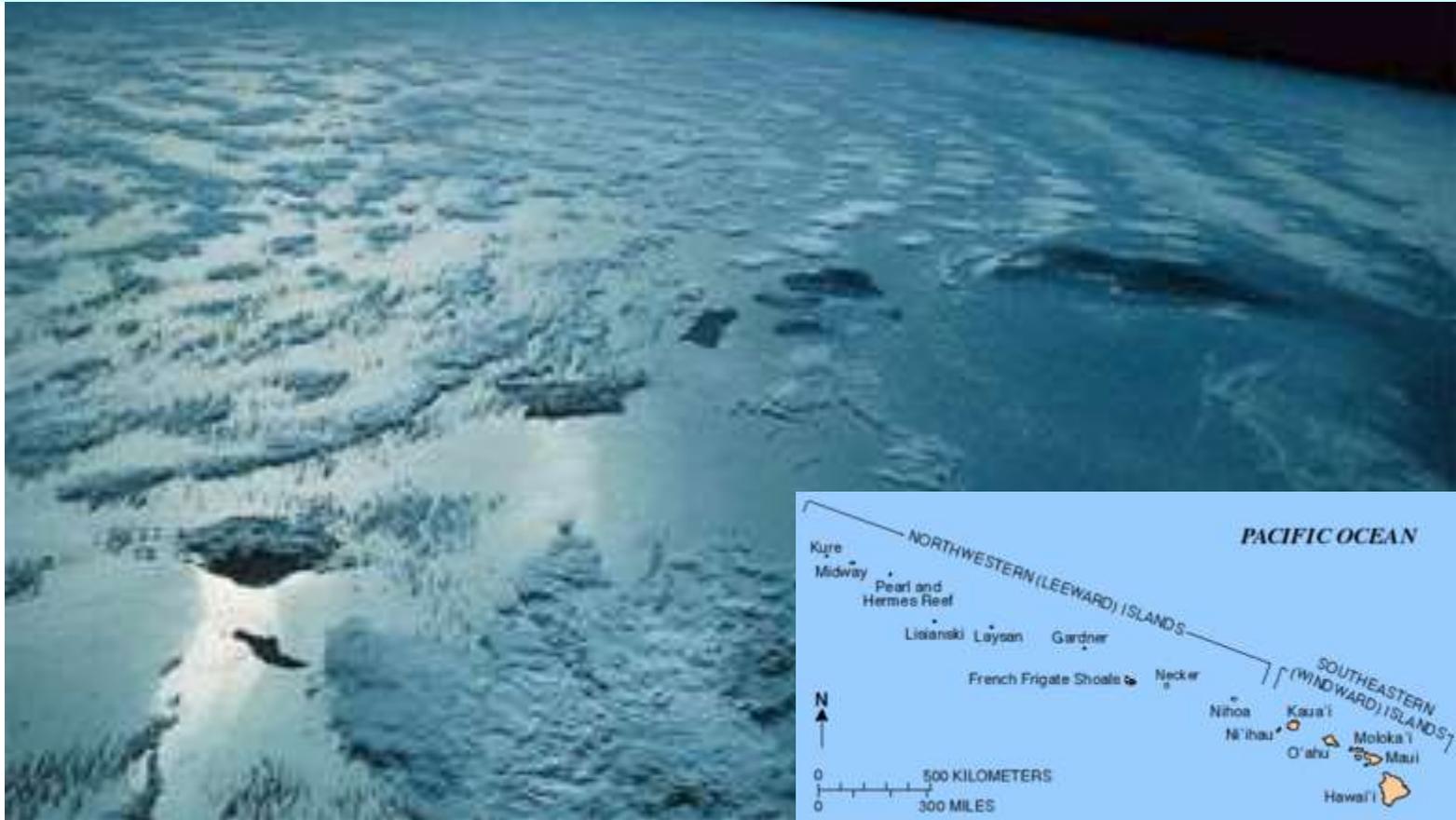


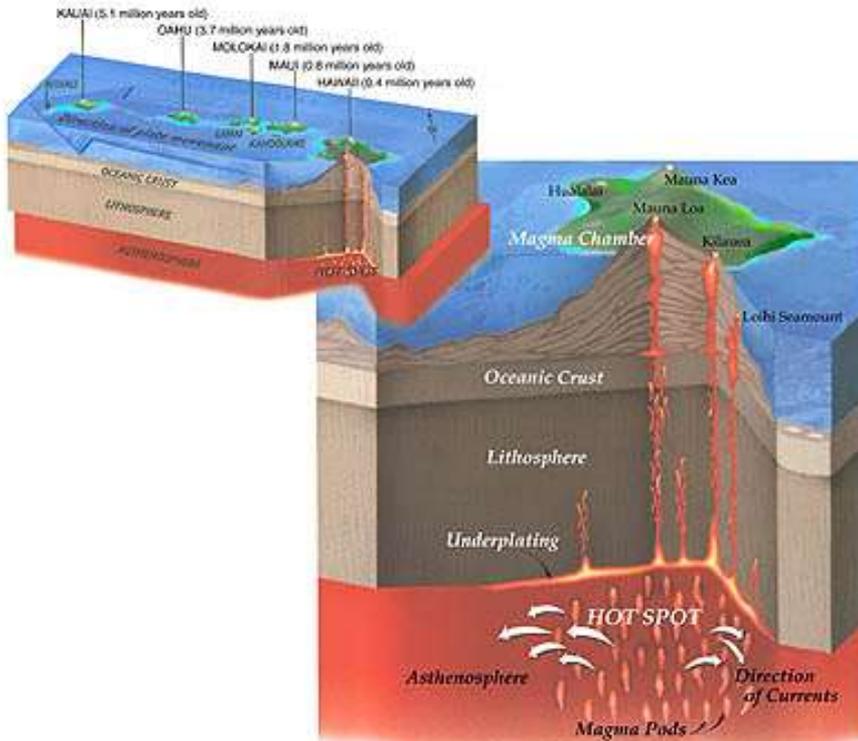
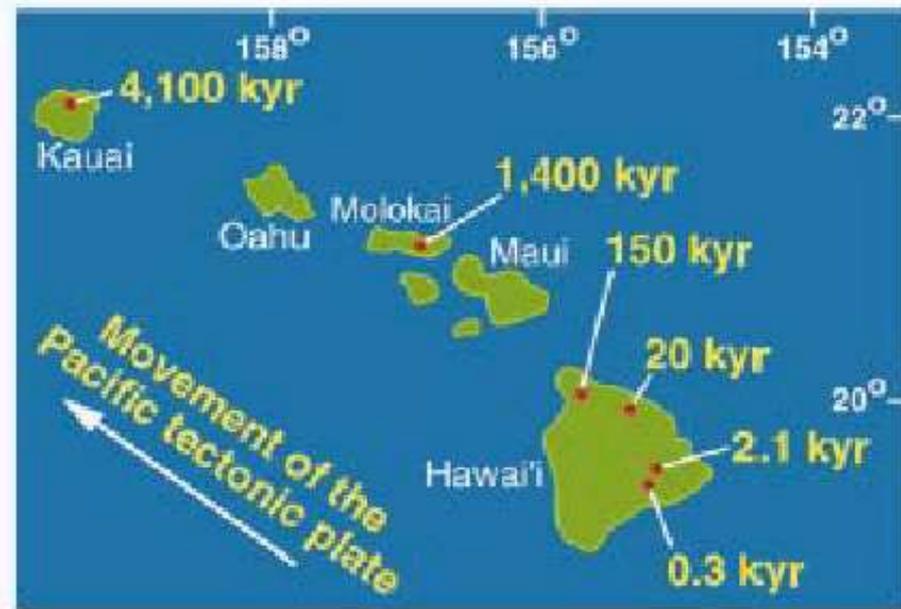
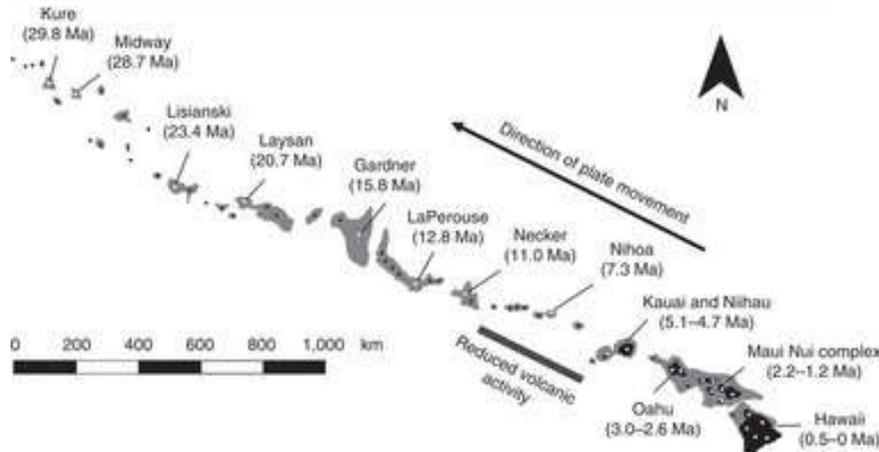
Tropical islands, speciation & distribution of biodiversity



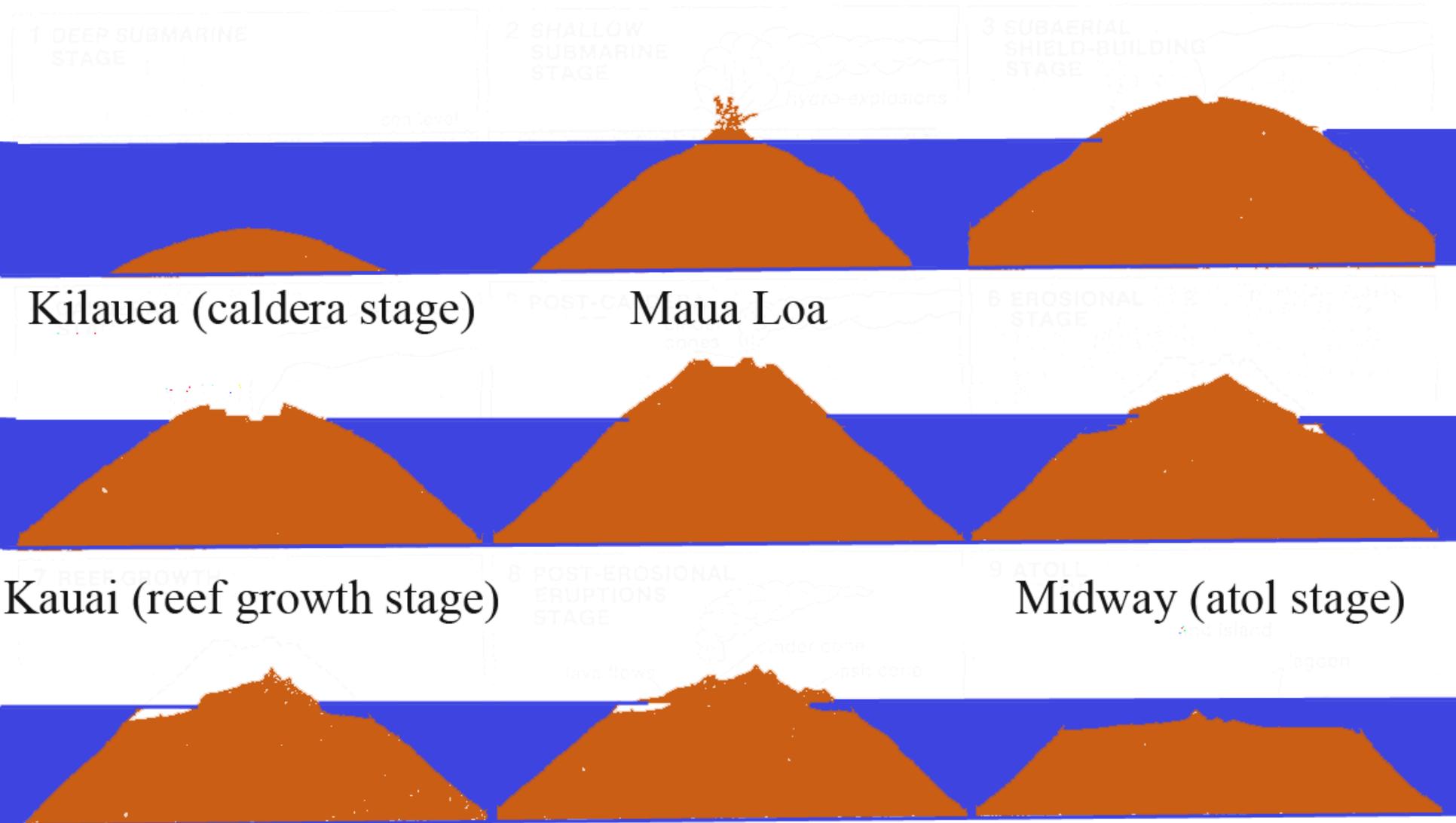
Hawaii Islands - a classic study site



Hawaii island is sitting on a magmatic hotspot



Development of a typical oceanic volcanic island





Hawaii: the creation of new ground (hot lava flow meets the ocean)



Molokai: 1.4 million years of erosion



Kauai: 4 million years of erosion

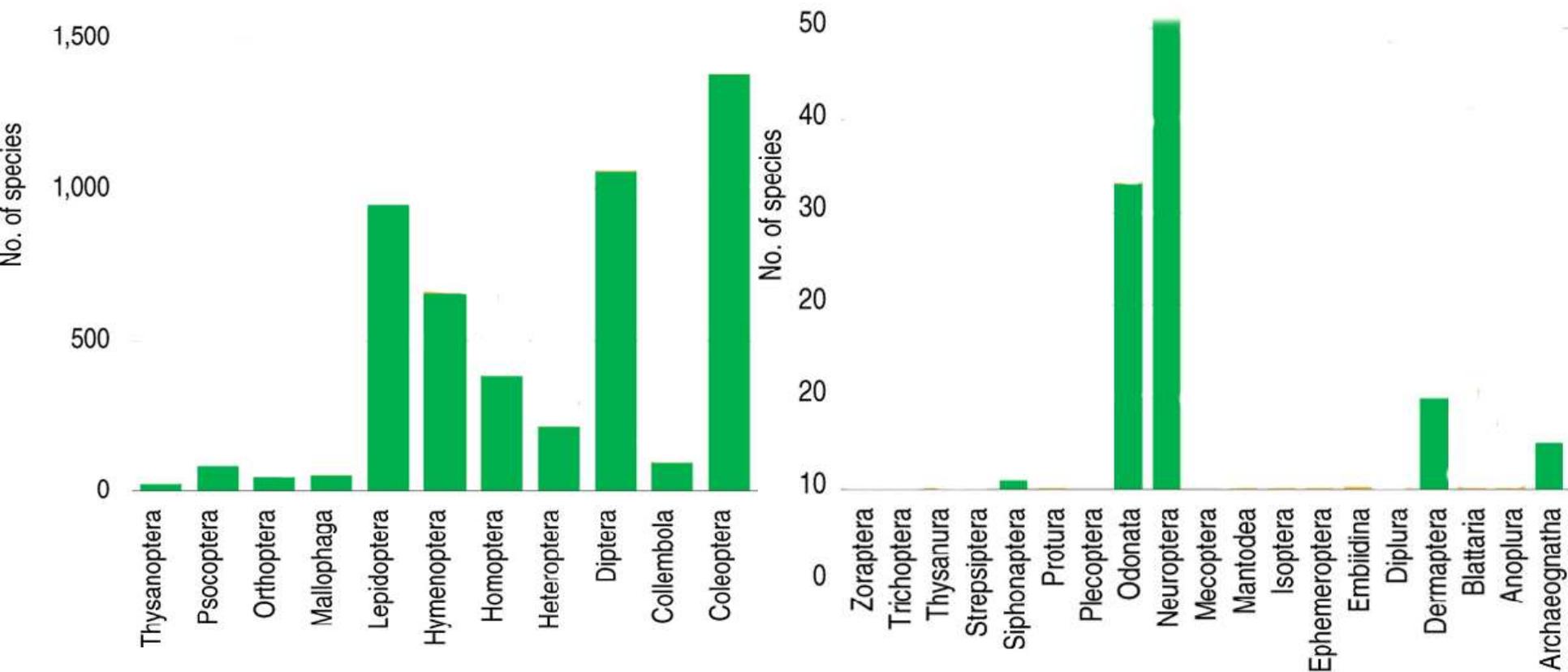
Key features of island biota

- semi-random taxonomic composition
(chance plus dispersal ability)
- empty niches → explosive radiation
- empty niches → wide niches
- empty niches → unusual shifts of ecological niches
- empty niches → susceptibility to invasive species

- random taxonomic composition

Hawaii: only 50% of insect orders present

- no Ephemeroptera, Plecoptera, Trichoptera (freshwater larvae)
- no termites
- no ants



Dispersal options for Hawaii

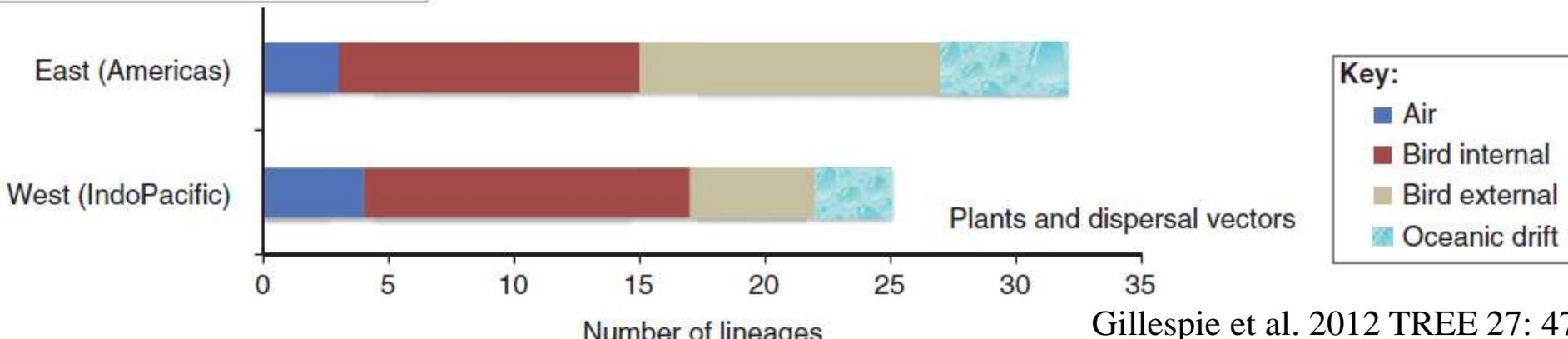
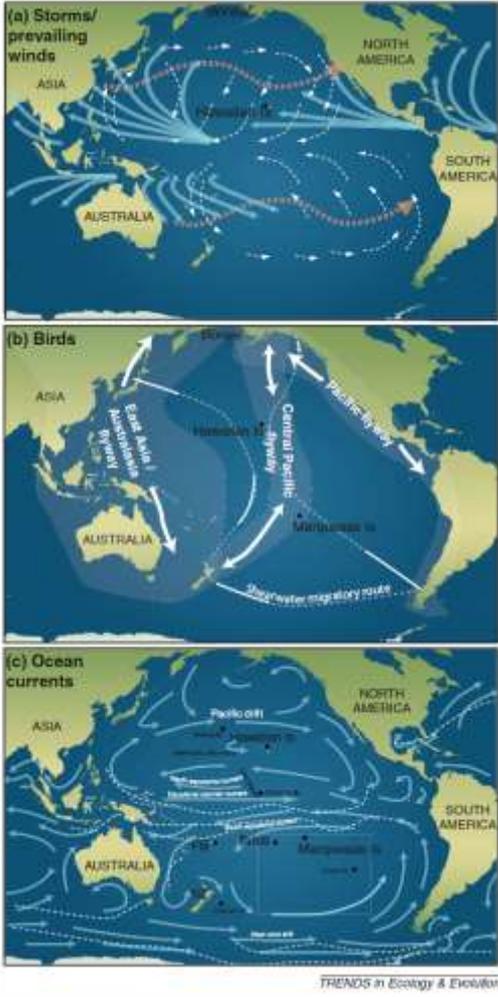
Modes of long-distance dispersal.

(a) Storms and prevailing winds; eastward subtropical jet streams (orange); prevailing trade winds (white).

(b) Bird migratory routes: major migratory pathways; routes by shearwaters and petrels (broken lines).

(c) Oceanic currents.

Plant lineages colonizing Hawaii from East and West by different means of dispersal



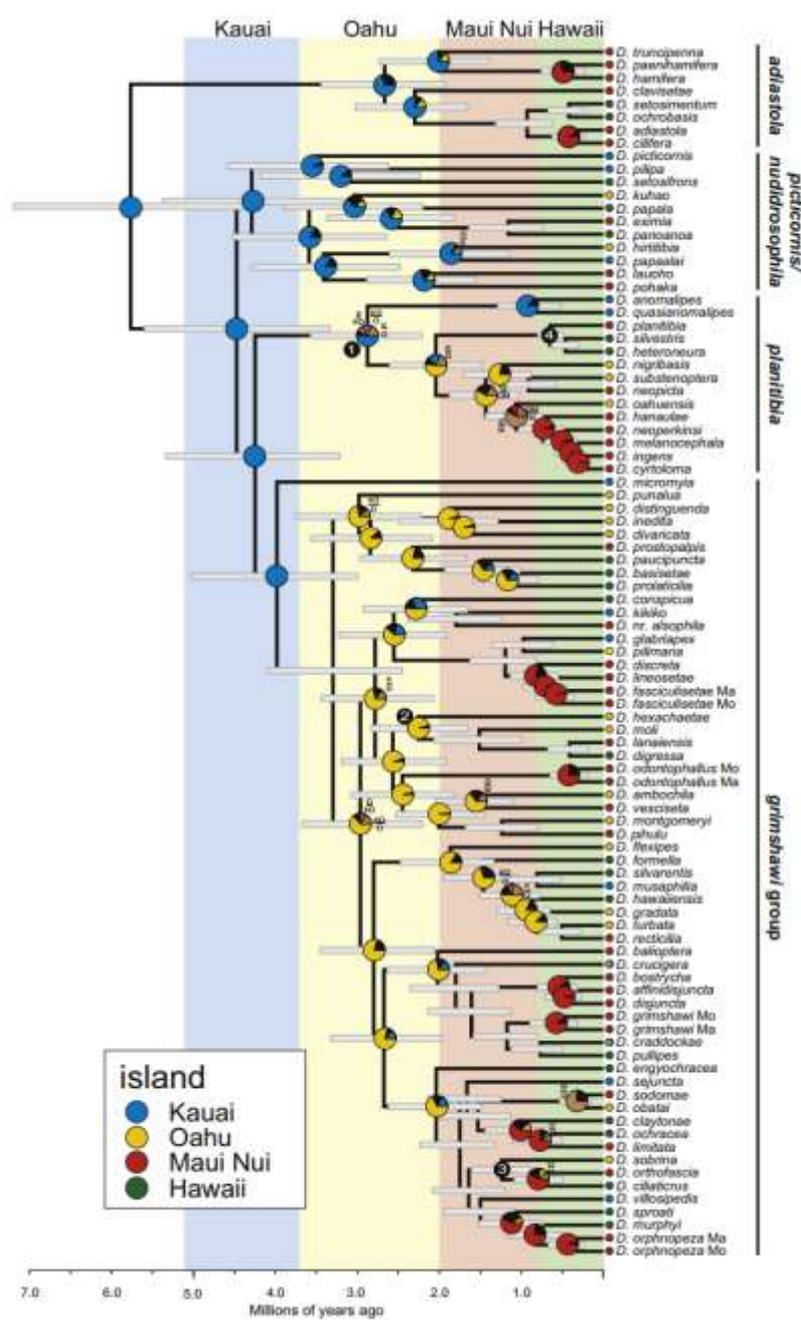
- explosive radiation

The 6,000-10,000 insects native to Hawaii evolved from 300 - 400 ancestral immigrant species (Hardy 1983; Gagné and Christensen 1985);

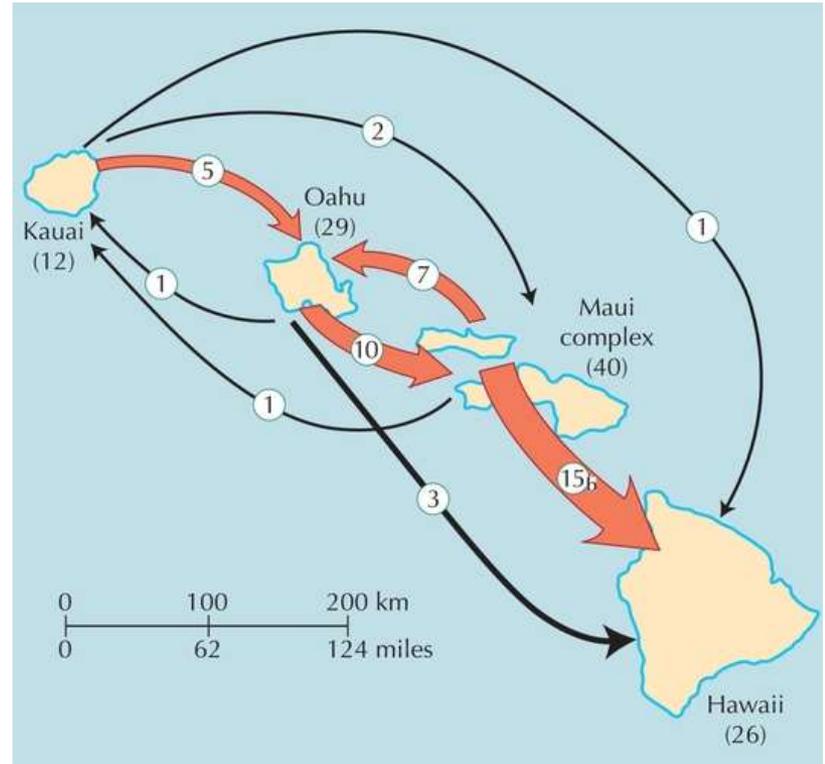
Drosophila:

Hawaii 600 spp. all from a single ancestor during 40 mil years;
100 spp. on the youngest Hawaii island evolved during past 1 mil years
Hawaii species represent 40% of world's Drosophila





Picture-wing *Drosophila* spp.

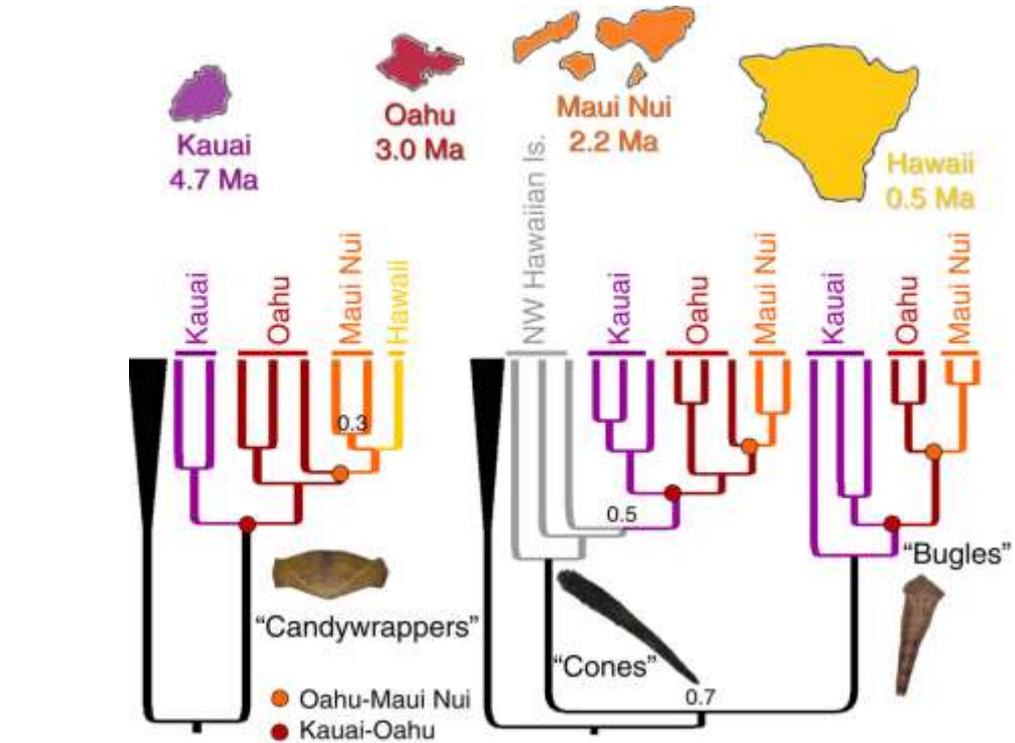


Drosophila phylogeny shows jumping from older to younger islands

The number of founder events reconstructed for the phylogeny of 103 spp. Of picture-wing *Drosophila* (No. of spp on each island in brackets).

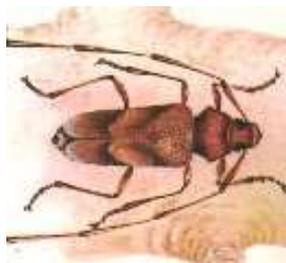
Further examples of explosive insect radiation in Hawaii:

Hyposmocoma (Cosmopterigidae): 400 spp., evolved in 15 M years,
Represent >1/3 of all Lepidoptera spp on Hawaii



Phylogenies of 3 *Hyposmocoma* case-bearing lineages

Kawahara et al. unpubl 2015 Haines et al. Nature Communications 2014, doi 10.1038/ncomms4502

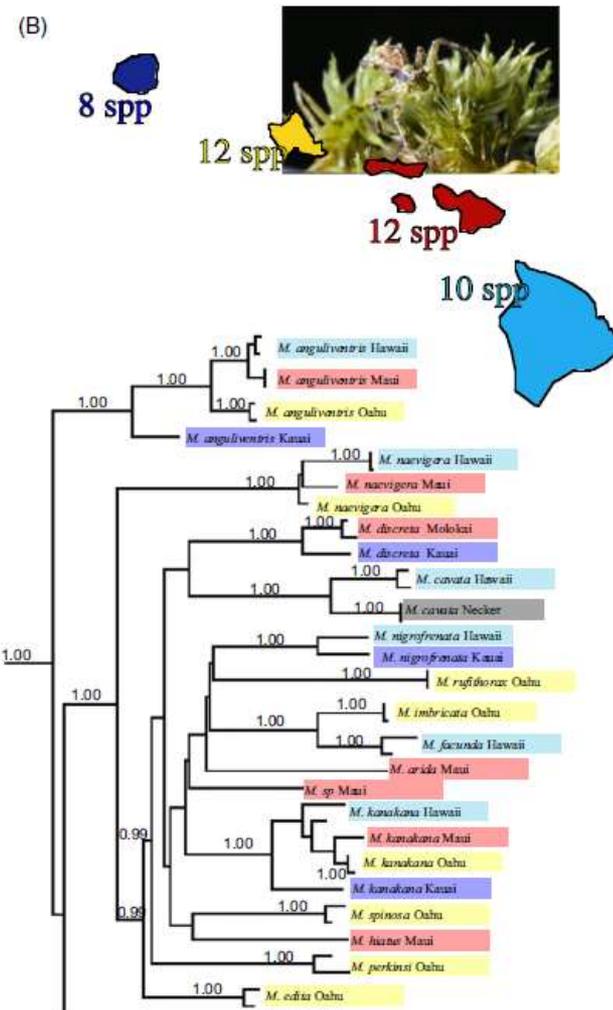
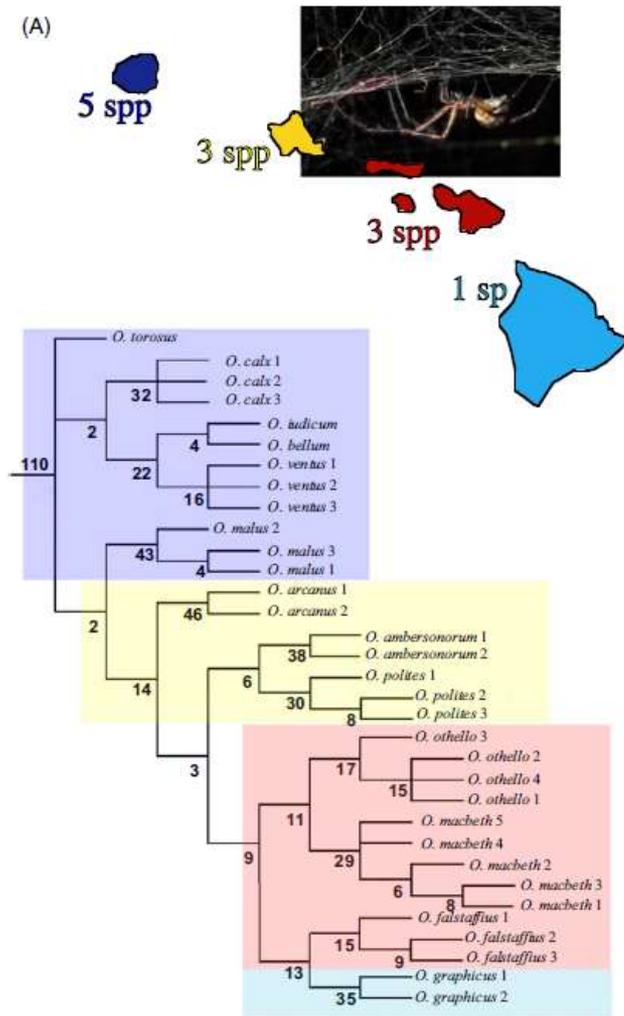


Plagithmysus (Cerambycidae): 139 spp.,
other cerambycids: 2 spp.

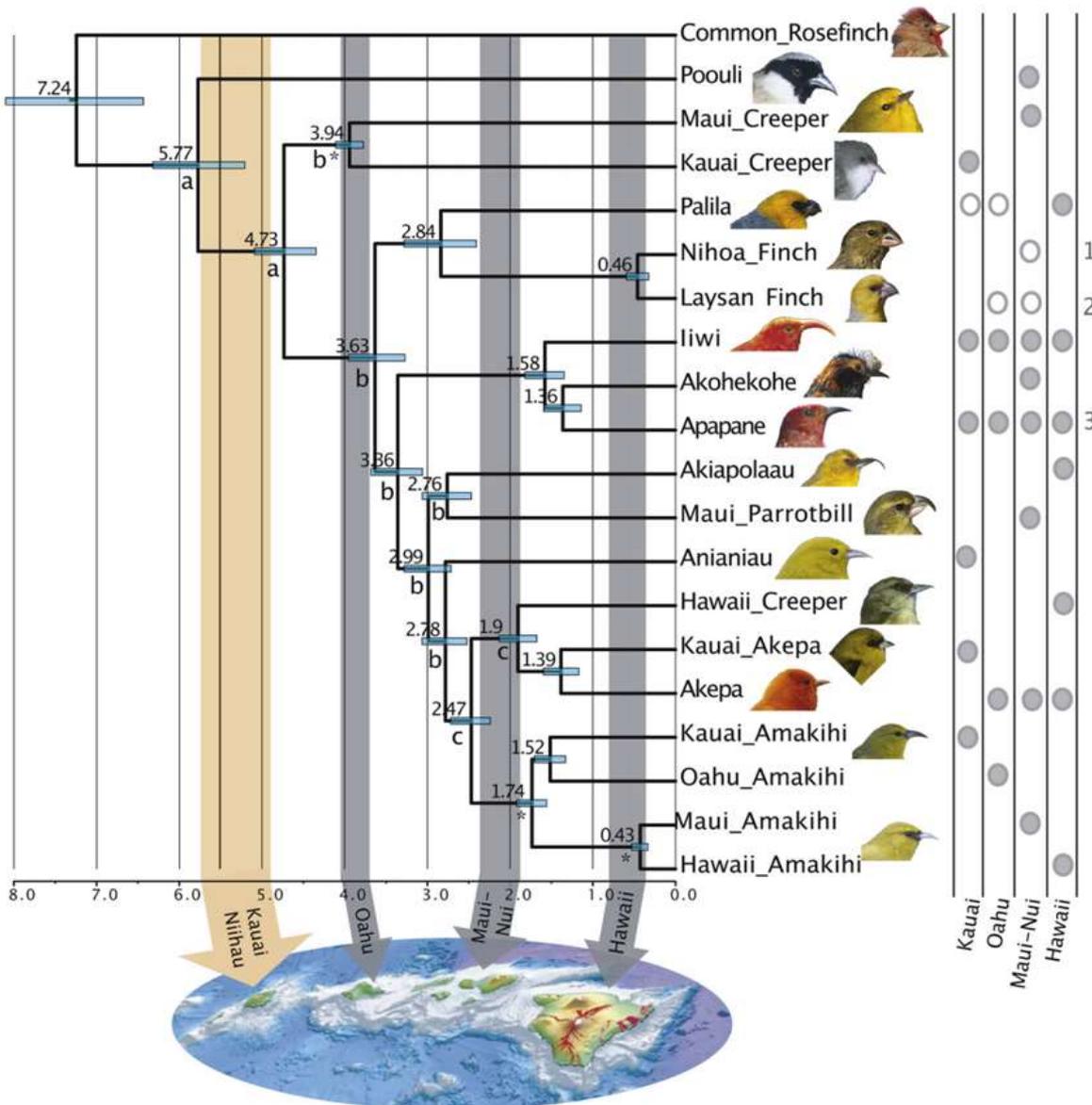
Spiders: speciation between and within islands

(A) *Orsonwelles* spiders, radiation progressed down the island chain

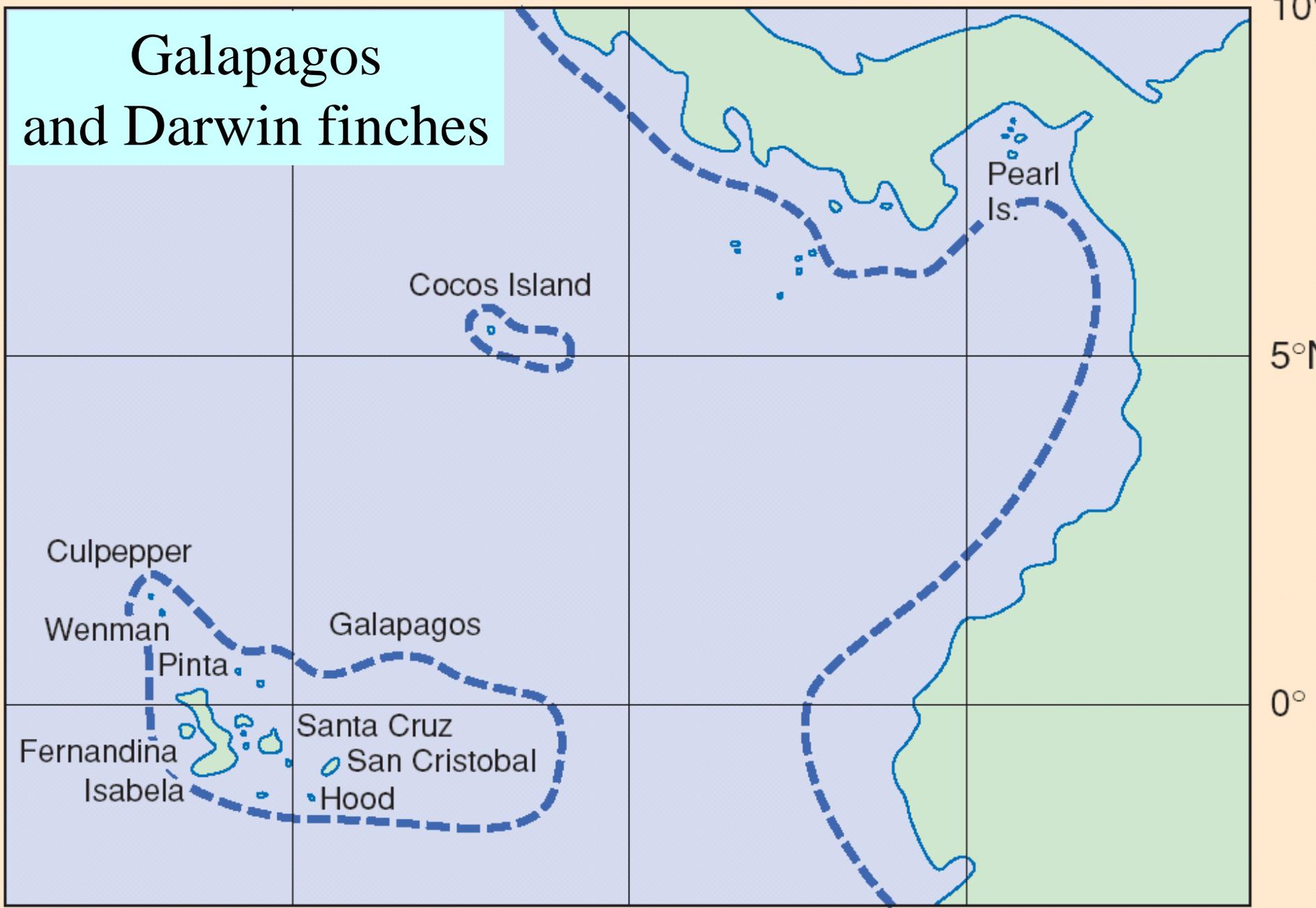
(B) *Mecaphesa* spiders, early diversification into different ecologically defined taxa, subsequent progression down the island chain in each species.



Drepanididae: and endemic Hawaiian family, 52 spp., incl. 18 extinct



Galapagos and Darwin finches



(a)

90°W

85°W

80°W

10°

5°

0°

Geospiza on Galapagos: coexistence and beak size

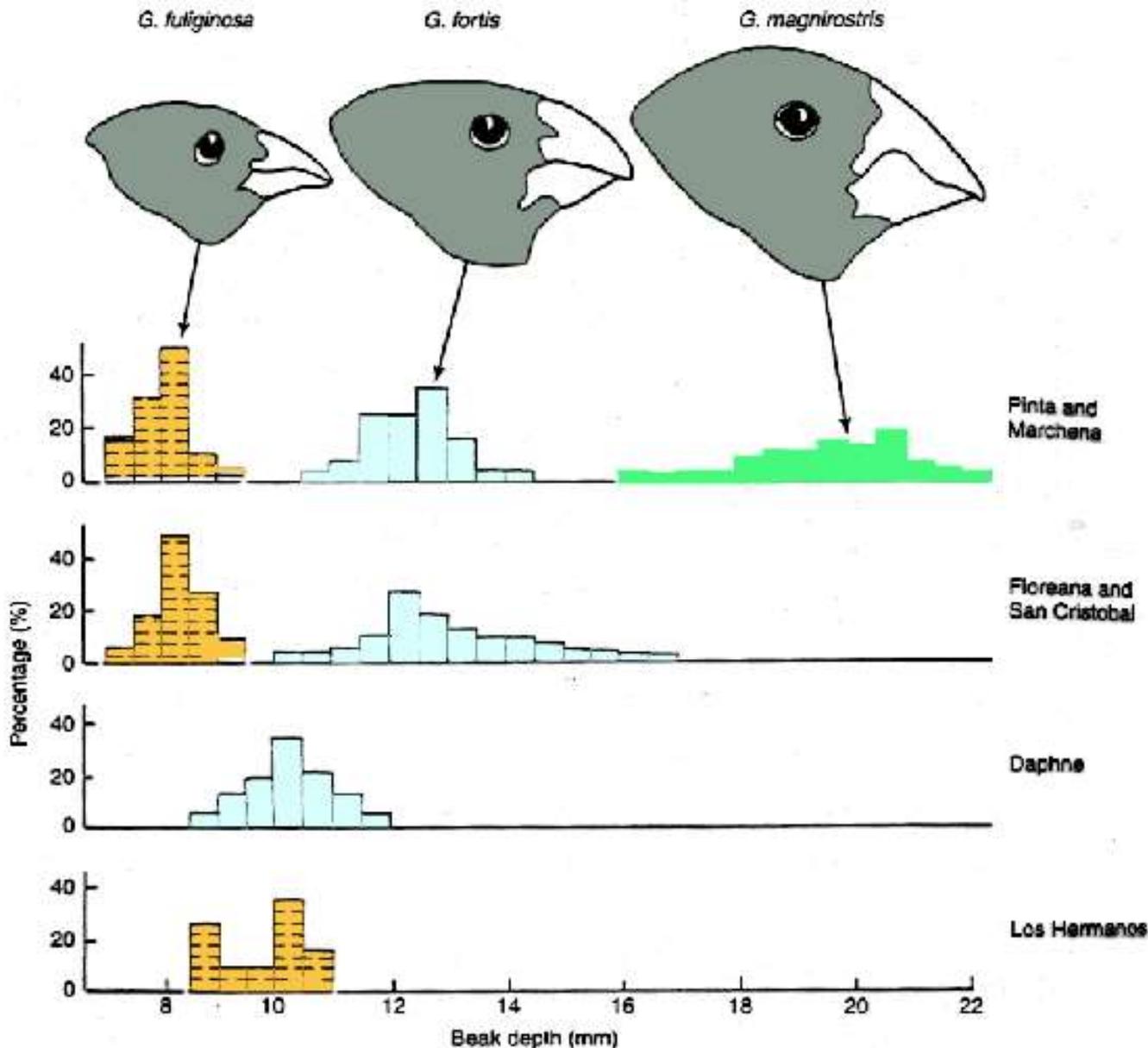


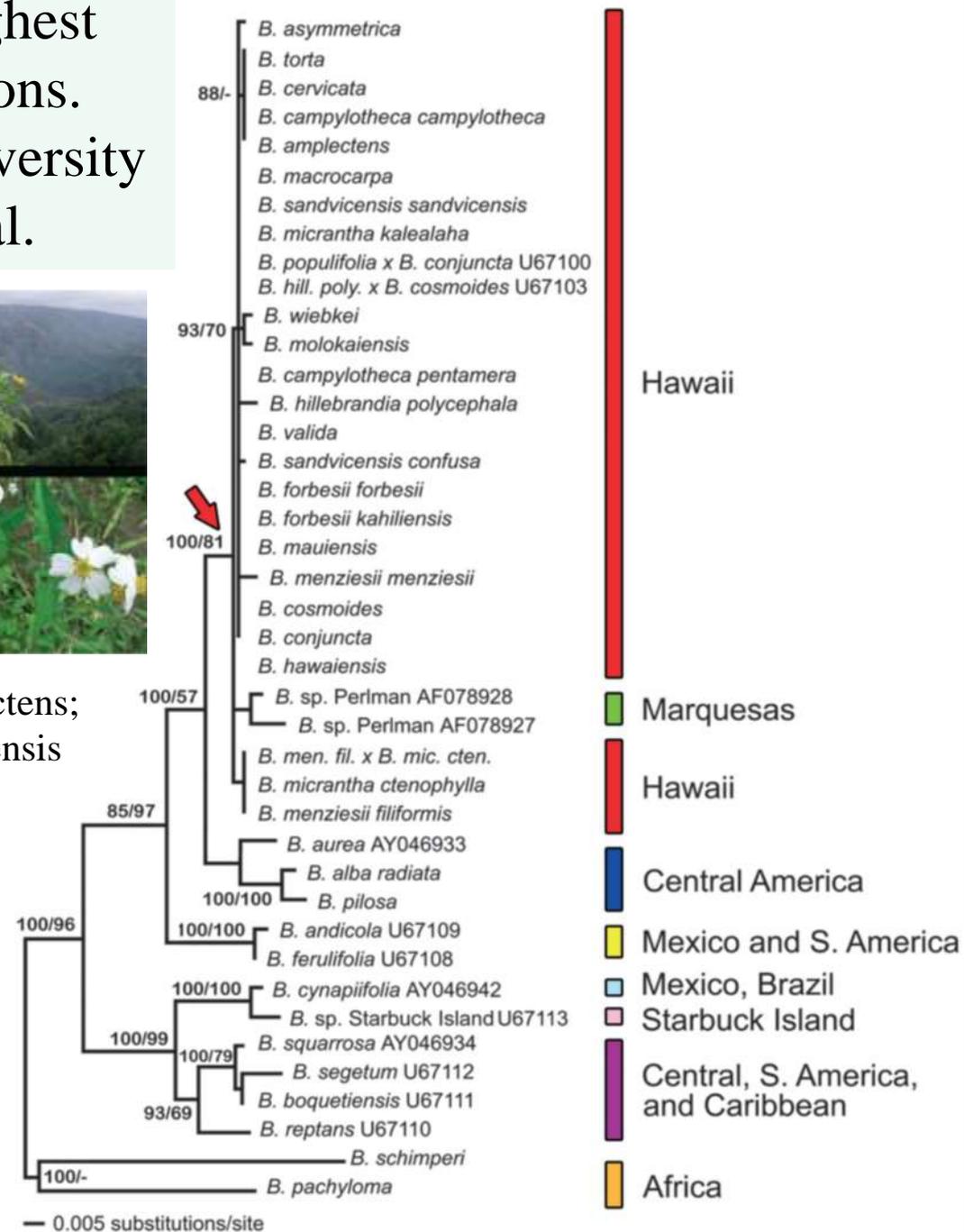
Figure 12.13 Percentages of individuals with beaks of different depths in three species of ground finches (*Geospiza* spp.) on islands in the Galapagos Archipelago. Note the increase in beak depth in *G. fortis* on Floreana and San Cristobal Islands where *G. magnirostris* is absent and the altered beak size distributions of *G. fortis* and *G. fuliginosa* on Daphne and Los Hermanos Islands respectively (after Lack 1947; Riecherts 1997 with kind permission from Peter Lack and Cambridge University Press).

Bidens in Hawaii: one of the highest speciation rates for plant radiations.
 Rapid diversification: habitat diversity and the adaptive loss of dispersal.



a: *B. hillebrandia*; b: *B. cosmoides*; c: *B. amplexans*;
 d: *B. sandvicensis*; e: *B. mauiensis*; f: *B. hawaiiensis*

Maximum likelihood phylogram based on ITS sequences for Hawaiian and outgroup *Bidens* spp.

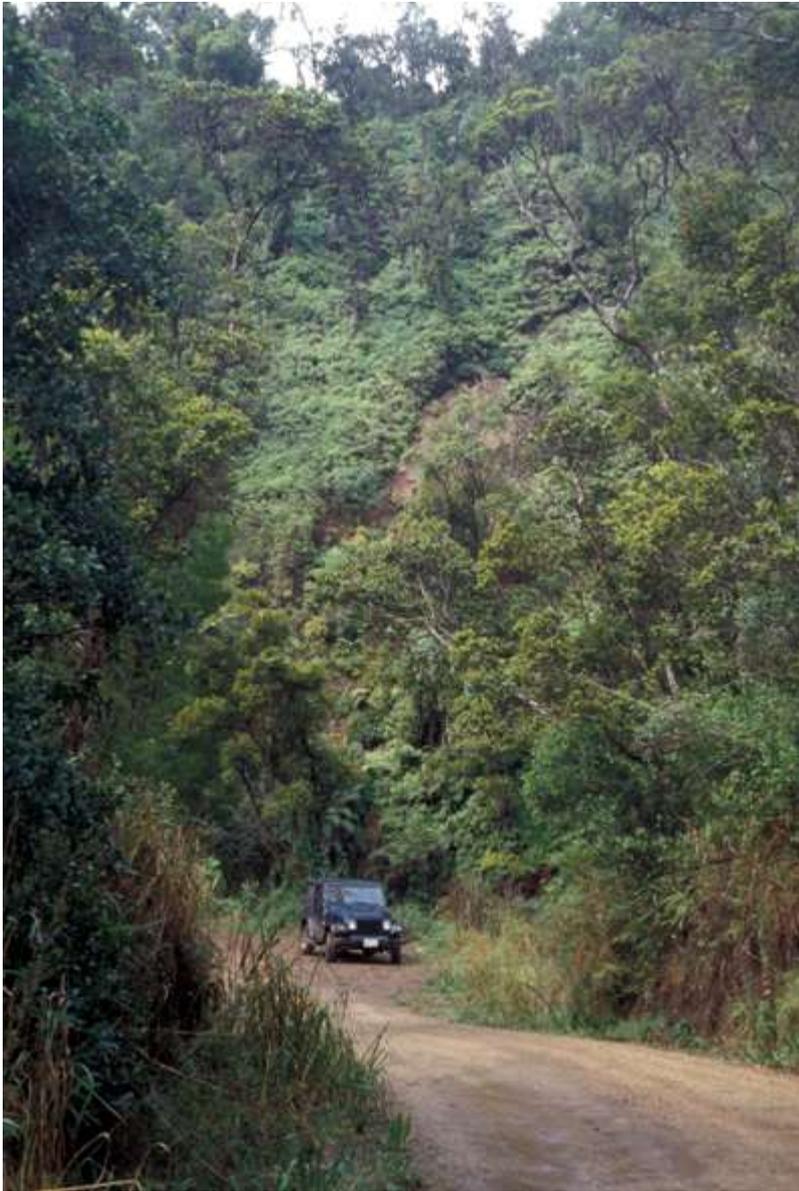


- wide niches

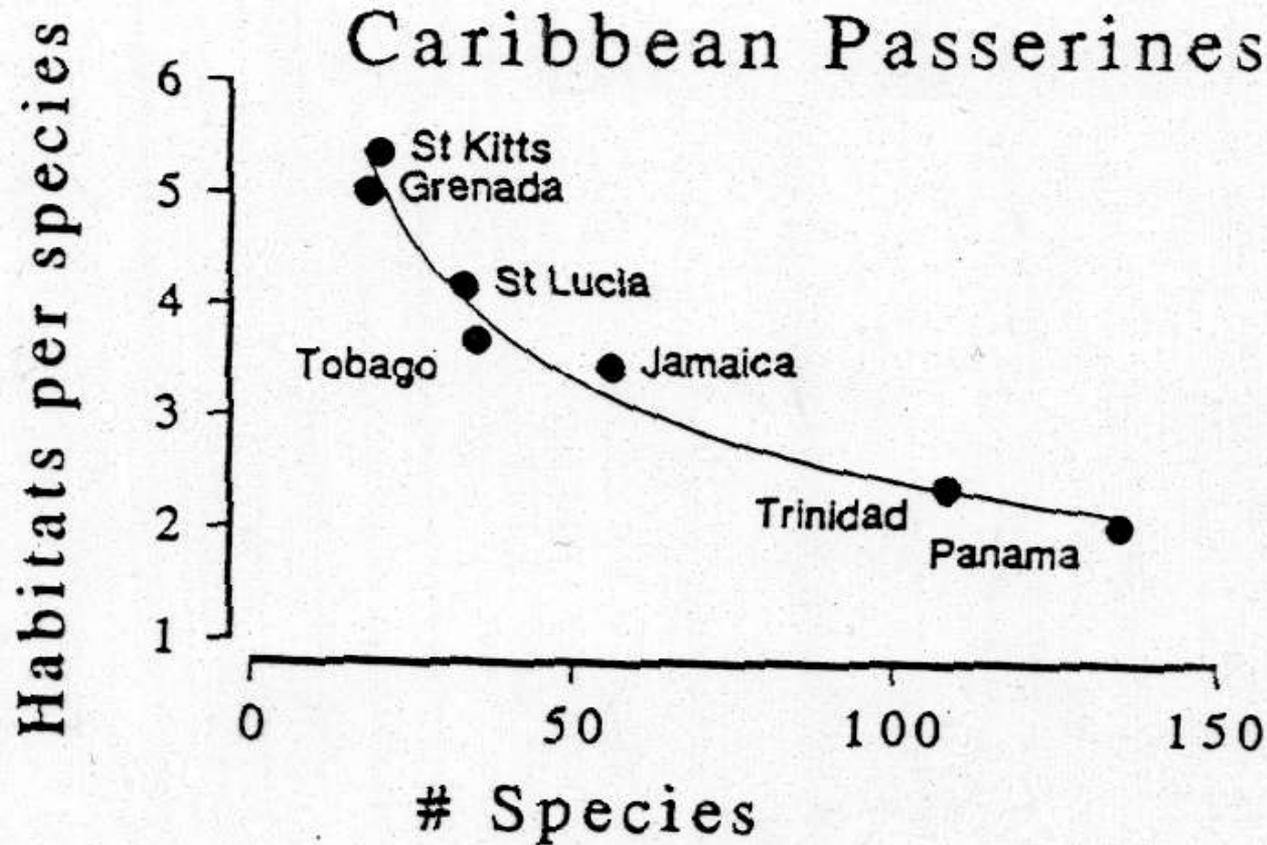
Metrosideros polymorpha (Myrtaceae): dominates Hawaiian forests from the sea shore to 2,600 m asl, as a tree or shrub



Hawaii forests: dominated by *Metrosideros polymorpha* and *Acacia koa*



Wider niches: bird species use more habitats on species poor islands



The more species of birds, the fewer habitats used by each species. Data from Cox and Ricklefs (1977) and Wunderle (1985).

- unusual shifts of ecological niches

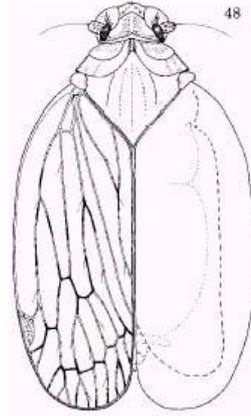
- *Euphitecia* (Geometridae): 18 spp. are the only known predatory caterpillars



- *Megalagrion oahuense* (Odonata): has terrestrial larvae
- Delphacidae (Hemiptera): ~1,800 spp. feed almost exclusively on monocotyledoneous plants, but all 135 Hawaiian spp. feed on dicotyledoneous hosts



Oliarus (Cixiidae, Hemiptera): 7 cavernicolous spp. in lava tubes, each by a separate cave colonization



wing, eye & pigment reduction



Hoch, H.
2002. Denisia
4:139-146

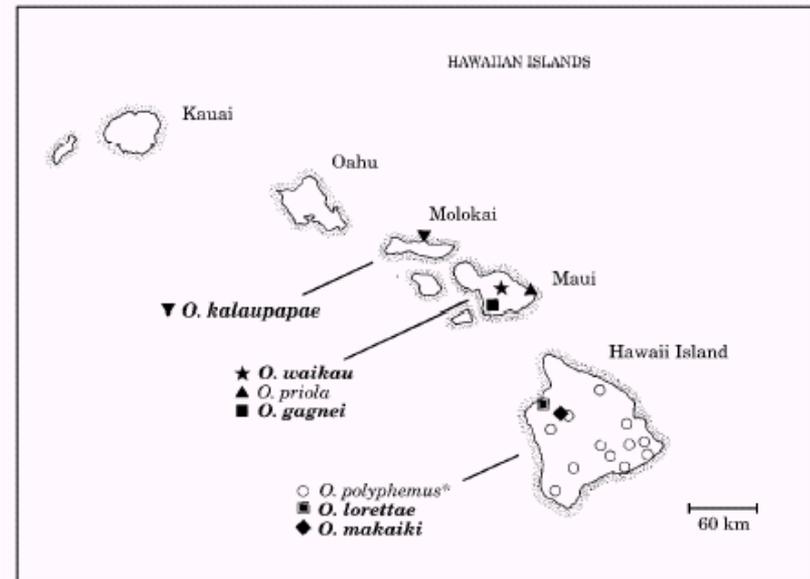


Figure 59. Distribution of cavernicolous *Oliarus* species in the Hawaiian Islands. *Localities after Hoch and Howarth (1993) and Hoch (unpublished data).

Some plants lost their anti-herbivore defence in Hawaii, such as secondary chemicals (*Mentha* spp.) or thorns (*Rubus* spp.)



Mentha sp.



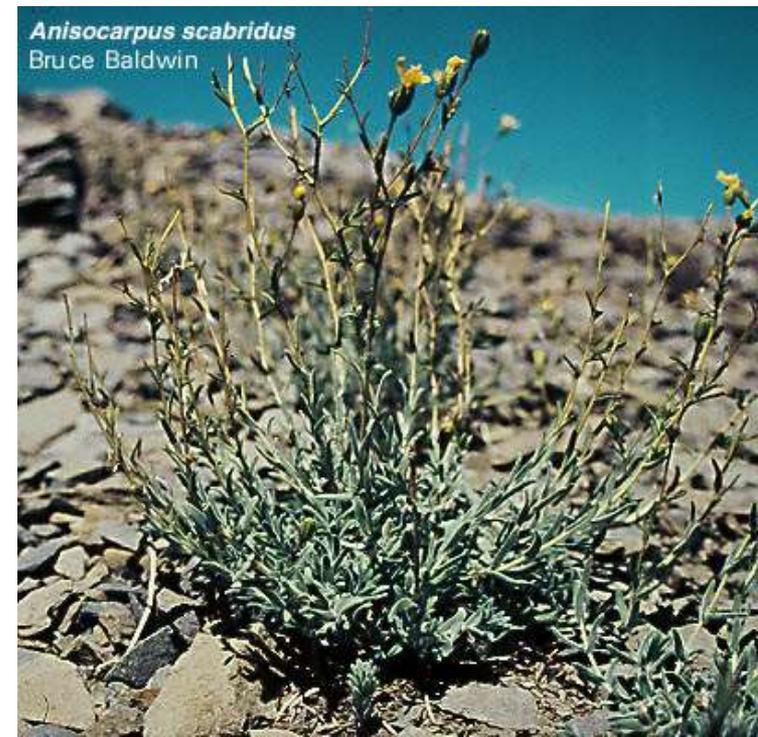
Rubus hawaiiensis

Sometimes, strange organisms evolve on islands

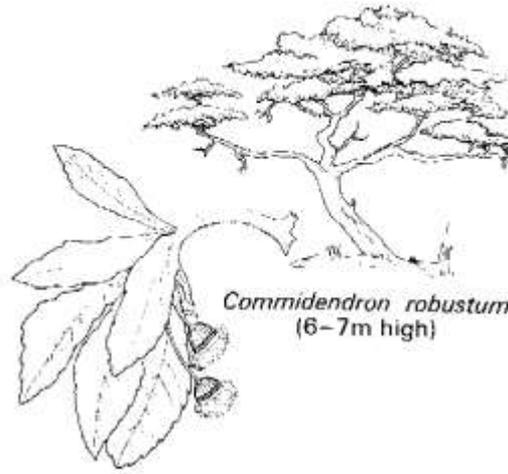
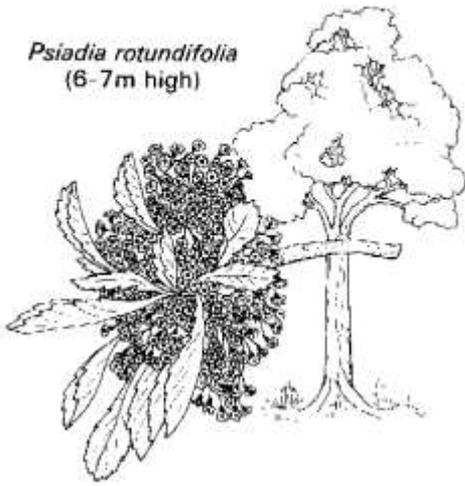


Agroxiphium sandwicense (silversword) Hawaii

Silverswords evolved after a single colonization by an Asteraceae plant near the extant *Anisocarpus*:



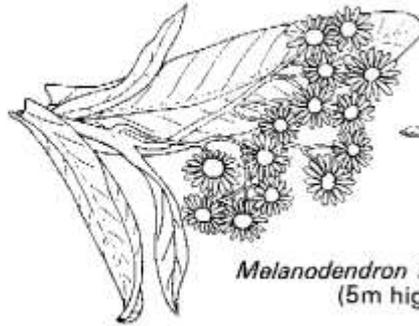
Psiadia rotundifolia
(6-7m high)



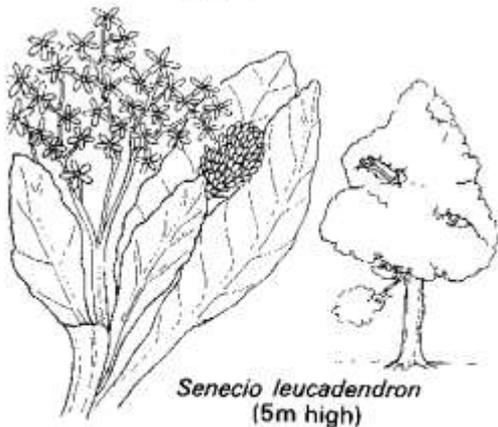
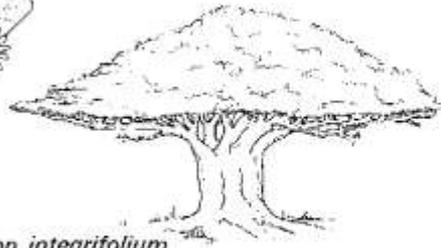
Commidendron robustum
(6-7m high)



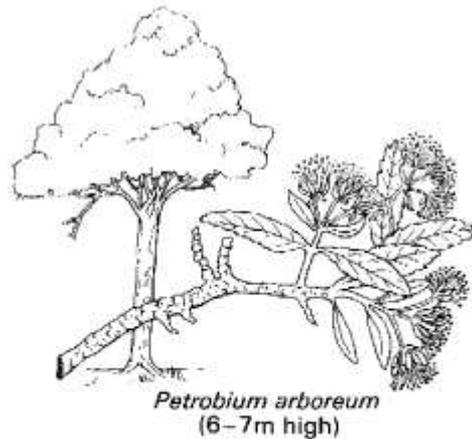
Radiation of Asteraceae on St. Helena island



Melanodendron integrifolium
(5m high)



Senecio leucadendron
(5m high)



Petrobium arboreum
(6-7m high)

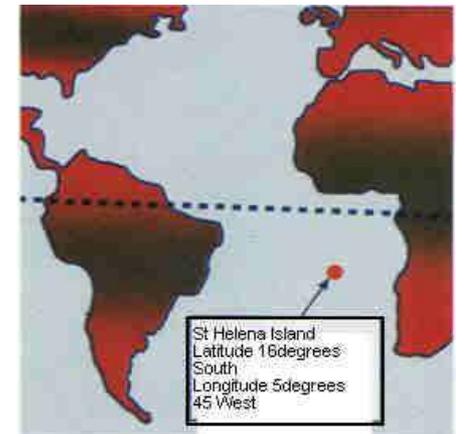
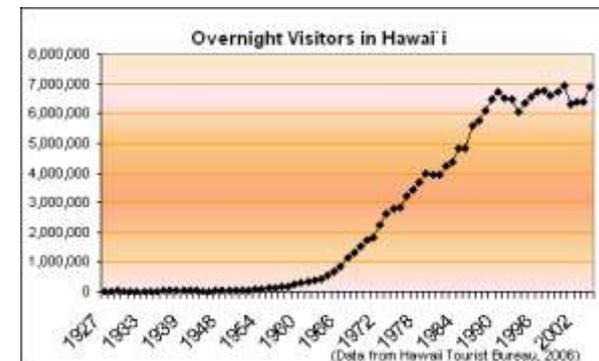
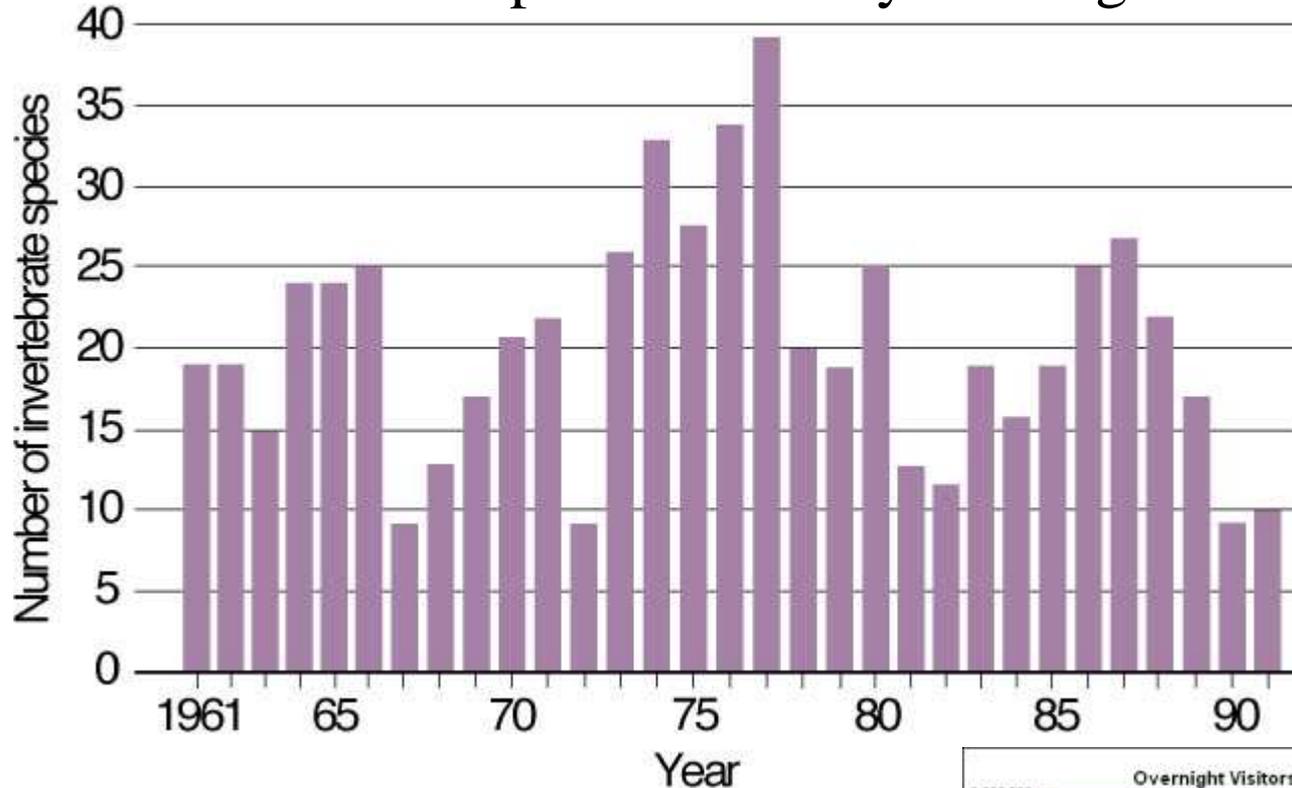


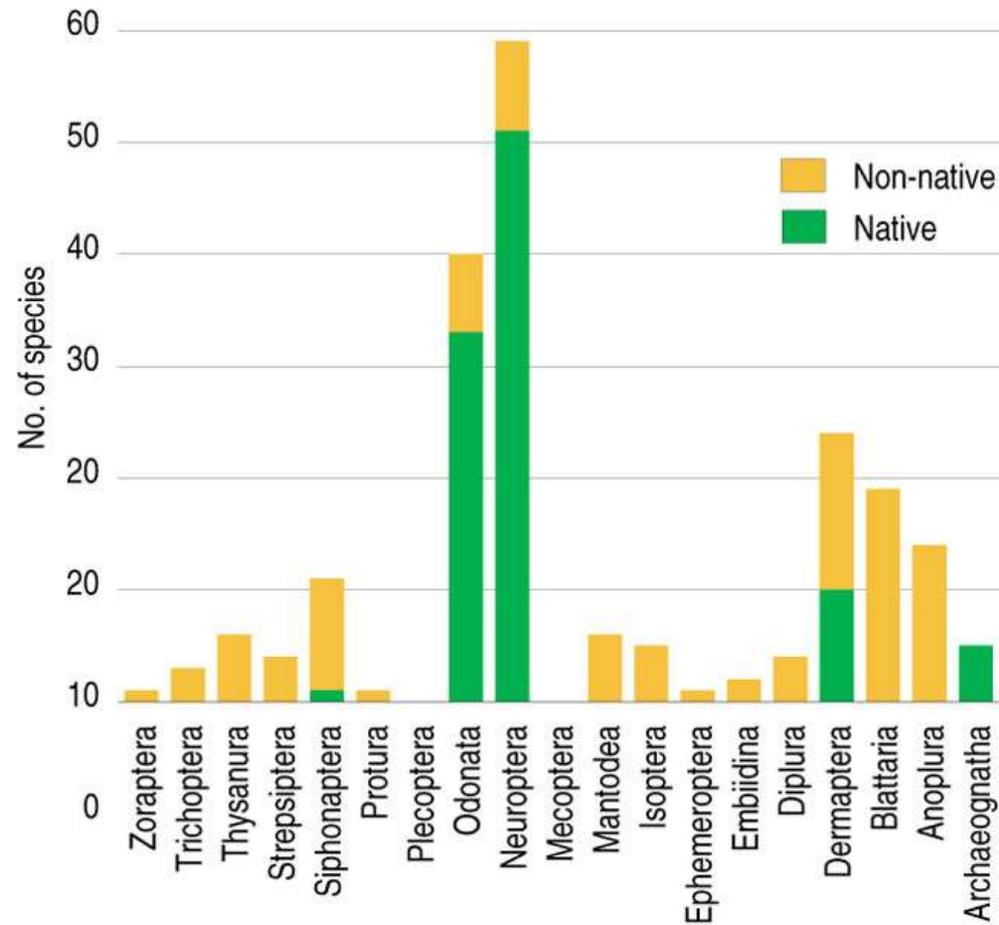
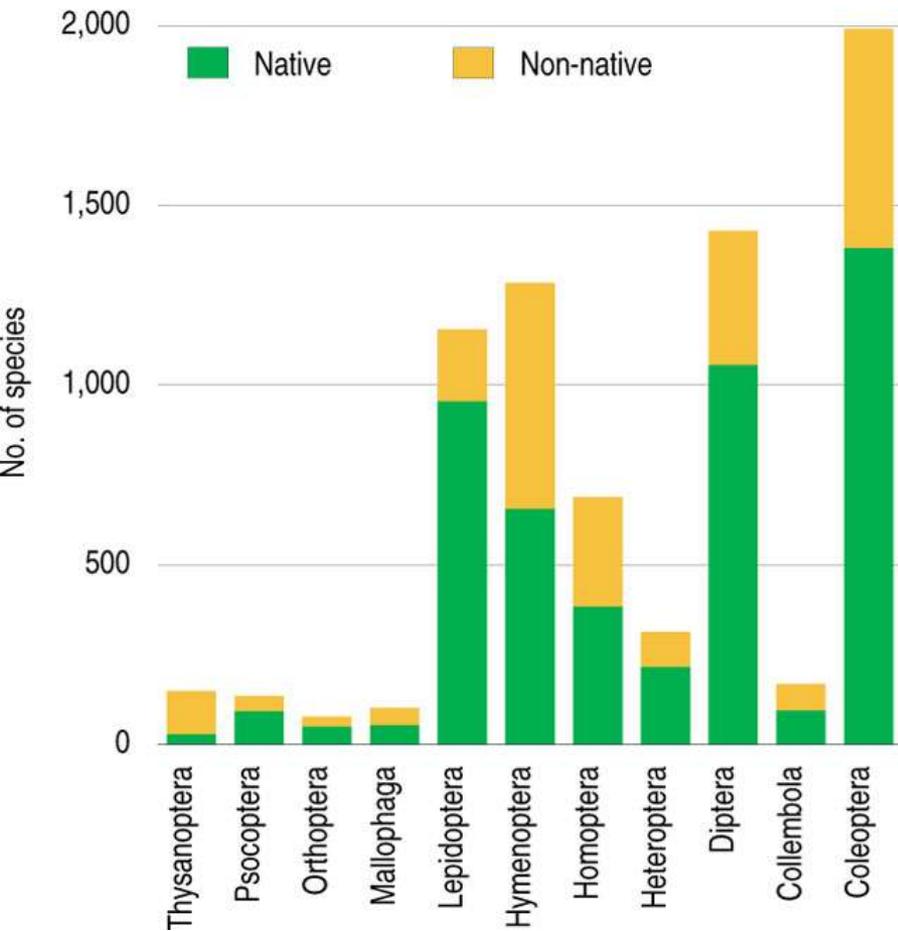
Figure 5.8. The varied trees which have evolved from immigrant sunflowers on St. Helena Island.

- susceptibility to invasive species

No. of alien invertebrate species annually arriving to Hawaii



Native and alien species of insects in Hawaii



HAWAII ISLES

endemic non-endemic alien

flowering

plants

1,100

87

800

ferns

105

37

21

birds

44

12

38

land

mammals

0

0

18

insects

5,000

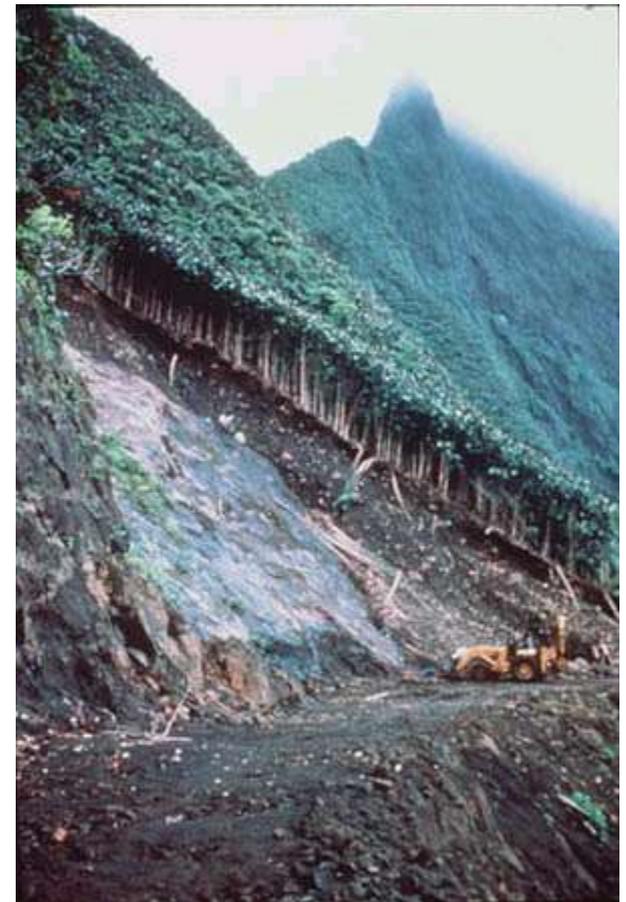
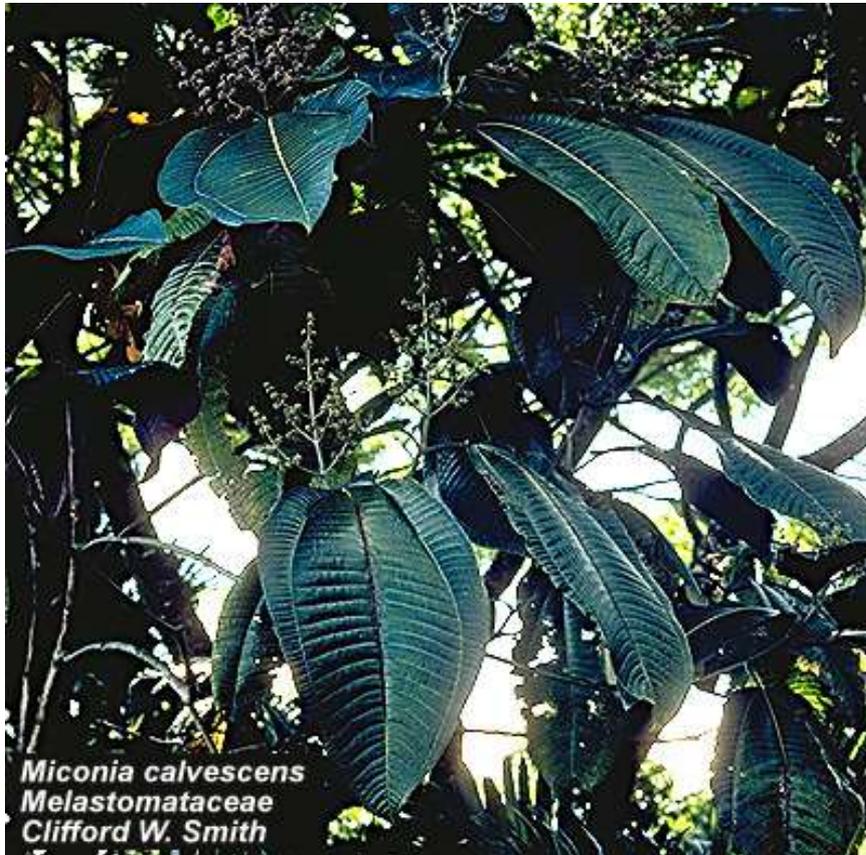
>100

2,700

(?10,000)

Miconia calvescens (Melastomataceae)

Origin in South America, spreading in Hawaii and the Pacific.
In Tahiti invaded native vegetation and now dominates >60% of local forests, often forming monospecific stands..



Monospecific *Miconia* stand in Tahiti

Falcataria moluccana (Fabaceae)

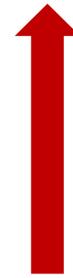
Large, fast growing N-fixing pioneer, colonizes disturbed sites on Pacific islands. In Hawaii on lava flows, its nitrogen input (240 kg N per ha and year - comparable to industrial fertilization levels for crops) was 4-55x greater than from native vegetation, altering successional trends – facilitating alien *Psidium cattleianum*, suppressing native dominant *Metrosideros polymorpha*



Falcataria moluccana



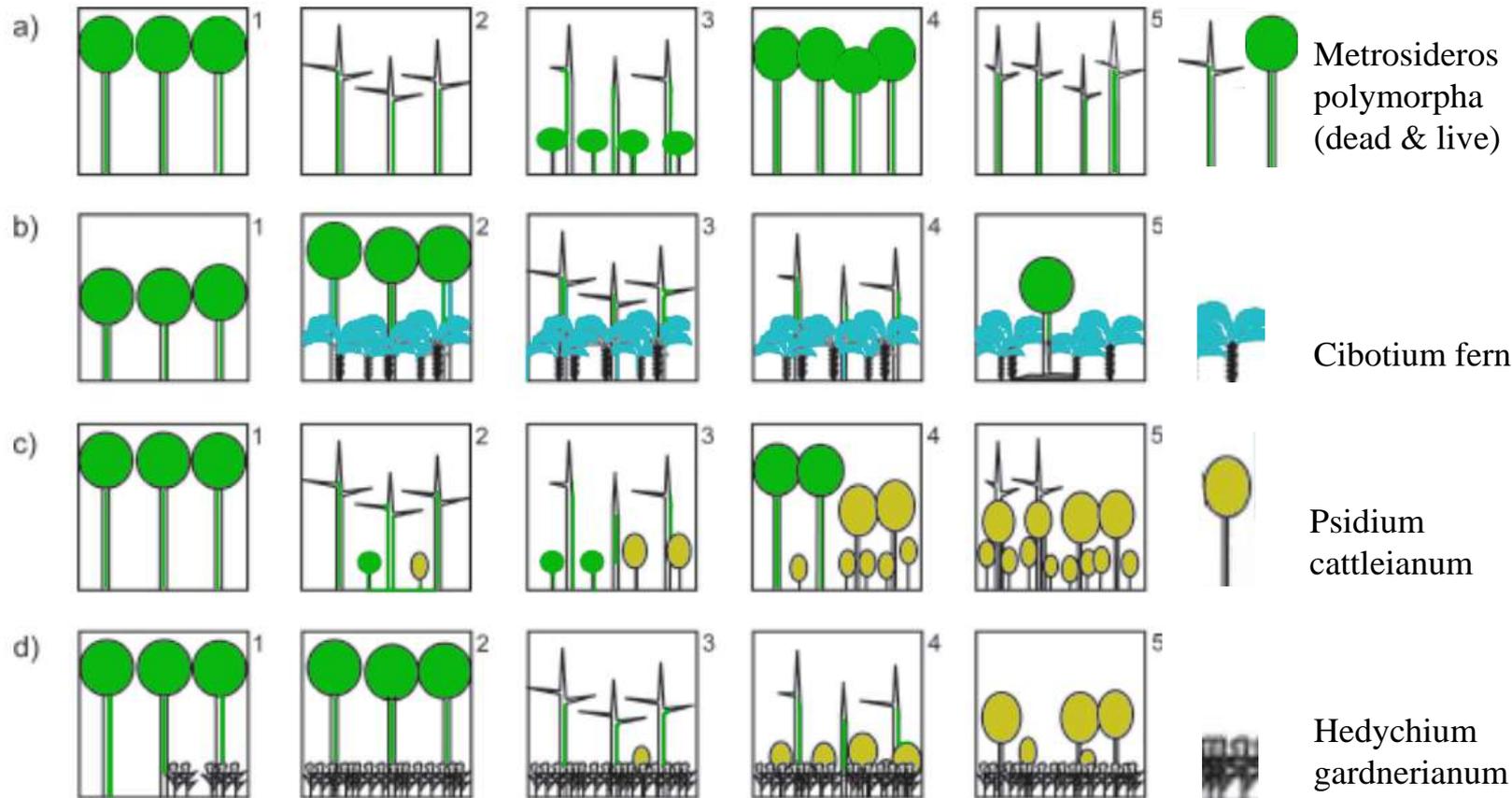
*Metrosideros
polymorpha*



*Psidium
cattleianum*



Invasive spp. changing Hawaii forest dynamics



M. polymorpha forest dynamics – simple replacement of dead trees by conspecific recruits (a) or the replacement is slowed on nutrient rich soils by native tree fern *Cibotium* (b).

Invasive *P. cattleianum* colonizes tree gaps and suppresses *Metroxylon* regeneration producing *Psidium* forest (c) or dominance in the understory by invasive ginger *Hedychium* that suppresses *Metroxylon* but not *Psidium*, resulting in *Psidium* forest with *Hedychium* understorey..



a



b

Christmas Island

Invasion of ‘crazy ant’
Anoplolepis gracilipes



Elimination of *Gecarcoidea natalis* crab



Increase in forest
understorey cover

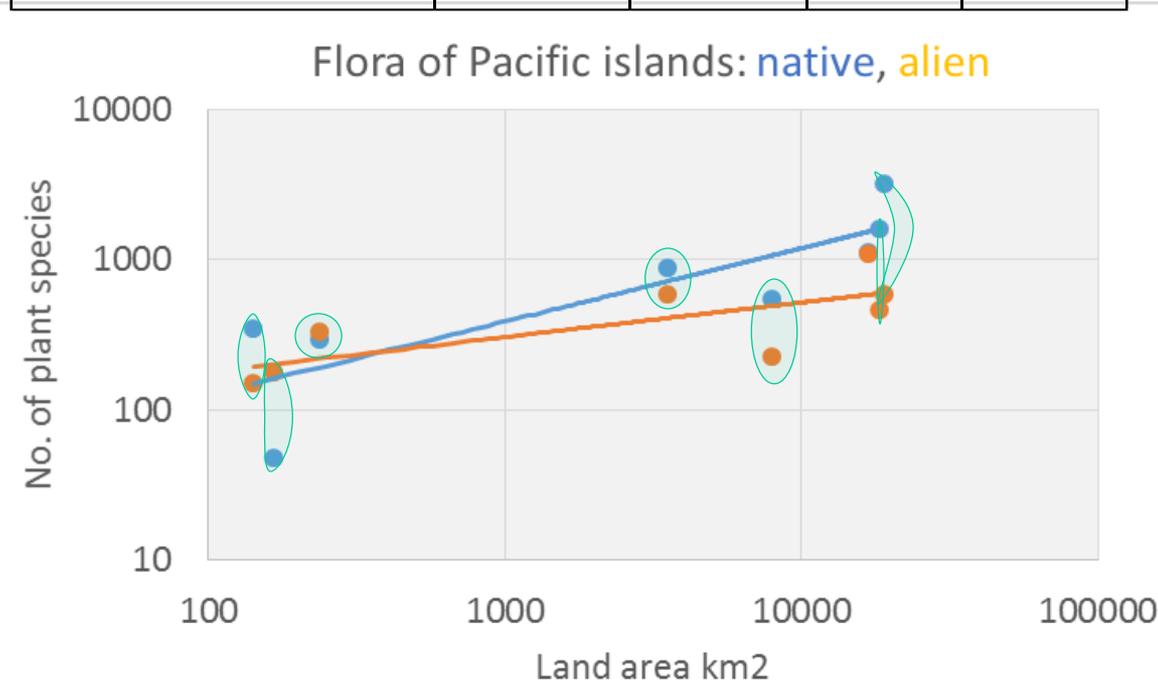
O’Dowd et al. 2003 Ecology Letters, 6: 812–817

community structure and ecosystem function. Here we show invasion by the alien crazy ant, *Anoplolepis gracilipes* causes a rapid, catastrophic shift in the site from an open area of a tropical oceanic island, affecting at least three trophic levels. In invaded areas, crazy ants exclude the red land crab, the dominant endemic consumer on the forest floor. In doing so, crazy ants indirectly release seedling recruitment, enhance species richness of seedlings, and thus alter forest dynamics. In the forest canopy, more associations between the invasive ant and *Acacia* are observed, leading to more *Acacia* recruitment and diversity impacts. Sustained high densities of foraging ants on canopy trees result in high population densities of *Homocidus* and other predators and growth of canopy insects, leading to canopy defoliation and even deaths of canopy trees. The indirect effects from the displacement of a major ‘keystone’

Figure 1 Impacts of invasion of island rain forest by the yellow crazy ant, *Anoplolepis gracilipes*. (a) Uninvaded site (Wainfred Track) with open understorey maintained largely by the foraging activities of the red land crab, *Gecarcoidea natalis*. (b) Invaded site (Dales) 1–2 years after ant invasion with a dense and diverse seedling cover and thick litter layer. Photographs by Peter Green.

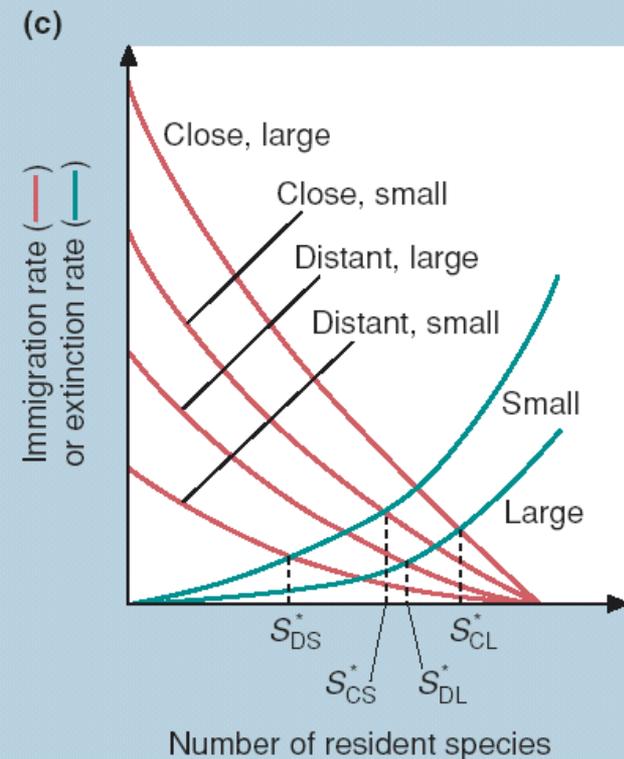
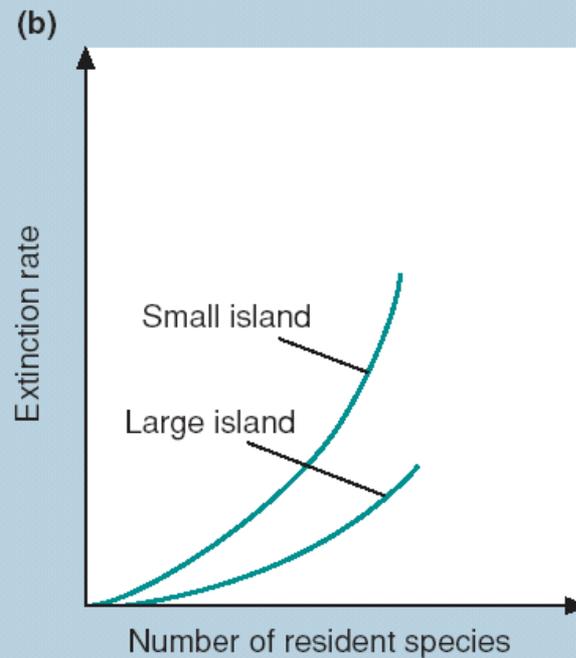
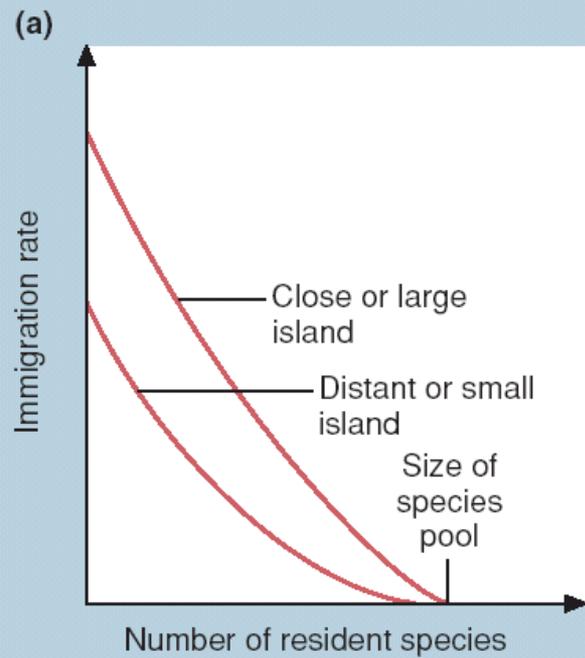
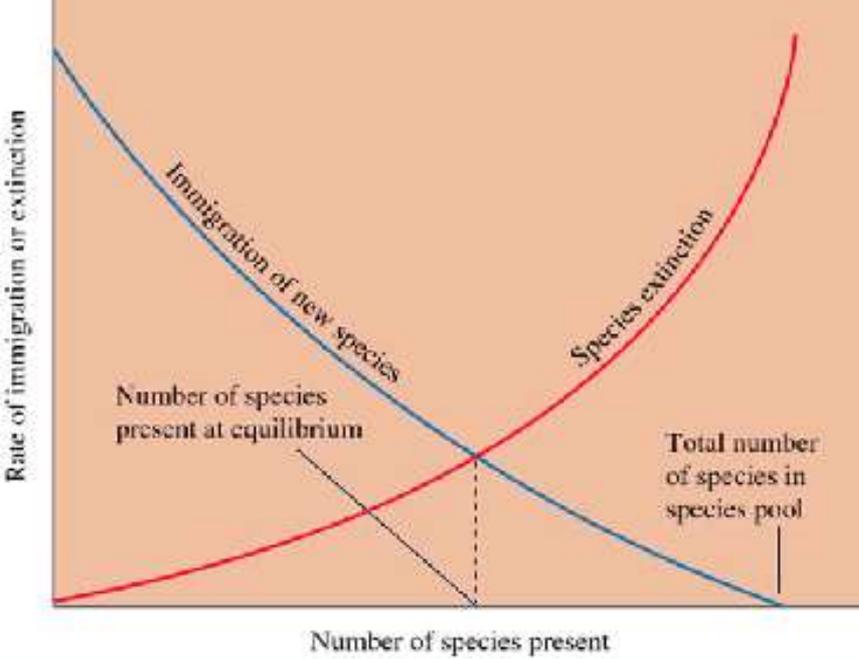
Pacific islands floras: 15-79% alien

	Area km ²	Native	Alien	% alien
New Caledonia	19060	3261	595	15
Fiji	18270	1622	461	22
Hawai'i	16880	1138	1104	49
Galápagos	7900	550	229	29
French Polynesia	3519	885	593	40
Cook Is.	238	296	333	53
Rapa Nui (Easter Is.)	166	48	180	79
Wallis et Futuna	142	351	151	30

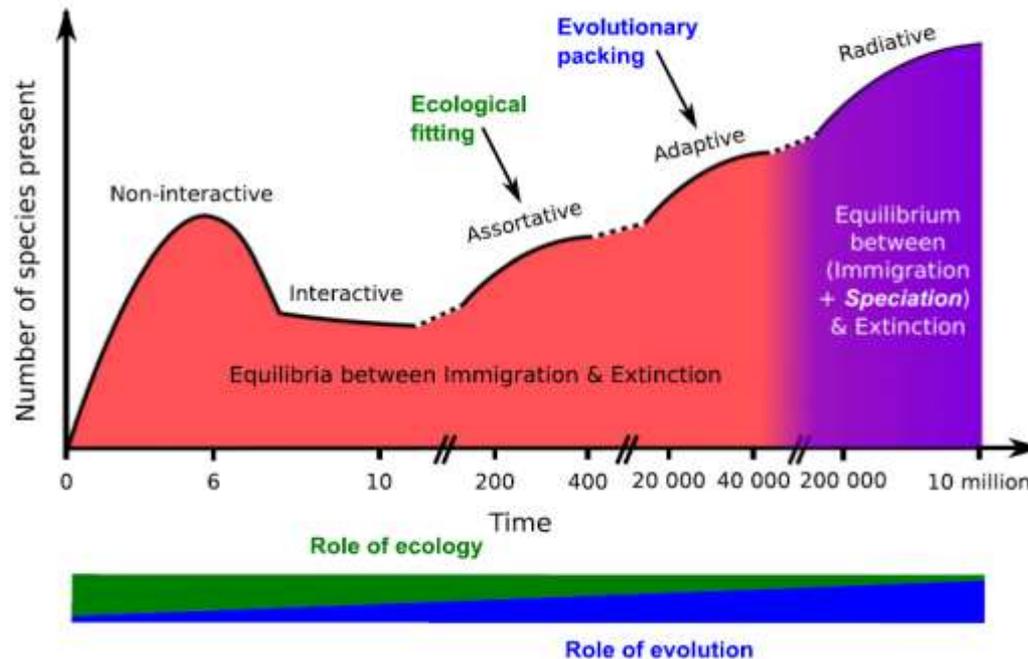


Native and alien data points for each site are connected:
At 3 sites, alien flora equals or exceeds native

Island biogeography



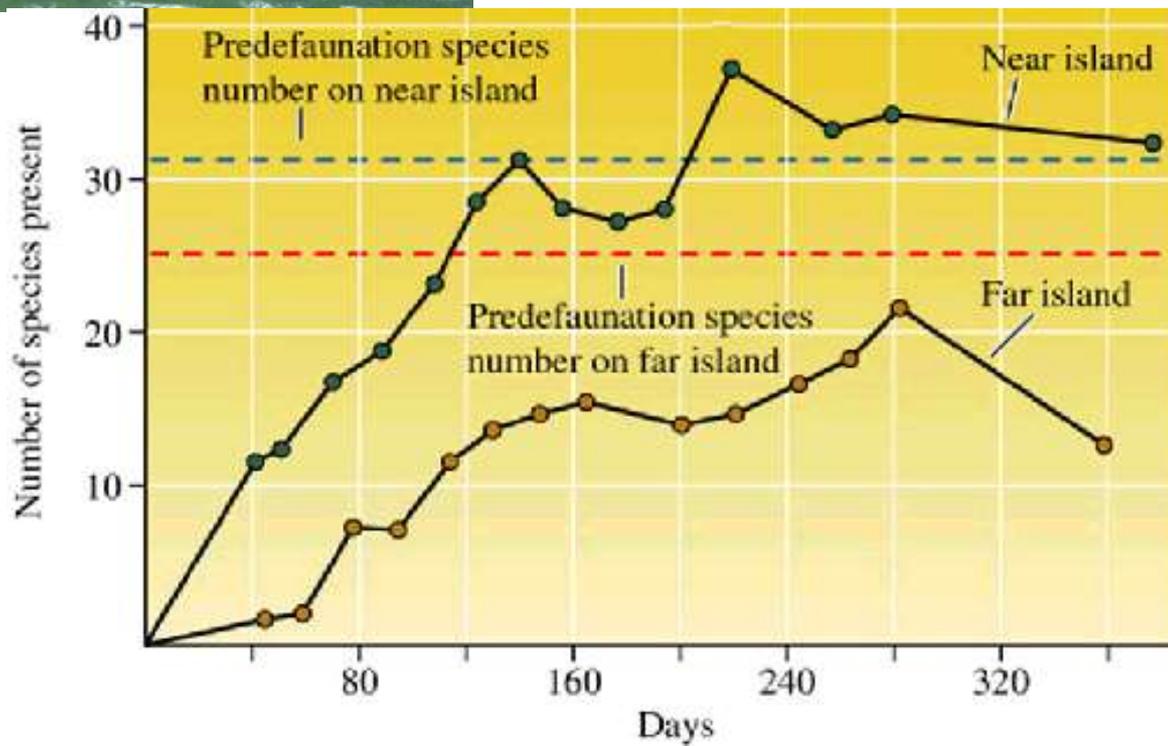
Ecological – evolutionary continuum in equilibrium number of species in communities



- (1) Non-interactive equilibrium: prior to the attainment of high population densities needed to make species competitive exclusion a major factor in extinction,
- (2) Interactive equilibrium: species interactions incl. competitive exclusion are a major factor
- (3) Assortative equilibrium: in response to environmental filtering, i.e. the conditions of the local environment and interactions with other species over the long term,
- (4) Adaptive equilibrium: reached when populations undergo evolutionary adaptive change in response to environmental conditions and other species.

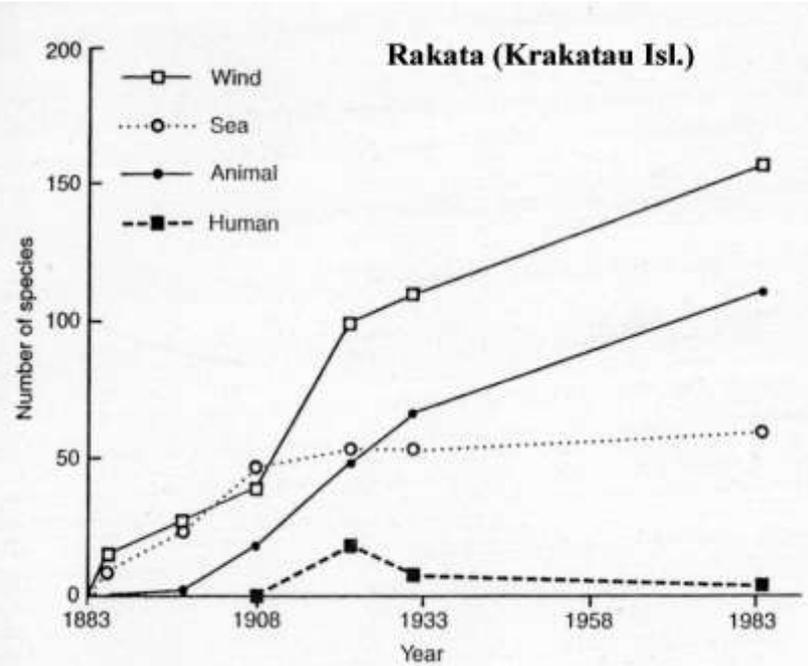
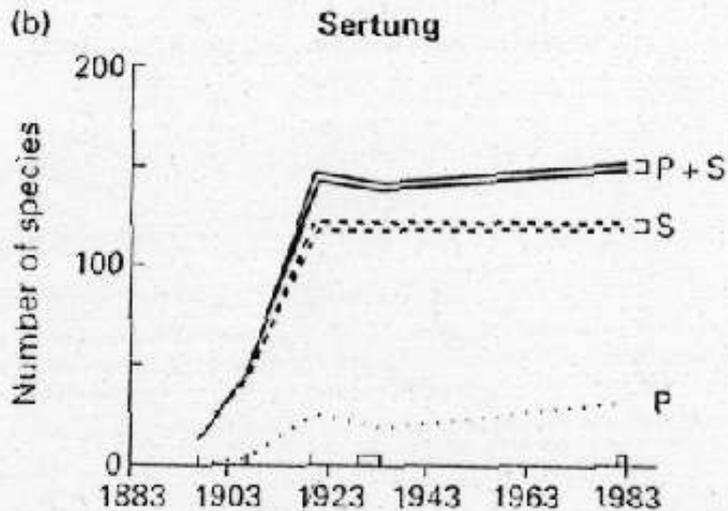
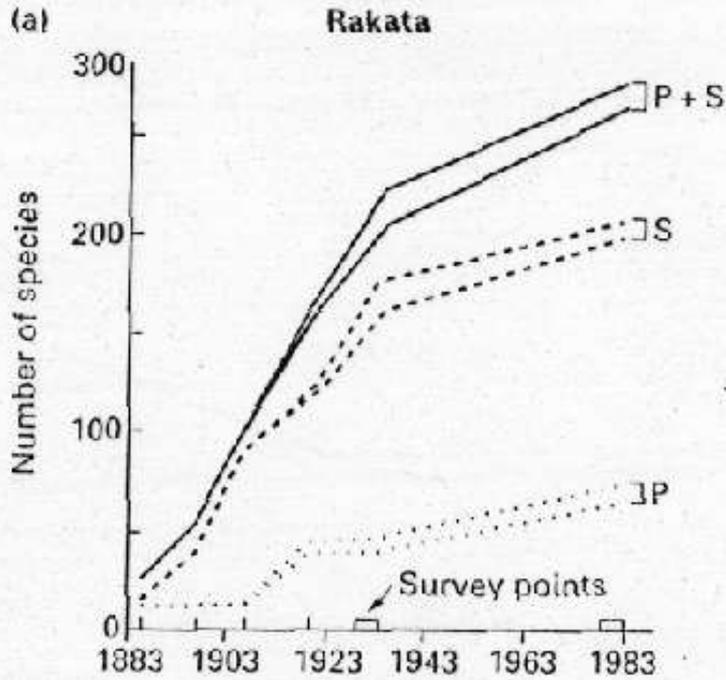


Wilson and Simberloff (1970):
experimental tests of the theory,
monitoring arthropod immigration and
extinction after complete defaunation
of small mangrove islands offshore
Florida



SUCCESSION ON KRAKATAU

S spermatophyta P pteridophyta

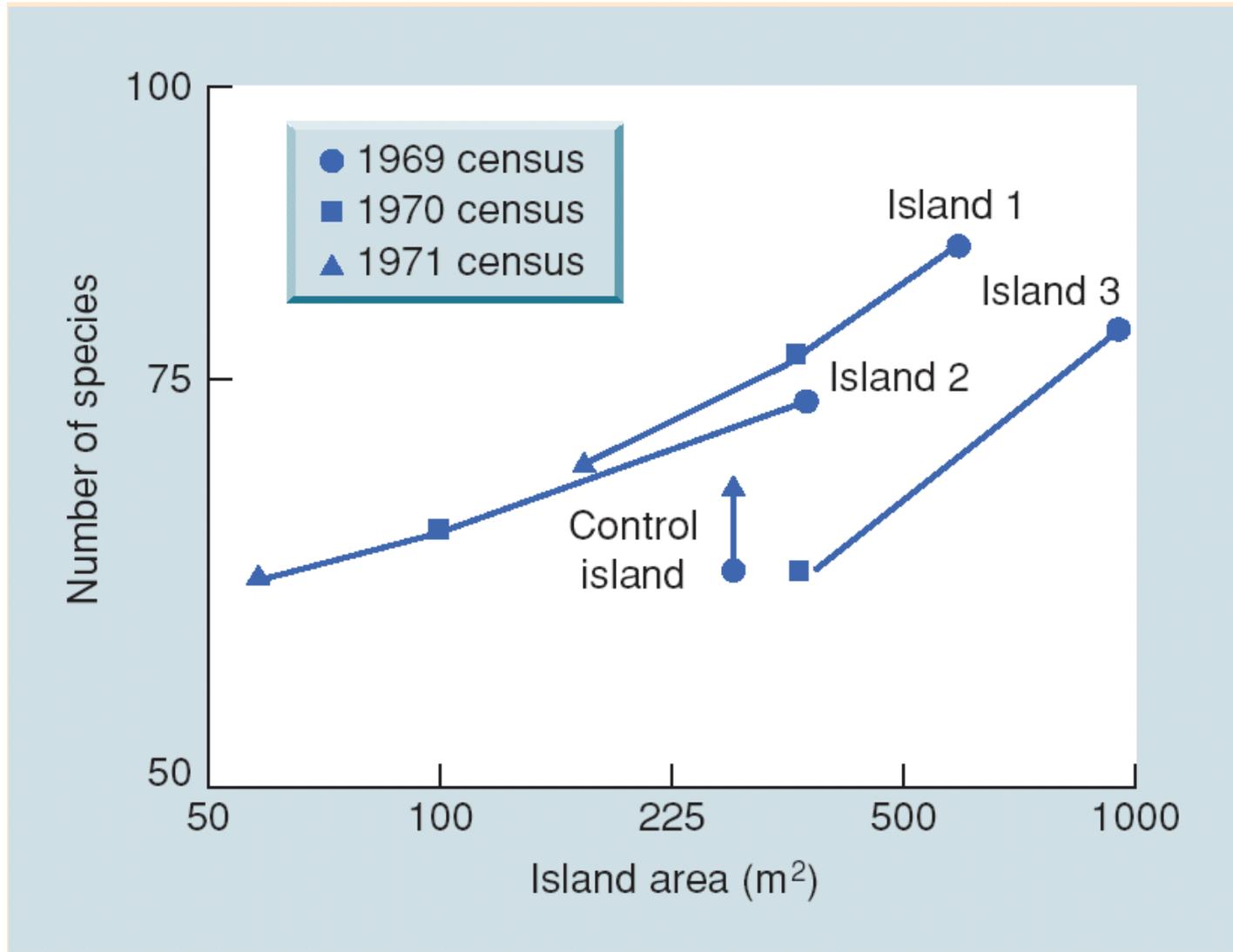


Species accumulation after defaunation of Krakatau

Fig. 4.18 Number of species recorded in particular survey periods for Pteridophyta (P), Spermatophyta (S) and all higher plants (P+S) for the three older Krakatau Islands: (a) Rakata; (b) Sertung; and (c) Rakata Kecil. The ranges take into account the uncertain identification of some taxa. (After Whittaker *et al.* 1989.)

Figure 12.3 Dispersal mode spectra of vascular plants on Rakata at successive survey periods. Surveys made in the periods 1920–24, 1929–34 and 1979–89 are grouped and the data plotted at the mid-point of these periods. Note: (1) how the presence of sea-dispersed plants levelled out after 1924; and (2) the increase in wind-dispersed plants between 1908 and 1924, which was largely due to the arrival and colonisation of species adapted to the more shady conditions provided by the developing forest canopy (adapted from Thornton 1996; Whittaker *et al.* 1992). Reprinted by permission of the publishers from Krakatau by Ian Thornton, Cambridge, MA: Harvard University Press, Copyright © 1996

Experimental test of the effect of island area on species richness



The effect on the number of arthropod species of artificially reducing the size of mangrove islands. Islands 1 and 2 were reduced in size after both the 1969 and 1970 censuses. Island 3 was reduced only after the 1969 census. The control island was not reduced, and the change in its species richness was attributable to random fluctuations. (After Simberloff, 1976.)

Reptiles and amphibians in the Caribbean: an example of species-area relationships for islands

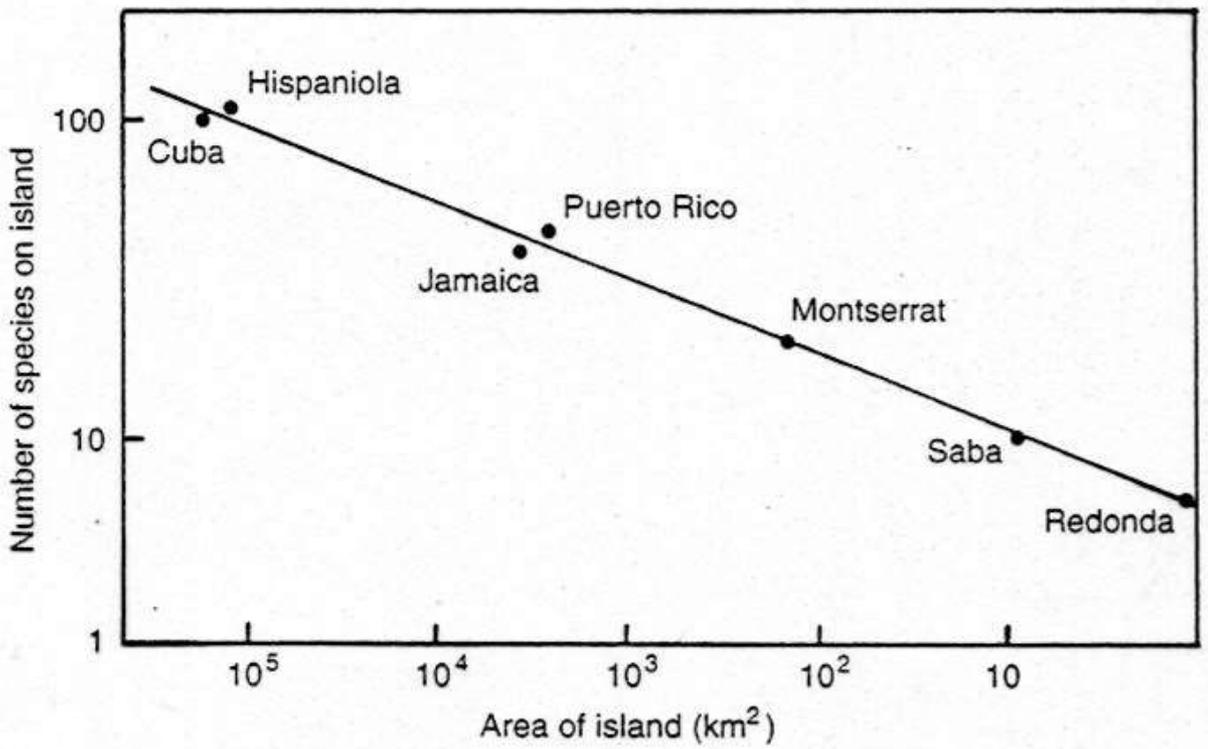
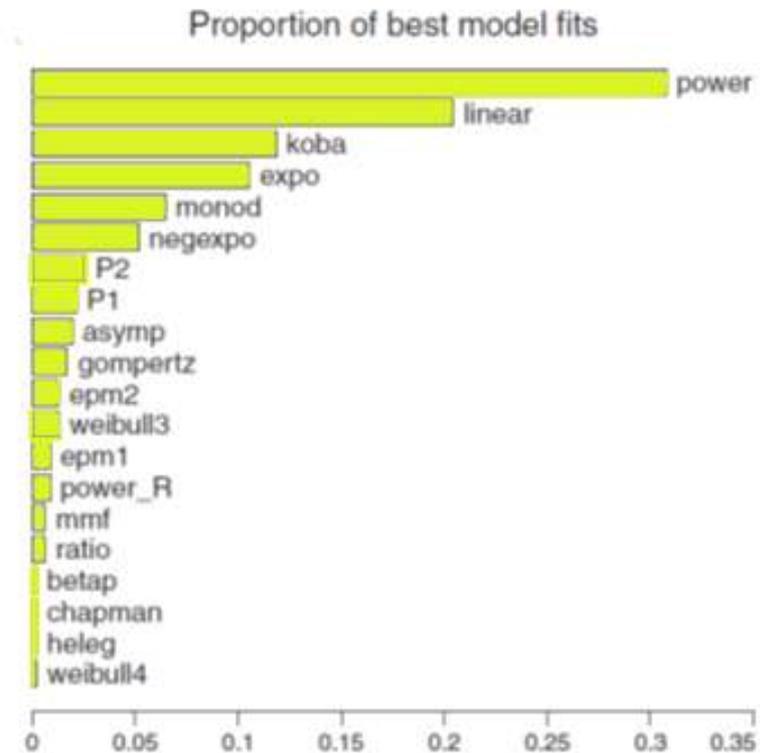


Figure 12.9 The number of species of reptiles and amphibians on seven Caribbean islands plotted against island size (after MacArthur and Wilson 1967; Wilson 1992).

Relationship between island size and number of species: always power?

Function name	Formula	Shape type	Asymptote
Linear	$S = c + zA$	Linear	No
Power	$S = cA^z$	Convex	No
Power Rosenzweig	$S = k + cA^z$	Convex	No
Extended Power 1	$S = cA^{zA-d}$	Both	No
Extended Power 2	$S = cA^{z-(d/A)}$	Sigmoid	No
Persistence Function 1	$S = cA^z \exp(-dA)$	Convex	No
Persistence Function 2	$S = cA^z \exp(-d/A)$	Sigmoid	No
Exponential	$S = c + z \log A$	Convex	No
Kobayashi Logarithmic	$S = c \log(1 + A/z)$	Convex	No
Monod	$S = d/(1 + cA^{-1})$	Convex	Yes (d)
Morgan–Mercer–Flodin	$S = d/(1 + cA^{-z})$	Sigmoid	Yes (d)
Logistic	$S = c/(f + A^{-z})$	Sigmoid	Yes (c/f)
Negative Exponential	$S = d[1 - \exp(-zA)]$	Convex	Yes (d)
Chapman–Richards	$S = d[1 - \exp(-zA)]^c$	Sigmoid	Yes (d)
Weibull-3	$S = d[1 - \exp(-cA^z)]$	Sigmoid	Yes (d)
Weibull-4	$S = d[1 - \exp(-cA^z)]^d$	Sigmoid	Yes (d)
Asymptotic	$S = d - cz^A$	Convex	Yes (d)
Rational	$S = (c + zA)/(1 + dA)$	Convex	Yes (z/d)
Gompertz	$S = d \exp[-\exp(-z(A-c))]$	Sigmoid	Yes (d)
Beta-P	$S = d[1 - (1 + (A/c^z)^{-f})^{-f}]$	Sigmoid	Yes (d)

Species-area functions: S = no. of species, A = area, c , d , f , z = fitted parameters; asymptote's value in brackets (last column)



Island species–area relationship models across 465 data sets

Species-area relationships from SE Asia

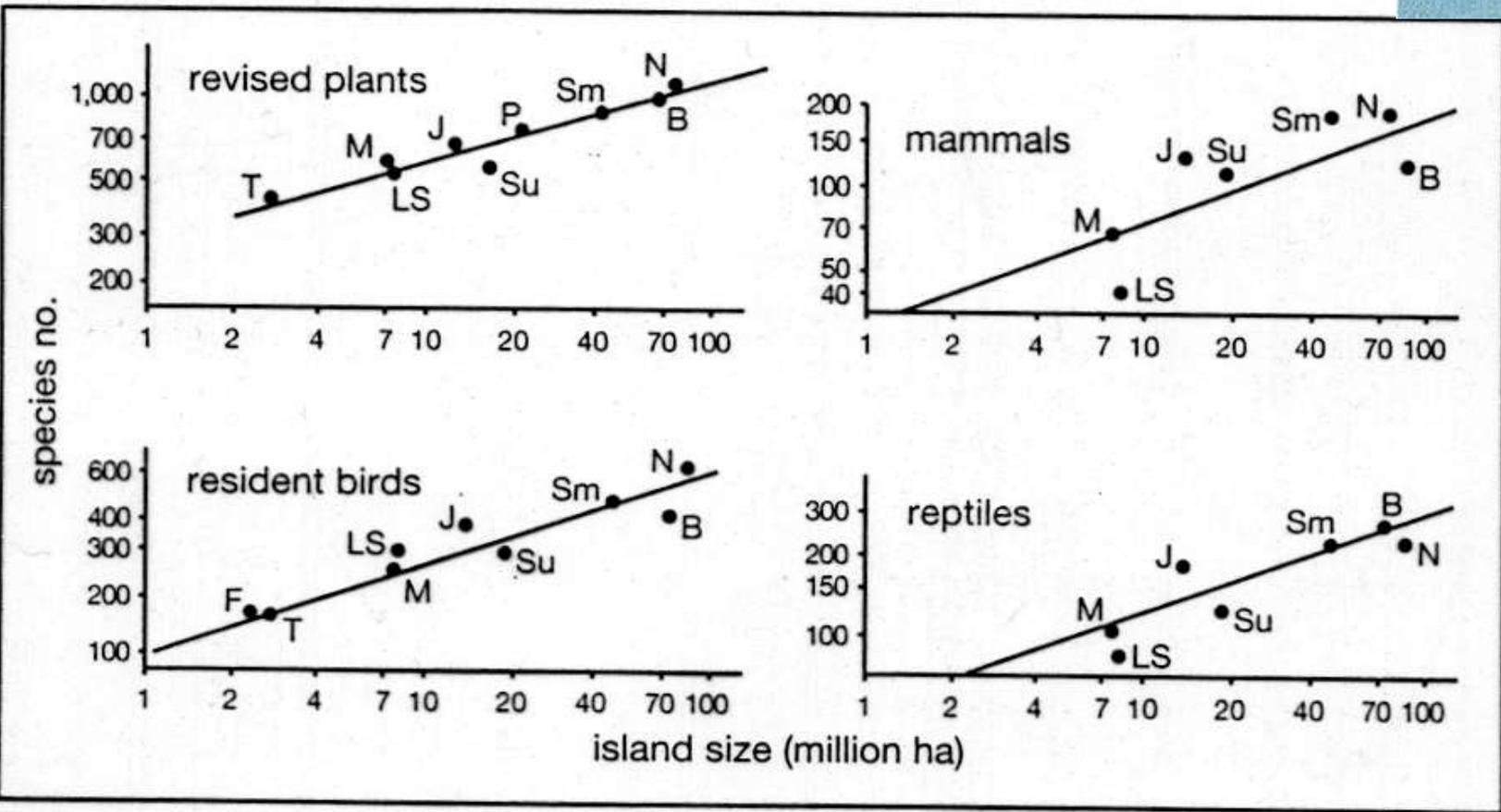
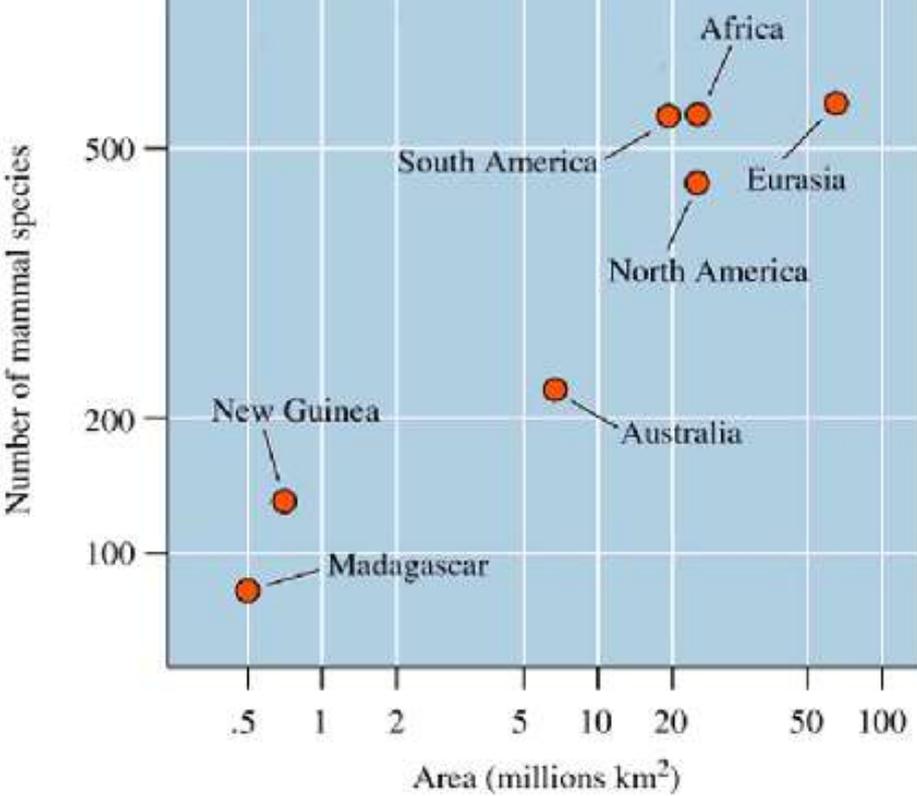
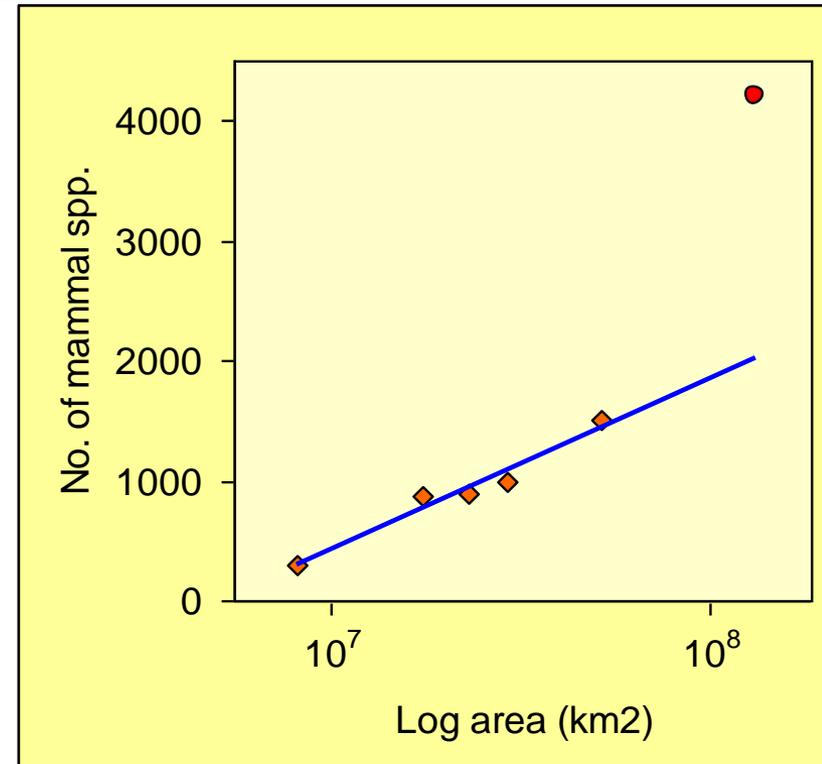


Figure 1.19. Relationship between number of species and island size for revised plants (reviewed in Flora Malesiana), resident birds, mammals and reptiles. B - Borneo, F - Flores, J - Java, LS - Lesser Sundas, M - Moluccas, N - New Guinea, Sm - Sumatra, Su - Sulawesi, T - Timor.



The fragmentation of land to five continents doubled species richness of mammal species in the world



Species-area relationship for large islands and continents



Species richness on islands tends to be lower than in mainland areas of the same size: ants in New Guinea and smaller islands

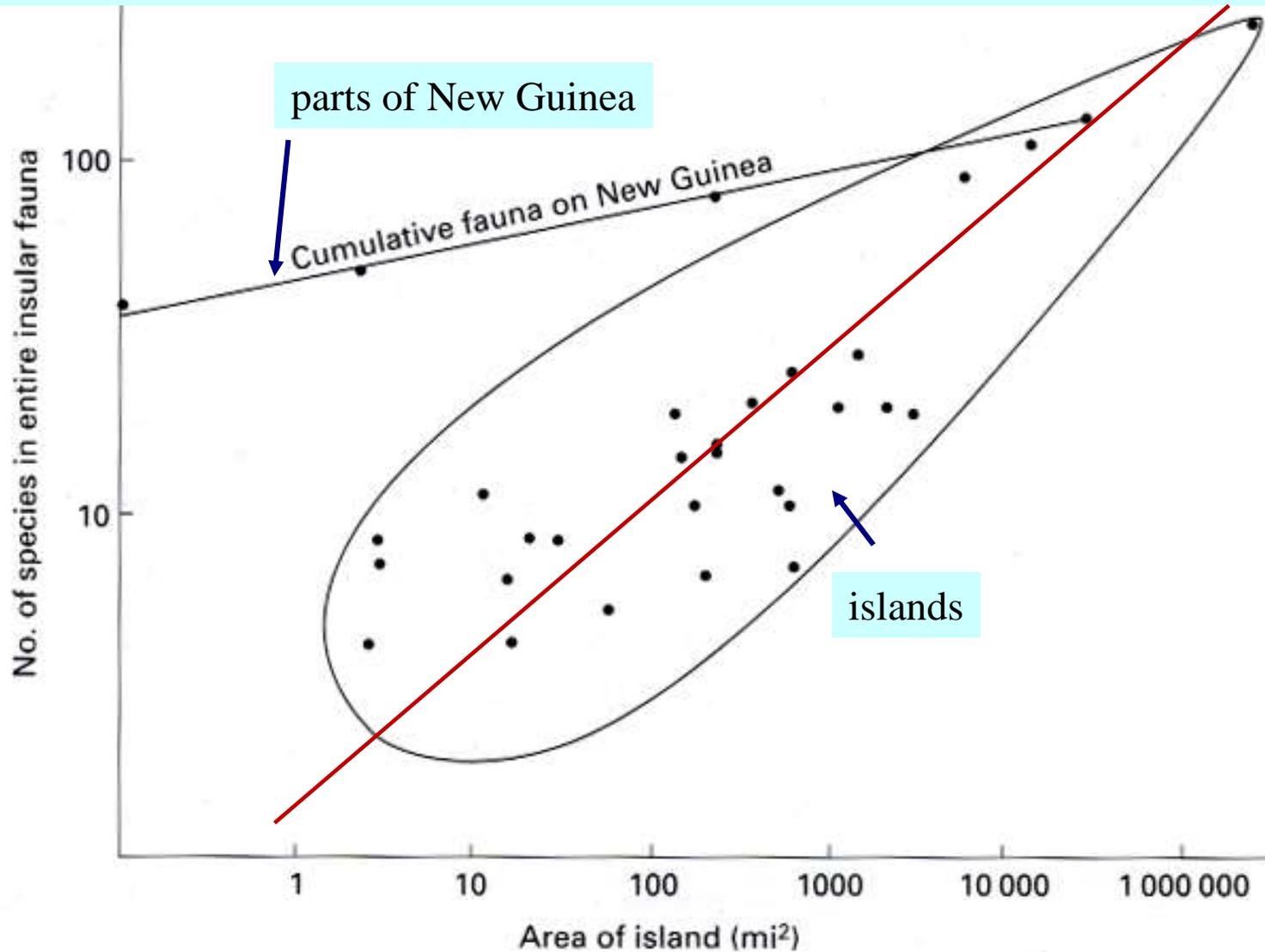
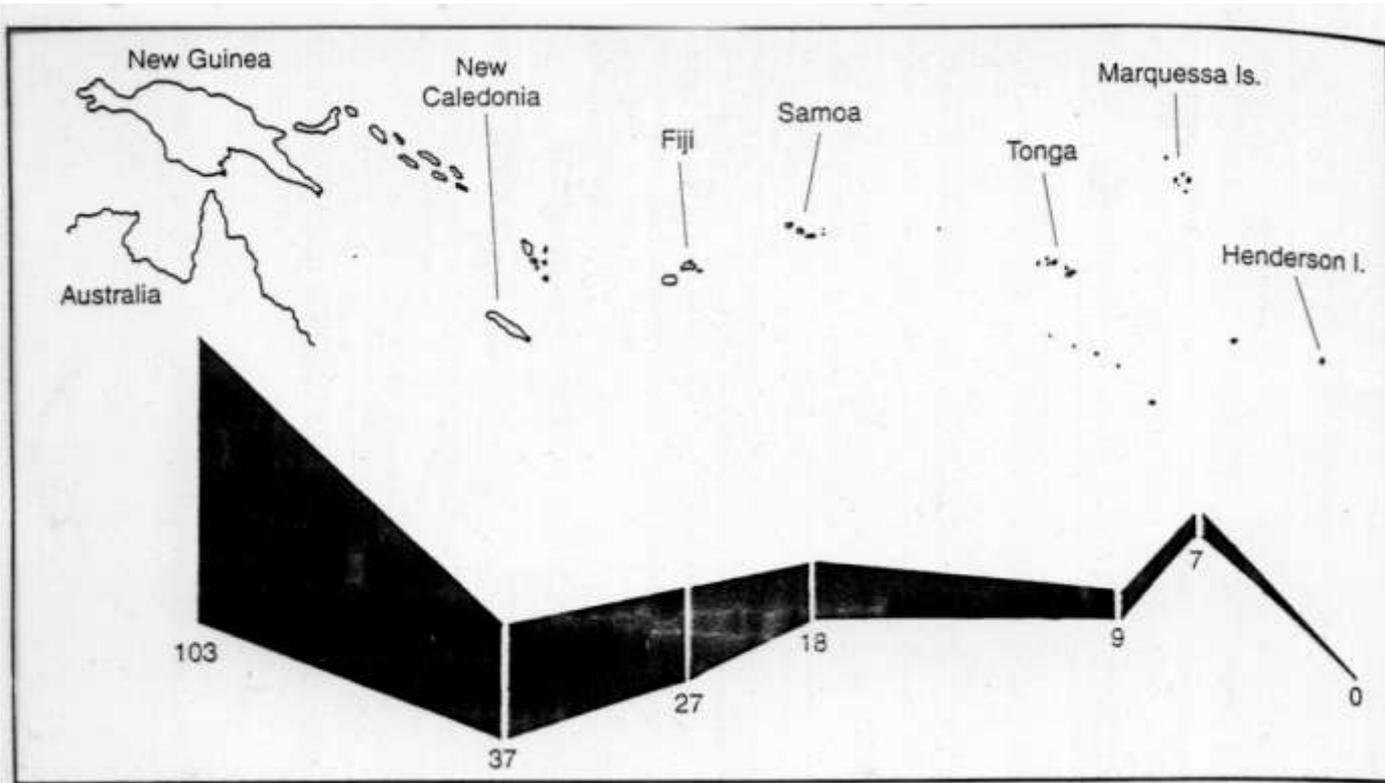


Fig. 8.14 The relationship between the number of (ponerine and cerapachyine) ant species found on different Maluccan and Melanesian islands and the area of these islands. (From Wilson 1961, with permission from The University of Chicago Press.)

Species-area relationship: combined effect of island isolation and size

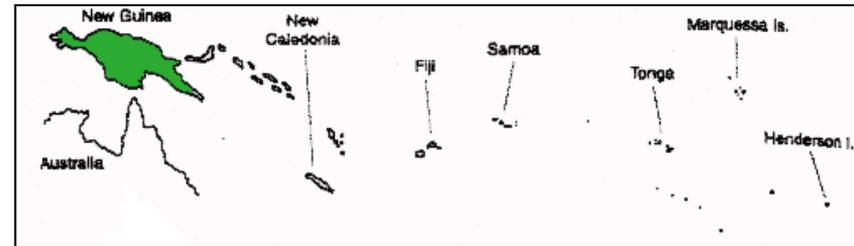
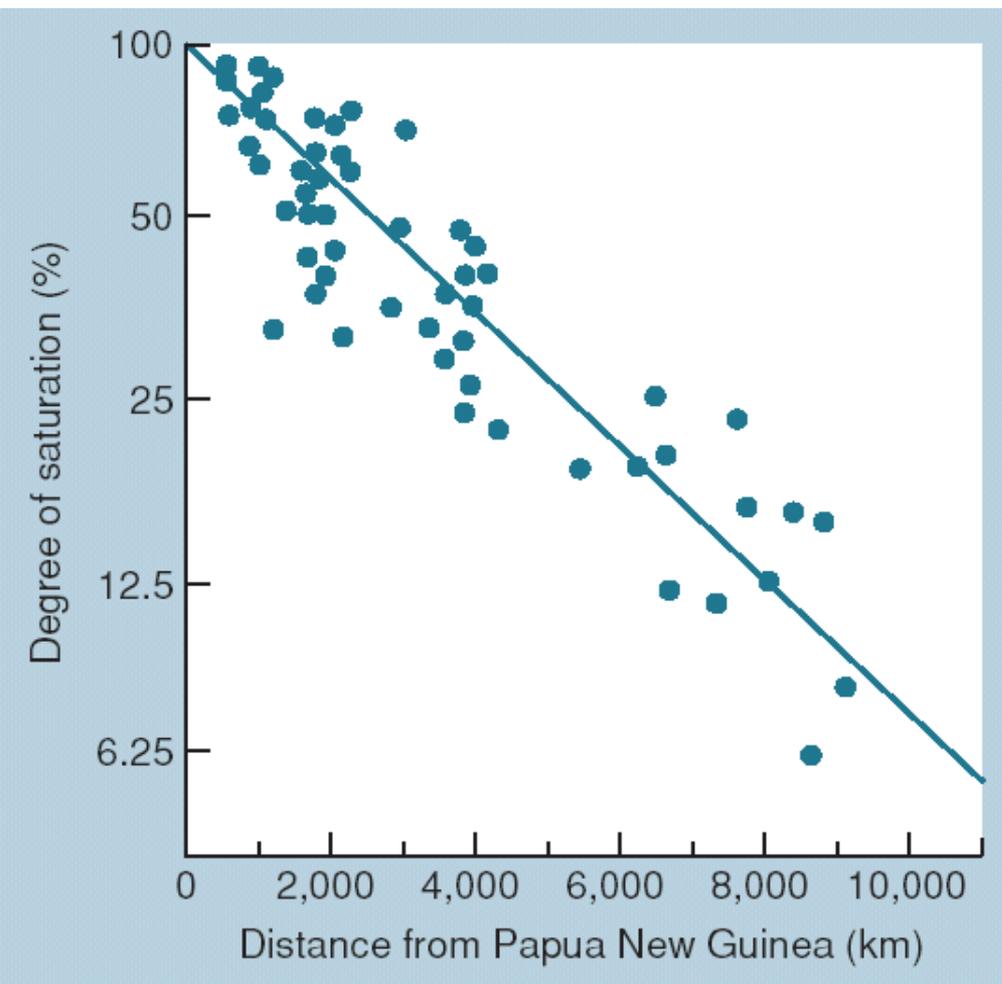


Species richness of Cryptorhynchidae: declining rapidly as a result of decreasing island size and increasing isolation

Figure 12.7 The number of genera in a weevil family (Cryptorhynchidae) declines progressively on islands more distant from the source area (New Guinea). The marked taper on this filter is exacerbated by island size as the more distant islands also happen to be smaller (adapted from Carlquist 1974, courtesy of the American Museum of Natural History).

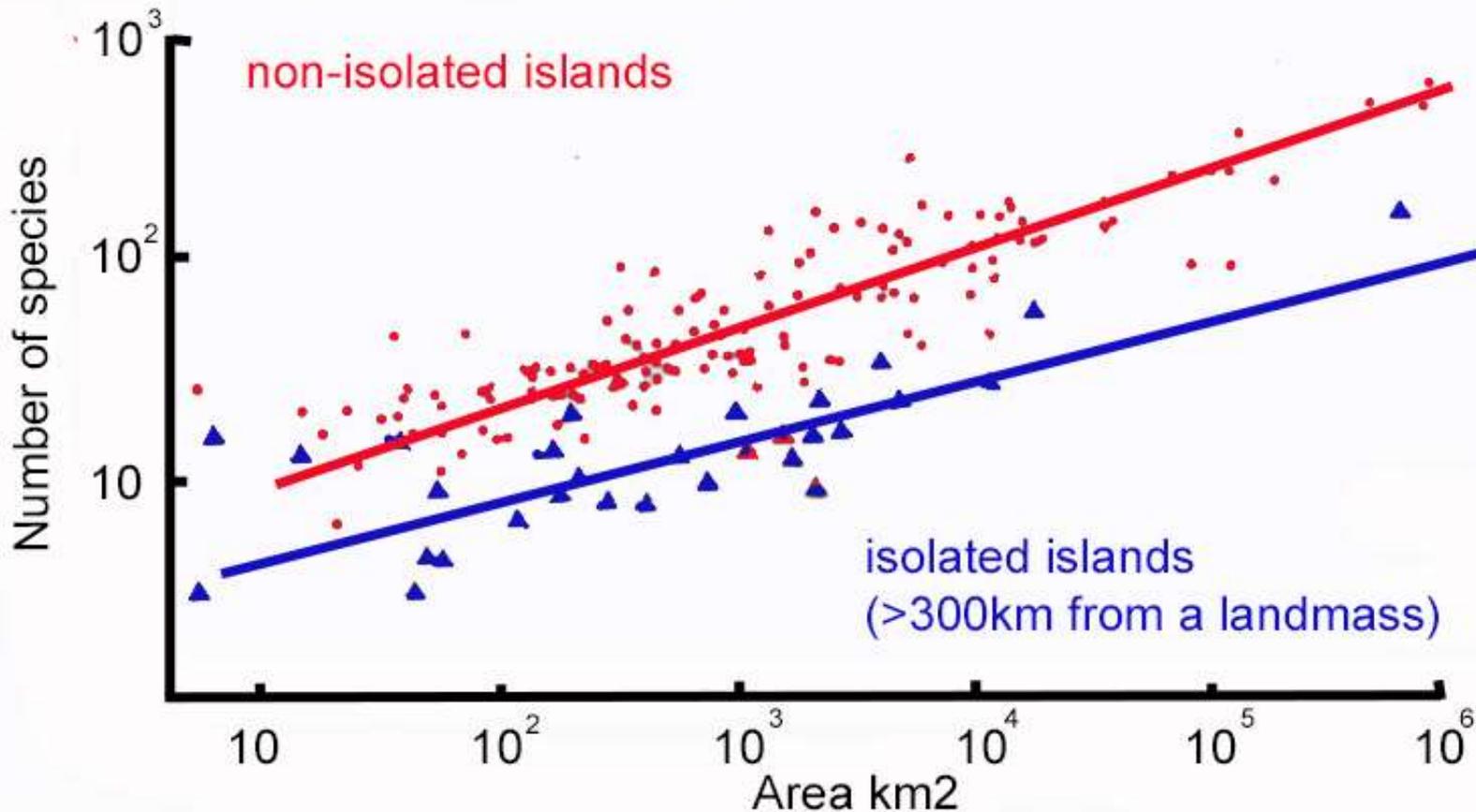
Species-area relationship: the effect of island isolation

Number of resident lowland bird species on islands far (>500 km) from New Guinea as % of species richness on islands of the same size adjacent to New Guinea



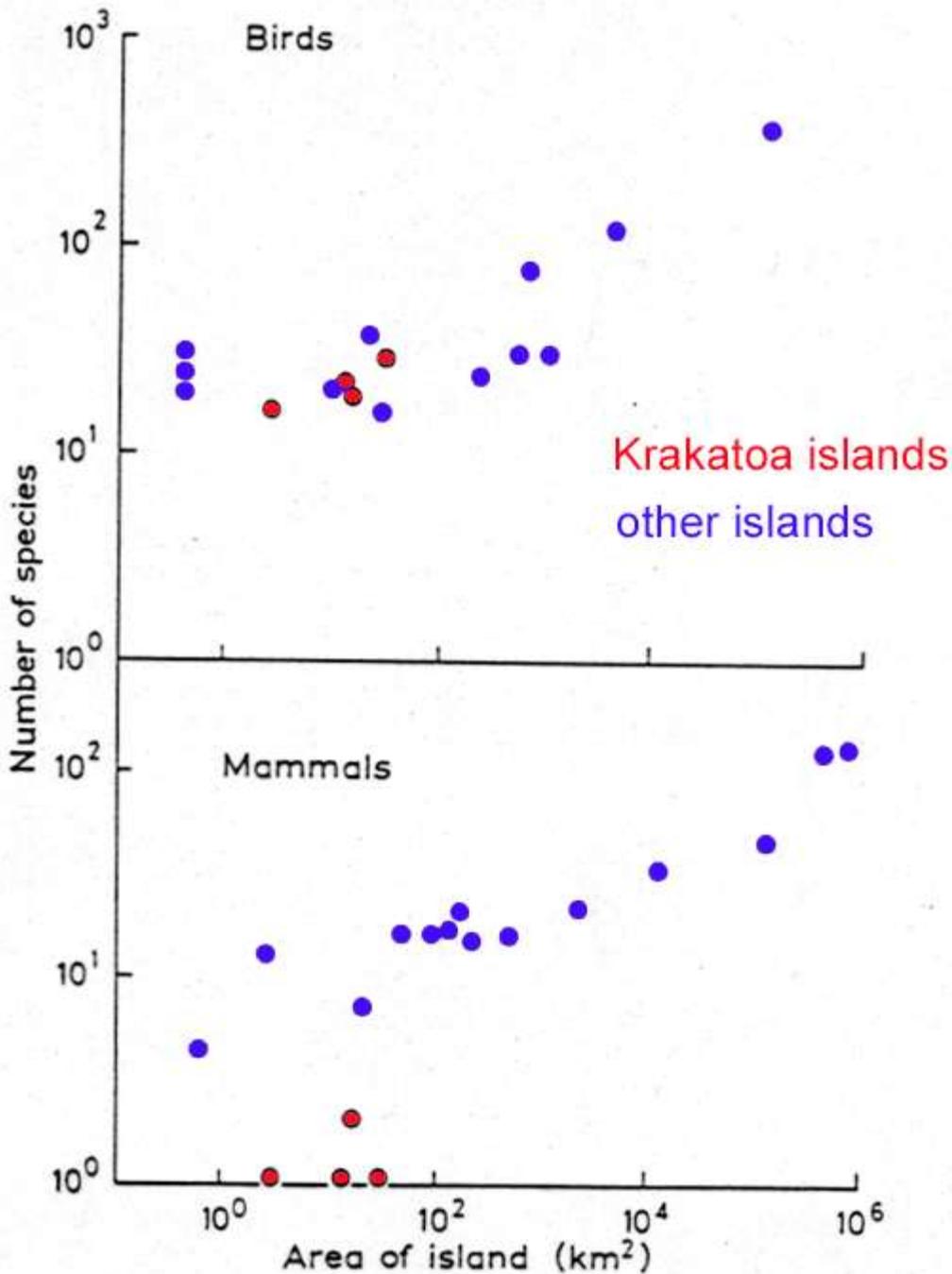
The number of resident, nonmarine, lowland bird species on islands more than 500 km from the larger source island of Papua New Guinea expressed as a proportion of the number of species on an island of equivalent area but close to Papua New Guinea and plotted as a function of island distance from Papua New Guinea. (After Diamond, 1972.)

Species-area relationship: the effect of island isolation



Land birds on tropical islands that are isolated (>300 km from a landmass) are poorer in species than on non-isolated islands

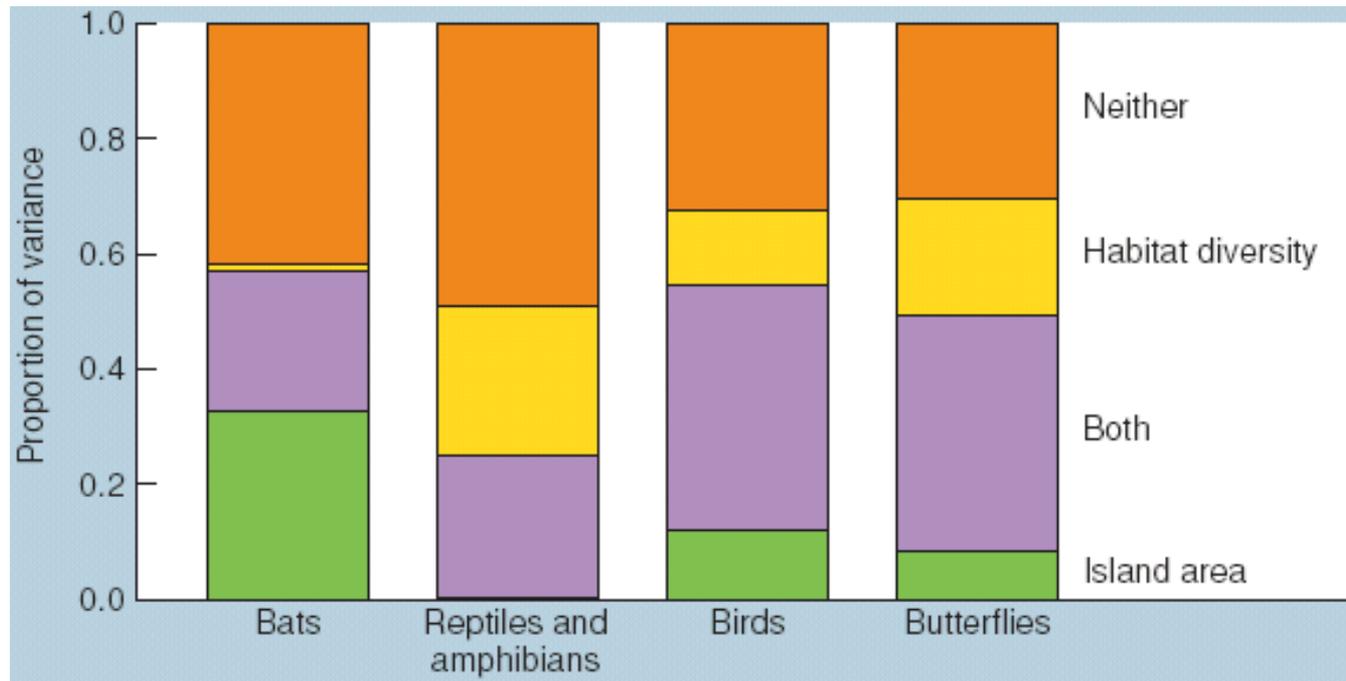
Species diversity



Species-area relationship:
the effect of recent
disturbance

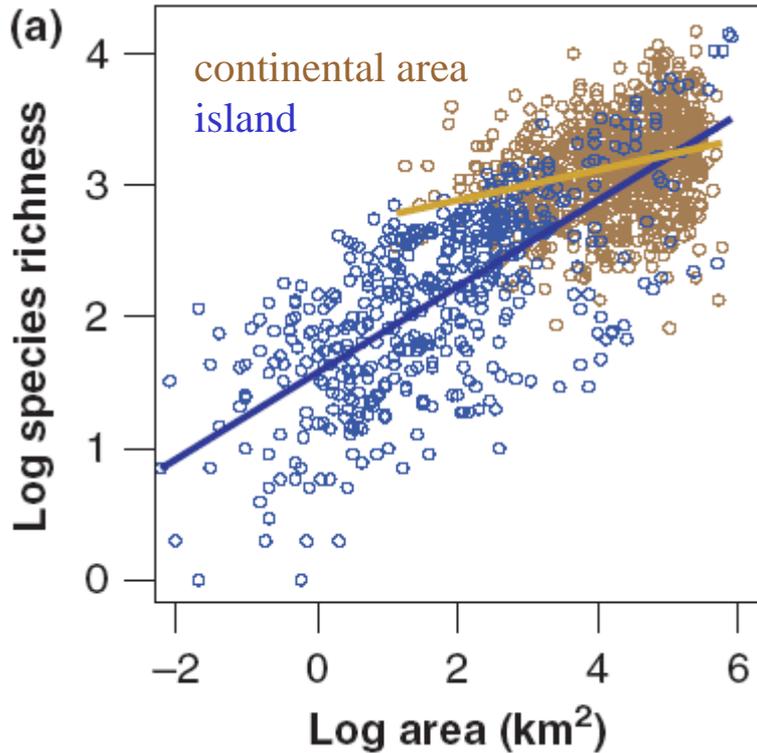
Bird diversities has recovered
since 1883 eruption – unlike
that of mammals.

Species-area relationship: combined effects of area and habitat diversity



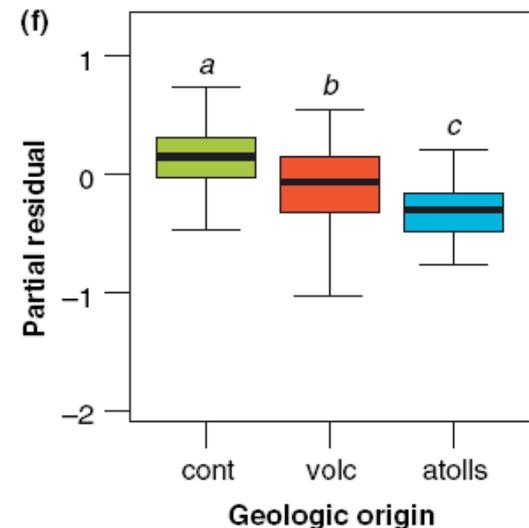
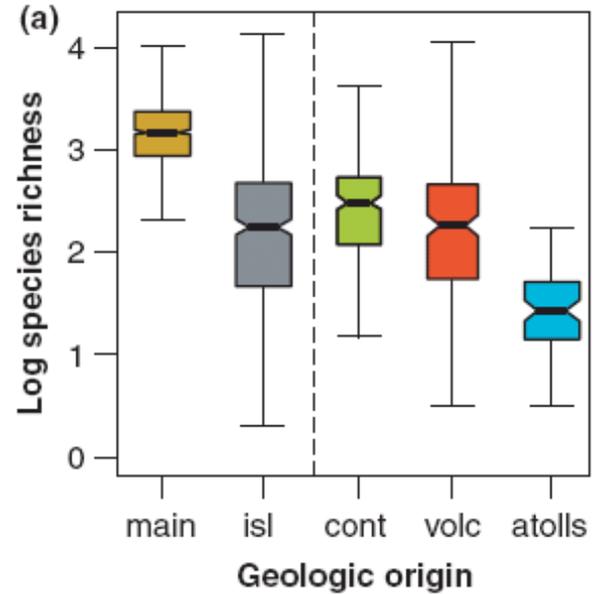
Variance in species richness among islands in Lesser Antilles explained by island area, habitat diversity, their interaction, and other factors

Species-area curves for vascular plants on islands and in continental areas

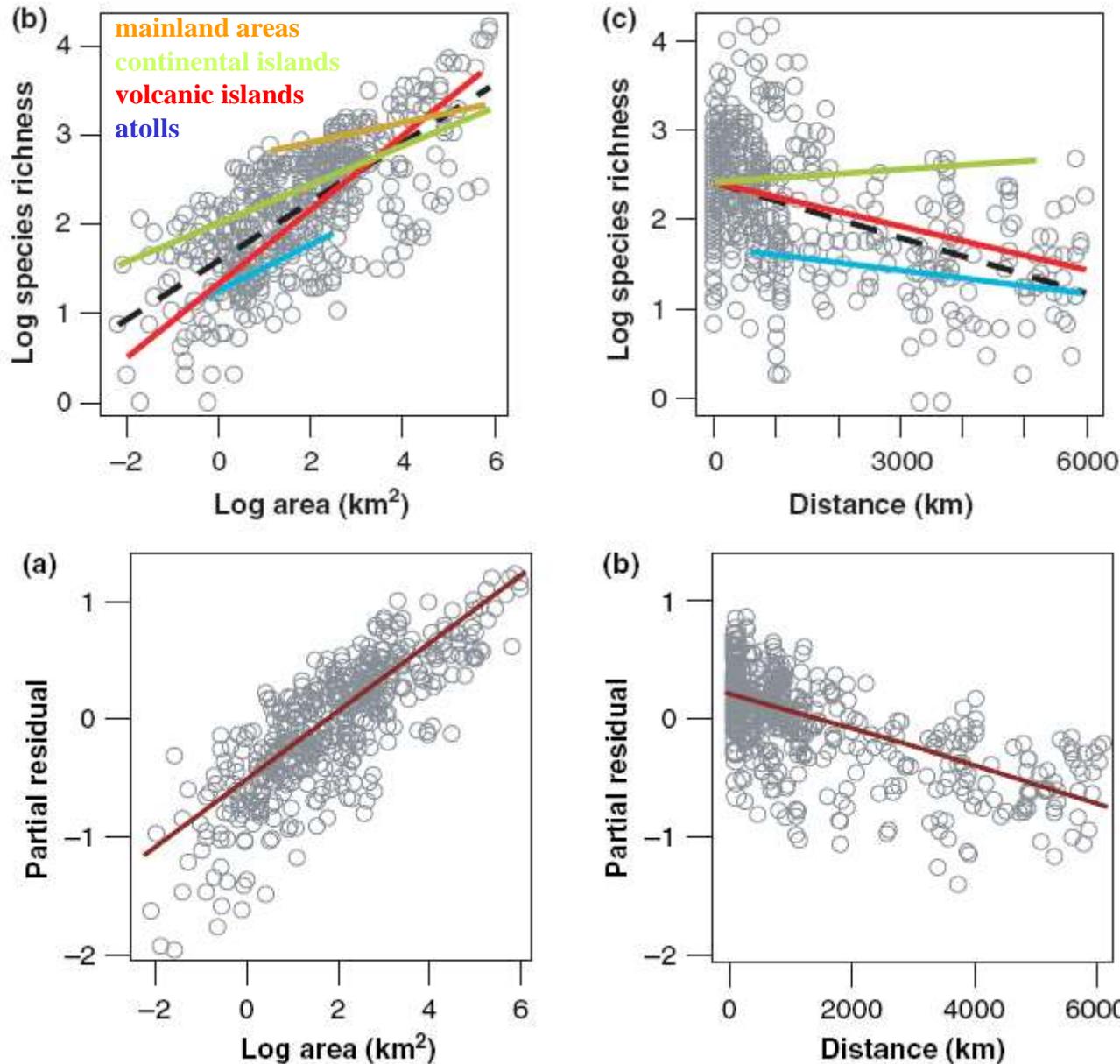


Species richness for islands of various origin
 [residuals after regression for size, distance to mainland, elevation range, precipitation and temperature]

Species richness for continental and island areas, and islands of various origin

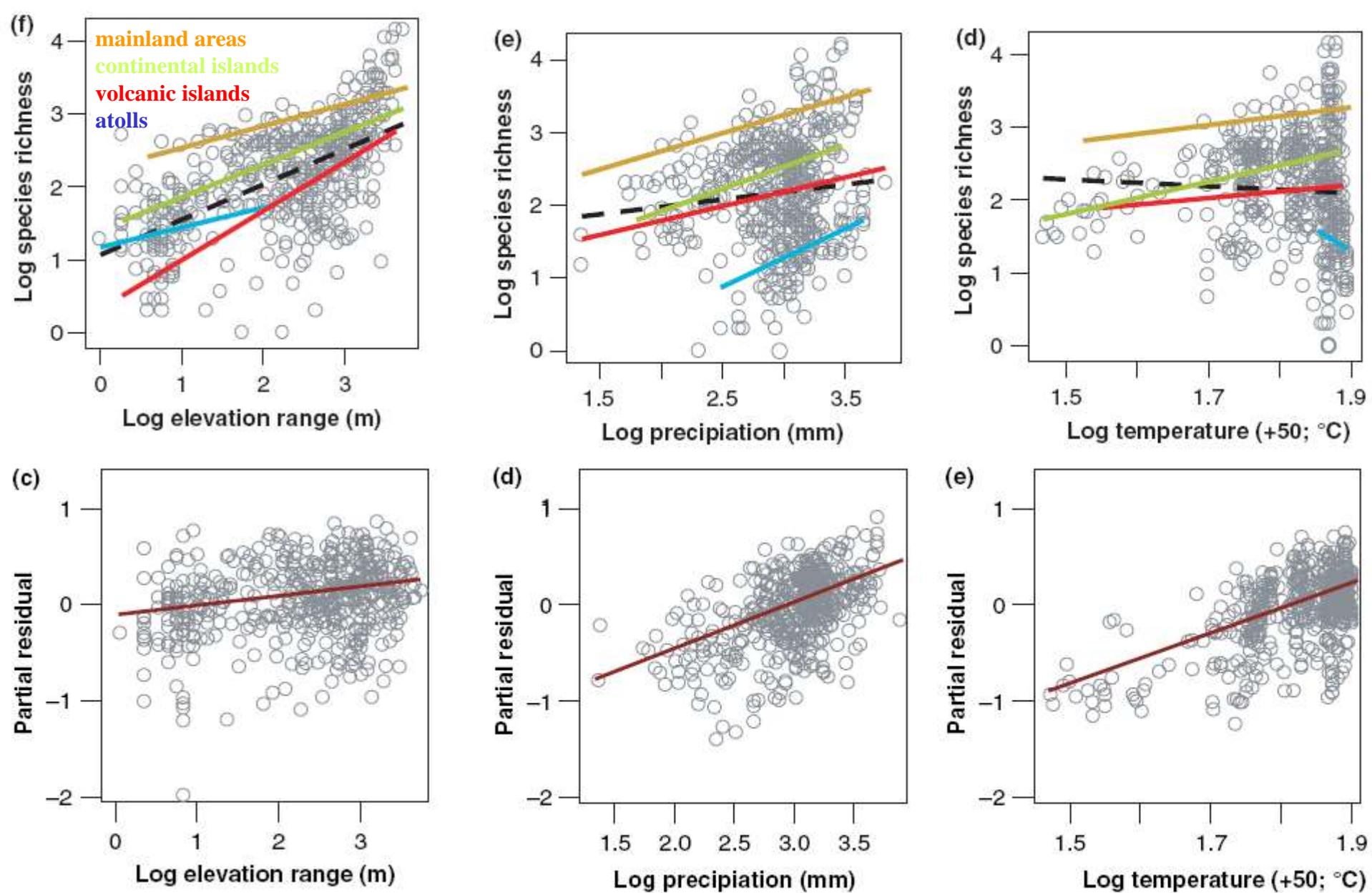


Relationships between plant species richness and (i) island area, and (ii) island distance from the mainland



Raw data (above) and residuals (below) after regression on:

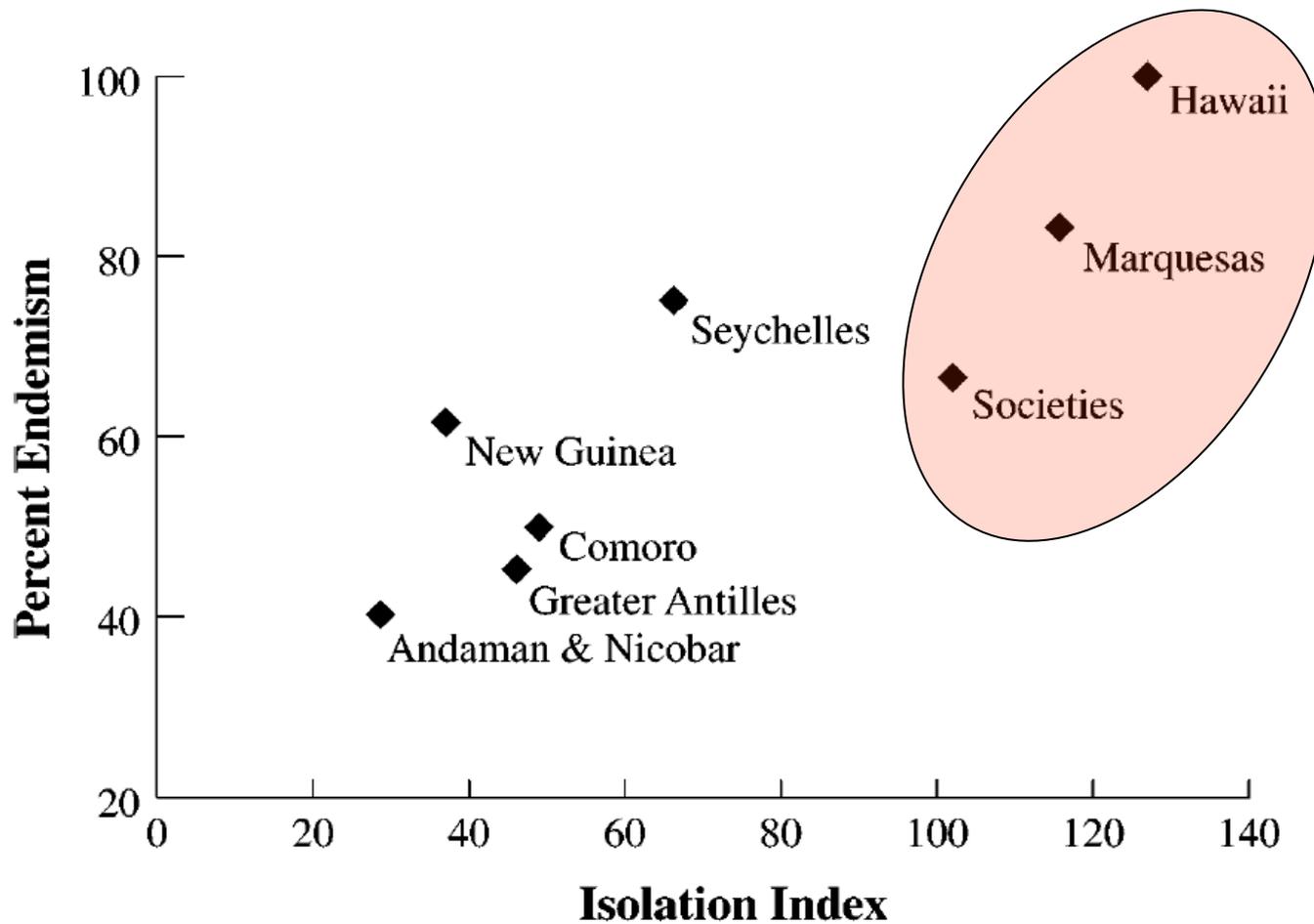
- island size
- distance to mainland
- elevation range
- mean precipitation
- mean temperature



Relationships between plant species richness and elevation range, precipitation and temperature

Raw data (above) and residuals (below) after regression on island size, distance to mainland, elevation range, mean precipitation and mean temperature

Island isolation and endemism



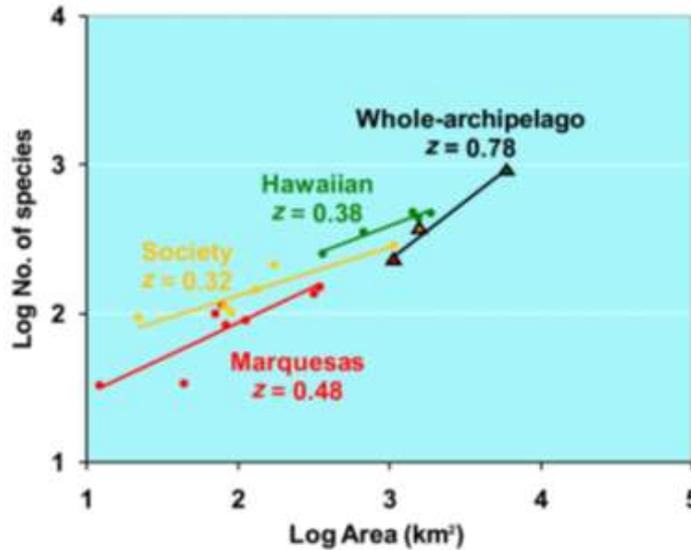
Tetragnatha sp.

Figure 3 The relationship between isolation and endemism for spiders in the genus *Tetragnatha* (R. Gillespie, unpublished data). Isolation index calculated as above.

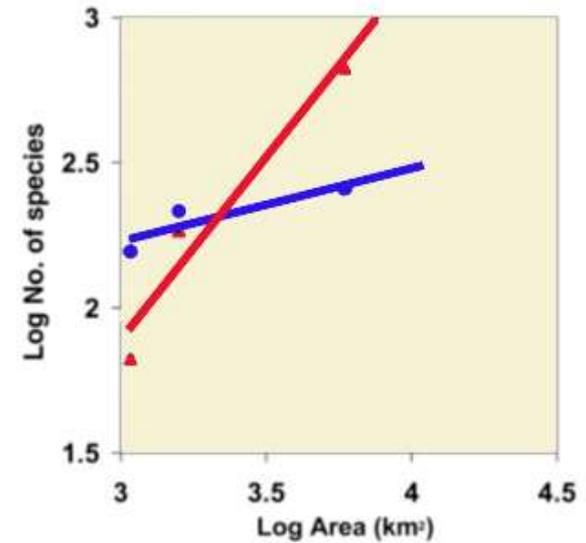
Colonization, anagenesis and cladogenesis on islands



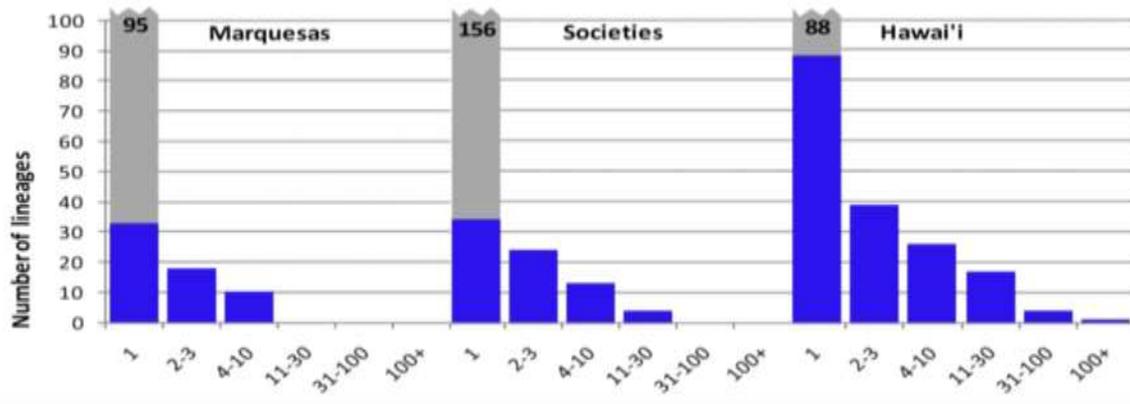
Three Pacific archipelagoes



Species-area curves

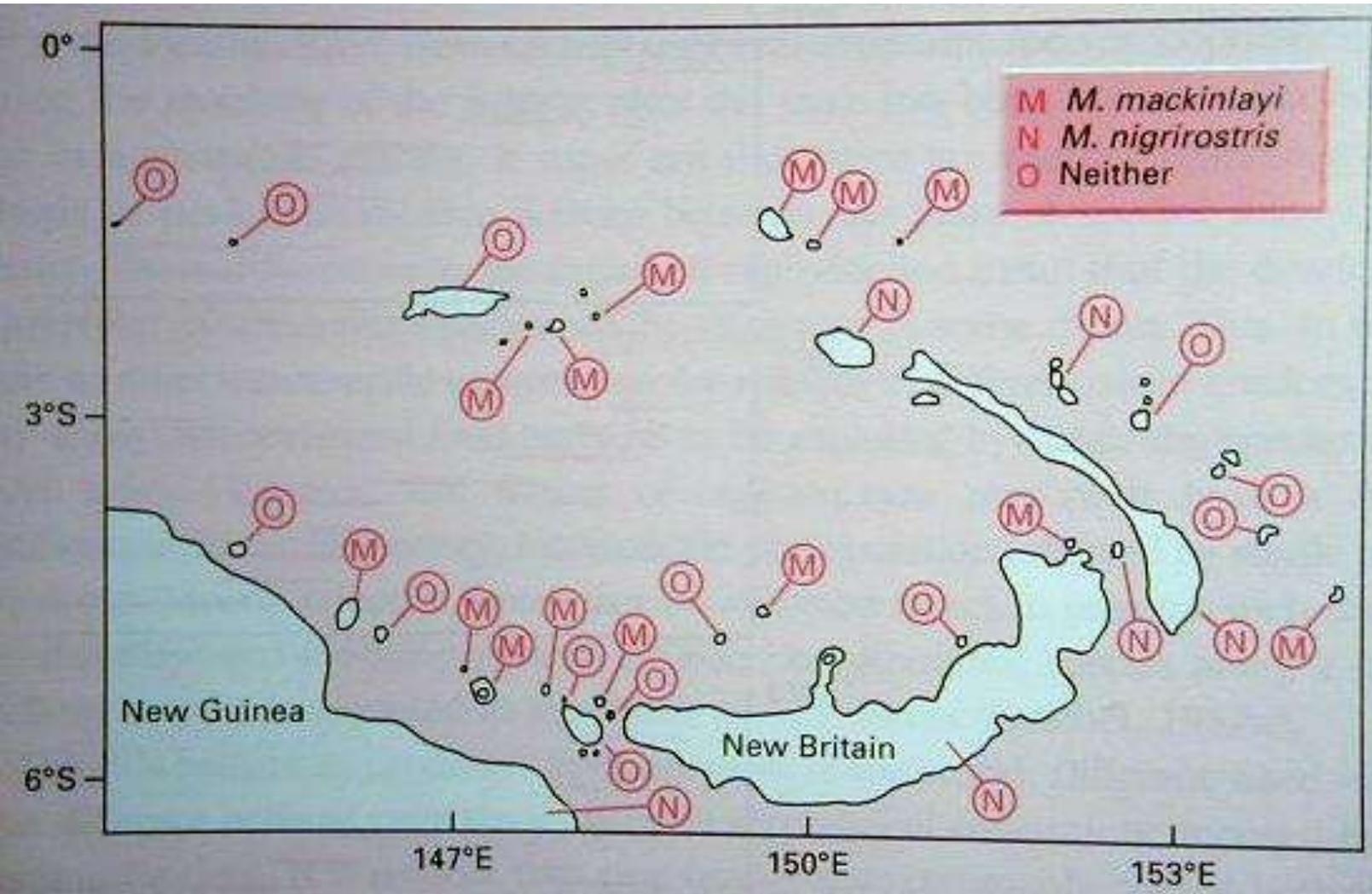


Contribution of colonization (dots) and cladogenesis (triangles) to the species pools of the archipelagoes



Single-species lineages that have differentiated from ancestral species to form an endemic species (anagenetic lineages) and lineages with multiple endemic species (cladogenetic lineages) in blue. Single-species lineages consisting of nonendemic species in gray.

“Checkboard distribution” - not predicted by island biogeography



M. nigrirostris



M. mackinlayi

Cockoo-dove *Macropygia mackinlayi* and *M. nigrirostris*

Checkerboard distribution: *Zosterops* birds in New Guinea

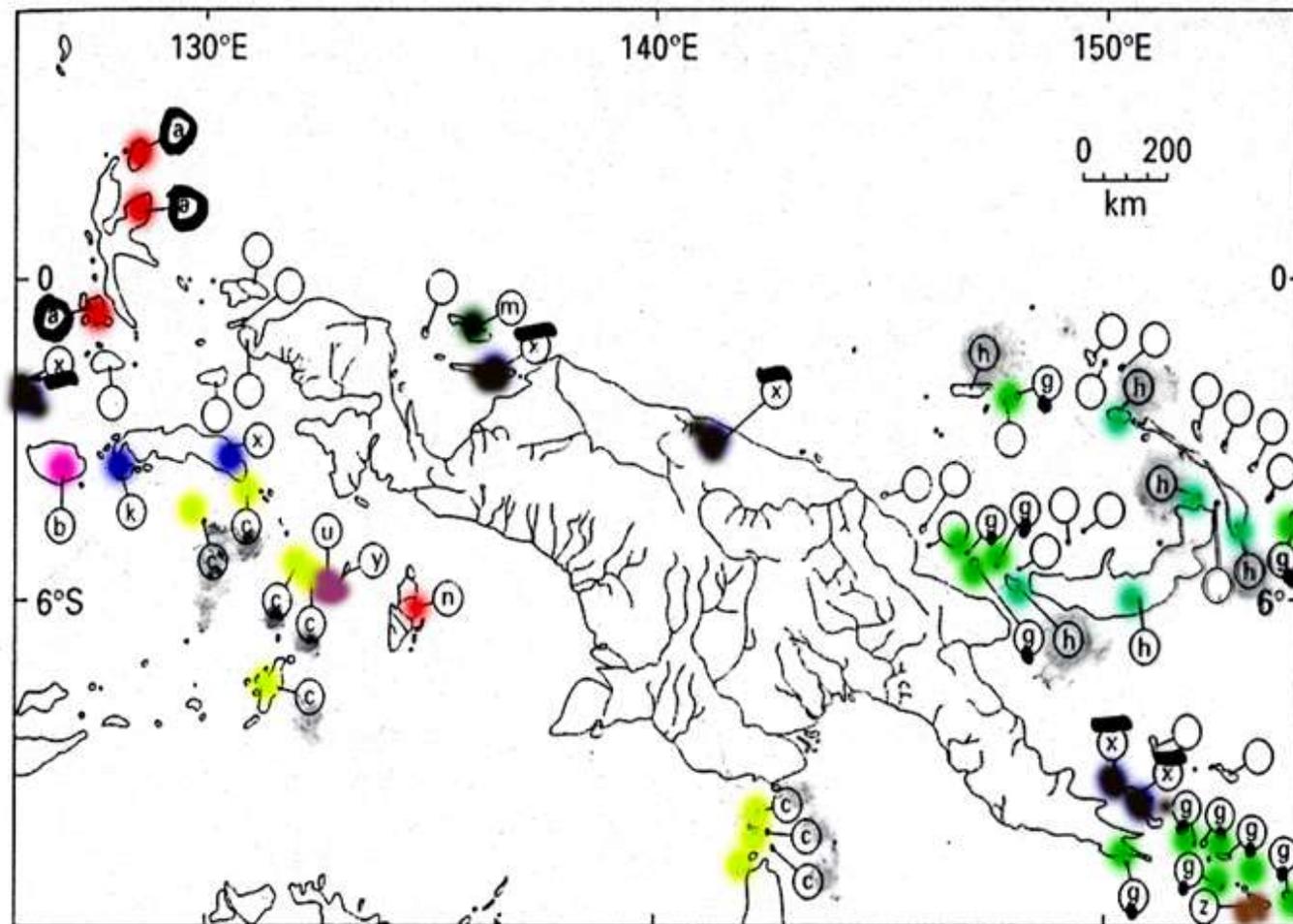
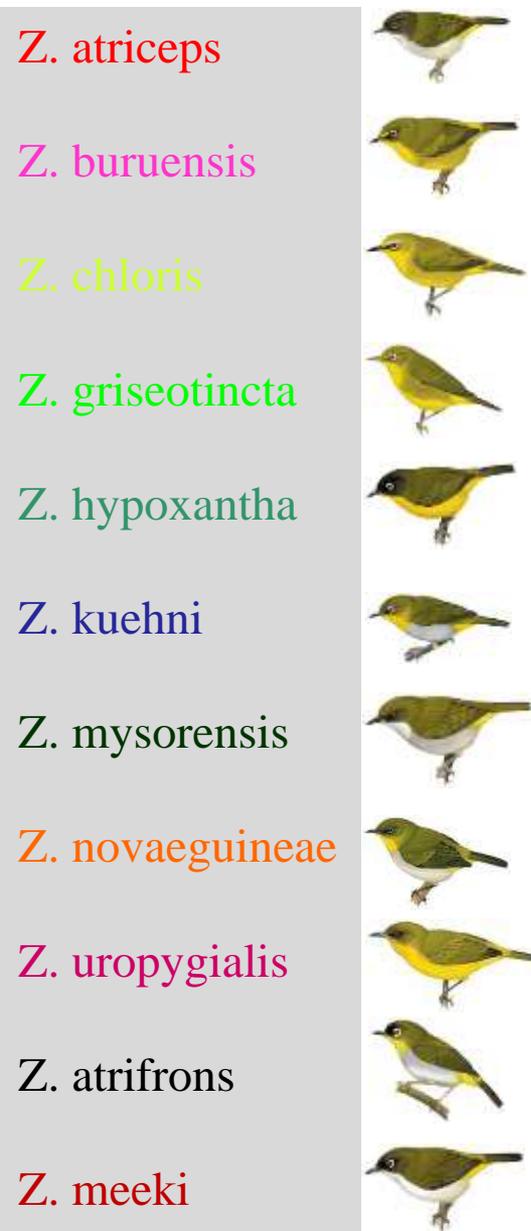
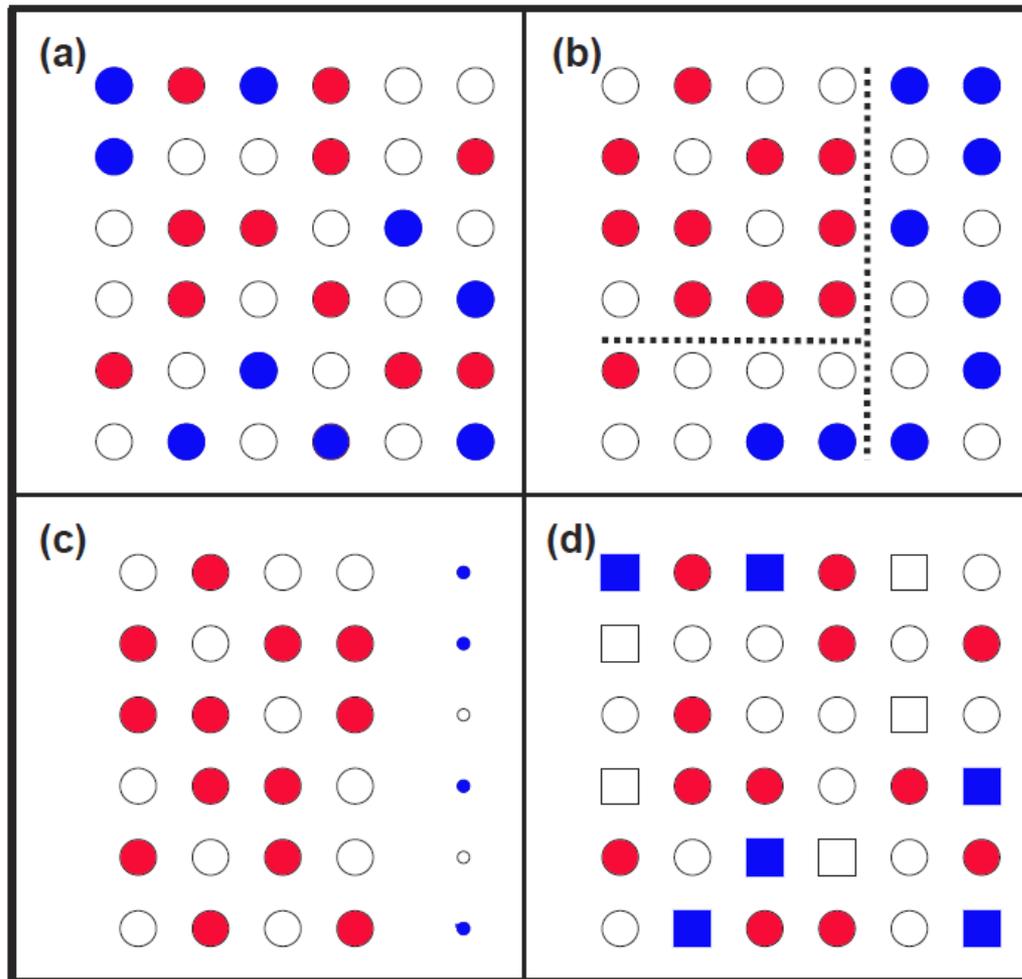


Fig. 6.12 Checkerboard distribution of 12 species of white-eyes (the genus *Zosterops*) on the islands of the New Guinea region. Symbols on the islands are: a, *Z. atriceps*; b, *Z. buruensis*; c, *Z. chloris*; g, *Z. griseotincta*; h, *Z. hypoxantha*; k, *Z. kuehni*; m, *Z. mysorensis*; n, *Z. novaeguineae*; u, *Z. uropygialis*; x, *Z. atrifrons*; y, *Z. grayi*; z, *Z. meeki*. Islands without a symbol in a circle have no *Zosterops* species. (Reprinted by permission of the publisher from *Ecology and Evolution of Communities* by M.L. Cody & J.M. Diamond, Cambridge, MA: Harvard University Press, Copyright ©1975 by the President and Fellows of Harvard College.)

Checkerboard distribution patterns



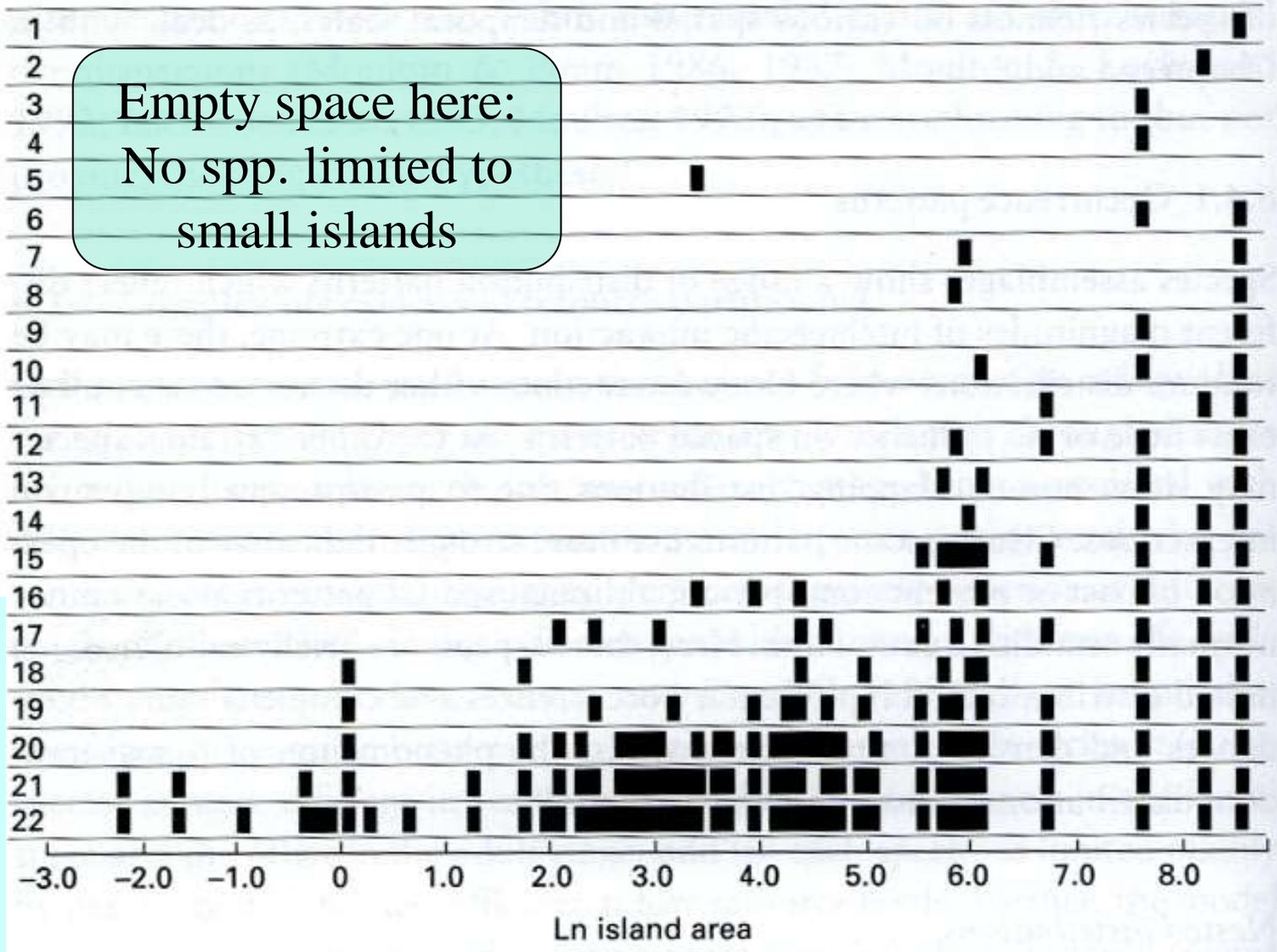
Checkerboard distribution tests:
how much to randomize the original communities?
No. of spp per site?
No of sites per spp?

A representation of (a) checkerboard distribution due to competition, (b) regional allopatry, (c) supertramp distributions, and (d) differences in habitat preference. Supertramp species are restricted to small, isolated or disturbed islands. Circles = islands; squares = islands with a different habitat type. Red and blue represent islands occupied by different species.

Nestedness: species on species-poor islands represent a subset of species on species-rich islands

Species
No. 1-22
from rare
(top) to
common
(bottom)

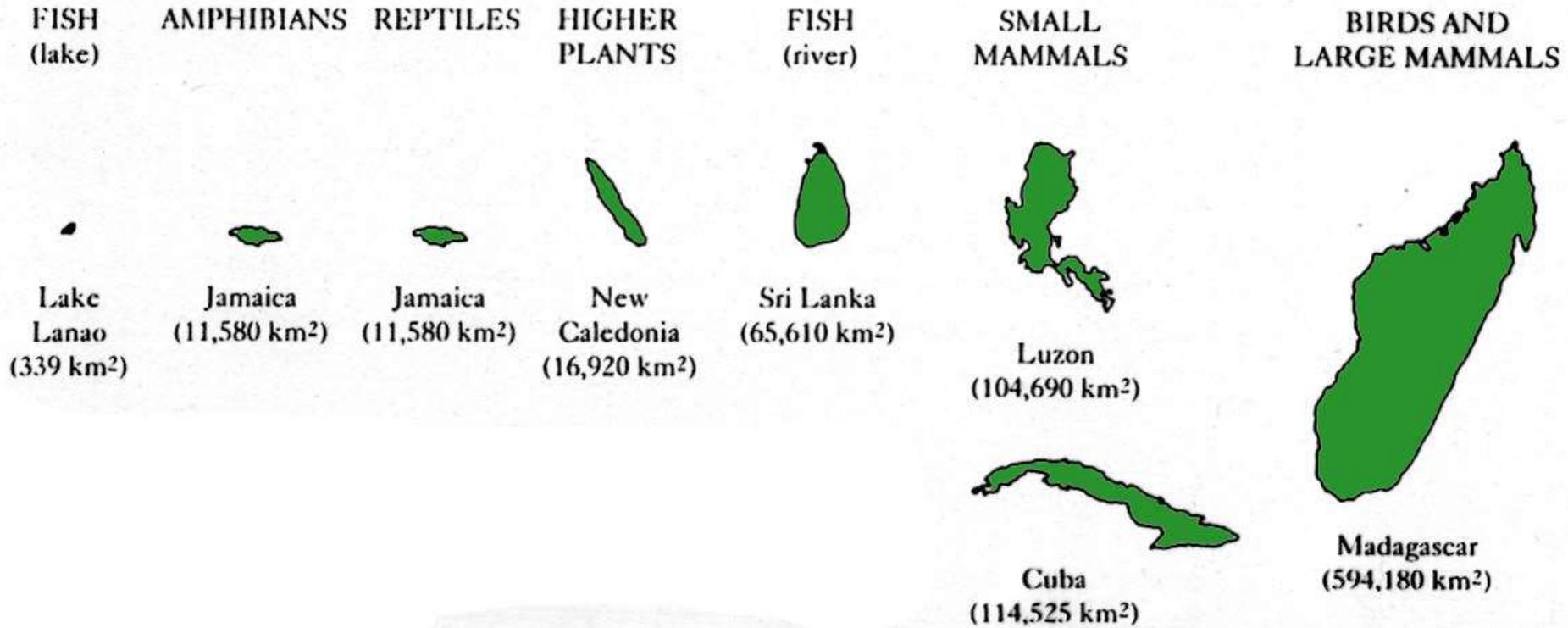
Empty space here:
No spp. limited to
small islands

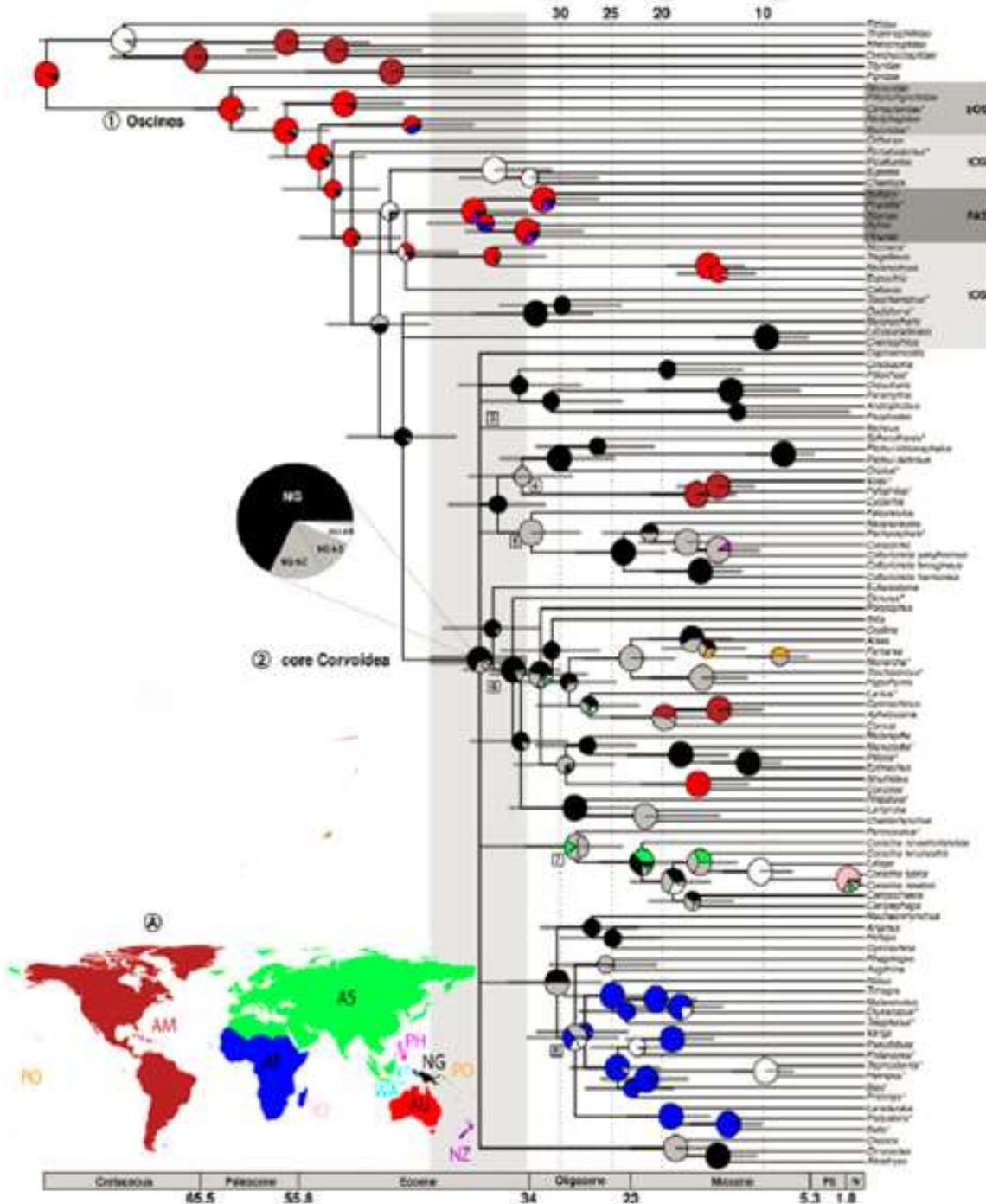


Herpetofauna
on British
Virgin
Islands:
a nested
pattern of
species
distribution

Fig. 6.11 Species occurrence of herpetofauna on the British Virgin Islands. Numbers on the left denote different species. (Data from Lazell 1983; Schoener & Schoener 1983a,b.)

Minimum area required for evolutionary radiation by different lineages

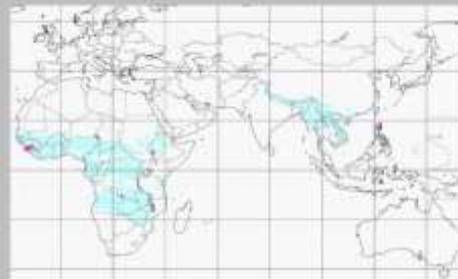
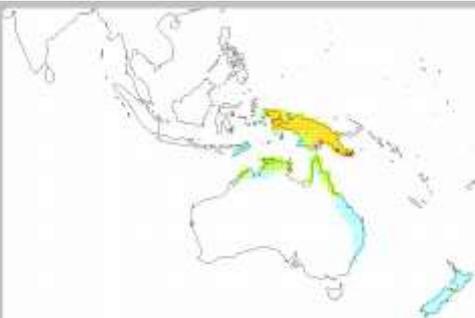
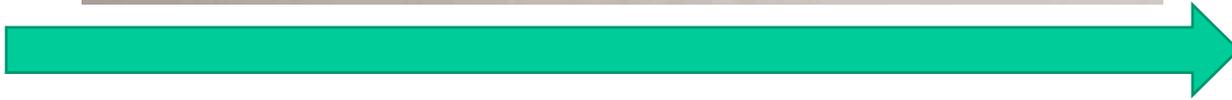




Islands can also serve as cradles for lineages spreading from them to continents

Core Corvoidea (>700 spp) spread from the Papuan archipelago

Oriole expansion: phylogenetic root-path quartiles, the deepest branches have Papuan area origin; younger lineages widespread Old World species.



RED MEAT

frying bacon in the bedpan

from the secret files of
MAX CANNON

It's true...no man is an island.



©1996 MAX CANNON

But if you take a bunch of dead guys and tie 'em together, they make a pretty good raft.

