

# Colonization of the Krakatau Islands by vertebrates: Equilibrium, succession, and possible delayed extinction

(species turnover/ecological refuges/island biogeography)

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**ABSTRACT** MacArthur and Wilson [MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ)] used the rate of recolonization of the Krakatau Islands (sterilized in the cataclysmic 1883 eruption) by birds and vascular plants to test their equilibrium model of immigration and extinction processes on islands. Working with data only up to 1933, they concluded that the number of resident land bird species had approached equilibrium by 1908–1919, 25–36 years after the eruption, when the number of vascular plant species was still increasing. Recent surveys of vertebrates on the archipelago show continuing colonization, as well as species turnover. Nonmigrant nonmarine birds and reptiles are only now approaching equilibrium species numbers; archipelago acquisition rates for these groups are lower than in the 40 years following the 1883 eruption. Apparent (minimal) annual extinction rates are an order of magnitude lower than those calculated for equilibrium by MacArthur and Wilson. The active volcano Anak Krakatau emerged in 1930 and suffered an eruption in 1952 that destroyed the vegetation. It is still at an early stage of succession and on the threshold of major vegetational change. This island and a physically dynamic, ever-young spit on Sertung I, also held at an early successional stage, may provide (i) ecological refuges for some species whose optimal habitat on the older islands is being extirpated by vegetational succession and (ii) ecological “windows” through which such species may still establish from the mainland, thus postponing their extinction on the archipelago.

The 1883 eruption of Krakatau Island (Krakatoa) resulted in the loss of some two-thirds of the island and extirpated the flora and fauna of its 813-m-high remnant, Rakata (now 777 m), and the adjacent islands Sertung and Panjang (1) (Fig. 1). The recolonization of the archipelago by plants and animals is a classical case study in biogeography and was used by MacArthur and Wilson (2, 3) to test their stochastic model of immigration and extinction processes on islands. Using data on the bird fauna only up to 1933, they concluded that the number of nonmigrant nonmarine bird species on Rakata and Sertung had approached equilibrium by 1908–1919 (28 species), at a time when the number of vascular plant species was still increasing. They (3) estimated the annual extinction rate at equilibrium to be surprisingly high, between 0.5 and 1.6 species per year, or “1% to 6%” (sic) of the standing fauna, with an equilibrium number of species of about 30. Mayr (4) had independently suggested an equilibrium number of 40–45 species.

MacArthur and Wilson were evidently unaware of a survey of Krakatau birds by the ornithologist Hoogerwerf (5) show-

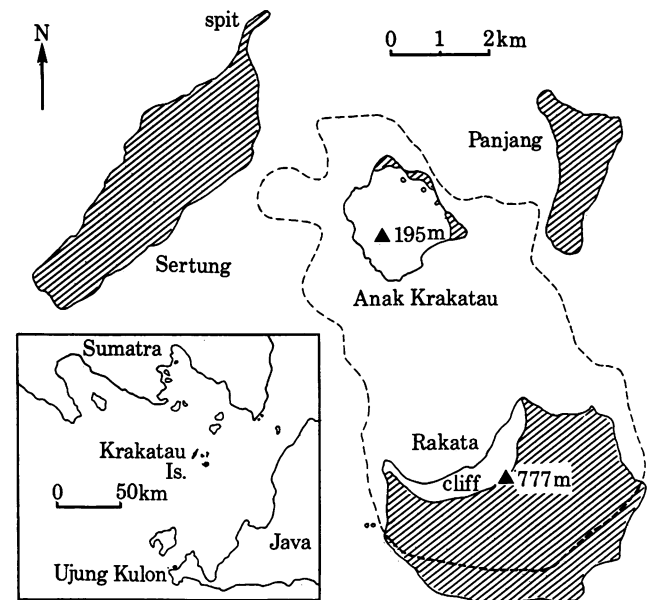


FIG. 1. Sunda Strait and the Krakatau Islands. Heights are given in meters; broken line shows outline of Krakatau before 1883 eruption; shading represents vegetation over 90% cover.

ing species numbers still rising in 1951. Faunal surveys were conducted by a Japanese team (which did not survey birds or bats) in 1982 (6) and by us from 1984 to 1986, so that two good datum points (1951–1952 and 1984–1986) are now available for birds, in addition to those used by MacArthur and Wilson, and one more (1984–1986 for birds and bats, 1982–1986 for reptiles and rats), the first since 1933, for other vertebrates. It is now possible to reassess the course of recolonization by vertebrates, including the last half-century.

In 1930 a new island, Anak Krakatau, emerged from the submarine caldera of Krakatau, and lava flows in the 1960s ensured its permanence. It is now 195 m high and still active. Successive eruptions since its appearance have set back biotic succession, and we believe the existence of Anak Krakatau has had a significant effect on the course of succession and species turnover on the archipelago as a whole.

In our surveys of the archipelago in August and September, 1984–1986, we censused nonmigrant nonmarine birds by mist netting [21,677 (rain-free hours of daylight during which the nets were set) × (m<sup>2</sup> of net)], broadcasting calls of expected species, recording calls and songs, 411 man-hours of visual survey, and 63 man-hours of spotlighting. Bats were detected by ultrasound (19 man-hours) and captured in mist nets [7675 (rain-free hours of night during which the nets were set) × (m<sup>2</sup> of net)] and harp traps (34 trap-nights). Reptiles were caught

by hand, and Elliott traps (400 trap-nights) were used for rats. Forty man-days of specialist effort was expended on reptiles, 80 on birds, and 43 on mammals. We know of no record of the previous use of sound or ultrasound recorders, harp traps, mist nets, or Elliott traps on the islands.

### Turnover and Increase in Number of Species

We found apparent turnover and increases in number of species in the last 50 years in all groups but rats (Table 1, Fig. 2). *Rattus rattus* has occurred on Rakata since 1919 and is now also on Anak Krakatau. *Rattus tiomanicus* has been on Sertung and Panjang since 1933 and 1928, respectively (1). The increases in birds and reptiles, however, do not satisfy Schoener's arbitrary nonequilibrium criterion (8) that species number increase "for at least two consecutive time periods by 15% or more." Observed increases in species of bats, particularly insectivorous species, in 1984 and 1985 must be treated with great caution because monitoring techniques were more refined than in previous surveys. When only Rakata and Sertung data are considered, for comparison with data available to MacArthur and Wilson (3), turnover and increase in species number are still evident. Panjang was adequately surveyed only in the 1980s, but no vertebrate species was found to be restricted to that island.

We believe that some species first recorded in the 1980s are recent colonizers, either because they are conspicuous by sight or sound and unlikely to have been missed in previous surveys, or because they have a restricted archipelagic distribution, or both. They include the carnivorous Malay false vampire bat (*Megaderma spasma*), the insectivorous whiskered bat (*Myotis muricola*), the large fruit bat (*Pteropus vampyrus*), and the tokay (*Gekko gecko*) and king gekko (*Gekko monarchus*) (which have loud calls but were not recorded in 1982; ref. 6), all of which have restricted distributions on the islands. All these species except *P.*

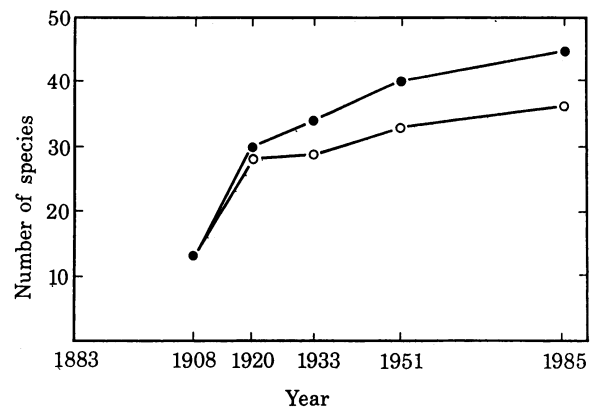


FIG. 2. Increase in number of species of nonmigrant nonmarine birds recorded on the Krakatau Islands since 1883. Filled circles, cumulative number; open circles, actual number.

*vampyrus* were present in the 1980s at Zwarte Hoek, Rakata, which is a part of the archipelago visited by every zoological expedition in the past. A colony of *P. vampyrus* was present on Sertung near the base of the spit, also a much-visited part of the archipelago. Thus it is unlikely that their restricted distributions have led to these species being missed in previous surveys; they are in fact confined to the areas that have received the most attention in the past. The paradise tree snake (*Chrysopelea paradisi*) is fairly conspicuous, frequent, and now occurs on all islands. A blind snake, *Rhamphotyphlops brahminus*, first seen in 1984, probably arrived some time after 1933, perhaps with a termite nest on flotsam (9); Dammerman's expeditions paid particular attention to soil and litter (1). The black eagle (*Ictinaetus malayensis*) and the imperial pigeons *Ducula aenea* and *Ducula bicolor* are all fairly conspicuous, and the two pigeons have

Table 1. Number of vertebrate species on the Krakataus and changes in composition of the fauna in surveys since 1883

	1889	1908	1919–1924	1928–1934	1951–1952	1984–1986
<b>Land reptiles</b>						
Actual	1	3	7	7		9
Gains	+1	+2	+4	+1		+5
Losses	—	0	0	—1		—3
Cumulative	1	3	7	8		13
<b>Resident land birds</b>						
Actual	?	13	28	29	33	36
Gains	—	+13	+17	+4	+7	+7*
Losses	—	—	—2	—3	—3	—4
Cumulative	—	13	30	34	40	45
<b>Bats</b>						
Actual	0	0	2	4		15†
Gains	—	—	+2	+2		+13†
Losses	—	—	—	0		—2
Cumulative	—	—	2	4		17†
<b>Total vertebrates, including rats</b>						
Actual	1	16	38	42		62
Gains	+1	+15	+24‡	+8‡		+25§
Losses	—	0	—2	—4		—7§
Cumulative	1	16	40	48		75

Data for first four surveys from Dammerman (1), for 1951–1952 from Hoogerwerf (5), for 1984–1986 our surveys.

\*Assumes two recolonizations.

†Includes one species recorded only in 1974 (7).

‡Includes one species of rat.

§Not totals of gains and losses shown under 1984–1986; bird gains and losses since 1928–1934 (+9, —2) rather than 1951–1952 are included, to conform with mammals and reptiles.

loud calls and are unlikely to have been missed in 1951. Other evident gains since Hoogerwerf's survey include the barn owl (*Tyto alba*), Pacific swallow (*Hirundo tahitica*), house swift (*Apus affinis*), and chestnut-capped thrush (*Zoothera interpres*).

Species that were unrecorded in the 1980s and that appear to represent extinctions include the distinctively colored, large insectivorous bat *Hipposideros diadema*, the previously common (1) coastal skink (*Emoia atrocostatum*), the serpent eagle (*Spilornis cheela*), and the koel (*Eudynamis scolopacea*). The koel is a nest parasite of crows; its host appears to be on the point of extinction on the islands (see below). We believe that all the above absences represent extinctions. The peaceful dove (*Geopelia striata*) was restricted to Sertung in 1951 (5) and was not recorded in the 1980s; it now may also be extinct. We believe that *Rhaphidura leucopygialis*, a swift restricted to Rakata in 1951 (5) and also not recorded in the 1980s, may have been missed in our survey. The python (*Python reticulatus*) now appears to be very rare, but the paradise tree snake has become well established in recent years and a successful recolonization by the serpent eagle may be expected.

### Equilibrium Number of Resident Land Bird Species

The 164 nonmigrant nonmarine bird species recorded from Ujung Kulon (Fig. 1) by Hoogerwerf (10) and later observers may be regarded as the mainland pool for this island group (3). From immigration and extinction rates during the most recent intersurvey period, based on two good bird surveys, the equilibrium number of species on the Krakataus can be calculated by following MacArthur and Wilson (3). The data from Table 1, which is based simply on actual records, give an equilibrium number of 51. Calculations based on various other assumptions of absences indicating extinctions and presences indicating residence give numbers ranging from 44 to 57. These differences in estimated equilibrium numbers underscore the problems of intersurvey comparisons where small faunas are involved. In any case, the present number of bird species (36 species) is clearly not the equilibrium figure, which is higher than that (about 30) estimated by MacArthur and Wilson (3); the 1919–1924 number (28 species) represents not equilibrium but a point after which the rate of increase sharply declined (Fig. 2). This pattern is repeated in the figures for reptiles (Table 1), and the rate of increase of vascular plant species on Rakata also declined from this time (11), which was when canopy closure began (12). The increase in nonmigrant nonmarine bird species since 1921 is 29%, about one additional species every 8 years, compared to about one every 18 months previously. The present extinction rate for birds is between 0.09 and 0.15 species per year, from 0.25% to 0.42% of the standing fauna, and for reptiles is 0.06 species per year (0.70%). These rates are decidedly lower than the annual extinction rates at equilibrium calculated for birds by MacArthur and Wilson (2). Because of cryptoturnover (13) (species becoming extinct and reimmigrating within the intersurvey period) such values are clearly minimal and underestimate true extinction rates, which may be several times higher (14, 15).

### Colonization of Anak Krakatau

Anak Krakatau emerged in 1930 and suffered a devastating eruption in 1952 (5, 16), with several damaging ones since then; the biota is thus no more than about three decades old. Grassy areas and a *Casuarina* association comprise the 5% (14 ha; 1 ha = 10<sup>4</sup> m<sup>2</sup>) of its area that is now vegetated (17, 18) (Fig. 1). These were early successional stages on the three older islands, which now are covered in secondary forest. The species-acquisition rate of nonmigrant nonmarine birds

by Anak Krakatau since 1952 is 0.75 species per year (25 species now present), similar to the rate for the other islands in the 38 years following 1883 (0.74 species per year), in spite of the very small vegetated area available for colonization on Anak Krakatau. However, Anak Krakatau is much closer to potential sources, the three older islands, than were they at the time of their recolonization.

Of true forest birds present on the other islands, as yet Anak Krakatau lacks the brown-capped woodpecker (*Picoides moluccensis*) and orange-bellied flowerpecker (*Dicaeum trigonostigma*), specialists of large trees, first recorded on the archipelago 36–38 years after the cataclysmic eruption. However, the scarlet sunbird (*Aethopyga mystacalis*) and chestnut-capped thrush (*Zoothera interpres*), birds of dense undergrowth not recorded until 1951 and 1984, respectively, were seen on Anak Krakatau in the 1980s and may be recent components of its avifauna.

Five (possibly 6) of the 11 species of frugivorous birds on the archipelago occur on Anak Krakatau (including the omnivorous, near-extinct crow; see below), and 4 of these were early colonizers of Rakata. The little cuckoo-dove (*Macropygia phasianella*) and pink-necked pigeon (*Treron vernans*) are the only 2 of the 6 species of fruit-eating pigeons on the islands to occur on Anak Krakatau. The Philippine glossy starling (*Aplonis panayensis*), which was heard on the island, is a known disperser of *Macaranga*, a tree important in the plant succession to mixed secondary forest and which may have become established very recently on the island (18). The black-naped oriole (*Oriolus chinensis*), another specialist frugivore, is certainly breeding on the island; the island's only resident bats (*Cynopterus sphinx*, *Cynopterus tittaechilus*, and *Rousettus amplexicaudatus*) are frugivorous; and in 1986 a stray individual of the large flying fox *Pteropus vampyrus*, also a fruit-eater, was seen on the island.

The two fig species on Anak Krakatau were first seen fruiting there in 1985, and fig wasps are present. Thus, with fruiting figs and several frugivorous vertebrate species, an avenue for plant colonization of great importance for subsequent plant succession on the island (19) is now open. Of 76 species of spermatophytes recorded from Anak Krakatau from 1979 to 1983 (17, 18), 19 are of genera dispersed by birds and/or *Cynopterus*, *Rousettus*, or *Pteropus* species (1, 15, 19, 20), and 8 of these were not recorded on the island until 1982 (18, 20). At least a further 53 species of genera recorded as being dispersed by birds, *Cynopterus*, *Rousettus*, or *Pteropus* in Southeast Asia or Australasia (21, 22), including 16 species of *Ficus*, occur on the other islands of the Krakataus (23, 24). The succession on Anak Krakatau may thus be on the threshold of change from the present *Casuarina* association toward mixed secondary forest. Indeed, recent botanical surveys show that there has been a significant enrichment of forest species on the island since 1979 (18). Five forest trees were recorded there for the first time in 1983, including, besides *Macaranga tanarius* (see above), *Dysoxylum caulostachium* and *Timonius compressicaulis*, both of which are also important successional components and, like *M. tanarius*, bird-dispersed.

### Ecological Refuges and "Windows": Postponement of Extinction

Three birds of open country occur on Anak Krakatau: the lesser coucal (*Centropus bengalensis*), savanna nightjar (*Caprimulgus affinis*), and white-breasted waterhen (*Amaurornis phoenicurus*). These are absent from (the waterhen) or rare on the other islands, from which open habitats have been extirpated by successional processes, apart from small areas of Sertung on its northern spit (Fig. 1), which, like Anak Krakatau, is physically (25, 26) and successionally young.

The early stages of plant succession on Anak Krakatau and the Sertung spit are now, and have for decades been, prevented from proceeding to the next seral stage. Anak Krakatau's periodic eruptions continually set back its vegetational succession, and the Sertung spit is a dynamic, ever-young physical entity as a result of erosional and prograding regimes on its western and eastern coasts, respectively (26). These areas thus provide, and probably have provided for some time, ecological refuges for open-country species on the archipelago that may otherwise have lost their preferred habitat through succession, such as the three birds mentioned above. These areas may also act as ecological windows through which such open-country species may establish themselves on the islands from the mainland, either for the first time (e.g., the barn owl, *Tyto alba*), having missed the earlier opportunity, or as reinvasions, thus giving rise to a "rescue effect" (27) by augmenting and enriching declining conspecific populations already present.

The spit may not persist but, volcanic activity permitting, Anak Krakatau may long continue to have such an influence on species numbers on the archipelago. The result of both these processes would be to delay extinction on the archipelago, and this may well explain why observed annual extinction rates are lower than those estimated for equilibrium by MacArthur and Wilson.

The large-billed crow (*Corvus macrorhynchos*) has evidently not been saved by the provision of an ecological refuge on Anak Krakatau, nor has the peaceful dove (*Geopelia striata*). Recorded on every island surveyed from 1908 to the 1930s (1), in 1951 the crow was seen on Sertung only (4); by 1984 only a single pair remained, on Anak Krakatau, and in 1985 and 1986 these birds were gone. The dove has not been seen for over 65 years, although it was heard on Sertung in 1951. Perhaps in these cases grassland habitats on the older islands disappeared too quickly to be fully compensated for by their limited development on Anak Krakatau and persistence on a small part of Sertung.

No true primary-forest tree species has yet become established on the Krakataus; *Disoxylum caulostachium*, previously considered a primary-forest species, is now thought to be typical of certain secondary-forest formations (28). On the three older islands the change from the present "secondary" forest to "primary" forest, if it occurs at all (and it may not), is likely to be more gradual than the changes that have occurred over the past century (11). Under these circumstances the species numbers of vertebrate groups on the archipelago may reach temporary equilibria that could be long-lasting; reassortment and a move toward a final equilibrium will probably follow the slow changes in the composition of the vegetation.

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