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THE COLONIZATION OF THE KRAKATAU ISLANDS BY FIG WASPS AND OTHER CHALCIDS (HYMENOPTERA, CHALCIDOIDEA)

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CONTENTS

This paper describes aspects of the chalcid fauna of the Krakatau Islands in relation to recolonization and floral succession. Chalcids of the family Agaonidae (fig wasps) are the obligate pollinators of fig trees (*Ficus* spp.). The years 1984–86 appear to have spanned a critical period in the colonization of Anak Krakatau by *Ficus* and its associated animals. Within this period, flowering and successful pollination have taken place for the first time and the diversity of fruit-eating vertebrates has multiplied.

The chalcids present on Anak Krakatau were compared with those found on other islands in the group. The chalcid fauna of Anak Krakatau had most in common with that of the spit area of northern Sertung, with which it shares a *Casuarina*-dominated vegetation. Comparisons between chalcids collected by similar methods on the Krakatau Islands and in tropical West Africa indicated that at the family level the faunas are remarkably similar.

Introduction

In common with many other groups of small and taxonomically complex insects, the chalcid fauna of the Krakatau Islands has not been well documented. Dammerman (1948) noted records of only 10 species. Because of their involvement in a wide range of ecological

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interactions, ranging from pollination to intricate parasitoid–host relations, information on the diversity and taxonomic composition of the group is of considerable value in understanding habitat complexity and succession, and their use as bio-indicators in surveys is coming to be more widely recognized. This paper discusses two important aspects of Chalcidoidea on the Krakatau Islands:

(1) the interaction between figs (*Ficus* spp.) and their obligate agaonid pollinators in relation to colonization and floral succession on Anak Krakatau;

(2) an appraisal of the comparative taxonomic composition of the superfamily on the four islands in relation to their vegetation.

The return of figs and fig wasps to the Krakataus

The recolonization of the Krakatau Islands by fig trees (*Ficus* spp., Moraceae) is of interest on two counts. Firstly, fig trees are an important component of both primary and secondary rainforests, both in terms of numbers of species and numbers of individuals. Secondly, the flowering phenology and unique pollination system of fig trees may make it particularly difficult for them to establish viable populations on islands.

The colonization of islands by fig trees has certainly not been a rare event, for as Ridley (1930) observed, 'there is hardly any tropical island of any size but possesses one or more species of *Ficus*'. It is, however, rare to have an opportunity to monitor the process of colonization as it actually takes place. The recent zoological expeditions to the Krakataus provided such an opportunity.

With few exceptions, each of the 750 or so *Ficus* species is pollinated by its own unique species of fig wasp (Hymenoptera, Agaonidae), the larvae of which develop only in the seeds of that species of fig (Michaloud *et al.* 1985; Wiebes 1986). The flowering phenology of fig trees is generally characterized by synchrony of fruit production within individual trees, but marked asynchrony between trees (Janzen 1979; Milton *et al.* 1982). This fruiting pattern normally prevents individual trees from supporting their own population of pollinators because crops may be separated by periods of several months and adult fig wasps are believed to have a life-span of only a few days.

A feature of fig biology may serve to reduce this apparent handicap to island colonization. Trees that receive an abundant supply of pollinators tend to abort any figs that remain unpollinated (Galil & Eisikowitch 1968; S. G. Compton & A. J. Gardiner, unpublished results). However, if few or none of the figs are pollinated, abortions are inhibited and the figs can remain attractive to pollinators for much longer (Murray 1985). A consequence of this is that figs on one tree are pollinated at different times and the normal within-tree synchrony is disrupted. In this way isolated fig trees gain more time to attract pollinators.

The establishment of independent fig-tree populations on a new island requires two phases of colonization. Fig seeds must first be carried to the island. Once these have eventually produced mature trees, agaonids from elsewhere must reach them at a time when their figs are at a suitable stage for pollination (Galil & Eisikowitch 1986). In the absence of any within-tree asynchrony, this dependence on immigrant pollinators will only decline when a critical population size has been achieved and a resident agaonid population can be supported.

Today, Rakata, Sertung and Panjang have a well-developed covering of secondary rainforest (Flenley & Richards 1982). The course of recolonization since the catastrophic

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sterilizing eruption of 1883 (summarized by Thornton & Rosengren (1988)) is best documented for Rakata, where *Ficus* species were among the first trees to reappear, with *F. fulva* Reinw. and *F. montana* Burm. f. being recorded by Penzig as early as 1896–97. By 1934 a *Macaranga–Ficus* forest had developed on the island's lower slopes and a total of 14 fig species had been detected (Docters Van Leeuwen 1936). Subsequently, five additional species were noted by the 1979 Hull University Expedition and two more by the 1983 Kagoshima University Expedition (Flenley & Richards 1982; Tagawa 1984). At least two of the figs recorded from Rakata are early successional species that are known to exploit disturbed ground and other open sites (*F. fistulosa* Reinw. ex Bl. and *F. ampelas* Burm. f., in Corner (1958)).

Fig trees and fig wasps on Anak Krakatau

The vegetation of Anak Krakatau was extensively damaged by volcanic activity in 1952 and 1957, and consequently the plant succession is still at an early stage. At present, only a small section of the eastern foreland is vegetated, supporting a *Casuarina–Saccharina*-dominated community of 66 seed-plant species (Bush *et al.* 1986). Small- and medium-sized fig trees are a conspicuous feature of the vegetation. Two species have so far been recorded, *F. fulva* Reinw. and *F. septica* Burm. f. (Flenley & Richards 1982; Partomihardjo 1983). Given the difficulties of separating immature *Ficus*, others may also be present.

Janzen (1979) predicted that the colonization of islands by figs was likely to be achieved by the extension of a mainland fig-seed shadow by fruit pigeons or bats, followed by wasp colonization. Observations from Anak Krakatau are in broad agreement with this hypothesis.

The fig species established on Anak Krakatau (*F. fulva* and *F. septica*) are known to be dispersed by bats (Van der Pijl 1957). Fruit bats were first noted on Anak Krakatau by members of the 1982 Kagoshima University Expedition (Tagawa 1984). Two years later, in September 1984, about 40 *Cynopterus sphinx angulatus* (lesser dog-faced bats) were captured during one night's mist-net trapping on the island (R. Zann in Thornton (1985)). This species was sighted again in 1985 and 1986, together with two other fruit eating species, *Rousettus amplexicaudatus infumatus* and *Pteropus vampyrus*.

The *C. sphinx* captured in 1984 were seen to be regurgitating and defaecating fig seeds. These seeds were almost certainly produced by trees on other islands because no fruiting *Ficus* were found on Anak Krakatau at that time. Previous searches by members of the 1979 and 1983 Hull University Expeditions had also failed to detect fruiting *Ficus* on the island (N. Barker, M. Bush & P. Jones, personal communications). Given the small vegetated area on Anak Krakatau (only *ca.* 17 hectares†) it is unlikely that fruiting *Ficus* would have been overlooked.

The lack of figs and other fruits on Anak Krakatau suggests that *C. sphinx* was using the island as a feeding roost rather than as a feeding site (Fleming 1982). The central position of Anak Krakatau in the archipelago may make it an ideal staging post for bats travelling between the islands. Long-distance flights between roosts are well documented for fruit bats, with travelling distances of 10 km or more being recorded (Heithaus 1982; Osmaston 1965; Williams & Williams 1967). The presence of fig seeds in faeces produced at roosts was noted by Osmaston (1965), and specialist insect faunas have evolved to exploit this resource. Various

† 1 hectare = 10^4 m^2.

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species of lygaeid bug that use *Ficus* seeds as their major food are found only in caves inhabited by fruit bats (Slater 1984).

In addition to the dispersal of fig seeds via defaecation, *C. sphinx* may also be transporting whole or partly eaten figs to Anak Krakatau. *C. sphinx* trapped in mist nets in Rakata in 1984 were found to be carrying whole figs in their claws. The carrying of figs to roosts has also been observed in other *Cynopterus* bats (Ridley 1930), and Osmaston (1965) describes figs being dropped hundreds of metres from the nearest feeding sites.

If Anak Krakatau is being used as a feeding roost by *C. sphinx*, then seeds of *Ficus* and other fruit-bearing trees will have been transported routinely to the island. *C. sphinx* was recorded from the Krakataus as early as 1919 (as *C. brachyotis*, see Dammerman (1948)) and may well also have had a major role in the initial dispersal of figs to the islands.

Fruit-eating birds appear to be much less important than bats for the transport of figs to Anak Krakatau. The generalist frugivores *Oriolus chinensis* and *Pycnonotus goiavier* were first observed on the island by a zoological–botanical expedition from Bandung in July 1983. Both species were sighted during the Zoological Expeditions of 1984, 1985 and 1986. Zann (in Thornton 1986) estimated that in 1985 there were 5–7 pairs of *O. chinensis* and 15–20 pairs of *P. goiavier* on the island.

Five species of obligatory fruit-eating pigeon have been recorded from the Krakataus, but a single pair of the cuckoo-dove *Macropygia phasianella* were the only representatives of this group on Anak Krakatau in 1985 (Zann in Thornton (1986)). In 1986 three individuals were seen, together with three individuals of the pink-necked pigeon, *Treron vernans*. Pigeons may be more sedentary than bats and Anak Krakatau may not until now have been producing sufficient fruits to support resident fruit specialists. This situation is already changing because in August 1985 both *F. fulva* and *F. septica* were observed fruiting on Anak Krakatau for the first time. The success of these and future crops is dependent on the numbers of agaonid wasps available on the island.

Observations of the dispersal of agaonids are generally difficult to obtain. Condit (1920) believed that the pollinators of cultivated figs. (*F. carica* L.) could be carried for long distances by the wind, and Ramirez (1970) provided indirect evidence of pollinators travelling for several kilometres between individual trees. Perhaps the most dramatic example of fig-wasp dispersal was provided by the colonization of figs on Kauai in the Hawaiian Islands from source islands at least 100 km distant (Pemberton 1934; Corner 1958).

Fig wasps were first collected on the Krakataus by Karny in 1920 (Dammerman 1948). The agaonids *Blastophaga javana* Mayr and *Ceratosolen bisulcatus* Mayr were recorded, together with the inquiline fig wasps *Philotrypesis spinipes* Mayr and *Sycoryctes simplex* Mayr (both Torymidae). *C. bisulcatus* was also collected subsequently by Dammerman in 1933. No additional records are available.

Figs from four species of *Ficus* were collected on Rakata and Sertung by E. Hall during the 1983 Hull University Expedition. Agaonids and inquiline torymids were present in each (S. G. Compton, unpublished results) and the indications are that the trees on these islands are supporting fig wasp faunas that are comparable to those on the mainland.

Three sweep-net collections of chalcids were made on Anak Krakatau in September 1984. Among the material collected were four species of agaonids, each represented by a single female. *C. bisulcatus*, the pollinator of *F. septica*, was the only species positively identified. Also present were a *Blastophaga* species (not *B. javana*), a *Liporrhopalum* sp. and a *Platyscapa* sp.

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Sweep netting of the vegetation on Anak Krakatau in 1985 produced further agaonid females (mainly *Waterstoniella* spp. (J. T. Wiebes, personal communication)). Two non-pollinating fig wasps (subfamily Sycoecinae) were also collected in white-water traps positioned on the western side of the island near sea level, with a third turning up in a pitfall trap placed on the outer cone. These traps were set up on barren lava and ash, with the nearest vegetation a kilometre to the north and separated from the traps by the volcanic cone (Thornton *et al.* 1988). Sycoecines are seed predators, entering figs but failing to pollinate them effectively. All three individuals were *Diaziella macroptera* Grandi, a species previously recorded from Sumatra (Wiebes 1974; Gardiner & Compton 1987).

No fruiting *Ficus* were present on Anak Krakatau in 1984 and the agaonids collected there must have been transported from fig trees elsewhere. Similarly, the insects collected in the water traps are believed to represent wind-borne fall-out carried from the other islands or the mainland. The origin of the agaonids collected in the vegetated area in 1985 is more problematical and although no fig trees with mature fruit were observed on Anak Krakatau at that time, some wasps may have emerged from trees that had fruited earlier.

The longevity of adult agaonids is believed to be only a few days (Janzen 1979), yet these collections on Anak Krakatau show that this is sufficient time for potential pollinators to be reaching the island on a regular basis. It was not established whether or not pollinators had reached the figs that were produced on Anak Krakatau in 1985, but confirmation of pollination taking place was achieved in 1986, when wasps were found inside figs of both *F. fulva* and *F. septica*. The following adult wasps were reared from *F. fulva*: *Blastophaga inopinata* Grandi (Agaonidae), *Philotrypesis grandii* Wiebes and a ?*Sycoryctes* sp. (both Torymidae). The torymids are inquiline species and show that a well-developed fig-wasp community was already present.

The years 1984–86 appear to have spanned a critical period in the colonization of Anak Krakatau by fig trees and the animals associated with them. The available information can be summarized as follows.

1979–83. No fruiting figs found, despite specialist attention. *C. sphinx* noted in 1982.

1984 Fig seeds are being transported to the island by *C. sphinx*. Moderate-sized trees are present, but not yet producing figs. Fig wasps are arriving as aerial fall-out and could pollinate the figs if any were available. Fruit-eating birds are effectively absent from the island, although some facultative frugivores present.

1985 *F. fulva* and *F. septica* are observed fruiting for the first time. Cuckoo-doves (obligatory frugivores) appear on the island.

1986 The successful pollination of both *F. fulva* and *F. septica* is confirmed and inquiline fig wasps are already present. Further fruit-eating pigeons are observed, together with two additional species of fruit bat.

The situation on Anak Krakatau is now at a most interesting stage of development. Figs are being produced and agaonids are arriving to pollinate them. The progeny of these colonizing agaonids should be in sufficient numbers to ensure improved pollination rates and in time the establishment of a fig tree population that is effectively independent of pollinators arriving from other islands. The change from a *Casuarina*-dominated vegetation to mixed lowland rainforest may now be expected to accelerate.

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The chalcid fauna of the Krakatau Islands

The Chalcidoidea is one of the largest groups of parasitic wasps, including in excess of 100000 species worldwide, although only a few of these have been described (Noyes 1978). With the exception of certain families (Pteromalidae, Torymidae) the group appears to be particularly species-rich in the tropics (Noyes 1978; Compton 1986). Given the problems of naming large numbers of tropical chalcids, many of which are likely to be new to science, it was decided to adopt a quantitative approach to the study of the chalcids on the Krakataus. This involved the sampling of chalcids at various sites on the islands and the assignment of the insects collected to nominal taxa.

(a) *Methods*

Insects were collected by sweep-net sampling of vegetation by using a 'Boucêk-style' triangular net with a long handle (Noyes 1982). After short periods of sweeping the net bag was examined and any chalcids present were extracted. Care was taken to search the bag thoroughly for the smaller species, but despite this some bias towards the collection of larger individuals is likely.

Insects were mounted individually on card rectangles before being grouped into 'nominal' species. *Tetrastichus* males (Eulophidae, Tetrastichinae) were excluded from the counts because of difficulties with associating the sexes. Additional specimens obtained by alternative collecting methods or by 'casual' sweep-netting were also excluded.

(b) *Results*

Sweep-net collections were made on 11 occasions in September 1984. Table 1 summarizes information on the sample sites and the number of insects collected. Coverage of the four islands varied considerably. The small vegetated area on Anak Krakatau was sampled three times and the collections may represent a reasonably complete census of the species present on the island at that time. This is not the case with the other islands, where the coverage was much less comprehensive.

A total of 1216 individuals were present in the samples (excluding *Tetrastichus* males). These were from 14 families and 266 nominal species. The Eulophidae was the dominant family in

Table 1. Sweep-net collections of chalcids on the Krakatau Islands

(Coastal vegetation was sampled at all the sites except the northwest ridge on Rakata.)

island	collection site	habitat description	collection code/date (1984)	sample size (chalcids)
Anak Krakatau	vegetated area on east side	*Casuarina* and *Saccharum*	A 10 Sep. E 13 Sep. L 21 Sep.	342
Sertung	spit at north end of island	*Casuarina* woodland	B 11 Sep. G 15 Sep.	117
Sertung	forested area south of spit	secondary lowland forest	C 11 Sep. H 15 Sep.	289
Rakata	Zwarte Hoek	secondary lowland forest	D 12 Sep. J 16 Sep.	175
Rakata	northwest ridge alt. 250 m approx.	secondary forest	F 14 Sep.	102
Panjang	'Transect' across north of island	secondary forest	K 20 Sep.	191

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terms of both numbers of species and specimens and the Encyrtidae were also well represented (table 2). Species counts from the four islands were as follows: Rakata, 121 species; Sertung, 109 species; Panjang, 47 species and Anak Krakatau, 84 species. Because of the variable coverage of the different islands it is inappropriate to relate these totals to factors such as island size or successional status.

Table 2. The numbers of species of chalcids collected in the Krakatau Islands during September 1984

family	Anak Krakatau	Sertung spit	Sertung forest	Rakata Z.H.	Rakata N.W.R	Panjang
Agaonidae	4	0	2	3	1	0
Aphelinidae	8	1	7	4	3	1
Chalcididae	5	3	7	3	0	3
Elasmidae	2	1	2	1	1	2
Encyrtidae	20	12	9	16	13	11
Eucharitidae	0	1	3	2	1	1
Eulophidae[a]	21	22	28	30	24	14
Eupelmidae	5	3	1	1	1	4
Eurytomidae	6	2	1	0	0	1
Mymaridae	6	2	2	3	3	2
Perilampidae	0	0	0	0	0	1
Pteromalidae	3	3	10	10	7	7
Torymidae	0	0	1	1	7	0
Trichogrammatidae	4	1	0	0	0	0
totals	84	51	83	74	63	47

[a] *Tetrastichus* males excluded.

The composition of the chalcid assemblages at the six sample sites is compared in figure 1, which shows the proportion of the species shared by pairs of sites. The chalcid collections from Anak Krakatau had most in common with those from the Sertung spit (figure 1*a*, *b*), whereas those from the lowland forests of Rakata (Zwarte Hoek), Sertung and Panjang also shared a relatively large proportion of their species (figure 1*c*, *d*). The most distinct collection was from the montane forest on Rakata, which had at most 11.6% of its (pooled) species shared with another site.

A more detailed examination of the chalcids on the islands was done by correspondence analysis (reciprocal averaging). This is a graphical display technique which provides a means of plotting both sample sites and individual species on the same axes. Sample sites plotted close together have relatively similar faunas, and species plotted close together have similar distributions. The uses of this technique have been discussed by Gauch (1982), Greenacre (1984) and Underhill & Peisach (1985). The results of the ordination are given in figure 2. Samples (in chronological order) are labelled A–K (no sample I). Dots indicate the coordinates of individual species on the two axes, whereas numbers indicate positions where more than one species is situated at the same coordinates. Where large numbers of species are plotted at the same coordinates this reflects species that were only collected in one sample. For example, 7 species were unique to sample B, 37 to sample F and 16 to sample H (figure 2).

The *x*-axis (with an Eigen-value of 0.18) divides the sample sites into two groups. The first group comprises those from Anak Krakatau (samples A, E and L) and those from Sertung spit (samples B and G). The second group contains the forest sites on Sertung (samples C and H),

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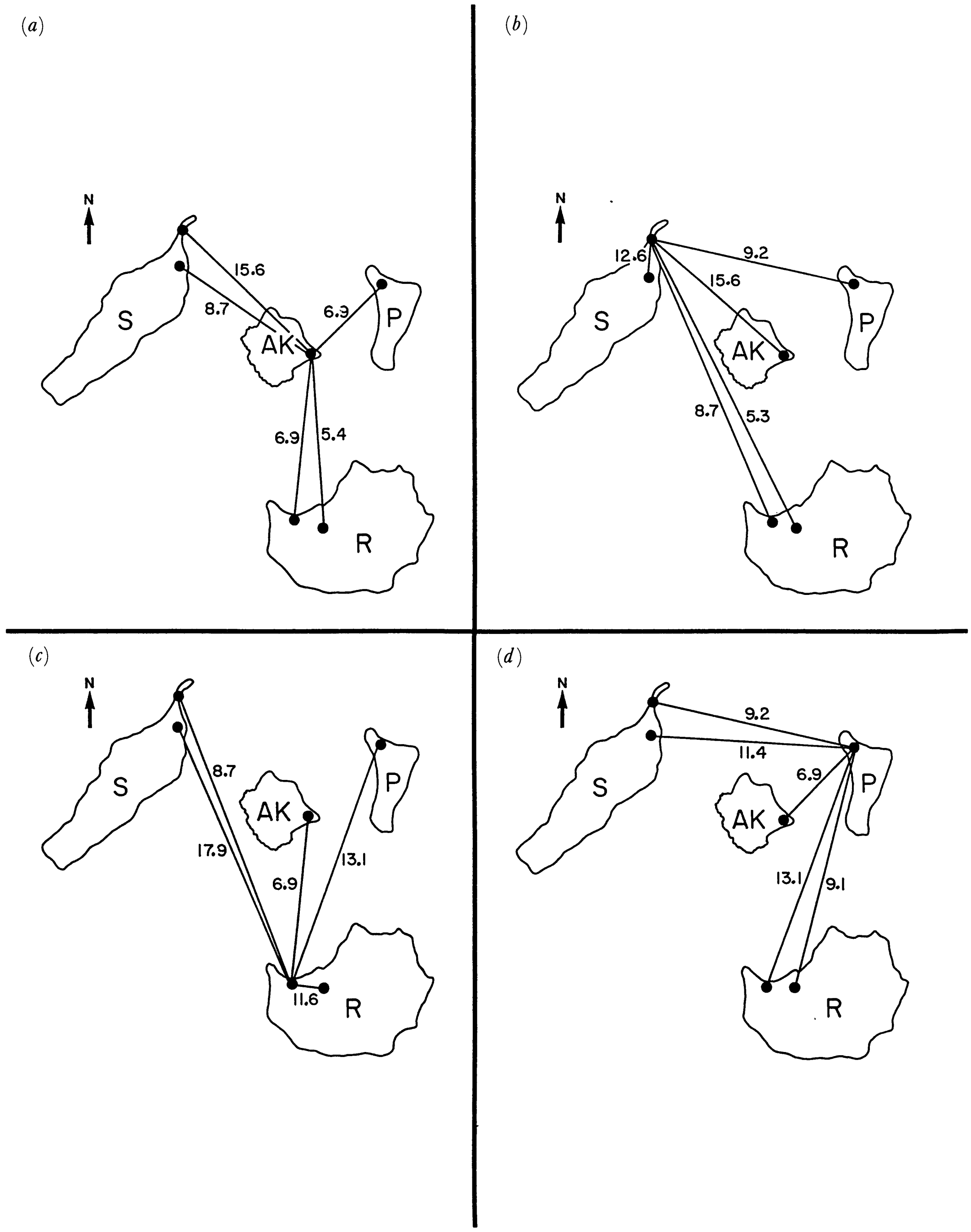

FIGURE 1. The numbers of chalcid species shared by sample sites. Each value represents the percentage of the (pooled) faunas shared by each pair of sites. Not illustrated are the species shared by Rakata northwest ridge and Sertung forest (10.8 %).

Panjang (sample K) and Rakata (samples D, F and J). The y-axis (with an Eigen value of 0.14) highlights the difference in the Rakata montane forest sample (F) from the other forest samples.

The position of each species on the ordination provides a means of distinguishing its habitat preferences. Those species plotted at the higher values on x-axis are characteristic of *Casuarina*

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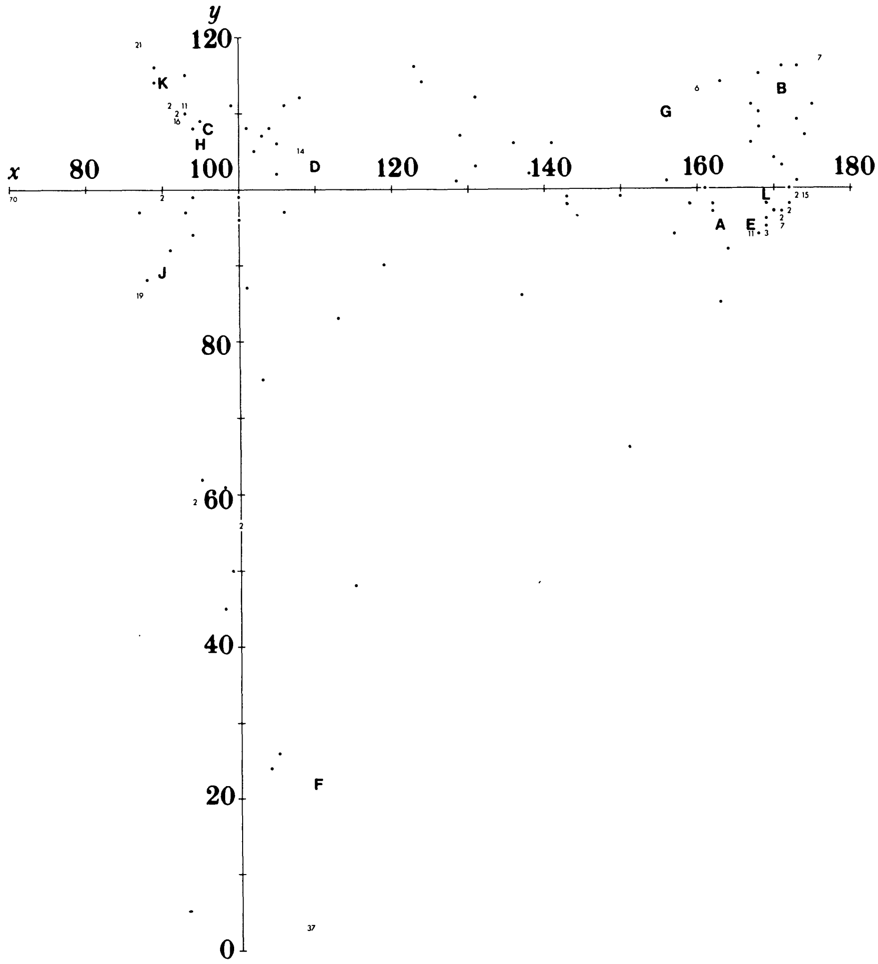

FIGURE 2. Ordination of the chalcid species and samples on the Krakatau Islands. Samples are coded A–K (table 1) and each species is indicated by a dot. Numbers indicate where more than one species is plotted at the same coordinates.

woodland, whereas those plotted at lower values on this axis are more typical of secondary rainforest. An examination of the species plotted at intermediate positions along the x-axis showed that these included several chalcids that had been noted as being associated with coastal vegetation. This vegetation type was sampled at all the collection sites except F.

Is the chalcid fauna of the Krakataus 'disharmonious', with a mixture of species different from that of equivalent habitats on the mainland? This question cannot be addressed directly because there is no information available on the composition of the chalcid faunas of Java or Sumatra. Collections made in a way similar to those described here are available, however, from Cameroun in tropical West Africa (Compton 1986). Table 3 compares Cameroun collections at Musone and Victoria with the overall Krakatau fauna. The vegetation at the two sites in Cameroun consisted of lowland secondary forest and scrub. Encyrtidae are not included in the table because data from Cameroun are not available. At the family level, the composition of the Krakatau fauna is remarkably similar to that from mainland West Africa. The Krakataus may be relatively depauperate in trichogrammatids, but are rich in agaonids and torymids, two groups associated with fig trees, and in eupelmids and chalcidids.

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Table 3. A comparison of the composition of sweep-net collections from the Krakatau Islands and Cameroun

(Comparable data for Encyrtidae were not available.)

	Krakatau Islands		Cameroun: Musone		Cameroun: Victoria	
	number of species	rank	number of species	rank	number of species	rank
Agaonidae	6	9	1	12	0	13
Aphelinidae	15	3	19	3	9	4
Chalcididae	11	5	4	8	5	7
Elasmidae	2	12	3	9	4	8
Eucharitidae	4	11	3	9	1	11
Eulophidae[a]	48	1	45	1	22	1
Eupelmidae	11	5	6	7	3	9
Eurytomidae	8	7	7	6	6	5
Mymaridae	12	4	15	4	12	3
Perilampidae	1	13	2	11	1	11
Pteromalidae	24	2	24	2	13	2
Torymidae	8	7	1	12	2	10
Trichogrammatidae	5	10	9	5	6	5
totals	155		139		84	

[a] *Tetrastichus* spp. excluded.

A noticeable feature of the Krakatau fauna was the small number of brachypterous species that were present. Throughout the islands as a whole, only three short-winged species were collected (two encyrtids and one eupelmid). These small numbers are in marked contrast to, for example, the collections from Cameroun, which included numerous flightless encyrtids and eupelmids.

Discussion

Numerically, chalcids are clearly a major component of the insect fauna of the Krakataus. In the samples described here 266 species were represented, a total for the superfamily that considerably exceeds those of, for example, psocopterans (approximately 80 spp.), Aculeate Hymenoptera, excluding ants (86 spp. (Yamane 1983)) or butterflies (55 spp. (New *et al.* 1988)). Moreover, and unlike some of these groups, the collections are clearly not exhaustive. Almost half of the species were represented by only a single specimen in the collections and assuming that the species–abundance curve for chalcids on the islands approximates to the log-normal, then there are many more species on the islands that await discovery (Preston 1948; May 1976). This projection is supported by evidence from the examination of chalcids collected by alternative methods or by other members of the expedition. These collections contain additional species absent from the major samples.

The abundance of chalcids on the Krakataus can be related to their abundance on the mainland and to their dispersal ability. Chalcids are small insects, a characteristic which facilitates dispersal by air currents (Askew 1968). In temperate latitudes, chalcids are frequent members of the aerial plankton and are known to be carried many miles out to sea (Cheng & Birch 1978; Hardy & Cheng 1986). A similar degree of wind dispersal in the tropics would ensure a steady flow of immigrants to the Krakataus.

The correspondence analysis of the distribution of chalcid species on the islands suggests that

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assemblages may be associated with different stages of the vegetation succession. The primary colonizer *Casuarina equisetifolia* J. R. and G. Forst. is the dominant tree on Anak Krakatau and the Sertung Spit. Several chalcids appear to be associated with this vegetation type and as succession proceeds it is this group of species which would be predicted to decline. The ordination of the species also emphasizes the distinctive nature of the upland sample on Rakata, relative to the other areas of secondary rainforest. In part this may be due to the absence of coastal species at this inland site, but it also implies that some vertical stratification may be present.

Despite the abundance of chalcids on the islands it is unlikely that the entire complement of mainland species can have become established there. The absence of certain chalcids, or other parasitoids, may have been a factor in the outbreaks of phytophagous insects that have occurred on the islands. Yukawa (1984*a*, *b*) has described outbreaks of the tephritid fly *Dacus albistrigatus* De Meijere and the scale insect *Crypticerya jacobsoni* (Green) that took place in 1982. He found no evidence of attacks by parasites on *C. jacobsoni*, despite its abundance and its presence on the islands since at least the 1920s (Dammerman 1948).

The scarcity of brachypterous chalcids on the Krakataus may be related to the short period of time that the insects have been established on the islands. It is interesting to note, however, that one brachypterous encyrtid was already established on Anak Krakatau in 1984. Polymorphism for wing length is not uncommon in chalcids and, as dispersal to the islands must be almost entirely by air, the brachypterous individuals are likely to be descendants of winged colonizers.

This paper has examined general patterns in the composition of the chalcid fauna of the Krakataus and has looked in detail at one particular group, the fig wasps. The chalcids collected on the islands are available for study by taxonomists and in the coming years it is hoped to extend these general conclusions and investigate the distribution and abundance of individual species.

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