Spatio-temporal dynamics of regime shifts in ecosystems.

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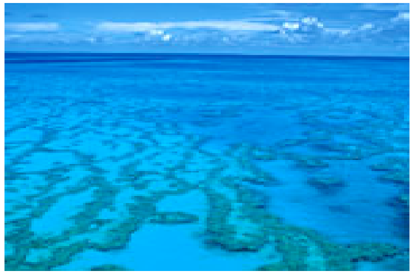
Regime shift

A dramatic change of ecosystem state

Outbreak of plankton

Disruption of coral reefs



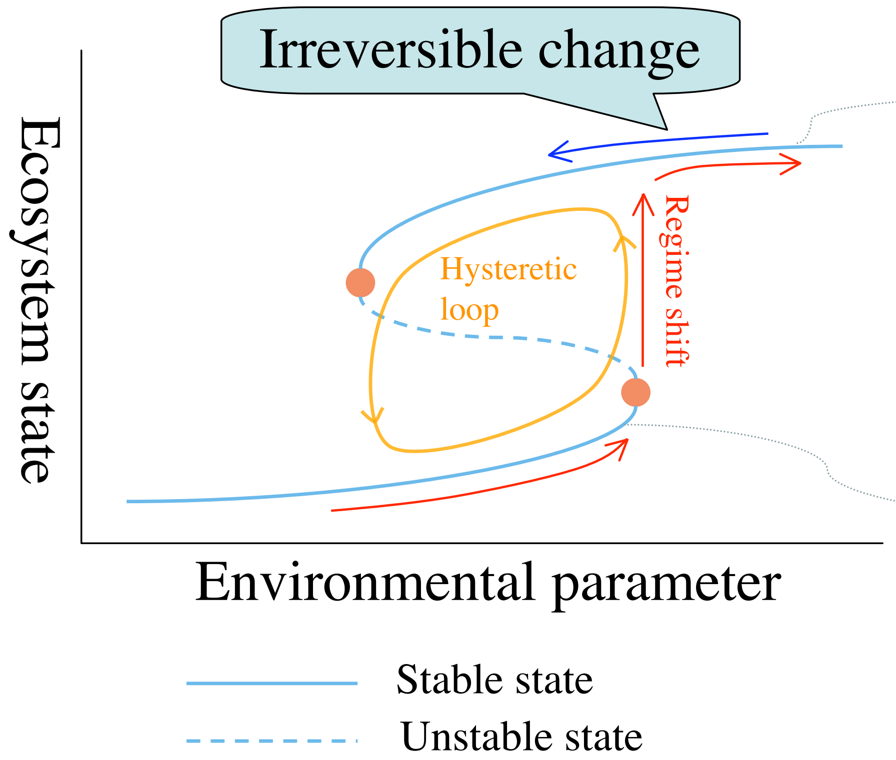
Desertification

Regime shifts are reported in various scenes of environmental disruption.

Seemingly caused by a gradual change of environmental (exogenous) parameter.
(E.g. temperature, eutrophication, precipitation etc.)

A possible mechanism of regime shifts

Bistability can cause regime shifts.



Environmental parameter is nutrients…

Stable state of
dense phytoplankton population.

Stable state of
scarce phytoplankton population.

Outline

We investigated two models about a regime shift.

Model 1

Budworm - Leaf

May, *Nature*, 1977

$$\frac{dN}{dt} = N\left(1 - \frac{N}{\kappa S}\right) - \frac{rN^2}{N_0^2 + N^2}$$

$$\frac{dS}{dt} = S\left(1 - \frac{S}{S_{max}}\right) - bN$$

Model 2

Vegetation - Water

(in water-limited region)

Hardenberg et al.,

Physical Review Letters, 2001

$$\frac{dn}{dt} = \frac{\gamma w}{1 + \sigma w} n - n^2 - \mu n$$

$$\frac{dw}{dt} = p - (1 - \rho n)w - w^2 n$$

May's model（No space）

$$\frac{dN}{dt} = N\left(1 - \frac{N}{\kappa S}\right) - \frac{rN^2}{N_0^2 + N^2}$$

$$\frac{dS}{dt} = S\left(1 - \frac{S}{S_{max}}\right) - bN$$

N：Population of budworm

S：Average leaf area per tree

N_0： Budworm population without predation

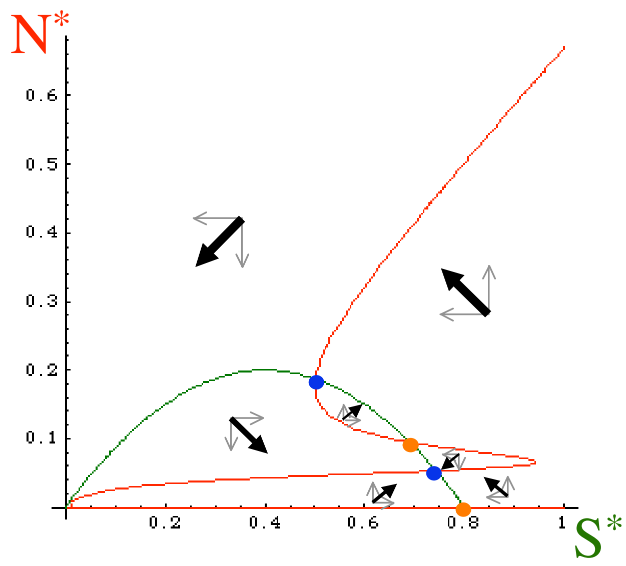
S_{max}： Maximum leaf area per tree

κ： Utilization rate of leaf

r： Predation rate of budworm

b： Predation rate of leaf

Isocline （$S_{max} = 0.8$）



● Stable equilibrium points

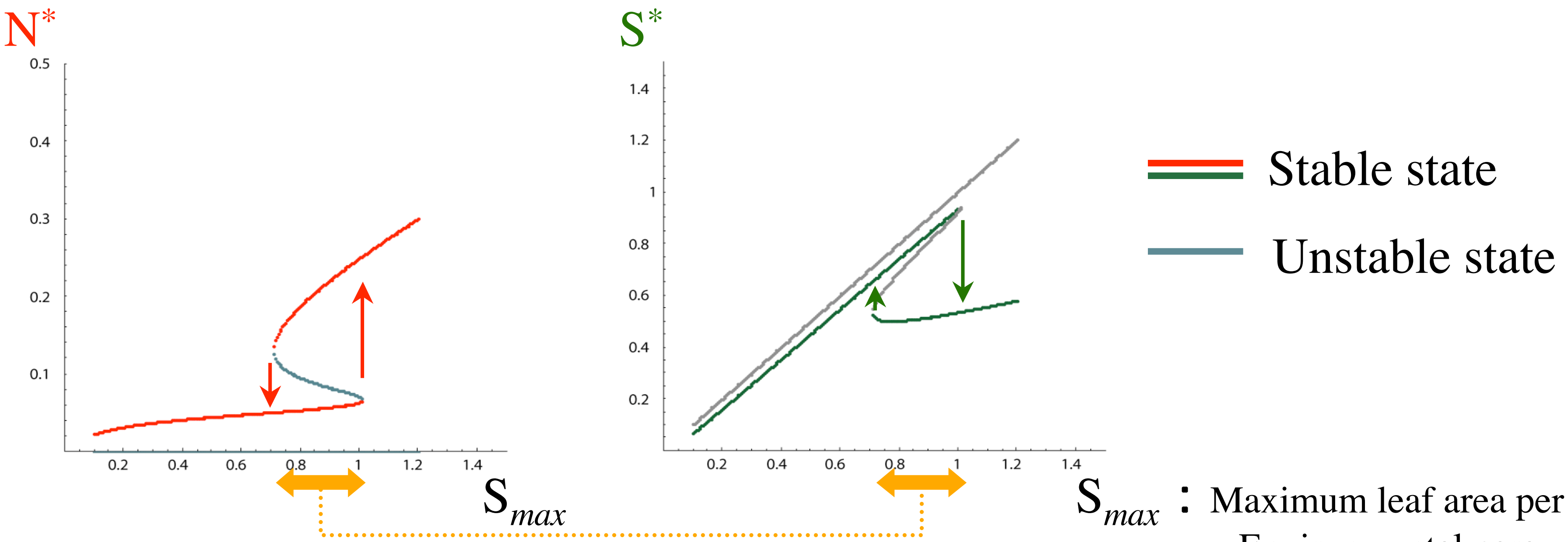
● Unstable equilibrium points

$N_0 = 0.06$, $r = 0.11$, $\kappa = 0.8$, $b = 1$

Bistability of May's model

Bistability occurs as dependent of S_{max}.

Equilibrium points vs. Maximum leaf area per tree



S_{max} : Maximum leaf area per tree
= Environmental parameter

Range of S_{max} arising bistability

Regime shifts and hysteretic loop to S_{max} occur.

May's model + Space

$$\frac{\partial N}{\partial t} = \underbrace{N\left(1-\frac{N}{\kappa S}\right) - \frac{rN^2}{N_0^2+N^2}}_{=f} + \nabla^2 N$$

$$\frac{\partial S}{\partial t} = \underbrace{S\left(1-\frac{S}{S_{max}}\right) - bN}_{=g} + d\nabla^2 S$$

d : The diffusion coefficient of S as that of N is 1

Conditions of diffusion-driven instability

$$J = \begin{pmatrix} \frac{\partial f}{\partial N} & \frac{\partial f}{\partial S} \\ \frac{\partial f}{\partial N} & \frac{\partial g}{\partial S} \end{pmatrix} = \begin{pmatrix} f_N & f_S \\ g_N & g_S \end{pmatrix}$$

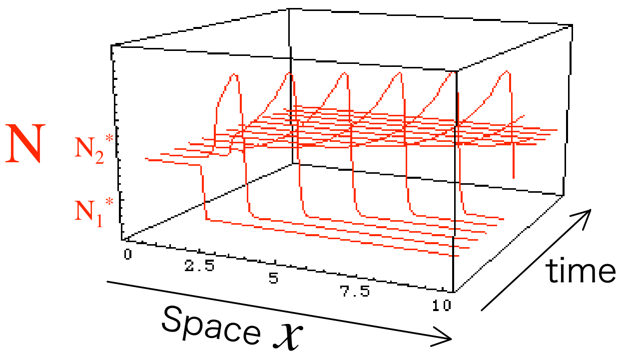
For heterogenous patterns to emerge, the following conditions must be met.

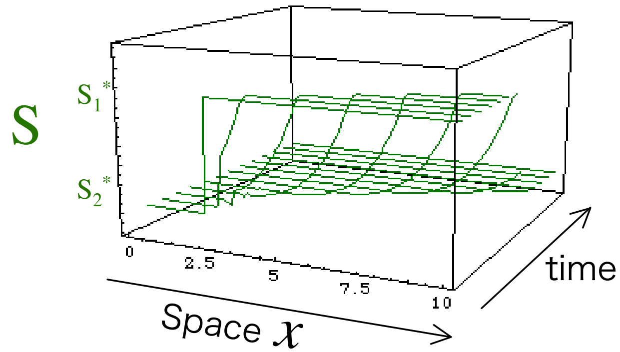
$$df_N + g_S > 0 \qquad (df_N + g_S)^2 - 4d(f_N g_S - f_S g_N) > 0$$

Unlikely to be met for budworm - leaf area dynamics（d>>1）

Examples of May's model + Space

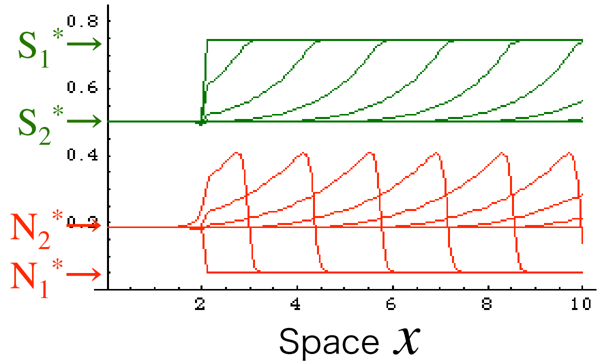
We investigated which stable state solution is converged with one dimension model.





$N_0 = 0.06$, $r = 0.11$, $\kappa = 0.8$,
$b = 1$, $S_{max} = 0.8$, $d = 0.01$

We gave initial distribution having two stable states.



The solution forms a traveling wave and converges to spatially homogenous equilibrium state （N_2^*,S_2^*）.

We can confirm that heterogenous pattern did not appear.

Summary of May's model

- In May's model, bistability is possible.
  - Holling typeⅢ is used in the second term of N's ODE.
  - We can confirm regime shift and hysteretic loop to S_{max} in no diffusion.

- When we introduced conventional diffusion term...
  - Either of the two bistable equilibria is homogenously realized.

    → The system didn't satisfy condition of diffusion-driven instability, and spatially pattern didn't appear.

Hardenberg's model（No space）

$$\frac{dn}{dt} = \frac{\gamma w}{1+\sigma w} n - n^2 - \mu n$$

$$\frac{dw}{dt} = p - (1-\rho n) w - w^2 n$$

n : Biomass density of vegetation

w : Density of ground water

p : Precipitation

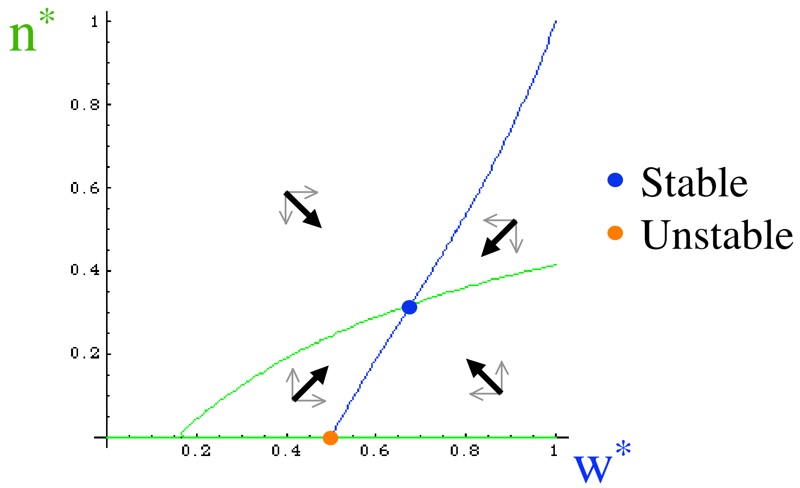
γ, σ : Vegetation growth rate depending on w

μ : Mortality and herbivory rate

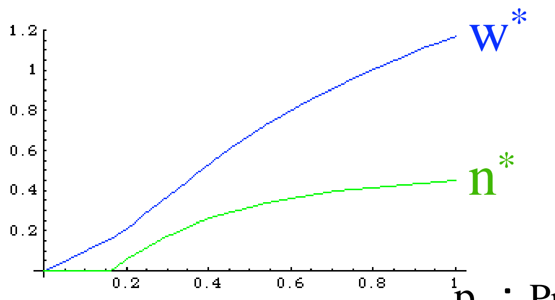
ρ : Alleviation of evaporation by vegetation

$\gamma = 1.6$, $\sigma = 1.6$, $\mu = 0.2$, $\rho = 1.5$

Isocline（p=0.5）



Equilibrium points vs. Precipitation



p : Precipitation
= Environmental parameter

No bistability occurs!!!

Hardenberg's model with space

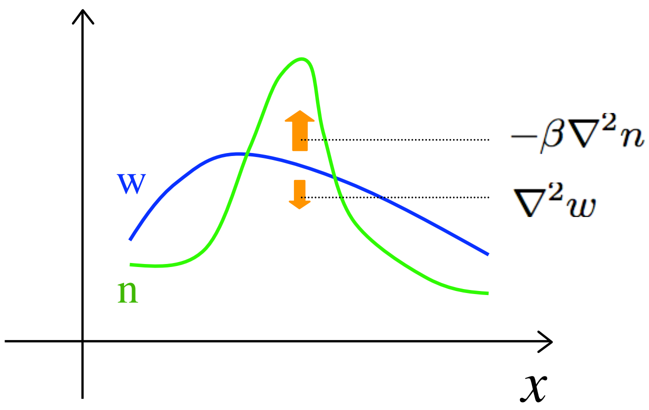
To describe heterogenous vegetation pattern,
Hardenberg introduced cross diffusion term of water effected by vegetation.

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

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

Cross diffusion term

Diffusion of ground water
depends on vegetation.



☜ This diffusion term makes increase ground water in region which vegetation biomass is distributed concavely.

Diffusion-driven instability of Hardenberg's model

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

$$\frac{\partial w}{\partial t} = \underbrace{p - (1-\rho n) w - w^2 n}_{= g} + \delta \nabla^2 (w - \beta n)$$

δ : The diffusion coefficient of w as that of n is 1

Conditions of diffusion-driven instability

$$J = \begin{pmatrix} \frac{\partial f}{\partial n} & \frac{\partial f}{\partial w} \\ \frac{\partial f}{\partial n} & \frac{\partial g}{\partial w} \end{pmatrix} = \begin{pmatrix} f_n & f_w \\ g_n & g_w \end{pmatrix}$$

For heterogenous patterns to emerge, the following conditions must be met.

$$\delta(f_n + \beta f_w) + g_w > 0$$

$$(\ \delta(f_n + \beta f_w) + g_w\ )^2 - 4\delta(f_n g_w - f_w g_n) > 0$$

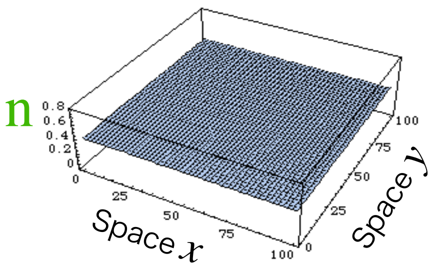
Vegetation pattern will emerge, if β is larger than a certain value.

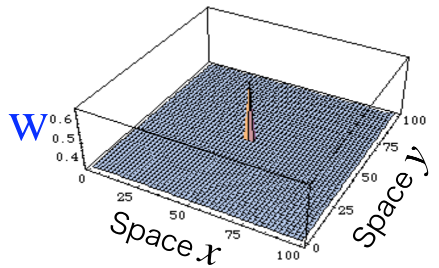
Examples of Hardenberg's model

Precipitation as an environmental parameter and vegetation pattern

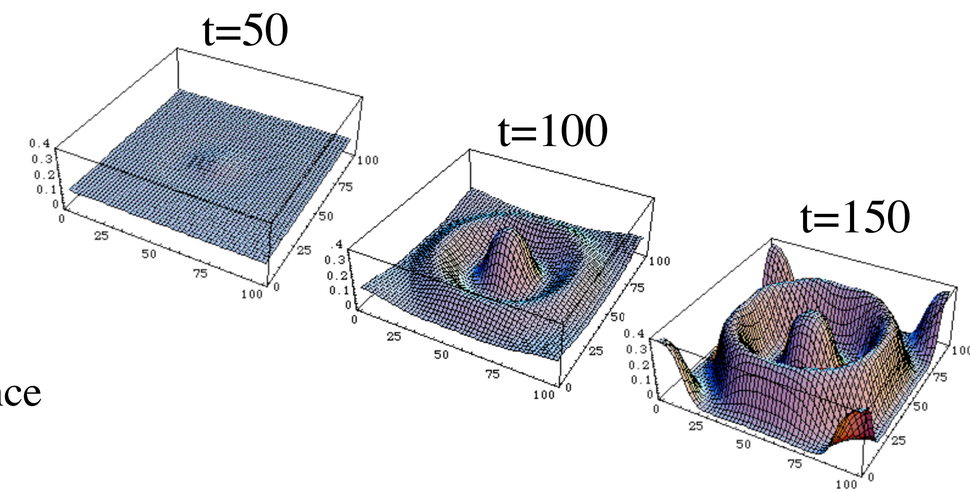
Initial distribution

Dynamics of vegetation patterns（p=0.25）

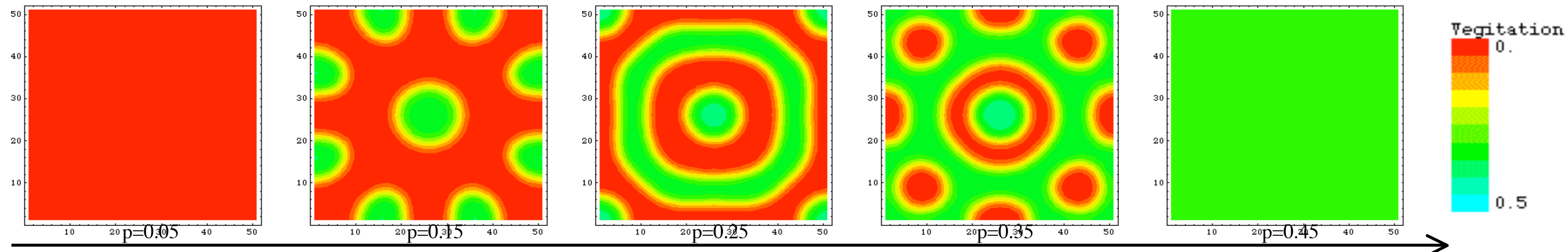




n=0.4（Flat） w=p（Frat）＋ Disturbance

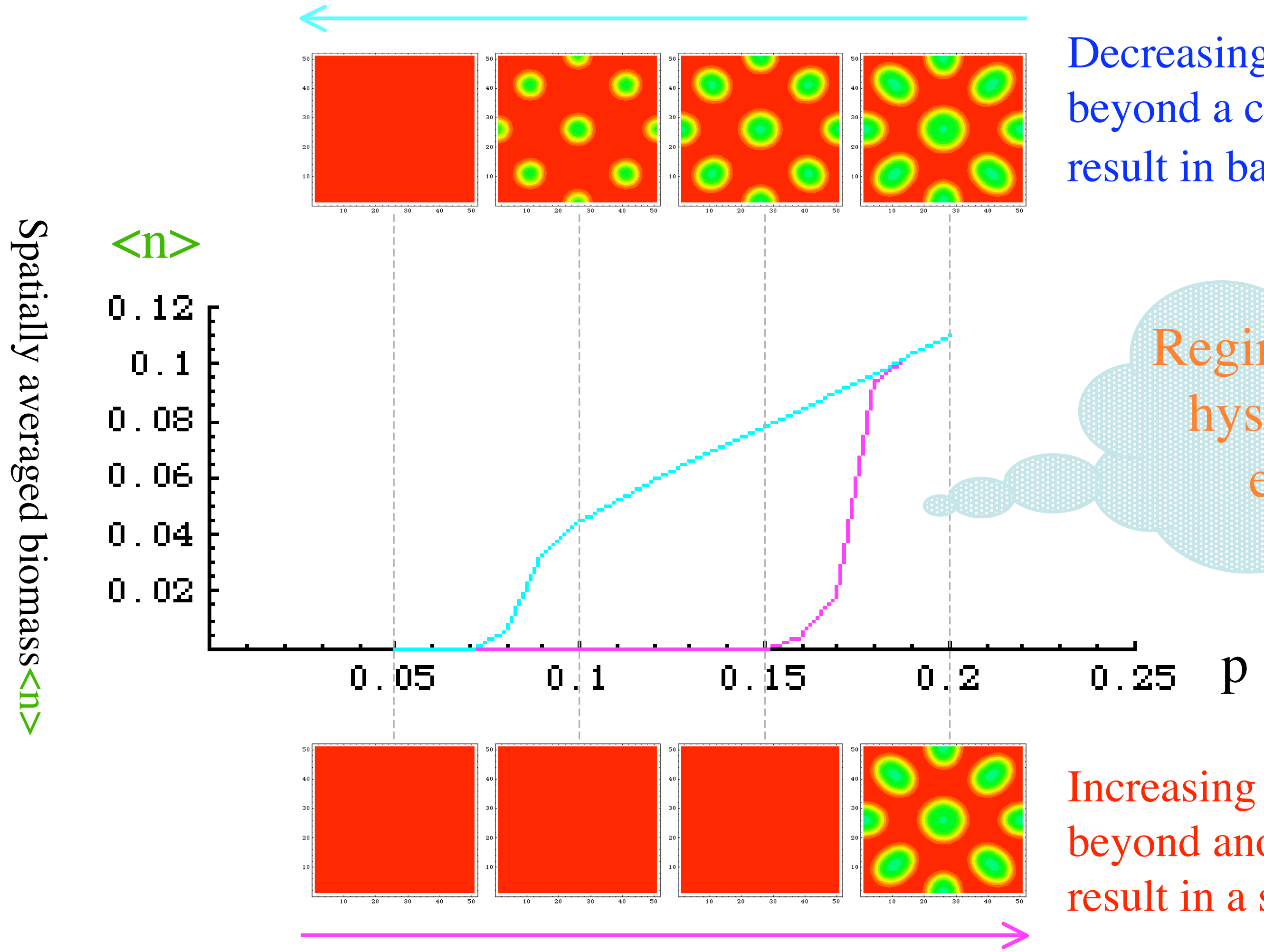


Vegetation patterns (n) after time passed enough（t=1000）



Small p Large

Stable spatial patterns and precipitation



Decreasing precipitation beyond a certain threshold result in bare soil（no vegetation）.

Regime shifts and hysteretic loop emerged.

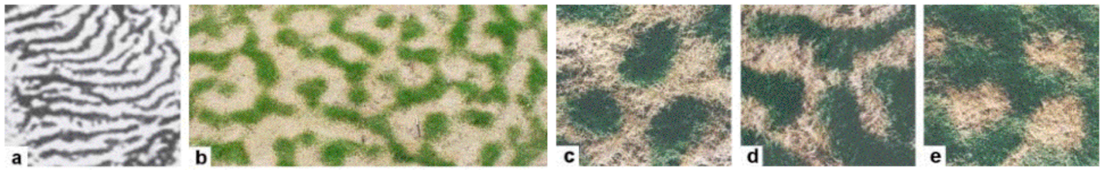
Increasing precipitation beyond another threshold result in a spatial pattern.

Summary of Hardenberg's model

- In Hardenberg's model, there is no bistability, but regime shifts occur mediated by spatial pattern.
  - Cross diffusion term makes it possible regime shifts by spatial pattern.

    → This patterns consistent with field observations.

Observed pattern（Hardenberg et al., *Physical Review Letters*, 2001）



  - We can confirm regime shift and hysteretic loop to P by spatially pattern.

Conclusion and future prospects

- To cause regime shift, bistability is not always necessary.
- In the future, we will introduce cross diffusion term to May's system to study regime shifts in space.
- References

  - Robert M. May, Thresholds and breakpoints in ecosystems with a multiplicity of stable states, *Nature* (1977)
  - J. von Hardenberg et al., Diversity of Vegetation Patterns and Desertification, *Physical Review Letters* (2001)
  - J. D. Murray, Mathematical Biology II, 1993. Springer-Verlag Berlin Heidelberg.