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United Nations
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WORKSHOP ON QUANTITATIVE ECOLOGY
9 to 20 May 2005

Maximum entropy production and ecosystems

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These are preliminary lecture notes, intended only for distribution to participants.

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Maximum entropy production and ecosystems

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Workshop on Quantitative Ecology, Abdus Salam ICTP Trieste, 9-20 May 2005

- Natural selection and diversity in physics
- MaxEnt and maximum entropy production
- Natural selection and diversity in ecology

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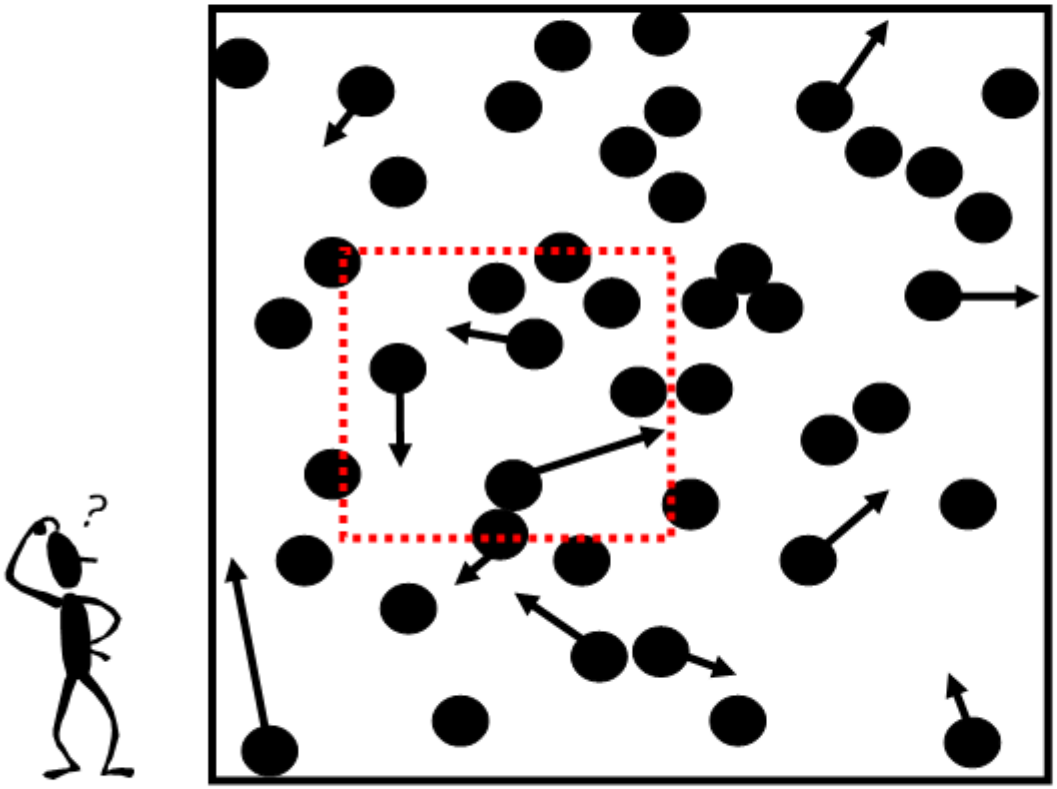
Why is there such a diversity of molecular positions and velocities ?



$\langle N_s \rangle$, $\langle E_s \rangle$, V_s fixed

N, E, V fixed

Macroscopic description *A*

spatial distribution of molecules in box

Microscopic description *i*

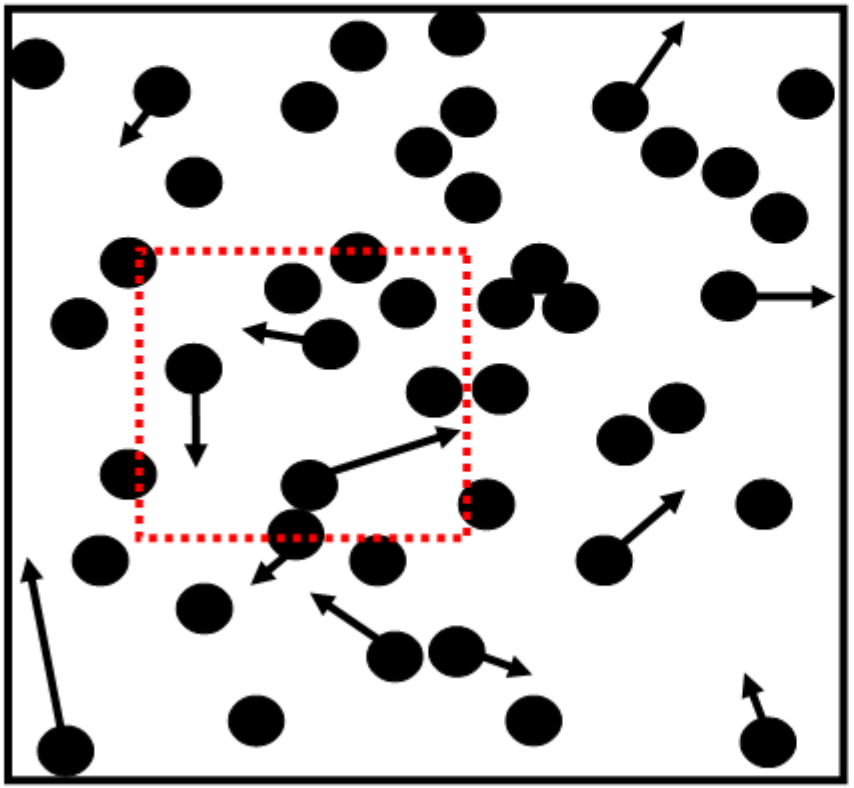
individual positions of every molecule

S_A = entropy of *A*

W_A = number of ways *A* can be realized microscopically

Ludwig Boltzmann
(1844 - 1906)

Diverse (spread-out) distributions are more probable (W is bigger)



$\langle N_s \rangle$, $\langle E_s \rangle$, V_s fixed

N, E, V fixed

- Natural selection and diversity in physics
- MaxEnt and maximum entropy production
- Natural selection and diversity in ecology

Summary

- Under given constraints (N, E, V), nature selects the most diverse (spread-out) distribution simply because it is the most probable one (max S = max log$W$)

- The maximum diversity (max S) attainable under given constraints increases as those constraints are removed

- Natural selection and diversity in physics
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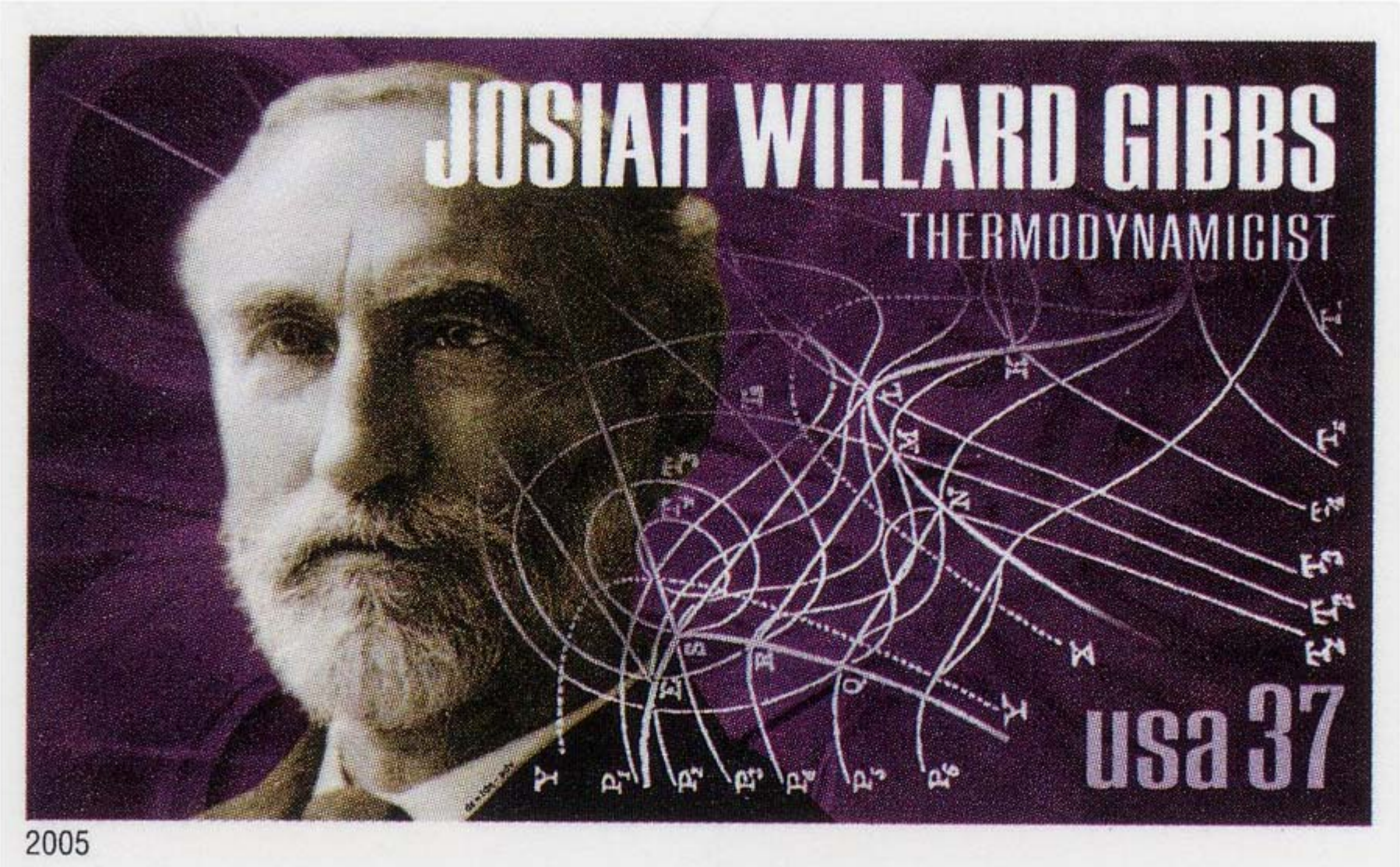


(1839 - 1903)

The Gibbs algorithm (MaxEnt) ...

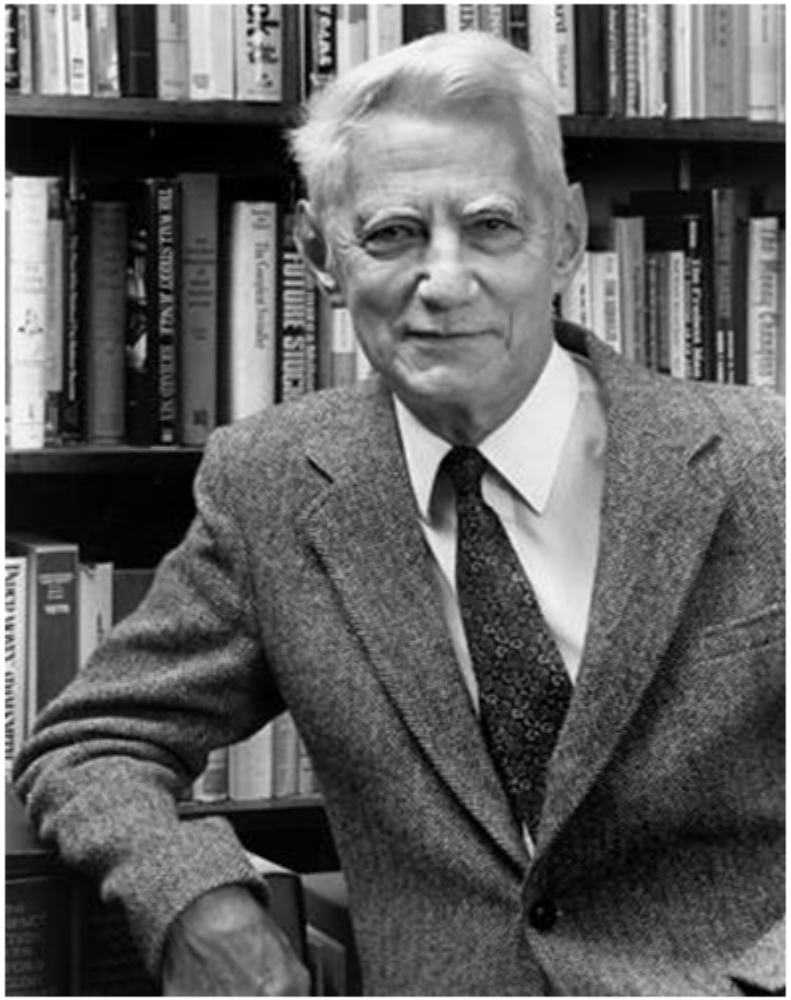
p_i : probability that the system is in microstate i
Given $\langle E \rangle$, what is p_i ?

Maximise : $H = -\Sigma_i \, p_i \log p_i$

Subject to : $\Sigma_i \, p_i E_i = \langle E \rangle$ (given energy)
$\Sigma_i \, p_i = 1$ (normalisation)

Solution : $$p_i = \frac{1}{Z} \exp\left(-\frac{E_i}{kT}\right)$$ (= Boltzmann)

… it worked but what did it mean ?



Claude Shannon
(1916 - 2001)

$$H = -\Sigma_i \, p_i \log p_i$$

- H is a measure of the missing information about outcomes i
- (H = uncertainty)

- H is larger if p_i is more spread-out
- (H = diversity)

- $H \approx \log W$ where W is the number of outcomes i with $p_i > 0$
- ($H \approx$ Boltzmann entropy S)

$$\max H = -\Sigma_i \, p_i \log p_i$$

- MaxEnt is a completely general algorithm for contructing p_i from known constraints C

- it works because it gives the most probable distribution under C (Gibbs ~ Boltzmann)

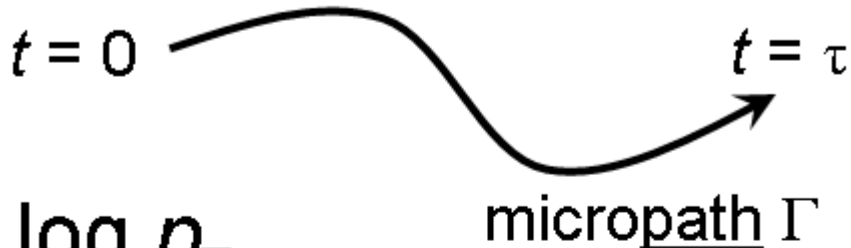
- it predicts the behaviour that is <u>reproducibly selected</u> under C

- it can be applied to non-equilibrium systems (e.g. climate, ecosystems ...)

Edwin Jaynes (1922 - 1998)

MaxEnt for non-equilibrium systems

J Phys A **36**, 631-641 (2003)
J Phys A **38**, L371-L381 (2005)



Maximise : $H_{\text{path}} = -\Sigma_\Gamma\, p_\Gamma \log p_\Gamma$

Subject to :

$\Sigma_\Gamma\, p_\Gamma J_\Gamma = \langle J \rangle$ (given energy flux)

$\Sigma_\Gamma\, p_\Gamma = 1$ (normalisation)

$\partial \rho_\Gamma / \partial t = -\nabla \cdot J_\Gamma$ (local continuity)

Solution :

$$p_\Gamma = \frac{1}{Z_{\text{path}}} \exp\left(\underbrace{\frac{\tau}{2k} \int_V J_\Gamma \nabla \left(\frac{1}{T} \right)}_{\text{entropy production } (\mathrm{EP}_\Gamma)} \right)$$

Two fundamental implications of the MaxEnt solution $p_\Gamma \propto \exp(\tau EP_\Gamma/2k)$

- *Maximum entropy production*
- *(or, sometimes, maximum flux) :*

The average entropy production $\langle EP \rangle$ (or, sometimes the average flux $\langle F \rangle$) takes its maximum possible value under the imposed constraints

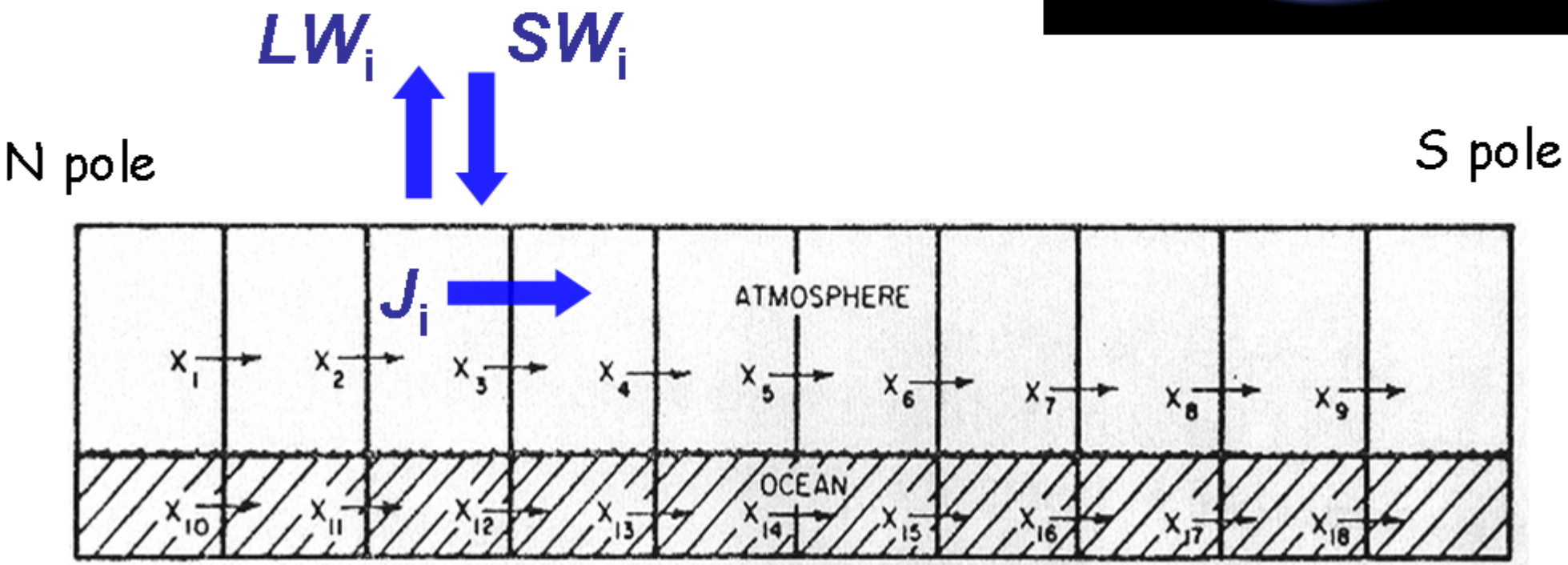
- *Fluctuation theorem :*

$\langle EP \rangle = (\tau/2k)\,Var(EP)$

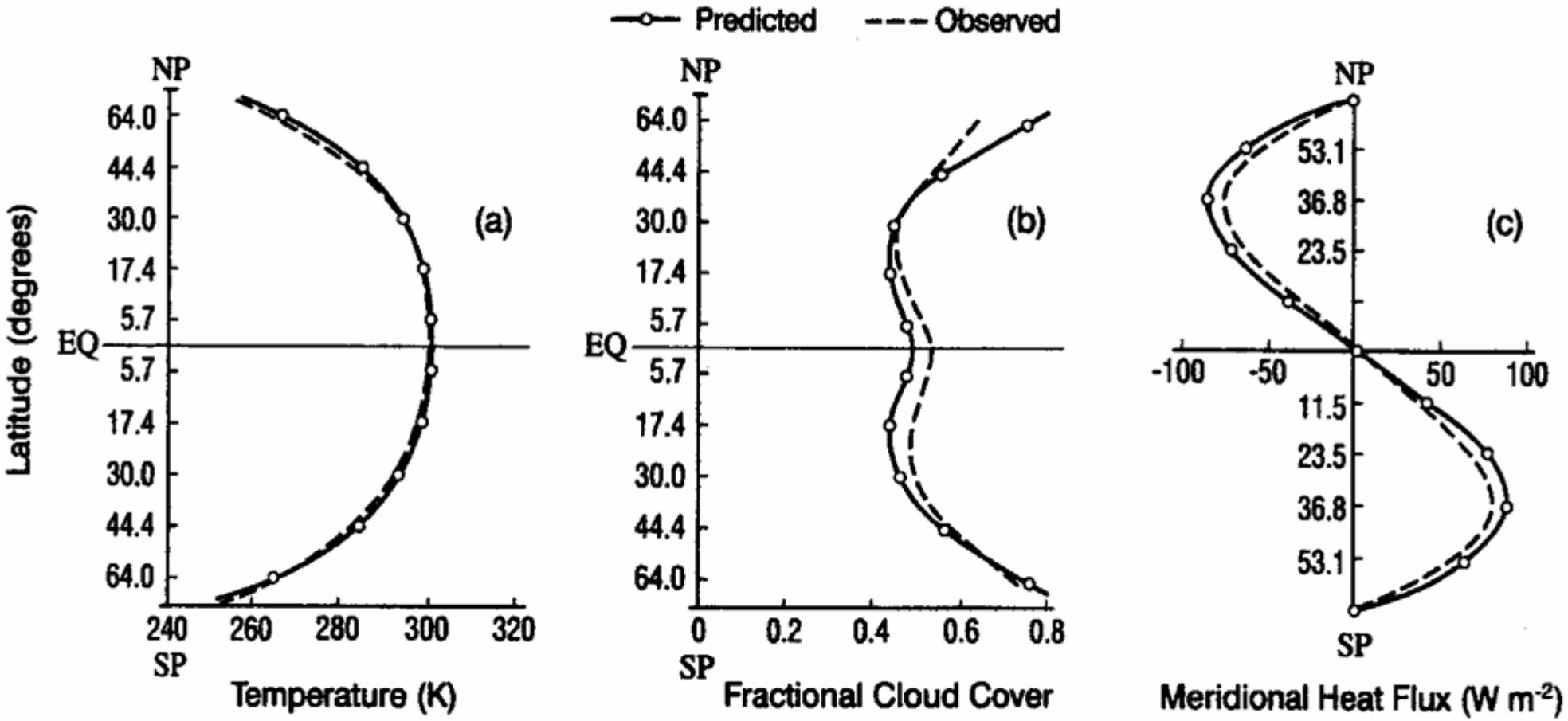
Paltridge (1978) :

10-zone climate model

$$EP_{planet} = \sum_{zone\ i=1}^{10} J_i \left(\frac{1}{T_{i+1}} - \frac{1}{T_i} \right)$$



Paltridge (1978) : MEP predictions from a 10-zone climate model



- Natural selection and diversity in physics
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Summary

- MaxEnt is a very general algorithm for predicting the behaviour which nature selects reproducibly under given constraints
- For non-equilibrium systems, MaxEnt predicts that nature selects the stationary state with the greatest entropy production
- Empirical evidence so far mainly from physics (planetary climates, thermal and shear turbulence, crystal growth ….)

- Natural selection and diversity in physics
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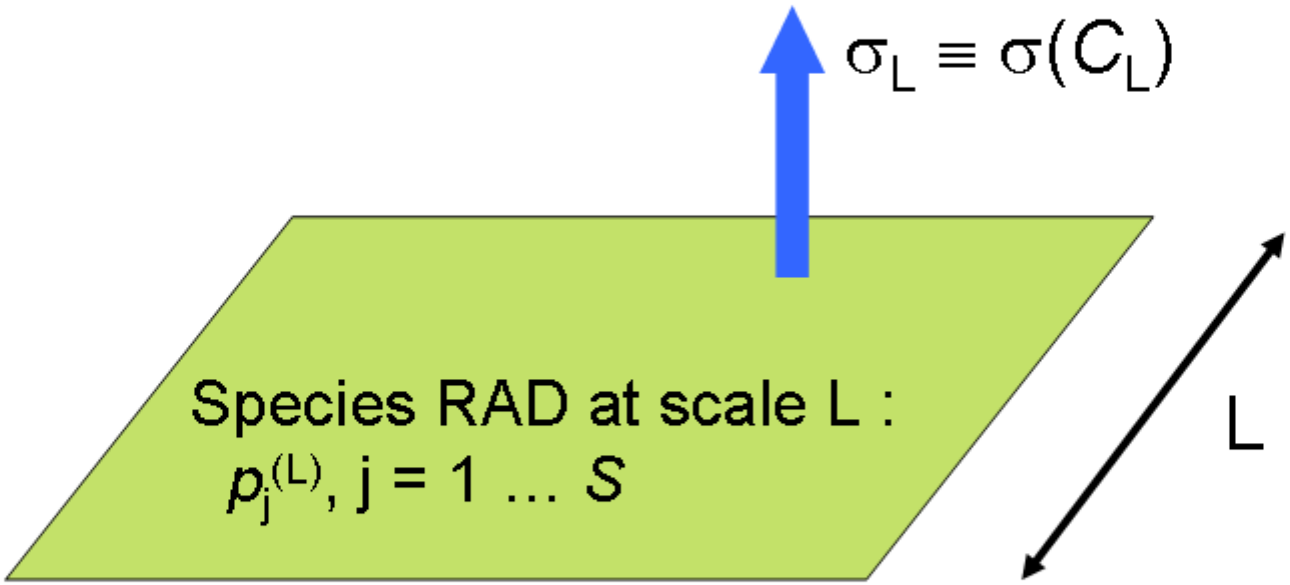
- C_L = constraints at scale L (J_{solar}, $J_{precipitation}$ …)
- Apply MaxEnt to p_Γ subject to C_L
- $\Rightarrow$ maximum $\langle EP_L \rangle$ at scale L = $\sigma(C_L)$



- What is the most probable RAD, $p_j^{(L)}$?
- Apply MaxEnt to $p_j^{(L)}$ subject to σ_L

Maximise : $$H_L = -\sum_{j=1}^{S} p_j^{(L)} \log\left(p_j^{(L)}\right)$$ (log # species)

Subject to : $$\sum_{j=1}^{S} p_j^{(L)} \sigma_j = \sigma_L$$ (given σ_L, *i.e.* C_L)

$$\sum_{j=1}^{S} p_j^{(L)} = 1$$ (normalisation)

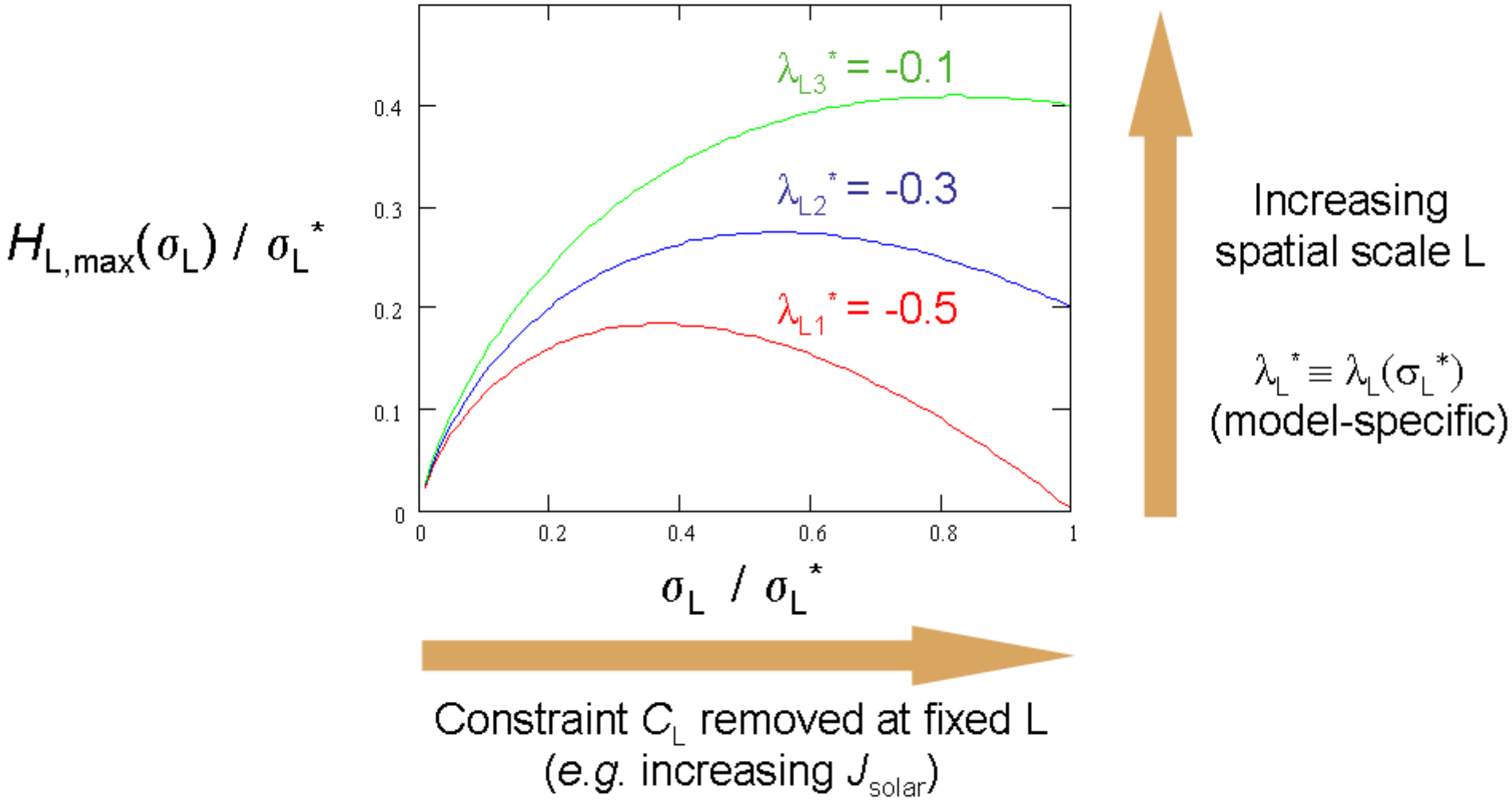
Solution : $$p_j^{(L)} = \frac{1}{Z_L} \exp\left(-\lambda_L \sigma_j\right)$$ where $\lambda_L = \lambda_L(\sigma_L)$

$$\lambda_L(\sigma_L) = \frac{\mathrm{d}H_{L,\max}(\sigma_L)}{\mathrm{d}\sigma_L}$$

$$\frac{\mathrm{d}\lambda_L}{\mathrm{d}\sigma_L} = -\frac{1}{\mathrm{Var}(\mathrm{EP}_L)} = -\frac{1}{2\sigma_L}$$

fluctuation theorem !

log (# species) vs. σ_L on different spatial scales



Some other ongoing applications of maximum entropy production

Global climate patterns (G Paltridge, GD Farquhar)

Biosphere-climate feedbacks (A Kleidon, J Ogée, F Million)

Turbulent transport in atmospheric boundary layers (J-F Wang)

Leaf stomatal behaviour (S Delzon)

Optimal molecular structure of chloroplast ATP-synthase
(D Juretić, P Zupanović)

conclusions & conjectures

- MaxEnt is a general statistical method for predicting the most probable behaviour under given constraints

- For non-equilibrium systems, MaxEnt predicts that nature selects the stationary state with the greatest entropy production (MEP)

- Natural selection in both physics and biology
- = selection of the most probable 'macroscopic' state
- = selection of maximum 'microscopic' diversity

- Ecosystem diversity and functioning at different spatial scales reflects behaviour of maximum entropy production (σ_L) under scale-dependent changes in resources (C_L)