

#### Goals and learning objectives

- 1) Describe patterns expected with the species-area and species-isolation relationship
- 2) Interpret the theory of island biogeography, the basic figure that shows expected species richness and turnover at equilibrium, given rates of colonization and extinction, and the rescue and target effects
- 3) Understand the expected shifts in island community structure with decreasing colonization rates, moving from those composed of species shared with the mainland to island endemics to groups of species that undergo in situ diversification on islands
- 4) Outline the relative strength of different ecological and evolutionary factors that influence the suite of species found on islands types: large – near, large – isolated, small – near, small – isolated



In the marine realm, islands can be assigned to the following:

1) Oceanic (volcanic) islands

Arise from oceanic crust, have never been connected to a mainland landmass



#### 2) Land bridge (or continental shelf) islands

Are situated over continental shelf and can be colonized by species dispersing over land at times of lower sea level

#### **3)** Continental fragments

Islands that were split apart from continental plates by tectonic processes







Madagascar

Other island-like systems include species inhabiting archipelago-like habitats, such as forest-associated species of mountaintop 'sky islands'



Islands of subalpine coniferous forest (black areas) in the American Southwest. Contour lines show the lower edge of montane conifer forest. The Rocky Mountain boreal forest extends northward in Colorado (from Frey *et al.* 2007).

#### Why study islands?

Characterized by isolation, a principal factor driving evolutionary change.

Smaller, perhaps simpler, ecosystems that are usually more tractable in terms of ecological and evolutionary processes operating within species and communities.



The Equilibrium Theory of Island Biogeography was perhaps the single greatest contribution in the field during the 20<sup>th</sup> century

In part, it brought the notion of 'dynamic insular communities' to the forefront of ecological biogeography

**Robert MacArthur** 



E.O. Wilson



#### Island biogeography has generally centered on three major approaches:

- 1. Describe diversity and composition of island biotas and how they differ from continental flora and fauna, and the nature of adaptations that influence dispersal to and colonization of islands
- 2. Identify and quantify factors that influence rate of dispersal to islands, rates of extinction on islands, and the numbers and kinds of species islands can support
- 3. Understand evolution of communities in novel environments following colonization



#### Island biogeography has generally focused on two major patterns:

- 1. The tendency for species richness of insular communities to increase with island area (species-area relationship)
- 2. The tendency of species richness to decrease with island isolation (species-isolation relationship)



#### The species-area relationship

Diversity of conifer and flowering plant genera and endemics in the Pacific islands.



More isolated islands are shown as triangles. Other islands (circles) show a pattern very close to the regression, indicating high correlation.



Species-area relationship for butterflies on islands off the British Isles, shows a marginally significant relationship with substantial scatter (from Dennis & Shreeve 1997)

The species-area relationship



(from Lomolino *et al.* 2010, after Brown 1978) <sup>13</sup>



Species-area relationship for freshwater fish from North American lakes (triangles) and African lakes (circles).

African lakes are much older (>1 million years) than North American lakes (post-glacial; < 10,000 years ago) and have a steeper slope (z) (from Barbour and Brown 1974)



The species-area relationship

African lakes are much older (>1 million years) than North American lakes (post-glacial; < 10,000 years ago) and have a steeper slope (z) (from Barbour and Brown 1974)

The older African lakes have been a center for speciation – particularly in the long term historical diversification of African Cichlids

#### The species-area relationship

Explanations:

- Larger areas hold more individuals, sampling of more individuals should result in more species on larger islands
- Since larger areas hold more individuals, and extinction is less likely in large populations, there will be less extinction on larger islands
- Higher geographic/habitat diversity on larger islands (e.g., elevation ranges, topographic complexity)
- Higher likelihood of abiotic disturbance on smaller islands, leading to higher extinction rates
- More evolutionary diversification on larger islands (more opportunity for within-island separation of populations and allopatry)
- *Target effect*: larger islands have a larger shoreline, which leads to higher immigration rates (higher chance of intercepting dispersing individuals)

# The species-area relationship Log (Species Richness) OR.... $\bigcirc$ Log (Area)

Small isolated islands have fewer species than similarly sized areas on a continent. Populations are less likely to be rescued on islands - higher probability of extinction

Sampling larger areas of continuous habitat

Sampling islands

independently



Figure from Wilson 1961, black line added to emphasize slope across insular faunas

#### The species-isolation relationship

Assume the decline in richness results from decrease in dispersal opportunities with increasing isolation

The form of the species-isolation relationship reflects the dispersal curves for the *pool* of species (i.e., potential colonists from the mainland)

Species-isolation relationship:  $S = k_1 e^{-k_2(l^2)}$ 

S = number of species (or richness)

I = isolation

 $k_1$ ,  $k_2$  = fitted constants



#### The species-isolation relationship

Species-isolation relationship remains less well documented than the species-area relationship

In part, it is tough to accurately measure isolation in a way that represents the likelihood of immigration to an island



Measured routes of dispersal between patches

Actual routes species use between patches



The species-isolation relationship

Sq. Root Isolation (km to mainland)

Species-isolation relationship for butterflies on islands off the British Isles. A significant relationship with substantial scatter (Dennis & Shreeve 1997)

#### The species-isolation relationship



Figure shows number of high Andean bird species on each mountain island (black) plotted against distance to the main Andes (gray) in Central-Western Argentina

(from Nores 1995)

#### The species-isolation relationship

**Explanations:** 

- Low immigration rates prevent far islands from attaining equilibrium
- Low immigration rates lead to a lower number of species at equilibrium
- Lower diversity of habitats on isolated islands
- *Rescue effect*: populations on near islands are less likely to go extinct due to immigration from the mainland



Routes of dispersal in and out of Melanesia followed by the ponerine ants (from Wilson 1959)  $\frac{1959}{24}$ 

#### E.O. Wilson's "Taxon Cycle" for Melaniesian ant fauna (Species turnover in time)



1) Adaptation to marginal habitat on mainland. 2) Cross water gap and establish in marginal habitat on an island. 3) Go extinct, or 4) colonize inner rain forest. 5) Diversify in structured forest habitat. 6) Adapt to marginal habitat, continue cycle on further islands

#### (Wilson 1959)

#### the Equilibrium Theory of Island Biogeography (ETIB)

Proposed by E.O. Wilson and R.H. MacArthur (1963, 1967) to explain three characteristics of island biotas:

- 1. Species-area relationship
- 2. Species-isolation relationship
- 3. Species turnover (T)



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#### the Equilibrium Theory of Island Biogeography (ETIB)

Two assumptions of the ETIB:

- 1. Rate of immigration of new species decreases with increasing species on the island. Reaches zero when all species in the source area (*P*) are on the island.
- 2. Rate of extinction increases with increasing number of species on the island.



#### the Equilibrium Theory of Island Biogeography (ETIB)

- As more species arrive, the chance of having deleterious (extinction-inducing) interactions increases.
- Variation in extinction/immigration probabilities between species:
  - Best dispersers arrive quickly, poorer dispersers arrive later and later.
  - When many species are present, more extinction-prone species are lost first.



the Equilibrium Theory of Island Biogeography (ETIB)

Equilibrium prediction: colonization curve



Time

#### Significance of the ETIB

1. Reinvigorated interest in role of contemporary processes to explain species distributions and diversity (e.g., dispersal).

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- 2. Conservation biology.

Relevant to the design of wildlife reserves.

- Figure depicts different designs for reserves based on a given available area. In each case, the design on the left is preferred.
- Scenario (A) is a depiction of the "SLOSS debate" is it better to have a "single large or several small" reserves?
- Which scenarios can be understood based on the principles of the ETIB?



### Significance of the ETIB

- 1. Reinvigorated interest in role of contemporary processes to explain species distributions and diversity (e.g., dispersal).
- 2. Conservation biology.
- 3. The ETIB made testable predictions.

e.g.,

• With equilibrium species richness:

S<sub>LN</sub> > S<sub>LF</sub> (Large islands Near mainland will have more species than large islands Far from mainland)

 $S_{SN} > S_{SF}$  (Small islands Near mainland will have more species than Small islands Far from mainland)

- $T_{SN} > T_{LN}$  (Small islands Near to mainland will experience higher turnover than Large islands near the mainland)
- $T_{SF} > T_{LF}$  (Small islands far from the mainland will have higher turnover than Large islands far from mainland)