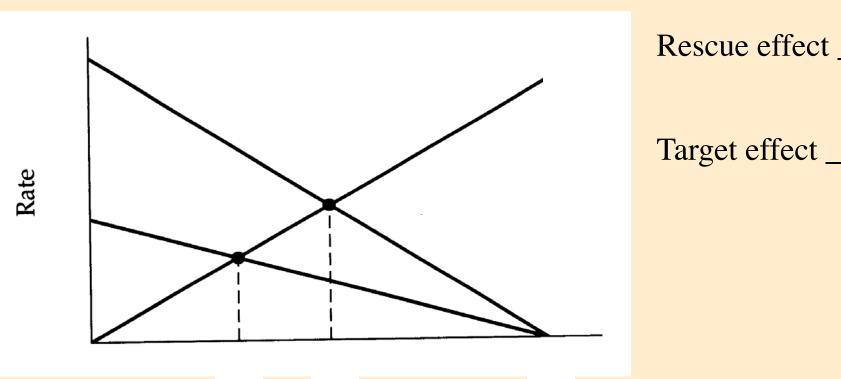
## Theory of Island Biogeography



Three assumptions of the M-W Theory of Island Biogeography:(1)(2)(3)

## Island Biogeography II

Island Biogeography Theory has been widely applied to habitat islands at a range of scales:

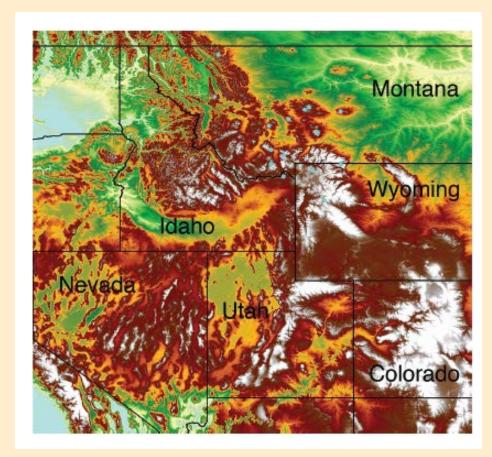
- Fungi growing on rotting logs (Ferrer 2001)
- Fish in lakes in Wisconsin (Tonn and Magnuson 1982)
- Beetles in forest fragments (Kehler 1999)
- Invertebrates in vernal ponds (March 1995)
- Earthworms on river islands in N. Sweden
- Domestic booklice in Madrid apartments (Baz 1999)

Support for theory is mixed.

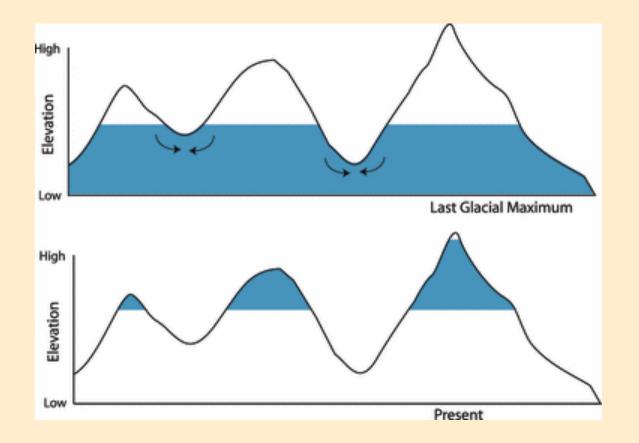
Island biogeographic theory has been especially influential in Conservation Biology

What utility does Island Biogeography have?

Brown (1971) Community composition of forest mammals on isolated mountain ranges ('sky islands', Great Basin of western N. America



## Key feature: Great Basin = montane habitats surrounded by desert scrub



Blue = habitat suitable for species currently restricted to montane habitats

#### Predictions:

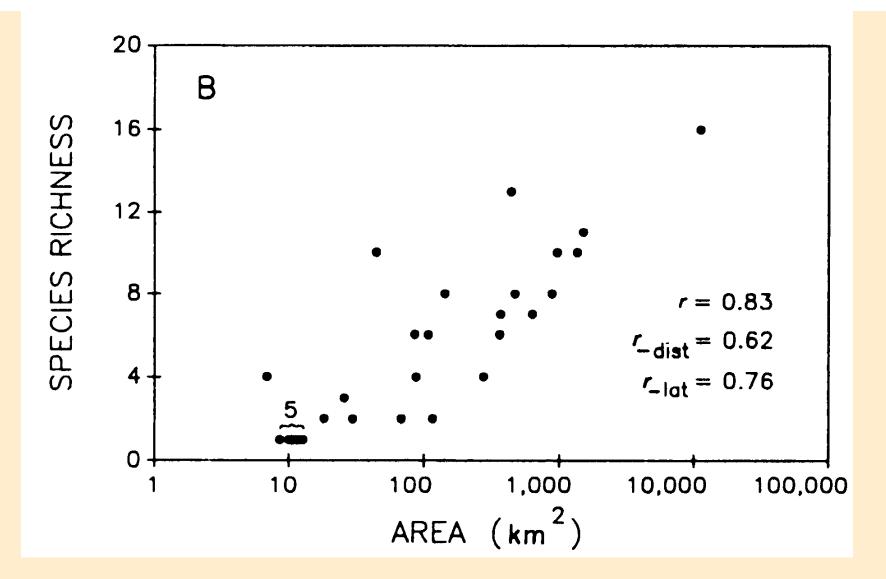
Expectation that fragmentation of a *once continuous habitat* into relatively isolated patches of small size should result in *decrease in species richness through time* (**'relaxation**' hypothesis), as the more resource-demanding species (e.g. large carnivores) become extinct.

*Good evidence for extinction*: lower *S* on smaller islands of habitat, but *little evidence of colonization* (intervening matrix too different from that of woodland habitat to permit migration?)

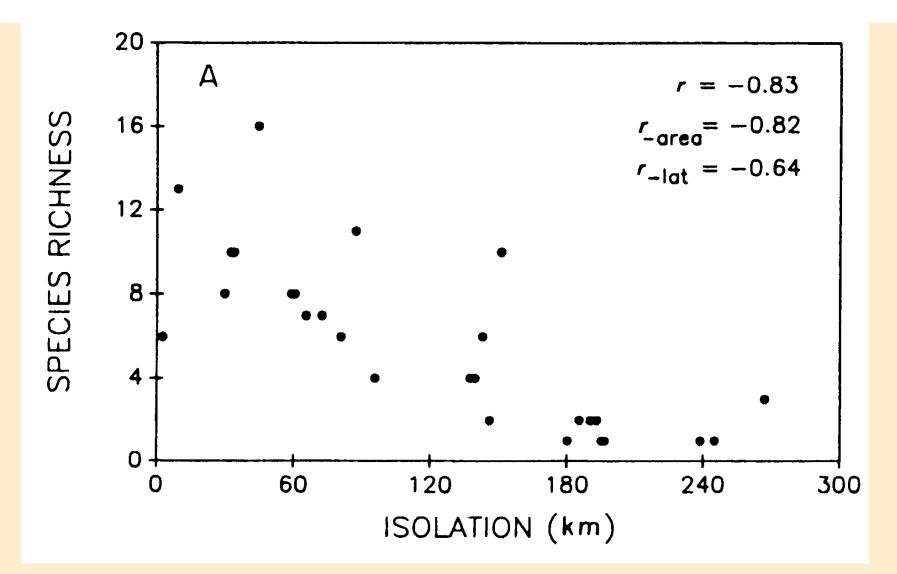
Lomolino et al (1989): Forest fragments in the South of the Great Basin. These are forests mostly within a matrix of *woodland rather than desert-scrub*. Matrix more permeable than desert?

What would you expect for distance and size effects if the matrix can be crossed or not?

Looked at distribution of 26 non-flying mammals on 27 islands with known association with montane environments.



Species richness strongly correlated with area of forest island (n=27) for forest mammals – suggesting that *extinction* has been an important process

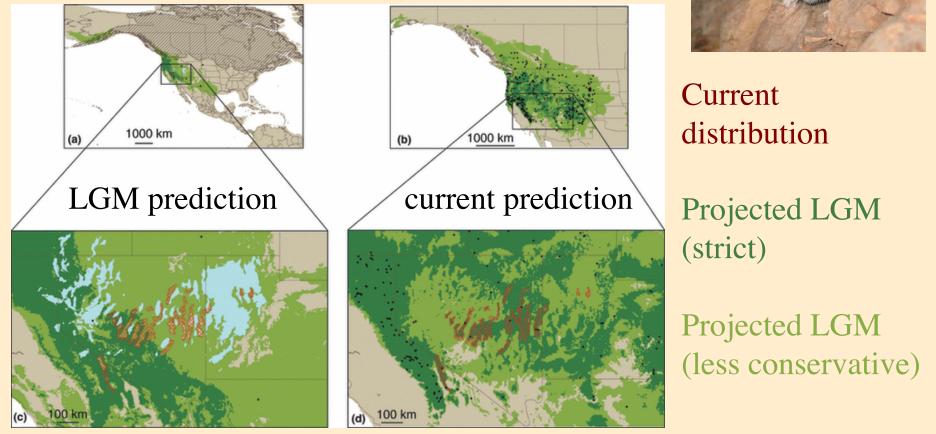


However also a strong effect of isolation of forest island... Suggests that post-pleistocene immigration through the matrix of woodland and chapparal surrounding forest islands has been important

## Waltari and Guralnick (2009) J. Biogeography 36:148

Re-evaluation of assumptions of habitat connectivity during the last glacial maximum (LGM) using *ecological niche modelling* 

*Neotoma cinerea* (wood rat)



## What about actual islands?



## Barro Colorado Island (BCI), Panama



*Relaxing on islands in the Panama Canal...* 

Leigh et al (1993) looked at species composition on many small islands (<2 ha) around BCI

- Small islands isolated by creation of freshwater lake in 1913. Found that by 1980 tree diversity on these islands was substantially lower than that on equivalent sized areas of the mainland or BCI

- Constructed Hubbell-style **random drift model** to determine whether random extinction could predict the species composition of these islands.

## Leigh's islands dominated by just a few common taxa:



Why the same species on each island?

Asquith *et al* (1997) evaluated the effect of different mammal compositions on different sized islands for seedling recruitment.

<u>Mainland</u>: spiny rats, agoutis, rabbit, paca, peccary, squirrel, deer, tapir, jaguarundi, margay, ocelot, puma, jaguar

BCI (1600 ha): all above except jaguar

Medium islands (15-18 ha) spiny rats, agouti, rabbit, paca

<u>Small islands</u> (<2 ha) spiny rats only







Asquith: 5 replicate sites at each of the 4 island sizes (mainland, L, M, S islands)...

Set out seeds of species likely to be dispersed or predated by mammals either in cages or in the open with threads attached to the seed.

No differences in removal rates across the 4 locations (all gone)

Large differences in the *fate* of seeds removed: Small islands - all consumed Medium islands - 34 % dispersed and buried Large island (BCI) - 43 % dispersed and buried Mainland - 77 % dispersed and buried

Also looked at the fate of established seedlings after by removing cages after seed germination 6 x higher survival of caged seedlings on small islands
3 x higher survival on medium islands
2 x higher on mainland
1.5 x higher on BCI

Conclusion: extreme mammal defaunation on small and medium islands has large and consistent effects on seedling recruitment.

Poaching is having similar effects across large areas of the mainland forests of Panama and elsewhere. *Will most protected areas end up looking like Leigh's small islands a century from now?* 

Wright (2000) evaluated sites in central Panama with different poaching intensities. Large effects on seedling recruitment success for palm species.

## What about fragmentation of continuous habitat?

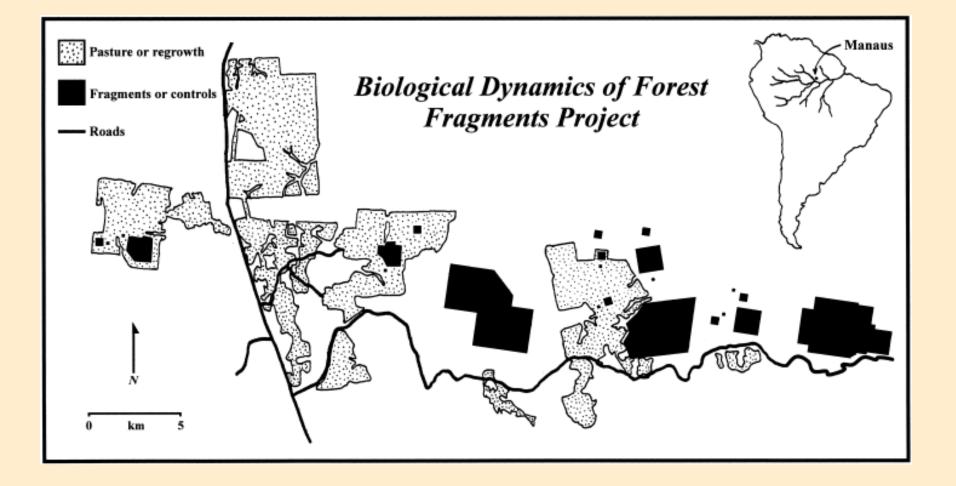


Brazilian government policy in 1970s mandated that a fraction of each ranch must be retained as forest.

What would be the capacity of these fragments to retain diversity?

What causes loss of spp from (even moderately large) fragments?

*Biological dynamics of forest fragments project* (BDFFP) looked at changes in species composition of artificially isolated 1, 10, 100 ha fragments and continuous forest controls on ranches around Manaus, Brazil.



What has happened in 32 years since experiment was started?

Laurance et al. Biological Conservation, in press.

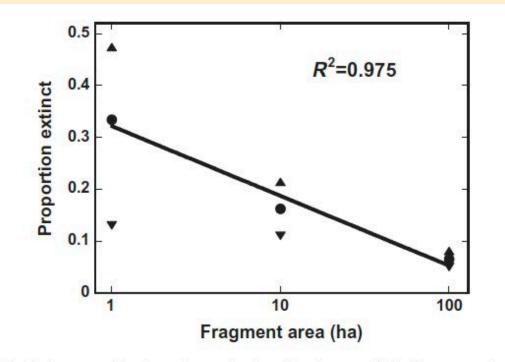
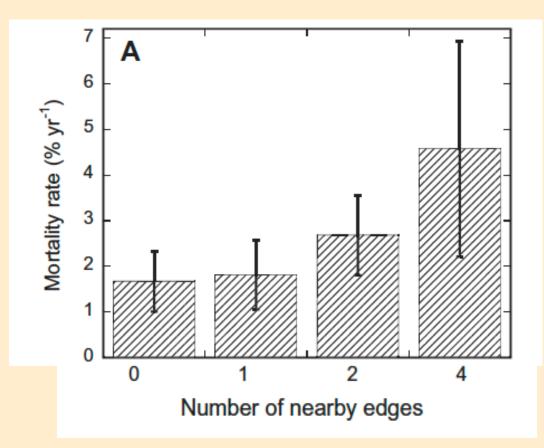


Fig. 2. Fragment-size dependent extinction of understory birds. Shown are the mean, minimum, and maximum proportion of bird species captured in each fragment in 1992 that were locally extinct in the same fragment in 2001 (after Stouffer et al., 2008).

Declines in mammals, insectivorous birds, bryophytes, seedlings...

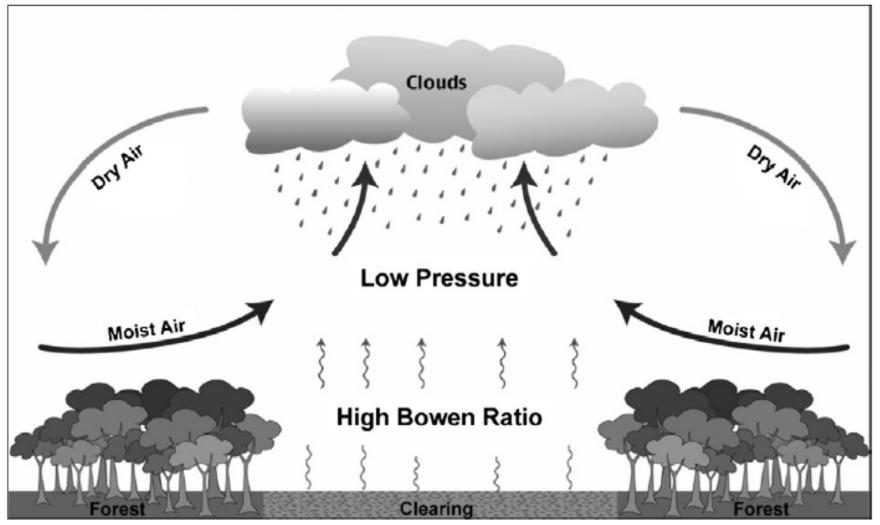
Smaller fragments lose spp more quickly.

Much larger areas needed to maintain species long-term >10,000 ha = 100 km<sup>2</sup>



# Tree mortality is highly sensitive to edge effects





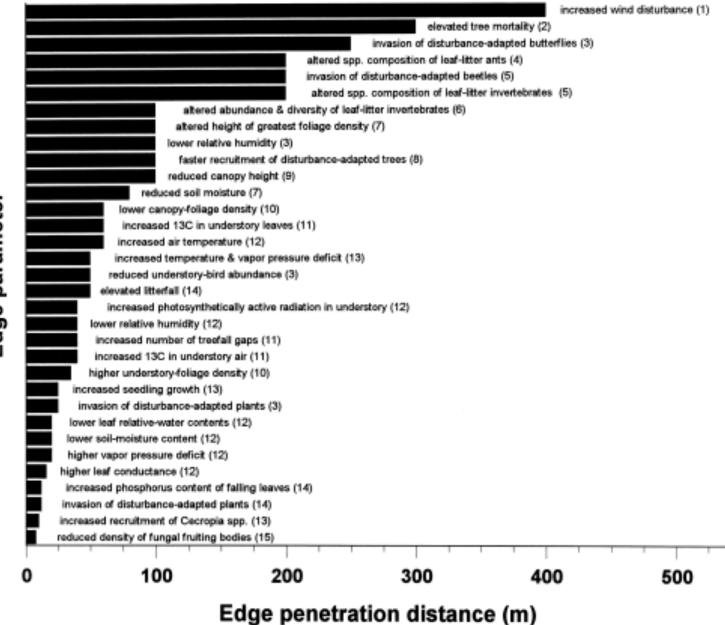
#### Laurance and Peres 2006



Laurance et al (1997, 2001) Tree mortality rates three fold higher at edge than center of fragments results in a 'biomass collapse'

Significantly more lianas stems and higher diversity at the edge. Colonization by lianas may have long lasting effects on forest composition by inhibiting tree seedling recruitment (Schnitzer et al 2000)

## Laurance et al. 2002 Conservation Biology



# Edge parameter

Since BDFFP initiated many pastures abandoned.

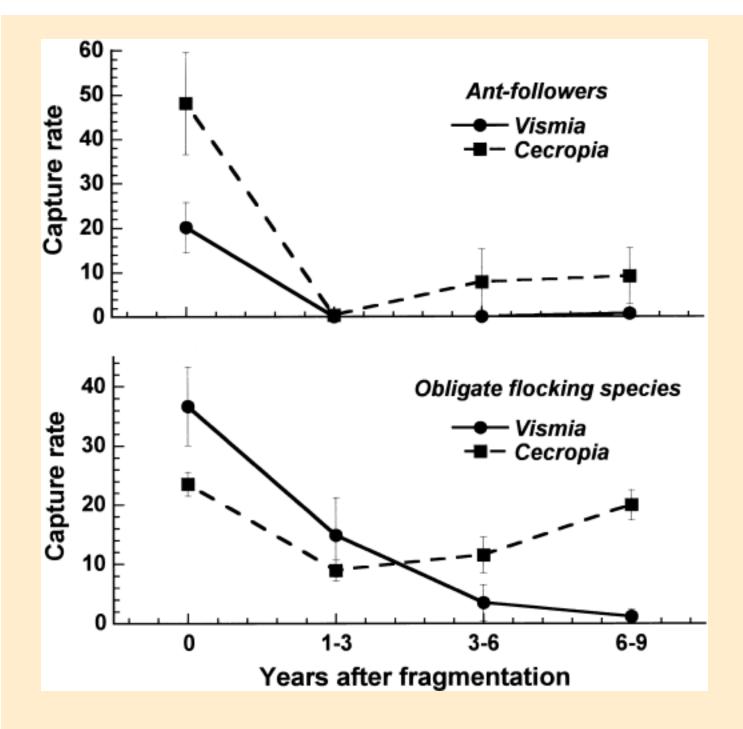
Fragments now have a matrix of regenerating forest





Cecropia

Vismia



Once matrix surrounding the forest fragments regrew then some recolonization of the fragments could occur

(more soon when regrowth was *Cecropia* dominated)

## Lago Guri, Venezuela: Another case study of contemporary relaxation.





Hydroelectric lake in Bolivar State, Venezuela, formed by damming the Rio Caroní in 1986.

Largest man-made lake in world? Lake = 4300 km<sup>2</sup>

Natural vegetation in forestsavanna matrix Rao et al (2001): Increased herbivory in forest isolates: implications for plant community structure and composition

Leaf-cutter ants (*Atta* spp), remove as much as 5% of annual leaf production...

- Small islands (0.3-3 ha): 5.6 colonies/ha
- Medium islands (7-12 ha): 2.3 colonies/ha
- Large islands (100-350 ha): 0.7 colonies/ha
- Mainland: 0 colonies.

## Possible release from predation?

Army ants: need large habitat areas (30 ha +) - observed to disappear soon after fragmentation Armadillos: dig up young ant colonies. Home range 3.5 ha Consequences of increased Atta herbivory for plants?

Inventoried saplings (<10 cm DBH) and juveniles (<1 cm DBH) on plots on six small, 4 medium, 2 large islands

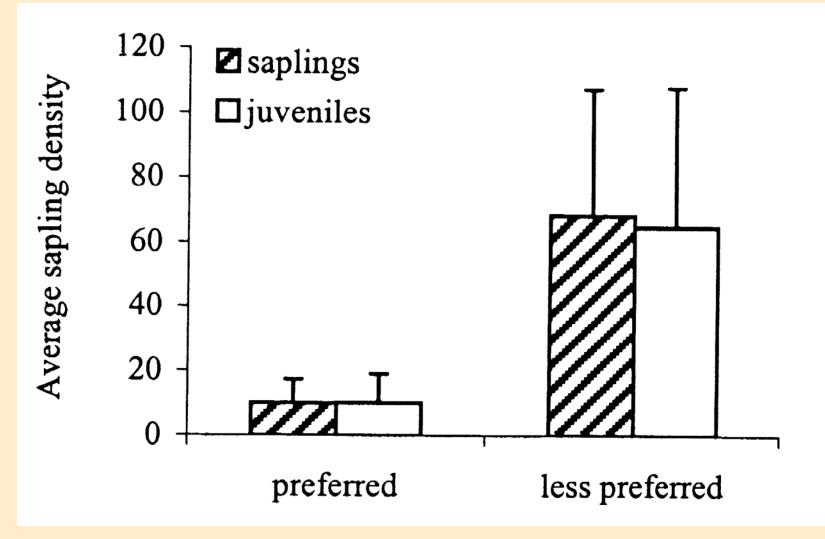
Tested palatability of the 43 most common plant species on the islands to determine *Atta* preferences.

Ranked species by ant preference and compared relative abundance of the top ten most palatable and bottom ten least palatable species on small and large islands.

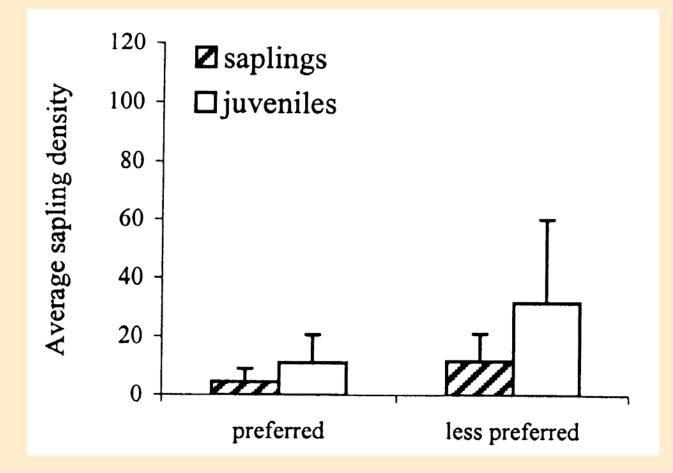
Result: **no difference** in abundance of saplings and juveniles of preferred spp **on large islands**.

However preferred spp were significantly less abundant on medium and small islands:

Difference in preferred v. less preferred -- medium islands



## Small islands:



Note: Stem densities of both preferred and less preferred species are lower than on medium islands and mainland -- ant effect or seed predation and other factors?? Lago Guri also provides example of how island formation can influence bird communities

Terborgh et al (2000) Censused bird communities on the mainland, and on 8 small islands (~1 ha) and 3 medium islands (~10 ha) and one large island (350 ha).

No evidence that relaxation resulted in consistent loss of particular bird species - species composition on islands was very variable, with few resident species on small (9) and medium sized (11) islands. However, most islands actually maintained higher bird densities on the islands than the mainland (in contrast to findings by Ferraz et al. for the Brazilian fragments). Due to?

- High densities due to cavity nesters (using stumps sticking out of the lake around the margin of the island).

- Lots of pigeons - able to fly between islands and nest on small islands because they are predator-free.

- '*Ecological release*'- in the absence of mainland competitors, island birds can exploit greater range of resources and increase in numbers. Some resources more abundant at Guri? e.g. Arthropod food resources (no army ants).

## However, low bird densities on 2 medium sized islands

- fewer resident pairs than the small islands despite 10 x area of small islands

- Low bird densities on these islands likely due to increased nest predation?

- Placed artificial nests containing Quail eggs out on all the islands. Found 100 % nest predation on the 2 medium sized islands versus average of 30 % predation elsewhere.

- Medium sized islands contained populations of Cebus monkeys



Territory size of *Cebus* in continuous forest ~ 150 ha On medium islands constrained to 10 ha could result in greater intensity of nest predation = *'ecological amplification'*.

### **Conclusions:**

The MW theory quickly became a **paradigm** in the 1960s strongly influencing population, community, and conservation biology

Now seems overly simplistic, and many assumptions no longer tenable:

Assumption that communities are in equilibrium Assumption that islands and intervening matrix are equivalent or homogeneous with respect to factors influencing immigration and extinction

Overlooks *in situ* speciation