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Phil. Trans. R. Soc. Lond. B 1990 **328**, 131-165
doi: 10.1098/rstb.1990.0112

Phil. Trans. R. Soc. Lond. B **328**, 131–165 (1990) [131]
Printed in Great Britain

COLONIZATION OF THE KRAKATAU ISLANDS BY ANIMALS: A PERSPECTIVE FROM THE 1980S

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(*Communicated by Sir David Smith, F.R.S. – Received* 13 *September* 1989)

CONTENTS

An examination of cases of turnover in animal species on the Krakataus since 1883, particularly vertebrates, supports the findings of plant ecologists that very little, if any, turnover is stochastic. Successional, rather than equilibrium turnover is still occurring in all animal groups for which analyses can be made; for no group of animals is there evidence that an equilibrium of species number has been achieved, although for resident land birds there are indications that this is now imminent. Approach to equilibrium is not uniform; the colonization curves for resident land birds, reptiles, cockroaches and nymphalid and hesperiid Lepidoptera, as examples, have flattened markedly in the past 50 years, whereas numbers of species of land molluscs and many other insect groups are still increasing at a rate similar to that in the first half century since 1883. The period of the beginning of forest formation (1908–21) was the time when immigration reached a peak, and the period of canopy closure (1921–33) was the time of highest extinction rates.

Successful colonists, over a range of animal groups, appear to be species with wide distributions and broad ecological tolerances. There is indirect evidence that successional processes have precluded colonization by several animal groups present in the mainland pool because of unavailability of their preferred habitat, and it is suggested that the effective available pool, as opposed to the theoretical one, changes in size and species complement as succession proceeds on the target islands. We believe that the brief open-habitat phase was too short for the establishment of several animal groups that were available in the pool. Animals of mature forest are, in general, absent as the archipelago's forests are still relatively impoverished and early successional.

Anak Krakatau, in general terms, offers an analogy with the early decades of colonization after 1883. The role of animals in the first stages of forest diversification from casuarina woodland has been monitored on this island, and an ash-lava aeolian ecosystem based on an allochthonous energy source was identified, which parallels similar systems on volcanic substrates in Sicily, the Canaries and, particularly, the island of Hawaii.

1. Introduction

The data obtained on our 1984–1986 La Trobe University – L.I.P.I. expeditions to the Krakataus (Thornton & Rosengren 1988), those of the Kagoshima University zoologists in 1983 (Yukawa *et al.* 1984) and that of the Institut Teknologi Bandung in 1982 (Ibkar-Kramadibrata *et al.* 1986), have now been sufficiently well-studied to permit an overview of the fauna of the archipelago about a century after the life-extirpating 1883 eruption. The representation of some animal groups can now be assessed in the context of previous faunal surveys (in 1908, 1919–23, 1928–34 and 1951 (birds only)) although the taxonomic treatment of some ecologically important groups, such as ants and spiders, is not yet complete. In addition, recent conclusions on the flora from the 1979, 1983 and 1984 Hull University expeditions (Whittaker *et al.* 1989) and the 1983 Kagoshima University expeditions (Tagawa 1984) permit a consideration of the fauna within a definitive botanical framework.

The prime aims of our expeditions were to characterize the 1980s fauna and so provide a datum point for comparison with past and future surveys, and to assess the extent, if any, to which various segments of the fauna were proceeding towards equilibrium number of species. Interest in the second aim was stimulated by MacArthur & Wilson's (1967) reference to the Krakataus' avifauna as the only actual case study of the natural achievement of equilibrium on islands. They believed that by 1919, less than four decades after the devastating eruption of 1883, when the number of plant species was still rising, the archipelago's resident land bird fauna had reached equilibrium.

We also wished to characterize the fraction of the source faunas that had become established on the islands after a century, examine the sequence of colonization, and assess the effect of the emergence in 1930 of the virgin island Anak Krakatau (figure 1) on the faunal dynamics of the archipelago and the reassembly of a tropical forest ecosystem.

Ours was the first attempt at a comprehensive faunal survey since the end of the Dammerman series of surveys in 1933 (Dammerman 1948). The Institut Teknologi Bandung (I.T.B.) expedition of 1982 (Ibkar-Kramadibrata 1986) spent three days on each of Anak Krakatau and Panjang (a total of 40 man-days) and concentrated on soil and litter animals, and the Kagoshima University expedition of 1983 (Tagawa 1984) spent a total of 67 zoologist-days on the islands. Results of the latter expedition so far published have dealt with plants (Tagawa *et al.* 1985), aculeate hymenoptera other than ants (Yamane 1983), termites (Abe 1984), Lepidoptera (Yukawa 1984*a*, 1986), tephritid (Yukawa 1984*c*), chloropid (Kanmiya & Yukawa 1985) and bombyliid Diptera (Evenhuis & Yukawa 1986), Odonata and Hemiptera (Yukawa & Yamane 1985), and Neuroptera (Tsukaguchi & Yukawa 1988). Other papers resulting from this expedition have concerned an outbreak of a margarodid homopteran (Yukawa 1984*b*), and observations on the migratory flight of a butterfly species (Yukawa 1983) and on the mammals, reptiles and crabs (Iwamoto 1986).

We attempted to complement the work of these expeditions by a wider coverage of invertebrates and by specialist vertebrate surveys. We have investigated or are investigating soil nematodes (Winoto *et al.* 1988; Rashid *et al.* 1990), oligochaetes, terrestrial molluscs (Djayasasmita 1985; Smith & Djajasasmita 1988), symphylans (Scheller 1988), myriapods, a wide range of insect groups (Bush 1986*a*; Compton *et al.* 1988; New *et al.* 1985, 1988; New & Sudarman 1988; New & Thornton 1988; Roth 1989; Strassen 1990; Sturm & Bach de Roca 1988; Thornton *et al.* 1988*a*, *b*; van Tol 1988; Vaughan *et al.* 1989), arachnids (Harvey 1988), terrestrial crabs (Morgan 1990), terrestrial isopods (Green *et al.* 1990), reptiles and rats (Rawlinson *et al.* 1990), birds (Adhikerana 1985; Thornton *et al.* 1990; Zann *et al.* 1990*a*, *b*) and bats (Tidemann *et al.* 1990). In addition, we have made studies of antibiotic resistance patterns of soil bacteria and of the enteric bacteria of mammals and reptiles (Graves *et al.* 1988*a*–*d*; Thornton & Graves 1988), freshwater communities (Thornton & New 1988*a*) and the dynamics of sea coasts (Rosengren 1985). A brief summary of colonization by vertebrates (Thornton *et al.* 1988*c*) and an overview of invertebrate colonization (Thornton & New 1988*b*) have also been published.

In this paper we attempt to provide an overview of the fauna in the 1980s in the context of physical and biotic changes on the archipelago since the 1883 eruption.

2. The archipelago

(*a*) *Physical and vegetational change*

Among the most important physical changes to the archipelago that were not the direct result of the 1883 events (see Thornton & Rosengren (1988) for a summary of these), have been the partial consolidation of the 1883 deposits and soil formation, the reshaping of the islands' coastlines by rain and marine erosion and the redeposition of material eroded both during gully formation and by wave action to form cuspate forelands, and the emergence, growth and activity of Anak Krakatau. The vegetational changes of most significance to animals have been the formation of open savanna grassland, the change to woodland and forest formation, and the closure of the forest canopy.

Gully formation occurred on all three islands soon after the 1883 event, and marine erosion since then, resulting in cliff formation, is evident particularly on Sertung and Rakata. The creation of forelands is most significant on southern Rakata, northern and eastern Anak Krakatau, and northern Sertung (where a persistent but mobile and morphologically variable spit of land was built up) (Bird & Rosengren 1984; Rosengren 1985; Thornton & Rosengren 1988). The most dramatic change was the emergence in 1930, from the 1883 caldera, of Anak Krakatau, and its subsequent growth, consolidation by lava flows in the 1960s, and periodic activity. Its post-1930 volcanicity has affected not only the development of a biota on Anak Krakatau itself, but also, by periodically damaging ash-falls, the course of succession of the biotas of Sertung and Panjang. We believe that the long-term successional asynchrony resulting from the creation and physically dynamic nature of Sertung's spit and the emergence and periodic activity of Anak Krakatau also have implications for turnover and approach to equilibrium of the archipelago's fauna (see §2*f*)

In general, the flora has been more frequently and more thoroughly surveyed since 1883 than the fauna, and in the past decade has been the subject of attention of teams from Kagoshima University and from Hull University and the Bogor Herbarium. Tagawa *et al.* (1985) and Whittaker *et al.* (1984, 1989) have provided definitive floral lists for each island,

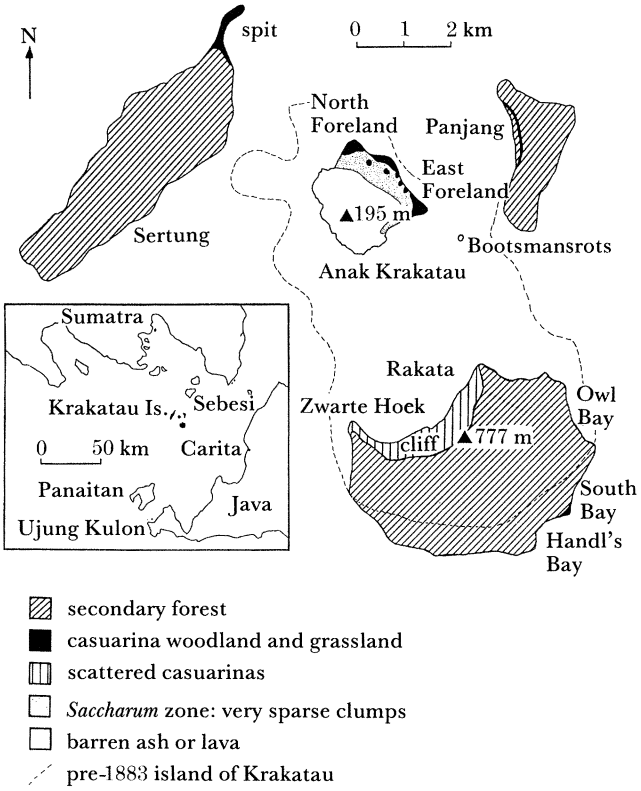


FIGURE 1. The Krakatau Islands, 1985, showing vegetation cover.

and comprehensive discussion of the vegetational succession on the archipelago since 1883. This has involved, on Rakata at least, an early development (within three years) of blue-green algae that acted as a substrate for a fern cover extending over the interior, which by 1897 gave place in the lowlands to savanna grassland dominated by *Saccharum spontaneum* and *Imperata cylindrica*, and incorporating patches of *Casuarina* woodland with *Ficus* and other forest species. By this time the fern cover was retreating to the higher slopes and *Ipomoea pes-caprae* formations had developed on the beaches, often with the beginnings of coastal *Terminalia*, *Barringtonia* and *Casuarina* communities behind them. Open savanna woodland-grassland was prevalent in 1906, with *Casuarina* of greater importance. From 1919 to the 1930s the *Casuarina* savanna grassland was gradually displaced by species-poor mixed secondary forest and the canopy began to close. The change from grassland to woodland, and the closure of the forest canopy have both had a great impact on faunal succession.

Tagawa's and Whittaker's groups are basically in agreement regarding the present development of mixed secondary forest on the archipelago, both recognizing differences between the associations on the three forested islands on the basis of dominant species (see introduction to this series, Thornton & Rosengren (1988)). Briefly, in 1982 and 1983 *Terminalia*-rich coastal forest occurred on Rakata, Sertung and Panjang (with strong intermixture of *Ficus fulva* and *Ficus septica* on Sertung), but whereas forests dominated by *Timonius compressicaulis* or *Dysoxylum gaudichaudianum* covered considerable areas of Sertung and Panjang (*Dysoxylum* forest being less extensive on Sertung), the inland forests of Rakata were dominated by *Neonauclea calycina* or by *N. calycina* and *Ficus* species, particularly *Ficus pubinervis*.

Whittaker's group have recently found that the Sertung and Panjang forests have changed considerably since 1983, particularly the latter. Over most of Panjang's interior, the *Timonius* has now given way to other canopy dominants, principally *D. gaudichaudianum*, which overtop the *T. compressicaulis*, and in the lowland forests of Rakata the *N. calycina* is now diminishing, and *D. gaudichaudianum* increasing in importance (R. J. Whittaker, personal communication). The inland forests of the islands are early successional, impoverished compared with mature mainland forests, and dominated by a small minority of tree species that are early successional dominants (Whittaker *et al.* 1989). At the higher elevations of Rakata, *N. calycina* becomes progressively less important, the wet cloud forest of the summit region being dominated by *Saurauia nudiflora*, *Schefflera polybotrya* and *Ficus ribes*.

Docters van Leeuwen (1936) and Tagawa's group suggested that the inter-island differences in the type of forest may be due to the different relative timing of arrivals of dominant species on the various islands. More recently, Whittaker *et al.* (1989) have invoked disturbance due to the volcanic activity of Anak Krakatau as a preferred explanation (together with the greater height of Rakata). They believe that, during and since 1930, periodic volcanic disturbances by this new active volcano have deflected vegetational succession on Sertung and Panjang away from the course followed on Rakata, which has been unaffected. Bush (1986*b*) has suggested differential ash fall has resulted in different dominants within the Sertung forests. Although damage to the vegetation of Sertung and Panjang by the 1930, 1933 and 1952 activity of Anak Krakatau has been documented (see for example, Dammerman 1937; van Borssum Waalkes 1954, 1960), there is no evidence of the extent of damage, if any, between 1933 and 1952, or from 1953 to 1979. Both explanations probably are valid; they are not mutually exclusive.

The accounts of Tagawa *et al.* (1985) and Whittaker *et al.* (1989) differ fundamentally in their interpretations of forest succession and their predictions of the future vegetational succession on the islands. Tagawa and his colleagues suggest that Sertung and Panjang have the most mature, advanced forests (*Dysoxylum*-dominated) on the islands and that in time this forest type will succeed the *Timonius* and *Neonauclea* forests now present on Rakata. Whittaker and his colleagues, however, believe the *Dysoxylum* forests of Sertung and Panjang are very young, representing a disturbance-induced secondary succession, and that *D. gaudichaudianum* will not become the forest dominant over much of Rakata, but will contribute to floral diversification, leading to a more patchy mosaic. In 1989 R. J. Whittaker (personal communication) found that on Rakata below about 150 m *N. calycina* appeared to be diminishing and *D. gaudichaudianum* gaining in importance.

(*b*) *Development of the fauna and approach to equilibrium since* 1933

Dammerman (1948) provided an admirable account of faunal development from 1883 to 1934, based on Jacobson's 1908 faunal survey (Jacobson 1909) and his own surveys from 1919 to 1934. This can now be augmented by incorporating the results of Hoogerwerf's 1951–52 survey of the avifauna (Hoogerwerf 1953*a*) and surveys in the 1980s. A table showing colonization of the archipelago and species turnover of various invertebrate groups was provided by Thornton & New (1988*b*, table 10). To this can now be added data for reptiles, resident land birds and mammals (table 1).

Problems of cryptoturnover and pseudoturnover have been discussed in earlier papers of this series (Thornton & Rosengren 1988; Thornton & New 1988*b*; Thornton *et al.* 1990). There are, of course, problems of pseudoturnover with all groups of animals, and, for vertebrates, they

Table 1. Turnover on the Krakataus of various animal groups for which data from at least four survey periods are available

(*a*, Actual species number; *c*, cumulative species number; +, immigrants; −, extinctions in intersurvey intervals.)

		1908	1919–24	1928–33		1982–86
Oligochaeta	(*a*)	1 (+3−1)	3 (+1−0)	4 (+3−1)		6
	(*c*)		4	4		7
land molluscs	(*a*)	2 (+4−0)	6 (+5−0)	11 (+8−0)		19
	(*c*)		6	11		19
scorpions[a]	(*a*)	1 (+0−0)	1 (+1−0)	2 (+1−0)		3
	(*c*)		1	2		3
Odonata	(*a*)	2 (+10−0)	12 (+3−4)	11 (+7−7)		11
	(*c*)		12	15		20
Blattodea	(*a*)	3 (+6−2)	7 (+5−0)	12 (+10−5)		17
	(*c*)		9	14		24
Thysanoptera	(*a*)	0 (+12)	12 (+4−12)	4 (+25−3)		26
	(*c*)		12	14		39
Neuroptera	(*a*)	1 (+3−1)	3 (+2−1)	4 (+8−2)		10
	(*c*)		4	6		13
Diptera, bombyliid, chloropid, lauxaniid	(*a*)	11 (+1−10)	2 (+4−0)	6 (+20−5)		21
	(*c*)		12	15		27
butterflies	(*a*)	6 (+28−1)	33 (+8−11)	30 (+27−3)		54
	(*c*)		34	42		64
ants	(*a*)	21 (+20−5)	36 (+17−13)	40 (+42−11)		71
	(*c*)		41	58		100
other aculeates	(*a*)	16 (+26−11)	31 (+18−9)	40 (+56−10)		86
	(*c*)		42	56		107
braconids	(*a*)	2 (+4−2)	4 (+4−4)	4 (+62−4)		62
	(*c*)		6	10		72
land reptiles[b]	(*a*)	3 (+3−0)	6 (+0−0)	6 (+5−2)		9
	(*c*)		6	6		11
resident land birds[c]	(*a*)	16 (+14−2)	28 (+4−2)	30 (+6−2)	34(+6−3)	37
	(*c*)		30	34	40	45
bats[d]	(*a*)	0 (+2)	2 (+2−0)	4 (+12−2)		14
	(*c*)		2	4		16
rats	(*a*)	0 (+1)	1 (+1−0)	2 (+0−0)		2
	(*c*)		1	2		2

[a] Data for scorpions from Vachon & Abe (1988), for other invertebrates from authorities cited in table 7 of Thornton & New (1988*b*).

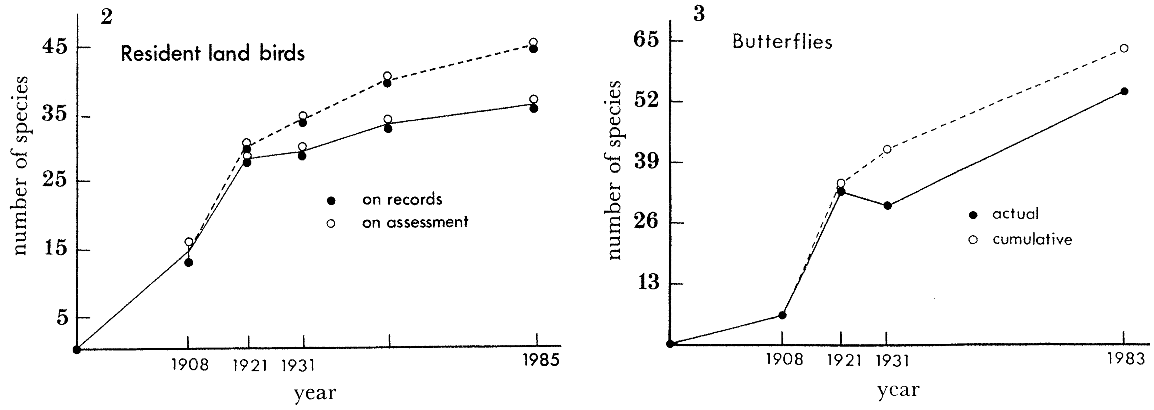
[b] Ignores records of *Crocodylus porosus* (1924 and 1984) and *Cosymbotus platyurus* (1928), regarded as incidentals; data from Rawlinson *et al.* (1990).

[c] Based on table 6, Thornton *et al.* (1990); includes data for survey 1951–52.

[d] Data from Tidemann *et al.* (1990), counting *Macroglossus sobrinus* (1974 record) as now present.

are greatest with the bats, for which monitoring techniques have changed considerably since the 1930s. Although the turnover in bat species since the last survey in the 1930s (+12, −2 species) almost certainly includes a high proportion of pseudoturnover, the size of the increase and comments on the lack of bats (particularly microchiropterans) in reports of earlier surveys, suggest that a substantial actual increase has occurred in the past 50 years. Tidemann and his colleagues accept that frugivores, with their relatively unspecialized roosting requirements and good dispersal abilities, were earlier colonizers (the first species was recorded in 1919, three being present by 1933) than insectivores, which probably became established after 1939, in the second half-century after the eruption (Tidemann *et al.* 1990). This conclusion has important implications for the development of the flora (Whittaker *et al.* (1989) and see below) and thus for the colonization of other animals, including microchiropterans. It is likely that the colonization curve for bats, if pseudoturnover could be discounted, would still resemble that for butterflies, for example, more than that for resident land birds (figures 2 and 3).

In the case of resident land birds we have shown (Thornton *et al.* 1990) that the assumption (MacArthur & Wilson 1967) that the resident land bird fauna had reached equilibrium by 1919 is not supported. The present size of the fauna (36 or 37 species, depending on presence or absence of *Corvus macrorhynchos*) falls short of estimates of the equilibrium number, S, (44–58) calculated by using colonization data for the last intersurvey interval and a pool (resident land birds of Ujung Kulon) of 165 species (table 2), but close to estimates made after correcting for pseudoturnover and cryptoturnover (38), and by fitting the colonization equation to the whole of the data, a method that is free from cryptoturnover error (36) (Thornton *et al.* 1990). Species number of resident land birds now appears to be close to equilibrium but this has been achieved only in the past 30 years. There are indications that birds first colonized the islands only in the second decade after 1883.



FIGURES 2 AND 3. Colonization curves of resident land birds (figure 2) and butterflies (figure 3) to the Krakatau Islands. Data from Thornton *et al.* (1990) and New *et al.* (1988), respectively. In these and subsequent colonization curves, continuous lines are used for actual numbers at the time of the survey, dashed lines for cumulative numbers.

Similar estimates cannot be made for bats with any precision because a high proportion of pseudoturnover is almost certainly involved as a result of changes in survey methods, and this cannot be assessed and discounted as was done for birds (Thornton *et al.* 1990). However, taking the pool as 31 species, the number of species recorded in recent surveys of the West Java coast, Ujung Kulon, Sumur, Panaitan Island and Sebesi Island (Tidemann *et al.* 1990), and the present fauna as 14 species, with 12 immigrations and two extinctions over 52 years, the estimated equilibrium number on the basis of data from the last two surveys is 22 species (table 2). Fourteen species were recorded from 1974 to 1986. Although the lack of mature primary forest, bamboo thickets and other mainland habitats on the Krakataus means that the *effective* mainland pool size is less than the total number of mainland species, it is likely that the recent mainland surveys resulted in an underestimate of the size of the fauna, and taking P arbitrarily as 50 species increases the value of $\hat{S}$ to 28 species. Assuming that 6 species were missed in the earlier survey and thus halving the number of immigrants from 12 to 6 species to take some account of pseudoturnover, results in estimates of $\hat{S}$ of 20 and 24 species for pools of 31 and 50 species, respectively. By analogy with the birds, however, considerations of cryptoturnover could reduce these estimates considerably.

Table 2. Estimated equilibrium number of species ($\hat{S}$) of vertebrate groups on the Krakataus

(Calculated from data over the most recent intersurvey interval (T, in years) by the formula $\hat{S} = \lambda P/(\lambda+\mu)$ (MacArthur & Wilson 1967). P, number of species in assumed pool population; S_1, number of species in earlier survey; S_2, number of species in later survey; $\bar{S}$, average number of species in intersurvey interval; imm, number of immigrant species in the interval; ext, number of extinctions in the interval.)

	T	P	S_1	S_2	$\bar{S}$	imm	ext	$\hat{S}$
1. resident land birds[a]	33.5	165	34	37[j]	35.5	6	3	58
2. resident land birds[b]	33.5	165	34	36[j]	35.0	6	4	47
3. resident land birds[c]	33.5	165	33	35[j]	34.0	7	5	44
4. bats[d]	52.0	31	4	14	9.0	12	2	22
5. bats[e]	52.0	50	4	14	9.0	12	2	28
6. bats[f]	52.0	31	10	14	12.0	6	2	20
7. bats[g]	52.0	50	10	14	12.0	6	2	24
8. reptiles[h]	52.0	25	6	9	7.5	5	2	13
9. reptiles[i]	52.0	50	6	9	7.5	5	2	15

[a] Data based on assessment of survey records (Thornton *et al.* 1990, table 6), P is number of species recorded from Ujung Kulon (Hoogerwerf 1970; Blower & van der Zon 1977, and our observations).

[b] As (1) but counting *Corvus macrorhynchos* as extinct.

[c] Data based on unadjusted records but *C. macrorhynchos* counted as extinct.

[d] P is the number of species found in recent years on the West Java coast adjacent to Sunda Strait, Ujung Kulon, Sumur, Sebesi I., Panaitan I. (Tidemann *et al.* 1990). S_2 includes one species found only in 1971.

[e] As (4) but P arbitrarily set at 50.

[f] As (4) but taking S_1 as 10 and imm as 6 to take account of pseudoturnover.

[g] As (6) but P arbitrarily set at 50.

[h] P is the number of land reptile species (discounting *Crocodylus porosus* and *Chelone mydas*) recorded from the Ujung Kulon wildlife reserve by Hoogerwerf (1970). *C. porosus* (1924, 1984) and *Cosymbotus platyurus* (1928) records on the Krakataus are regarded as incidental.

[i] As (8) but P arbitrarily set at 50.

[j] One Krakatau species absent from assumed pool (Ujung Kulon) not counted in calculating available pool (P-$\bar{S}$).

Hoogerwerf (1970) listed 27 species of reptiles for the Ujung Kulon wildlife reserve, a region that he surveyed frequently over a number of years. Discounting the crocodile *Crocodylus porosus*, for which there is no suitable habitat on the Krakataus, and the green turtle, *Chelone mydas* (not a land reptile) the pool may be regarded as 25 species. Treating the 1924 and 1984 Krakatau records of *C. porosus* and the 1928 record of the gecko *Cosymbotus platyurus* as incidental (Rawlinson *et al.* 1990), and by using the colonization data for the last intersurvey period, the estimated equilibrium number is 13 species, and if the pool is taken as 50 species $\hat{S}$ becomes 15 species. The estimates would be reduced according to the extent of cryptoturnover if this could be corrected for. An exponential colonization curve can be fitted to all the data within the observational limits (see Thornton *et al.* 1990) (except that the number of species in 1908 must be four, rather than three) when t_r (Diamond 1972) $= 50$ years, t_0 (time since 1883 of first colonization) $= 2$ years, and $S = 11$ species. This suggests that reptiles first colonized only in the third year after 1883 (the first report, of *Varanus salvator*, was in 1889), that the present fauna, nine species, is not far from equilibrium but that it is approaching equilibrium relatively slowly (compared to birds).

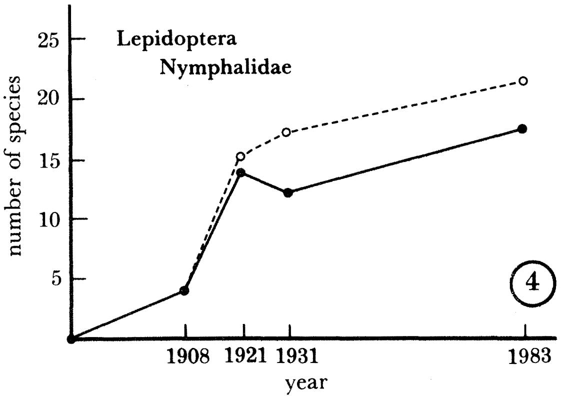
No estimates can be made for terrestrial mammals as only two species (of *Rattus*) are present on the islands and there has been no change in the past 52 years. However, discounting 11 large species (rhino, banteng, leopard, deer, cats, wild dogs, pigs and binturong) Hoogerwerf (1970) lists 20 small mammals such as rodents, monkeys, civets, squirrels, tree shrews and mongoose for Ujung Kulon. Of these, only the two rats have succeeded in colonizing the Krakataus in over 100 years.

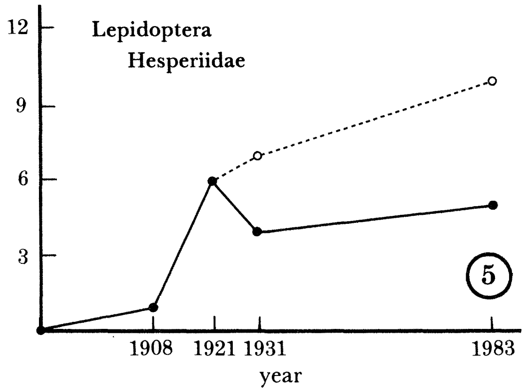
It is clear from our studies and those of other workers in the last decade that successional turnover rather than equilibrium turnover is still occurring; for no group of animals is there evidence that a dynamic equilibrium of species numbers has been achieved, although there are indications that for resident land birds this is imminent. Colonization curves for various groups of animals show that approach to equilibrium species numbers is by no means uniform (figures 2–16). In some groups, such as nymphalid and hesperiid Lepidoptera (4, 5), Blattodea (6), Odonata (7), reptiles (8), and non-migrant, non-marine birds (2), the rate of increase in number of species has flattened markedly in the past 50 years. In contrast, other groups, for example, lycaenid Lepidoptera (9), ants (10), other aculeate and braconid Hymenoptera (11, 12), Diptera (13), Thysanoptera (14), Neuroptera (15) and land molluscs (16) are building up species numbers at a rate little different from that in the first half century since 1883.

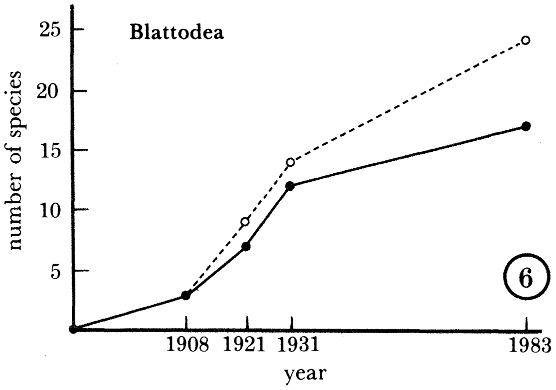
Brown (1988) has used our data and those for unspecified undisturbed islands to plot species–area curves that reveal the contrast between birds, which were shown to have built up a species complement on all islands of the archipelago comparable with those of undisturbed islands of similar area, and mammals, for which no such correspondence was evident. Brown used incorrect data for the Krakataus; by using correct data for 1986, his graphs can be modified (figure 17). When bats are included in the mammals (our plots 1–5 of the mammal graph), the older Krakatau islands are almost in conformity with undisturbed islands. Plotting only non-volant mammals (our plots 6–8), all islands are of course strikingly impoverished. It is likely that if similar species–area curves for other animal groups present on the Krakataus could be plotted they would reveal a continuum between these extremes.

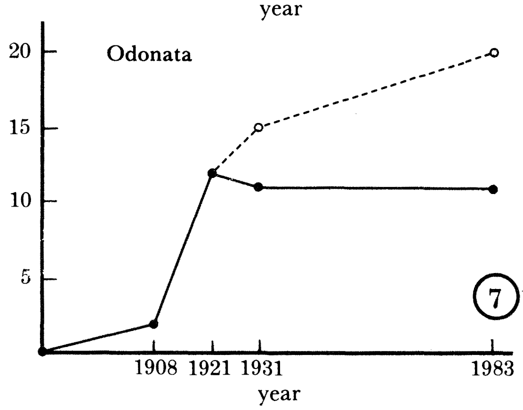
The change from open grassland habitats to closed forest has had a most important impact on the fauna. Of the animal groups for which previous survey records permit turnover calculations, the second intersurvey period (1908–19), when forests were forming, was the time when immigration rates were highest, and the third period (1920s and early 1930s), when the forest canopy was closing, was the time of highest extinction rates. This is exemplified in the data for butterflies, ants, other aculeate Hymenoptera, Thysanoptera and resident land birds (New *et al.* 1988; Thornton & New 1988*b*; Thornton *et al.* 1990). Dammerman (1948) stressed the changes in representation of invertebrate groups from the 1908 survey of Jacobson to the Dammerman surveys of 1919 to 1934, changes that were clearly correlated with the succession from extensive open grassland habitat to one of closed forest. There is some indication (Thornton *et al.* 1990) that after forest canopy closure there was a change in the resident land bird fauna towards more specialized feeders, and the data clearly show differences in the proportions of immigrants that were true forest birds and open country species. When the two halves of the century since 1883, pre- and post-canopy closure, are compared, the percentage of immigrants that are forest birds has increased significantly since 1933, and the proportion of open-country immigrants decreased. During the period of forest formation in the 1920s many ecologically important plant species that are bird- or bat-dispersed first made their appearance (Whittaker *et al.* 1989).

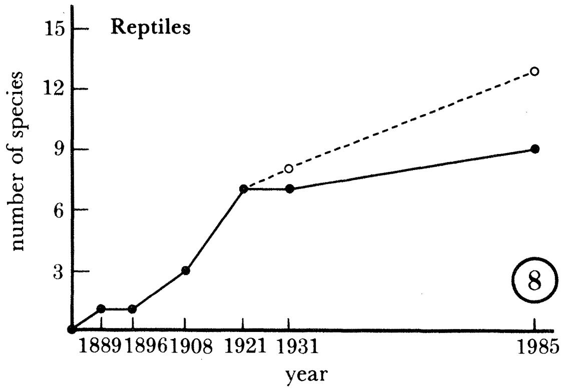
The colonization curves of resident land birds for the archipelago, and for Rakata alone, differ slightly (Thornton *et al.* 1990). The curve for the archipelago rises steadily, although less steeply, after 1921, when forests were becoming established. The Rakata curve, however, levels out from 1921 to 1951–52, after which it rises again to the 1980s value. These differences may

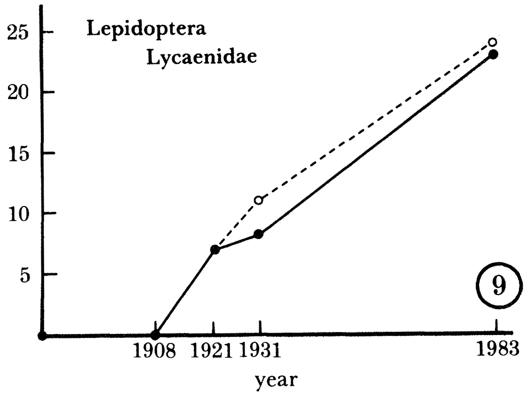


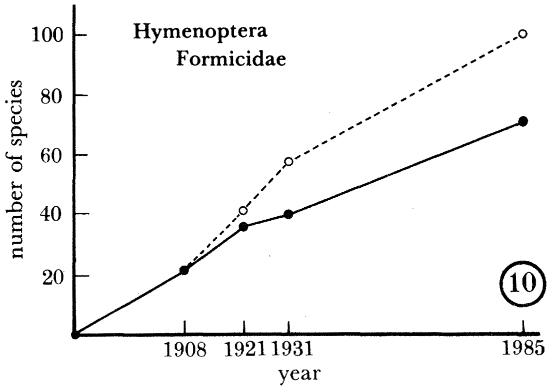




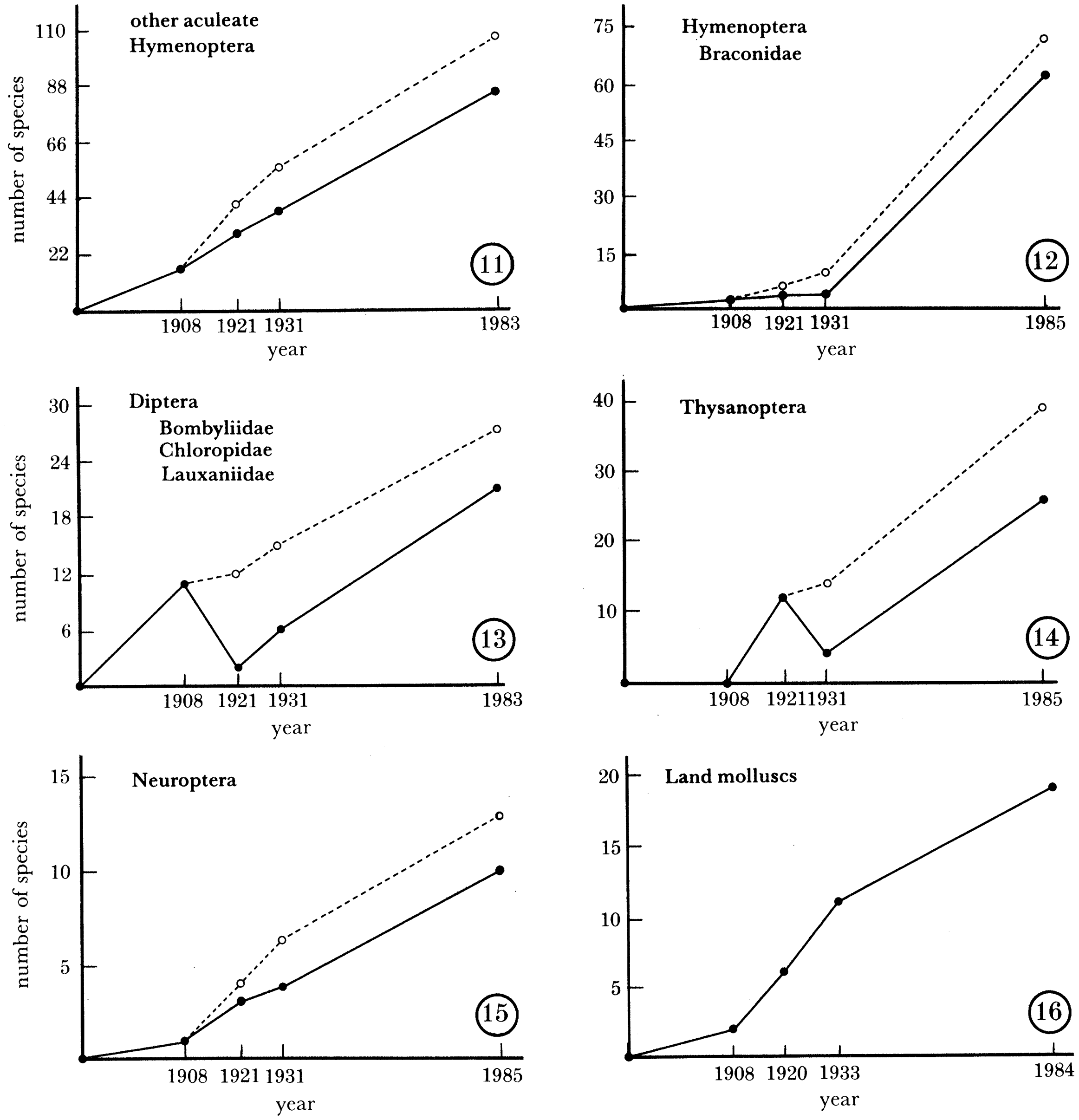








FIGURES 4–10. For description see opposite.



FIGURES 4–16. Colonization curves for various animal groups to the Krakataus. Data from sources cited in table 7 of Thornton & New (1988*b*) and Rawlinson *et al.* (1990). Continuous lines are used for actual numbers at the time of the survey and dashed lines for cumulative numbers.

reflect the differential disturbance to the archipelago by Anak Krakatau's activity, Rakata alone remaining almost unaffected, and the persistence of open habitat on the archipelago (on Sertung and Anak Krakatau) but not on Rakata. The rise in the Rakata curve for the last intersurvey period coincides with changes that Whittaker's group have recently found to be occurring in Rakata's lowland forests.

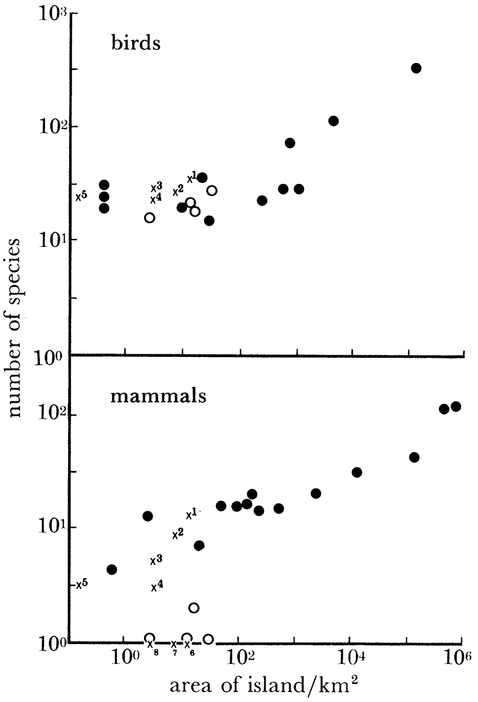


FIGURE 17. Correction of Brown's figure 3.6 (Brown 1988) showing the species–area relations of birds and mammals on unspecified undisturbed islands (filled circles) and the Krakataus (empty circles). Our corrections are plotted as crosses with superscripts as follows: resident land birds – 1, Rakata; 2, Sertung; 3, Panjang; 4, Anak Krakatau (counting total area); 5, Anak Krakatau (counting only vegetated area); mammals – 1, Rakata; 2, Sertung; 3, Panjang; 4, Anak Krakatau (total area); 5, Anak Krakatau (vegetated area); terrestrial mammals (rats) only – 6, Rakata; 7, Sertung; 8, Panjang; Anak Krakatau has no terrestrial mammals.

(c) *The nature of successful animal colonists*

Successful colonizers in many animal groups appear to comprise species known to have wide distributions and broad ecological tolerances. This is particularly clearly shown in the Krakatau land birds. A high proportion (about 75%) of the resident land bird colonists are known to be inhabitants of urban or semi-urban garden areas and other open disturbed habitats in southeast Asia. Almost half of the Krakataus' present resident land birds (17 of 37 species) were listed by Whitten *et al.* (1987) for Ujung Pandang, an urban area on Sulawesi. Thornton *et al.* (1990) pointed out that four fifths of the species immigrating to the Krakataus in the first 50 years after the 1883 eruption (27 out of 34 species) were birds of coastal scrub, mangrove, and open habitats that have also been recorded recently in Singapore, and 62% of those present in the 1980s (23 out of 37 species) are known from Singapore. They also showed that almost half (45%) of the 62 species recorded from *both* the Ujung Kulon (West Java) and Barisan Selatan (southern Sumatra) national parks have been recorded from the Krakataus, a very much higher proportion than that for species recorded from only one of these parks (16% of 103 for Ujung Kulon, 0% of 59 for Barisan Selatan). The arrival and success of two species of kingfisher on the archipelago nicely illustrates this point. Two kingfishers were recorded in 1908, the white-collared, *Halcyon chloris*, and the small blue, *Alcedo caerulescens*. The former, a bird of open, particularly coastal country, was regarded by Diamond (1975) as a 'supertramp' and is an aggressive, pioneer colonist, that at least on the Krakataus has been successful in the absence of mangroves (one of its preferred habitats). It now occurs on all islands, including a thriving population on Anak Krakatau. The small blue kingfisher normally inhabits trees beside small streams, brackish ponds and mangroves (MacKinnon 1988). None of these habitats occurred on the Krakataus in 1908, and in contrast to *H. chloris*, it was evidently unable to adapt to the conditions then existing; it has not been encountered since 1908.

Similarly, the bat colonizers of the Krakataus, are, in general, widespread species without specialized roosting requirements. They are not species of primary forest; rather they are species that appear to tolerate disturbed habitats fairly well, and which L. R. Heaney (personal communication) has found to occur on small isolated islands of the Philippines.

The reptiles also comprise predominantly species that are widely distributed and either associated with urban situations or good candidates for dispersal by sea (Rawlinson *et al.* 1990). Of 13 identified species known to have arrived in the last century, 4 are geckos associated with human habitations; *Gekko gecko*, *Hemidactylus frenatus*, *Lepidodactylus lugubris* (now absent) and the transient *Cosymbotus platyurus*. These, and the skink *Mabuya multifasciata* are thought to have arrived adventitiously by sea traffic. There is evidence that *H. frenatus* can survive substantial volcanic ashfalls, and this species and *Varanus salvator* are the most successful terrestrial vertebrate colonists of the archipelago, being found on all islands and established by 1908 and 1889, respectively. The monitor, *V. salvator*, probably arrived by swimming, like the python *Python reticulatus* (present by 1908) and the gliding paradise tree snake *Chrysopelea paradisi*, probably from the island of Sebesi some 12 km to the north.

Four species, the king gecko *Gekko monarchus*, the widely distributed gecko *Hemiphyllodactylus typus*, which occurs around houses as well as in natural situations including the axils of *Pandanus* leaves, the coastal skink *Emoia atrocastata*, and the parthenogenetic termite-feeding blind snake *Ramphotyphlops braminus*, probably arrived by rafting on driftwood. All Krakatau's seven termite species are wood or tree nesters, although over a third of the termite source fauna comprises subterranean or epigeal nesters (Abe 1984). A species of the termite genus *Nasutitermes*, which makes carton nests in trees, occurs on all islands and is likely to have arrived by rafting, and *R. braminus* possibly arrived with such a nest. *E. atrocostata* became well established on the Sertung spit by 1919, but was not recorded over the period 1982–86 and Rawlinson *et al.* believe it to have become extinct on the islands, probably as a result of habitat destruction by Anak Krakatau's activity in 1952.

The two carnivorous *Gekko* species are probably recent arrivals; they have conspicuous calls that would have been noticed by earlier survey groups, and have a localized distribution. The paradise tree snake also appears to be a recent colonist, and a most successful one, occurring on all islands by 1984; it feeds chiefly on geckos. Two other reptilian carnivores, *P. reticulatus* and *V. salvator*, were early arrivals. The monitor's diet consists chiefly of shore crabs (Iwamoto 1986), and these, carrion, and green turtle eggs (Rawlinson *et al.* 1990) would provide available food on arrival. In the words of Rawlinson *et al.*, 'as with *H. frenatus*, not only is *V. salvator* predisposed to disperse to new volcanic islands, it is also well adapted to survive on them'. The python, which inhabits areas around human settlements, has a staple food on the islands – rats.

Two species of rat, *Rattus rattus* and *Rattus tiomanicus*, occur on the group (on Rakata, and on Panjang and Sertung, respectively) and both probably arrived as a result of human activity, *R. rattus* by 1918 and *R. tiomanicus* by 1928 (possibly in 1896–97, see, for example, Rawlinson *et al.*

1990). *R. rattus* is the urban house rat and *R. tiomanicus* the 'field rat', common in agricultural areas as well as natural situations. We captured one sub-adult *R. rattus* on Anak Krakatau in 1985, and believe it to have been introduced inadvertently on a tourist boat. The distribution of the two species on the archipelago is allopatric, and Yukawa *et al.* (1984) and Iwamoto (1986) noted morphological differences between the Panjang and Sertung populations of *R. tiomanicus* which led them to conclude that three separate introductions of rats had occurred and that the natural dispersal rate within the archipelago is low.

These characteristics of good colonists may also be seen in the insects. For example, two of the three families of psocopteran insects with the greatest relative colonization ratios to the Krakataus are the exploitative, r-strategy Lepidopsocidae and Ectopsocidae (Thornton *et al.* 1988*b*), which exploit frequent but ephemeral habitats, such as dead or dying leaves, that are almost always available. Kanmiya & Yukawa (1985) also noted that the chloropid fauna of the islands consists of saprophagous or littoral species, and many of the known species are widespread. In comparing the butterfly faunas of disturbed, transitional, and closed climax forest habitats in the mountains of North Vietnam, Leps & Spitzer (1990) showed that many widely distributed species were closely associated with the disturbed (ruderal) habitat and were recorded recently from the Krakataus.

(*d*) *Preclusion by lack of habitat*

There is indirect evidence that successional processes have precluded colonization by several groups of animals because their optimal habitat is (or was) not available. We have noted, with respect to non-migrant land birds (Thornton *et al.* 1990), that the effective pool (as opposed to the theoretical pool) of potential immigrants to islands still undergoing successional processes is not constant, but changes with time as the potential habitat on the islands moves away from the optima of some species and towards the optima of others, possibly precluding the establishment of different sets of species as succession proceeds. Conceivably, the rate of environmental change on the islands may be so great that there may be insufficient time even for members of the effective available pool for a particular environmental stage to exploit the transient opportunity.

Dammerman (1948) believed that the grassland fauna had not reached its maximal development by the time forests began to form, and pointed out that the grassland plant formation had reached its greatest extent by 1908, 25 years after the 1883 eruption, and at about that time 'mixed forest was beginning to supplant the grass', so that less than two decades had been available for its colonization by animals (grassland was first recorded in 1897). By the time Dammerman's surveys began (1919) the grassland was 'to a large extent replaced by mixed forest, at any rate on the lower areas' and by 1933 Rakata was 'almost entirely covered by trees even up to a great altitude and the grass jungle, at any rate as covering large areas, had almost disappeared' (Dammerman 1948).

There are some indications that the brief timespan of the open habitat phase was too short for the establishment of several animals that might have been expected to colonize successfully. Yamane (1983), for example, noted that although species of the sphecid wasp genera *Sceliphron*, *Chalybion* and *Ammophila* are characteristic of open sites on the Javan and Sumatran mainlands, these genera have never been recorded on the Krakataus, having failed to colonize the archipelago during the two decades or so when their optimal habitat was extensive. Similarly, Thornton *et al.* (1990) suggested that the grassland phase was 'missed' by granivorous birds such as sparrows and munias (Ploceidae), 13 species of which occur in coastal areas of West Java, in some cases only 44 km from the archipelago.

Twenty-two families (comprising 145 species of non-migrant, non-aquatic bird species) that are recorded from the Sunda Strait area (coastal West Java including Ujung Kulon, southern Sumatra and Barisan Selatan National Park, Benkulu and Lampung in southern Sumatra) (Blower & van der Zon 1977; Chasen 1937; Dammerman 1923; Hoogerwerf 1953*b*, 1970; van Marle & Voous 1988; MacKinnon 1988; de Wulf *et al.* 1981, and our observations) have never been recorded from the Krakataus. Twelve of these families comprise or include birds of open country and grassland. The Phasianidae, for example, includes birds of open country such as quails and peacocks, and some that are forest species, such as argus pheasants and jungle fowl, all, incidentally, poor fliers. These, and the frogmouths (Podargidae), tree swifts (Hemiprocnidae), bee-eaters (Meropidae), drongos (Dicruridae) and white-eyes (Zosteropidae) of these areas together contain 12 open country species. Other families absent from the archipelago consist entirely of open grassland species: buttonquails (Turnicidae) (also poor fliers), Richard's pipit (Motacillidae), sparrows and munias (Ploceidae) and a finch, *Serenus estherae* (Fringillidae), a further 19 species in all.

Twenty-one species of Old World warblers (Sylviidae) are recorded from the Sunda Strait area, 14 of them inhabiting reeds, scrub or open grassy country, but only one has become established on the Krakataus, and this (*Gerygone sulphurea*) is (exceptionally) a bird of coastal scrub and mangroves. Only one species of granivore (*Geopelia striata*) has ever been recorded from the islands, and this (in 1919 and 1951) since 1908 when grasslands were extensive.

The most obvious category affected by lack of specialized habitat comprises animals of mature forest. Apart from the large mammals, smaller non-volant mammal species such as squirrels, gliding lemurs, tree shrews, civets, small cats and monkeys, as well as many bats, common on the Ujung Kulon peninsula, are absent. Tidemann *et al.* (1990) listed 15 bat species, four pteropodids, a nycterid, two rhinolophids, seven vespertilionids and a molossid that were collected in Java but not found on the Krakataus. Two of the vespertilionids, *Pipistrellus imbricatus* and *Tylonycteris pachypus*, are known from the island of Sebesi, only some 15 km to the north of the Krakataus. *Tylonycteris*, two species of which were collected in West Java in the last decade, is unrepresented on the archipelago; its species are exclusively bamboo roosters (Medway & Marshall 1970) and bamboos have not become established on the Krakataus. Other species, such as the pteropodid *Chironax melanocephalus*, which appears to be restricted to primary forest (Suyanto *et al.* 1985), may be precluded from establishment on the islands because the vegetational succession has not proceeded to their habitat optima. This probably also applies to several reptile species common, for example, in the forests of Ujung Kulon, such as species of *Draco* and many snakes. The bamboo snake or green whip snake (*Dryophis trasinus*) is the analogue of *T. pachypus* in this respect.

Many land bird species that are characteristic of mature forests in the Sunda Strait area have never become established on the Krakataus (Thornton *et al.* 1990). Nine out of the 22 families absent from the Krakataus mentioned above comprise forest birds. Trogons (Trogonidae) inhabit forest mid-storey, hornbills (Bucerotidae) require mature hollow trees for nesting, barbets (Capitonidae) are tree-hole nesters of the upper storey, pittas (Pittidae) are reluctant fliers and inhabitants of forest undergrowth, ioras and leafbirds (Chloropseidae) are, with one exception, birds of the forest canopy, parrots (Psittacidae), nuthatches (Sittidae) and broadbills (Eurylaimidae) are forest birds, and babblers (Timaliidae) are birds of deep forest, many that inhabit undergrowth and the forest floor in addition being poor fliers. These nine families together comprise 85 species known from areas adjacent to the Sunda Strait, of which the babblers make up 42.

Several families that are represented on the archipelago are composed largely of forest species, the Krakatau representative being, exceptionally, a bird of open scrub or mangroves. For example, of the 19 species of thrushes (Turdidae) in the Sunda Strait area, 17 are forest species. Apart from *Zoothera interpres*, the only other colonizer of the Krakataus is *Copsychus saularis*, a species of gardens, open woodland and mangroves. The only other non-forest species in the family is *Saxicola caprata*, a bird of open country and grasslands that did not colonize the islands when these habitats were extensive. The oriole on the Krakataus, *Oriolus chinensis*, is the only one of four in the area that inhabits open country, grassland and mangroves, the others being forest birds. Similarly, of 21 species of flycatchers (Muscicapidae) in the Sunda Strait area, the only representative on the Krakataus (*Cyornis rufigastra*) is one of only two that are normally inhabitants of mangroves; the other, *Rhipidura javanica*, would be a likely colonist were *C. rufigastra* not already established. *C. rufigastra* is listed by MacKinnon (1988) as rare on Java and its status a matter of concern; on the Krakataus, however, it is one of the most abundant species (Zann *et al.* 1990*a*).

This possible case of habitat expansion (and there are others, particularly involving birds usually associated with mangroves) may have parallels among invertebrates. Instances of insects that have become unusually dominant on the islands, and which they suggested may be undergoing 'outbreaks' were noted by Yukawa & Yamane (1985), and Thornton & New (1988*b*) discussed apparent increases in the plant host range of some phytophagous insects, suggesting a form of 'ecological release'.

Some species well-known to be highly vagile, such as the butterflies *Anapheis java*, *Phalanta phalantha*, species of *Delias* and *Papilio demoleus*, have not become established on the Krakataus, which lack their food-plant families (Capparidaceae, Loranthaceae, Santalaceae, Rutaceae), although the first two species mentioned are recorded as having reached the islands.

Whereas stenophagous insects, such as some butterflies, are precluded from establishment by absence of their host-plants (New *et al.* 1988), others, with a less narrow food range but with other specialized habitat requirements that are satisfied in mature forest, are also lacking from the islands, although present on adjacent mainland areas. Families of psocopteran insects that occur predominantly in closed forest habitats (Amphientomidae, Psocidae, Myopsocidae, Calopsocidae) are poorly represented proportionally on the Krakataus compared with either the total known Indonesian fauna, or with that of the well-studied islands of Bali and Lombok, for example (Thornton *et al.* 1988*b*). Dammerman (1948) suggested the absence of ascalaphid neuropterans from the island group by the 1930s reflected the lack of their preferred forested habitat; the family is still unrepresented, and several forest-inhabiting chrysopid lacewing taxa that occur on Java or Sumatra or both, are also absent (New & Sudarman 1988). Yamane (1983) also noted the poor representation on the Krakataus of forest aculeate hymenopterans (other than ants). There are few habitual deep-forest butterflies on the Krakataus; only *Loxura atymnus* and one or two other lycaenids are established (New *et al.* 1988). Many forest lycaenids have obligate relations with particular species of ants, adding another environmental dimension to their need, and barrier to their colonization.

Just as phytophagous insects with specialist food requirements cannot successfully colonize until their food plant has become established, so parasites, of course, must be preceded by their hosts. Braconid Hymenoptera, for example, were particularly late colonists to the archipelago (figure 12; K. Maeto, personal communication). Anak Krakatau, which is at an earlier successional stage than the other islands, having a biological age of only three decades or so, supports only five of the archipelago's 13 braconid subfamilies. It lacks all 15 of the archipelago's species that are endoparasites of cyclorrhapous Diptera and has only 1 of the 10 that parasitize wood-feeding beetles. By analogy, it is likely that the poor early representation of braconids on the archipelago as a whole was also because of preclusion of some groups due to lack of appropriate insect hosts, in turn perhaps the result (as with xylophagous beetles) of the lack of the appropriate vegetational successional phases. The nest-parasitizing koel, *Eudynamys scolopacea*, did not colonize until after potential host species (*Corvus macrorhynchos* and *Oriolus chinensis*) had already become established.

The almost total lack of permanent bodies of freshwater on the islands precludes the establishment of five families of birds known from the Ujung Kulon peninsula: Podicipedidae (grebes), Phalacrocoracidae (cormorants), Ciconiidae (storks), Anatidae (ducks) and Jacanidae (jacanas). Of insect orders with aquatic larvae, stoneflies (Plecoptera) have never been recorded, and mayflies (Ephemeroptera) and caddis flies (Trichoptera) were first noted by Thornton & New (1988*a*) in 1984 and 1986. The mayflies found in the 1980s were of a family (Baetidae) that includes species with unusually long-lived adults (up to 14 days) and some that are associated with brackish water. One adult was taken in a light trap on Anak Krakatau, and larvae in an artificial pond on Panjang. Caddis larvae of two families (Hydropsychidae and Psychomyiidae) were found in a small artificial pool on Sertung. No psychodid or simuliid Diptera, nor gyrinid beetles have been recorded from the Krakataus, and dytiscid and hydrophilid beetles, and hydrometrid, gerrid, corixid and notonectid hemipterans have only been found rarely, and then generally associated with the brackish lagoons that existed on Sertung for several decades from before 1919 to after 1934, or in a fisherman's well present on Rakata from 1933 to 1934. An aquatic snail, *Melanoides tuberculata*, that was present in the Sertung lagoons in 1933 was found in numbers in the Sertung pool in 1986, together with an adult dytiscid beetle. Other aquatic molluscs were present only during the period of existence of the Sertung lagoons (Smith & Djajasasmita 1988). A surface-film dwelling aquatic bug, *Microvelia* (Veliidae), was breeding in one of the Panjang ponds in 1986 (Thornton & New 1988*a*); the family was previously unrecorded. The only insects with aquatic larvae that are well represented on the Krakataus are the Odonata (Yukawa & Yamane 1985; van Tol 1988); most are undoubtedly adventive and non-resident, although a libellulid dragonfly larva was present in the Sertung pool in 1986. We found no zygopterous larvae.

An estuarine crocodile, *Crocodylus porosus*, was captured in 1924 near the brackish lagoon on Sertung; one member of our 1986 expedition (D. J. Kitchener) saw one in the shallows off Zwarte Hoek beach, Rakata, but the species is of course precluded from establishment on the islands.

(*e*) *The nature of turnover in animal species*

Whittaker *et al.* (1989) pointed out that plant species present on only one of the islands have the poorest persistence, those occurring on all three older islands the best persistence; this, of course, would be expected from stochastic considerations. More importantly, they noted that turnover of plants largely involves 'ephemerals', species lost due to habitat destruction, species introduced by humans, and successional turnover; there has been little 'stochastic' turnover.

A consideration of animal extinctions (particularly vertebrates, for which there is most data) supports the points made by Whittaker and his colleagues.

Inadvertent introduction by humans appears to have been responsible for a proportion of the turnover of animal species similar to that of plants. The only cases of vertebrate species being possibly introduced by humans are those mentioned by Rawlinson *et al.* (1990): four geckos, the coastal skink and the two species of rat, and Thornton & New (1988*b*) discuss the relatively few cases of possible invertebrate introductions.

The volcanic and physically dynamic nature of the islands has also probably been responsible for some turnover of animal species through habitat changes. The eruptions of Anak Krakatau that Whittaker *et al.* (1989) thought to have played such an important role in the diversification of the archipelago's forests by deflecting forest succession on Panjang and Sertung, are also thought to be responsible for the loss of the coastal skink *Emoia atrocostata* from the archipelago (Rawlinson *et al.* 1990). The skink appeared in numbers between high- and low-water marks on the Sertung spit in 1919, and was persisting there (and there only) in numbers in 1933 (Dammerman 1948). The 1952 eruption of Anak Krakatau is known to have devastated this area (van Borssum Waalkes 1954) and the skink could not be found in the 1980s in spite of intensive searches of the spit's littoral and supralittoral zones. Dammerman found its restriction to the Sertung spit 'curious'. The skink's eggs or adults are very probably dispersed by driftwood and the Sertung spit has the greatest accumulation of driftwood in the islands. The direction of the surface drift generated by ocean swell (Bird & Rosengren 1984; Rosengren 1985; Thornton & Rosengren 1988) renders it highly unlikely that a population established only on the spit would be able to re-disperse to others parts of the archipelago by this means.

Whittaker *et al.* (1989) have shown that the coastal plant association is one of the most stable and persistent on the archipelago. The islands' coastal areas, consisting generally of partially consolidated pyroclastic deposits emplaced during the 1883 eruption of Krakatau, are physically very susceptible to marine forces, resulting in substantial mobility of coastlines (see §2*a*), and it may be that this persistent dynamism is, paradoxically, responsible for the essential stability of plant associations that are specialized for such dynamic substrate conditions.

Rawlinson *et al.* (1990) believed the overall reduction in extent of beach associations was partly responsible (together with canopy closure, see below) for the loss of the coastal gecko *Lepidodactylus lugubris* from the islands. Apart from buildings, this gecko inhabits very open coastal habitats, rocks and the trunks and crowns of mangroves (there is not and has never been a mangrove association on the islands), palms and near-shore vegetation, although it has also been collected up to about 300 m altitude.

New *et al.* (1988) stressed the importance for butterfly colonization of the *Ipomoea pes-caprae* associations, now restricted to the few extant low-energy beaches, and although they did not suggest that a decline in butterfly diversity has been associated with the reduction in extent of such beaches, they registered concern for the butterfly fauna if the remaining beaches are modified by more intensive use for landing and recreational areas as a result of increased tourist activity.

There are a few cases in which two closely related (congeneric) species, or species with similar ecological requirements, have successfully colonized the islands and one has become extinct, the other persisting, often very successfully, to the 1980s. The fruit bats *Cynopterus sphinx* and *Cynopterus horsfieldii* were first recorded on the archipelago in 1919 and 1920, respectively, but whereas *C. sphinx* now occurs on all islands, having already colonized Anak Krakatau, *C. horsfieldii* has not been recorded in the 1980s. There are parallel cases in the birds. The lesser coucal, *Centropus bengalensis*, a bird of grassland and open country, had colonized the islands by 1908, the date of the first zoological survey, and the greater coucal, *Centropus sinensis*, which inhabits scrub, grassland and open woodland, was heard once on Sertung in 1919, when the lesser coucal was already present on at least Rakata and Sertung. The greater coucal has not been recorded since. Although the preferred habitats of the two species are closely similar, *C. sinensis* is less common on Java and Bali than *C. bengalensis* (MacKinnon 1988). Both the yellow-vented bulbul, *Pycnonotus goiavier*, and the sooty-headed bulbul, *Pycnonotus aurigaster*, occurred on Rakata by 1908. *P. aurigaster* frequents open woodland and forest edges – wooded, bushy habitats – and includes more fruit in its diet than *P. goiavier*, which is a bird of open country and scrub – more open habitats – and spends more time on the ground than other bulbuls, including worms, beetles and crickets in its diet (Zann *et al.* 1990*b*). The Krakataus' habitat in 1908 (savannah grassland with small patches of woodland) was more suited to *P. goiavier* than *P. aurigaster*, which did not persist. *P. aurigaster* was only ever encountered once, on Rakata in 1908 (Jacobson 1909); Dammerman (1948) did not regard it as having successfully colonized the islands. A third bulbul species, the olive-backed bulbul, *Pycnonotus plumosus*, was first recorded in 1951 (Hoogerwerf 1953*a*), on Rakata and Sertung, and persists on these two islands. *P. plumosus* is a bird of forest edges in well-wooded country, inhabiting the middle and upper canopy, and feeds on figs and berries as well as flies, caterpillars and beetles (MacKinnon 1988). Its habitat overlaps with *goiavier* less than does that of *P. aurigaster*. We suggest that *aurigaster* may have arrived too early (before forest development) for successful coexistence with *goiavier*; *plumosus* and *goiavier*, however, are now able to coexist. We postulated above that the small blue kingfisher, *A. caerulescens*, also arrived too early, before its preferred habitat (trees by forest streams) was even approached on the islands.

The most important successional changes so far as animals are concerned were the formation of forest and the closure of its canopy. 'Successional' extinctions, losses of species as a result of successional processes, include the long-tailed shrike, *Lanius schach*, a bird typical of open country and grassland, that became established before 1908 and was breeding on both Rakata and Sertung in 1919–20, but was not recorded in the surveys of 1928–34 when the forest canopy was closing, nor in any subsequent surveys. The peaceful dove, *Geopelia striata*, is another example. A ground seed eater, it was first recorded in 1919. By 1951 it was 'heard' on north Sertung (Hoogerwerf 1953*a*), one of the few areas of grassland persisting by that time, but was not recorded in the 1980s. The drastic reduction of open country habitat probably also accounts for the demise of the large-billed crow, *Corvus macrorhynchos*, which by 1951 was confined to north Sertung, and by 1984 one pair remained, on Anak Krakatau. The species was not encountered in our surveys of 1985 and 1986, a pair was seen on the island in 1988 by I.W.B.T. but the species was again absent in 1989 (K. Richards, personal communication). We believe this crow to be now on the verge of extinction from the archipelago. Its decline may have been partly responsible for the extinction of its nest parasite, the koel (*Eudynamys scolopacea*). The crow had become established before 1908, and the koel was first recorded in 1919, but declined in numbers after 1921 (Dammerman 1948). The koel was present in 1951 but was not seen or heard in our surveys of 1984, 1985 or 1986. The large-billed crow, however, is not the koel's only host. MacKinnon (1988) lists crows, orioles and drongos. No other crow species has become established on the archipelago, nor have drongos ever occurred there, but the black-naped oriole, *Oriolus chinensis*, was an early colonist like the crow, arriving before 1908; unlike the crow, the oriole has persisted well, having been recorded on all islands surveyed at every survey, and in the 1980s there were from two to seven pairs even on the small vegetated area of Anak Krakatau (Zann *et al.*, 1990*b*). Thus the large-billed crow's decline cannot be the only explanation for the loss of the koel, which, being a bird of dense forest, is likely to have been favoured rather than disadvantaged by the development of forest and closure of the canopy during the period (1919 to 1951 as a minimum) of its presence on the Krakataus.

Rawlinson *et al.* (1990) offer habitat reduction by vegetational succession and canopy closure (together with marine erosion, see above) as an explanation for the extinction of the gecko *Lepidodactylus lugubris*, which prefers open coastal habitats. Present on all three older islands from 1920 to 1934, it was absent in the 1980s.

Dammerman noted that several species of ants normally associated with grassland and found in large numbers by Jacobson in 1908, had greatly declined in numbers by the 1920s, for example species of *Crematogaster*, *Tetramorium*, *Plagiolepis* and *Tetraponera*. *Tetraponera rufonigra* was abundant on Rakata in 1908 (Jacobson 1909) and Dammerman found it common also on Sertung in the 1920s (Dammerman 1948); by the 1980s it was found only on Anak Krakatau (which still offers open habitats) and Panjang (Thornton & New 1988*b*). Similarly, sphecid wasps of the genera *Crabro*, *Larra* and *Tachytes* have never been collected since 1908, nor have several species of sapromyzid flies. Dammerman noticed that 11 out of the 19 species of fulgorid homopterans collected between 1919 and 1921 were not found on his later visits, the number of jassid species was halved over this period, and the density of ground-living tenebrionid beetles, which prefer dry to moist surface habitats, was greatly reduced (Dammerman 1948). The large, aggressive centipede *Scolopendra subspinipes* and a millipede of the genus *Spirostreptus*, which were both common in 1908, the *Scolopendra* being particularly noteworthy, had declined by 1920, and declined further by 1933, but the centipede still occurs on Rakata and Sertung (J. G. E. Lewis, personal communication).

The succession from grassland to forest of course had a great impact on the grass-feeding hesperiid Lepidoptera. There has been substantial extinction and turnover of hesperiids since the 1920s and 1930s, six species present from 1908 to 1934 were not found in the 1980s (Yukawa 1984*a*; New *et al.* 1988). Both extinction rate and extinction rate coefficient for butterflies were highest for the period of canopy closure (1919–34), the latter being over eight times that for other intersurvey periods (New *et al.* 1988).

Other extinctions probably come under the Whittaker *et al.* (1989) category of 'ephemerals': species that are likely never to have bred on the islands, and, strictly, should be excluded from colonization and turnover considerations. Examples among vertebrates are marine, shore and migrant birds; the 2.8 m long male estuarine crocodile, *Crocodylus porosus*, shot near the Sertung lake in 1924; the gecko *Cosymbotus platyurus*, obtained on Rakata only in 1928; and the cavernicolous microchiropteran *Hipposideros diadema*, one female of which was collected at 600 m on Rakata in 1928. Tidemann *et al.* (1990) pointed out that *H. diadema* (of which the identification has been checked) has not been recorded on the adjacent mainland in spite of three relatively thorough bat surveys in the 1980s, and believe that this specimen may have been a chance lone stray. Most of the 20 species of dragonfly that have been recorded on the islands (11 species in the 1980s) are ephemerals in the sense that they were unlikely to be breeding on the archipelago, and there are instances of wide-ranging butterfly species that lack appropriate food plants on the islands being recorded on but a single occasion (see above).

Apart from the koel, there remain but two vertebrate extinctions that cannot be explained in any of the ways outlined above: the crested goshawk, *Accipiter trivirgatus*, and the serpent eagle, *Spilornis cheela*. The goshawk, a bird of lowland and hill forest, was seen on the archipelago in 1920 and 1933, and has not been recorded in the 1980s. The serpent eagle is the commonest eagle over forested hills in Java (MacKinnon 1988), and was heard frequently over Sertung in 1951 by Hoogerwerf, but seen only once. However, it is described by MacKinnon as 'a very vocal eagle, frequently uttering a loud shrill cry', and the 1951 record may represent a single bird and thus be an 'ephemeral' in the sense of Whittaker *et al.* (1989).

(*f*) *Ecological refuges and windows*

We have suggested elsewhere (Thornton *et al.* 1988*c*; Thornton & New 1988*b*) that Anak Krakatau and the northern spit of Sertung may provide ecological refugia for open country species that would otherwise be doomed by vegetational succession to extinction from the islands. Whittaker *et al.* (1989) hypothesized that Anak Krakatau's volcanic activity, by interrupting successional processes on Panjang, similarly enhanced the persistence of the early pteridophyte flora on that island (table 6 of Whittaker *et al.*), although if this were so one might have expected the same on Sertung, which was at least similarly affected by Anak Krakatau's activity.

Sertung's spit is a highly mobile, ever-young feature, with a physical life of about a rolling decade or two (Rosengren 1985; Thornton & Rosengren 1988), and is held at an early stage of vegetational succession by its short period of physical turnover. Thus, like Anak Krakatau, it offers for animals stages of vegetational succession that are earlier and simpler than those present on the rest of Sertung, or on Panjang and Rakata. Winoto *et al.* (1988), for example, found 18 genera of soil nematodes on the spit, compared with 41 in the more complex soils of the adjacent mixed forest. The lycaenid butterfly *Catachrysops panormus*, found on Rakata in 1933, is now restricted to localized early seral stages of vegetation on the Sertung spit. A vespid and a sphecid wasp, *Ropalidia variegata* and *Bembix borrei*, and two scoliid wasps, *Campsomeris phalarata* and *Triscolea azurea*, all found on the other islands in the half century after 1883 (and all but the last species found in the first 25 years) are now confined to Anak Krakatau. The ant *Tetraponera rufonigra*, which was common on Rakata and Sertung in 1933, was found in the 1980s only in open sunny areas of Anak Krakatau. The peaceful dove, *G. striata*, had not been seen since the early 1920s, but was heard on the Sertung spit in 1951. It was not seen or heard in the 1980s: evidently in this case the refuge was inadequate. The large-billed crow, *C. macrorhynchos* (mentioned above), another open country bird, was recorded on every island surveyed from 1908 to 1934 but in 1951 was seen on the Sertung spit only. By 1984 only a single pair remained, on Anak Krakatau. In this case the refuges were more effective, but in all likelihood the crow is now on the verge of extinction. The white-breasted waterhen, *Amaurornis phoenicurus*, which frequents open scrub, is now confined to Anak Krakatau and the savannah nightjar, *Caprimulgus affinis*, a grassland, open-country inhabitant, is now rare except on that island.

As well as providing ecological refuges, these areas have also re-opened an ecological 'window', closed elsewhere on the archipelago by vegetational succession, for the immigration of species that missed the short grassland phase in the early 1900s. Seven out of the 10 owl species in the Sunda Strait area are forest birds. The barn owl, *Tyto alba*, normally frequents open coastal country and mangroves. It was seen in the 1980s at Owl Bay, Rakata, the Sertung spit, and on Anak Krakatau, and has evidently taken the opportunity afforded by the provision of open habitat to become established on the archipelago recently. Other open-country species to arrive in recent years, although not resulting in establishment, are the house crow, *Corvus splendens*, and the tiger shrike, *Lanius tigrinus*, which is a migrant. The ecological window, of course, also offers the possibility of 'ecological rescue' (in the sense of the 'rescue effect' of Brown and Kodric-Brown 1977) of animal species that may otherwise have become extinct as a result of declining populations because of vegetational succession. On balance, the effect of such successional asynchrony will reduce faunal turnover and delay the achievement of equilibrium on the archipelago (Thornton *et al.* 1988*c*).

3. Anak Krakatau

Anak Krakatau (figures 1 and 18) emerged in 1930 from Krakatau's sunken caldera. It erupts every few years and its destructive eruption in 1952 evidently extirpated its biota (Hoogerwerf 1953*a*; van Borssum-Waalkes 1954, 1960). There have been periodic eruptions since then, so that the island's biota was a maximum of 32–34 years old in 1984–86. The island is largely barren lava and ash; vegetation cover is confined to 14 ha† (5 % of the island's area), of which 5 ha is grassland. The northern foreland is largely *Imperata cylindrica* and *Saccharum spontaneum* grassland with clumps of *Casuarina equisetifolia*, *Ficus fulva*, *Ficus septica* and *Pandanus tectorius*. The eastern foreland, which was grassland as late as 1971 (photograph by Professor. K. Yoda in Tagawa 1984), by 1979 was a casuarina woodland, with the two species of fig, *Terminalia catappa*, *Pandanus*, *Melastoma affine* and *Hibiscus tiliaceus*. The two forelands are now connected by casuarina-dominated vegetation along the shore, extending about 100 m inland in places. Scattered clumps of *Saccharum* occur on the slopes of the outer ash cone, with occasional specimens of *Casuarina*. Sixty-six species of vascular plants were recorded in 1983 (Barker & Richards 1986) and a total of 82 between 1979 and 1983.

(*a*) *Analogy with the early biota of the three older islands*

Whittaker *et al.* (1989) took issue with suggestions by Dammerman (1948), Tagawa *et al.* (1985) and Thornton (1984*a*) that an analogy can be drawn between the biota of Anak Krakatau and that of the main islands in the early post-1883 period. Tagawa *et al.* (1985) incorporated the plant communities of Anak Krakatau as pioneer associations in their schema of vegetational succession on the archipelago. Whittaker and his co-workers contended that it is rash to draw such an analogy, citing 'such major environmental and ecological differences' as the poor representation of ferns in surveys of Anak Krakatau ('they have never been an important constituent of the vegetational cover'), the presence of close sources (the other islands), the volcanic activity of Anak Krakatau ('regularly noxious and spasmodically violent, and has caused repeated disruption of the developing vegetation cover...' '...history of disruption'), and the marine-deposited cuspate forelands ('atypical of the majority of the Krakatau group').

There is indeed no evidence of either an early blue-green alga phase or a subsequent fern phase (both seen on Rakata after 1883, but *not* seen to predominate to the same degree on Sertung or Panjang) on Anak Krakatau, but these were present on Rakata three years after

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† 1 hectare = 10^4 m^2.

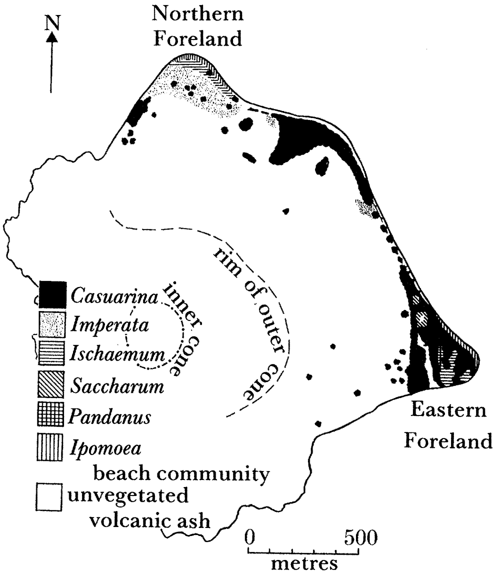

FIGURE 18. Anak Krakatau in 1986, showing major vegetation types in areas of more than 10% cover. The extent of scattered *Saccharum* clumps up the northern and eastern slopes of the outer cone may be seen in figure 1.

1883 (Treub 1888) and had been replaced by grassland except at high elevations 11 years later (Penzig 1902). Anak Krakatau was not surveyed for 22 years after emerging in 1930, and not for a further 26 years after its devastating 1952–53 eruptions. Absence of evidence is not evidence of absence, although it might be expected that had a fern cover developed on parts of Anak Krakatau, ferns would be better represented now on the island than they are. Eroded gullies, a prime habitat for ferns, are limited in extent on Anak Krakatau relative to the other islands, and are still being actively eroded.

Except for the 1930, 1933 and 1952 eruptions, the suggestion that activity of Anak Krakatau has affected the plant succession on the other islands rests entirely on the results of soil studies by Shinagawa *et al.* (1984). They found differences between the soils of Rakata and the other islands, those of Rakata being more advanced, with higher contents of organic matter, clay, free iron and aluminium hydroxides. Pedogenesis on Sertung and Panjang was found to be occurring in five or six layers of volcanic ash and scoria derived from Anak Krakatau, emplaced on top of the pyroclastic deposits of Krakatau's 1883 eruption. The thickness of the various layers varied between islands, for example, Sertung: scoria 6 cm, scoria 5 cm, lava fragments 10 cm, scoria 8 cm, scoria 12 cm, scoria 10 cm, A horizon 10 cm, fresh ash 10 cm; Panjang: lava fragments 21 cm, scoria 1 cm, scoria 1 cm, scoria 1 cm, scoria 1 cm, scoria 5 cm, ash 5 cm, A horizon 8 cm, fresh ash 2 cm. Obviously, the two islands have received different deposits as a result of Anak Krakatau's activity, but the evidence for the link with plant succession is indirect. Although in 1989 Whittaker and his colleagues found that most of Panjang and Sertung was covered with from one to two metres of post-1930 volcanic ash (R. J. Whittaker, *in litt.*), Anak Krakatau has surely suffered from its own activity more drastically than it has affected Panjang, for example. Its vegetation exhibits a classic interrupted succession, yet its flora in the 1980s was almost as rich as Panjang's (Whittaker *et al.* 1989), in spite of the vegetated area being only one sixteenth that of the older island.

The two main vegetated areas of Anak Krakatau in the 1980s were on the north and east cuspate forelands (figure 18), which are indeed largely of marine origin (Bird & Rosengren 1984), and the two have been out of successional synchrony for at least the past twenty years. Vegetation, however, is not confined to these areas; a coastal *Casuarina* woodland now links them. The evidence does not support the assertion that such marine-deposited forelands are atypical of the Krakataus. The northern spit of Sertung, for example, is certainly marine derived (Rosengren 1985). Moreover, an area of over 4.6 km^2 was added to Rakata's west, south and southeast coasts by pyroclastic deposits during the 1883 eruption (figure 1 of Verbeek 1885, surveyed in October 1883), and by 1919 much of the new area formed west of Zwarte Hoek had been removed and a large lobate beach foreland of longshore drift deposits had been built up south of what is now known as Handl's Bay (figure 1), with a marine-derived beach extending north of this for over a kilometre (plate 1 of Stehn 1929, from a map published by Escher). The erosion of western Rakata left pyroclastic-deposit cliff-stacks of unstratified tuff (presumably on lava basement) isolated from the island. Photograph 8 of Stehn (1929), taken either in 1922 or 1928, shows two stacks, an inner one about half the height of the main island's cliffs and close to them, and an adjacent outer smaller stack. By the 1980s the outermost small stack had been eroded to a sea break, the large one was still extant, and a third, larger stack was now the innermost and isolated by some 200 m of sea from the main island (figure 11 of Thornton & Rosengren (1988)). The lobate foreland south of Handl's Bay had become reduced to some 12 ha in area by the 1980s and supported a remnant of casuarina woodland (figure 2 of Bird & Rosengren (1984)). Escher's map also shows marine-deposited foreshore areas on north and northeast Panjang and southeast Sertung, as well as the then very extensive northern spit of Sertung. It seems likely that the pyroclastic-formed shores of the islands in the decades after 1883 would have been subjected to both marine erosion and subsequent marine accretion in much the same way as Anak Krakatau and northern Sertung are today, and the evidence supports rather than precludes the presence of earlier marine-deposited forelands.

As far as spermatophytes are concerned, the data provided by Whittaker *et al.* (1989) actually support the suggestion of a broad analogy between Anak Krakatau in the 1980s and the early vegetation stages of the three older islands. Of the 60 species of spermatophytes recorded from Rakata, Sertung and Panjang (Appendix I of Whittaker *et al.* 1989) that have also been recorded from Anak Krakatau (Appendix II of Whittaker *et al.* 1989), almost half (28 species) were presented on the archipelago by 1897, within 14 years of the 1883 eruption, and 48 species (80%) were recorded by 1908, within 25 years. Evidently the early colonizers of the older islands are predominantly the early colonizers of Anak Krakatau, albeit over much shorter distances.

Thornton & New (1988*b*) have shown (their table 8) that for various invertebrate groups the present size of the fauna of Anak Krakatau is similar to that of Rakata three or four decades after 1883. Also, Anak Krakatau's acquisition rate for resident land birds since 1952 is very similar to the rate for the other islands in the first four decades after 1883 (Thornton *et al.* 1990). Non-migrant non-marine birds have colonized Anak Krakatau at a rate of three species every 4 years (0.75 per year) since 1952 (25 species present in 1986), the same rate at which the other islands were colonized in the 38 years after the 1883 eruption (0.74 per year). Presumably the very much smaller area available for colonization on Anak Krakatau is balanced by the additional very much closer sources (the other islands). A substantial proportion of the species of several animal groups represented on Anak Krakatau by 1985

(33 years after its self-devastating eruption), had arrived on the archipelago 38 years after 1883 (table 3). Over 70% of Anak Krakatau's present resident land bird fauna is comprised of species that became established on the archipelago in the first fifty years after 1883 (20 of the 31 species established by that time). Whereas nine out of the 11 resident land bird species established on the islands 25 years after 1883 now occur on Anak Krakatau (and one of the two remaining became extinct on the archipelago before 1934), only four out of the 11 to arrive in the last half century occur on that island (Thornton *et al.* 1990, table 2). Of the frugivorous-insectivorous and obligatorily frugivorous birds that are important in the development of mixed forest, including fig species, three facultative frugivores (a crow, oriole and bulbul) and two obligatory frugivores (a pigeon and a cuckoo-dove) were recorded on the archipelago at the first survey, 25 years after 1883. These same 5 species constitute the only frugivorous birds yet recorded from Anak Krakatau (Zann *et al.* 1990*b*), the two obligatory frugivores having been recorded only since the island's two fig species first fruited. Moreover, Tidemann *et al.* (1990), who accepted the evidence of previous surveys that fruit bats arrived on the archipelago before insectivorous and carnivorous bats, found two species of fruit bats established on Anak Krakatau in 1985, but no insectivorous or carnivorous species. The two species now on Anak Krakatau were the first two of 14 species of bats to successfully colonize the islands; they were first recorded in 1919 and 1933, respectively 36 and 50 years after the 1883 eruption.

Colonization rate of most groups of invertebrates has also been in accord with the colonization of Rakata after 1883, although colonization of Anak Krakatau has been faster for aculeate Hymenoptera excluding ants, braconid Hymenoptera, Neuroptera, and land crabs

TABLE 3. NUMBER OF SPECIES IN ANIMAL GROUPS REPRESENTED ON ANAK KRAKATAU (AK) IN 1985 (33 YEARS AFTER 1952) THAT ALSO OCCURRED ON THE ARCHIPELAGO (KS) BY 1908 (25 YEARS AFTER 1883) AND 1921 (38 YEARS AFTER 1883).

(Percentages of the present AK fauna are in brackets. Sources as acknowledged in Thornton & New (1988*b*, table 7), Rawlinson *et al.* (1990), Thornton *et al.* (1990), and Tidemann *et al.* (1990).)

	A recorded on Ks by 1985	B present on AK 1985 (+33)	C B present on Ks by 1908 (+25)	D B present on Ks by 1921 (+38)
land molluscs	19	1	0	0
oniscidean Crustacea	11	2	0	0
Odonata	20	3	1 (33)	2 (67)
Orthoptera	51	10	0	4 (40)
Blattodea	24	6	0	3 (50)
Thysanoptera	39	5	?	2 (40)
Neuroptera	13	7	0	1 (14)
lauxaniid Diptera	10	5	0	0
Hesperiidae	10	2	0	1 (50)
Lycaenidae	24	9	0	3 (33)
Nymphalidae	21	7	2 (29)	5 (71)
Pieridae	5	3	0	2 (67)
Papilionidae	4	2	0	1 (50)
butterflies	64	23	2 (9)	12 (52)
braconid Hymenoptera	72	13	0	1 (8)
non-ant aculeate Hymenoptera	107	43	9 (21)	14 (33)
reptiles	13	3	2 (67)	2 (67)
resident land birds	42	24	9 (38)	17 (71)
bats	17	2	0	1 (50)

(Thornton & New 1988*b*). Some aculeate Hymenoptera are open site species, and Anak Krakatau and small areas of Sertung spit are the only parts of the archipelago on which such habitats now occur. The proximity of the other three surrounding islands is also undoubtedly a factor in the cases of accelerated colonization, particularly in land crabs.

We believe that although the analogy cannot be a precise one, it does have heuristic value, at least as far as animals are concerned, provided that the differences between the two situations are constantly borne in mind.

(*b*) *The role of animals in the development of mixed forest*

There has been a significant enrichment of forest species on Anak Krakatau from 1979 to 1984 (Whittaker *et al.* 1989); in table 4 we summarize the incidence of bird and/or bat dispersed plants that were not found until 1979, and of animals associated with them. Five forest trees first recorded on the island in 1983 include *Macaranga tanarius*, *Dysoxylum gaudichaudianum* and *Timonius compressicaulis*, which were important successional components of the other islands and are bat and bird (the first two) and bird dispersed (the last).

Philippine glossy starlings (*Aplonis panayensis*), known dispersers of *Macaranga*, were heard on the island in 1985 and 1986. Altogether, five (possibly six) of the archipelago's 11 species of frugivorous birds have been recorded from Anak Krakatau in the 1980s, and four of them were early colonists of Rakata. Apart from the starling, the Anak Krakatau frugivores include the omnivorous large-billed crow *C. macrorhynchos* (one pair 1984 and 1988) the facultative frugivores black-naped oriole *O. chinensis* (5–7 pairs 1985) and yellow-vented bulbul *P. goiavier* (15–20 pairs 1985), and two of the archipelago's six species of fruit-eating pigeons: the Sunda island cuckoo-dove *Macropygia phasianella* (one pair 1985, three individuals 1986) and the pink-necked pigeon *Treron vernans* (three individuals 1986). Zann *et al.* (1990*a*) believe the island's raptors, the hobby, the owl and the white-breasted sea eagle *Haliaeetus leucogaster*, have aborted several recent possible colonization events by fruit-eating birds (*T. vernans* and the green-winged pigeon *Chalcophaps indica*). These observations suggest that it is only recently that Anak Krakatau has provided sufficient fruit to support resident obligatory frugivorous pigeons.

Seeds of *Terminalia catappa*, another forest tree found on Anak Krakatau, in 1985 littered the floor of caves on Panjang occupied by the fruit bat *Cynopterus titthaecheilus* (Tidemann *et al.* 1990). The related *Cynopterus sphinx* has been on Anak Krakatau since 1982. It is likely that bats were more important than fruit-eating birds in the colonization of Anak Krakatau by another important component (both in number of species and individuals) of the archipelago's mixed forests: fig species.

The phenology of *Ficus* flowering and their unique pollination mechanism (requiring the presence of particular agaonid wasps, usually *Ficus* species specific) theoretically make the initial establishment of fig species on islands difficult (Compton *et al.* 1988), and yet they have successfully colonized tropical islands as remote as the Hawaiian archipelago. Because the larva of an agaonid develops only in the seeds of its particular fig species, and the fig species is pollinated only by its particular agaonid, the bond between plant and insect is absolute.

As discussed by Compton *et al.* (1988), for the establishment of viable island populations of figs, fig seeds must be dispersed to an island and when the resulting trees mature, agaonids (which must perforce also have come from elsewhere) must be present at the appropriate time for pollination. Since fruit production is generally synchronous within individual trees but asynchronous between trees, when there are only a few fig trees present their crops may be

TABLE 4. ROLE OF ANIMALS IN DEVELOPMENT OF MIXED FOREST FROM CASUARINA WOODLAND ON ANAK KRAKATAU 1979–86

(T, important forest tree; d, bird dispersed; t, bat dispersed; n.f., not fruiting; e/d figs, eating figs and defaecating fig seeds; s. net, sweep net capture; r. *F. fulva*, reared from syconia of *F. fulva*; w/p traps, water trap and pit trap captures.)

				1979	1982	1983	1984	1985	1986
td	*F. fulva* (T)		figs	n.f.	n.f.	n.f.	n.f.	fruit	fruit
td	*F. septica* (T)			n.f.	n.f.	n.f.	n.f.	fruit	fruit
t	*C. papaya*		other plants	—	—	✓	✓	✓	✓
td	*M. tanarius* (T)			—	—	✓	✓	✓	✓
td	*D. gaudichaudianum* (T)			—	—	✓	✓	✓	✓
d	*Melastoma affine*			✓	✓	✓	✓	✓	✓
td	*Passiflora foetida*			—	✓	✓	✓	✓	✓
d	*T. compressicaulis* (T)			—	✓	✓	✓	✓	✓
d	*Cayratia trifolia*			—	—	✓	✓	✓	✓
	C. sphinx		fruit bats	—	✓	✓	e/d figs	✓	✓
	R. amplexicaudatus			—	—	—	✓	✓	✓
	P. vampyrus			—	—	—	—	—	straggler
	C. bisulcatus (pollinator of *F. septica*)		agaonid fig pollinators; fig chalcids	—	—	—	s. net	✓	✓
	Blastophaga sp.			—	—	—	s. net	✓	✓
	Liporrhopalum sp.			—	—	—	s. net	✓	✓
	Platyscapa sp.			—	—	—	s. net	✓	✓
	Waterstoniella spp. (2)			—	—	—	—	s. net	✓
	B. inopinata			—	—	—	—	—	r. *F. fulva*
	D. macroptera – sycoecine fig seed predator			—	—	—	—	w/p traps	✓
	P. grandii		torymid inquilines	—	—	—	—	—	r. *F. fulva*
	Sycoryctes sp.			—	—	—	—	—	r. *F. fulva*
	O. chinensis	oriole	facultative frugivores		✓	✓	✓	✓	✓
	P. goiavier	bulbul			✓	✓	✓	✓	✓
	C. macrorhynchos	crow			—	—	1 pair	—	—
	A. panayensis	starling			—	—	✓	✓	?
	M. phasianella	cuckoo dove	obligatory frugivores		—	—	—	1 pair	1 pair +
	T. vernans	pigeon			—	—	—	—	1 pair +
	Z. interpres –	thrush	deep forest bird		—	—	—	—	1 individual

separated by intervals greater than the lifespan of adult fig-wasps (a few days), so that individual trees cannot support their own population of agaonids. In this situation, dependence on immigrant agaonid pollinators will continue until a critical population size of figs is reached and a resident population of agaonids is supportable. The attainment of this critical population size depends on further successful dispersal of fig seeds. Thus for successful establishment of a fig population the dispersal of seed is first necessary, then the dispersal of agaonids, but both these processes must be extended beyond the initial event. Our opportunity to monitor the colonization of Anak Krakatau by figs broadly supports Janzen's (1979) prediction that island colonization by figs is likely to occur by extension of a mainland fig-seed shadow through the agency of fruit pigeons or bats, followed by colonization of agaonids.

Both fig species (*Ficus fulva* and *Ficus septica*) present on Anak Krakatau occur on the other islands, and both are known to be dispersed by bats (Van der Pijl 1957). They were not fruiting on Anak Krakatau in 1979, 1982, 1983 or 1984. Bats were first seen on Anak Krakatau in 1982 (Tagawa 1984); they were fruit bats, probably *Cynopterus sphinx angulatus* (short-nosed fruit bat), of which 40 individuals were captured by us in one night's trapping on the island in 1984. This species was present also in 1985 and 1986. In 1984 the bats were spitting out and defaecating fig seeds, although the few figs on Anak Krakatau were not fruiting. *C. sphinx* was evidently roosting on Anak Krakatau but using the other islands as feeding sites. Individuals of the same species captured on Rakata were carrying whole fruit in their claws, and other *Cynopterus* species have been seen carrying figs to feeding roosts (Ridley 1930). Osmaston (1965) reports bats dropping figs hundreds of metres from feeding sites, and the central position of Anak Krakatau in the archipelago, 2–4 km from the other islands, means that it could be used as a staging post for a number of inter-island routes. Tidemann *et al.* (1990) report the finding of *Ficus* seeds in several places on areas of bare lava on Anak Krakatau, showing that bats move over these areas in their journeys, and our tents, pitched in casuarina woodland on Anak Krakatau, were stained with bat excrement containing fig seeds at the end of the 1985 expedition.

In 1985 fruit was collected from both the *Ficus* species, but no agaonids could be found within the fruit. In 1986 another fruit bat, *Rousettus amplexicaudatus*, Geoffroy's rousette, was collected on the island (it was recorded on Panjang as early as 1933 and occurs also on Rakata and Sertung). It was not found there in the two previous years in spite of fairly extensive trapping and netting. Excreta of this species in Panjang caves contained many fig seeds (Tidemann *et al.* 1990). A camp of several hundred *Pteropus vampyrus* (large flying fox) was discovered on north Sertung in 1985, but was not there the following year, when a single individual was seen on Anak Krakatau's east foreland, although in 1989 the colony was again present on north Sertung (K. Richards, personal communication). Tidemann and colleagues believe that pteropodid bats probably move freely between the islands, and perhaps the mainland, to feed, and may change their feeding locations in response to availability of food.

The fig species on Rakata and Sertung at least, are supporting fig-wasp faunas that are comparable to those on the mainland; pollinating agaonids and inquiline torymids were present in figs from four species from those islands in 1983 (Compton *et al.* 1988). In 1984, before Anak Krakatau's fig trees first fruited, four species of agaonids, including *Ceratosolen bisulcatus*, the pollinator of *F. septica* (first collected on the archipelago in 1922), were captured by sweep-net in Anak Krakatau's vegetation, and further species were collected there the next year. Also in 1985, two individuals of *Diaziella macroptera*, a sycoenine fig-chalcid that is a seed predator rather than a pollinator, were captured in water traps on the barren ash-lava fields of western Anak Krakatau a kilometre from the nearest vegetation and separated from it by the volcanic cone. One individual of this species was found in a pit-trap on the barren eastern rim of the outer cone. We believe the 1984 *C. bisulcatus* specimens, and probably the *D. macroptera* specimens caught in 1985, were carried to Anak Krakatau as wind-borne fall-out, which we showed by water-trap studies on the island in 1986 (Thornton *et al.* 1988*a*) is considerable and must provide a regular income of living agaonids. Although in 1985 we could not obtain emergence of pollinators from the syconia of Anak Krakatau's figs, in the following year we succeeded; an agaonid (*Blastophaga inopinata*) and two inquiline torymids were reared from figs of *F. fulva*, and fig-wasps were also found in figs of *F. septica*.

Fig-wasp communities have thus already become established on the island, and agaonids are arriving, so pollination rates should improve. Fruit bat and pigeon populations are also now present, and the scene is set for the arrival of further fig species and an acceleration of the change from casuarina-dominated woodland to mixed forest (table 4).

(*c*) *The ash-lava aeolian ecosystem: a conduit for an extra-island energy source*

The extensive barren ash and lava fields that make up over 80 % of Anak Krakatau's surface are by no means an ecological desert. Thornton *et al.* (1988*a*) showed that aerial wind-borne fall-out in these areas was considerable. Living fall-out, and insects swept up to the crater area and rim of the outer cone by air currents, were preyed upon in the 1980s by a number of aerial insectivores including three species of dragonflies, the swallows *Hirundo rustica* and *Hirundo tahitica*, the house swift *Apus affinis* and the edible-nest swiftlet *Collocallia fuciphaga*. In this barren habitat these birds are themselves exposed to predation by the oriental hobby, *Falco severus* (Zann *et al.* 1990*a*, *b*).

On the surface, the fall-out was exploited by a guild of species, including earwigs, lycosid spiders and mantids, and dominated by a nocturnal, cryptic, flightless cricket (*Speonemobius* sp.) of the tribe Nemobiini that seems to be a specialist in this habitat (New & Thornton 1988). The cricket was breeding on the ash-lava, was not trapped or seen in vegetated areas, and was shown to be feeding on (presumably wind-borne) arthropods.

Such aeolian ecosystems have been known for some time (Mani 1962; Swan 1963; Edwards 1987) above the vascular plant line at high altitudes and latitudes. Their existence on new volcanic substrates (*a'a* lava) was first noted on Mount Etna in Sicily, by Wurmli (1974), and a salticid spider that he found exploiting allochthonous wind-borne prey may be restricted to these lava flows. Howarth (1979) subsequently found a community that is closely paralleled by that on Anak Krakatau, on unvegetated *pahoehoe* lava flows near Kilauea volcano, Hawaii, at about 1000 m elevation. An apterous nemobiine cricket, *Caconemobius fori*, which is also cryptic and nocturnal, dominated this community. The cricket was not found in adjacent vegetated areas, and appeared to be confined to new flows. The Kilauea community also included a fairly abundant lycosid spider, and an exotic earwig and mantis.

Ashmole & Ashmole (1988) have recently reported more diverse, evidently less specialized arthropod communities supported by aerial fall-out on recent lava flows in the Canary Islands. On the high-altitude almost barren flows of Tenerife a lepismatid thysanuran, *Ctenolepisma* sp. was dominant, with an opilionid, dermapteran, lithobiid chilopods, a cricket, a reduviid, a collembolan, and spiders of seven families making up the community. The low altitude flows of Lanzarote, some of which had many lichens, supported communities dominated by either an entomobryid collembolan (in one case an *Entomobrya* species, in another a *Seira* species) or a melyrid beetle. These communities also included a thysanuran, two species of cricket, a possibly exotic *Porcellio*, and spiders of three families. The communities on Tenerife were themselves exploited by a mimetid spider (a spider predator), possibly a phorid dipteran whose larvae feed on spider eggs, a pipit and lizards.

Howarth notes that barren lava habitat has been available for colonization on Hawaii island for about 700000 years. Specialization for the exploitation of fall-out in this habitat probably has an even longer history in the Hawaiian Archipelago, encompassing a long succession of islands at this geological hot spot. Thornton (1984*b*) showed that the physical life of islands and the time intervals between their emergences were such as to permit the transfer of Hawaiian forest insect faunas from island to island for over 70 million years; the constraints are greater of course in the case of a fauna confined to unvegetated lava, but the coexistence of extensive barren areas on Haleakala, Maui, with those on Hawaii, shows that such transfer could be possible, although perhaps not encompassing as many links as could the transfer of components of a forest fauna.

Volcanic activity in the Sunda arc has been extensive and long-lasting, and although it is not surprising that such a specialist community has also evolved there, the close parallels with the Hawaiian community are remarkable. In the case of Anak Krakatau the system could have provided, in the last few decades, a conduit for energy flow from outside the island itself, without the necessity for the prior colonization of the substrate by plants.

4. The future

Our studies on Krakatau, together with those of other workers cited in this paper, have helped to indicate how complex tropical terrestrial communities may develop, either from land completely sterilized by volcanic activity or (in the case of Anak Krakatau) from land which has not itself existed until recently. Within the bounds of sampling adequacy, intensity, and methods employed there are parallels between Anak Krakatau over the past 30 years and faunal development on the older islands in the years after 1883. Some anomalies must remain as such: we are unable to examine in retrospect some critical stages of colonization, and loss of some specimens from earlier surveys (especially of some invertebrates) ensures that their specific identity remains doubtful. The data for vertebrates are more robust, although there are doubts over the timing and extent of colonization by microchiroptera. We have seen some critical stages in community integration occurring on Anak Krakatau during the past few years, and the extent of overlap with the taxa present in earlier colonization of the older islands is sometimes substantial.

If the system remains on its present course, Tagawa *et al.* (1985) predicted that the *Timonius* forests on Sertung and Panjang, the *Neonauclea* forests on Rakata, and the mixed forests of the archipelago will progressively change to *Dysoxylum* forest, and in 1989 R. J. Whittaker (personal communication) found evidence of this change in Rakata's lowland forests. Whittaker *et al.* (1989), however, believed that the flora of Rakata, Panjang, and higher more stable parts of Sertung will increase in complexity and floristic diversity. Whichever occurs, environments will be provided for a range of animal taxa that cannot colonize these islands at present. The animal-dispersed component of the flora was the slowest to colonize but has suffered a very low rate of losses and shows the highest rate of increase in numbers since 1934

(Whittaker *et al.* 1989). Animals have been of great importance in the natural afforestation process, all forest types except the *Neonauclea* forest on Rakata being dominated by zoochorous species. As the number of species of frugivorous vertebrates increases, plant species attractive to birds and fruit bats will play an important role, through positive feedback, in the continued diversification of inland forest. Diversification may also be fostered by the effects of Anak Krakatau's continuing activity, as Whittaker's group believe has occurred already on Sertung and Panjang.

In the (most unlikely) absence of further eruptions, the flora of Anak Krakatau may move progressively, according to the scheme of Tagawa *et al.* (1985) through *Casuarina* forest towards *Terminalia* and mixed forest, present now in some coastal and inland areas of the older islands, thence possibly to *Timonius* or *Neonauclea* forest, and in due course the islands may converge further as the *Dysoxylum* forest climax phase is approached. Whittaker *et al.* (1989), however, believe this is unlikely; they believe that Anak Krakatau's ash substrate differs from the post-1883 ash cover in ways that make it less conducive to plant colonization, and do not attempt to predict, even implicitly, a future vegetational succession in the absence of further activity.

The future development of Anak Krakatau's entire biota, which is in a state of intermittently interrupted succession, is indeed difficult to predict. At its present stage of development, the major communities are highly vulnerable. Although another 1883-type eruption appears unlikely for some time (Newhall *et al.* 1985), regular eruptions of Anak Krakatau are likely to have at least transient effects on the biota. Another eruption of the intensity of that in 1952 may not only affect the biota of the older islands, but also set back that of Anak Krakatau itself again to a zero base-line, thereby providing an opportunity to monitor the resulting renewed primary xerosere.

Lowland regions of the archipelago are also subject to considerable physical change: we have earlier stressed the transient nature of the Sertung spit and the physical dynamism of the shoreline of Anak Krakatau, but Zwarte Hoek (Rakata) had undergone massive physical transformation between our visits in 1984 and 1986.

Superimposed on the effects of physical dynamism and probable periodic eruptions is the effect of encroaching and intensifying human activity. Although valued as a National Park, the archipelago receives many visitors not all of whose attitudes are clearly environmentally sensitive. Visitors comprise three major categories: tourists, including increasing numbers from overseas lured by increasing publicity for the Krakataus, local fishermen and scientists. Tourist visits are concentrated on Anak Krakatau and some of the more accessible beaches of southern Rakata and the Sertung spit, and many are for only a few hours. Some tourists camp on the beaches for 1–3 nights, and most attempt to ascend at least the outer rim of Anak Krakatau. Fishermen habitually shelter on the islands and have considerable potential to introduce other animals, ranging from geckos and arthropods usually present on boats, to rats and even domestic fowl, pigs and other domestic animals. The establishment in 1986 of a P.H.P.A. conservation post on Sertung should reduce the chances of accidental wildfires being started by visitors and provide some control over the extent of sampling by scientists, but it will also lead to intensification of human activity on the islands, and inadvertent contamination may increase. The beach sites favoured for tourist visits are, unfortunately, close to some of the most interesting, sensitive and vulnerable areas of the archipelago, the east foreland of Anak Krakatau and the Sertung spit, and Genolagani's (1985) implication that these will become the focus of increased tourism is viewed with concern. A balance needs to be struck between the permanent presence of P.H.P.A. personnel with the attendant risks, and the effective control of the activities of visitors. Unless this is achieved it is possible that future faunal surveys will reveal progressively greater effects of human intrusion rather than of a truly 'natural' process, and the time for monitoring pristine natural colonization processes, in particular of Anak Krakatau, may have already passed.

We again thank our main supporters, the Australian Research Grants Committee, the *Australian Geographic* magazine, CRA Pty Ltd, the Ian Potter Foundation, the Melbourne *Age*, the Melbourne public, and La Trobe University. We also gratefully acknowledge the assistance of many taxonomic specialists in invertebrate groups (noted in table 7 of Thornton & New (1988*b*)) and the 37 other participants in our 1984, 1985 and 1986 expeditions. Permission to work in this National Park was granted by L.I.P.I. (Indonesian Institute of Sciences) and P.H.P.A. (Indonesian Directorate-General of Forest Protection and Nature Conservation). We also thank Mrs J. Browning, Ms J. Cheah and Mrs T. Carpenter for their technical and clerical support in producing this series of papers.

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