We will integrate all three island phenomena in the context of the Hawaiian Islands.
Hawaiian archipelago - the example for island biogeography

“Getting there is half the problem . . . but then they can’t go home again”

Sherwin Carlquist, 1965
Hawaiian archipelago - the example for island biogeography

“If one were to stand at the top of Mauna Loa, he could see all the climes of the world at a single glance of the eye”

Mark Twain, 1866

4,169 m OR 13,679 ft
Hawaiian archipelago - the example for island biogeography

“Assume nothing in Hawaiian natural history”

Frank Howarth, 1992
Hawaiian archipelago - the example for island biogeography

Most remote island system in the world

- settled in 1st millenium by Polynesians
- made known to science by Captain Cook in 1778
Hawaiian Biota

Hawaiian biota: most are found nowhere else in the world and exhibit traits uncharacteristic of their taxa

- around 1,000 species of flowering plants
- 225 species of ferns and allies
Hawaiian Biota

Hawaiian biota: most are found nowhere else in the world and exhibit traits uncharacteristic of their taxa

- nearly 5,800 species of insects
- 130 species of spiders

Happyface spider

Kamehameha butterfly
Hawaiian biota: most are found nowhere else in the world and exhibit traits uncharacteristic of their taxa

- 230 species of birds
- 800 species of terrestrial molluscs
Hawaiian Biota

Hawaiian biota: most are found nowhere else in the world and exhibit traits uncharacteristic of their taxa

- no amphibians
- no terrestrial mammals

Hawaiian hoary bat
Hawaiian monk seal
Hawaiian Biota

Hawaiian biota: extinction on-going process both in past and present

Hawaiian hoary bat
- arrived 10,000 years ago

Extinct small Hawaiian bat
- arrived 320,000 years ago
- extinct 1,100 years ago
Hawaiian Biota

Hawaiian biota: extinction on-going process both in past and present

Extinct snail, flightless duck, lobeliad

Hawaiian honeycreepers
Hawaiian Archipelago

- 132 islands, reefs, & shoals
- 2,580 km on SE-NW line
- 99% of land lies on 8 main islands near the hot spot below Lo’ihi
Hawaiian Archipelago

- hot spot stationary relative to Pacific Plate motion
- forms hot spot trace
- potassium-argon dating indicates oldest islands furthest from hot spot
- newest island Loihi still underwater - seamount
Hawaiian Archipelago

- plate motion changed 43 mya
- oldest seamounts subducted into Aleutian Trench
Hawaiian Archipelago

- Islands (and shoals) are simply emergent tops of great underwater volcanoes
- up to 10km above ocean floor

Mauna Kea – 10.2 km (4.2 km)
Maua Loa - 37 m lower but most massive
Hawaiian Archipelago

- actually double hot spot 30km apart
- Lo’ihi to Mauna Loa
- Kilauea to Mauna Kea
Hawaiian Climate

• primary weather pattern is northeasterly trade winds
• severe kona winds come from leeward side

Hilo (windward and wet) vs. Kona Coast in Hawaii (leeward and dry)
Hawaiian Climate

rainfall patterns

• double mountain system (as in Oahu) sets up complex rainfall gradient and a diversity of ecosystems

Figure 10. The Koʻolau Mountains, which run perpendicular to the direction of the trade winds, condense most of the moisture from this moist air. The Waiʻanae Mountains are in a rain shadow. Only Mt. Kaʻala in the Waiʻanae Mountains is high enough to receive much moisture from the trade winds.
Hawaiian Climate

- extraordinary rich and diverse habitats available
- 38 community types recognized
Hawaiian Climate

rainfall patterns

- Wai’ale’ale on oldest (most eroded) island of Kauai is wettest spot in Hawaii and possibly in the world

- 11.5 m of rain and presence of the Alakai Swamp
Hawaiian Climate

rainfall patterns

• Pu’ukukui (5,788 ft) on west Maui is 2nd wettest spot; xeric summit of Haleakala on east Maui is 10,023 ft

Greensword bog - west Maui
Flora of Hawaii

“Assume nothing in Hawaiian natural history”
Flora of Hawaii

- since so isolated, it has a depauperate flora and consists entirely of waif elements derived from LDD

native or weeds

Argyroxyphium sandwicense - Haleakala silversword  Passiflora mollissima - Banana poka
Flora of Hawaii

- individual islands tend to fit the expected number of species based on area - except most recent Hawaii

**Figure 5** Species–area regression for whole islands. Abbreviations are given in Table 2.
Flora of Hawaii

- **endemism** high in flowering plants (highest in the world)

956 native species
  - 89% endemic

216 native genera
  - 15% endemic

87 native families
  - 0% endemic

1,817 including introduced

649 including introduced

146 including introduced

*Brighamia* (Lobeliaceae)
Flora of Hawaii

- disharmonic flora
- only 3 native orchid species
- but many introduced orchids that become naturalized

Dendrobium & honey bees
Flora of Hawaii

- disharmonic flora

- only 1 native palm genus (coconut?)

- native gymnosperms and primitive angiosperms absent

Pritchardia beccariana
Flora of Hawaii

- **disharmonic** flora - 15 largest families of native species

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Campanulaceae</td>
<td>110</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>92</td>
</tr>
<tr>
<td>Rutaceae</td>
<td>55</td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>54</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>54</td>
</tr>
<tr>
<td>Gesneriaceae</td>
<td>53</td>
</tr>
<tr>
<td>Poaceae</td>
<td>47</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>45</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td>33</td>
</tr>
<tr>
<td>Piperaceae</td>
<td>25</td>
</tr>
<tr>
<td>Malvaceae</td>
<td>24</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>21</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>20</td>
</tr>
<tr>
<td>Solanaceae</td>
<td>9</td>
</tr>
<tr>
<td>Myrtaceae</td>
<td>8</td>
</tr>
</tbody>
</table>

- **large** source area families under represented
- **small** Campanulaceae - lobeliads and bellflowers - over represented
Flora of Hawaii

- **immigrants**: 270 (or less!) gave rise to 956 native angiosperms

- 1/10th of colonist generates 1/2 of species!

**TABLE 3. Twenty most speciose genera of Hawaiian flowering plants and presumed numbers of colonists.**

<table>
<thead>
<tr>
<th>Genus</th>
<th>Number of species</th>
<th>Presumed number of colonists</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyrtandra</td>
<td>53</td>
<td>4–6</td>
</tr>
<tr>
<td>Cyanea</td>
<td>52</td>
<td>1</td>
</tr>
<tr>
<td>Pelea</td>
<td>47</td>
<td>1</td>
</tr>
<tr>
<td>Phylllostegia</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>Peperomia</td>
<td>25</td>
<td>3–4</td>
</tr>
<tr>
<td>Clermontia</td>
<td>22</td>
<td>—</td>
</tr>
<tr>
<td>Schiedea</td>
<td>22</td>
<td>1</td>
</tr>
<tr>
<td>Dubautia</td>
<td>21</td>
<td>1</td>
</tr>
<tr>
<td>Lipochaeta</td>
<td>20</td>
<td>2 (polyphyletic)</td>
</tr>
<tr>
<td>Stenogyne</td>
<td>20</td>
<td>—</td>
</tr>
<tr>
<td>Myrsine</td>
<td>20</td>
<td>1–2</td>
</tr>
<tr>
<td>Hedyotis</td>
<td>20</td>
<td>1–2</td>
</tr>
<tr>
<td>Bidens</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Pritchardia</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td>Chamaesyce</td>
<td>15</td>
<td>1–2</td>
</tr>
<tr>
<td>Labordia</td>
<td>15</td>
<td>1</td>
</tr>
<tr>
<td>Sicyos</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Coprosma</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>Lobelia</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>Wikstroemia</td>
<td>12</td>
<td>1</td>
</tr>
</tbody>
</table>

Totals 469 26–32

*Images of Cyanea, Cyrtandra, and Pelea*
Flora of Hawaii

- **immigrants**: similar story with other biota
- one American finch gave rise to 33 extant and 14 extinct species of honeycreepers
Flora of Hawaii

• *immigrants*: similar story with other biota

• 800 land molluscs from 20 colonists
• 5,800 insects from 250 colonists
Flora of Hawaii

- **immigrants**: but different story for ferns!

- 168 ferns from 135 colonists - implying constant immigration (lack of genetic isolation) and/or few speciation events

*Sadleria* - 6 species vs. *Polypodium* - 1 species
**Flora of Hawaii**

- **LDD mechanisms**

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>Code</th>
<th>Description</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air</td>
<td>A</td>
<td>internal</td>
<td>1%</td>
</tr>
<tr>
<td>Internal</td>
<td>BI</td>
<td>mud</td>
<td>39%</td>
</tr>
<tr>
<td>Viscid</td>
<td>BV</td>
<td>barbs/hooks</td>
<td>13%</td>
</tr>
<tr>
<td>Barbs/hook</td>
<td>BB</td>
<td>barbs/hooks</td>
<td>10%</td>
</tr>
<tr>
<td>Drift</td>
<td>DF</td>
<td>drift</td>
<td>12%</td>
</tr>
<tr>
<td>Drift - rare</td>
<td>DR</td>
<td>drift - rare</td>
<td>14%</td>
</tr>
</tbody>
</table>

- **Leptocophylla BI**
- **Argyroxyphium BB**
- **Acacia - koa DR**
- **Viola BM**
Flora of Hawaii

- floristic affinities

- despite proximity of Hawaii to N America, almost half of colonists are of Austral-asian origin

**Leptocophylla**
Epacridaceae
Flora of Hawaii

- floristic affinities

Viola
- few from Arctic-Beringia

Plantago - plantain
Flora of Hawaii

• **floristic affinities**

Viola

*Viola langsdorfii*

• woody violets *once* considered closely related to South American violets

• all native Hawaiian violets are polyploid and derived from polyploid races of one Beringian tundra species - the Alaskan violet
Flora of Hawaii

- floristic affinities

- 18-22% from western North America

Argyroxyiphium
Flora of Hawaii

• adaptive radiation of Hawaiian silverswords

• silversword alliance of 3 genera and 28 species

• trees, shrubs, subshrubs, rosette plants, cushion plants, vines
Flora of Hawaii

- **adaptive radiation** of Hawaiian silverswords

- B. Baldwin verified that the Hawaiian silversword radiation derived from California
  - the closest species is now called *Carlquistia muirii*
  - this origin occurred about 5 mya
  - rapid radiation at base
**Flora of Hawaii**

- **inter-island biogeography** [“island hopping” – “stepping stones”]
  - most speciation events occur on individual islands
  - few successful inter-island colonizations
  - movement is from older to younger islands

---

*Argyroxyphium*

---

*Rosemary Gillepsie*

---

*Argyroxyphium*
Flora of Hawaii

• extinction: on-going process on islands (as well as immigration)

• but due to humans . . .

• 107 of 956 angiosperm species — 11% extinct
• 423 of 956 species — 38% extinct or threatened
Flora of Hawaii

- **extinction**: rogue gallery of exotics

*Passiflora mollissima* - banana pokal
Flora of Hawaii

- extinction: rogue gallery of exotics

*Miconia* introduced into Hawaii as ornamental

*Miconia calvescens* “green cancer”
Biogeography of Hawaii

Adaptive radiations

Hawaiian lobeliads
Hawaiian Lobeliads

Why the Hawaiian lobeliads?

- **largest group**: 6 genera, 140 species
- **1/8th of native flora**
- considered derived from **3-5 separate colonizations**
- phenomenal variation in habitat, life form, flowers, and fruits
Why the Hawaiian lobeliads?

- appear to have co-evolved with the endemic Hawaiian honeycreepers
- honeycreepers represent a separate adaptive radiation
DNA supports common ancestry of **ALL** Hawaiian lobeliads – one single ancestral seed dispersed to Hawaii & radiated into the more than 140 species
Two approaches for dating and placing the Hawaiian colonization

1. Calibration using an external phylogeny of the order Asterales and 5 well characterized fossils outside the family Hawaiian lobelioids.
Hawaiian Lobeliads

Two approaches for dating and placing the Hawaiian colonization

2. Calibration using island shifts / island ages

- Nihau vs. Kauai
- Kauai vs. Ohau
- Ohau vs. Maui
- Maui vs. Hawaii
Hawaiian Lobeliads

Two clock calibrations - using Asterid fossils or using Hawaiian Island ages - place the differentiation of Hawaiian lobeliads at 13-14 mya
Hawaiian Lobeliads

Two clock calibrations - using Asterid fossils or using Hawaiian Island ages - place the differentiation of Hawaiian lobeliads at 13-14 mya

Original colonist arrived in LaPerouse/Gardner Pinnacles - large volcanic islands 10-15 mya
Hawaiian Lobeliads

Two clock calibrations - using Asterid fossils or using Hawaiian Island ages - place the differentiation of Hawaiian lobeliads at 13-14 mya.

Original colonist arrived in LaPerouse/Gardner Pinnacles - large volcanic islands 10-15 mya.

Figure 3. Island configurations at 5 Myr intervals. We adjusted a rough digital elevation model of the estimated pre-erosion surface according to height estimates for different points in time. Ku, Kure; PH, Pearl and Hermes; Li, Lisianski; La, Laysan; Ma, Maro; G, Gardner; LP, LaPerouse; Ne, Necker; Ni, Nihoa; Ka, Kauai; Oa, Oahu; MN, Maui Nui; Ha, Hawaii.
Hawaiian Lobeliads

One of the oldest radiations of extant Hawaiian biota - honeycreeper pollinators would not arrive for another 7-9 my
Hawaiian Lobeliads

But . . . a 2008 paper shows that the 5 recently extinct Hawaiian Honeyeaters – thought to be recently derived from AustralAsian Honeyeaters – are in fact 14-17 my old and derived from an American clade - waxwings, silky flycatchers, and palm chats

Hawaiian lobeliads 13-14 mya

Hawaiian Honeycreepers 7 mya
Hawaiian Lobeliads

- Early lobeliads had initial radiation with Hawaiian honeyeaters
- Later radiation of two large genera (Cyanea and Clermontia) primarily with Hawaiian honeycreepers
“Assume nothing in Hawaiian natural history”