PATTERNS OF GEOGRAPHICAL DISTRIBUTION: ANIMALS

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Contents

Summary

The faunas of oceanic islands generally differ from continental faunas in at least four significant ways. They are generally impoverished, disharmonic and have a high percentage of endemic species. Island faunas are also thought to be unsaturated, although this is a matter of some debate. In addition there are a number of evolutionary trends in which island species tend to have noticeably larger or smaller body sizes than do their continental counterparts. For groups that can fly, such as birds and insects, there is a trend toward flightlessness on islands. There is also a trend, most pronounced on isolated islands and archipelagos, for initial colonizing species to undergo adaptive radiation. Although islands in general support smaller faunas than do nearby mainland areas, the high number of endemic species found on islands is an important component of the world's biota. Overall, islands comprise about 3% of the earth's land surface but harbor about 15% of the biota. Tragically, island species are also for a variety of reasons, highly susceptible to extinction from human-related disturbances; the native fauna that is found on islands today is a fraction, often a small fraction, of what once occurred there.

1. Introduction

The animals found on oceanic islands are generally derived from nearby continents. The taxonomic composition of island faunas therefore tends to vary geographically and to reflect the world-wide distribution of different animal groups. However, the ecological characteristics of island faunas tend to be rather similar in that they are impoverished but have a high rate of endemism. Island faunas tend also to be disharmonic. Depending on island size, distance from source areas and other factors, some taxonomic groups that are poor over-water dispersers (e.g., amphibians) tend to be poorly represented or absent from islands. Other groups (e.g., geckos) tend to be well represented. Islands also tend to disproportionately harbor relict taxonomic groups that have gone extinct on adjacent mainland areas, possibly because insular environments tend to be more stable than those on continents.

In many respects islands differ from continents only in that they are smaller and more difficult to reach. These features, however, combine to greatly influence the composition of the fauna. The initial animal colonists are generally those most adept at dispersal and establishment. In the absence of a full array of mainland predators and competitors these species often take on broader ecological characteristics than they exhibit on continental areas. This, together with the founder effect, in which the initial colonists represent a small fraction of the genetic diversity of the species, can lead to divergent evolution and the development of unique island biotas. It is in fact these features that have made islands model systems for the study of evolutionary biology beginning with Darwin's visit to the Galapagos Islands.

A number of different evolutionary trends have been identified on islands. These include reduction in dispersal capabilities, changes in body size, changes in reproductive strategies, changes in population densities and expansion of ecological niches. This chapter begins with brief summaries of the faunas of different groups of islands in order to understand geographic patterns of species richness and endemicity

and then examines ecological and evolutionary trends within these groups.

In this analysis the focus is mainly on vertebrate groups because the distribution and diversity of these taxa are far better known than are those of invertebrates. For example in the Hawaiian Islands, which have been intensely studied for more than two centuries, upwards of a quarter of the insects may be undescribed. The vertebrates have essentially been known for the better part of a century.

1.1. Definition of Oceanic Islands

For the purposes of this study oceanic islands are those islands that have never been connected by land with continental source areas (see Oceanic Islands: Introduction). This includes islands formed volcanically or by crustal upthrust. It also includes some islands that formed as tectonic fragments, such as the Seychelles in the Indian Ocean and New Caledonia in the southwestern Pacific, which seem to have retained some of their original continental biota but subsequently have been isolated for millions of years.

1.2. Geographical Distribution of Oceanic Islands

There are thought to be at least 25,000 islands in the world of which about half are in the Pacific region. In order to understand general geographic trends in the ecology and evolution of island animal communities, islands are examined in geographic groups. These are arbitrarily divided into islands of the eastern Pacific, central and western Pacific, north Atlantic, south Atlantic, Indian and Caribbean. This is not meant to be an exhaustive treatment; the selection of islands and island groups is somewhat arbitrary and is intended to be broadly reflective of islands in different geographic areas of the world.

2. Island Faunas

2.1. Eastern Pacific Ocean

The eastern Pacific tends of be rather devoid of islands. The best known groups include the Galapagos archipelago and the Juan Fernandez Islands. In addition, there are a number of small isolated islands and island groups off the coast of Mexico. The faunas of the eastern Pacific islands are derived largely from North, Central, and South America.

2.1.1. Revillagigedo Archipelago

This isolated archipelago consists of four main volcanic islands and numerous islets with a total area of about 637 km^2 located approximately 600 km west of the Mexican state of Colima. The oldest islands are probably Pliocene in age and at least one of them, San Benedicto, remains volcanically active with the last eruption having taken place in 1952. The islands lack native amphibians and land mammals. The two largest islands, Soccoro and Clarión, are each inhabited by an endemic phrynosomatid lizard in

the genus *Urosaurus*. In addition, Clarión is inhabited by an endemic colubrid snake, *Masticophis anthonyi*. The two species of *Urosaurus* are most closely related to *Urosaurus ornatus*, which has an extensive distribution from southern Wyoming to Sonora and Sinaloa. The *Masticophis* is apparently also most closely related to species occurring in Sonora and Sinaloa. Twenty-five species of breeding birds are known from the archipelago. Ten of these are seabirds of which one, *Puffinus auricularis*, is endemic and the rest are land birds of which three, all passerines, are endemic. The passerines all likely originated from mainland Mexico. The invertebrate fauna is depauperate and like the vertebrates, appears to have originated from Sonora-Sinaloa or in some cases from southern Baja California.

2.1.2. Clipperton

This small island, an oval-shaped atoll about 4 km long, is located at 10° north latitude about 1300 km southwest of the Mexican state of Guerrero. It is the eastern-most atoll in the Pacific. Clipperton lacks native amphibians, reptiles and mammals but has eight species of breeding birds. These include the American coot and seven species of seabirds. None is endemic.

2.1.3. Galapagos Islands

The Galapagos Islands are among the best known islands in the world. They consist of 13 main islands and occupy a total area of 770 km^2. The climate is generally arid and there are no native amphibians. However, there are 21 native species of reptiles representing eight genera and five families, including snakes, lizards and the famous Galapagos tortoises (one species with many insular races). All but one of the reptile species are endemic. There are 58 native species of breeding birds including 21 species of passerine birds. Overall, 27 (47%) of the birds are endemic. Among the passerines, 18 (86%) of the species are endemic. There are five extant species and at least six extinct species of native oryzomyine murid rodents comprising three genera. The genera are closely related and probably represent the same radiation. Two of the genera are endemic and the third, *Oryzomys*, is represented by a single endemic species. There are nearly 40 other species of *Oryzomys* occurring in the Neotropical region. Two species of widely distributed vespertillionid bats in the genus *Lasiurus* also inhabit the Galapagos Islands as does an endemic fur seal, *Arctocephalus galapagoensis*. There are at least 2000 native terrestrial invertebrates, primarily insects and land snails.

2.1.4. Juan Fernandez Islands

This small archipelago consist of two main islands, Masatierra and Masafuera, and several smaller islands located about 600 km west of Valparaiso, Chile. The only native terrestrial vertebrates are nine species of birds, of which four (44%) are endemic. There are small radiations of land snails and insects.

2.2. Central and Western Pacific

This region includes at least 12,000 islands, most of which are volcanic in origin but some of which were formed from crustal uplift or as tectonic fragments rafted off

mainland areas. The large island of New Guinea has served as a major source area for the biota of the Pacific region, and this influence extends for some groups all the way to Hawaii (6,800 km to the northeast). New Guinea began forming in the late Oligocene at the leading edge of the Australian plate. This involved considerable uplift, volcanism and the accretion of more than 30 terranes to form a geological composite, a process that facilitated the evolution of an enormous biota that today comprises 5-7% of the world total. At the same time, the formation of island arc systems to the north and east provided dispersal pathways by which elements of this biota have expanded into the Pacific Basin. In general those islands closest to New Guinea are biologically most similar to it.

Frogs show the simplest pattern. The Admiralty Archipelago and Bismarck archipelagos support 19 species of frogs, of which 12 (60%) are endemic. The Solomon Islands (including the islands of Buka and Bougainville which are politically part of Papua New Guinea) have 26 species of which 22 (85%) are endemic. There are no native frogs on Vanuatu or New Caledonia. but there are two species of ranid frogs in the genus *Platymantis* endemic to Fiji. Frogs in this genus undergo direct development from eggs laid in moist substrate (e.g., leaf litter) and this may help explain the wide distribution of the genus which in addition to the areas mentioned also occurs in the Philippines, Palau, the Moluccas, New Guinea, the Bismarck and Admiralty Archipelagos and the Solomon Islands.

Lizards and snakes are much more adept than frogs at crossing ocean gaps between islands. There are at least 46 species of lizards and 13 species of snakes inhabiting the Bismarck Archipelago. Five of the lizards (11%) and 3 of the snakes (23%) are endemic. Most of the remaining species also occur in New Guinea. The Solomon Islands have 55 species of lizards of which 22 (40% are endemic) and 20 species of snakes including 9 (45%) that are endemic. The adjacent archipelago of Vanuatu has 25 species of lizards of which 6 (24%) are endemic. Only two species of snakes occur in Vanuatu; both are widespread Pacific species.
The island of New Caledonia (18,760 km^2 in area), which formed as a volcanic arc off the northeastern coast of Australia during the Permian and rafted east to its present position beginning in the late Cretaceous, has a herpetofauna of 71 species. This includes 68 species of lizards native to New Caledonia and the nearby Loyalty Islands and three species of snakes. The lizards represent large radiations of skinks and geckos and all but seven of the species are endemic. Only one of the snakes, a blind snake, is endemic.

Fiji, which at 18287 km^2 in area is slightly smaller than New Caledonia, has 26 species of terrestrial squamates, including 24 lizards (9 endemic) and three species of snakes (one endemic). Remarkably Fiji also has two endemic species of ranid frogs in the genus *Platymantis*.

The small archipelagos of Samoa and Tonga (752 km^2 and 3033 km^2, respectively) have what is essentially a subset of the Fijian fauna. The widespread Pacific boa, *Candoia bibroni*, occurs in all three archipelagos. There are 19 (two endemic) and 14 (one endemic) species of lizards known, respectively, from Tonga and Samoa. There doesn't appear to be any native terrestrial reptiles north or east of the Cook Islands, although a

number of species appear to have been inadvertently dispersed by humans throughout much of Oceania, including Hawaii.

The New Guinea fauna also extends in the western Pacific north to Palau, which in addition to the single endemic frog species (*Platymantis pelewensis*) mentioned above, has 27 species of lizards and five snakes. Ten of the lizards (4 geckos and 6 skinks) are endemic. The other high islands of Micronesia - e.g., Pohnpei, Yap, and Kosrae, and the Marianas - each supports a small herpetofauna that overall includes a few endemic skinks and geckos.

The Pacific region, including New Guinea, is home to about 1035 species of terrestrial and non-marine breeding birds. About 500 of these occur in Polynesia, Micronesia and Melanesia, exclusive of New Guinea, and slightly more than 300 of them are endemic to this latter region. As with other animal groups, species diversity is greatest on the islands close to New Guinea and drops of with distance. The Bismarck and Admiralty Archipelagos have 168 species of which 48 (29%) are endemic. The Solomon Islands have 169 species and 59 (37%) endemics. New Caeldonia has 75 total species of which 20 (27%) are endemic. The avifauna of Vanuatu is rather impoverished with a total of 56 species, but 20 of these (36%) are endemic. The remaining parts of the Pacific have 215 species of native land birds; at least 175 (81%) of these are endemic (Table 1). For the most part, birds of the southwestern Pacific have affinities to those of New Guinea and Asia. The birds of Micronesia have these same affinities but with a greater proportion of the species derived from Asia. Hawaii, the most isolated archipelago in the world, has species derived from North America and well as from Asia and the Pacific region. More than half of Hawaii's birds are in the finch subfamily Drepeninae that includes at least 33 extant and historically extinct species that are thought to have been derived from a single carduine finch ancestor that likely came from Asia or North America.

	Total	**Indigenous**	**Endemic**	**% Endemic**
Subregion	**Species**	**Species**	**Species**	**Species**
Fiji	54	30	24	44.4
South Polynesia	38	26	12	31.6
East Polynesia	47	8	39	83.0
Central Polynesia	6	5	1	16.7
Hawaii	53	4	49	92.5
Micronesia	61	21	40	65.6
TOTAL	**215**	**40**	**175**	**81.4**

Table 1. Number of indigenous and endemic species of land birds found in different regions of Polynesia and Micronesisa

Compared to birds the terrestrial mammalian fauna of the Pacific is rather impoverished with 102 species known from Melanesia (exclusive of New Guinea), Micronesia and tropical Polynesia, including four species that have gone extinct in historical times. A

total of 69 species are endemic to this region. The remaining 33 species are mostly shared with New Guinea and satellite islands. The Admiralty Archipelago has a total of 17 native species of mammals. Fifteen of these, all bats, are shared with the Bismarck Archipelago and two species, a cuscus, *Spilocuscus kraemeri* and a rat, *Melomys matambui*, are endemic. Both species endemic to the Admiralties have their closest affinities to New Guinea; the cuscus may represent an ancient human introduction to the Admiralties.

The Bismarck Archipelago has a total of 47 species. In addition to the 15 species shared with the Admiralties, there are 22 additional non-endemic ones. One of these, a fruit bat, is shared only with Manus; the other non-endemic species are mostly widespread southwestern Pacific species. The remaining ten species are endemic to the Bismarcks. These include seven species of bats and three species of rodents; all have affinities with New Guinea.

The Solomon Islands have 49 native species of mammals of which 29 are endemic. The non-endemic species, all bats, are mostly widespread southwewstern Pacific species. The endemic species include 21 species of bats (17 species of fruit bats and four species of insectivorus bats) and eight species of murid rodents. Two of the rodent genera are shared with the Bismarcks and New Guinea; the third, *Solomys*, comprising a radiation of four species, is endemic.

The only terrestrial mammals found east of the Solomon Islands are bats. Species diversity declines markedly past the Solomon Islands. There are 11 species found in Vanuatu of which two are endemic. New Caledonia has six endemic and three indigenous species. Fiji has a total of six species, one of which is endemic. Samoa and Tonga have a total of four species, none of which is endemic. In addition, an endemic subspecies of the widespread New World bat, *Lasiurus cinereus*, occurs in Hawaii.

The widely dispersed islands of Micronesia have a total of ten species of bats. Nine of these are fruit bats in the genus *Pteropus* of which eight species are endemic to Micronesia. The other bat that occurs in Micronesia is an emballonurid, *Emballonura semicaudata*, that occurs through much of the Pacific Basin.

The insects show patterns similar to the birds - in general they have clear affinities with New Guinea and Asia. The numbers of genera and species tends to decrease away from New Guinea. This is likely the result of two combined factors: increasing distance from the source area and a somewhat irregular trend towards a decrease in island size away from New Guinea.

There are thought to be about 4000 species of Pacific land snails (exclusive of the ca. 1000 species found in New Guinea). These are generally thought to have originated from the Asian/Australian region. However, one family, the Achatinellidae, is restricted entirely to the Pacific region; it may have originated from the Nearctic or Neotropical region. Land snails have radiated extensively on some islands and there are 752 species known from Hawaii.

The many islands that are politically part of the Phillipines and Indonesia have a large,

diverse biota that has primary affinities to Asia. It is beyond the scope of this chapter to treat this fauna in detail.

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Much of the information on the geographical distribution of animals on islands is scattered through an enormous literature. For the preparation of this more than 200 journal articles and books were consulted. The ten major references used are listed below.

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Biographical Sketch

Allen Allison specializes on the classification, ecology and biogeography of vertebrates, particularly amphibians and reptiles. He received his B.Sc. in 1972 and his Ph.D. in 1978 from the University of California at Davis. Born and raised in California, he has spent most of his career in the Pacific region. In 1978 he was appointed as assistant director of the Wau Ecology Institute, an independent research organization in Papua New Guinea, that originated as a field station of the Bishop Museum in Hawaii. In 1983 he accepted a research position with the Bishop Museum and relocated to Hawaii. In 1985 he was

appointed chair of the Museum's Department of Zoology and in 1991 was promoted to Vice President for Science. He has also since 1984 served on the affiliate graduate faculty of the University of Hawaii and as an officer numerous scientific organizations.

Dr. Allison's research interests currently center on the systematics and biogeography of Pacific amphibians and reptiles. He is also actively involved in efforts to develop information systems from the data contained in museum specimen collections. This has led to the establishment of the Hawaii Biological Survey, a program of the Bishop Museum that has produced a complete inventory of the plants and animals of Hawaii. Dr. Allison and colleagues are currently expanding that effort into a Pacific Biological Survey. He resides in Honolulu with his spouse, Isabella Forster and two daughters, Zora and Hana.