Neutral Theory

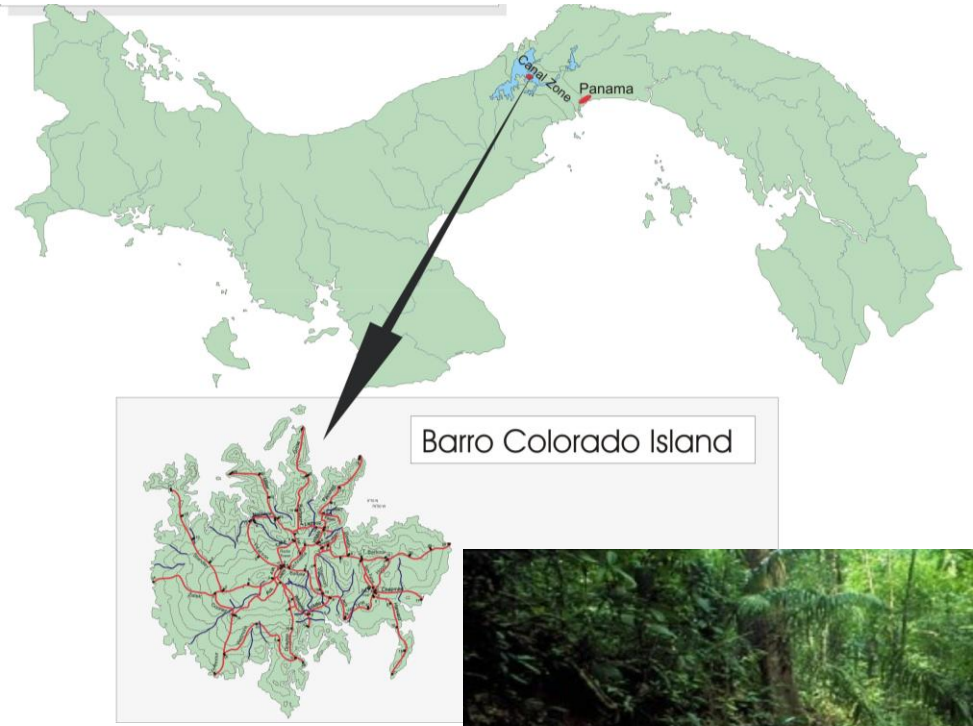
ECOL 4000

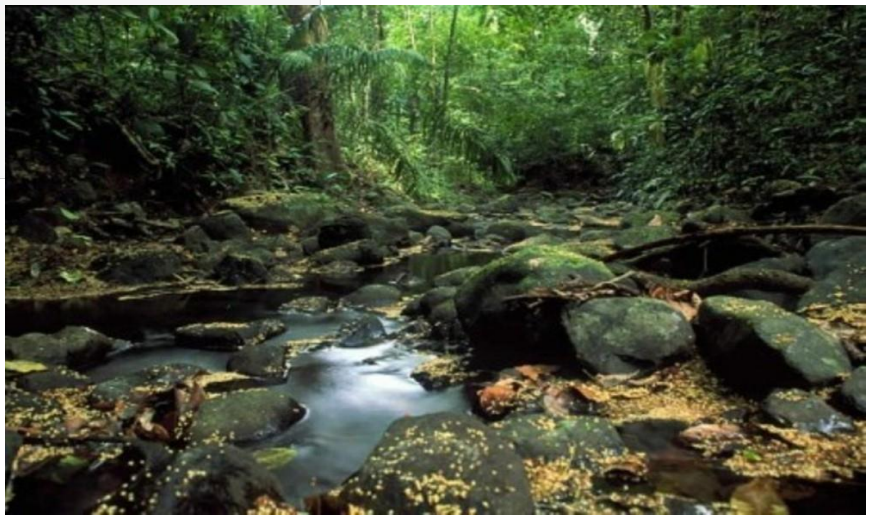
Quiz:

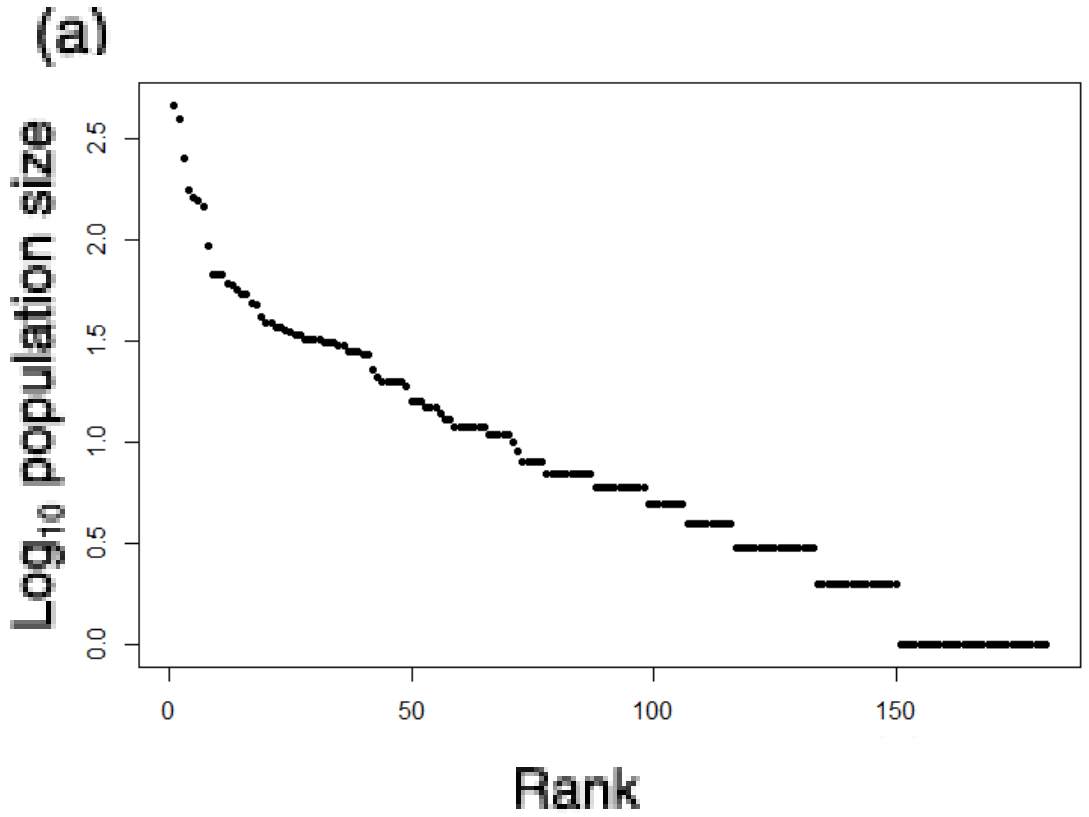
Which of the following are assumptions of neutral theory:

A) All species have an equal probability of being removed by disturbance
B) There is no speciation, only migration/dispersal
C) Species interactions have no effect or are not present
D) Species colonization probability depends on the local environment
E) A and B
F) A and C

Species abundance distributions vary from community to community





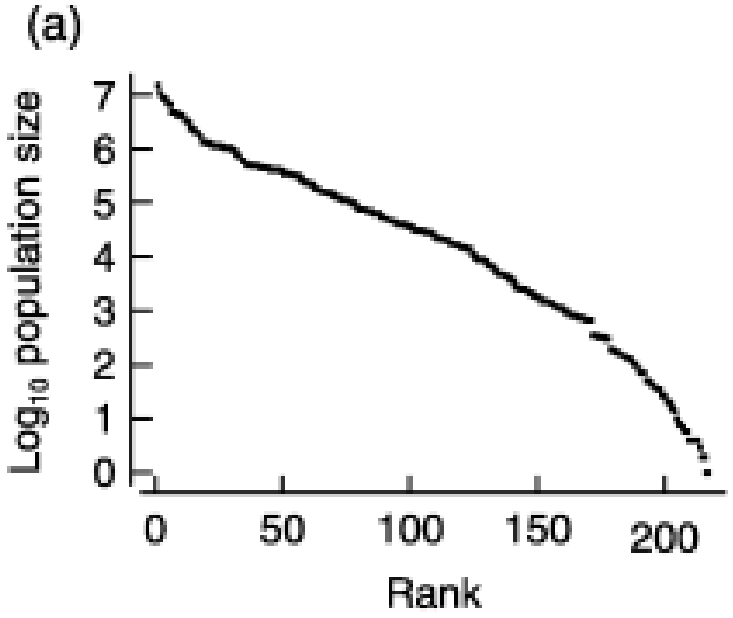


Hubbell 2000

Learning Objectives

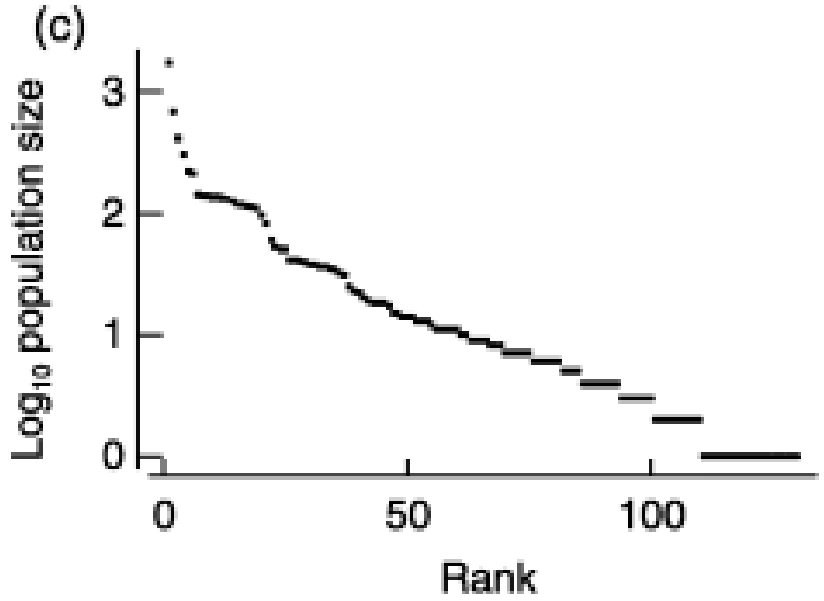
1. Describe the Unified Neutral Theory of Biodiversity and Biogeography and the evidence supporting it
2. Explain the differences in processes behind Niche based and Neutral community assembly
3. Predict the effect of changes in parameters on the output of Neutral Theory Models

Species abundance distributions vary from community to community



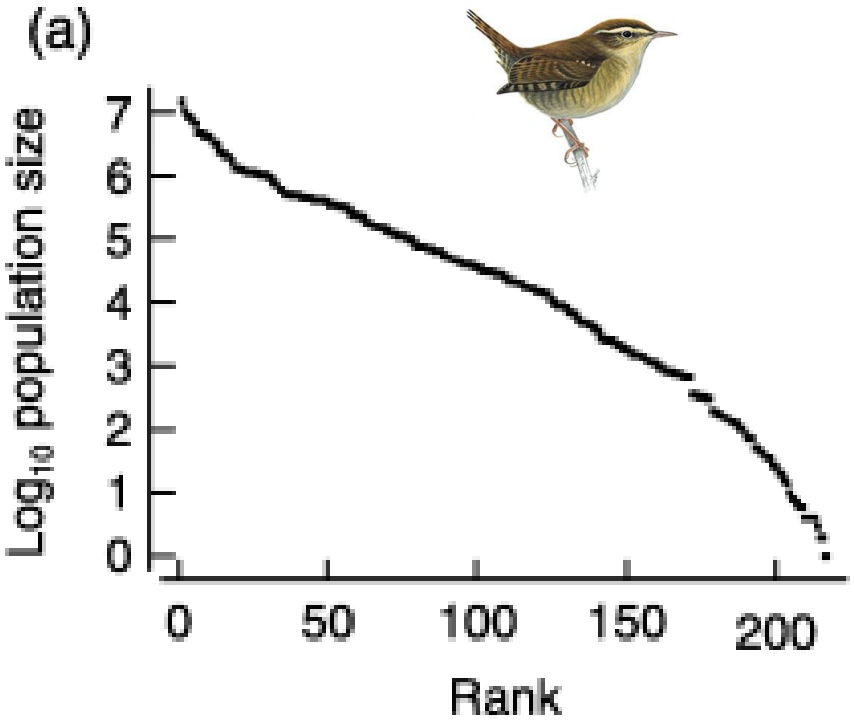
Williamson and Gaston 2005;
Gaston and Blackburn 2000

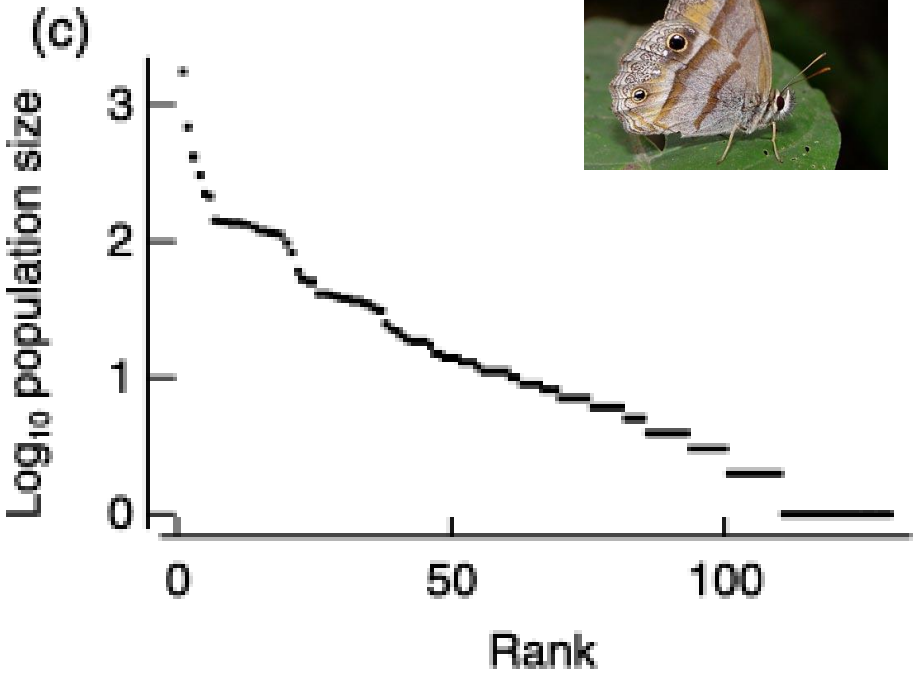
Species abundance distributions vary from community to community



DeVries et al. 1997

Describe some differences between these distributions.





But what can these differences tell us about how communities are assembled?

Broken Stick Model

The Environment

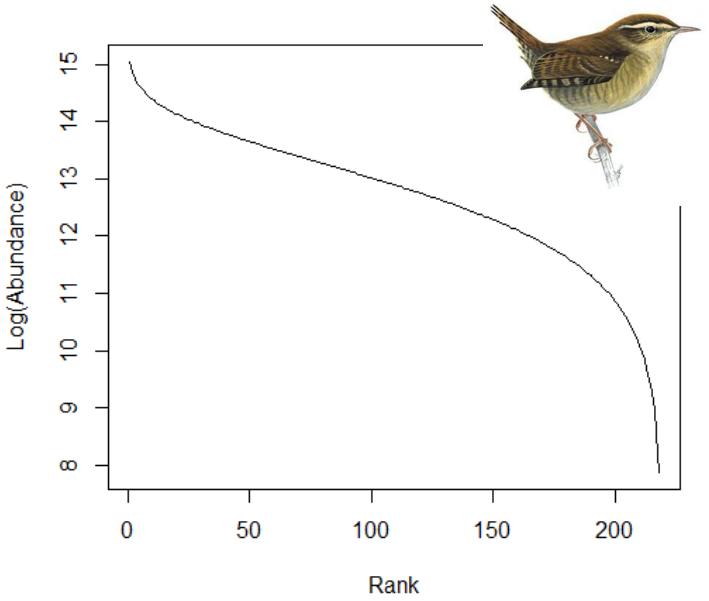
N Species ➔ N segments

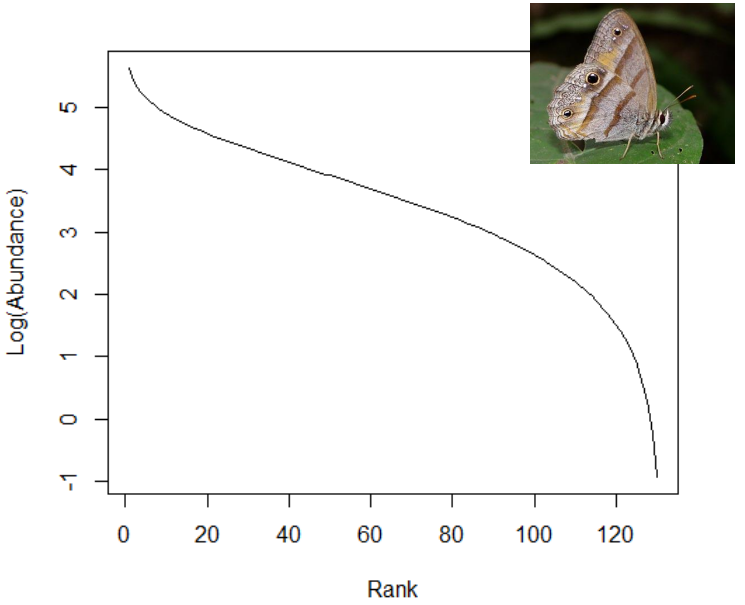
- Species abundances are relative to the length of the segments
- **This represents N species with non-overlapping niches occupying an environment**
- The expected length of the r^{th} shortest segment is:

$$\frac{1}{n}\sum_{i=1}^{r}\frac{1}{n-i+1}$$

- So in a community of m individuals the abundance of the r^{th} least abundant species is:

$$\frac{m}{n}\sum_{i=1}^{r}\frac{1}{n-i+1}$$

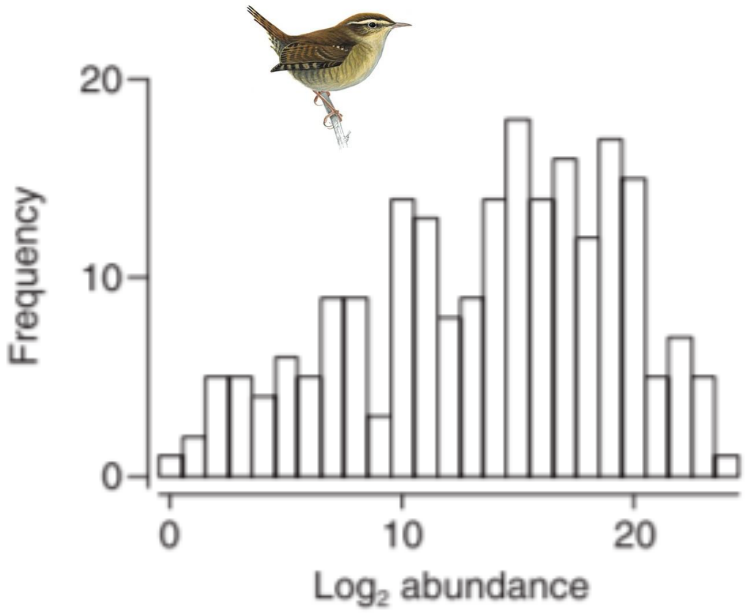


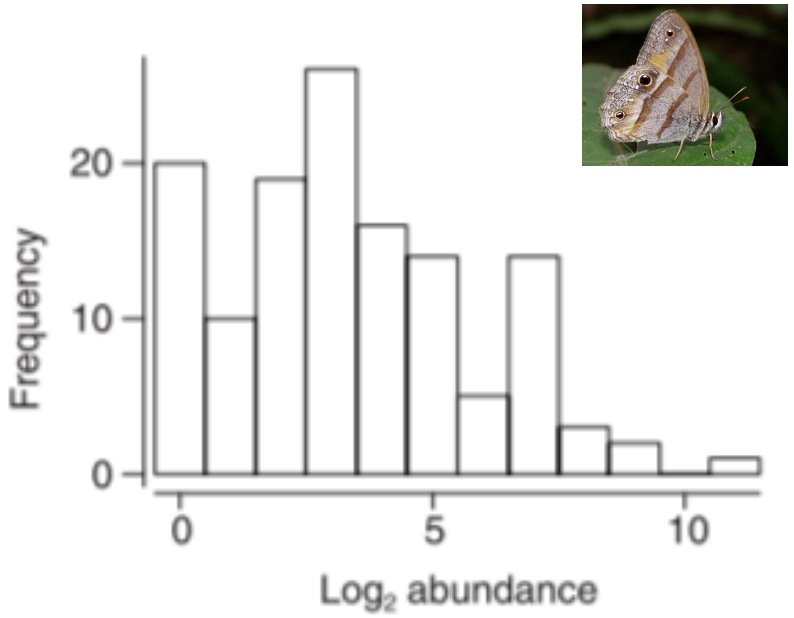


MacArthur 1957

Log Normal Model

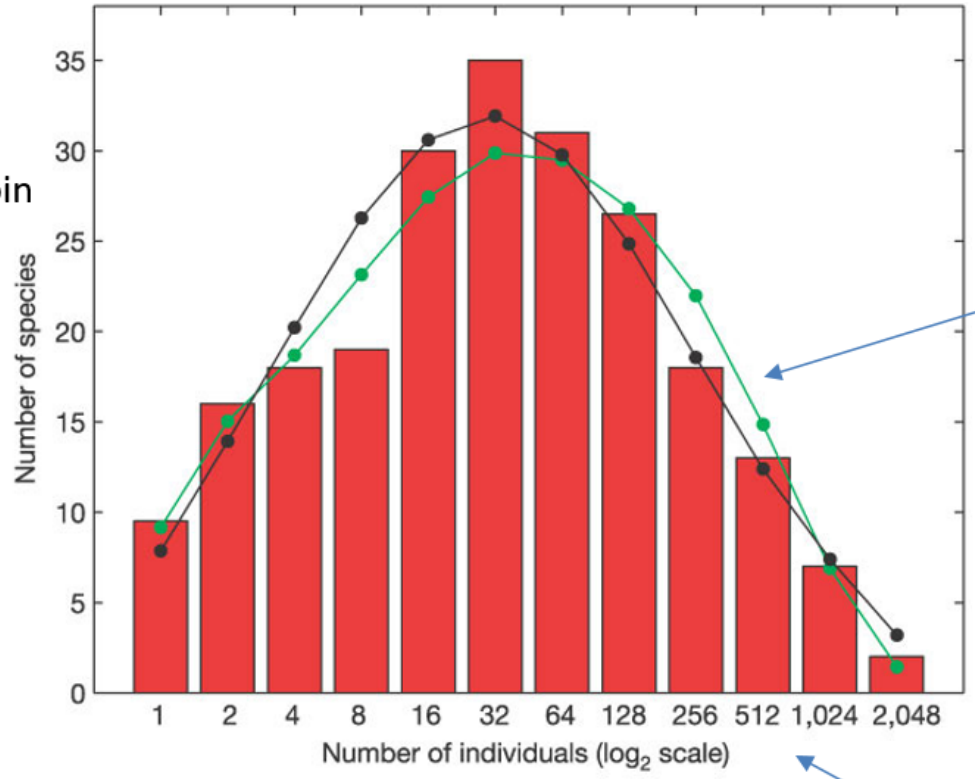
- Preston (1946) suggested that species abundances follow a Lognormal distribution
- Meaning that the frequency of the log abundances should follow a normal distribution
- Widely applied but largely phenomenological





Preston Plots

Frequency of each bin

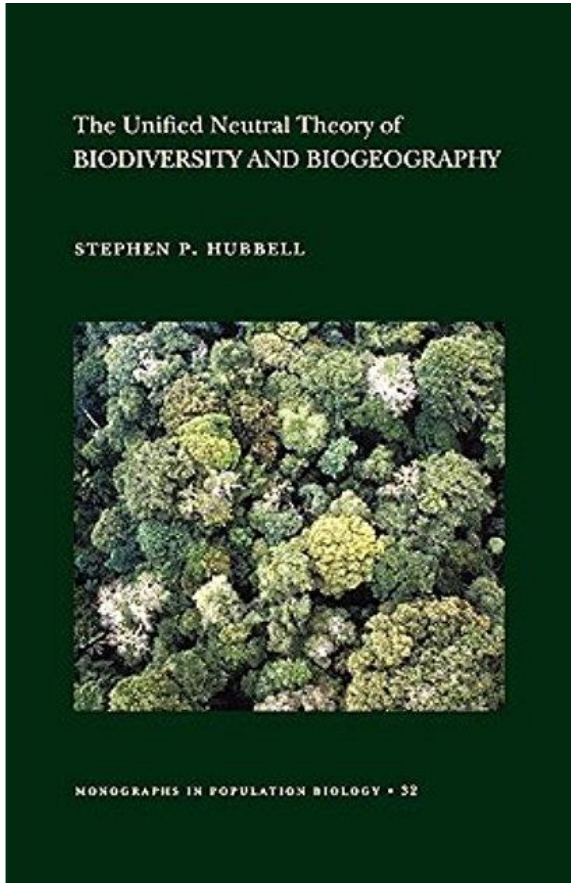


Different models will make different predictions about the frequency of bins

Each species belongs to a bin on a log scale (here a log2 scale) for the number of individuals in a sample

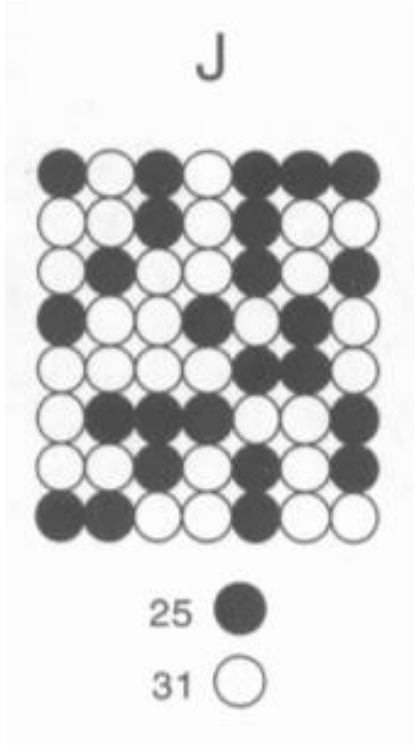
But how do we know if a model fits “well enough”?

The Unified Neutral Theory of Biodiversity and Biogeography



- Stephen Hubbell proposed his Neutral Theory as a macroecological null model based exclusively on dispersal and speciation
- Key Components
  - Processes structuring ecological communities are stochastic
  - Species differences have little effect on community composition

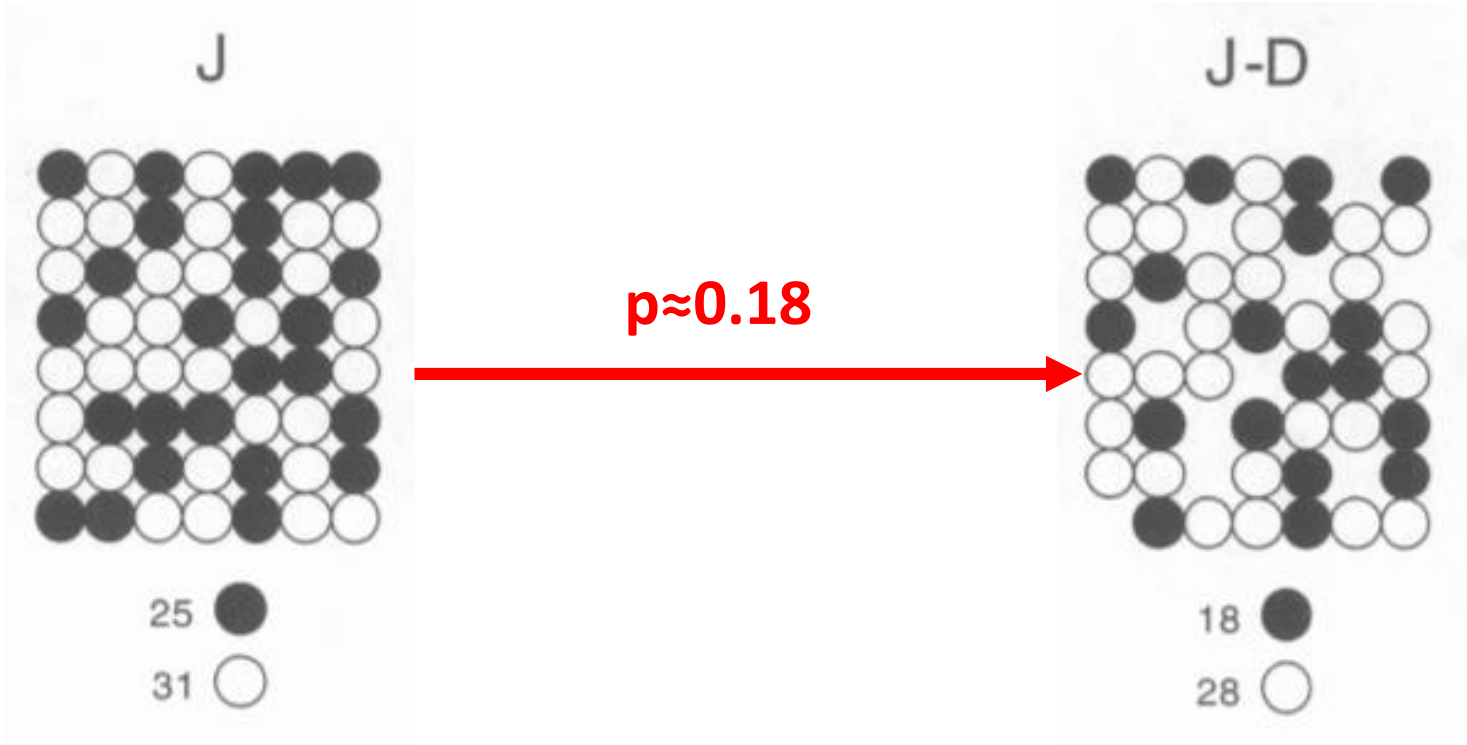
The Unified Neutral Theory of Biodiversity and Biogeography



- A community is made up of J individuals of a variety of species
- Each individual occupies its place in the community independently of others
  - **They Don’t Compete**

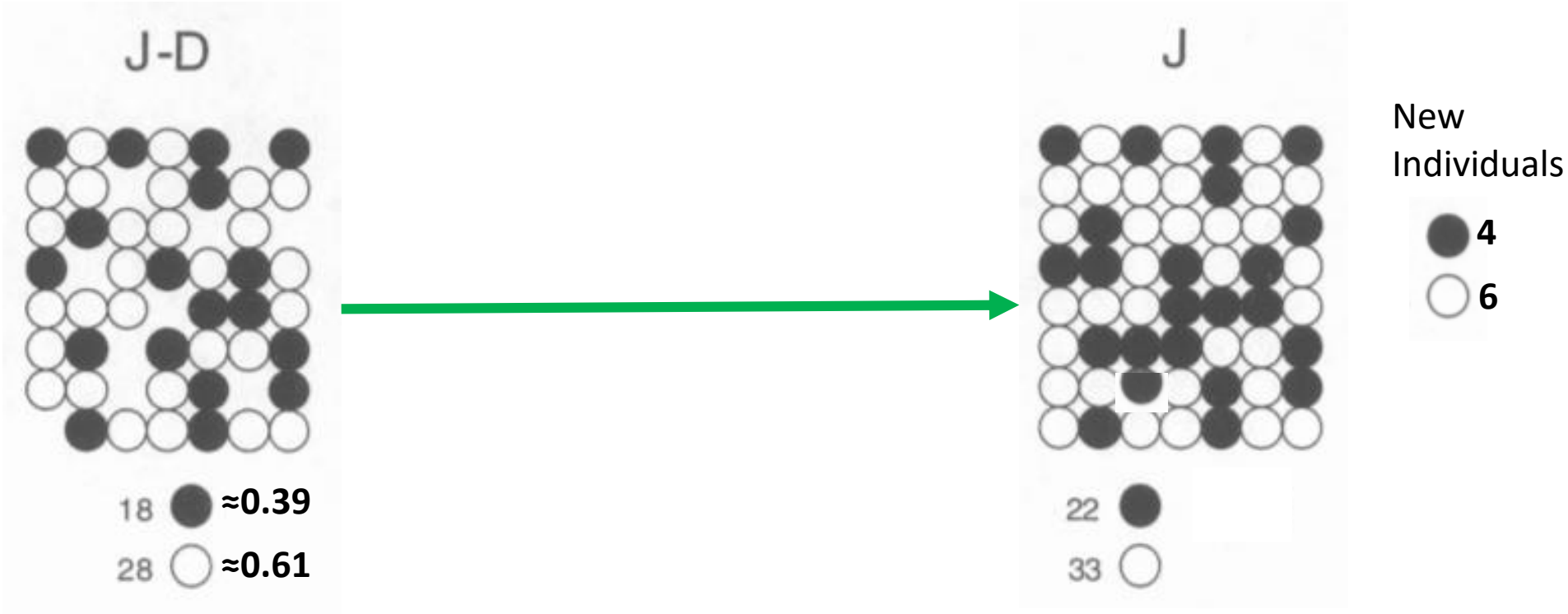
The Unified Neutral Theory of Biodiversity and Biogeography

- Disturbance removes individuals of all species with the **same probability p**



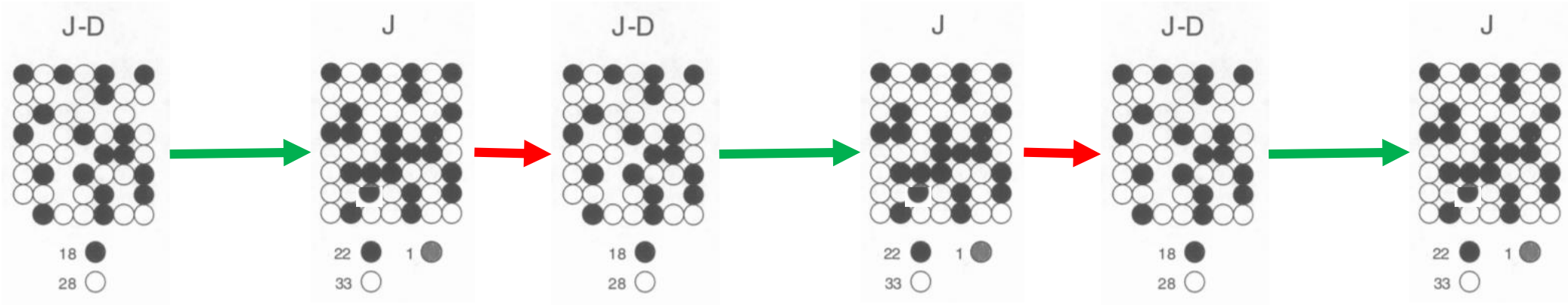
The Unified Neutral Theory of Biodiversity and Biogeography

- All gaps left by removed individuals are filled in **direct proportion to their relative proportions in the community** after disturbance



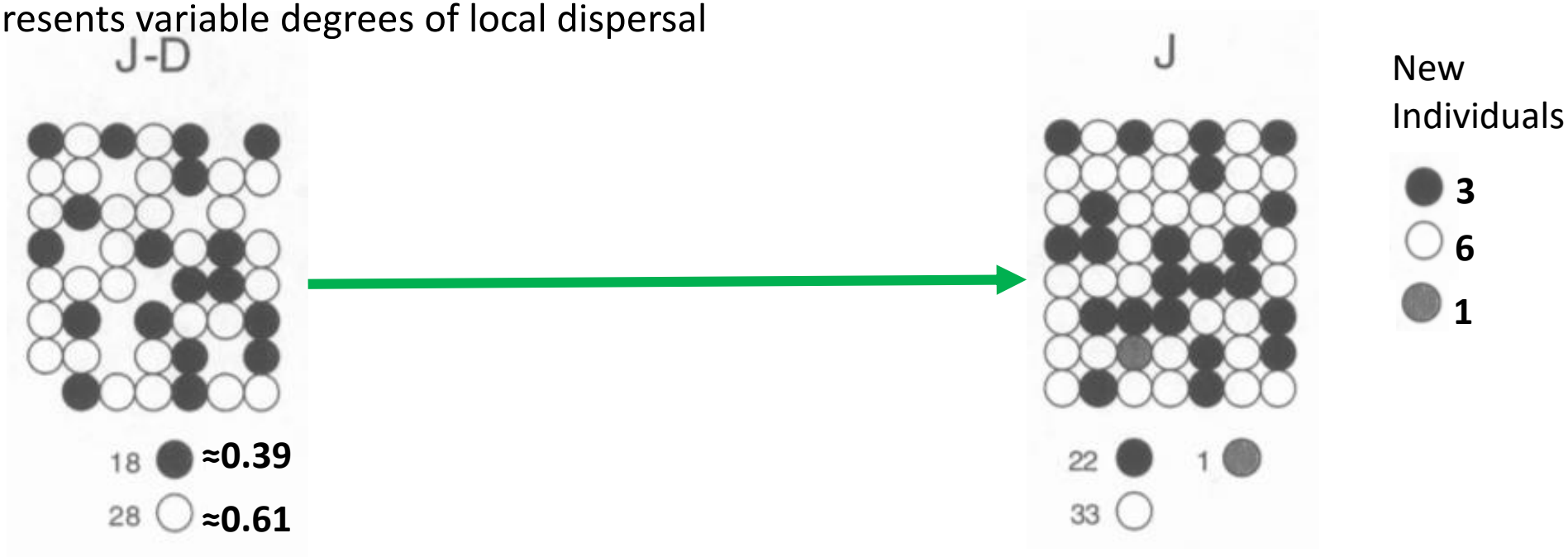
The Unified Neutral Theory of Biodiversity and Biogeography

- This process of disturbance and filling of gaps is repeated



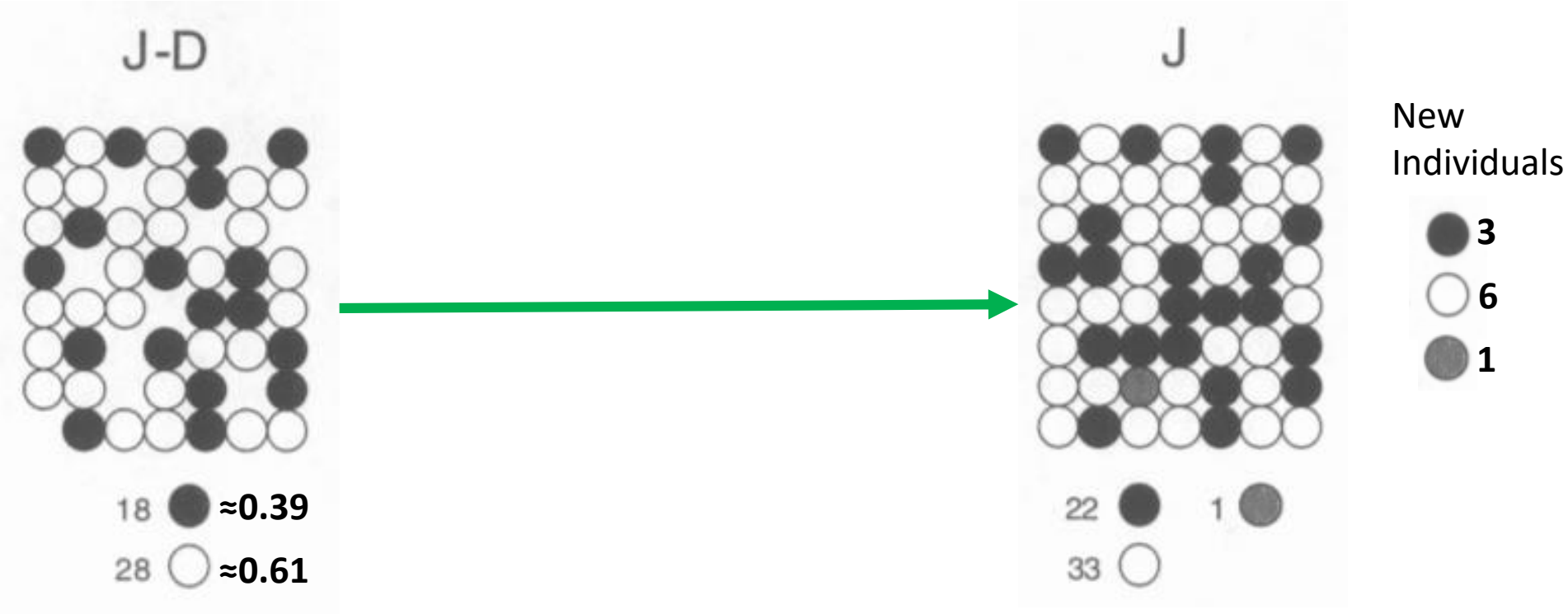
The Unified Neutral Theory of Biodiversity and Biogeography

- Migration from outside the community can also occur
- We denote this migration rate m and the identities of the migrants are proportional to the relative proportions of species in the metacommunity
- m=1 means that the metacommunity is entirely mixed so the local community is a random sample of the meta community
- m=0 represents no migration from the metacommunity
- 0<m<1 represents variable degrees of local dispersal



The Unified Neutral Theory of Biodiversity and Biogeography

- There can also be speciation in which a single individual is replaced by a individual of a novel species
- We denote this speciation rate v and it is typically quite small



Neutral Theory: Parameter Summary

- J is the fixed number of sites for individuals within a community
- p is the probability of the removal of an individual by disturbance (same for all species)
  - Alternatively births and deaths can be continuous
  - All species have the same birth rate (b) and death rate (d)
- m represents dispersal
- v is the speciation rate (constant for all places, times, and species)
- The fundamental biodiversity number $\theta=2Jv$

Predictions of Neutral Theory: Group Exercise!

1. Divide into 6 groups
   a) Each group will receive a neutral theory parameter on a sheet of paper
2. Make predictions about the effect of changing your parameter (5 minutes)
   a) Do this BEFORE opening R
3. Open R and load the script file from the website (2 Minutes)
4. Run your code with different values of your parameter (5 Minutes)
5. Describe how varying your parameter changes the shape of the SAD (5 Minutes)
   a) Does the result of your experiment match your predictions?
6. Find the other group with your parameter and compare notes (5 Minutes)
   a) Do your observations and conclusions agree with theirs?
7. Nominate 1-3 group members to present your observations to the class (2 Minute presentation)

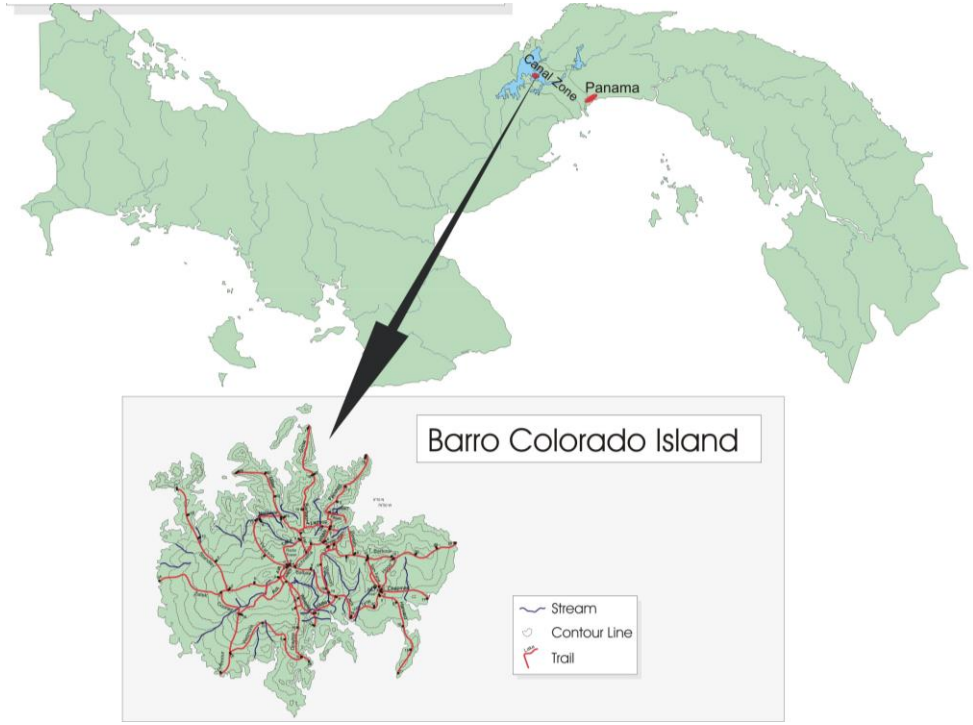
How do we know if models have a good enough fit?

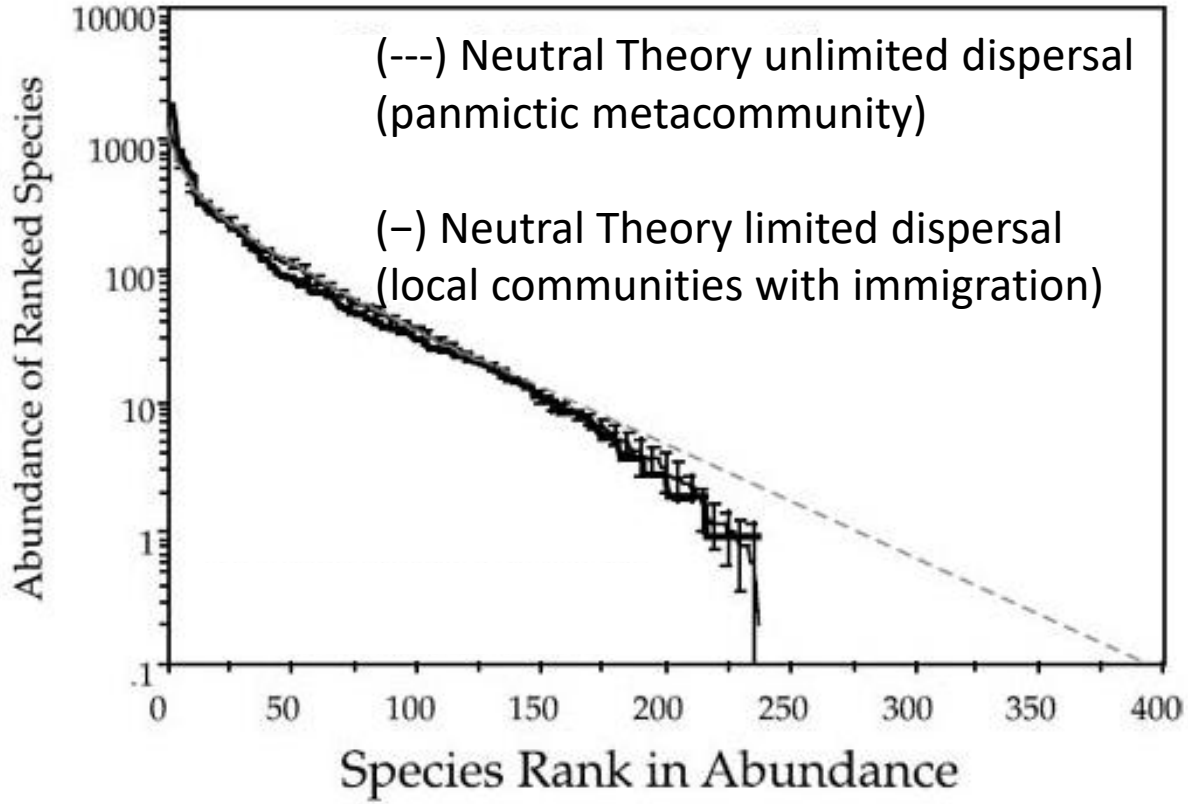
How does Neutral theory serve as a null model?

- Assumes:
  - No differences between species
  - No effect of environment
- Provides predictions for communities based exclusively on neutral processes
  - Dispersal
  - Speciation
- What can be explained without the use of more complex ideas like niche competition or the intermediate disturbance hypothesis
- This allows us to compare more complex models and determine whether and how they outperform Neutral Theory

Do we have evidence for the Neutral Theory?

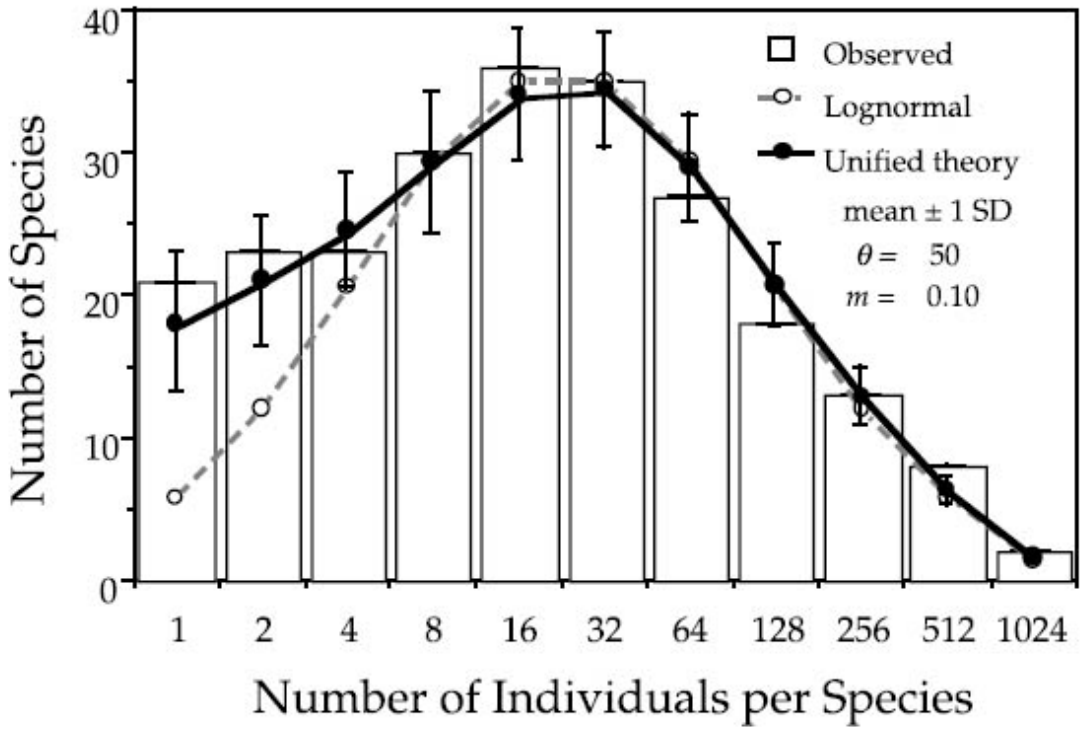
Case Study: Barro Colorado Island





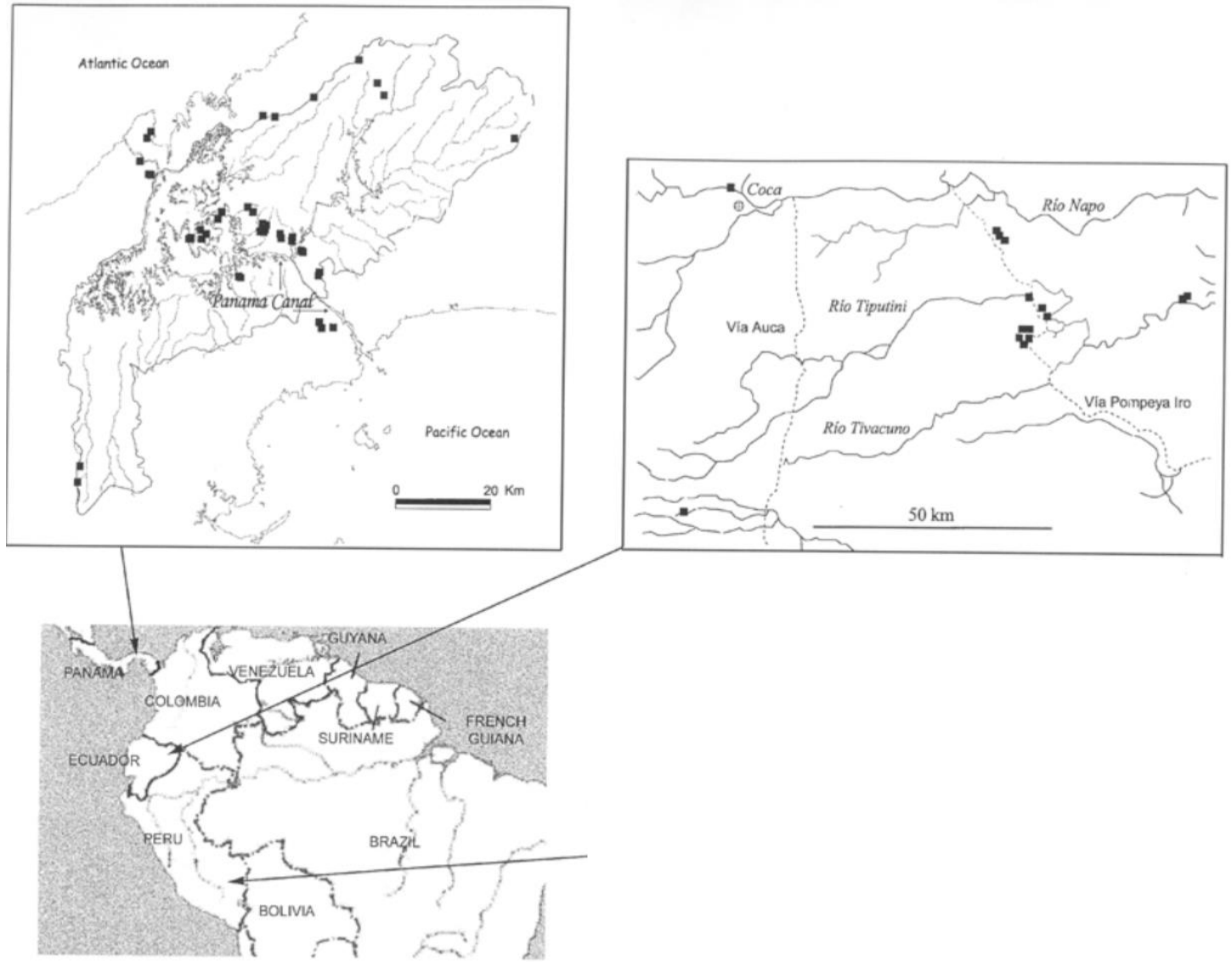
Case Study: Barro Colorado Island- Preston Plots

- Neutral theory predictions better supported by data than Lognormal



The Neutral Model Predicts β diversity

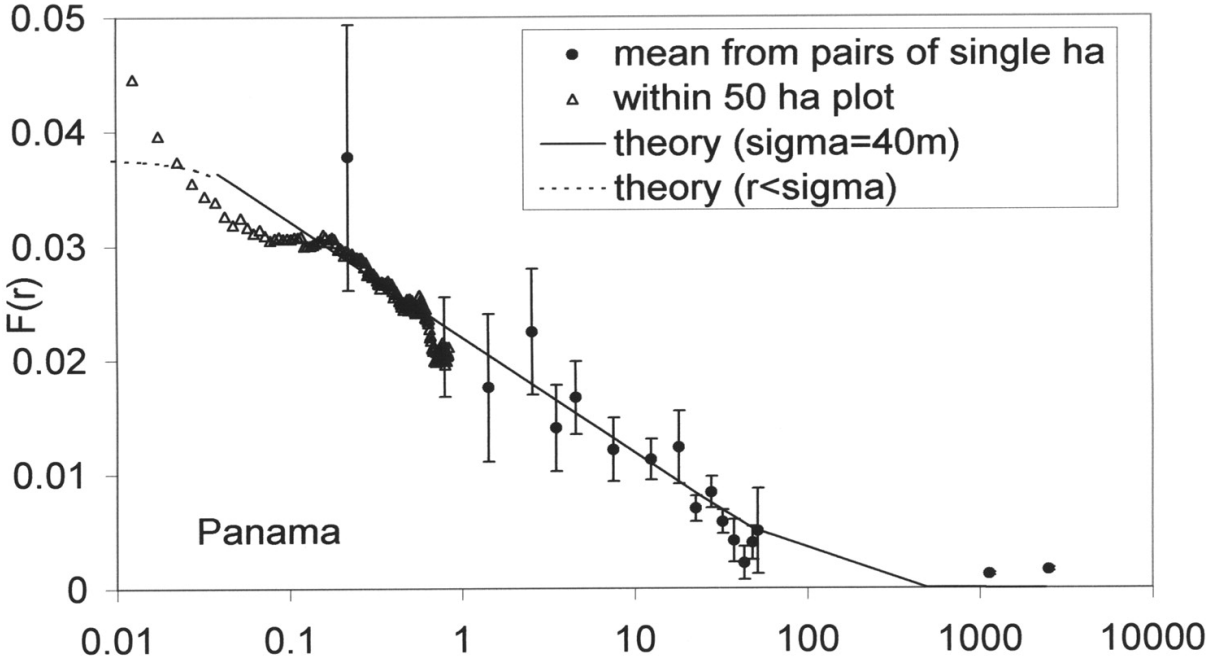
- Reminder: β diversity is the turnover in species composition along an environmental gradient
- One way to measure β diversity is the probability (F) that two individuals, drawn at random, separated by a given distance (r) are the same species

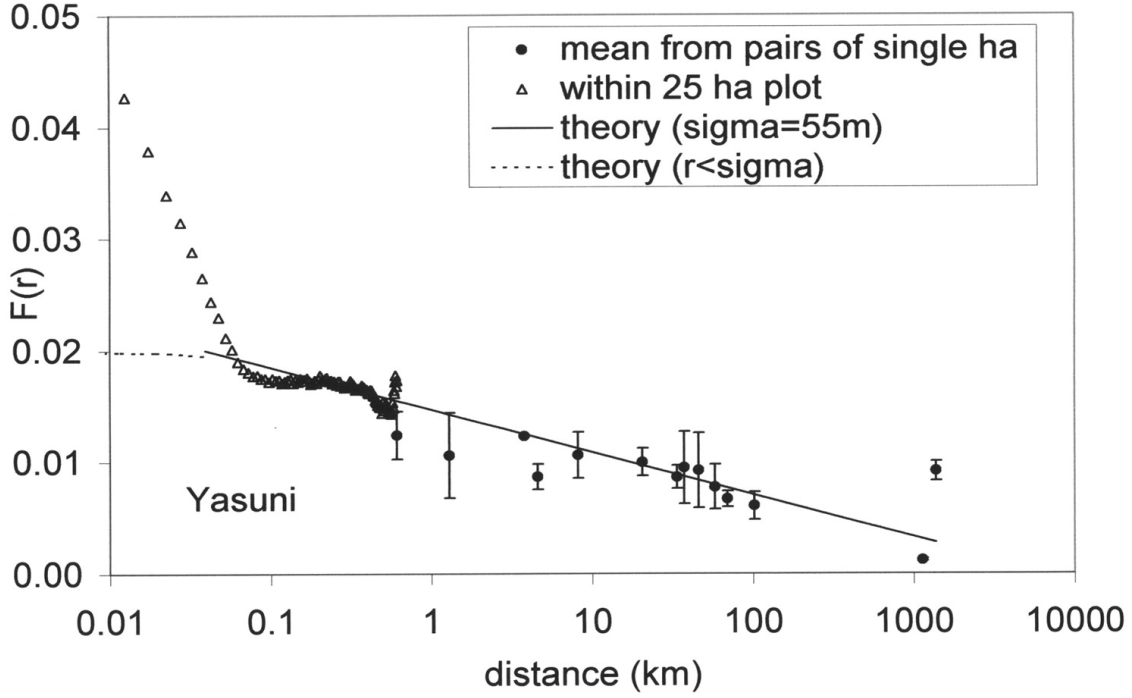


Condit et al. (2002) Science 295:666-669

The Neutral Model Predicts β diversity

- But only at intermediate distances (r=0.2 – 50km)





Conclusions: Neutral Theory

- Neutral theory suggests that species differences are unnecessary to explain observed macroecological patterns (e.g. species abundance distributions)
  - This would make community ecology irrelevant to biogeography!
- Neutral Theory is more consistent with some species abundance distributions than alternatives
- Neutral theory is consistent with beta diversity measures over a wide range of distances
- Neutral theory serves as a viable null model for models of macroecological processes.

Implications for Conservation

- What are we trying to conserve?
  - Individual Species?
  - Whole ecosystems?
  - Diversity itself?
- The dominant processes driving species abundances determines the appropriate scale of action/policy
  - Microenvironment (Habitat requirements, obligate mutualists, etc.)
  - Ecosystem boundaries (Transport processes, cycles)
  - Biogeography (speciation, dispersal)