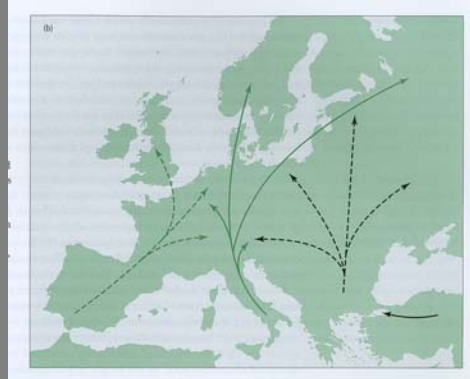


L10. Evolutionary Biogeography



Ole Seehausen
www.fishecology.ch



Aquatic Ecology,
 Institute of Zoology,
 University of Bern

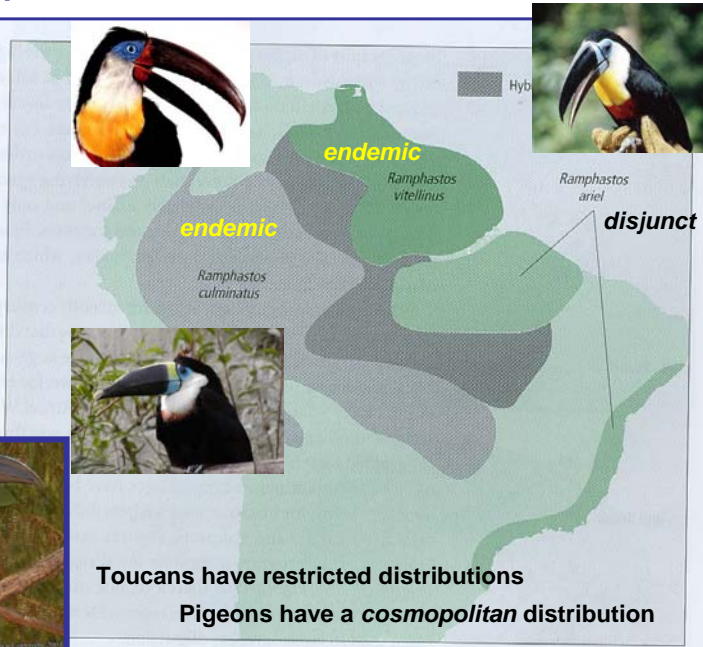
Fish Ecology & Evolution,
 ETH-EAWAG Limno. Res.
 Centre, Kastanienbaum



Kinds of geographical distributions

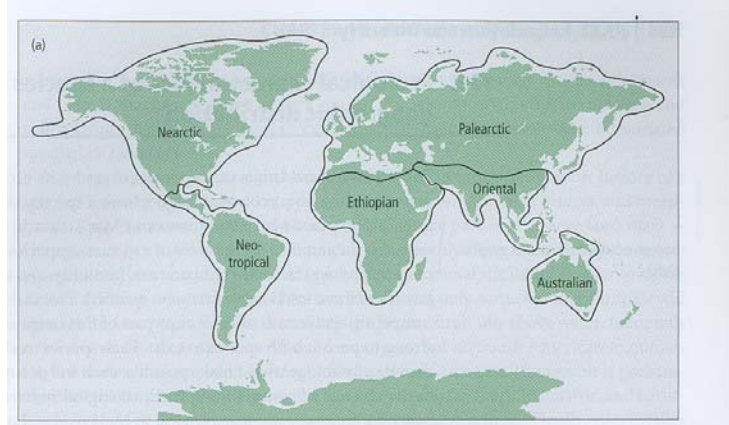
Figure 17.1

The natural distribution of three species of toucans in the genus *Ramphastos* in South America: *R. vitellinus* and *R. culminatus* have endemic distributions, whereas *R. ariel*'s distribution is disjunct. There is an extensive hybrid zone between the species. Modified, by permission of the publisher, from Haffer (1974).



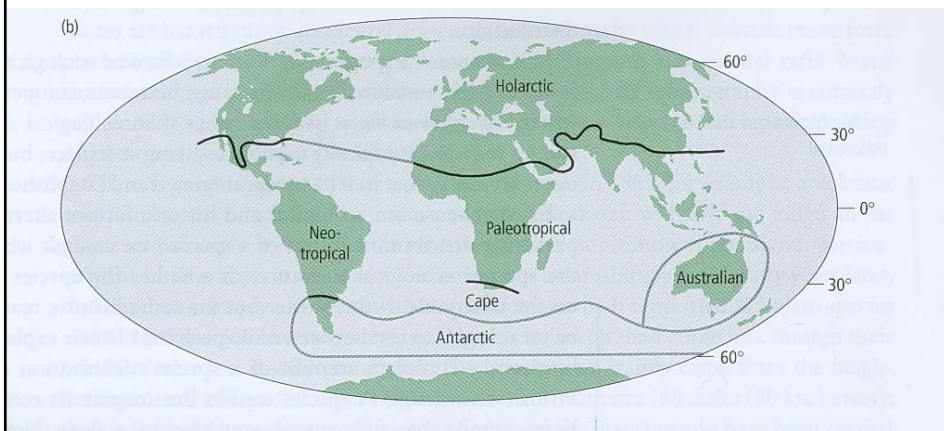
Toucans have restricted distributions
 Pigeons have a *cosmopolitan* distribution

The six main faunal regions of the world, based on the distribution of animals, and particularly of birds and mammals



The discontinuity between the Australian and Oriental regions is called the Wallace's line

The six main floral regions of the world, based on the distribution of angiosperms (flowering plants)



Simpson's index of biogeographical similarity:

N_1 = number of taxa in the area with smaller n taxa

N_2 = number of taxa in the other area

C = number of taxa in common between the two areas

$$\text{Simpson's index} = C/N_1$$

Table 17.1 Faunal similarity is often given as $(C/N_1) \times 100$

Indexes of similarity for the mammalian species of various regions. Data from Flessa *et al.* (1979).

	North America	West Indies	South America	Africa	Madagascar	Eurasia	South East Asian islands	Philippines	New Guinea	Australia
North America										
West Indies	67									
South America	81	73								
Africa	31	27	25							
Madagascar	38	27	35	65						
Eurasia	48	27	36	80	69					
South East Asian islands	37	20	32	82	63	92				
Philippines	40	20	32	88	50	96	100			
New Guinea	36	21	36	64	50	64	79	64		
Australia	22	20	22	67	38	50	61	50	93	

Ecological characteristics of a species limit its geographic distribution range



Figure 13.1 Distribution of the holly *Ilex aquifolium* in Europe.

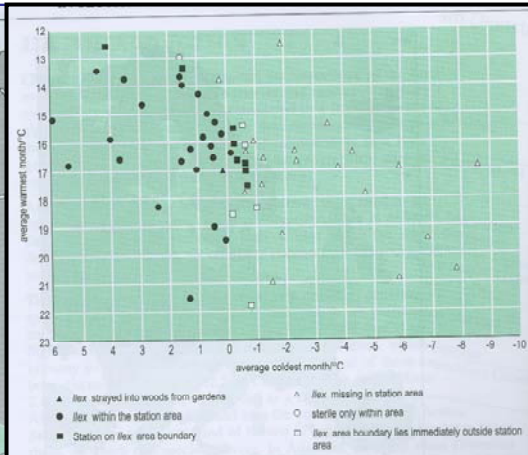


Figure 13.2 The status of holly *Ilex aquifolium*, correlated with average warmest and coldest month temperatures, in the neighbourhood of meteorological stations in Denmark.

Dispersal biogeography: dispersal abilities/opportunities of a species limit its geographic distribution range too

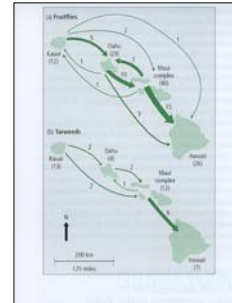
Various dispersal routes might have been followed in the biogeographic history of a species.

Simpson distinguished dispersal by means of

corridors,

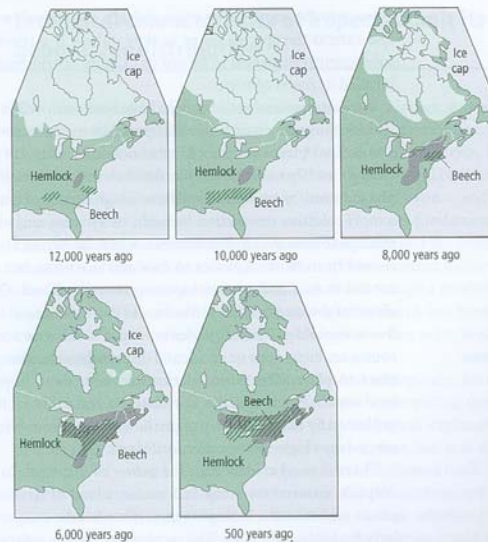
filter bridges,

sweepstakes



Because the environment has changed a lot over time, history, ecology and dispersal interact to determine species' ranges

Figure 17.3
Changing American geographic distribution of beech (*Fagus*) and hemlock (*Tsuga*) as the polar ice cap retreated after the most recent ice age.



The genetic legacy of the Quaternary ice ages

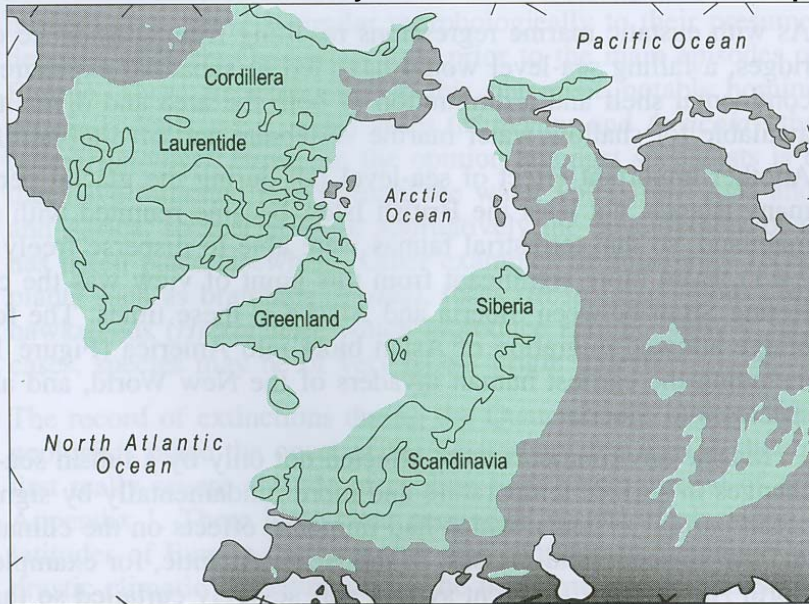
Godfrey Hewitt

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

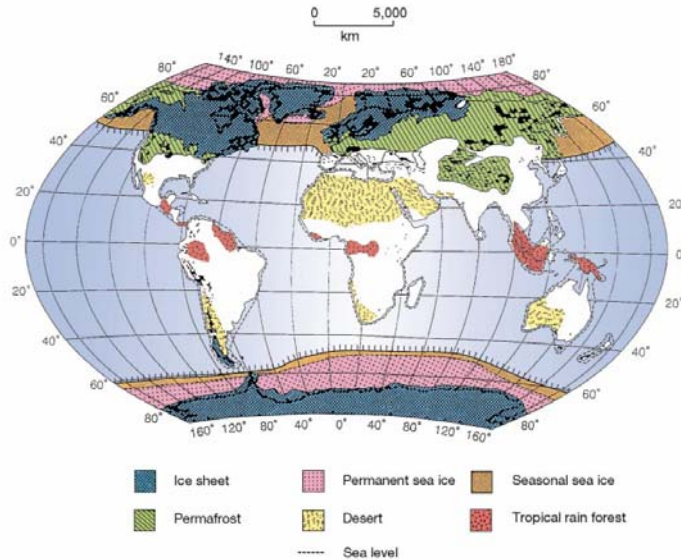
Global climate has fluctuated greatly during the past three million years, leading to the recent major ice ages. An inescapable consequence for most living organisms is great changes in their distribution, which are expressed differently in boreal, temperate and tropical zones. Such range changes can be expected to have genetic consequences, and the advent of DNA technology provides most suitable markers to examine these. Several good data sets are now available, which provide tests of expectations, insights into species colonization and unexpected genetic subdivision and mixture of species. The genetic structure of human populations may be viewed in the same context. The present genetic structure of populations, species and communities has been mainly formed by Quaternary ice ages, and genetic, fossil and physical data combined can greatly help our understanding of how organisms were so affected.

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Maximum extent of Quaternary ice-sheets in the Northern Hemisphere



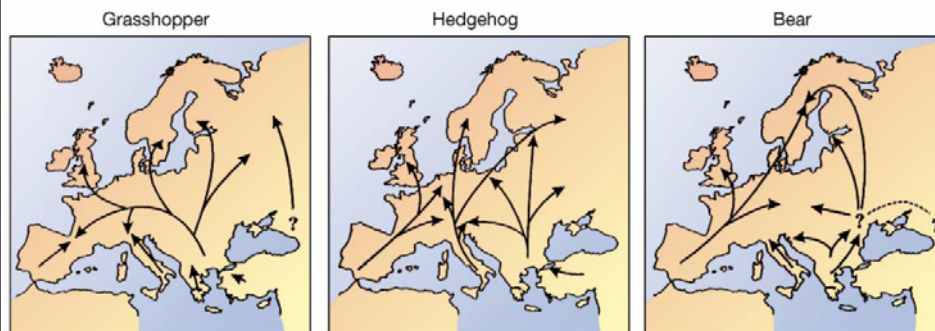
The ice ages affected climate worldwide: The maximum extent of ice and permafrost at the end of the last ice age 20,000 yr BP. The lowered sea level, large deserts and main blocks of tropical forest are indicated.



Glacial refugia and postglacial recolonization of the North

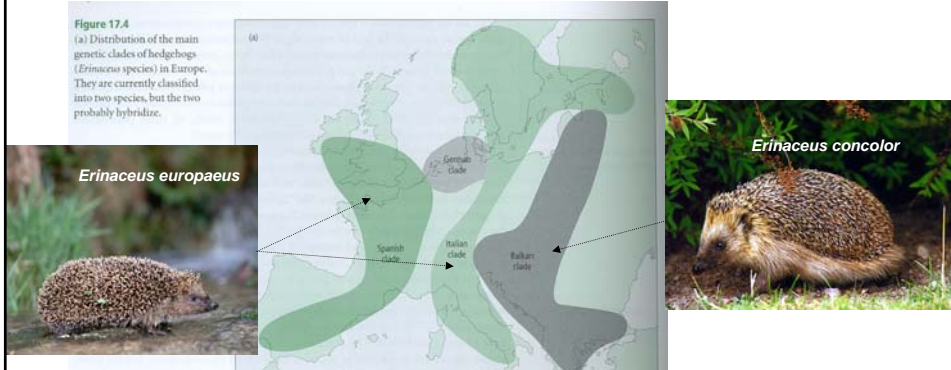
Three paradigm postglacial colonizations from southern Europe deduced from DNA differences for the grasshopper, *Chorthippus parallelus*, the hedgehog, *Erinaceus europeus/concolor*, and the bear, *Ursos arctos*.

The main refugial areas, **Iberia, Italy, the Balkans and Caucasus**, contributed differently to the repopulation of northern parts.



Glacial refugia and postglacial recolonization of the North are reflected in current distribution patterns of genetic lineages within species, and sometimes sister species

Figure 17.4
(a) Distribution of the main genetic clades of hedgehogs (*Erinaceus* species) in Europe. They are currently classified into two species, but the two probably hybridize.



However, the molecular clock suggests that species splits are usually a lot older than the beginning of the last ice age, e.g. 3 million years in the case of the hedgehog



Suture zones

Many species have migrated from similar glacial refugia and form hybrid zones where the different clades meet in rather similar areas. Such areas where several species form hybrid zones are called **suture zones**

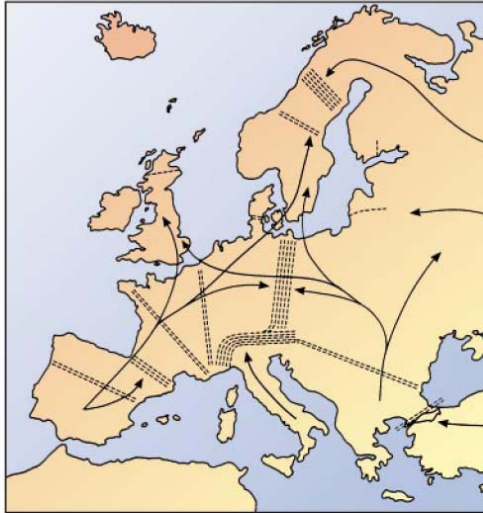


Figure 3 The general position of some well-known hybrid zones in Europe, which show major clustering in Scandinavia, central Europe and the Alps. Other clusters are apparent in the Pyrenees and the Balkans. These suture zones are caused by commonalities of ice-age refugia, rate of postglacial expansion and physical barriers. There is further subdivision in the southern regions.

Evolutionary biogeography can also rule out geographical causes for diversity

The case of the Anoline lizard radiation on the Greater Antilles

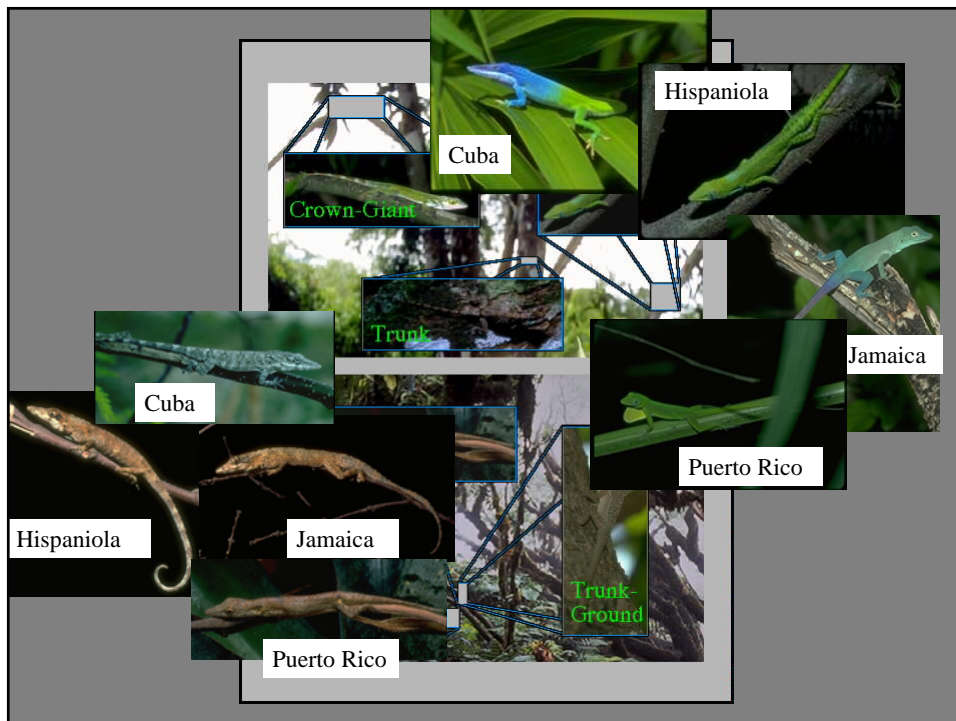


Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards

Jonathan B. Losos,* Todd R. Jackman, Allan Larson,
Kevin de Queiroz, Lourdes Rodríguez-Schettino

The vagaries of history lead to the prediction that repeated instances of evolutionary diversification will lead to disparate outcomes even if starting conditions are similar. We tested this proposition by examining the evolutionary radiation of *Anolis* lizards on the four islands of the Greater Antilles. Morphometric analyses indicate that the same set of habitat specialists, termed ecomorphs, occurs on all four islands. Although these similar assemblages could result from a single evolutionary origin of each ecomorph, followed by dispersal or vicariance, phylogenetic analysis indicates that the ecomorphs originated independently on each island. Thus, adaptive radiation in similar environments can overcome historical contingencies to produce strikingly similar evolutionary outcomes.

www.sciencemag.org • SCIENCE • VOL. 279 • 27 MARCH 1998



The distribution of adaptive phenotypes over islands is predominantly explained by repeated ecological differentiation within islands, rather than by vicariance or dispersal between islands

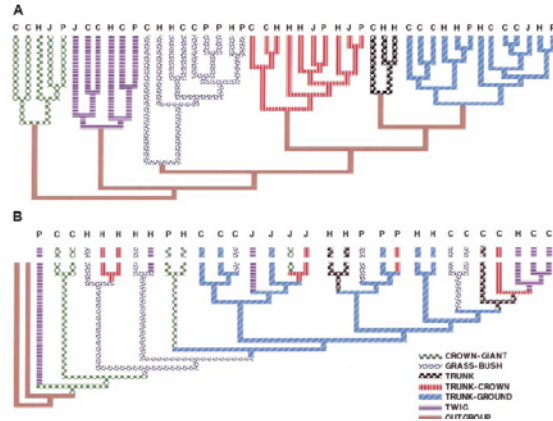


Fig. 1. (A) UPGMA phenogram showing that members of the same ecomorph class cluster in morphological space regardless of geographic affinities. Branch lengths are proportional to the distance separating species or clusters in morphological space. Letters indicate the island on which a species is found (C, Cuba; H, Hispaniola; J, Jamaica; P, Puerto Rico). The shading of the branches connecting the ecomorph classes has no significance. (B) The most parsimonious tree derived from the molecular data indicates frequent transitions among ecomorph classes. The lengths of the branches have no significance. (C)

Other species radiations are more strongly determined by dispersal, or by an interaction of local diversification and dispersal

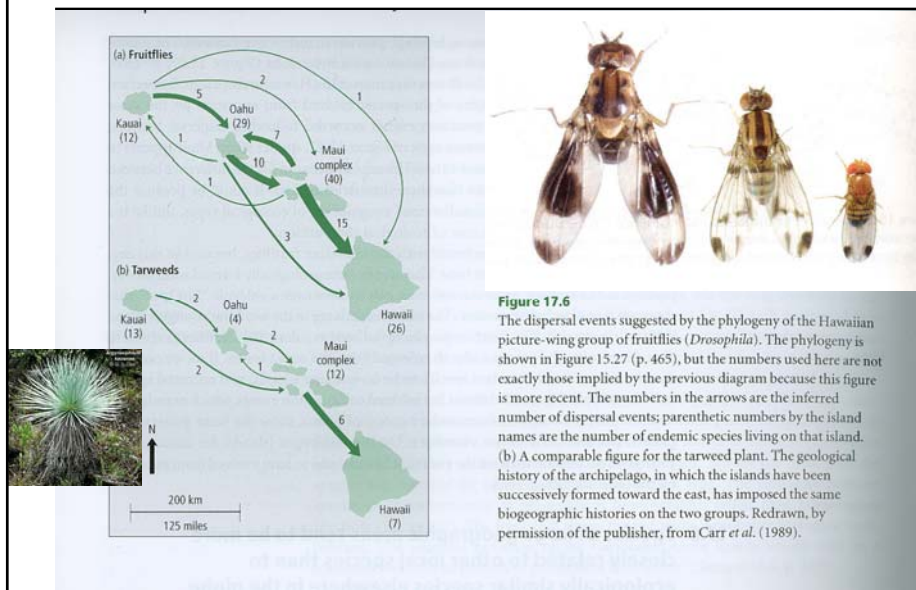


Figure 17.6 The dispersal events suggested by the phylogeny of the Hawaiian picture-wing group of fruitflies (*Drosophila*). The phylogeny is shown in Figure 15.27 (p. 465), but the numbers used here are not exactly those implied by the previous diagram because this figure is more recent. The numbers in the arrows are the inferred number of dispersal events; parenthetical numbers by the island names are the number of endemic species living on that island. (b) A comparable figure for the tarweed plant. The geological history of the archipelago, in which the islands have been successively formed toward the east, has imposed the same biogeographic histories on the two groups. Redrawn, by permission of the publisher, from Carr *et al.* (1989).

Vicariance biogeography

Plate tectonics (“continental drift”).

(a) The movements of the continents during the past 200 million years.

(b) The positions and direction of movement of the main tectonic plates today

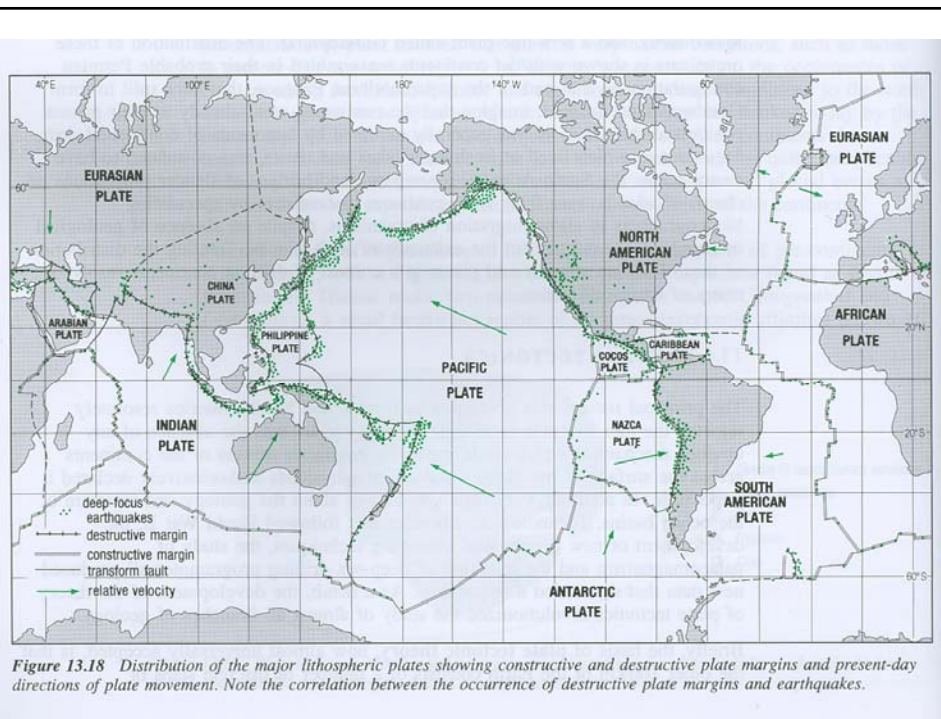
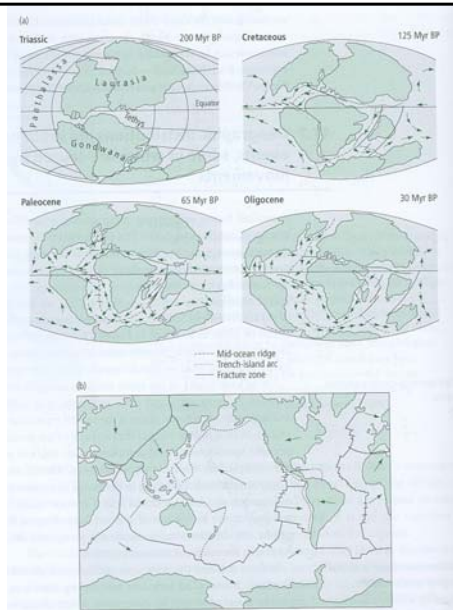
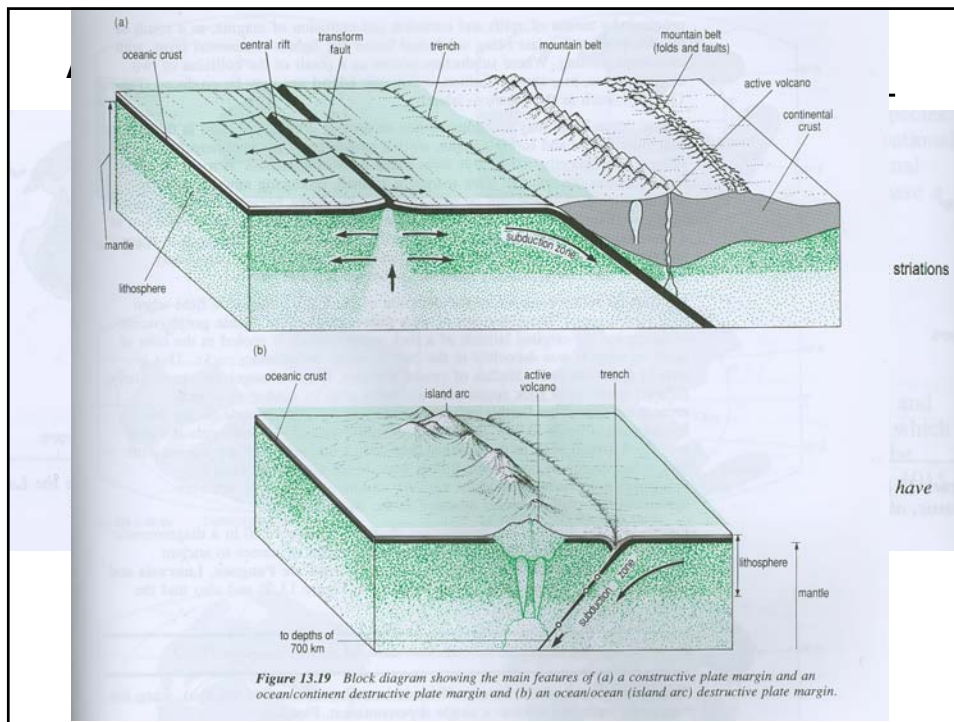


Figure 13.18 Distribution of the major lithospheric plates showing constructive and destructive plate margins and present-day directions of plate movement. Note the correlation between the occurrence of destructive plate margins and earthquakes.



Alfred Wegener and the early palaeoenvironmental evidence for Plate Tectonics



Figure 13.16 Wegener's map showing palaeoenvironmental evidence for climatic belts as they might have existed about 300Ma ago during the Late Carboniferous to Early Permian

Palaeontological evidence for the existence of supercontinents

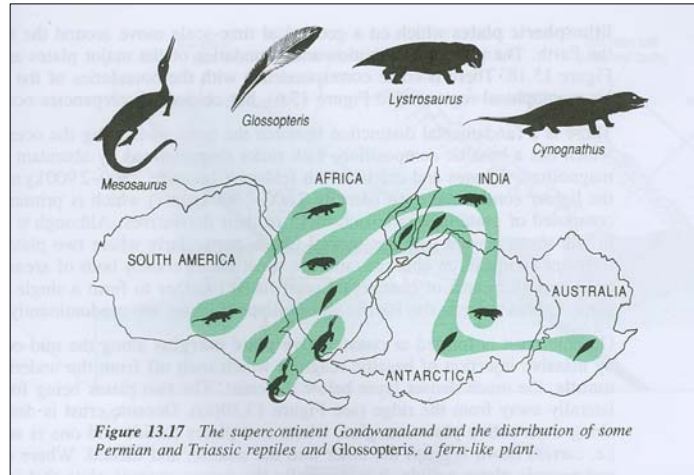
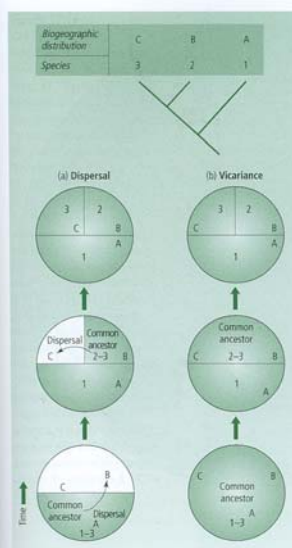


Figure 13.17 The supercontinent Gondwanaland and the distribution of some Permian and Triassic reptiles and Glossopteris, a fern-like plant.

Dispersal and vicariance (range splitting) can be alternative hypotheses to explain the biogeography of a group and tests are required to determine the fit of their predictions with observed patterns



The most common way of testing the predictions made by the alternative hypotheses is by means of building **area cladograms**

Multiple area cladograms can be compared for congruency, or individual area cladograms can be dated with a molecular clock

Figure 17.8 Dispersal and range splitting can be alternative hypotheses to explain the biogeography of a group. (a) An ancestral species with its center of dispersal in area A dispersed first to area B and a descendant from there then dispersed to area C. (b) An ancestor occupying area A + B + C had its range split first into A and B + C and then the descendant in B + C had its range split.

The first rough test is to see whether the branching order in the area cladogram is consistent with the vicariance hypothesis

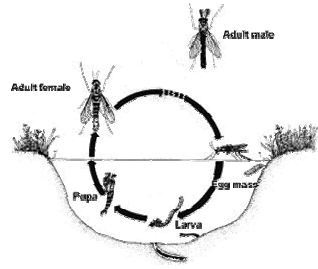


Figure 17.9
The biogeography of chironomid midges in the southern hemisphere. Reprinted, by permission of the publisher, from Brundin (1988).

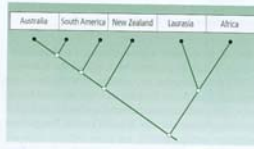
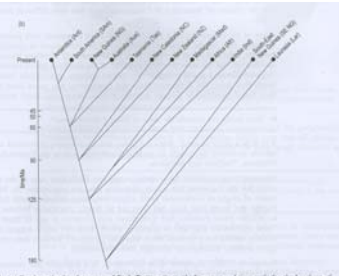
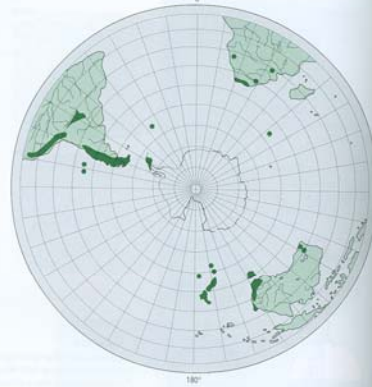


Figure 17.10
An area cladogram of chironomid midges. The diagram shows the phylogenetic relations between the midges from different areas: the midges of Australia, for example, are phylogenetically more closely related to those of South America than those of South Africa. (To see the location of Laurasia, see Figure 17.7.) Reprinted, by permission of the publisher, from Brundin (1988).

Figure 13.11 (a) Gondwanaland in Jurassic and Early Tertiary times. (b) Sequence and time-scale for the break-up of Gondwanaland.

Sequence and time-scale for the break-up of Gondwanaland

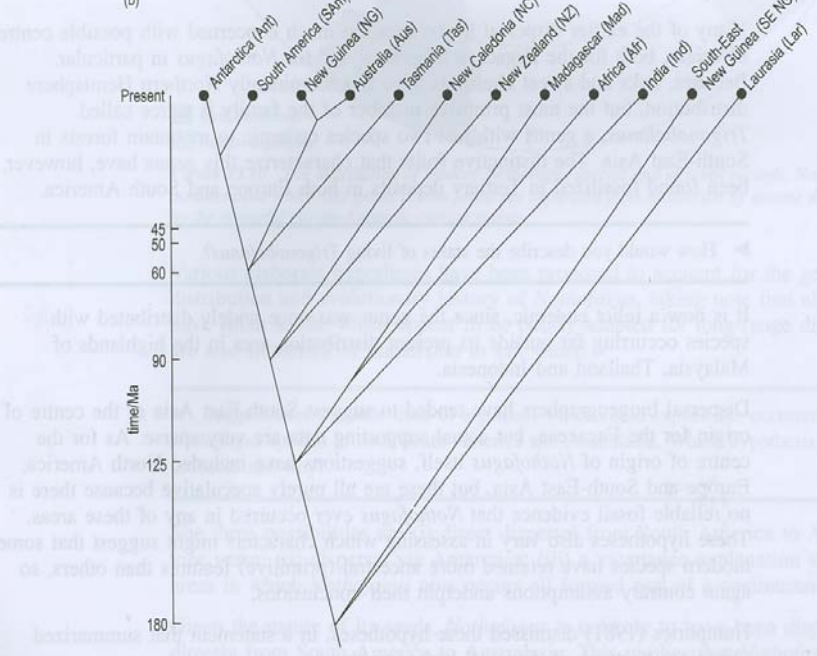
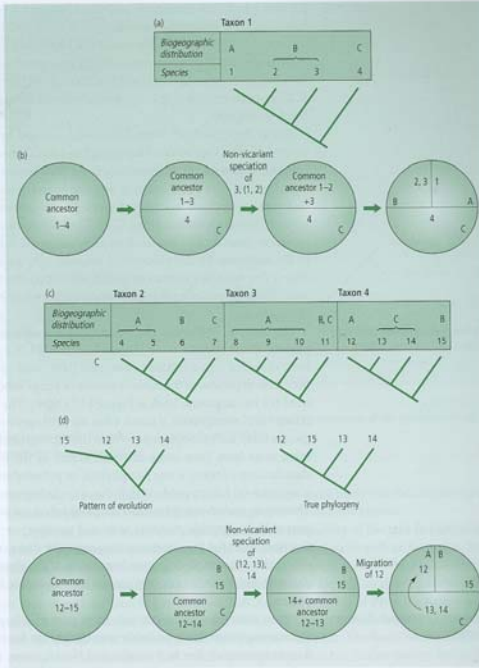
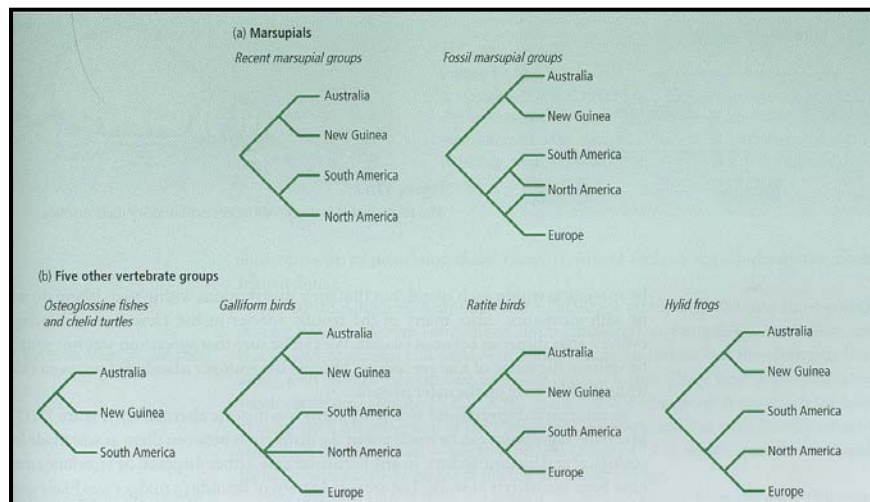


Figure 17.11

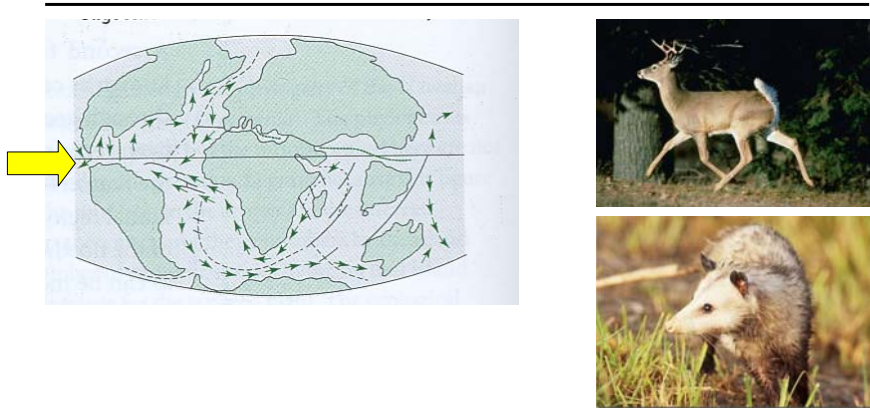
Testing vicariance biogeography by comparing the area cladograms of four taxa. (a) The phylogeny and biogeography of four species. The species are symbolized by numbers (1, 2, 3, 4) and the places where the species live by letters (A, B, C). (b) Inferred vicariant history of the distributions. (c) Taxa 2-3 have distributions that are congruent with taxon 1, but taxon 4 is incongruent. (d) Either there were dispersal events in the history of taxon 4, or its phylogeny is wrong. Species 15 may have been wrongly classified, for example, because it has evolved rapidly (the group of species 12-14 in (c) is then an example of a paraphyletic group). The suggested history with migration is only one of a number of possibilities that are compatible with a range split in the order $A + B + C \rightarrow A + B/C \rightarrow A/B/C$.



(a) Area cladograms of recent and fossil marsupials. (b) Area cladograms of five other taxa with congruent biogeographic distributions



Faunal interchange



The great American faunal interchange: after >100 million years of separate evolution, the North and South American continents became connected through a land bridge about 3 million years ago. Two very different mammalian faunas interchanged members.

The great American faunal interchange



The South American fauna was dominated by marsupials, xenarthrans (armadillos, sloths, anteaters), and ungulates. After the faunal interchange it became distinctly North American and several conspicuous South American species disappeared

Similar fractions of species moved into both directions, but NA contained more species to begin with than SA, and the species of NA origins speciated more

Table 17.2

Pattern of faunal exchange between North and South America in different time periods. The table gives the total numbers of genera of South or North American origin in each region (these are the numbers plotted in Figure 17.15), and breaks down the immigrant genera according to whether they were "primary" (that genus itself immigrated) or "secondary" (that genus descended from a primary immigrant genus, e.g., a secondary immigrant in North America evolved in there but came from a genus that itself evolved in South America). The total of the immigrant genera in the bottom two rows equals the number of alien genera in the "number of genera" row above. Note: (i) the similar proportions of primary immigrant genera moving in each direction, and (ii) the much greater numbers of secondary immigrants in South America than in the north. Modified from Marshall *et al.* (1982).

Time period (Myr BP):	South America						North America			
	9-5	5-3	3-2	2-1	1-0.3	0.3-Recent	9.5-4.5	4.5-2	2-0.7	0.7-Recent
Duration (Myr)	4	2	1	1	0.7	0.3	5	2.5	1.3	0.7
Number of genera										
North American	1	4	10	29	49	61	128	99	90	102
South American	72	68	62	55	58	59	3	8	11	12
Total	73	72	72	84	107	120	131	107	101	114
Number of immigrant genera										
Primary	1	1	2	10	18	20	2	6	8	9
Secondary	0	3	8	19	31	41	1	2	3	3

Similar fractions of species moved into both directions, but NA contained more species to begin with than SA, and the species of NA origins speciated more

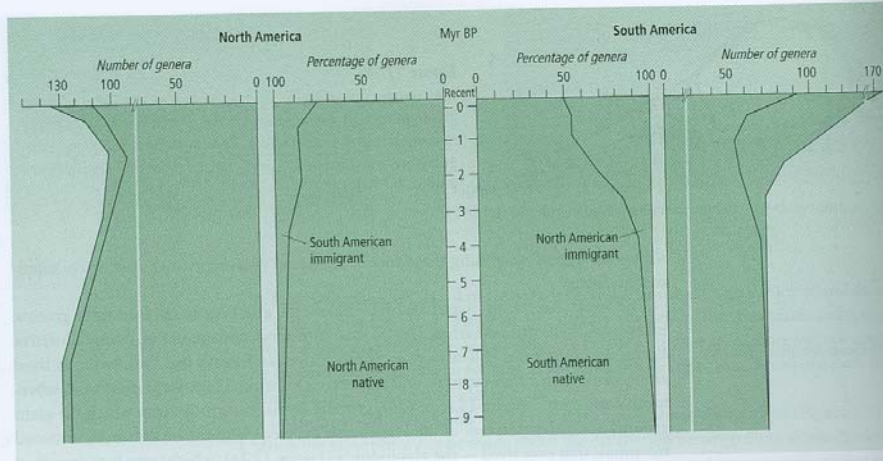


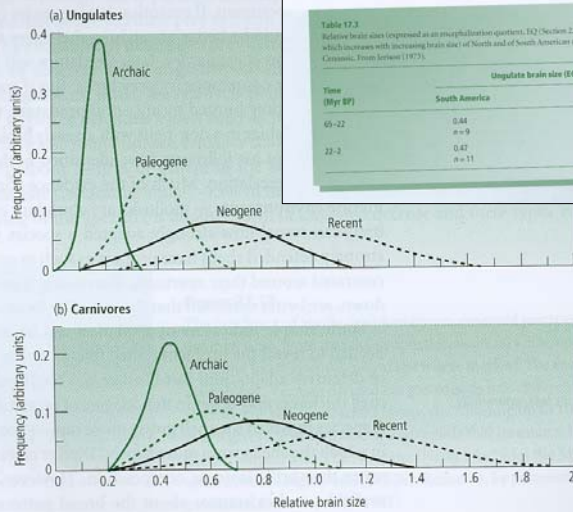
Figure 17.15

Numbers (and percentages) of genera of land mammals in the last 9 million years in North and in South America. Immigrant and native genera are distinguished in both places. Note the

wave of immigration after about 3 million years ago. Redrawn, by permission of the publisher, from Marshall *et al.* (1982). © 1982 American Association of the Advancement of Science.

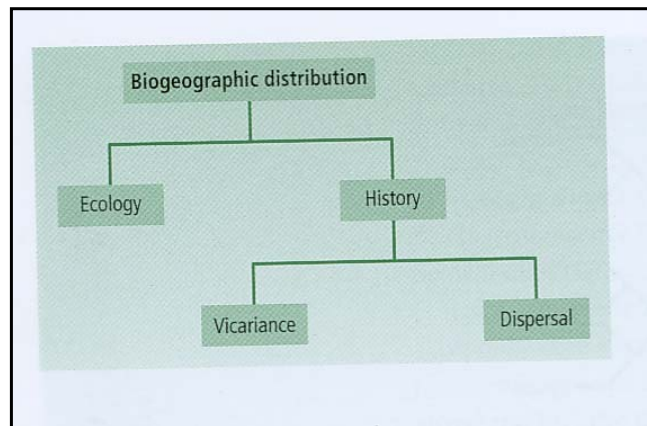
One of several hypotheses is that NA mammals had evolved in a more competitive environment and had evolved larger brains (Jerison 1973)

Figure 22.11
The distribution of relative brain sizes for (a) ungulates (prey) and (b) carnivores (predators) through the Cenozoic. Brain size increased over time and at any one time carnivores had bigger brains than ungulates. Redrawn, by permission of the publisher, from Jerison (1973).

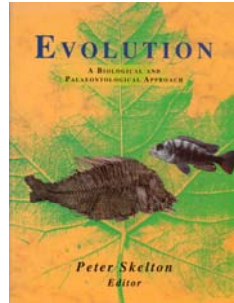
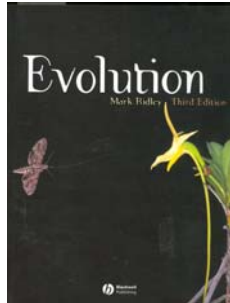


However, this is just a hypothesis, and the reasons for the differential speciation rates are not known.

The relationship between different explanatory dichotomies in Biogeography



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