Biogeographic Kinetics: Estimation of Relaxation Times for Avifaunas of Southwest Pacific Islands

(immigration/extinction/birds/tropical rainforest/conservation)

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ABSTRACT When species diversity S on an island is displaced from the equilibrium value by injection or removal of species, S relaxes to equilibrium by an imbalance between immigration and extinction rates. Estimates of exponential relaxation times, t_r, for avifaunas of New Guinea satellite islands are calculated from analysis of four "experiments of nature": recolonization of exploded volcanoes, contraction in island area due to rising sea level, severing of land bridges, and disappearance of land-bridge relict species. t_r is in the range 3,000–18,000 years for avifaunas of islands of 50–3000 square miles (130–7800 km²), and increases with island area. Immigration coefficients decrease and extinction coefficients increase with increasing S. The results may be relevant to the design of rainforest preserves.

If one compares the faunal or floral diversity on different islands, one finds that the number of species increases with island area, but decreases with distance from the mainland. MacArthur and Wilson (1, 2) interpreted this pattern to mean that insular species diversities represent an equilibrium between immigration rates and extinction rates. Immigration rates due to random dispersal of individuals from the mainland should fall off with increasing distance, and extinction rates due to fluctuations in small populations should fall off with increasing area (hence, increasing population size). Comparisons of bird censuses taken several decades apart on the California Channel Islands (3), on Karkar Island off New Guinea (4), and on Mona Island in the Caribbean (5) have confirmed that the avifaunas of these islands actually are in dynamic equilibrium, and have provided estimates of immigration and extinction rates under steady-state conditions.

An alternative approach to these studies under steady-state conditions depends upon displacing an island fauna from equilibrium and measuring the "relaxation time" with which species diversity returns to the equilibrium value or "relaxes." For example, Simberloff and Wilson (6) fumigated mangrove trees near the Florida coast and measured the rates at which insects and other arthropods recolonized the trees. The present paper reports methods for estimating relaxation times of avifaunas on the satellite islands of New Guinea, utilizing "experiments of nature" or natural relaxation processes, rather than experimental manipulation of the fauna. Four sets of conditions are identified under which both a nonequilibrium species diversity at some time in the past and the expected species diversity at equilibrium can be estimated and compared with the species diversity at present, providing three points on the relaxation curve.

Theory

We describe faunal relaxation by a highly schematic treatment that the present paper will show to represent an over-simplification, but that nevertheless serves as a useful starting point.

The measured relaxation times of island faunas are a resultant of two relaxation processes, immigration and extinction, whose respective rates I and E (expressed in species per year) depend on the instantaneous species diversity $S(t)$ (t represents time). Let us assume constant coefficients K_i and K_e (expressed in year^{-1}) of immigration and extinction, respectively:

$$E = K_e S(t) \quad [1] \qquad\qquad I = K_i [S^* - S(t)] \quad [2]$$

$$dS/dt = I - E = (K_i + K_e)$$
$$\times [K_i S^*/(K_i + K_e) - S(t)] \quad [3]$$

where S^* is the mainland species pool. Straightforward integration under various boundary conditions yields the following equations:

At equilibrium ($dS/dt = 0$), the species diversity S_{eq} is given by

$$S_{eq} = K_i S^*/(K_i + K_e). \quad [4]$$

Furthermore, $\qquad I = E = K_i K_e S^*/(K_i + K_e). \quad [5]$

Relaxation to equilibrium from an initial species diversity $S(0)$ that differs from S_{eq} is described by:

$$[S(t) - S_{eq}]/[S(0) - S_{eq}] = e^{-t/t_r} \quad [6]$$

where the relaxation time t_r is given by

$$t_r = (K_i + K_e)^{-1}. \quad [7]$$

The relaxation time is the length of time required for the departure of species diversity from equilibrium, $|S(t) - S_{eq}|$, to relax to $1/e$ (or 36.8%) of the initial departure, $|S(0) - S_{eq}|$, where e is the base of natural logarithms. Relaxation is 90% complete after 2.303 relaxation times.

Species diversity at equilibrium

First, we need a formula predicting S_{eq}, the bird species diversity on New Guinea satellite islands at equilibrium. We assume that most tropical islands of the southwest Pacific resemble Karkar, the California Channel Islands, and Mona in being at avifaunal equilibrium, except for those few islands recently perturbed by the four "experiments of nature" to be discussed. The number of land and fresh-water bird species coexisting on each tropical island of the southwest Pacific varies from 1 for some isolated atolls up to 513 for New Guinea itself. These differences in S are predictable from an island's area, A (expressed in square miles), its distance from New Guinea, d (expressed in miles), and its elevation, L (expressed
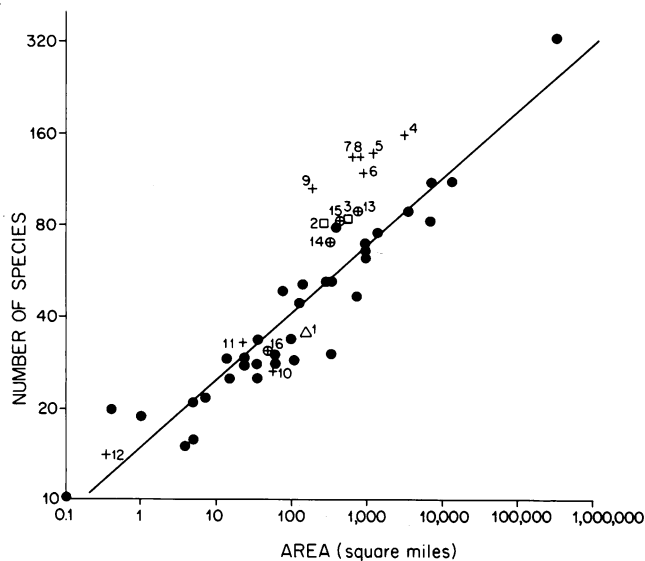
FIG. 1. Number of resident land and fresh-water bird species on New Guinea satellite islands, plotted as a function of island area on a log–log scale. ●, Islands whose avifaunas are presumed to be at equilibrium. The avifaunas of the numbered, remaining islands are in various stages of relaxation. △, Exploded volcanoes: *1* = Long. □, Contracted islands: *2* = Goodenough, *3* = Fergusson. +, First-order land-bridge islands: *4* = Aru, *5* = Waigeu, *6* = Japen, *7* = Salawati, *8* = Misol, *9* = Batanta, *10* = Pulu Adi, *11* = Ron, *12* = Schildpad. ⊕, Second-order land-bridge islands: *13* = Batjan, *14* = Amboina, *15* = New Hanover, *16* = Tidore. The straight line is Eq. 8, the least-mean-squares fit to all points except the first-order land-bridge islands. Note that large land-bridge and contracted islands deviate in the direction of an excess of species, that small islands do not, and that the deviation is more marked for the first-order land-bridge islands than for second-order land-bridge islands or contracted ones.

in feet). The present analysis of the empirical dependence of S on A, d, and L is similar to previous analyses by others (1, 2, 7), but is based on more extensive data, derived from the unpublished journals of the Whitney South Sea Expedition, from published literature, and from my expeditions (8–10).

Fig. 1 depicts the number of bird species, S, occurring at sea level on islands between 5 and 300 miles from New Guinea, as a function of island area, A. Over a three-millionfold range of areas the results fit the exponential equation

$$S = 15.1 \, A^{0.22} \qquad [8]$$

with an average error of 19%. The numbered deviant points represent islands undergoing various types of relaxation, as discussed later.

Fig. 2 plots, as a function of island distance, d, from New Guinea, the ratio of an island's actual S at sea level to the S value predicted from the island's area and Eq. 8, based on islands near New Guinea. This ratio decreases exponentially with distance, by a factor of 2 for each 1620 miles from New Guinea. Thus, the most remote islands of the southwest Pacific (Mangareva and the islands of the Pitcairn group, 5000–5700 miles from New Guinea) have a bird species diversity only 12% that of islands of similar size near New Guinea. Figs. 1 and 2 mean that, for that segment of the New Guinea avifauna capable of crossing a 5-mile water gap at all, mean dispersal distances of species are many hundreds of miles, taking into account secondary radiation

from intermediate stepping-stone islands. A qualitatively similar conclusion for California birds is implied by the fact that avifaunal equilibrium turnover rates on the California Channel Islands are virtually independent of d between at least 8 and 61 miles (3). This does not necessarily imply that the mean dispersal distance of an individual bird in the absence of stepping-stones would be comparable. Nor does it imply comparable dispersal distances for the California or New Guinea avifauna as a whole: many California and New Guinea species are stopped by a water gap of 5 miles or even 60 yards (see below).

The mountains of the higher southwest Pacific islands harbor additional bird species not occurring at sea level. On the average, each 1000 ft of elevation, L, enriches an island's avifauna by several montane species equal to 2.7% of its avifauna at sea level. Thus, bird species diversity on the New Guinea satellite islands may be summarized by the empirical formula

$$S = (15.1) \, (1 + 0.027 \, L/1000) \, (e^{-d/1620})(A^{0.22}). \qquad [9]$$

The following discussion of avifaunal relaxation concerns only species found at sea level, and only islands within 300 miles of New Guinea.

Method 1: Recolonization of Exploded Volcanic Islands. Long, Ritter, Krakatau, and some other islands are volcanoes whose fauna and flora were apparently completely destroyed by cataclysmic eruptions within historical times. Long Island off northeastern New Guinea was surveyed by W. F. Coultas of the Whitney South Sea Expedition in 1933, about two centuries after an explosion that apparently blew out part of the island and buried the remainder under lava. Coultas found 36 resident land-bird species, 78% of the equilibrium value predicted from Eq. 8 for an island of Long's area (151 square miles, S_{eq} = 46 species). Substitution of t = 200 years, $S(0)$ = 0, $S(t)$ = 36, and S_{eq} = 46 into Eq. 6
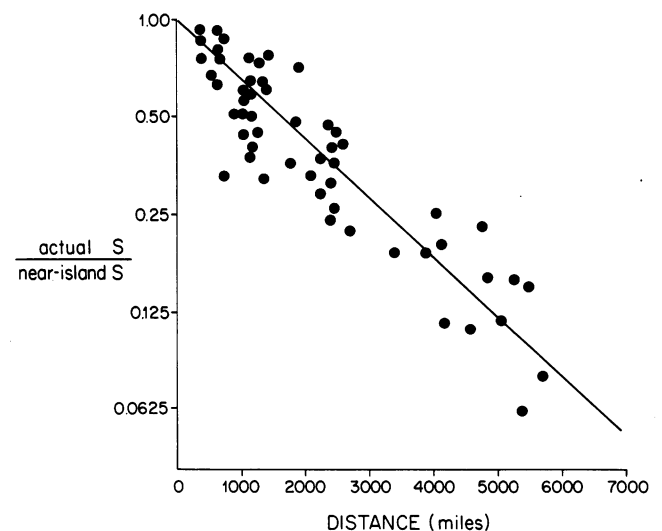

FIG. 2. *Ordinate* (logarithmic scale), number of resident land and fresh-water bird species on tropical southwest Pacific islands more than 300 miles from New Guinea, divided by number of species expected on an island of equivalent area less than 300 miles from New Guinea (calculated from Eq. 8). *Abscissa*, island distance from New Guinea. Note that species diversity decreases by a factor of 2 per 1620 miles.

yields a relaxation time of 129 years. A similar calculation for the famous explosion of Krakatau, based on $S(t)/S_{eq}$ = 0.48 at t = 25 years (ref. 2, p. 45), yields t_r = 38 years. For equilibration of the bird fauna itself, t_r is likely to be considerably shorter; these figures serve only as upper limits, since part of these t_r estimates arises from the t_r for regeneration of the vegetation on which birds ultimately depend. The shorter t_r for Krakatau than for Long Island reflects the more rapid regrowth of forest on Krakatau.

Method 2: Contraction in Area. An opposite situation, in which species diversity decreases rather than increases towards an equilibrium value, is provided by the islands of the D'Entrecasteaux Shelf. This shelf off southeastern New Guinea is now submerged under shallow water less than 100-m deep and is separated from New Guinea by a channel at least 600-m deep. During the most recent Pleistocene glaciation up to about 10,000 years ago, when much water was sequestered in glaciers, sea level is thought to have been about 100 m below its present level (11), and the area of the D'Entrecasteaux Shelf above the sea was about 7430 square miles. From Fig. 1 or Eq. **8**, an island of this size would have had 108 species at equilibrium. At present, the largest fragment of the shelf above water is Fergusson Island, with 86 lowland species and an area of 494 square miles. Eq. **8** predicts only 59 species for A = 494 square miles. Thus, the avifauna of Fergusson has decayed, by an excess of extinction over immigration, from the 108 species it presumably supported when it was part of a larger island, but it has not yet decayed to the equilibrium value for its contracted post-Pleistocene size. Substituting t = 10,000 years, $S(0)$ = 108, $S(t)$ = 86, and S_{eq} = 59 into Eq. **6** yields a relaxation time of 16,700 years for the avifauna of Fergusson Island. The values for a slightly smaller fragment of the D'Entrecasteaux Shelf, Goodenough Island [A = 263 square miles, $S(0)$ = 108, $S(t)$ = 81, S_{eq} = 51], yield a slightly shorter t_r of 15,600 years. For fragments of 100 square miles (Kiriwina) or less there is no significant excess of $S(t)$ over S_{eq}, implying $t_r \ll$ 10,000 years. Thus, the faunas of the smaller islands relax more rapidly, because extinction rates increase with decreasing area.

Method 3: Severing of Land Bridges. During glacial epochs of the Pleistocene, those few New Guinea satellite islands that are separated from the New Guinea mainland by water less than 100-m deep would have formed part of the New Guinea mainland and supported virtually the full New Guinea lowland fauna of 325 species. Since the severing of the "first-order" land bridges (i.e., bridges to New Guinea itself) by rising sea level about 10,000 years ago, S on each "land-bridge island" must have been relaxing towards the value expected for an "oceanic" island of the same area, by an excess of extinction over immigration. As shown in Fig. 1 (points marked +), the largest first-order land-bridge islands are still supersaturated—i.e., their present $S(t)$ values are still considerably in excess of the equilibrium value, although considerably less than the initial value of 325. For instance, Misol has an area of 788 square miles and should have 65 species at equilibrium (from Eq. **8**) but actually has 135 species. Substituting $S(0)$ = 325, S_{eq} values from Eq. **8**, and t = 10,000 years into Eq. **6** yields relaxation times of 6200–8200 years (average, 7400 years) for the five largest land-bridge islands with areas of 630–3000 square miles, and t_r = 6450 years for an island of area 175 square miles (Table 1).

TABLE 1. *Relaxation times of bird communities on New Guinea satellite islands*

Island	Area (square miles)	t_r (years)	$S(0)/S_{eq}$*
Equilibrium turnover			
Karkar	142	286	—
Recolonization of volcanoes			
Long	151	<129	—
Krakatau	8	<38	—
Contraction in area			
Fergusson	494	16,700	1.83
Goodenough	263	15,600	2.12
Kiriwina	102	≪10,000	2.59
Land bridges, first-order			
Aru	3,000	8,210	3.69
Waigeu	1,218	7,320	4.39
Japen	860	6,240	4.88
Misol	788	7,600	4.96
Salawati	630	7,700	5.21
Batanta	175	6,450	6.92
Pulu Adi	56	≪10,000	8.78
Ron	21	≪10,000	10.84
Schildpad	0.36	≪10,000	27.08
Land bridges, second-order			
Batjan	781	15,390	1.72
New Hanover	458	16,900	1.81
Amboina	305	17,600	1.57
Tidore	46	≪10,000	3.14
Land-bridge relict species			
Aru	3,000	9,000	—
Waigeu	1,218	7,610	—
Japen	860	8,440	—
Misol	788	7,940	—
Salawati	630	9,150	—
Batanta	175	6,100	—
Pulu Adi	56	2,630	—
Ron	21	3,040	—
Schildpad	0.36	≪10,000	—

* This ratio is the factor by which the fauna was supersaturated at the time that relaxation began.

Fig. 1 also shows that, in contrast, S values for three small land-bridge islands (56, 21, and 0.36 square miles) are close to the equilibrium curve, implying $t_r \ll$ 10,000 years. As for contracting islands, the more rapid relaxation of smaller land-bridge islands is due to higher extinction rates.

Consideration of the 100-m ocean depth contour also indicates that certain islands of the Bismarck Archipelago and the Moluccas must have been connected by Pleistocene land bridges to larger and more species-rich islands of these groups, though not to New Guinea itself [New Hanover connected to New Ireland, $S(0)$ = 105 species; Batjan and Tidore connected to Halmahera, $S(0)$ = 110 species; Amboina connected to Ceram, $S(0)$ = 83 species]. Fig. 1 shows that the larger of these "second-order" land-bridge islands (points marked ⊕) are also still supersaturated. For instance, the present $S(t)$ on New Hanover, 84, is greater than the equilibrium value of 58 predicted from Eq. **8** for New Hanover's area of 458 square miles, but is less than New Ireland's total of 105 species, nearly all of which must have been shared with New Hanover 10,000 years ago. Substitution into Eq. **6** yields t_r = 16,900 years for New Hanover, and comparable values for the similar-sized islands of Batjan and Amboina (Table 1). On the smaller island of Tidore (A = 46 square miles), there is no significant difference between $S(t)$ (= 31) and S_{eq} (= 35), implying $t_r \ll$ 10,000 years. Relaxation times for the three larger second-order land-bridge islands are close to those for the similar-sized contracted D'Entrecasteaux islands, but double those for similar-sized first-order land-

bridge islands (Table 1). The reason for this difference is discussed below.

Method 4: The Land-Bridge Relict Fauna. The preceding analysis treats average turnover rates and relaxation rates for the fauna as a whole. However, there are gross differences between the colonizing abilities of different species. These differences make it possible to identify a subset of the New Guinea avifauna that cannot cross water gaps and to calculate its relaxation rate on land-bridge islands.

Only 191 of the 325 New Guinea lowland species have crossed water gaps more than 5 miles wide, as proven by their having been recorded from one or more islands lacking a recent land bridge. The successful colonists are drawn disproportionately from species characteristic of New Guinea second-growth (regenerating vegetation on cleared land). Under natural conditions, areas of second-growth are short-lived, appearing when a landslide or falling tree makes a clearing in the forest and disappearing as the forest re-establishes itself. To have persisted on New Guinea, second-growth species must have evolved high dispersal abilities in order to seek out the shifting bits of habitat suitable to them. These dispersal abilities predispose them to become successful over-water colonizers.

The 134 species that have been unable to cross water gaps of 5 miles or more are drawn disproportionately from the avifauna of the New Guinea forest, especially the forest understory. They are also drawn disproportionately from the birds considered most characteristic of the Papuan region, its endemic genera and families. No bower bird, only six birds of paradise, and only five species in endemic genera of the Papuan region occur on an island lacking a recent land bridge. Distributions on the Madang Archipelago, a group of islands lying 60–3900 yards from the New Guinea mainland, illustrate the dispersal abilities of these 134 species: only 10 of them occur on an island 60 yards offshore, 3 on an island 550 yards offshore, and none on five islands 820, 2030, 3210, 3500, and 3900 yards offshore. Thus, more than 90% of these species are stopped by a water gap only 60-yards wide. Only three of these species are flightless, all of the remainder are capable of flying 60 yards in a fraction of a minute, and some are strong fliers that normally cover more than 100 miles overland each day. Thus, the reasons for their failure to cross water gaps are psychological, not physiological. Some tropical forest species are even reluctant to cross a road a few yards wide. This extreme selection against dispersal in most tropical forest species may arise because their low reproductive potential would make them poor colonists even if they did reach islands. Similarly poor water-crossing ability in characteristic forest species of the Asian continental shelf islands may explain the vivid impression of an avifaunal break that field observers report on crossing Wallace's Line, an impression that has been difficult to understand from the modest differences in zoogeographic affinities of the avifaunas on opposite sides of Wallace's Line (12).

Although most of the 134 species that do not cross water must have been present on most of the first-order land-bridge islands when the land bridges were intact, their present distributions indicate varied abilities to persist as isolated populations once the land bridges were severed. At the one extreme are species like the Black Cockatoo, *Probosciger aterrimus*, and the Frilled Monarch, *Monarcha telescophthalmus*, which are still present on all seven first-order land-bridge islands with areas greater than 175 square miles (but on no

oceanic island). At the other extreme are some distinct Papuan endemics like the New Guinea Harpy Eagle, *Harpyopsis novaeguineae*, and the Vulturine Parrot, *Psittrichas fulgidus*, which are now confined to the New Guinea mainland and must have become extinct on all the land-bridge islands. Both the number of species that do not cross water, and the percentage of the total island avifauna they represent, decrease with decreasing area among the first-order land-bridge islands: 36–45 species that do not cross water and 26–35%, respectively, on islands of 630–3000 square miles; 26 species and 25% for an island of 175 square miles; 3 species and 11% for an island of 56 square miles; and 0 species and 0% for an island of 0.36 square miles (which, nevertheless, has 14 water-crossing species). From these data, if one applies Eq. 6 and if one assumes that each first-order land-bridge island initially held all 134 species that do not cross water [$S(0) = 134$], and assumes further that the number has been decreasing exponentially due to extinction since the severing of the land bridge and that there has been no recolonization over water ($S_{eq} = 0$), one may calculate the following relaxation times for this segment of the avifauna: 9000 years, 7600–8400 years, 6100 years, 2630 years, and infinitely short, as compared to 10,000 years, on islands of 3000, 788–1218, 175, 56, and 0.36 square miles, respectively. These estimates are in good agreement with the estimates based on the number of all bird species on the same land-bridge islands (*method 3:* see Table 1).* Thus, with decreasing area a land-bridge island approaches an oceanic island in species composition, as well as in species diversity, due to increasing extinction rates and decreasing relaxation times.

Interpretation of relaxation times

Table 1 summarizes relaxation times obtained by the four methods. Also included for comparison is t_r derived from equilibrium turnover rates on Karkar. The measured E, I, $S(t)$, and S^* values for Karkar (4) were inserted into Eqs. 1 and 2 to obtain $K_e = 0.00297$ year^{-1} and $K_i = 0.000527$ year^{-1}, which yield $t_r = 286$ years from Eq. 7.

The t_r values in Table 1 yield the following conclusions:

(*i*) t_r calculated from recolonization of Long is less than 129 years, probably considerably less. The value of 286 years calculated from equilibrium turnover on Karkar is more than twice as high, even though Long and Karkar have virtually the same area and Long is three times more distant from New Guinea. The reason for this difference in t_r obtained from the two methods is that K_i is not constant but decreases with increasing $S(t)$, as predicted by MacArthur and Wilson (ref. 2, p. 21). That is, New Guinea mainland species differ in their

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* Brown (13) has shown that small mammal species on the tops of isolated mountains in the western United States probably arrived from the Sierra Nevada or Rocky Mountains via former "land bridges" of montane vegetation, and that the number of these mammal species has subsequently been decaying by extinction without immigration since the "land bridges" were severed. These populations are thus analogous to the populations of birds that do not cross water on the New Guinea land-bridge islands. From Brown's data and Eq. 6, one may calculate that t_r ranges from 10,800 years for mammal faunas on the largest mountaintops, with an average area of 734 square miles, down to 3900 years for the smallest mountaintops, with an average area of 43 square miles. The values for New Guinea birds on similar-sized islands are very similar (8500 years for an average area of 759 square miles, 2630 years for 56 square miles).

colonizing abilities. The species with highest dispersal ability tend to be the first to recolonize an initially empty island, and subsequent immigrants as equilibrium is approached are drawn from a residual mainland species pool consisting of progressively poorer colonists.

(*ii*) t_r values for contracted islands and second-order land-bridge islands agree well with each other, but are twice as long as values for first-order land-bridge islands of similar size. The reason is that the first-order land-bridge islands were much further from equilibrium when relaxation began [$S(0)/S_{eq} = 3.69 - 27.08$, as opposed to 1.57–3.14 for the contracted and second-order land-bridge islands], and that K_e is not constant, but decreases with decreasing $S(t)$ (as predicted in ref. 2, p. 22). This is partly because some species are more prone to extinction than others (hence, the more extinction-prone species become extinct first), and partly because disappearance of some species may tend (by diminishing competition) to increase the population densities and, hence, the survival chances of the remaining species. The initial value $S(0)$ before relaxation began was 108 species for Goodenough and Fergusson, 110 species on Batjan, 105 species on New Hanover, and 83 species on Amboina, but 325 species on the first-order land-bridge islands connected to New Guinea itself, yielding higher mean K_e and lower t_r values for the latter islands.

(*iii*) The value $t_r = 286$ years calculated from equilibrium turnover during the past 55 years on Karkar is much lower than the values of about 6,000 or 16,000 years calculated from the net decay of species during the past 10,000 years on land-bridge islands or contracted islands of similar size. This difference also reflects the nonconstancy of K_e, which is much higher for recently arrived species with low population densities than for established species (ref. 2, chap. 4). Most of the extinctions occurring at equilibrium on Karkar and on the California Channel Islands involve recent arrivals doomed to disappear before they can saturate available island habitats with a stable population. This consideration is also related to the finding that t_r is at least an order of magnitude lower for approach to equilibrium from below [$S(0) - S_{eq}$] than from above [$S(0) > S_{eq}$], compare Batanta and Long.

Thus, these three types of comparisons show that a more-refined treatment will have to treat K_i and K_e as functions of $S(t)$, and will have to treat the relaxation process as a sum of exponentials rather than as a single exponential.

(*iv*) A decrease in t_r with decreasing area is expected from the predicted inverse relation between extinction rates and area. Enough islands were available for comparison by *method 2*, by *method 3* applied to first-order land-bridge islands, and by *method 4*, to confirm this expectation. A similar relation between area and relaxation rates calculated from equilibrium turnover was apparent for the California Channel Islands, when area was weighted to take account of habitat differences between islands (3).

(*v*) An increase in t_r with increasing distance is expected from the predicted inverse relation between immigration rates and distance. It has not been possible to test this prediction in the present analysis because the distances from New Guinea of the islands studied are too small, compared to dispersal distances of New Guinea species.

Implications for the design of rainforest preserves

Primary tropical rainforest is the most species-rich, ecologically complex habitat on earth. For millions of years it has served

as the ultimate evolutionary source of most plant and animal groups (14). Throughout the tropics today, it is being destroyed at a rate such that little will be left in a few decades. Since many rainforest species cannot persist in other habitats, the destruction of the rainforests would destroy many of the earth's species and would permanently alter the course of evolution (15).

The governments of some tropical countries, including New Guinea, are attempting to set aside some rainforest tracts now for conservation purposes. If these plans succeed, the rainforests, instead of disappearing completely, will be broken into "islands" surrounded by a "sea" of open country in which forest species cannot live. What is likely to happen to forest species is suggested qualitatively by the parallel case of the New Guinea land-bridge islands, which were also part of a formerly continuous forest, but are now isolated by ocean. On an island of 3000 square miles, about 51% of the original species have become extinct after 10,000 years, and about 72% of the survivors are widespread second-growth species rather than the endemic forest species that require protection. Comparable figures for an island of 56 square miles are 92% of the original species extinct, and 89% of the survivors second-growth species. This ominous process is further illustrated by Barro Colorado Island, a former hilltop that became an island in Gatun Lake when construction of the Panama Canal flooded adjacent valleys 60 years ago. Since then the populations of several forest species have died out and have not recolonized from the nearby forest on the shore of Gatun Lake.

Some implications for national park systems in the tropics are that, in a faunally homogeneous area, one large park is preferable to an equivalent area in the form of several smaller parks; that continuous nonforest strips (e.g., wide highway swaths) through the park should be avoided; and that, if several small parks cannot be avoided, connecting them by strips of forest might significantly improve their conservation function at little further cost in land withdrawn from development.

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