The neutral theory of biodiversity and other competitors to maximum entropy

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Biodiversity

Biodiversity maintenance: Niche or Neutral?

- **Niche theory** proposes species differences allow coexistence of competitors
  - → *stable coexistence (i.e. species can invade from low abundance)*
  - → *species richness determined by number of niches*
  - → *species' relative abundance determined by relative prevalence of their niches*
- **Neutral theory** proposes coexistence of competitors is due to species similarities
  - → *dynamics are not stable, instead dominated by stochasticity*
  - → *species richness determined by balance between colonization/ speciation and extinction*
  - → *species' relative abundances shaped by stochasticity and dispersal limitation*

What is the idea behind Niche Theory?

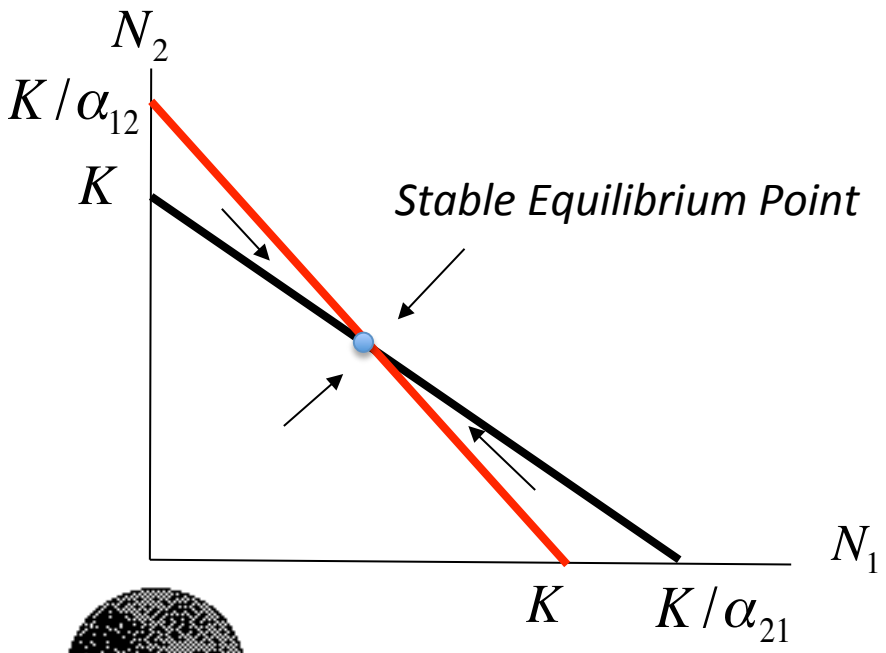
Coexistence through species differences

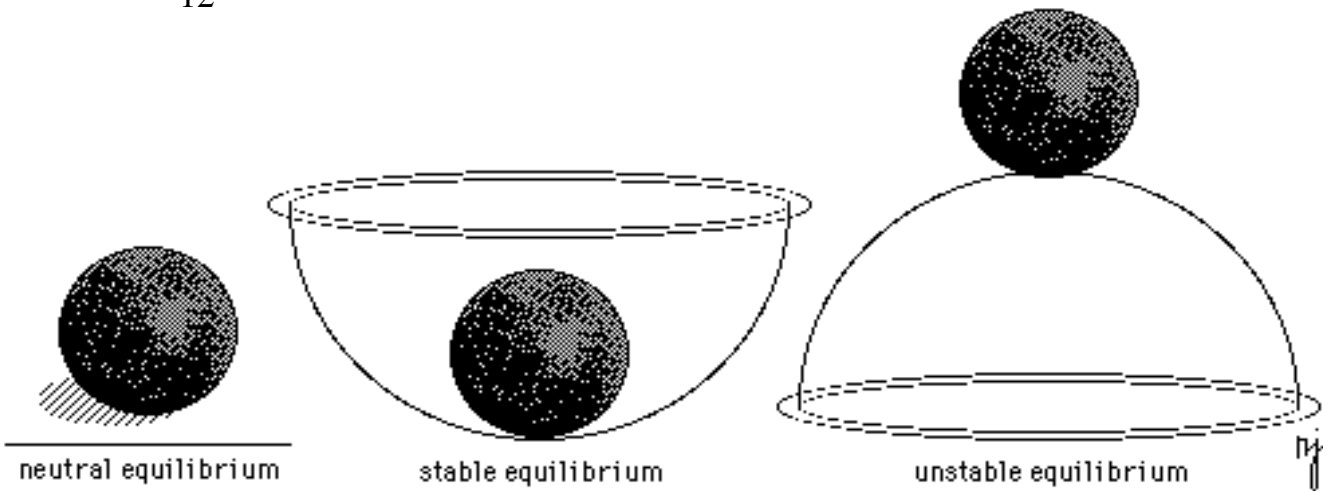
In the context of the Lotka-Volterra competition model (with $K_1=K_2=K$):

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K - N_1 - \alpha_{12} N_2}{K} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K - N_2 - \alpha_{21} N_1}{K} \right)$$

$$\alpha_{12} < 1 \qquad \alpha_{21} < 1$$

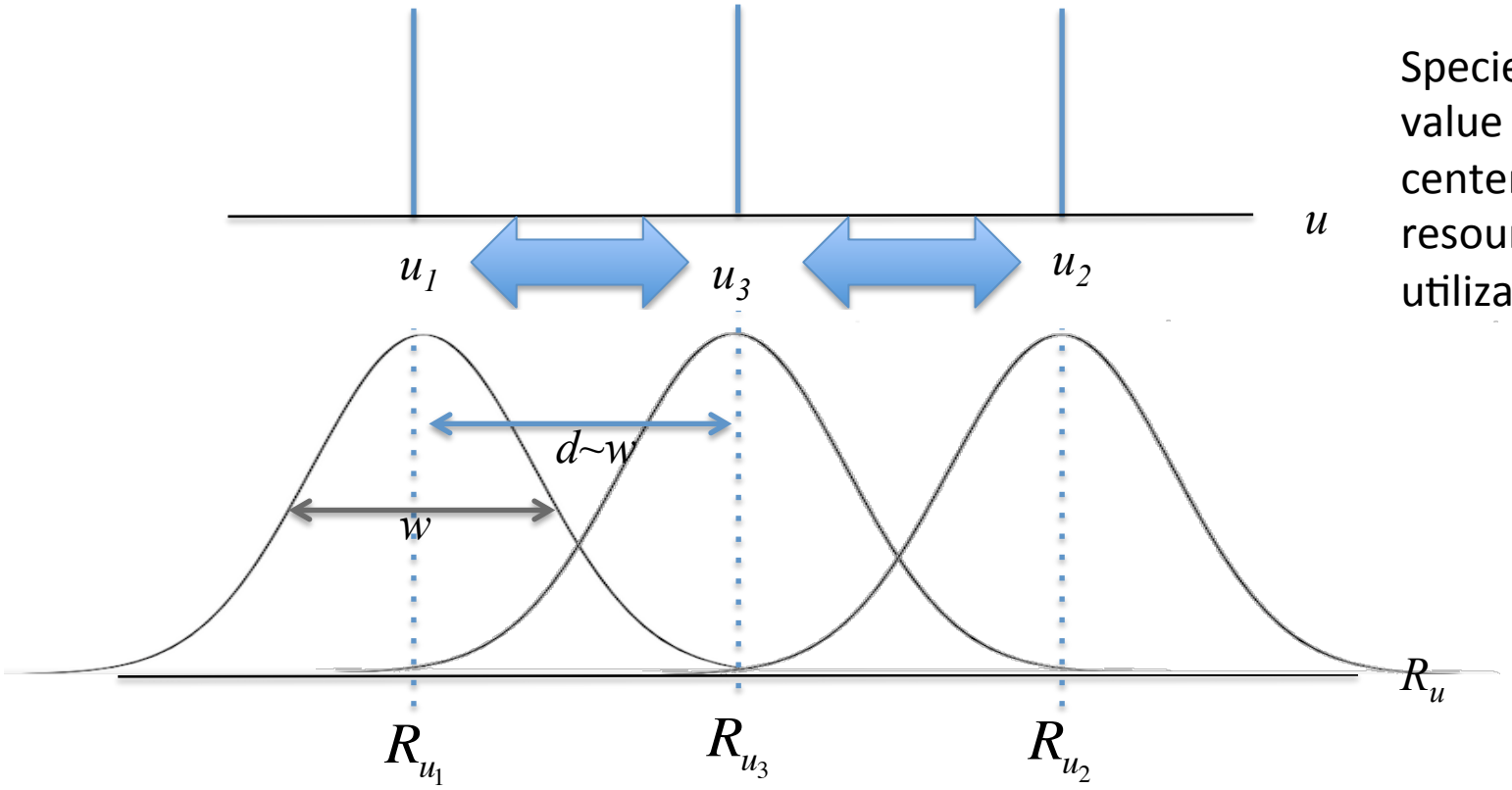




What is the idea behind Niche Theory?

The differences have to be large enough!

- Mac Arthur and Levins (1967) derived the principle of limiting similarity from model of competition among species on a 'niche' axis:



Species' niche value u indicates center of its resource utilization

$$\frac{dN_i}{dt} = r\left(N_i/K_i\right)\left(K_i - N_i - \sum_{j=1}^{S}\alpha\left(u_i,u_j\right)N_j\right)$$

$\alpha\left(u_i,u_j\right)$ decreasing function of $|u_i - u_j|$

What is the idea behind Niche Theory?

Differences in interaction with regulating factors

- early definition of niche (Grinnell 1917):

  set of conditions allowing persistence of population

- here I am taking a definition of niche differences focused on what enables stable, robust coexistence of competitors:

  differences in interaction with "regulating factors"

Can show such differences are present when coexistence is robust across a large family of models:

Barabas, Pastor, Meszena, Ostling Ecology Letters (2014)

Factors that influence and are influenced by population sizes e.g. classic "resource", or number of available patches with required conditions

What is the idea behind Neutral Theory?

Coexistence through Similarity

In the context of the Lotka-Volterra competition model (with $K_1=K_2=K$):

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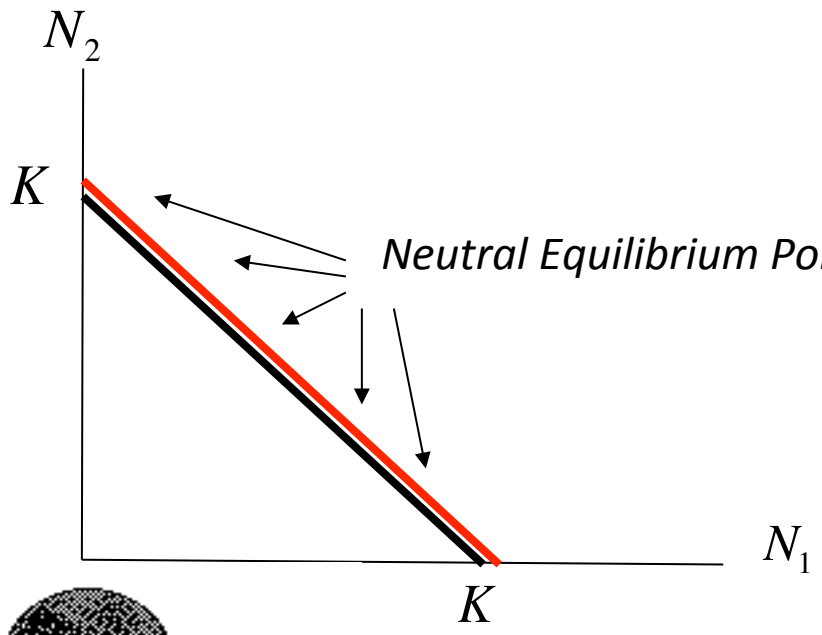
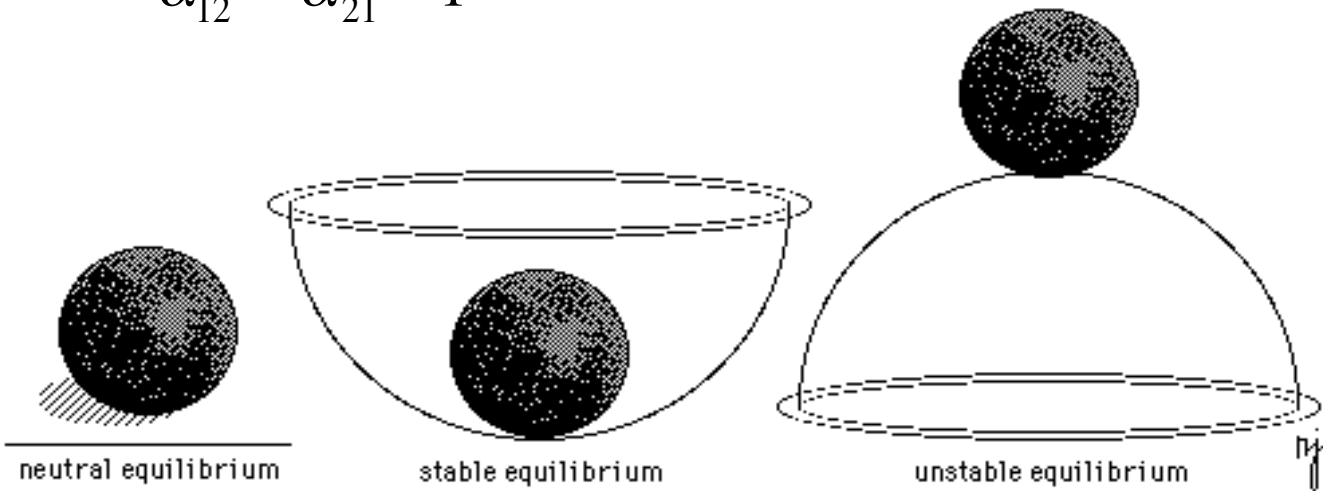
$$\alpha_{12} = \alpha_{21} = 1$$

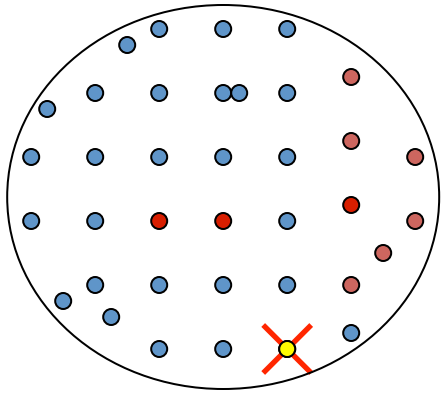




What do Neutral Models look like?

Neutral Model: *Local community*

Local community at carrying capacity



Metacommunity ⟶

In each death and replacement event:

- a randomly chosen individual dies, and then…

2 options:

- with probability m, it is replaced with the offspring of a random individual from the regional community ("metacommunity")

or

- with probability $(1\text{-}\ m)$ it is replaced with an offspring of a random individual in the local community

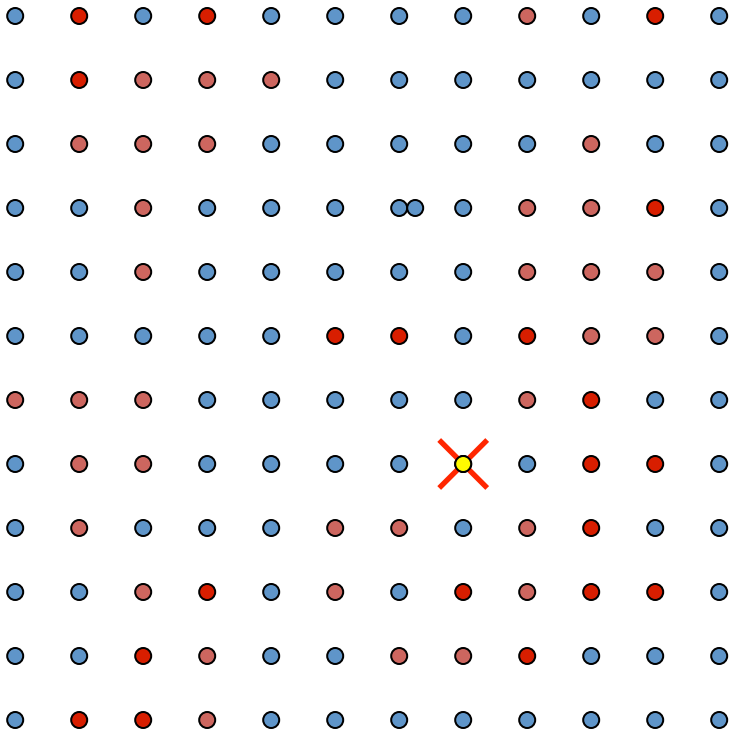
m = immigration rate

Assumes **all** individuals are
demographically equivalent

What do Neutral Models look like?

Neutral Model: *Metacommunity*

Metacommunity at carrying capacity



In each death and replacement event:

- a randomly chosen individual dies, and then…

2 options:

- with probability ν, it is replaced with an individual of a new species

or

- with probability (1-ν) it is replaced with the offspring of a randomly chosen individual

ν = speciation rate

Local community predictions depend on $\theta=2J_M\nu$ and m

Species abundance distribution

$P(n,t) \equiv$ probability species has abundance n at time t after arising from speciation

Note: $\tilde{P}(n) = \delta_{n0}$

$$\frac{dP(n,t)}{dt} = W_{n-1}^{+}P(n-1,t) + W_{n+1}^{-}P(n+1,t) - \left(W_n^{+} + W_n^{-}\right)P(n,t)$$

zero-sum $$W_n^{+} = \left(\frac{J_M - n}{J_M}\right)(1-\nu)\left(\frac{n}{J_M}\right)$$

non-interactive $$W_n^{+} = bn$$

$S(n,t) \equiv$ expected # of species in community with n individuals at time t

$$= \int_0^t dt' \nu P(n, t-t') \quad + \text{terms going to 0 at large } t$$

Species abundance distribution

$$\frac{dS(n,t)}{dt} = W_{n-1}^{+} S(n-1,t) + W_{n+1}^{-} S(n+1,t) - \left(W_n^{+} + W_n^{-} \right) S(n,t)$$

$$+ \nu \delta_{n1}$$

$$\tilde{S}(n) = \frac{W_{n-1}^{+} W_{n-2}^{+} \cdots W_1^{+} \nu}{W_n^{-} W_{n-1}^{-} \cdots W_1^{-}}$$

non-interactive $$\tilde{S}(n) = \frac{\nu}{b} \frac{\left(b/d \right)^n}{n}$$

Species clearly differ in traits, and often in ways that could stabilize coexistence.

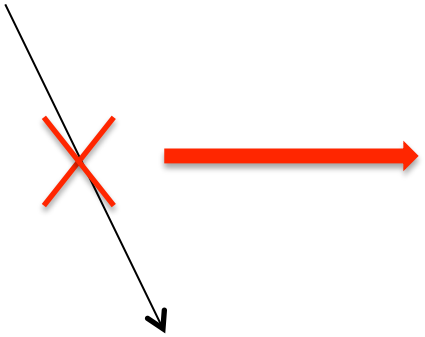
However, what is less clear is…

- How strong of a role do differences play in maintaining diversity?
  - Are there enough niches for all species?
  - How strongly stabilized is the coexistence?

- How strong of a role do they play in shaping species' relative abundances and other patterns of community structure?

Neutral theory as a "Null Model"

Neutral Theory may not be true. But…



Niches, Habitat filtering!

Patterns in Community Structure

- Species richness & degree of consistency of composition
- Species abundances and the distribution of abundance across species (i.e. how many rare versus common species)

Problems with existing tests of Neutral Theory

- When neutral theory has succeeded, seems a stochastic niche model could do just as well

- When neutral theory has failed, typically easy to argue due to neutral model used ignoring "demographic complexity" that has little to do with niches

Testing Neutral Theory in ecology vs. in evolutionary biology

- In evolutionary biology context, can deal with 'demographic complexity' using calibration on a large number of genes, or comparisons across similar species

- In ecological context, more difficult to achieve calibration or comparison

Overcoming problems with tests of Neutral Theory

- Figure out what differences in community structure are produced by niches through study of stochastic niche models

- Figure out what demographic complexity is important to neutral model predictions

- Figure out how to construct tests of neutral theory so that we can ignore more of the demographic complexity

Our stochastic niche model

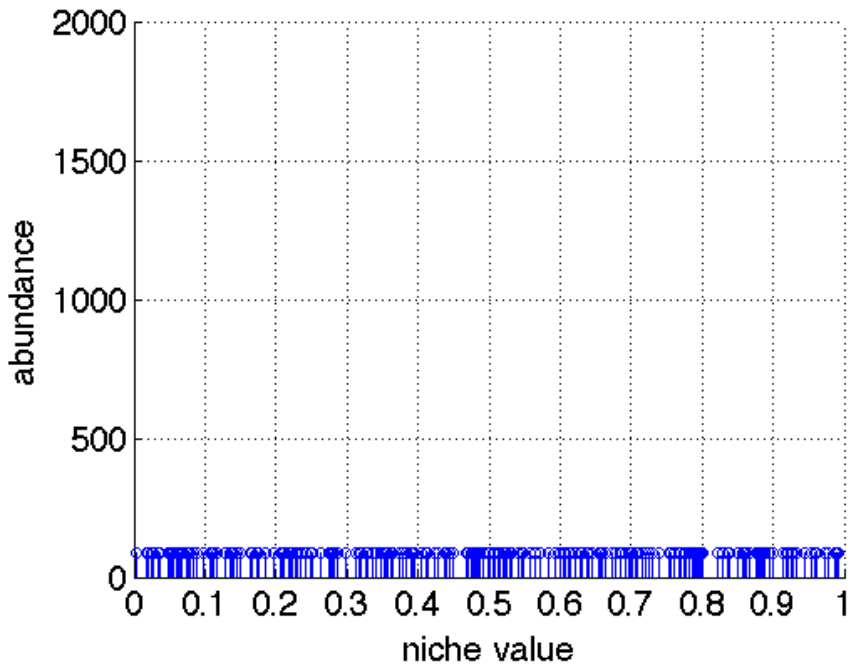
Study stochastic version of Lotka-Volterra competition on trait axis:

Niches emerge on the trait axis.

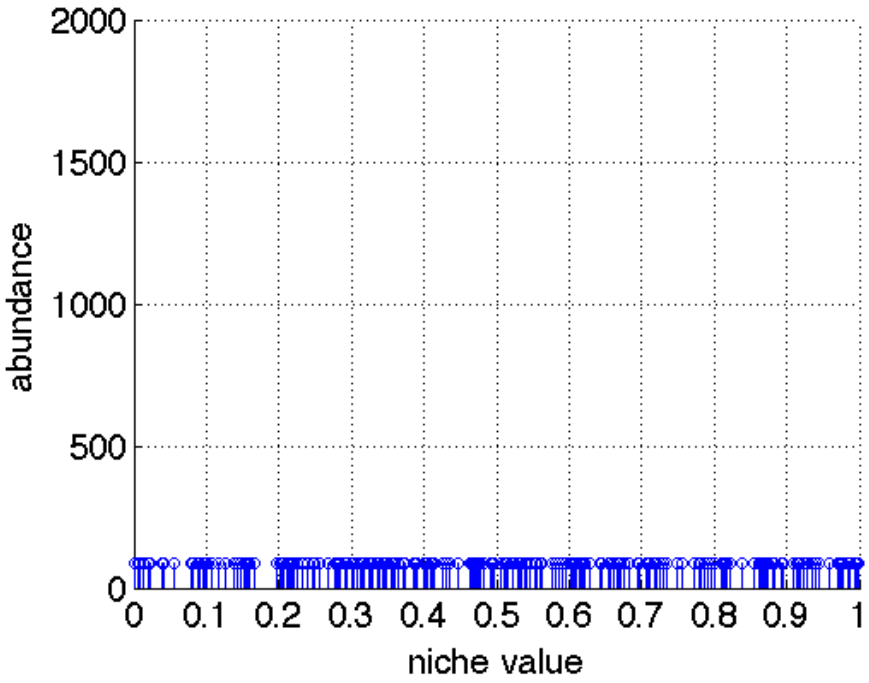
Species clustered rather than dispersed if # species > # niches.

Larger effect of niches on SAD than previously thought.

neutral



niche



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Opinion

CellPress

Maximum information entropy: a foundation for ecological theory

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Species abundance distributions, statistical mechanics and the priors of MaxEnt

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The application of statistical physics to evolutionary biology

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