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# *Maximum entropy production and ecosystems*

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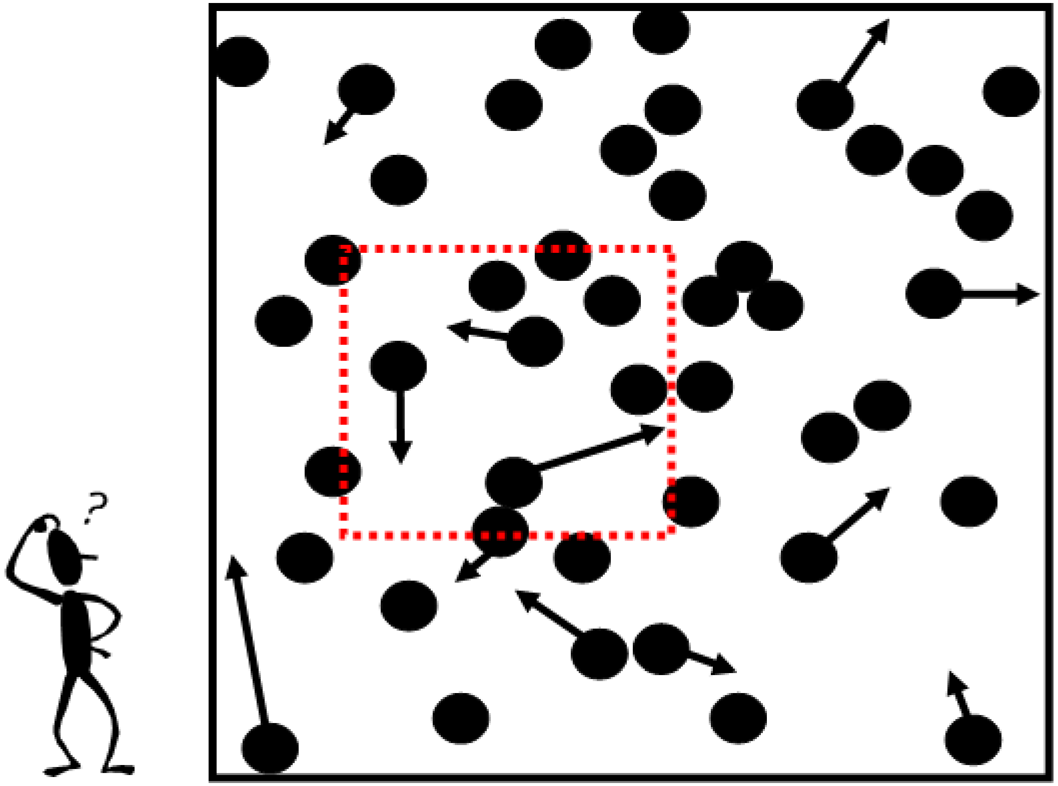
# Why is there such a diversity of molecular positions and velocities ?



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

N, E, V fixed

Macroscopic
description *A*

*spatial distribution of molecules in box*


Microscopic
description *i*

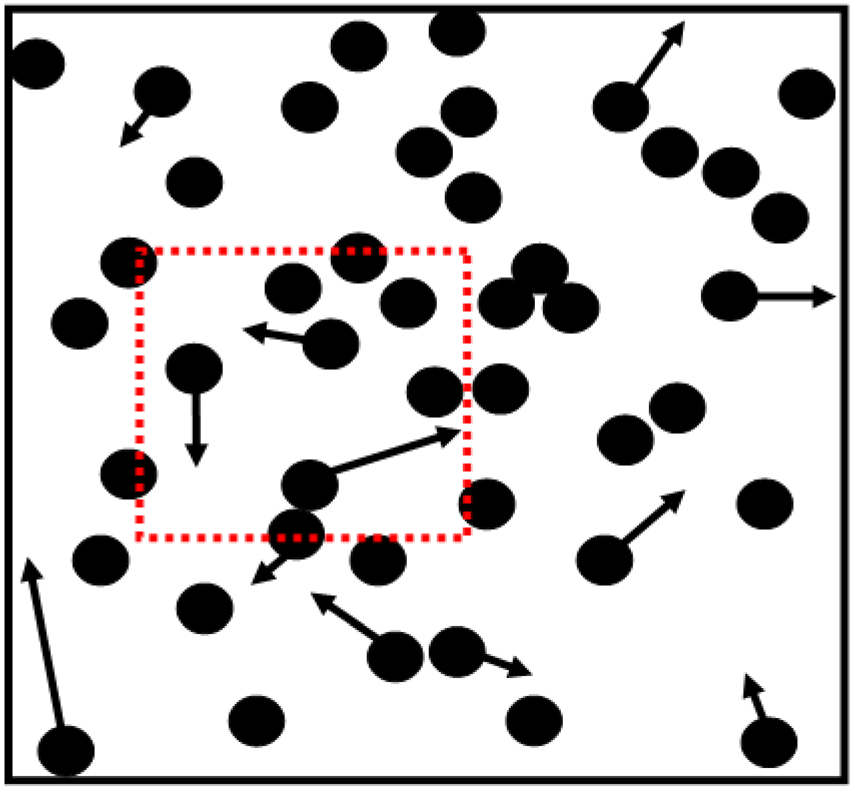
*individual positions of every molecule*

$S_A$ = 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
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## 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

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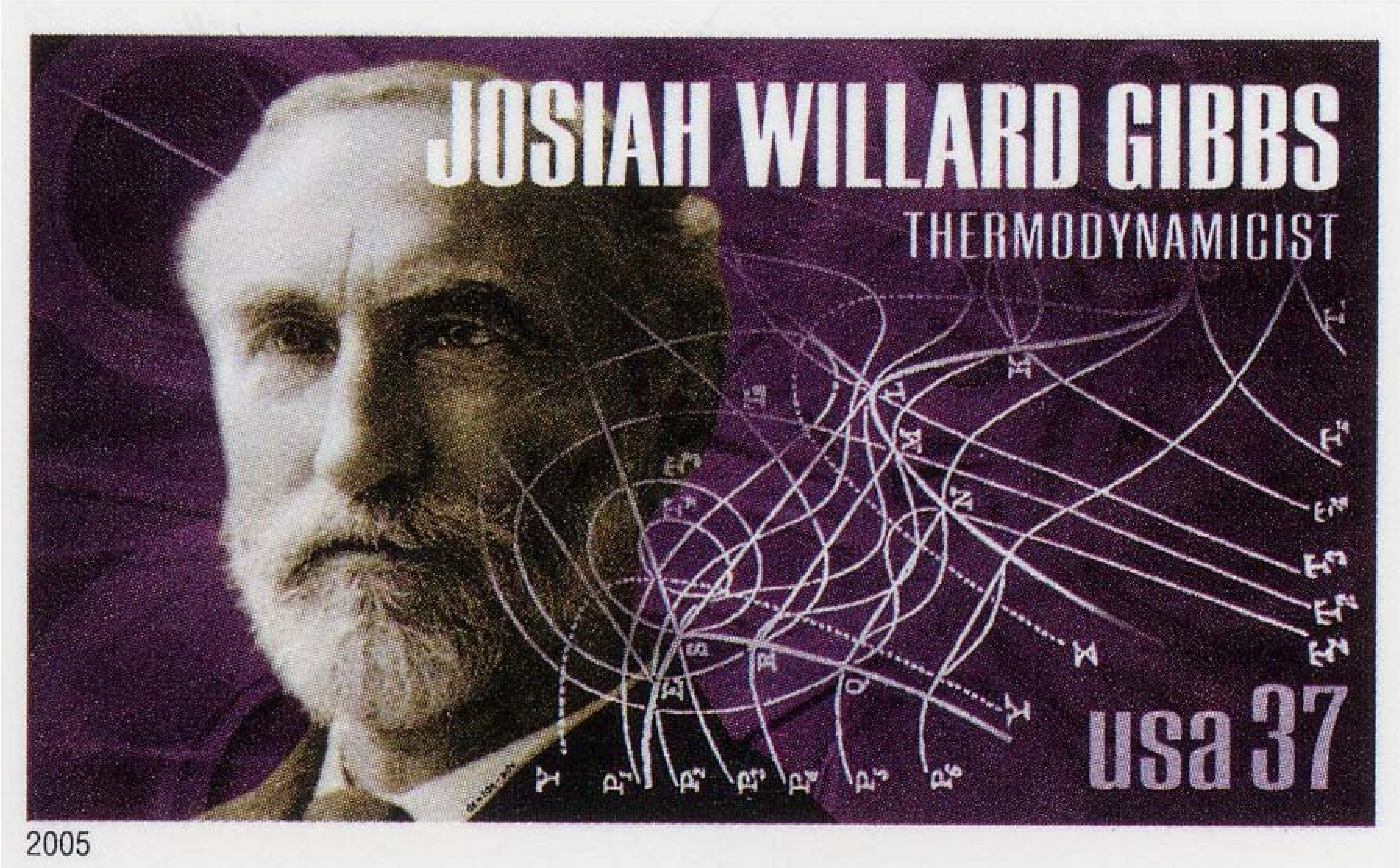



(1839 - 1903)

# The Gibbs algorithm (MaxEnt) ...

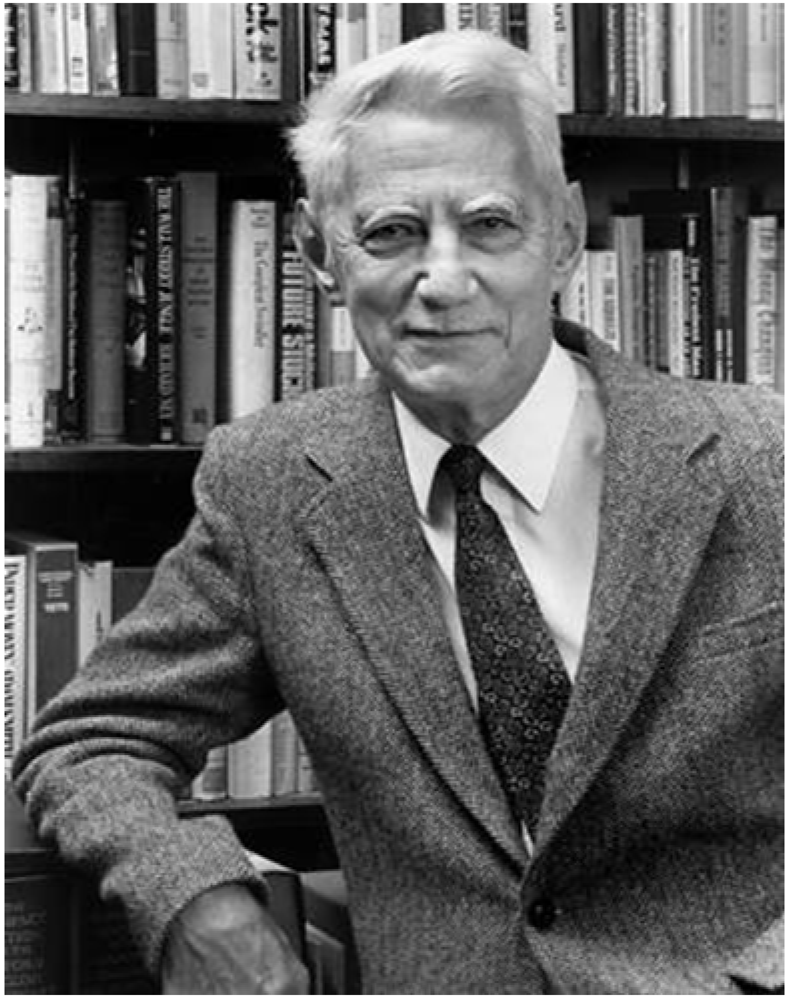
$p_i$ : probability that the system is in microstate $i$
Given $\langle E \rangle$, what is $p_i$ ?

**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*)

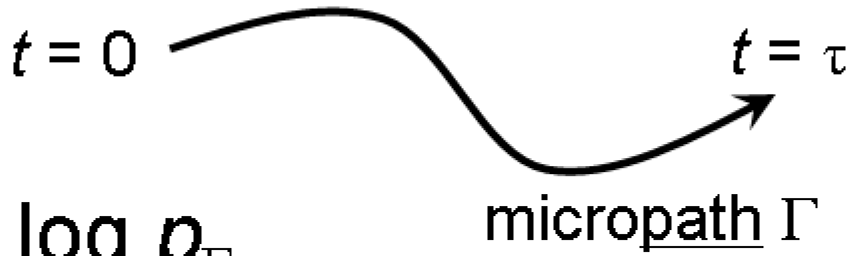
$$\max H = -\Sigma_i \, p_i \log p_i$$

- 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 :**

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

entropy production ($EP_\Gamma$)

# Two fundamental implications of the MaxEnt solution $p_\Gamma \propto \exp(\tau \mathrm{EP}_\Gamma / 2k)$

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

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

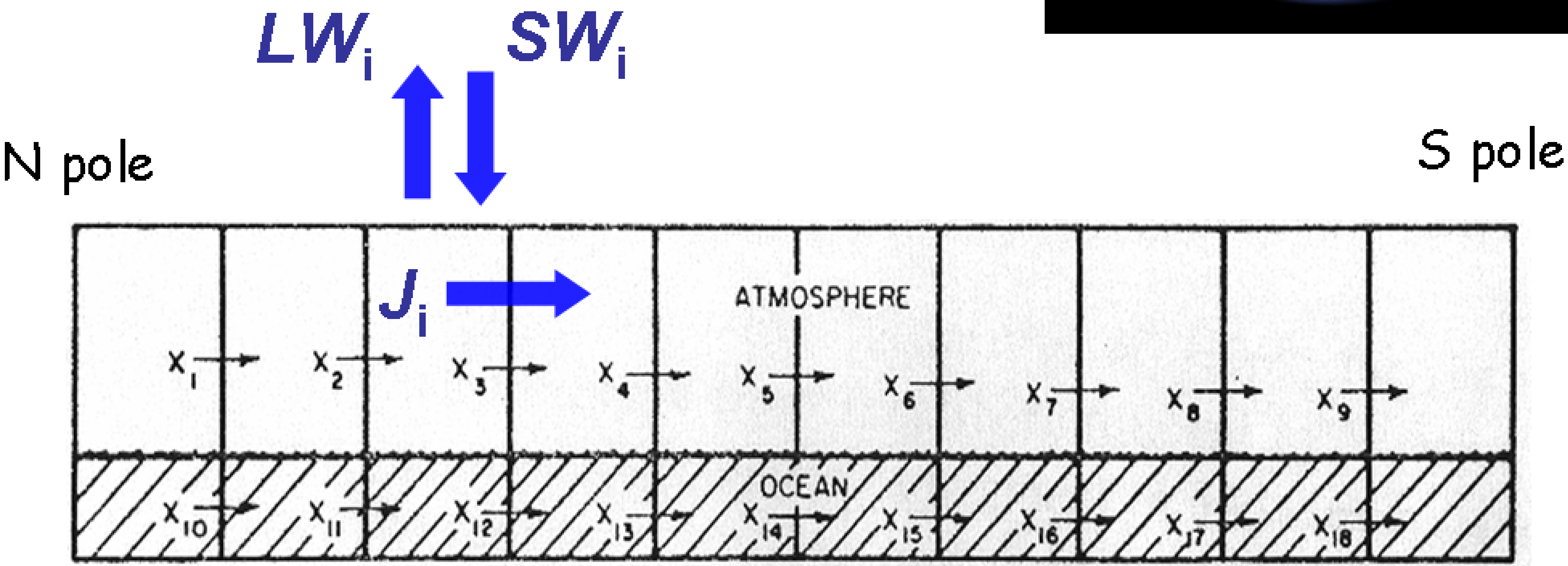
- *Fluctuation theorem :*

$\langle \mathrm{EP} \rangle = (\tau/2k) Var(\mathrm{EP})$

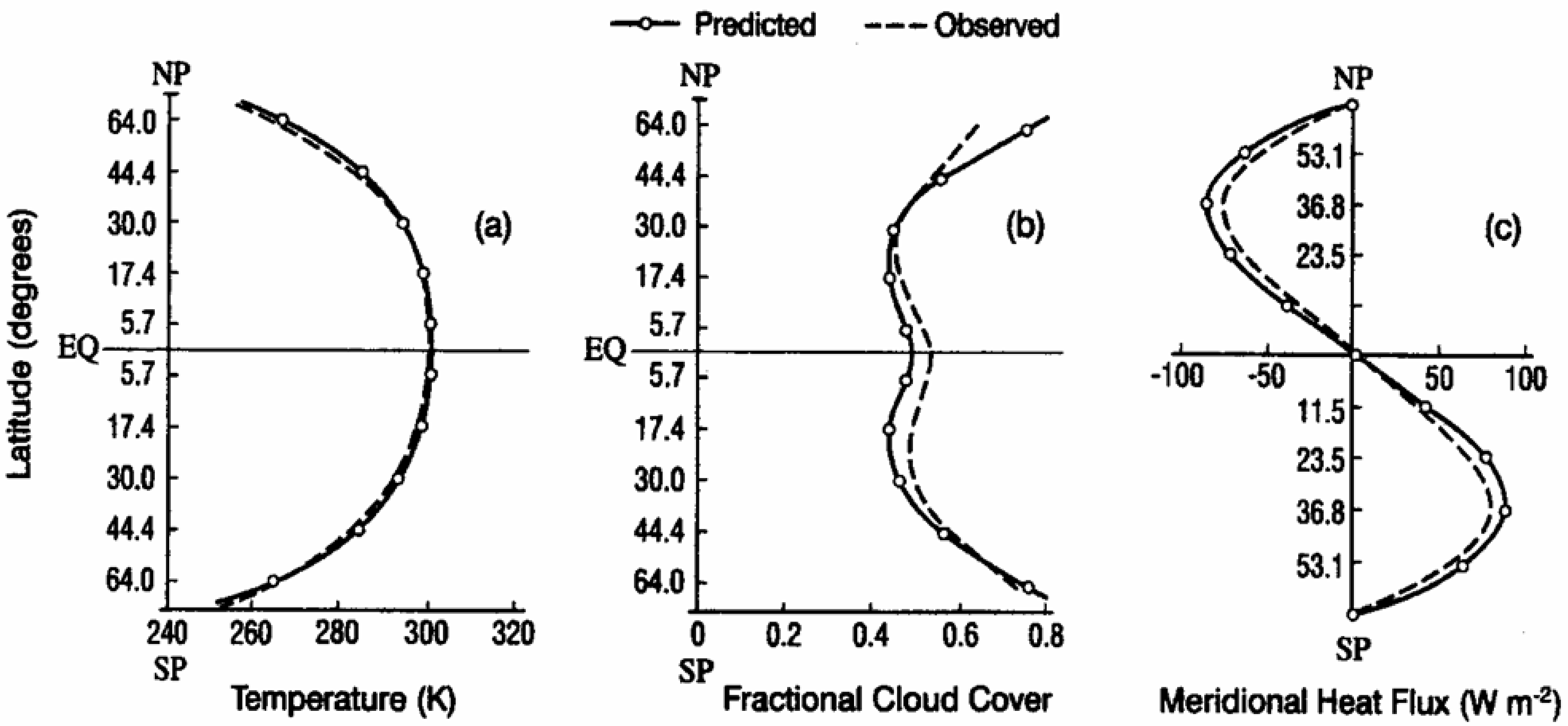
# Paltridge (1978) :

## 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 ….)

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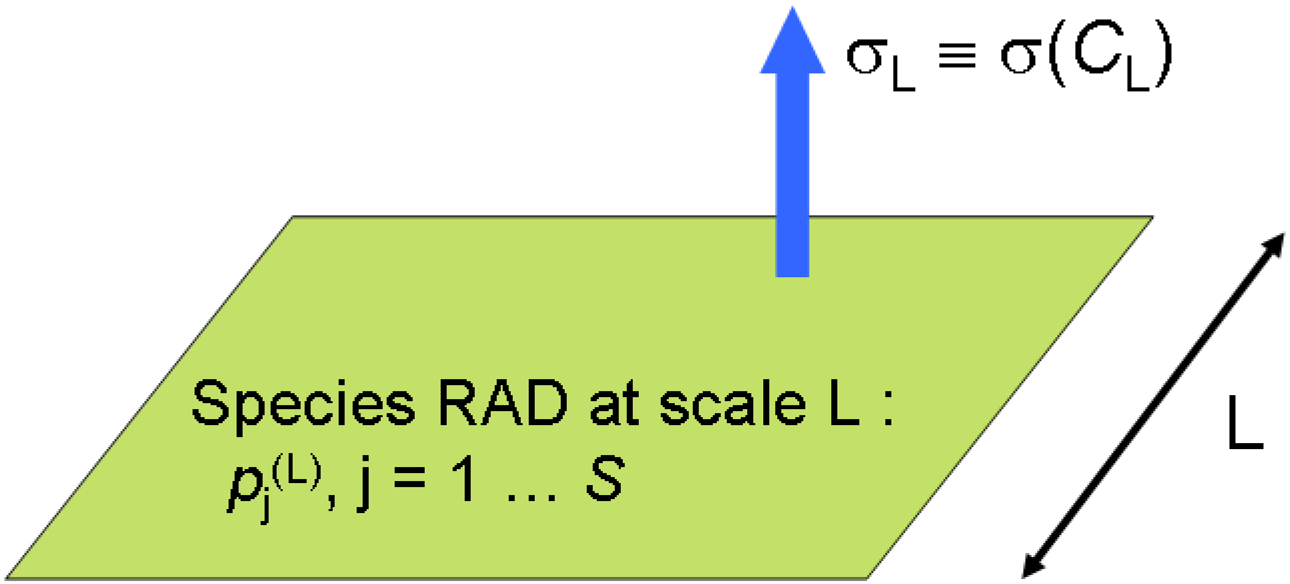
- $C_L$ = constraints at scale L ($J_{solar}$, $J_{precipitation}$ …)
- Apply MaxEnt to $p_\Gamma$ subject to $C_L$
- $\Rightarrow$ maximum $\langle EP_L \rangle$ at scale L = $\sigma(C_L)$




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

**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 $\sigma_L$, *i.e.* $C_L$)

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

**Solution :**

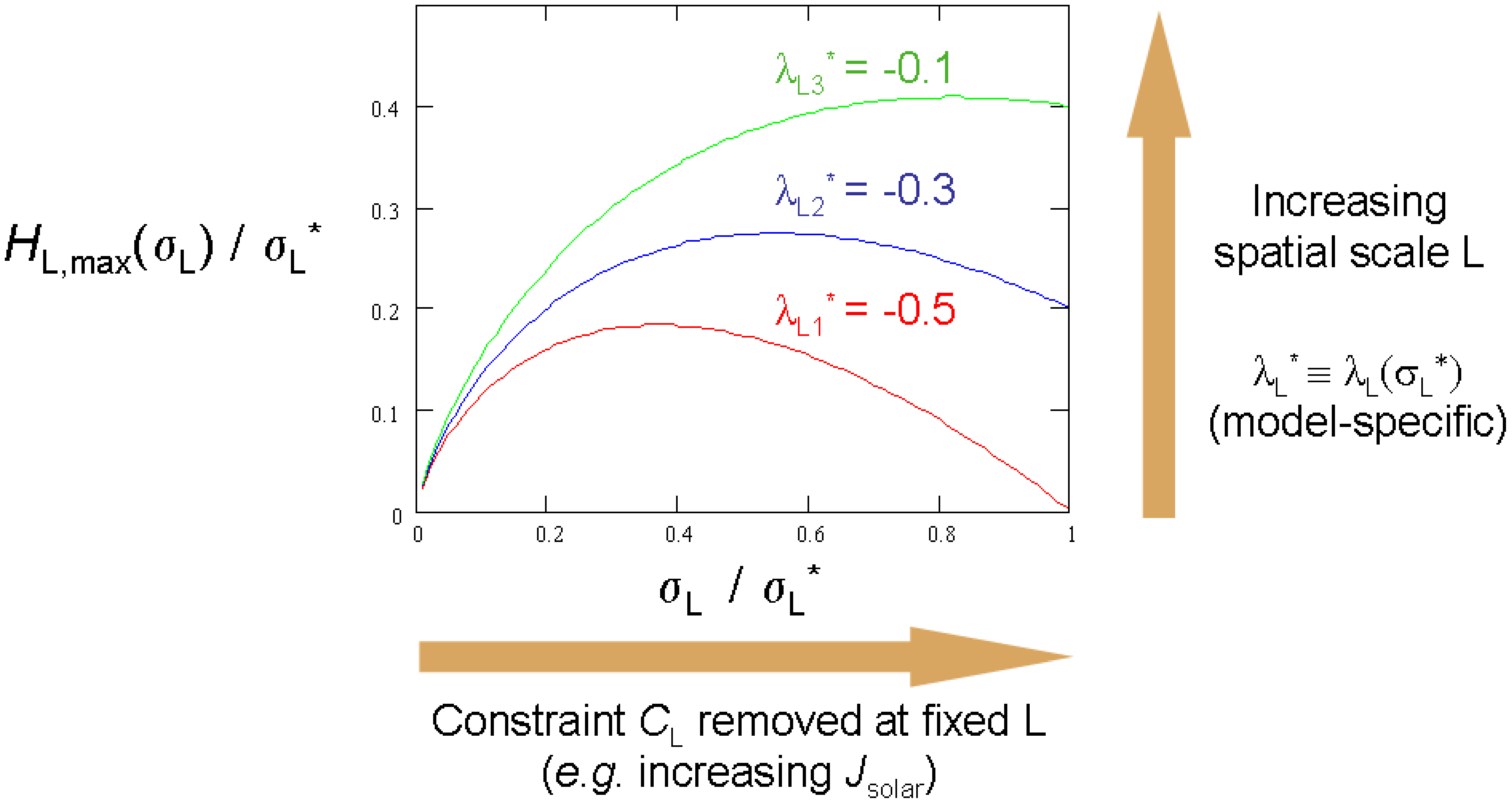
$$p_j^{(L)} = \frac{1}{Z_L} \exp\left(-\lambda_L \sigma_j\right)$$ where $\lambda_L = \lambda_L(\sigma_L)$

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

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

*fluctuation theorem !*

# log (# species) vs. $\sigma_L$ 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 ($\sigma_L$) under scale-dependent changes in resources ($C_L$)