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KRAKATAU INVERTEBRATES: THE 1980s FAUNA IN THE CONTEXT OF A CENTURY OF RECOLONIZATION

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CONTENTS

The results of surveys made of the invertebrate fauna of the Krakatau Islands in the 1980s, about 100 years since Krakatau's destructive eruption, are reviewed in the context of earlier surveys, and as a reference for future work on the islands as colonization continues.

The possibility of invertebrates surviving the 1883 eruption is discussed and, on balance, rejected. Dispersal modes of invertebrate groups are related to their archipelagic distributions; prerequisites for successful establishment and the sequence of colonization are discussed.

The present fauna of the young island of Anak Krakatau (emerged 1930) is discussed in relation to records of recolonization of the three older islands in the first fifty years after 1883.

We identify three early pioneer animal communities that exploit energy sources outside the island system and thus are able to establish themselves before plants have successfully colonized.

Invertebrate groups are at differing stages on the route towards an equilibrium number of species, and ecological changes involved in equilibration of the fauna as a whole should be the subject of future studies.

Introduction

In this paper we attempt to give an overview of the invertebrate fauna of the Krakatau islands based on the results of recent expeditions, in the general context of a century of recolonization of Rakata, Sertung and Panjang since Krakatau's 1883 explosive eruption, and the colonization of Anak Krakatau, the fourth island of the archipelago, since its emergence from the sea in 1930 (figure 1).

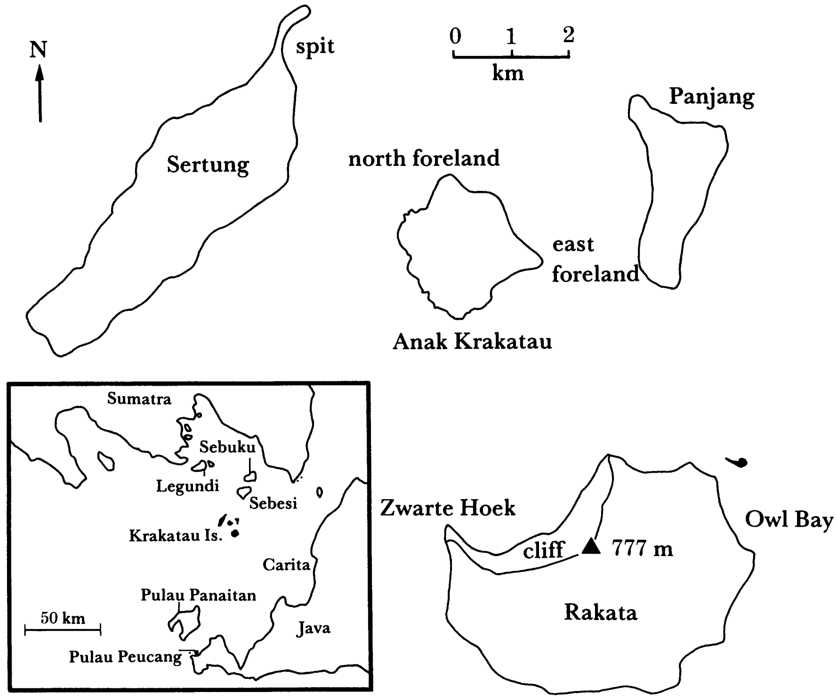

Figure 1. Krakatau Islands in the 1980s.

Such a synthesis must necessarily suffer from several shortcomings. As a result of our collections many groups are known to be very diverse on the islands but they have not yet been fully appraised by specialists. Important examples include Coleoptera, Diptera, Hemiptera and ants. For some non-insect groups, such as spiders and nematodes, even initial examination based on rather few samples has revealed very high numbers of taxa. The 78 genera of soil-dwelling nematodes recorded by Winoto *et al.* (1988), for example, were from samples which are likely to be representative rather than comprehensive.

Some of the better-known groups (that is, those examined by taxonomists during the past few years) must be considered in the context of inadequate or no earlier records of their incidence on the islands, although it is virtually certain that they were present there at the time of earlier surveys. These include land isopods, pseudoscorpions, Collembola, Psocoptera and chalcidoid wasps. Thornton *et al.* (1988*b*) note, for example, that the 80 species of Psocoptera recorded from the islands for the first time in the 1980s are highly unlikely to be all recent colonists. Together with many other groups of small and inconspicuous animals, they are likely to have been overlooked during earlier surveys for two main reasons: (1) the lack of specialist interest and consequently (2) lack of specialized or selective collecting techniques. The case of land crabs is somewhat exceptional in this regard. Only three species have been recorded earlier

(Dammerman 1948), over 50 years ago. Two are estuarine forms that were present when brackish lagoons existed on Sertung. There are now 11 species present (Morgan 1988), and it is almost inconceivable that some of the larger of these, which, unlike the groups mentioned above, are fairly large, active, intrusive animals, would not have been collected or recorded by Dammerman's expeditions. It is thus likely that several species of terrestrial crab have become established in the past half century. For some invertebrate groups, such as land isopods, substantial material was collected on earlier surveys but identifications were simply not completed, a fate all too common for much important expedition material. Dammerman (1948), in his invaluable compendium of the fauna, and also Jacobson (1909) noted that some collections from the earlier surveys were lost, spiders having suffered particularly in this regard.

The problems of inter-survey comparisons are discussed briefly by Thornton & Rosengren (1988). They include differences in (1) degrees of attention to the same animal groups in successive surveys; (2) duration of surveys; (3) sites surveyed; and (4) numbers and bias of participating scientists, these together influencing 'collecting intensity'. Dammerman (1948) commented that Jacobson's 1908 survey was less extensive than his own first group of surveys (1919–24), and some of the techniques Dammerman employed (light trapping, soil and litter extraction) had not been used earlier on the Krakataus. Moreover, some of the methods employed in the 1980s, for example Malaise traps, water traps, pitfall traps, and lures, were probably not used previously. For most groups of invertebrates, therefore, the rigorous data needed to assess such ecologically informative parameters as colonization and turnover rates are simply not available and a major value of our own team's work is to provide relatively sound 'baseline' information for a wide range of groups, to be appraised in relation to the results of future expeditions.

However, several groups of invertebrates do lend themselves to constructive discussion at present. They include land molluscs and a range of arthropod groups, predominantly those containing taxonomically tractable forms and including some in which our results complement those of the 1982 Japanese expedition (Tagawa 1984). In the cases of Odonata, Blattodea, Isoptera, Thysanoptera, Neuroptera, butterflies and some aculeate Hymenoptera, productive comparison with earlier data is feasible.

In this overview, where existing data make it possible, we consider the colonization of the islands by invertebrates from the point of view of dispersal, establishment, archipelago distribution, turnover and approach to equilibrium. The situation on Anak Krakatau, which emerged from the sea in 1930, is considered separately.

Survival from the 1883 eruptions

The question of whether or not any of the Krakatau biota could have survived the 1883 volcanic events (Thornton & Rosengren 1988) to provide a foundation for a renewed biota which developed into the present one has been discussed by several authors. Most notable are the contributions of Jacobson (1909), Michaelson (1924), Scharff (1925), Backer (1929), Bristowe (1931), Ernst (1934), Doctors van Leeuwen (1936) Dammerman (1948), Richards (1952) and Richards (1982). Controversy was at its height in the 1920s and 1930s (Anon. 1929; Turrill 1935; van Steenis 1930, 1938).

Authors proposing survival of animals after Krakatau's 1883 eruption, like Backer, the chief proponent of incomplete biological sterilization, have relied on the possibility of survival below the soil surface. Scharff (1925), for example, maintained that earthworms deep in the soil could have survived the eruption and hot ash deposition in 1883, and Michaelson (1924), believing *Pheretima dammermani*, which was common in the first 'Dammerman period' (1919–24), to be a Krakataus endemic, considered that it was a survivor. This species, however, will soon be synonymized by Easton with a widespread Indonesian species found also in Sumatra, Enggano island, and Java (E. G. Easton, personal communication). Jacobson (1909) searched, without success, for earthworms in soil in 1908, and emphasized their absence in soil on Rakata, although he found an immature specimen of a *Pheretima* species in a decayed tree trunk. Dammerman (1948) found earthworms 'plentiful' (two species) on Rakata in 1921, and a third species was found on that island in 1933. However, 'after having made a minute study of the soil fauna' he found none on Sertung.

Dammerman, who did not mention Backer's paper, pointed out that four (actually five, von Martens (1867)) land mollusc species known to have been present on the archipelago before the eruption, all fairly large and two 'even very large and conspicuous', had not been collected since. Strubell, a malacologist, worked on the archipelago six years after the eruption but found no true land molluscs. The pre-1883 species have still not been found on the islands, although 19 other species have been recorded (Smith & Djajasasmita 1988).

Scharff (1925) also believed that insect larvae in soil could have survived, as well as adult insects, spiders and snails, sheltering in crevices.

Like his botanical counterpart Docters van Leeuwen (1936), Dammerman was an advocate of the theory of biological sterilization, at least so far as the macrofauna was concerned, and noted that insects with subterranean larvae comprise the very groups that were absent in 1908 and in some cases the 1920s or 1930s. He cited tiger beetles (Cicindelidae), six species of which occur on Sebesi Island, some 12 km to the north (figure 1), and cockchafers (Melolonthidae) of which there is a species on Sebesi. Neither group was found during the 1908 or 1919 to 1924 investigations, and it was not until 1933 that a cicindelid was found on each of Sertung and Panjang (both species occurring on Sebesi). One of the most numerous large insects now on the islands is the large green cicada, *Dundubia rufivena*, conspicuous by its morning and evening song and habit of coming to light; the larvae live in the soil feeding on shallow plant roots. Jacobson did not record the species in 1908, although Dammerman found it common in 1921: it seems unlikely that *D. rufivena* would have escaped notice had it been present earlier.

Dammerman (1948) stated that soil nematodes can withstand a temperature of 80 °C, and Winoto *et al.* (1988) noting the dearth of information on lethal conditions and vertical distribution of soil nematodes, and soil temperature gradients at the time of the 1883 eruption, believe that their survival must be treated as a possibility. Thus they note that the biogeographical significance of the Krakataus may be limited as far as soil nematodes are concerned. A diverse fauna of 78 genera is present, representing 8 orders and including parasites of higher plants and fungi, microbivores, saprophages and predacious forms. Winoto and his co-workers cite *Geomonhystera*, a genus with the capability of cryptobiosis and survival of environmental extremes, and *Eudorylaimus*, which has a diverse diet including blue-green algae, Protozoa and fungi and has been found in a wide variety of habitats, as possible survivors. However, the distribution of *Geomonhystera* on the islands (Sertung spit and Owl Bay, Rakata) (figure 1) coincides with the sites of occasional fishing camps; it was not found, for example, in the mid-level mixed forest or summit forest of Rakata, nor on Panjang, which is little visited by fishermen. *Eudorylaimus*, the other possible survivor, occurs on Anak Krakatau, which carries only a quarter of the Krakatau species, and where survival of the 1883 event is impossible, the island having emerged only in 1930. It was found on the beach. Thus the distributional data for *Geomonhystera* and *Eudorylaimus* do not support the hypothesis of post-1883 survival, and the possibility of post-eruption immigration or introduction or both must be considered at least as strong.

A week after Anak Krakatau's month-long activity in August 1930, Dammerman (1937) examined the surface of a 4 km wide region of Sertung that was covered with volcanic ash. Trees (except *Casuarina*) had been stripped of leaves, and the lower undergrowth largely destroyed. In the devastated forest the effect of this volcanic activity, very much less than that in 1883, was remarkable. Only 12 species (average seven species per square metre sample) made up the surface fauna, whereas in the unaffected mixed forest there was double this number, and in unaffected *Casuarina* forest 20 species per square metre. Spiders, pseudoscorpions, hemipterans, ground molluscs, myriapods, earwigs, and staphylinid and tenebrionid beetles were found in unaffected areas, but were absent from the area covered by ash. Anak Krakatau erupted again for six weeks in November and December 1933, and on that occasion the prevailing west monsoon carried the ash to Panjang, rather than to Sertung, where the vegetation had by then recovered. Dammerman's group visited Panjang eight days after the activity ceased; trees were leafless and a layer of ash 1 cm thick covered the area. Winged insects like butterflies, flies and wasps, plentiful on previous visits, were absent, as of course were exposed larvae like caterpillars, and *Dundubia rufivena* was very much rarer than usual. As on Sertung after the 1930 eruption, ants and termites were recorded. Thus Dammerman showed that Anak Krakatau's eruptions, resulting in ash deposits hundreds of times shallower than those emplaced as a result of the 1883 event, had a significant effect on the litter fauna of Sertung and Panjang in areas where the ash was deposited.

One of the themes of Dammerman's (1948) monograph is the sequence of first records of animals on the Krakataus after 1883 according to their feeding habits. He convincingly demonstrated that in general the sequence was: scavengers and carrion feeders; omnivores; phytophagous species; carnivores and parasites (with the exception of spiders, which appeared earlier in the sequence). If survival was the result of physical habitat preferences, then the generally relatively late appearance of carnivores, for example, is not explained. The sequence of appearance of the animal groups is only explicable on the basis of recolonization after extirpation on the islands. Similarly, another of Dammerman's themes, the preponderance of species (over 90%) which can either fly or be transported by air (and the lack, for example, of mygalomorph spiders, of doryline ants in which the females are always apterous, and of apterous or brachypterous tenebrionid beetles) is explicable only in the context of recolonization after destruction of the biota.

Thornton & Rosengren (1988), however, report the finding in 1985 on Rakata of an exposure of incompletely carbonized logs up to 30 cm in diameter below a 10 m thick layer of what appeared to be undisturbed 1883 pumice deposits. If this find was indeed of pre-1883 timber, then the question of animals surviving deep in the logs, albeit buried in thick volcanic deposits, must at least be left open, although their long-term survival without further food is unlikely.

In spite of the 1985 discovery, we believe that the weight of evidence supports the hypothesis of total destruction, at least of the macrobiota, in 1883. Fisher & Schmincke (1984) discuss

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

measured temperatures of pyroclastic flows, which conserve heat very well. They cite emplacement temperatures of 1980 pyroclastic flow deposits at Mount St Helens ranging from 750 to 850 °C, and temperatures of from 500 to 600 °C at depths of from 3 to 5 m in a flow at St Augustine volcano, Alaska, a few weeks after emplacement. They state that if deposits are several metres thick, high temperatures can persist in the interior for several years; fumarole temperatures in poorly welded ash deposits in the Valley of Ten Thousand Smokes, Alaska, were as high as 645 °C seven years after emplacement. Professor Noboru Oba of Kagoshima University, Japan, estimates (*in litt.*) that the surface of the Krakataus in the 1883 eruption would have been subjected to temperatures of 'from 300° to 850 °C, and that these temperatures would have been maintained for several years at least'. Sudradjat & Siswowidjojo (1987) report that in 1984 a pyroclastic flow from Mt Merapi, central Java, covering 60 km^2 had a temperature of 225 °C 6.5 km from the source.

Dispersal

Many land molluscs and insects known to be common on Java and Sumatra have not yet colonized the Krakataus. Colonization involves both the arrival of viable propagules and their subsequent successful establishment. Failure of species present in the source areas to colonize the Krakataus therefore may involve failure to disperse successfully, or failure to become established after dispersal. The barrier to dispersal for land organisms is obvious, 35–44 km of seawater, and this may be overcome in several ways: by hydrochorous dispersal (swimming, floating on the surface, or being carried on something that floats: rafting); by anemochorous means (flying, being carried in the air, or being carried on something that flies or is air-borne); and by being brought to the islands through the activities of humans. Many organisms can be dispersed by several of the above methods, but the likelihood of any one rather than others varies from group to group.

The beaches of the Krakataus are littered with flotsam (and jetsam) today, as they were in 1908 (Jacobson 1909), particularly with logs, pumice and human debris. Pumice has been suggested by McBirney & Williams (1968) as capable of carrying propagules over large distances. While on Anak Krakatau in August 1986, we found a freshly beached mass of vegetation, some 20 m^2 in area, which included palms 3–4 m high with green foliage, on the southern beach of the east foreland (Thornton 1987). A larger mass of floating vegetation has been recorded as floating for as far as 1000 nautical miles (*ca.* 1800 km) in the north Atlantic (Powers 1911). Although some vicariance biogeographers have recently attempted to ridicule the idea of rafting as a means of long-distance dispersal, there is no doubt that on the Krakataus beached natural rafts are commonplace and must be considered as viable vehicles for the passage of at least some animal groups to the islands.

The patterns of distribution of land molluscs within the Krakatau archipelago suggest that litter inhabitants are better dispersers than arboreal species over the relatively short inter-island distances of up to 6 km (table 1).

Nine of the 12 litter species of mollusc on the Krakataus occur on more than one of the islands, five occurring on three islands, whereas only two of the seven arboreal species occur on more than one island and none occurs on more than two. Smith & Djajasasmita (1988) suggest that this implies that rafting is a more effective dispersal mechanism than air currents. Implicit in this suggestion is the generally accepted assumption that litter species are more likely to be

Table 1. Archipelago distribution of Krakatau land molluscs, by habitat

number of species	arboreal	litter
confined to 1 island	5 (71%)	3 (25%)
on 2 islands	2 (29%)	3 (25%)
on 3 islands	0	5 (42%)
on 4 islands	0	1 (8%)
total	7	12

surface-dispersed than those inhabiting trees, and arboreal species the more likely to be wind-borne. Dammerman, however, noted that *Amphidromus porcellanus*, the only true tree snail present in the period 1908–34, and the only land snail to be recorded in 1908, is well adapted for rafting. It belongs to a group that produces a hardening secretion at the mouth of the shell, attaching it extremely firmly to the surface of bark. To assess the relative efficacy of these methods of dispersal over the 35 and 44 km of sea separating the archipelago from Sumatra and Java respectively, one would need to know whether the proportion of litter to tree-inhabiting species in the source areas differs significantly from the 12:7 ratio found on the islands. This information is not yet available, although similar data are available for an insect order containing ground nesters and arboreal-nesting taxa, the Isoptera (termites).

Abe (1984) concluded that rafting was more important than aerial dispersal in the colonization of the archipelago from the mainland by termites. Eight of the 21 species found on the west coast of Java nest under or on the surface of the soil, but none of the Krakataus' species are subterranean or epigeous. All are wood or tree nesters (table 2). The first termite to be found on Anak Krakatau, *Nasutitermes matangensis*, was first discovered there in 1963 (not, as Roonwal states, in 1949) 11 years after its destructive eruption; it is an arboreal nester, and colonies were found in two driftwood logs near the shore (Roonwal 1969). On one of the logs the nest was 'found attached to the head of the trunk'. One colony of *Glyptotermes caudomunitus* and two of a *Prorhinotermes* species were found, again in driftwood near the shore, in 1982 (Abe 1984), and were absent from fallen trees and branches inland. The termites found during our surveys entirely corroborate Abe's conclusion.

Abe (1987) noted that the maximum flight range of termites is only a few kilometres. Humus-feeding and soil-nesting termites have no opportunity to contact potential rafts, and although subterranean termites consume wood they nest in soil, so that any rafts would usually contain only soldiers and workers. In contrast, reproductives of wood-nesting termites would inhabit a potential raft that may also serve as food and shelter on arrival. Abe believed dry-wood termites to be pre-adapted for oversea dispersal in that they are coastal, their nest wood is resistant to the entry of seawater, they are relatively tolerant of seawater and of the coastal conditions experienced on arrival, and their caste differentiation is flexible. Thus dry-wood termites have been most successful in colonizing the Krakataus and now dominate the archipelago's termite fauna.

Of the 11 pseudoscorpion species on the archipelago (Harvey 1988), the two on Anak Krakatau also occur on two and three other Krakatau islands, so that only one pseudoscorpion species occurs on all islands. Species with subcortical habits are slightly in the majority on the Krakataus (7 of the 11) compared with litter inhabitants, although 6 of the 9 species in our collections at Ujung Kulon and southern Sumatra were from litter, and only one was found beneath bark (table 3). This trend parallels that seen in termites. One pseudoscorpion, *Goryphus*

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 2. Numbers of species of termites found on the Krakataus and parts of west Java (P. Panaitan and Carita), by nest type and food

(After Abe 1984.)

nest type	food	Krakataus	west Java	total
hard wood	hard wood	4	5	8
soft wood	soft wood	2	4	5
arboreal	soft wood	1	4	4
epigeous	soft wood, fallen leaves	0	1	1
subterranean	soft wood	0	4	4
subterranean	soft wood, fallen leaves	0	1	1
subterranean	humus	0	2	2
total		7	21	25

Table 3. Distribution of pseudoscorpion species found in 1984–85, by habitat

habitat	Krakataus	southern Sumatra and western Java
subcortical only	5	1
subcortical/litter	2	0
litter only	3	6
vegetation only	1	2
total	11	9

maldivensis, was found under the bark of a dead tree on the shore in 1984 and is a possible case of rafting.

Womersley (1932) regarded the collembolan *Mesira calolepis*, a common detritivore found in large numbers on Anak Krakatau's beach six months after the island's emergence, as having been carried by drift material, and Bödvarsson (1982) in studying the collembolan fauna of Surtsey, Anak Krakatau's temperate counterpart (Thornton 1984) that emerged from the mid-oceanic ridge in the North Atlantic in 1963, believed that three of the island's four halobiontic collembolan species established by 1978 arrived by drifting with ocean currents on the sea surface. Lindroth *et al.* (1973) showed that one of the species, first found on Surtsey four years after its emergence and which has often been seen in numbers floating on the sea surface, could easily withstand flotation on seawater for the time (four weeks) necessary to achieve a landfall from source islands 5–18 km away. They also showed that Collembola could survive in floating grass tussocks for seven days, and Bödvarsson found both halobiontic and non-halobiontic species in grass tussocks washed ashore in 1972 and 1974 (one species was present five years later).

Muir (1930) believed that the nymphs of Derbidae, a family of fulgoroid insects, may have been carried in old logs; they have poor flight powers, and have a high incidence of island endemism. Six species occurred on the islands by 1920.

In temperate climates 'ballooning' flights of (particularly) immature spiders are commonly reported.

In the two summers after the Mount St Helens eruption of 1980 in Pacific northwestern America, 43 species of spider arrived as ballooners in the blast zone from which life had been extirpated, and Edwards (1986) concluded that some originated from areas 30 km distant. Okuma & Kisimoto (1981) collected living spiders in the summers of 1979 and 1980 in nets set 18 m above the surface of the central East China Sea, on a ship 400 km from land. The nets were emptied every three hours and contained adults and second and third instars of *Tetragnatha* species (101 of 105 individuals) with one individual each of the Theridiidae, Erigonidae and Linyphiidae.

However, only a small percentage of spider species are definitely known to practise ballooning and the phenomenon is practically unrecorded in tropical regions, although Dammerman (1948) noted that local people in Java have a phrase 'hujan lawa' (spider rain) for unusual falls of spider gossamer. Whether this means of dispersal is rare or absent in tropical spiders or simply a sporadic individual occurrence that is likely to escape general notice (Robinson 1982) is not known. Main (1982) also emphasized that many groups do not balloon and believed that although ballooning of linyphiids is well known in the Northern Hemisphere there is some doubt that this capacity 'facilitates their geographic distribution in the Australian and Oriental regions'. Although some mygalomorph spider genera disperse by gossamer flights, most spiders of this primitive group are ground-dispersers. Main (1976) noted that populations of non-aerially dispersing mygalomorphs occur only on the *continental* islands of Australia, and this restrictive distribution is maintained even on a single archipelago. The Abrolhos group of islands, off Western Australia, include both continental and reef-formed islands, and Main has found that mygalomorphs occur only on the parts of the archipelago representing continental shelf cut off by rise in sea level. The families Araneidae, Thomisidae, Clubionidae, Salticidae, Oxyopidae, Lycosidae and Zodariidae, but again no mygalomorphs, occur on islands of Australia's Great Barrier Reef, and Main (1982) considered that 'obviously such populations can only be established as a result of aerial dispersal'. She believed that this may imply that 'much of the spider fauna of New Guinea and adjacent islands has been by windborne spiderlings', but acknowledged that other explanations are required for most mygalomorphs, detricolous species, and the very small web-weavers of the symphytognathoid group.

Toxopeus (1950) found no males of *Nephila* on Sertung in 1949, and remarked that if this lack was found on future visits it would imply that there was a continuous air-borne immigration. The predominant families of spiders known from the archipelago by the 1930s (the present fauna is yet undetermined) were araneids and salticids, followed by theridiids, thomisids and linyphiids (Bristowe 1931, 1934) (table 4). Immatures of all these families and lycosids, together with some clubionids, oxyopids and zodariids, are known to be ballooners. On the Krakataus these 'ballooning families' (9 out of 19 families) made up 82 % of the fauna (82 of about 100 species) in 1933. On Surtsey, all 7 species of spider found by 1981 (18 years after the island's emergence) were linyphiids (Ólafsson 1978, 1982).

In contrast to ballooning spiders, behaviour in some insects may be a disadvantage to dispersal over a stretch of sea. Yamane (1983), discussing the aculeate Hymenoptera of the Krakataus (other than ants which are as yet undetermined but which are diverse: our collections contain 72 species, R. W. Taylor, personal communication) made the point that there is a lack of the swarm-forming social Hymenoptera such as *Polybioides*, *Ropalidia* (*Icaridia*) and *Trigona* on the Krakataus; he believed this is because their swarms cannot maintain coherence over the distance (44 km) between the archipelago and the mainland. The exception, he noted, is *Apis dorsata*, which has been present on the islands since 1919 and is known to swarm for long distances (150–200 km). Of the three genera mentioned above, Yamane indeed recorded only one species of *Ropalidia* (*Icaridia*) on the Krakataus (Anak Krakatau) in 1982, but two species of this subgenus were recorded on Rakata in 1908, and

Table 4. Numbers of species of spider families on the Krakataus in 1934

(Data from Bristowe (1931, 1934) and Dammerman (1948).)

family	number of species	'ballooning' known
Pholcidae	2	no
Scytodidae	1	no
Dysderidae	1	no
Dictynidae	1	no
Uloboridae	3	no
Theridiidae	11	yes
Linyphiidae	9	yes
Araneidae	20	yes
Oxyopidae	3	yes
Zodariidae	1	yes
Lycosidae	4	yes
Pisauridae	1	no
Clubionidae	6	yes
Gnaphosidae	4	no
Sparassidae	4	no
Ctenidae	1	no
Thomisidae	10	yes
Salticidae	18	yes

Yamane reported only three species from west Java in 1982: two on Pulau Peucang, one at Carita, and none on Pulau Panaitan (figure 1). The evidence for *Trigona* is more conclusive. In 1982 Yamane recorded three species of *Trigona* from west Java (Pulau Peucang two, Pulau Panaitan one) and none has ever been known from the Krakataus. *Polybioides* also has never been represented on the Krakataus, but no species was found in 1982 in any of the areas of west Java sampled by Yamane's group.

The greatest representation of Neuroptera on the islands (4 of the 11 species) is by the small vagile Coniopterygidae (New & Sudarman 1988), which Ng & Lee (1982) found to be the most frequently encountered neuropterans in a Malaise trapping programme at various heights in a Malayan lowland primary forest, and which are diverse in Indonesia. Unexpectedly, several generalist and assumedly vagile hemerobiids that occur in Java and Sumatra are scarce or absent from the Krakatau islands. Ant-lions have reached the islands, but are not yet known from Anak Krakatau, and the strongly flying Ascalaphidae are absent from the archipelago.

Instances of mass flights were cited by Dammerman (1948) for 18 species of Lepidoptera, 11 of which had been found on the Krakataus by 1934 and a further three (*Graphium agamemnon*, *Euploea* sp. and *Precis atlites*) have been found in the 1980s. All the pierids now present on the islands, particularly *Catopsilia* species, including *C. pomona*, and *Eurema* species, including *E. hecabe*, are recorded as making mass flights in Java (Dammerman 1948; Yukawa 1983; New *et al.* 1985). *C. pomona*, *E. hecabe* and *Eurema blanda* are on all the Krakatau islands, *C. pomona* having been first seen in 1932 and the two *Eurema* species in 1921. A third species of *Eurema* (*E. alitha*) has recently been recorded (and may have been confused with *E. hecabe* in the past). *Anapheis java* is also strongly migratory, and a single specimen caught on Rakata in 1919 was recorded as probably a straggler.

The nymphalid butterflies *Hypolimnas bolina* (a migrant), *Danaus genutia*, and *Tirumala limniace*, and large numbers of Odonata are believed to have been diverted from their normal

BIOLOGICAL SCIENCES THE ROYAL SOCIETY PHILOSOPHICAL TRANSACTIONS OF

flight patterns in August 1983 by a monsoon storm and carried almost 2000 km over the sea from northwest India to Arabia (Larsen & Pedgley 1985). A very much smaller diversion would suffice to achieve a landfall on the Krakataus from the Sunda mainlands. *D. genutia* was recorded on Rakata in the first 1908 survey (Jacobson 1909), and thereafter on Sertung and Panjang (Dammerman 1948); it was recorded from Sertung in 1982 by Yukawa (1984*a*). Colonization of Canton Island (a mid-Pacific coral atoll 1100 km from Samoa) by *H. bolina* was witnessed by van Zwaluwenburg in 1941 (van Zwaluwenburg 1942). The species has been found in all Krakataus surveys since 1919, and the specimens found in 1984 by us appeared flight-worn and may have been migrants. *T. limniace* does not occur on the islands, but *Tirumala septentrionis* was captured on Rakata in 1983 (Bush 1986).

The almost cosmopolitan dragonfly, *Pantala flavescens*, seen in mass flights at sea some 460 km from land in the Indian Ocean (Dammerman 1948), and also observed becoming established (together with *Diplacodes bipunctata*) in rain pools on Canton Island by van Zwaluwenburg, has been on the Krakataus since 1921, and is there still. *Diplacodes trivialis* was one of the first two dragonfly species seen on the islands, in 1908, and was caught on all four islands between 1982 and 1985 (Yukawa & Yamane 1985; van Tol 1988). Because of the lack of suitable breeding sites (Thornton & New 1988) most Odonata present on the islands are undoubtedly adventives and non-resident.

Smaller, lighter insects such as Thysanoptera (25 species in 1984 (zur Strassen 1988)), Psocoptera (80 species (Vaughan *et al.* 1988)), chalcidoids (266 taxa (Compton *et al.* 1988)), and choloropid flies (7 species (Kanmiya & Yukawa 1985)) were undoubtedly borne to the islands on air currents as part of the broad spectrum of aerial plankton. Edwards (1927) noted that salt-water coastal mosquitoes are known to undertake long flights and believed that the coastal mosquitoes on the Krakataus from 1919 to 1921 probably were airborne, although 'it is by no means impossible that their larvae were carried by sea currents'. Bödvarsson (1982) believed that aerial disperal of non-halobiontic soil collembans to Surtsey was indicated.

Our simple water-trapping programme on the barren southwestern part of Anak Krakatau in 1984 and 1985 (Thornton *et al.* 1988*a*) showed that large numbers of airborne insects and spiders make land-falls on the island. Additionally, Malaise traps sited on the inner volcanic cone, the outer rim and the bare southwestern region of the island all captured a wide range of insects. The last-mentioned trap, for example, yielded 317 specimens from 18 to 29 September 1986. All the groups of small, light insects mentioned above were represented in our water traps, chloropid Diptera being the most abundant family. Also included were spiders, aphids and six other hemipteran families. That such fall-out is a regular occurrence is indicated by the existence of a guild of species, dominated by a species of nocturnal flightless cricket (*Speonemobius*), exploiting such air-borne insect debris (see below).

In September 1986 we surveyed three very small bodies of freshwater on Sertung (one) and Panjang (two) (Thornton & New 1988). Among the community in one of the pair of Panjang ponds were ephemeropterans, an insect order not known previously from the archipelago. They were of the family Baetidae, well known as colonizers of small oceanic islands and including some ovovivoparous species with adults living for up to 14 days, unusually long-lived for mayfly adults. Non-baetid mayflies, with characteristically short-lived adults, are poor colonists. The simple macroinvertebrate communities were different in the three ponds, suggesting random colonization by founders and little mixing since establishment. Another insect order found for the first time on the Krakatau Islands in the 1980s, the Trichoptera, is represented by two species resident in the Sertung pool but caddis flies are apparently absent from the Panjang ponds.

The overall role of human activity in the dispersal of invertebrates to the Krakataus is difficult to assess.

A settler, Mr Händl, and his family lived on Rakata from 1916 to 1920, and survey teams spent from August 1896 to January 1897 and, intermittently, from 1927 to 1940, on Panjang (Thornton & Rosengren 1988). Interference with the biological succession has probably been minimal; even Händl's plantings of some exotic species were soon lost from the island (Docters van Leeuwen 1936). However, significantly, it was on Rakata in 1919 and Panjang in 1928 that rats were first found (*Rattus rattus* and *Rattus tiomanicus* respectively).

Human activity on the Krakataus in the past half century has been confined to visits of volcanological and biological expeditions, fishermen and tourists. During our visits at least one fishing boat (often more) landed almost every day, and weekends and public holidays frequently saw an influx of tourists to Anak Krakatau. Several boats remained for at least one night, and periods of bad weather may lead to stays of longer duration. Fishermen typically spend some time ashore (on Sertung for ablutions at the pool), and remains of temporary encampments were present on all islands. Most tourists climb at least to the outer rim of Anak Krakatau, far fewer to the inner cone, and discarded soft-drink containers and other debris, including uncovered faeces on occasion, can be found along their route of climb. In terms of both accidental sporadic introductions and the conservation of the delicate developing ecosystems (particularly that on Anak Krakatau) the extent of unmonitored and non-quarantined casual visits is cause for concern. This may, of course, decline with the recent establishment of a permanent P.H.P.A. post on Sertung and the provision of a reliable seaworthy vessel. Timber, foodstuffs, vegetation, ballast and other jetsam discarded from boats, casually or deliberately, may be the mode of introduction of, for example, timber-infesting beetles and anthropophilic taxa such as cockroaches and some Diptera.

A few instances of possible transport of invertebrates by visitors are the pseudoscorpion *Haplochernes warburgi*, which is at least partly diurnal and was common in tents and around camp sites in 1984 (Harvey 1988); the cockroaches *Periplaneta americana* and *Periplaneta australasiae*; the tenebrionid beetle *Alphitobius laevigatus*, which Blair (1928) believed might have come to the Krakataus with expedition stores; several house spiders, including a species of *Scytodes* (Bristowe 1934); and three 'semidomestic' culicine mosquito species (Edwards 1927). Dammerman suggested that a geophilomorph centipede was brought to the summit of Rakata by a survey party that camped there in 1908, and a scolopendromorph centipede that has been on Rakata since 1908 and now occurs also on Sertung, *Scolopendra subspinipes*, is carried around by commerce, particularly in fruit (Dr. J. Lewis, personal communication). The symphylan *Millotelellina krakatauanus* may also have been introduced (Scheller 1988); it was found only on the Sertung spit and Zwarte Hoek, Rakata, both sites being visited by fishermen. Winoto *et al.* (1988) suggest that the dorylaimoid soil nematode *Xiphinema* may have been brought to the islands with plants, and R. W. Taylor (personal communication) believes that the present ant fauna includes a number of well-known semidomestic species.

The possibility of the introduction of molluscs attached to the feet of birds, and mites and other organisms being carried on insects was discussed by Dammerman (1948). This mode of transport was considered to be unlikely, a view endorsed, in the case of land molluscs, by Smith & Djajasasmita (1988).

Establishment and succession

It is obvious that animals arriving on the islands can only become established if they encounter, and can exploit, the resources they need to do so. The spectrum of major habitats available on the Krakataus is constantly changing, so that the sequences of vegetational succession and physical, floristic and faunal changes on the archipelago over the past century have clearly affected the chances of establishment of animal immigrants. As an example, the number of soil nematode genera (18) found in 1985 on the physically young and mobile northern spit of Sertung is much less than in the adjacent mixed forest (41), and Winoto *et al.* (1988) believe this may be partly explained by the more complex soils found under mixed forest vegetation providing a greater diversity of food sources.

Since the destruction of two brackish lagoons on the Sertung spit as a result of marine erosional processes (Rosengren 1985), the islands have been devoid of permanent water bodies apart from a very small freshwater spring pool on Sertung and small artificial rain ponds on northern Panjang (see above).

Dragonflies are one of several groups of aquatic animals that might have been expected to decline since the 1920s and 1930s, when the brackish lagoons existed on the Sertung spit (Yukawa & Yamane 1985), but the number of species in the 1980s is the same (11) as that in 1933 (van Tol 1988). Turnover in the interval has been high (seven species), but it is doubtful if this is a true dynamic equilibrium in the sense of MacArthur & Wilson (1967), because many of the species recently recorded are thought to be temporary migrants (Yukawa & Yamane 1985; van Tol 1988). In contrast, although 12 species of Trichoptera (caddis flies) were collected in 1984 on Java and Sumatra, only two were discovered on the Krakataus, a striking example of the need of suitable habitat for successful permanent colonization.

Six species of mosquito were present on Sertung in the period from 1919 to 1921, when one lagoon existed, and three have larvae that live in seawater. Two of these, *Aedes vigilax* and *Culex sitiens*, have very wide distributions and the third, *Aedes cancricomes*, breeds in crab holes on the shore. The remainder are semidomestic species breeding in small temporary bodies of standing freshwater (Edwards 1927) and, once introduced, could have become established by using rainwater in leaf axils, for example of *Pandanus*, and other small naturally occurring water bodies.

Clearly stenophagous insects, like some butterflies, are precluded from establishment if their larval food plant has not previously become established, although Bush (1986) and New *et al.* (1988) record instances of what appear to be established populations of which the known larval food plants are absent from the islands. Whether this indicates a shift to other related food plants present on the archipelago, or, more likely, simply reflects ignorance of the true range of food plants on the mainland of what are relatively polyphagous species, is not known.

Mention has been made above (p. 502) of the highly vagile butterfly *Anapheis java*. A single individual was found on Rakata in 1919 when its food-plant family (Capparidaceae) was absent. The species was not seen again in any surveys in the 1920s and 1930s, but was reported by Yukawa (1984*a*) on Panjang in 1982. Because the Capparidaceae is still unrepresented on the islands, it is unlikely that the species will become established. As early as 1908, an individual of *Phalanta phalantha*, a widely distributed nymphalid butterfly that has been recorded 400 km from land, was seen (on Panjang), but the species has never been observed again; like *A. java*, its food-plant families are absent.

We discussed earlier the 18 species of Lepidoptera listed by Dammerman as undertaking mass flights, and noted that 14 of them had reached the Krakataus by the 1980s. Of the four remaining species, Dammerman stated that *Vanessa cardui* is found only high on the mountains in Java, and believed that it lacks appropriate habitat on the Krakataus, *Delias* species have no food plants (Loranthaceae, Santalaceae) available on the island group, nor does *Papilio demoleus*, the larvae of which feed on Rutaceae. The absence of the fourth, *Agrotis ypsilon*, is difficult to explain, as this cosmopolitan migratory noctuid is polyphagous.

Another lepidopteran, the hesperiid *Hasora chromas*, has been seen in a mixed mass flight of at least 16 species of moths at sea some 20 km from the coast of the Malay peninsula, but has not colonized the Krakataus. The habitat on the islands has now changed dramatically from the point of view of grass-feeding hesperiids. Three species, one reported as early as 1908, were lost from the islands in the decade after 1920 when grasses and palms were declining in importance, and three others, seen in 1933–34, could not be found in the 1980s. By now, apart from *Notocrypta curvifascia*, which was found on Rakata in 1984–85 and may not be the *Notocrypta* species recorded from that island in 1919, and *Tagiades japetus*, regarded as the *Tagiades* species found on Sertung in 1933, the hesperiid fauna has changed completely since the days of the Dammerman expeditions. Five species seen in the period 1919–34 have been replaced by three new to the archipelago; only one is present on all islands. One species, *Potanthus ?confucius*, seems to be restricted on Anak Krakatau to the grass *Ischaemum muticum*.

The decline of grasses and palms between 1920 and 1933 was also reflected in a reduction in numbers of species of fulgoroid homopterans that feed on them. Muir (1930) noted 13 such species present by 1920, only three of which were collected 13 years later.

As assessed by their presence on the Krakataus in the 1980s, the lepidopteran groups with the best colonizing record as measured by their relative colonization ratios (*RCR*) (Thornton *et al.* 1988*b*) (table 5), are Satyrinae and Lycaenidae. The Nymphalinae are poor colonizers by this measure.

In contrast to the butterflies, moth diversity appears to be rather low. Yukawa (1986) found only 10 species, and our own light trapping was persistently disappointing in relation to the larger range of taxa encountered on Java, but an initial appraisal of our collections suggests many more than 10 species. Although there may be marked seasonality in time of appearance

TABLE 5. RELATIVE SUCCESS OF WEST JAVA BUTTERFLY GROUPS IN COLONIZING THE KRAKATAUS, AS MEASURED BY RELATIVE COLONIZATION RATIO (*RCR*) AFTER ABOUT 100 YEARS OF COLONIZATION

(WJ, Ujung Kulon peninsula, Pulau Peucang, Pulau Panaitan. K, Krakatau Islands. CR = total species K: (WJ+K only)[a]. $RCR = CR_{group} : CR_{total}$.)

	number of species				
	WJ	total K	K only	*CR*	*RCR*
Papilionidae	10	4	1	0.36	0.90
Pieridae	13	5	2	0.33	0.83
Nymphalidae					
Danainae	10	6	4	0.43	1.08
Satyrinae	8	6	1	0.67	1.68
Nymphalinae	30	5	1	0.16	0.40
Lycaenidae	27	23	14	0.56	1.40
Hesperiidae	11	5	4	0.33	0.83
total	109	54	27	0.40	

[a] Since collecting on the Krakataus has been more intensive than in west Java, species found on the Krakataus only are assumed to have been missed in west Java.

of tropical moths, our collections are very much less diverse than the 113 species noted by Dammerman (1948). The presumed *Ficus*-feeding *Asota heliconia* and the migratory *Utetheisa pulchelloides* (both arctiids) were found on Anak Krakatau, the former commonly, and the legume-feeding noctuid *Chalciope hyppasia* was found in association with *Ipomoea*. The large fruit-moth *Othreis fullonia* was caught on Anak Krakatau in all three years of our surveys and may be another migratory species. Small pyralids and other moths were captured in Malaise traps high on Anak Krakatau. Because of the very small overlap between his 1982 collections and the accumulated Dammerman records, Yukawa suggested that many species of moths may have been added to the Krakatau fauna since 1931–34, and that the number is likely to increase markedly with vegetational succession.

Apart from changes in the actual floral complement, vegetational succession has resulted in sequential change of the gross habitat for animals. In general, the vegetational change has been from algal cover with a fern community, to grassland, followed by open *Casuarina* woodland with a beach *Ipomoea* community and coastal '*Barringtonia* association', and then closed mixed secondary forest. Perhaps the most important of these changes has been that from open to closed forest, with the microclimatic changes (lower temperature, less light, higher humidity and less wind) attendant on closure of the canopy.

Forest closure may have led to decline in some butterflies dependent on open spaces or early successional vegetation, like hesperiids, and provided appropriate habitat for others, such as *K*-selected lycaenid species, permitting their establishment relatively late in the succession (New *et al.* 1988). Another example of possible decline, but of an ecologically more widespread species, is the ant *Tetraponera rufonigra*. Dammerman (1948) noted Jacobson's observation of its abundance on Rakata, and found it common also on Sertung. In the 1980s it was not collected on these islands, being found only on Anak Krakatau and Panjang (R. W. Taylor, personal communication).

Yamane (1983) remarked on the lack on the Krakataus of the sphecid wasp genera *Sceliphron*, *Chalybion* and *Ammophila*, all of which have never been recorded on the archipelago but are common in open sites in Java and Sumatra. In contrast, many forest-dwelling small *Trypoxylon* species were found on Rakata and Sertung. Presumably the three former genera failed to colonize when the Krakatau environment provided suitable open habitat, which is now very limited.

The forests of the Krakataus are still far from primary status (Richards 1982) and this may have precluded the establishment of many species with strict, primary or deep-forest requirements. For example, few deep-forest butterflies are present yet on the Krakataus, and specialized forest taxa of chrysopid neuropterans are absent (New & Sudarman 1988). Forest aculeate hymenopterans (other than ants) are few (Yamane 1983), and some psocopteran families typical of forest habitats are absent or poorly represented (Thornton *et al.* 1988*b*).

Yukawa & Yamane (1985) cited several examples of insects that were unusually dominant in 1982, and which they suggested might be undergoing 'outbreaks' in a relatively untramelled environment after colonization. The major species involved were the margarodid *Crypticerya jacobsoni* (Yukawa 1984*b*)and the fruit fly *Dacus albostriatus* (Yukawa 1984*c*). The former species was restricted to Rakata, but another scale insect (*Steatococcus samaraius*) occurred on Anak Krakatau. The fruit fly made up at least 97% of all fruit fly catches on all four islands, but was not captured at Carita, west Java (figure 1). Relatively few other species of fruit fly were captured, ranging from none on Anak Krakatau to five on Rakata. The difference between the patterns of *C. jacobsoni* and *D. albostriatus* is likely to reflect their differing dispersal powers. Intriguingly, *C. jacobsoni* appeared to be expanding its host range on Rakata. This widespread Oriental insect had not been recorded previously from *Ficus* in any part of its range but occurred, sometimes abundantly, on four species of this genus on Rakata.

Such apparent increases in host range, suggesting some form of 'ecological release', merit careful investigation in studies of colonization by phytophages. Several of the resident butterflies on the Krakatau islands must be utilizing larval food plants other than those recorded for the species elsewhere (Bush 1986), and for a few species (such as *Papilio memnon* on Rutaceae, *Graphium agamemnon* on Annonaceae) there are no taxonomically similar potential hosts on the islands. However, as noted above, background information on host range elsewhere is undoubtedly incomplete for these and other species.

Differences in dispersal abilities (see previous section) may affect the likelihood of establishment of particular species. Termites of the genus *Prorhinotermes* tend to be confined to tropical and subtropical islands (Abe 1987) and are common in both coastal and inland forests on the Krakataus, but have not invaded the inland forests on Java. They both nest and feed in wet wood, and their colony maturation time (about four years) is longer than wood of small diameter (less than 30 cm) would serve them for both food and nest: they are intolerant of wood with such a short life, whereas competing termite species, which feed but do not nest in wood, are tolerant of such a resource. Abe believes that this is why *Prorhinotermes* have become established only on islands, such as the Krakataus, from which such competitors are scarce or precluded because of difficulties of dispersal.

Predators and parasites may, in general, be expected to establish themselves late in the sequence, as Dammerman (1948) noted. An example of this is the evidently late establishment of the majority of braconid parasitic wasps on the islands (table 10).

There are exceptions to the general rule of phytophagous colonists preceeding carnivorous ones. Spiders were early colonists of the islands, about 28 species being present in 1908, and indeed a web-spinning spider was the first animal to be seen on the islands, nine months after the 1883 eruption (Cotteau 1885). Web-spinning spiders, of course, capture flying or air-borne prey, which need not necessarily imply the prior existence of vegetation. We also discovered a guild of aeolian scavenger–predators in 1985 subsisting on air-borne fall-out on Anak Krakatau (New & Thornton 1988). A mantis, lycosid spiders and a dermapteran were part of this community, which was dominated by a nocturnal, cryptic, flightless cricket, clearly a specialist for this niche. The community closely parallels similar aeolian ecosystems on bare lava flows on the island of Hawaii (Howarth 1979) and, less precisely, the diurnal and nocturnal guilds found on alpine snowfields of several mountains of northwestern North America, in the blast area resulting from the 1980 eruption of Mount St. Helens (Edwards 1986), and on snowfields of mountains in Austria (Liston & Leslie 1982), Scotland (Ashmole *et al.* 1983) and the Arctic (Kaisala 1952).

Large numbers of the dragonfly *Diplacodes trivialis* (together with swiftlets) were seen by the senior author in February 1988 on the barren outer rim of Anak Krakatau, hawking flies that had been brought up to the rim by air currents. Clearly this species would also be able to obtain insect food before the establishment of vegetation.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Origin of the immigrants

In most groups it is impossible to distinguish between immigrants of Javan and Sumatran origin because the species concerned occur on both major source islands and do not have identifiable subspecies on either, or because the fauna of those large islands is not sufficiently well known to permit categorical statements that particular species are definitely absent. Overall, Dammerman (1948) considered most of the fauna to be of Sumatran origin, but this interpretation should be treated with caution. Both these major source areas have clearly contributed to the Krakataus' fauna.

Yamane (1983) reported that two specimens of the eumenid wasp *Phi flavipictus* found on the Krakataus were intermediate between the Javan and Sumatran subspecies. The remaining two specimens were typical of the Sumatran subspecies. Dammerman had also noted such intermediate forms as evidence for immigration from both source areas. Similar evidence (both Javan and Sumatran subspecies present) was cited by van der Vecht & Krombein (1955) for *Sphex sericeus* on Rakata in 1928; only the Javan subspecies, however, was found in 1982 by Yamane. Yamane noted that four wasps in all are represented by the Javan subspecies (*Polistes tenebricosus*, *Polistes sagittarius*, *Vespa analis* and *S. sericeus*) and one by the Sumatran (*P. flavipictus*); this evidence favours a Javan over a Sumatran origin (table 6). A possible case of competitive exclusion was noted by van der Vecht (1957). The Javan subspecies (*analis*) of *V. analis* occurs on the west coast of Java, the islands of Sebesi, Sebuku and Legundi, and on southern Sumatra. The subspecies *indosinensis* of *Vespa affinis*, common in Sumatra, is rare or absent from Java, and van der Vecht believed this may be due to the presence there of *V. analis*. On the Krakataus, however, both were common in 1982, and collected together on two of the islands.

Butterflies are another group in which there are several species with distinct Javan and Sumatran forms, and Yukawa (1984*a*) cited two instances of species represented by both Javan and Sumatran subspecies on the Krakataus, *Danaus genutia* (noted by Dammerman, as present from 1928 to 1933) and *Pachliopta aristolochiae* (1919–1982). No intermediates between subspecies of the latter were found, although they co-exist on Rakata, Sertung and Anak Krakatau. Inter-mating was seen on Sertung by Toxopeus (1950). Yukawa has shown that, for butterflies, Javan subspecies predominate over Sumatran ones on the Krakataus. Of 10 species occurring on the archipelago that have distinguishable Javan and Sumatran subspecies, 9 are represented by the Javan, and 1 by the Sumatran form (table 6).

Yukawa believed that Dammerman's estimate of a preponderance of Sumatran forms in the fauna was because he based it largely on the birds. But the avifauna of Krakatau is equivocal in this respect, and Dammerman's reckoning gave a Sumatran:Javan ratio of 4:4 by 1934 for the birds. Sumatra is slightly closer (35 km) than Java (44 km) to the Krakataus, and the islands of Sebuku and Sebesi (figure 1) are available as stepping stones, the latter being only

Table 6. Representation on the Krakataus of Javan and Sumatran subspecies of butterflies and aculeate Hymenoptera (excluding ants)

	Javan subspecies	Sumatran subspecies
aculeate Hymenoptera	4	1
butterflies	9	1
total	13	2

12 km from Panjang. However, a century ago Sebesi and Sebuku were also devastated by ash fall-out from Krakatau; Cotteau (1885) reported a layer of dried mud 20 feet thick there in May 1884. The strongest prevailing winds, the northwest monsoon, would tend to bring immigrants from Sumatra rather than Java. These winds, however, predominate in the wet season, when butterflies are less likely to be available for wind assistance than in the dry season, when the winds are predominantly from Java. Toxopeus stressed that Sebuku, Sebesi and the Lampung district of southern Sumatra have lepidopteran faunas containing both Javan and true Sumatran elements, with 'Javanese influence being traceable in 25% of a collection of Kalianda butterflies in the Leyden museum'. As he noted, this may explain the implied predominance on the Krakataus of Javan over Sumatran forms, and advocated further collecting in southern Sumatra to test this.

Anak Krakatau

The total area of potential invertebrate habitat, and its complexity, are considerably less on Anak Krakatau (figure 2), which emerged in 1930 and because of a devastating eruption in 1952 is only about three decades old biologically, than on the other islands of the archipelago (Thornton & Rosengren 1988). Anak Krakatau, which is still active, now has an area of some 17 hectares† covered with vegetation (12 hectares with trees and 5 hectares grassed). *Casuarina equisetifolia* is still the dominant tree, with wild sugarcane, *Saccharum spontaneum*, and open areas on the eastern foreland have a cover of the grass *Ischaemum muticum*. The northern foreland has fewer trees, and a considerable area of alang–alang grass, *Imperata cylindrica*, as well as *S. spontaneum*. Mixed forest is beginning to develop, particularly on the eastern foreland, where two fig species, *Ficus septica* and *Ficus fulva*, are established, as well as *Terminalia* and other trees. A total of 82 species of vascular plants was recorded in the period 1979–83, with 66 present in 1983 (Barker & Richards 1986). The vast majority of the island, however, is barren; lava flows cover the south and southwest, the remainder is ash or lava overlain by ash. Eruptions have occurred fairly regularly since the island's emergence from the sea in 1930, the last very destructive one, which destroyed the vegetation, being in 1952.

Knowledge of the island's fauna up to the 1980s is confined to limited collections and observations made on a few short visits by individuals. A large cricket, *Brachytrypes portentosus*, was found on a predecessor of the present Anak Krakatau in May 1929. Bristowe (1931) in February 1931, six months after the emergence of Anak Krakatau IV and 11 months before the first vegetation was seen, spent part of a day ashore there, and recorded a pioneer and scavenging community. A collembolan, *Mesira catolepis*, was present in large numbers in drift debris on the shore, as was the widespread anthicid beetle *Anthicus oceanicus*. Three spiders (a linyphiid, *Maso krakatauensis*, which was fairly common, and immatures of a ctenid (*Ctenus periculosus*, found also on Rakata and Panjang) and a lycosid, *Trochosa reimoseri* (present also on Panjang)), were regarded as 'possibly established' by Bristowe (1934). Single specimens of a cosmopterygid moth and a mosquito were collected, and the ant *Camponotus variegatus* was present, although Bristowe regarded the ant and mosquito as 'not established'. Two species of ocypodid crab were found on the beach. In November 1932 another beach detritivore, the tenebrionid beetle, *Diphyrrhynchus vagabundus*, was regarded as an 'established inhabitant' by Dammerman (1948), and in January 1933 the chloropid *Eutropha noctilux* was found. This is a

† 1 hectare = 10^4 m^2.

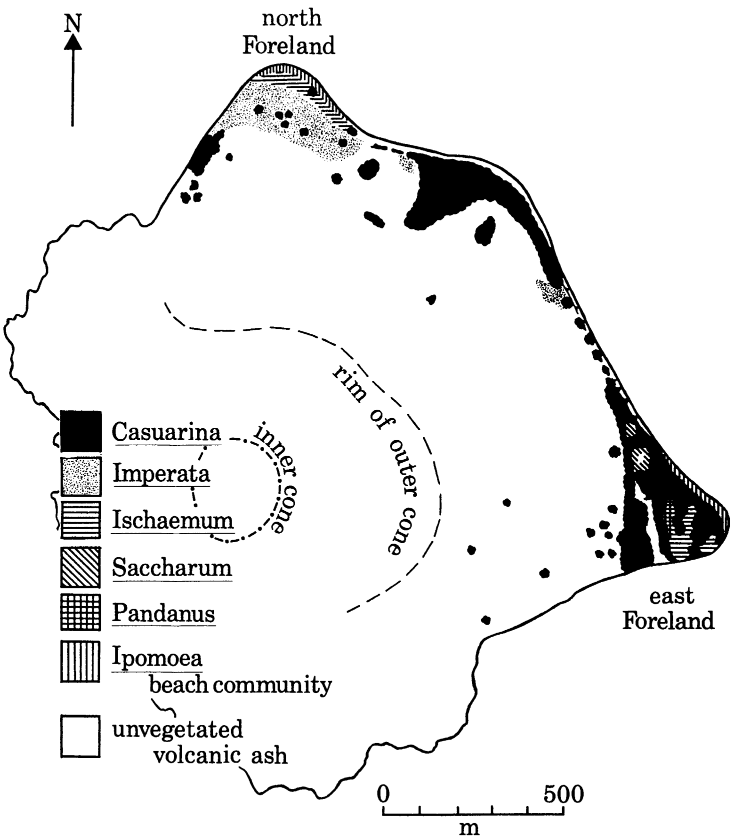

FIGURE 2. Anak Krakatau in 1986 showing major vegetation types.

member of a guild of several genera, four species of which occur on the islands and two of which were found in the first survey after 1883, which appears to be particularly associated with decaying marine animals on the shore (Kanmiya & Yukawa 1985) and so able to colonize islands before vegetation is established. Thus apart from the moth (a miner in palm and bamboo leaves), the early community was evidently dependent on marine detritus, and compares with those found by Heatwole (1971) on small bare cays of the Great Barrier Reef and Coral Sea, and Lindroth *et al.* (1973) on Surtsey. Most of the cays Heatwole studied, however, carried nesting sea-bird colonies, which provide an important conduit, lacking on Anak Krakatau, for energy flow to islands.

No zoologist visited the island again until 1949 when Toxopeus (1950) spent a morning there in August. He found acridids abundant and feeding on the vegetation, two certainly breeding, as well as two jassids, the carpenter bee *Xylocopa latipes*, and a *Halictus* species. An ant and a cosmopterygid (*Trachydora* sp.) were recorded, and three other lepidopterans, two (*Enarmonia* sp. and the lycaenid *Zizina otis*) on *Canavalia*, a component of the *Ipomoea* beach association. A tachinid fly, the mantid *Hierodula patellifera* and three dragonflies, *Potamarcha obscura*, *Orthetrum sabina* and *Diplacodes trivialis*, were found exploiting this fauna, but, remarkably, no spiders were seen. The mantid, the only one known on the islands and found on Rakata in 1919 and on Panjang in 1932, was breeding on Anak Krakatau in 1949 (and is still present). In October 1951 the botanist van Borssum Waalkes (1960) again saw 'large swarms of grasshoppers'.

It was not until the 1980s that zoologists again visited the island. Both an Indonesian expedition (Ibkar-Kramadibrata *et al.* 1986) and a Japanese expedition (Tagawa 1984) worked on the island in 1982, and our expeditions from 1984–86. Unfortunately, although botanists visited Anak Krakatau soon after the 1952 eruption (Van Borsumm Waalkes 1960), no systematic zoological survey was made for three decades.

Only one land mollusc, of 19 species on the archipelago, is present on Anak Krakatau (a litter inhabitant) and Smith & Djajasasmita (1988) suggest that two other litter dwellers will be the next invaders. Similarly, only one of the 18 types of plant gall present on the Krakataus in 1982 was found on Anak Krakatau (Yukawa *et al.* 1984). In contrast, about a third of the Krakatau group's insect fauna thus far determined occurs on Anak Krakatau's limited area of vegetation and the island now carries a good proportion of the Krakataus' complement of several invertebrate groups (table 7).

Distributional data on soil nematode genera (Winoto *et al.* 1988) suggest that the Krakataus' soil nematode fauna consists of a group of about 50 genera that are fairly widespread on the archipelago (27 of them on 3 or more islands), with Rakata, the highest, largest and most ecologically diverse island, carrying an additional set of about 24 genera (7 of these evidently confined to the higher altitudes). Anak Krakatau appears to be yet unsaturated, with four orders and even some of the very widespread genera found on the three older islands lacking. The genera found on Anak Krakatau all occur elsewhere on the archipelago and have been found in an average of 6.2 sample sites on the other islands. Those not found on Anak Krakatau are less widely distributed, occurring in an average of only 3.2 sample sites. Thus the soil nematodes that have succeeded in colonizing Anak Krakatau are, in general, those that are most widely distributed on the rest of the archipelago.

Yamane (1983) suggested that the surprising richness of Anak Krakatau's aculeate hymenoptera fauna (excluding ants) can be ascribed to the mutual source-area effect (the islands of the archipelago acting as sources for one another) and their preferences for open sites, now, apart from the Sertung spit, practically confined to Anak Krakatau. The colonization of Neuroptera, braconid Hymenoptera and land crabs also appears to have been faster than was the colonization of Rakata after 1883 when potential source areas were much more distant (table 8), although in other groups the rates are generally in accord. Accelerated colonization, where it occurs, can be largely ascribed to immigration from other Krakatau islands, although a coniopterygid neuropteran, *Heteroconis axeli*, was found in 1984 and 1985 only on Anak Krakatau and the possibility of direct colonization from the mainland cannot be entirely discounted.

For several species characteristic of early vegetational stages and with preferences for open sites, Anak Krakatau and the Sertung spit now represent the only available habitat, other such habitats on the archipelago having been extirpated by vegetational succession. This provision of an 'ecological refuge' has already been mentioned in the case of vertebrates (Thornton *et al.* 1988*c*). An insect example is the lycaenid butterfly *Catachrysops panormus* which is found now only on the Sertung spit in localized early seral stages of vegetation, but not on Anak Krakatau. Anak Krakatau now offers the only suitable habitat for several other Lycaenidae and Hesperiidae. Other insects found on the other islands in the first 50 years after 1883 but now confined to Anak Krakatau, are the vespid *Ropalidia variegata*, the scoliids *Campsomeris phalarata* and *Triscolea azurea*, and the sphecid *Bembix boorei*. The ant *Tetraponera rufonigra*, previously found on Rakata and Sertung, was not found on those islands by either our expeditions or the

Table 7. Number of species of various invertebrate groups on islands of the Krakatau group (Ks), 1982–85, and percentage of these on Anak Krakatau (AK)

(Rakata, Sertung and Panjang indicated by initial letters. Where no reference to an authority's publication is given, numbers are those following initial appraisals. Areas in parentheses take account of only vegetated area of Anak Krakatau.)

	R	S	P	AK	Ks	% on AK	authority
area of island/hectares	1250	790	275	235 (17)	2548 (2331)		
land planarians	1	0	1	0	2	0	L. Windsor
soil nematodes	68	41	34	19	78	24	Winoto *et al.* (1988)
Oligochaeta	4	2	1	0	6	0	E. G. Easton
land molluscs	16	14	7	1	19	5	Smith & Djajasasmita (1988)
Oniscidea	5	6	3	2	10	20	S. Taiti, F. Ferrara & A. Green
land crabs	7	3	9	6	12	50	Morgan (1988)
pseudoscorpions	11	5	4	2	11	18	Harvey (1988)
Chilopoda	3	3	1	0	5	0	J. Lewis
Symphyla	1	1	0	0	1	0	Scheller (1988)
Collembola	8	6	7	6	15	40	P. J. M. Greenslade
Archaeognatha	2	0	0	0	2	0	Sturm & Bach de Roca (1988)
Ephemeroptera	0	0	0	1	1	100	W. L. Peters
Odonata	3	5	5	3	11	27	Yukawa & Yamane (1985); J. van Tol (1988)
Blattodea	11	10	7	6	17	35	L. M. Roth
Isoptera	5	5	4	3	7	43	Abe (1984)
Mantodea	0	0	0	1	1	100	G. Milledge
Dermaptera	2	2	0	2	4	50	H. Steinmann
Orthoptera	8	15	3	14	30	47	Yukawa *et al.* (1984), F. Willemse
Embioptera	1	0	0	0	1	0	E. S. Ross
Psocoptera	57	27	48	27	80	34	Vaughan *et al.* (1988)
Hemiptera	6	9	8	3	16	19	Yukawa & Yamane (1985)
Thysanoptera	18	6	4	6	26	23	zur Strassen (1988)
Neuroptera	3	1	5	7	10	70	New & Sudarman (1988)
Coleoptera (Coccinellidae)	6	0	0	0	6	0	R. D. Pope
Diptera (7 families)[a]	20	12	4	10	39	26	S. Marshall, Yukawa Evenhuis & Yukawa (1986); Kanmiya & Yukawa (1985), M. Sasakawa
butterflies	47	38	24	23	54	43	New *et al.* (1988)
ants	46	33	22	35	71	49	R. W. Taylor
other aculeate Hymenoptera	55	47	45	43	86	50	Yamane (1983)
Braconidae	28	20	25	13	62	21	K. Maeto
Chalcidoidea	121	110	47	84	266	32	Compton *et al.* (1988)
total	663	421	318	317	949	33	

[a] Bombyliidae, Chloropidae, Sphaeroceridae, Tephritidae, Tethinidae, Clusiidae, Lauxaniidae.

Japanese–L.I.P.I. expedition of 1982, but was found to be persisting on Anak Krakatau and Panjang (R. W. Taylor, personal communication). The dorylaimoid nematode genus *Thornia* has been found only on the Sertung spit and on Anak Krakatau, and *Heterocephalobellus*, a rhabditid nematode, has only been collected on the Sertung spit.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 8. Number of species of various invertebrate groups present on Rakata and Anak Krakatau at surveys 25 and 38 years after the 1883 eruption of Krakatau, and 32 years after Anak Krakatau's 1952 eruption, respectively

(Authorities for Anak Krakatau's fauna as in table 7.)

	Rakata		Anak Krakatau
	25 years	38 years	32 years
Oligochaeta	1	4	0
land molluscs	2	6	1
Oniscidea	3	3?	2
land crabs	0?	1	6
Odonata	2	12	3
Blattodea	3	8	6
Isoptera	3	3?	3
Thysanoptera	0?	12	6
Neuroptera	1	3	7
chloropid Diptera	2	3	1
lauxaniid Diptera	7	1	5
butterflies	5	28	23
ants	21	36	35
aculeate Hymenoptera (excluding ants)	16	31	43
braconid Hymenoptera	2	4	13
totals	68	155	154

We have mentioned above three communities of animals that exploit energy sources deriving from outside the island 'system' itself: web-spinning spiders, which trap airborne prey; an aeolian scavenger–predator guild that is able to subsist in barren areas on insect fall-out; and a community of marine detritivores dominated by a collembolan and including chloropid flies and anthicid beetles. A web-spinning spider is now renowned as the only animal found on Rakata nine months after the destructive eruption of 1883 and the earliest recorded fauna of Anak Krakatau largely consisted of marine detritivores, established only six months after the island's emergence, before any vegetation had become established. The early decades of Anak Krakatau's colonization were, unfortunately, not monitored, but we speculate that the aeolian guild on bare ash, still extant, was also probably an early component of the fauna. These three communities and dragonflies (see above, p. 503), if established early, may short-circuit the normal successional sequence of plant–herbivore–carnivore and provide, almost at the outset, a basis for a further sequence of animal predators and parasites.

Development of the fauna, turnover and approach to equilibrium

The examples discussed in this overview represent an ecologically broad spectrum of invertebrates derived from two rather different ecological sequences. The three major islands of the archipelago have undergone progressive colonization since 1883, and the emergence of Anak Krakatau in 1930 has provided a sequence exemplifying seral stages now long passed on the older islands (see, for example, table 9), with the exception of the mobile Sertung spit. The spit has many features in common with the vegetated area of Anak Krakatau: both are dominated by *Casuarina* and have areas of grassland. However, the relative stability of Anak Krakatau since the last major devastating eruption has ensured that additional vegetation is starting to appear.

TABLE 9. TIMING OF STAGES IN THE DEVELOPMENT OF THE RAKATA BIOTA AFTER 1883 COMPARED WITH ANAK KRAKATAU SINCE THE DEVASTATING ERUPTION OF 1952

	Rakata years after 1883	Anak Krakatau years after 1952
ferns, blue-green algae	3	not monitored
grassland, some *Casuarina*	14–25	19 (east foreland) 30–36 (north foreland)
Casuarina open woodland	25	27 (east foreland)
Ficus first fruiting	23	33
obligatory frugivorous pigeon *Treron vernans* first recorded	25	34
obligatory frugivorous pigeon *Macropygia phasianella* first recorded	49	33
fruit bats (*Cynopterus* species) first recorded	36	30
mixed woodland	36–50	—

Ecological succession of plants on the islands is discussed by Whittaker *et al.* (1984) and Tagawa *et al.* (1985), and observations on plants and animals on the three older islands over the past century and on Anak Krakatau since its emergence in 1930 suggest the following sequence (in summary).

1. Bare ash beds, as at present on most of Anak Krakatau, supporting possibly a community of web-spinning spiders and probably a pioneer aeolian guild, characterized by *Speonemobius* crickets, with minor constituents such as lycosid spiders, the widespread earwig *Euboriella plebeja* and the mantis *Hierodula patellifera*, exploiting wind-borne animal food. A marine detritivore community consisting of collembolans, chloropid flies and anthicid and tenebrionid beetles exploiting sea-borne organic debris. Bacterial-feeding and saprophagous rhabditid soil nematodes, five genera of which occur on Anak Krakatau, are resistant to desiccation and high temperatures, and likely to be air-borne. Such nematodes were probably well represented in the pioneer soil fauna. A *Ditylenchus* species, probably a fungal feeder, was the only soil nematode found on Surtsey nine years after its emergence (Sohlenius 1974); six genera of the Tylenchida occur on Anak Krakatau (Winoto *et al.* 1988). Thus soil nematodes probably also were early exploiters of bacteria and fungi in the early pre-vegetation soils after 1883.

2. After three years a fern cover, with occasional flowering plants and a gelatinous layer of blue-green algae on the surface of pyroclastic deposits. This stage was not seen on Anak Krakatau; attempted surveys of that island in 1931, 1932 and 1933 were hampered by frequent eruptions and ash-falls, and the 1939 expedition again found that all vegetation possibly present was buried under a thick layer of ash from heavy eruptions from one to two months previously.

3. From 14 to 25 years after 1883, up to and including the 1908 expeditions, a savanna grassland, dominated by *Saccharum spontaneum* and *Imperata cylindrica* covering the lower slopes and a beach *Ipomoea pes-caprae* formation with a landward *Barringtonia* association present on the coasts. Anak Krakatau's eastern foreland was at this stage, with *Imperata cylindrica* dominant, in 1971 (Tagawa *et al.* 1985) and its northern foreland, which has been more strongly subjected to marine erosional and prograding régimes and has thus been less stable than the eastern foreland (Bird & Rosengren 1984), was at this stage in the mid-1980s. On the northern foreland alang–alang (*Imperata cylindrica*) is again the dominant grass, along with *S. spontaneum*.

The invertebrate fauna of the archipelago's grassland in 1908 was dominated by ants, spiders, Diptera, diplopods and chilopods, with acridid and gryllid Orthoptera, chrysomelid beetles, cockroaches, termites, and apid, sphecid and vespid hymenoptera. There is some evidence that Anak Krakatau is now relatively rich in these groups.

4. By 25 years after the eruption the grassland had incorporated extensive patches of *Casuarina* woodland, with some *Ficus* and other secondary forest species. The eastern foreland of Anak Krakatau and the Sertung spit are now approximately at this stage of succession, or at a little later stage, and it is also about 25 years since Anak Krakatau's self-sterilizing eruption of 1952.

5. From 1919 to 1932 a change from *Casuarina* savanna grassland to mixed secondary forest was seen, with *Casuarina* gradually declining in importance as the canopy began to close. Several different types of secondary forest, with different dominants, developed in the archipelago, possibly simply as a result of the different timing of the arrival of the dominants (Tagawa *et al.* 1985). This was a period of maximum turnover for most plant and animal groups, as the new range of potential habitats created by canopy closure permitted the establishment of a new set of immigrants, and many of the open grassland and *Casuarina* inhabitants were lost. Bark beetles, such as cucujids, fungus inhabitants such as nitidulids and inhabitants of rotten wood, passalids and lucanids, made their appearance, as well as cerambycid, scolytid, buprestid, bostrichid, and anthribid beetles, and other wood-borers. Myriapods and ants declined in importance and ground-living spiders and shade-loving gall-forming midges (Cecidomyidae) increased in diversity.

6. The Sertung spit's mobility and the emergence, growth and volcanic activity of Anak Krakatau since the 1930s have resulted in the establishment and extended existence on these of areas of *Casuarina* and grassland, which provide a continuity of habitat for species of open sites and early phases of vegetational succession, permitting some of them (some aculeate Hymenoptera and butterflies) to prolong their residence on the archipelago.

The only possible 'primary' forest tree now on the islands is *Disoxylum gaudichaudianum*†, but its true primary status is doubted; Richards (1986) believed it to have some characteristics of a 'secondary' forest tree, and that it should be considered to be *r* rather than *K* dispersed. Whittaker *et al.* (1984) suggested that the present vegetation of Rakata, which has increased in species number only slightly since 1951, may represent a 'pseudo-equilibrium' after which successful colonization of *K*-selected species may slowly proceed, but they doubted that a 'primary' rain forest as rich as those on the Sunda mainlands will ever be achieved.

Indications are that invertebrate groups are now at various stages on the route towards equilibrium of species numbers. The number of species of braconid parasitic Hymenoptera has risen dramatically since the last survey. This may be at least partly due to more specialized collecting (although we had no braconid specialist in our team), as suggested by the fact that Anak Krakatau, the braconids of which are mainly parasitoids of Lepidoptera larvae, has more braconid species per butterfly species than did the other islands at a comparable period after 1883 (table 10). But it may also be because host-specific braconids will generally lag behind their hosts in the colonizing sequence. Many species, though, can probably attack a wide range of hosts. In several groups, such as thrips, Neuroptera, aculeate Hymenoptera (other than ants) and braconid Hymenoptera, species numbers have more than doubled since the last surveys,

† Previously identified as *D. caulostachyum*.

TABLE 10. COLONIZATION OF THE KRAKATAUS AND SPECIES TURNOVER OF VARIOUS INVERTEBRATE GROUPS SINCE 1883

(a, Actual; c, cumulative number of species. Authorities for 1980s fauna as in table 7.)

		1908		1919–22		1928–33		1982–86
Oligochaeta	a	1	(+3−1)	3	(+1−0)	4	(+3−1)	6[a]
	c			4		4		7
land molluscs	a	2	(+4−0)	6	(+5−0)	11	(+8−0)	19
	c			6		11		19
terrestrial crabs	a	0	(+1)	1	(+1−1)	1	(+12−1)	12
	c			1		2		14
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
Isoptera	a	3		?3		?3	(+5−1)	7
	c			?3		?3		8
Dermaptera	a	0	(+1)	1	(+0−0)	1	(+3−0)	4
	c			1		1		4
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
bombyliid Diptera	a	1	(−1)	0	(+2)	2	(+4−2)	4
	c			1		3		7
chloropid Diptera	a	3	(+1−3)	1	(+1−0)	2	(+6−1)	7
	c			4		4		10
lauxaniid Diptera	a	7	(+0−6)	1	(+1−0)	2	(+10−2)	10
	c			7		8		10
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 aculeate	a	16	(+26−11)	31	(+18−9)	40	(+56−10)	86
Hymenoptera	c			42		56		107
braconid	a	2	(+4−2)	4	(+4−4)	4	(+62−4)	62
Hymenoptera	c			6		10		72
total	a	68	(+119−33)	154	(+72−55)	171	(+288−53)	406
	c			187		251		526

[a] Includes collections in 1973.

numbers of species of butterflies and ants have about doubled, but numbers of earthworm, land mollusc and cockroach species are rising more slowly (table 10) and may be closer to equilibrium numbers. The number of dragonfly species, surprisingly, has not changed since the Sertung lagoons disappeared (1908: 2; 1919–21: 12; 1923–33: 11; 1982–85: 11), although turnover since 1933 has been high (7 species). Because many of these species are probably migrant and not permanently resident, this apparent equilibrium must be regarded with caution. There is, of course, no reason why different segments of the fauna should approach equilibrium in unison, unless the diversity of one group is closely and synchronously dependent on the diversity of another. Successional asynchrony of the fauna has possibly resulted in several of the 'outbreak' situations discussed earlier.

Although in general there is no evidence of promixity to equilibrium, species numbers are greatest on Rakata, the highest (777 m) and largest (1250 hectares) island (table 7). Rakata's higher forests (from 500 m to the summit) are pedologically, climatically, structurally and to

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

some degree floristically distinct from the lower forests, taking on the character of mossy–submontane forests, which inland on larger land masses are characteristic of much higher altitudes (Whittaker *et al.* 1984). There is some evidence that this is reflected in the invertebrate fauna. Compton *et al.* (1988), found that an association of chalcidoid hymenopterans is characteristic of this region, having at the most 12 % of its species in common with other sites, and several other invertebrate taxa, for example species of the terrestrial isopod genus *Burmoniscus* and the pseudoscorpion genus *Tyranochthonus* and seven genera of soil nematodes, are evidently restricted to the region (Harvey 1988; Winoto *et al.* 1988).

Anak Krakatau's fauna is greater than might be expected considering the small area (about 17 of its 235 hectares) that is now vegetated. Colonization must have been rapid because of the proximity of the other islands that act as sources. Nevertheless, a complement of species of about the same as Panjang (275 hectares) (table 7) is quite unexpected and warrants explanation. For example, the Panjang collections of Orthoptera, ants, chalcidoid Hymenoptera, and lauxaniid and tethinid Diptera, are unexpectedly low compared with Anak Krakatau.

Coverage of the islands by recent expeditions has not been even. The work of the I.T.B. 1982 expedition was confined to Panjang and Anak Krakatau (Ibkar-Kramadibrata *et al.* 1986), and the Kagoshima University expedition (Tagawa 1984), also in 1982, concentrated on Rakata and Sertung (23 and 22 zoologist-days respectively, compared with 11 or 12 on each of Panjang and Anak Krakatau). On our expeditions (Thornton 1985, 1986, 1987) Rakata and Anak Krakatau received the most attention (194 and 154 zoologists-days respectively, against 64 on Sertung and only 57 on Panjang). The total coverage of the various islands on expeditions from 1982 and 1986 in zoologist-days is approximately: Rakata 217, Sertung 86, Panjang 75, Anak Krakatau 173. If one assumes, as is likely, that coverage by invertebrate zoologists reflected total coverage, then clearly intensity of invertebrate collecting has not been uniform.

Also, the theoretical reduction of Anak Krakatau's 235 hectares to the 17 hectares vegetated area is probably an oversimplification. The island does provide 235 hectares of surface for the land-fall of air-borne arthropods, which we have shown is considerable (Thornton *et al.* 1988*a*). Many of these arrive alive, and some may then successfully concentrate, actively or passively, in the small area of vegetation, which may act as an ecological trap. Similarly, the island's shore is about 7–8 km long, and animals making a successful land-fall may move along it after arrival.

Our work on Anak Krakatau was opportune in helping to clarify two examples of community integration involving insects.

1. The aeolian-based communities are not yet confused by an ubiquitous cover of vegetation. The *Speonemobius* species (the major constituent consumer) is relatively rare in or absent from vegetated zones, and the community may naturally be a rather transient one, specialized for the exploitation of this first post-volcanic stage.

2. The mutualism between figs and fig-wasps appears to have become established on Anak Krakatau only in the past year or two (Compton *et al.* 1988). Dr J. T. Wiebes has identified, from the syconia of *Ficus fulva* on Anak Krakatau, the agaonid *Blastophaga inopinata*, as well as its parasites (*Sycoryctes* sp.) and cleptoparasites (*Phylotrypesis grandii*). This may be a key stage in Anak Krakatau's vegetational succession, facilitating, through the agency of fruit bats and

frugivorous pigeons (Thornton *et al.* 1988*c*; Zann *et al.* 1989) the establishment of other species of figs and thus the transition from *Casuarina* woodland to mixed forest.

Many groups of insects now seem to be more diverse than noted by earlier authors, but the *caveats* noted in our introduction limit precise quantification of this. Of the well-represented groups, perhaps only for butterflies are the data now sufficiently rigid to allow unequivocal comparisons, although this will soon be possible also for the ants. The fauna so far appraised does not indicate any large degree of taxonomic differentiation from putative source populations. Several of the taxa formerly believed to be Krakatau endemics have either now been found elsewhere, or are recognized as synonymous with taxa described from elsewhere. We believe that much more intensive comparative sampling is needed before accepting any Krakatau invertebrate as endemic. Thus, for example, although some 28 species of Psocoptera have as yet been found only on the Krakatau islands (Vaughan *et al.* 1988), there is little reason to doubt that they will be found in our considerable unworked Javan collections or in due course, in Sumatra.

We suggest that future work on the islands should consist of representative faunal surveys of the archipelago at intervals of 5–10 years, with, if possible, more frequent monitoring of the young developing ecosystem of Anak Krakatau with emphasis on community relationships. The short paper by Iwamoto (1986) points to the direction that such future studies should take. Dr K. Maeto (personal communication) has noted that only 13 of the 62 species (21 %) of braconid parasitic Hymenoptera found on the Krakataus during our expeditions were taken on Anak Krakatau, and only 5 of the 13 subfamilies represented on the islands occur there. However, the island is particularly rich in the subfamilies Agathidinae, Cheloninae and Microgastrinae, which comprise endoparasitoids of lepidopterous larvae; in these subfamilies Anak Krakatau has 10 of the 16 (63 %) known species from the Krakataus. The island is poor (1 species of 10 on the archipelago) in ecto- and endoparasitoids of xylophagous beetles, which may only be expected to colonize in numbers and increase in diversity when mixed forest has become established, and it lacks any of the 15 species of braconids that are endoparasitoids of cyclorraphous Diptera. Close monitoring of the island's fauna may demonstrate future changes to a more 'balanced' faunal spectrum. Even if (and perhaps particularly if) volcanic eruptions set back the process of ecosystem assembly on Anak Krakatau, studies of ecological relationships on the island would be invaluable in providing knowledge of the early stages of colonization, knowledge which, so far as animals are concerned, we do not have and cannot now directly obtain for the archipelago as a whole.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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