Lecture 8

Adaptive Radiation and Additional Evolutionary Trends on Islands

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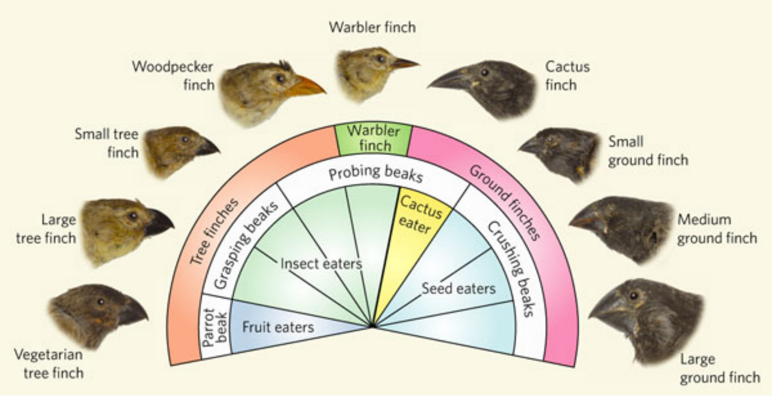
13 December 2012

Outline

1. More on adaptive radiations
2. Additional trends on islands
3. Summary of insular evolution

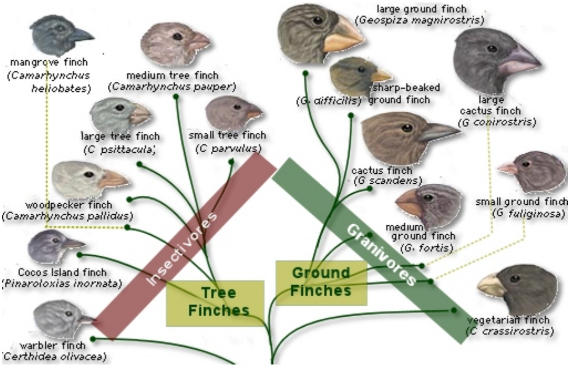
Adaptive radiation: the crowning glory of island evolution

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



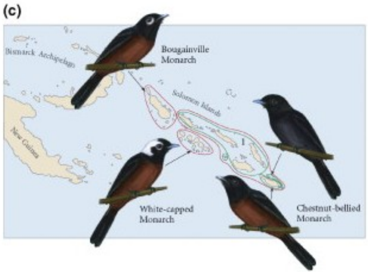
Why "adaptive" in adaptive radiation?

- In adaptive radiation the phenotypic (especially morphological) differentiation and diversification among the groups (species) is associated with niche shifts.
- Involves **adaptation** of the phenotype (morphology) to the new niche.
- For example, in Darwin finches beak morphology evolved and adapted to the changes in feeding niche.



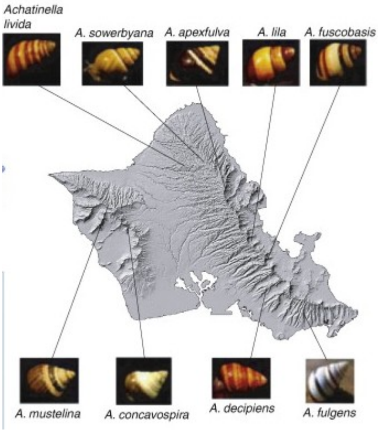
Why “adaptive” in adaptive radiation?

- But morphological differentiation and speciation may occur also without changes in the niches that each group (species) occupies.
- Simply because of isolation and accumulation of genetic and phenotypic differences.
- ⇒ **Non**adaptive radiation.
- Example: Flycatchers in Solomon islands.



Why “adaptive” in adaptive radiation?

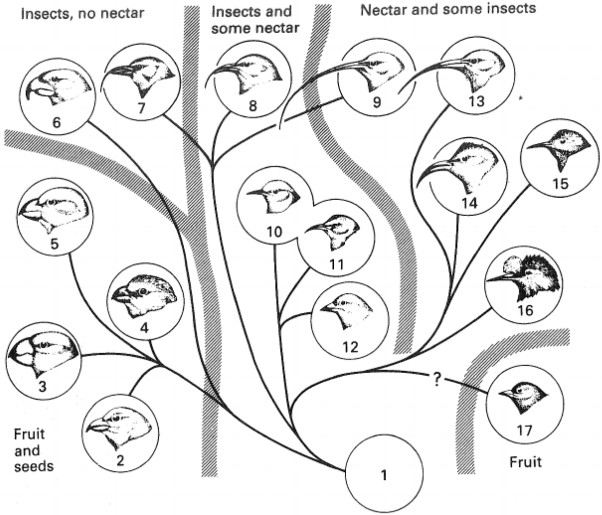
Another example of **nonadaptive** radiation: *Achatinella* – Hawaiian tree snails.



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

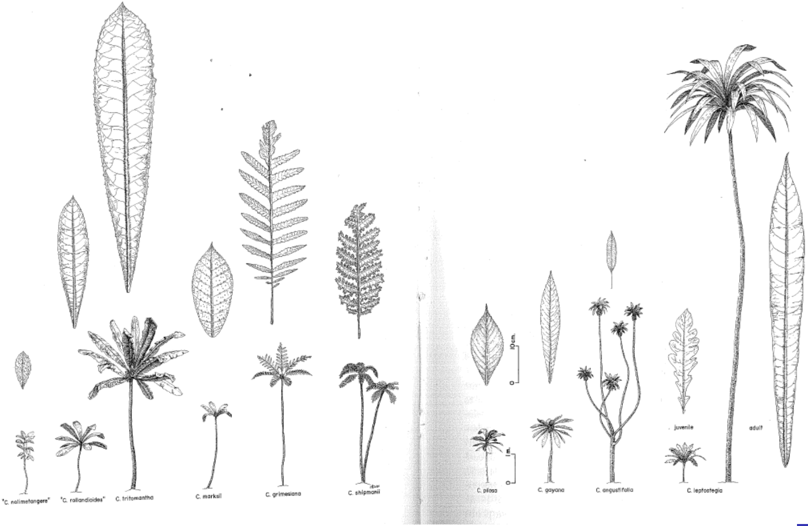
Sonchus on Canary Islands and Madeira

Europe:

Canary islands and Madeira:

Cyanea on Hawaii

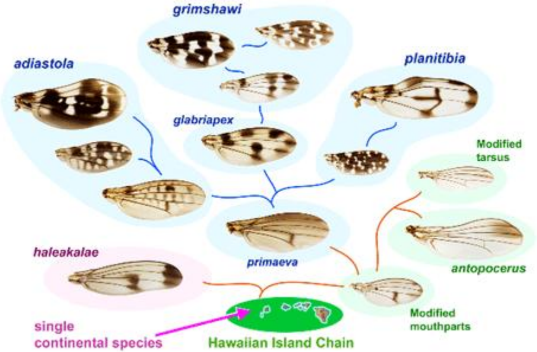
Cyanea is one genus of Hawaiian Lobelioids – Lobelioids radiated tremendously on Hawaii – 125 species in 6 genera (!).



Adaptive radiation in plants

- Diversification of growth form (herb, shrub, rosette tree, branched tree, etc.), in life history (annual vs. perennial), in leaf morphology, etc.
- Differentiation of growth forms and species according to different habitats.
- For example:
  - Forest vs. open habitats.
  - Coastal and lowland vs. upland, montane/sub-alpine, and cliffs habitats.
  - Dry or arid habitats vs. moist and wet.
- Radiation is often in families that are represented on mainland by weedy, annual, highly dispersive forms. For example, Asteraceae.

Hawaiian Droshophilids

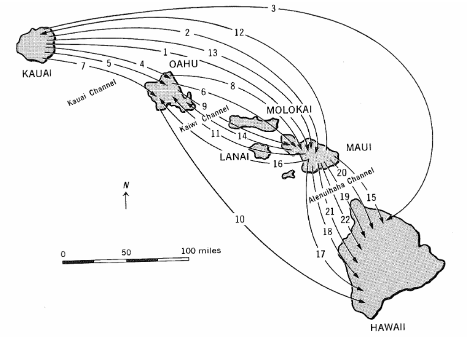


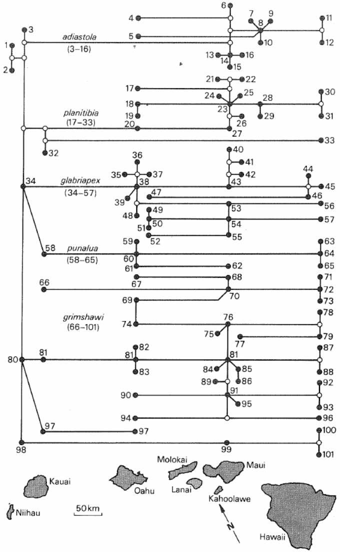
Hawaiian Droshophilids

- Probably, as high as 1000 species.
- Highly diversified in morphology, anatomy, mating behavior, feeding behavior, and habitats they occupy: rotting leaves, rotting bark, in mushrooms, in flowers, in slime fluxes, etc.
- Different from Drosophilids on continents, especially with regard to diet, habitats occupied, morphology and mating behavior.
- Most species occur only on a single island within the archipelago.
- Much of the speciation also occurred because of isolation between different populations on the same island – for example, in valleys separated by steep ridges, and forests divided by fresh lava flows.

Hawaiian Droshophilids

The geographic pattern of Drosophilids radiation on Hawaii:





Evolution on archipelagos and adaptive radiation

- Species poverty and disharmony ⇒ empty niches.
- Isolation from mainland, among islands within the archipelago, and also within parts of a single island.
- Availability of empty niches and isolation together promote differentiation and speciation leading to adaptive radiation.
- Occasional inter-island dispersal further promotes differentiation and speciation.
- For example, may bring together two subspecies that evolved allopatrically on different islands and differentiated in their niche (e.g., feed on different resources)
  ⇒ Competition leads to stronger niche specialization (the opposite of ecological release) and to further prezygotic isolation and differentiation among the now sympatric groups ⇒ Ultimately, leading to speciation.

Other examples of adaptive radiation

- Hawaiian tree crickets and spiders.
- Many plant groups on every oceanic archipelago.
- Wetas in New Zealand.
- *Anolis* lizards in the Caribbean (Greater and Lesser Antilles).

Outline

Niche shifts without radiation

- Adaptive radiations contribute much to insular endemicity – By definition they create a large number of endemic species.
- They are spectacular but extreme cases of insular evolution.
- Most immigrant species to islands do NOT show radiation – evolving into a single or only few species.
- But they still show significant evolutionary change and differentiation from ancestor and mainland relatives.
- Much of these changes are also adaptive – associated with niche shifts.
- Some are also observed in adaptive radiations – changes in body size, insular woodiness, etc.

Niche shifts without radiation

An example is the Marine Iguana on Galapagos – became a marine herbivore from an original land herbivore; shares the islands with a sister species of land iguanas.
A single species in the entire archipelago.

Insular Woodiness ("עיצוי")

- Disharmony in plants, because major groups of trees almost never arrive to oceanic islands.
- → Their seeds are relatively large – good in providing resources to the young plant in low-light conditions of forests, but have poor dispersal ability.
- Nonetheless, islands (especially high islands) offer a spectrum of environments –some suitable for trees.
- ⇒ Changes in woodiness on islands will occur in the direction of herb → shrub/tree (not the opposite).
- From a herbaceous pioneering species – originally specializing in unstable, open and drier habitats (such as coastal habitats) – a more woody growth form may evolve – associated with niche shifts.
- E.g., on Canary islands and Hawaii – adaptive radiations create both herbaceous and more woody species.

Insular Woodiness ("עיצוי")

- In the absence of "real" trees, the herbaceous forms are free to move into new habitats – more wet and stable habitats – upland habitats on high islands, with high and regular rainfall, and weaker temperature fluctuations, as occur on islands.

- Herbaceous forms experience **ecological release** and subsequent niche shifts (in comparison to the situation on continents):
  1. Less competition from "real" trees.
  2. Less predation because large herbivores are absent or few.
  3. More stable habitats – in term of physical conditions.

- Allowing herbaceous annuals to change into more woody perennials – investing more in growth and postponing reproduction.

Insular Woodiness ("עיצוי")

We have seen examples from adaptive radiations on Canary islands and Hawaii. Other example is ***Scalesia*** in Galapagos island – basically a giant sunflower. The genus belongs to the family Asteraceae – a family of mostly herbaceous plants on continents, common on islands (e.g., *Sonchus* example from last week). There are whole forests of *Scalesia* on some islands of the Galapagos.


Insular Woodiness ("עיצוי")

Another example is the "Cabbage tree" *Dendroseris liitoralis* in Juan Fernandez islands – also related to sunflower, and belongs to the family Asteraceae.

Insular Woodiness ("עיצוי")

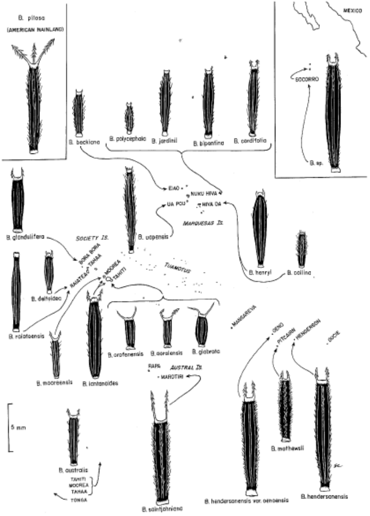
- Insular woodiness has occurred repeatedly and independently on many islands and in many originally herbaceous species.
- In a sense, repeating again and again the more ancient evolution of the tree groups on continents.
- Albeit on a much smaller scale –
  1. Spatially – on small isolated islands, rather than vast continents.
  2. Temporally – much more recent evolution – usually no more than few million years old.
  3. Evolutionarily – less differentiation and speciation from original herbaceous forms.
- ⇒ The natural laboratory paradigm.

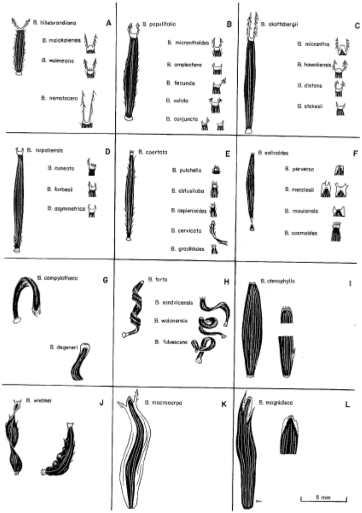
Loss of dispersal ability in plants

- **1.** Immigrants to islands tend to be good dispersers.
- ⇒ Changes in dispersal ability on islands will occur in the direction of good → poor dispersal ability (rather than opposite).
- Loss of dispersal ability in plants is associated with
  1. Evolution of larger seeds and fruits.
  2. Loss of special dispersal-related structures and traits of the seeds.
- **2.** Larger seeds are associated with more woody growth forms and growth in stable but low-light forest habitat (as in trees on continents).
- **3.** Precinctiveness ("מחוזיות") – dispersal to lower distances on the island prevents landing in sea or (for woody plants) away from stable habitats.

Loss of dispersal ability in plants

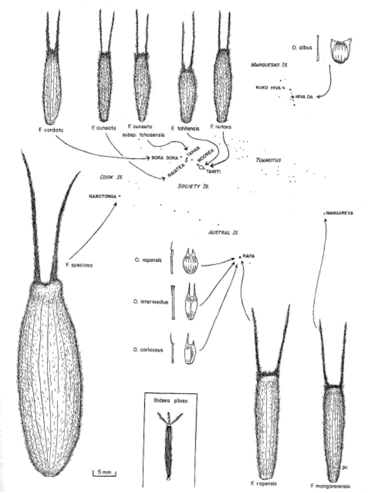
An example is the the genus ***Bidens*** on Pacific ocean islands – loss of barbs and dispersal structures.





Loss of dispersal ability in plants

Another example from pacific ocean: ***Fitchia*** – loss of dispersal structures and significant increase in seed size.



Loss of dispersal ability in plants

Examples from Hawaii – seed and fruit gigantism:

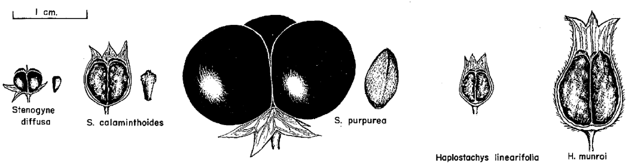


FIG. 11.11. Fruits of the Hawaiian genera *Stenogyne* and *Haplostachys* (Lamiaceae). Seeds with fleshy exocarp removed are shown to the right in each *Stenogyne* species. Fruits are shown with the facing portion of the enclosing calyx removed, except for *Stenogyne purpurea*.

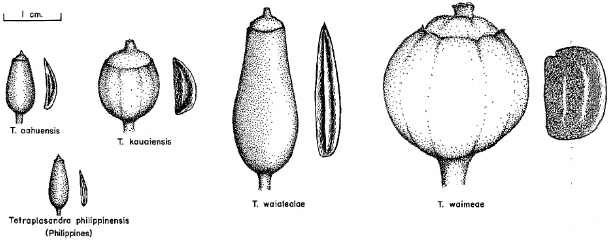


FIG. 11.1. Comparison of fruits and seeds of *Tetraplasandra* (Araliaceae). All species except *T. philippinensis* are endemic to the Hawaiian Is.

Loss of dispersal ability in plants

Another Hawaiian example:

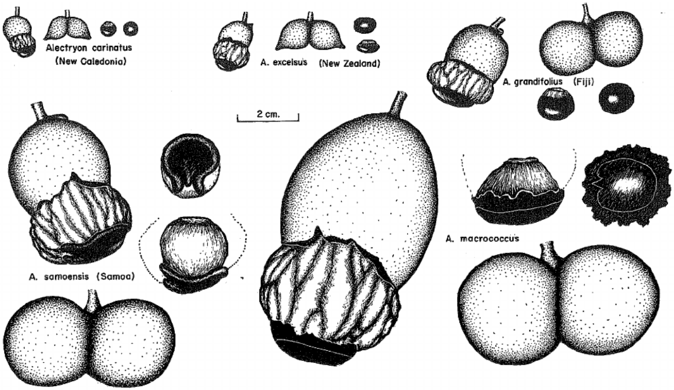


FIG. 11.14. Comparison of fruits and seeds of non-Hawaiian species of *Alectryon* (Sapindaceae) with those of the Hawaiian *A. macrococcus*. One or both cocci of the fruits may develop in all species. At maturity cocci are broken open by the expanding red aril, at the tip of which the seed is borne. For each species, an opened monococcate and an unopened bicoccate fruit are shown; also two views of each seed: one lateral view (chalazal end of seed above) and one polar view (surface opposite chalazal end). Dotted lines around lateral views of seeds of *A. samoensis* and *A. macrococcus* indicate outline of aril. Scale applies to all drawings.

Loss of dispersal ability in plants

Loss of sea flotation ability in Hawaiian *Erythrina*, in comparison to an Indomalesian relative.

Loss of dispersal ability in animals: Flightlessness

- Loss of dispersal ability is also common in island animals.
- Especially, in birds and insects, capable of flying.
- Loss of flight capability – from behaviorally reduced tendency to fly, up to degeneration or disappearance of wings.
- Loss of dispersal ability in animals is strongly associated with niche shifts
    1. Into more terrestrial lifestyles – e.g., in rails, which feed on the ground also on continents, but have become ground birds completely on many islands.
    2. Ecological release from predators – with few or none around, flight as an escape mechanism becomes less crucial.

Loss of dispersal ability in animals: Flightlessness

Flightlessness in rails has developed repeatedly and independently on dozens of islands worldwide:

Galapagos Cormorant - only flightless cormorant worldwide:

Loss of dispersal ability in animals: Flightlessness

Flightlessness in island moths and flies:

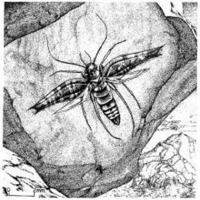


FIG. 12.1. *Tinearupa sorenseni*, a flightless moth from Campbell I.

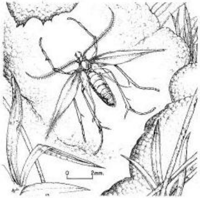


FIG. 12.2. *Campbellana attenuata*, a flightless moth from Campbell I.

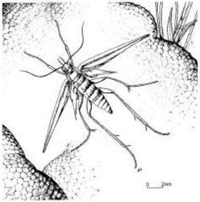


FIG. 12.3. *Exsilaracha graminea*, a flightless moth from Campbell I.

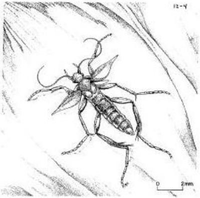


FIG. 12.4. *Pringleophaga kerguelensis*, a flightless moth from Kerguélen I. It is shown on a leaf of *Pringlea antiscorbutica*, the "Kerguélen cabbage."

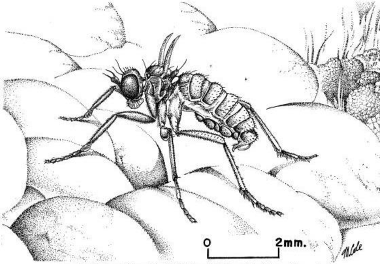


FIG. 12.5. *Schoenophilus pedestris* (Diptera: Dolichopodidae), from Macquarie I.

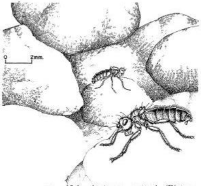


FIG. 12.6. *Apataenus watsoni* (Diptera: Coelopidae), from Macquarie I.

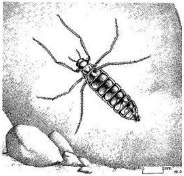


FIG. 12.7. *Belgica antarctica* (Diptera: Chironomidae), a flightless midge from the Antarctic mainland.

Loss of dispersal ability in animals: Flightlessness

Other examples include:

- Numerous flightless beetles in Madeira and close-by islands.
- The Dodo bird of Mauritius and other Indian ocean islands.
- Flightlessness or reduced flight ability in ducks from Laysan island and New Zealand islands.
- Reduced flight ability in New Zealand bats.

Summary of causes of loss of dispersal ability

1. Disharmony – immigrants to islands tend to be good dispersers $\Rightarrow$ changes will occur in the direction of good $\rightarrow$ poor dispersal ability (rather than opposite).

Additionally, in plants:

2. Larger seeds as part of the syndrome of more woody growth forms in more stable habitats.
3. Precinctiveness – both in the island and habitat scales.

Additionally, in animals:

2. Flightlessness associated with niche shifts.
3. Flightlessness associated with ecological release from predators.

Gigantism and Dwarfism

- Already seen that, in plants, niche shifts, insular woodiness and loss of dispersal ability lead to larger plants and seeds.
- Similar changes in size occur in animals: some becoming larger on islands – **Gigantism** – , while others become smaller – **Dwarfism** (or, nanism).
- Such changes in body size are usually associated with niche shifts and/or ecological release (especially, from predators).
- We have already seen some examples from adaptive radiations – e.g., in Darwin's finches, species that eat larger foods (e.g., larger seeds) have larger beaks and larger body sizes.

Gigantism and Dwarfism

Gigantism often associated with reduced flight ability:

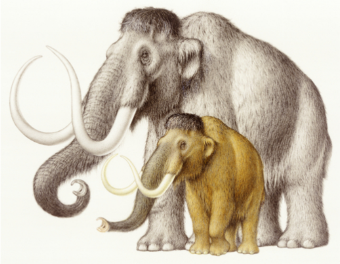
Buller, Walter Lawry, Birds of New Zealand, 1873.
Gould, John, Birds of Australia, 1840–48 - Public Domain

Gigantism in reptiles, rodents and insects:

Gigantism and Dwarfism

Dwarfism often occurs in large mainland mammals.

Examples include the dwarf elephant and hippo from Malta and the Wrangel island mammoth.



Other evolutionary trends on islands

- Island animals are more bold, or less timid, compared to mainland relatives – probably because of lack of experience with predators.
- In plants – tendency towards more sexual reproduction (dioecy) – division into male and female plants.
- In plants – tendency towards smaller less conspicuous flowers – because large pollinating insects usually do not reach islands.
- In animal reproduction – tendency towards fewer but larger eggs or offspring.

Outline

Summary of insular evolution

In light of the natural laboratory paradigm

- Adaptive radiation, Nonadaptive radiation, Woodiness, Loss of dispersal ability, Flightlessness, Gigantism and Dwarfism, etc. also occur on continents.
- For example, the radiation of mammals following the extinction of dinosaurs (creating disharmony and empty niches on a global scale), or evolution of trees on continents.
- However, on continents these are either rare events (adaptive radiation), or otherwise evolution occurs much more slowly.

Summary of insular evolution

In light of the natural laboratory paradigm

- **Numerous, small and discrete geographical units** – Isolation on a large number of islands have allowed for evolutionary trends to occur independently again and again in many different circumstances and in many different groups and original immigrants (e.g., flightlessness in rails occurred independently on many islands).
- **"Simple" biotas** – Species poverty and disharmony make these evolutionary phenomena exceptionally clear on islands (compared to the more complex biotas on continents).

Summary of insular evolution

In light of the natural laboratory paradigm

- **"Accelerated time"** – Relative recentness of these evolutionary changes have allowed for survival of intermediate forms and most member species of adaptive radiations (e.g., herbs, shrubs and trees evolving from same immigrant species), and ancestor species on continents for comparison.

- **"Telescoping" of environmental variability** – allows repeatedly to connect certain ecological circumstances with certain evolutionary trends (e.g., ecological release leading to flightlessness; stable habitats leading to woodiness).

Summary of insular evolution

In light of the natural laboratory paradigm

1. $\Rightarrow$ Allow for general conclusions that also apply to evolution on continents.
2. Teach us about the role of ecology, history and chance events in evolution of life on earth, in general.
3. Island studies have contributed again and again to development of theories in evolutionary biology and ecology, from before Darwin's time until today.