Lecture 6

Endemicity and Insular Evolution

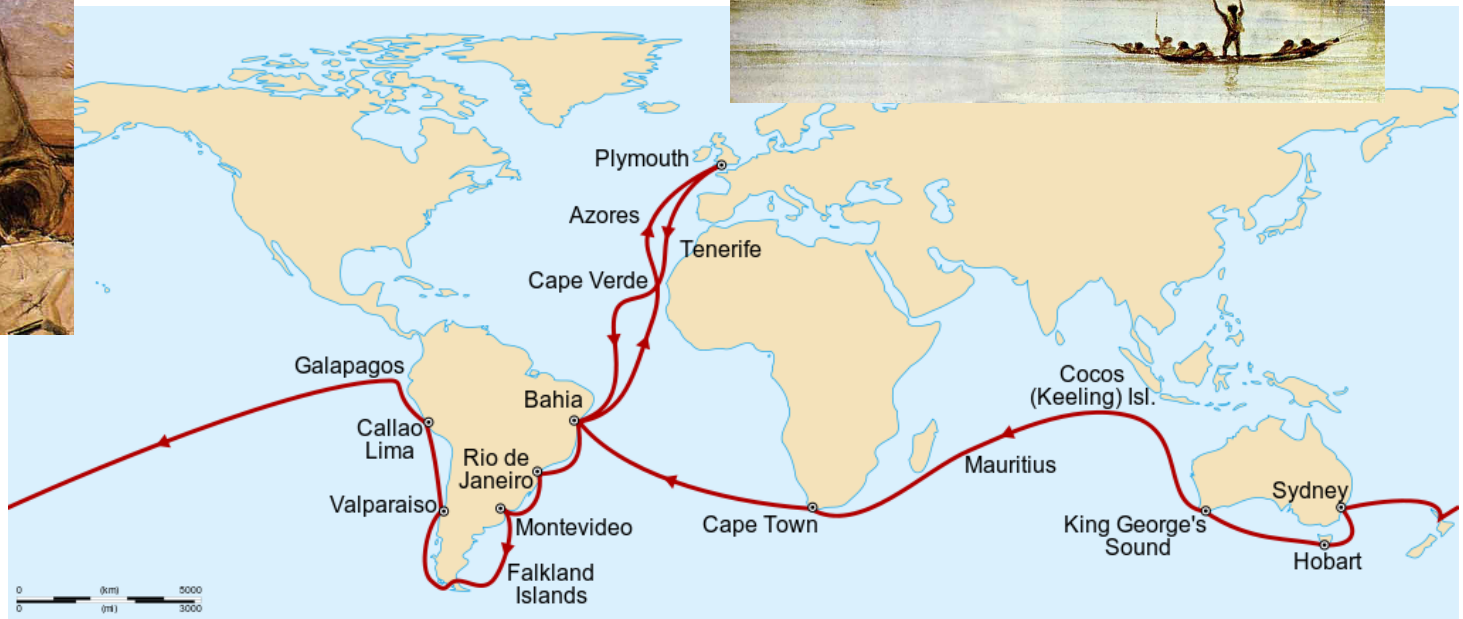
Dr. Ido Filin
ifilin@univ.haifa.ac.il

29 November 2012

Outline

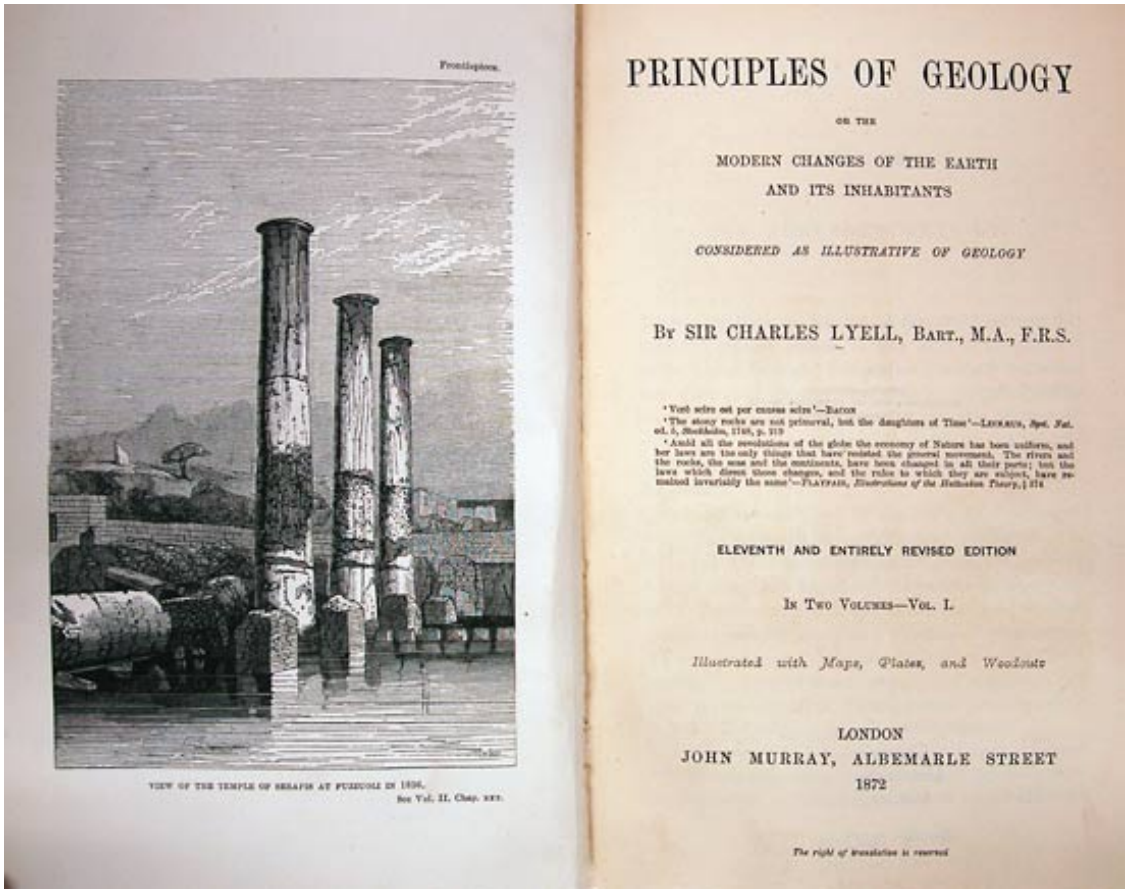
A tale of one man and some 45 islands

Dec 1831 – Charles Darwin, aged 23, embarks on a five-year circumnavigation of the globe aboard the HMS *Beagle*.



A tale of one man and some 45 islands

Darwin read Charles Lyell's *Principles of Geology*
→ Uniformitarianism – the idea that the earth was shaped by slow-moving forces still in operation today.



VIEW OF THE TEMPLE OF SERAPIS AT PUZZUOLI IN 1836.
See Vol. II. Chap. XIV.

PRINCIPLES OF GEOLOGY

OR THE

MODERN CHANGES OF THE EARTH
AND ITS INHABITANTS

CONSIDERED AS ILLUSTRATIVE OF GEOLOGY

BY SIR CHARLES LYELL, BART., M.A., F.R.S.

'Vetè scire est per causas scire'—BACON

'The stony rocks are not primeval, but the daughters of Time'—LUCRETIUS, *Rer. Nat.* ed. 5, Stockholm, 1765, p. 319

'Amid all the revolutions of the globe the economy of Nature has been uniform, and her laws are the only things that have resisted the general movement. The rivers and the rocks, the seas and the continents, have been changed in all their parts; but the laws which direct those changes, and the rules to which they are subject, have remained invariably the same'—PLAYFAIR, *Illustrations of the Huttonian Theory*, § 374

ELEVENTH AND ENTIRELY REVISED EDITION

IN TWO VOLUMES—VOL. I.

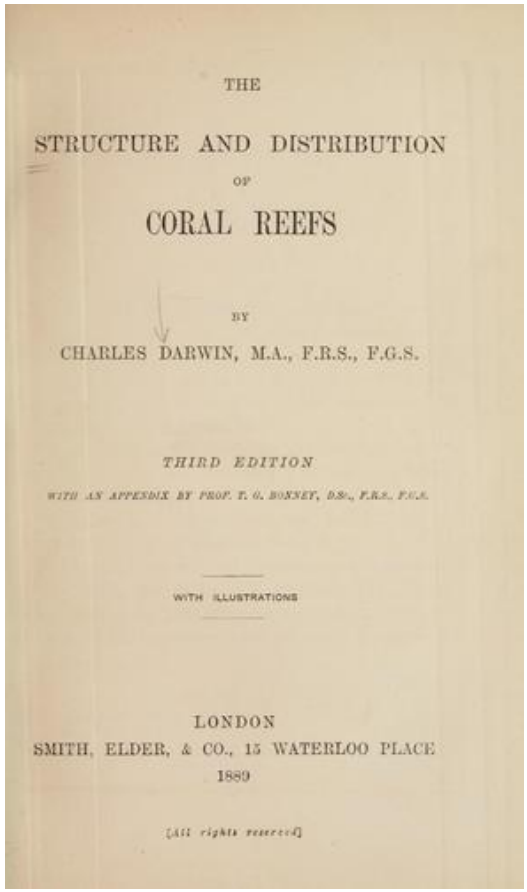
Illustrated with Maps, Plates, and Woodcuts

LONDON
JOHN MURRAY, ALBEMARLE STREET
1872

The right of translation is reserved

A tale of one man and some 45 islands

In that context, Darwin develops a theory on atoll formation, which he later publishes back in England → fringing reef, barrier reef and atoll are all stages of the same process of reef formation.



THE

STRUCTURE AND DISTRIBUTION

OF

CORAL REEFS

BY

CHARLES DARWIN, M.A., F.R.S., F.G.S.

THIRD EDITION

WITH AN APPENDIX BY PROF. P. G. MONNEY, D.Sc., F.R.S., F.G.S.

WITH ILLUSTRATIONS

LONDON

SMITH, ELDER, & CO., 15 WATERLOO PLACE

1889

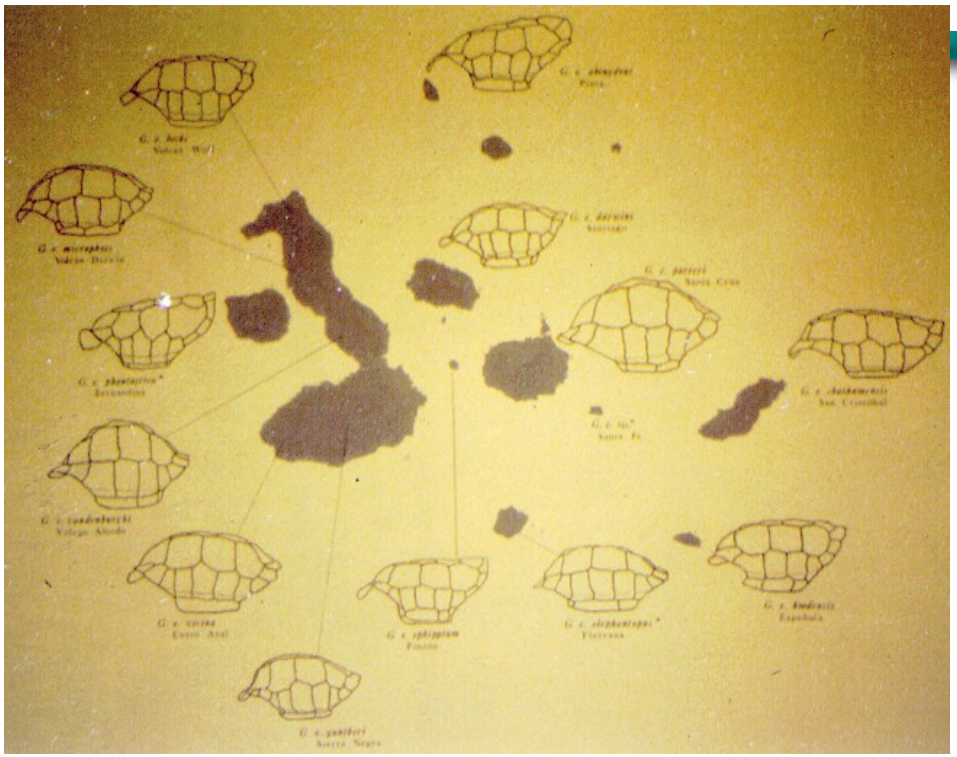
[*All rights reserved*]

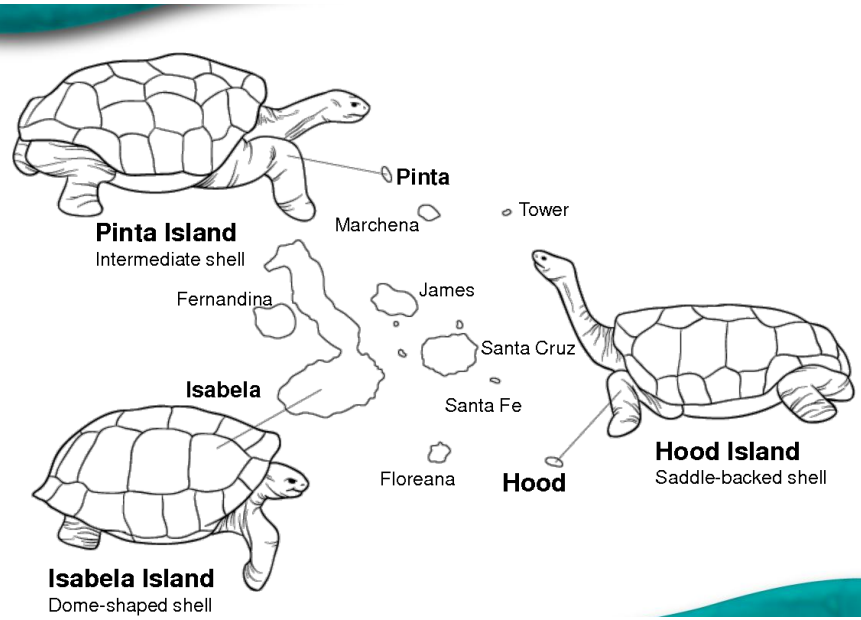
A tale of one man and some 45 islands

Sep-Oct 1835 – HMS *Beagle* visits the Galápagos islands. Darwin encounters a chain of islands, each with a very different topography and environment.

A tale of one man and some 45 islands

He encounters many strange creatures there, like the giant tortoises. Each a bit different on every island.





He begins to doubt the immutability of species.
Like the earth slowly changes over long periods of time, organisms may slowly change as their environment changes.

The tree of life – Taxonomy in a nutshell

Organisms are classified and named in a **hierarchical** fashion – representing both phenotypic similarity and common descent (common evolutionary history) within groups – **taxon / taxa**.

ממלכה **Kingdom:** **Animalia** Plantae Fungi . . .

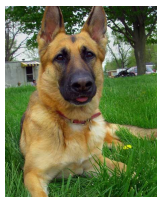
מערכה **Phylum:** **Chordata** Arthropoda Mollusca  . . .

מחלקה **Class:** **Mammalia** Aves Reptilia . . .

סדרה **Order:** **Carnivora**

משפחה **Family:** **Canidae** Felidae  Ursidae  . . .

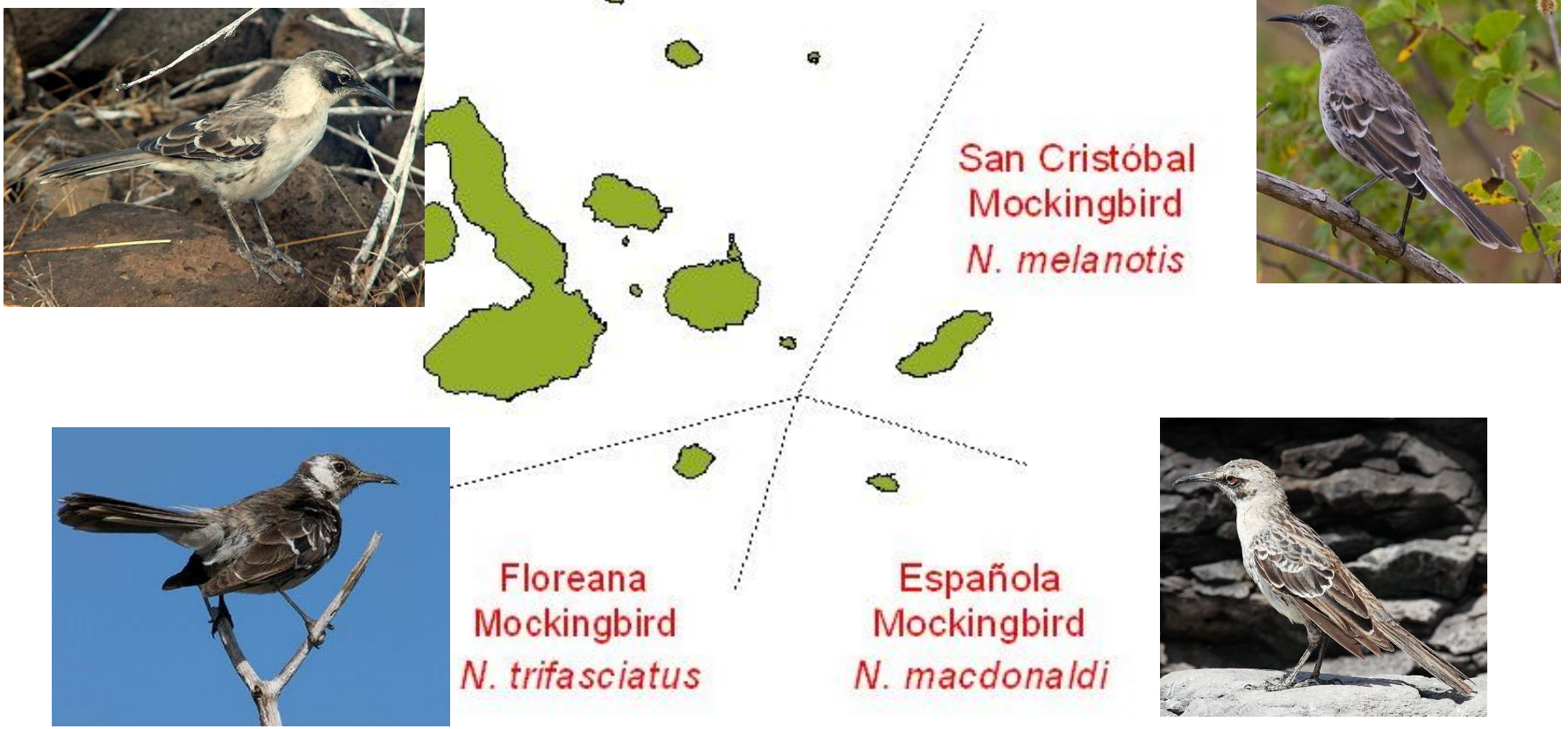
סוג **Genus:** ***Canis*** *Vulpes*  . . . 

מין **Species:**  ***Canis lupus*** *Canis mesomelas* . . .

Subspecies, Breed, Variant, Population, Growth form . . . 

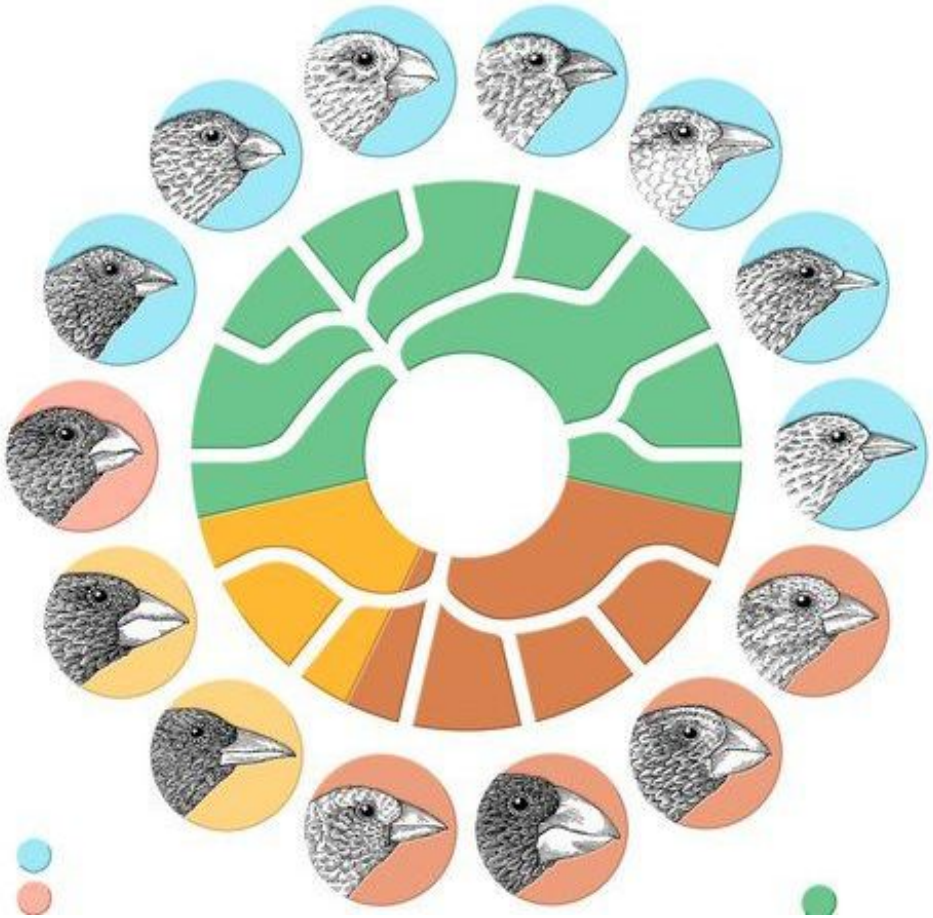
A tale of one man and some 45 islands

Another example of variability and change is displayed by the four species of Galapagos mockingbirds – each found in a different part of the archipelago.



A tale of one man and some 45 islands

Extreme variability and change is displayed by the Galapagos finches (later known as Darwin finches). A wide array of forms/species – not all present on every island.



Conditions promoting differentiation and speciation

- Isolation –
  - Between mainland and islands.
  - Among individual islands in an archipelago.

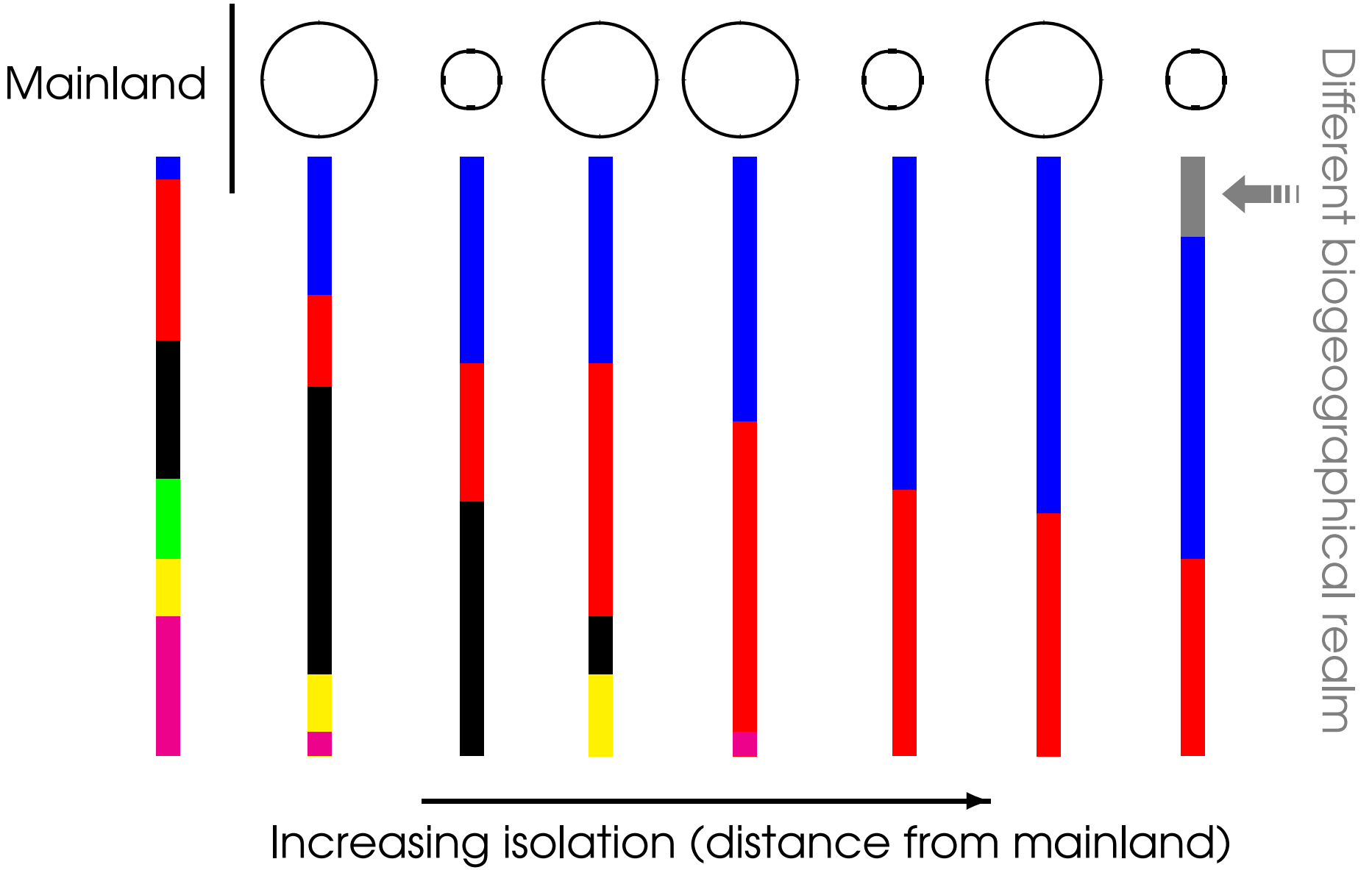
  Genetic and phenotypic differences may accumulate over time among unconnected populations – resulting in differentiation.

- Different environments – different subpopulations of a species may be exposed to different environments and eventually become differentiated phenotypically and genetically
  (if also some sort of isolating mechanism operates).

- **Speciation** (התמיינות) – the process by which new species are created from an ancestor species.
  In effect, differentiation at the extreme.

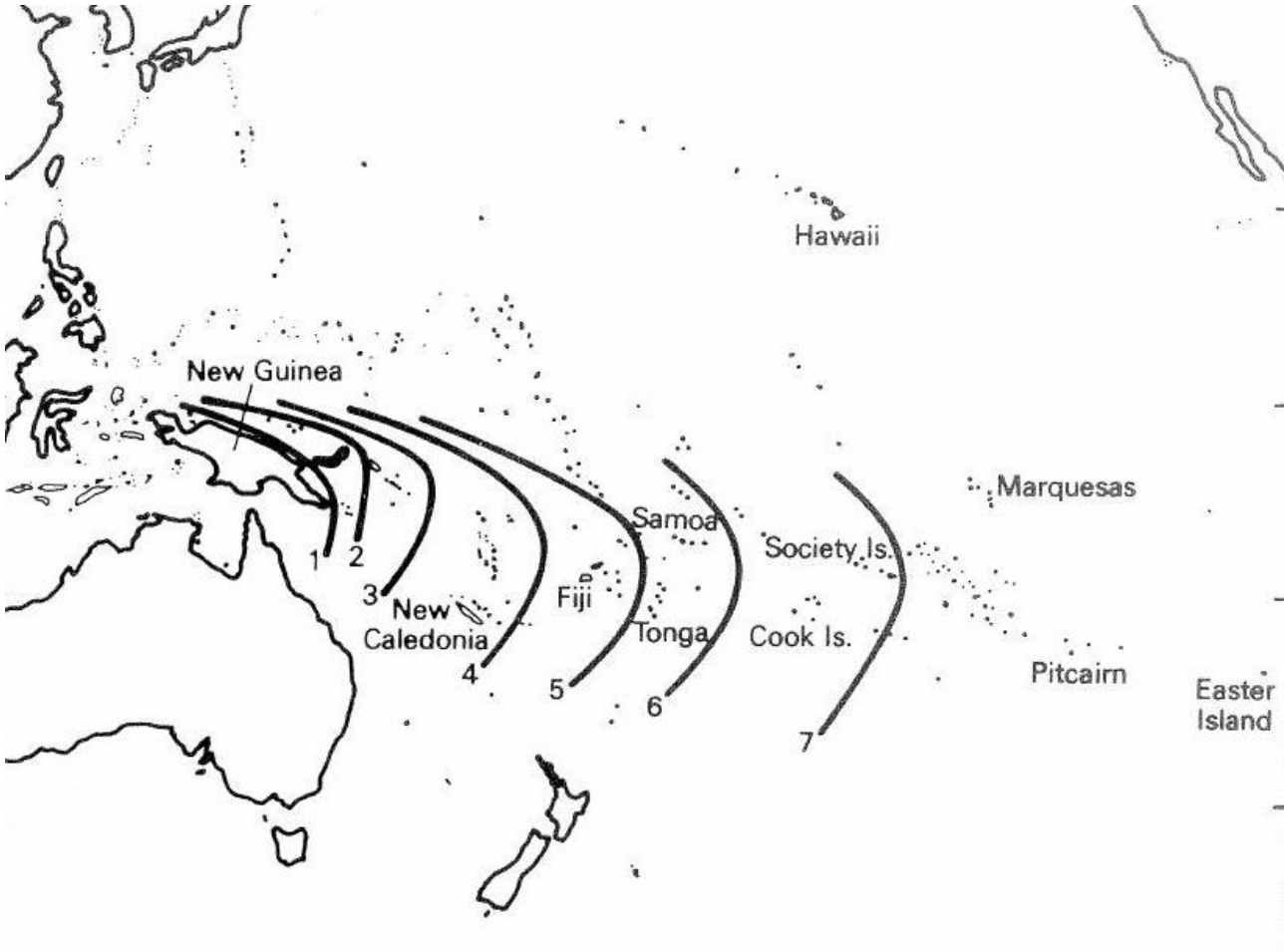
Outline

Species poverty and disharmony summarized



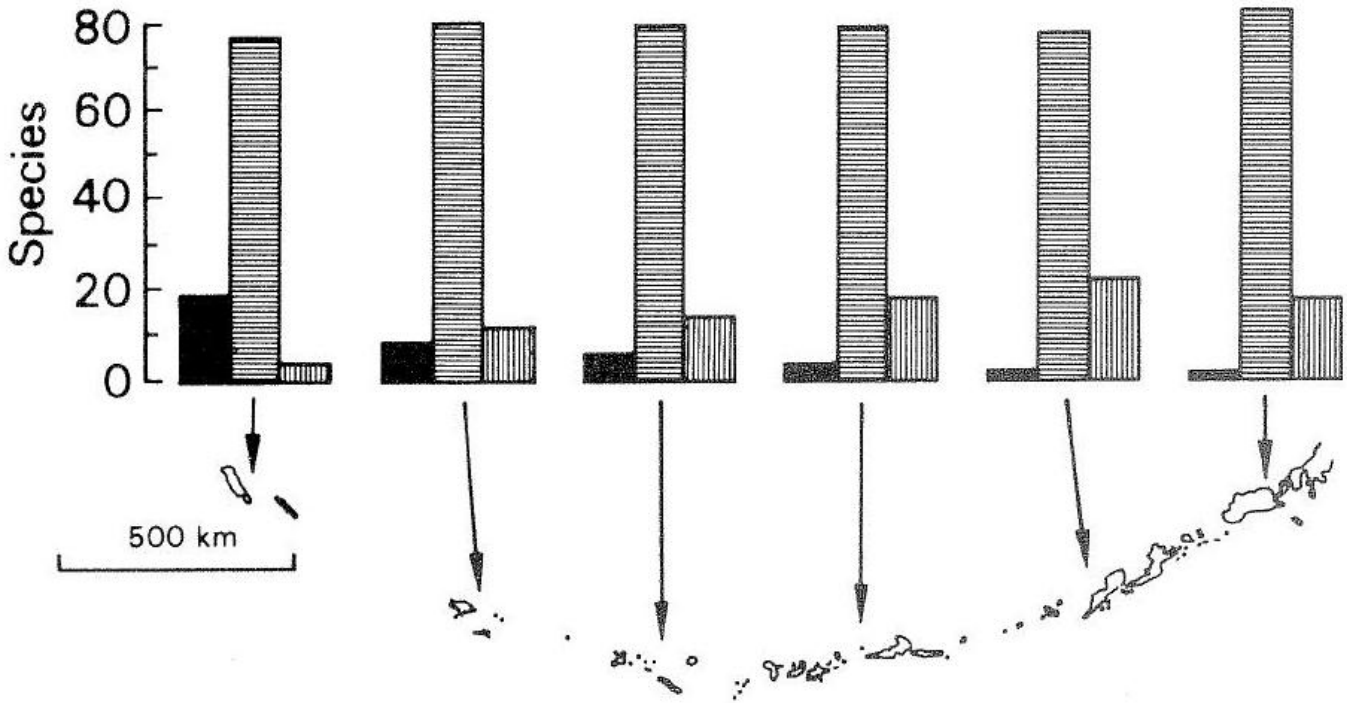
Distribution limits of New Guinea bird (sub)families on east pacific islands

1, -14 taxa → **2**, -2 taxa → **3**, -10 taxa → **4**, -7 → **5**, -4 → **6**, -7 → **7**, -3 → . . .



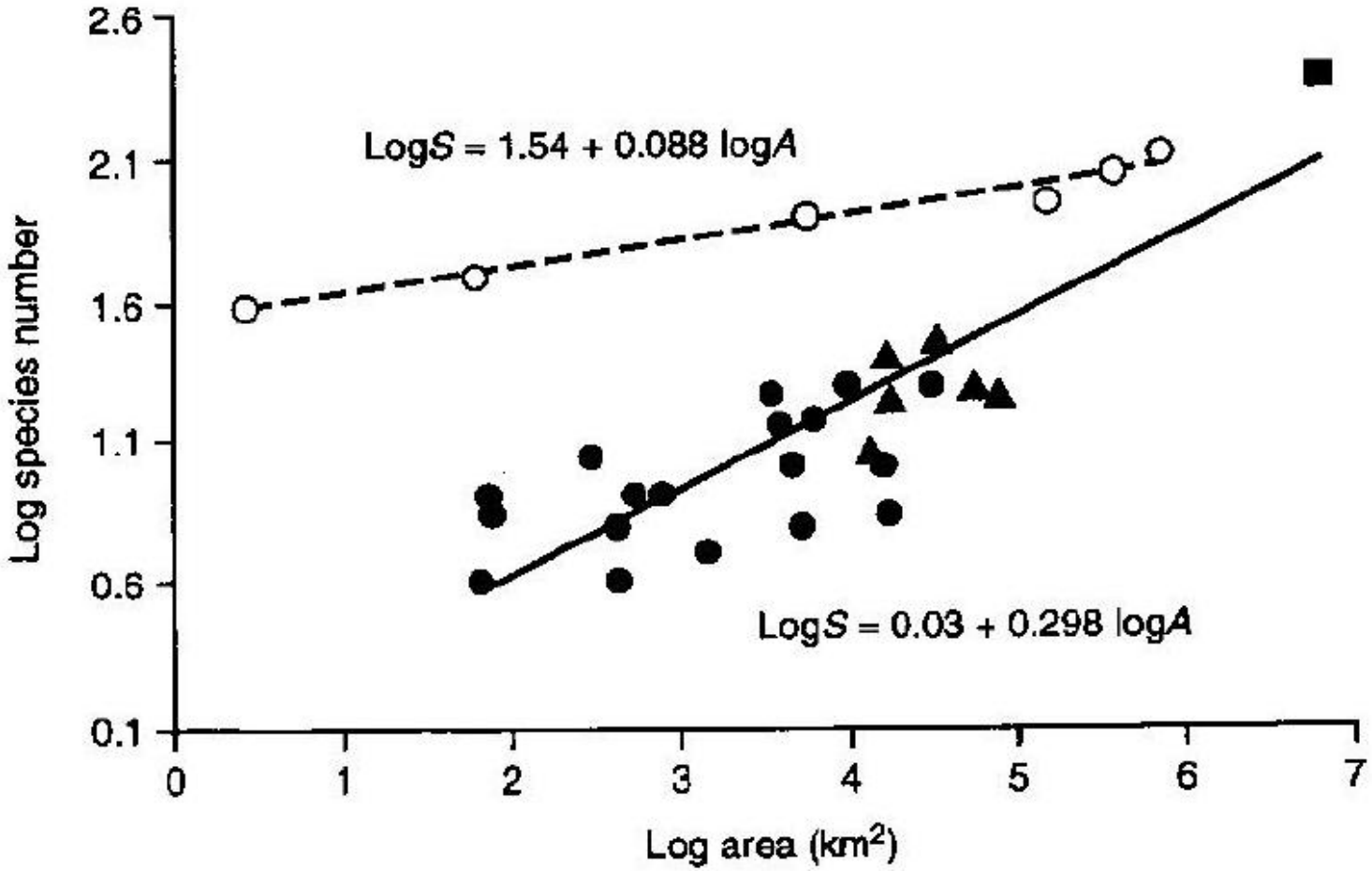
Disharmony due to mixing of biogeographic realms

Double filter effect in plant species of the Aleutian archipelago – Palearctic-dominated to the east; Nearctic-dominated to the west.



Island area and species richness species-area curves

Ant species in New Guinea and Melanesia.
Mainland-island comaprison.



Outline

Global biodiversity numbers

Islands comprise less than 3% of land area worldwide (much less if you consider only oceanic islands).

They however contribute disproportionately to global biodiversity (species richness):

Group	Global	On islands	Percent on islands
Higher plants	263,000	36,500	13%
Landsnails	35,000	-	8-9%
Birds	-	1750	17%
Anolis lizards	300	-	50%
Flying fox bats	161-174	55	31-34%

- How can we reconcile that with the clear observations of species poverty on islands?
  1. There are many islands (much more than continents).
  2. High proportion of **Endemicity** on islands.

Endemicity statistics

Levels of endemicity on (oceanic) islands are extremely high!

For example, for higher plants:

Island(s)	Species number	Endemics	% Endemic
Hawaii(flowering plants)	934	850	91%
New Guinea	15000-20000	10500-16000	70-80%
Cuba	6514	3229	50%
New Caledonia	3094	2480	80%
New Zealand	2371	1942	82%
Mauritius/Reunion	878	329	37.5%
St. Helena	74	59	80%

Endemicity statistics

Land snails:

Island(s)	Species number	Endemics	% Endemic
Hawaii	*c.*1000	*c.*1000	99.9%
Japan	492	487	99%
New Caledonia	300	*c.*299	99%
Madeira	237	171	88%
Canary islands	181	141	78%
Rapa	>105	>105	*c.*100%

Endemicity statistics

- **Hawaiian insects:**
  - Fruit flies (Drosophilids): 500-1000 endemic species.
  - Tree crickets: 3 genera, 68 species.
  - Endemic plant bug genus *Sarona*: 40 species.

- **Degrees of regional/local endemicity in selected Pacific and Indian ocean faunas:**

Group	Number	% Continental	% Regional	% Local
Pacific Ocean butterflies	285	55%	10%	35%
Pacific Ocean lizards	100	21%	13%	66%
Pacific Ocean birds	592	25%	10%	65%
Indian Ocean birds	139	43%	7%	50%

Continental = also occurring on continents.

Regional = species occurring on more than one island/archipelago.

Local = endemic to a single island/archipelago.

Island biology in a (coco)nutshell

Island Physics

- Isolation
- Small area
- Young age
-

Island Biodiversity

- Species poor
- Disharmony
- High Endemicity
-

Insular Evolution

- "Untypical" creatures
- Adaptive radiation
-

Outline

Establishment on islands

- Not enough to arrive on island (via long-distance dispersal).
- Need to succeed in growing, reproducing and establishing a stable resident population.
- Establishment success is another filter operating after dispersal success.
- **Examples:**
  - Abiotic and biotic conditions for growth and reproduction.
  - For obligate sexual organisms – several migrants arriving (more or less) together so one can find mates (unless pregnant female arrives alone).
  - Predators – require presence of prey.

The niche concept

- Ecological **community** – assemblage of (interacting) populations of different species occupying the same place and time.
  Example: Aquatic community of Lake Kinneret.

- Ecological **niche** – A role in the community, specifying the types of conditions and opportunities for organisms to obtain resources and avoid predators, so to survive and growth.
  Example: Zooplankton, Planktivorous fish, Piscivorous fish.

- In the island context, **empty niche** means ecological/evolutionary opportunity for immigrants to islands – opportunity that is occupied by other forms in the mainland.

The niche concept

- In the island context, **empty niche** means ecological/evolutionary opportunity for immigrants to islands – opportunity that is occupied by other forms in the mainland.
- For example:
  1. herbaceous immigrant developing/evolving into a tree-like growth form.
  2. Another example: availability of nectar from flowers in Hawaii, not consumed by hummingbirds or sunbirds that never reached Hawaii.

The niche concept

- In the island context, **empty niche** means ecological/evolutionary opportunity for immigrants to islands – opportunity that is occupied by other forms in the mainland.
- For example:
  1. herbaceous immigrant developing/evolving into a tree-like growth form.
  2. Another example: availability of nectar from flowers in Hawaii, not consumed by hummingbirds or sunbirds that never reached Hawaii.
- Empty niches on islands are a direct consequence of:

The niche concept

- In the island context, **empty niche** means ecological/evolutionary opportunity for immigrants to islands – opportunity that is occupied by other forms in the mainland.
- For example:
  1. herbaceous immigrant developing/evolving into a tree-like growth form.
  2. Another example: availability of nectar from flowers in Hawaii, not consumed by hummingbirds or sunbirds that never reached Hawaii.
- Empty niches on islands are a direct consequence of:
  1. Species poverty and disharmony.
  2. On high islands, a variety of unoccupied habitats.

The niche concept

- In the island context, **empty niche** means ecological/evolutionary opportunity for immigrants to islands – opportunity that is occupied by other forms in the mainland.
- For example:
  1. herbaceous immigrant developing/evolving into a tree-like growth form.
  2. Another example: availability of nectar from flowers in Hawaii, not consumed by hummingbirds or sunbirds that never reached Hawaii.
- Empty niches on islands are a direct consequence of:
  1. Species poverty and disharmony.
  2. On high islands, a variety of unoccupied habitats.
- Immigrants experience different environments (biotic and abiotic) than on their homeland: latitude, elevation, temperatures, rainfall, competitors, predators etc.

Establishment on islands

- The niche of a species helps to determine in which habitats it would establish itself, upon arrival on the island.
- For example:
  - A sea-dispersed plant (strand-line plant) that can tolerate saline environments may establish itself on coastal/littoral habitats.
  - A fern may establish more inland – wetter and less saline lowland habitats.

- Over time, may establish in other habitats.
- For example:
  - The strand-line plant may expand inward into lowland habitats.
  - The fern may expand upwards into higher altitudes (highland habitats) – contributing to formation of cloud forest and maybe even changing into tree growth form.

Outline

Niche shifts on islands

- Species poverty and disharmony means that there are far less species on islands than on continents, to compete against for food, nesting sites, habitats etc.
- On an island a species may use sites/habitats/resources that it would not ordinarily use on the continent.
- $\Rightarrow$ Reduced competition leads to **ecological release**.
- $\Rightarrow$ The **niche breadth** of the species is wider.
- For example, a seed-eating finch, in the absence of other bird species, may also begin to occasionally consume insects and nectar.
- Even more so if occasionally (or seasonally) there is a shortage of seeds.

Niche shifts on islands

- Island species typically exhibit higher degrees of variability within species (intraspceific variability) and plasticity – ecological, morphological, behavioral etc.
- **Plasticity** – the ability of the same genotype (an individual or a group of genetically identical individuals) to display different phenotypes – morphologies, behaviors, etc. – in different environments or circumstances.
- In the opposite direction, it may be that more plastic species are more successful in establishing on islands.
- **Examples:**

1. Fijian fruit bats being more diurnal (compared to less isolated islands), in the absence of predatory eagles on Fiji.

Niche shifts on islands

2. Ohi'a lehua – *Metrosideros polymorpha*.
   Tremendous variety of growth forms: from low shrubs on lava flows to tall trees in moist cloud forests.

Niche shifts on islands

3. Cocos island finch – shows **within species** a stunning array of feeding behaviors – comparable to variation **among species** in Galapagos finches, and **among bird families(!)** on continents.

   However, this is a single species!

Adaptive radiation: the crowning glory of island evolution

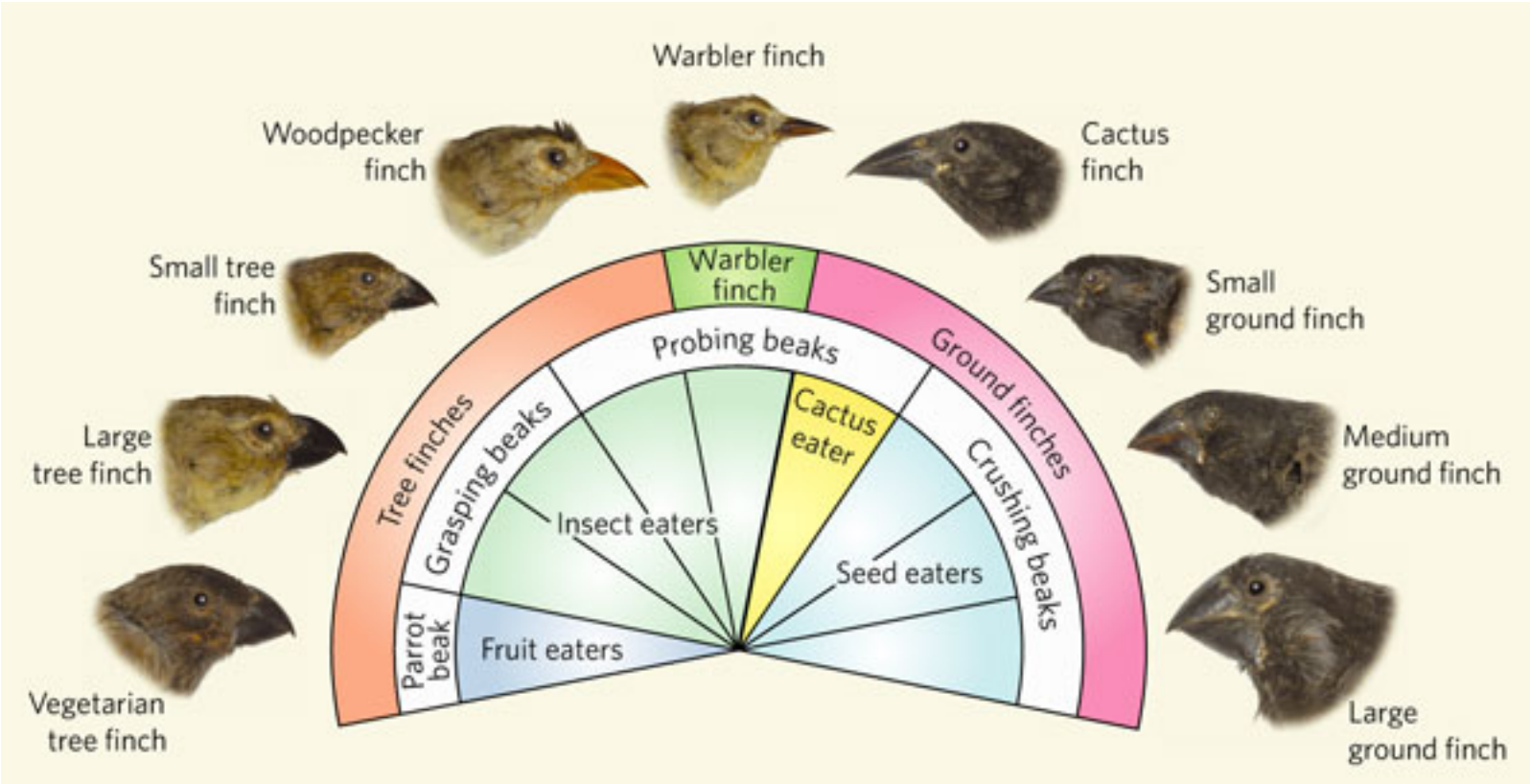
- When ecological release and occupation of empty niches combines with the presence of isolating mechanism, speciation may occur.

- In the extreme case, this leads to **adaptive radiation** – a single ancestral immigrant species diversifies into a large number of daughter species.

- Perhaps the most famous example of adaptive radiation is the **Galapagos (Darwin) finches**.
- A single immigrant species of seed-eating finch evolved into 13 insectivorous, granivorous and frugivorous species.
- Remarkably, sharp-billed ground finches even eat ticks off tortoises and iguanas, and drink blood by inflicting wounds on boobies.

Adaptive radiation: the crowning glory of island evolution

Accompanying the diversification in feeding behavior, was a diversification in beak morphology and overall body size (unlike in the cocos island finch).



Adaptive radiation: the crowning glory of island evolution

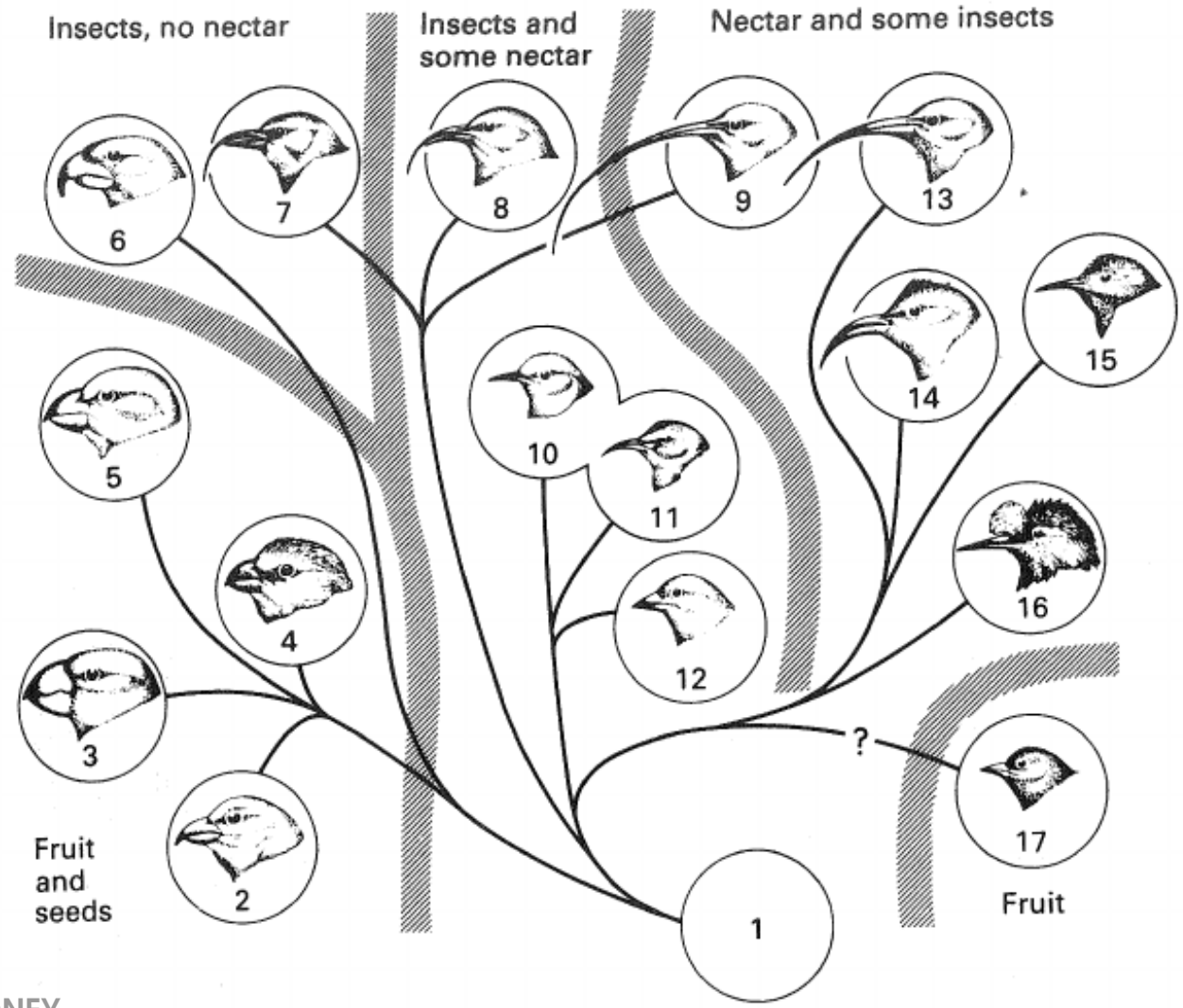
Darwin finches:

- High variability and plasticity also within species – in morphology, body size and behavior (for example, among populations of the same species occupying different islands).
- When comparing species of different body sizes, the largest of the smaller species is almost as large as the smallest of the larger species.
- Morphological variability among species of Galapagos finches is comparable to that among different bird families on continents.
- Genetic differentiation is very low – comparable to that found within a single population of finches on the American continent.
- This suggests that the diversification was very fast and relatively recent.
- Phenotypic differentiation not always correlates with genetic differentiation and vice versa.

Adaptive Radiation: Hawaiian honeycreepers

Adaptive Radiation: Hawaiian honeycreepers

Diversification associated with a wide array of feeding niches.



Adaptive Radiation: Hawaiian honeycreepers

- Even greater radiation than on Galapagos – one immigrant seed eating species of finch from Asia evolved into over 30 species.
- In the absence of hummingbirds and sunbirds, and in the presence of flowers year round (Ohia lehua and other plants) many nectarivorous species evolved.
- In the absence of woodpeckers and similar bird species, a honeycreeper that bores into wood in search of insect larvae also evolved.
- Additional species specialize in feeding on seeds, insects or fruits.
- Even more spectacular morphological diversification than on Galapagos.

Adaptive Radiation: *Echium* on Canary Islands