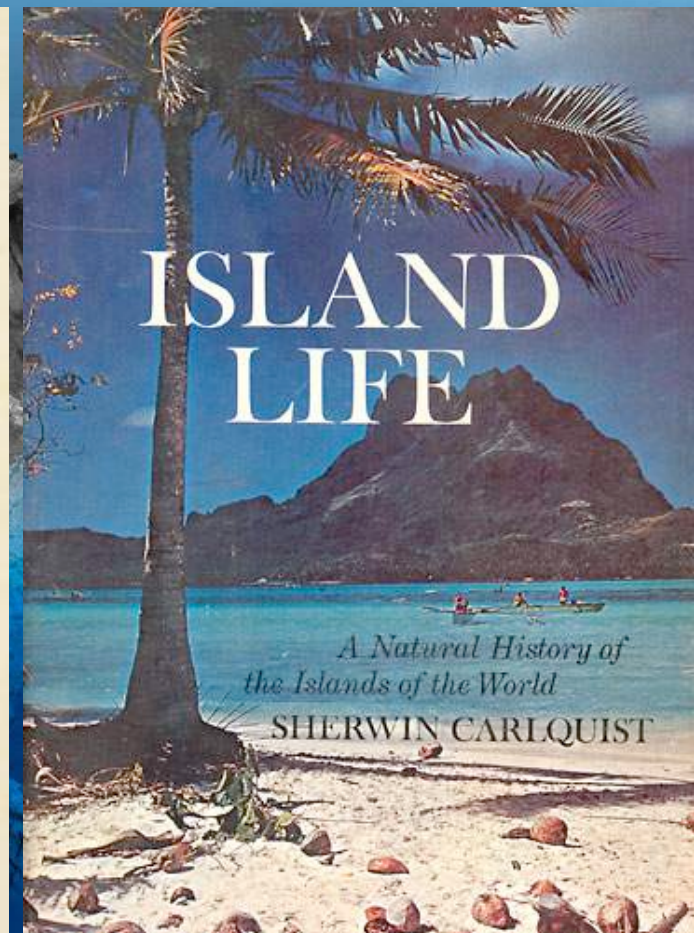
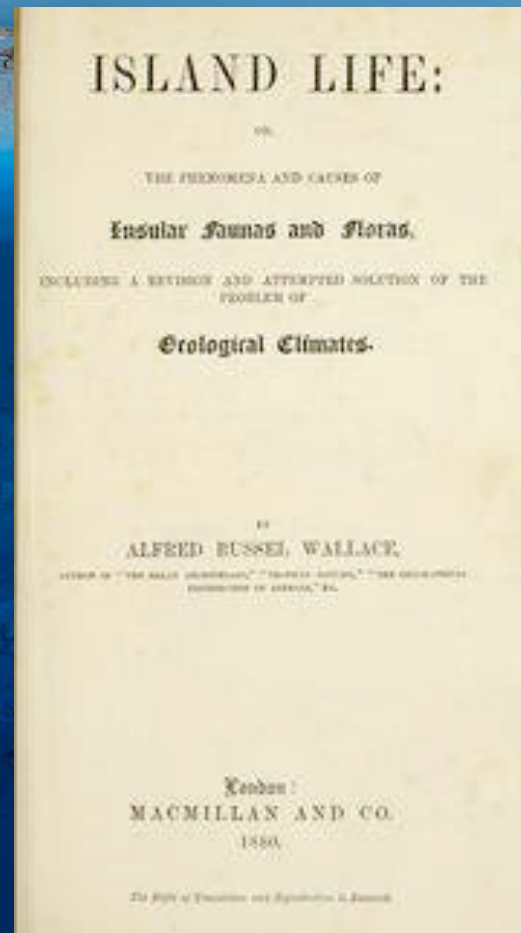


# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”



# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments



Dwarfism: dwarf elephants on Channel Islands

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments



Gigantism: lizards and tortoises on Galapagos Islands

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments



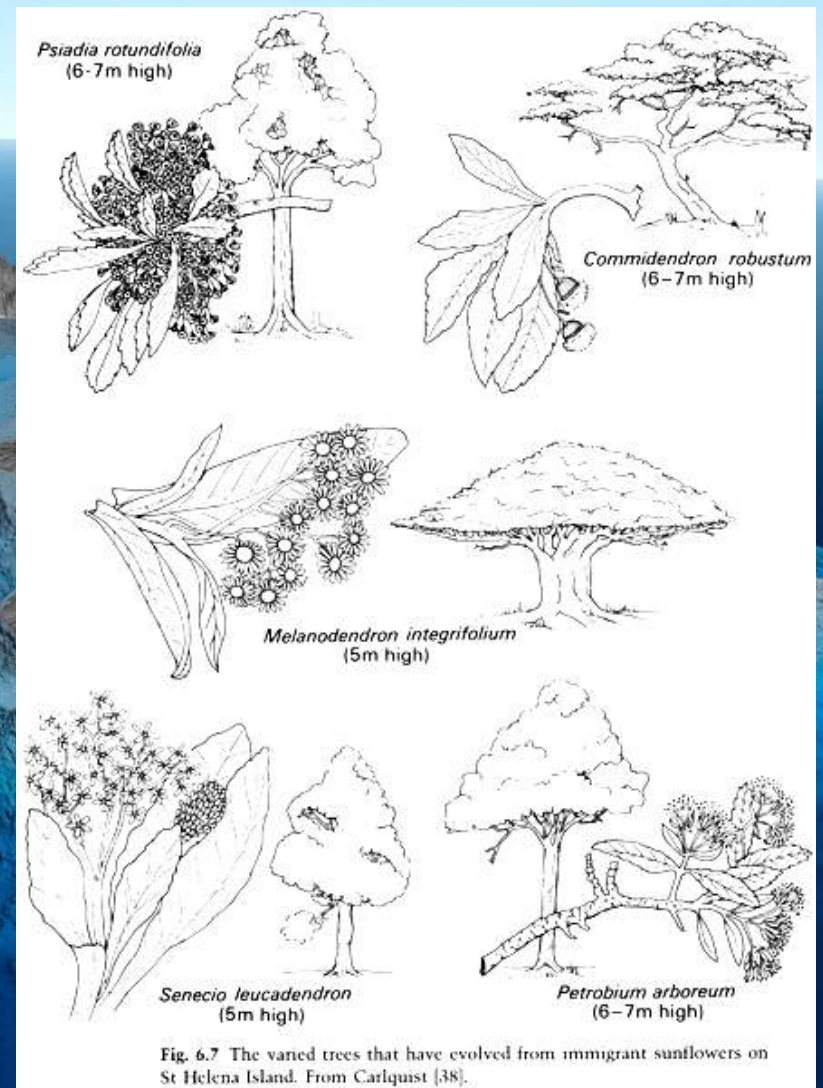
Gigantism: “lily” trees on Canary Islands

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”

- replicate experiments

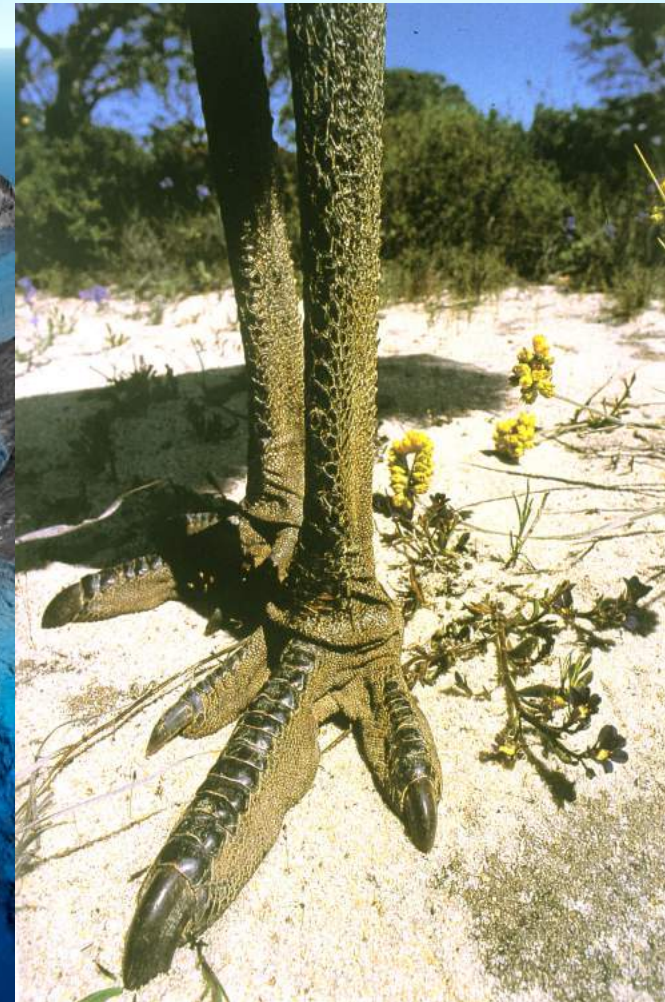


Gigantism: convergent  
“sunflower” trees - St. Helena

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments

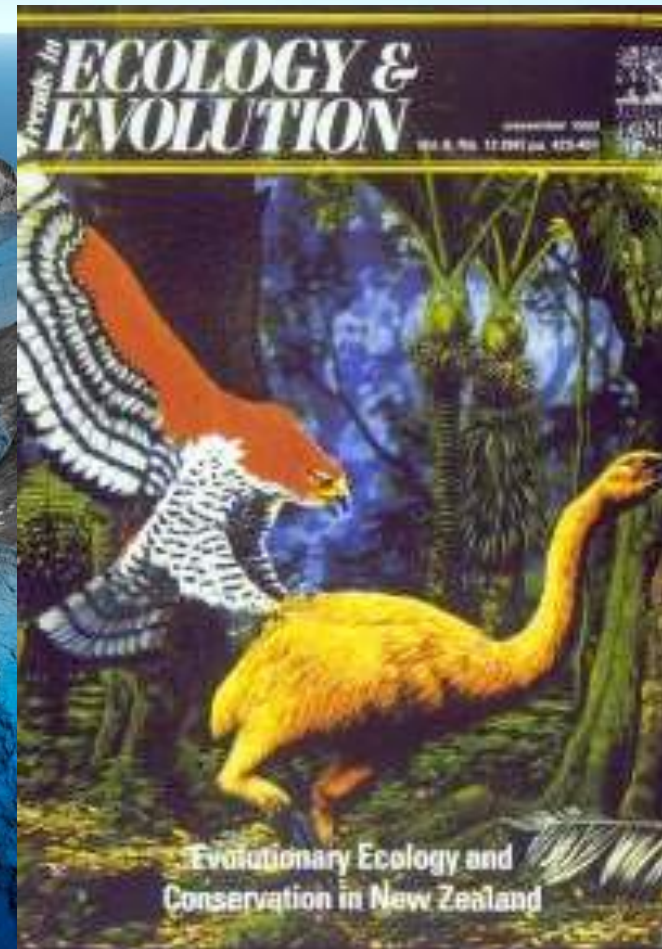


Flightlessness: emu on Australia

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments



Flightlessness: extinct moas on New Zealand

# Biogeography of Islands

Special things go on in islands

- “island life” or “insular biology”
- replicate experiments



Niche shifts: NZ giant wetas (Orthoptera) as small mammals



# Biogeography of Islands

**Special things go on in islands**

- “island life” or “insular biology”
- replicate experiments
- extreme isolation

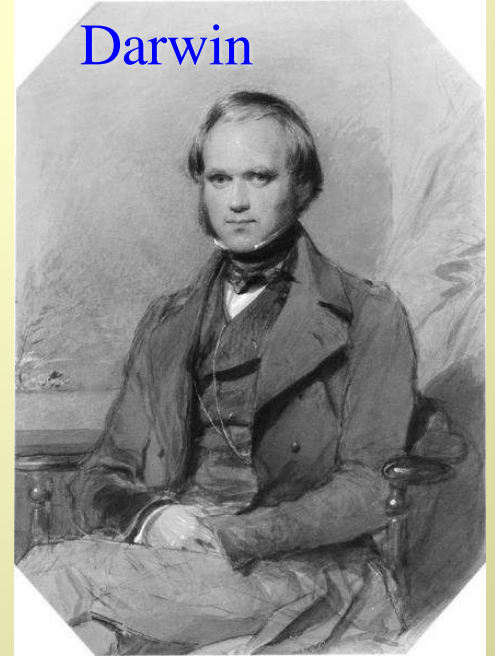
Sweepstakes dispersal

Complete genetic isolation

# Biogeography of Islands

Islands historically important in biogeography

Darwin

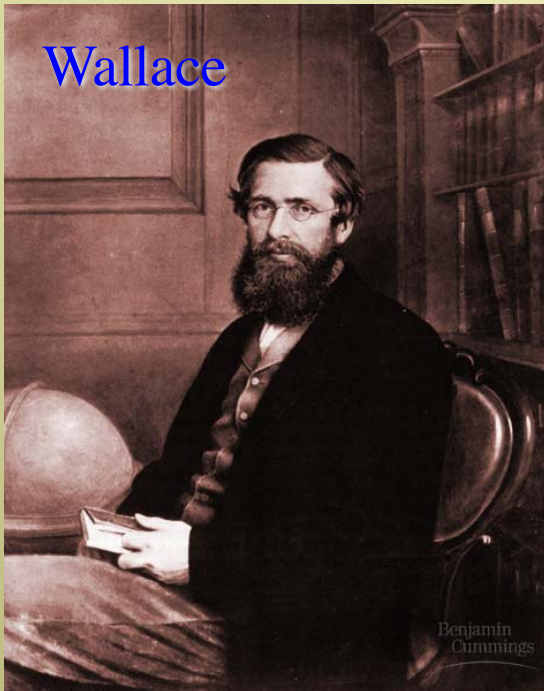


Galapagos

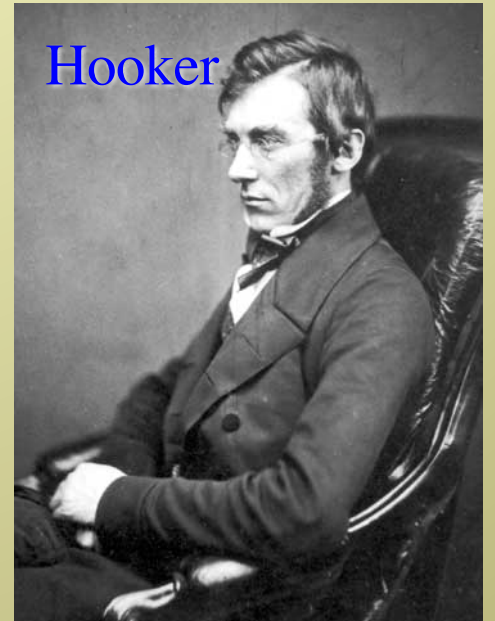
East Indies

South Pacific

Wallace

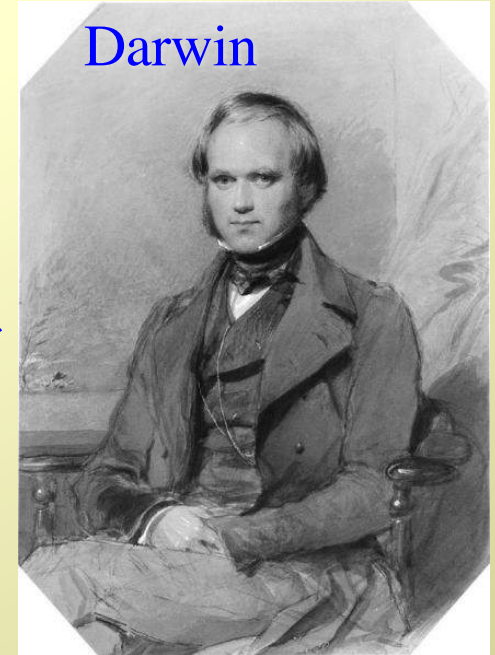


Hooker



# Biogeography of Islands

Islands historically important in biogeography



Galapagos

East Indies

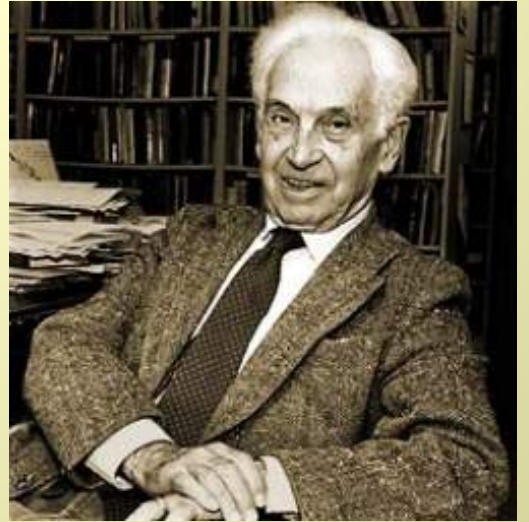
South Pacific



Rosemary & Peter Grant:  
specialists on Darwin's  
finches

# Biogeography of Islands

Islands historically important in biogeography

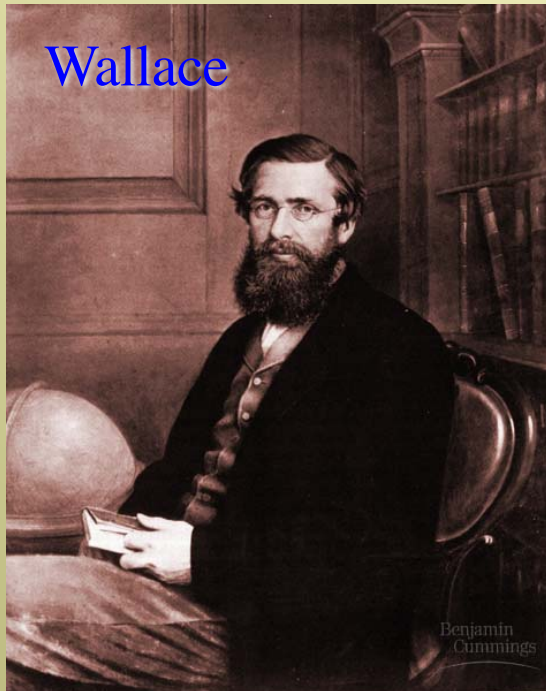


Ernst Mayr: specialist on Australasian birds

Galapagos

East Indies

South Pacific



Wallace

# Biogeography of Islands

Islands historically important in  
biogeography



Rosemary Gillepsie: animal  
specialist on Pacific islands

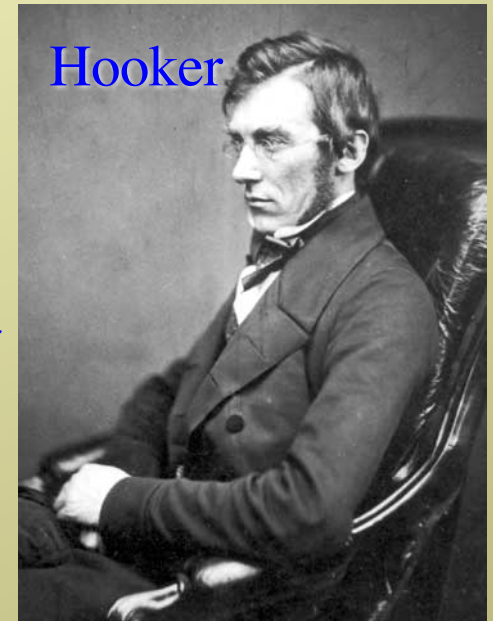


Sherwin Carlquist: plant  
specialist on Pacific islands

Galapagos

East Indies

South Pacific



Hooker

# Biogeography of Islands

Islands biologically important in biogeography

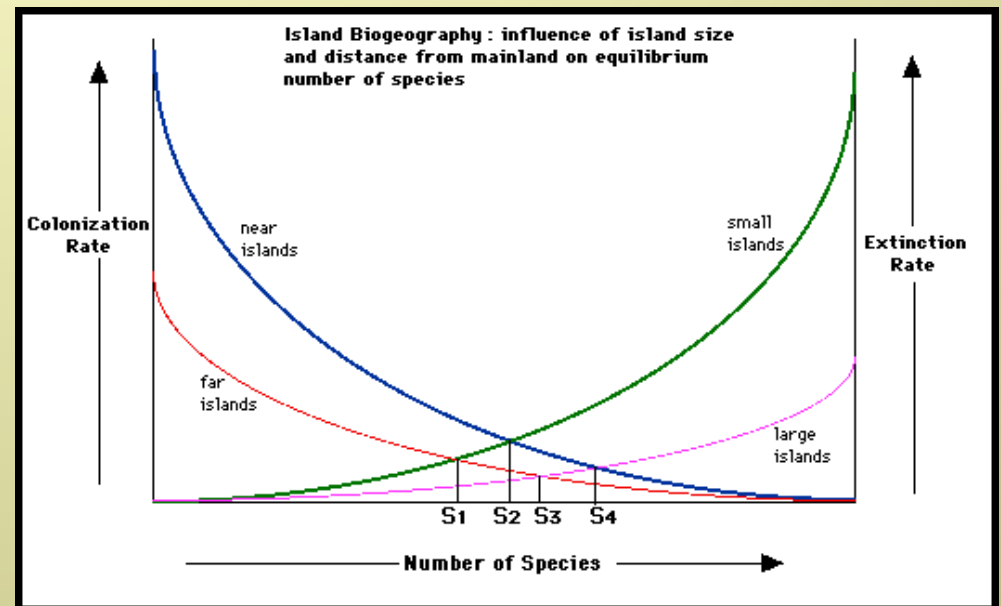
## 1. Island Biogeography

Identifying and quantifying the factors that control 3 phenomena:

rate of island immigration

rate of island extinction

number of species per island

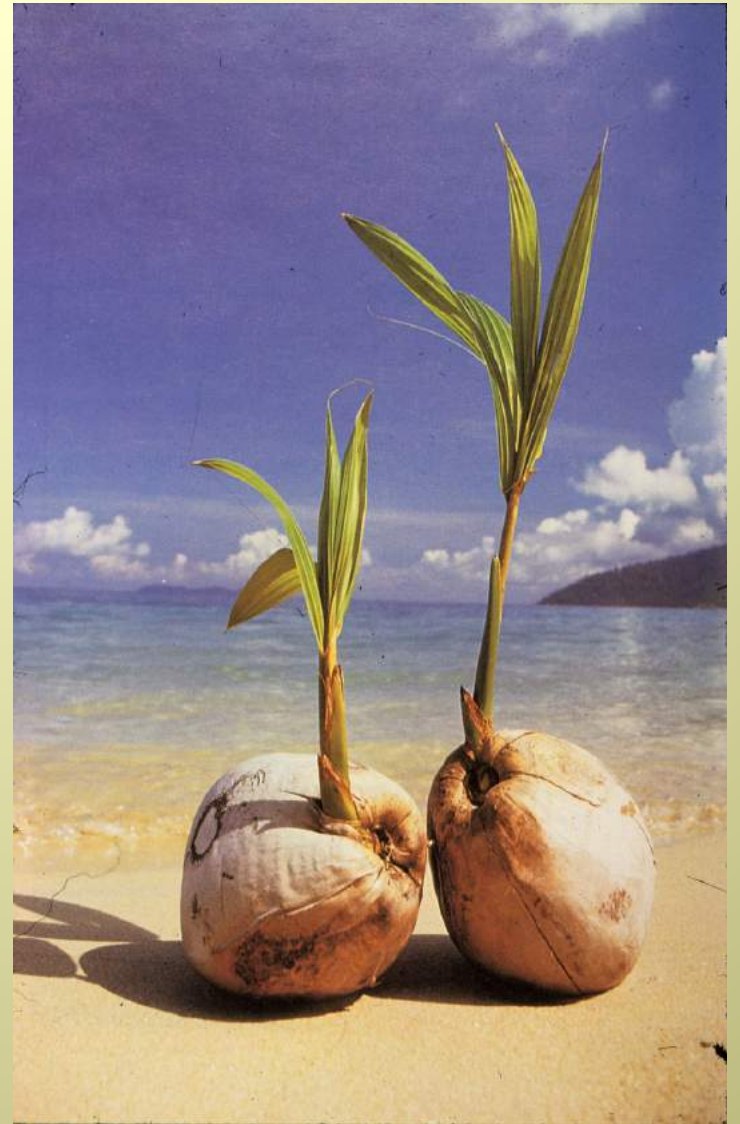


# Biogeography of Islands

Islands biologically important in biogeography

## 2. Dispersal biology

Nature of island biota: how it differs from that of the source-area, and the nature of adaptations of the successful immigrants that permitted them to reach and colonize the island



# Biogeography of Islands

Islands biologically important in biogeography

## 3. Adaptive radiations

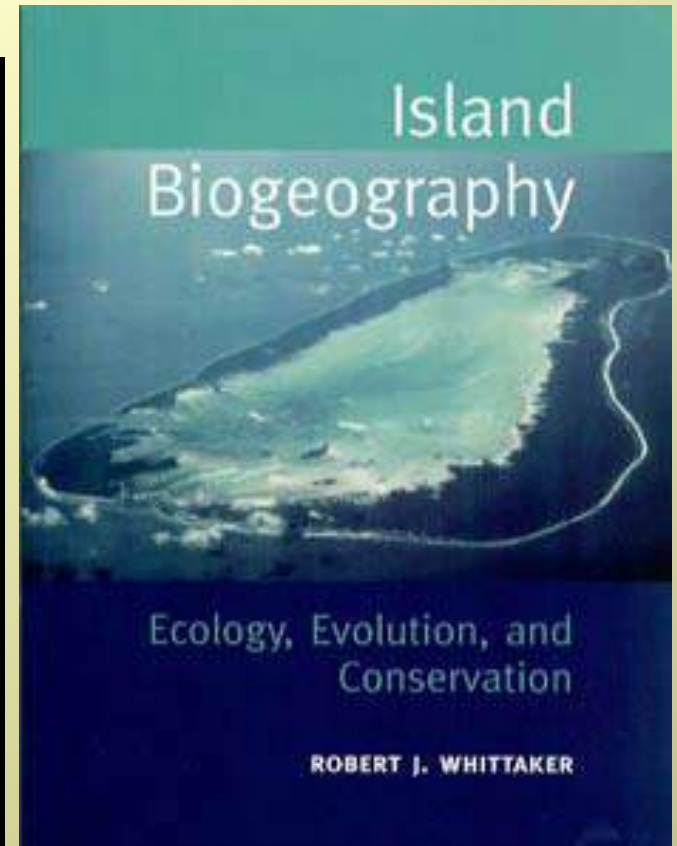
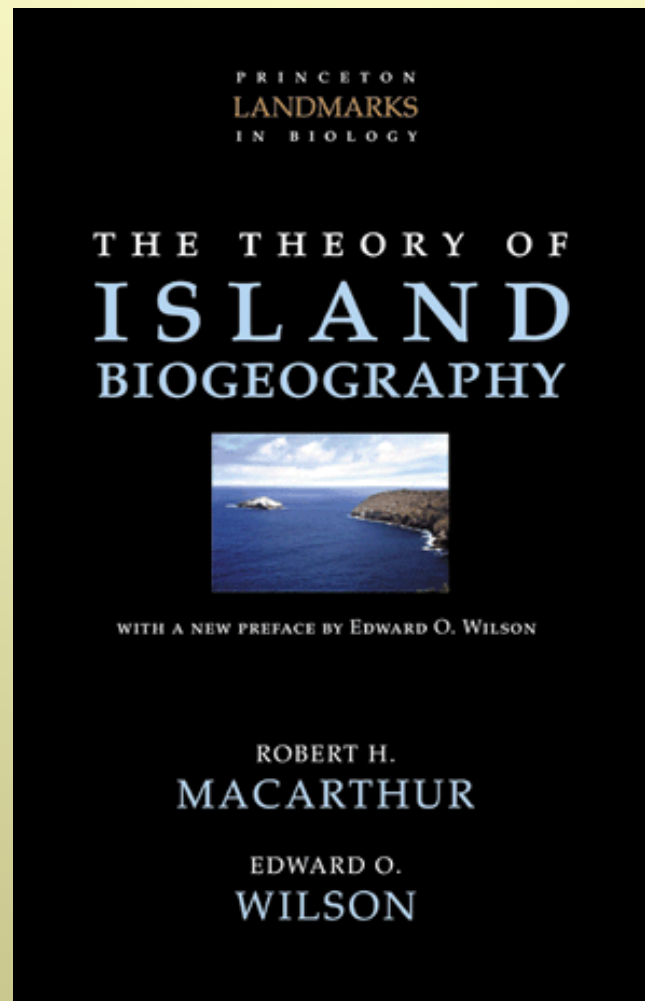
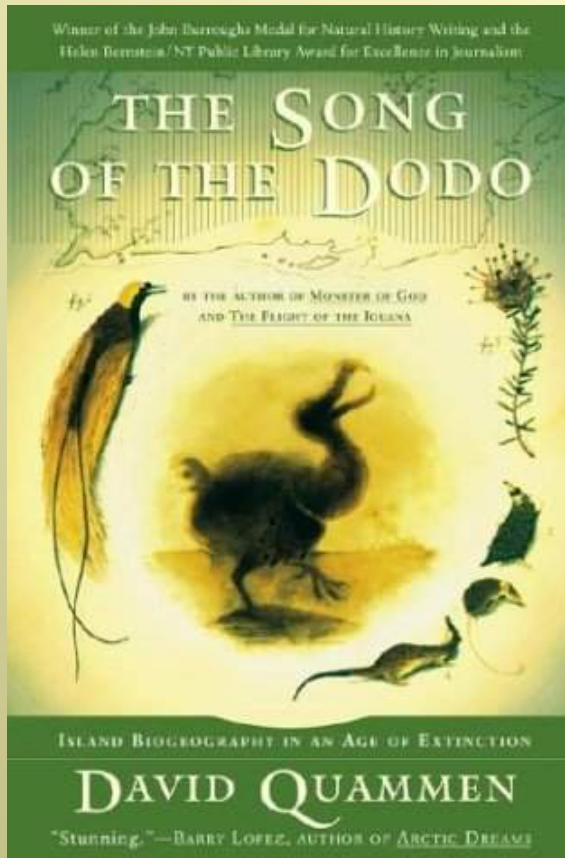
Processes of evolutionary change by which immigrant species diversify and radiate to occupy ecological niches that on the mainland are normally occupied by other groups





# Island Biogeography

Three interrelated ecological and biogeographical patterns seen on islands



# Island Biogeography

1. Species-area relationships - relationship within archipelagos between the sizes of individual islands and the number of species that comprise their biota

- de Candolle recognized that larger islands contain more species than small islands
- Philip Darlington in 1938 quantified this relationship with the herp-fauna of the West Indies



*Darlingtonia*  
Haitian ground snake



*Darlingtonia*  
Cobra lily

Darlington, Philip J. (Museum of Comparative Zoology, Harvard University, Coleoptera-Carabidae) Harvard University, April 1961



THE ORIGIN OF THE FAUNA OF THE GREATER ANTILLES, WITH DISCUSSION OF DISPERSAL OF ANIMALS OVER WATER AND THROUGH THE AIR

By P. J. DARLINGTON, Jr.

Museum of Comparative Zoology, Cambridge, Mass.

#### INTRODUCTION AND ACKNOWLEDGMENTS

THE purpose of this paper is to find how the fauna of the Greater Antilles, the four big islands of the West Indies, has been derived from the mainland, whether across the water or over land connections. This problem, like any other in biogeography, involves the recent history of the earth's surface. It is of interest to geologists as well as to biologists, and has been discussed many times, most recently by Schuchert (1935), who concludes that the fauna of the islands has come from Central America over land connections. However, a good deal still remains to be said. Some of what I shall say is elementary, but is necessary for a proper approach to the subject.

It must be remembered throughout that, except where otherwise stated, this paper deals exclusively with the Greater Antilles. The Lesser Antilles have had a different geological origin and have received their fauna largely from different sources, and to lump them in discussion with the Greater Antilles would introduce many complications. The origin of the fauna of the Greater Antilles is a sufficiently complex subject in itself, so much so that, in attempting to simplify it and to keep the length of this paper within bounds, I may occasionally be guilty of "reducing to baldness an argument that is entitled to hairsplitting."

During the writing of this paper I have become indebted especially to Dr. Thomas Barbour, who, although he does not agree entirely with my conclusions, has given me much information and repeated encouragement. Under Dr. Barbour's directorship, the Museum of Comparative Zoology is a perfect headquarters for work on the Antilles. I wish it were possible (but it is not) to acknowledge in detail the facts and ideas which have come my way from members of the staff during conversations on the back steps of the museum. Most of the meteorology in this paper has come from or been checked by Prof. C. P. Brooks of Harvard. Information received from specialists is acknowledged at various points in the text below.

#### THEORY AND MATHEMATICS OF DISPERSAL OF ORGANISMS ACROSS WATER GAPS

Biogeographers customarily refer to dispersal of terrestrial animals across water as "accidental dispersal" or "random dispersal." These terms, however, are bad ones. In this paper the non-committal term "over-water dispersal" will be used in their place.

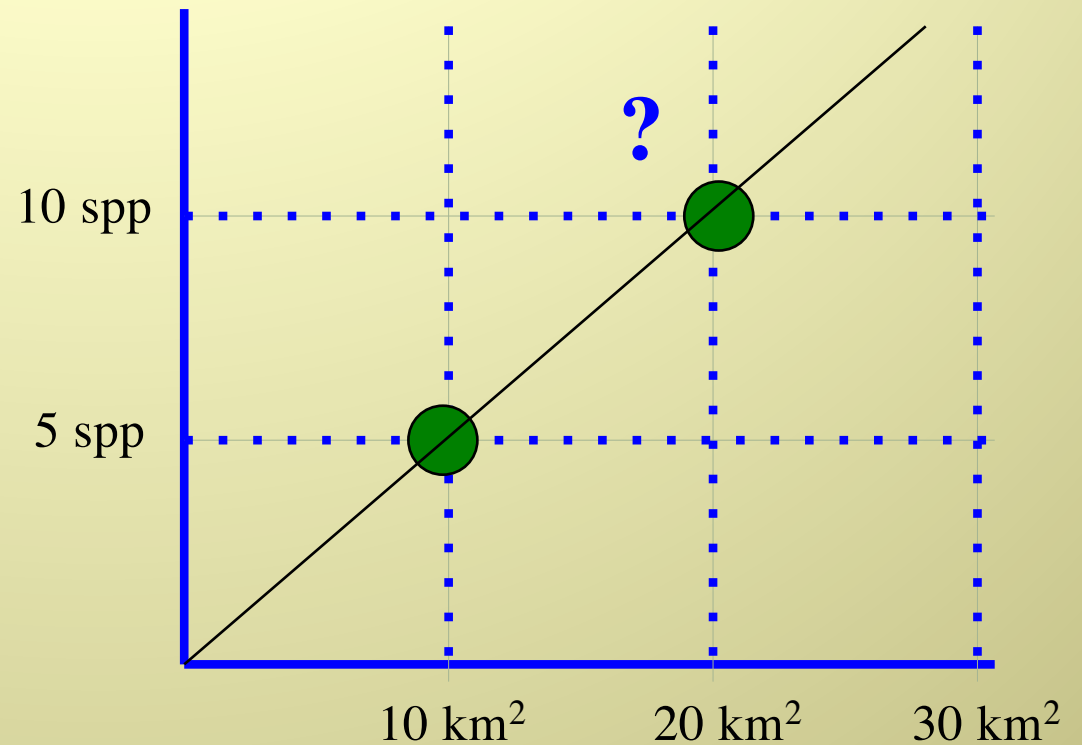
The first objection to the term "accidental dispersal", as applied to dispersal across water, is that many factors besides accident are involved. It is no accident that some organisms, because of their nature and behavior, cross water more often than others, and it is no accident that some islands, because of their nature and position, the direction of winds and currents, and the nature of neighboring land, receive more organisms than other islands do. There is, of course, no doubt

# Island Biogeography

- Darlington's species area relationship – is it arithmetic, e.g. simply double island size to get double species number?



*Anolis*



# Island Biogeography

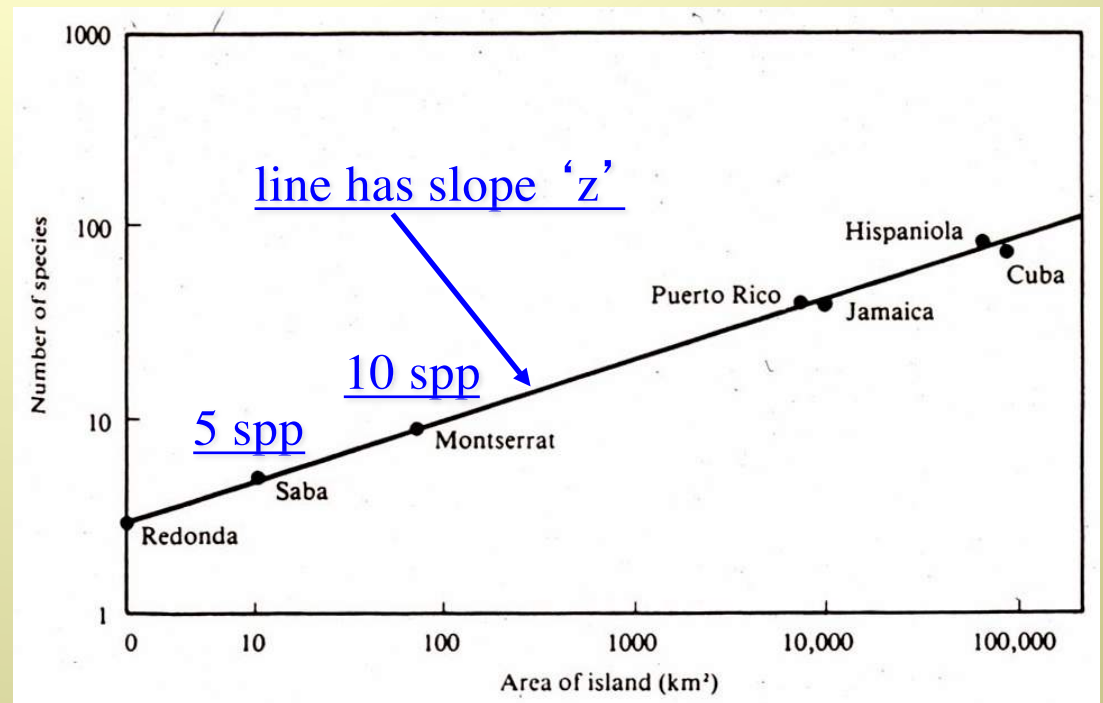
- Darlington's species area relationship – NO, increase island size ~10X to get 2X number of species

$$S = CA^z$$

$$\log S = C + z \log A$$



*Anolis*



Relationship between number of species (S) and island area (A) for reptiles and amphibians of the West Indies (Darlington 1957)

# Island Biogeography

- Similar patterns are seen in Pacific islands for **angiosperm** and **bird** genera

... but with **exceptions**

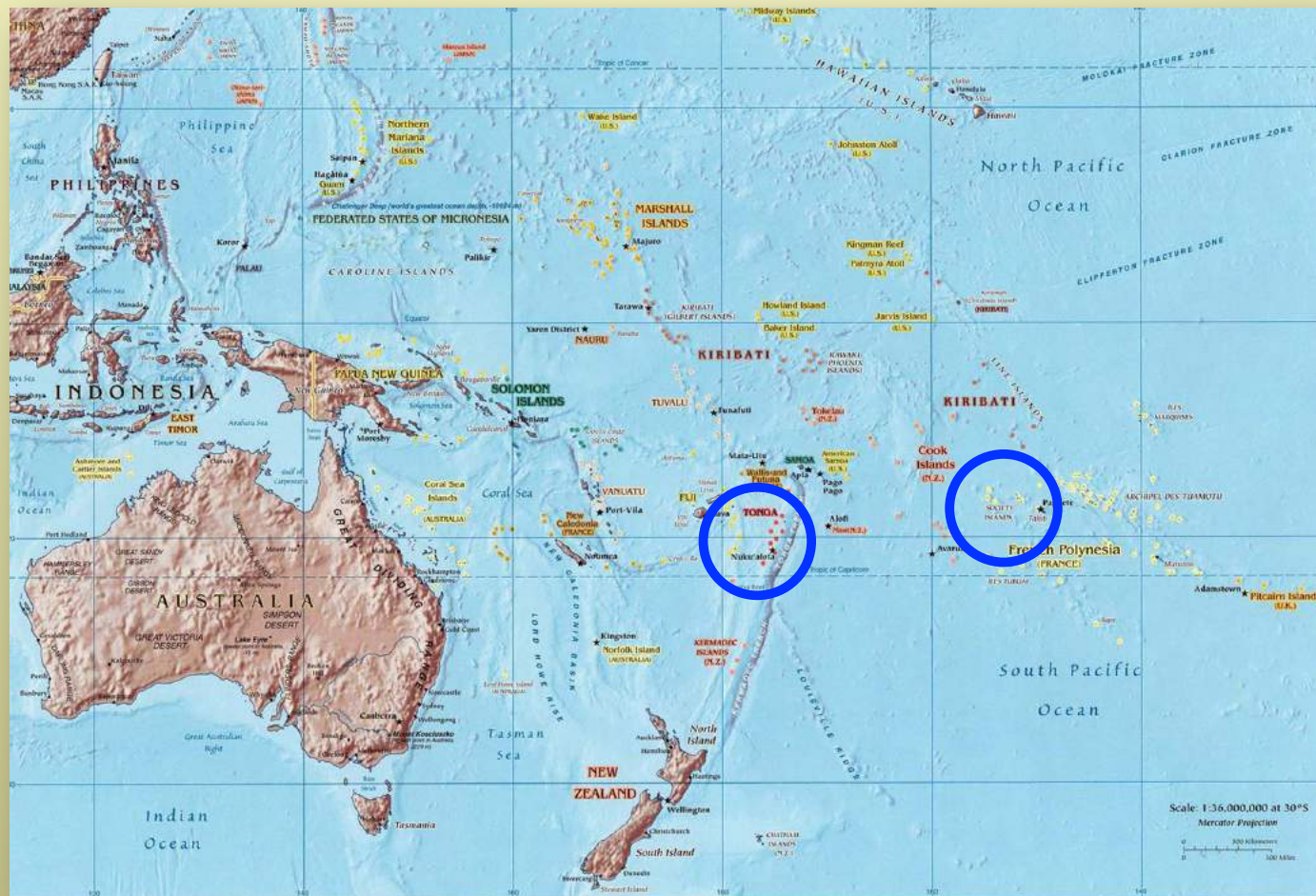
**Table 6.1** The relationships between island area and the diversity of bird genera and non-endemic flowering plant genera in some Pacific islands. Data from Van Balgooy [5]; Mayr, [6]; MacArthur & Wilson [7]

	Area (km <sup>2</sup> )	Angiosperm genera	Bird genera
Solomon Islands	40 000	654	126
New Caledonia	22 000	655	64
Fiji Islands	18 500	476	54
New Hebrides	15 000	396	59
Samoa group	3100	302	33
Society Islands	1700	201	17
Tonga group	1000	263	18
Cook Islands	250	126	10

# Island Biogeography

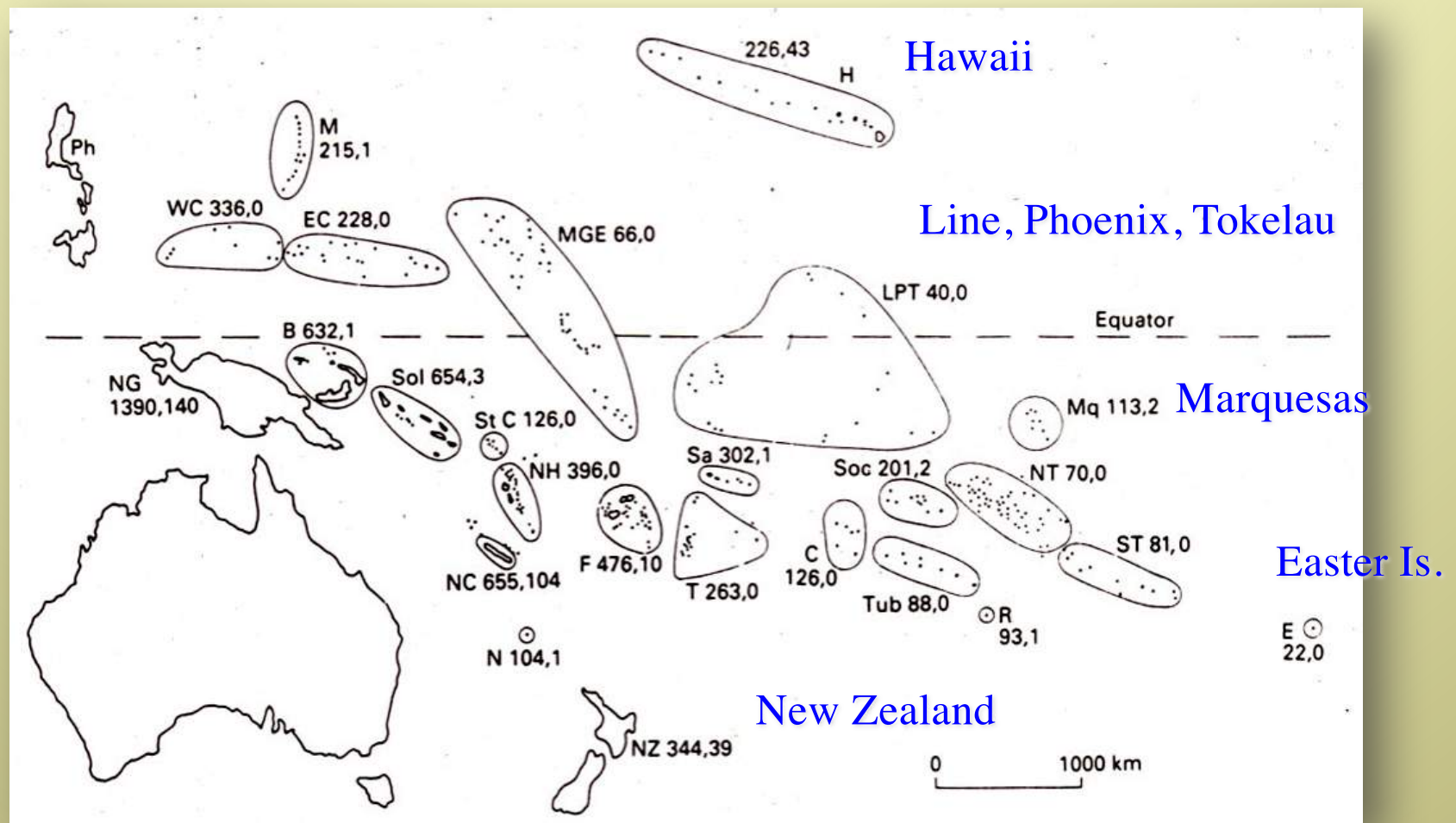
## 2. Effect of isolation - isolated islands have fewer species than expected

- Pacific islands show this dramatically



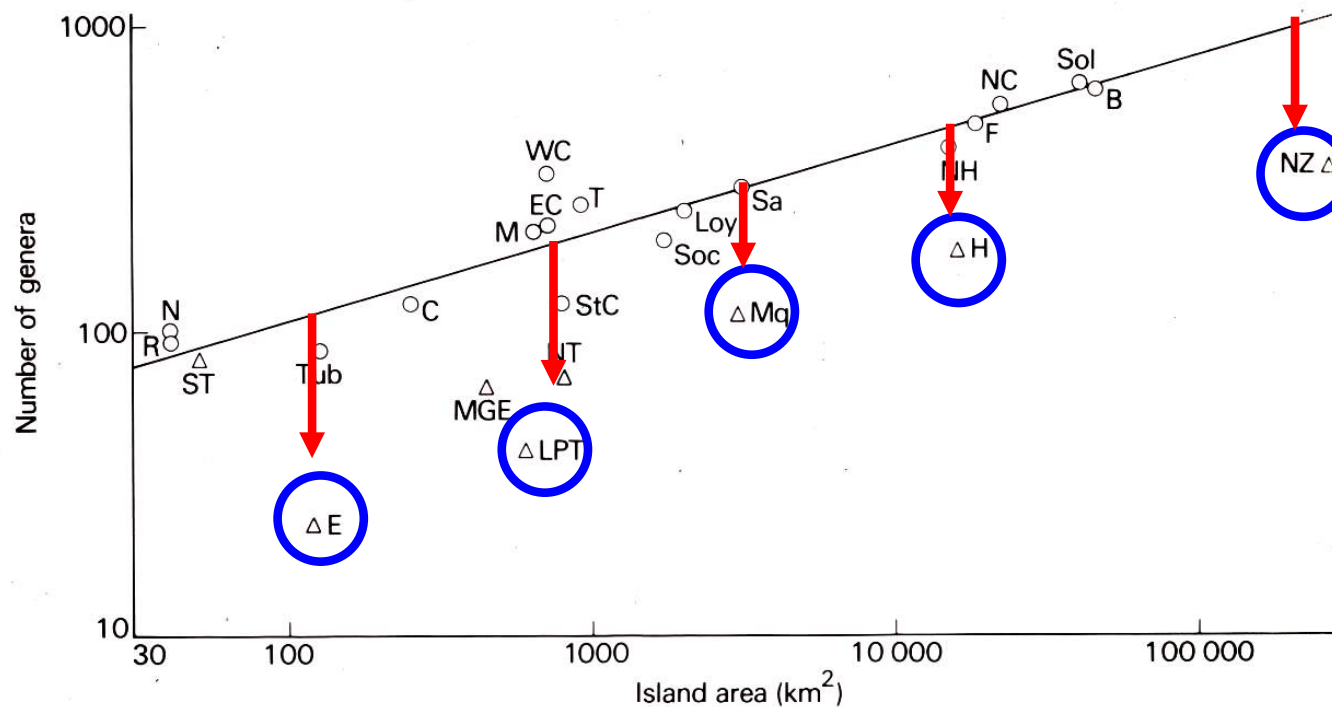
# Island Biogeography

- Distribution of **seed plant genera** in Pacific islands (#genera / #endemic)



# Island Biogeography

- Species area relationship has high correlation coefficient (0.94)  
but isolated islands too low

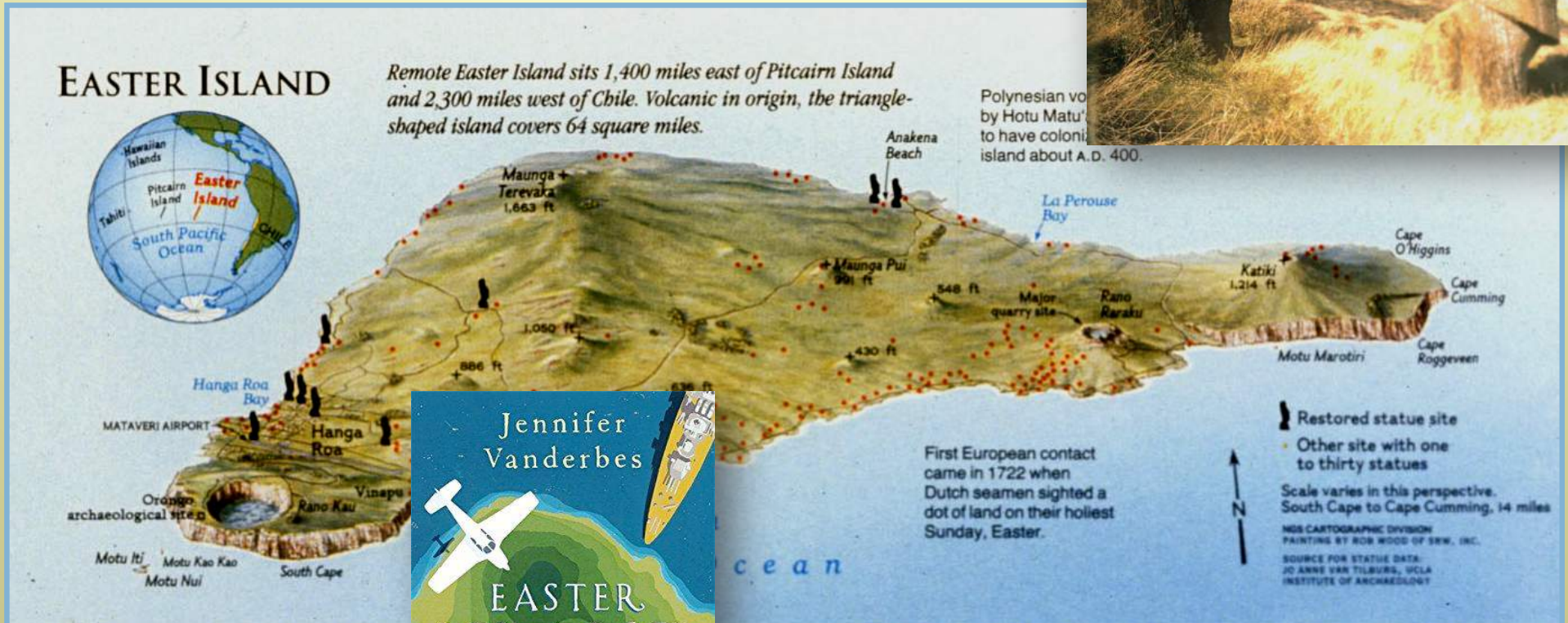


**Fig. 6.2** The relationship between island area and diversity of conifer and flowering plant genera in the Pacific Islands. The more isolated islands are indicated by triangles. The data from the other islands lie very close to a straight line (the regression coefficient), suggesting that generic diversity in these islands is almost wholly controlled by island area – the correlation coefficient is 0.94, indicating a very high degree of correlation. For abbreviations, see legend of Fig. 6.1, plus Loy, Loyalty Islands. Data from Van Balgooy [5].



# Island Biogeography

- Easter Island (Rapa Nui) is one of the most isolated - 22 seed plant genera



Dr. Greer Farraday, an American botanist, travels to Easter Island to research the island's ancient pollen, but more important, to put back the pieces of her life after the death of her husband.

# Island Biogeography

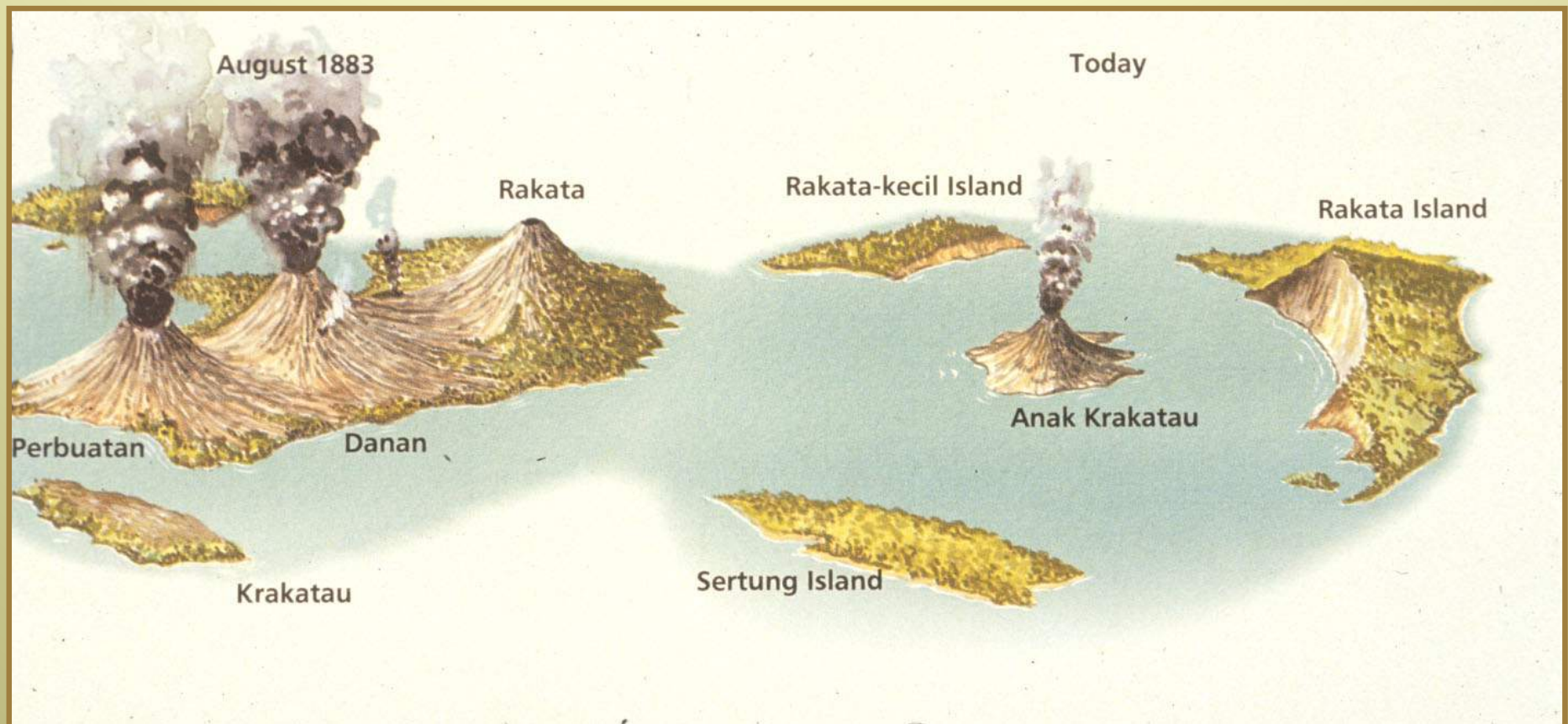
- Extreme impoverishment of isolated islands indicates **distance** limits successful colonization
- Supported by observation that successful colonists have **special** features allowing for **long distance dispersal**



# Island Biogeography

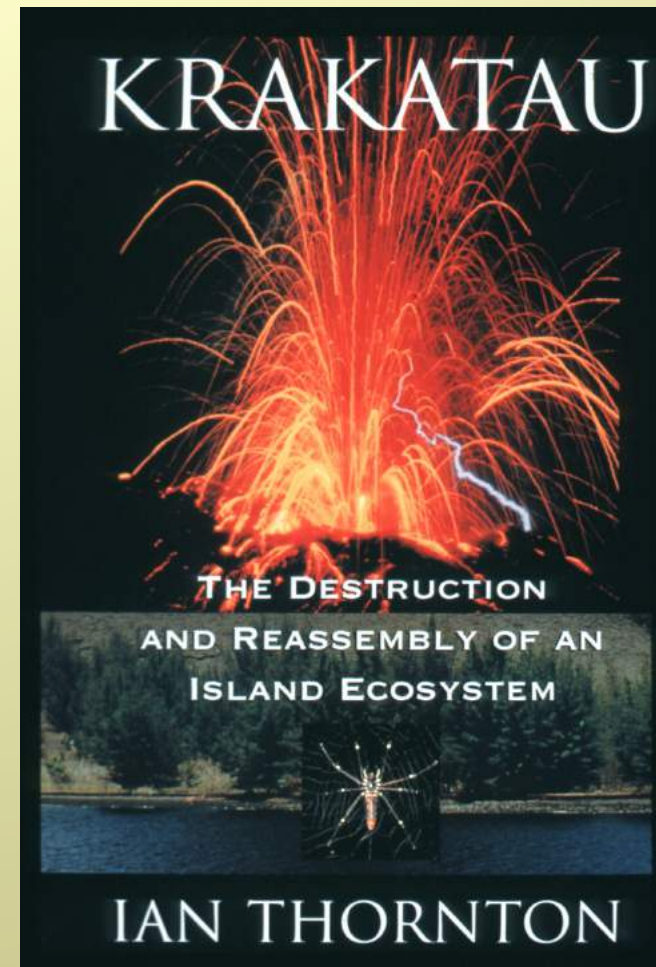
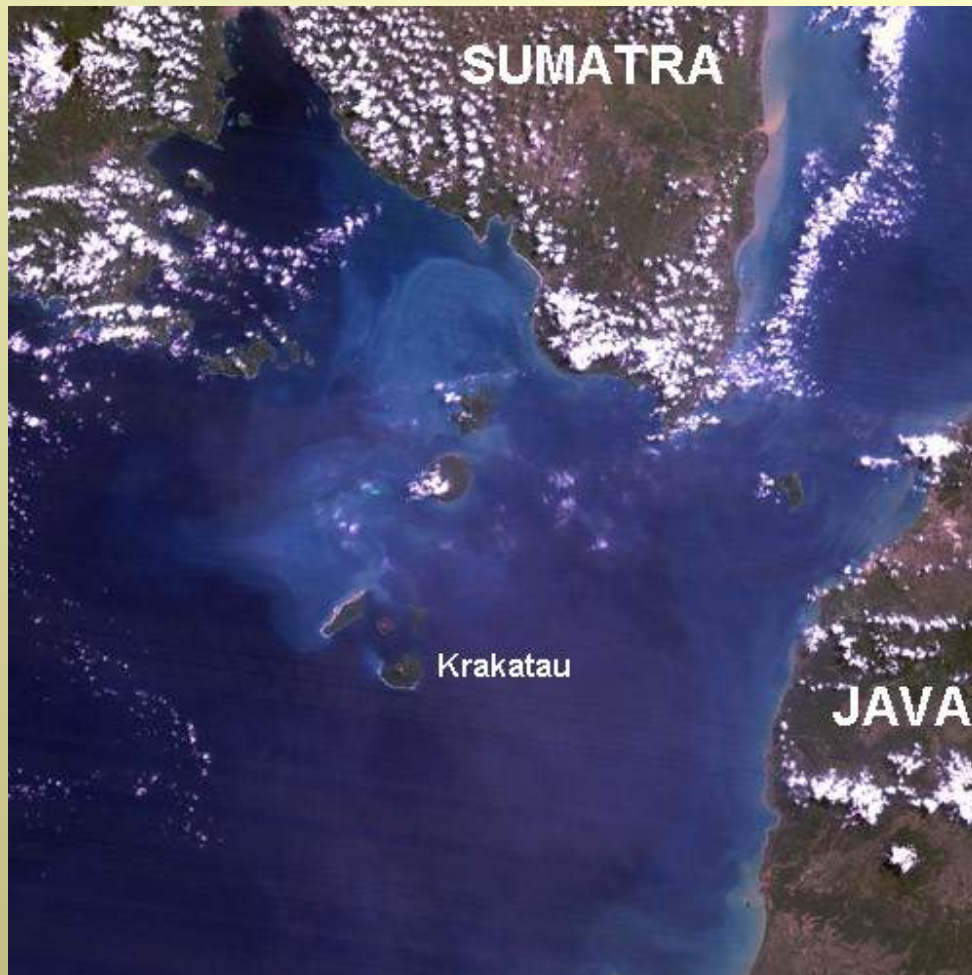
3. **Species turnover** - islands have higher species turnover than continental mainlands

- 136 years of Krakatau recolonization



# Island Biogeography

- recolonization from Sumatra and Java; extensive data collected on species composition ever since



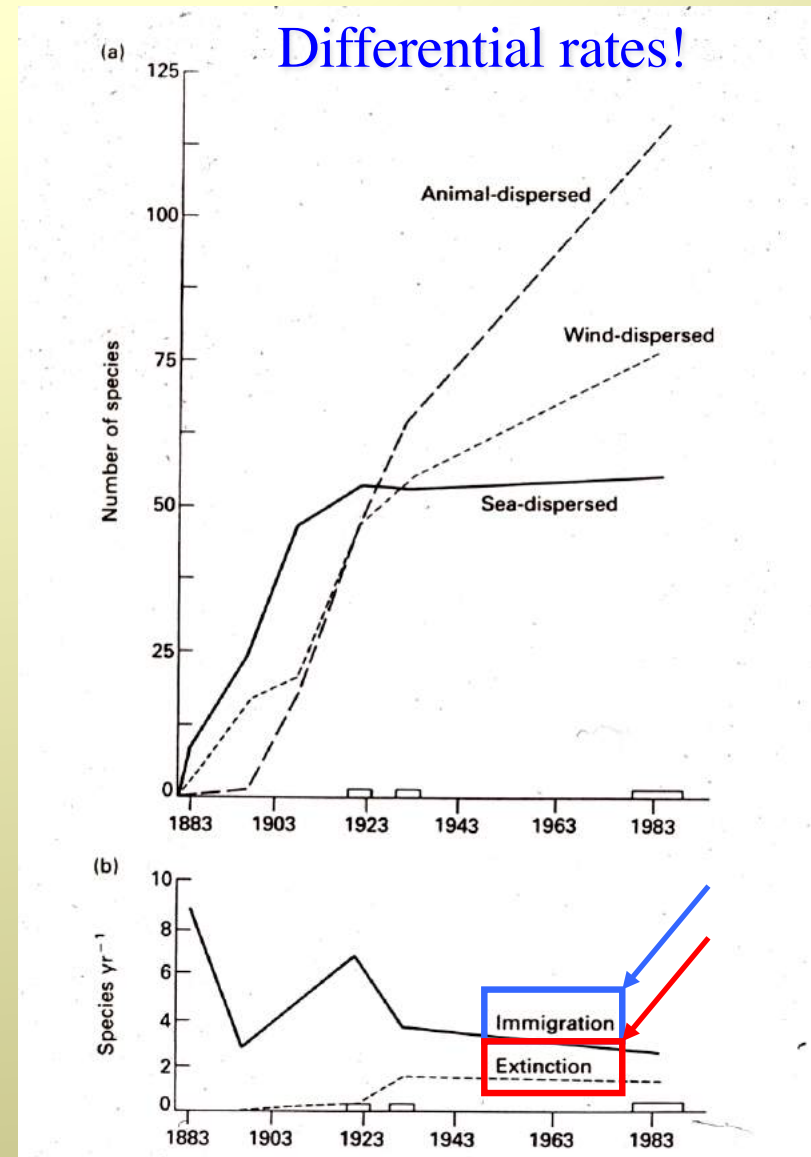
# Island Biogeography

- by the 1930s a tropical forest had developed
- number of bird species increased until 1920, then has remained fairly constant despite changes in avifauna
- some later colonists were successful, replacing about same number of bird species that went “extinct”



# Island Biogeography

- water dispersed plants arrived quickly and have maintained at about 50 species
- wind and then animal dispersed species arrived later
- immigration rates slowing down, extinction rates increasing



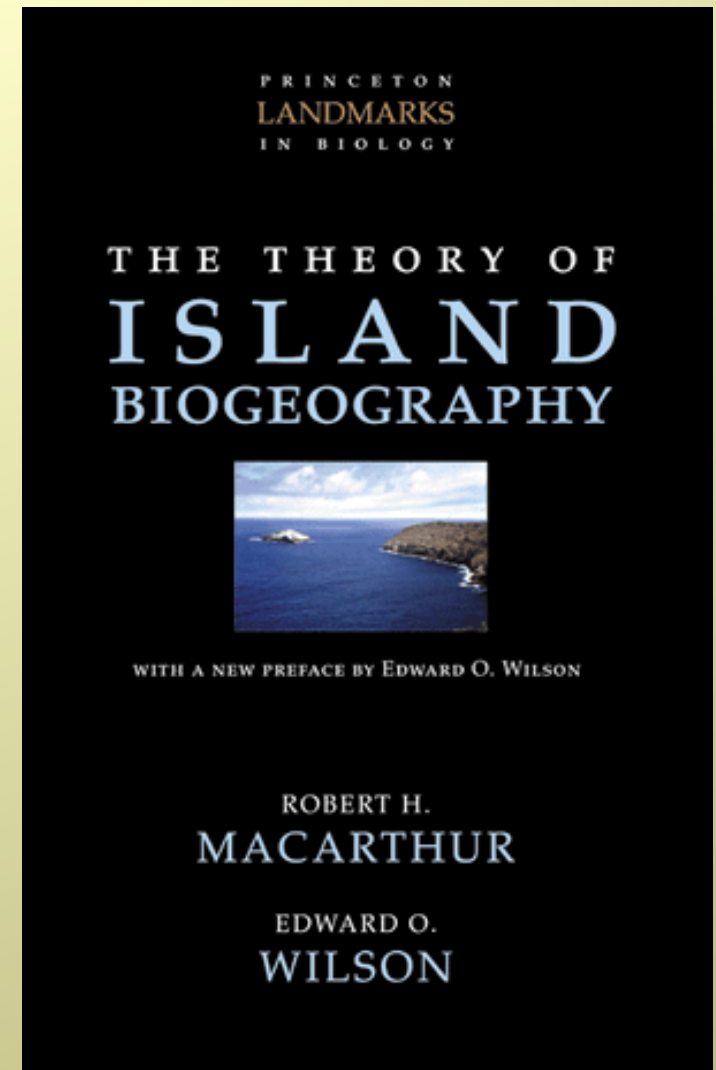
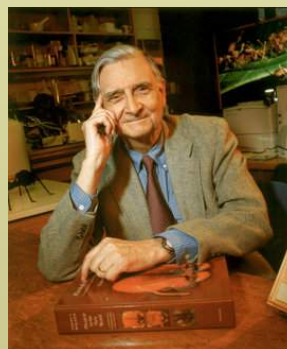
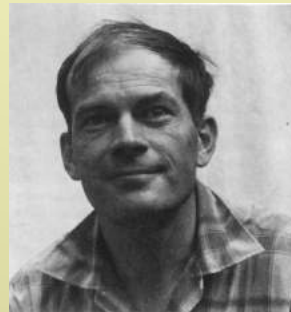
# Island Biogeography

**Theory of Island Biogeography** - unifying theory to explain these three basic characteristics of insular biotas (1963 article, 1967 book)

1. Species-area relationships
2. Effect of isolation
3. Species turnover, but numbers same

Robert MacArthur - ecologist,  
competition

E. O. Wilson - ant taxonomist,  
biogeographer



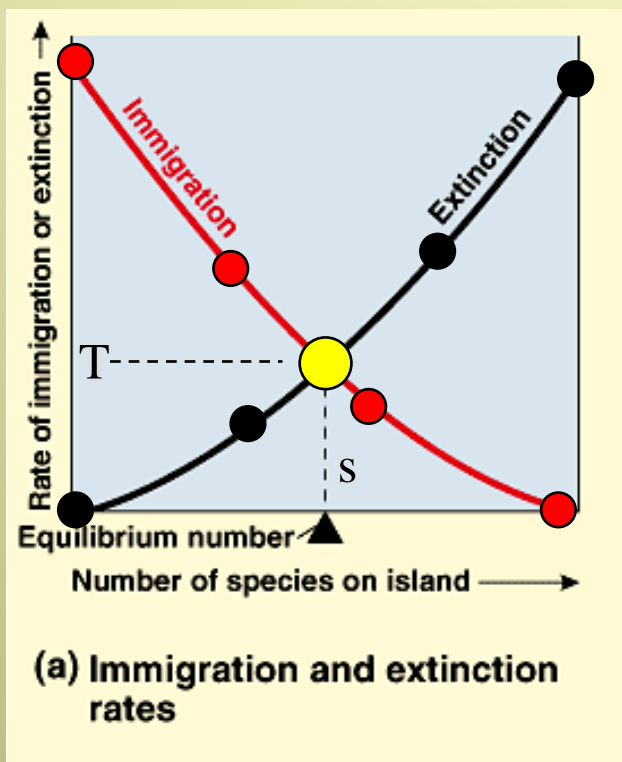
# Island Biogeography

## Equilibrium Theory of Island Biogeography

immigration rate - starts high, then saturates

extinction rate - starts low, then rises

equilibrium species (s) number - where two rates (T) intersect



- Species turn over through time, but same number (s) of species
- Island size?
- Island distance?

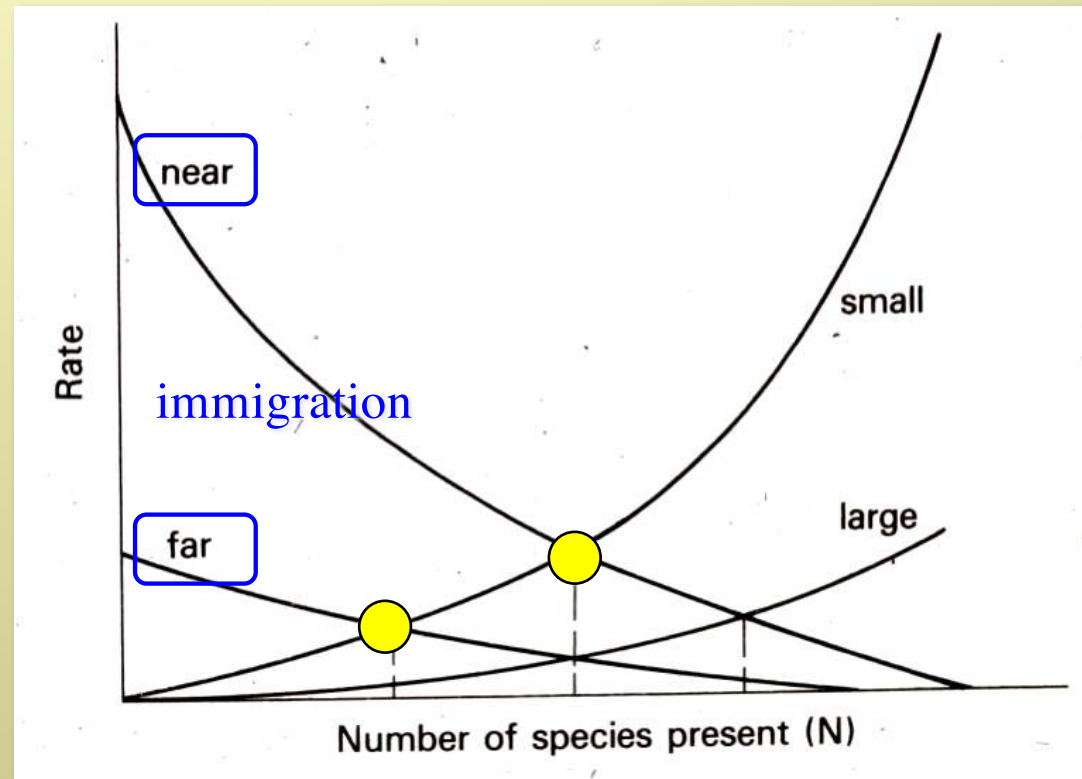
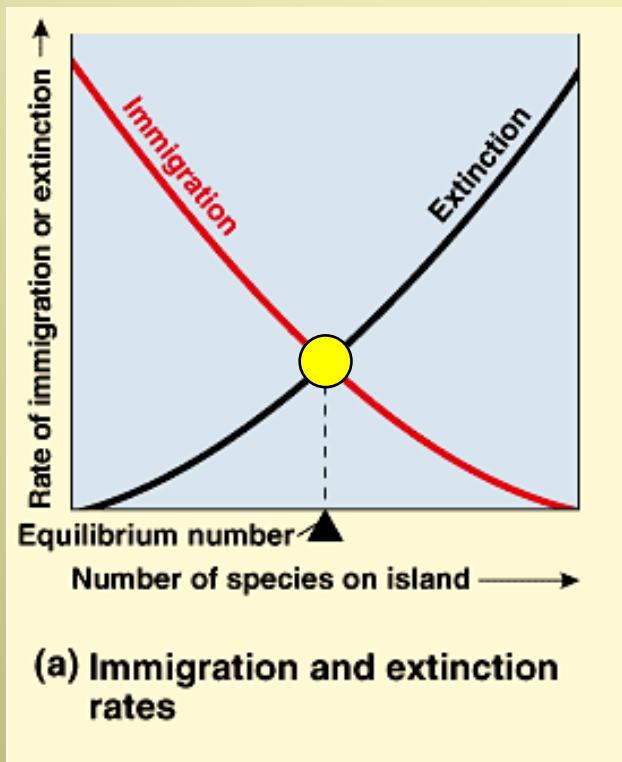


# Island Biogeography

## Equilibrium Theory of Island Biogeography

distance effect - near vs. far island will have different colonizations

equilibrium species (s) number varies!



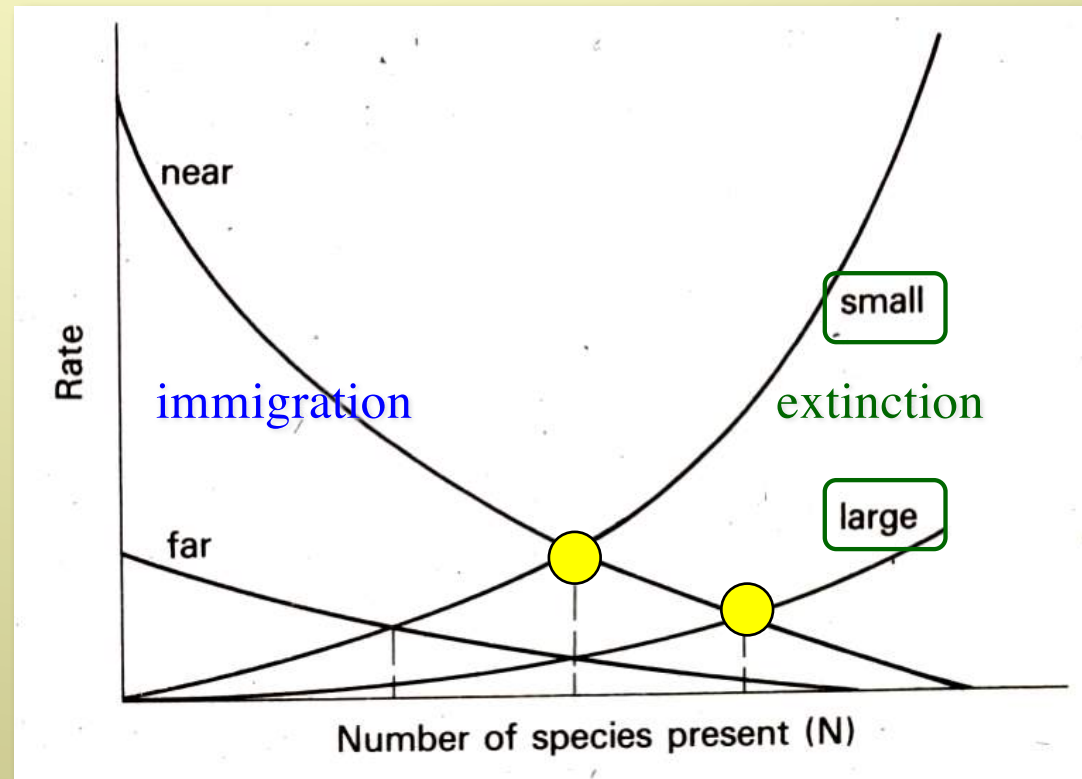
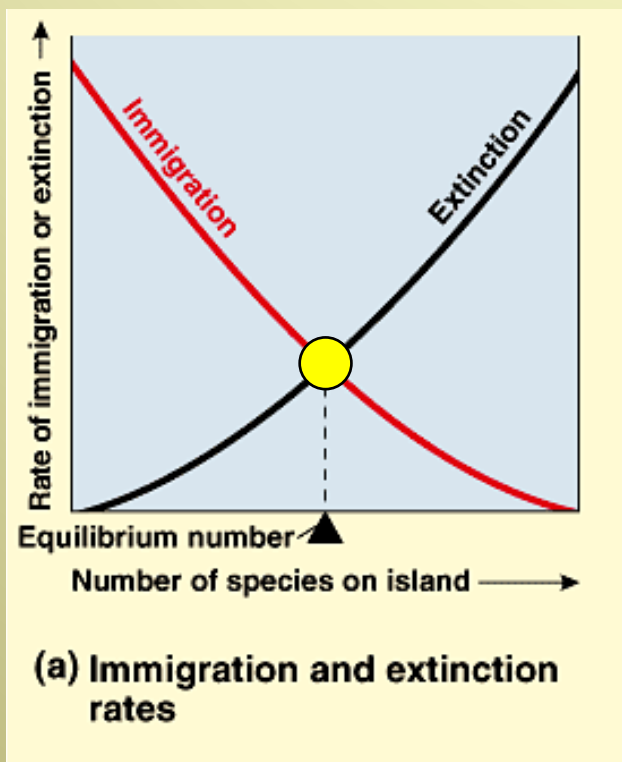
# Island Biogeography

## Equilibrium Theory of Island Biogeography

distance effect - near vs. far island will have different colonizations

size effect - large vs. small island will have different extinction rates

equilibrium species (s) number varies!



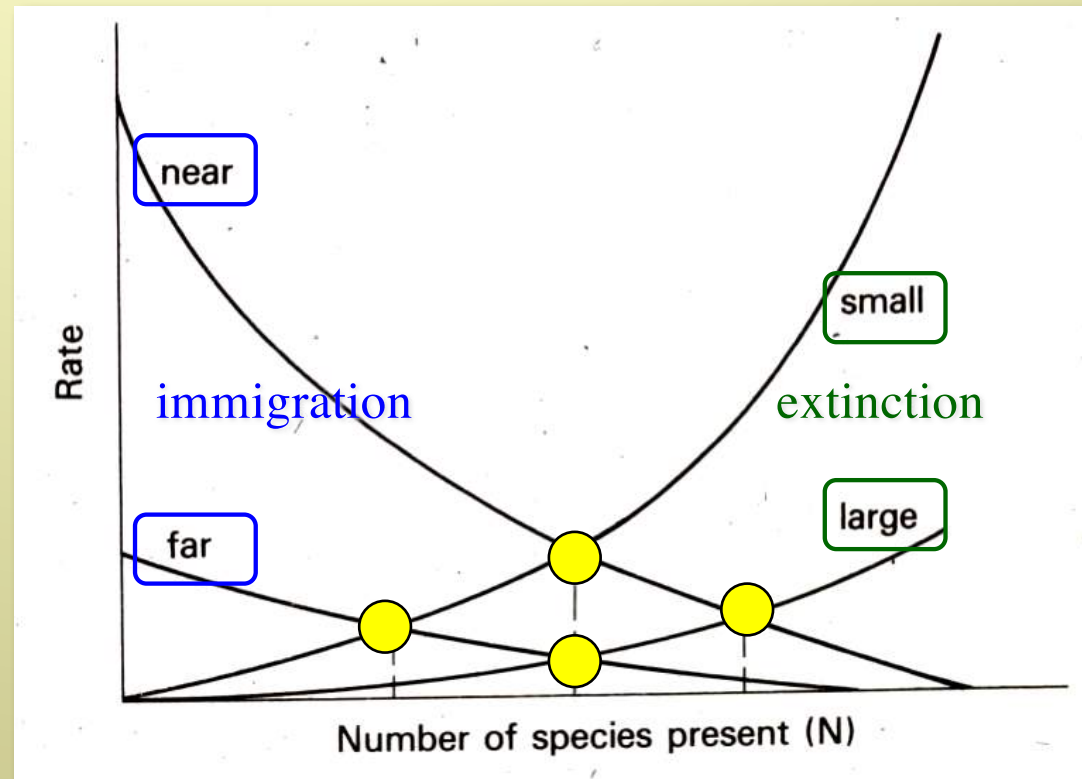
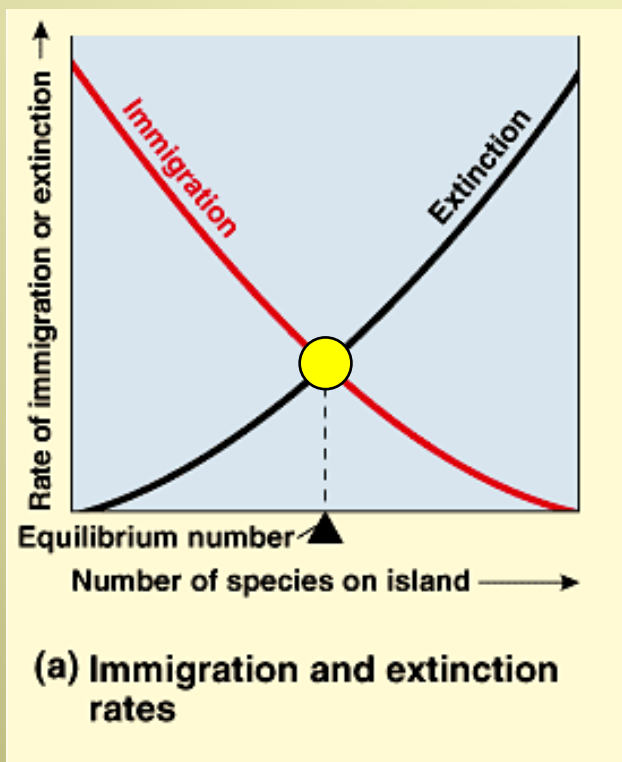
# Island Biogeography

## Equilibrium Theory of Island Biogeography

**distance effect** - near vs. far island will have different colonizations

**size effect** - large vs. small island will have different extinction rates

equilibrium species (s) number varies!

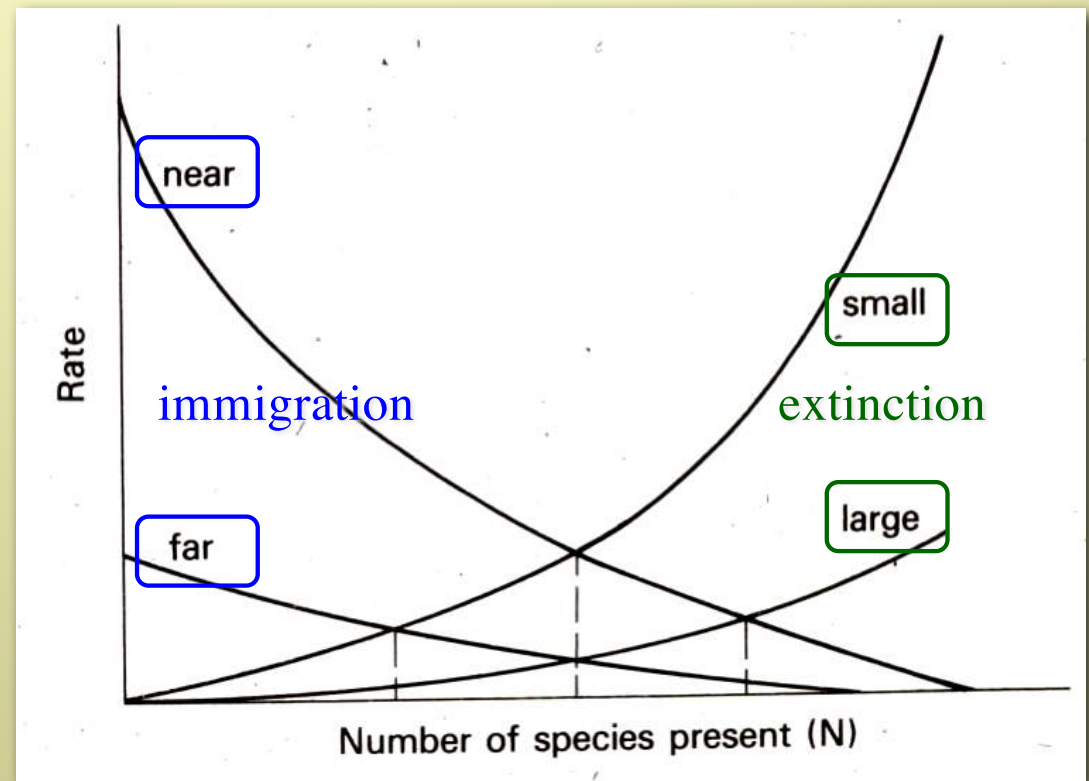
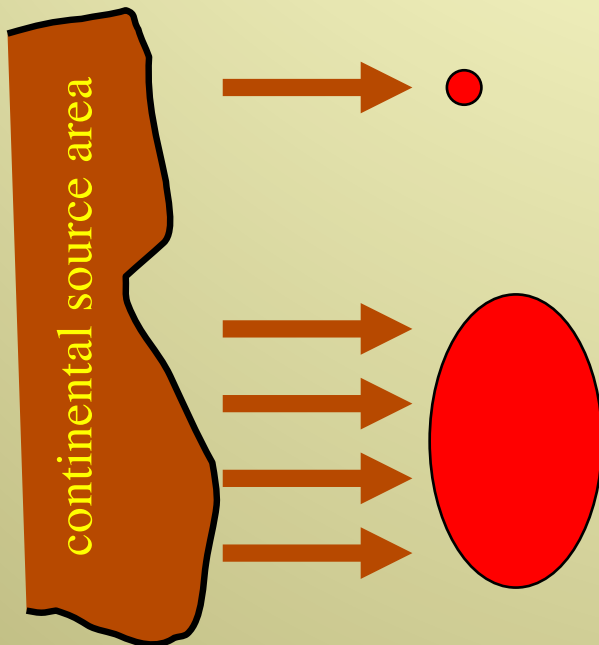


# Island Biogeography

Equilibrium Theory of Island Biogeography - shortcomings!

1. immigration - not just affected by distance, but also island size

'target' effect

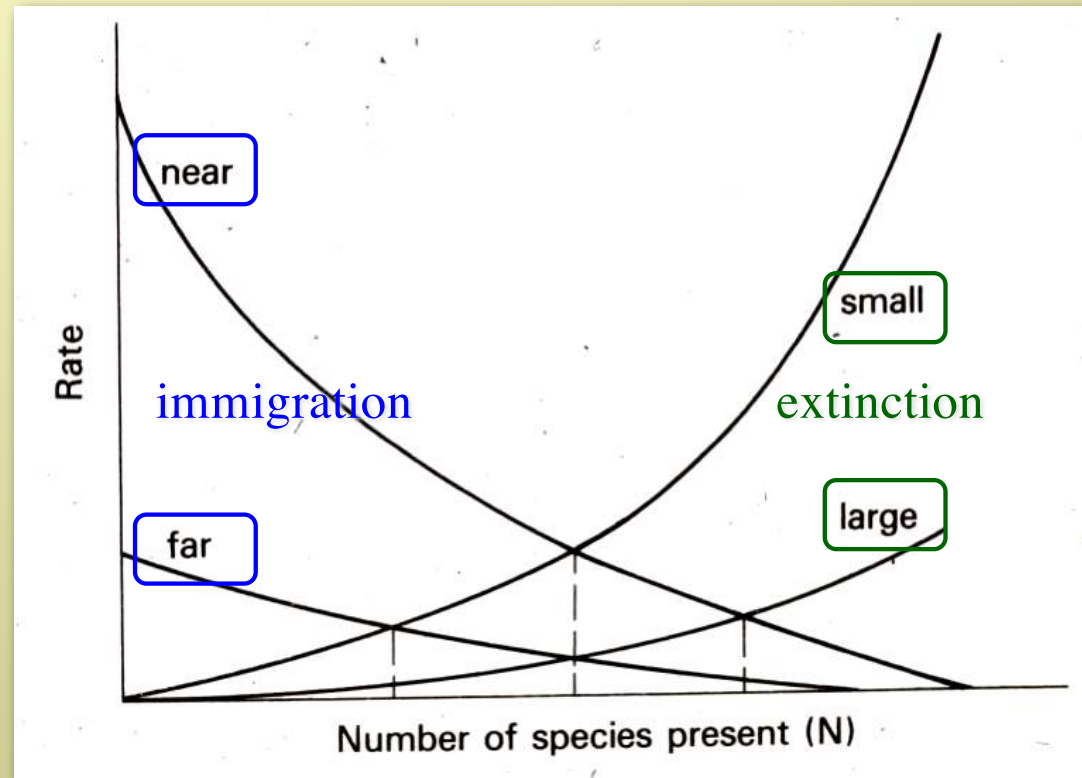
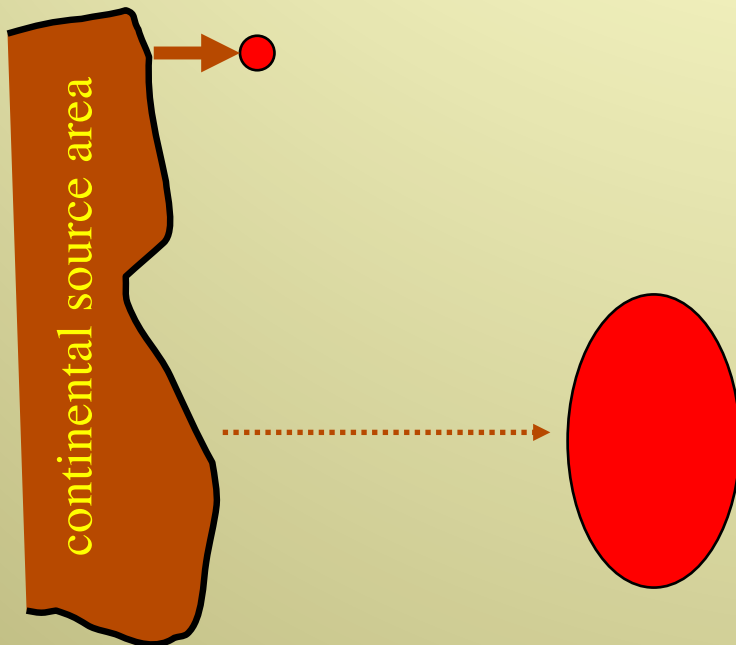


# Island Biogeography

Equilibrium Theory of Island Biogeography - shortcomings!

2. extinction - not just affected by size, but also distance

'rescue' effect - extinction bailed out by recolonization



# Island Biogeography

Equilibrium Theory of Island Biogeography - short comings!

## 3. Diversity of habitats increases with island size



*Metrosideros* - ohia

- keystone species change carrying capacity
- permits *in-island* speciation (~300 introductions → 3000 species in Hawaii)

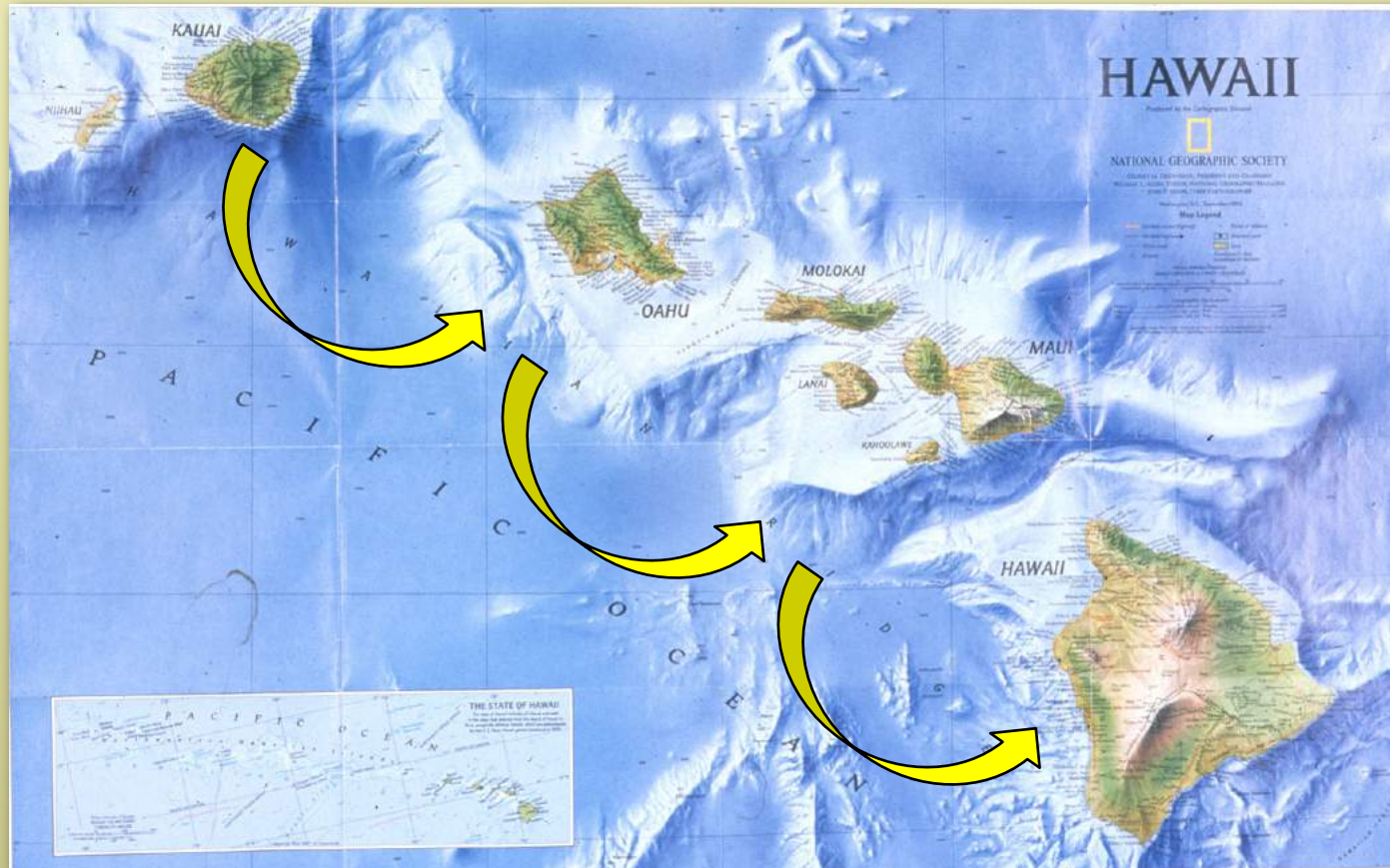


Hawaiian bird diversity increases

# Island Biogeography

Equilibrium Theory of Island Biogeography - short comings!

4. Archipelago effect - islands influence each other

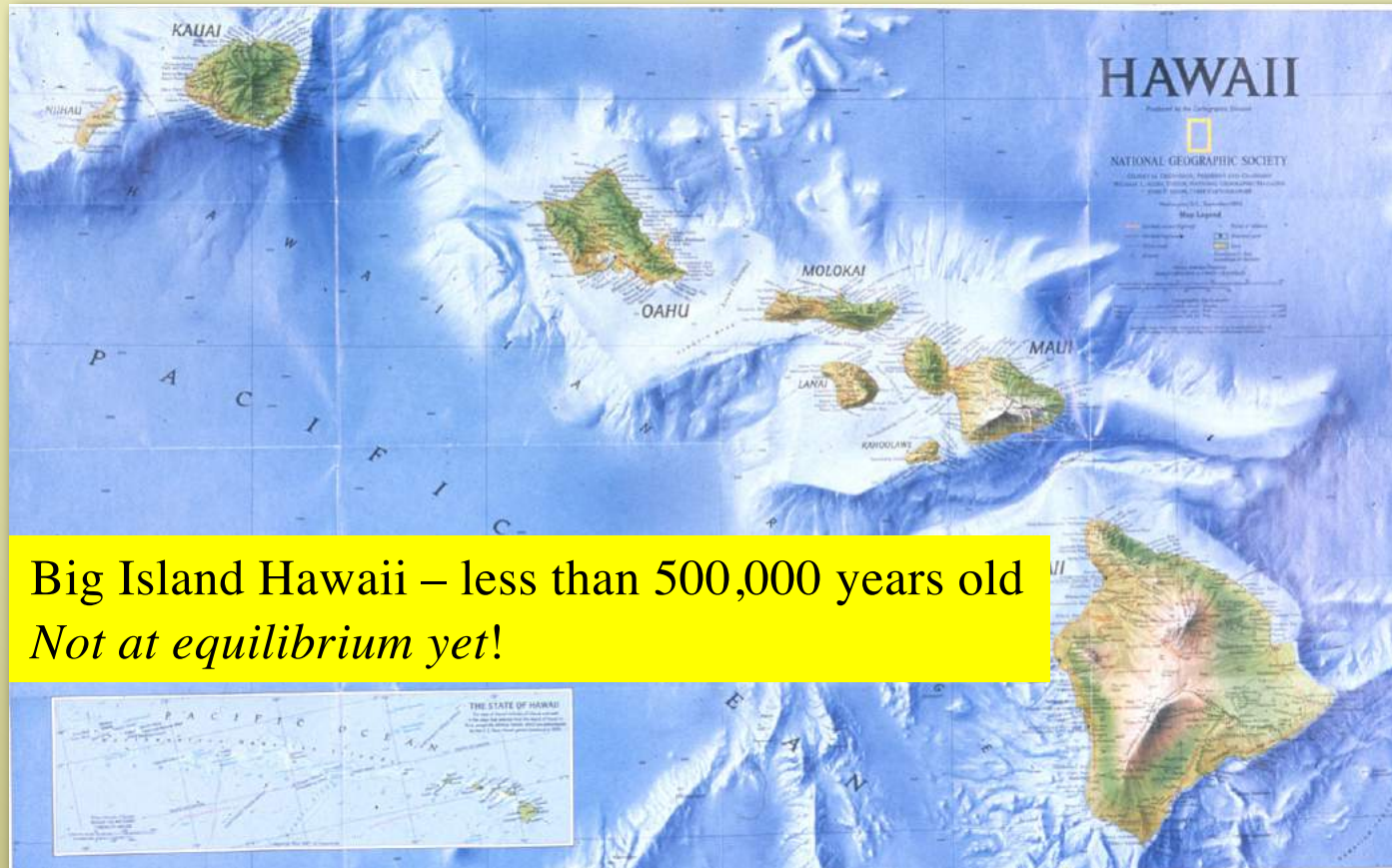


# Island Biogeography

Equilibrium Theory of Island Biogeography - shortcomings!

5. “Equilibrium” not yet reached in some cases

Oceanic islands - equilibrium typically met



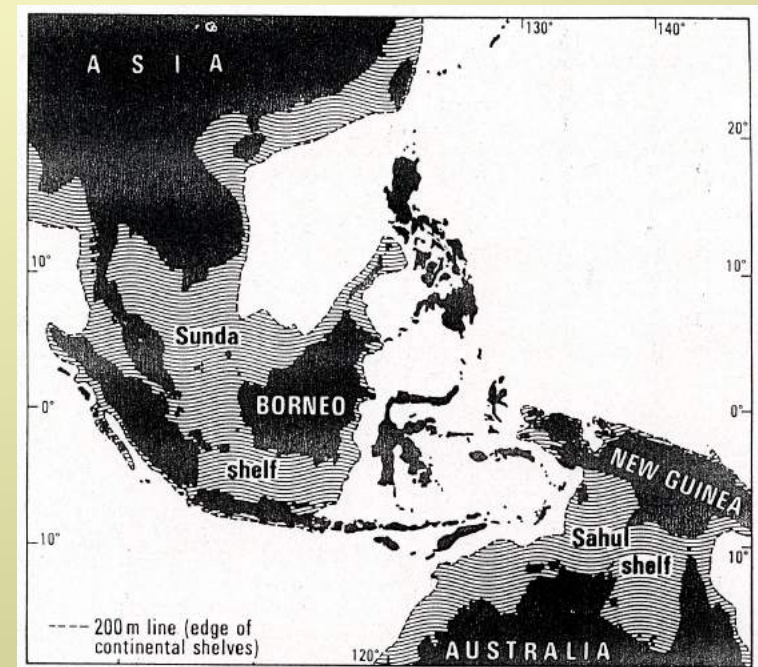


# Island Biogeography

Equilibrium Theory of Island Biogeography - short comings!

5. “Equilibrium” not yet reached in some cases

Continental islands - equilibrium typically **not** met

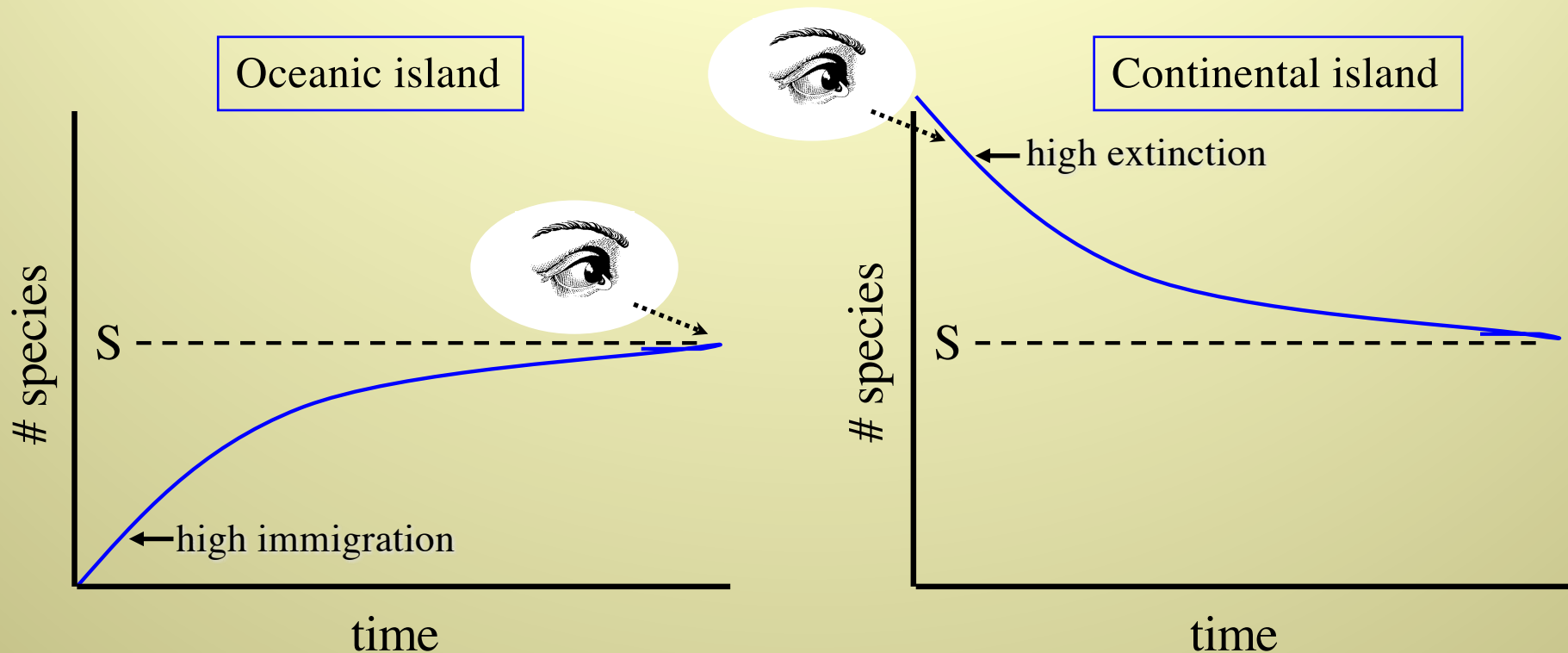


Malay Archipelago “islands” were recently **continental** during Pleistocene!

# Island Biogeography

Equilibrium Theory of Island Biogeography - short comings!

5. “Equilibrium” not yet reached in some cases



- we view oceanic islands late when at equilibrium

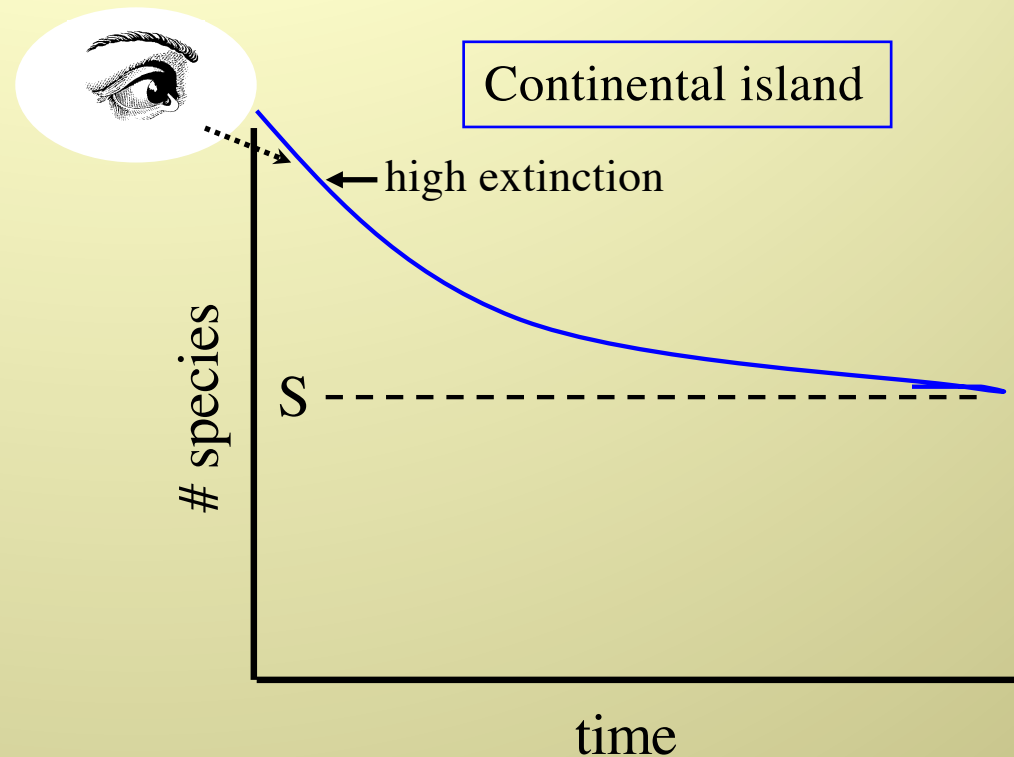
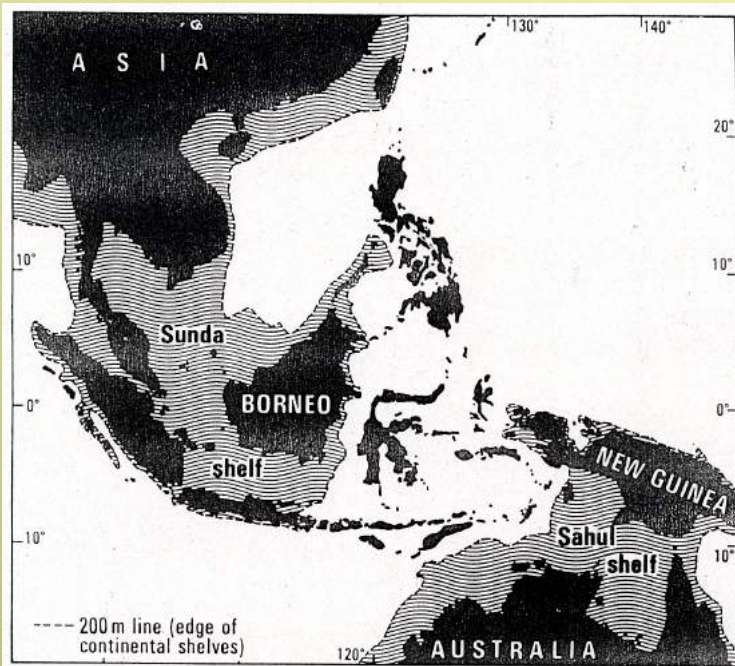
- we view continental islands early (faunal/flora collapse, relaxation)

# Island Biogeography

## Equilibrium Theory of Island Biogeography - short comings!

### 5. "Equilibrium" not yet reached in some cases

- Faunal collapse in Sunda Shelf 0.5% decline/generation
- Time to equilibrium very slow



- we view continental islands early (faunal/flora collapse, relaxation)

# Island Biogeography

## Equilibrium Theory of Island Biogeography - short comings!

### 5. “Equilibrium” not yet reached in some cases

- Great Britain - continental island - shares many orchid and bee pollinators with Europe, including bee mimic orchids and their pollinators
- 120 native bee species, but declining
- *Ophrys apifera* apparently has lost its specific bee pollinator and is now entirely selfing



# Island Biogeography

Equilibrium Theory of Island Biogeography - short comings!

6. Not predicted outcomes (or real life is more complex!)

- Barro Colorado Island - continental island (formed with Panama Canal)
- Carnivores went “extinct” almost immediately
  - Seed eating herbivores increased tremendously
  - Rapid changes in plants not predicted by EToIB



# Island Biogeography

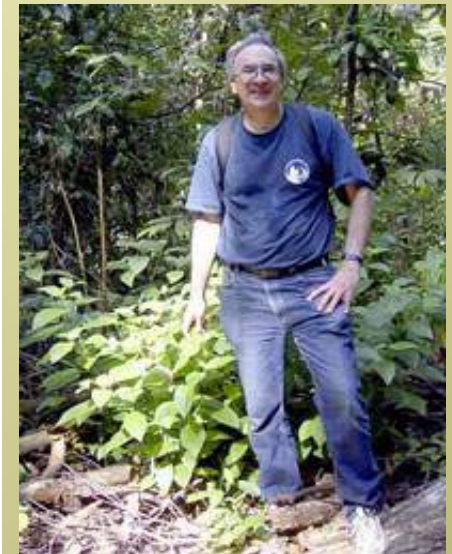
## Equilibrium Theory of Island Biogeography - short comings!

### 6. Not predicted outcomes (or real life is more complex!)

- Florida Key mangrove arthropod communities - experimental test by Dan Simberloff
- Four islands, far and near, had arthropod community exterminated and then biodiversity assessed at regular intervals



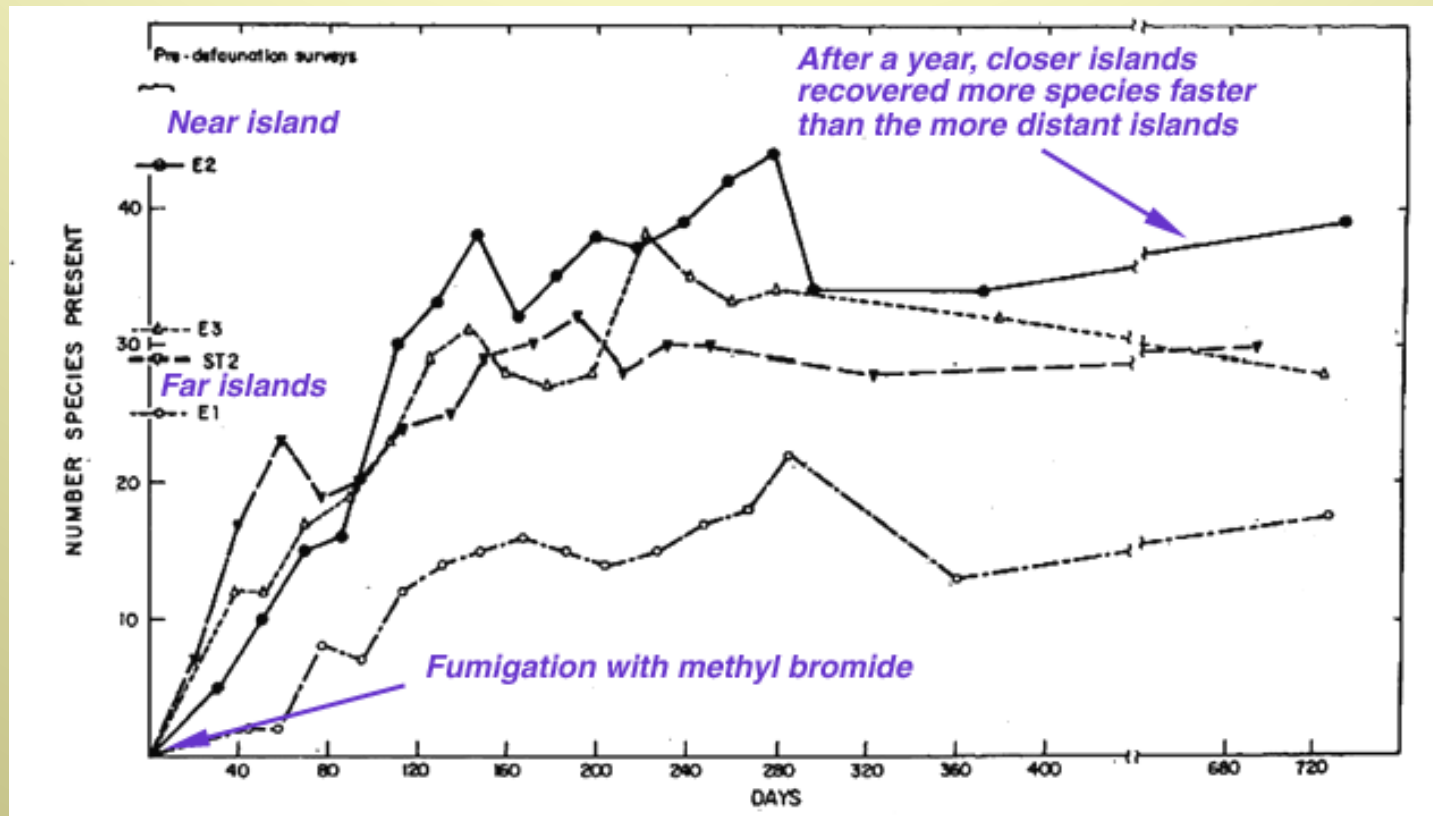
**54.10 Testing the Equilibrium Species Richness Model** Scaffolding is erected by scientists to enclose a small mangrove island in the Florida Keys. Methyl bromide introduced into the enclosure killed all arthropods inside it. When the enclosure was removed, arthropods quickly recolonized the island.



# Island Biogeography

## Equilibrium Theory of Island Biogeography - shortcomings!

- Equilibrium reached within a year, but ‘overshooting’ before stabilizing
- Species number fit distance of islands and pre-defaunation levels
- Actual species varied

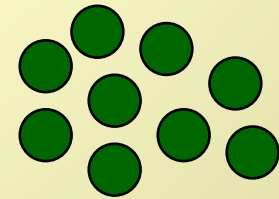
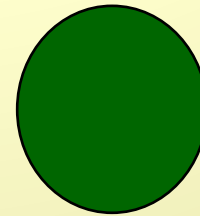


Simberloff & Wilson 1970. Experimental zoogeography of islands: a two-year record of colonization. *Ecology* 51: 934-937.

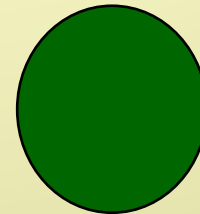
# Island Biogeography

## Applications of Equilibrium Theory of Island Biogeography

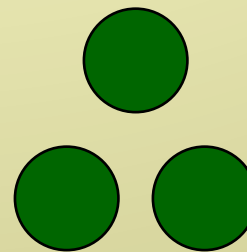
- design of nature preserves - the SLOSS debate (single large or several small):  
*sum of species in series of small areas does not sum to list of one large area!*



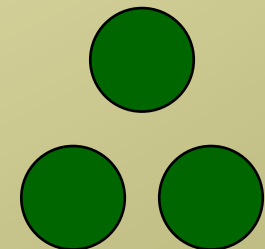
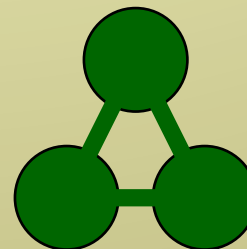
- circular vs. 'peninsular'



- clumped vs. spread out



- corridors vs. unconnected





# Island Biogeography

## Applications of Equilibrium Theory of Island Biogeography

- Oceanic islands
- Sky islands (mountain tops)
- Forest fragments
- Prairie potholes
- **Prairie remnants**

### Ecological Determinants of Species Loss in Remnant Prairies

Mark K. Leach and Thomas J. Givnish

Recensuses of 54 Wisconsin prairie remnants showed that 8 to 60 percent of the original plant species were lost from individual remnants over a 32- to 52-year period. The pattern of species loss was consistent with the proposed effects of fire suppression caused by landscape fragmentation. Short, small-seeded, or nitrogen-fixing plants showed the heaviest losses, as did species growing in the wettest, most productive environments. The interruption of landscape-scale processes (such as wildfire) by fragmentation is an often overlooked mechanism that may be eroding biodiversity in many habitats around the world.

*Science* 1996



# Island Biogeography

## Applications of Equilibrium Theory of Island Biogeography



- 54 prairie patches undergoing ‘relaxation’ or species loss since mid-1800s
- resampled 50 years after the mid-1900’ s

### Ecological Determinants of Species Loss in Remnant Prairies

Mark K. Leach and Thomas J. Givnish

Recensuses of 54 Wisconsin prairie remnants showed that 8 to 60 percent of the original plant species were lost from individual remnants over a 32- to 52-year period. The pattern of species loss was consistent with the proposed effects of fire suppression caused by landscape fragmentation. Short, small-seeded, or nitrogen-fixing plants showed the heaviest losses, as did species growing in the wettest, most productive environments. The interruption of landscape-scale processes (such as wildfire) by fragmentation is an often overlooked mechanism that may be eroding biodiversity in many habitats around the world.

*Science 1996*

1. size of patch determined rate of species loss
2. number of species originally determined rate of species loss
3. correlated species features to species loss

# Island Biogeography

## Applications of Equilibrium Theory of Island Biogeography

*Platanthera leucophaea* - prairie finged orchid



- loss of herbs with small seeds, N<sub>2</sub> fixers, and sphingid moth-pollinated

