GE/BI307, Feb 27, 2007   Reading: Quammen pp. 21-114

1. Early theories of biogeography: beyond Noah's ark
2. Barriers and Isolation: a foundation of biogeographic theory
   - Exemplified by Wallace's Line

Thinking during Linneaus' time:

From maximizing noah's ark size to "special creation"

"This newly imagined God of the late 18th century was a hands-on, follow-through sort of guy who committed himself to details and showed no knack for delegating power" - Quammen

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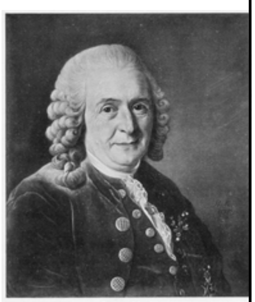
1. Early theories of biogeography

Linnaeus' (1707-78) Theory:

- Accepted Noah's Ark hypotheses

•Species Immutable
•Plato, Aristotle (300-400 BC)
•The Bible
•Linneaus (1700s) →



Carl von Linné
Painting by A. Roslin, 1775

Linnaeus theory of origin of species treated species as immutable:

•Noah's Ark landed on Mt. Ararat and species disembarked.

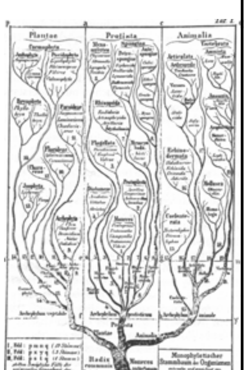
•Species found suitable habitats in the heterogeneous environments of Mt. Ararat.

•When flood waters receded, species migrated to suitable locations throughout earth

Ironically, while Linneaus *treated species as immutable*, his Binomial Classification scheme recognized relatedness of species (grouped into genera), and was an early form of a 'tree of life'.

Also, Linneaus got the "niche" concept right.

Linneaus' scheme became a focus for Darwin …

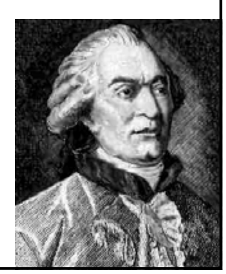


Haeckel's version of the tree of life

There are a couple of problems with this explanation:

1. **Organisms would have to cross inhospitable boundaries to get to suitable environments**
2. **We see different kinds of animals and plants in very similar, but isolated environments (Buffon's Law)**

Comte de Buffon (1707-88) pointed these problems out and offered another explanation…



Buffon's key contribution was to posit the *mutability of species*:

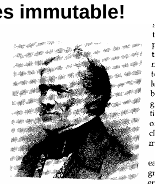
- •Northern Origin hypothesis
- •Species originated in the North during a warmer period (climate variation!)
- •During climate cooling, species migrated and *adapted* to new habitats.

Lamarck (1744-1829) got closer:

- •Key contribution: Species evolve in response to environment
- •They do so by inheritance of acquired traits (e.g. Giraffe's necks). There is no evidence for this.
- •Unfortunately, Lamarck is most remembered for being wrong.

Some other major contributors:

•Charles Lyell (1797-1875, Geologist extrodinaire): changeable earth, climate, but species immutable!

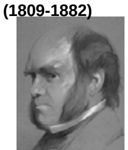


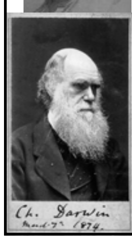
•Alexander von Humboldt (1769-1859): floristic belts, latitude=altitude
•Johann Forster (1729-98): island size and species diversity

Darwin and Wallace's Breakthrough

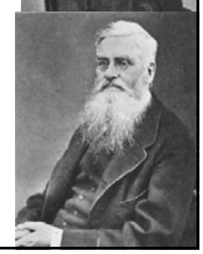
(jointly published July 1, 1858 – The Linnaen Society of London)

Charles Darwin (1809-1882)





Alfred Wallace (1823-1913)



Some of their key observations:

- •Darwin: Mockingbird (not finch) variation on Galapagos Islands led Darwin to question the fixity of species.
- •Wallace: was a paid specimen collector; thus he collected many individuals of species rather than single individuals. Variation among individuals was prominent in his mind.
- •Wallace (1855): "Every species has come into existence coincident both in space and time with a pre-existing closely allied species"

Darwin and Wallace's Breakthrough

Thomas Malthus provided a key insight that crystallized the concept of natural selection to both Darwin and Wallace:

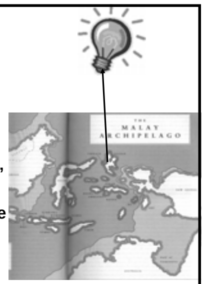
- •***Almost all species can reproduce at far greater rates than the environmental carrying capacity and observed population sizes.***
- •***So what keeps the population numbers stable? It must be that relatively few individuals survive. Which ones survive? The ones that are best fitted to their environment*.**

Thomas Malthus (1766-1834)

A Eureka Moment:

Wallace: "…no satisfactory conclusion was reached till February 1858. At that time I was suffering a rather severe attack of intermittent fever at Ternate in the Moluccas, and one day while lying on my bed during the cold fit… the problem again presented itself to me, and something led me to think of the 'positive checks' described by Malthus in his "Essay on Population"…these checks – war, disease, famine and the like – must, it occurred to me, act on animals as well as on man. Then I thought of the enormously rapid multiplication of animals, causing these checks to be much more effective than in man; and while pondering vaguely on this fact there suddenly flashed upon me the *idea* of the survival of the fittest.

… In the two hours that elapsed before my fit was over I had thought out almost the whole of the theory, and the same evening I sketched the draft of my paper…"



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1. Barriers and Isolation: a foundation of biogeographic theory
   - Exemplified by Wallace's Line
2. Filters versus corridors versus barriers

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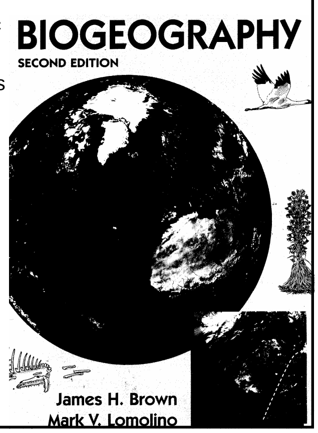
2. Barriers and Isolation: a foundation of biogeographic theory
   - Exemplified by Wallace's Line



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2. Barriers and Isolation: a foundation of biogeographic theory

Background: Before Wallace there were already 6 recognized major faunal regions:

1. Palaearctic
2. Nearctic
3. Neotropical
4. Ethiopian
5. Oriental
6. Australian

Lyell and others assumed impassable barriers were the cause (they were generally correct)

But the regions between 5 and 6 presented a puzzle – not a lot of water separation, and not explained by simple water distance…

Wallace's Line

•Wallace spent 8 yrs in the Malay Archipeligo

•In 3rd yr of travels (1856) made his way from Bali to Lombock

"on crossing over to Lombock, I naturally expected to meet with some of these birds again, but during a stay there of 3 months I never saw one of them, but found a totally different set of species…"

Also, Sulawesi (Celebes) "was at once the poorest in number of species and the most isolated in character of its productions of all indonesian islands

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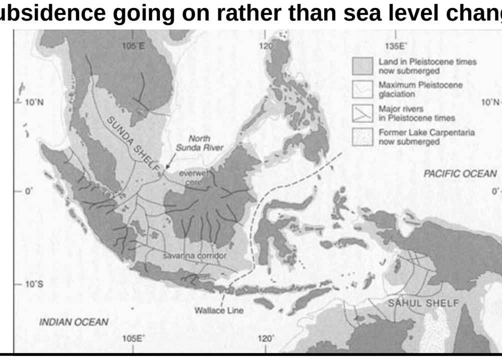
Wallace noted that species break corresponded to the edge of the deep water shallow seas on the Sunda Shelf. He thought there was land subsidence going on rather than sea level change.



Wallace also didn't know about plate tectonics

We now know that the deep water channel between Bali and Lombock represents the edge of the eurasian continent. Further east is the australian continent. In between are continental fragments and volcanic arcs.

Wallace also didn't appreciate glacial cycles and influence on barrier formation/removal

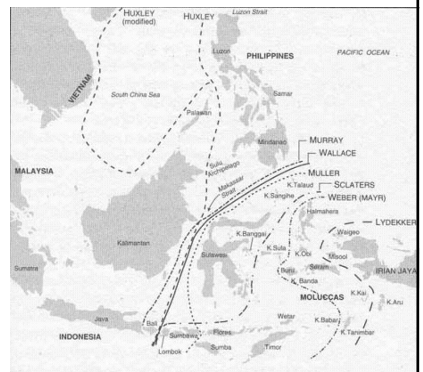
There are other lines besides Wallace's, for different taxonomic groups.

Murray, Sclater: mammalian groups

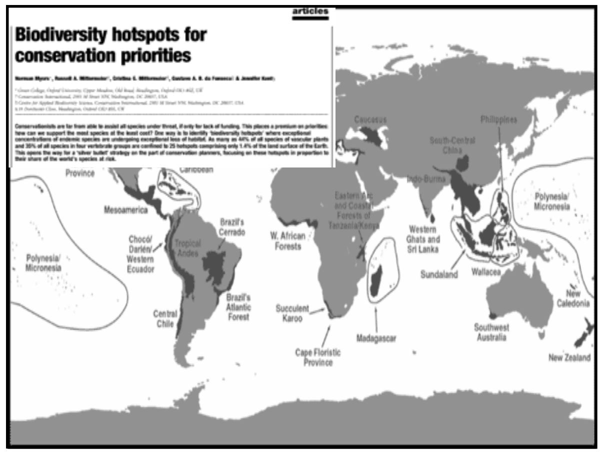
Huxley: birds

Weber: 50% split line.

Lydekker: bounds Australian from "Wallacean" transition zone



Wallace's line continues to have relevence to biogeographic research and conservation today.



current relevence to human biogeography research…

Polynesian origins

Slow boat to Melanesia?

The origin of the Polynesian islanders and of the Austronesian languages that they speak has been debated for more than 200 years. Diamond has presented the predominantly held modern viewpoint, described as the 'express train to Polynesia' model, which proposes that the ancestors of the Polynesians were early farmers who dispersed south from a homeland in South China/Taiwan, through Island Southeast Asia (replacing an indigenous 'Australoid' hunter-gatherer population), and then on east, out into the Pacific — all within the past 6,000 years[8]. However, evidence is accumulating from several genetic markers that Polynesian lineages have a much deeper ancestry within tropical Island Southeast Asia than this hypothesis would suggest. The new evidence implies that the Polynesians originated not in China/Taiwan, but in eastern Indonesia, somewhere between Wallace's line and the island of New Guinea.

NATURE | VOL 410 | 8 MARCH 2001 | www.nature.com

PALEOANTHROPOLOGY:

Ancient Island Tools Suggest *Homo erectus* Was a Seafarer

Ann Gibbons

In 1968, a Dutch missionary living on the Indonesian island of Flores found stone tools alongside the bones of an extinct type of elephant called a *Stegodon*, known to have lived at least 750,000 years ago. If the tools were as old as the *Stegodon*, this was a spectacular discovery, for Flores lies beyond a deep-water strait that separates most Asian and Australian faunas. The tools meant that the only human species then living in Southeast Asia, *Homo erectus*, must have been able to cross this biological barrier, called **Wallace's line**.

2. Filters versus corridors versus barriers

Wallace's line and others really represent a biotic 'filter' rather than a barrier.

"Filters" differentially allow/exclude organisms based on dispersal ability

"Corridors" allow most species to pass – e.g. Bering strait, Great American Exchange

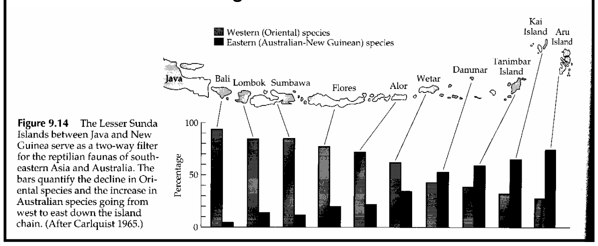


Figure 9.14 The Lesser Sunda Islands between Java and New Guinea serve as a two-way filter for the reptilian faunas of southeastern Asia and Australia. The bars quantify the decline in Oriental species and the increase in Australian species going from west to east down the island chain. (After Carlquist 1965.)

The Great American Interchange was really actually a filter…

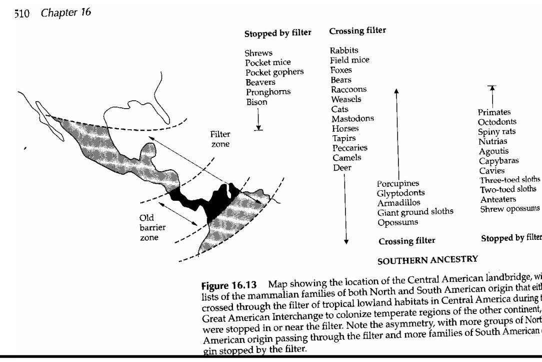


Figure 16.13 Map showing the location of the Central American landbridge, with lists of the mammalian families of both North and South American origin that eithe crossed through the filter of tropical lowland habitats in Central America during th Great American Interchange to colonize temperate regions of the other continent, o were stopped in or near the filter. Note the asymmetry, with more groups of North American origin passing through the filter and more families of South American or gin stopped by the filter.

Many other biogegraphic lines – an example from N. America

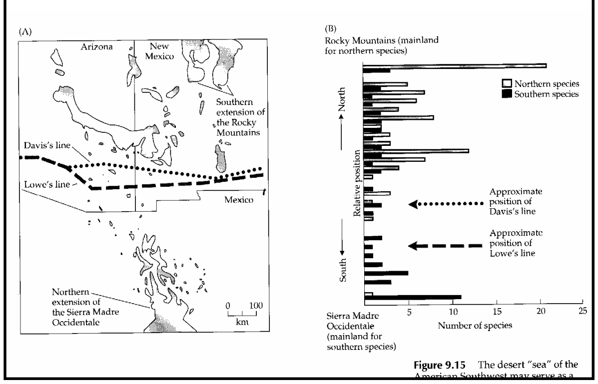


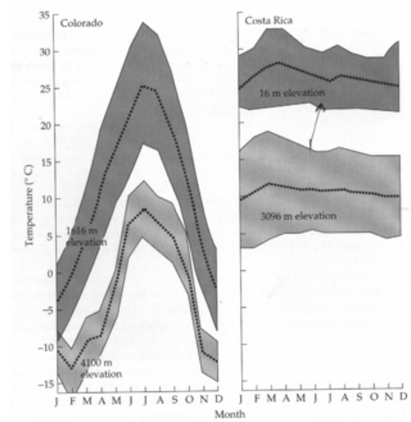
Figure 9.15 The desert "sea" of the American Southwest may serve as a

Mountain barriers are 'higher' in the tropics.

(Janzen 1967)

Climate modifies the nature of barriers/filters!

(new guinea)



The role of dispersal:

Clearly, the nature of barriers depends not only on the physical/environmental separation between habitats, but on dispersal properties of plants and animals.

Two kinds of dispersal:

1. **Active**
2. **Passive**

Active Dispersal:

Flying, locomotion.

Sometimes surprising:

- Golden plover covers the globe each year.

Active Dispersal:

Other examples of active dispersal:

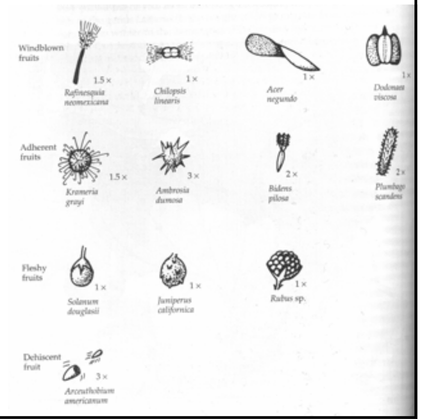
-**Monarch butterflies (canada to mexico)**

-**Elephant cow+calf documented to voluntarily swim 50 km from Sri Lanka!**

Passive Dispersal:

Rafting (lizards, rodents)

Windblown, hitchhiking.



Differential dispersal ability is a key reason for selective filtering – I.e. why 'barriers' are almost always really 'filters'

On islands, this leads to 'disharmonic biotas'. That is, island communities do not represent a balanced subset of the species on mainlands.

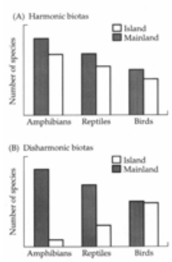


Figure 14.1 Two hypothetical examples of patterns in species composition illustrating the difference between harmonic and disharmonic biotas. In both examples, the insular communities have fewer species of each taxonomic group than the mainland biota. Disharmony refers to marked differences in the composition of insular communities from that of mainland biotas, with overrepresentation of some taxonomic or functional groups (e.g., birds in B) and scarcity of others that tend to be common elements of the mainland biota (amphibians and reptiles in B).

Evolution

1. **Patterns of Evolution on Islands: insightful absurdities**
2. **Mechanisms of Evolution I: without natural selection**
3. **Mechanisms of Evolution II: by natural selection**

1. Patterns of Evolution on Islands: insightful absurdities

- **Gigantism and Dwarfism**
- **Flightlessness/reduced dispersal ability**
- **Loss of defensive adaptations**

Examples: Giant jumping rat, madagascar (hypogeomys antimena) (size of rabbit)

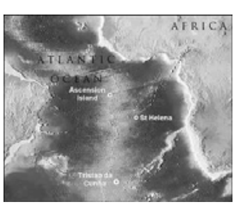
Komodo dragon (varanus komodoensis)

Giant burrowing cockroach (macropanesthia rhinoceros) - Australia

Nestor notabilis, carnivorous parrot, New Zealand

Flightless duck (anas aucklandica), auckland island

Flightless moth, dimorphinoctua cunhaensis, Tristan da Cunha



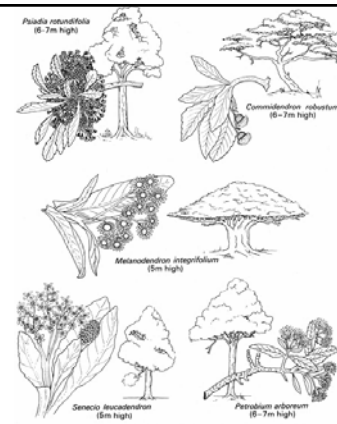
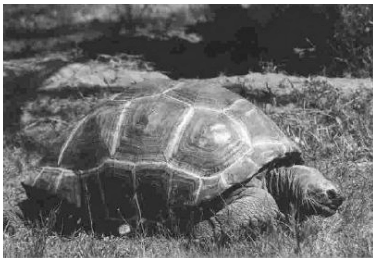
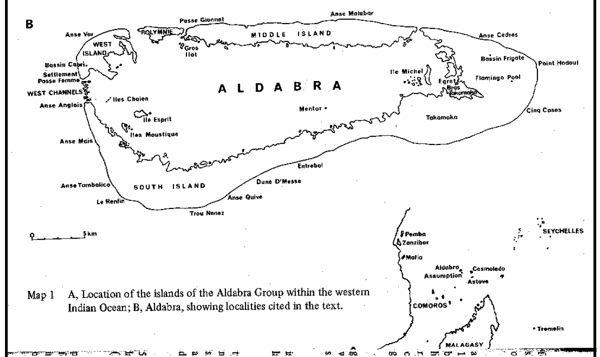


Fig. 6.7 The varied trees that have evolved from immigrant sunflowers on St Helena Island. From Carlquist [38].

Giant tortoise, Geochelone gigantea, Aldabra





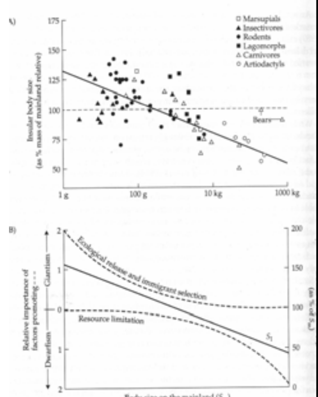
Gigantism/Dwarfism
Foster's Island Rule

Small mainland organisms become large on islands

Larger mainland organisms become smaller on islands

Ecological release: small organisms can appropriate more resources due to less competition (also, komodo dragon and pygmy elephant example)

Resource limitation: large organisms with large energy needs struggle to get enough resources, and are selected out



- **Flightlessness/reduced dispersal ability**
- **Loss of defensive adaptations**

Lack of selective forces (predation, competition) lead to evolutionary stagnation.

The Taxon Cycle:

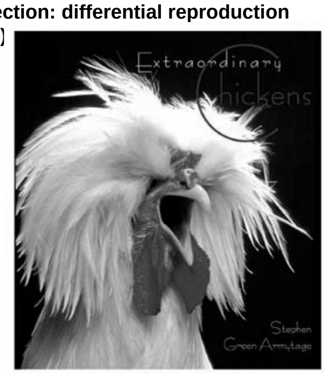
1. **Invasion by generalists adapted to disturbed envts.**
2. **Differentiation to highly specialized and restricted habitats**
3. **Extinction by envt. Change or new invaders**

Evolution

1. **Patterns of Evolution on Islands: insightful absurdities**
2. **Mechanisms of Evolution I: without natural selection**
3. **Mechanisms of Evolution II: by natural selection**

There *is* Evolution without natural selection:

A. Artificial Selection (can be intense, but basically operates similarly to natural selection: differential reproduction based on favored traits)



There *is* Evolution without natural selection:

To understand, first lets consider when there isn't.

B. In large, isolated populations, with random mating, without natural selection, the Hardy-Weinberg theory says that there should be no population evolution (frequency of allelles):

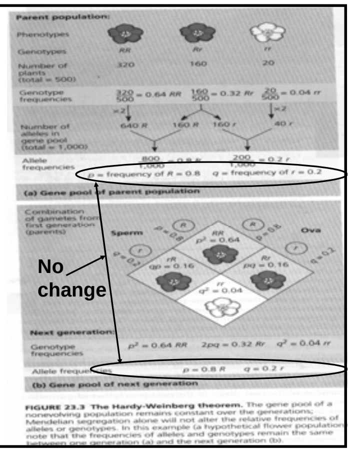
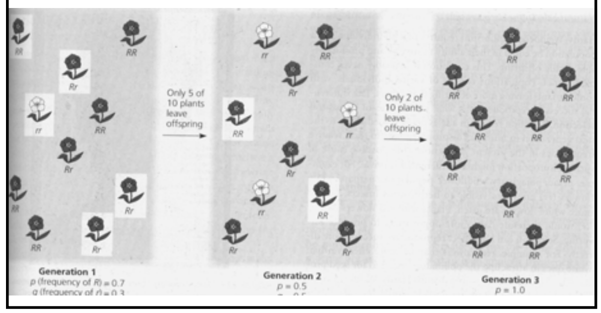


FIGURE 23.3 The Hardy-Weinberg theorem.

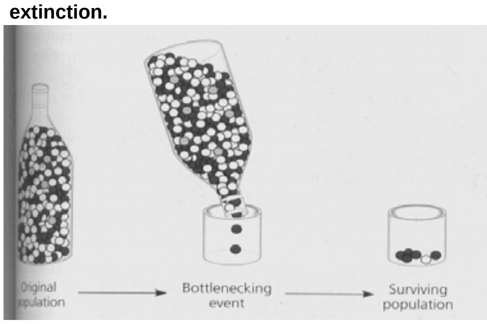
There *is* Evolution without natural selection:

B. Genetic Drift: In *small* populations, evolution over time may simply be due to 'rolls of the dice' of allele transmission. This is purely random and has nothing to do with environmental selection.



There *is* Evolution without natural selection:

B. The bottleneck effect is genetic drift that occurs with a catastrophic reduction in population size – it reduces population genetic variability – and can presage extinction.



David Quamman on Genetic Drift:

these are alleles of the sock gene…

Imagine a selection of variants…black socks and brown socks and argyles and flamingo pink socks…

Some alleles are common in a population; some are rare.
If the population is large, the rare alleles and common will be passed on.

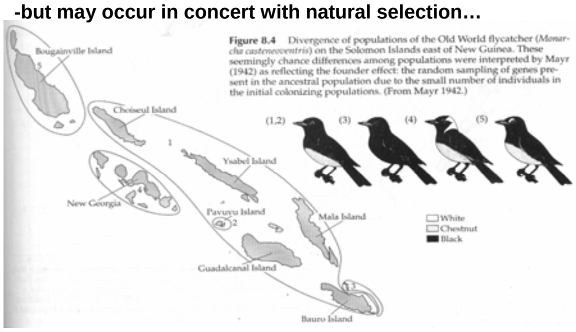
If the population is small, the rare alleles will most likely disappear in the course of reproduction, because chance operating at low numbers produces aberrations…

When you pack hastily for a trip, groggy in the early morning darkness and grabbing socks at random, you're likely to miss the one flamingo pink pair. But what if your plane makes an unscheduled stop in Las Vegas on Halloween. Of course you'll wish you had them…

Genetic drift deprives small populations of rare and seemingly useless alleles that might later, under changed circumstances, turn out to be useful."

The Founder Effect is an example of Genetic Drift

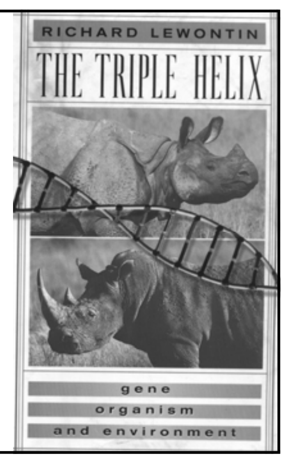
Small, colonizing populations diverge with no apparent differences in environment
-but may occur in concert with natural selection…



There *is* Evolution without natural selection:

B. Genetic Drift: If those small populations then grow back to large populations, the chance allele differences can lead to relatively 'fixed' different phenotypes.

Horn differences between african and indian rhinos likely not due to natural selection. (at least according to Lewontin)

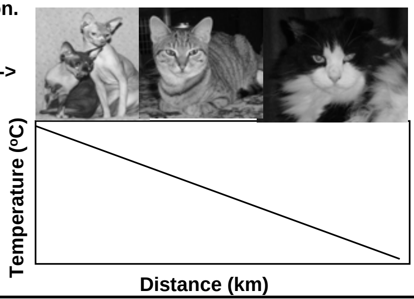


There *is* Evolution without natural selection

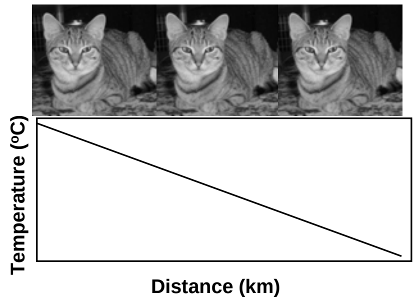
(or more precisely with gene flow, lack of evolution *with* natural selection):

C. Gene Flow: Genetic exchange *between* nearby populations can prevent local adaptation to the environment. This is a force that counters natural selection.

Without Gene Flow->



With Gene Flow:



Recap: Artificial Selection, Genetic Drift and Gene Flow are *not* examples of evolution by natural selection.

Let's discuss evolution by natural selection now…

Evolution

1. **Patterns of Evolution on Islands: insightful absurdities**
2. **Mechanisms of Evolution I: without natural selection**
3. **Mechanisms of Evolution II: by natural selection**

2. Evolution by natural selection

- A) Micro and Macro Selection
- B) Sympatric vs. Allopatric selection/speciation
- C) The Ecological Niche
- D) Adaptive Landscapes
- E) Character Displacement

2. How does the Environment Select?

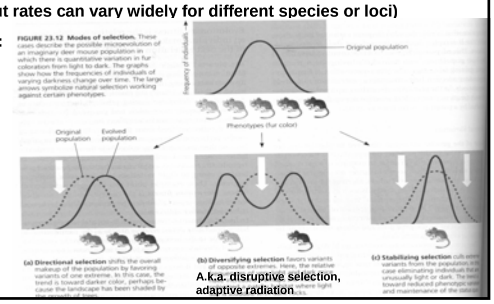
A) Micro Selection:

- Generation-to-generation change in a population's allele frequencies, *in response to the environment*.

-Evolution on the smallest scale - populations

-Gradual (but rates can vary widely for different species or loci)

***An example*:**



2. How does the Environment Select?

A) Macro Selection:

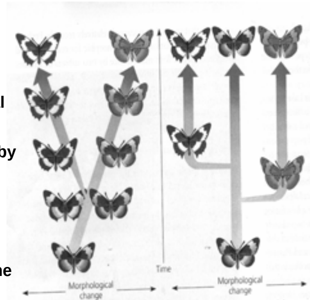
-Puncuated Equilibrium:

-Paleontologists rarely find gradual transitions in fossils

-Long periods of stasis separated by rapid speciation.

-May mirror the time pattern of climate and environmental change

-This is not incompatable with micro-selection, but emphasizes the widely variable rate of micro-selection.



(a) **Gradualism model.** Species descended from a common ancestor gradually diverge more and more in morphology as they acquire unique adaptations.

(b) **Punctuated equilibrium model.** A new species changes most as it buds from a parent species, and then changes little for the rest of its existence.

FIGURE 24.17 Two models for the tempo of speciation.

2. How does the Environment Select?

A) Macro Selection:

- Species Selection: Analagous to selection on individuals, but instead at the species level (or higher).

-Big example: Dinosaur extinction, mammal proliferation 65 Mya.

-Metabolic temperature regulation in mammals may have conferred an advantage during the nuclear winter.

Don Davis, NASA

Dinosaur extinction likely had nothing to do with "the traditional view of them as being slow, stupid, lethargic beasts…"

Old view

Recent thinking

Credits: Tom Weller

2. How does the Environment Select?

A) Micro and Macro Selection

B) Sympatric vs. Allopatric selection/speciation

C) The Ecological Niche, character displacement, adaptive Landscapes

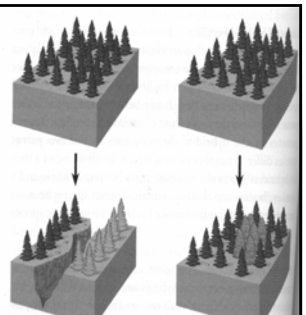
2. How does the Environment Select?

B) Sympatric vs. Allopatric selection/speciation

Sympatric – selection/speciation occuring in the same location

Allopatric – selection/speciation occuring in geographically isolated populations.

Allopatric speciation can be due to both natural selection and genetic drift.



(a) **Allopatric speciation:** a population forms a new species while geographically isolated from its parent population

(b) **Sympatric speciation:** a small population becomes a new species without geographic separation from its parent population

FIGURE 24.6 Two modes of speciation. These sketches simplify the geographic relationships of new species to their parent species.

Sometimes geographical isolation leads to speciation, sometimes not. Often it is a matter of length of time of separation, and differential environmental selection.

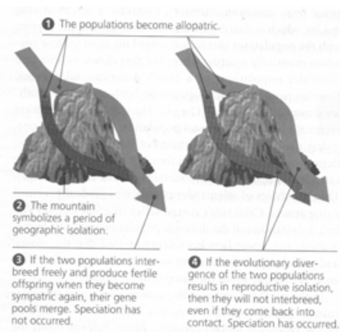
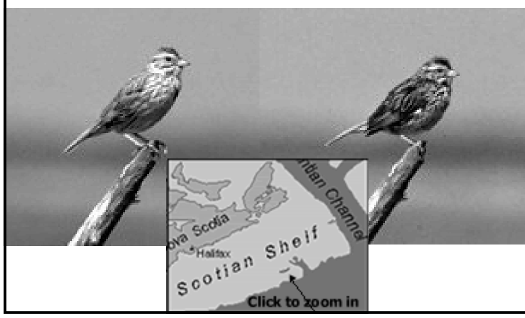


FIGURE 24.8 Has speciation occurred during geographic isolation?

Are these different species?

Ipswich Sparrow — **Savannah Sparrow**

Passerculus princeps — **Passerculus sandwichensis**



What is a species, anyway?

Several definitions. The two most prevalent are:

1. **The Biological Species concept: Based on sexual reproduction. E.g. Horses and Donkeys represent distinct species because they do not produce viable offspring. Problem: asexual reproducing organisms?**
2. **Morphological species concept: The classic definition. Based on phenotypic (physical) characters. Now uses genetic characters. Criteria for determining which traits are important and how much they must differ are subjective.**

One key mechanism of Sympatric Speciation: Polyploidy

Polyploidy – mistakenly unreduced gametes can recombine

It's a rare event, but if it happens, a new species is formed 'immediately' due to reproductive isolation.

Natural selection works on these 'hopeful monsters'

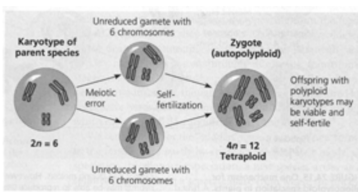


FIGURE 24.13 Sympatric speciation by autopolyploidy in plants.

This is an example of a self fertilizing plant – but a similar process can occur even across different species (allopolyploidy)!

One allopolyploidy mechanism:

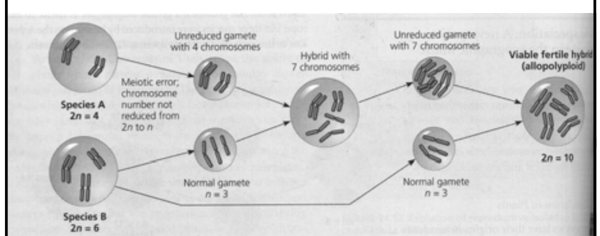


FIGURE 24.15 One mechanism for allopolyploid speciation in plants. A hybrid between two species is normally sterile because its chromosomes are not homologous and cannot pair during meiosis. However, the hybrids may be able to reproduce asexually. This diagram traces one mechanism that can produce fertile hybrids as new polyploid species. The new species has a chro number equal to the sum of the chro in the two parent species.

Example: polyploidy in goatsbeard:

Genus Tragopogon, native to Europe, 3 species introduced to Pacific NW US early 1900s (T. dubius, T. pratensis, T. porrifolius)

Two new species arose in mid 1900s:

T. Miscellus = allotetraploid hybrid of T. dubius and T. pratensis

T. Mirus = alloploid from T. dubius and T. porrifolius

T. pratensis

Other mechanisms of sympatric speciation

-**sexual selection (e.g. coloration)**
-**Adaptive radiation**

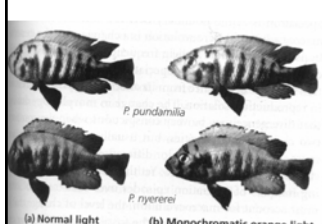
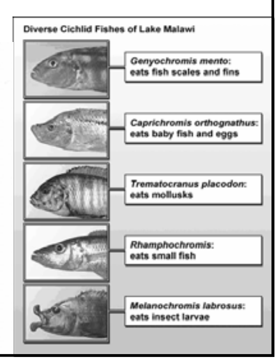


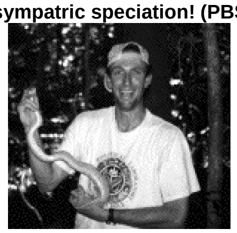
FIGURE 24.16 Mate choice in two species of Lake Victoria cichlids. (a) In normal lighting, two sympatric species of the cichlid genus Pundamilia are noticeably different in coloration. Females of each species mate only with males of their own species. (b) With monochromatic lighting in laboratory experiments, females apparently cannot distinguish males of the two species and mate indiscriminately, producing fertile hybrids.



Traditionally, more importance has been placed on allopatric speciation rather than sympatric speciation.

However, active research is revealing that sympatric speciation is a strong force of evolution.

Researchers at BU currently examine relative strengths of allopatric vs. sympatric speciation! (PBS - Evolution)



Prof. Chris Schnieder, BU Biology Dept.

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2. How does the Environment Select?

A) Micro and Macro Selection

B) Sympatric vs. Allopatric selection/speciation

C) The Ecological Niche, Character Displacement, Adaptive Landscapes

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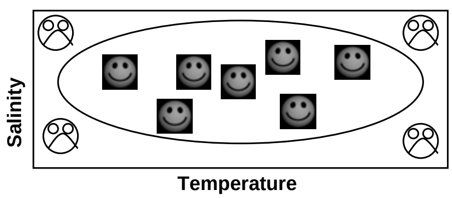
The Ecological Niche and Evolution

The environment selects species that 'fit' into resource niches.

Temperature range, light level, salinity, size range of prey, all can be dimensions that describe a niche space.

Niche space is easily visualized in two dimensions:

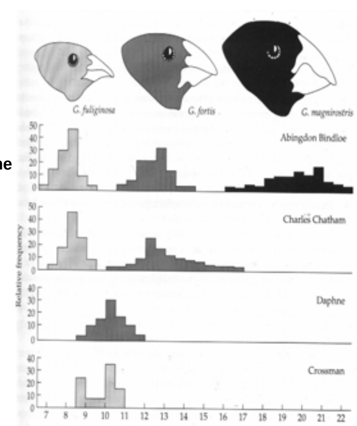


And can easily be mapped onto geographical space.

The Ecological Niche and Character Displacement

Competition tends to prevent different species occupying similar niches.

Clear evidence of this is the observation of Character Displacement:

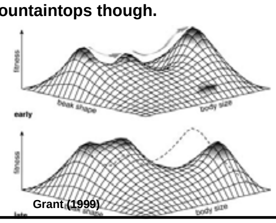


Ecological Niches map how species fit within their environment.

Conversely, adaptive landscapes are maps of what phenotypes the environment favors in organisms.

Natural Selection leads to 'peak climbing'

Species often get stuck on local mountaintops though.



Grant (1999)

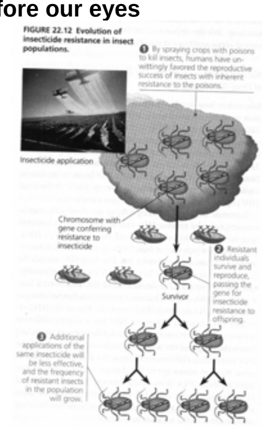
Cactus Finch, Geospiza scandens

Photo credit: Fritz Polking/Peter Arnold

Evolution before our eyes

Evidence of Natural Selection

A contemporary example: DDT selects for insecticide resistance



A famous example of natural selection: Kettlewell's Peppered moth and industrial melanism

GE/BI307: Mar. 8 2007

Extinction: A Litany of Cases and Causes

1. Factors causing extinction

- **Rarity: intrinsic or forced**
  - **Trophic cascades**

2. Examples

The fate of all species is extinction

-The Taxon Cycle

-The Red Queen Hypothesis: "it takes all the running you can do to keep in the same place" – cessation of evolutionary change may lead to extinction.

-Abiotic and biotic environments are always changing, and it becomes increasingly difficult for highly evolved, specialist species to respond

Factors causing extinction

- **Rarity: *intrinsic* or forced**

Key points:

Small populations are vulnerable to extinction, whether intrinsic to that species (e.g. top predators) or caused by external forces.

Once a population is small, it is the population's smallness itself that drives it to extinction.

This is what Quammen implies by 'rarity unto death'

Why?

The extinction vortex:

Even in a favorable environment, small populations may lose genetic diversity due to the bottleneck effect and inbreeding, leading ultimately to even smaller populations until extinction.

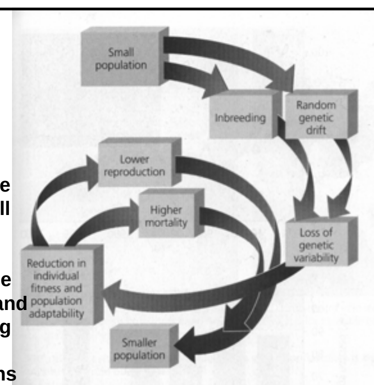
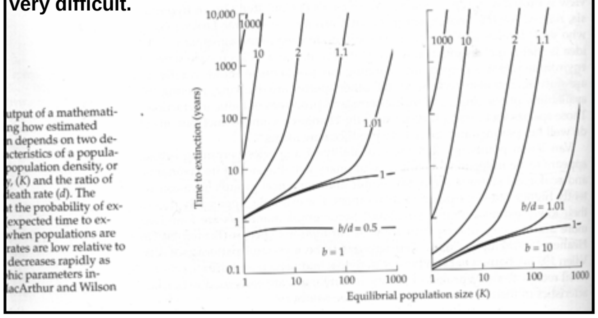


FIGURE 55.10 The extinction vortex of the small-population approach. Small populations can fall into a vortex of positive feedback loops leading to smaller and smaller population size.

Population growth models suggest that even with high birth/death ratios, extinction becomes likely at low population sizes.
Potentially exponential population growth leads to very non-linear population growth, which makes extinction estimates very difficult.



Researchers have tried for a long time to determine Minimum Viable Population sizes (we'll talk more about this later in the semester)

Population Viability Analysis: predicts probability of survival over a given time range (e.g. 15% chance of extinction in next 50 yrs).

It is not simply the number of individuals that matter in population viability analyses: it is the effective population size:

-depends on % of individuals capable of breeding, and the sex ratios:

$N_e = 4N_fN_m/(N_f+N_m)$

N_e = effective population size
N_f = # females that can effectively breed
N_m = # males that can effectively breed

e.g. 1000 individuals, all can breed, 50% male/female:

$N_e = 4*500*500/(500+500) = 1000$

e.g. 1000 individuals, 50% can breed, 25%male/75%female:
Ne = 4*375*125/(375+125) = 375

So how do populations become small and endangered?

Five major threats:

1. Habitat destruction
2. Introduced species
3. Overexploitation
4. Food Chain Disruptions (trophic cascades)
5. Climate Change (can act as #1)

Often, these factors interact

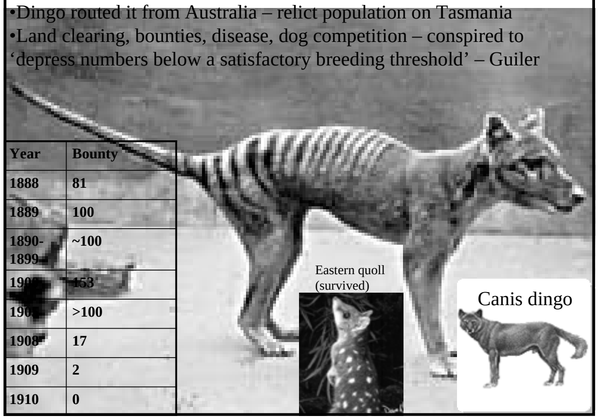
So how do populations become small and endangered?

A central point of Quamman:
humans often reduce population numbers to a point of diminishing returns, but do not directly finish species off.

The low population sizes then finish off the species.

Examples Galore:

Tasmanian ‘tiger’, Thylacinus cynocephalus:
•Dingo routed it from Australia – relict population on Tasmania
•Land clearing, bounties, disease, dog competition – conspired to ‘depress numbers below a satisfactory breeding threshold’ – Guiler



Year	Bounty
1888	81
1889	100
1890-1899	~100
190[illegible]	153
190[illegible]	>100
1908	17
1909	2
1910	0

Eastern quoll (survived)

Canis dingo

Mauritius kestrel 6 in 1970s

Dodo: humans + introduced pigs, monkeys – eat eggs.

‘swept into a vortex of compounded woes’? - Quamman

Lophopsittacus mauritianus largest parrot ever - extinct

Crab-eating macaque Macaca fascicularis Native: southeast asia

Passenger Pigeon: Ecopistes migratorious

Social behavior (huge dense flocks) eased killing. But likely not coup de grace.

1880’s still nesting in millions.

1888: sighting of 175 was noteworthy.

Last wild bird killed 1900

“5000 thylacines may be sufficient in tasmania, 5 million too few for pigeons. Why? Social structure and its ecological correlates impose different thresholds of population stability on different species” - Quamman

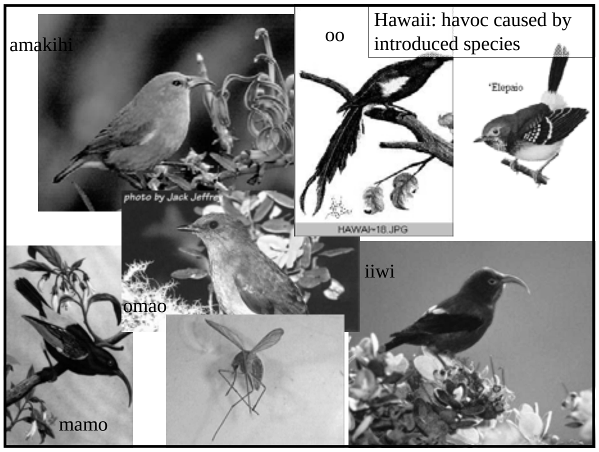
“The puzzling aspect of the passenger pigeon’s demise lies in the fact that during the last years the species continued to decline at a rate that seems too great to be accounted for simply by hunting” - Halliday

“this bird had to live in vast numbers or not at all”

-**finding food, guard against enemies, incubating eggs, fledging young, thythms of mating/nesting, all apparently were supported by big population sizes.**

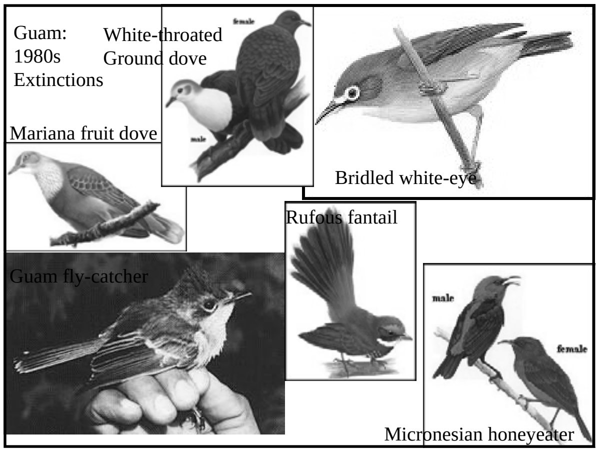
“Critical Mass” – here social factors, rather than genetic extinction vortex likely played a role.

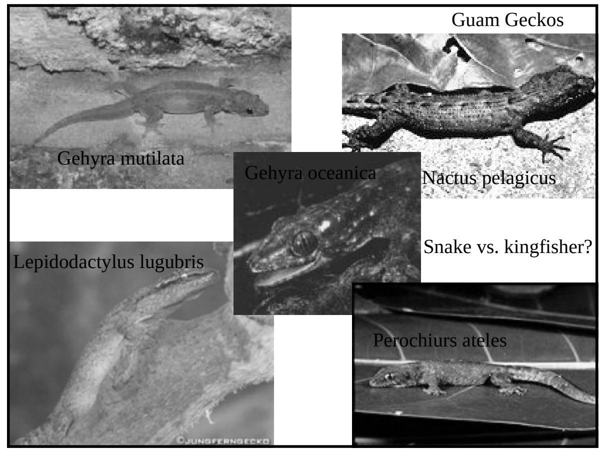
Hawaii: havoc caused by introduced species

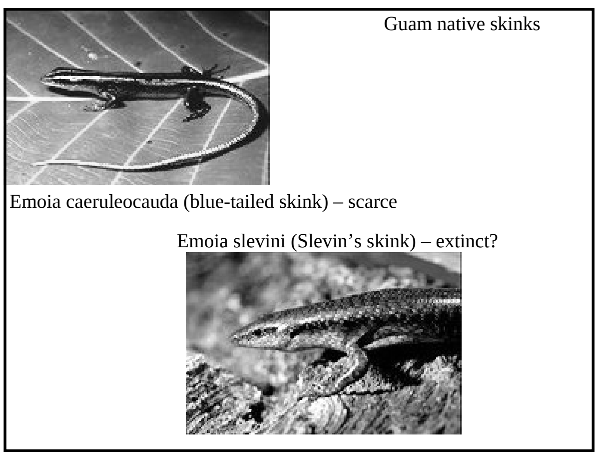


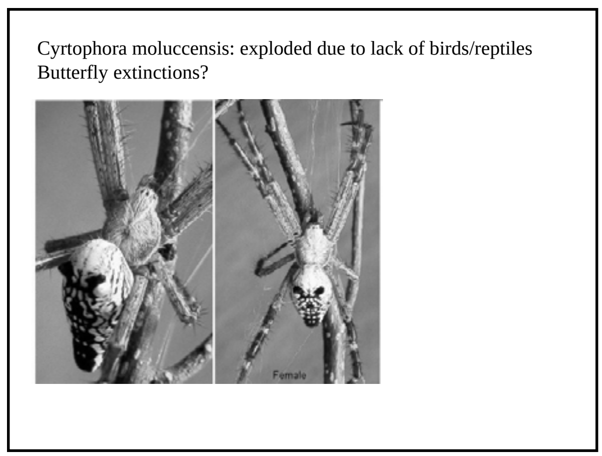
Trophic cascades: examples from Guam, Panama

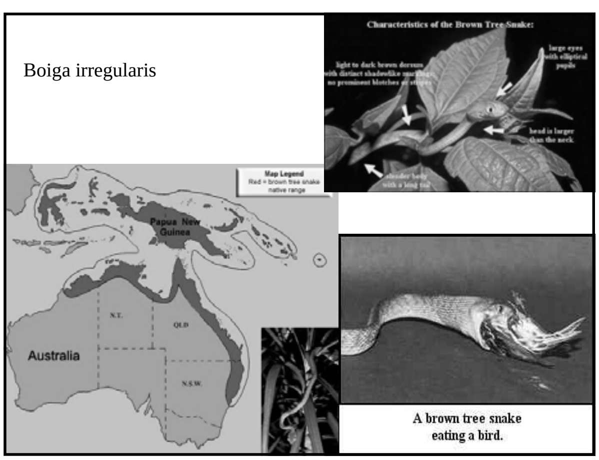
Definition (Diamond): “Since species abundances depend on each other in numerous ways, disappearance of one species is likely to produce cascading effects on abundance of species that use it as prey, pollinator, or fruit disperser. “At the low extreme of abundance, a species faces rarity unto extinction”





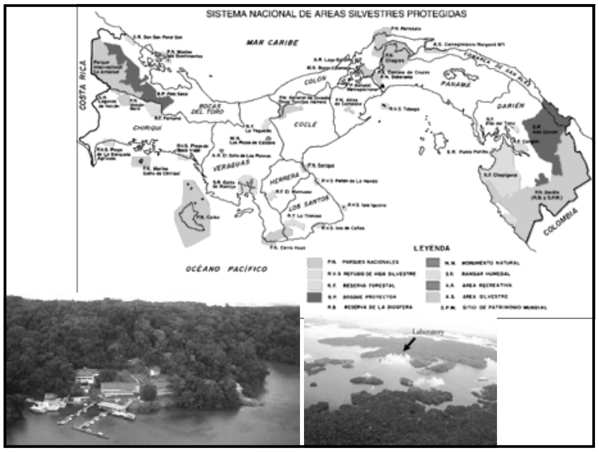






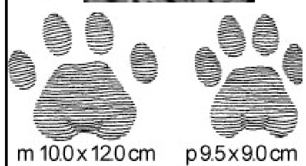
Trophic cascades: example from Panama

- **Lake Gatun dammed early 1900s, BCI protected beginning 1923**
- **By 1980s, 45/108 breeding birds locally extinct: why?**



Top predators left first (died or swam away)

Pantera Onca centralis
But Tracks on BCI: 1993



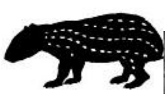
Harpy Eagle

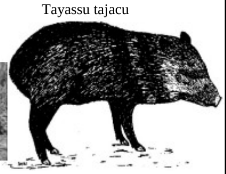
Led to profusion of mid-sized omnivores, feeding on ground bird eggs

Howler monkey

Gato solo, Coati mundi,
white nosed coati
Nasua narica

Collared Peccary
Tayassu tajacu



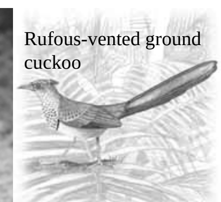


Agouti paca, Paca

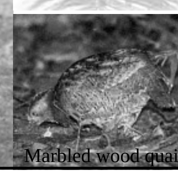
9 banded armadillo

A few of the many dozens of local extinctions on Barro Colorado Island

Great curassow
Marcus G. Martin



Rufous-vented ground cuckoo



Marbled wood quail

Black faced antthrush

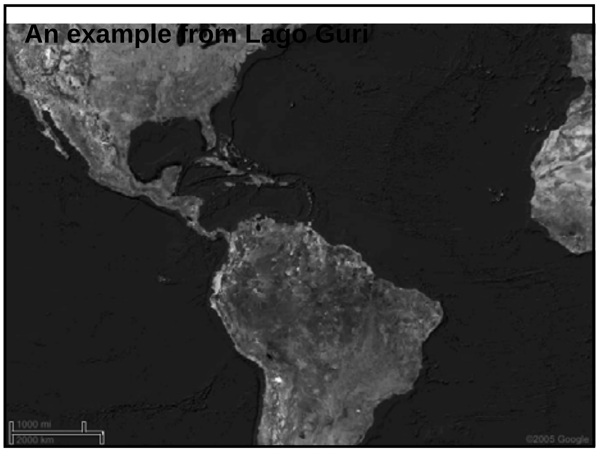
Harvard NHM Field Trip Thursday

- Bring your BU ID!
- Look for and spend time at Dodo, Moa, Passenger Pigeon displays
- Find an animal from a region related to your term project.
- Visit the Peabody Archeological and Ethnographic Museum for NZ, NG artifacts: http://www.peabody.harvard.edu/ethno/oceania.html

Summary: Fragmentation and trophic cascades

Insularization -> extinction -> more extinctions

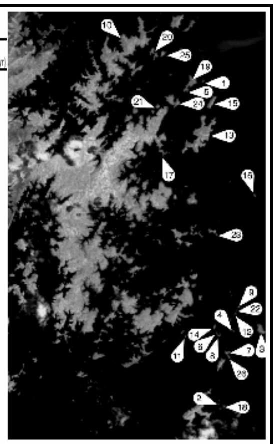
An example from Lago Guri

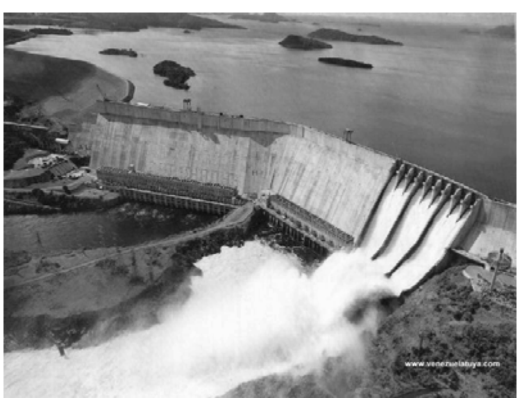


Lago Guri

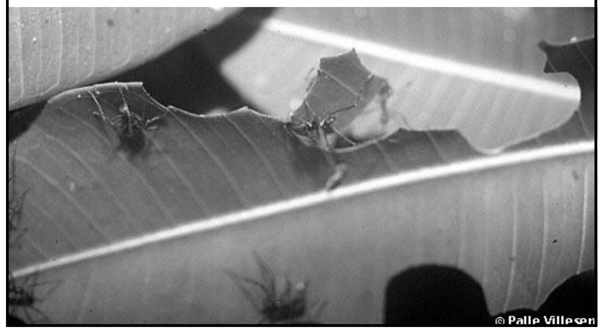
Table 1: Attributes of study islands

Island	ID #	Area (ha)	Tree Diversity (Fisher's Alpha)	Canopy Closure (%)	Basal Area (m^2/ha)	Stand Density (stems/ha)	AWI (m^2/ha/yr)
Afuera	1	0.2	4.88	74.31	12.79	301.94	-0.03
Aguila	2	0.7	5.42	76.24	-	-	-
Ambar	3	14.7	24.32	-	-	-	-
Baya	4	0.6	10.19	78.44	10.46	313.33	0.22
Bumeran	5	0.9	13.70	72.36	-	-	-
Chigüire	6	0.3	8.72	74.39	13.84	399.86	0.28
Chotacabra	7	4.0	13.29	85.25	-	-	-
Cola	8	1.0	9.58	77.00	12.27	326.41	0.21
Colon	9	0.6	10.99	80.55	13.87	425.00	0.17
Danto Machado	10	180.8	26.86	85.43	-	-	-
Densa	11	0.5	9.71	71.56	4.44	195.59	0.05
Facil	12	0.3	8.76	84.81	12.50	346.32	0.17
Grande	13	88.0	13.77	-	-	-	-
Iguana	14	0.7	13.75	85.73	17.35	461.43	0.39
Lomo	15	12.0	15.88	-	-	-	-
Miedo	16	0.7	6.51	82.37	4.69	137.14	0.14
Palizada	17	1.8	17.21	79.68	7.87	198.33	
Paloma	18	0.5	4.23	81.29	7.25	226.46	0.04
Panarama	19	11.1	17.64	-	-	-	-
Perimetro	20	1.7	21.37	-	-	-	-
Quina	21	0.6	10.76	83.84	-	-	-
Reinita	22	0.2	6.35	77.08	11.84	400.00	0.00
Rocas	23	0.6	9.29	76.92	-	-	-
Solitario	24	2.4	12.34	75.67	-	-	-
Triangulo	25	2.3	8.82	80.91	-	-	-
Tucucito	26	1.5	14.01	77.18	-	-	-





Leaf cutter ants: herbivores
Leaf cutter colonies on small islands ~ 1-7 /ha
On large islands/mainland: .01-.04/ha



Howler monkeys: 10-50 x as dense on small islands as on mainland

Capuchin monkeys: omniverous, absent from small, and medium Islands…

Persisting on small islands:
Predators of invertebrates: spiders, anurans (frogs/toads), lizards, birds
Seed predators (small rodents)
Herbivores (howler monkeys, iguanas, leaf cutter ants)

Absent from small islands:
Frugivores (principal seed dispersers) and predators of vertebrates.

Medium islands: + armadilos, agoutis, phorid fly parasitouds of ants

Large islands: + deer, peccaries, tapir, monkeys

Mainland: jaguar, puma, harpy eagle

Diverse, bizarre outcomes of insularization too numerous to list!

Meeting Society for Conservation Bio

Loss of Dung Beetles Puts Ecosystems in Deep Doo-Doo

Like an overengineered airplane, ecosystems are thought to have redundant functions that should prevent a single extinction from triggering more serious consequences. Many animal species disperse seeds, for example. So when one such species disappears, others face less competition and ought to become more abundant, taking up any slack.

Backlog. When key dung beetle species disappear, monkey dung goes unburied.

New research suggests that may not always be true. The study examined the fate of dung beetles, which collect dung, bury it, snack on it, and lay their eggs in it. Burying the seed-laden dung also enriches the soil and helps plants regenerate. Trond Larsen, a graduate student at Princeton University, found that the beetle species best at burying dung were the first to disappear from forest fragments. Alarmingly, related species did not become more abundant. Much dung then went unburied. "It tells us that the level of resilience in ecosystems to damage or biodiversity loss could be much less than we thought," says Richard Ostfeld of the Institute of Ecosystem Studies in Millbrook, New York.

Larsen studied 42 species of dung beetles in eastern Venezuela, where a hydroelectric dam completed in 1986 flooded 4300 square kilometers of tropical forest and created more than 100 forest islands. He found that smaller islands had fewer species of beetles and that the larger beetles were most frequently missing.

The main cause of the beetle's decline was a bad sense of direction. Most dung beetles are used to flying in contiguous forest, where they don't need to be expert navigators. By marking some 15,000 beetles and recapturing as many as possible, Larsen showed that beetles couldn't find their way back if they flew off the island. "Once they hit open water, they're done for," he says. Big beetles fly faster and farther than small beetles, he discovered, and are more likely to go AWOL. The problem is worse on smaller islands, where there is a larger perimeter relative to the area. To retain a viable population, three of the largest dung beetle species needed at least 85 hectares—a surprisingly large amount of habitat for an insect, Larsen says.

When beetle diversity declined, much less dung was buried. The remaining species of dung beetle on the smaller islands didn't become more abundant and dig into the surplus dung, Larsen found. The reason, he suspects, is that they too are accidentally leaving the islands, although at a lower rate. With fewer seeds being buried, forest diversity ultimately will decline.

The worrisome conclusion is that species diversity is less of a safeguard against ecosystem collapse than had been assumed, Larsen says: "Even the loss of just one or two species may have a much greater impact than we previously thought." Like top carnivores, the large dung beetles appear to be the most sensitive to extinction and extremely important for ecosystem integrity, he adds. Moreover, it's surprisingly hard for others to fill their shoes, Ostfeld says: "I wouldn't have expected to see this effect with a dung beetle."

Larsen's discovery that the beetle's larger body size and flying behavior make it more vulnerable to decline is an important contribution, says Ostfeld. "Finding a clear mechanism makes it more likely that ecologists can predict the systems that should behave similarly," Ostfeld says. "That's a big deal for environmental managers and policy specialists."

30 27 AUGUST 2004 VOL 305 SCIENCE

Summarizing the trophic cascade on Lago Guri:

1. Insularization: top predators gone quickly
2. Herbiverous consumers flourish
3. Recruitment of trees severly diminished (only 20% of saplings on small islands vs. mainland)
4. Lianas, shrubs, grasses favored, canopy trees eaten.

"Hyperabundant folivores threaten to reduce species-rich forests to an odd collection of herbivore-resistant plants… the endpoint is likely to be a biologically impoverished system, much like that found today on 85-yr old islands in Lake Gatun, Panama" – Terborgh et al.

Lessons from the trophic cascade on Lago Guri:

- Hyperabundant grazers in US (cows, deer, etc) – e.g. native grasses -> shrubs
- Top-down regulation of ecosystem primary productivity and diversity can be as important as 'bottom-up' regulation.

A trophic cascade that turned out not to be true…

Calvaria major:
The "dodonut" tree

Temple 1977 hypothesis

GE/BI307 – Mar 20, 2007

The Species-Area Relationship

"The species-area relationship is one of ecology's oldest and most profound generalizations… It pertains to the preservation or loss of biological diversity on our planet, where the total area of natural landscape grows smaller and more fragmented every year."

- David Quammen

History of the Species-Area relationship

Forster 1778: "Islands only produce a greater or less number of species, as their circumference is more or less extensive"

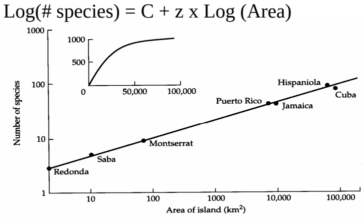
Watson (1859), deCandolle (1855), Jaccard (1902, 1908), Brenner (1921), Arrhenius (1921), Gleason (1922, 1926).

Arrhenius was the first to generalize the relationship in mathematical form.

The species-area relationship: A fundamental pattern of biodiversity

$\# \text{ of species} = C \times \text{Area}^Z$

or, $\text{Log}(\# \text{ species}) = C + z \times \text{Log}(\text{Area})$



Reptiles/amphibians of West Indies, Darlington 1957

Plants in pacific islands

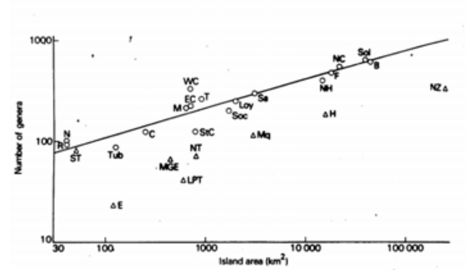


Fig. 6.2 The relationship between island area and diversity of conifer and flowering plant genera in the Pacific Islands. The more isolated islands are indicated by triangles. The data from the other islands lie very close to a straight line (the regression coefficient), suggesting that generic diversity in these islands is almost wholly controlled by island area — the correlation coefficient is 0·94, indicating a very high degree of correlation. For abbreviations, see legend of Fig. 6.1, plus Loy, Loyalty Islands. Data from Van Balgooy [5].

Beetles in urban UK roundabouts

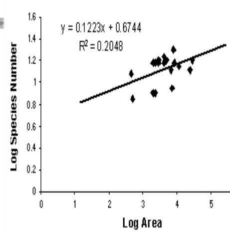
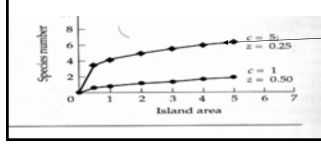


Figure 1. Relationship between Area and Number of Species

A few comments on the Species-Area Curve:

$S = C \times A^Z$

- •The C and Z values of the Species-Area Curve differ by taxonomic group (family or genus). "One size does not fit all"
- •The C and Z parameters do not lend themselves easily to ecological intepretation and are really more just statistical fits to data
- •For example, high Z has been equated with rapid increase in species richness with area (due to perhaps small body sized organisms), but that is not necessarily true.
- •When plotted linearly, we see diminishing returns at larger areas – implications for conservation?
- •Useful for estimating # of species, not necessarily how much we value them.



Species # increases more here,
Even though Z is smaller

A few comments on the Species-Area Curve:

$S = C \times A^Z$

- •The species-area curve depends on whether we are considering area "samples" within a large, uniform area, versus true "isolates", like islands or landscape fragments.
- •Samples typically have higher species richness for the same area. Why?

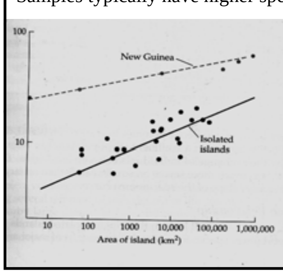
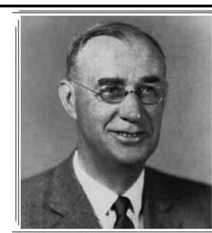


Figure 13.3 The slope of the species-area relationship in log-log space is much steeper for isolated islands than for sample areas of different sizes within a single large landmass. These data are for pomerine ants on the Moluccan and Melanesian islands (below) and in regions of increasing size on New Guinea (above). The difference between the two curves can be attributed to the greater likelihood of extinction without replacement by immigration of rare species on isolated islands. (From Wilson 1961.)

Frank Preston:



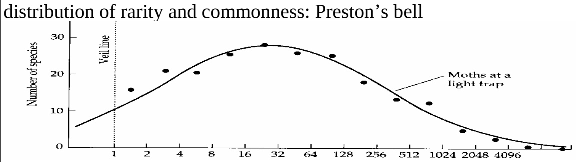
Dr. Frank Preston in 1961

"…on isolated islands we must have an approximation to internal *equilibrium*…since an island can hold only a limited number of individuals… but on the mainland a small area is not in internal equilibriumm; it is in equilibrium with areas across its boundaries and is a sample of a vastly larger area"

What causes the species-area relationship?
2 factors:

Larger areas provide more habitat/resources/range size for more species. Also, the statistical probability of finding rare species increases with area – the smaller the area, the less the chance. (analagous to bottleneck effect on rare alleles in small populations)

In stats jargon, the species-area r'ship arises from the lognormal distribution of rarity and commonness: Preston's bell



Rare species ---→ moderate ------→ common
Ferrari mercedes ford
Abundance

Frank Preston:

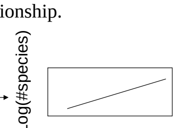
"…it is not possible to preserve in a state or national park, a complete replica on a small scale of the fauna and flora of a much larger area"

Of what practical use is the Species-Area relationship?

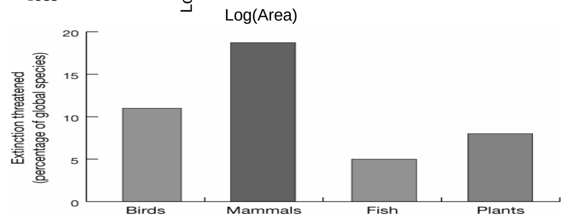
1. Puts biodiversity on a quantitative basis: underpins the Equilibrium theory of Insular Biogeography
2. Local: Allows conservationists to estimate how big a patch is needed to preserve X% of flora and fauna.
3. Global: Can be used to estimate global biodiversity and expected biodiversity loss.

Estimates of global extinction threats: Based on applying the species – area relationship.

Habitat loss →

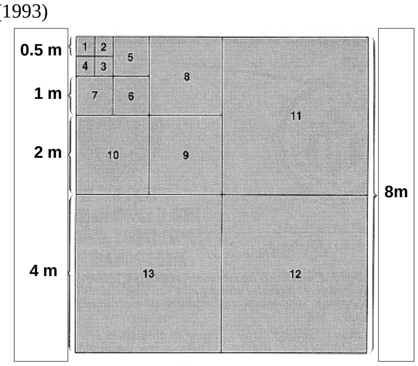


→ Estimated Species loss



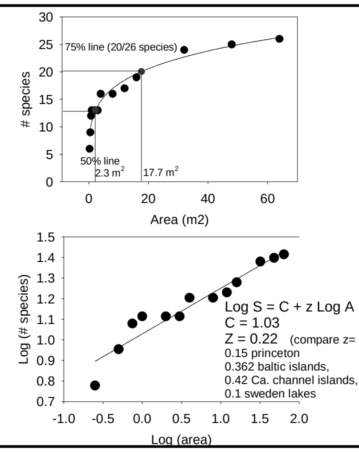
Source: Chapin et al. 2000 (Nature) Estimates
From Pimm et al. Science 269:347-350 (1995)

Biogeography in the backyard – adapted from Henry Horn (1993)



SPECIES	BLOCK NUMBER 1	2	3	4	5	6	7	8	9	10	11	12	13
TURKEYTRACK GRASS	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
SCOTT'S TOOTH GRASS	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
LITTLE BROAD-LEAVED GRASS	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
FAT-LEAVED GRASS	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
WHITE CLOVER	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓	✓
ALSIKE CLOVER	✓	✓	✓	✓	✓		✓		✓	✓	✓	✓	✓
HOP CLOVER				✓			✓			✓			✓
YELLOW WOOD SORREL	✓		✓	✓		✓	✓	✓			✓		✓
MOUSE-EAR CHICKWEED	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
JAMES'S 3-LEAF							✓			✓			✓
SMOOTH-LEAVED BARBARA		✓		✓	✓		✓		✓	✓			✓
HAIRY HARRY				✓	✓		✓						✓
BROAD-LEAVED PLANTAIN	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
FANCY MARY	✓	✓			✓				✓		✓	✓	✓
DANDELION	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓
ITTY-BITTY					✓		✓						✓
WHITE ASH TREE								✓		✓			
SPEEDWELL		✓	✓		✓	✓	✓	✓	✓		✓	✓	✓
BERT WEED							✓						✓
INDIAN STRAWBERRY			✓			✓		✓			✓	✓	✓
BROWN-TOP MUSHROOM					✓								
PETITE LISA	✓				✓							✓	
BOSS MOSS	✓	✓		✓	✓		✓			✓			
FIELD SPEEDWELL	✓											✓	
FUZZY CHICKWEED											✓	✓	
SCARLET PIMPERNEL										✓			✓
TWIN BETTY												✓	
NARROW-LEAVED PLANTAIN					✓								
MYSTERY PLANT					✓						✓		✓
NOVA TERRA SHARON											✓		
PRINCETON PARSLEY											✓		
POISON IVY											✓		
LINDA BERRY													✓
ERNIE WEED											✓		
TOTAL PER BLOCK	14	13	11	13	19	11	18	11	12	15	19	13	22
CUMULATIVE TOTAL	14	16	17	19	23	23	25	26	26	27	32	33	34
AREA OF BLOCK	1	1	1	1	4	4	4	16	16	16	64	64	64
CUMULATIVE AREA	1	2	3	4	8	12	16	32	48	64	128	192	256

						Block Number							
Species	**13**	**12**	**11**	**10**	**9**	**8**	**7**	**6**	**5**	**4**	**3**	**2**	**1**
Butter and Eggs Linaria vulgaris – invasive europe	X	X	X				X	X	X	X	X	X	X
Saw Sedge	X	X	X				X	X	X	X	X	X	X
Dandelion		X	X										
Purple starberry	X	X	X										
Woody clover	X	X	X										
Fuzzy Leaf		X					X						
Little Leaf	X	X						X	X	X	X	X	
Brown bulb		X	X				X						
Fool’s cilantro	X	X	X									X	X
Feather	X	X	X	X									
Tree of Heaven	X	X	X								X		
Brown rose	X	X	X										
Softgrass	X	X	X									X	
Baby oak	X	X	X							X			
Clusters					X								X
Purple Daisy		X								X			X
3-prong	X		X	X	X	X	X	X	X		X		
Grass X	X			X	X								X
Little Tabby	X		X		X								
Sweet Money	X			X									
Sawtooth					X				X		X	X	
Shamrock			X										
?	X	X	X	X	X	X					X		
Heartleaf							X						
Mini-tomato		X											
Juicy leaf	X												
TOTAL PER BLOCK	17	17	16	5	6	2	6	4	5	5	7	6	6
CUMULATIVE TOTAL	26	25	24	19	17	16	16	13	13	13	12	9	6
AREA OF BLOCK	16	16	16	4	4	4	1	1	1	.25	.25	.25	.25
CUMULATIVE AREA	64	48	32	24	16	8	4	3	2	1	.75	.5	.25



GE/BI307 – March 29, 2007

The equilibrium theory of insular biogeography

- a framework for predicting biodiversity in all kinds of fragmented landscapes.

Question:

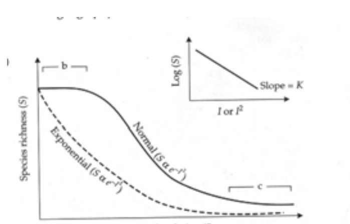
Now we know something about how the size of an ‘island’ influences biodiversity…

What’s another major geographical factor that you might think influences biodiversity of landscape fragments?

Answer:

Degree of Isolation of the Fragment from other fragments or the ‘mainland’

While species richness increases with area of habitat, it declines with degree of habitat isolation.



The form of the relationship is generally much less general than the species-area relationship and reflects taxonomic differences in mechanisms/effectiveness of dispersal.

Some examples of species-isolation relationships.

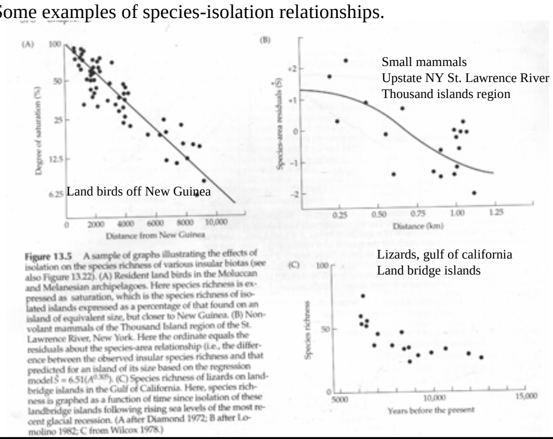


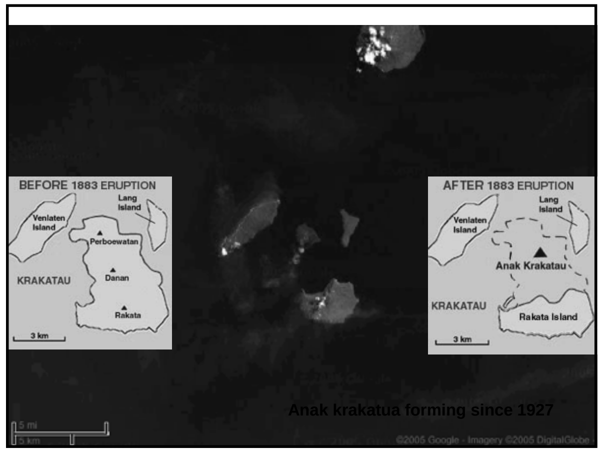
Figure 13.5 A sample of graphs illustrating the effects of isolation on the species richness of various insular biotas (see also Figure 13.22). (A) Resident land birds in the Moluccan and Melanesian archipelagoes. Here species richness is expressed as saturation, which is the species richness of isolated islands expressed as a percentage of that found on an island of equivalent size, but closer to New Guinea. (B) Nonvolant mammals of the Thousand Island region of the St. Lawrence River, New York. Here the ordinate equals the residuals about the species-area relationship (i.e., the difference between the observed insular species richness and that predicted for an island of its size based on the regression model $\hat{S} = 6.51(A^{0.305})$. (C) Species richness of lizards on landbridge islands in the Gulf of California. Here, species richness is graphed as a function of time since isolation of these landbridge islands following rising sea levels of the most recent glacial recession. (A after Diamond 1972; B after Lomolino 1982; C from Wilcox 1978.)

We’ve discussed two ingredients of a theory of insular biogeography

1. Species Richness increases with area
2. Species Richness decreases with isolation.

A third and last key ingredient:

3. Species turnover: Colonized islands over time tend toward a balanced rate of immigrations and extinctions. Example: Rakata/krakatau



Painting of the River Thames Nov. 26, 1883 (William Ascroft) (eruption Aug. 26-27)

The wave lifted the steamship Berouw up the Koeripan River valley, depositing the ship over a mile inland, thirty feet above sealevel, killing all 28 of its crew members.

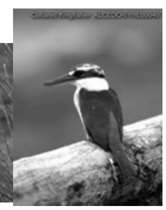
http://www.geology.sdsu.edu/how_volcanoes_work/Krakatau.html

A few species on Anak Krakatau

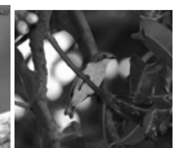
Komodo dragon

Mangrove whistler, Pachycephala cinerea

Casuarina equisetifolia



Halcyon chloris



Flyeater, Gerygone sulphurea

Krakatau flora and fauna (MacArthur, Wilson)

•After eruption, species quickly colonized, and approached an equilibrium species richness

•Species ‘turned over’ – some new ones came, some went extinct, equilibrium roughly maintained.

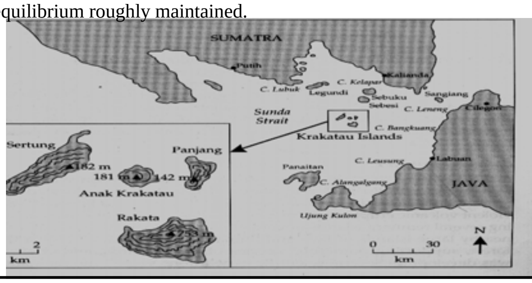


Table 13.1
Number of species of land and freshwater birds on Rakata and Sertung

Number of species found

	Rakata			Sertung		
	Nonmigrant	**Migrant**	**Total**	**Nonmigrant**	**Migrant**	**Total**
1908	13	0	13	1	0	1
1919–1921	27	4	31	27	2	29
1932–1934	27	3	30	29	5	34

Number of extinctions and colonizations between censuses

	Rakata		Sertung	
	Extinctions	**Colonizations**	**Extinctions**	**Colonizations**
1908 to 1919–1921	2	20	0	28
1919–1921 to 1932–1934	5	4	2	7

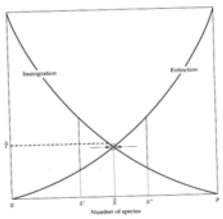
Source: After MacArthur and Wilson 1967.

Note: The number of species increased from the census of 1883 to that of 1919–1921 and then remained relatively constant despite extinction of some species and colonization of others.

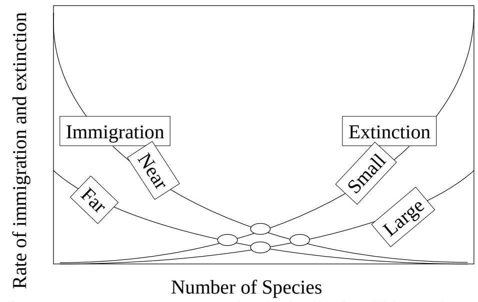
Robert MacArthur and E.O. Wilson put fragment area, isolation and turnover together in an elegant theory called "The Equilibrium Theory of Island Biogeography"

Hypothesis: For any island (or isolate), there is a dynamic equilibrium between the influx and extinction of species.

Kind of like water molecules evaporating and condensing at equal rates in a closed, half-filled jar.



Then, they considered how island size and isolation would change equilibrium species richness:



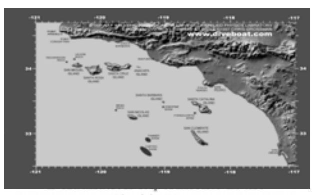
Predictions: Large, near-to-mainland islands should have the most species richness, small, far islands the least

Also, small, near islands should show the most species change over time, large far islands the least

There have been many indications that the general processes described by the theory do indeed occur.

California Channel Island birds (Diamond) – large turnover, most on smallest islands

Florida keys insects (Simberloff & Wilson) – approach to equilibrium.



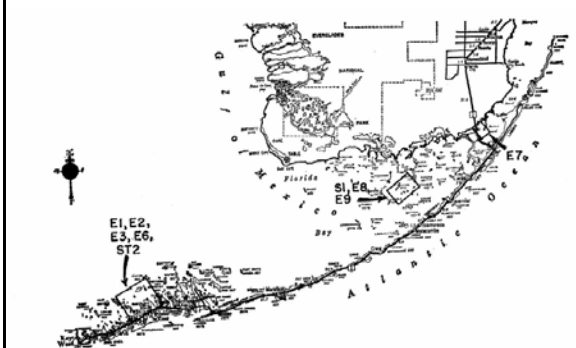


FIG. 1. The southern tip of Florida and the Florida Keys. The rectangles enclose the experimental areas shown in detail in Figures 3–5.

Florida keys insects (Simberloff & Wilson)

•Insects quickly recolonized after fumigation ("relaxation")
•Farthest, smallest islands had fewest species at equilibrium

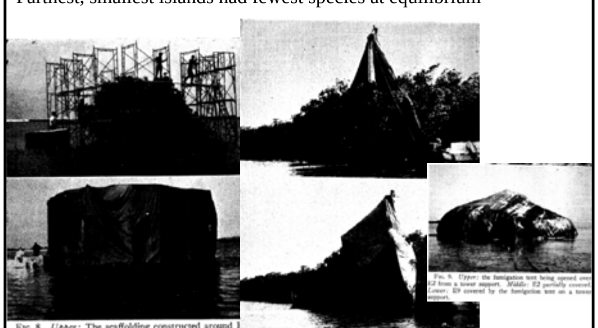
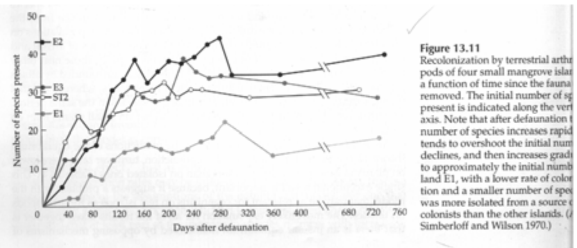


FIG. 8. *Upper:* The scaffolding constructed around E complete except for the top walkway. *Lower:* the fum gation tent over E2.

FIG. 9. *Upper:* the fumigation tent being spread over E2 from a tower support. *Middle:* T2 partially covered. *Lower:* E9 covered by the fumigation tent on a tower support.

FIG. 2. *Upper:* Island E1, the second smallest island in the experimental series. *Lower:* Island E9, the largest island in the experimental series; note also the presence of supratidal mud.

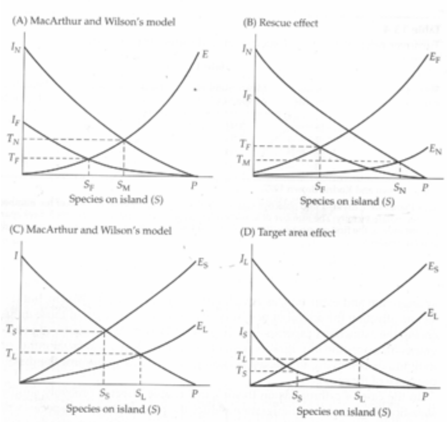
Florida keys:
-relaxation (works the other way too!)
-Overshoot (non-interactive equilibrium?)
-Interactive equilibrium – decrease after overshoot
-Assortative equilibrium – slow subsequent increase: succession, niche filling…



But there are important limitations to the equilibrium theory

- All species treated the same, disregards requirements for range size by different species.
- Doesn't account for Speciation
- Doesn't account for habitat heterogeneity

•Extinction also depends on island isolation (rescue effect) and immigration depends on island size (target area effect). Rescue effect provides both individuals and genetic diversity to near islands. Target island effect – larger islands may be better seen or encountered by potential immigrators. **"The factors affecting the arrival of new species are not independent of those influences the extinction of species already present" – James Brown.**



Examples of the target area effect

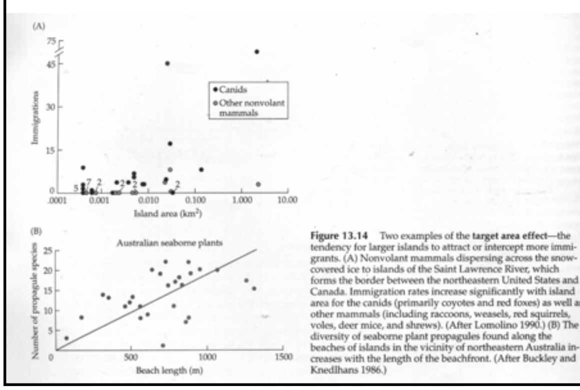


Figure 13.14 Two examples of the **target area effect**—the tendency for larger islands to attract or intercept more immigrants. (A) Nonvolant mammals dispersing across the snow-covered ice to islands of the Saint Lawrence River, which forms the border between the northeastern United States and Canada. Immigration rates increase significantly with island area for the canids (primarily coyotes and red foxes) as well as other mammals (including raccoons, weasels, red squirrels, voles, deer mice, and shrews). (After Lomolino 1990.) (B) The diversity of seaborne plant propagules found along the beaches of islands in the vicinity of northeastern Australia increases with the length of the beachfront. (After Buckley and Knedlhans 1986.)

Finally, we know that not all islands are at equilibrium: great basin isolation of small mammals is near perfect – distance doesn't matter, there is zero immigration.

"instead of turnover, Brown found only extinction" - Quamman

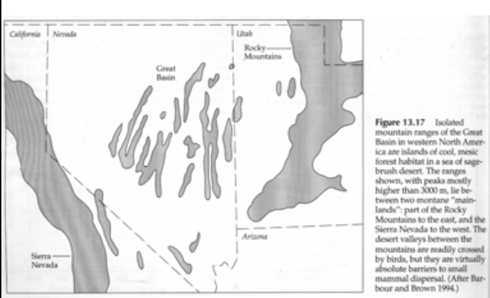
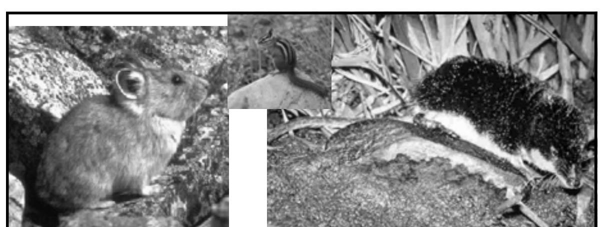


Figure 13.17 Isolated mountain ranges of the Great Basin in western North America are islands of cool, mesic forest habitat in a sea of sagebrush desert. The ranges shown, with peaks mostly higher than 3000 m, lie between two montane "mainlands": part of the Rocky Mountains to the east, and the Sierra Nevada to the west. The desert valleys between the mountains are readily crossed by birds, but they are virtually absolute barriers to small mammal dispersal. (After Barbour and Brown 1994.)



Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Lagomorpha
Family: Ochotonidae
Genus: Ochotona (26 species)
Species: **Ochotona princeps**

Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Insectivora
Family: Soricidae
Subfamily: Soricinae
Genus: Sorex (dozens of N. Am. species
Species: **Sorex palustris**

-All species treated the same -> limitations to theory

Islands usually show ‘disharmonic’ biotas – immigration is selective.

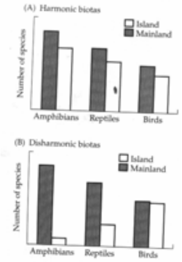


Figure 14.1 Two hypothetical examples of patterns in species composition illustrating the difference between harmonic and disharmonic biotas. In both examples, the insular communities have fewer species of each taxonomic group than the mainland biota. Disharmony refers to marked differences in the composition of insular communities from that of mainland biotas, with overrepresentation of some taxonomic or functional groups (e.g., birds in B) and scarcity of others that tend to be common elements of the mainland biota (amphibians and reptiles in B).

Strengths of the theory:

-Graphical model accessible, easily understandable

-Leads to clear, testable predictions based on measureable variables.

-Implications for conservation, reserve design

One example of the theory’s utility:

Insular distrubution functions.

Turns equilibruim theory on its head by focusing on single species dependence on area/isolation:

Based on immigration/extinction rates of individual species, and how related to area/isolation.

Intercept: measure of minimum area needed for survival

Slope: increases with decreasing immigration ability (rescue ability)

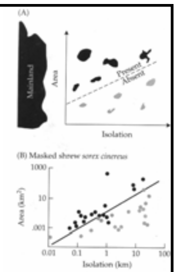
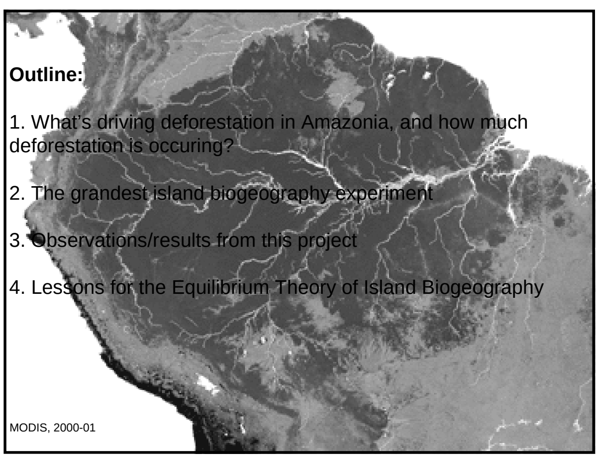


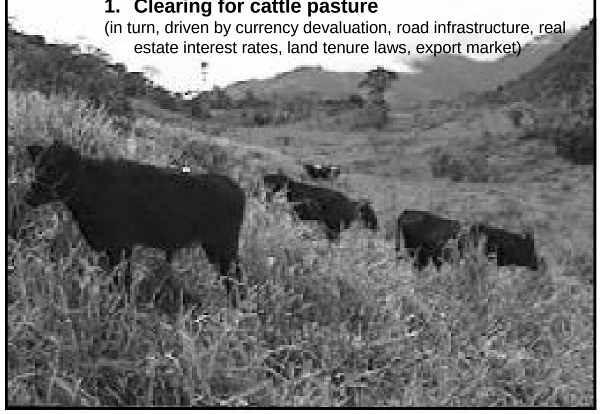
Figure 14.8 Insular distributions of species should be influenced by the combined effects of immigration and extinction. Species populations may persist on small islands if they are close enough to the mainland to experience frequent immigrations. Because immigration rates should decrease with isolation, the minimum area required to maintain insular populations of a focal species should increase with isolation. The predicted pattern (A) has been observed for a variety of organisms, including small mammals (B, after Lomolino 1986 and 1998), fishes (see Figure 18.26), and butterflies (see Figure 18.27).



Why: Principal Drivers of Amazon Deforestation

1. **Clearing for cattle pasture**

(in turn, driven by currency devaluation, road infrastructure, real estate interest rates, land tenure laws, export market)



Why: Principal Drivers of Amazon Deforestation

2. Subsistence crop farming (squatters rights)

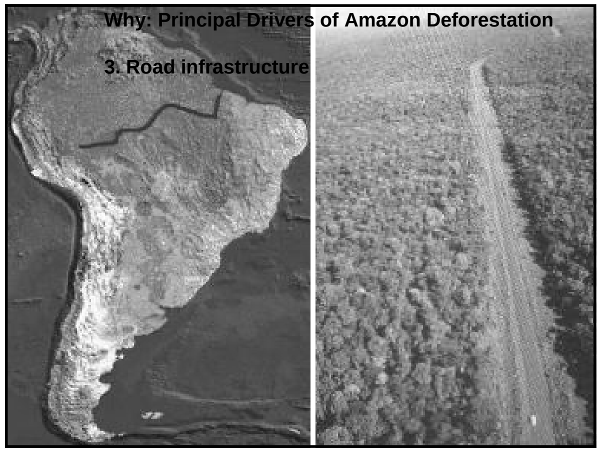
Vicious cycle:

- **Burn**
- **Plant (bananas, palms, manioc, corn, rice)**
- **Deplete soils**
- **Abandon**
- **Burn new land**

Small-scale Subsitance Farm Field - Amazonas

Why: Principal Drivers of Amazon Deforestation

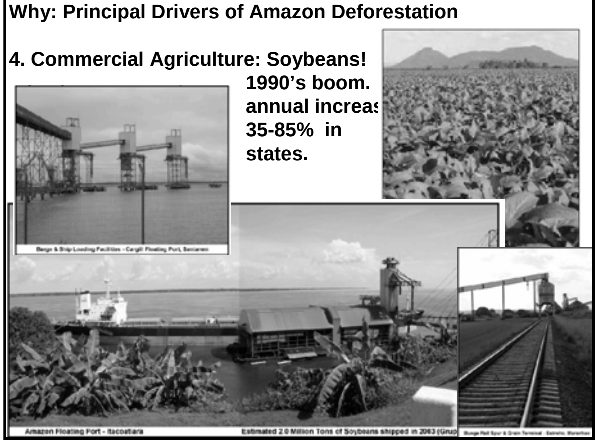
3. Road infrastructure



Why: Principal Drivers of Amazon Deforestation

4. Commercial Agriculture: Soybeans!

1990's boom. annual increas 35-85% in states.

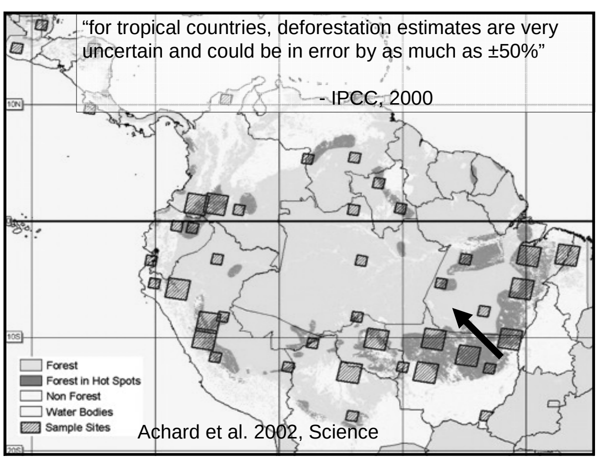


Why: Principal Drivers of Amazon Deforestation

5. Timber extraction.
- Strict licensing, lax enforcement.

"for tropical countries, deforestation estimates are very uncertain and could be in error by as much as ±50%"

- IPCC, 2000



Achard et al. 2002, Science

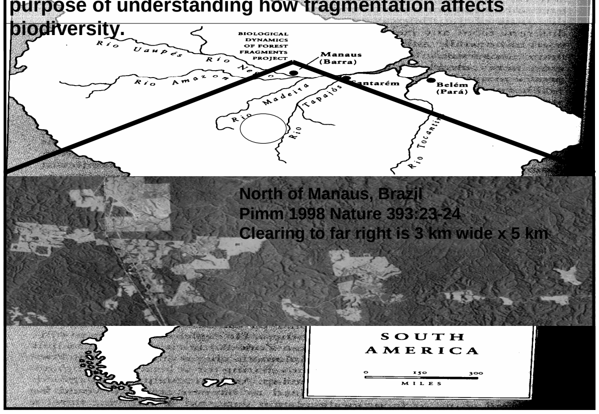
Even the low estimates of tropical deforestation are large.

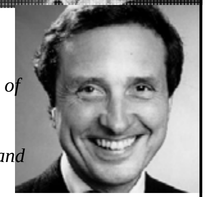
Table 3. Annual deforestation rates, as a percentage of the 1990 forest cover, for selected areas of rapid forest cover change (hot spots) within each continent.

Hot-spot areas by continent	Annual deforestation rate of sample sites within hot-spot area (range)
Latin America	0.38%
Central America	0.8-1.5%
Brazilian Amazonian belt	
Acre	4.4%
Rondônia	**3.2%**
Mato Grosso	1.4-2.7%
Pará	0.9-2.4%
Colombia-Ecuador border	~1.5%
Peruvian Andes	0.5-1.0%
Africa	0.43%
Madagascar	1.4-4.7%
Côte d'Ivoire	1.1-2.9%
Southeast Asia	0.91%
Southeastern Bangladesh	2.0%
Central Myanmar	~3.0%
Central Sumatra	3.2-5.9%
Southern Vietnam	1.2-3.2%
Southeastern Kalimantan	1.0-2.7%

Achard et al. 2002 Science

Ecologists have been carving up forests too. But for the purpose of understanding how fragmentation affects biodiversity.





-Idea conceived 1976 by Thomas Lovejoy as direct result of Equilibrium Theory debate.

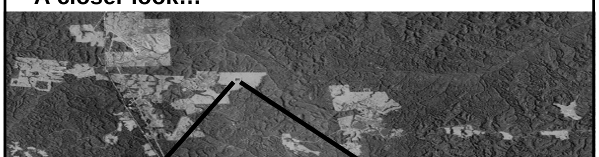
-Mission: "*Determine ecological consequences of habitat destruction and fragmentation in the Amazon, and to disseminate this information widely in such a way as to foster conservation and rational use of forest resources*"

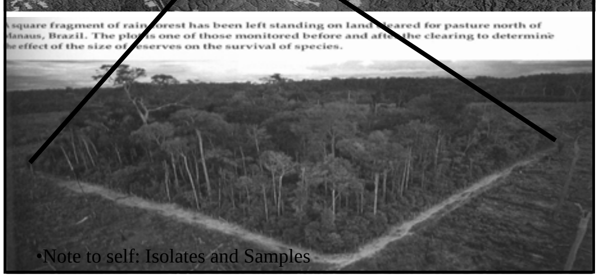
-Collaboration between Brazilian Institute for Research in the Amazon (INPA) and Smithsonian

-opportunistic use of the Manaus Free Zone "50% provision"

-pre-sampling 1979, isolates created starting 1980.

A closer look…





•Note to self: Isolates and Samples

Study Layout: Variation across scale important for evaluating equilibrium theory (why?)

Fragment size (ha)	1	10	100	1000	Mainland
Edge (km)	0.1	0.3	1.0	3.1	-
No. fragments	8	9	5	2	1
Currently under study	8	8	5	2	1
Currently isolated	5	4	2	0	0

Appears very neat, clean, cartesian, but…

Masks a great deal of habitat heterogeneity, even within "lowland terra firma rainforest":

Reserve 2303 (100 ha): "Bisected terrain. High hill to NW, draining with valleys to SE. Swamp area long S edge. Soil with more sand than other reserves, as well as thicker/shorter canopy. Extensive area NW has poor drainage, lots of edges w/ young trees, few large trees, no palms…"

"Mainland" Control: "Several forest physionomic types, several streams, 2 lakes…", peculiar soil types.

Observations from this project:

•Smaller 'islands' lost far more species.

•Due to both range size requirements and edge effects (dry winds drying out interior)

•Lots of 'secondary effects' – "trophic cascades"

- e.g. Peccaries leave, no wallow pools, three species of frog couldn't breed anymore and went extinct, beetles that feed on frog waste disappeared, etc. etc.

It would be nice if these effects could be predicted in advance…

It could help us decide how big we need to make reserves.

Lessons from this project:

•Some consistency with equilibrium theory, but many more 'autecological' results and edge effects.
•Sloss debate not settled in probably the cleanest experiment that could address it.
•Some studies flat out say equilibrium theory irrelevent (Barbara Zimmermann frogs):

"The inescapable conclusion [is that MacArthur/Wilson] has taught us little that can be of real value planning real reserves in real places"

Nevertheless, this project has yielded a great deal of information on the many impacts of habitat fragmentation over 25 yrs, and would never have been conducted if it weren't for the equilibrium theory.