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Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion

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Abstract

Location, aims Long Island's biota was destroyed by volcanic eruption in *c.* 1645, and Motmot, an emergent island in its caldera lake, was re-created in 1968, providing a nested pair of natural colonization sequences. In 1999 we surveyed the plants and vertebrates of Long and the entire biota of Motmot for comparison with previous surveys of Long (1932, 1972, birds only) and Motmot (1969–88).

Results The known flora of Long is 305 vascular plants (thirty-two pteridophytes, 273 spermatophytes), including thirty-one *Ficus* species, the sixteen fruiting all having pollinating wasps, and there were eleven species of effective fig dispersers. There were two frog species, a crocodile, a monitor, seven skinks, four geckos, a boid snake, fifty species non-migrant land birds, seven bats, two rats, a cuscus (probably introduced) and feral pigs, dogs, cats and chickens.

Most of Motmot's surface was barren or sparsely vegetated ash, cinder and lava fields. There were seven pteridophyte and thirty-eight spermatophyte species, including eight *Ficus*, and the cumulative known flora comprises eleven pteridophytes and fifty-one spermatophytes, mainly zoochorous and anemochorous, with sedges, grasses and herbs predominating. All *Ficus* individuals but one were small; three plants of two species bore syconia but had not been pollinated and had not set seed. Motmot's known invertebrate fauna comprises thirty-five species, mainly predators and scavengers; two spider and one ant species dominating. An insectivorous bat and eight land bird species (three breeding) were the only vertebrates.

Main conclusions Long's biota comprised mainly widely distributed species with broad ecological tolerances, well-adapted for colonizing species-poor islands. The mid-level caldera plateau, as in 1932, was covered in fairly open forest of similar-sized trees with a few much larger individuals and little or no understorey. Primary rain forest tree species from the region were under-represented or absent but secondary forest species were common. There were few regional endemic *Ficus* species. The avifauna comprised species with good dispersal ability, lacked endemic subspecies and probably for at least the past seven decades has been held at a quasi-equilibrium of fifty species, fourteen below the theoretical number. More than half the fifty-four resident land birds known from Long (and three of the seven bats) are high class tramps in the sense of Diamond; only two birds are high-S species. Turnover has been low and none of the bird super-

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tramps has been replaced. The non-avian fauna comprised mostly high-category tramp-type species with relatively broad habitat requirements and extensive geographical ranges. Non-volant vertebrates comprised a number of highly vagile species associated with humans. Several groups, especially snakes and amphibians, were depauperate compared with the fauna of other islands in the area. Long's biota is evidently held at an arrested stage of development by some physical factor, possibly the extremely porous substratum and relatively dry climate.

The allochthonous input of lake insects to Motmot evidently provides the major energy source for its animal communities, with a very minor contribution from organic flotsam. Reflecting Motmot's very isolated situation, plant colonization has been slow, but when more fig individuals mature and fig–wasp populations become established fruit production should attract frugivores and start a positive feedback process which will accelerate the growth of Motmot's community.

Long's colonization shows similarities with that of Krakatau (Sunda Strait, Indonesia) after the 1883 eruption, and species shared by the two include a high proportion of pioneer species. Motmot's triple isolation (sea, land and fresh-water barriers) means that its colonization differs markedly from those on two marine emergent islands of the region, Tuluman (Admiralty Group) and Anak Krakatau.

Keywords
Island colonization, dispersal, establishment, community assembly.

INTRODUCTION

The introductory paper to this series (Thornton, 2001) provides a general introduction to the geographical and geological setting, volcanic history and pre-1999 biological surveys of Long Island and Motmot, and is summarized here.

In about 1645 AD, Long Island, 55 km north of New Guinea (Fig. 1), erupted explosively, almost certainly destroying its macrobiota and leaving a 13-km diameter caldera in which a deep fresh-water lake, Lake Wisdom, developed. Long Island's present biota is thus no more than 350 years old. In the 1940 and 1950s volcanic activity

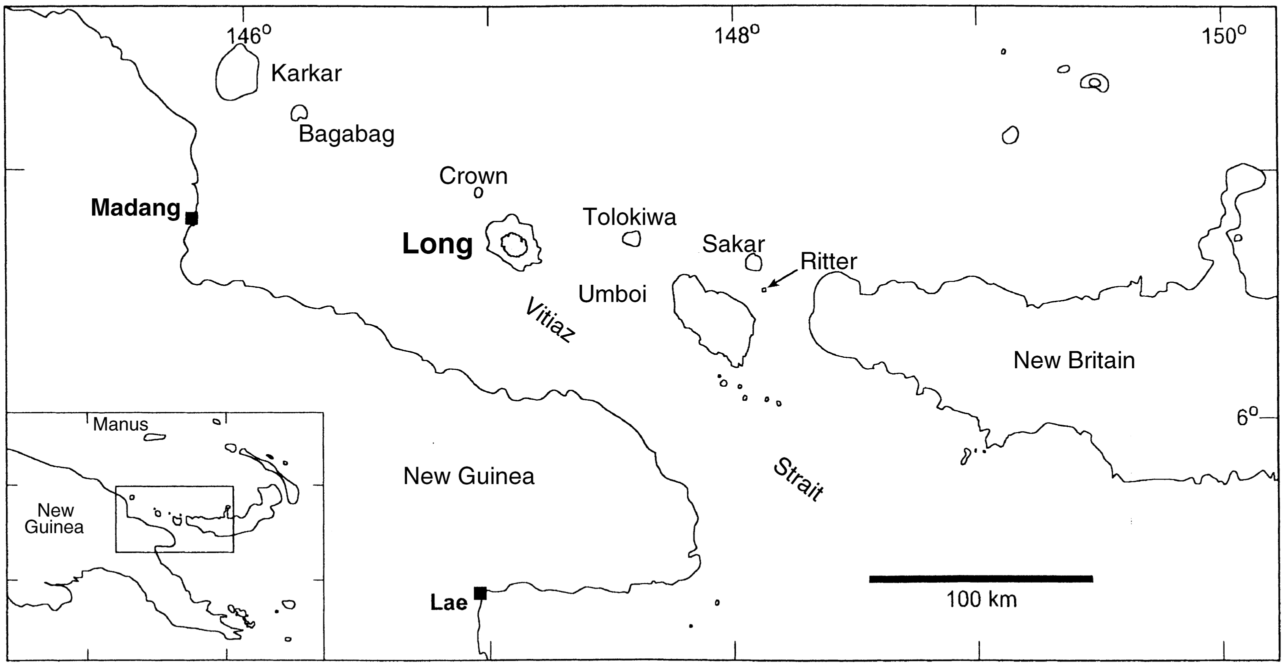

Figure 1 Small islands of the western Bismarck Volcanic Arc, off the northeast coast of New Guinea. Modified from Ball & Hughes (1982), with permission.

resumed and a succession of low ash islets emerged from the caldera lake until in 1968 an eruption re-created the present island, Motmot. This grew and was colonized by animals and plants, probably largely from the surrounding ring of Long Island. Further eruptions on Motmot in 1973 and 1974 included lava flows, thus ensuring the island's permanence but setting its young developing biota back to almost zero.

We surveyed Long Island and Motmot in June–July 1999 in order to provide an additional datum in the study of a nested pair of natural colonization sequences: first, the oversea recolonization of Long Island from islands unaffected by the eruption and over 60 km away in Vitiaz Strait, or from the mainlands of New Britain and New Guinea, 125 and 55 km distant, respectively (Fig. 1); and secondly, colonization of Motmot, presumably predominantly from Long Island over at least 4 km of fresh water (Fig. 2).

We aimed to investigate Long's hitherto unknown flora and its vertebrate fauna, of which only the birds had been surveyed, in 1932 (Coultas, 1933–1935) and 1972 (Diamond, 1974a, b, 1975, 1976; 1977, 1981; Diamond *et al.*, 1989). In order to further monitor the early development of Motmot's new community, we surveyed its entire biota, which had been surveyed earlier by Bassot & Ball (1972), Ball & Glucksman (1975, 1981) and Osborne & Murphy (1989).

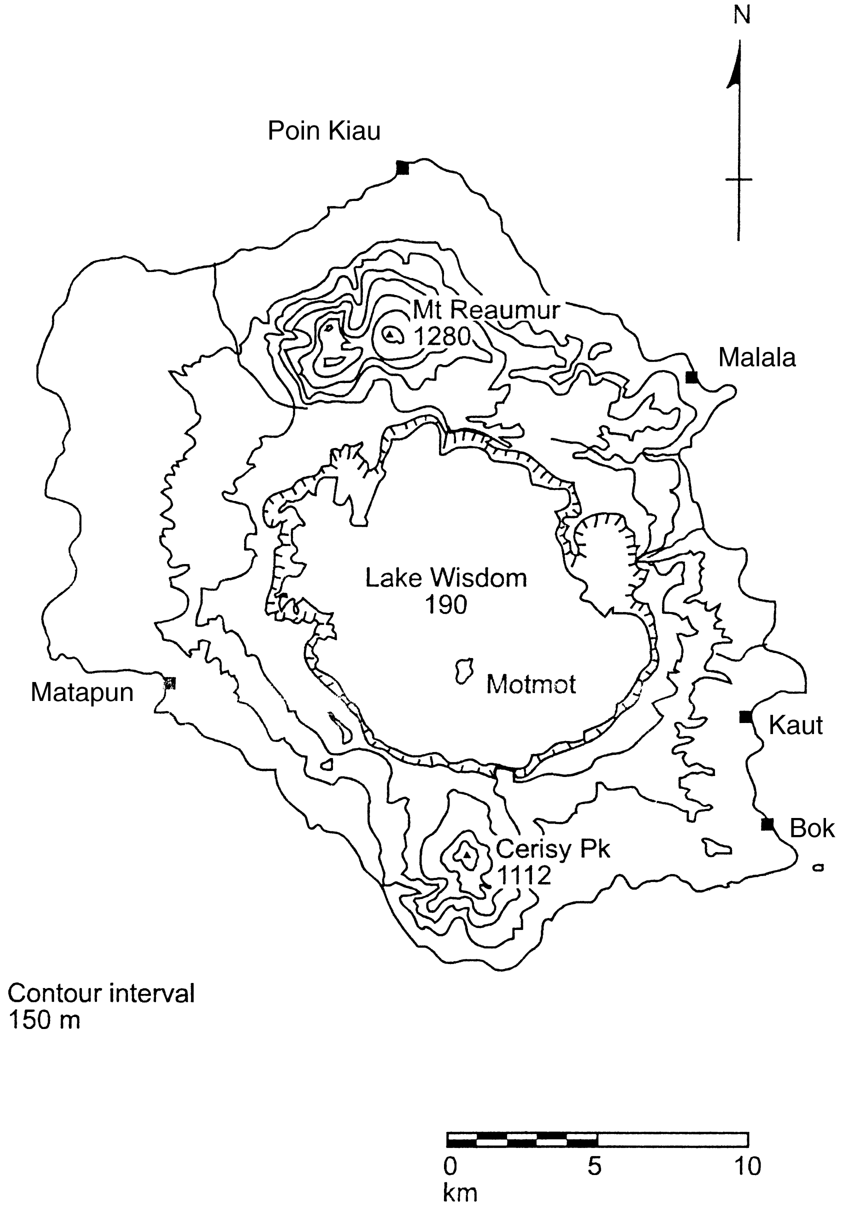

Figure 2 Long Island, showing caldera cliff-wall hatched. Modified from Ball & Hughes (1982), with permission.

Table 1 Numbers of species of selected taxa recorded from Long Island and Motmot in 1999. Numbers in brackets include herbarium records from the Forest Research Institute, Lae, and earlier records from Motmot, and assume species found only on Motmot are present also on Long Island itself

	Long	Motmot
Pteridophytes	17 (32)	7 (11)
Spermatophytes	145 (273)	38 (51)
Frogs	2	0
Crocodile	1	0
Snake	1	0
Varanid lizard	1	0
Geckos	5	0
Skinks	7	0
Resident land birds	50	3*
Pigeons and doves	8	0
Rats	2	0
Megabats	6	0
Microbats	2	1
Cuscus	1	0
Feral pig, dog, cat, chicken	4	0

*Further seven species recorded with no evidence of breeding, two only as prey remains.

RESULTS

Long Island

We surveyed the west central part of Long Island from the shore up to the caldera lake and made a short excursion to 700 m on Mt Cerisy (Fig. 2). The caldera plateau (*c.* 400 m), as in Diamond's days, was a rather open forest of low-stature trees of similar size, with a few much larger trees and free-standing hemi-epiphytic figs, especially *Ficus virens* Ait., and little or no understorey. The forest was dominated by a few very common species, such as *Horsfieldia tuberculata* (K.Sch.) Warb., *Melanolepis multiglandulosa* Reich.f.&Z., *Poikilospermum poxianum* (Winkl.) Merr., *Dendrocnide longifolia* (Hemsl.) and *D. schlectri* (Winkl.) Chew. We found 162 species of vascular plants (seventeen pteridophytes, 145 spermatophytes). Including hitherto unpublished records of plants from Long Island in the herbarium of the Forestry Research Institute, Lae, the island's known vascular flora totals 305 species, thirty-two pteridophytes, 273 spermatophytes (Table 1). Twenty-nine species (six pteridophytes, twenty-three spermatophytes) are known only from Motmot, although we assume that they are present but unrecorded on Long Island (Harrison *et al.*, 2001).

The 1999 non-migrant land bird fauna comprised fifty species (Schipper *et al.*, 2001) (Table 1). The loss of one bird species since 1933 was confirmed. In the past 27 years, three species have colonized and three are believed to have become extinct, a turnover rate of 0.22% per year. The non-avian vertebrate fauna included two anuran amphibians, at least fourteen reptile species and at least nine indigenous mammals. The reptiles comprised a crocodile, boid snake, varanid lizard, four geckos and seven skinks, and the mammals two rats and seven bat species, including six pteropodids and an emballonurid (Cook *et al.*, 2001). An introduced cuscus was abundant, and pigs, dogs, cats and chickens were feral.

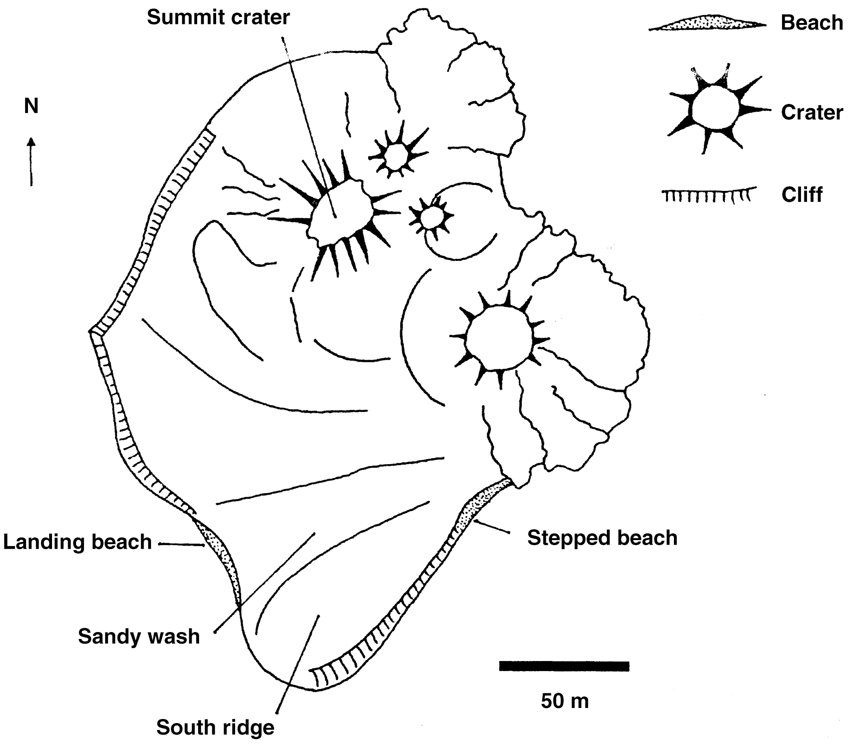

Figure 3 Sketch map of Motmot, based on aerial photographs in 1976 (Ball & Glucksman, 1981) and 1988 (Osborne & Murphy, 1989), sketches in Cooke *et al.* (1976), and observations and bearings made in 1999.

Motmot

In 1999 Motmot's area was about 0.25 km^2 and its height about 50 m (Fig. 3). Its surface of lava, cinder and ash fields was still barren or very sparsely vegetated, largely by sedges and grasses. We found seven pteridophytes and thirty-eight spermatophyte species (including eight species of *Ficus*), all typical early colonists in the region (Harrison *et al*., 2001; Shanahan *et al*., 2001a). The minimum cumulative known flora (assuming plants identified only to genus in early collections are referable to identified species of the same genus collected later) of sixty-two vascular plants includes eleven pteridophytes and fifty-one spermatophytes (ten *Ficus* species) (Harrison *et al*., 2001). Motmot's 1999 flora was similar to that on Long Island in terms of proportions of species in the subclasses, seed-dispersal syndromes and life-forms, although of course there were no specialist littoral species with sea-dispersed propagules. One individual of *F. benjamina* L. was large enough to produce a crop of fruit but individuals of other zoochorous species were probably too small, and no individuals with ripe fruit were observed. *Ficus wassa* Roxb. and *F. nodosa* Teysm. et Binn. were found bearing a few syconia but none had been pollinated.

Two chironomid midge species were present in 1969, four in 1972 and at least eleven in 1976, and caddis larva of a *Triplectides* species were abundant in 1969–72 (Ball & Glucksman, 1975). In 1999 adults of four chironomid species and the caddis fly *T. helvolus* Morse & Neboiss (an Australian species hitherto unknown from the New Guinea region) were rising in numbers from the Motmot lake shore in the evenings. Damselflies, *Xiphiagrion cyanomelas* Selys (first seen in 1969) were common and the dragonflies *Tramea liberata* (Lieftinck) (seen 1969), *Orthetrum sabina* (Drury) and the hitherto unrecorded *Pantala flavescens* (Fabricius) were present (Edwards & Thornton, 2001).

The rapid growth of the ant fauna was noted by Ball & Glucksman (1975), from two species in 1971 to seven in the following year. In 1999 the previously unrecorded *Anoplolepis gracilipes* (Smith) was dominant and widespread and there were at least nine other species. Earwigs, *Labidura riparia* Pallas, which had been found only under rocks near the beach in 1971, were almost ubiquitous in 1972 but in 1976 again occupied a much reduced area (Ball & Glucksman, 1975, 1981). In 1999 they were found only under half-submerged lava rocks at one site on the eastern coast.

A ground-hunting lycosid spider, '*Trochosa*' *papakula* (Strand), had been noted in 1969, was almost ubiquitous in 1972 but very much less extensive in 1976 (Ball & Glucksman, 1975, 1981). In contrast to the earwig, in 1999 it was again widely distributed, abundant, and reaching densities of 22 m^{-2} although ground insects were scarce (Edwards & Thornton, 2001). Tetragnathid spiders had not been reported previously but in 1999 *Tetragnatha nitens* Audouin was abundant, and a second species of the genus was less common.

We found no amphibia or reptiles. The only vertebrates recorded were an insectivorous bat, the emballonurid *Mosia nigrescens solomonis* (Thomas) (the Lesser Sheath-tailed Bat), and eight bird species (two more as prey remains only). Pacific Black Duck, *Anas superciliosa* Gmelin, Pacific Swallow, *Hirundo tahitica* Gmelin (both nesting by 1969) and the Melanesian Megapode, *Megapodius freycinet* Gaimard, were breeding, the first two in numbers. Red-throated Little Grebe, *Tachybaptus ruficollis* (Pallas), were seen off-shore and other birds recorded included Rufous Night-heron, *Nycticorax caledonicus* (Gmelin) and three raptor species previously recorded by Ball & Glucksman (1975): Brahminy Kite, *Haliastur indus* (Boddaert); White-breasted Sea-eagle, *Haliaeetus leucogaster* (Gmelin); and a pair of Peregrine Falcons, *Falco peregrinus* Tunstall. An Osprey, *Pandion haliaetus* (Linnaeus) had been seen passing over in 1971 and 1972 (Ball & Glucksman, 1975) but we did not record it from Motmot. Skeletons of five ducks, a megapode, three Collared Kingfishers [*Halcyon chloris* (Boddaert)], an *Aplonis* starling and a sea-eagle were found (Schipper *et al*., 2001).

DISCUSSION

Long Island

The nature of the colonists

Tramps and supertramps. Diamond (1974a, 1975) gave the designation 'supertramps' to bird species of the Bismarcks that are specialists of small, isolated or young islands with small avifaunas, and not found on larger, species-rich islands. Supertramps are important early colonists but cannot survive the competition that comes with more species. As species number increases it is expected that the supertramps will be replaced by more sedentary, 'high-S' species, that specialize in competitive ability rather than dispersal ability, flourish in competitive situations of many species and are restricted to species-rich islands. Ten of Long Island's fifty non-migrant land bird species in 1999 are supertramps (Schipper *et al*., 2001). The 'Long group' [Long, Crown and Tolokiwa islands (Fig. 1) all severely affected by Long's eruption] has three times the number of supertramps expected of a Bismarck island of similar total species number. In contrast, Long's larger neighbour, Umboi, which was relatively unaffected, has only three supertramps, and two of these are of localized occurrence (Diamond, 1981; Diamond *et al*., 1989).

Diamond established various categories of tramps (A–D), which occur on large species-rich islands and on a varying number of smaller islands of varying degrees of remoteness, size and impoverishment. D-tramps are the closest to supertramps in distributional characteristics, A-tramps the most similar to high-S species. Diamond noted that as well as containing ten of the Bismarcks' thirteen supertramps, the fifty-four known Long Island species also include all fourteen of the Bismarcks' D-tramps, eleven of nineteen C-tramps, nine of seventeen B-tramps and only six of twenty-six A-tramps.

As well as an over-representation of supertramps, Long Island has a dearth of high-S species (Diamond *et al*., 1989). In fact, although Long has twenty-four of the Bismarcks' twenty-seven supertramp/D-tramp species, it has only two of the Bismarcks' fifty-two high-S species (compared with Umboi's sixteen). Diamond's group also observed that Long's avifauna has other youthful characteristics: a lack of island endemic subspecies (which occur on all other Bismarck islands of its size), a species number below the theoretical equilibrium, and evidence from elsewhere in the Bismarcks (Vuatom Island) that most of its species have been selected for good over-sea dispersal ability.

Thus at least a fifth of Long's avifauna (the supertramps) has arrived, not from the large sources of New Britain or New Guinea (which is closer than Umboi to Long Island) but from smaller islands stocked with species well-adapted for dispersal. This is a minimum proportion. Long Island populations of species with distributions that include small as well as large islands may not have originated on the large ones. In one case we know this to be so. Long's White-collared Kingfisher, *Halcyon chloris* (a D-tramp), is of a subspecies, *stresemanni* Hartlaub, that has supertramp characteristics, occurring also on Witu, Unea and/or Umboi, but not on New Guinea or New Britain (J. M. Diamond, pers. comm.). Other populations that are not of distinct subspecies revealing that they arrived from small islands, may nevertheless have done so.

High-category tramps may also be recognized among the bats. Koopman (1979) established a number of bat tramp categories in the manner of Diamond (1975), based on incidences on New Guinea, New Britain, and some twenty smaller islands, mainly of the NE New Guinea 'offshore' islands of the Bismarcks Volcanic Arc. He listed eight high-S species, one A-, eight B/C- and two D-tramps, and two 'peculiar' supertramps (peculiar because, although absent from New Guinea and New Britain, they occurred on only one of the small arc islands). According to Bonaccorso (1998), however, the Variable Flying Fox, *Pteropus hypomelanus* Temminck (listed as a B/C-tramp by Koopman) is a supertramp (*sensu* Diamond, 1975), being almost restricted to species-poor small islands throughout its extensive range (Thailand to Philippines, Solomons) and having been collected from New Guinea island only twice (and once from New Britain), although present on over a score of small islands to the north and east of New Guinea. It occurs regularly on mainlands only on the southeast coast of Indochina. Chasen & Kloss (1927, p. 807) noted that in the Mentawi Islands to the west of Sumatra this species generally replaces *Pteropus vampyrus* (Linnaeus) on deep-water or oceanic islands, and 'is not found on the continent or any of the large land-masses.' The Bismarck tube-nosed bat, *Nyctimene vizcaccia* (Thomas), according to Bonaccorso also prefers small-to-medium-sized islands. It occurs on Long, Umboi, Manus, New Ireland and Bougainville and, although present on New Britain, is absent from New Guinea. This species, as now known, comprises two species listed by Koopman as a D-tramp and a supertramp. The black-bellied bat, *Melonycteris melanops* (categorized as a B/C-tramp by Koopman), has a very similar distribution, occurring on Long, Tolokiwa, Umboi, New Ireland and New Britain, and being absent from New Guinea island. Both may be classed as D-tramps, if not supertramps. Thus three of a known bat fauna of seven species are supertramps/D-tramps, about the same proportion as in the avifauna.

Only the avifauna, which has been surveyed three times, can provide evidence of more slowly dispersing high-S or lower-category tramp species displacing supertramps. There is no evidence that this is happening. Nine bird supertramps were established by 1933 and the tenth, the Torres Strait pigeon, *Ducula spilorrhoa* (G. R. Gray), had arrived by 1972. The only extinction since 1933 is of a B-tramp, the eastern black-capped lory, *Lorius hypoinochrous* Gray. It became extinct between 1933 and 1972 in spite of being a preferential feeder on the flowers and young fruit of coconuts (LeCroy & Peckover, 1983), which were being cultivated on Long Island. The three new colonists in 1999 had all been recorded in 1933. The Golden-headed Cisticola, *Cisticola exilis* (Vigors & Horsfield) is a B-tramp, Meyer's Goshawk, *Accipiter meyerianus* (Sharpe), is a high-S species but did not replace a supertramp, and the Nicobar Pigeon, *Caloenas nicobarica* Linnaeus, is itself a supertramp. The proportion of supertramps has not changed in 66 years (Schipper *et al.*, 2001).

Thus no bird supertramp has become extinct, turnover has been very low, and the avifauna is far from achieving an equilibrium number appropriate to an island of Long's area in the region. We believe, along with Diamond (1974a, b, 1976) and Ball & Hughes (1982), that tree growth is constrained and vegetational development arrested at a subclimax stage by some physical factor, probably the poor water retention of the porous, ashy substrata combined with extreme seasonal aridity (an 8-month drought in 1972 was described by Ball & Hughes (1982)), which, in turn, may be holding the avifauna below the theoretical species number, thus allowing supertramps to persist.

Wide-ranging eurytopic species. Diamond recognized that 'supertramps have extraordinarily catholic and unspecialized habitat preferences, and high dispersal ability' (Diamond, 1975, p. 343). As on the Krakatau Islands (Thornton *et al.*, 1990a; Thornton, 1996a), where the biota is little more than 100 years old, a number of successful colonists to Long Island have broad ecological tolerances and extensive geographical ranges.

Although Long Island's flora is incompletely known, it is remarkable that many typical rain forest genera of the Bismarck Archipelago were absent in 1999. The forest on Long Island's caldera plateau lacked many important Bismarcks rain forest genera, such as *Pometia* (Sapindaceae), *Octomeles* (Datiscaceae), *Campnosperma*, *Dracontomelon* (Anacardiaceae), *Pterocymbium* (Sterculiaceae), *Cryptocarya* (Lauraceae), and *Intsia* (Leguminosae) (Mueller-Dombois & Fosberg, 1998). *Eucalyptus deglupta* (Myrtaceae) described by Mueller-Dombois & Fosberg as a common native rain forest species as far as New Britain, has also not been recorded from Long Island (Harrison *et al.*, 2001). In contrast, common species on Long Island such as *Melanolepis multiglandulosa*, *Elaeocarpus sphaericus* (Gaertn.) K.S.

(Elaeocarpaceae), and *Poikilospermum paxianum* (Winkl.) Merr. (Cecropiaceae) are typical secondary forest species elsewhere (Paijmans, 1976; Mueller-Dombois & Fosberg, 1998).

Of Long Island's thirty-one *Ficus* species, for which the nomenclature is more reliable than in other plant groups, only seven (22%) are endemic to New Guinea and New Britain, compared with 56% endemicity in the *Ficus* flora of the area (Corner, 1965). Nine of Long Island's *Ficus* species have ranges extending from Asia to Australia, and seven are amongst the twenty-four species that have colonized the Krakataus (Thornton, 1996a), a substantial overlap considering that these islands lie in different phytogeographical zones.

Many of Long's *Ficus* species also clearly have broad habitat requirements (Corner, 1940). For example, *F. virgata* Reinw. ex Bl., with a range extending from southern Japan to Australia, may be found as a common coastal shrub, growing on rocks, and as a large hemi-epiphyte in inland forests. *Ficus benjamina* L., found naturally from India to northern Australia, on Long Island occurred as a hemi-epiphyte on the caldera plateau and as a free-standing tree on the coast. On Motmot an individual of this species was the largest tree on the island, growing in the harsh environment of an *aa* lava field just beneath the summit crater (Shanahan *et al*., 2001a, b). *Ficus septica* Burm. f., found from Japan to Australia, is a common roadside and disturbed-habitat species and was also one of the early colonists of Anak Krakatau (Thornton, 1996a), a volcanic island which emerged from Krakatau's submarine caldera in 1930 and was self-devastated in 1952.

Hence, on Long Island typical rain forest tree species from the region are under-represented or absent, while secondary forest species are common, and amongst *Ficus* there are relatively few regional endemics and an over-representation of species with very wide distributions and broad ecological tolerances.

Motmot's arthropod community consists largely of tramp-type opportunistic species with wide tropical distributions, which may be loosely regarded as arthropod analogues of Diamond's high-category tramp species (Edwards & Thornton, 2001). The strongly flying dragonfly *Pantala flavescens*, a fugitive species that colonizes rain pools throughout the tropics, the cricket *Teleogryllus oceanicus* Le Guillou and the scavenger/carnivore earwig *Labidura riparia*, are examples of cosmopolitan species which reach very isolated islands. Motmot's most numerous and ecologically dominant ant, the formicine *Anoplolepis gracilipes*, is spread widely by human activity in tropical Africa, Asia and the Australian region and has generalized feeding habits. The spiders also have these characteristics. Tetragnathids are known long-distance dispersers (Okuma & Kisimoto, 1981) and lycosids are part of the aeolian-dependent communities found on lava fields on Hawaii, ash/lava beds on Anak Krakatau, and barren areas of the Mount St Helens blast zone.

The small, turret-shelled *Melanoides tuberculatus* Muller, the commonest of Long's four fresh-water molluscs, was abundant on Motmot in 1969 (Bassot & Ball, 1972) and in 1999 was widespread on the lake's outer shores. It is ingested by ducks (Ball & Glucksman, 1975) and small enough to be occasionally dispersed in adhering mud. Possibly originating in the West Indies, now tropicopolitan, it has colonized the very small bodies of fresh water on the Krakataus (Thornton & New, 1988). In Lake Wisdom it occurs in mud or algae at all depths down to about 350 m (Ball & Glucksman, 1978), and Bassot & Ball (1972) noted that it can live in temporary ponds, streams, lakes, rivers and in hot or brackish waters.

The two Long Island amphibians are frogs, a hylid, the giant tree frog, *Litoria infrafrenata* (Gunther), and a ranid, *Platymantis papuensis* Meyer. The hylid's range extends from E. Indonesia to NE Australia. In the Papuan region it is the most widely distributed of all hylids below 1200 m and, of about eighty New Guinea hylids, is one of only three to reach New Britain (Menzies, 1976). Breeding in shaded swamps, it is a forest frog but one of the few New Guinea frogs to inhabit gardens and suburbs. On Long Island it was found in a banana plantation. *Platymantis papuensis* is a terrestrial forest frog with adaptations that reduce its dependence on free water, important on a volcanic island with very porous substrata (Cook *et al*., 2001). It ranges from E. Indonesia to the Trobriands and may have been introduced by humans to Long Island. Menzies (1976, p. 26) noted that in New Guinea it can also be found 'in gardens where there is extensive shrubbery and long grass'.

The Pacific Boa, *Candoia carinata* (Schneider), Long's only snake, is live-bearing and was common in 1999 (Cook *et al*., 2001). Its distribution extends from Ceram to Samoa. An inhabitant of cultivated areas as well as forests and mangroves, it feeds on lizards, mammals (including rats), birds, flying foxes and fish (McCoy, 1980; Whitaker *et al*., 1982).

Long Island's lizards are mostly widespread species with generalist habits, although these characteristics are not as marked as in the bats (Cook *et al*., 2001). The mangrove monitor, *Varanus indicus* (Daudin), ranges from Timor to the Solomons and Micronesia. Rather like a supertramp, in the Solomons it is uncommon on large islands but may be abundant on small ones (McCoy, 1980). Usually coastal, inhabiting mangrove swamps, it occurs also in forest but prefers semi-open areas and is common in coconut plantations on small islands, foraging for crabs, smaller lizards, snakes, rats, birds, birds' eggs and turtle eggs. On Long Island it was common around the shores of Lake Wisdom and the gardens around Matapun but rarely seen in closed canopy rain forest.

Two of Long's eleven small lizards are known to have broad habitat tolerances and to be associated with forest recovery. In a study of twenty-two lowland forest plots in northern Papua New Guinea, ranging from newly established, cultivated, harvested and abandoned gardens, through secondary forest 26 years after clearing to untouched primary forest, the skink *Emoia jakati* (Kopstein) occurred in all habitats and the ground-foraging gecko *Nactus pelagicus*

(Girard) (which has a range extending to Tonga) in all but newly established garden plots (Bowman *et al.*, 1990). *Emoia jakati* was found in all Long Island habitats (including disturbed ones) except closed forest, and *N. pelagicus* was the most widely distributed gecko on Long Island.

Skinks generally have a smaller geographical range than geckos but the terrestrial *E. mivarti* (Boulenger) ranges from New Guinea and the Solomons to Micronesia. This forest skink enters clearings to forage and in the Admiralties is common in gardens and secondary growth, in which it was found on Long Island. *Lamprolepis smaragdina* (Barbour) (not found in 1999) has the same geographical distribution. Almost completely arboreal, it sometimes occurs on coconut palms, and although largely insectivorous it takes some fruit and flowers. *Sphenomorphus solomonis* (Boulenger) ranges to the Solomons and is a litter-foraging forest lizard which sometimes occurs in plantations; it was found in both these habitats on Long Island (McCoy, 1980; Whitaker *et al.*, 1982).

Although New Guinea has 128 skink species and only thirty-three geckos (Allison, 1996), the disparity is reduced on Long Island (seven skinks, four geckos), and further into the Pacific representation is equal. Allison noted that this suggests that geckos are the better dispersers, and pointed out that they are the more likely to be rafted with drifting flotsam; their eggs are more salt resistant, and many that reach remote Pacific islands are represented by all-female races and are probably parthenogenetic. None of Long's skinks reach Vanuatu but two of its geckos do. *Lepidodactylus lugubris* (Dumeril & Bibron) has been recorded from India to Central America and *N. pelagicus* reaches Samoa. Both are parthenogenetic.

Several of Long's arboreal geckos are associated with humans and so perhaps more likely than most skinks to be accidentally dispersed through traditional boat traffic. Long has an undetermined species of *Gehyra*, two New Guinea species of which [*Gehyra oceanica* (Lesson) and *Gehyra mutilata* (Wiegmann)] are eurytopic, have very wide distributions extending into the Pacific, and are sometimes found in human habitations. *Lepidodactylus lugubris* is another arboreal gecko often found in houses, its only known habitat on Long Island.

Of Long Island's fifty-four resident land bird species, only thirteen are restricted to the Melanesian subregion, and only five to New Guinea and its islands. Forty-one have ranges extending into one or more adjacent regions. There are proportionately fewer frugivore–insectivores than in the younger fauna of Krakatau (see below), although ground-feeding herbivore–insectivores are well-represented. The supertramp megapode, *Megapodius freycinet* Gaimard, is an example of the latter, being practically omnivorous. It is also an unusually eurytopic megapode. Jones *et al.* (1995) reviewed twenty-two species and stated (p. 50) that this has 'the most diverse array of incubation techniques of any megapode' (mounds of vegetation, ground heated by the sun, and ground heated by volcanic activity).

The ecological breadth of a supertramp may sometimes play a determining role in an island's colonization. For example, the Louisiades White-eye, *Zosterops griseotinctus* Gray, inhabits Manus Island, over 300 km to the north of Long, but is absent from all islands off north-eastern New Guinea, except Long. Diamond believed that it probably became established on Long early, perhaps as a result of the chance occurrence of a 'bloom' in species numbers at the right time. This small omnivore then flourished to become abundant in all habitats, and may have severely restricted the entry of other small bird species into Long's community (Diamond, 1975).

Only one of Long Island's seven bat species has a strong habitat preference for closed-canopy forest – the fig specialist *Nyctimene vizcaccia* (Thomas). The rest tolerate a wide range of habitats, often including human-disturbed ones, and most are wide-ranging. *Pteropus hypomelanus* Temminck ranges from Thailand to the Philippines and in New Guinea forages in 'primary and secondary lowland and hill forest, small gardens, and plantations' (Bonaccorso, 1998, p. 127). *Pteropus neohibernicus* (Peters) is unknown outside the New Guinea region but occurs in a wide range of forest types. Long's three blossom bats all take some fruit as well as nectar and pollen (Start & Marshall, 1976; Smith & Hood, 1981; Utzurrum, 1984; Bonaccorso, 1998) and two are eurytopic and widely distributed. *Macroglossus minimus* (E. Geoffroy) ranges from Thailand to the Solomons and Australia and inhabits *Sonnateria* mangroves (Start & Marshall, 1976), banana plantations and dense primary rain forest (Kitchener *et al.*, 1990), and *Melaleuca* swamps, bamboo thickets and monsoon scrub (Kitchener *et al.*, 1978). It is common in a wide variety of New Guinea habitats but uncommon in primary rain forest (Bonaccorso, 1998). *Syconycteris australis* (Peters), found from Ambon to NE Queensland, is a 'habitat and feeding generalist' which occurs in all types of forest and woodland (Bonaccorso, 1998, p. 205). Long's third blossom bat, *Melonycteris melanops* (Dobson), is a Bismarck Archipelago endemic, Long Island being its westernmost record. In New Guinea it occurs up to 1600 m altitude, is frequent in plantations (as on Long Island) and gardens but rare in primary rain forest. The range of the emballonurid *Mosia nigrescens* extends from the Moluccas to the Solomons, and Bonaccorso (1998, p. 235) described it as a 'habitat generalist, foraging in primary and secondary tropical broadleaf forests, mangroves, gardens, coconut plantations, and villages.

Long's two rat species are the Polynesian rat, *Rattus exulans* (Peale) and the variable spiny rat, *Rattus praetor* (Thomas). They are the only rats known from the six NE New Guinea 'offshore' Bismarck Arc islands (Koopman, 1979) and both are human commensals. *Rattus exulans* has the widest distribution of any New Guinea *Rattus* species, having been carried inadvertently as far as Easter Island (Taylor *et al.*, 1982). In New Guinea it occurs in a wide range of human-disturbed habitats and is the main village rat (Menzies & Dennis, 1979). Both arboreal and ground-dwelling, it was the only rodent shown to benefit substantially from slash-and-burn agricultural practices (Dwyer, 1978, 1984). *Rattus exulans* may successfully share its range in the Bismarcks and Solomons with *R. praetor* (as on Long) and the more recent arrival, *R. rattus* Linnaeus. Johnson (1946) described its success in military camps on Bougainville in World War II in the presence of these two considerably larger species, although in many New Guinea coastal villages it is being replaced by *R. rattus* (Menzies & Dennis, 1979). *Rattus praetor* is the only autochthonous New Guinea *Rattus* species to occupy the Bismarcks and Solomons. Unlike the introduced *R. exulans* and *R. rattus*, and in spite of being an opportunist in human environments, it does not seem to accompany human excursions and there is no evidence of it crossing straits in sea-going cargo (Menzies & Dennis, 1979).

The Oriental Cuscus, *Phalanger orientalis* (Pallas), is abundant on Long Island. As an important protein source it is literally carried about the region and undoubtedly was introduced to Long Island (Cook *et al.*, 2001).

Colonization of Long Island by Ficus *species*

There are thirty-one species of *Ficus* on Long Island and the island's *Ficus* flora is disharmonic only in the absence of representatives of the section *Rhizocladus*, a group of climbers which makes up 20% of New Guinea's 147 *Ficus* species (Shanahan *et al.*, 2001a, b). Possible explanations of this absence are the dearth of large mature trees as substrates in Long's relative young forests, and the W-E decline in representation of this section of the genus across New Guinea, only four species being known among the fifty-five *Ficus* species of Madang Province, for example. Long Island's proportion of dioecious to monoecious *Ficus* species is similar to that for Madang Province, which is similar to that for New Guinea as a whole (about 70% monoecious) (Shanahan *et al.*, 2001a, b) and the comparison provides no evidence that either reproductive system was advantageous in Long's colonization (see discussion in Thornton *et al.*, 1996; Thornton, 1996a). All seven species that reached the Krakataus within 25 years of the 1883 eruption were dioecious, but there are no comparable data for Long Island's early colonization.

Two species each of flying foxes (*Pteropus* species), fruit doves (*Ptilinopus*), imperial pigeons (*Ducula*) and *Aplonis* starlings were the likely agents of fig dispersal to the island (Shanahan *et al.*, 2001a, b). Fruit doves and imperial pigeons do not digest fig seeds and are effective dispersers. Flying foxes are wide-ranging fig-eaters and should seeds be retained in the gut and remain viable during long flights they would also be very effective dispersers. Seeds of twelve *Ficus* species from faeces of Madang town's *Pteropus conspicillatus* Gould were planted in Port Moresby and grew into seedlings, and some, including *F. gul* Laut. et K. Schum., one of the Long Island species, into trees (J.I. Menzies, pers. comm.). Small fruit bats of the genus *Cynopterus* confined in small cages retain fig seeds in the gut overnight – much longer than was previously thought (Shilton *et al.*, 1999) – and if such long retention times occur during free flight and in fruit bats generally, dispersal of figs by bats making the 2- or 3-h flight to Long from the mainland or Umboi would be as likely as dispersal by frugivorous birds.

In 1999, sixteen of Long Island's *Ficus* species were bearing ripe figs and had therefore been pollinated by their species-specific fig–wasps. Over thirty species of potentially or known fig-eating vertebrates now occur on Long and, as well as the dispersers noted above, a range of smaller dispersers, making fourteen dispersers in all, are available to assist *Ficus* dispersal within Long Island (Shanahan *et al.*, 2001a, b). The most important of the smaller dispersers are probably the Bismarck Tube-nosed Bat, *Nyctimene vizcaccia*, which feeds primarily on figs (Bonaccorso, 1998); the Common Blossom Bat, *Syconycteris australis*, which in New Guinea feeds mainly on fruit, fig seeds having been found in its faeces (Bonaccorso, 1998); and the abundant cuscus, *Phalanger orientalis*. The Black-bellied Bat, *Melonycteris melanops*, is a blossom bat that has eaten soft fruit in captivity; the common koel, *Eudynamys scolopacea* (Linnaeus), is a large cuckoo that feeds on insects, small invertebrates, berries and figs; and the omnivorous Louisiades White-eye, *Zosterops griseotinctus* Gray, also takes figs. *Macropygia* cuckoo-doves and Rainbow Lorikeets, *Trichoglossus haematodus* (Linnaeus), are considered to be predominantly fig-seed predators rather than dispersers.

Comparison between Long Island and the three pre-1883 Krakatau Islands

It is of interest to compare the biotic recovery of Long Island with that of the Krakatau Islands, some 4500 km to the west, in Sunda Strait. Three of the Krakataus were devastated by the 1883 eruption and the fourth, Anak Krakatau, emerged from Krakatau's submarine caldera in 1930 (Thornton, 1996a). Although Long Island and the Krakataus are about equally distant from large species-rich source

Table 2 Numbers of genera and species (separated by a colon) of vascular plants in the known cumulative Long Island (L) and Krakataus (K) floras; numbers common to the two (L/K); proportions of L/K species also known from Motmot (M), Anak Krakatau (AK), and Anak Krakayau and/or Motmot; for comparison, proportions of Long and Krakatau floras known from Motmot and Anak Krakatau, respectively

	Pteridophytes	Spermatophytes	Vascular plants
L flora	24 : 32	202 : 273	226 : 305
K flora	56 : 118	282 : 447	338 : 565
Number shared L/K	22 : 14	117 : 80	139 : 94
Proportion of L/K spp. that are on M	5/14 (36)	20/80 (25)	25/94 (27)
Proportion of L/K spp. that are on AK	7/14 (50)	48/80 (60)	55/94 (59)
Proportion of L/K spp. on M and/or AK	10/14 (71)	54/80 (68)	64/94 (68)
Proportion of L spp. that are on M	11/32 (34)	51/273 (19)	62/305 (20)
Proportion of K spp. that are on AK	20/118 (17)	168/447 (38)	188/565 (33)

Values in parentheses are percentages.

islands (55 and 44 km from New Guinea, and Java and Sumatra, respectively), Long Island is the larger by an order of magnitude (Long 330 km^2, Krakataus 24.5 km^2) and its new biota has been re-assembling for some 350 years, about three times as long as that of the Krakataus (117 years).

Many of the taxa mentioned in the previous section have colonized both Long Island and the Krakataus. For example, 62% of Long's vascular plant genera and 31% of its species are shared with the Krakataus (Table 2). Interestingly, the majority (68%) of the shared species are early pioneers, as evidenced by their presence on one or both of the emergent islands, Anak Krakatau and Motmot. This is much higher than the proportions of species in the Long Island and Krakatau floras that have been found on Motmot (20%) and Anak Krakatau (33%), respectively (Table 2), and confirms the theoretical findings of Ward & Thornton (2000) that early colonization is relatively deterministic compared with the greater stochasticity later in the process. Fifty-nine per cent of the shared species and 86% of the early pioneers (as defined above) occur on Anak Krakatau, compared with 27% and 39%, respectively, occurring on Motmot, reflecting the fact that most of these species are sea-borne and of course Motmot is an inland island.

Colonization of Long Island and Motmot by animals also has similarities with that of Krakatau. A common Long Island dragonfly, *Pantala flavescens*, was an early immigrant to Krakatau, 38 years after the 1883 eruption, and another, *Orthetrum sabina*, was found on Anak Krakatau in 1949, 19 years after its emergence. A labidurid earwig was important in Motmot's early community and one had colonized all three recovering Krakatau Islands within 25 years of the 1883 eruption. *Anoplolepis gracilipes*, the commonest ant on Motmot, was the most widespread and abundant ant on the Krakataus at the first zoological survey after 1883 (Jacobson, 1909). Long Island has at least three species of *Tetragnatha* spiders, two of which occur on Motmot (Edwards & Thornton, 2001); two tetragnathid species were found on Krakatau by the first spider specialist to visit the islands after the eruption (Bristowe, 1931; Reimoser, 1934).

Almost half (seventeen) of the thirty-eight resident land bird genera recorded from Krakatau in the last 15 years occur also on Long Island, where they are represented by twenty-seven species, and eleven of Krakatau's forty-two species are present also on Long (Table 3). These are impressive similarities considering the generally very different avifaunas of New Guinea and Indonesia west of Wallace's Line, and most involve widespread good colonizing species that have crossed the line and have been able to exploit both opportunities.

The percentage turnover rate (%T; Thornton *et al.*, 1990b) for Long Island's avifauna is lower than those calculated for the Krakataus. The %T on the Krakataus over the last 44 years (1952–96, seven gains seven losses) was 0.44% per year, and in the last 10 years (1986–96, two gains three losses) 0.68% per year (Runciman *et al.*, 1998). In comparison, in the 27 years between the last two Long Island surveys (1972–99, three gains three losses) %T was 0.22% per year. A lower turnover rate would be expected in a larger island (Long) on which forest succession is relatively slow.

Table 3 Numbers of non-migrant land bird genera and species recorded from Krakatau (1983–96) (including *Egretta* and *Esacus*) and Long Island (1972, 1999), and the numbers shared

	Krakatau	Long	Combined	Shared
Genera	39	46	66	19
Species	40	54	82	12

Excluding Long Island's two aquatic species (there is no extensive fresh-water habitat on the Krakataus), one notable difference between the guild spectra of the two bird communities is that Long has greater proportions of ground insectivore–herbivores and of predators on large invertebrates and small vertebrates (Schipper *et al.*, 2001), and this may be related to the fact that Long Island is the richer in small vertebrates. Another difference is that the Krakataus have a relatively high proportion of the frugivore–insectivore guild, which, by analogy with Anak Krakatau, is believed to have been important in the earlier stages of natural re-afforestation (Thornton, 1996a) and may have been more important at an earlier stage of Long's recovery, when no surveys were made.

Motmot

Colonization of Motmot by plants

The high proportion of sea-dispersed species that characterizes the early phase of succession on emergent marine islands in the region is not a feature of Motmot's flora, of course (Thornton, 1996b; Harrison *et al.*, 2001). Wind-borne and zoochorous plants make up 86% of the known flora. In 1999 the dominant vegetation comprised sedges, particularly *Cyperus polystachyos* Rottb., the first plant species to become established on the island, in 1968. Sedges were almost certainly carried to Motmot by the Pacific Black Duck, itself an early colonist; Ridley (1930) cited ducks as a prime means of dispersal of sedges. Two important pioneer ferns were *Pityrogramma calomelanos* (L.) Vink., first recorded in 1972, and *Nephrolepis hirsutula* (Forst.) Presl., which may also have been present in 1972 (Harrison *et al.*, 2001). These two species were also pioneers of ash-covered lava flows on Anak Krakatau and species of both genera are well-known colonists of recent lava flows in Hawaii and Japan (Thornton, 1996a). Other common wind-borne pioneers on Motmot included kunai grass, *Imperata cylindrica* (L.) Beauv., the composites *Emilia sonchifolia* (L.) DC and *Vernonia cinerea* (L.) Less. (all of which colonized between 1973 and 1988), and the composite *Mikania micrantha* H.B.K. and the asclepiad *Tylophora flexuosa* R.Br. (neither previously recorded). The most frequent of the eight *Ficus* species present in 1999 were *F. benjamina* (present by 1988), *F. copiosa* Steud. and *F. wassa* (both first recorded 1999).

Assuming that species recorded on Motmot but not found on Long Island itself occur also on Long, Motmot has been

Table 4 Dispersal modes (Shanahan *et al*., 2001a, b) of *Ficus* species (a) on Long Island that have and that have not reached Motmot in the first 31 years of its existence; (b) on the three older Krakatau Islands that have and have not reached Anak Krakatau in the 46 years following its devastating eruption in 1952–53; and (c) that colonized the Krakataus in the first 25 years after the 1883 eruption

		ba	ba/bi	bi	bi/ba	?	Total
a	On Long and Motmot	3	1	3	1	0	8
	On Long, not on Motmot	2	1	2	3	15	23
b	On older Krakataus and Anak Krakatau	1	5	0	2	0	8
	On older Krakataus, not on Anak Krakatau	3	2	1	4	5	15
c	On Krakataus in first 25 years	2	6	0	2	2	12

ba = bat-dispersed, bi = bird-dispersed, ba/bi = primarily bat-dispersed, bi/ba = primarily bird-dispersed, ? = dispersal agents not known.

colonized by 20% (62/305) of Long Island's vascular plant species. This includes a greater proportion of the anemochorous pteridophytes (34%, eleven of thirty-two) and the zoochorous *Ficus* species (26%, eight of thirty-one) than that of spermatophytes as a whole (19%, 52/273). No doubt reflecting Motmot's double isolation, the small flora in 1999 (seven ferns and thirty-eight seed plants) is at a relatively early stage for its age, consisting largely of sedges, grasses and herbs, with very few trees of stature. One plant each of *Paraserianthes falcataria* (L.), *Alstonia scholaris* R. Br., *Dendrocnide latifolia* (Gaud.) Chew, and *F. benjamina* attained heights of 4–6 m.

Perhaps not surprisingly, some of Motmot's woody plants were present in 10–12-year-old regenerating lowland New Ireland rain forest plots following selective logging (Saulei & Kiapranis, 1996). *Leea indica* (Burm. f.) Merr. and *F. wassa* occurred in unlogged plots only, *Albizia procera* (Roxb.) Benth., *Alstonia scholaris* and *F. septica* Burm. in logged plots only, and *Canarium indicum* L., *F. copiosa*, *Ficus pachystemon* Warb., *Ficus polyantha* Warb., *Ficus variegata* Bl. and *Mallotus philippinensis* (Lam) Muell.-Arg. in both logged and unlogged plots. These common and widespread woody species illustrate the general pioneer nature of Motmot's plant community.

Ficus species reached Motmot within 3 years of its establishment. Ball & Glucksman (1975) in 1972 found what were thought to be seeds of *F. benjamina* on Motmot's shore and figs of *F. virgata* Reinw. ex Bl. floating on the lake. Both species were early colonists of Motmot. It is possible that some colonization by *Ficus* species may have been via the lake surface, but none now grows at the shore, so secondary dispersal would have to be invoked. Flotsam beached on Motmot's windward shore in 1972 included seeds of seven other plant species but none of them has since colonized the island. In contrast to earlier years (Ball & Glucksman, 1981), in 1976 and 1999 little flotsam and no plant seedlings were seen on Motmot's beaches. Zoochory is a much more likely means of *Ficus* dispersal. The sixteen *Ficus* species found fruiting on Long Island in 1999 all had their pollinating wasps, so that all Long's *Ficus* species probably have the potential to reach Motmot by means of the available volant dispersers.

The largest fig tree on Motmot, a free-standing *F. benjamina* probably also recorded in 1988 (Osborne & Murphy, 1989), was not fruiting in 1999 but was large enough to have a crop of thousands of figs. Most of Motmot's other fig plants were small and probably immature, but two individuals of *F. wassa* and one of *F. nodosa* were bearing syconia, although none had been pollinated and so the flowers had not set seed (Harrison *et al*., 2001; Shanahan *et al*., 2001a, b). The only fruit-eater on Motmot in 1999 was the almost omnivorous *Megapodius freycinet*. Although often regarded as a poor, reluctant flier, during our visit a disturbed bird was watched flying towards the lake's outer shore, 5 km distant. This megapode has been seen eating figs (W.R.J. Dekker, pers. comm.), and could be a disperser of *Ficus* species to Motmot and important in their spread within the island once immigrants have set seed. Megapode numbers on Motmot were low, however (probably one pair), and in 1999 other more specialized frugivores, had little reason to spend time there. Motmot's 1999 *Ficus* flora was probably the legacy of frugivorous birds or bats occasionally visiting or over-flying the island.

Raptors were taking a toll of ducks, kingfishers and megapodes in 1999, and a starling skeleton was evidence of a frugivore and possible *Ficus* disperser either being killed on Motmot or brought thither as prey. The presence of diurnal raptors may be thought to have an inhibitory effect on potential bird but not bat dispersers of figs; if so, as on the Krakataus, pioneer *Ficus* colonists would tend to be bat-dispersed rather than bird-dispersed. However, a comparison of dispersal modes between those Long Island *Ficus* species that have become established on Motmot and those that have not (Table 4) shows that bat-dispersed species are no more successful as colonists of Motmot than bird-dispersed ones. In South Africa, bats may form a significant portion of the diet of opportunistic raptors (Fenton *et al*., 1994) and, although on the Krakataus bat-dispersed *Ficus* species appear to be better (earlier) colonizers than bird-dispersed ones, there is evidence that fruit bats may suffer as much raptor pressure as birds. On Anak Krakatau diurnal raptors, particularly the peregrine, took small fruit bats and flying foxes (*Cynopterus* and *Pteropus* species) as well as birds, and pellets of the barn owl (also present on Long) contained skeletal remains of *Macroglossus minimus minimus* (E. Geoffroy), a subspecies of the blossom bat that also occurs on Long Island (Thornton *et al*., 1996).

In 1999, any of Motmot's fig species that produced syconia would have been dependent on incoming fig–wasps for pollination, and the unpollinated syconia of *F. nodosa* and *F. wassa* suggest that, for these species at least, pollinator dispersal was limiting. Because so few individuals are fruiting, any pollinators arriving from Long Island are unlikely to become permanently established. At this early stage of the colonization process, increase in numbers of *Ficus* individuals and species on the island will largely depend on viable seeds being brought from Long Island by dispersers successfully running the gauntlet of raptors, so establishment of a reproductive *Ficus* community may take some time.

There are two possible models for the future pollination of Motmot's *Ficus* species. Some, perhaps most, *Ficus* species on such a small island will never reach sufficient numbers to maintain populations of their pollinators continuously and will always depend on pollinators arriving from Long Island. The wasps of some monoecious species in Panama have been shown to disperse regularly over long distances (Nason *et al.*, 1996). If the wasps of any of Motmot's species, perhaps the monoecious *F. benjamina*, have similar dispersal abilities, then pollination success on Motmot should not be limited by pollinator availability. Shanahan *et al.* (2001a, b) raise the possibility that the saplings of *F. benjamina* on Motmot may be the offspring of the large tree there. Other *Ficus* species, usually dioecious ones, may have poorer-dispersing wasps (Harrison, 2000a), as indicated by the unpollinated syconia of *F. wassa* and *F. nodosa*, but normally occur in higher densities and produce syconia more often, so can maintain their pollinator population between only a few trees (Kameyama *et al.*, 1999). One such species studied by RDH in Borneo needed just one male tree to maintain its pollinator population over an 18-month period (Harrison, 2000b). After a rare colonization event such species could maintain their wasp populations even on a very small island.

On Anak Krakatau in 1992 Compton *et al.* (1994) found that two rare *Ficus* species, *F. fistulosa* Reinw. and *F. hispida* L. f., apparently had 100% of their syconia pollinated, whereas common species, *F. fulva* Reinw. ex Bl. for example, had pollination rates on Motmot substantially lower than on older islands of the group. It may be, as suggested by Thornton *et al.* (1996), that for the two rare *Ficus* species the few incoming pollinators were sufficient to fully service the very small number of trees, whereas the *F. fulva* population was too large for this to be possible yet below the critical size for self-maintenance of its pollinators. Another explanation is possible, however. There were only four male trees of *F. hispida* (the trees that produce the wasps in dioecious figs) but all syconia were pollinated. This species produces syconia asynchronously (Compton *et al.*, 1994; Patel, 1996), which enables the wasp cohorts to cycle between a few trees or even within a single tree (see above). For this species, therefore, there was probably a regular supply of pollinating wasps on the island. *Ficus fulva*, however, in which only 18% of syconia were pollinated, produces syconia synchronously and only intermittently (Compton *et al.*, 1994; Harrison *et al.*, 2000), hence requiring a large population of trees to maintain its pollinator population. Thus in spite of its greater abundance on Anak Krakatau it was probably still dependent on wasps arriving from outside the island, which would account for its relatively poor pollination success. The discussion in this and the preceding paragraph is based on evidence from phenological studies, for as yet there are no data on the relative dispersal abilities of fig-wasps in this region, data which might have been provided by our expedition had there been more mature trees on Motmot.

When Motmot's *Ficus* trees mature and, assuming pollination occurs, produce fig-fruit which attract frugivores, a feed-back loop may be set up that will accelerate the colonization both of *Ficus* species and other fruiting trees. Motmot's large *F. benjamina* tree may play a crucial role in this process (Shanahan *et al.*, 2001a, b). On Anak Krakatau this stage was reached after 34 years (Thornton *et al.*, 1996).

Food relationships on Motmot

The duck, swallow, raptors and emballonurid bat all derive much of their sustenance from material originating outside the island. Raptors, of course, require territories very much larger than Motmot. A pair of sea eagles, for example, cannot survive on islands smaller than about 13–40 km^2, their normal foraging range (Diamond, 1975). The prey remains found on Motmot (see above) probably derived from outside the island (except perhaps the megapode). The Pacific Black Duck strips seeds from shore or water plants, takes floating seeds from the surface, and forages in mud at the bottom of shallows for invertebrates. The grebe dives for insects, tadpoles, and (absent from Lake Wisdom) fish and prawns, and takes seeds and shoots of aquatic plants. Both must feed largely on insects and other invertebrates in Lake Wisdom, for there is no aquatic vegetation around Motmot and little elsewhere on the lake. Many individuals of the small fresh-water snail *Melanoides tuberculatus* have been found in the stomach of the duck, along with seeds (including sedge seeds) and parts of insects (Ball & Glucksman, 1975).

Scavenging and predaceous earwigs, which played an important role in Motmot's early succession (Ball & Glucksman, 1975), were still present in 1999 but, as in the very early years, confined to the shore and in very low numbers. A shore-scavenging anthicid beetle (*Anthicus* sp.), found some 30 years earlier, was also persisting. There was no beached organic flotsam at the time of our visit and the large fluctuations in earwig numbers may reflect fluctuations in this resource. Earwigs had spread inland on Motmot by 1976 and may then also have been exploiting aerial fallout.

The dusk and early evening emergence flights of aquatic insects almost certainly constitute the main energetic input for the Motmot island food chain. In daylight the swallow, a damselfly and three dragonflies were taking chironomids, caddis flies and other lake insects in the air. At and after dusk some may be taken by the few Lesser Sheath-tailed Bats, although Cook *et al.* (2001) believe that the bats are more likely to commute to Long Island to forage in dense foliage, taking insects in flight and by gleaning. Vestjens & Hall

(1977) examined forty-two stomachs of this bat and found mostly wingless ants. Ants were the commonest insect on the vegetation in the summit crater (Fig. 3), where the bats roosted.

Crepuscular and nocturnal tetragnathid spiders were common and widespread on Motmot, trapping chironomids and caddis flies in their threads close to the ground. In spite of the paucity of ground insects, a dense population of the large wolf spider '*Trochosa*' *papakula* was active at night on the barren ash and lava fields from the shore to the top of the highest cone, taking lake insects that reached the ground. Lycosids are one of the spider families occurring on islands of Australia's Great Barrier Reef, on which, Main (1982) believed, colonization could only have been by aerial dispersal. A lycosid was the only spider present on Coral Sea cays devoid of vegetation that were surveyed by Heatwole (1971), and lycosids were part of the pioneer fauna of Anak Krakatau's ash-lava (New & Thornton, 1988; Thornton *et al*., 1988) and Hawaii Island's Kilauea pahoehoe lava flows (Howarth, 1979). They were also the initial spider colonists of barren sites on the Pumice Plain of Mount St Helens, an area from which all biota was eliminated by the 1980 eruption, part of another arthropod community dependent on airborne organic fallout (Edwards *et al*., 1986; Edwards & Sugg, 1993; Crawford *et al*., 1995). Earwigs, crickets and a wide variety of spiders are also part of a lavicolous community probably subsisting on such fallout on the Canary Islands (Ashmole & Ashmole, 1988). Recent studies of terrain exposed by retreating glaciers in the high Arctic have shown that there, too, allochthonous aerial fallout is the staple food resource of an arthropod community (Prof. I. Hodkinson, *in litt*).

Ants (*Anoplolepis gracilipes*) were also taking grounded lake insects. In addition, they attacked large numbers of adult dragonflies (*Pantala flavescens*) emerging from the nymphal exuviae before the cuticle had hardened sufficiently for flight. It is not clear what animals, if any, were exploiting the rich energy source represented by the lycosid population. It is possible that the megapode, which normally feeds on ground insects and small fruit (Kisokau, 1974 found small seeds and simuliid and muscid flies in its gut on Long) takes some lycosids. More likely, perhaps, the Rufous Night Heron, *Nycticorax caledonicus*, a crepuscular and night feeder on arthropods which was seen on Motmot in 1999 but is not resident there, exploits them. If so there is evidently little effect on numbers.

Absences from Motmot

It may be thought that if a species has colonized Long Island it should be able to reach Motmot, yet most of Long's bird guilds are absent or poorly represented, only one of the seven bats is present and none of the reptiles or frogs. There are a number of possible explanations. First, animals have had 350 years to reach Long Island but only 30 years to reach Motmot. Secondly, for birds and bats the flight from Long to Motmot, although fairly short (4–8 km), is exposed, without cover, and in the presence of raptors. For pigeons, white-eyes and finches, and even for some bats, the presence of falcons may be a sufficient deterrent (see above, Thornton *et al*., 1996). Thirdly, Motmot's small size (about 0.1 km^2) will preclude potential colonists with large activity ranges. Finally, the niches for many of Long's species are not yet available on the young island.

The paucity of vegetation is almost certainly a major restraint on establishment for many animals. Termites reached Motmot by 1972 but we found none; the 1972 observation was probably a mating flight from Long Island, as suggested by Ball & Glucksman (1975); establishment of a colony on what was then an extremely sparsely vegetated island would have been unlikely. Considering the state of the vegetational succession and paucity of fruiting trees (Harrison *et al*., 2001), it is not surprising that, apart from the omnivorous megapode, no frugivorous bats or birds have colonized Motmot. Similarly, colonization by nectarivores will be delayed until after the arrival of the appropriate flowering plants.

Aerial insects are the chief conduit for energy to Motmot (see above) and aerial insectivores are among the bird species that may be expected to colonize the island and join the swallow, bat and dragonflies in exploiting the large numbers of aerial prey. Long's nightjar, which would not compete with the swallow, is a likely candidate. The emballonurid bat is the only one of Long Island's non-avian vertebrates to inhabit Motmot. Weighing just 2.5 g, it is one of the smallest of bats and in that regard well-adapted for survival on a very small island. Other insectivores, such as skinks and geckos, are probably precluded by the paucity of shelter and cover from predators (the bats roosted in the locality with most shelter and thickest cover – the summit crater; Fig. 3). As vegetation develops and provides cover, and ground insects increase in numbers and diversity, other types of Long Island insectivores may colonize.

Birds such as munias may begin to exploit the grass and sedge seeds available on Motmot before frugivores are able to colonize, although it is doubtful that they would find sufficient sustenance now for a population to become established, and munias were not seen around the caldera rim. Munias have not yet colonized Anak Krakatau, although they have reached there (Thornton *et al*., 1993). The limited resources now available on Motmot are probably beyond the reach of finches that must make a crossing of at least 4 km with no cover in the presence of falcons.

The kingfisher skeletons on Motmot may represent failed colonization attempts. Collared Kingfishers do not require trees for either nesting or foraging. On Anak Krakatau they

Table 5 Number of vascular plants species in the two successions on Motmot and Anak Krakatau, and the number and percentage of species in the first succession (S1) that were present in the second (S2)

	S1	S2	In common (%)
Motmot	23	49	10 (43)
Anak Krakatau	39	182	33 (85)

nest in the sides of ash-cliffed gullies or arboreal termite nests and feed on shore crabs (Zann & Darjono, 1992). This kingfisher, and bee-eaters, which also nest in holes made in soft cliffs, may be early colonists of Motmot. A resident and a migrant bee-eater occur on Long, and we observed the former over Lake Wisdom whilst *en route* to Motmot (Schipper *et al*., 2001). As noted above, there is an abundance of food on Motmot for any animal immigrants capable of exploiting the dense population of fairly large spiders.

Motmot compared with two emergent marine islands in the region

Motmot and Anak Krakatau. Like Motmot, Anak Krakatau is an emergent island volcano, having risen from Krakatau's submarine caldera in 1930 and, also like Motmot, its first biota was destroyed by its own activity. With an area of about 3.5 km^2 it is an order of magnitude larger than Motmot (about 0.1 km^2), and some 400 m high (compared with 50 m), but it is about equally isolated, from 2 to 5 km from other islands of the Krakatau group.

Apart from size, there are two major differences between Anak Krakatau and Motmot. First, Anak Krakatau's volcanic activity has continued intermittently up to the present, retarding colonization. For example, of 125 vascular plant species present on Anak Krakatau in the year before the 1992–95 eruptions, only thirty-five were present 2 months after the episode ended (Thornton *et al*., 2000). In contrast, the last recorded eruption of Motmot was in 1976. Secondly, and most important, Anak Krakatau is a marine island and can receive sea-borne propagules and food items as flotsam; Motmot lacks this important conduit for immigrants and energy.

In 1999 *Imperata cylindrica* was dominant in several places on Motmot, and, until the eruptions beginning in 1992 (Thornton *et al*., 2000), in one back-beach zone on Anak Krakatau. The wide distribution on Motmot of pioneer sedges, however, has had no parallel on Anak Krakatau, which has lacked ducks, their probable dispersers to Motmot.

On both islands there have been two successions. Eruptions of Anak Krakatau in 1951–52 destroyed the first succession of its developing biota and the second succession has been set back repeatedly. Motmot's first succession, starting from 1968, was truncated by eruptions in 1972–73 and the second, from 1974, is proceeding without disturbance from eruptions. In all, of the 305 vascular plant species (thirty-two pteridophytes, 273 spermatophytes) known from Long Island, in the two successions sixty-two species (eleven pteridophytes, fifty-one spermatophytes) have reached Motmot, 20% of the known Long flora (34% of pteridophytes, 19% of spermatophytes, Table 2). Some 188 species of vascular plants, 168 of them spermatophytes, are now known from Anak Krakatau (Thornton *et al*., 2000; T. Partomihardjo, pers. comm.), 33% of those known from the Krakataus (17% of the pteridophytes, 38% of spermatophytes). There are two possible reasons for the reversal of the proportions, with relatively more pteridophytes and fewer spermatophytes on Motmot. First, Anak Krakatau has lacked any sheltered, shaded habitat equivalent to Motmot's small ravine-like summit crater (Fig. 3), so that Anak Krakatau's pteridophyte community is largely restricted to heliophilous species. Secondly, Motmot lacks any equivalent of Anak Krakatau's deterministic core of early successional, widely distributed, largely sea-borne spermatophytes derived from the older Krakataus. The latter point may also explain the fact that on Motmot ten species were part of both successions (43% of the twenty-three in the first succession), whereas on Anak Krakatau thirty-three (85%) of the thirty-nine species in the first succession were present again in the

Table 6 Colonization (cumulative numbers of species) by groups pertinent to the establishment of *Ficus* species: (a) on Anak Krakatau by 1992 following its eradicating eruption of 1952 and (b) on Motmot by 1999 following its eradicating eruption in 1968

(a) Anak Krakatau 1952–92								
Years since eruption	30	32	33	34	37	38	39	40
Raptors	1	1	2	3	3	3*	3	3
Fruit bats	1	1	2	2	2	2	2	4
Facultative avian frugivores	2	3	5	6	5	5	5	6
Specialist avian frugivores	0	0	0	1	1	1	2	2
Ficus species	2	2	2	2	3	5	6	7
Ficus species fruiting	0	0	2	2	2	3	3	5
Pollinating fig–wasp species	0	4	5	6	6	6	6	7
Other zoochores	5	7	7	7	10	13	15	15
(b) Motmot 1968–99								
Years since eruption	3	4	20	31				
Raptor species†	4	4	?	3				
Frugivore species	0	0	?	1				
Ficus species	2	2	5	8				
Ficus with syconia	0	0	0	2‡				
Pollinating fig–wasp species	0	0	0	0				
Other zoochorous plants	3	1	1	1				

**Falco peregrinus* replaced *Falco severus*. †Not breeding on Motmot. ‡But the syconia were unpollinated.

second (Table 5), although the difference is not statistically significant.

Seven of Motmot's eight *Ficus* species are dioecious (Shanahan *et al*., 2001a, b). The Motmot proportion does not differ significantly from that of Long, and this comparison, like that between Long and New Guinea (above), provides no evidence that either dioecy or monoecy is advantageous in colonization. Six of the seven *Ficus* species on Anak Krakatau are dioecious, a proportion similar to that of Motmot.

The first colonists of Anak Krakatau were wading shorebirds (Zann *et al*., 1990), and some eleven species of seabirds and shorebirds have been recorded on Long Island (Table 2 of Schipper *et al*., 2001). Although isolated from the sea by land and fresh-water barriers, Motmot is only a 10–15 km flight from the sea shore and there is evidence that shore- and seabirds have reached there. Ball & Glucksman (1975) saw three unidentified species of waders on Motmot, and found the mummified bodies of a Sharp-tailed Sandpiper, *Calidris acuminata* (Horsfield), Pacific Golden Plover, *Pluvialis fulva* (Gmelin), and a frigatebird, probably the Lesser Frigatebird, *Fregata ariel* (G. R. Gray). Ball and Glucksman (1975) found the mummified bodies of a Sharp-tailed Sandpiper, *C. acuminata* (Horsfield), Pacific Golden Plover, *P. fulva* (Gmelin), and a frigatebird, probably the Lesser Frigatebird, *F. ariel* (G. R. Gray). The skull of a tern, probably the Common Tern, *Sterna hirundo* Linnaeus, was thought to have been the remains of raptor prey, which may or may not have been taken on Motmot. Whilst crossing Lake Wisdom we saw the Pacific Reef Egret, *Egretta sacra* (Gmelin). As well as its isolation, Motmot, unlike Anak Krakatau, does not offer habitat suitable for any shorebirds or seabirds that may reach there.

In 1971 and 1972 White-bellied Sea-eagle and Osprey were seen passing over and peregrines had a feeding roost on Motmot (Ball & Glucksman, 1975). The early appearance of raptors and aerial insectivores (the Pacific Swallow was breeding by 1971) is very similar to the situation on Anak Krakatau (Zann *et al*., 1990).

There is evidence for the second-hand dispersal of *Ficus* species in Africa by a falcon, through fig seeds contained within disgorged pellets composed of the indigestible remains of its fruit-eating avian prey (Hall, 1987). Also on Anak Krakatau in 1992 seeds of the palm *Oncosperma tigillarium* (Jack) Ridl. were brought to the island in the body of a Green Imperial pigeon, *Ducula aenea* (Linnaeus) killed by a raptor, probably a peregrine (Thornton, 1994, 1996a; Thornton *et al*., 1996). Peregrines were seen on Motmot 27 years ago, and Ball & Glucksman (1975) suggested that such transfer of plant seeds was conceivable. The first plant to flower on Motmot (a sedge) was high on the crater rim among prey skeletons beneath a feeding roost of the peregrine (Ball & Glucksman, 1975; Ball, 1977). Until there is more plant cover, however, the presence of raptors is likely to deter potential bird colonists, particularly pigeons, as was believed to be the case on Ritter Island in Vitiaz Strait (Diamond, 1974b) and on Anak Krakatau (Zann *et al*., 1990).

Table 7 Numbers of species of vascular plants in common between the following 30–31-year sequences: Motmot from its prisere in 1968–99; Anak Krakatau from its devastating eruptions of 1952–53 to 1983; Tuluman from its emergence in 1954–84. Numbers of species on islands in these periods are shown after island names. Anak Krakatau data from Partomihardjo *et al*. (1992), Tuluman data from Kisokau *et al*. (1984)

	Anak Krakatau 90	Tuluman 35*
Motmot 62	10	2
Anak Krakatau 90	–	22

*Identified species only.

Dermapterans, lycosid spiders and anthicid beetles, all part of Motmot's early pioneer community, have been found in other primary colonizing situations (see above and Thornton, 1996a, b, 2000) and the early communities exploiting organic flotsam and aerial fallout were very similar on Motmot and Anak Krakatau. The anthicid beetle found on Motmot in 1971 and 1999 may be *Anthicus oceanicus*, found on many island shores under washed-up seaweed, which was on the Krakataus by 1921 and found in numbers among drift material on Anak Krakatau only 6 months after its emergence, before any plants were established (Bristowe, 1931; Reimoser, 1934). On both Anak Krakatau and Motmot, Pacific Swallows and odonates (in both cases including the libellulids *Pantala flavescens* and *Orthetrum sabina*) exploited aerial organic fallout. Earwigs and lycosid spiders were part of similar pioneer ground communities subsisting on aerial fallout on Motmot and on *aa* lava-ash fields on Anak Krakatau (New & Thornton, 1988; Thornton *et al*., 1988). On Anak Krakatau, as on Hawaii, flightless crepuscular crickets, specialists in exploiting fallout in barren areas, dominated the ground community. Motmot's crickets are evidently not specialists in this role, which is taken by the lycosid and tetragnathid spiders.

Eruptions in 1951–52 destroyed Anak Krakatau's developing biota but after 34 years of recovery its pioneer *Ficus* trees bore fruit and their fig–wasps were already coming on to the island (Table 6). The fruiting coincided with an increase of volant frugivore species from four to seven, and this set off a colonization cascade. The number of fig species rose from two to seven in the next 5 years and the number of other zoochorous plants doubled (from seven to fifteen). Once figs were present in numbers and variety, specialist frugivorous birds colonized (Thornton, 1994, 1996a, b; Thornton *et al*., 1996). On Long Island there are at least thirty-one *Ficus* species and an abundance of excellent fig dispersers (Shanahan *et al*., 2001a, b), and the triggered sequence that occurred on Anak Krakatau may begin also on Motmot, perhaps in the next decade or two. The first full fruiting of figs on Motmot may attract facultative frugivores such as starlings, which occur on Long and were the first fruit-eating colonists on Anak Krakatau. These, in turn, would be likely to bring in more *Ficus* species and attract specialist frugivores, to further augment fig numbers and diversity and bring in other fruiting trees.

Motmot and Tuluman. Between 1954 and 1957, in the Admiralty Group some 300 km north of Long Island, a new island, Tuluman, emerged from the sea as a result of volcanic activity about 1 km south of Lou Island, a 7-km-long island which is some 30 km south of Manus Island (Johnson & Smith, 1974; Reynolds & Best, 1976). Tuluman's biota was surveyed in March 1984, 30 years after its emergence, when the island was about 500 m in diameter, 23 m high and 0.28 km^2 in area (Kisokau *et al.*, 1984).

Tuluman and Motmot are thus of similar size and their young biotas of similar age. Kisokau stated that fifty-nine plants were found on Tuluman in 1984, only thirty-five of which were identified. Of these, at least twenty are dispersed by sea. Tuluman's wind-dispersed grass, *I. cylindrica*, was an important pioneer on both Anak Krakatau and Motmot. Bearing in mind that there are about a score of yet unidentified species in the Tuluman collection, a comparison can be made between three sequences: on Tuluman since its 1954 emergence (30 years); on Anak Krakatau up to 1983 following its devastating eruptions of 1952–53 (30 years) and Motmot up to 1999 since its prisere began in 1968 (31 years). At least twenty-two species (seventeen of them sea-dispersed) are common to the Tuluman and Anak Krakatau sequences, over half of Tuluman's known flora (Table 7). The sea-dispersed core of pioneer plants has no access to land- and-lake-locked Motmot, although many of its component species are present along the sea coast of Long Island. This probably accounts for the contrast between the Tuluman/Anak Krakatau comparison and those involving Motmot. The sequences on Motmot and Anak Krakatau have ten species in common, only four of which are dispersed by flotation. Those on Motmot and Tuluman have in common only *I. cylindrica* (L.) and *F. opposita* Miq. (probably misidentified *F. nodosa* on Motmot), at most 5% of Tuluman's known flora (Table 7). Tuluman species of each of *Cyperus*, *Pipturus* and *Timonius*, all with representatives on Motmot, are unidentified.

Only two reptile species have been reported from Tuluman, a crocodile and a monitor, both probably the same species as on Long Island, which have not been reported from Motmot.

Kisokau's group listed nine non-migrant land bird species from Tuluman in 1984. Diamond has pointed out to us that one record must be regarded as doubtful. The Black-billed Cuckoo-dove, *Macropygia nigrirostris* Salvadori, has never been recorded from the Admiralties and is very similar to Mackinlay's Cuckoo-dove, *Macropygia mackinlayi karkari* Rothschild & Hartet, which does occur in the group (and on Long). Although only one of Tuluman's bird species – the Black Bittern, *Dupetor flavicollis* (Latham) – has not been recorded from the much older and larger Long Island, of the Tuluman species that are known from Long [Beach Kingfisher, *Halcyon saurophaga* Gould, Olive-backed Sunbird, *Nectarinia jugularis* (L.), Rainbow Lorikeet, *Trichoglossus haematodus* (L.), Singing Starling, *Aplonis cantoroides* (Gray), Metallic Starling, *Aplonis metallica* (Temminck), *Egretta sacra* and *Megapodius freycinet*], only the almost omnivorous megapode has colonized Motmot (although one of the starlings, as evidenced by prey remains, may have reached there).

The only mammal seen on Tuluman was the Admiralty Flying Fox, *Pteropus admiralitatum* (Thomas), smallest of the flying foxes. Two larger species of *Pteropus* have colonized Long (see above) but the bat living on Motmot is a very small emballonurid insectivore.

CONCLUSIONS

Long Island

Long Island's community appears to be undeveloped for its age compared with the recovering Krakatau Islands. The vegetation appears to be at an arrested stage of development.

At middle elevations a rather open forest of largely similar-sized trees with little or no understorey and only a few much larger trees has persisted for more than seven decades. Typical rain forest tree species from the region are under-represented or absent, while secondary forest species are common. The *Ficus* flora has an under-representation of regional endemics, and a number of species with very wide distributions and broad ecological tolerances.

A number of characteristics of the vertebrate fauna indicate that it has been assembled over a considerable sea barrier and is still at an early stage of development. Freshwater fish are absent. Several groups of ground vertebrates, especially snakes and amphibians, appear to be depauperate compared with other islands in the area. The reptile fauna comprises largely skinks and geckos, with a relatively high proportion of geckos. The non-avian fauna comprises largely ecologically tolerant, wide-ranging species, and many (geckos, frogs, rats, cuscus) are associated with humans to some degree and may have been carried to the island, intentionally or otherwise. There is a preponderance of bird and bat supertramps and D-class tramps and a relative lack of high-S bird species, there are no island-endemic bird subspecies, and the number of resident land bird species is well below that expected for an island of Long's size and isolation.

Long Island's highly porous soil and poor water retention, relatively low rainfall, and frequent extreme seasonal aridity together may be responsible for the slow growth of trees and arrested vegetational development, which may in turn inhibit the maturation of Long's animal community.

Long Island's colonization has a number of similarities to that of the three older Krakatau Islands and in vascular plants this is largely because of the presence in both of seaborne early pioneer species.

Motmot

Motmot's vegetation is still at a very early stage of development, sedges, grasses and herbs being the most frequent plants, with only four trees of stature. All but one of the *Ficus* individuals are small and most are probably immature. The *Ficus* community is still at an early stage of dependence on pollinating wasps arriving from Long Island.

Motmot's animal community is largely dependent on energy from outside the island, chiefly the fallout of lake insects, and is dominated by two spider and one ant species. The island's vegetational immaturity precludes frugivores and nectarivores and the presence of raptors and lack of cover may preclude the establishment of rats, reptiles or frogs. Of the four resident vertebrates, two (a swallow and a bat) are aerial insectivores, one (a duck) is also dependent on the lake for food, and one (a megapode) is a ground-feeding insect/herbivore.

Motmot's isolation from the sea precludes two important features of the colonization process. Marine flotsam, which serves as an energy conduit to young coral sand cays and to marine emergent islands such as Surtsey, Anak Krakatau and Tuluman, has no access to Motmot. Similarly, thallassochorous plants, many of which are important pioneers on marine emergent islands, cannot reach Motmot unless they are diplochorous and the secondary dispersal mode is very effective. On marine emergent islands like Anak Krakatau such pioneer diplochores are visited by facultatively frugivorous birds which may bring in more numbers and species of fruit-bearing trees. These attract obligate frugivores which, particularly through the establishment of pioneer heliophilous *Ficus* species in good numbers, accelerate the process of plant diversification. Marine diplochorous plants cannot initiate this train of colonization processes on Motmot, and diversification is likely to be slower. It should accelerate when vegetational cover increases and there are sufficient mature *Ficus* plants to attract frugivores to the island.

SUGGESTIONS FOR FUTURE WORK

Probably the most pressing need in the study of the Long/Motmot colonization system at present is a thorough survey of the flora of Long Island. It is also important that suggestions by zoologists that the vegetation of Long is unusually undeveloped and the growth of its trees retarded be checked by field botanists on Long Island and by comparison with relatively unaffected islands in the area, for example, Umboi. A thorough, specialist bat survey is also needed.

On Motmot investigations into the maturation of the various *Ficus* species and the arrival of their specific pollinating fig–wasps would provide useful information on fig–wasp dispersal and the establishment of *Ficus* populations. Motmot's simple food chain offers an ideal opportunity to measure true flux of biomass from water to land, and rate of accumulation of organics leading to soil formation. The apparent absence of a predator on the high lycosid population deserves further investigation.

Surveys of Long and Motmot should continue at intervals of 5–10 years in order to continue the monitoring of these colonization processes. Biological investigations at shorter intervals should follow closely upon any further volcanic activity.

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BIOSKETCHES

Ian Thornton, leader of the Long Island research group, is interested in the assembly of communities on pristine isolates, and over the past two decades has led research teams working on the Krakatau Islands. **Simm Cook** is completing his doctorate on processes determining species richness in Australian tropical lizards. **John Edwards** has research interests in the ecology of alpine and volcano arthropods, especially in the recolonization of Mount St. Helens volcano since the 1980 eruption. **Mike Shanahan** and **Rhett Harrison** are fig biologists with experience in Borneo, specializing in the dispersal of figs by frugivores, and their pollination, respectively. **Clinton Schipper** is an ornithologist with experience in Australia and Africa, **Rose Singadan** is a vertebrate conservationist and ecologist, and **Ruby Yamuna** a coral conservationist with interests in New Guinea plants.