

Habitat Fragmentation & Island Biogeography

David Quammen (a local!) wrote *The Song of the Dodo*, which examines the relationship between declining biodiversity and island biogeography. He coined the Persian Rug analogy — if you take a 10'x10' Persian rug and cut it into 100 pieces, do you get 100 nice little replicas of the original rug? No, you get 100 frayed pieces of junk.

Habitat Islands - an area of habitat surrounded by an area of unsuitable habitat. Can be treated like an island, w.r.t. the processes determining how many species occupy it.

Examples of habitat islands:

1. Man made: forest surrounded by area that has been converted to grassland
2. Natural: alpine habitat on mountaintops, isolated from other alpine habitat by lower land
3. Natural, very small scale: dung piles, habitat for dung beetles.

Islands generally hold fewer species than an area of the same size in continuous habitat. This is true for genuine oceanic islands and for habitat islands.

(Fig. 2.9c Pianka: Ants on New Guinea and small Indonesian islands)

Barro Colorado became island in 1923, during construction of Panama Canal, and has subsequently lost 45 species of birds.

Island Biogeography largely grew out of the observation that islands hold fewer species than expected, based on area alone. Robert MacArthur & Edward Wilson (1967) developed much of the theory.

Two basic patterns underlying the major ideas in Island Biogeography

1. Larger islands hold more species.

Overhead: Fig. 9.3 Diamond & May 1981: New Guinea birds on mountain ranges)

This seems obvious, but why? Three reasons:

1. Statistically, large areas more likely to include sparsely distributed species.
2. Large areas likely to hold a greater variety of habitats than small areas.
3. Large areas can support species that require large home ranges (e.g. mammalian top carnivores)

$$S = CA^z$$

S = # of species

A = area of island

C and z, constant and exponent that vary among places and taxonomic groups.

On a log-log plot, this equation describes a straight line with slope = z :

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

In general, $0.18 < z < 0.35$ on islands.

Rule of thumb from empirical values of z :

The observation that $0.18 < z < 0.35$ gives a useful rule of thumb — reducing area by factor of 10 will reduce species present by factor of 2. Can be used to make predictions about the number of species likely to be preserved under alternative course of action. E.g. reduce area of tropical rainforest to 10% of current size → expect 50% of original species to be retained. Reduce to 1% of current size → expect 25% of original species to be retained.

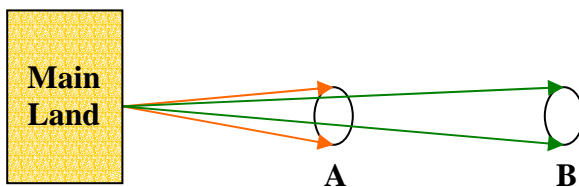
Note - this is a very rough guide that ignores many ecological details. If possible, desirable to use more detailed information on population sizes and specific habitat requirements of the species actually present in an area.

2. **The Distance Effect** - the farther an island is from a potential source of colonists, the fewer species it holds

(Overhead: Fig 9.2 Diamond & May 1981, bird species vs distance in S. Pacific)

Two reasons for this:

1. Only species with good dispersal ability can cross wide gaps
2. As distance increases, the arc of dispersal angles that will strike island decreases.



A and B same size. Because A is closer to mainland, a wider arc of dispersal angles will strike it.

The Equilibrium Theory of Island Biogeography

The observations described above lead MacArthur & Wilson (and others) to a simple model of the number of species expected on an island, as functions of the island's size and degree of isolation. Under this theory, the expected number of species, S , stabilizes when the opposing forces of **immigration** and **local extinction** are exactly balancing.

(Overhead: Fig 2.11 Pianka: I, E, S)

How will immigration and extinction rates vary with the number of species already on an island?

Immigration: Consider a new island formed by volcanic activity in ocean. Initially, no species present. At first, rate at which new species are established will be high, for two reasons:

1. Every immigrant species is likely to be new (unrepresented on the island) initially. As time passed, immigrants are less likely to be novel.
2. Competition is initially low, so establishment is initially easy. As niches become filled, establishment is harder.

Consequently, immigration rates will decline as S increases through time (Fig. 2.11 Pianka)

Local Extinction: No species present initially, so extinction rate = 0. As time passes, rate of extinction rises, for two reasons:

1. As more species are established, the odds increases that one will go extinct by chance alone (assuming that the likelihood of extinction, per species, is constant).
2. The likelihood of extinction, per species, will increase as the number of species increases (\uparrow interspecific competition) and as population sizes increase (\uparrow intraspecific competition).

Consequently, extinction rates will increase as S increases through time (Fig 2.11 Pianka).

The equilibrium number of species occurs when these two processes balance each other.

(Overhead: Fig 2.11 Pianka)

If the rates of extinction and immigration change in a linear fashion as S increases:

$$\lambda_s = \lambda_0 - \alpha S$$

Where λ_0 = immigration rate with no species present

λ_s = immigration rate at equilibrium

α = change in rate of immigration of species as S increases

S = number of species present

$$\mu_s = \beta S$$

Where μ_s = extinction rate at equilibrium (note $\mu = 0$ when $S = 0$)

β = change in rate of extinction of species as S increases

Setting $\lambda_s = \mu_s$ gives equilibrium number of species:

$$S_s = \lambda_0 / (\alpha + \beta)$$

Important to note that this predicts the number of species at equilibrium, but it is a **dynamic equilibrium**. The number of species is constant, but the particular species present may be changing as immigration and local extinctions occur.

Modifications to increase biological realism.

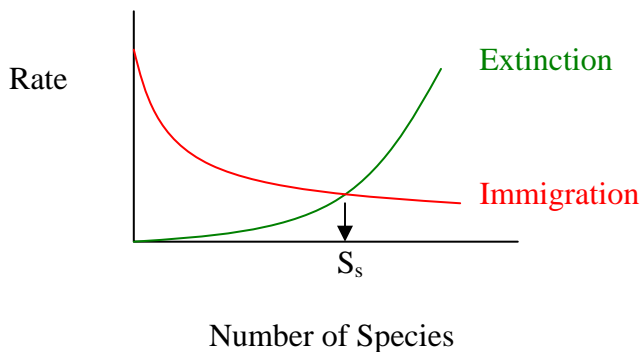
The linear relationships between λ and μ implicitly assume that:

- each species has the same chance of immigrating as every other species
- each species has the same of going locally extinct

In real data, the immigration and extinction curves will rarely be linear.

(Overhead: Fig 9.7 Diamond & May 1981, p174: E & I curves for 3 Sisters).

It is generally argued that immigration and extinction curves will be concave up:



Immigration - initially at a high rate as species with good dispersal ability colonize. Eventually, most if the good colonist species in the pool of potential immigrants are present, so rate of immigration of new species slows.

Extinction - as species with poor dispersal ability but good competitive ability (K-selected species) arrive, they drive poor competitors that arrived earlier (r-selected species) extinct. As more species are accumulate, population sizes decrease, competition intensifies, so the total risk of extinction accelerates.

Adding the island size effect.

Island size is likely to have large effect on extinction rates by limiting population sizes. May also affect immigration rates (smaller effect) by affecting size of target for dispersers.

(Overhead: Pianka Fig. 2.14 - effect of area on equilibrium number of species)

(Overhead: Meffe & Carroll 94, Fig 9.6, p. 245 - size effect in Atlantic coast birds)

Adding the distance effect.

Distance is not likely to affect extinction rates, but more distant islands will have lower rates of immigration

(Overhead: Pianka Fig 2.12 - data on distance and immigration probabilities)

(Overhead: Pianka Fig 2.13 - effect of distance on equilibrium number of species)

(Overhead: Meffe & Carroll 1994, Fig 9.7, p.245: Combining the distance and area effects)

Adding an island type effect.

Up to now, the theory discussed has implicitly been applicable to *de novo* islands, arising anew (e.g. by volcanic activity). Often called ***oceanic islands*** to distinguish them from ***land bridge*** islands. Land bridge islands are areas that used to be connected to a mainland but have become isolated.

For a land-bridge island, most or all of the pool of potential colonists are already present when the island is formed. Therefore, S decreases or ***relaxes to equilibrium***. (The equilibrium itself is same as for oceanic islands - a balance between immigration and extinction rates sets dynamic equilibrium).

(Overhead: Fig 9.8 Meffe & Carroll, p. 246 - model of oceanic and land bridge islands with same size and distance to mainland)

(Overhead: Fig 23.8 Begon et al, p. 869, lizards on land bridge islands, Gulf of CA)

(Overhead: Terborgh 1974, Table 1, land-bridge extinctions)

A large-scale experiment in island biogeography.

Simberloff & Wilson tested most of the above ideas on islands of red mangrove in the Bay of Florida, which support communities of insects, spiders, scorpions and isopods (sounds inviting). Censused original community, removed animals by setting up tent over entire island and gassing with methyl bromide. Then recensused periodically over next two years.

As predicted, found that most islands returned to similar equilibrium number of species, with S higher on large islands and those close to mainland.

(Overhead: Fig 5.2 MacArthur 1972, p. 82 - S pre and post defaunation)

Also as predicted, found that the equilibrium was dynamic - similar number of species, but *different* species). Island E-9 had 29 species prior to removal, and 24 species a year later. Only 8 of those 24 were present prior to the removal.

(Overhead: Fig. 5.3 MacArthur 1972, p.83 - results from island E-9.)

Simberloff also manipulated island size (a very rare experiment) by chainsawing away portions of the mangrove thicket. Found the expected area effect

(Overhead: Begon et al. Fig 23.7, p.869 - island size reduction experiment)

Edge effects

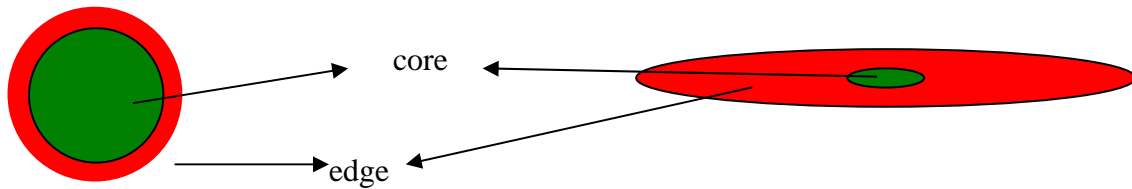
Habitat islands aren't surrounded by water, they're surrounded by another type of habitat. Edges of habitats tend to have different physical characteristics (e.g due to light penetration in forests) and different species composition than central portions. Over past 15 years discussion of *edge effects* has hypothesized that edges may be of lower quality than central portions. (Important to remember that edges also tend to have high productivity, and some species thrive there.)

Example with birds - data suggest that predation and nest parasitism by cowbirds is greater at edges. Data generally support this hypothesis, but not always, and only when 'edge' is defined to be 50m wide or less. (Some authors have argued that edges are much wider.)

(Overhead: Paton 1994, Table 1 - nest predation vs distance from edge)

(Overhead: Paton 1994, Table 2 - nest parasitism vs distance from edge)

Edge effect has implications for *optimal shape of reserves*. A circle has the minimum circumference for a given area. Reserves with highly irregular shape have a lot of edge per unit area. Long, thin reserves may be 'all edge'



Edge effect has implications for SLOSS debate - if a fixed area can be protected, is it better to have a *single large or several small reserves*. If several small reserves, then a large proportion of protected area will be edge. However, several reserves avoids putting all your eggs in one basket. Will return to this in last two lectures, on conservation biology.

Corridors. Because habitat islands are surrounded by land, it is possible to reduce the distance effect. Distance effect is really an isolation effect - farther away, lower immigration rates. For habitat islands, can reduce isolation (distance) effects by leaving corridors of suitable habitat that facilitate immigration.

Considerable debate on how useful corridors are, and how wide they must be. The answer depends on the species under consideration. Corridors would probably help beetles:

(Overhead: Meffe & Carroll, Fig 9.12, p. 248 - effect of road on beetle movements)

But species like coyotes and wolves can disperse across large tracts of 'unsuitable' habitat, without a corridor.

Case Studies of Corridor and Edge Effects

Thirgood et al – Serengeti wildebeest

Beier – California mtn lions