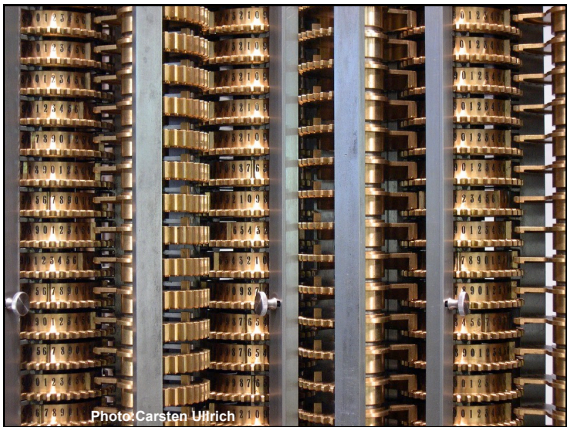


Photo: Carsten Ullrich

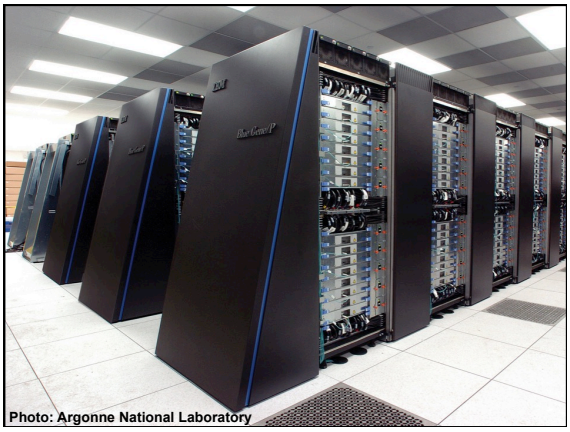
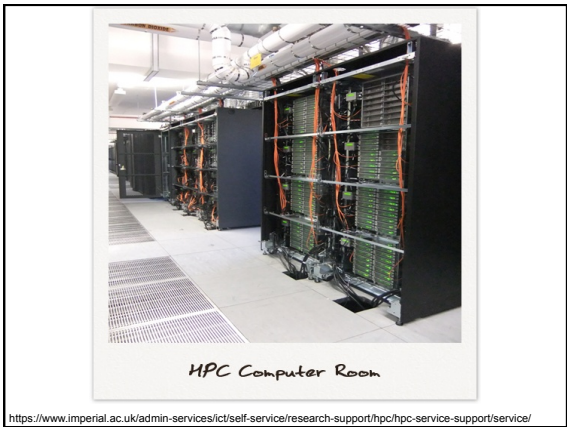
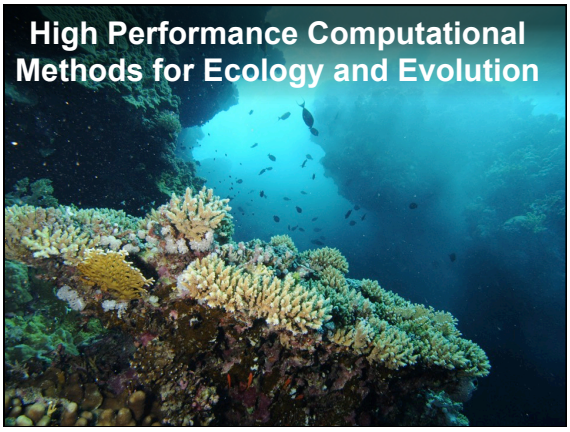


Photo: Argonne National Laboratory

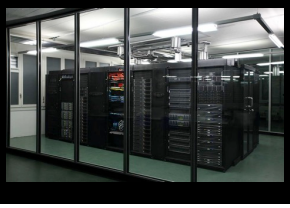

OAK RIDGE
IBM
summit
Photo: Carlos Jones/ORNL - flickr.com


HPC Computer Room
https://www.imperial.ac.uk/admin-services/ict/self-service/research-support/hpc/hpc-service-support/service/


High Performance Computational Methods for Ecology and Evolution

Course objectives

Learn about computers and programing
Good programming practice
Running code in parallel on a cluster
Code optimisation

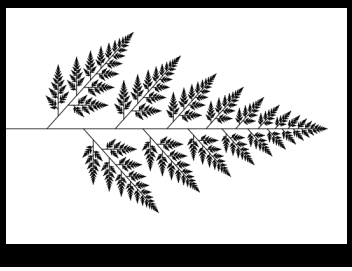


Course objectives

Ecological neutral theory
Stochastic and event based models

Course objectives

Fractals in biology
Iterative functions and chaos



A few other things

- Fewer lectures more practical
- Worksheet to hand in for credit
- J.Rosindell@imperial.ac.uk
- Kennedy building ground floor

Ecological Neutral Theory:

Assumes all individuals are ecologically equivalent

(Caswell 1976)
(Hubbell 1979)
Hubbell 1997)
(Bell 2000)
(Bell 2001)
(Hubbell 2001)

Ecological Neutral Theory: Madness or Misunderstood?

"This flies in the face of years of ecological theory (supported by data) maintaining that species are *not ecologically equivalent*"

Jerry Coyne

"A preoccupation with neutral theory could marginalize biodiversity science, competing for resources with process-based studies, while having little to offer conservation and policy."

Jim Clark

"It's probably the most misunderstood theory in contemporary ecology"

Arne Schroder

Ecological Neutral Theory: Madness or Misunderstood?

1.) What is neutral theory?

2.) Example neutral models

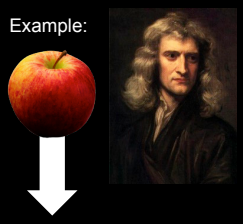
3.) Uses of neutral theory

4.) Applications in island biogeography

A few words about theory in physics …

- Scientific theory conforms with empirical data and puts forward an 'explanation' for observed phenomena

Example:



$$F = G\frac{m_1 m_2}{r^2}$$

A few words about theory in ecology …

Any ecological work that uses mathematical formulas or a computer

Ecological Neutral Theory

Assumes all individuals are ecologically equivalent

Is not a claim that all individuals are ecologically equivalent

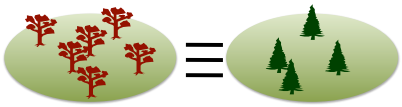
Is about making some assumptions and seeing where they get us

(Caswell 1976)
(Hubbell 1979)
Hubbell 1997)
(Bell 2000)
(Bell 2001)
(Hubbell 2001)

Common misconceptions about what neutral theory is …

~~The term 'neutral model' can be used interchangeably with 'null model'~~

'neutral models' assume all **species** are the same



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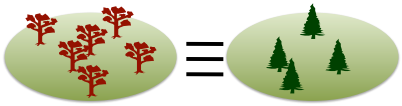

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The demographic properties of an individual are independent of its species identity

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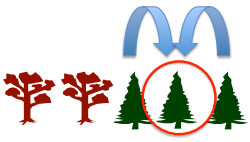
A model in which species are interchangeable is neutral

The demographic properties of an individual are independent of its species identity



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Ecological Neutral Theory: Madness or Misunderstood?

1.) What is neutral theory?

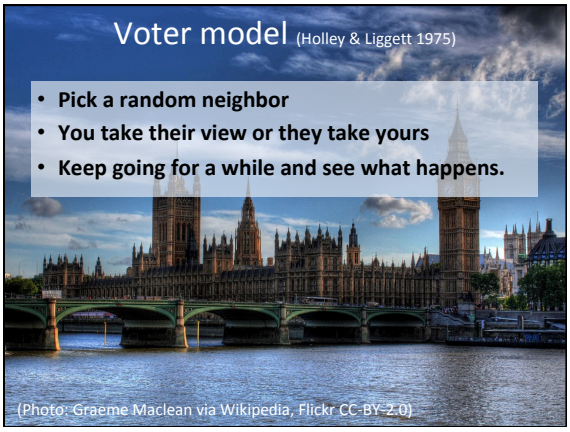
2.) Example neutral models

3.) Uses of neutral theory

4.) Applications in island biogeography

Voter model (Holley & Liggett 1975)

- Pick a random neighbor
- You take their view or they take yours
- Keep going for a while and see what happens.



(Photo: Graeme Maclean via Wikipedia, Flickr CC-BY-2.0)

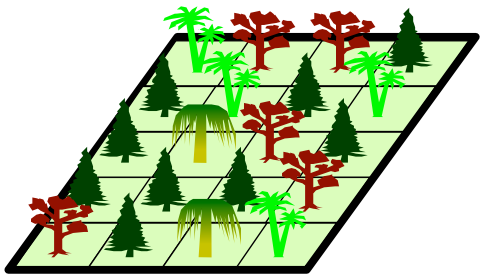
Voter model – relating to biology

- Political view becomes species identity
- People become places in space where an individual could live
- Dispersal is over very short distances

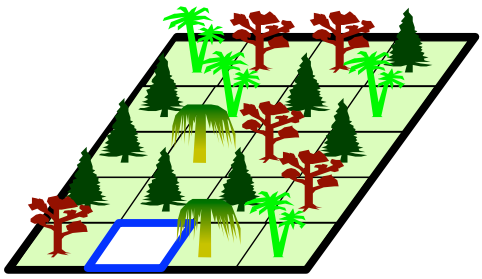
Voter model – what we found

- Found some impenetrable clumps forming
- There are edge effects
- Eventually everyone in each connected group holds the same view
- Hence we introduced mutation

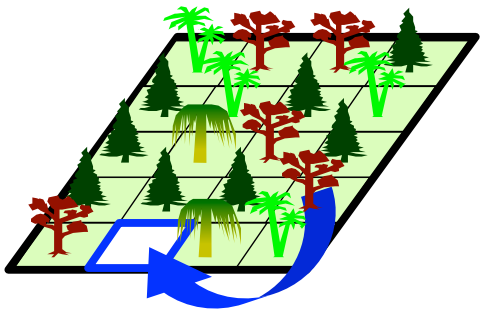
The model rules in brief



The model rules in brief



The model rules in brief



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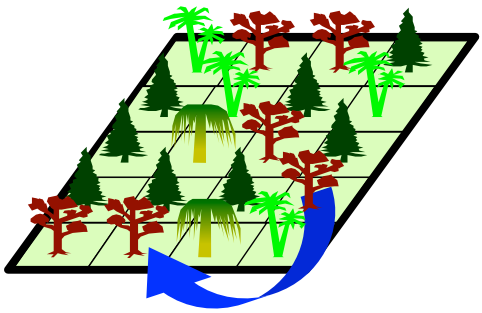

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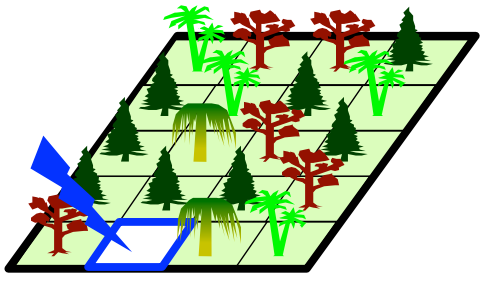
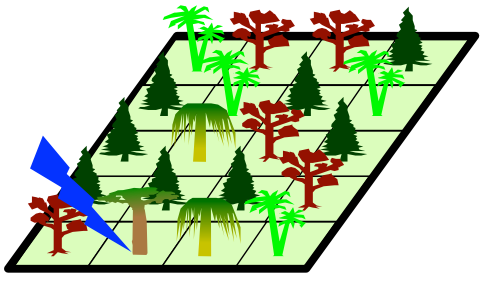
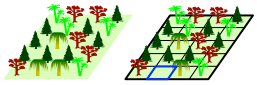


The model rules in brief



Variations on the theme

- The zero sum assumption

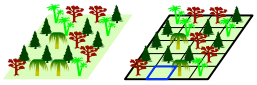


- Speciation mode (none)

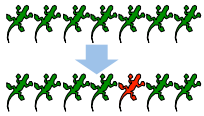
(Caswell 1976)
(Bell 2000)
(Bell 2001)

Variations on the theme

- The zero sum assumption



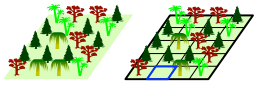
- Speciation mode (point mutation)



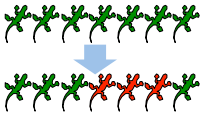
(Hubbell 1997)
(Hubbell 2001)

Variations on the theme

- The zero sum assumption



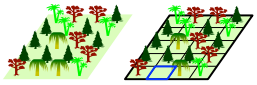
- Speciation mode (random fission)



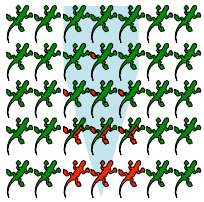
(Hubbell 2001)
(Hubbell & Lake 2002)

Variations on the theme

- The zero sum assumption



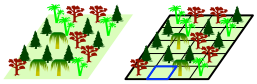
- Speciation mode (protracted)



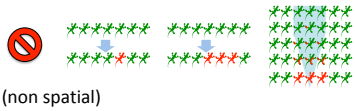
(Rosindell *et al.* 2010)

Variations on the theme

- The zero sum assumption



- Speciation mode

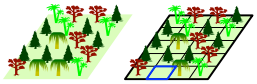


- Spatial structure (non spatial)

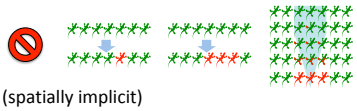
(Caswell 1976)

Variations on the theme

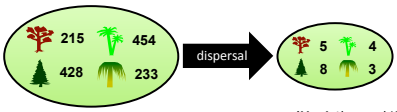
- The zero sum assumption



- Speciation mode



- Spatial structure (spatially implicit)



(MacArthur and Wilson 1963)
(Hubbell 2001)

Variations on the theme

- The zero sum assumption
- Speciation mode
- Spatial structure (spatially explicit network)

(Economo & keitt 2008)
(Warren 2010)
(Vanpeteghem & Haegeman 2010)
(Muneepeerakul *et al.* 2008)

Variations on the theme

- The zero sum assumption
- Speciation mode
- Spatial structure (fully spatially explicit)

(Holley & Liggett 1975)
(Bramson et al. 1998)
(Durett & Levin 1996)
(Hubbell 2001)
(Chave et al. 2002)
(Chave & Leigh 2002)
(Zillio et al. 2005)
(Rosindell & Cornell 2007,2009)
(Pigolotti & Cencini 2009)
(O´Dwyer & Green 2010)
(Etienne & Rosindell 2011)

Variations on the theme

- The zero sum assumption
- Speciation mode
- Spatial structure

Variations on the theme

- The zero sum assumption
- Speciation mode
- Spatial structure

(Hubbell 2001)
(Leigh 2007)
(Leigh *et al.* 2010)

Variations on the theme

- The zero sum assumption
- Speciation mode
- Spatial structure

Your exercise questions

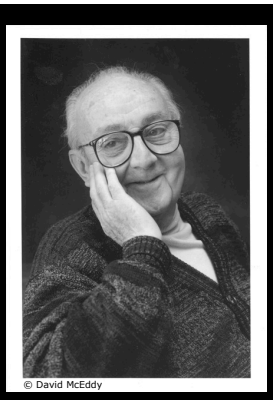
Ecological Neutral Theory: Madness or Misunderstood?

1.) What is neutral theory?

2.) Example neutral models

3.) Uses of neutral theory

4.) Applications in island biogeography



George E P Box (Box & Draper 1987)

Essentially, all models are wrong,

All models can fail upon being challenged with data

That's Okay!

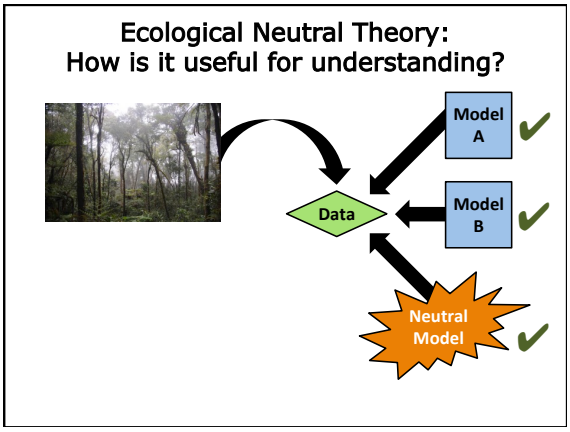
but some are useful

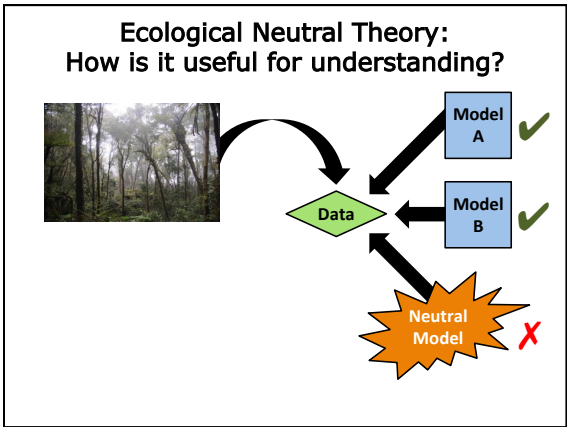
1. Helping to understand
2. Helping to predict

Ecological Neutral Theory: How is it useful for understanding?

Ecological Neutral Theory: How is it useful for understanding?

Ecological Neutral Theory: How is it useful for understanding?


Ecological Neutral Theory:
How is it useful for understanding?
Model A
Model B
Data
Neutral Model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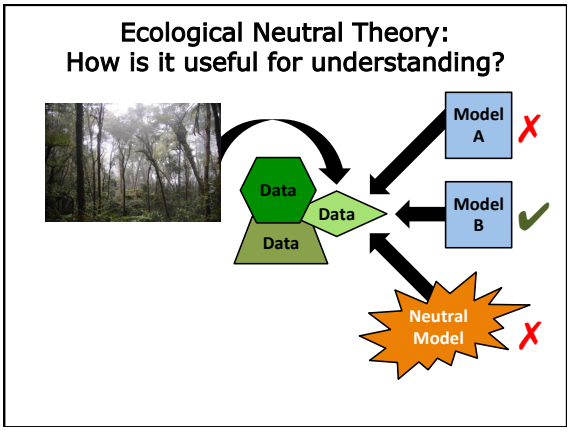
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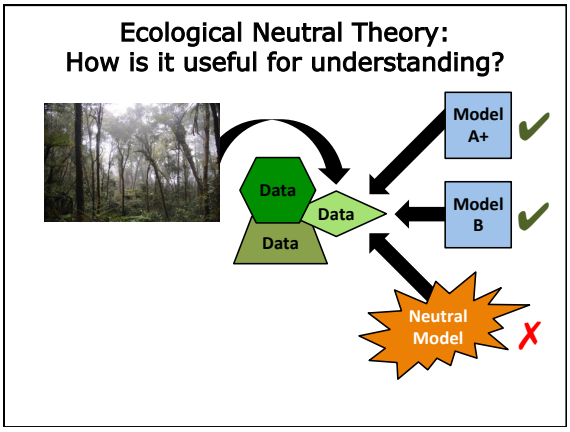
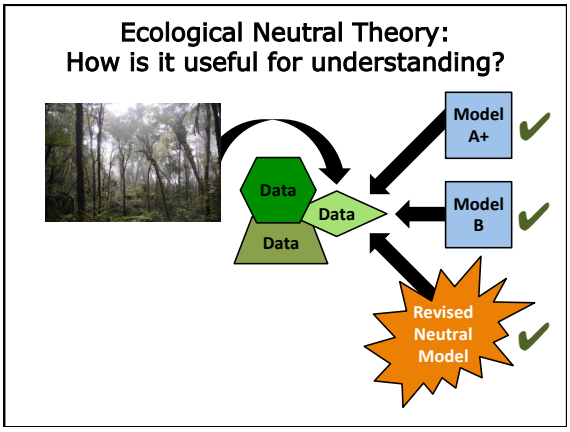
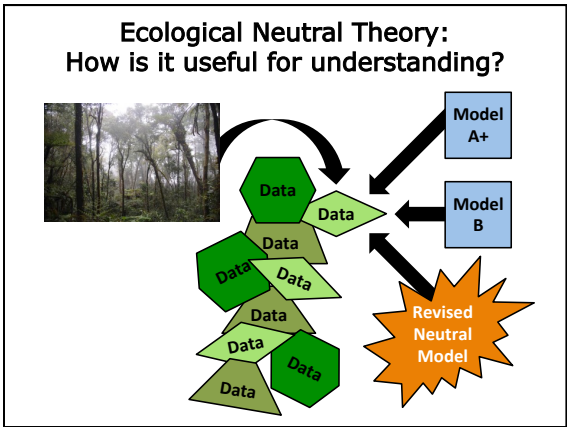
Data
Data
Data
Neutral Model

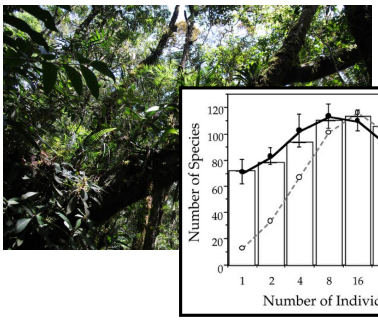

Ecological Neutral Theory:
How is it useful for understanding?
Model A+
Model B
Data
Data
Data
Neutral Model


Ecological Neutral Theory:
How is it useful for understanding?
Model A+
Model B
Data
Data
Data
Revised Neutral Model


Ecological Neutral Theory:
How is it useful for understanding?
Model A+
Model B
Data
Data
Data
Revised Neutral Model

Example data comparison

Species abundance distributions

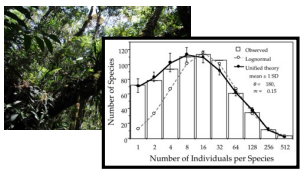


(Hubbell 2001)

Example data comparison

Mean species lifetimes are too short

(Ricklefs 2003, Nee 2005, Ricklefs 2006)

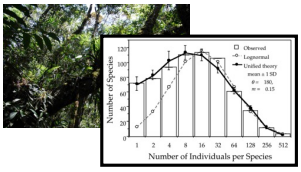


Example data comparison

Mean species lifetimes are too short

(Ricklefs 2003, Nee 2005, Ricklefs 2006)

but that was for point mutation speciation



Protracted Speciation

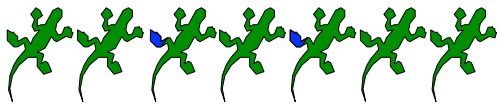
Not an instantaneous event

Protracted Speciation

Not an instantaneous event

Protracted Speciation

Not an instantaneous event



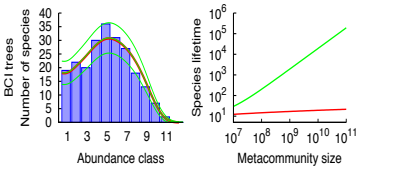
Protracted Speciation

Not an instantaneous event

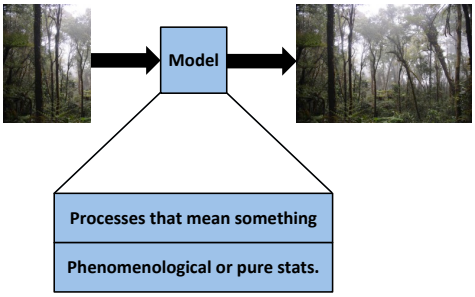
Protracted Speciation

Not an instantaneous event

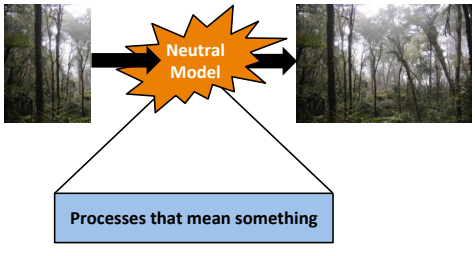
Tropical Forest Tree Data



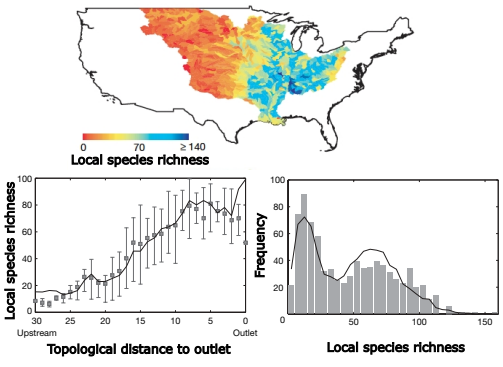
Ecological Neutral Theory: How is it useful for predicting?



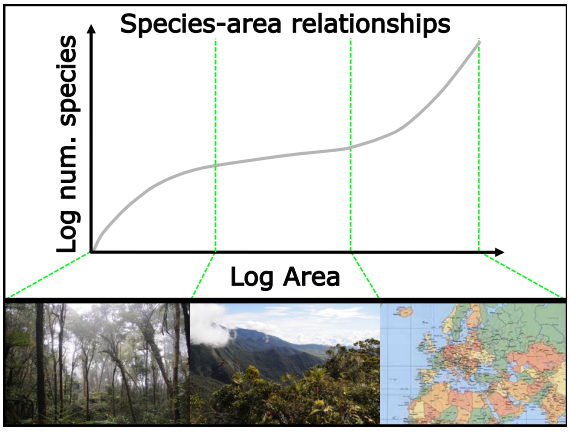
Ecological Neutral Theory: How is it useful for predicting?

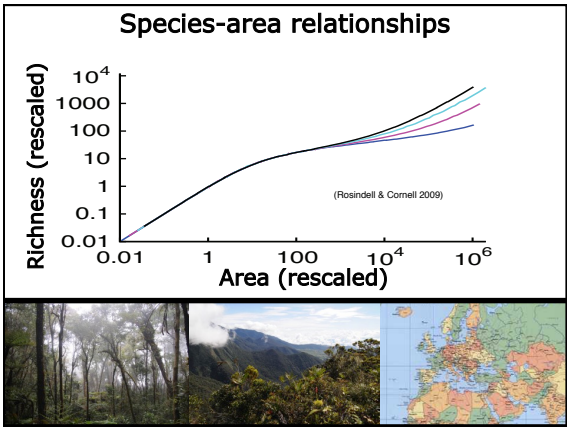


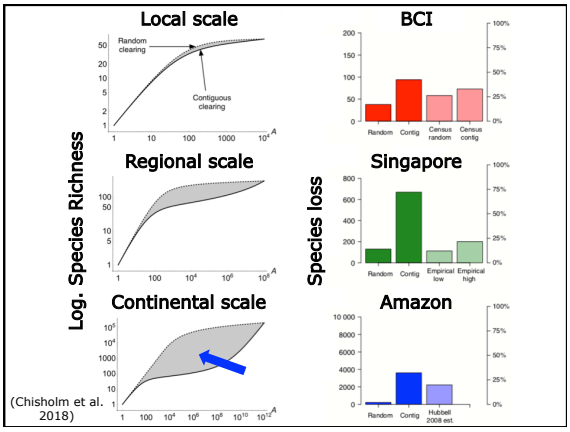
Riverine fish diversity patterns

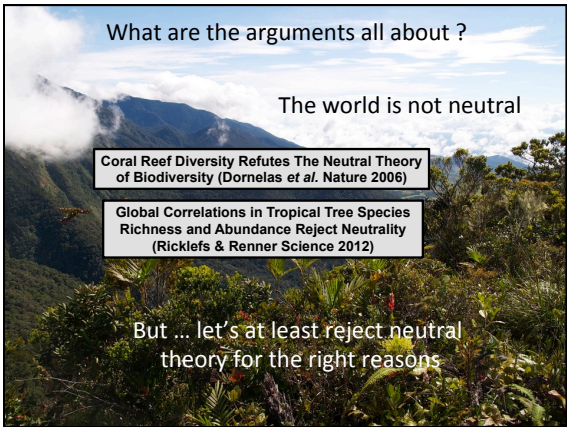


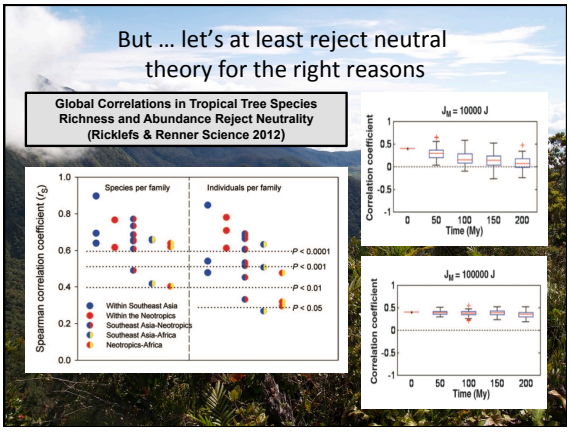
Diagrams from (Muneepeerakul *et al.* 2008)

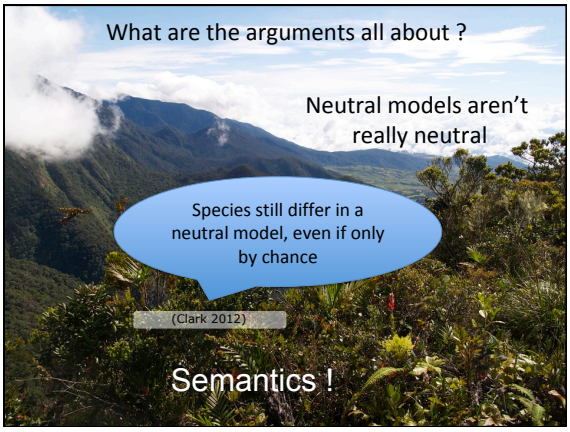

Species-area relationships
Log num. species
Log Area

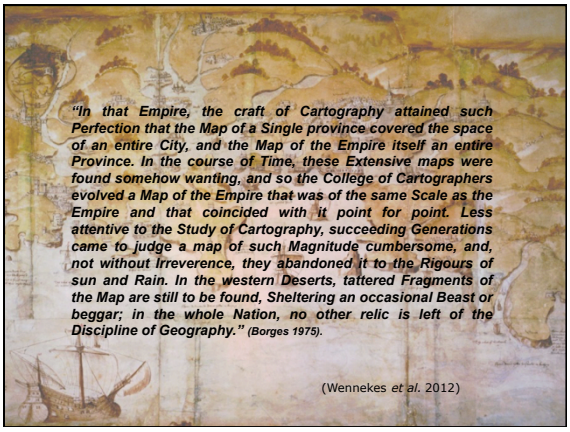

Species-area relationships
Richness (rescaled)
Area (rescaled)
(Rosindell & Cornell 2009)

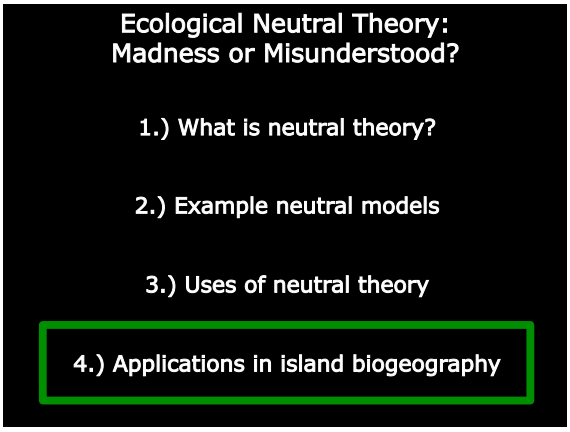

Local scale
Regional scale
Continental scale
Log. Species Richness
BCI
Singapore
Amazon
Species loss
(Chisholm et al. 2018)

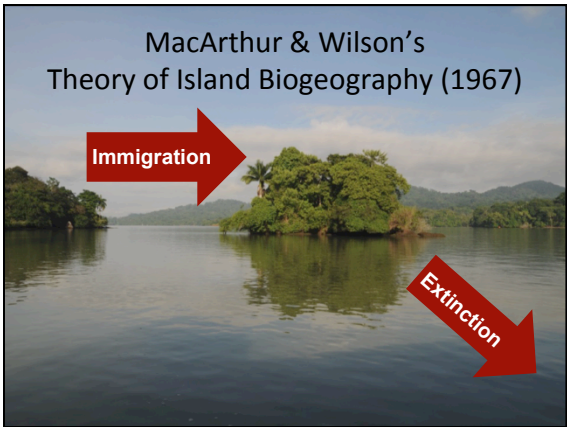

What are the arguments all about ?
The world is not neutral
Coral Reef Diversity Refutes The Neutral Theory of Biodiversity (Dornelas et al. Nature 2006)
Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality (Ricklefs & Renner Science 2012)
But … let's at least reject neutral theory for the right reasons

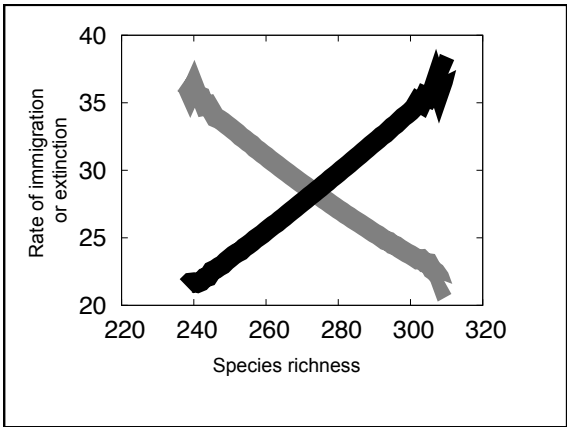

But … let's at least reject neutral theory for the right reasons
Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality (Ricklefs & Renner Science 2012)
Species per family
Individuals per family
Spearman correlation coefficient
Correlation coefficient
Time (My)

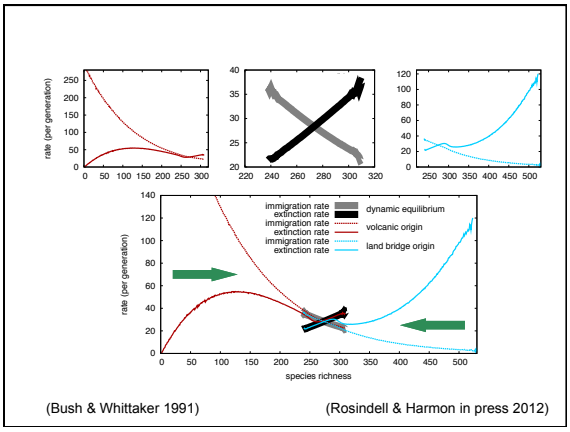

What are the arguments all about ?
Neutral models aren't really neutral
Species still differ in a neutral model, even if only by chance
(Clark 2012)
Semantics !





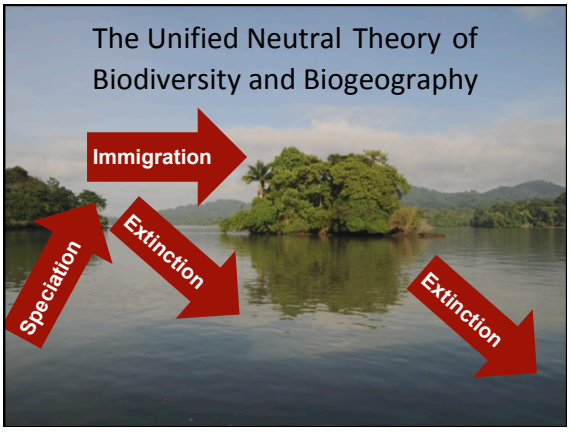


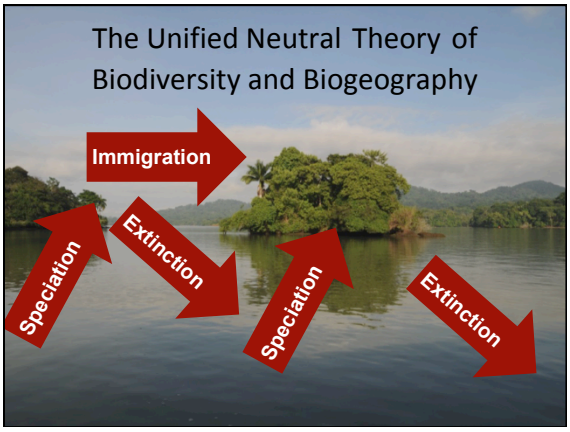




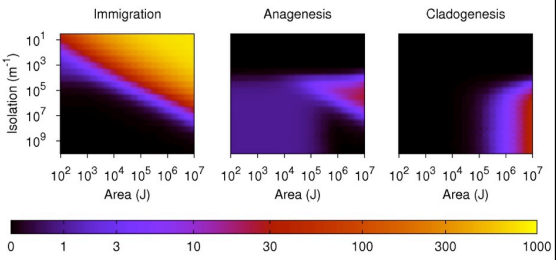
(Bush & Whittaker 1991)

(Rosindell & Harmon in press 2012)



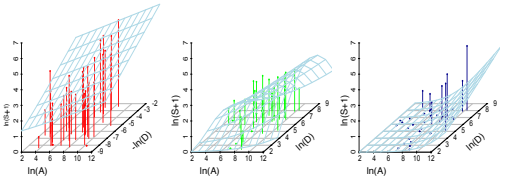


Model results



(Rosindell & Phillimore 2011)

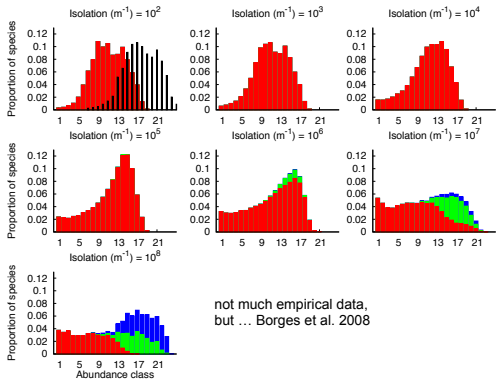
Empirical data: island avifauna



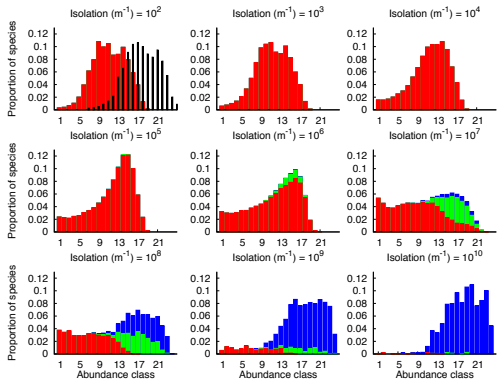
Immigrant Species

Anagenetic Species

Cladogenetic Species

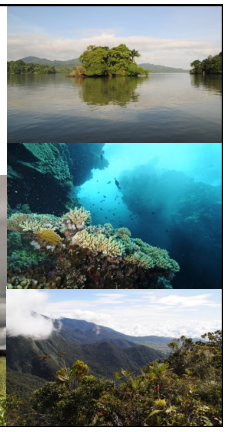


not much empirical data, but … Borges et al. 2008



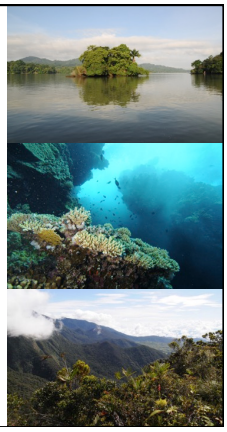
What have we learned about modeling

- John von Neumann "Give me four parameters, and I can fit an elephant. Give me five, and I can wiggle its trunk".



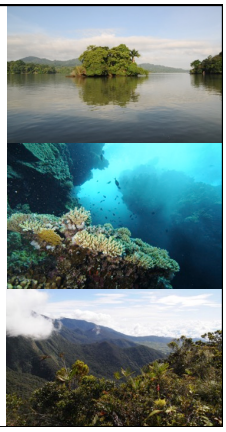
What have we learned about modeling

- John von Neumann "Give me four parameters, and I can fit an elephant. Give me five, and I can wiggle its trunk".
- Theories in biology and in physics are very different
- Modelling for making predictions, and for gaining understanding are two different types of exercise
- Not all data are very informative
- Simplicity vs. complexity – only add complexity when it's needed, use computers when needed
- Start with the end in mind



Neutral theory conclusions

- Neutral theory is a collection of neutral models assuming the demographic properties of an individual are independent of its species identity
- Uses for understanding and predicting but not both at the same time.
- Explains species area relationships and other spatial biodiversity patterns.
- Makes rich predictions about biodiversity and endemicity on islands.
- Neutral theory is one of the many useful tools you have in your tool box.



Ecological Neutral Theory