# Modelling evolutionary and ecological processes in biogeochemical cycles

A MarQUEST workshop held at University of East Anglia, 15th/16th February 2010.

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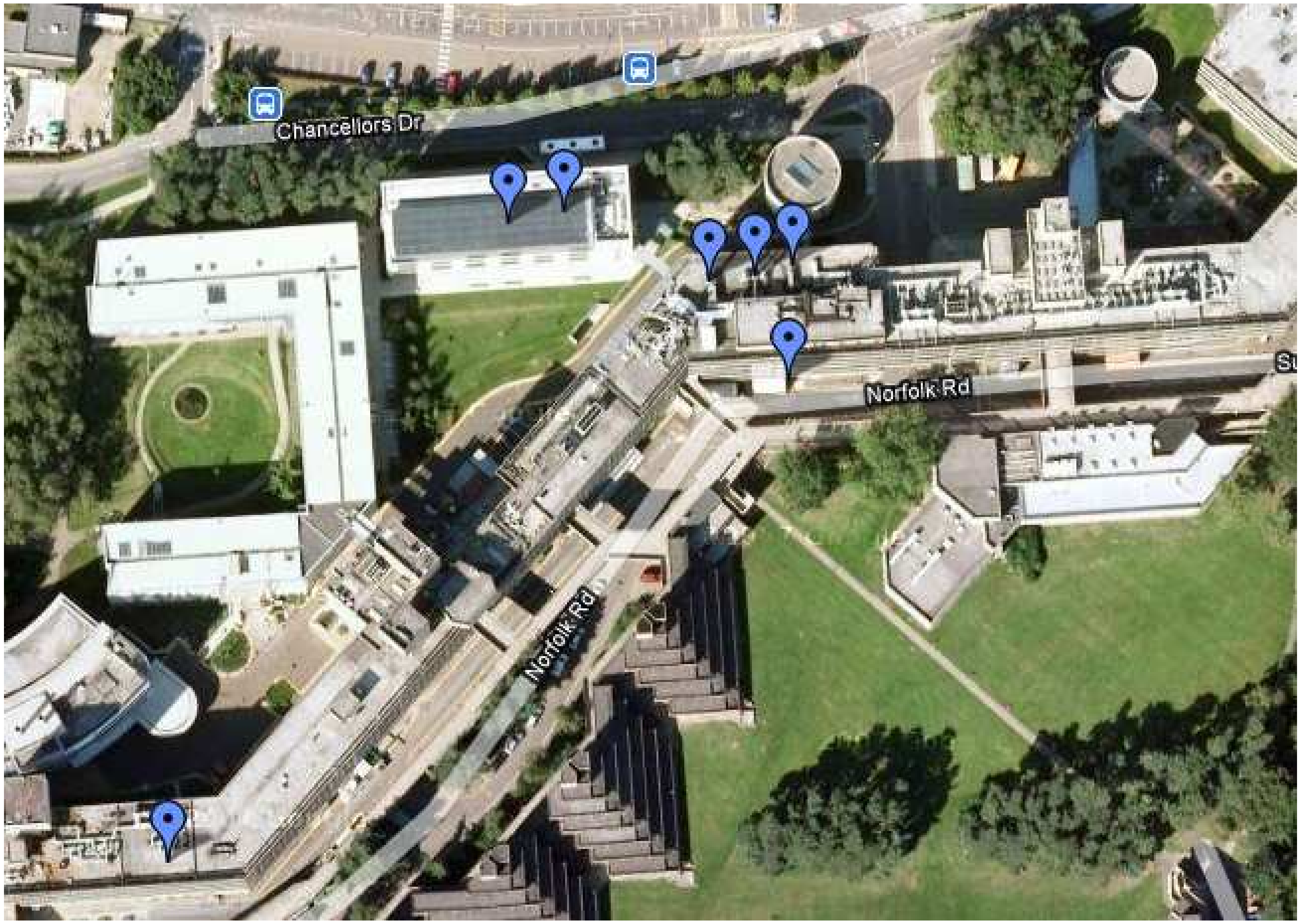

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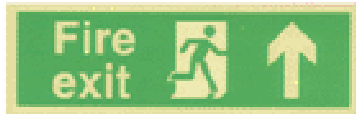

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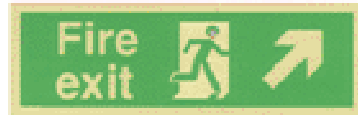

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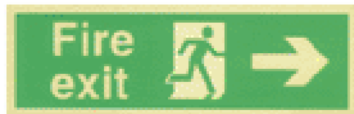

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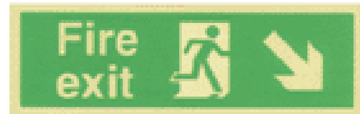

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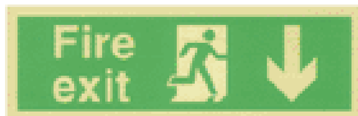

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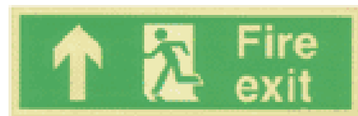

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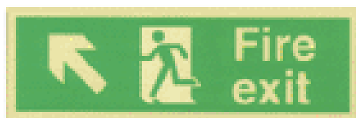

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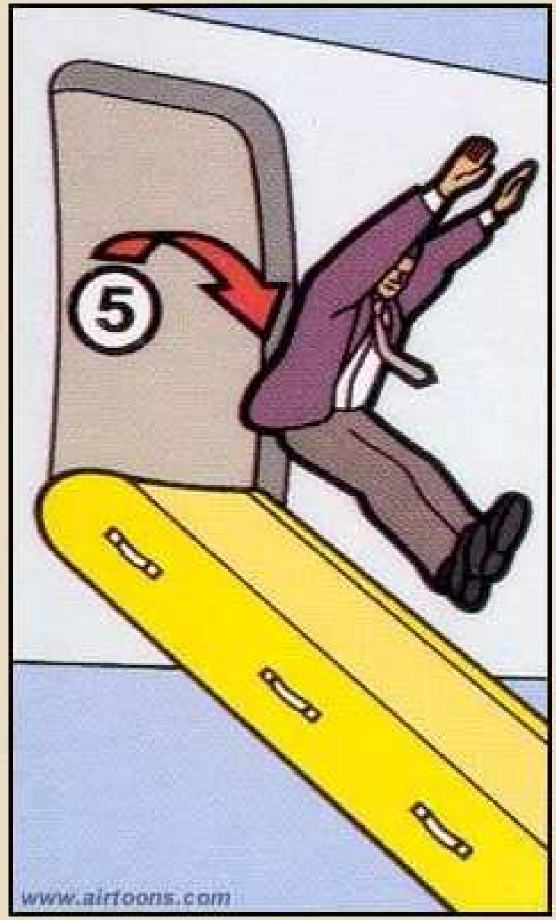


**In the event of an aircraft evacuation, style points will be given according to style and artistic impression.**

# Housekeeping

- Tea/coffee and lunches will be served in the ZICER exhibition space (outside this room)
- Speakers – please check your presentation in the break before your slot (laptop available)
- Wireless internet is available - ask Ben/Piotr/Phil
- Dinner tonight is 7.30pm at the Last Wine Bar in Norwich
- Transport for dinner...
- Drinks after today’s presentations

# Why are we here?

- Emerging trend for including adaptive biological processes (acclimation, ecology, evolution) in models of biogeochemical cycles
- Review the **scientific rationale**, the current **state of the art**, and the most promising **future directions** for adaptive modelling of biogeochemical cycles
- Target outcomes
  - characterise existing modelling approaches
  - identify outstanding scientific questions
  - highlight opportunities
  - review paper?

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## Modelling evolutionary and ecological processes in biogeochemical cycles

**A MarQUEST workshop at University of East Anglia, 15th/16th February 2010.**
**ZICER Seminar Room (Top Floor of ZICER building).**

| MONDAY 15th FEBRUARY 2010 | | | |
|---|---|---|---|
| 10.00am | WELCOME | | |
| 10.10am | Hywel Williams | University of East Anglia | Evolutionary modelling of life-environment interaction |
| 10.40am | Stephanie Dutkiewicz | Massachusetts Institute of Technology | Exploring biogeography and competitive advantage in a global ecosystem model |
| 11.10am | TEA/COFFEE | | |
| 11.30am | Andy Ridgwell | University of Bristol | Cancelled |
| 12.00 | Luca Polimene | Plymouth Marine Laboratory | Modelling stress responses in phytoplankton cells |
| 12.30pm | Richard Geider | University of Essex | Applications of cost-benefit analyses to phytoplankton ecophysiology |
| 1.00pm | LUNCH | | |
| 2.00pm | James Dyke | Max Planck Institute | Bringing Earth System Models To Life: Capturing evolutionary dynamics in biogeochemical processes. |
| 2.30pm | Drew Purves | Microsoft Research Cambridge | Modelling the Global Terrestrial Carbon Cycle: physiology → trees → stands → landscapes → grid-cell → globe |
| 3.00pm | Thomas Mock | University of East Anglia | Biogeochemical insights from marine algal genomes |
| 3.30pm | TEA/COFFEE | | |
| 4.00pm | Ivana Gudelj | Imperial College London | Mathematical models of metabolic cooperation |
| 4.30pm | Stuart Daines | University of Oxford | How can understanding prokaryotic genomics and evolution contribute to modelling the marine ecosystem (and vice-versa)? |
| 5.00pm | DISCUSSION & CLOSE | | |
| 7.30pm | DINNER | | |

Last Wine Bar

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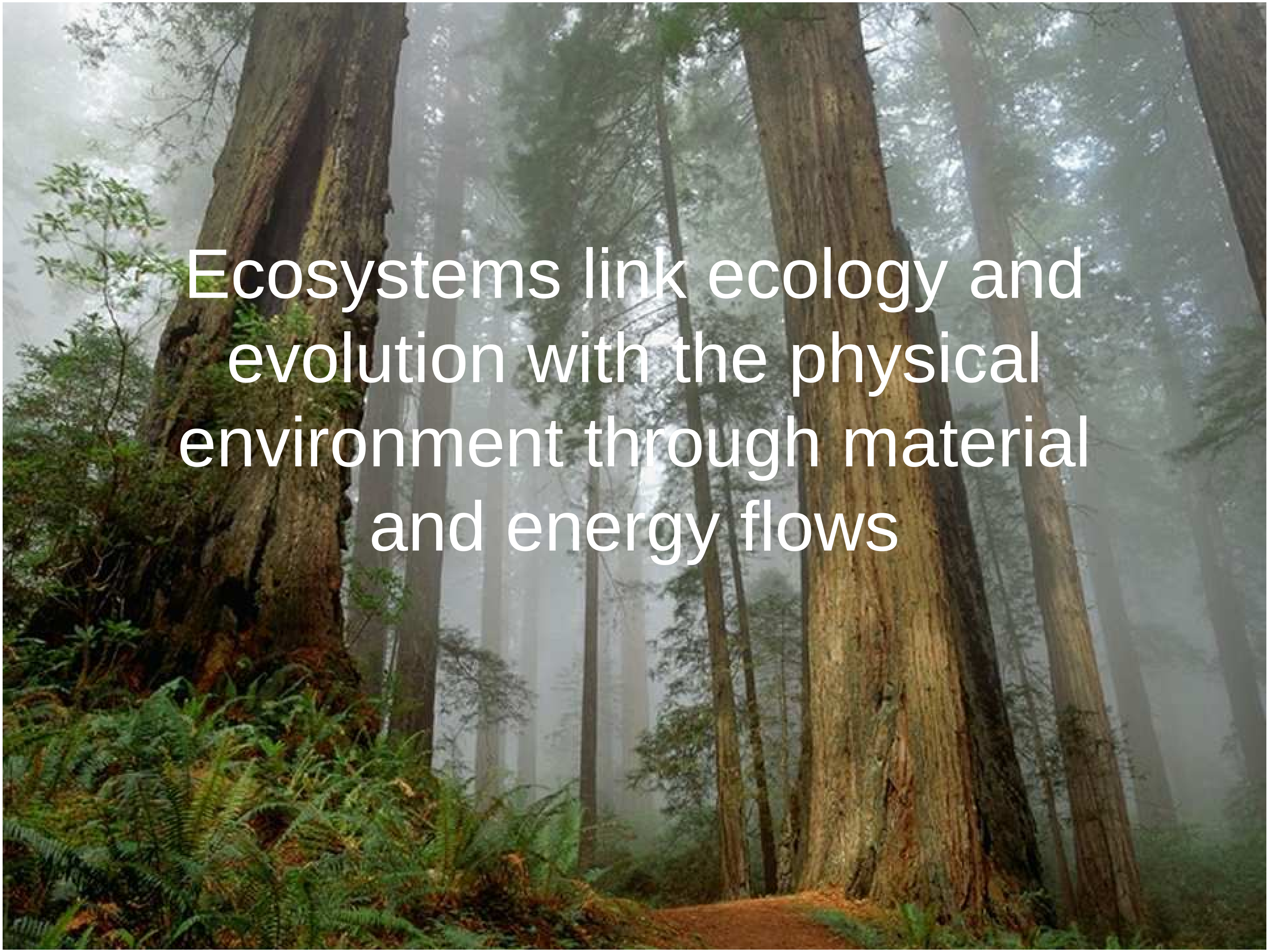
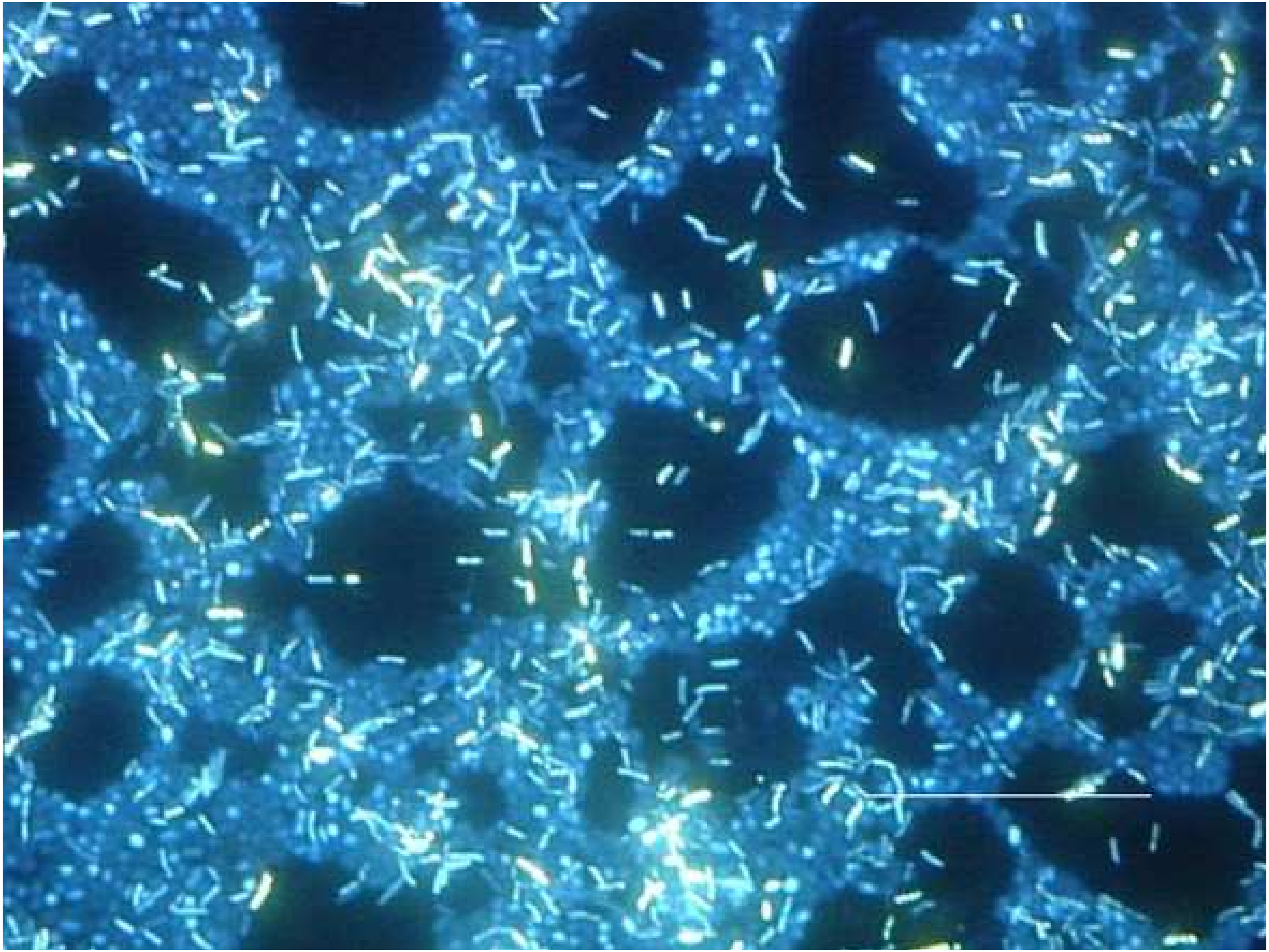
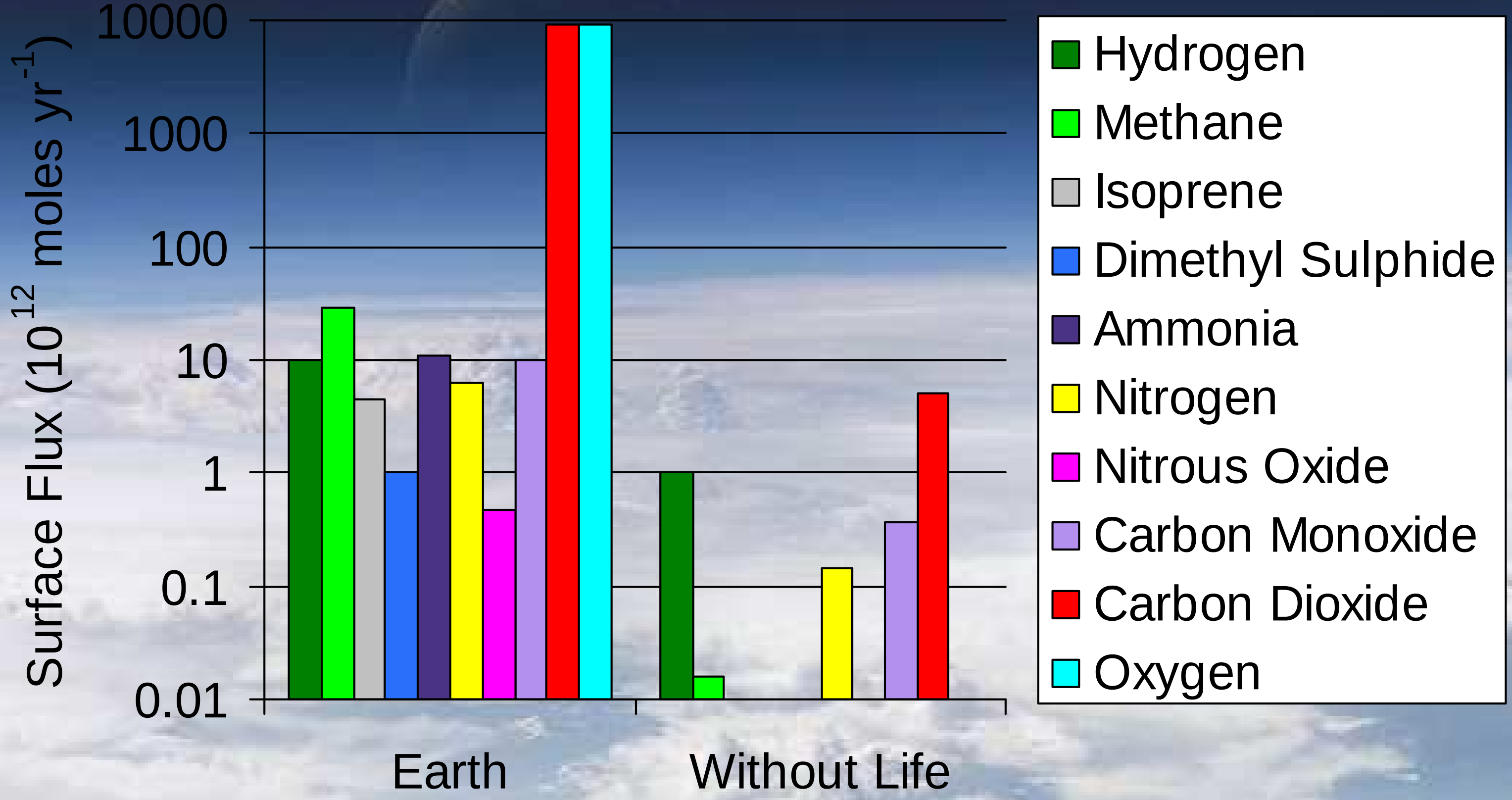
| TUESDAY 16TH FEBRARY 2010 | | | |
|---|---|---|---|
| 9.15am | Erik Buitenhuis | University of East Anglia | Acclimation to iron-light colimitation in a 0D and 3D model. |
| 9.45am | Jorn Bruggeman | University of Oxford | The plankton community as an evolving distribution of functional traits |
| 10.15am | Duncan Menge | National Center for Ecological Synthesis & Analysis, USA | Insights from simple biogeochemical models that incorporate evolutionary ecology of nitrogen fixation |
| 10.45am | TEA/COFFEE | | |
| 11.15am | Kristin Bohn | Max Planck Institute | A diverse adaptive biosphere: Population dynamics in the JEna DIversity (JeDi) model |
| 11.45am | Ferdi Hellweger | Northeastern University | Modeling the Evolution of Light Adaption in Marine Viruses using Systems BioEcology |
| 12.15pm | Corinne Le Quere | University of East Anglia | Controls on lower-trophic ecosystem composition in the global ocean |
| 12.45pm | LUNCH | | |
| 1.45pm | Rich Boyle | University of East Anglia | Neoproterozoic glaciations, kin selection & the origin of animals |
| 2.15pm | Jim Clark | University of East Anglia | Coupling evolutionary dynamics with an agent-based modelling approach: insights into the existence of oxygen oases circa 2.7 Ga |
| 2.45pm | DISCUSSION | | |
| 3.15pm | TEA/COFFEE | | |
| 3.45pm | DISCUSSION | | |
| 5.00pm | CLOSE | | |

Paper planning?

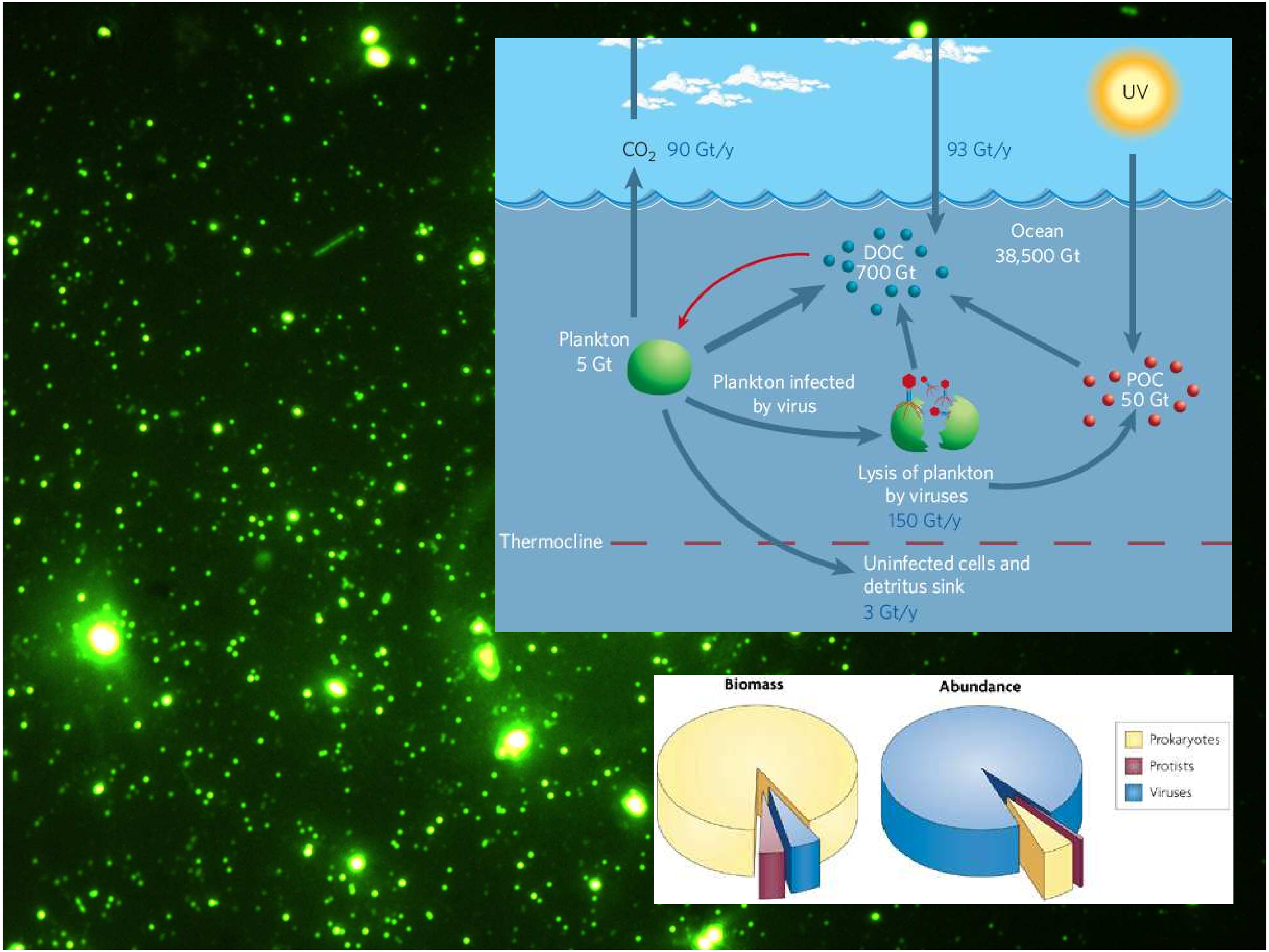

Ecosystems link ecology and evolution with the physical environment through material and energy flows



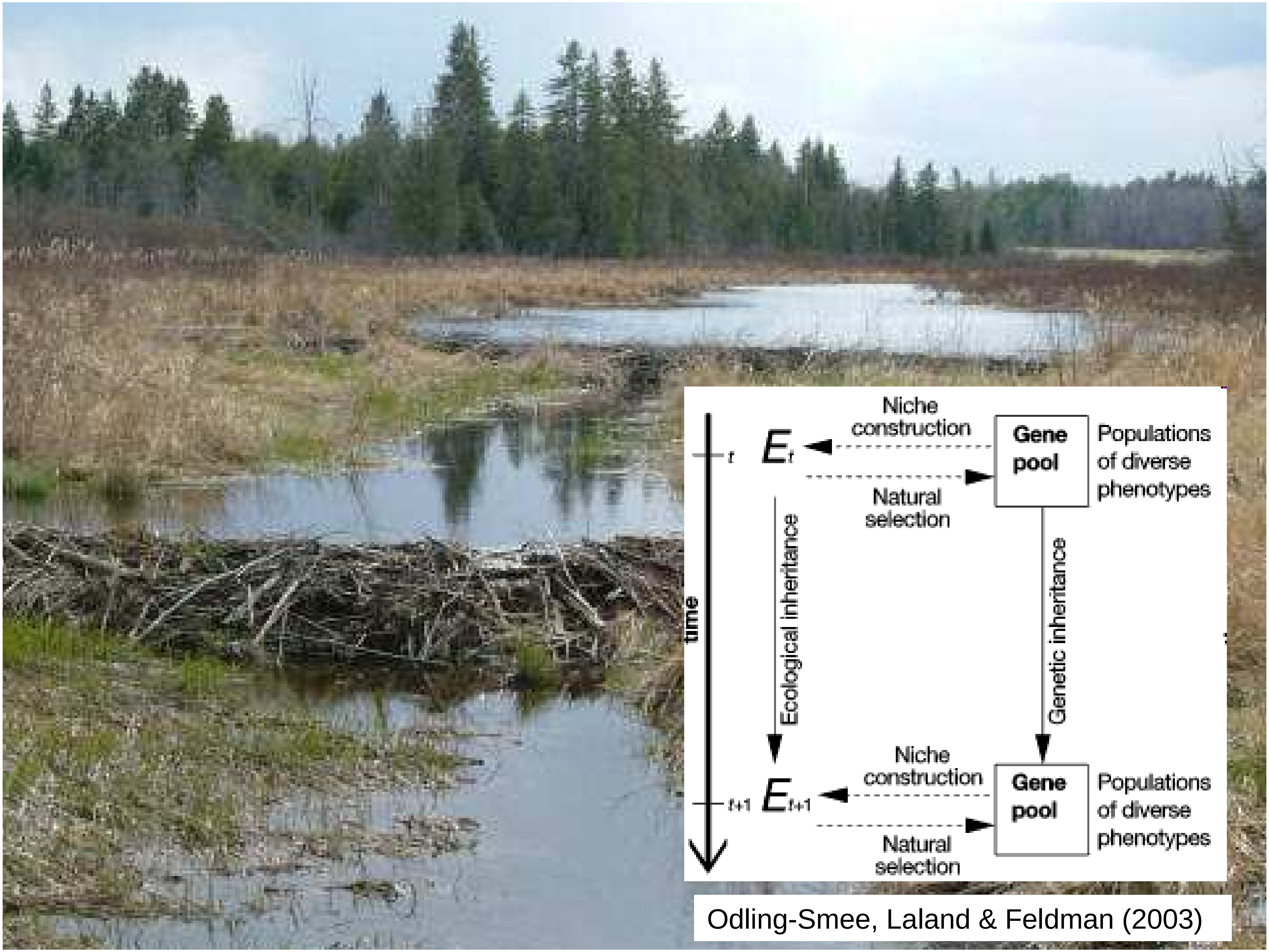
# Earth's atmosphere with and without life



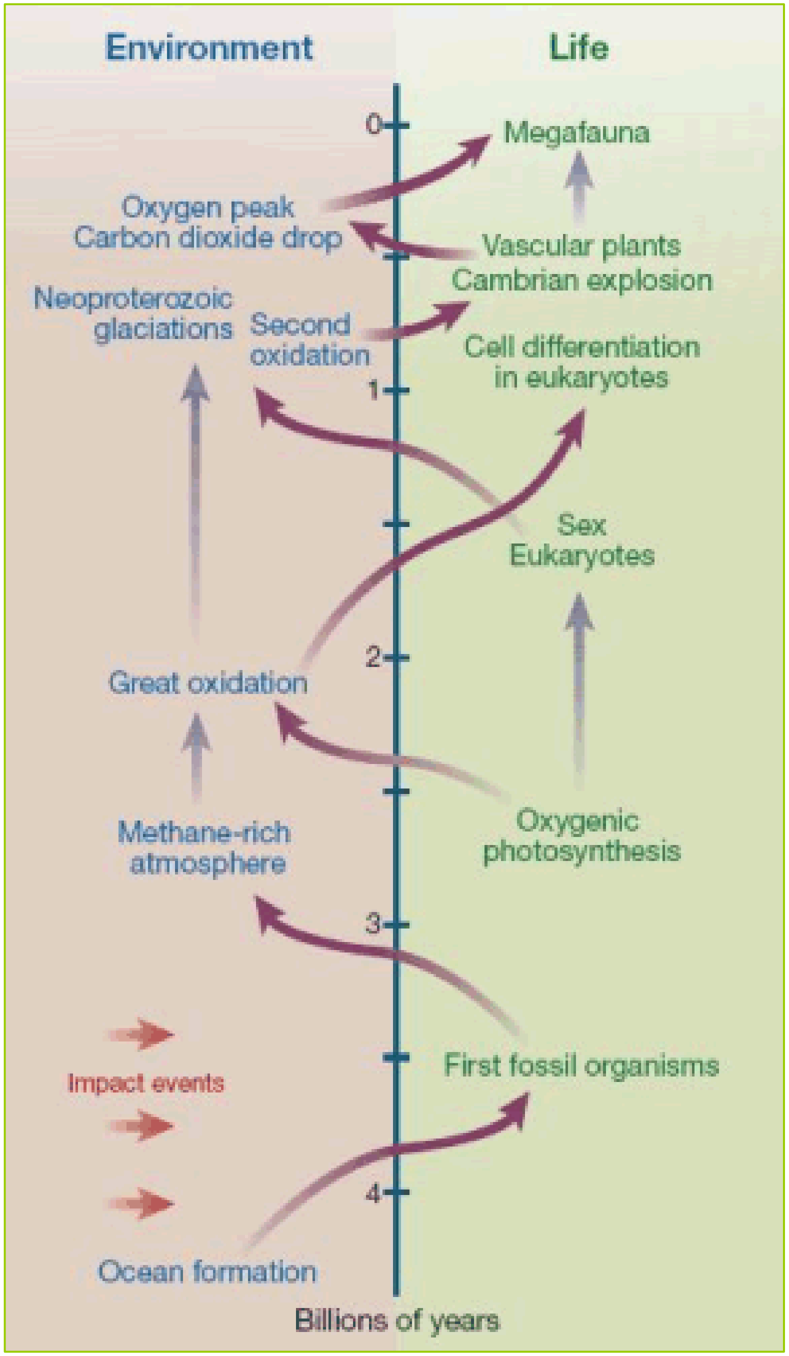

*Thanks to Tim Lenton*



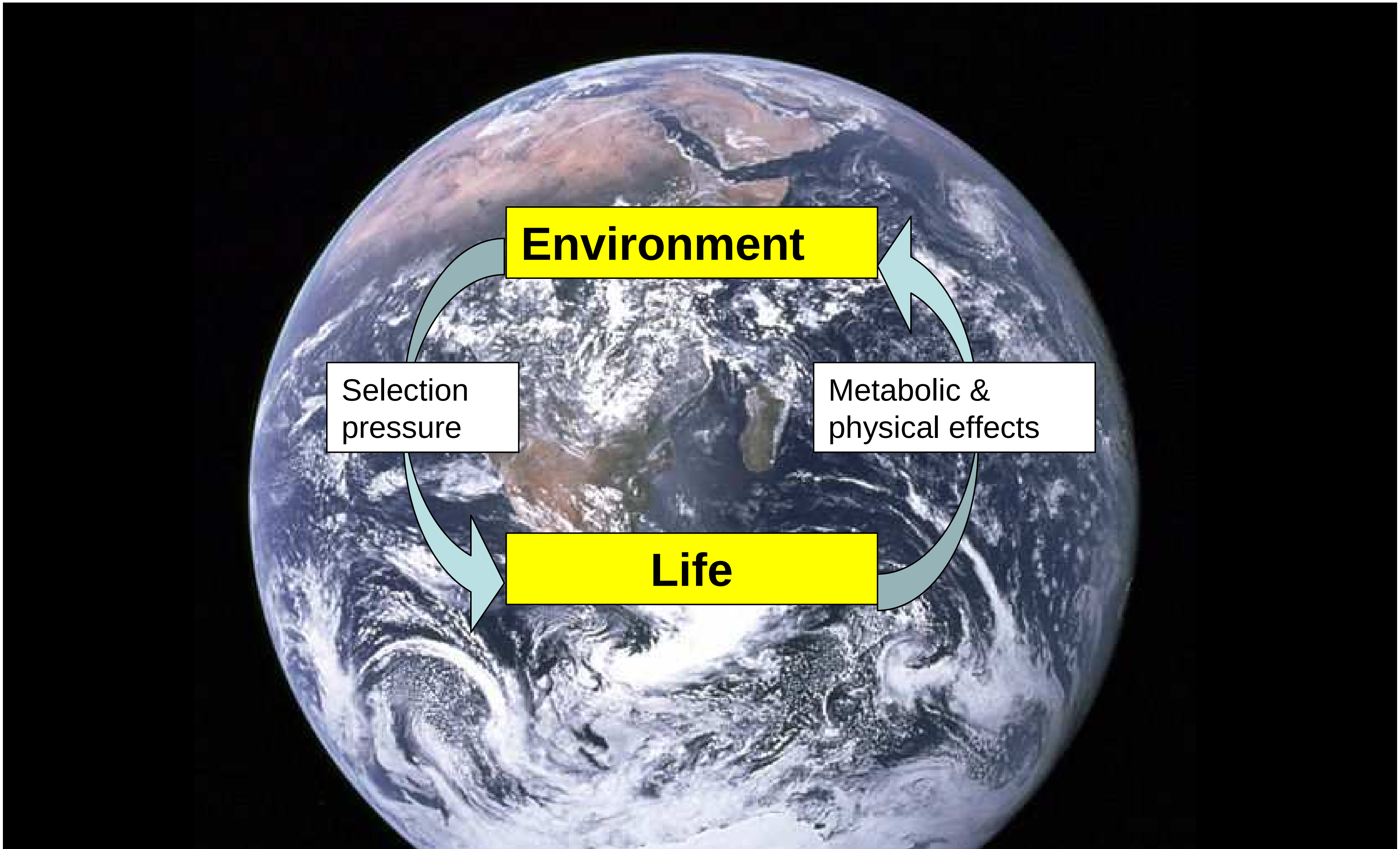
UV
CO2 90 Gt/y
93 Gt/y
Ocean
38,500 Gt
DOC
700 Gt
Plankton
5 Gt
Plankton infected
by virus
POC
50 Gt
Lysis of plankton
by viruses
150 Gt/y
Thermocline
Uninfected cells and
detritus sink
3 Gt/y
Biomass
Abundance
Prokaryotes
Protists
Viruses




Odling-Smee, Laland & Feldman (2003)




Lenton, Schellnhuber & Szathmary (2004)




Nothing in biogeochemistry makes sense except in light of evolution (and ecology, and acclimation,...)?

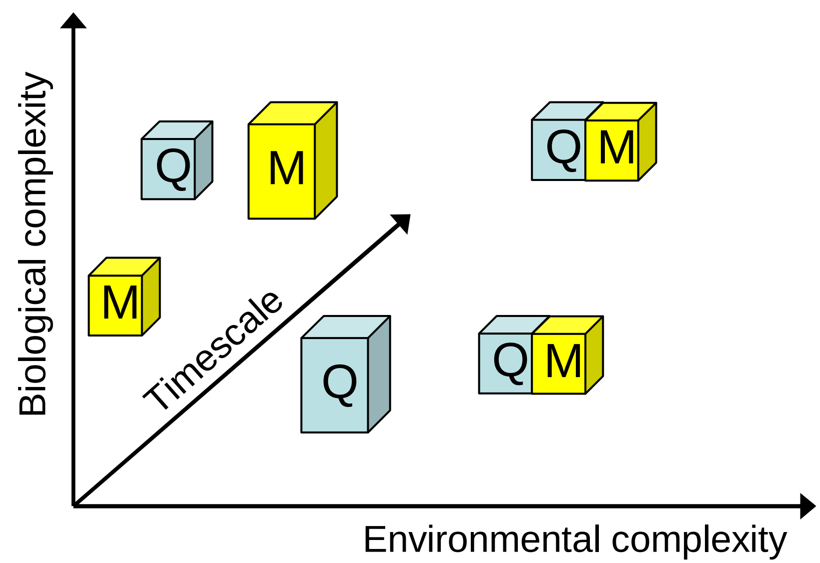
# Discussion points

- Science questions where adaptive models might help:
  - How did the systems we observe today come to exist? Why are they stable? How will they change over time?
  - In which ecosystems and on what timescales are adaptive processes an important part of biogeochemical cycles?
  - How will modern ecosystems respond to rapid environmental change?
  - Is evolution of the coupled life-environment system predictable?
  - Can we use genomic data to link the tree of life to Earth history?

- Methodological questions:
  - What contribution can modelling make? What are the limits of modelling?
  - Which modelling approaches are equivalent?
  - Is adaptive modelling best used to provide better parameterisations or to learn about the processes themselves?
  - Do you need to model everything to model anything?
  - How can we use genomic data to improve biogeochemical models?
  - Descriptive vs predictive modelling

# Fitting modelling approaches to scientific questions/hypotheses

- Timescale
- Spatial scale
- Environmental complexity
- Biological complexity
- Levels in the biological hierarchy
- Marine/terrestrial
- Formalism



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# Evolutionary modelling of life-environment interaction


**Hywel T.P. Williams**
University of East Anglia, UK



"Modelling evolutionary and ecological processes in biogeochemical cycles", UEA, February 15th 2010.

The Leverhulme Trust

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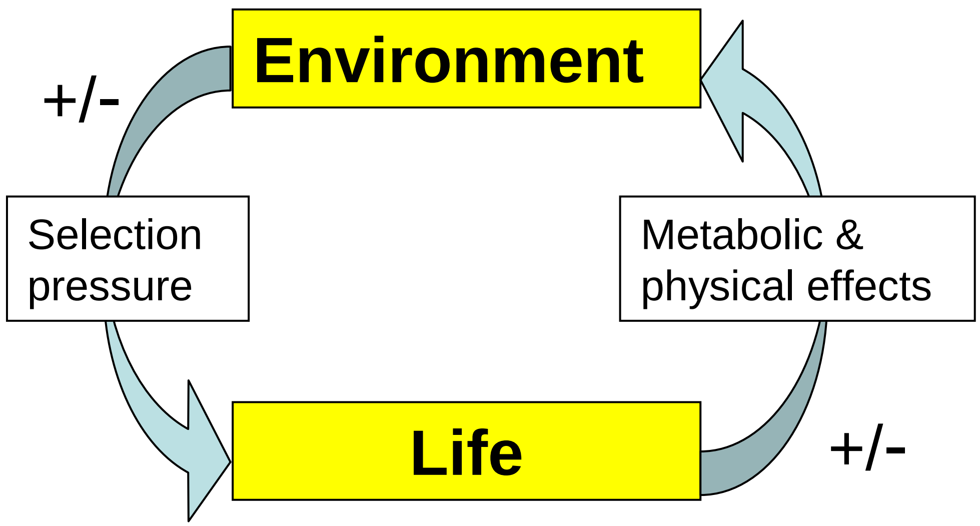
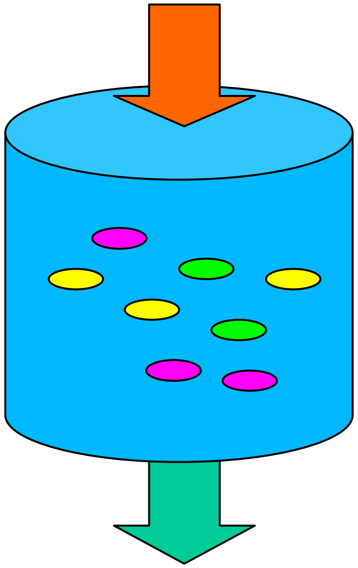
NATURAL ENVIRONMENT RESEARCH COUNCIL

# Feedbacks between life and its physical environment are inevitable and can create complex dynamics




- How will the coupled system evolve over time?
- How to handle complex dynamics?

# The Flask model



Individual-based evolutionary simulation model.

Continuous culture of “microbes” suspended in liquid medium.

Flow of liquid through flask supplies nutrients and alters abiotic environment (e.g., pH, temperature, salinity, etc.).

Microbial metabolism affects -- and is affected by – abiotic environment.

Conceptual model / thought experiment - qualitative predictions.

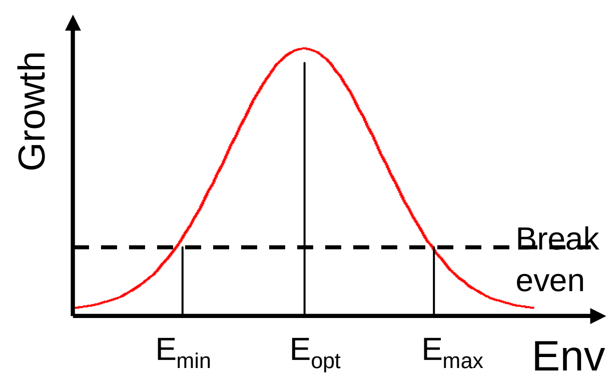
# Brief model description

- Individual-based evolutionary simulation
  - Model individuals = many real individuals
  - Evolution in response to selection pressures emergent from ecological processes

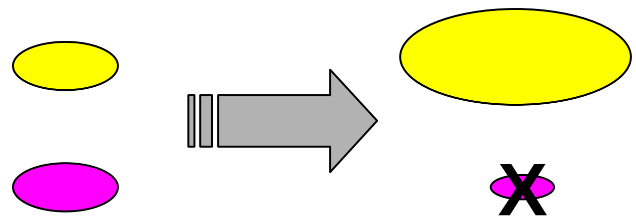
$$
\begin{array}{c} 0010110 \\ \downarrow \\ (\alpha, \beta, \ldots) \end{array}
$$

- Genotype → Metabolic traits
  - Nutrient consumption/release pattern
  - Optimum environment for growth
  - By-product effect on environment

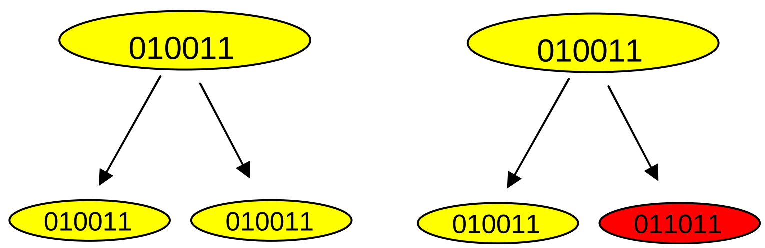
- Metabolism ↔ Environment
  - Growth by converting nutrients to biomass
  - Environmental conditions affect growth rate
  - Metabolic by-products affect abiotic environment

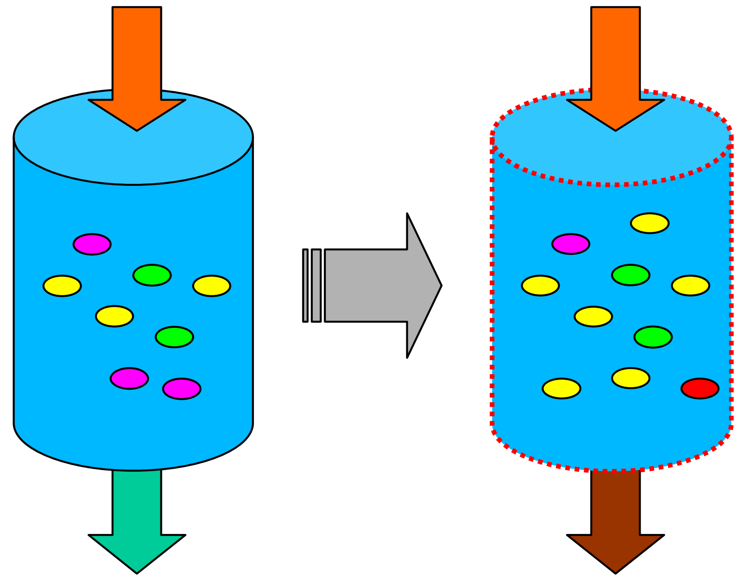


# Flask ecosystem processes



Microbes that are well-suited to the environment grow and reproduce. Unsuccessful microbes starve and die. Mutation may occur during reproduction, introducing new species to the system.



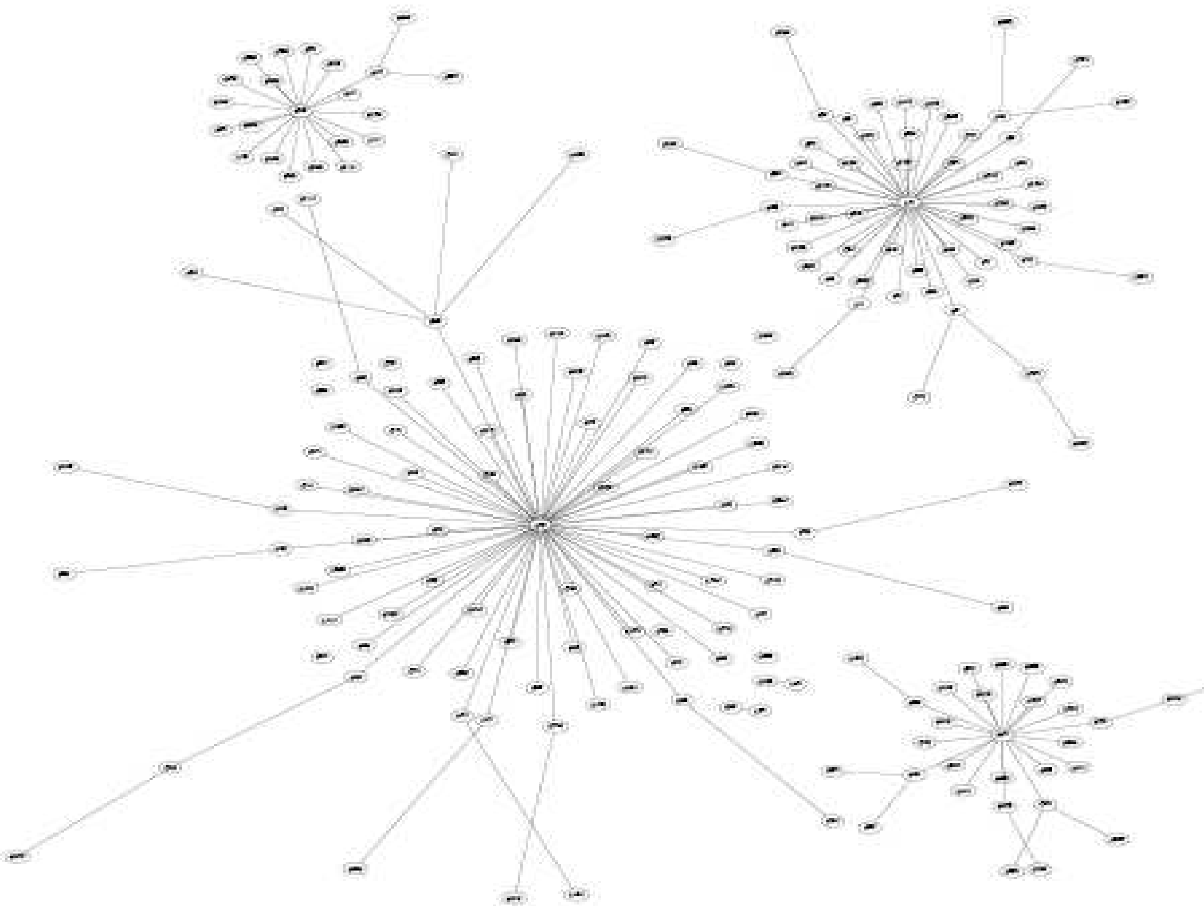



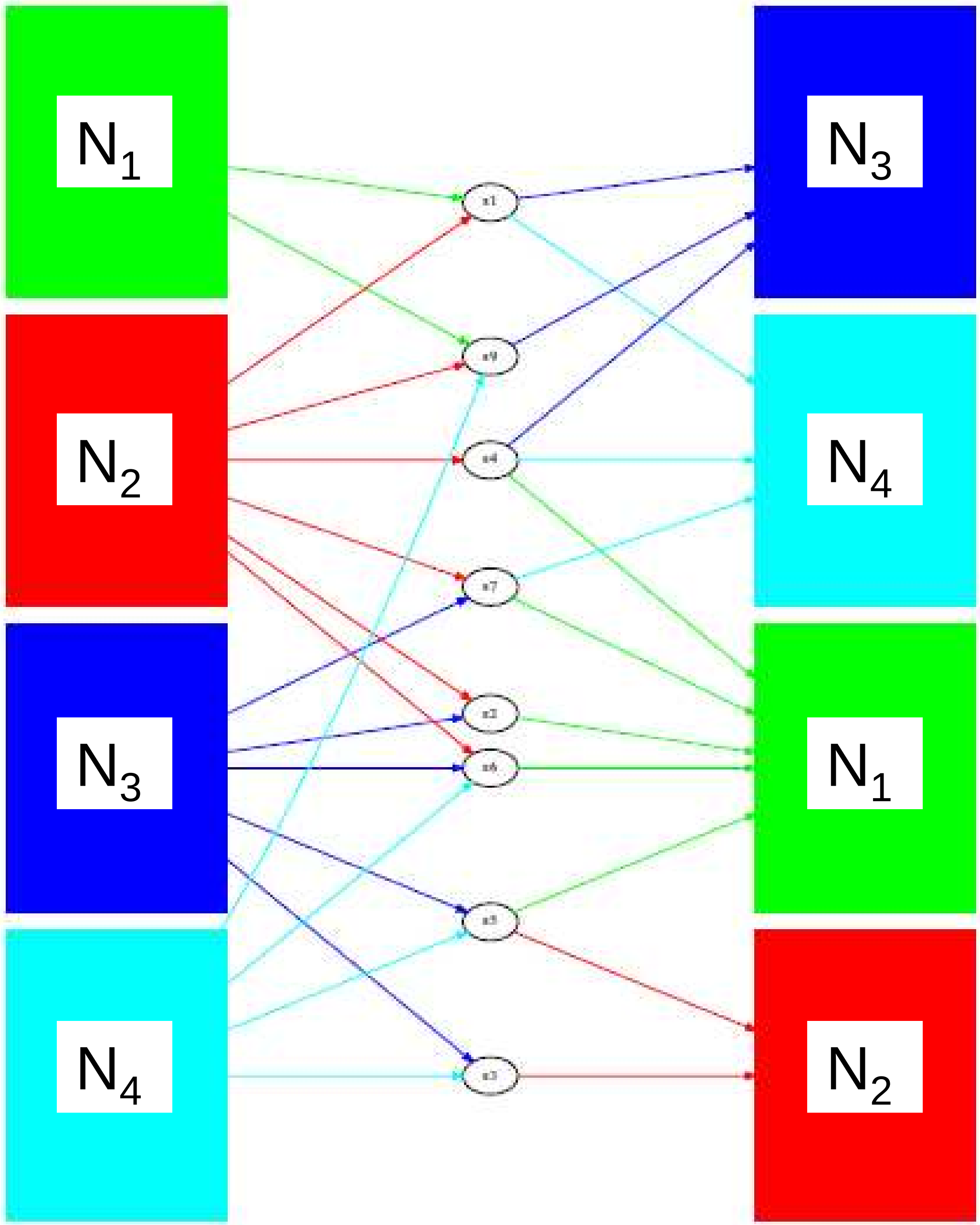
Over time ecological and evolutionary processes change the composition of the community. The combined metabolic activity of the community alters the state of the environment.

Williams & Lenton (2007) *Oikos* 116 (7), 1079-1253.

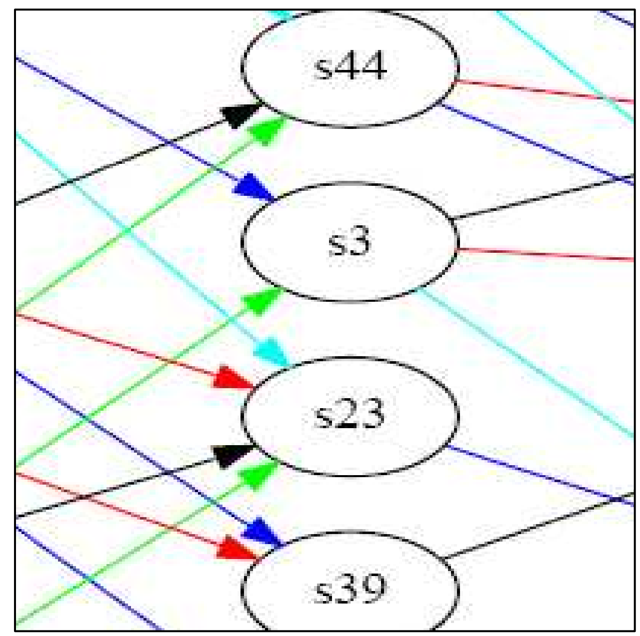
# Adaptive radiation

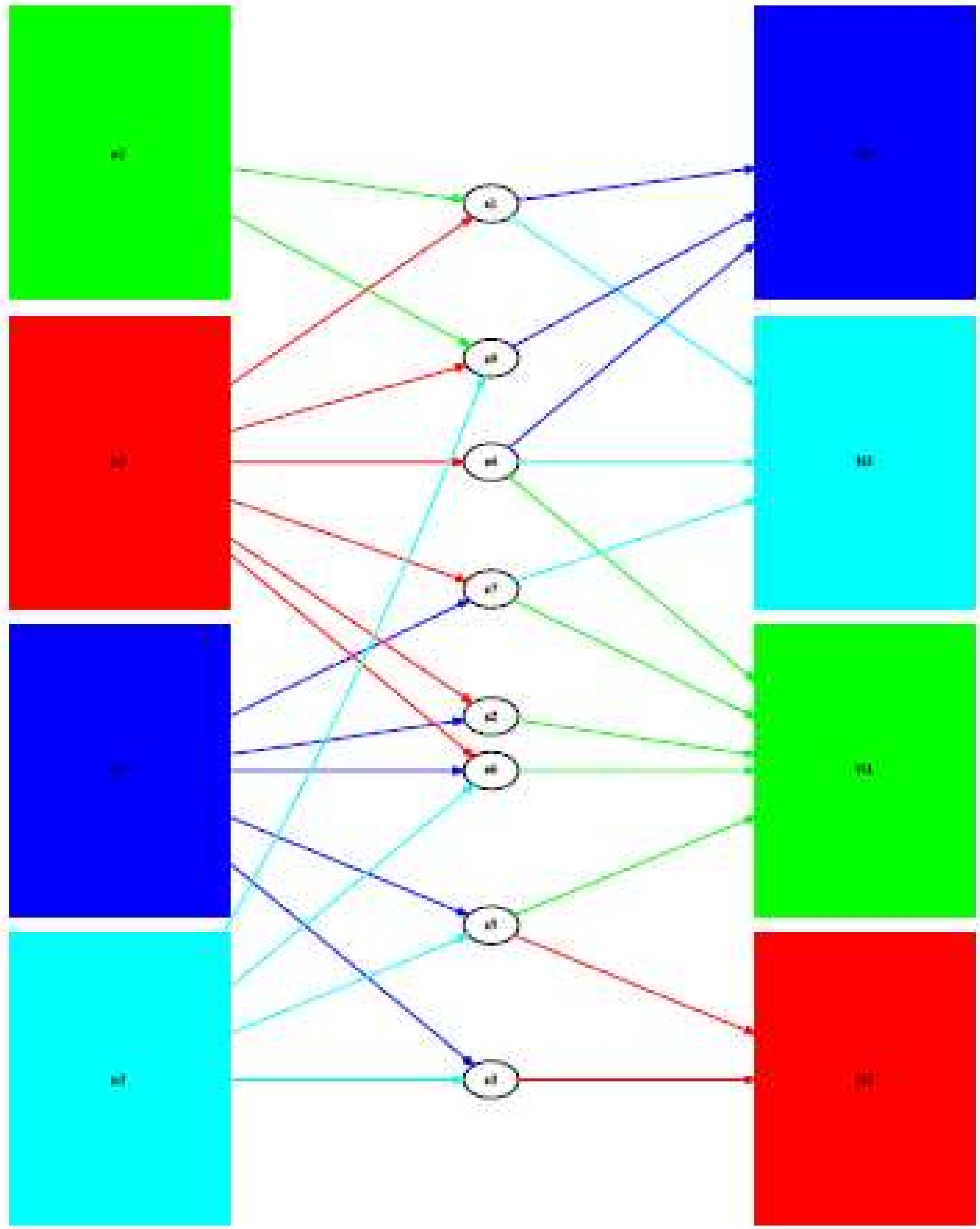
# Divergence of differentiated ecotypes






Cross-feeding network supports nutrient recycling





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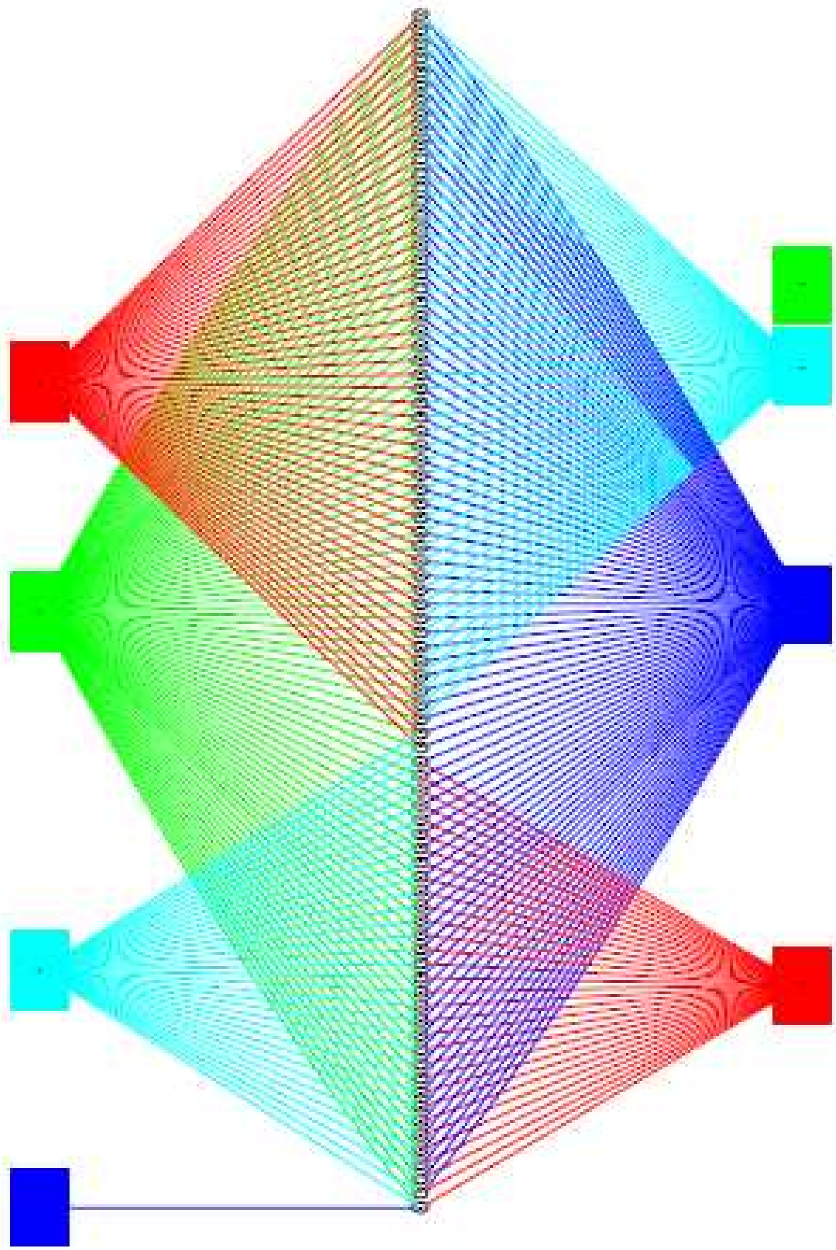
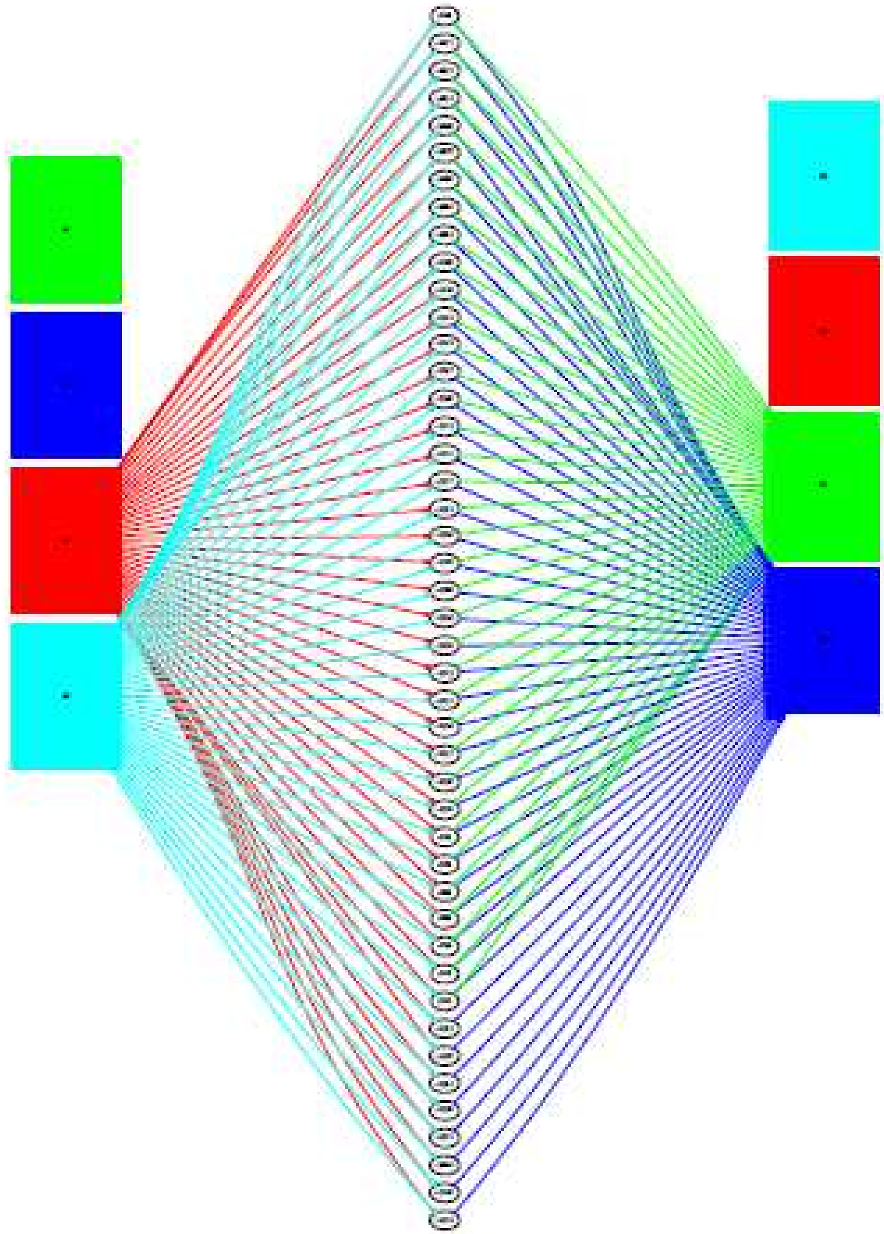
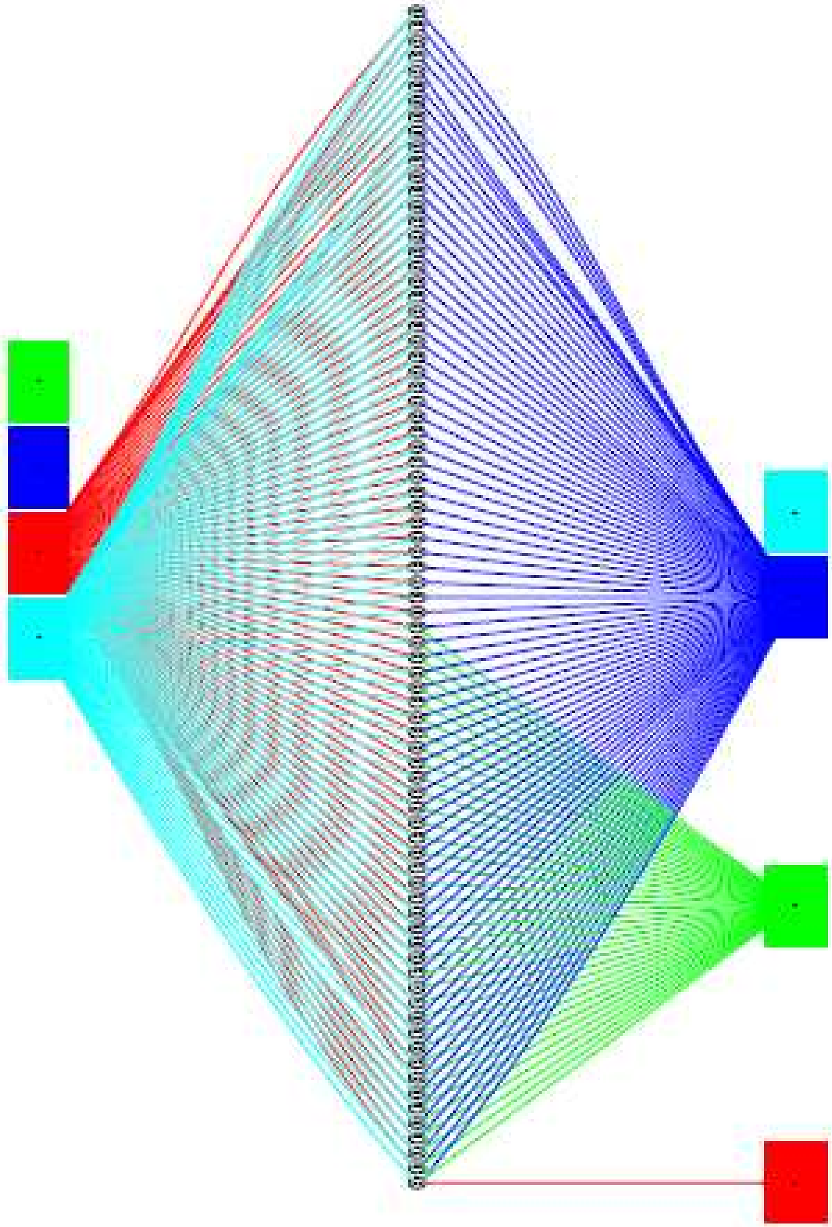


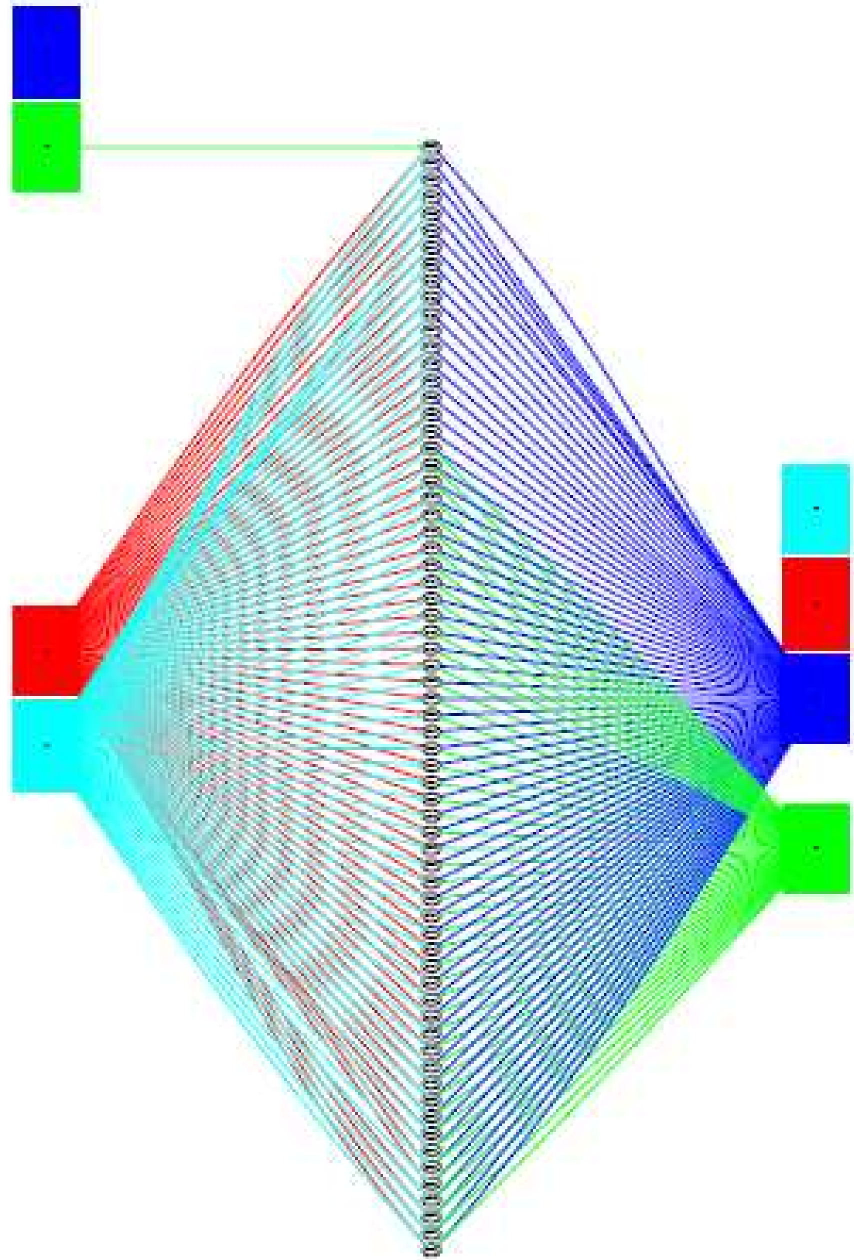
$t = 5000$



$t = 10000$



$t = 15000$



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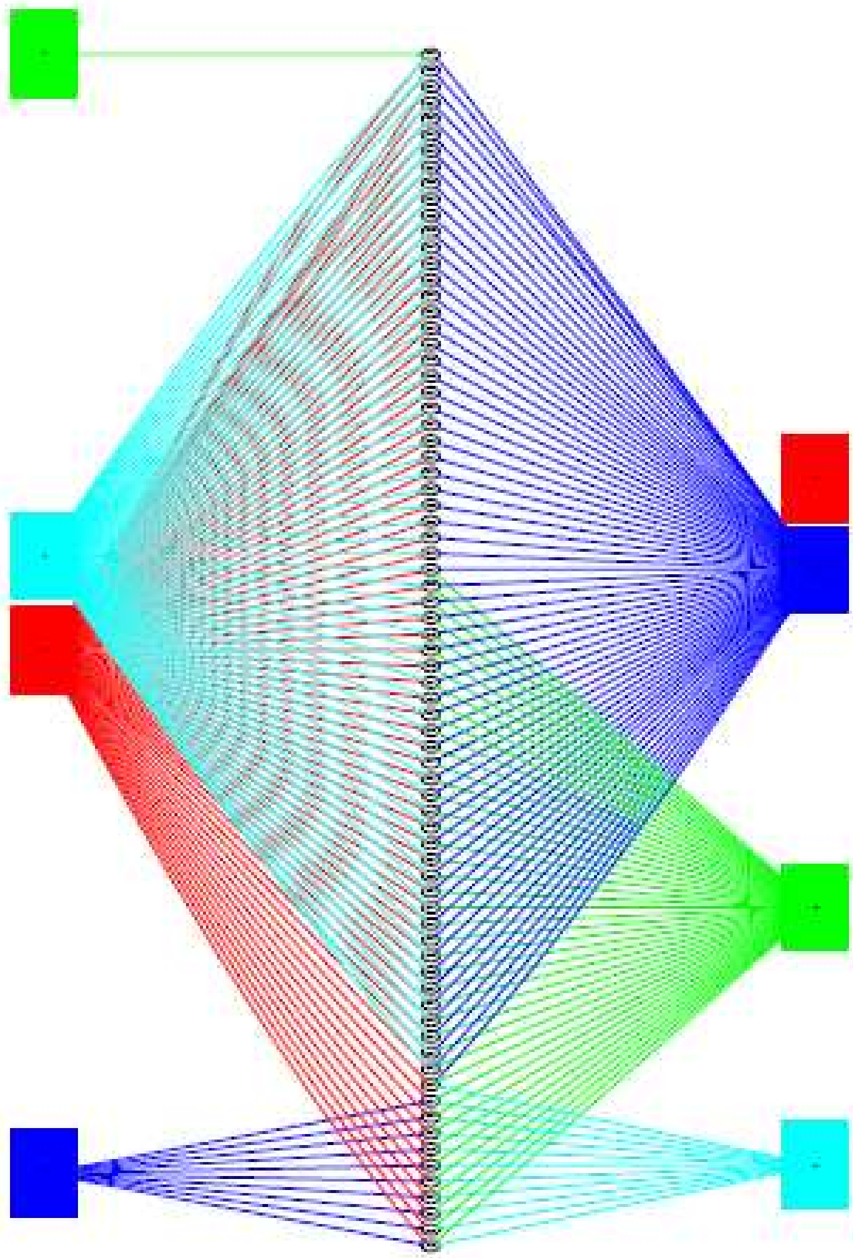

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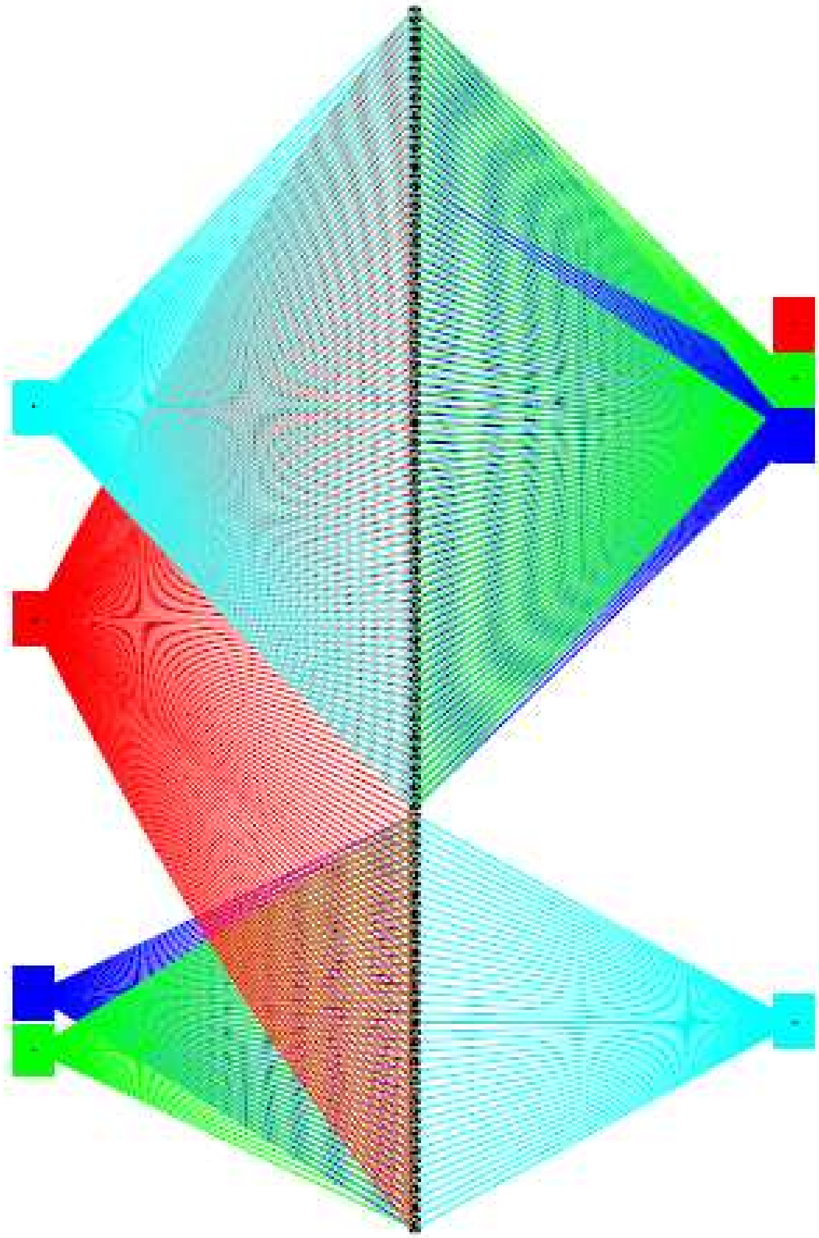

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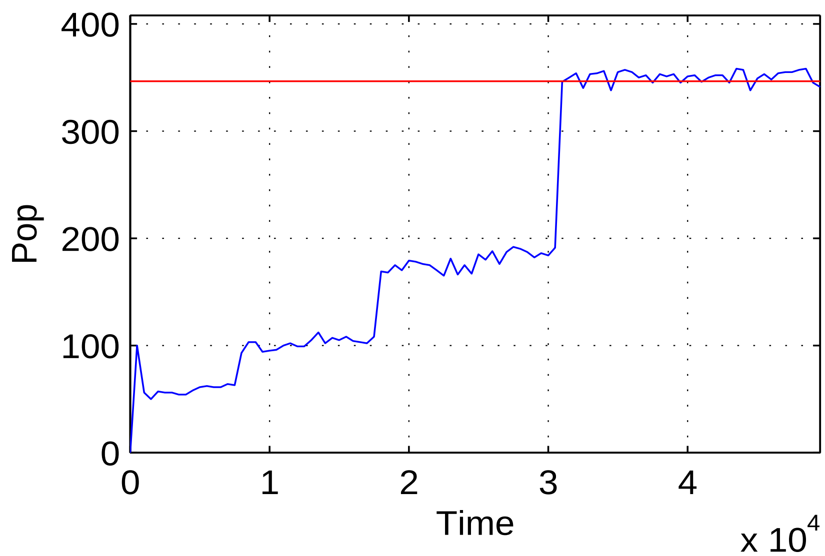
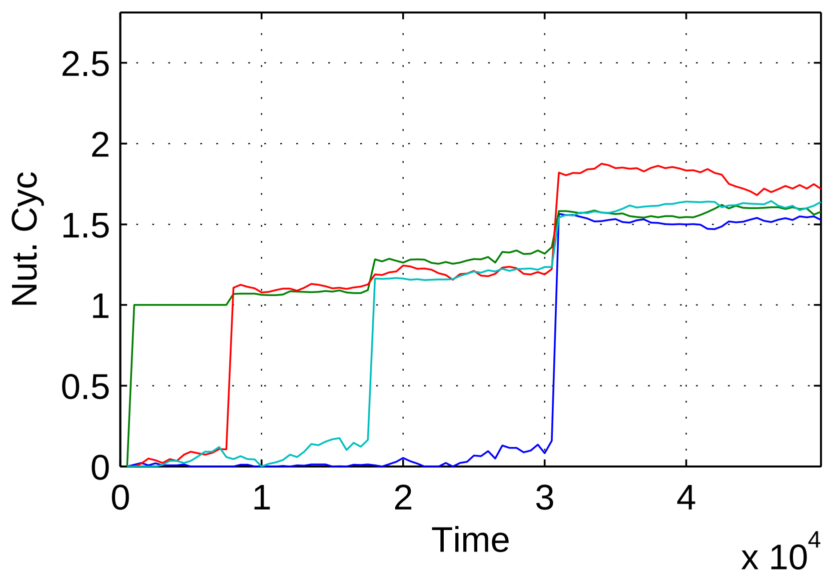


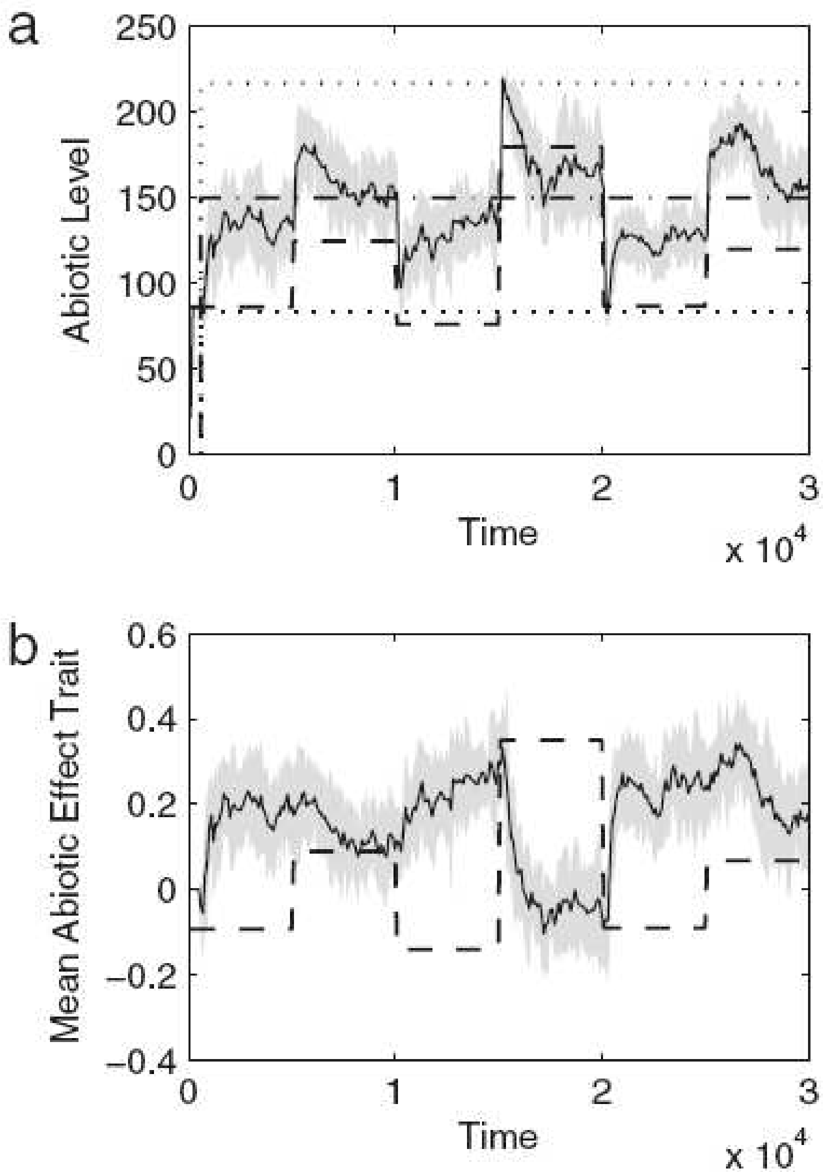



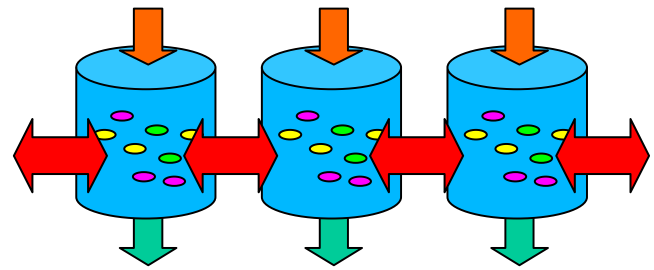

Nutrient recycling supports increased productivity and is a robust emergent feature of flask ecosystems.

Efficiency is increased by natural selection.

Williams & Lenton (2007) *Oikos* 116 (7), 1079-1253.

# Environmental regulation in spatial model



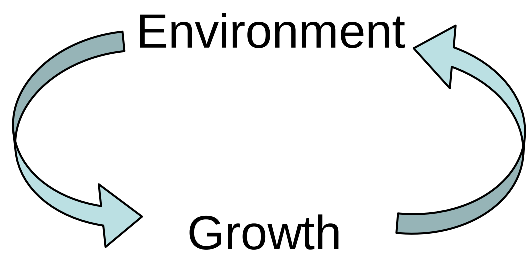



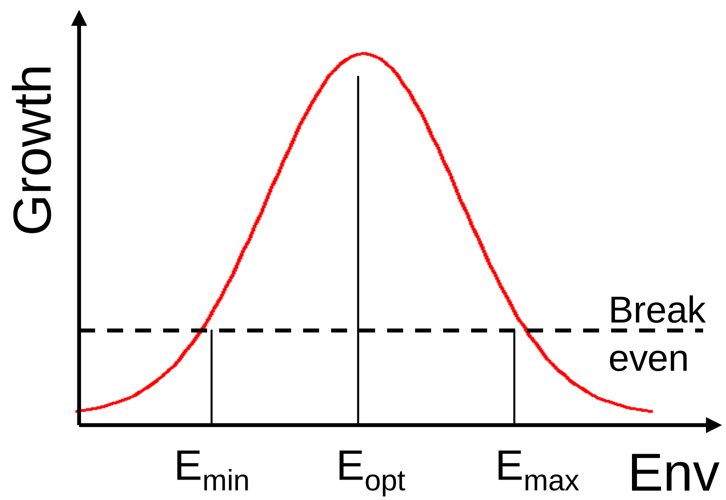
- ‘Niche-constructing’ action of biota maintains environment in habitable state and counteracts perturbations

- Change in mean value of environment-altering trait correlated with environmental change

Williams & Lenton (2008)
*PNAS* 105 (30), 10432-10437.

# Regulatory feedback mechanism

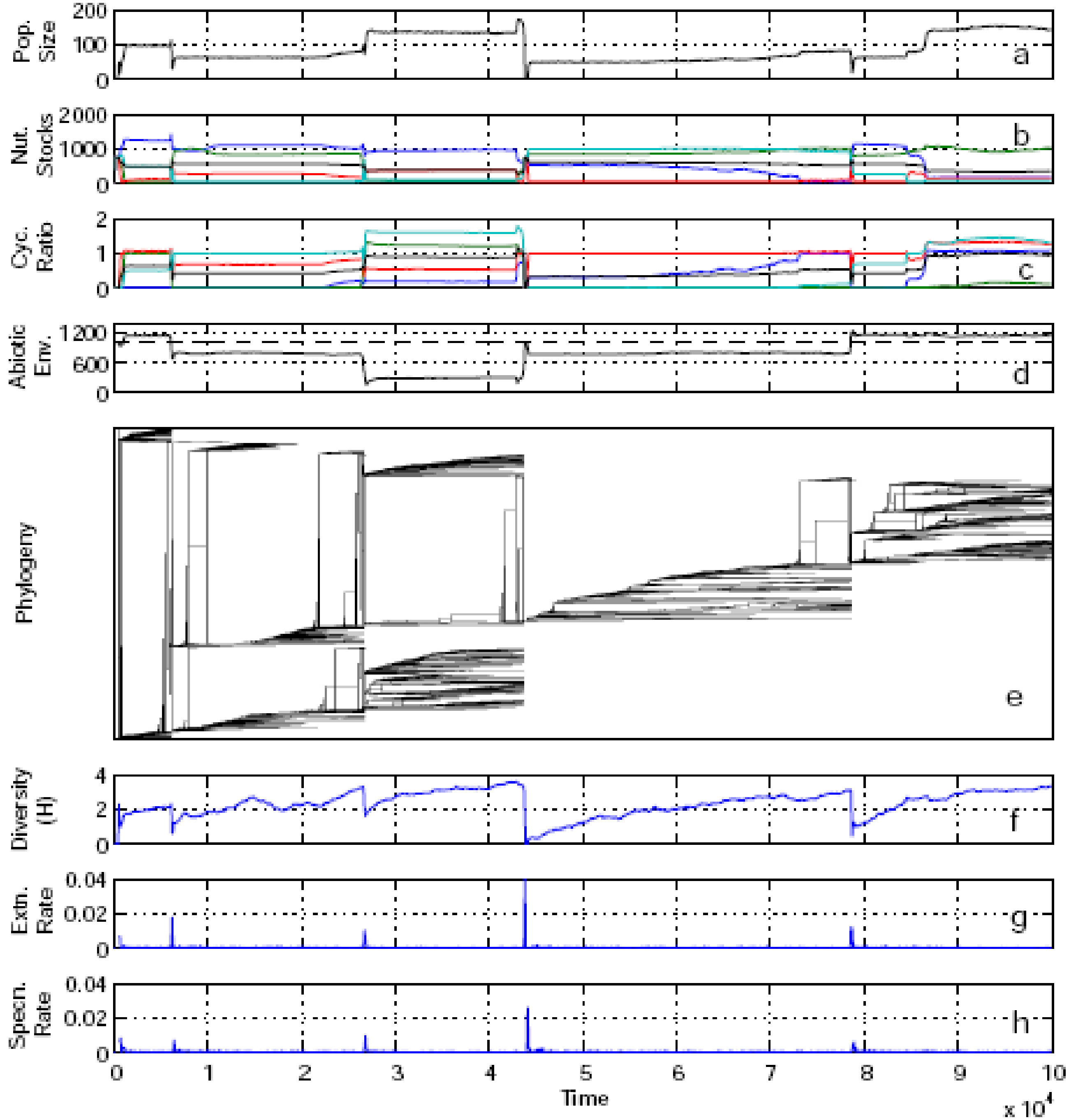



Extreme environments constrain growth and create selection pressure for environment-improving traits

- Local communities that improve their environment grow rapidly
- Local communities that degrade their environment starve
- Big communities are better colonisers
- Environment-improving communities spread rapidly across system

Williams & Lenton (2008) *PNAS* 105 (30), 10432-10437.

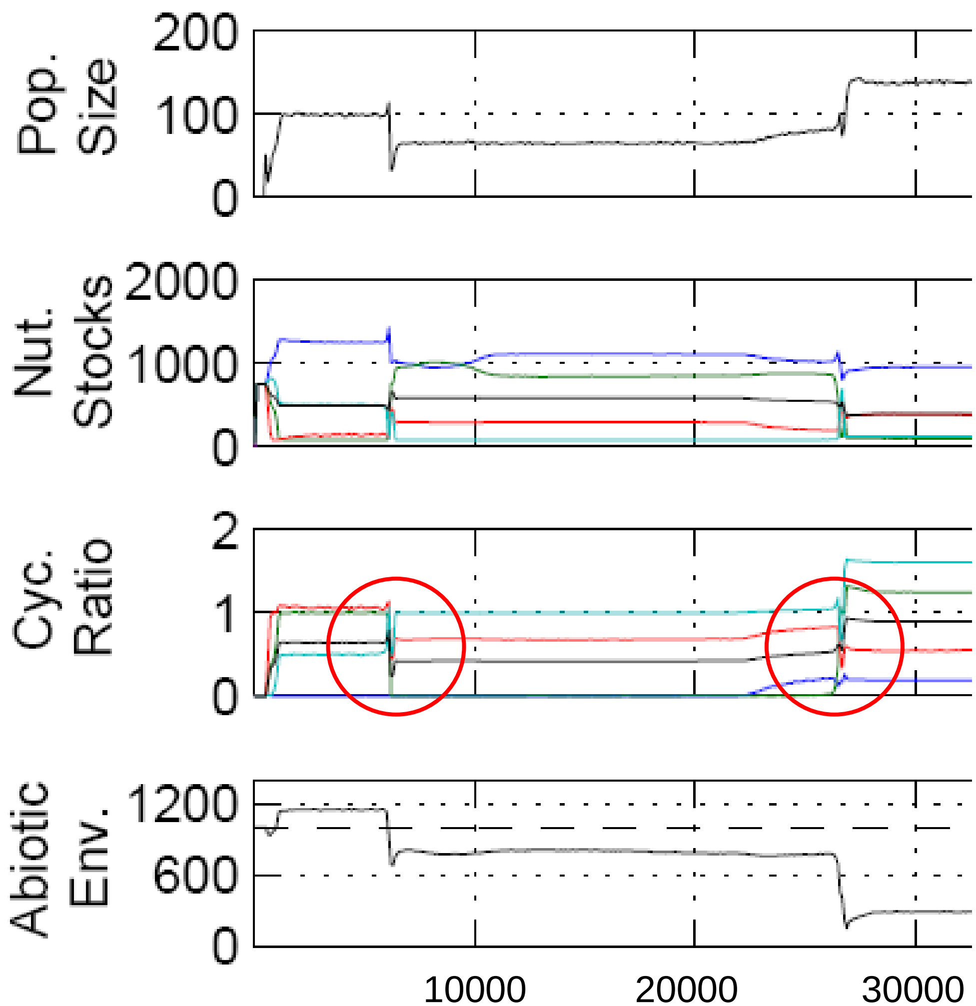



# Evolutionary regime shifts punctuate periods of stability

Unforced spatial model shows punctuational mode. Regulating feedbacks give periods of stability with increasing diversity. Infrequent system-wide transitions to new steady state are coupled to mass extinction events.

Williams & Lenton (in press).

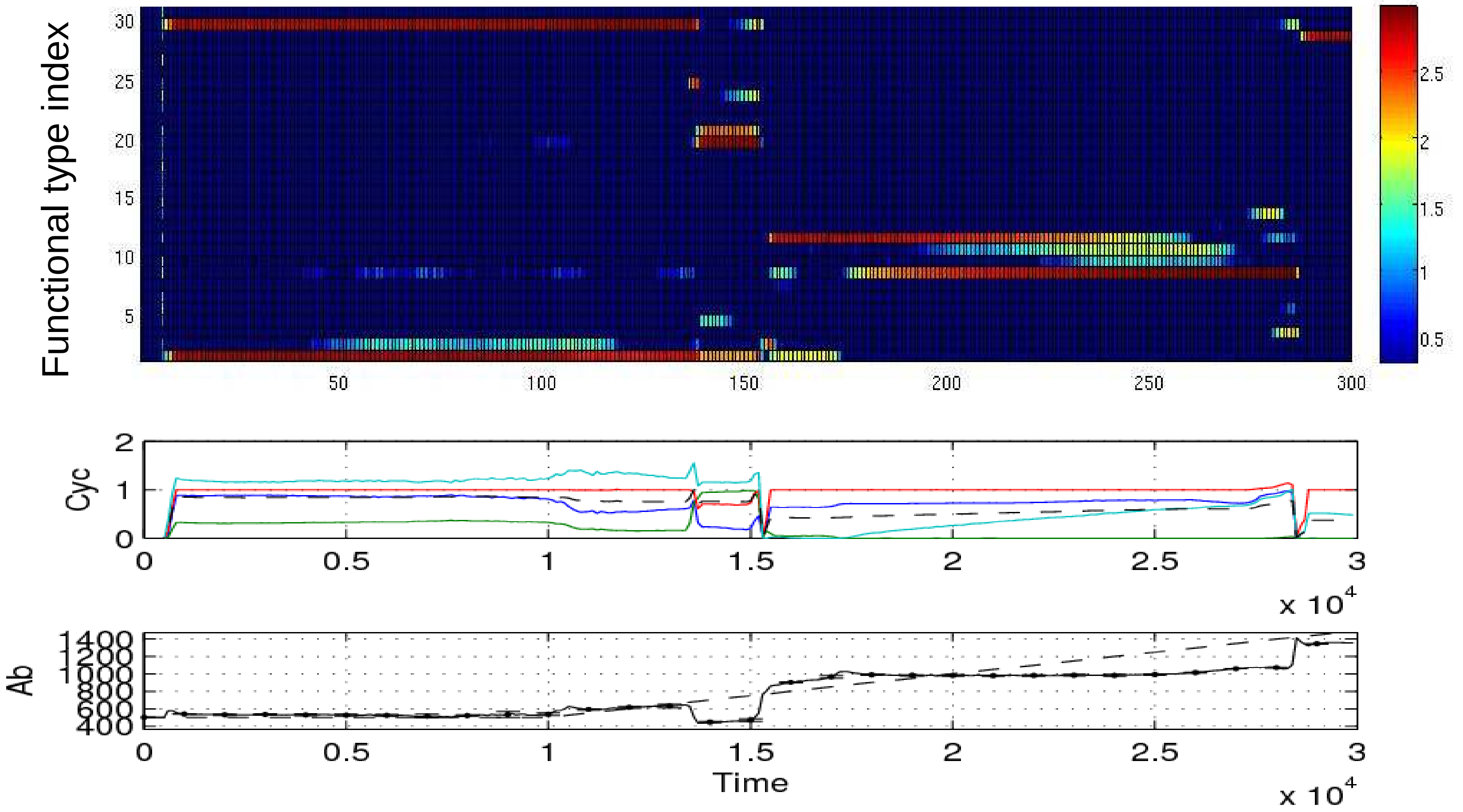
# Evolutionary regime shifts are triggered by adaptations allowing access to unutilised resources




- Metabolic evolution gives access to an unutilised resource
- Rapid growth creates sudden environmental change, driving many incumbent species extinct
- Disruption to nutrient cycling triggers further extinctions, leading to further environmental change…
- …leading ultimately to ecosystem collapse.

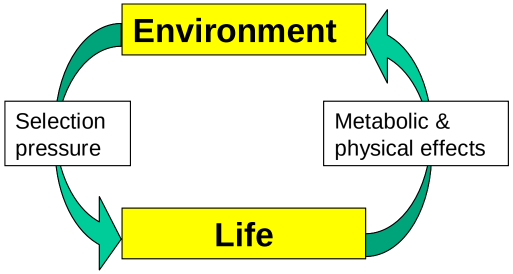
Williams & Lenton (in press) *Oikos.*

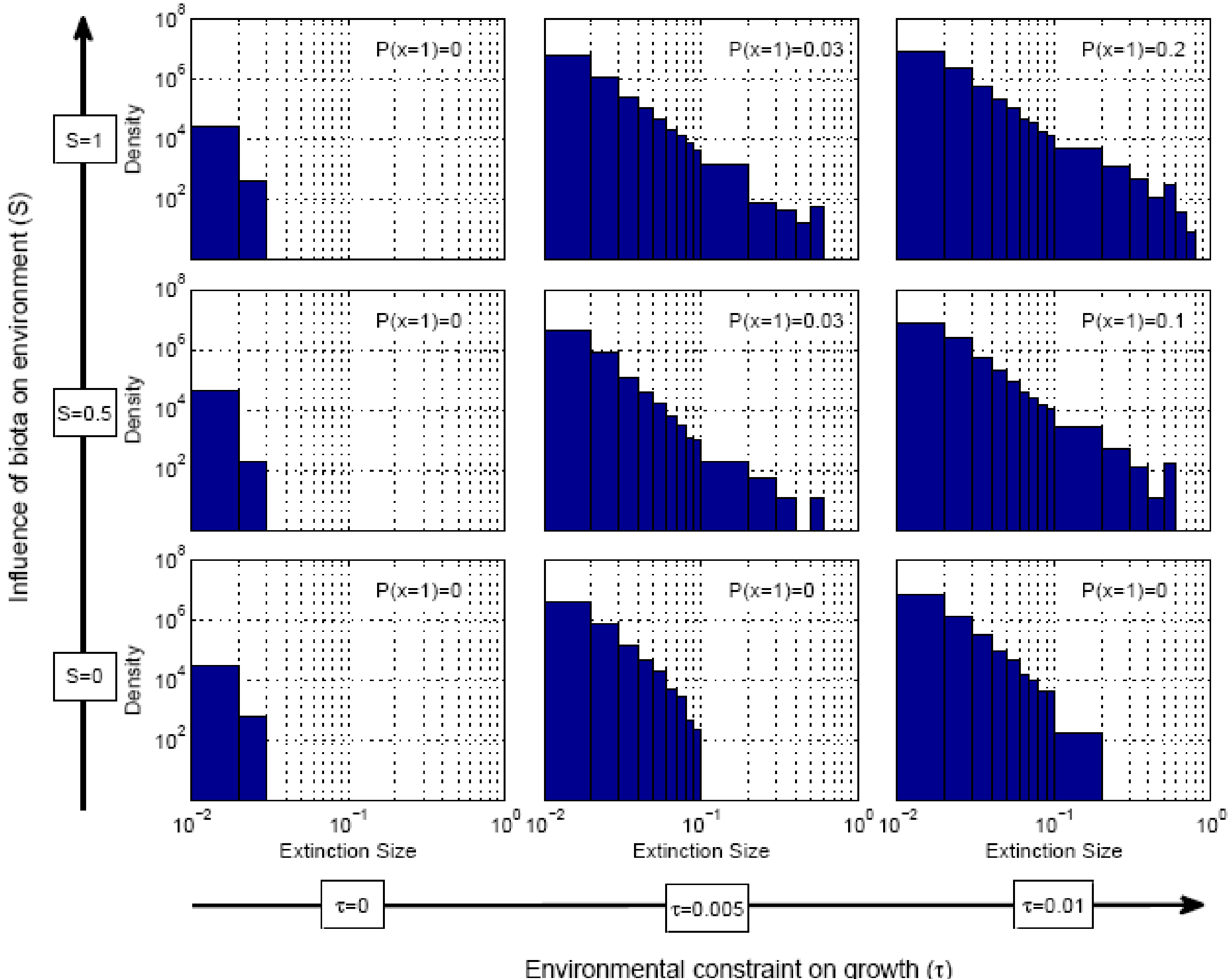
# System may recover to a different steady state




- Extinction events create opportunity for new ecological structure to emerge. "Ecosystem character" change is correlated with state change.

# Life-environment feedbacks create large extinction events



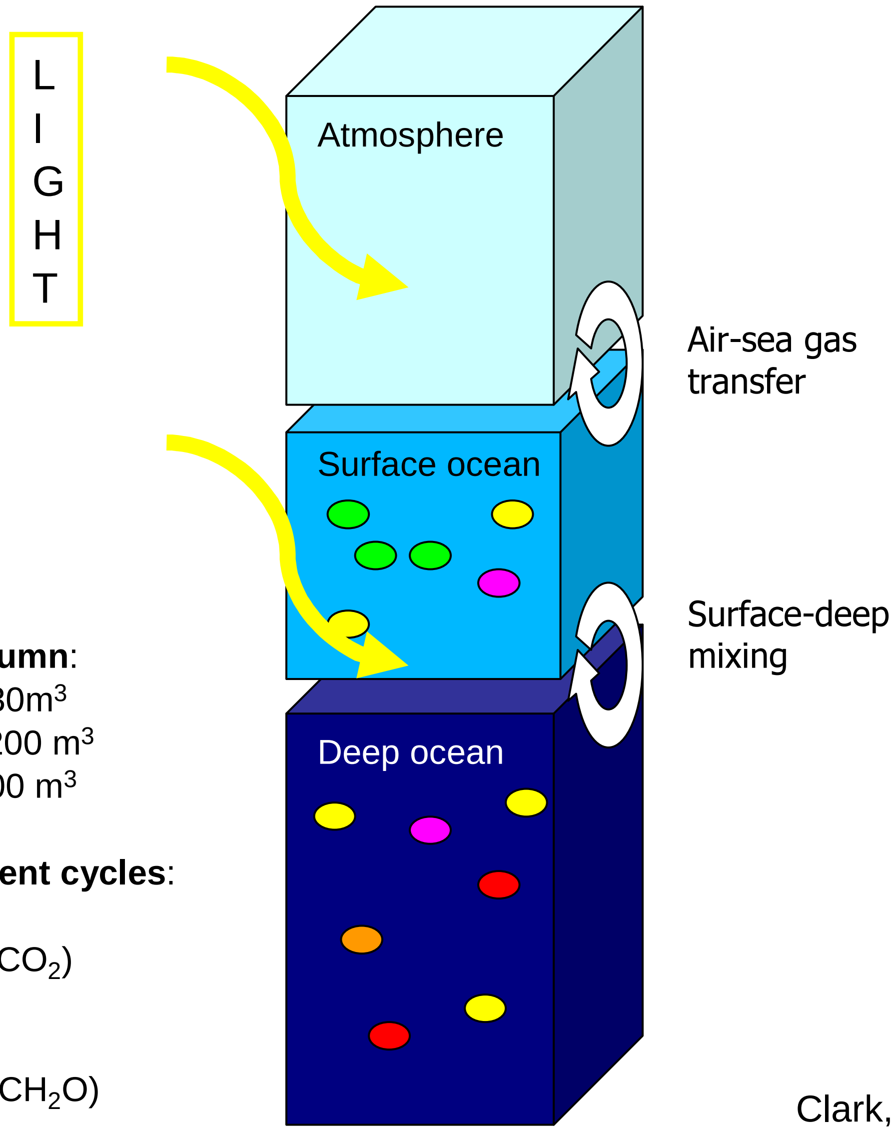

Williams & Lenton (in press) *Oikos.*

# An inconvenient observation…

# Summary

- Feedbacks between evolution and environmental change are important
- **Theoretical** results:
  - Natural selection on metabolic traits robustly creates efficient nutrient cycling loops
  - Metacommunity effects lead to biotic regulation of the environment
  - Metabolic evolution can drive “evolutionary regime shifts” and mass extinctions
- Critique of model
  - Evolution by natural selection in response to emergent selection pressures
  - Life-environment feedbacks implemented via constraints on growth and niche construction
  - Good for qualitative predictions, hypothesis generation
  - But very (too?) abstract, with many assumptions, lack of real chemistry

# ADAM: the ADaptive Archean Model




**1m² vertical column**:
Atmosphere: 8430m³
Surface ocean: 200 m³
Deep ocean: 3500 m³

**Restricted nutrient cycles**:
Light
Carbon dioxide ($CO_2$)
Water ($H_2O$)
Oxygen($O_2$)
Formaldehyde* ($CH_2O$)
Methane ($CH_4$)

**Photoautotroph**
$CO_2 + H_2O + \text{light} \rightarrow CH_2O + O_2$
$CH_2O + O_2 \rightarrow CO_2 + H_2O$

**Heterotroph**
$CH_2O \rightarrow CH_2O$
$CH_2O + O_2 \rightarrow CO_2 + H_2O$

**Methanotroph**
$CH_4 + O_2 \rightarrow CH_2O + H_2O$
$CH_2O + O_2 \rightarrow CO_2 + H_2O$

**Methanogen***
$CH_2O \rightarrow CH_2O$
$2CH_2O \rightarrow CH_4 + CO_2$

Clark, Williams, Lenton, Watson (submitted)

# Appendix 1: The Maths

# Flask environment

- Well-mixed, homogeneous liquid medium
- Simple abstract chemistry
- Steady influxes/outfluxes of N nutrients, A abiotic factors
- State a function of flux and biotic activity
- Reaches steady state in absence of biota

$$\frac{dv_i}{dt} = I_i - O_i v_i + E_i$$

$v_i$ = level of state variable $i$

$I$ = influx (parameter)

$O$ = outflux (parameter)

$E$ = biotic activity

# Microbe = (fixed genotype, variable biomass)

## Genotype:

Specifies metabolic reaction:

- Nutrient consumption ratio
- Nutrient excretion ratio
- Preferred abiotic environment (in which metabolic rate is maximised)
- By-product effect on abiotic environment

Encoded as 2(N+A) values from [-1.0,1.0]

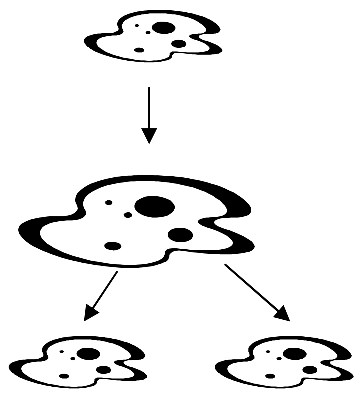
- Gives $21^{2(N+A)}$ different genotypes
- Simple developmental mapping

## Death:

- If biomass drops below threshold
- At random with low probability
- Biomass washed out of environment

## Reproduction:

- Metabolism increases biomass
- Reproduction by splitting when biomass reaches threshold
- Offspring is clone of parent with half parental biomass
- Mutation may occur (by copying error with low probability)
- No crossover/conjugation



# Metabolism

- Microbes consume nutrients in genetically specified ratios
- Consumed nutrients converted to biomass with fixed efficiency
- Fixed maintenance cost per timestep (thermodynamic inefficiency / heat loss)

$$\frac{dB}{dt} = \delta \mu_{\max} \lambda S - \gamma$$

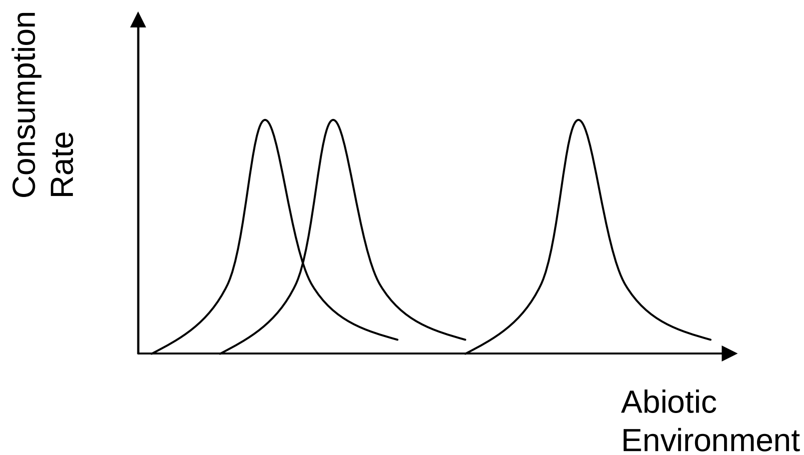
| | | |
|---|---|---|
| $B$ | = | individual biomass |
| $\delta$ | = | metabolic efficiency (global parameter) |
| $\mu_{\max}$ | = | max consumption rate (global parameter) |
| $\lambda$ | = | scaling for nutrient limitation |
| $S$ | = | environmental fit |
| $\gamma$ | = | maintenance cost (global parameter) |

# Environment affects metabolism

- Nutrient consumption limited by availability and by abiotic conditions
- Each microbe has genetically specified preferred conditions in which metabolic rate is maximised
- Consumption rate falls with distance from optimum

$$S = e^{-T\rho^2}$$

$$\rho = \sqrt{\sum_i (a_i - a_{opt})^2}$$




| | | |
|---|---|---|
| $S$ | = | environmental fit |
| $T$ | = | level of abiotic influence |
| $\rho$ | = | distance of environment from ideal |
| $a_i$ | = | level of abiotic factor $i$ |
| $a_{opt}$ | = | preferred level of $a_i$ |

# Metabolism affects environment

- Metabolism affects environment by:
  - Removing / adding nutrients
  - Altering levels of abiotic factors
- For every unit of biomass created, there is a by-product influence on abiotic factors
  - Genetically specified
  - Can be positive or negative
- When microbes die their stored biomass is washed out of the flask.

$$E_n = \sum_{living} (-cons + prod + dtr)$$

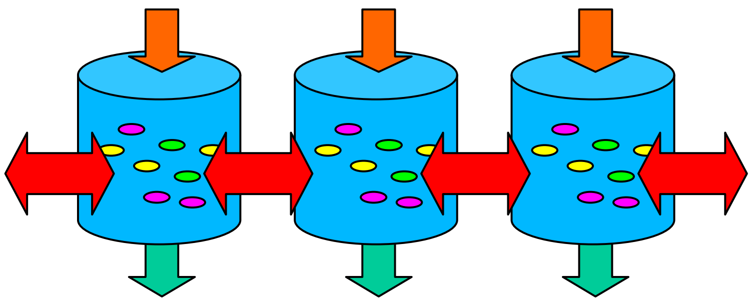
$$E_a = \sum_{living} \frac{dB}{dt} \cdot effect$$

$E_n$ = population effect on nutrients

$E_a$ = population effect on abiotic factors

$B$ = biomass

# Spatial Flask model



$$\Delta v_i = -R v_i + \frac{R}{2} v_{i-1} + \frac{R}{2} v_{i+1}$$

$$\Delta M_i = -R M_i + \frac{R}{2} M_{i-1} + \frac{R}{2} M_{i+1}$$

$M_i$ = population size in flask $i$

$v_i$ = level of environmental variable in flask $i$

$R$ = diffusion rate

- Continuous diffusive transfer between neighbouring flasks carries microbes and material
- Transport of material reduces environmental gradients
- Transport of microbes reduces density gradients and carries genetic information