f31 Biogeography < Fiji, Galapagos >

> Fore women [of Papua New Guinea highland] told her they ate the dead because they were 'delicious.'
> —Richard Roads in a letter about what Shirley (Glasse) Lindenbaum calls "gourmet cannibalism."[1]

Given that natural selection is ongoing (***Footnote f31.1***), the science of biogeography [2] seeks to explain such regularities as:

The species-area relationship.

Philip Darlington noted that for beetles the recurrent ratio of a tenfold decrease in area was matched roughly with a twofold decrease in species diversity.[3]

A species diversity-area equilibrium.

On an island, new species are gained by speciation and by immigration. Of the two, speciation is slow and can be ignored as a factor when there is a nearby large source of new species that can emigrate. Equilibrium is then a balance between immigration and extirpation (that is local, and not global, extinction). Equilibrium is achieved because successful immigrations decrease in frequency as an island becomes crowded with species and because extirpations increase in frequency as crowding increases. So an island of a given area has a *normal* complement of species if this has remained roughly constant through time. Equilibrium with turnover: one species arrives, another species of that genera dies out.

Remote islands support fewer species than do less remote islands.

This pattern shows itself in several different ways. An island of some given size, if located near a mainland, generally supports more species than a similar-size island far offshore. Also, a small island near a large island (for instance, one of the satellite islands around New Guinea) generally supports more species than a small island with no big neighbor.

Or as David Quammen puts it: "Biogeography is the study of animal and plant distribution around the planet. It addresses two simple questions: Which kinds of creatures live where, and why do they live there but not elsewhere?"[4]

In *The Theory of Island Biogeography* Robert H. MacArthur and Edward O. Wilson recount that they hypothesized that on a geologic time scale, the world's island ecosystems should be in a state of equilibrium which reflects ongoing processes and not short-term historical contingencies.[5]

Among the ant species of Asia and the Pacific Islands, Wilson noticed that newly evolved species seem to originate on the large landmasses of Asia and Australia and to disperse adventurously from there out to far-flung islands such as Fiji. As the new arrive, old species (those that had gotten there before) become extinct with the effect of no net loss or gain.

Wilson found that there were more ant species on the bigger islands and fewer ant species on the smaller islands. The same held for beetles and the reptiles and amphibians of the Antilles and for the land birds of certain Indonesian islands. For each group, a linear relationship exists between area and species diversity.

Because of their area, small islands harbor fewer species than large islands.

Because of their remoteness, remote islands receive fewer immigrants and suffer more extirpations. Area and distance determine the balance between immigration and extinction.

To test the *Theory*, Wilson used the historical record of Krakatau, a volcano in the Sunda strait between Java and Sumatra. In 1883, Krakatau blew up and vanished beneath the waves. A volcanic island Rakata emerged to take its place. On this, pioneer species were spiders, insects and fern spores. Wilson used his model that, given the calibrations of earlier measurements and curve fittings, mathematically described what to expect to predict for Rakata's birds: an equilibrium number of 30 species, a time to equilibrium of 40 years, and a turnover of one species per year.

> The actual record for Rakata is: 13 resident bird species in 1908. The number of bird species rose to 27 between 1908 and 1921. No net change in bird species between 1921 and 1934 but, by turnover, 5 species were new bird species.

An explanation for distinctive island species is a *founder effect*; one being that colonists, which survived the trip, are atypical of the average homelander. Natural selection on the progeny of the colonists can lead whither? This question has its fascinating answer for the case of some Canadian islands' weeds.

When a species of the daisy family (Asteraceae) colonizes an island, it is atypical (***Footnote f31.2***) compared to the average mainland species. The island colonists descendants are then subject to natural selection that fosters stay at home characteristics. This finding by Martin Cody and Jacob Overton in 1996 has bearing on the broader question of how come some plants and animals without *any* suitable dispersal characteristics are found on islands.[6] Much pondered cases are flightless birds (as the now-extinct dodo, and many surviving rails) and trees with gigantic seeds (as the "double coconut" of the Seychelles islands palm *Lodoicea maldivica*) that cannot be wind borne or be carried by a bird and which are intolerant of saltwater.[7]

A "Darwinian demon" (Richard Law's term for an organism that reproduces immediately after birth, has an infinite number of offspring, and lives forever)[8] mercifully has no existence. However, Jonathan Silvertown posits that "all species must go through a demon phase [grace time of maximal fitness] in their evolutionary history" when these go "from obscurity to dominance in just a handful of generations, producing evolutionary change."[9]

Recent arrivers in North America running amuck are tamarisk and Chinese tallow that degrade ecosystems by altering their physical or chemical properties, the rosy wolfsnail and brown tree snake that deplete native wildlife by preying on them, and the zebra mussel and balsam wooly adelgid aphid that set off cascading biological changes in the natural systems they invade.[10] Tim Flannery in *The Eternal Frontier*, 2001, delves into North America's ecological history of mammalian arrival events through to human colonization from when 57 million years ago the now-extinct uintatheres and *Arctostylops* came here from Asia. He illustrates that migrants pioneering any frontier exhibit:[11]

- the *founder effect,* which is that their populations are unrepresentative subsets of their source population: different on average in, say, longer legs, or stronger wings, or a larger sampling of "venturesome peasants than complacent landowners."
- *ecological release* of the immigrants, which is how they benefit from escaping a constellation of competitors, predators, parasites and diseases that bedeviled them in the old place.
- and finally, when "the fool's holiday of ecological release comes to an end," *adaptation* to the vagaries of the new environment. However, adaptation takes time and, as the mastodons and the uintatheres exampled, sometimes there isn't enough. Evolution is slow; extinction can be fast.

Consider the *Impatiens wallerana* a tropical weed native to east Africa between Mozambique and Tanzania. Somehow it had been transported to Central America where it grew in the shade of fence rows. Then one day in the 1940s, atop this gangly upright annual, its few inconspicuous orange blooms caught the eye of horticulturist Claude Hope. "Immediately enchanted," he set about to transform this denizen of riverbanks and the shady jungle understory to the branching, floriferous mound that blooms its head off in no fewer than eight colors. Michael Pollan who has essayed its floral conquest writes: "As is usually the case in such evolutionary success stories, the impatiens had the good fortune to find itself in a wide-open ecological niche, called the Post-war American Suburb. By the early 1970s, the trees and shrubs that the first generation of suburbanites had planted around their new split levels and Capes had matured, and a flower that could thrive in their deepening shade had it made. Before long, Hope's shade-loving hybrids had won the Darwinian competition to spread their leaves and flowers around the ankles of America's maples, beneath the poised hindquarters of her dogs and above her decks and patios, spilling out from white polyethylene hanging baskets."[12]

Do species see the forest or the trees?

“Neutral theory” predicts that the species in a habitat randomly come and go (the species do not see the trees). This is falsified by R. Condit’s study in 2002 of sawfly species that feed on birch trees in Finland.[13] Each sawfly species is specialized to feeding on leaves of a particular age (the species see the trees). But such examples are few and experimental evidence to supports the idea of niches is little.[14] Graham Bell, a proponent of the neutral theory, points out that if plants are closely matched to their local environments, they should perform poorly if transplanted.[15] But when he and his team in 2001 tried moving plants within Canadian forests: “The results puzzled us—they clearly didn’t point to any powerful degree of local adaptation, and sometimes the rarest species was the most successful in a new location.”[16] To remind: Neutral theory predicts that the species in a habitat randomly come and go. Stephen P. Hubbell’s *Neutral Theory of Biodiversity and Biogeography*, 2001, documents that at certain scales this is true.[17] But do the predictions of neutral theory merely mimic reality?

What is learned from these studies and tales has application to the understanding of paleogeographies. To quote Preston Cloud: “According to the basic principle of uniformitarianism, which uses observable and testable processes and dynamic relations as the keys to past events, the interpretation of ... paleogeographic data is based on analysis of the mechanisms that affect the survival and dispersal of organisms and organic remains ...”[18] In considering the marine realm, he illustrates the play of three variables: external, internal (reproductive) and cobiotic (dispersal), which need to be considered when reconstructing paleogeographies. ❑

Footnote f31.1 Bernard Kettlewell’s famous evidence of natural selection in action was the coincident rise and fall in *two* widely separate geographic areas (industrialized Birmingham, England, and Boston, America) of the frequency of dark coloration (melanism) in the peppered moth (*Biston betularia*) with industrial soot pollution from 1850 to 1900 when a dominant mutation produced an all-black form (called *carbonaria*) that proliferated and, later, a return to the normal coloration (white speckled with dark markings) form (called *typica*) after clean-air policies became enacted.

Two hypotheses for the rise of melanism by Kettlewell and his mentor E. B. Ford were respectively:

1) Typica moths being more conspicuous than carbonaria moths in a sooty environment, are selectively preyed on by sharp-eyed birds.
2) Carbonaria moths as breeding experiments show, are more resistant than are typica moths to pollution.

The role of natural selection by as the above in the frequency changes of the moth has been firmly established by numerous later studies; notably the careful ongoing one by Michael Majerus.[19] However, the popularizing book *Of Moths and Men* by Judith Hooper, 2002, might lead nonbiologists to conclude otherwise.[20] To quote Bruce Grant: “The case for natural selection in the evolution of melanism in peppered moths is actually much stronger today than it was during Kettlewell’s time. Textbook accounts should be expanded to reflect this newer information, and they should not cite *Of Moths and Men* as a credible resource.” [21]

Footnote f31.2 An example of biogeographic selection

Asteraceae species propagate by wind-dispersed seed. Like the familiar dandelion seed these have a fluff-ball parachute (pappas) and a dangling seed-case (achene). The distance that the seed can be wind-borne is measured by the parameter: pappus volume / achene volume.

Censuses showed that island weed-patches survive only a few seasons before going extinct. Also, fresh daisy colonizations in areas barren for 9 years are not the germination of buried seeds.

For several daisy species populations of known ages, from an age of 1 year to decades, the founder effect is colonists with a larger pappus and a smaller achene than is the norm of mainland individuals. Thereafter, insular achene volume increases through about 8 years after which this is at mainland size. And insular pappus volume decreases through about 6 years after which this remains much smaller than mainland size. The selective force in this peripatric evolution is winnowing.