## Island Biogeograhy and Community Diversity



## Islands differ in species number



Hawaii


A somewhat smaller island

Much of this variation is explained solely by the size of the island...

## In general, larger islands have more species



## Also applies to habitat islands



# The relationship is remarkably constant within groups and locations 

| Taxonomic group | Location | Slope (z) |
| :---: | :---: | :---: |
| (A) Oceanic islands |  |  |
| Birds | West Indies | 0.24 |
| Ants | Melanesia | 0.30 |
| Beetles | West Indies | 0.34 |
| Land plants | Californian islands | 0.37 |
| (B) Habitat islands |  |  |
| Zooplankton (lakes) | New York State | 0.17 |
| Snails (lakes) | New York State | 0.23 |
| Fish (lakes) | New York State | 0.24 |
| Mammals <br> (mountains) | Great Basin, USA | 0.43 |

From Preston, 1962; May, 1975; Gorman, 1979; and Browne, 1981

This association is formalized as the "species area relationship"

## The species area relationship

$$
S=c A^{z}
$$



## Re-writing the species area relationship

$$
\log (S)=\log (c)+z \log (A)
$$

- In this form, it is easy to see that $c$ represents the intercept and $z$ the slope of the species area relationship



## Using the species area relationship

- The number of fish species in a series of mountain lakes has been estimated
- The area of each lake has been estimated


$$
\begin{gathered}
\mathrm{S}=52 \\
\mathrm{~A}=300 \mathrm{~km}^{2}
\end{gathered}
$$

## Using the species area relationship

- As a result of irrigation, one of these lakes has had its water level reduced
- The new area of this lake has been estimated
- How many fish species do you predict will survive in this lake?



## Why does the species area relationship exist?

- Habitat diversity
- Explains the S.A. relationship as a function of availability of ecological niches
- The equilibrium model of island biogeography
- Explains the S.A. relationship as a balance between immigration and extinction


## Habitat diversity

- Perhaps larger island simply have more niches


This small island has only two niches and thus only two species

This large island has four niches and thus four species

## An example from Australian Gobies

(Kodric-Brown and Brown, 1993)


- Spring pool size explains the \# of species
- Spring size ALSO explains the identity of the species
- This is because larger springs have all the habitats of smaller springs plus more


## A counter example from red mangrove islands

(Simberloff, 1976)


Studied arthropod diversity on monospecific mangrove islands Rhizophera mangle

- Experimentally reduced island size (using brute force)
- Because the islands consisted of only a single host/habitat species (Rhizophera mangle) this manipulation changed only island size
- The number of arthropod species declined after island area was reduced even though the number of habitat types remained constant
- Not consistent with diversity of habitats as explanation


## The equilibrium model of island biogeography

## (MacArthur and Wilson, 1967)

- Hypothesized that the change in species number on an island represents the difference between rates of immigration and extinction

$$
\frac{d S}{d t}=\lambda_{S}-\mu_{S}
$$

- The equilibrium \# of species on an island should occur whenever:

$$
\lambda_{S}=\mu_{S}
$$

But what are the rates of immigration and extinction?

## The equilibrium model of island biogeography

- Assume that the rate of extinction ( $\mu_{\mathrm{S}}$ ) depends upon $S$


$$
\mu_{S}=\left(\frac{E}{P}\right) S
$$



- The number of species going extinct per unit time increases with $S$, simply because there are more species to possibly go extinct. When $\mathrm{S}=\mathrm{P}, \mu_{\mathrm{S}}=\mathrm{E}$


## The equilibrium model of island biogeography

- Assume that the rate of immigration $\left(\lambda_{\mathrm{S}}\right)$ depends upon $S$


$$
\lambda_{S}=I-\left(\frac{I}{P}\right) S
$$



- The number of species immigrating per unit time decreases with $S$, simply because there are fewer species to immigrate. When $\mathrm{S}=\mathrm{P}, \lambda_{\mathrm{S}}=0$.


## The equilibrium model of island biogeography

- Substituting terms for immigration and extinction shows that:

$$
\frac{d S}{d t}=I-\left(\frac{I}{P}\right) S-\left(\frac{E}{P}\right) S
$$

- As a result, the equilibrium species number on the island is:

$$
\begin{gathered}
0=I-\left(\frac{I}{P}\right) S-\left(\frac{E}{P}\right) S \\
\hat{S}=\frac{I P}{I+E}
\end{gathered}
$$

This is a dynamic equilibrium which occurs because extinctions precisely balance immigrations!
Thus the MacArthur-Wilson model is characterized by species turnover

## The equilibrium model of island biogeography

- The equilibrium \# of species on the island can also be found graphically
- So too, can the rate of species turnover, $\hat{T}$



## How would you calculate the equilibrium rate of species turnover?

$$
\lambda_{S}=I-\left(\frac{I}{P}\right) S
$$

$$
\mu_{S}=\left(\frac{E}{P}\right) S
$$



$$
\hat{S}=\frac{I P}{I+E}
$$

## The equilibrium model of island biogeography

## So far we have seen that:

- The number of species on an island represents an equilibrium between extinction and recolonization
- This equilibrium is dynamic, and characterized by continual species turnover

Time 1: $\left\{\mathbf{S}_{1}, \mathbf{S}_{3}, \mathbf{S}_{5}, \mathbf{S}_{6}\right\} \rightarrow$ Time 2: $\left\{\mathbf{S}_{1}, \mathbf{S}_{3}, \mathbf{S}_{5}, \mathbf{S}_{7}\right\} \rightarrow$ Time 3: $\left\{\mathbf{S}_{2}, \mathbf{S}_{3}, \mathbf{S}_{5}, \mathbf{S}_{7}\right\}$

But how does any of this explain the species area effect?

## The equilibrium model of island biogeography

We must make two additional assumptions:

1. The total population size of a species is proportional to island area

- Makes sense if resources are limiting

2. Extinction risk is less for large islands with large populations sizes

- Unavoidable because of demographic stochasticity


## The equilibrium model of island biogeography




- Larger islands should have more species
- Consistent with the species area relationship


## The equilibrium model of island biogeography

- Because travel to the near island is easier, the maximum immigration rate ( $I_{1}$ ), to this island should exceed that of a more distant island ( $\mathbf{I}_{2}$ )


- Closer islands should have more species
- Consistent with a distance effect


## Summarizing the equilibrium model of island biogeography

- The species richness of an island represents a balance between extinction and colonization
- There is continual species turnover

- Larger islands have a greater species richness at equilibrium
- Islands closer to the mainland have a greater species richness at equilibrium



## Tests of the equilibrium model

- Is there evidence for a distance effect?
- Is there evidence for species turnover?
- Is there evidence for "relaxation" of diversity?


## Evidence for a distance effect

Birds of the Bismarck islands (Diamond, 1972)



Species richness decreases with distance from New Guinea (mainland)

## Evidence for species turnover: Insects on mangrove islands

(Wilson and Simberloff 1969; Simberloff and Wilson 1969)


Everglades National Park Photo

- Identified 6 mangrove islands of varying size and distance from the mainland
- Carefully censused the arthropod community of each island
- Covered each island with canvas and fumigated to kill all arthropods
- Tracked recolonization of the islands over several years


## Evidence for species turnover: Insects on mangrove islands

## (Wilson and Simberloff 1969; Simberloff and Wilson 1969)



- Species richness approached its prefumigation levels within $\mathbf{2 8 0}$ days
- Species richness was greater on large islands closer to the mainland
- Both results support the equilibrium theory of island biogeography but is there turnover?

Species turnover is the critical test

## Evidence for species turnover: Insects on mangrove islands

(Wilson and Simberloff 1969; Simberloff and Wilson 1969)
$\left.\begin{array}{lll}\text { Orthoptera } & \text { Gryllidae } & \begin{array}{l}\text { Cycloptilum sp. } \\ \text { Cyrtoxipha confusa }\end{array} \\ \text { Dermaptera } & \text { Labiduridae } & \begin{array}{l}\text { Orocharis sp. } \\ \text { Labidura riparia }\end{array} \\ \text { Coleoptera } & \text { Anobiidae } & \begin{array}{l}\text { Cryptorama minutum } \\ \text { Tricorynus sp. }\end{array} \\ & \text { Anthicidae } & \begin{array}{l}\text { Sapintus fulvipes } \\ \text { Vacusus vicinus }\end{array} \\ & \text { Buprestidae } & \begin{array}{l}\text { Actenodes auronotata } \\ \text { Chrysobothris tranquebarica }\end{array} \\ & \text { Cantharidae } & \text { Chauliognathus marginatus }\end{array}\right\}$

Black squares $=$ species present Grey squares = species inferred to be present

- Substantial species turnover occurred over the course of the experiment
- Estimated the turnover rate to be . 67 species per day!
- Provides essential support to the equilibrium theory

Taken together, these results support the equilibrium model

## Evidence for relaxation of diversity

- Does diversity decrease after geographic isolation?

Initially, the land mass is cohesive


Over time, a piece becomes isolated


## Evidence for relaxation of diversity

- Pieces of mainland which become isolated should become less species rich over time and approach an equilibrium between immigration and extinction



## Evidence for relaxation of diversity

(Wilcox, 1978)

- Studied lizard species \# on former land bridge islands in the Gulf of California
- Estimated the length of time these islands had been isolated
- Plotted the relationship between time of isolation and number of species

- Found evidence for "relaxation" of the lizard fauna
- Consistent with the equilibrium theory


## Applying equilibrium theory to reserve design

 (A practice problem)- You are tasked with selecting between three potential locations for a new national park
- Your goal is to maximize the long term species richness of passerine birds within the park
- Previous research has shown that the birds meet the assumptions of the equilibrium model



## Applying equilibirium theory to reserve design

 (A practice problem)
## Previous research has also shown that:

- $I=2 / x$ where $x$ is distance to the mainland
- $E=.4 / A$ where $A$ is the area of the island
- Which of the three potential parks would best preserve passerine bird species richness?



## Exam 3 results

## You grade is shown in points (out of $\mathbf{1 6 0}$ total points)

Exam average: $\mathbf{1 2 3}$ points or $\mathbf{7 6 . 9 \%}$


