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Primary Succession and the Effect of First Arrivals on Subsequent Development of Forest Types

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ABSTRACT: The three Krakatau islands in Indonesia were completely denuded by the great eruption in 1883. One century after the eruption, the vegetation of Rakata on the one hand and of Panjang and Sertung on the other are quite different. Indigenous or exogenous *Neonauclea* seeds successfully formed *Neonauclea* forest on Rakata island but completely failed to do so on Panjang and Sertung islands. The dispersal of seeds, soil conditions and volcanic activity of Anak Krakatau were all found to be contributing factors.

The *Timonius* and *Dysoxylum* forests found on Panjang and Sertung originated on both islands after the appearance of Anak Krakatau. These dominants have larger seeds than *Neonauclea* and were able to germinate and grow under the regenerated mixed forest canopy but it was not so easy for them to colonize the *Neonauclea* forest. At the present time, their invasion progresses only gradually on Rakata.

Ardisia scrub on steep coastal slopes on the Satsunan islands, SW Japan, is thought to be a somewhat parallel case of the retarding effect on the subsequent development of communities of the first arrivals. *Ardisia* scrub in these habitats appears to be a stable community, withstanding salt-laden wind. This shrub produces a number of stem and root sprouts, in a mop-headed growth. Their drupes are carried by birds and few seedlings were found in the scrub. The scrub floor was heavily shaded when its canopy was covered by lianes. The deep shade and frugivore activity prevent the invasion of other dominant species which would change the scrub into another type of forest. In milder habitats the scrub gradually becomes tall and the number of sprouts decreases, the forest then changes into another type such as *Persea* or *Castanopsis* forest.

Introduction

Since Clements published the first conceptual synthesis of plant succession in 1916, several facts and ideas have been proposed (Tansley 1935; Watt 1947; Whittaker 1956; etc.) to clarify the outline of succession. However, in the process of succession we still have many problems to solve by intensive studies and experiments.

A plant succession has a larger number of seral stages in the tropics than in the temperate zone, but the time necessary for one seral stage would be shorter in the tropics. In normal succession, there is a gradual and successive replacement of canopy species, but if one type of forest has once come into existence in the course of succession, it will last for a long time, preventing the

invasion of other canopy species. This case is frequently observed on small islands.

In the Krakatau islands we can observe an example of the important effects of first arrivals on the subsequent development of forests. Another example of the effect was observed on small islands of SW Japan. The effect was produced by the heavy production of sprouts or mop-headed growth. In the present paper I describe two cases of long-existing vegetation in the course of a succession, and seek out the mechanisms of the long existence. The data used in the present paper were partly cited from Tagawa et al. (1985 b) and Tagawa and Suzuki (1985 a).

I would like to express sincere gratitude to the members of the research team, and also to Prof. Dr. I. W. B. Thornton, Dept. of Zoology, La Trobe University, Australia

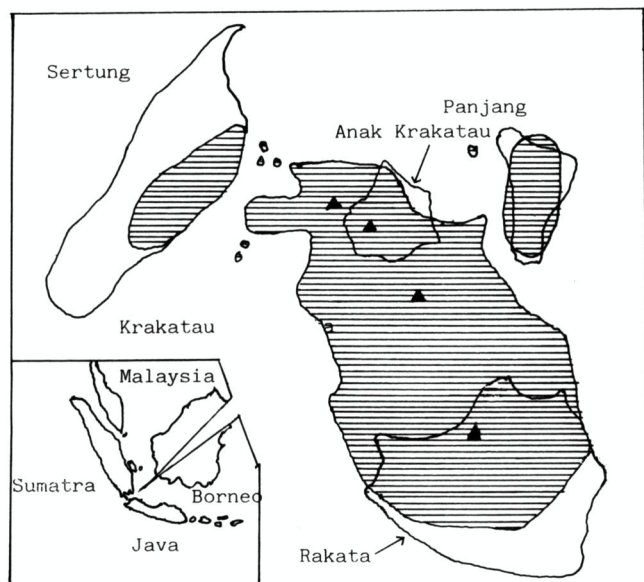


Fig 1 Map of the Krakatau islands. Shared areas show the islands before the eruption, and the solid line those at the present time. Black triangles show the craters; from north Perbuatan, Anak Krakatau, Danan and Rakata. Only the Anak Krakatau crater is active now.

correspond to 9 types of forest and their transitions:

- Group I and II: young and old stands of *Casuarina equisetifolia* forest
- Group III: *Terminalia catappa* forest
- Group IV: transitional from *Terminalia catappa* forest to *Timonius compressicaulis* forest
- Group V: *Timonius compressicaulis* forest
- Group VI: *Neonauclea calycina* forest
- Group VII: *Schefflera polybotrya* shrub
- Group VIII: transitional from *Terminalia catappa* forest to *Dysoxylum gaudichaudianum** forest
- Group IX: *Dysoxylum gaudichaudianum* forest

* cited as *Dysoxylum caulostachium* in Tagawa et al. 1985 b.

Several herbaceous communities were also identified. The forests and herbaceous communities identified by us and those recorded since 1883 were synthesized into a scheme of primary succession by Tagawa et al. (1985 b). This scheme contains plant communities that were not found in 1982 on the Krakatau islands, such as a blue-green algae community and mangrove.

Which is the more Advanced Community in Terms of Succession?

who invited me to the symposium, "The Krakatau islands - a case study of natural change in biodiversity", at the 17th Pacific Science Congress held in Honolulu, 1991. Almost all of this paper was read at the symposium.

The Case of the Krakatau Islands

Process of Plant Succession

The tremendous eruption of Krakatau Island in 1883 blew off two thirds of its volume, and all living things are said to have been killed on the island as well as the two neighbouring islands of Sertung and Panjang (Fig 1). The Indonesian government invited international research teams to the Krakatau islands as a centennial commemoration of the great eruption in 1883, and I organized an ecological team.

In 1982 our team made two expeditions to the Krakatau islands to do research in cooperation with Indonesian scientists. By observations during a short period of the dry season, the outline of the primary succession of a tropical monsoon area was obtained, making reference to the pioneer works of many scientists (Docters van Leeuwen 1936; van Borssum Waalkes 1960; Flenley and Richards 1982). Based on the 1982 observation and using the similarity index, $C_{\lambda(w)}$, which takes species composition and tree size into consideration, 9 groups of quadrats were identified (Tagawa et al. 1985 b). They accurately

According to Shinagawa et al. (1991), the soil of Rakata island contains much more clay material and exchangeable potassium than the soils of the other islands. He concluded that soil development was much more advanced on Rakata than on the other islands. Plant succession improves soil conditions by increasing organic matter in the mineral soil, and prepares soils for a new type of vegetation. If this statement is always true, the *Neonauclea calycina* forest, existing exclusively on Rakata, should be the most advanced forest type on the Krakatau islands.

Fig 2 shows the DBH (diameter at breast height) distribution of trees in the quadrats taken in the *Neonauclea* forest (Group VI). In five quadrats there were juveniles of *Neonauclea calycina*, and in one quadrat a number of juveniles of *Dysoxylum gaudichaudianum* and *Terminalia catappa*, a dominant species of other forest types. In the *Dysoxylum gaudichaudianum* forests (Fig 3) on Sertung and Panjang (in the original paper, Rakata Kecil) we could find a fair number of *Dysoxylum* juveniles but no *N. calycina*. In *Timonius compressicaulis* forest on Panjang, both *Dysoxylum* and *Timonius* juveniles were frequently found under the canopy of *Timonius compressicaulis* (Fig 4).

If it is true that species more resistant to shade appear later in a succession, then it is obvious from the above that *Dysoxylum* forest may be a more advanced type of forest than *Neonauclea* and *Timonius* forests.

Richards and Whittaker (1990) made vegetation maps of the Krakatau islands. On Sertung and Panjang there are

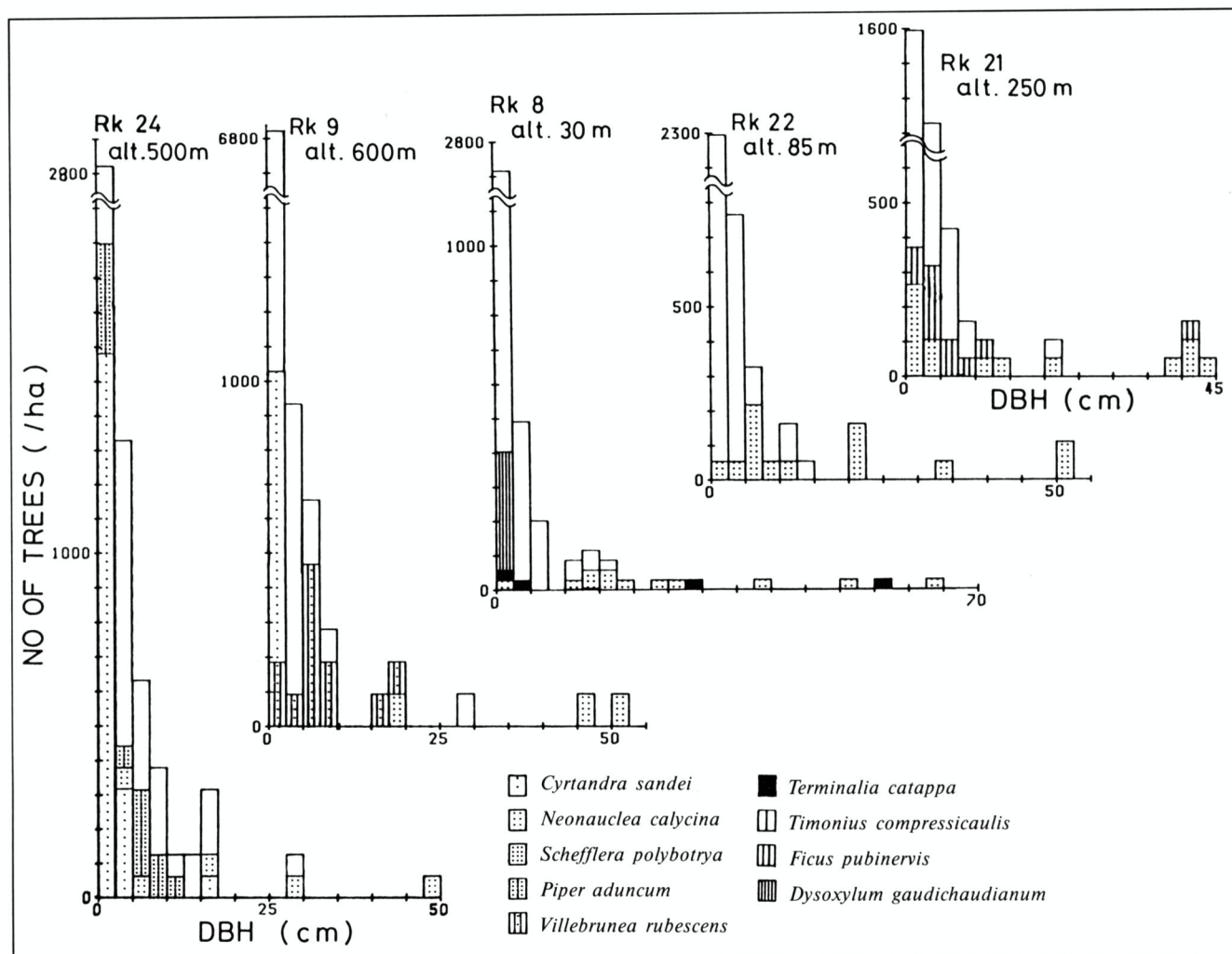


Fig 2 DBH (diameter at breast height) distribution of trees in the quadrats of Group VI, *Neonauclea* forest. The blank sections of the columns represent species other than those listed in the legend.

no *Neonauclea* forests, although small trees of *Neonauclea* were found on Panjang in 1920 by Doctors van Leeuwen. Hilly areas were covered by *Timonius* and *Dysoxylum* forests in 1982 (Tagawa et al. 1985 b). A *Neonauclea* forest was found only on Rakata island although its western area was not explored by us nor by Flenley's team. Then, why is *Dysoxylum* forest not a leading forest type on the rich soil of Rakata? And why doesn't *Dysoxylum* invade the *Neonauclea* forest?

The Problem of the Formation of *Neonauclea* forest

Invasion and extinction of species on islands were clearly explained in the equilibrium model of MacArthur and Wilson (1963) but from the standpoint of plant ecology it is very hard to determine the extinction of plant species,

because seeds, especially of pioneer trees and herbaceous species are dormant in the soil for a fairly long time, as Richards (1952) described. If there is an "ecological window" (Thornton et al. 1988) seeds have a possibility of germinating after a few decades of disappearance above the ground. Small scale ecological windows may be gaps in forests. Landslides and volcanic eruption make large windows.

I have two suggestions to account for the formation of *Neonauclea* forests only on Rakata island.

The first is that the seeds of *Neonauclea* had been stocked up in the old top soil before the 1883 eruption and afterwards germinated in deep gullies, the bottom of which reached to the surface of the old top soil. Many deep gullies were quickly developed on Rakata because of the steeper slopes (down from a peak about 800 m high) than on the other islands. This idea is not inconsistent with the

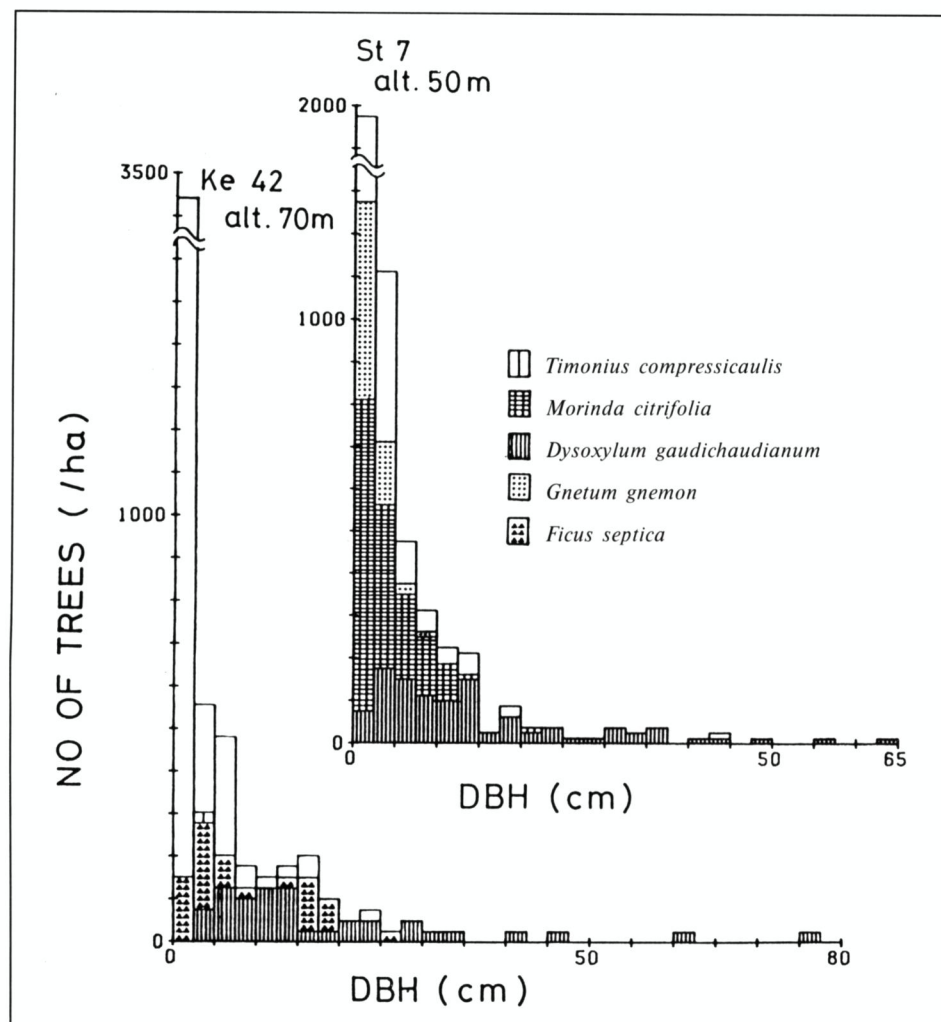


Fig 3
DBH distribution of trees in the quadrats of Group IX, *Dysoxylum* forest. The blank sections of the columns represent species other than those listed in the legend.

description of Docters van Leeuwen (1936) that thickets developed in the gullies and their outstanding *Neonauclea* trees gradually became dominant to make *Neonauclea*

forests. On the islands of Sertung and Panjang he recognized that mixed thickets also developed but the dominants were *Macaranga tanarius*, *Terminalia catappa* and a few species of *Ficus*.

There was controversy concerning the sterilization of plants on the Krakatau islands after the 1883 eruption, at the 4th Pan-Pacific Science Congress held in Batavia (now Jakarta) in 1929. At that time few paid attention to the question of seeds. We do not yet have a conclusion on this problem.

The second idea is that *Neonauclea* seeds invaded Rakata, Panjang and Sertung uniformly from Java but growing conditions on Panjang and Sertung were quite different from Rakata. The anemochorous seeds produced were able to spread over the whole island of Rakata without disturbance from the volcanic fall-out from Anak Krakatau, as described below. *Neonauclea* was first collected in 1905 by Valeton (Tab 1) and became the only dominant forest before 1919 (Docters van Leeuwen 1919, 1921), and in 1928 the forest became 20 m in height and

Tab 1 The first record of three dominant species on the Krakatau Islands. DvL, Tagetal, W&F, Valeton mean Doctors van Leeuwen (1936, Tagawa et al. (1985 b), Whittaker and Flenley (1982), and Valeton (Doctors van Leeuwen 1919), respectively. "<" means that the invasion was much earlier than the year indicated

Species	Rakata	Panjang	Sertung
<i>Neonauclea calycina</i>	1905 Valeton	1925 DvL	<1920 DvL
<i>Timonius compressicaulis</i>	1929 DvL	1929 DvL	<1982 TAGetal
<i>Dysoxylum gaudicaudianum</i>	1979 W&F	<1932 DvL	<1982 TAGetal

extended up to 750 m altitude. Thus within 23 years a high stature and extended distribution had been achieved, an astonishingly high speed for forest formation and extension. The fertile soil of Rakata played an important role in this.

I witnessed the seed rain of *Radermachera glandulosa* in the *Neonauclea* forest for several minutes in August, 1982. It looked like a snow fall. The seed fall of *Neonauclea* would be the same.

It is assumed that germination and early growth of *Neonauclea* was uniform on the three islands because it is hard to conceive of anemochorous seeds falling locally only on Rakata island. *Neonauclea* was found 15 and 24 years earlier on Rakata than on Sertung and Panjang, respectively. When Docters van Leeuwen found *Neonauclea* on Sertung in 1920, the trees were large and its first arrival would have been much earlier than 1920. On Panjang the situation may be the same. Volcanic activity then disturbed the subsequent growth of *Neonauclea* and the extension of its distribution on Panjang and Sertung.

In december 1927 volcanic activity on the bottom of the sea created Anak Krakatau. Repeated violent eruptions had a great effect on the vegetation of the flat islands of Sertung and Panjang. Rakata has a high and steep cliff facing Anak Krakatau, and the vegetation on the other, S side, sustained little damage. Even after the appearance of Anak Krakatau IV (the present island) above the sea in 1930, vegetation on the islands of Sertung and Panjang sustained great damage in 1934–1935 and 1952–1953 (van Borssum Waalkes 1960). I can easily imagine the heavy damage to forests by the thick accumulated ash, as the same situation occurs on the active Sakurajima volcano in my home town of Kagoshima. Under these conditions *Neonauclea* forest could not become established on the islands of Sertung and Panjang. Docters van Leeuwen (1936) wrote that many secondary trees produced vigorous stem sprouts and leaves on branches after defoliation by the eruption. This phenomenon was also observed on the devastated area after the great eruptions of Sakurajima (Kagoshima Ken 1927) and on Miyake-jima volcano, the Bonin islands (Matsuda & Honma 1987). *Neonauclea*, however, produces neither stem nor root sprouts, and has difficulty in germinating under a canopy of regenerated mixed forest.

Timonius compressicaulis was recorded in the late twenties after surviving the volcanic damage on Panjang, and *Dysoxylum gaudichaudianum* in the early thirties on those devastated areas. Their zoochorous seeds are much larger than those of *Neonauclea calycina* and their seeds and seedlings may be more resistant to burial under volcanic ash. The seeds can germinate on darker forest floors than those of *N. calycina*. The areas occupied by *Timonius* and *Dysoxylum* forests are small considering the period since they were first collected. Zoochorous dispersal of seeds of both species is responsible for their slow extension of distribution.

Unfortunately there is no precise record of *Timonius compressicaulis* and *Dysoxylum gaudichaudianum* on

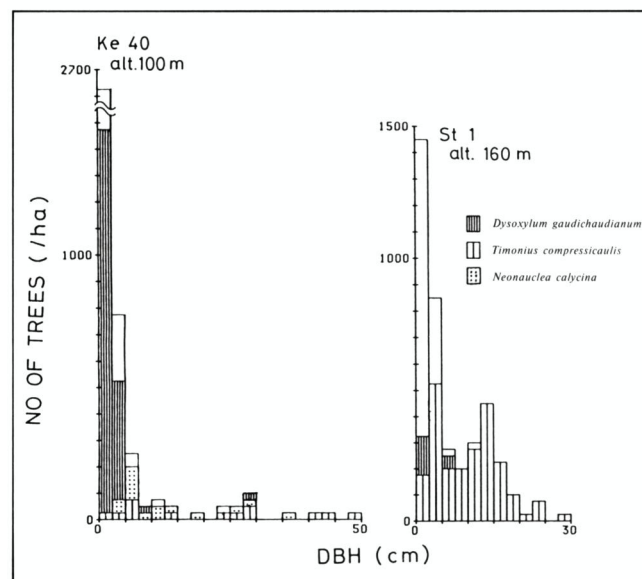


Fig 4 BDH distribution of trees in the quadrats of Group V, *Timonius compressicaulis* forest. The blank sections of the columns represent species other than those listed in the legend

Sertung until we found them in 1982; the time of their invasion is thought to be the same as on Panjang. The first colonization of Panjang by *Dysoxylum* might be much earlier than 1932, because Docters van Leeuwen found *Dysoxylum* trees in fruit and many seedlings around the trees in 1932, and the same situation probably applied to Sertung.

Regardless of the indigenous or exogenous origins of *Neonauclea* seeds, a nearly pure forest was formed over a large area of Rakata, and for about 70 years, from 1919 to 1991, the forest has prevented other dominant species from invading. In recent years we have found seedlings, saplings and juveniles of such dominant tree species as *Timonius*, *Dysoxylum* and *Ficus* (Fig 2–4) in the *Neonauclea* forest. In contrast, in the hilly areas of Panjang and Sertung there are no *Neonauclea* forests but *Timonius* and *Dysoxylum* forests, in which no *Neonauclea* juveniles were found.

I earlier described how *Neonauclea* forest would gradually be replaced by *Dysoxylum* forest (Tagawa et al. 1985; Tagawa 1989). I still think it is probable, apart from the possibility of invasion of a shade-tolerant species other than *Dysoxylum* from the large islands of Sumatra and Java. Thus, the first arrival, *Neonauclea*, delayed the subsequent development of the forest. As this first arriver was excluded on Panjang and Sertung by volcanic activity and other species (*Macaranga* and *Casuarina*) were the early dominants, subsequent forests on these two islands have been dominated by *Dysoxylum* and *Timonius*.

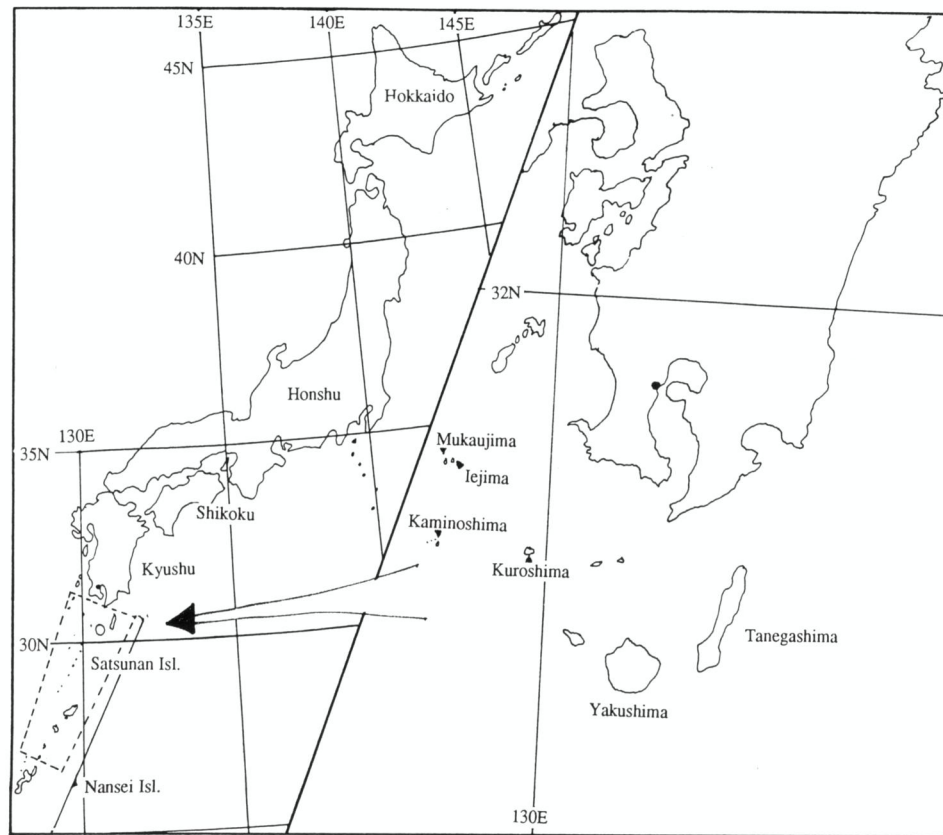


Fig 5
Map of Japan and the Satsunan
Islands

To test the two hypotheses outlined above we need experiments and long term observations such as those of Docters van Leeuwen in botany and Dammerman in zoology.

The Case of Satsunan Islands

The Satsunan Islands

Japan has land-bridges to the Kamchatka peninsula through Chishima Retto (Kuril islands), to the Russian mainland through Sakhalin island, to Micronesia through Izu Shoto and Ogasawara Gunto (Bonin islands), to the Korean peninsula through the Tsushima islands and to Taiwan and the China mainland through the Nansei

islands. These land-bridges have played an important role in the dispersion of plants and animals between the Asian continent, tropical Asian islands, Pacific islands and from the north, and have been the places for the evolution of a number of endemic species.

In the Satsunan islands, the northernmost part of the Nansei islands, there are a few islets that have hitherto been uninhabited (Fig 5). The islands concerned are Kaminoshima, Iejima and Mukaujima; they are of Tertiary volcanic origin and are fringed with bold cliffs. Nearly all the slopes on the cliffs are usually covered by herbage and almost pure scrub of the evergreen *Ardisia sieboldii*. On the flat islands of coral origin in the southern Nansei islands no such pure *Ardisia* scrub was found by the shore. *Ardisia* is strongly resistant to salt-laden wind, especially to sea water thickly driven ashore in typhoons. After such an

Islands	Area (km ²)	Maximum altitude (m)	Distance from Kyushu (km)	Water system
Kaminoshima	0.26	158.5	90	none
Iejima	0.60	95	80	a small stream
Mukaujima	1.70	324.6	80	a river
Kuroshima	15.70	621.9	55	several rivers

Tab 2
Summary of geographic features of
the islands studied

Species	Quadrat Altitude (m) Size (m ²)	K-1 150 100	K-5 120 100	K-10 80 50	U-1 90 100	U-2 40 100	U-5 75 25	U-6 50 25	M-1 135 100	M-2 135 100	M-3 160 100	M-4 160 100	M-10 200 100												
<i>Ardisia sieboldii</i>		52	5391	18	1080	61	6316	33	3458	2	105	5	363	11	2052	11	620	20	2085	6	480	17	4827		
<i>Litsea japonica</i>		2	298	1	37	1	95	6	487	13	1319	3	127	4	205	8	442	3	64	4	56	2	36	7	678
<i>Cinnamomum japonicum</i>		2	512													5	246	3	290	7	36	5	39	4	265
<i>Persea thunbergii</i>		1	295	2	428	1	384	1	1379	2	1521	1	122			7	708	6	1701	7	1432	6	2134	4	4077
<i>Morus australis</i>				2	428			1	398																
<i>Ficus erecta</i>				4	318	1	67	1	1	4	212	2	40	1	16	2	15				1	2	6	100	
<i>Callicarpa japonica</i> v. <i>luxurians</i>		1	1													2	32	1	17		4	15	7	181	
<i>Elaeagnus macrophyllus</i>		1	8							3	48					1	9	1	18	1	33		1	34	
<i>Aralia elata</i>				3	158																				
<i>Symplocos cochinchinensis</i>		1	19			2	204	1	311																
<i>Microtropis japonica</i>						1	40									2	30	2	14	9	410	2	3	4	84
<i>Celtis boninensis</i>																2	147								
<i>Cinnamomum daphnoides</i>																									
<i>Pueraria lobata</i>						6	7	21	15																
<i>Trachelospermum asiaticum</i>						20	16																		
<i>Paederia scandens</i>						1	-		1																
<i>Smilax maritima</i>						10	2	4	1																
<i>Ficus wrightiana</i>				2	5515											3	115	1	76						
<i>Mallotus japonicus</i>				1	2											2	100	2	280			1	4	6	363
<i>Dendropanax trifidus</i>																7	526	9	339			12	748	11	762
<i>Illicium anisatum</i>																4	159	2	31	1	2	1	2		
<i>Euonymus japonicus</i>																3	9			1	2			5	18
<i>Fatsia japonica</i>																1	323			2	1858	3	701		
<i>Eurya japonica</i>																3	48			2	150				
<i>Pittosporum tobira</i>																				8	18			3	5
<i>Tarenna gracilipes</i>																				2	76			1	19
<i>Elaeocarpus decipiens</i>																				1	4			1	365
<i>Ilex integra</i>																				6	2829	1	755		
<i>Lithocarpus edulis</i>																3	167								
<i>Camellia japonica</i>																				2	966				
<i>Livistona chinensis</i>																								1	1
<i>Rubus rosaeifolius</i>																								4	1851
<i>Castanopsis sieboldii</i>																									
The number of species		7		6	7	11		8	10		8	17	11	15	11										16

Tab 3 Species composition of the *Ardisia sieboldii* scrub on Kaminoshima (K), Iejima (U) and Mukaujima (M). The left column of each quadrat shows the number of individuals in the quadrat, and the right column the total basal area (m²) of the species. “-” means negligible proportion of the total basal area.



A



B



C

Fig 6 Sprouts from a stump of *Ardisia sieboldii* in a Kaminoshima quadrat K-1 (A), the *Ardisia* forest floor without undergrowth in Mukaujima quadrat M-1 (B), and undergrowth of a *Persea* tree on Kaminoshima quadrat K-1 (C). The *Persea* tree has many sprouts on its stem.

event all the leaves turn brown and fall, but immediately after the leaf fall, new leaves sprout. This scrub is a disclimax which survives under the severe conditions of the shore environment of the warm temperate region of Japan.

Mechanism of Self-Maintenance of *Ardisia* Scrub

A geographic summary of each island studied is provided in Tab 2. Kaminoshima is the smallest island and Kuroshima the largest. The number of higher plant species is 78 for Kaminoshima, 152 for Iejima, 170 for Mukaujima and 644 for Kuroshima. The larger the island, the more the habitats for plants, therefore the greater the species richness. In addition to species richness, there were diversified plant communities in response to a larger number of habitats on the larger islands. This is an interesting phase of island ecology, but in this paper I refer only to *Ardisia* scrub.

The species composition of the *Ardisia* scrub on each island is shown in Tab 3. *Ardisia sieboldii* is the sole dominant on the smallest island, Kaminoshima, but on larger and higher islands its dominance is shared by other conspicuous plants such as *Persea thunbergii* and *Castanopsis sieboldii*.

On the open slope facing the sea *Ardisia* produces vegetatively a number of stem sprouts and roots sprouts to make a mop-headed crown. The maximum number of sprouted stems was 74 for one individual in K-5 on Kaminoshima. The mean number of stems per individual in each quadrat, shown in Tab 4, decreases on the larger islands. Kuroshima island has an area of 15.7 km², and the mean number of stems was 1.9. The *Ardisia* drupes are carried by birds, and on the forest floor seeds are eaten by rats and mice. In the *Ardisia* scrub it is extremely hard to find seedlings, but according to general observation genets are found in open places and thought to be effective in the colonization of *Ardisia* on to bare ground. The *Ardisia* scrub, therefore, seems to be maintained by producing sprouts, not by seedlings.

Tab 4 The number of sprouted stems per individual of *Ardisia sieboldii* and *Persia thunbergii* on four islands. “-” means no record of the species

Island	Quadrat	Species	
		<i>Ardisia sieboldii</i>	<i>Persea thunbergii</i>
Kaminoshima	K-1	6.3	9.0
	K-5	23.9	2.5
	K-10	4.7	8.0
	Mean	9.7	5.5
Iejima	U-1	2.5	3.0
	U-2	4.0	3.0
	U-5	1.0	2.0
	U-6	3.5	-
	Mean	3.1	2.8
Mukaujima	M-1	4.1	2.8
	M-2	1.6	2.7
	M-3	2.8	1.1
	M-4	2.7	2.3
	M-10	4.0	2.3
	Mean	2.5	2.1
Kuroshima	Mean	1.9	1.6

In the quadrats taken on Kaminoshima no dead *Ardisia* stems were observed but there were a few scars of the dead stems left on the stumps. Seven dead stems in the Iejima quadrats and 3 in the Mukaujima quadrats were observed, but only one and two dead individuals were observed in the Iejima and Mukaujima quadrats, respectively. This shows that the *Ardisia* scrub, once established, is maintained vegetatively by producing sprouts whenever there is the least loss of stems and stumps. If one stem dies, leaving a small gap, the gap is closed by growth of branches from the neighbouring stems and filled up by leaves. In such a small gap there is no probability of seedlings becoming established.

Quadrats M-3, M-4 and M-10 were taken in a ravine of Mukaujima, where plants are sheltered from the strong salt wind. Although there were *Ardisia* shrubs in these stands, the dominant was *Persea thunbergii*. U-1 and U-2 were also taken in a ravine on Iejima, but the *Persea* here do not have a large basal area. The reason for this may be many lianes. *Pueraria lobata* (Legum), *Trachelospermum asiaticum* (Apocyn) and *Paederia scandens* (Rubia), covered

the canopy of the *Ardisia* scrub, heavily shading the floor, which was devoid of plants, as seen in Fig 6 B. There was one *Persea* tree in K-1 and two in K-5, but no seedlings were found around the trees (Fig 6 C). In the *Persea* forests on the Kyushu mainland or on larger islands such as Tanegashima island there are many *Persea* seedlings around the mother trees after a mast year. Another reason for the scarcity of seedlings under the canopy covered with lianes may be an outbreak of rats. Around stumps there were many empty snail shells and the apex of every shell was broken by rats. *Persea* seeds would be a suitable food for rats.

Thus other dominant tree species have difficulty invading such a shaded floor in a habitat with a high density of frugivores. In a more normal situation invasion may be successful by plants reproducing vegetatively or by ramets. Except for unusual incidents like land-slides, large gaps do not form and the *Ardisia* scrub will continue to exist without change. This is another example of the retarding effect of the first arrival, in this case *Ardisia sieboldii*, on the subsequent development of communities.

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