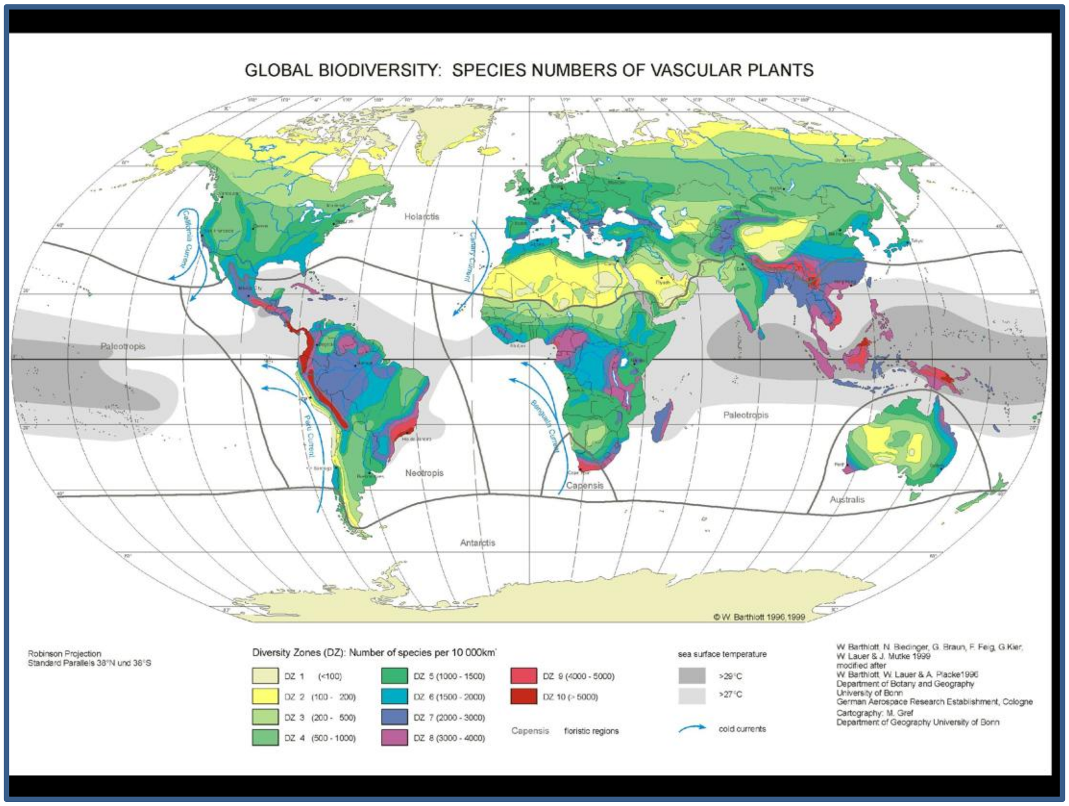
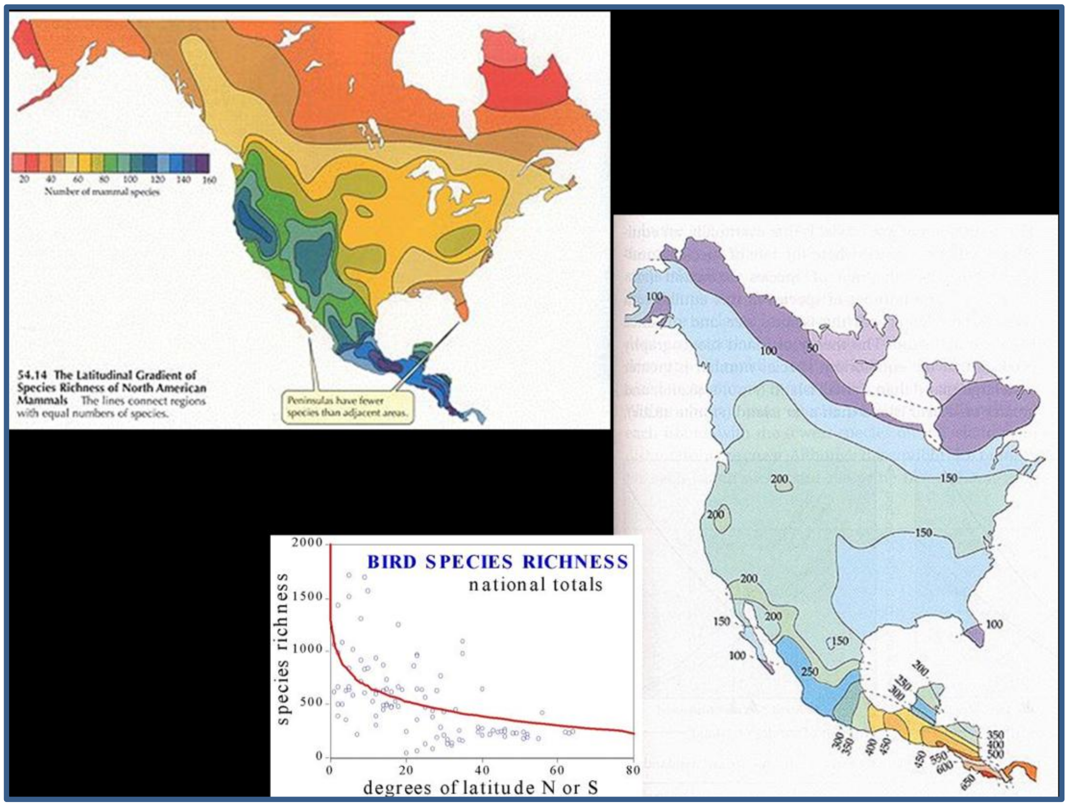
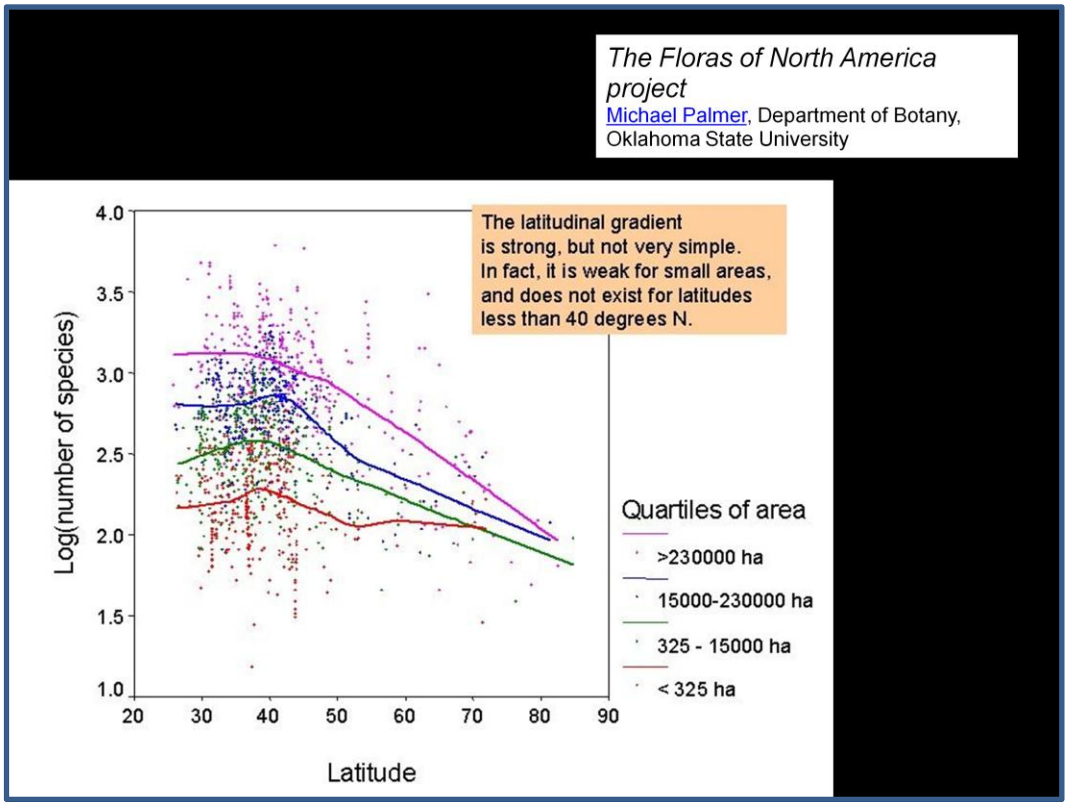


The problem of DIVERSITY. What regulates how many species occur together at a given time and place? What factors might promote diversity? What factors might constrain or limit it? Are factors controlling diversity linked to ecosystem properties and to the factors limiting (for example) ecosystem productivity? Patterns shown here in PLANT diversity are echoed by most other groups of terrestrial organisms, although there are a few exceptions; marine diversity patterns are somewhat more complicated. The most evident pattern is the so-called latitudinal diversity gradient; there are more species per given area at lower latitudes. Does this suggest an ‘energy’-related hypothesis (sunlight availability? Temperature?)? However, other patterns are superimposed; you suggested these might be related to moisture or terrain (habitat diversity in mountainous areas, for example). In fact, many hypotheses for all these patterns have been suggested. They’re difficult to test; people continue to explore them.



Mammal and bird diversity patterns for North America. Both show strong latitudinal diversity gradients. Are there other patterns visible?



But another pattern in diversity emerges by looking at data from a different angle. Here, plant diversity (simply the number of species) for well-studied sections of landscape is plotted against latitude (note that species number is on a logarithmic axis; MAKE SURE you understand what this means). Overall, diversity decreases with latitude again. BUT, these samples are of a wide range of sizes (The FoNA project -- http://botany.okstate.edu/floras/ -- collects species lists for areas of any size). Purple dots are for large areas; red ones for very small areas; blue and green in between). The colored lines are best 'fits' to to the points for each size class (imagine a graph with JUST the purple points or JUST the red points; the dots would be roughly centered around corresponding lines). There is a latitude relationship for the large area, but not much for the smallest ones.

This data-set demonstrates that another factor must be considered in understanding diversity patterns – how much area (or habitat) is being looked at).

In fact – perhaps surprisingly – the world record for plant species richness of a single square-meter area (about 90) is for these mowed grasslands in the White Carpathian Mts., Czech Republic, and other areas with near-record diversity are also in temperate regions (North Carolina pine savannas, Estonian wet meadows…). (The lower photo is an international group of plant ecologists tabulating species in a square-meter plot.)

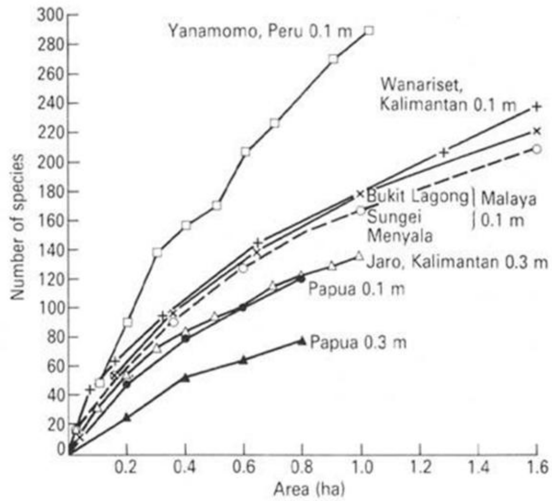
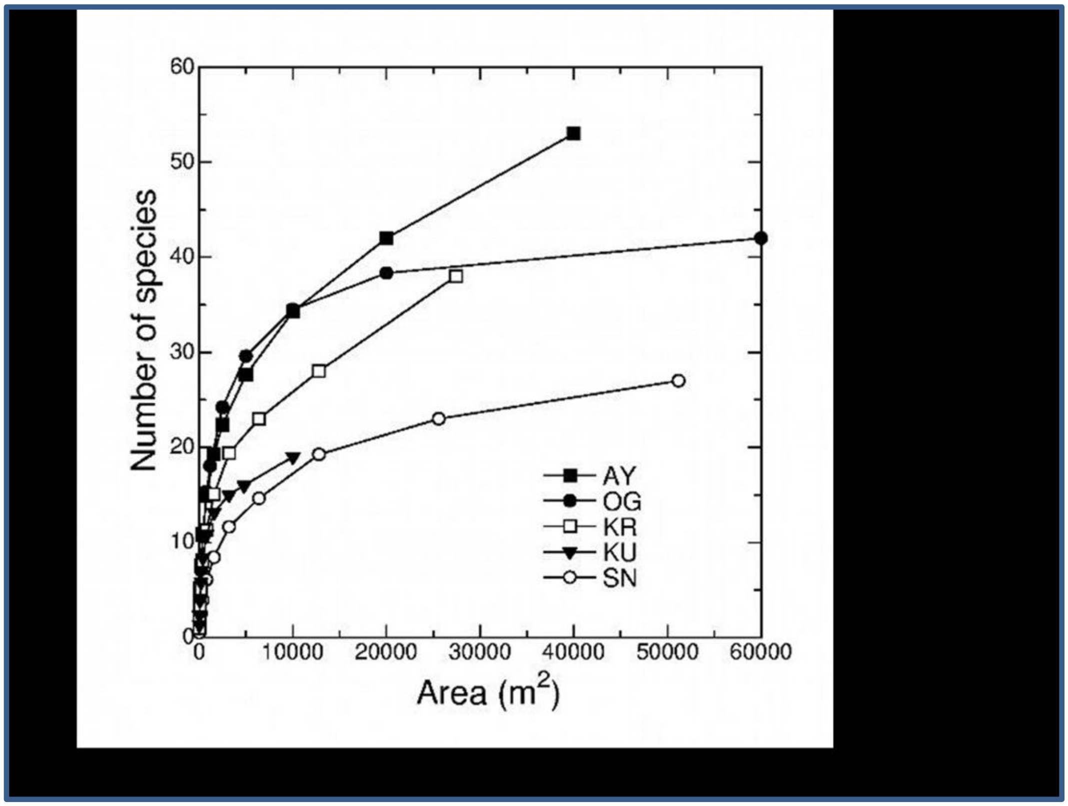


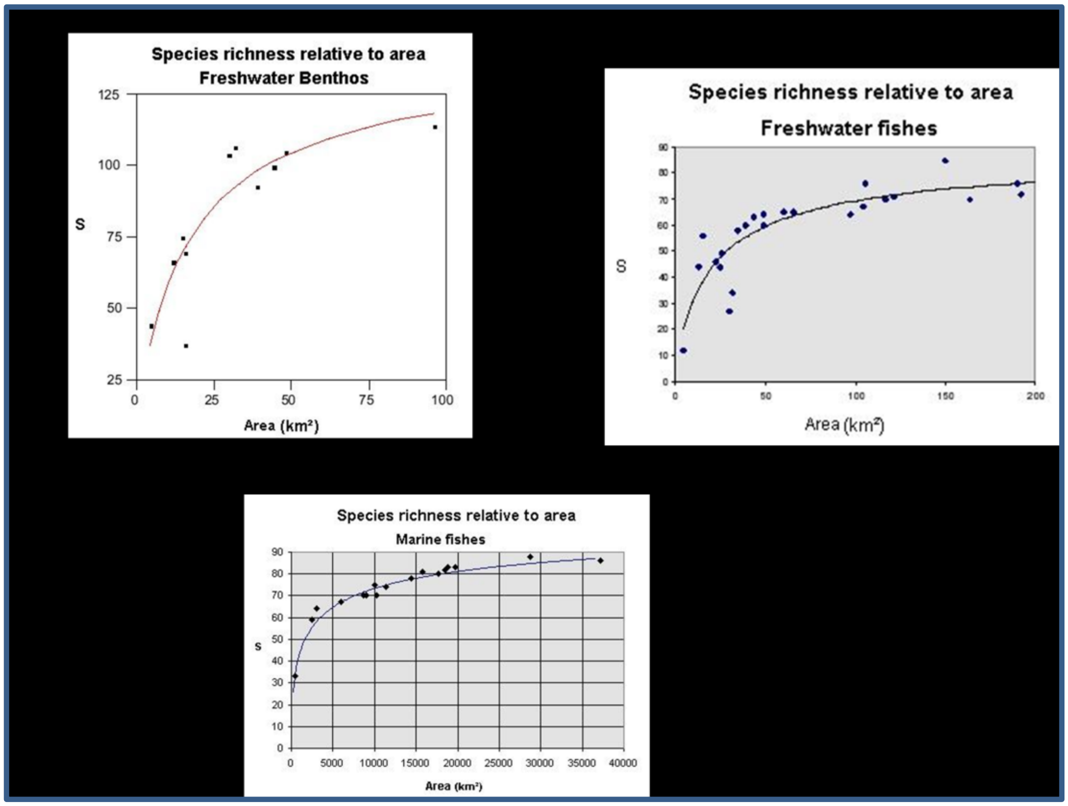
Fig. 2.28. Species area curves for tropical lowland evergreen rain forests. (After Whitmore 1984*a* and Genry 1988*b*).

The Yanamomo forest is the richest yet found, every second tree on the hectare plot was a different species. These curves were mostly made by adding together the number of species found on contiguous subplots. See also Figs. 2.29, 6.16*b*.

Relationships between species number (or ‘species richness’) and area sampled are, once again, extremely general. Here are some *species-area curves* for tropical forest trees (one hectare – ha – is 100 x 100 m or about 2.5 acres; there are almost 300 species of trees per ha in some tropical forests. There are about 600 species in all of the U.S. and Canada). Note the shape of the curves; they seem to have a slight arch, suggesting that, as area increases linearly, the *rate at which* the number of species increases will go down; it may even be a ‘saturating’ curve, with the line leveling off at a large enough area. While the curves for different regions clearly have different rates of increase, the possibility that there is a general *form* of curve has been of great interest; if this is really the case, it may suggest some sort of general mechanism for how species diversity is shaped with respect to area…



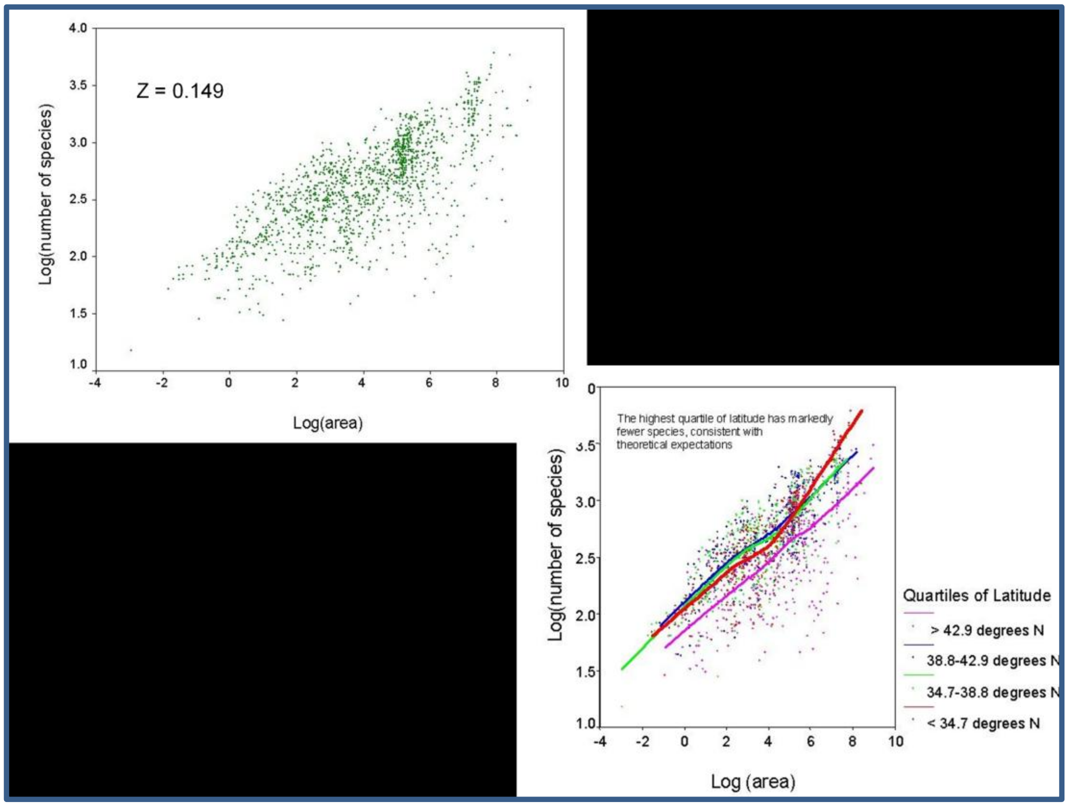
Here are similar curves for tree species in several stands of temperate forest in Japan (10,000 square m is one ha); these forests are much less diverse, and the curves do begin to level off at the largest areas.



Similar curves for some aquatic organisms; this curve form appears to be nearly universal for all kinds of organisms in all sorts of habitats. The shape of the resulting curves is best fit by a 'power equation' of the form $S = kA^z$ where S is species richness, A is area, and k and z are constants. Z is the interesting one; it determines how quickly species numbers increase with area. Taking the log of both sides of the equation gives:

$\ln(S)=\ln(k) + Z\ln(A)$

Which makes a straight line on logarithmic (or log-log) graphs with slope Z and y-intercept ln(k).



Going back to data from the ‘floras of North America’ project, and graphing the entire data-set onto log-log axes, there is a roughly linear relationship between log(S) and log(area); it’s slope is about 0.149. In the lower graph, the data set is broken up by latitudinal bands, and lines are fitted to each group of samples. Unsurprisingly, perhaps, the northernmost samples for any particular area tend to have lower species richness than samples of similar area but lower latitude. The more interesting patterns, however, is that all latitudinal groupings produce lines of very similar slope. The effect of area on diversity seems to be independent of latitude!

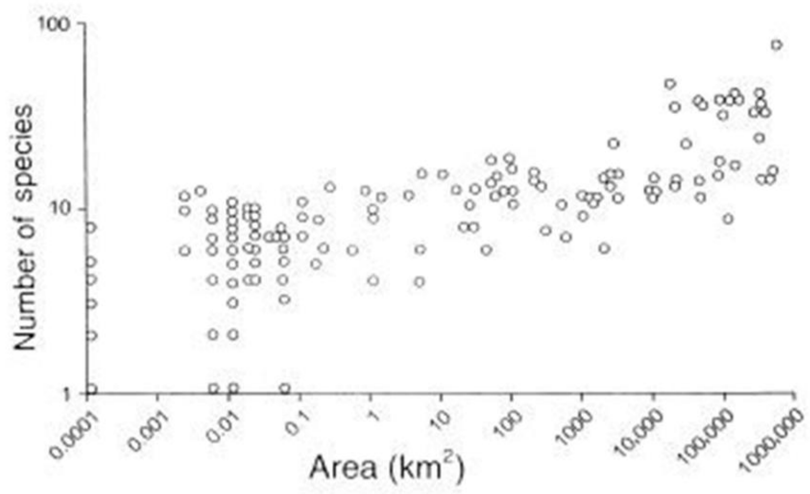
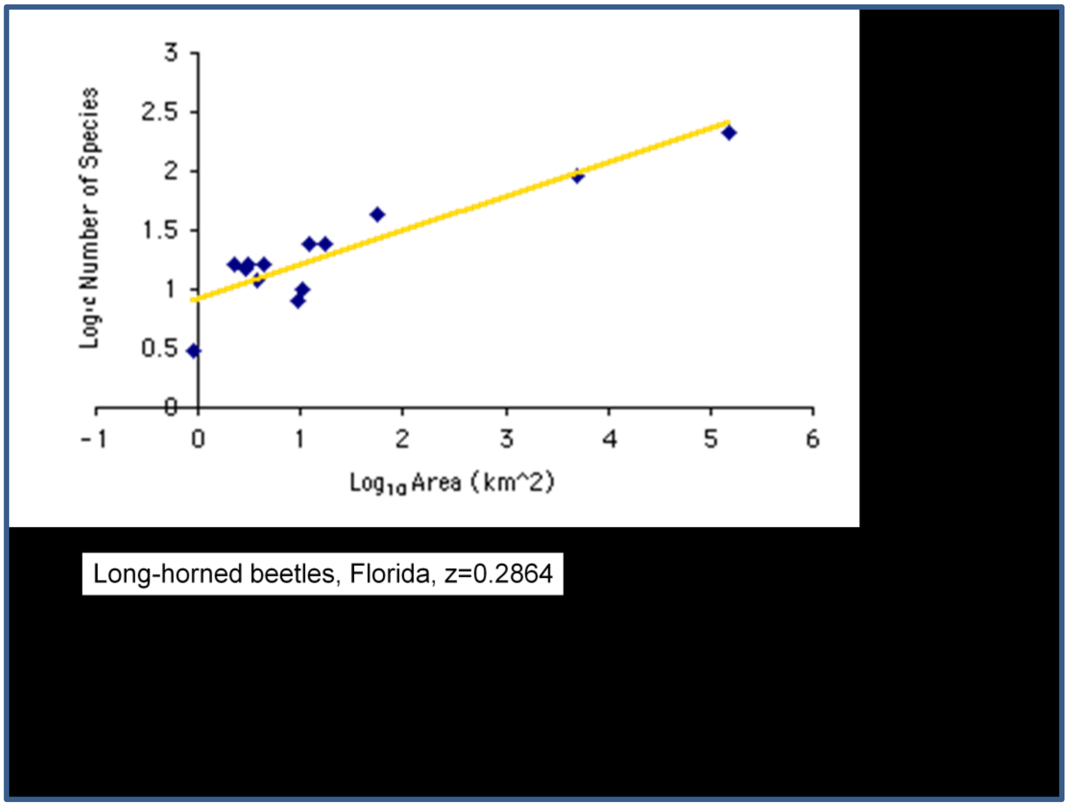


Figure 3 Species–area relationships for Lumbricidae (Annelida, Oligochaeta) in Europe. From Gaston & Spicer (1998) and Gaston (2000), from data in Judas (1988).

Species-area curves on log-log axes have been compiled for many types of organisms and many regions: earthworms in Europe.



A particular family of beetles in Florida. Most such curves have ‘z’ values (slopes) of around 0.15 to 0.25

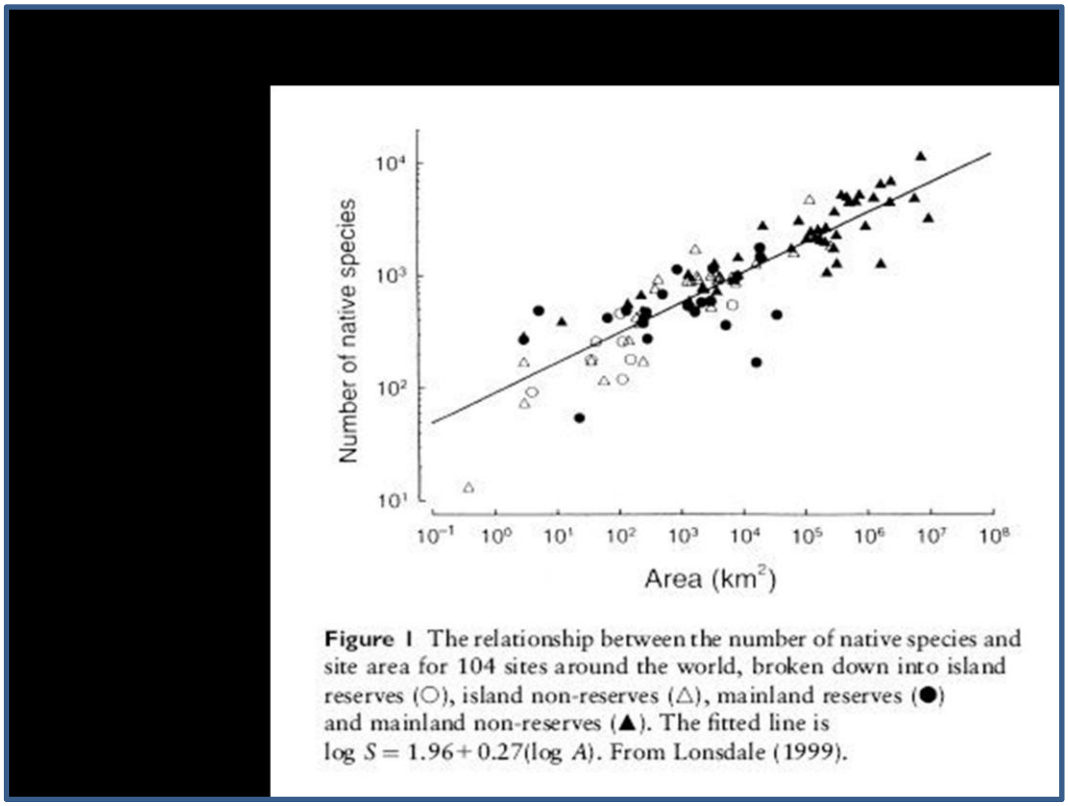
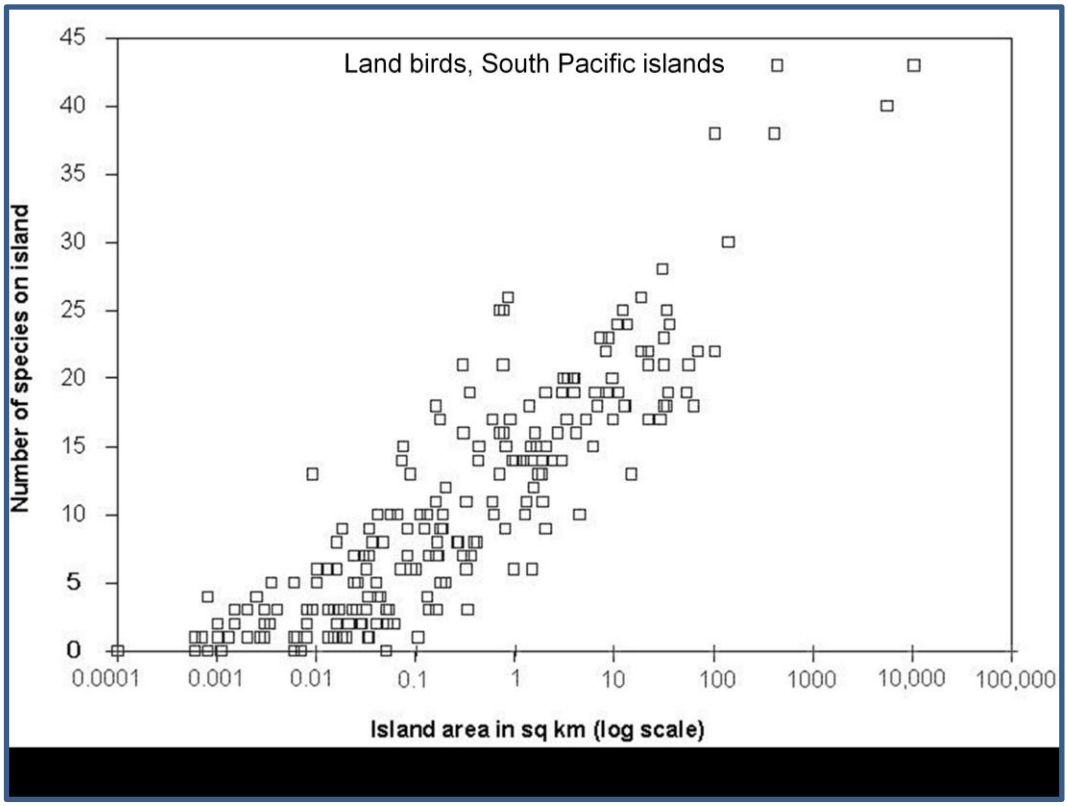
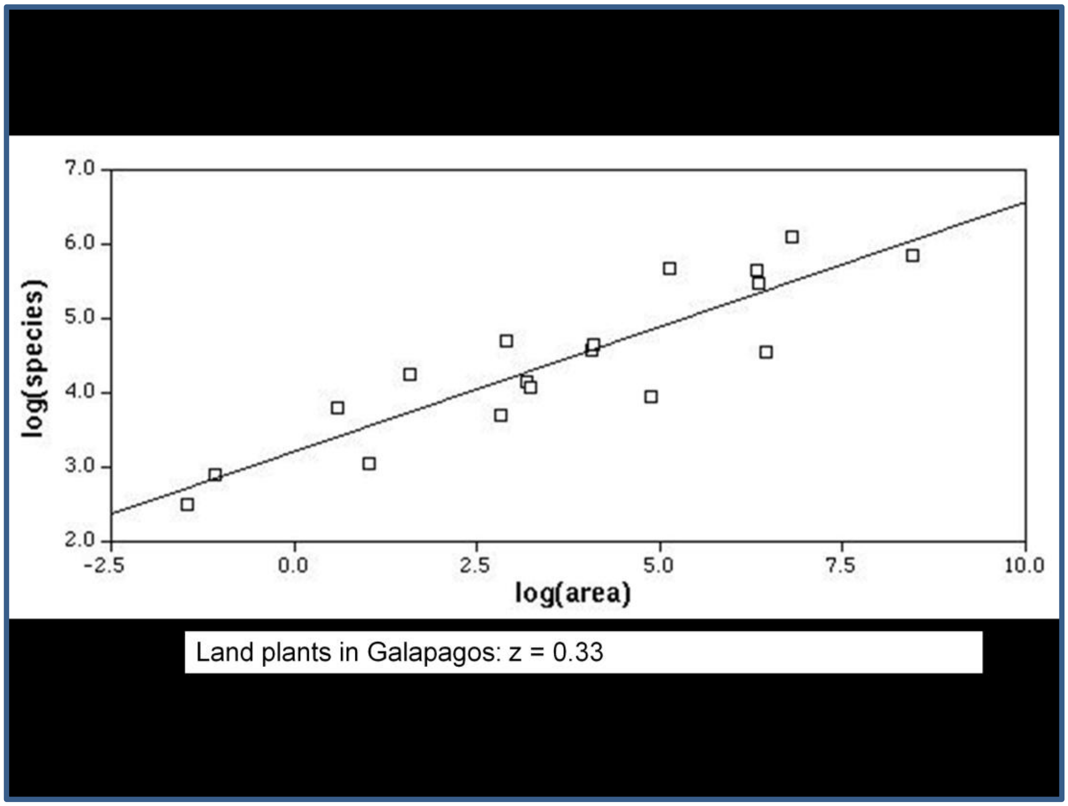


Figure 1 The relationship between the number of native species and site area for 104 sites around the world, broken down into island reserves (○), island non-reserves (△), mainland reserves (●) and mainland non-reserves (▲). The fitted line is $\log S = 1.96 + 0.27(\log A)$. From Lonsdale (1999).

And birds

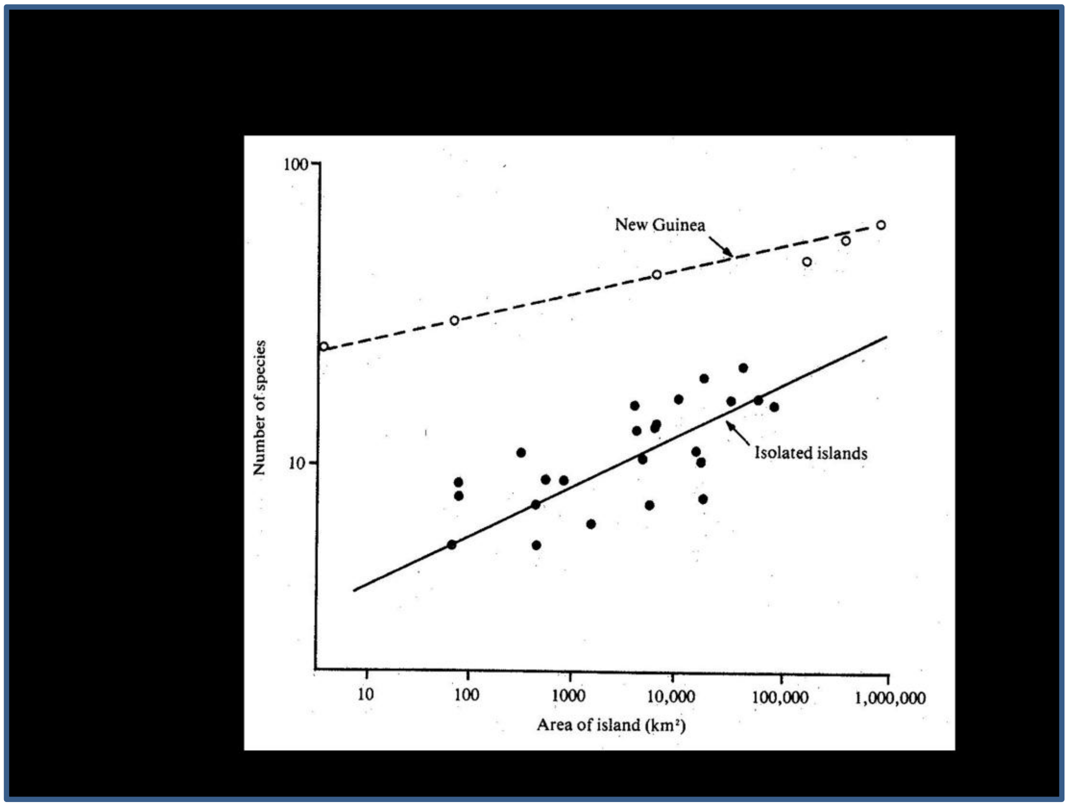


Similar patterns turn up when the total diversity of islands is plotted against island area; here each dot is an entire island.



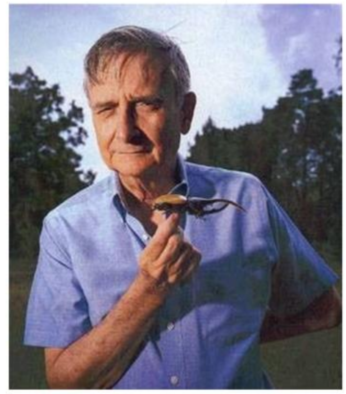
Land plants in Galapagos: z = 0.33

Islands often have Z-values on the order of 0.30-0.35 – higher than those for mainland sequences. Consider possible geometric explanations for this.



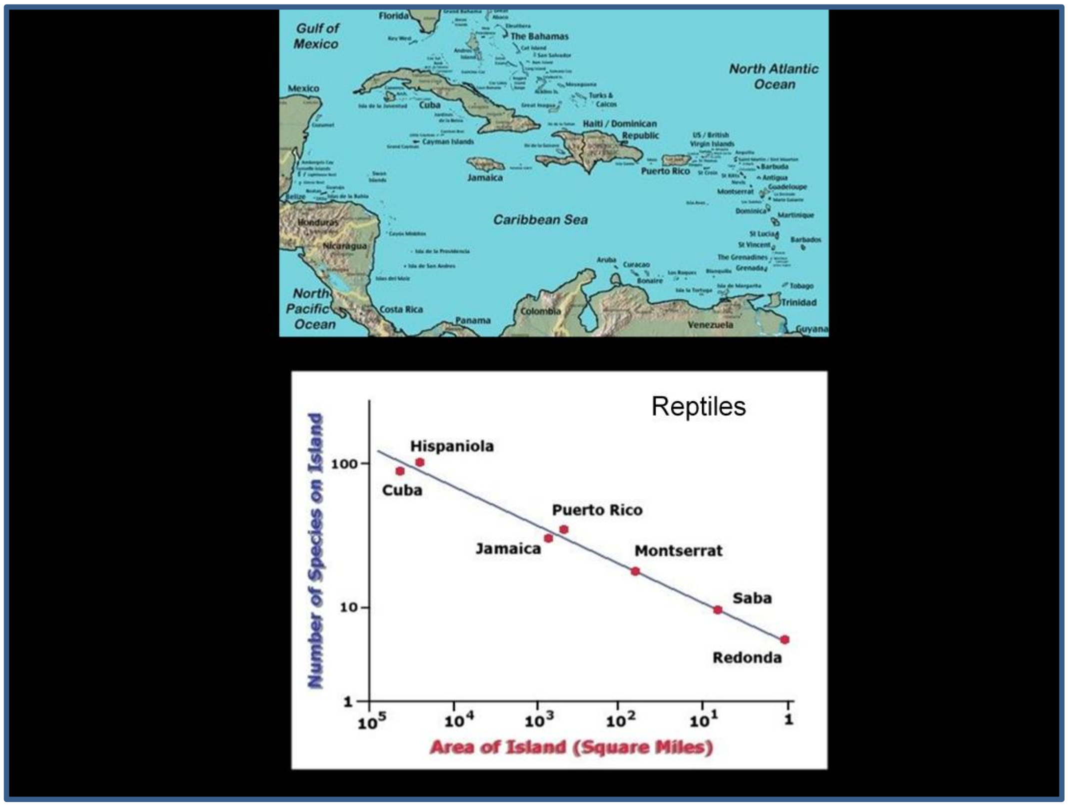
Now, as people made lots of species-area graphs in this manner, they began to notice some general patterns in differences in the slope of the curves; the Z-values for islands are higher than for curves based on similar areas within a mainland. Here, the number of ant species in a given area within New Guinea is higher than the number on a separate island of the same area. But *the difference decreases with increasing area* – that is, the z-value (slope) is higher for the islands *because* the y-intercept is lower for islands, but large islands become more and more like comparable areas on 'mainlands'. In other words, *small islands are extremely species-poor.*

Robert MacArthur (1930-1972)

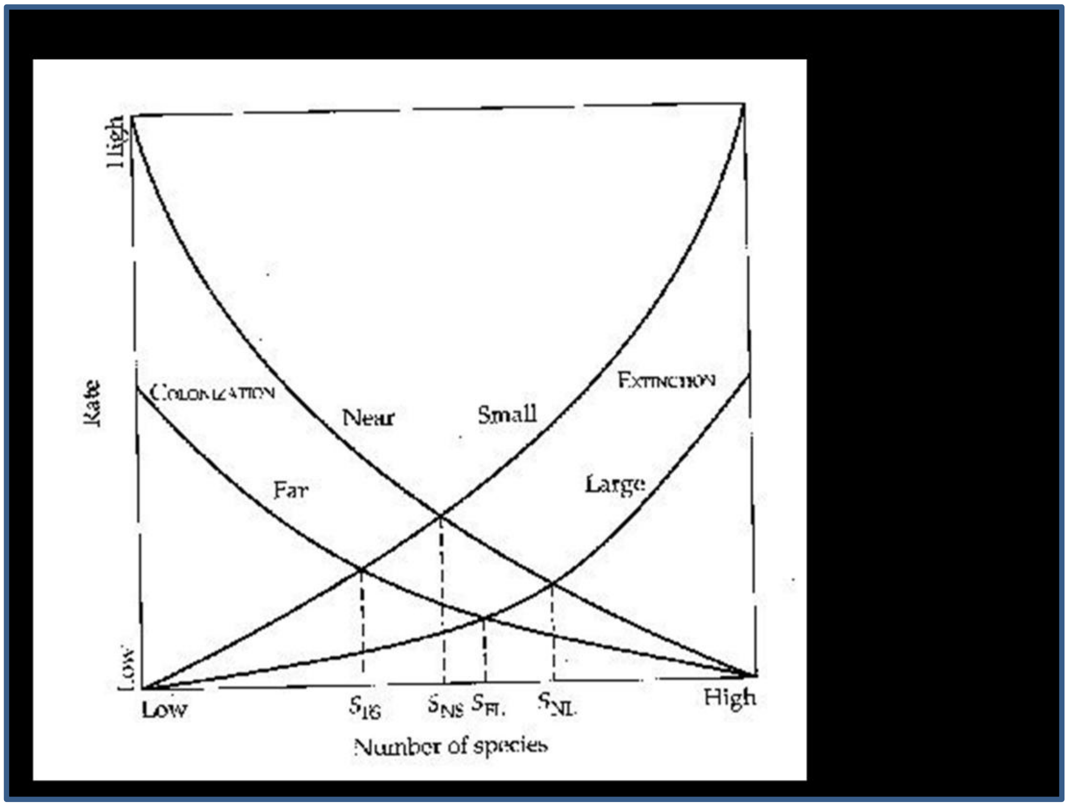


Edward O. Wilson (1929-)

These two individuals are among the most influential biologists of the 20th century; both made many contributions to ecology and evolution (Wilson continues to do so). Early in their careers, they became interested in islands as 'natural laboratories' for the study of patterns of diversity, and began to think about *processes that might regulate species richness on islands*.



They began their book *Island Biogeography* with this data-set for reptiles of the West Indies; a classic island species-area curve (note that they had the area axis run the opposite direction from other graphs here; small is to the right).

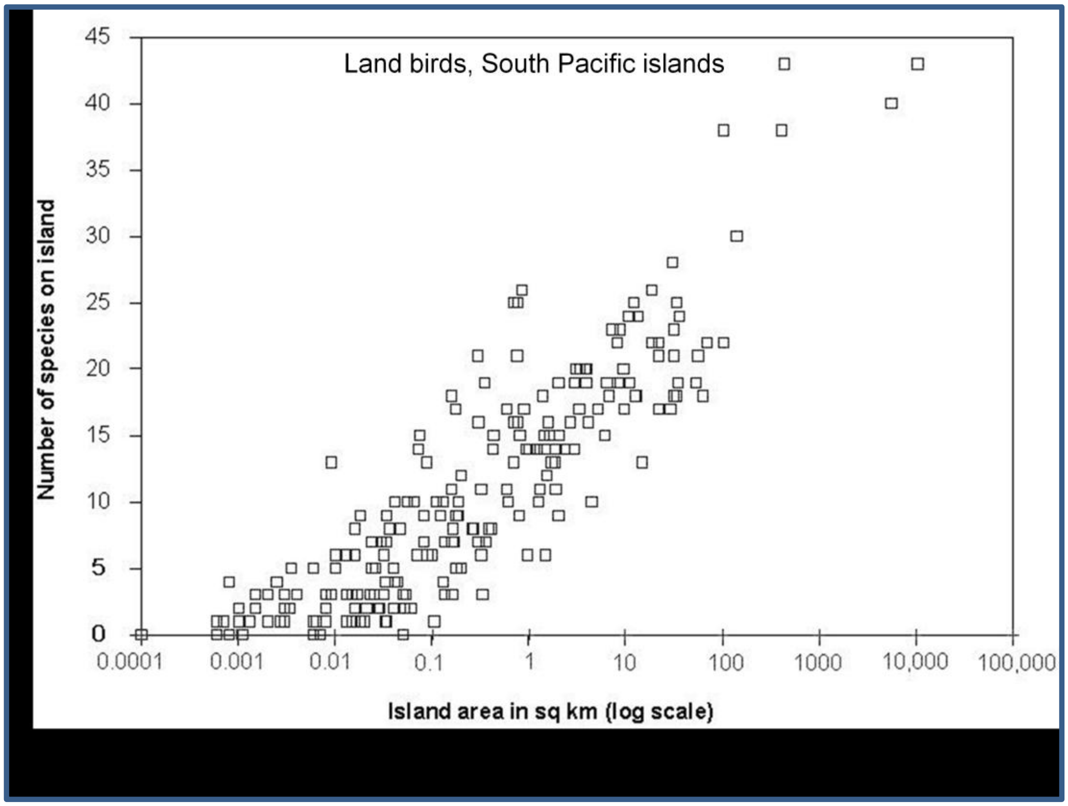


As we discussed in class; they approached the general question – what regulates diversity on islands? – by reducing the problem to the simplest *necessary* elements. Diversity MUST be determined by the balance between the rate at which new species colonize islands and the rate at which existing species go extinct. Many other factors MAY matter, but these MUST. This is a good example of how scientific models (hypotheses) are developed by really good theoretical thinkers; start with the essential skeleton, then see if it's enough. Add complications only as necessary.

The first complications – additional variables – added by M&W were island area and island remoteness. They reasoned that island remoteness would surely affect the rate of colonization; which would be lower for islands further from a source of colonists (a single 'continent' – or 'species pool' -- in their simplified model). Island SIZE would affect extinction rate; all else equal, a small island must have fewer individuals of any given species (due to resource constraints), so each species would have a higher chance of going to extinction.

Further, the number of species *already on the island* (S) would influence BOTH colonization and extinction rates. If S is higher, new immigrants are more likely to be of species already there, so they won't add to S. And if S is high average population sizes will be lower, so extinction more likely.

NOW, use the above graph to figure out how S (number of species) will change (or not) for different combinations of island size, island remoteness, and species richness. For any combination of size and remoteness, there's an *equilibrium* richness (where the curves cross, so colonization and extinction rates are the same). It is a *stable equilibrium* (make sure you understand this) This model has come to be called the MacArthur-Wilson Equilibrium Theory of Island Biogeography.



Island birds again: consider the variation in diversity for islands of approximately the same size: is it just random variation? Like any good or useful hypothesis, the M-W model makes testable *predictions* about this kind of thing; it predicts that particular differences in island properties should lead to particular differences in observed diversity? FAR islands (remote from source of immigrants) should have fewer species than otherwise similar NEAR islands; SMALL islands lower diversity than otherwise similar LARGE islands. (Remember that predictions of this sort always have an understood ‘all else being equal’ condition. If other things ARE very different then the comparison may not make a good test of the theory…)

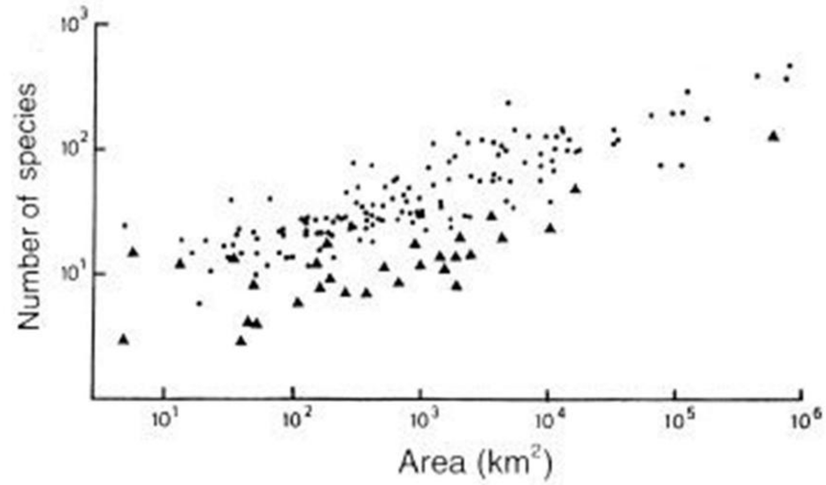
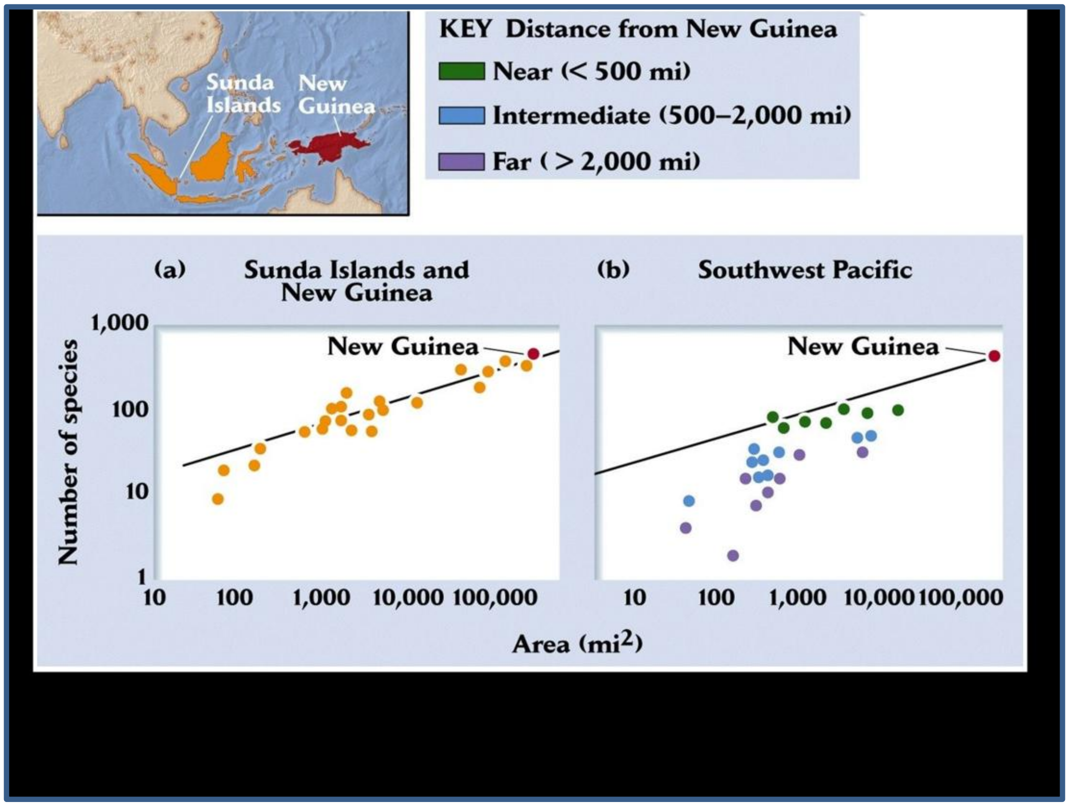
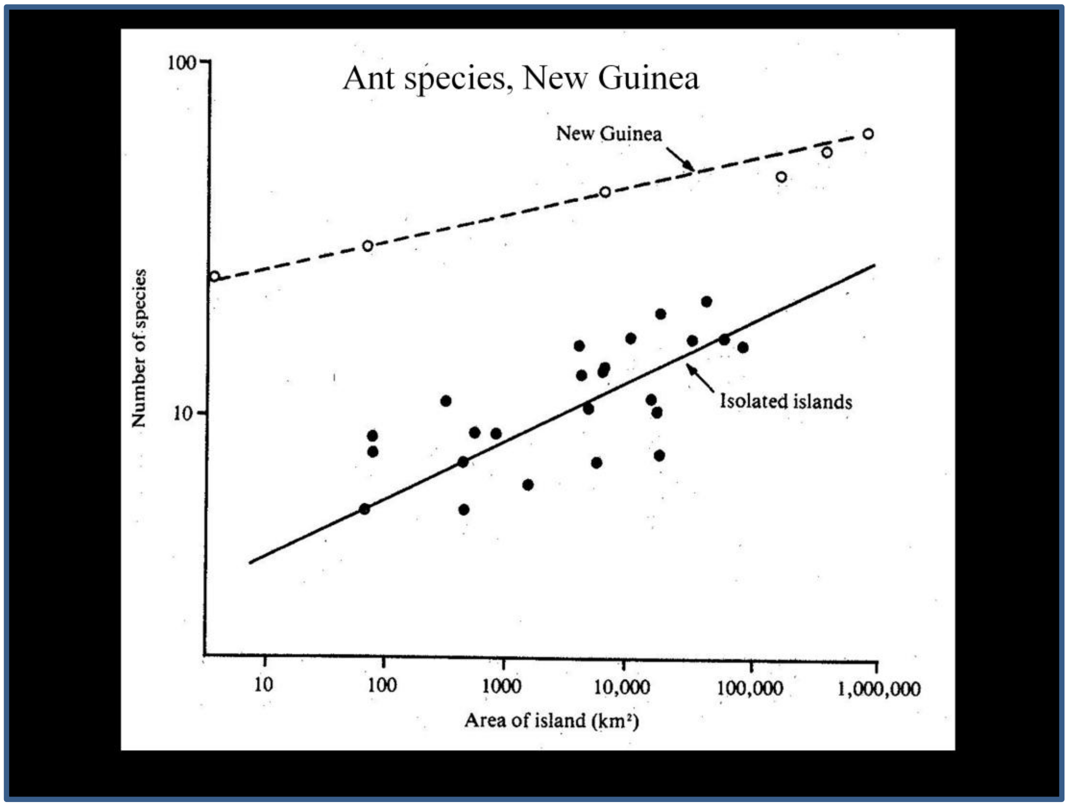


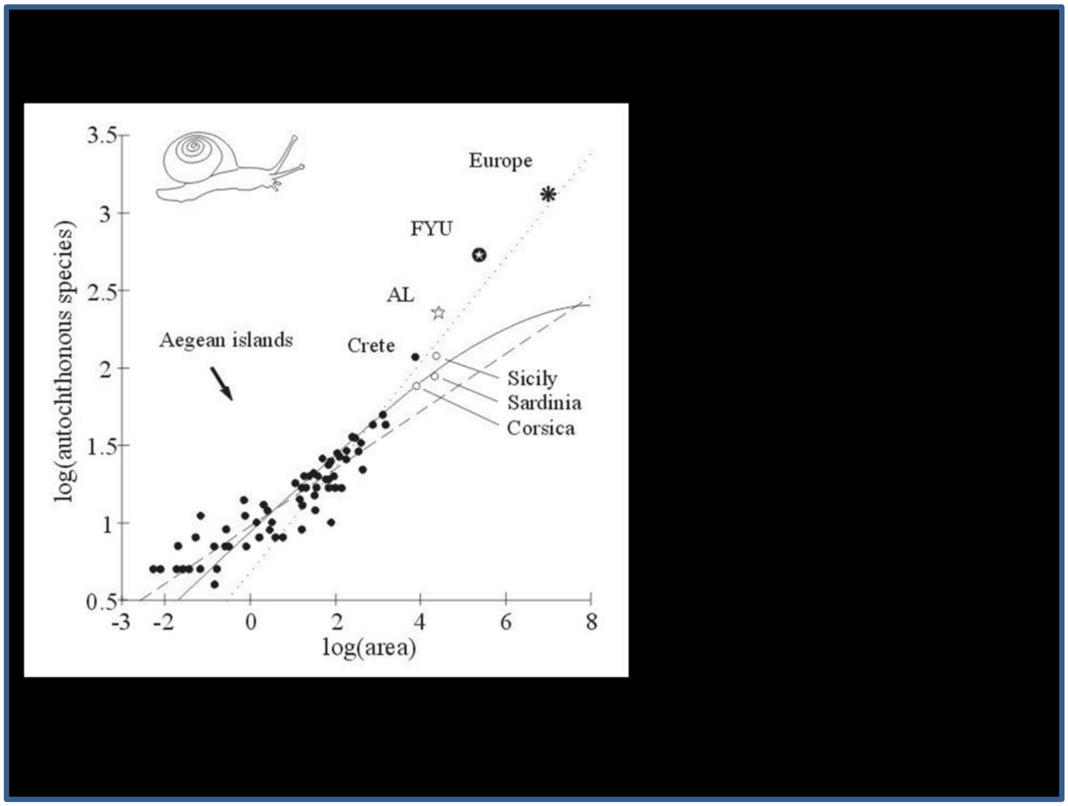
Figure 2 Species–area plot for the land birds on individual island in the warmer seas. (▲) Islands more than 300 km from the next largest land mass, or in the Hawaiian or Galapagos archipelagos. From Williamson (1981) and (1988), from data in Slud (1976).

A test of the hypothesis by partitioning a simple island data-set according to remoteness; ‘far’ islands (islands farther from any larger land-mass that might serve as a ‘pool’ of immigrants) are generally less species-rich than ‘near’ islands of similar size – as predicted. Model supported



Often, further refinements of hypotheses are suggested by patterns that don't seem, initially to 'fit' predictions of the basic model/hypothesis. Here, plant diversity for islands in south Pacific: Left-hand graph = islands that were connected to mainland until ca. 10,000 years ago. Why the difference between left and right? This confirms a more subtle prediction of the M-W model; if something changes about the island (here, disconnecting island from mainland is like making it smaller), then the equilibrium diversity should change, too – BUT IT MIGHT TAKE A LONG TIME (M-W called it 'relaxation time'). The Sunda Islands (those formerly connected to mainland Asia, when sea-levels were lower) are much more diverse than never-connected islands ('oceanic' islands). Among oceanic islands, distance from mainland is very important; it is not so important for islands of the Sunda Shelf. (Also, some of the 'near' islands on right were once connected to the very large island of New Guinea…)


Ant species, New Guinea
New Guinea
Isolated islands
Number of species
100
10
10
100
1000
10,000
100,000
1,000,000
Area of island (km²)



Here, note that species-area relationships for snail diversity on Mediterranean islands become more ‘continent-like’ on the largest islands.

Powerful hypotheses can often make predictions about phenomena and patterns not initially considered in the building of the hypothesis. Jared Diamond recognized that the M-W model ALSO implies that, even though there may be an equilibriium diversity for a given island, that doesn't mean things are static; there should be continuous turnover, with extinctions and new colonizations occurring at about equal rates. Further consideration shows that M-W predicts higher species turnover rates for small, near islands than for large, far islands, EVEN THOUGH their equilibrium species richness might be similar. He looked at the birds of the Channel islands of California (the red line shows shoreline during low sealevels of last glacial; not really pertinent for birds. Why?).

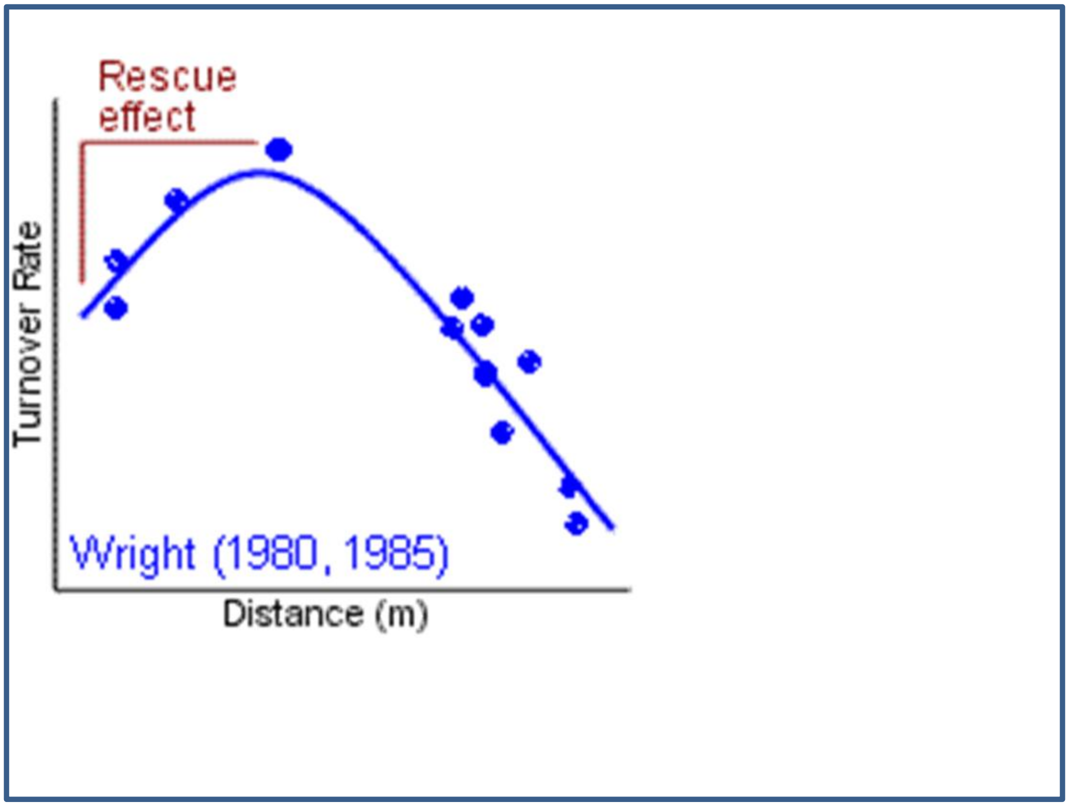
Equilbrium Island Biogeography & Turnover

Turnover on "Landbridge" islands (California Channel Islands)

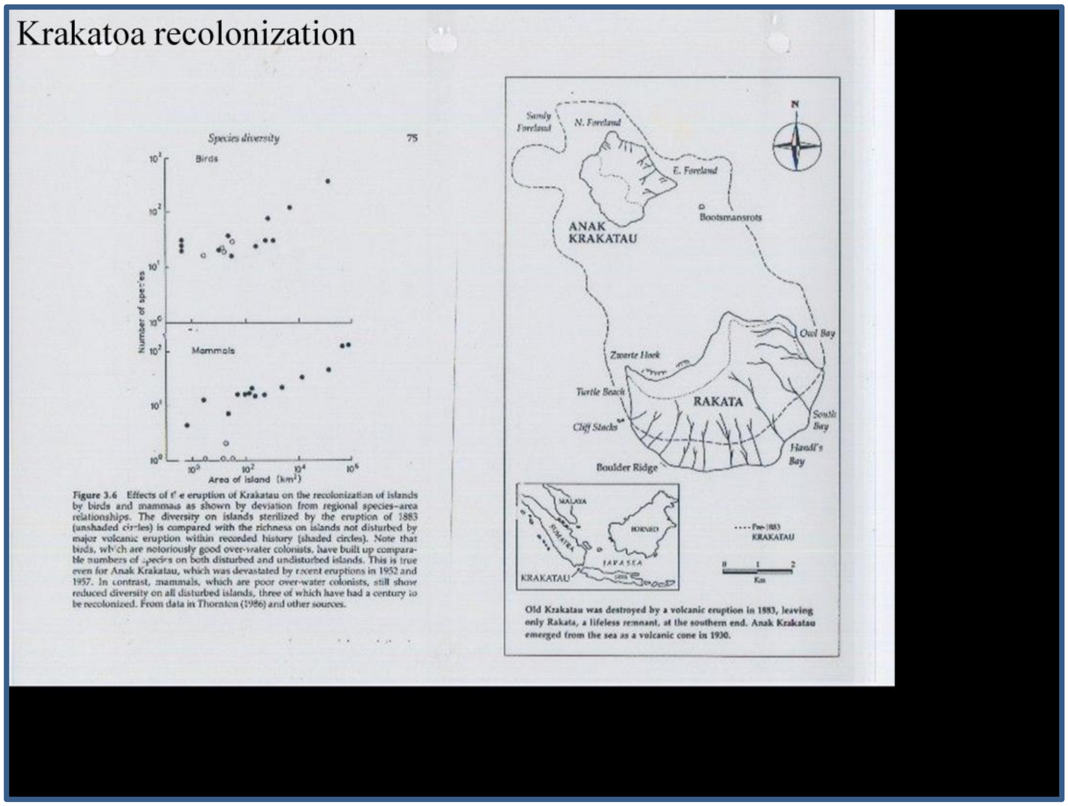
Island	Area km2	Distance km	Bird Spp. 1917	Bird Spp. 1968	Extinctions	Human Introd.	Immigrations	Turnover %
Los Coronados	2.6	13	11	11	4	0	4	36
San Nicholas	57	98	11	11	6	2	4	50
San Clemente	145	79	28	24	9	1	4	25
Santa Catalina	194	32	30	34	6	1	9	24
Santa Barbara	2.6	61	10	6	7	0	3	62
San Miguel	36	42	11	15	4	0	8	46
Santa Rosa	218	44	14	25	1	1	11	32
Santa Cruz	249	31	36	37	6	1	5	17
Anacapa	2.9	21	15	14	5	0	4	31

Diamond, J.M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Natl. Acad. Sci 64: 57-63. Jones, H.L. and Diamond, J.M. 1976. Short-time-base studies of turnover in breeding bird populations on the Channel Islands of California. Condore 73: 526-549. [+]

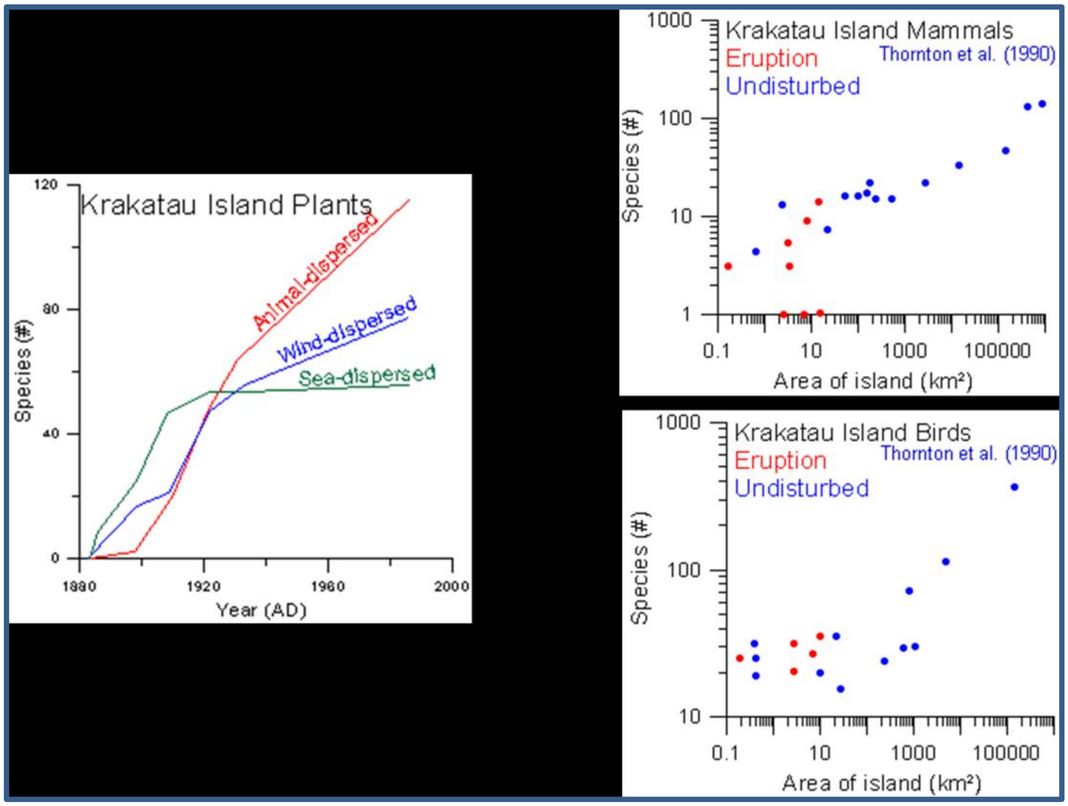
Diamond was able to compare data number of bird species on each of the islands from two censuses 50 years apart. While diversity changes little on most islands, there are extinctions and new species established on almost all of them. More or less as predicted; small islands have higher turnover. BUT there are exceptions, which offers fertile ground for more detailed hypothesis generations. Also note that distance doesn't seem to matter so much here. What might explain this?



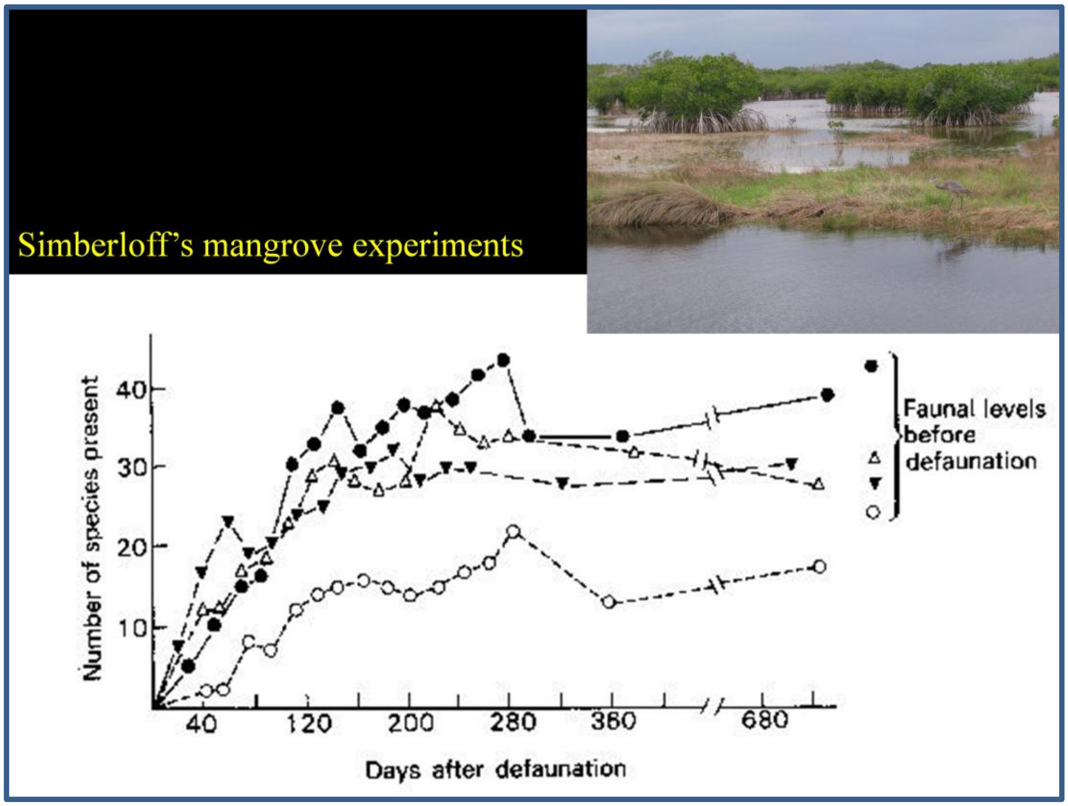
Later workers elaborated on the M-W hypothesis (as always happens with simple hypotheses that seem to be pretty good; such models are called 'fertile'). Wright noted that islands that are really close to source of immigrants are likely to have very low apparent extinction rates because there's high likelihood that new individuals of species that would otherwise go extinct will keep arriving from the mainland; this has come to be called the 'rescue effect' and is often incorporated in thinking about *conservation of rare species*. Think about why that would be.



“Tests” of the M-W hypothesis generally involve clever comparisons of existing systems – not classical experiments (with controls and manipulations). It can be very difficult to do whole-system experiments with natural communities. However, natural situations sometimes mimic what we’d like to do (and are often called ‘natural experiments’). The eruption of Krakatoa split one large island into several smaller ones, and all were essentially sterilized. M-W model would make predictions about how diversity would increase subsequently… Here, it’s clear that colonization rates will be different for *different groups of organisms* . Bird diversity on ‘sterilized’ islands has almost recovered to diversity observed on other islands of similar size. Not for mammals… (You can make hypotheses about what groups of organisms will see fastest reestablishment of equilibrium diversity.)



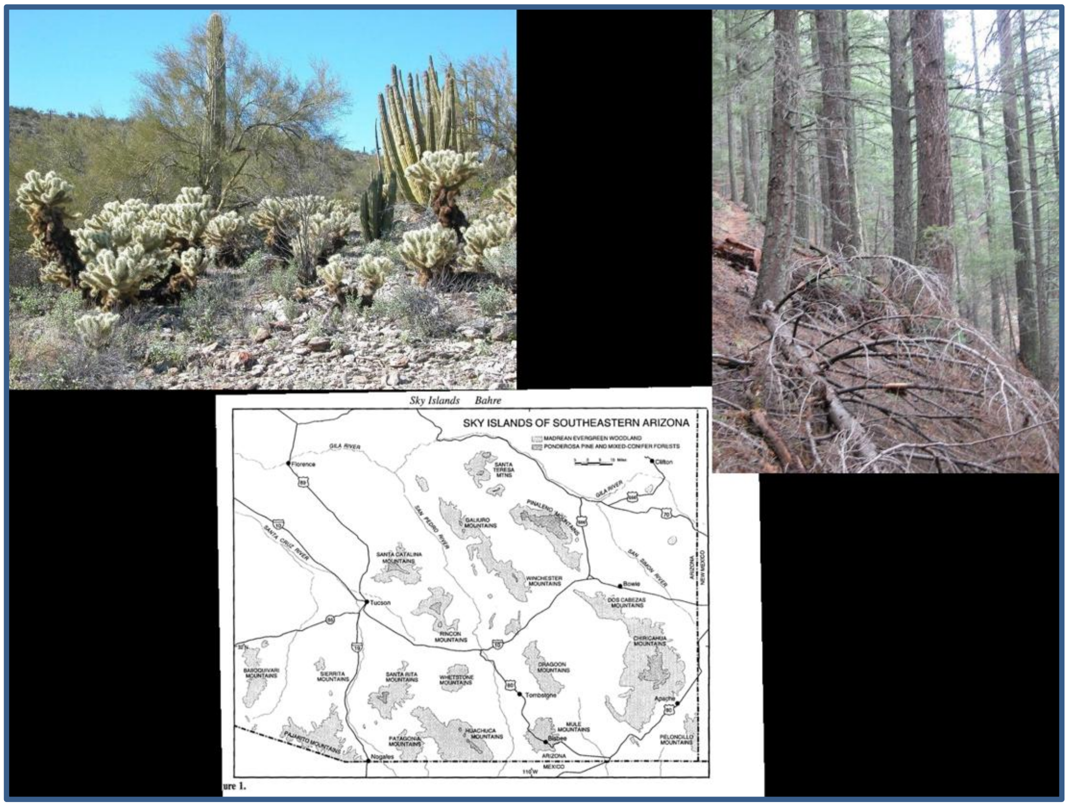
Krakatau Island Plants
Animal-dispersed
Wind-dispersed
Sea-dispersed
Species (#)
0
40
80
120
1880
1920
1960
2000
Year (AD)
Krakatau Island Mammals
Eruption
Undisturbed
Thornton et al. (1990)
Species (#)
1
10
100
1000
0.1
10
1000
100000
Area of island (km²)
Krakatau Island Birds
Eruption
Undisturbed
Thornton et al. (1990)
Species (#)
10
100
1000
0.1
10
1000
100000
Area of island (km²)



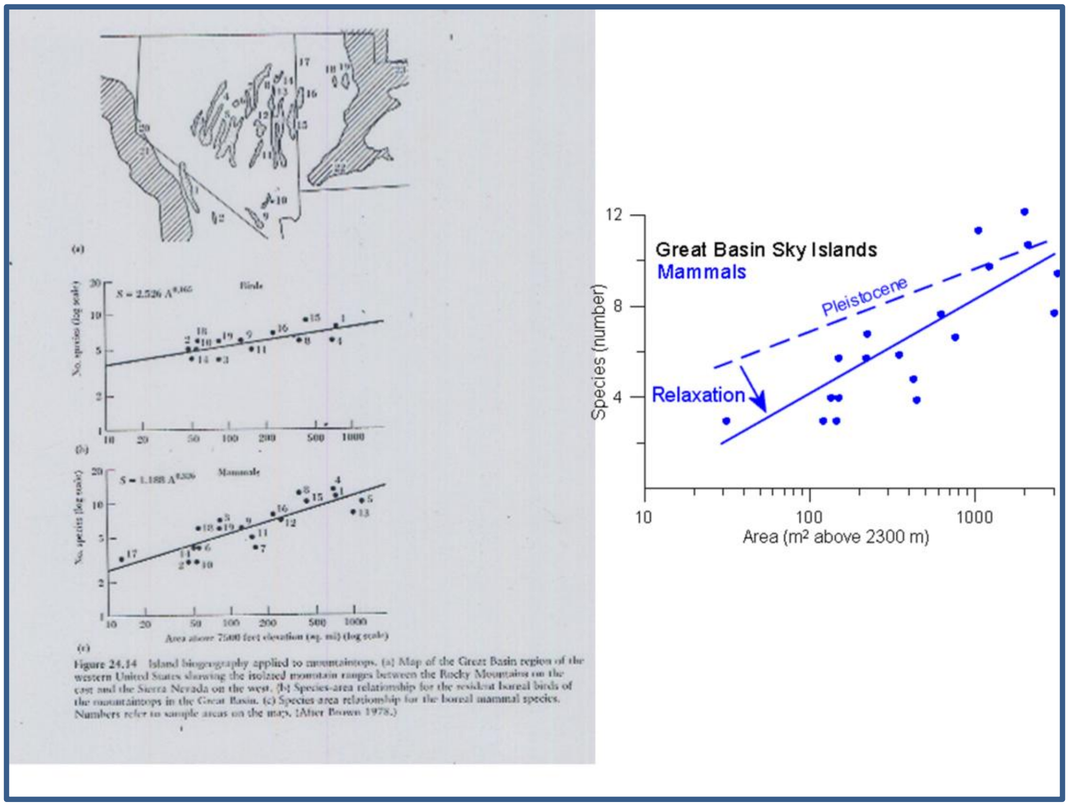
But natural experiments have their problems; they are *poorly controlled*; the researcher can't be confident that other, unmeasured factors aren't influencing thing. 'Manipulative' experiments are often the goal (like the hubbard brook study in ecosystem section).

Dan Simberloff did manipulative experiments with small mangrove islands in Tampa Bay, Florida. Because the islands are extremely numerous, replication was possible, and because they're very small and simple (they're just individual or a small number of mangrove trees standing in the water), the study is reasonably well-controlled.

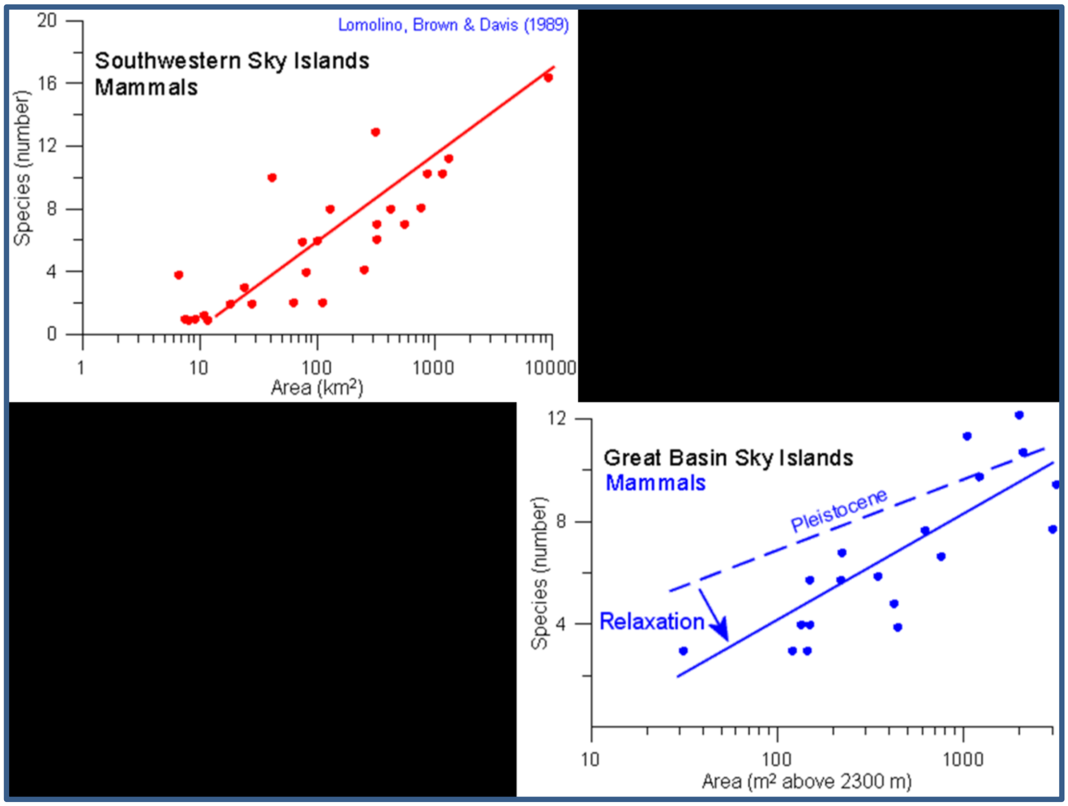
Simberloff eliminated arthropods (mostly insects and spiders) from individual islands (by covering them with a plastic sheet and fumigating with pyrethrin), then monitored the recovery of diversity PREDICTION: islands should recover to about same diversity as before 'defaunation'. Rate of colonization by new species function of distance. Results much as predicted – but NEW PATTERN observed. Note 'overshoot' of equilibrium and subsequent decline of diversity for some islands; these tend to be NEAR islands (i.e., where lots of immigrants arive right away). Is this consistent with processes invoked by M-W? Consistent with model? Can you offer hypotheses for what's going on here? Why should NEAR islands overshoot, but not FAR ones?



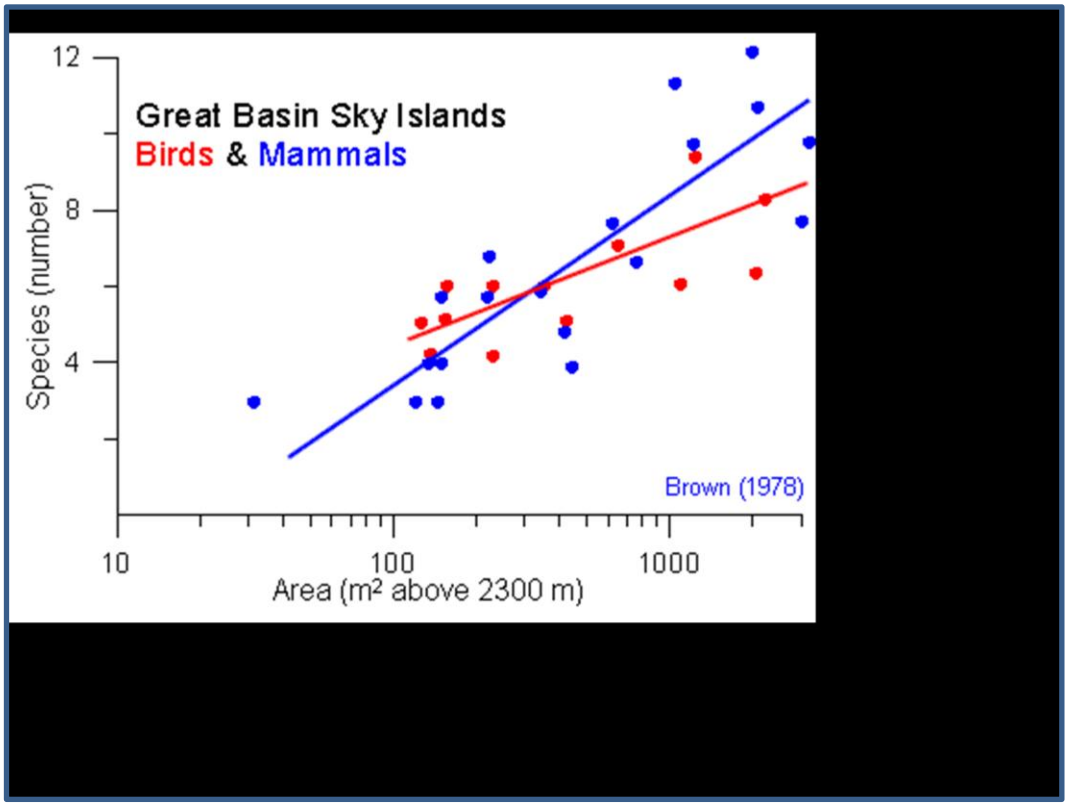
Like any powerful body of theory, the M-W model has been extended beyond its original scope. When is an island not an island? The basic reasoning of the model should apply, perhaps to ANY isolated patch of distinctive habitat – like ‘islands’ of cool, moist forests on mountain ranges in the desert southwest, surrounded by a ‘sea’ of desert. Do the plants and animals restricted to these habitats follow the same general patterns as those on ‘true’ islands?



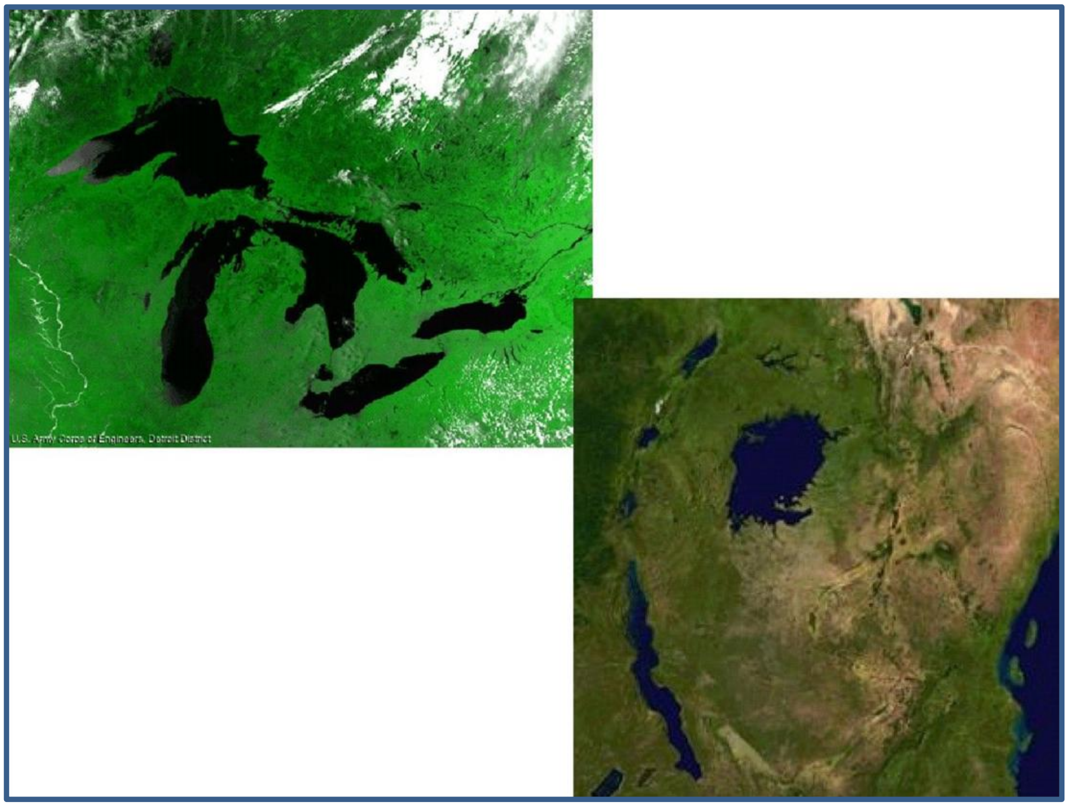
Sometimes yes, sometimes no; for example mammal diversity on sky islands is clearly related to area – but there may be effectively NO colonization… (Note that, in the Pleistocene – the glacial epoch – cool forests were continuous across this region…)



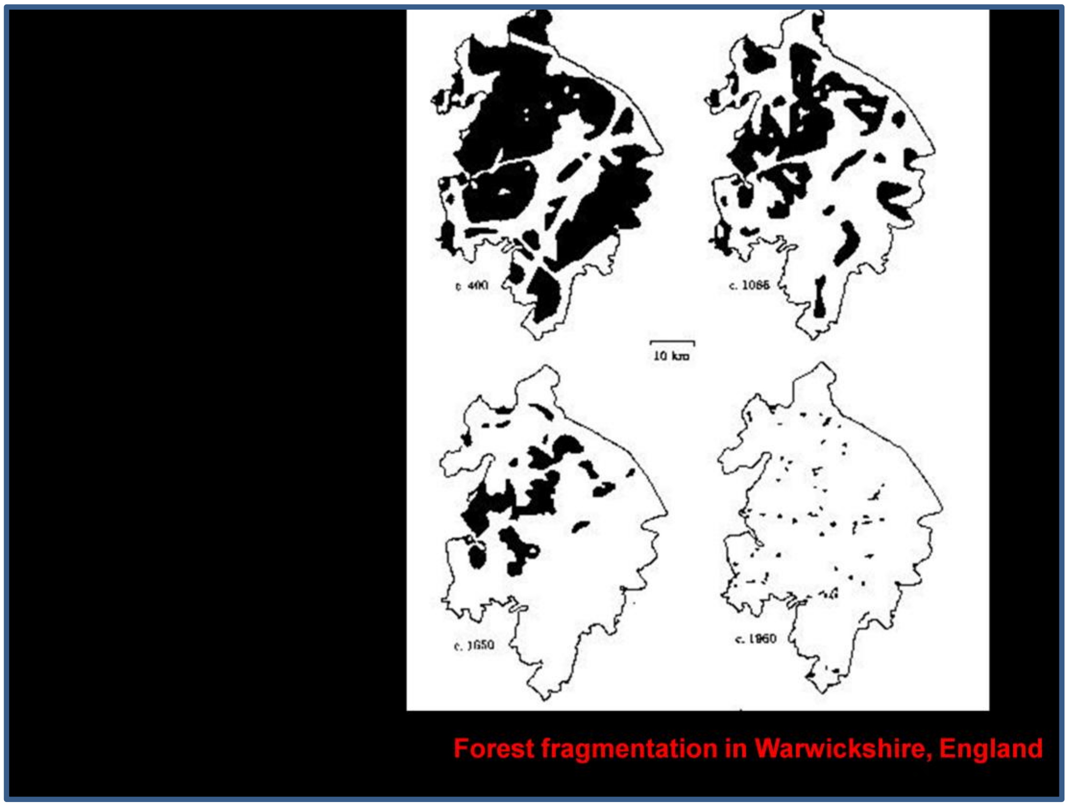
It appears that there's no real migration of mammals between 'sky islands' since they became isolated by valley deserts; the diversity patterns among high-elevation patches are determined almost entirely by differences in area causing differences in 'relaxation rates' (extinction rates).



Birds, however, don't experience these mountain ranges as 'islands' to the same degree, and their species-area curve has a slope more typical of areas within a large land-mass than of islands.

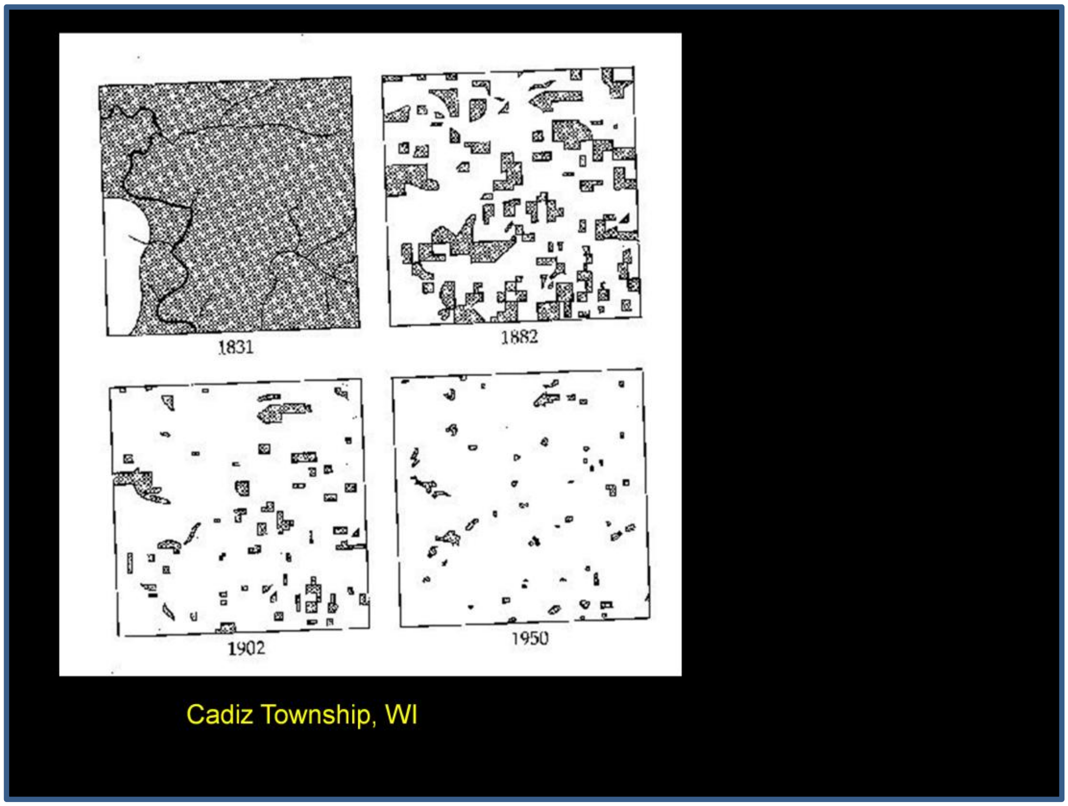


Lakes might be considered ‘inverse islands’ – but does the same thinking about what controls colonization and extinction rates apply?

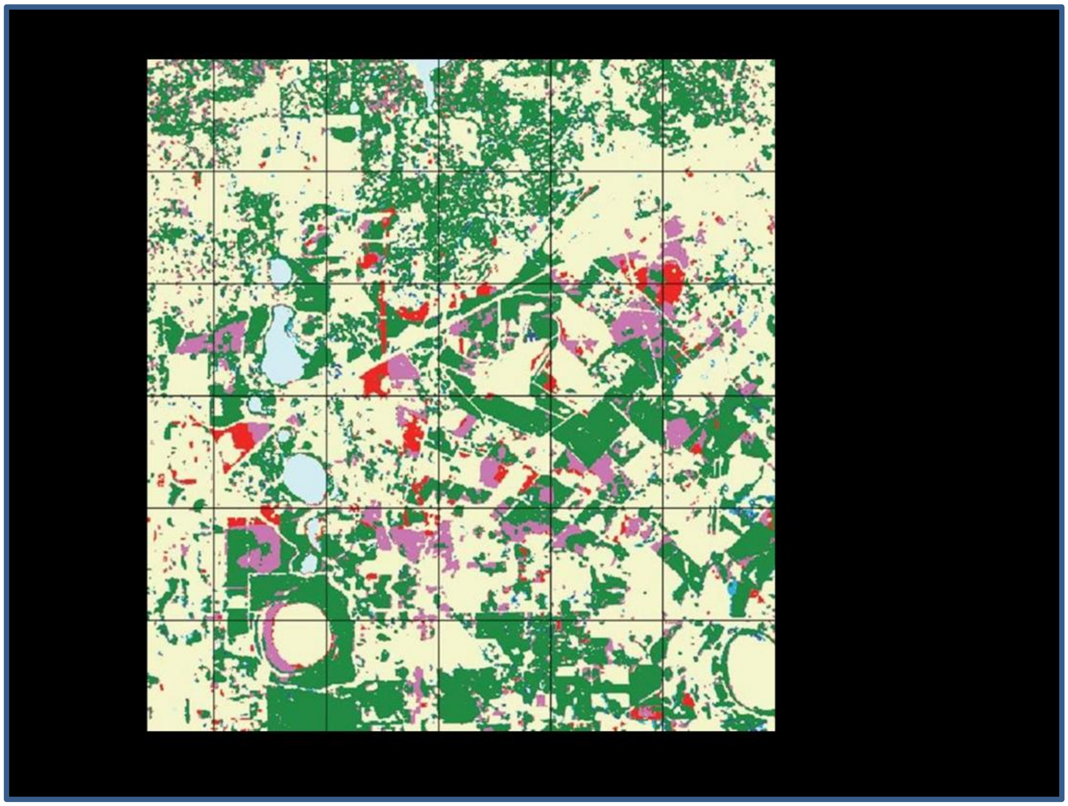


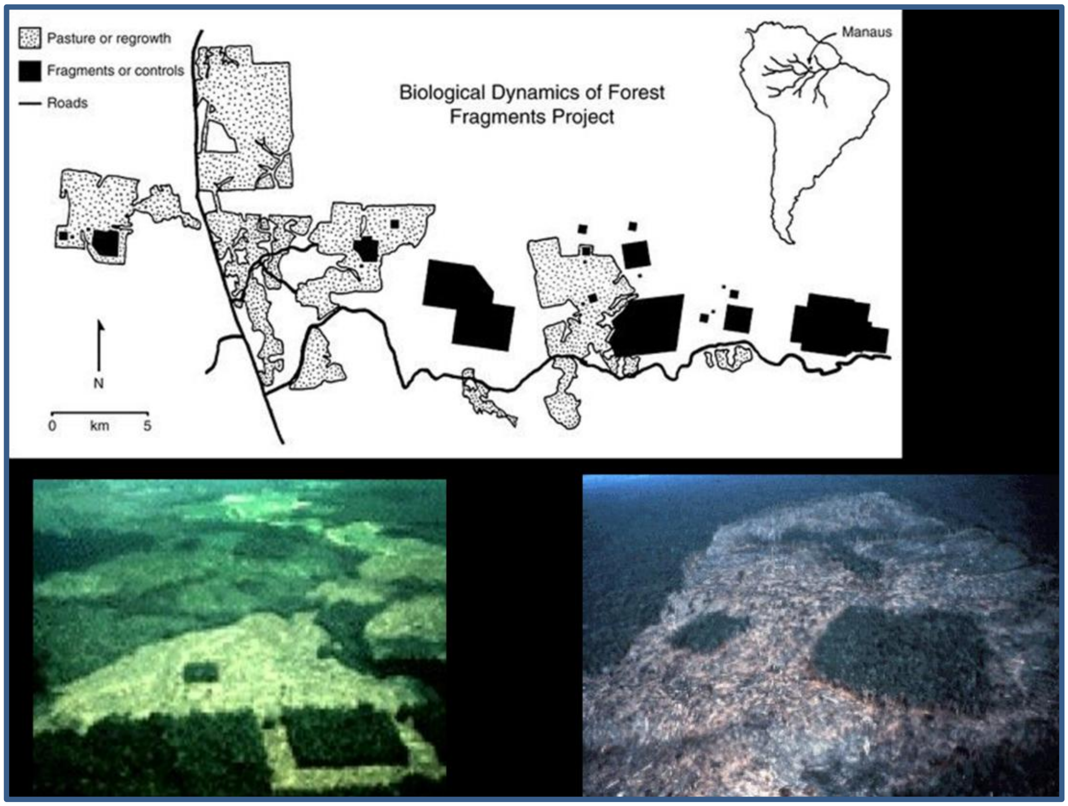
Forest fragmentation in Warwickshire, England

What about forested landscapes that have become fragmented? Do the fragments have ‘island’ properties in the M-W sense? If so, what does that say about expectations regarding diversity in such landscapes?



Maps of forest cover in a township in Wisconsin





An experiment in Brazil: In an area scheduled to be logged in the 1970s, ecologist Tom Lovejoy arranged with the Brazilian government for patches of various sizes and isolation to be left as habitat islands. These have been monitored now for over 30 years; there have been many publications from this project. (you could find them using the project name above)

What the Brazilian study looks like now.

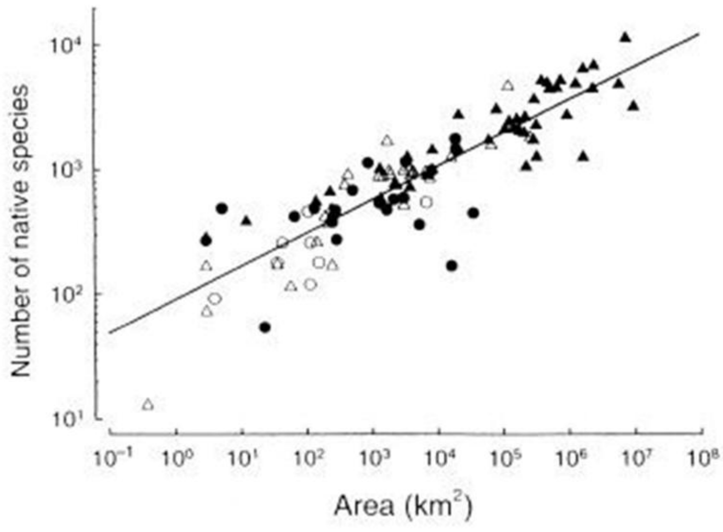


Figure 1 The relationship between the number of native species and site area for 104 sites around the world, broken down into island reserves (○), island non-reserves (△), mainland reserves (●) and mainland non-reserves (▲). The fitted line is $\log S = 1.96 + 0.27(\log A)$. From Lonsdale (1999).

Several types of habitat 'islands' on one graph. Think about it; what would this mean for you if you were a conservationist or manager charged with maintaining diversity of a region?