

Standard course – Modelling

Lesson SM1.1 – How to write and ecological model

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How to write an ecological model



All models are wrong. But some are useful



How to write an ecological model

Define the question to be asked. For example:

1. what are (if any) the environmental parameters affecting the population density of white ptarmigan?
2. What is the effect of introduced fish in a oligotrophic mountain lake ecosystem?
3. Under what conditions desert shrubs act as ecosystem engineers?



How to write an ecological model

Then:

Choice of the relevant dynamical variables:
biomass, individuals, species, size class,
functional groups, ...

And: whole population, age or stage structure



How to write an ecological model

Further: Do we want an homogeneous model or a model that takes into account the spatial structure and distribution of the population?



Rietkerk et al., *The American Naturalist*
160 (4), 2002



How to write an ecological model

Then we have to decide whether we want continuous or discrete variables.

Usually, we have space, time and the variable(s)

Continuous time: differential equations

Discrete time: difference equations (maps)

Continuous space: Partial differential equations

Discrete space: system of temporal equations



How to write an ecological model

Once defined the models structure, we have to estimate of model parameters

A difficult task, especially because the possibility of bifurcations and «tipping points» in dynamical systems



DETERMINISTIC AND STOCHASTIC MODELS



Single species, infinite resources

The simplest ecological model:
Single “species” with infinite resources
and Malthusian growth

$$dX/dt = A X = (r - d) X$$

$$X(t) = X(0) \exp [A t]$$



Single species, finite resources

A touch more realistic:

Single “species” with finite resources and the logistic equation

$$dX/dt = A X (1 - X / K)$$

Two equilibrium solutions:

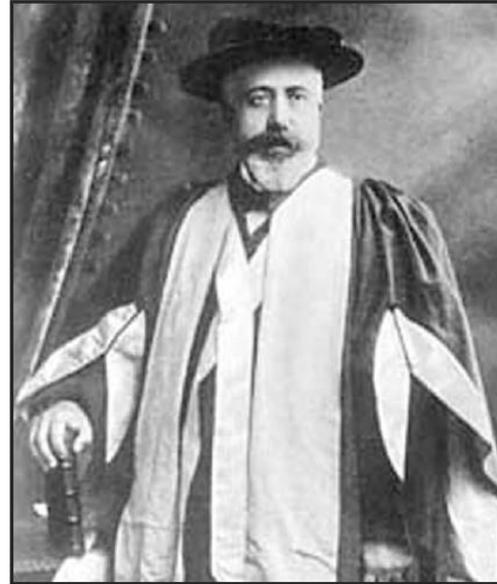
Void, $X = 0$ and $X = K$

K is the «carrying capacity»

In this model, the population reaches a finite density K determined by the value of the parameters

Two species: resource-consumer (predator-prey)

Lotka
(1932)



Vito Volterra, in full academic regalia. From The Biology of Numbers: The Correspondence of Vito Volterra on Mathematical Biology.

Volterra
(1926)

$$dX/dt = A X - C X Y$$

$$dY/dt = -A' X + C' X Y$$

Two species: resource-consumer (predator-prey)

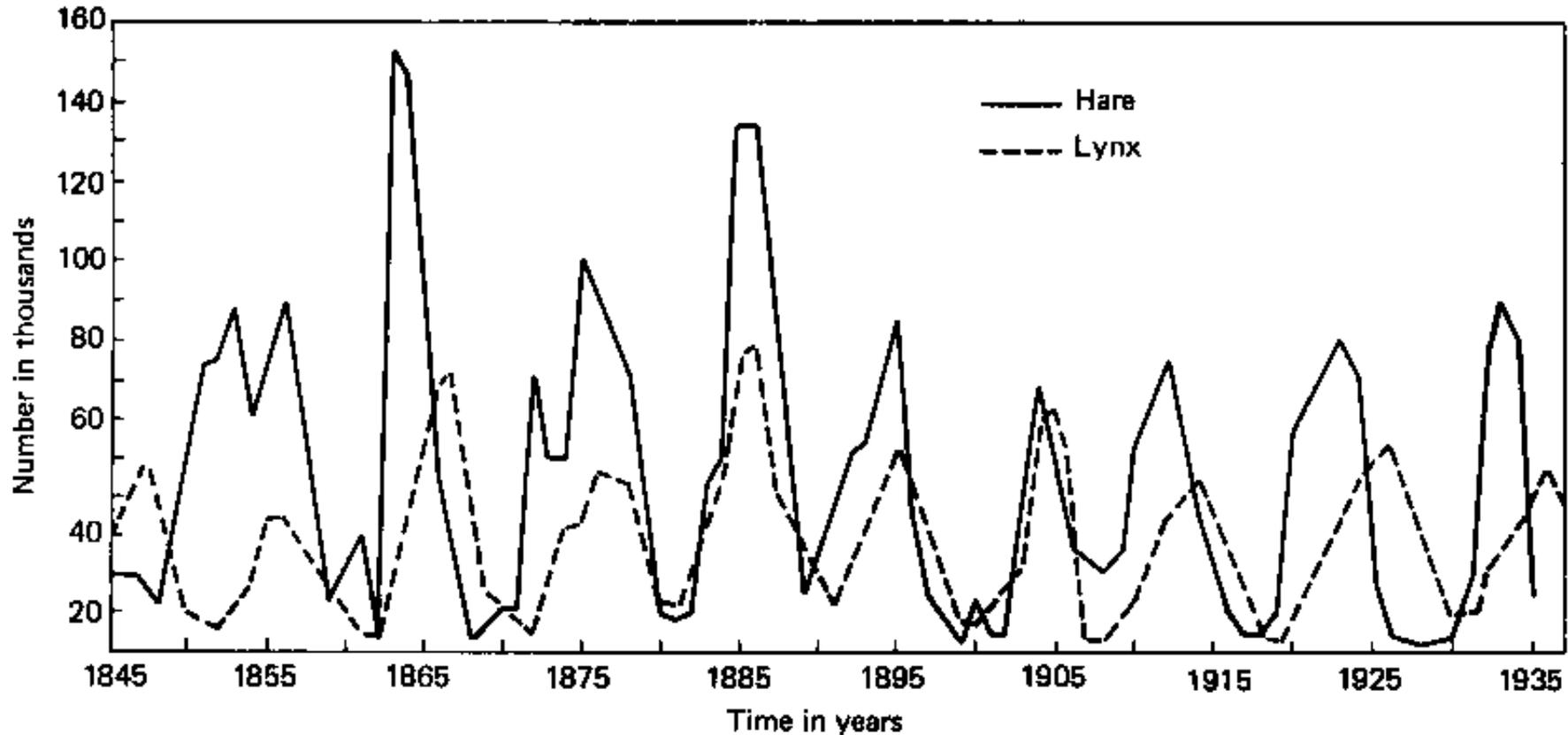


Figure 9-3. Changes in the abundance of the lynx and the snowshoe hare, as indicated by the number of pelts received by the Hudson's Bay Company. This is a classic case of cyclic oscillation in population density. (Redrawn from MacLulich 1937.)



Two species: resource-consumer (predator-prey)

Carissimo Papà:

• • •

I also feel that to leave in the word “heredity” will not greatly bother the biologists. It will be appropriate, however, to add a note explaining what you mean by “heredity” and saying that you use this word in a sense quite different from the conventional one.

• • •

Among the three titles you propose [for your book] I believe that the second one, *Théorie mathématique de la lutte pour la vie*, is the best. The first too could go, *Principes mathématiques de la lutte pour la vie*. On the other hand, I don’t like the third, *Principes mathématiques de biologie*. The part of biology that your work refers to is ecology or ethology, that is, the study of customs and of the environment. This being the case, it would perhaps be preferable even to mention to which part of ecology you refer, and specifically the study of biological associations or biocenosis of the relations among species.

In the case in which, of three species, the 1st simultaneously eats the 2nd and the 3rd, I don’t think that one may separately consider the 1st and the 2nd, and then the 1st and the 3rd. The more the 1st species eats of the 2nd, the less it eats of the 3rd, and vice versa. On the other hand, the nutritional values of the 2nd and the 3rd species will be different. But I believe that one could analyze [lit.: calculate] this case by taking the sum of the numbers of individuals of species 2 and 3, each multiplied by a coefficient. Don’t you think?

What you mention of plant parasites seems to agree fully with your theory. Indeed, the plant parasite *Icerya* (the one that one finds in Ariccia [a town near Rome] on the mimosa trees) has not been destroyed by *Novius*, although the presence of the latter keeps the former in proportions that are not greatly damaging.

• • •

In what way should one carry out this analysis using a series of statistical data over some number of years? This I believe should be the first practical item to solve.

I am glad to hear that you are well and you like it there. Mamma [Umberto’s mother-in-law] will join you in a few days. Today we were down there for lunch. We are all well.

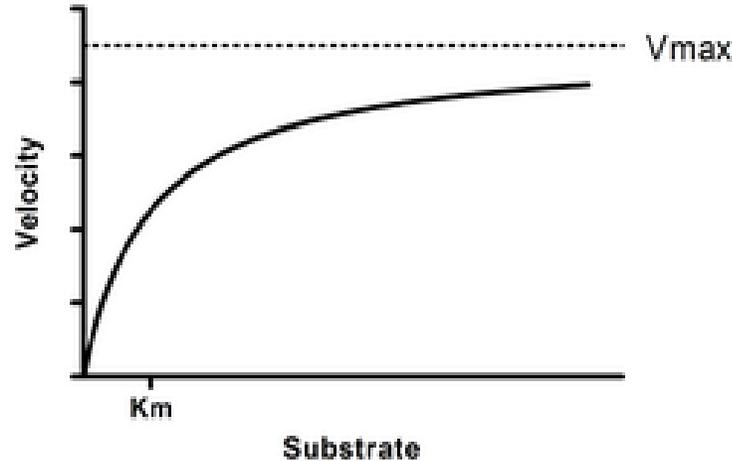
Tanti saluti affettuosi:
Umberto

Letter of Umberto D’Ancona to Vito Volterra

Two species: resource-consumer (predator-prey)

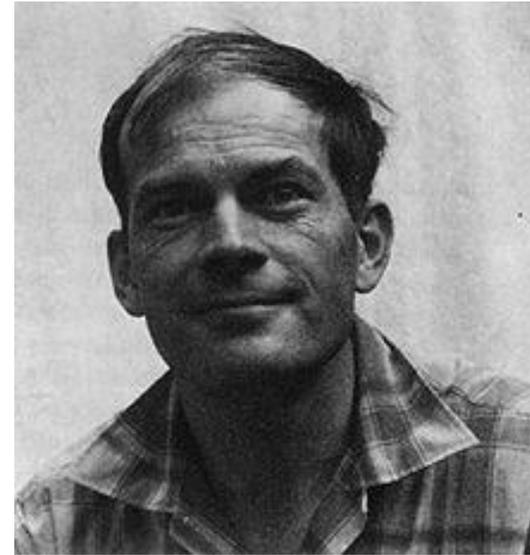
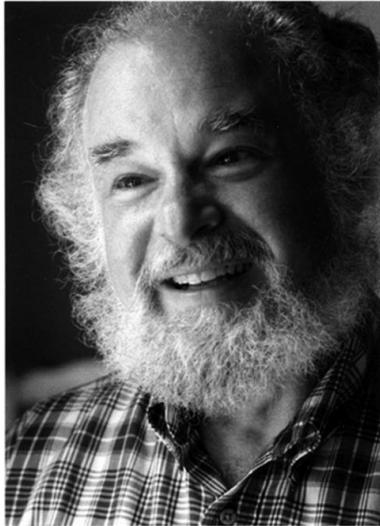
Functional form for predation/consumer
Michaelis-Menten, or Monod, or
Holling type II form

$$\text{Predation: } \frac{CXY}{(1+bX)}$$



Two species: resource-consumer (predator-prey)

the Rosenzweig-McArthur model (1963)



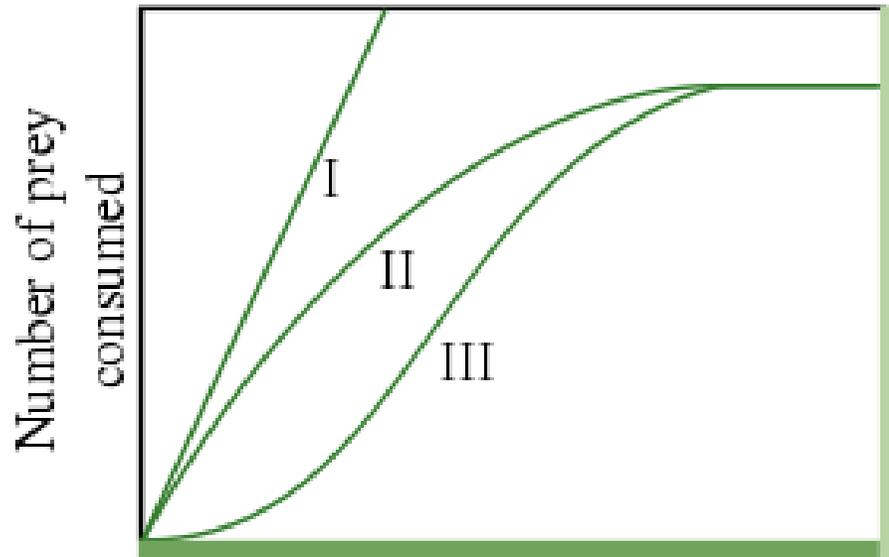
$$\frac{dX}{dt} = A X \left(1 - \frac{X}{K}\right) - \frac{C X Y}{1 + bX}$$

$$\frac{dY}{dt} = -A' X + \frac{C' X Y}{1 + bX}$$

Two species: resource-consumer (predator-prey)

Usually, Holling type II is good for a predator (consumer) that does not search for prey

For a predator that spends time looking for prey, a more appropriate functional form for predation is the Holling type III form



The three types of functional forms for predation

Predation type III:

$$C X^2 Y / (1 + d X^2)$$



A three species food chain

Nutrients, Grazers (Herbivorous),
Predators (Carnivorous)

Chemostat models: source of nutrients

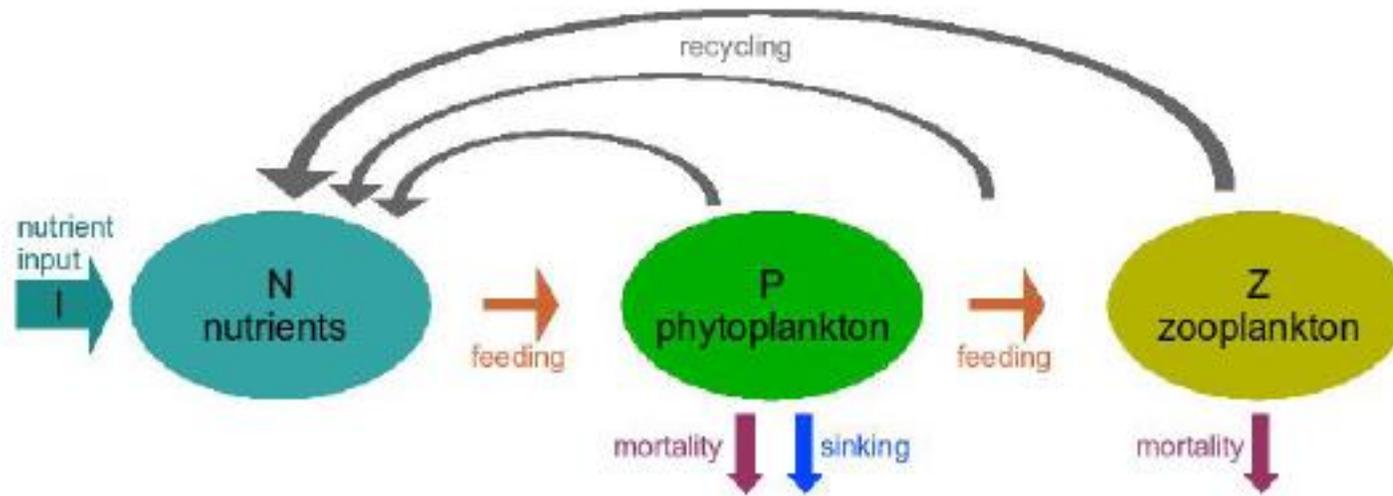
$$dN/dt = \alpha (N_0 - N)$$

N: nutrient density

N_0 = fixed nutrient reservoir density

A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)





A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)

$$\left\{ \begin{array}{l} \frac{dN}{dt} = f(N, P, Z) \equiv \Phi_N - \beta \frac{N}{k_N + N} P \\ \quad \quad \quad + \mu_N \left((1 - \gamma) \frac{a\epsilon P^2}{a + \epsilon P^2} Z + \mu_P P + \mu_Z Z^2 \right) \\ \frac{dP}{dt} = g(N, P, Z) \equiv \beta \frac{N}{k_N + N} P - \frac{a\epsilon P^2}{a + \epsilon P^2} Z - \mu_P P, \\ \frac{dZ}{dt} = h(N, P, Z) \equiv \gamma \frac{a\epsilon P^2}{a + \epsilon P^2} Z - \mu_Z Z^2. \end{array} \right.$$

$$\Phi_N = S(\mathbf{x}, t)(N_0 - N)$$



A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)

$$\left\{ \begin{array}{l} \frac{dN}{dt} = f(N, P, Z) \equiv \Phi_N - \beta \frac{N}{k_N + N} P \quad \Phi_N = S(\mathbf{x}, t)(N_0 - N) \\ \\ \frac{dP}{dt} = g(N, P, Z) \equiv \beta \frac{N}{k_N + N} P \end{array} \right.$$

Nutrient flux (chemostat) and Holling type II uptake by phytoplankton P

Holling type II grazing by phytoplankton on nutrients



A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)

$$\left\{ \begin{array}{l} \frac{dP}{dt} = g(N, P, Z) \equiv - \frac{a\epsilon P^2}{a + \epsilon P^2} Z \\ \frac{dZ}{dt} = h(N, P, Z) \equiv \gamma \frac{a\epsilon P^2}{a + \epsilon P^2} Z \end{array} \right.$$

Holling type III predation
by zooplankton on
phytoplankton

Holling type III growth of
zooplankton thanks to
predation on phytoplankton



A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)

$$\left\{ \begin{array}{l} \frac{dP}{dt} = g(N, P, Z) \equiv \\ \frac{dZ}{dt} = h(N, P, Z) \equiv \end{array} \right. \begin{array}{l} \text{Linear mortality of} \\ \text{phytoplankton} \\ \\ - \mu_P P, \\ \\ - \mu_Z Z^2 \\ \text{Quadratic mortality of} \\ \text{zooplankton representing} \\ \text{the effect of higher trophic} \\ \text{levels (fish)} \end{array}$$



A trophic chain

Nutrient-Phytoplankton-Zooplankton (NPZ)

This term represents recycling of dead biomass and excreta into nutrients by bacterial activity

$$+ \mu_N \left((1 - \gamma) \frac{a\epsilon P^2}{a + \epsilon P^2} Z + \mu_P P + \mu_Z Z^2 \right)$$



A trophic chain

The various components can be advected by a (turbulent) velocity field.

In the NPZ example, for 2D horizontal advection the model becomes:

$$\left\{ \begin{array}{l} \frac{dN}{dt} = f(N, P, Z) - u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} \\ \text{Here, } x \text{ and } y \text{ are the horizontal coordinates and} \\ \text{ } u, v \text{ are the fluid velocities of the horizontal advection field} \\ \frac{dP}{dt} = g(N, P, Z) - u \frac{\partial P}{\partial x} - v \frac{\partial P}{\partial y} \\ \frac{dZ}{dt} = h(N, P, Z) - u \frac{\partial Z}{\partial x} - v \frac{\partial Z}{\partial y} \end{array} \right.$$

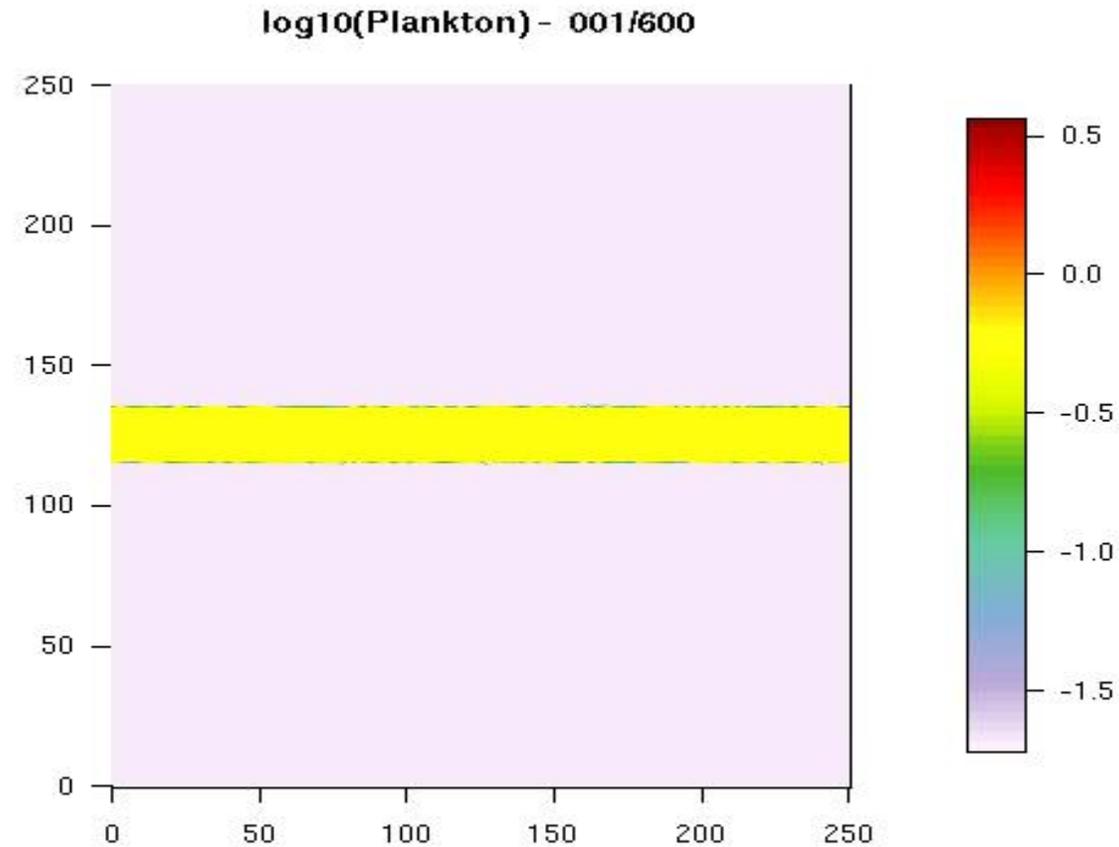


NPZ model

Phytoplankton in a 2D turbulent field

Nutrients enter at the horizontal strip at mid domain

View from above of an horizontal turbulent domain



A model for nutrient-poor (oligotrophic) Alpine lakes



Lake Trebecchi, GPNP, Italy
2729 m a.s.l.



Lake Nivolet sup, GPNP, Italy
2538 m a.s.l.



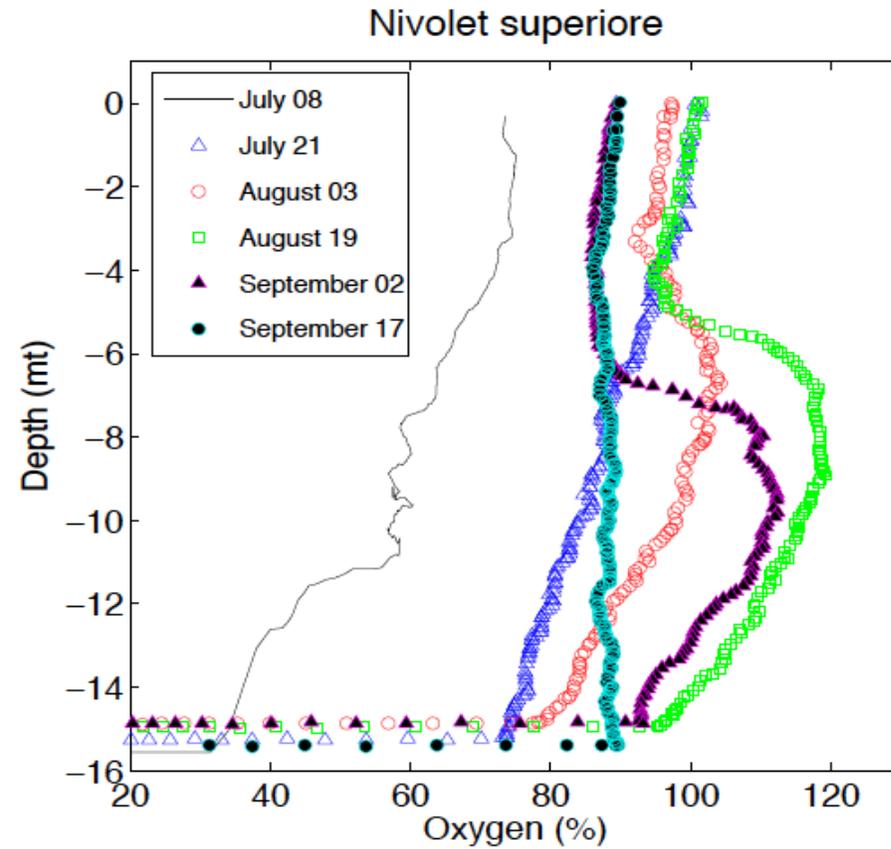
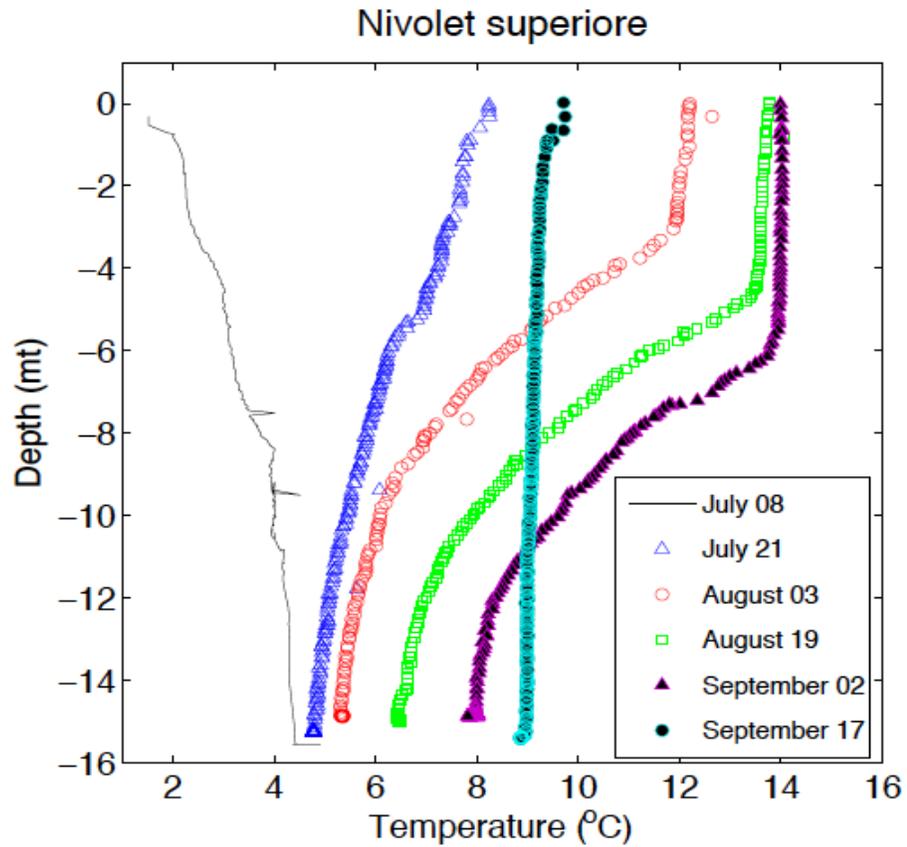
Sampling water properties and biology





Vertical structure of the lake

temperature and oxygen



Three types of zooplankton

rotifers, copepods, cladocerans





Properties of the species from biological sampling

Zooplankton	Average body length (μm)		Average dry weight (μg)		Number of lakes where found (2006 – 07)	
	No fish	Fish	No fish	Fish	No fish	Fish
Rotifers	119	119	0.15	0.15	6	6
Copepod nauplii	254	251	0.47	0.41	6	6
Copepodites	763	691	3.17	2.54	6	6
<i>Arctodiaptomus alpinus</i>	1236	1257	13.03	13.58	6	5
<i>Cyclops abyssorum</i>	1267	1249	17.33	16.57	6	5
<i>Eucyclops serrulatus</i>	–	740	–	4.21	0	1
<i>Daphnia middendorffiana</i>	2103	–	47.04	–	4	0
<i>Daphnia gr. longispina</i>	1307	1002	14.14	6.42	5	5
<i>Alona quadrangularis</i>	699	652	5.85	4.30	3	2
<i>Acroperus harpae</i>	327	592	1.23	2.05	1	1
<i>Chydorus sphaericus</i>	352	323	1.78	1.32	2	5



Structure of the mathematical model

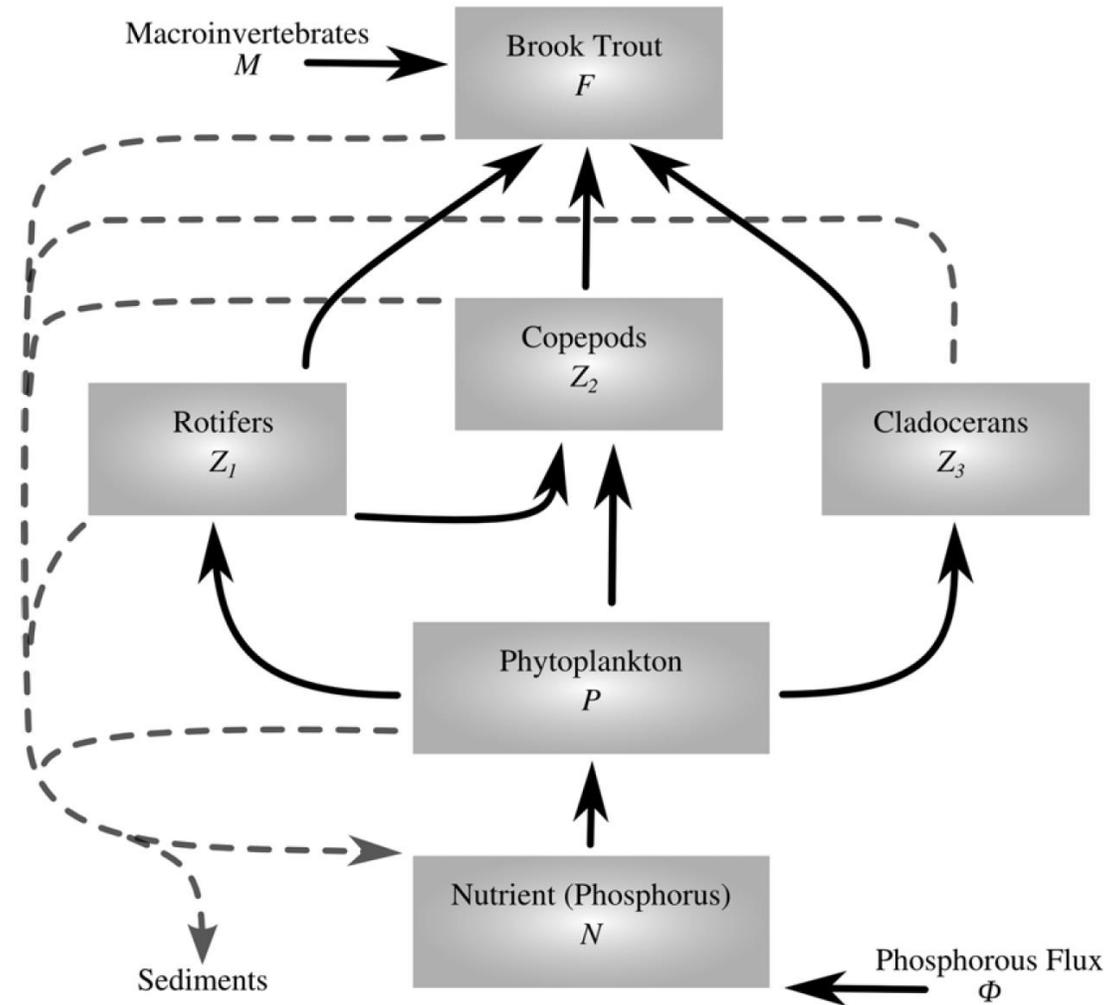


Fig. 1. A conceptual diagram representing the model adopted here. Each box represents a model compartment, whose dynamics is described in the text. The solid arrows indicate energy and biomass fluxes which are explicitly represented in the model; dashed arrows indicate fluxes of dead and/or egested biomass which are partly recycled and partly deposited in the sediment. External inputs are the phosphorus flux Φ and the constant pool of invertebrates entering the diet of the brook trout.



Values of the model parameters

Param.	Explanation	Value	Units	References
V_U	optimal ultrapl. P uptake rate	65	d^{-1}	[11], Tab. 4.2, [36], Tab. 5
κ_U	half-sat. c. for ultrapl. P uptake	0.5	$\mu\text{mol-P L}^{-1}$	[11] Tab. 4.2, [36], Tab. 5
Q_U	ultraplankton P:C molar ratio	1/70	mol-P/mol-C	[15, 35, 37]
r_{oi}	organic to inorg. P recycling rate	2.5	d^{-1}	[15] (pp. 258–259)
Φ	allochthonous phosphorus input	0.0007	$\mu\text{mol-P L}^{-1} \text{d}^{-1}$	[15] (p. 270), using $\bar{z} = 6.3 \text{ m}$
g_U	GE for ultraplankton	0.30		[40, 41]
g_0	GE for ciliates	0.68		[42]
g_1	GE for rotifers	0.55		[29]
g_2	GE for copepods	0.34		[29]
g_3	GE for cladocerans	0.83		[29]
g_F	GE for <i>S. fontinalis</i>	0.75		[43, 44]
q_0	ciliate P:C molar ratio	1/82	mol-P/mol-C	[42]
q_1	rotifer P:C molar ratio	1/111	mol-P/mol-C	[45]
q_2	copepod P:C molar ratio	1/114	mol-P/mol-C	[35]
q_3	cladoceran P:C molar ratio*	1/85	mol-P/mol-C	[46]
q_F	<i>S. fontinalis</i> P:C molar ratio	1/62	mol-P/mol-C	[47]
m_U	ultrapl. mort. rate (lysis and cell death)	1/3	d^{-1}	[15] (pp. 366, 508), [48]
d_0	ciliate mortality rate	1/7	$\text{d}^{-1} \text{L} (\mu\text{mol-C})^{-1}$	[15] (p. 402, Tab.16-3), [49]
d_1	rotifer mortality rate	1/14	$\text{d}^{-1} \text{L} (\mu\text{mol-C})^{-1}$	[50, 51, 52]
d_2	copepod mortality rate	1/53	$\text{d}^{-1} \text{L} (\mu\text{mol-C})^{-1}$	[53, 54]
d_3	cladoceran mortality rate	1/24	$\text{d}^{-1} \text{L} (\mu\text{mol-C})^{-1}$	[55, 56, 57, 58]
d_F	<i>S. fontinalis</i> mortality rate	1/1825	$\text{d}^{-1} \text{L} (\mu\text{mol-C})^{-1}$	[59]
α_U	ultrapl. constant in sinking rate (Stokes' law)	1240	$\mu\text{m}^{-1} \text{d}^{-1}$	[11] (at 10°C)
\bar{z}	average depth of water column	6.3	m	[9]
τ	time scale of P loss to sediment	90	d	[29]
p	parameter in predation function (??)	1		
γ	parameter in predation function (??)	3.605		

An example of the model behavior

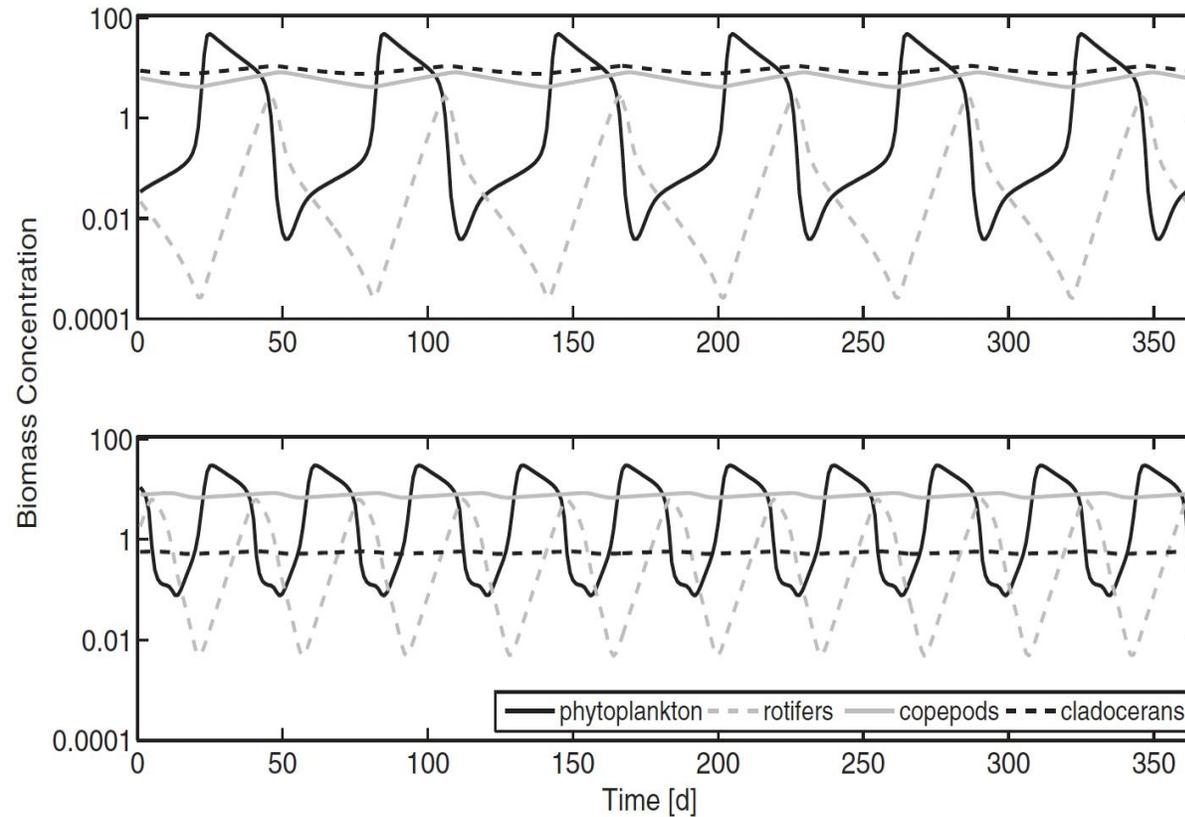


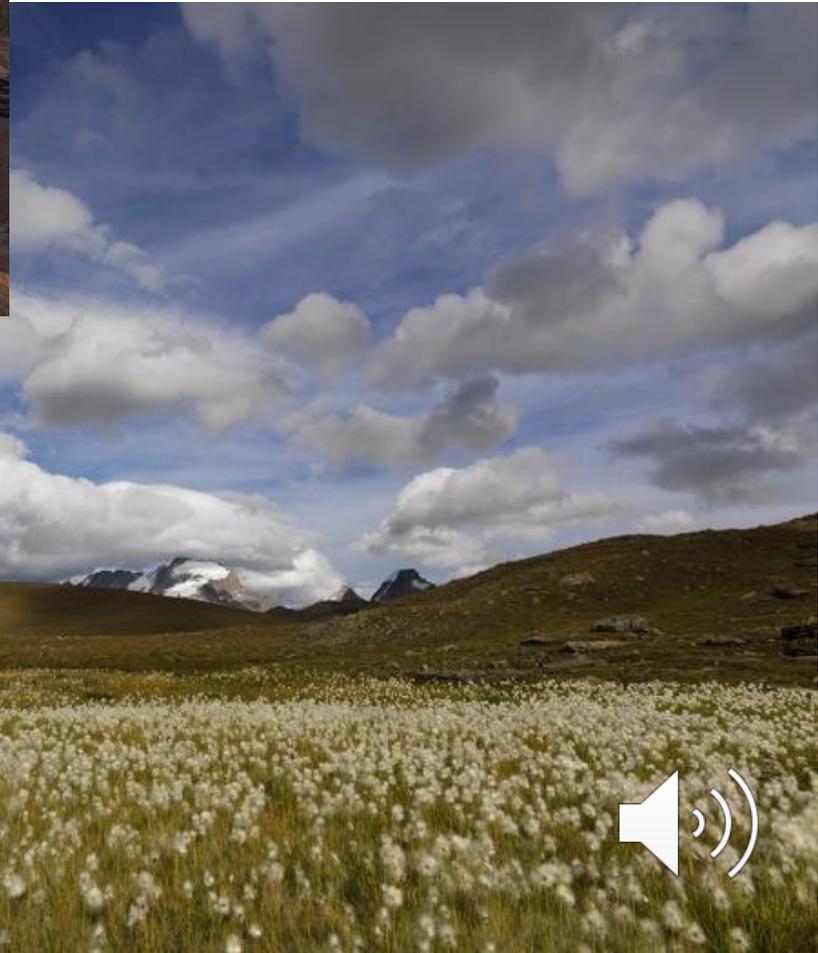
Fig. 2. Upper panel: temporal dynamics of the five-compartment ecosystem for a fishless lake. Lower panel: same as above but for lake with fish. Biomass concentrations are reported on logarithmic scale.



MODELS OF VEGETATION DYNAMICS



Vegetation dynamics models





Example 1: Savanna dynamics



Baudena et al, J. Ecology 2009
D'Onofrio et al, Water Resources Research 2014





Starting point: the conceptual model



Starting point: the conceptual model

$$\frac{db_1}{dt} = g_1 b_3 - \mu_1 b_1$$

Adult trees

$$\frac{db_2}{dt} = c_2 b_2 (1 - b_1 - b_2) - \mu_2 b_2$$

Grasses

$$\frac{db_3}{dt} = c_3 b_1 (1 - b_1 - b_2 - b_3) - \mu_3 b_3 - g_1 b_3 - c_2 b_2 b_3$$

Tree seedlings 

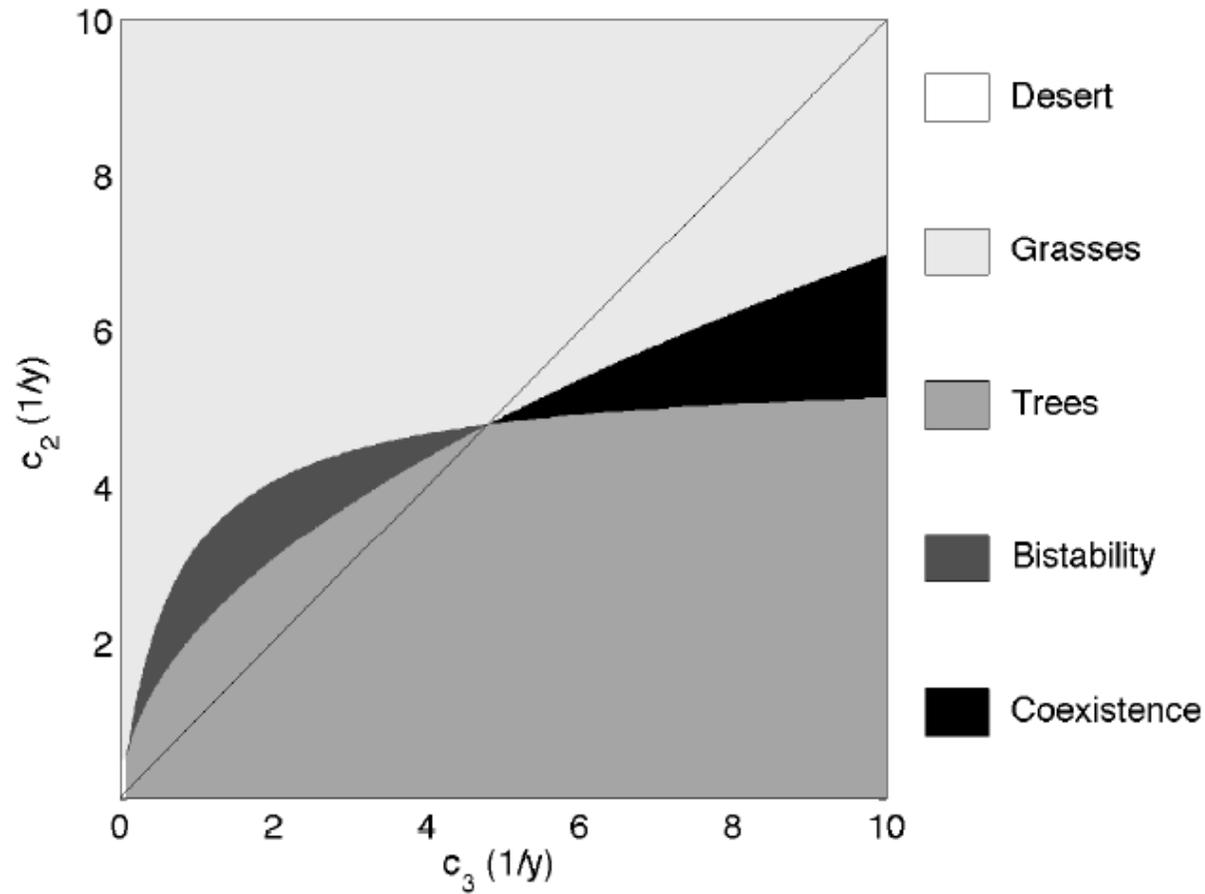
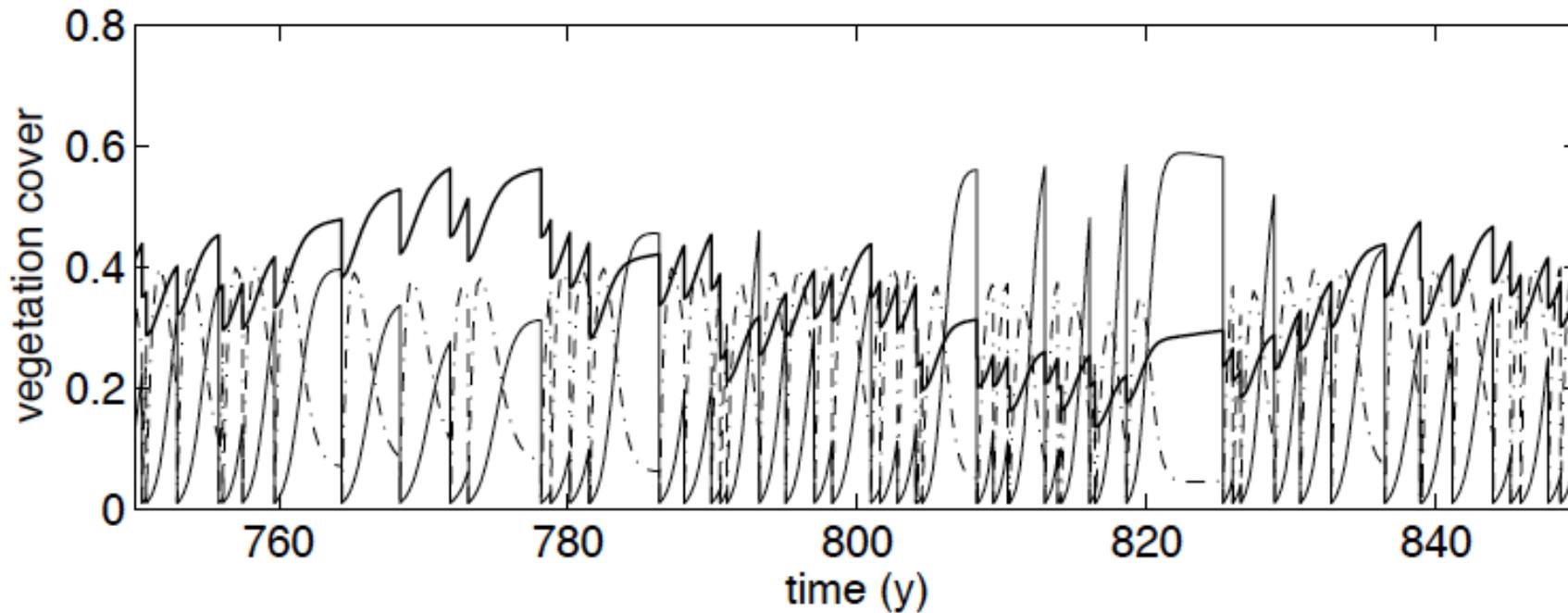


Fig. 1. Equilibrium states of the model in the subset of parameter space spanned by the colonization rate of tree seedlings, c_3 , and of grass, c_2 . The values of c_3 (x -axis) and c_2 (y -axis) vary from 0 to 10 y^{-1} ; other parameter values are $g_1 = 0.2 \text{ y}^{-1}$; $m_1 = 0.02 \text{ y}^{-1}$; $m_2 = m_3 = 0.5 \text{ y}^{-1}$. See the legend for the gray-scale code.



Stochastic fire disturbances

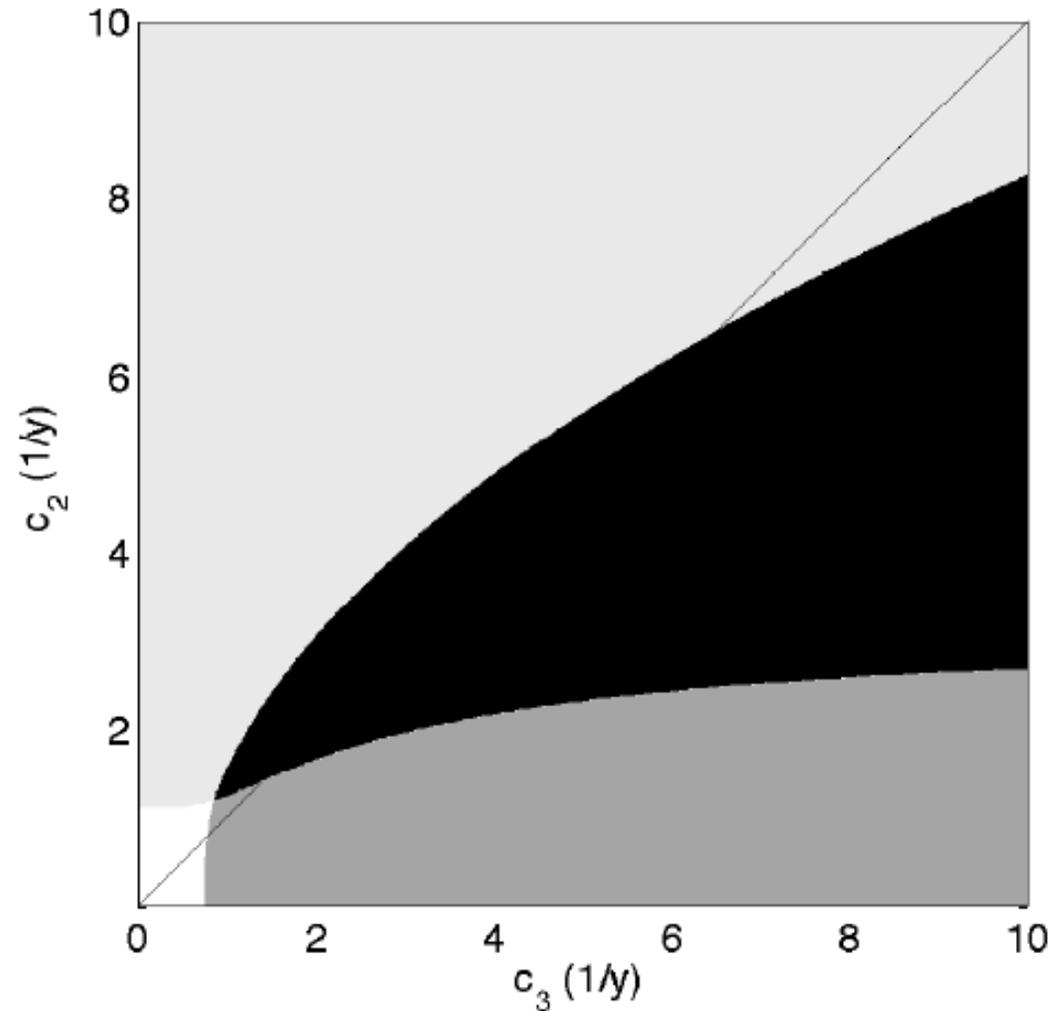
Significantly reduce grasses and seedlings,
leave trees almost unaffected





Stochastic fire disturbances

The coexistence range is extended



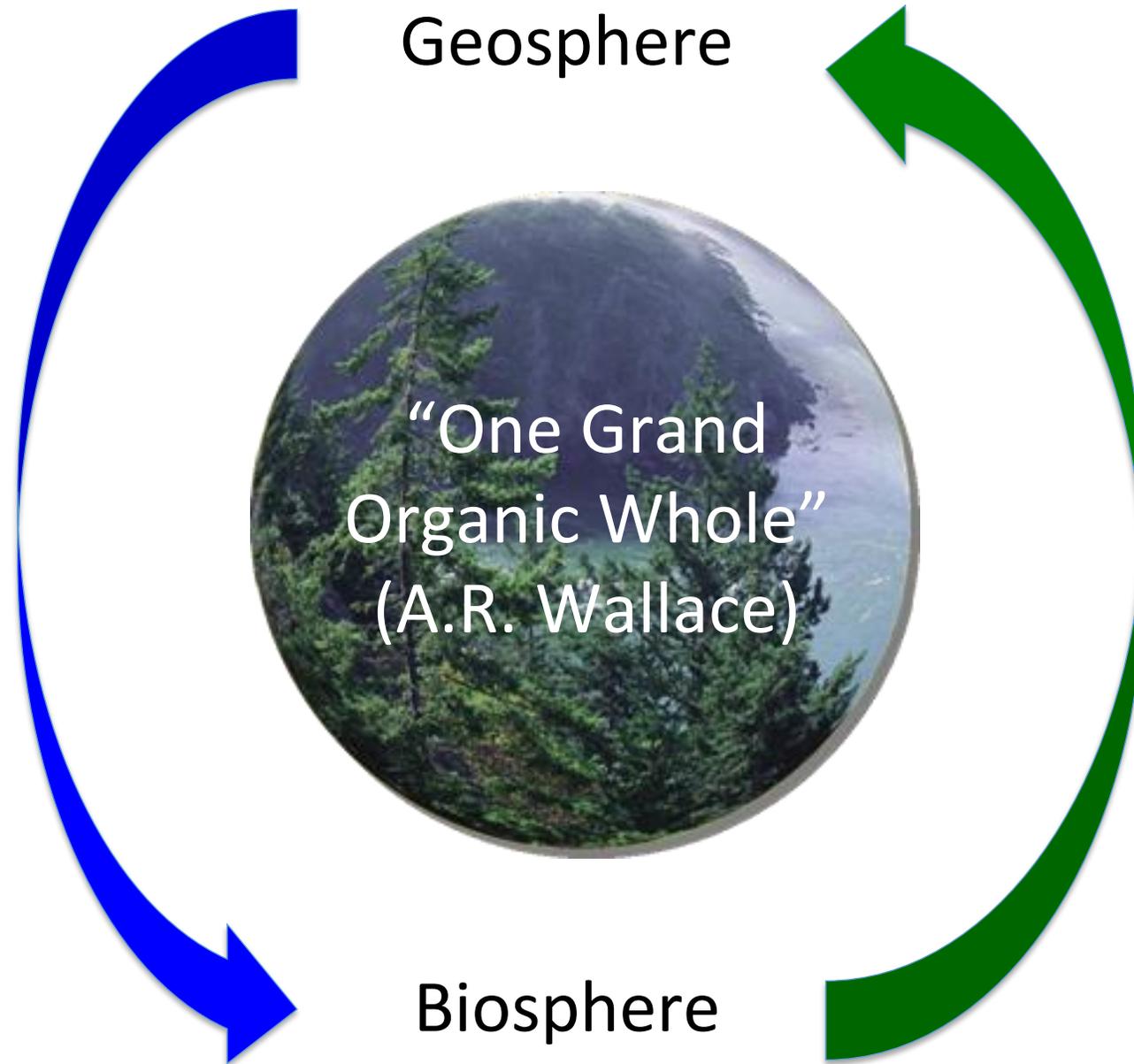
Stochastic fire disturbances

The circular structure of the model
allows for tree-grass coexistence

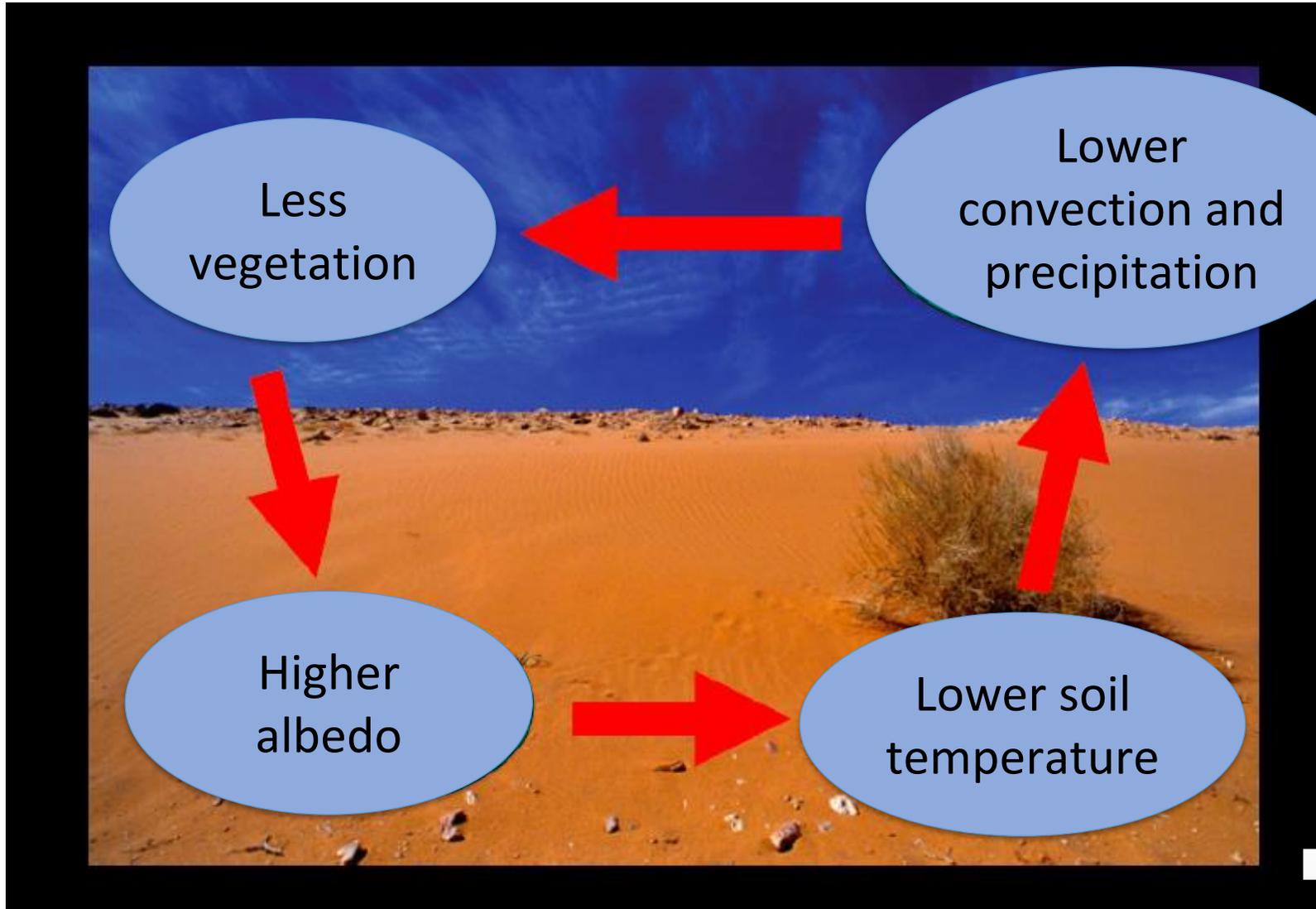
Depending on parameter values, we get either
a pure tree state,
pure grassland,
coexistence of trees and grass
or bistability between trees and grass

Stochastic fire disturbances
significantly widen the region of parameter space
where coexistence is possible

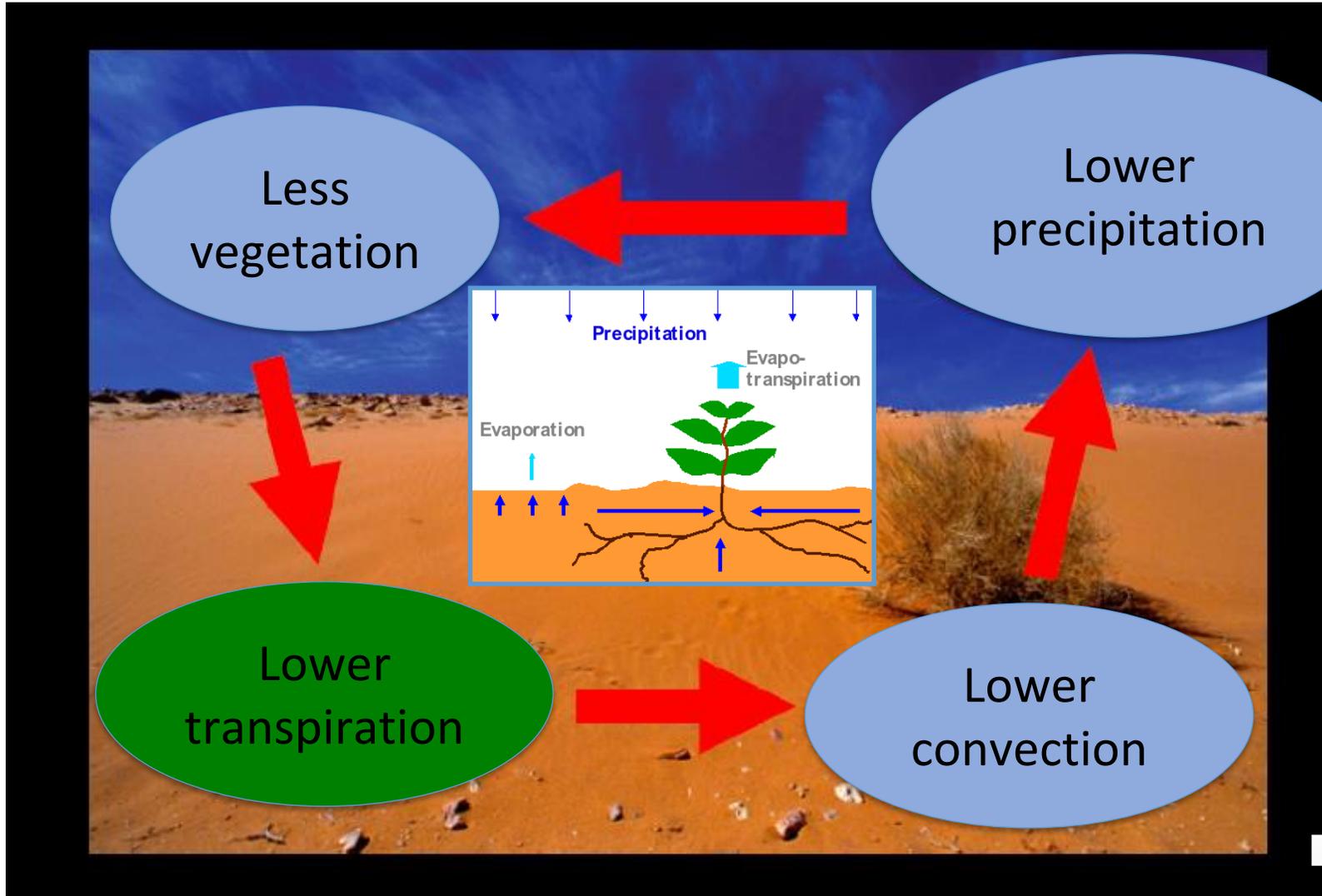


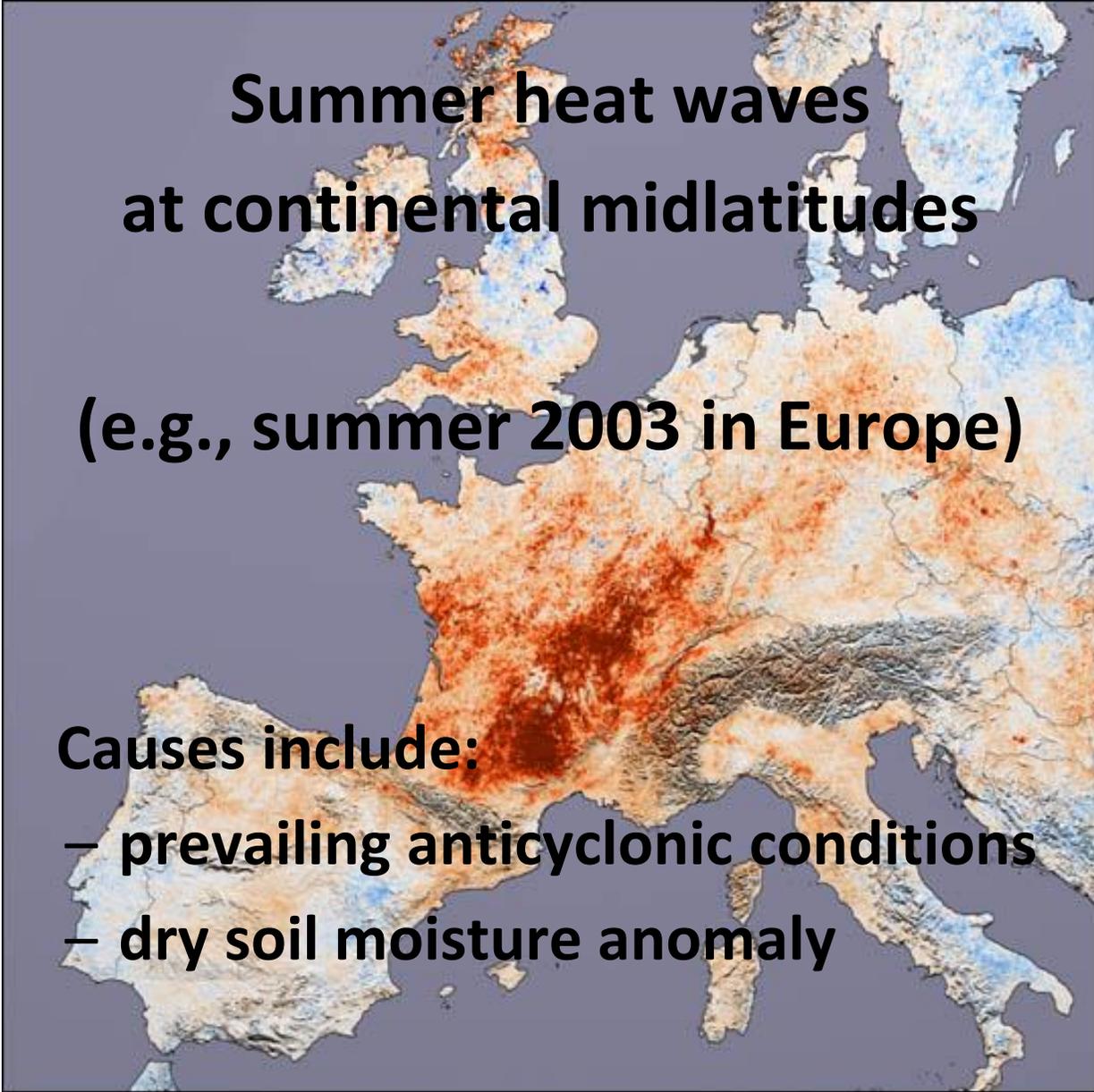


Albedo and the Charney mechanism (1975)



Plant transpiration and the hydrological cycle



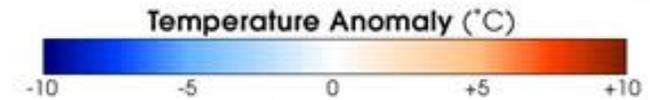


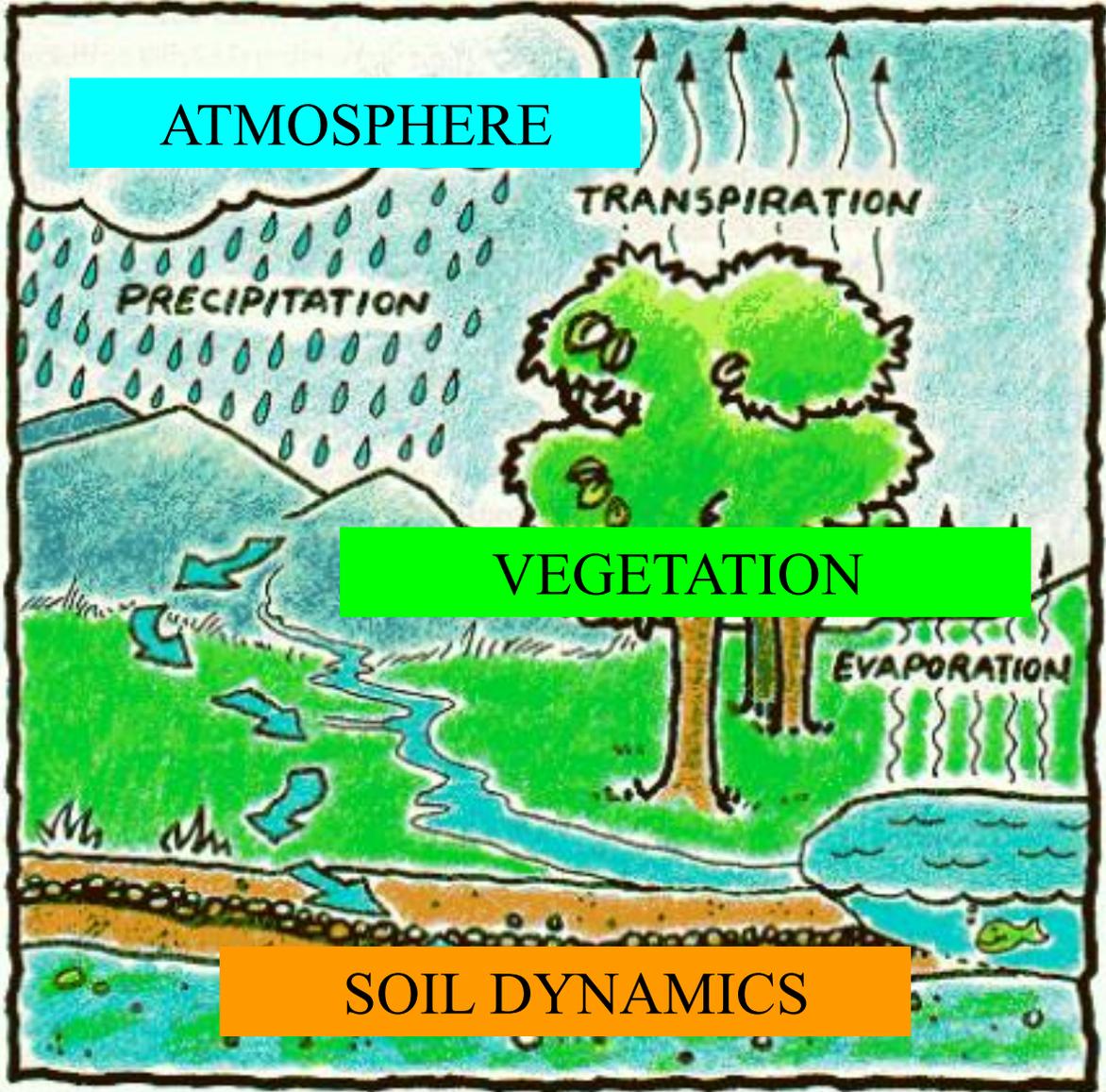
Summer heat waves at continental midlatitudes

(e.g., summer 2003 in Europe)

Causes include:

- prevailing anticyclonic conditions
- dry soil moisture anomaly





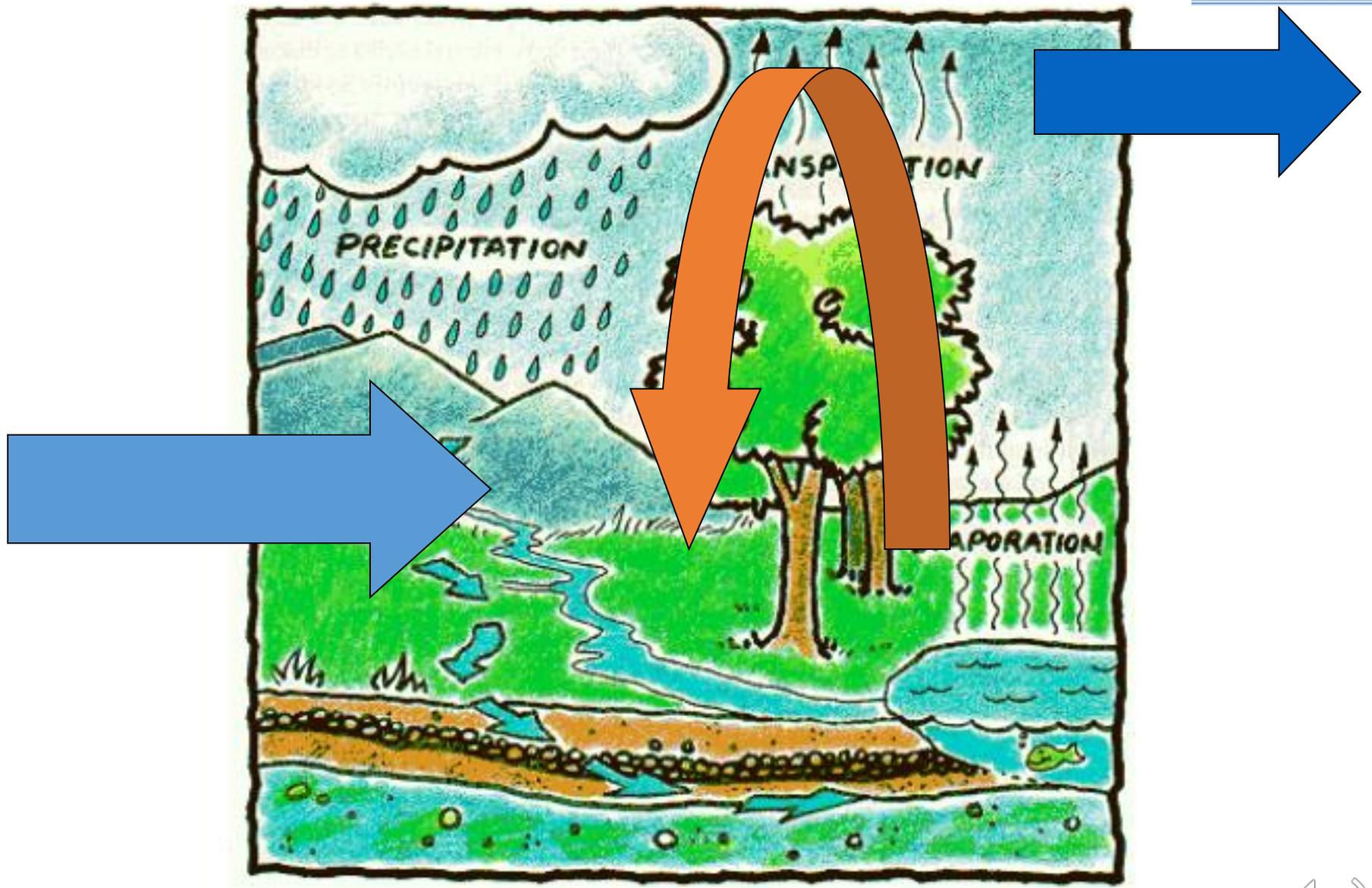
ATMOSPHERE

VEGETATION

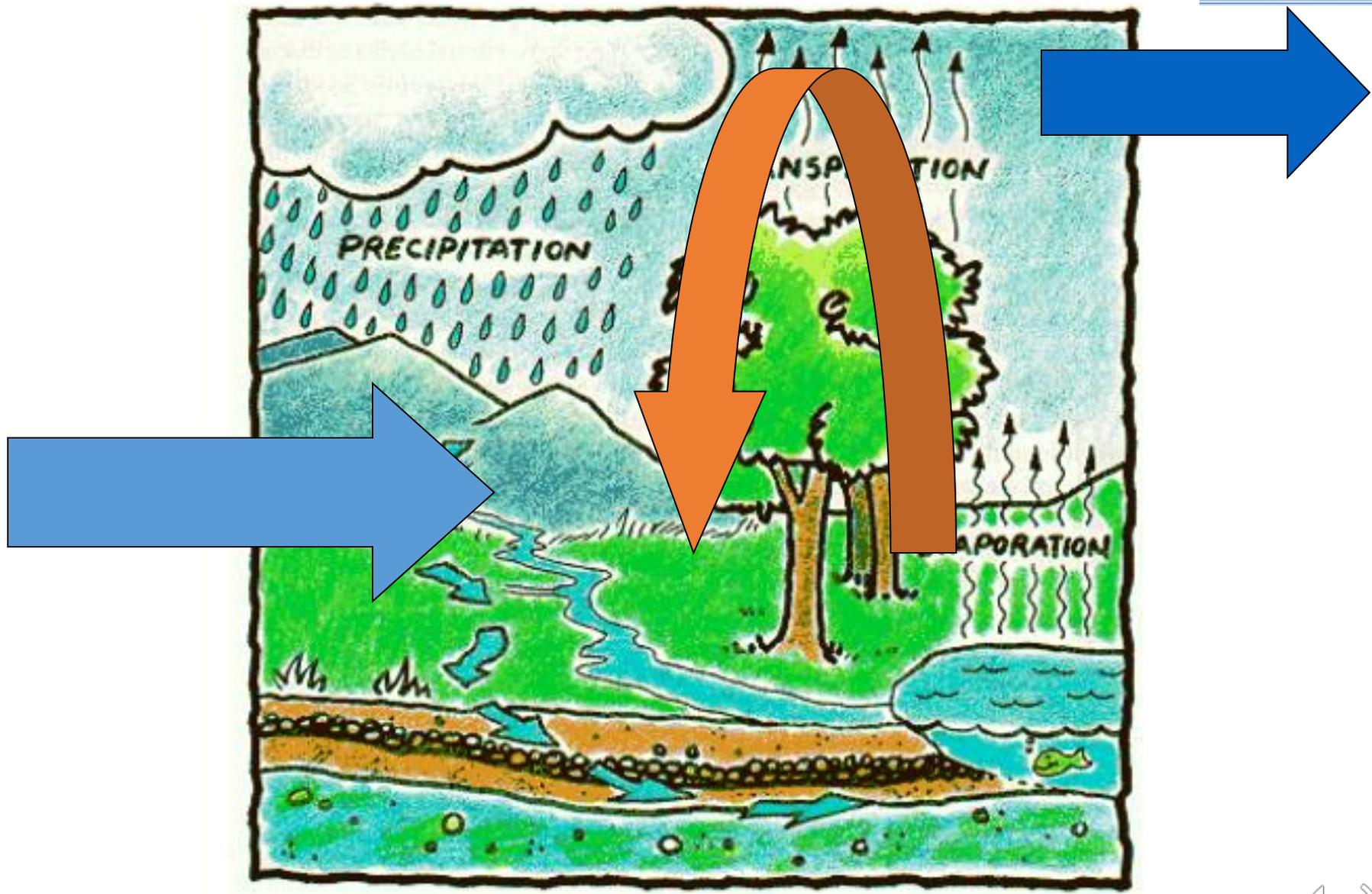
SOIL DYNAMICS

Hydrologic cycle on land





Closing the cycle: Long-range transport vs “local” recycling



Question: how important is the recycling in summer droughts?



$$\rho c_p h_a \frac{d\theta_a}{dt} = \epsilon_a \epsilon_s \sigma T_s^4 + Q_s - \rho c_p h_a \frac{d\Delta\tilde{\theta}_a}{dt} + \frac{1}{\tau_a} (\theta_a^* - \theta_a)$$

$$\rho h_a \frac{dq_a}{dt} = E - \rho h_a \frac{d\Delta\tilde{q}_a}{dt} + F_q$$

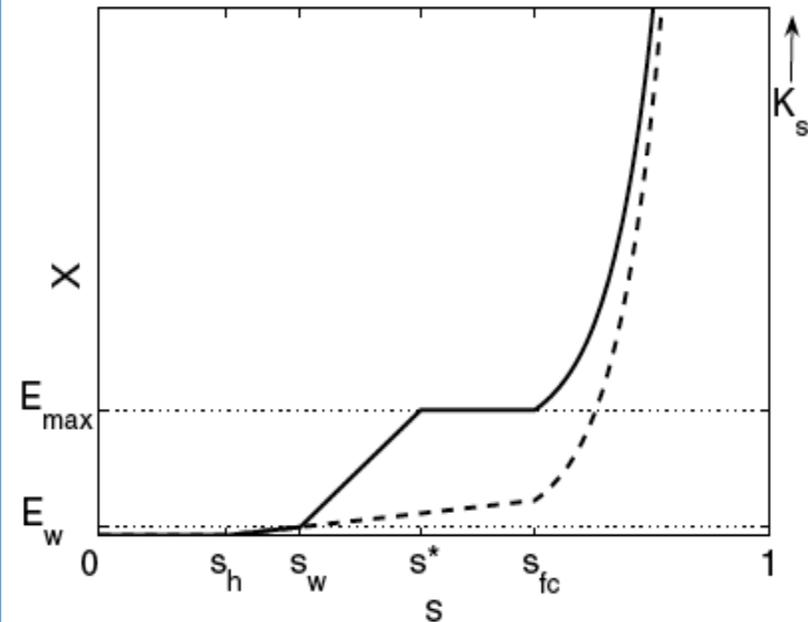
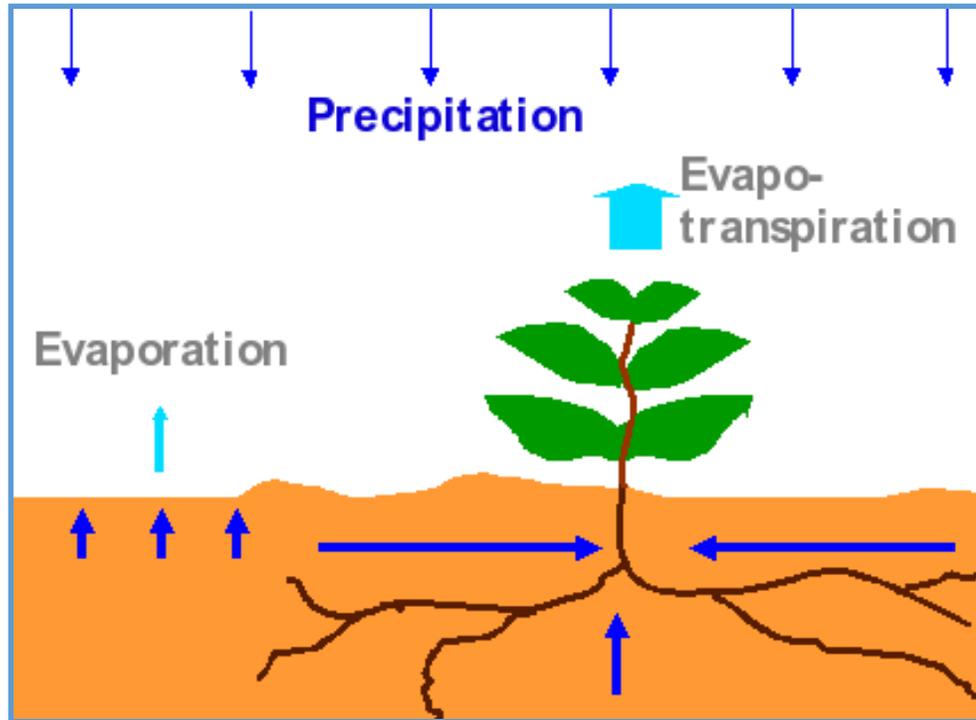
$$\rho_s c_{ps} h_s \frac{dT_s}{dt} = (1 - \alpha) F_{rad} - Q_s - \epsilon_s \sigma T_s^4 - L_e E$$

$$w_0 h_s \frac{dq_s}{dt} = I - E - L$$

$$\frac{db}{dt} = gb(1 - b) - \mu b$$



Evapotranspiration



$$X(s, b) = E + L = bC_b(q_s) + (1 - b)C_0(q_s)$$

Baudena, D' Andrea, AP, WRR, 2009



Albedo

$$\alpha = b\alpha_b + (1 - b)\alpha_0$$

$$\alpha_0 = 0.35$$

$$\alpha_b = 0.14$$

As in Charney [1975]

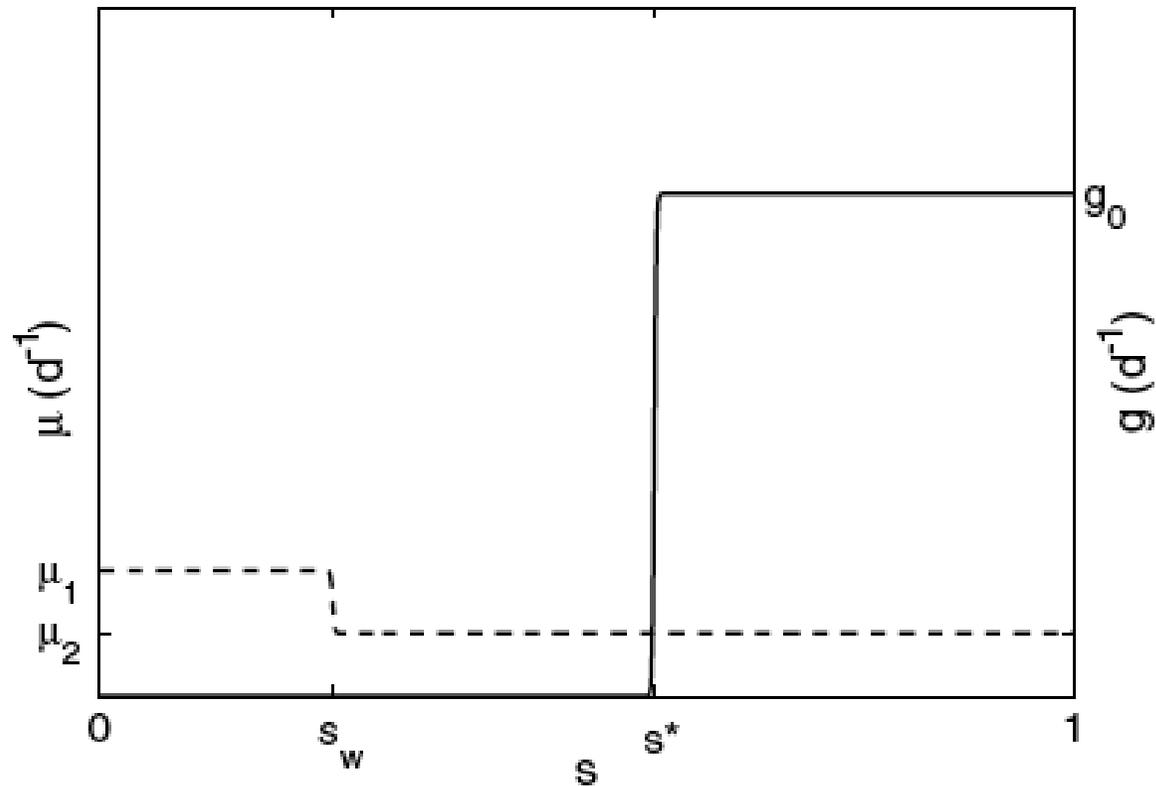




Vegetation dynamics

Levins, *Bull. Entomol. Soc. Am.* 1969; Tilman, *Ecology* 1994

$$\frac{db}{dt} = gb(1 - b) - \mu b.$$



Baudena, AP, HESS 2008; Baudena, D' Andrea, AP, WRR 2009



Convection parameterization

If $q_e = q_a \exp \frac{L_e q_a}{c_p q_a} > q_e^*$ convection occurs

We assume relative humidity is conserved
and that convection is instantaneous

$$\Delta \tilde{\theta}_a = \frac{\theta_e - \theta_e^*}{1 + \frac{L_e}{c_p} q_{rel} \delta q_{sat}},$$

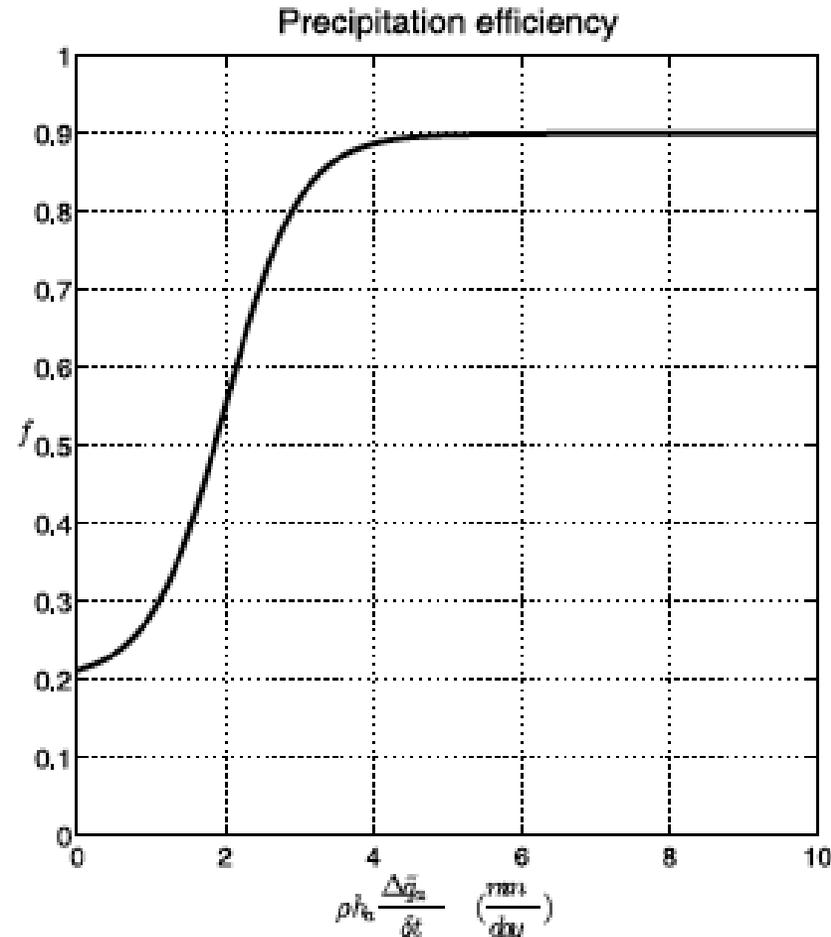
$$\Delta \tilde{q}_a = q_{rel} \delta q_{sat} \Delta \tilde{\theta}_a,$$





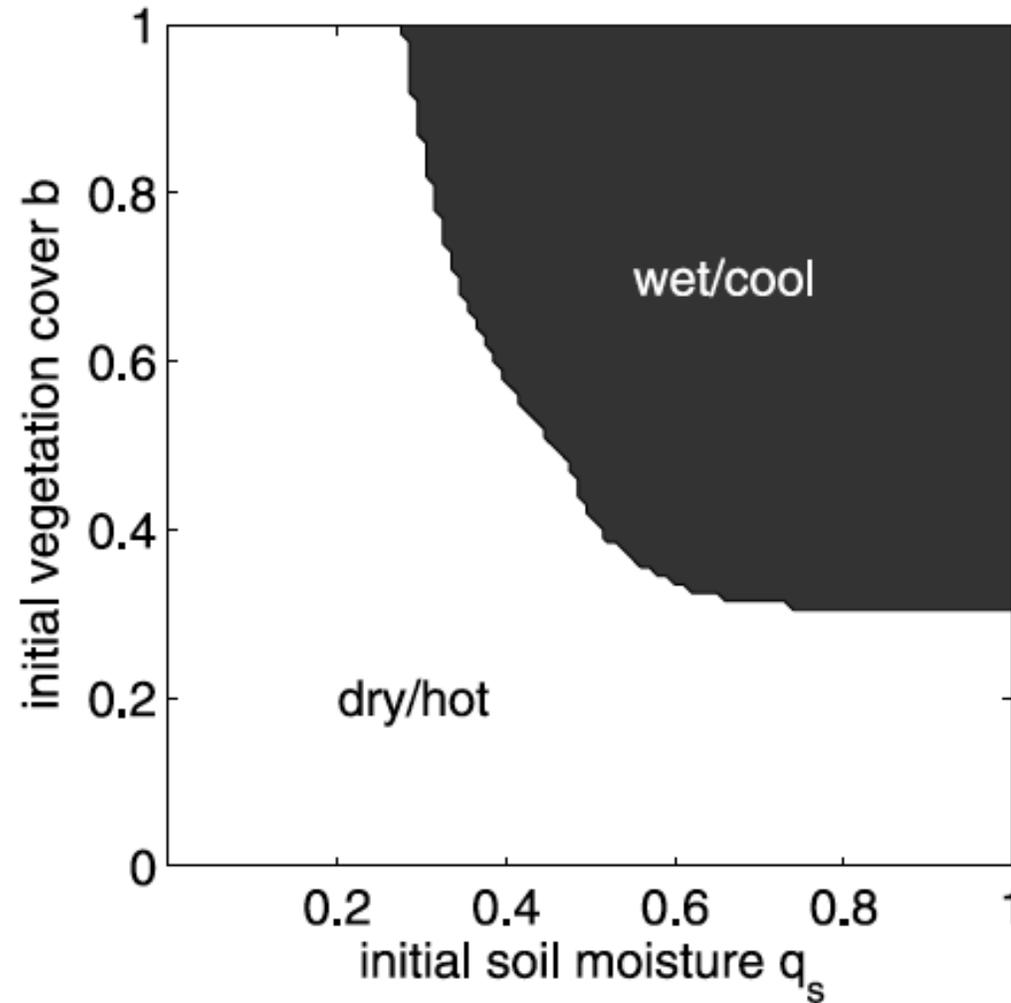
Precipitation efficiency (crucial feedback)

The amount of moisture transformed into local precipitation depends on the intensity of convection





Multiple equilibria of the soil-atmosphere system



D'Andrea et al *GRL* 2006, Baudena et al *WRR* 2009



Insurgence of summer droughts much dependent on the soil-moisture conditions at the end of spring

For realistic parameter values one obtains a bimodal distribution of soil moisture values

Vegetation cover is important:
below a minimal vegetation cover droughts are more probable

With dynamic vegetation, the “preferred” state is moist summers. When vegetation is frozen, summer droughts become more probable.

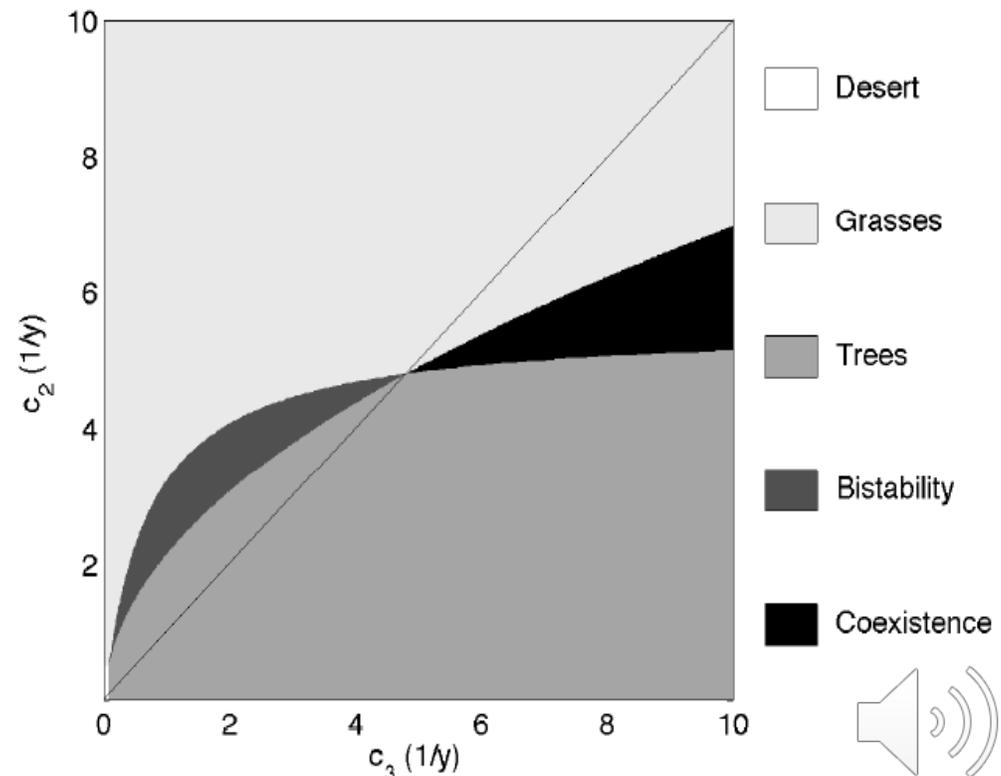
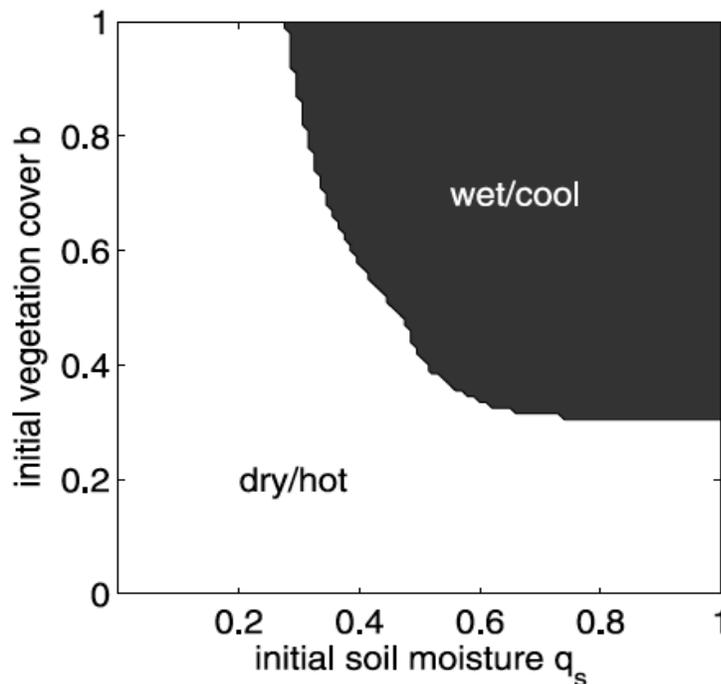
The crucial feedback is related to precipitation efficiency
Evapotranspiration feedback more importante than albedo feedback



Remarks on feedbacks and upscaling

(perspective paper, Rietkerk et al 2011)

In many cases, local ecohydrological systems are characterized by multiple equilibria



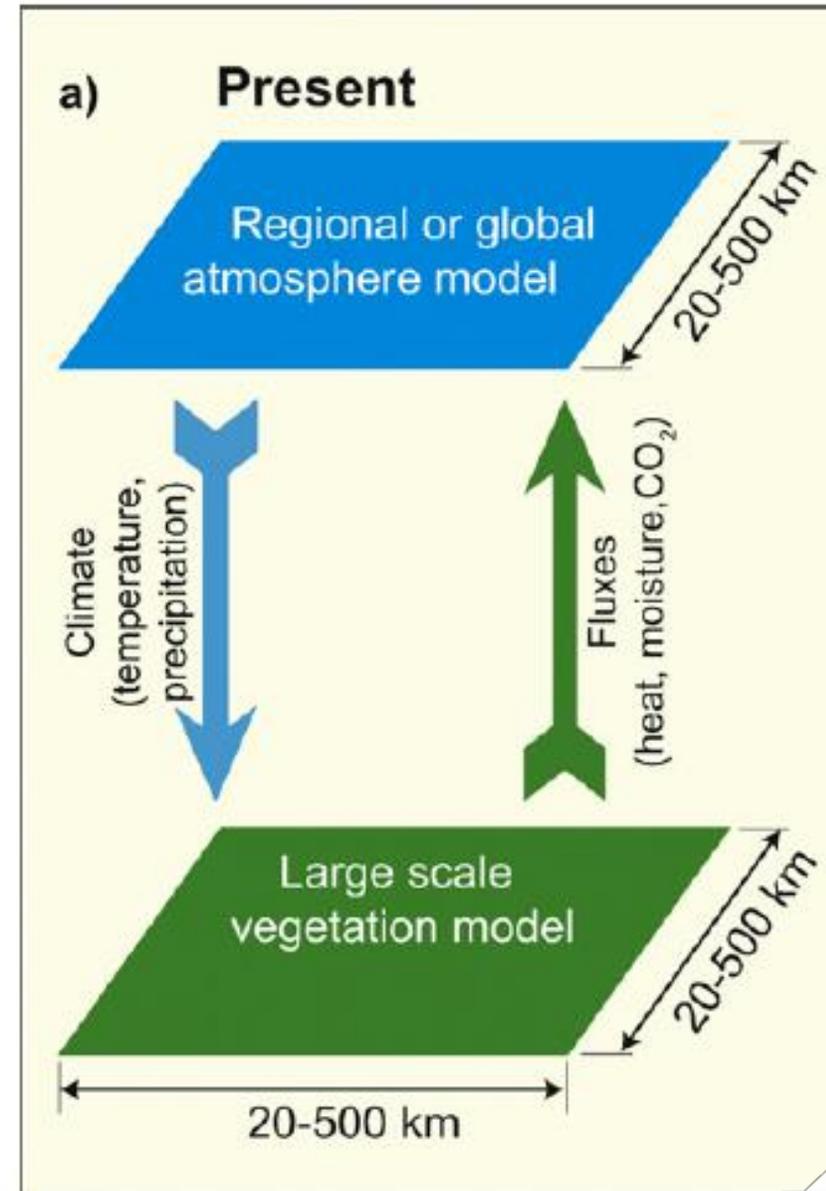


Cross-scale feedbacks

(Rietkerk et al 2011)

(Soranno et al 2014)

Modelling climate-vegetation feedbacks: Current situation



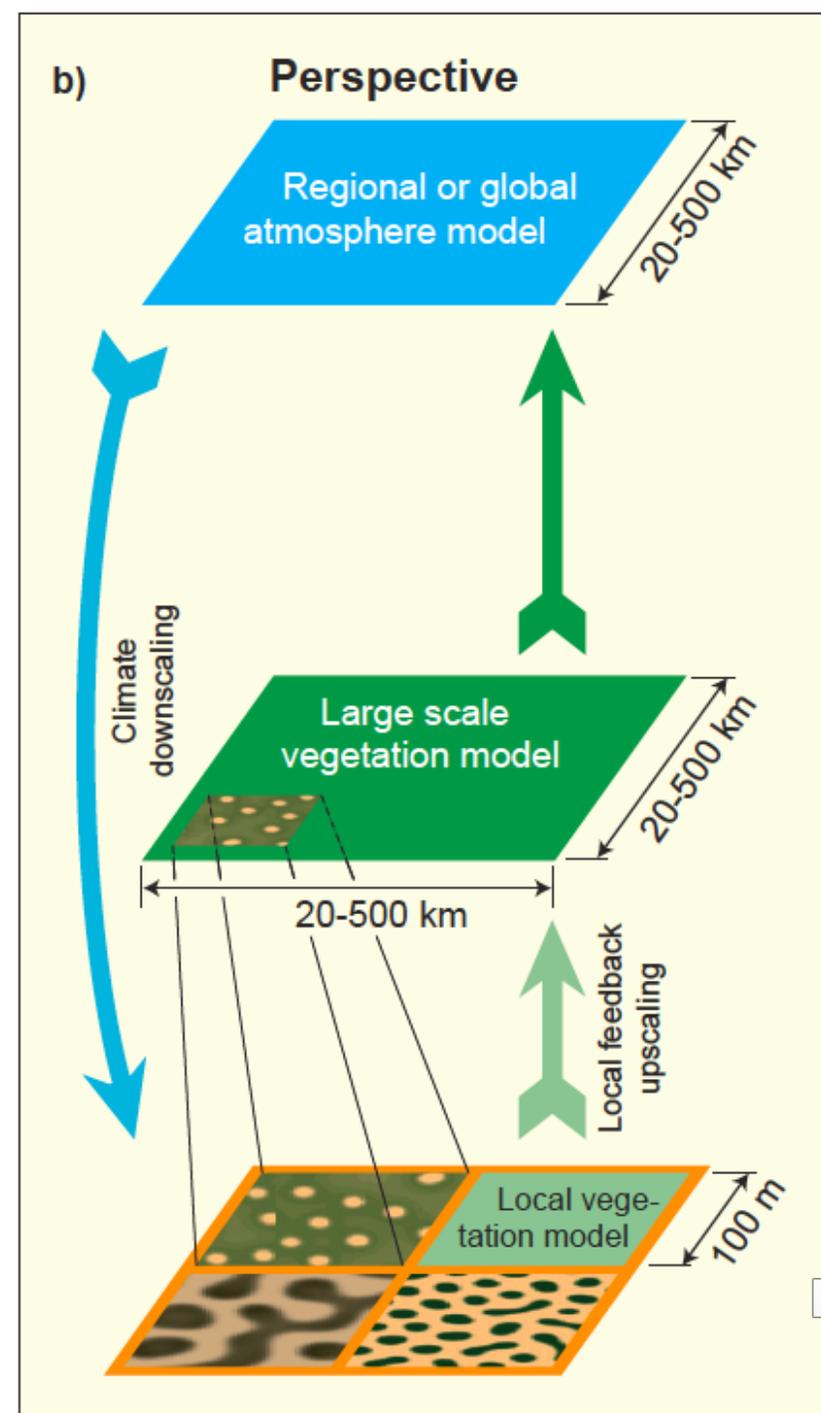


Cross-scale feedbacks

(Rietkerk et al 2011)

(Soranno et al 2014)

**Do changes
in small scales
affect
large-scale
behavior
(and how and where)?**





Challenge

Impact of climate change on the environment and the role of uncertainties

