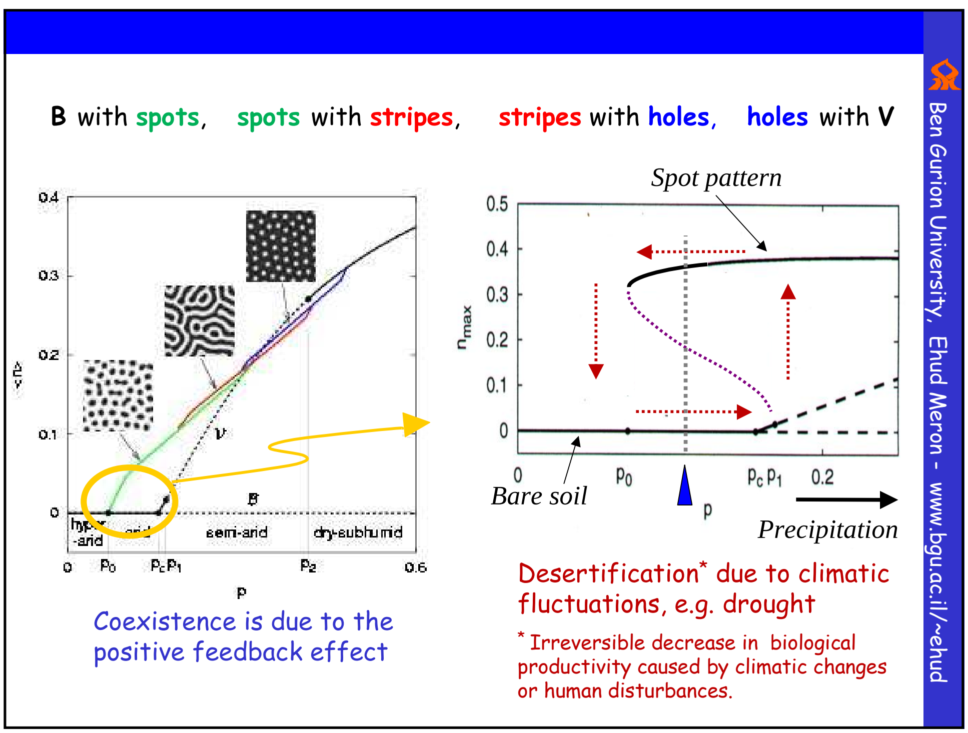

B with spots, spots with stripes, stripes with holes, holes with V
0.4
0.3
0.2
0.1
0
<n>
V
B
semi-arid
dry-subhumid
0
P0
Pc P1
P2
0.6
p
Coexistence is due to the positive feedback effect
Spot pattern
0.5
0.4
0.3
0.2
0.1
0
n_max
0
P0
Pc P1
0.2
Bare soil
p
Precipitation
Desertification* due to climatic fluctuations, e.g. drought
* Irreversible decrease in biological productivity caused by climatic changes or human disturbances.
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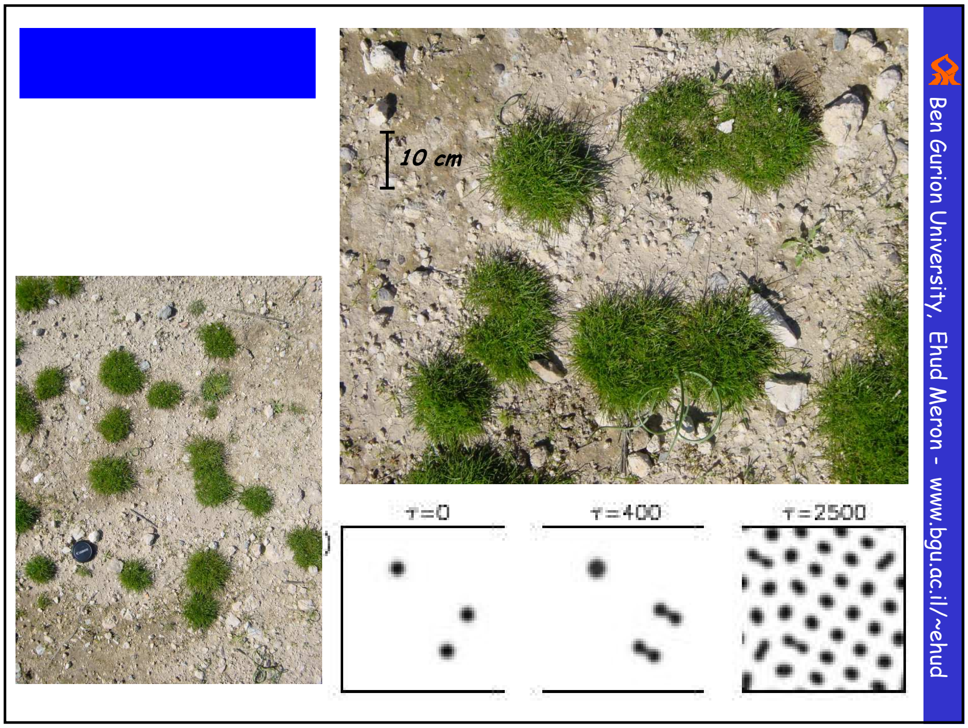
10 cm
τ=0
τ=400
τ=2500
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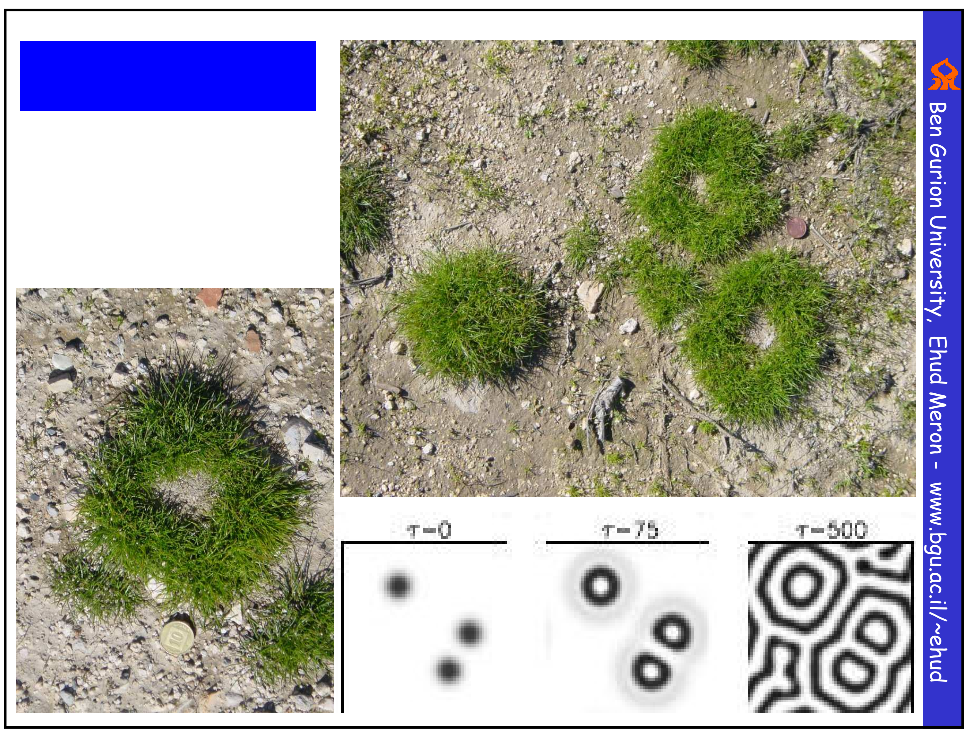
τ=0
τ=75
τ=500
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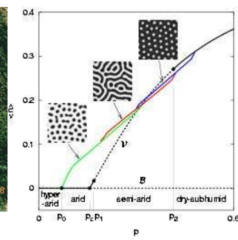
Spots

Stripes

Holes



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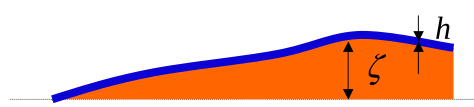
Explicit modeling of the two positive feedback mechanisms

b(**x**,*t*) - Plant biomass density
w(**x**,*t*) - Soil water density
h(*x*,*t*) – Surface water height



Okayasu and Aizawa (2001); Rietkerk et al. (2002)

$$\frac{\partial b}{\partial t} = b(1-b)\int_{\Omega} K_b(\vec{r},\vec{r}\,')w(\vec{r}\,')d\vec{r}\,' - \mu b + \delta_b \nabla^2 b$$

$$\frac{\partial w}{\partial t} = I - (1-\rho b)w - \beta w\int_{\Omega} K_w(\vec{r},\vec{r}\,')b(\vec{r}\,')d\vec{r}\,' + \delta_w \nabla^2 w$$

$$\frac{\partial h}{\partial t} = p - I + \nabla^2(h^2) + 2\nabla h\cdot\nabla\zeta + 2h\nabla^2\zeta$$

$$K_w(\vec{r},\vec{r}\,') = \exp\left\{-\frac{|\vec{r}-\vec{r}\,'|^2}{2\sigma_0[1+\eta b(\vec{r}\,')]^2}\right\}, \qquad K_b(\vec{r},\vec{r}\,') = \exp\left\{-\frac{|\vec{r}-\vec{r}\,'|^2}{2\sigma_0[1+\eta b(\vec{r})]^2}\right\}$$

$$I = \alpha h(\vec{r},t)\frac{b(\vec{r},t)+kf}{b(\vec{r},t)+k}$$

PF 1: Increased infiltration

PF 2: Water uptake by roots

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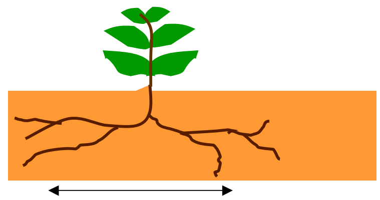
$\eta = dL/db$

– the rate at which the roots extend in response to plant growth



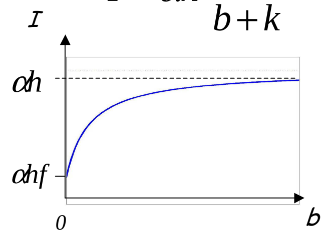
$$L = \sqrt{2\sigma_0}\,[1 + \eta b(\vec{r})]$$

f – parameterizes the dependence of the infiltration rate I on biomass b:

$$I = \alpha h \frac{b + kf}{b + k}$$

$f=1$ no biomass dependence

$f<<1$ infiltration rate increases dramatically with biomass →



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Uniform states (linear stability analysis):

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

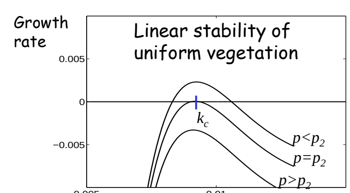
Fully vegetated state ($b \neq 0$):
Exists for $p > p_c$
Unstable for $p_c < p < p_2$
(dotted line)

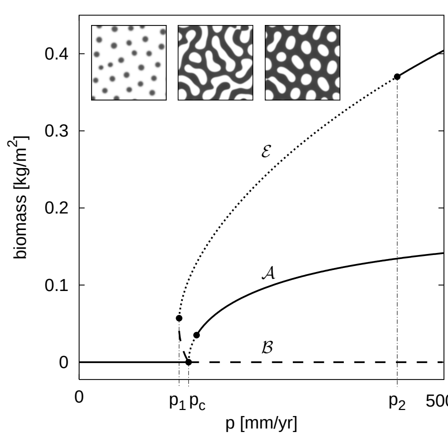
Pattern states (numerical simulations):

Spots, stripes, holes

Each of the positive feedbacks alone leads to pattern formation

Instability of bare soil becomes subcritical when $R = \dfrac{2\eta}{1-\rho+\beta} > 1$





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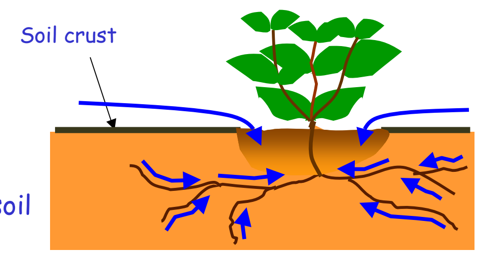
Ecosystem engineers are key species which modulate the landscape, organize the flow of resources, and strongly affect the number of other species in the ecosystem.

Engineering:

Cyanobacteria - form soil crusts which reduce infiltration

Shrubs – prevent the growth of soil crusts and increase infiltration



The combined engineering effect - accumulation of soil water. Can it create habitats for other species (e.g. annual plants) ?

Resilience:

Disturbances may destroy the fragile crust. What controls the resilience of the system, is it recoverable ?

$$\frac{\partial b}{\partial t} = b(1-b)\int_{\Omega} K_b(\vec{r},\vec{r}\,')w(\vec{r}\,')d\vec{r}\,' - \mu b + \nabla^2 b$$

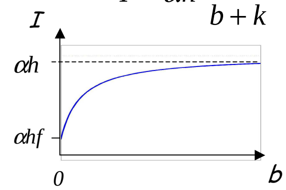
$$\frac{\partial w}{\partial t} = I - (1-\rho b)w - \beta b\int_{\Omega} K_w(\vec{r},\vec{r}\,')b(\vec{r}\,')d\vec{r}\,' + \delta_w \nabla^2 w$$

$$\frac{\partial h}{\partial t} = \nabla^2(h^2) + \nabla h \cdot \nabla \zeta + h\nabla^2\zeta + p - I$$

$$K_b(\vec{r},\vec{r}\,') = \exp\left\{-\frac{|\vec{r}-\vec{r}\,'|^2}{2\sigma_0[1+\eta b(\vec{r})]^2}\right\}, \qquad K_w(\vec{r},\vec{r}\,') = \exp\left\{-\frac{|\vec{r}-\vec{r}\,'|^2}{2\sigma_0[1+\eta b(\vec{r}\,')]^2}\right\}$$

$$I = \alpha h \frac{b+kf}{b+k}$$

1. Associate b with the shrub biomass
2. Model the existence of crust by $f \ll 1$



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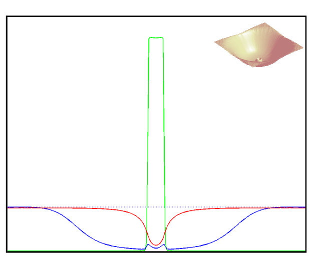
η

Biomass
Soil water
Surface water

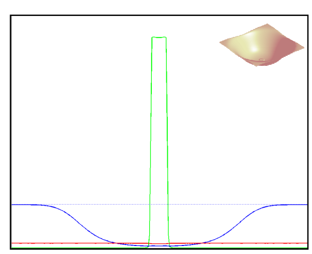
$\eta = 12 \quad (>>1)$

$f=0.1$



No engineering

$f=0.9$



System is resilient

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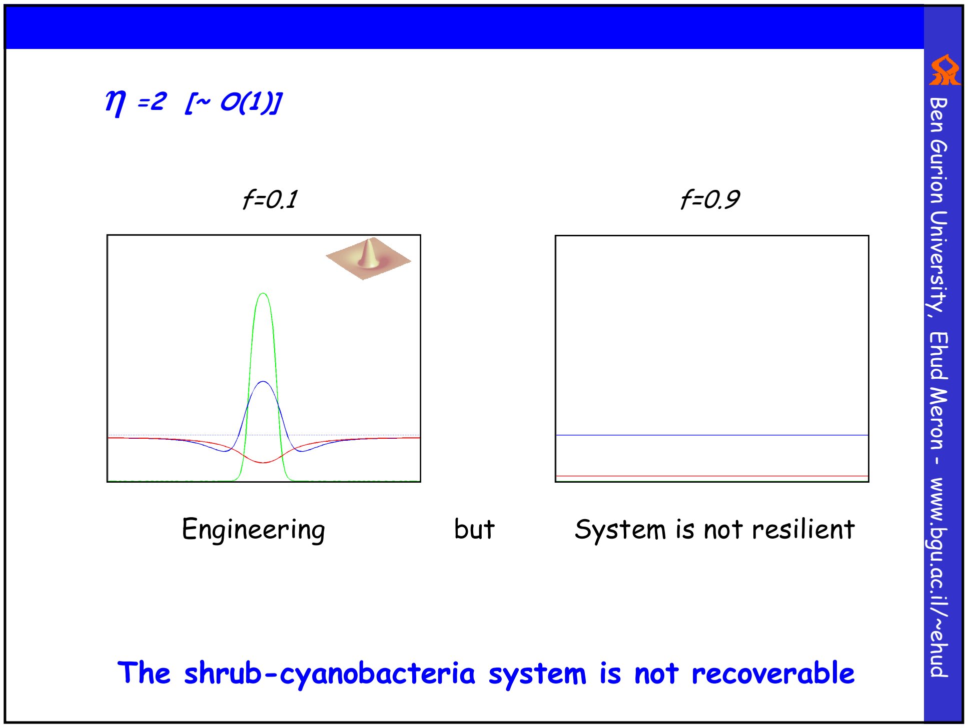
η =2 [~ O(1)]
f=0.1
f=0.9
Engineering
but
System is not resilient
The shrub-cyanobacteria system is not recoverable
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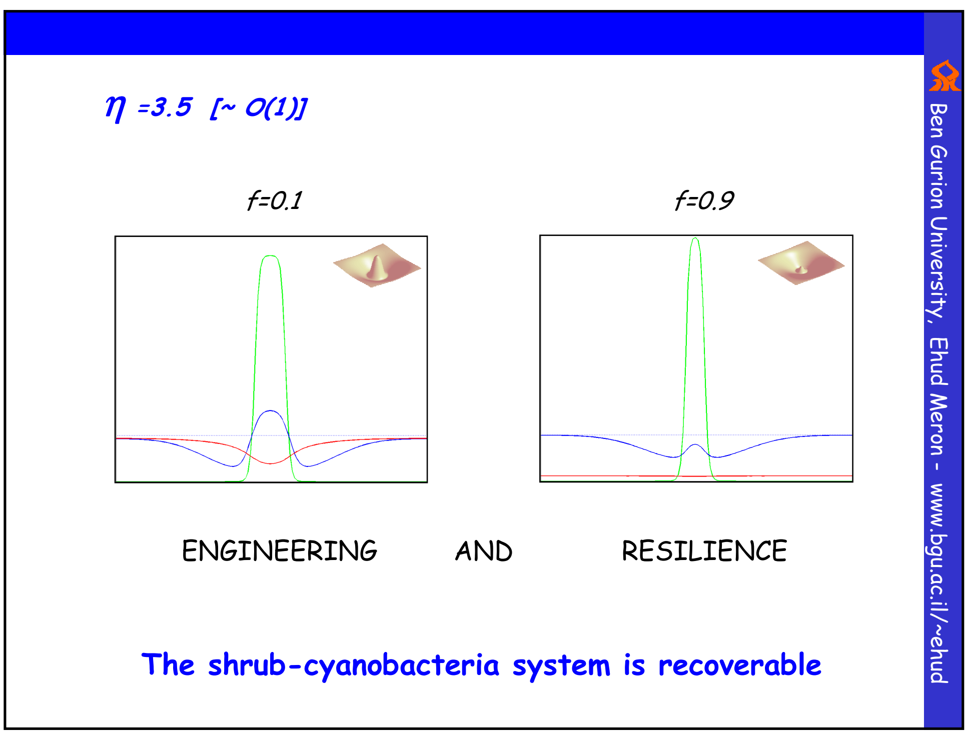
η =3.5 [~ O(1)]
f=0.1
f=0.9
ENGINEERING
AND
RESILIENCE
The shrub-cyanobacteria system is recoverable
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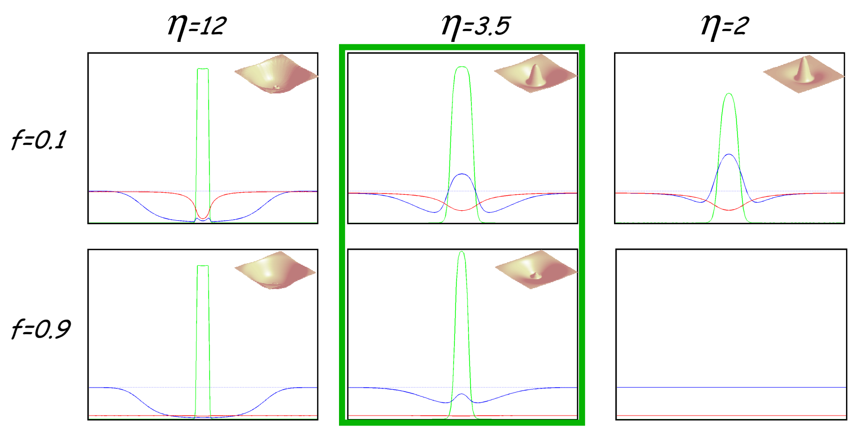
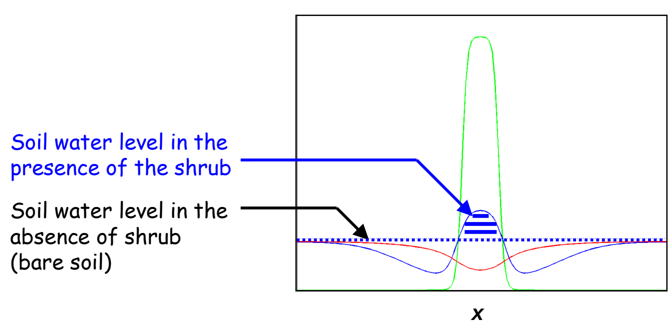


The model can be used to identify conditions for optimal ecosystem engineers in terms of soil water accumulation and resilience.

Soil water accumulation at vegetation patches may **exceed** the soil-water level of a bare soil at the same precipitation



The combine shrub-crust engineering effect provides habitats for weak species that may not survive in the absence of the engineers.

So far – conditions that favor the introduction of new species. What determines their **number**?

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Niche theory in ecology: the more diverse the landscape the more habitats or growth niches it provides and the richer the species that can be accommodated.

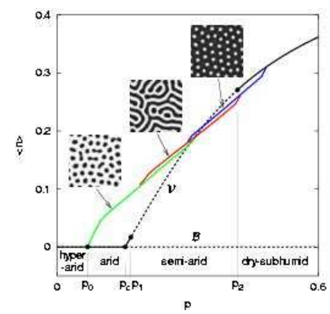
Landscape diversity in our case is determined by the spatial patterns the shrub forms.

The model suggests two mechanisms for pattern diversity:

1. Bistabilty of states:

← Bistability of bare soil and spots

← Bistability of spots and stripes



2. Spatial chaos (yet to be found)

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Ecosystems are going today through unprecedented loss of species and their habitats in response to environmental changes and human disturbances.

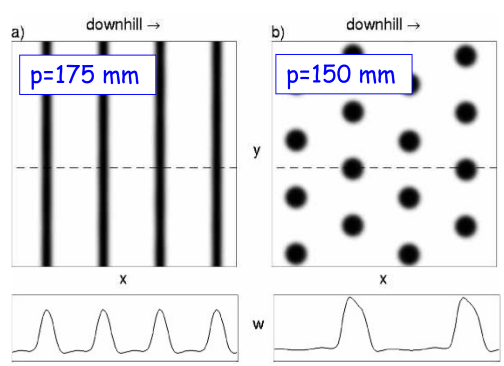
The model suggests a new mechanism:

Transitions between states or patterns of the ecosystem engineer that involve habitat loss, induced by climatic changes or human activities.

Example:
Spots ⟶ **bands**
on a slope

Counterintuitively species loss may result from *increasing* precipitation

Soil-water redistributions creating habitats →



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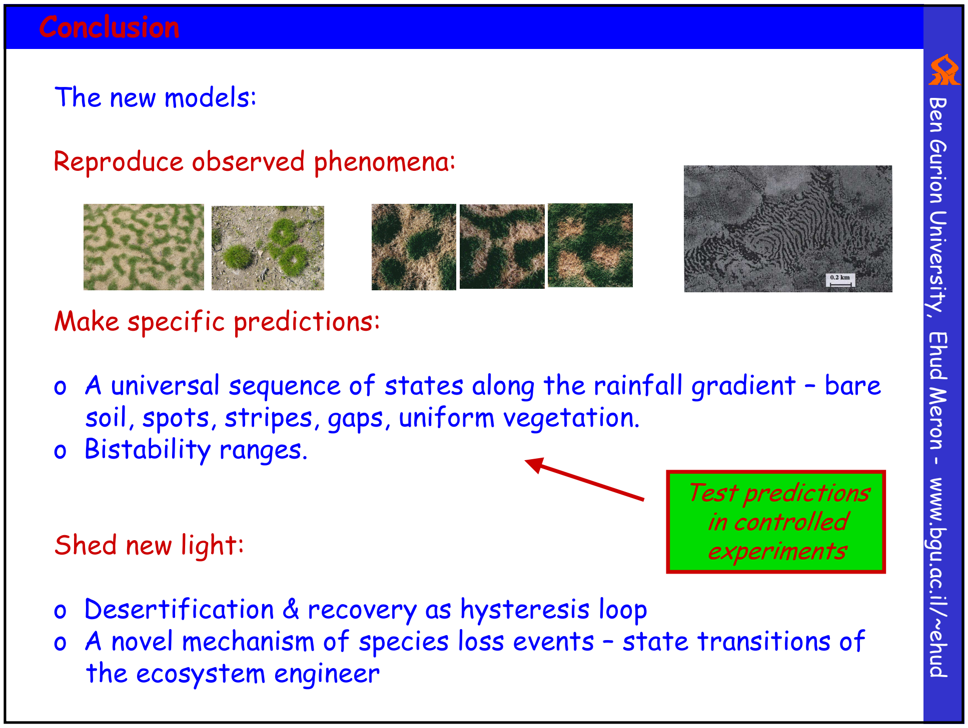
Conclusion
The new models:
Reproduce observed phenomena:
Make specific predictions:
o A universal sequence of states along the rainfall gradient – bare soil, spots, stripes, gaps, uniform vegetation.
o Bistability ranges.
Test predictions in controlled experiments
Shed new light:
o Desertification & recovery as hysteresis loop
o A novel mechanism of species loss events – state transitions of the ecosystem engineer
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