

Forest Structures, Composition, and Distribution on a Pacific Island, with Reference to Ecological Release and Speciation¹

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ABSTRACT: Native forest and scrub of Chichijima, the largest island in the Bonins, were classified into five types based on structural features: *Elaeocarpus-Ardisia* mesic forest, 13–16 m high, dominated by *Elaeocarpus photiniaefolius* and *Ardisia sieboldii*; *Pinus-Schima* mesic forest, 12–16 m high, consisting of *Schima mertensiana* and an introduced pine, *Pinus lutchuensis*; *Rhaphiolepis-Livistonia* dry forest, 2–6 m high, mainly occupied by *Rhaphiolepis indica* v. *integerrima*; *Distylium-Schima* dry forest, 3–8 m high, dominated by *Distylium lepidotum* and *Schima mertensiana*; and *Distylium-Pouteria* dry scrub, 0.3–1.5 m high, mainly composed of *Distylium lepidotum*. A vegetation map based on this classification was developed. Species composition and structural features of each type were analyzed in terms of habitat condition and mechanisms of regeneration. A group of species such as *Pouteria obovata*, *Syzygium buxifolium*, *Hibiscus glaber*, *Rhaphiolepis indica* v. *integerrima*, and *Pandanus boninensis*, all with different growth forms from large trees to stunted shrubs, was subdominant in all vegetation types. *Schima mertensiana*, an endemic pioneer tree, occurred in both secondary forests and climax forests as a dominant canopy species and may be an indication of “ecological release,” a characteristic of oceanic islands with poor floras and little competitive pressure. Some taxonomic groups (*Callicarpa*, *Symplocos*, *Pittosporum*, etc.) have speciated in the understory of *Distylium-Schima* dry forest and *Distylium-Pouteria* dry scrub. Speciation seems to have occurred exclusively where there are comparatively small numbers of component species, historically stable habitats, some opportunity for regeneration without large-scale disturbance, and the occasional occurrence of canopy gaps.

THE BIOTA OF OCEANIC ISLANDS is derived from ancestors that arrived by chance across an open sea and became established. The fauna and flora of those islands have many characteristics that distinguish them from those of continents (see Carlquist 1974). There are many oceanic islands in the Pacific Ocean, but there is relatively little information about their vegetation except for the well-known Hawaiian Islands (Rock 1913, Fosberg 1961,

Mueller-Dombois 1981), Galápagos Islands (Wiggins and Porter 1971, Eliasson 1984, Hamann 1984), and Ponape, in the Caroline Islands (Nakamura 1985). Moreover, the structure and quantitative composition of plant communities have been analyzed without consideration of insular phenomena such as ecological release and speciation.

The Bonin Islands (Ogasawara-shoto in Japanese), located about 1000 km south of Tokyo in the northwestern Pacific Ocean (Figure 1), are Japan's only typical oceanic islands. They consist of about 30 islets occurring in four main groups located linearly north to south: Mukojima, Chichijima, Hahajima, and Iwojima. Even the largest island, Chichijima, is comparatively small, 2395 ha in

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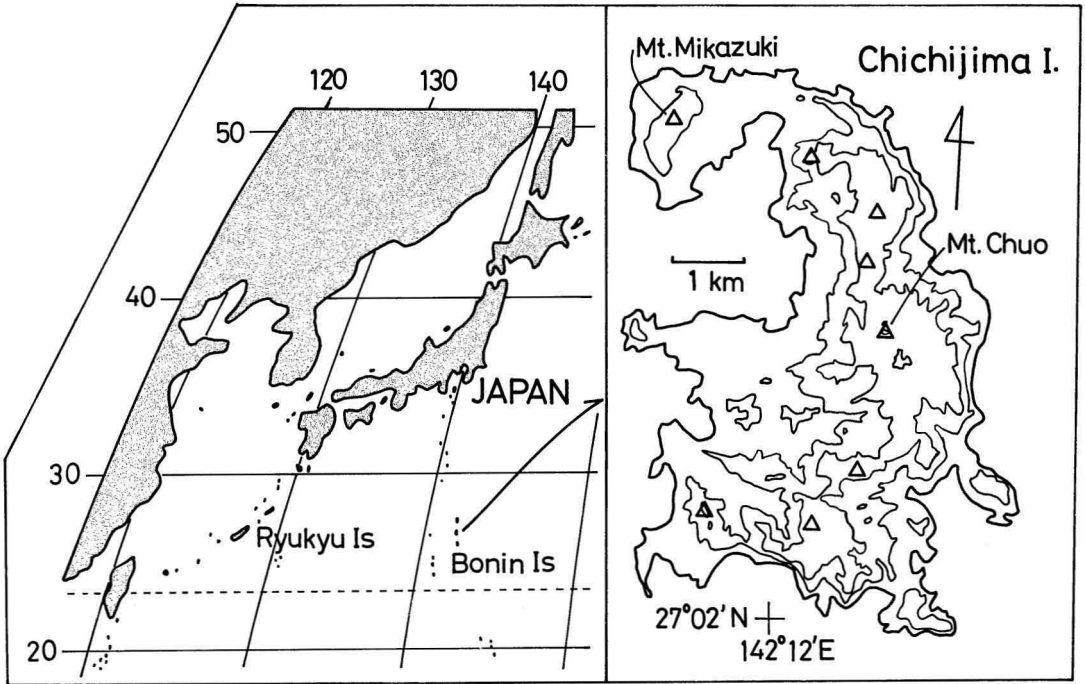


FIGURE 1. Location of the Bonin Islands and a geographical map of Chichijima Island. Thin lines on the map show the 100-m contour. Triangles mark principal mountains.

area and 319 m highest elevation. The islands are volcanic, dating back to the Tertiary (Mukojima, Chichijima, and Hahajima) or Quaternary (Iwojima) (Kuroda et al. 1981). The climate is subtropical. It rains almost year round, but soil water deficiency occurs in mid-summer in areas with shallow soil (Figure 2).

Ninety-nine families, 256 genera, and 369 species of vascular plants are found in the Bonins. The proportion of endemism is 42.5% for all flowering plants and 74.7% for arboreal species alone (Kobayashi 1978). The flora of the Bonins is related to that of subtropical Southeast Asia, Formosa, and the Ryukyu Islands (Hosokawa 1934, Tuyama 1970, Yamazaki 1981). However, some genera, such as *Quercus* and *Castanopsis*, which are the dominant species in the Ryukyu Islands, are absent in the Bonins (Shimizu, 1984a).

Toyoda (1975) classified the vegetation based on dominant species and proposed a

vegetation map for Chichijima. Okutomi et al. (1985) published vegetation maps for the main islands of the Bonins. Ohba and Sugawara (1977) and Okutomi et al. (1985) made a detailed classification based on the Braun-Blaunquet method of analysis. There are also ecological studies of the vegetation of Chichijima and Hahajima by Numata and Ohsawa (1970) and Ohga et al. (1977). None of these is sufficient, however, to describe a situation in which forest and scrub represent a stage on which a drama of evolution is played.

In this paper we classify the native forest and scrub of Chichijima with emphasis on structural characteristics and show some unique features. We also attempt to relate vegetation structure and composition to the phenomena of ecological release and speciation.

Nomenclature follows Yamazaki (1970) except for *Rhaphiolepis indica* v. *integerrima* and *Cinnamomum insularimontanum*.

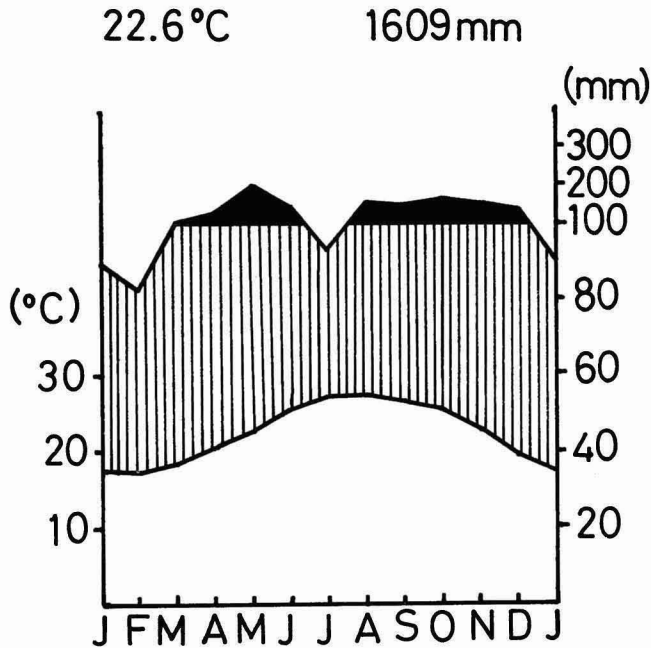


FIGURE 2. Climate diagram of Chichijima Island based on monthly mean temperatures and precipitation recorded from 1907 to 1939.

METHODS

The native forest and scrub of Chichijima was typified mainly by structural characteristics derived from field observation. Aerial photographs (scale 1 : 12,500) and ground observations were combined to produce a vegetation map.

Fifty plots, including each type of forest and scrub, were sampled in 1977 and 1979. The forest vegetation was stratified into four height layers: T1, the canopy tree layer; T2, the low-stature tree layer; S, the shrub layer; and H, the herbaceous plant layer including seedlings of canopy species. Fewer layers were recognized in scrub. An emergent layer consisting exclusively of mature *Pinus lutchuensis* trees was designated the E layer.

All vascular plant species were enumerated. Tree diameters (≥ 3 cm) were measured at 1.2 m above ground except for shrubs less than 1.5 m high, for which stem girth was measured at ground level. Seedlings in the H layer and saplings (< 3 cm) were counted.

Herbs and vines were tallied in 1 m \times 1 m

quadrats, randomly placed in each plot and covering at least 10% of the plot area.

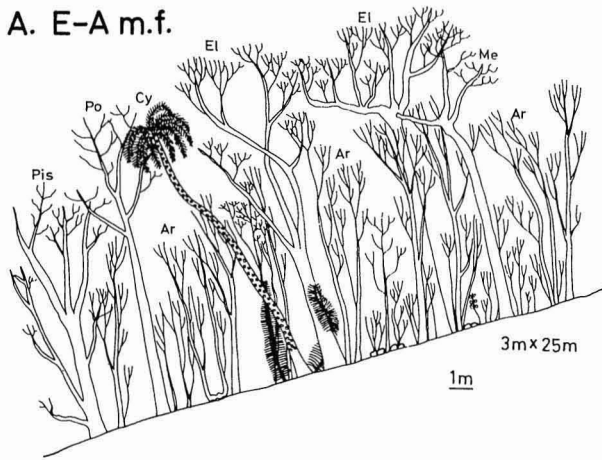
Profile diagrams were drafted, light intensity was measured at ground level, and leaf size (length and width) of all component species was measured with collected samples in the typical forest and scrub of each type.

RESULTS

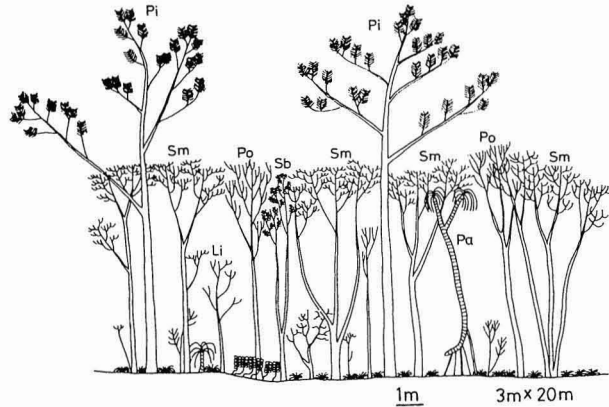
Typification

The native forest and scrub on Chichijima were classified into three main groups on the basis of average height of canopy trees: mesic forest with tall trees, 10–15 m high; dry forest with low-stature trees, 2–10 m high; and dry scrub with shrubs less than 2 m high. These groups were subdivided into five types (Figure 3) in terms of structural features other than tree height (e.g., presence of an E layer and development of undergrowth shrubs). Types were named by dominant or subdominant species.

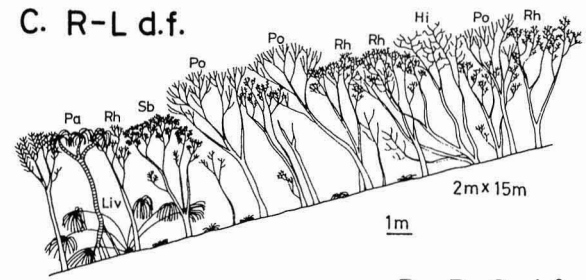
A. E-A m.f.



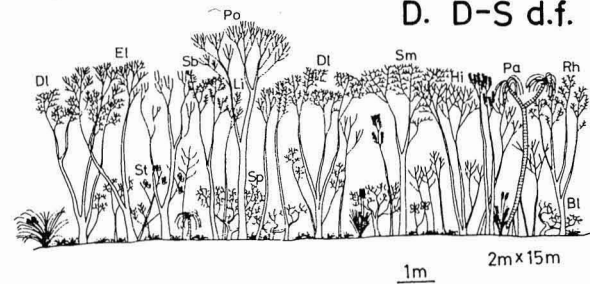
B. P-S m.f.



C. R-L d.f.



D. D-S d.f.



E. D-P d.s.

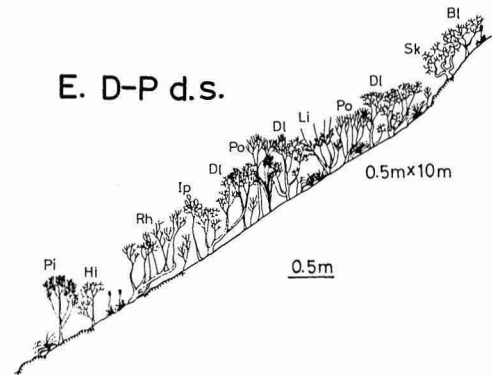


FIGURE 3. Profile diagrams of the five vegetation types. The size of sample strips is shown at bottom right of each. Keys to abbreviations: Ar, *Ardisia sieboldii*; Bl, *Boninia glabra*; Cy, *Cyathea mertensiana*; Dl, *Distylium leptotum*; El, *Elaeocarpus photiniaefolius*; Hi, *Hibiscus glaber*; Ip, *Ilex percoriacea*; Li, *Ligustrum micrantum*; Liv, *Livistonia chinensis*; Me, *Melia azedarach*; Pa, *Pandanus boninensis*; Pi, *Pinus lutchuensis*; Pis, *Pisonia umbellifera*; Po, *Pouteria obovata*; Rh, *Rhaphiolepis indica* v. *integerrima*; Sb, *Syzygium buxifolium*; Sk, *Symplocos kawakamii*; Sm, *Schima mertensiana*; Sp, *Symplocos pergracilis*; St, *Stachyurus praecox* v. *matsuzakii*.

Elaeocarpus-Ardisia mesic forest (E-A m.f.) is the tallest forest of all. Canopy trees attain 15 m in height. *Elaeocarpus photiniaefolius* is abundant in the canopy layer; lower layers are dominated by *Ardisia sieboldii* (Figure 3A).

Pinus-Schima mesic forest (P-S m.f.), 12–15 m high, is dominated by an introduced pine, *Pinus lutchuensis*, and an indigenous pioneer tree, *Schima mertensiana*. The crowns of the pine trees reach far above those of the other species, forming an emergent layer (Figure 3B)

Rhaphiolepis-Livistonia dry forest (R-L d.f.), 2–6 m high, is dominated by *Rhaphiolepis indica* v. *integerrima* (Figure 3C). There are few shrub species in the S layer.

Distylium-Schima dry forest (D-S d.f.), 3–8 m high, is mainly composed of *Distylium lepidotum* and *Schima mertensiana*. Many

undergrowth shrubs occur in this kind of forest (Figure 3D).

Distylium-Pouteria dry scrub (D-P d.s.), of 0.3–1.5-m-high vegetation, is also dominated by *Distylium lepidotum*. Almost all species in this scrub have stunted growth forms (Figure 3E).

Figure 4 shows the similarity relationships of the sample plots based on the Bray-Curtis (1957) ordination method. The index of similarity is $IS = 200c/(a + b)$, in which a and b represent the total number of species in Plots A and B, and c is the number of species common to both plots. The ordination, based on the composition of woody species, indicates that the plots of each vegetation type, except those of the *Pinus-Schima* mesic forest, are distinctively grouped. *Pinus-Schima* mesic forest is a secondary forest (Shimizu 1983),

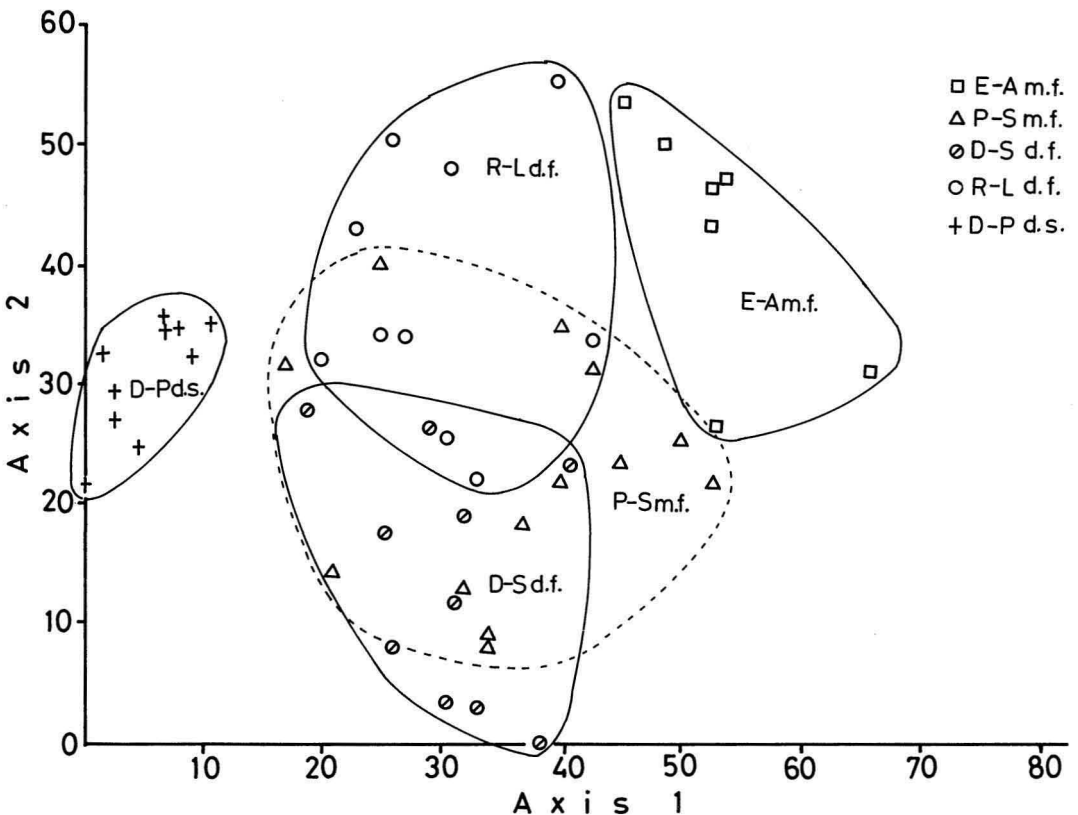


FIGURE 4. Ordination of 50 sample plots by the Bray-Curtis (1957) method based on similarity of composition of woody species.

thus the plots of this type are scattered in the ordination (Figure 4) because of varied species composition, which is affected by surrounding climax forests. Typification by structural features also seems to be reasonable from the standpoint of species composition.

The variation on axis 1 in Figure 4 shows a gradient from mesic forest to dry scrub. Field observation of a cross section along a road showed that tree height is roughly proportional to soil depth. Thus the gradient may be related to soil depth and moisture conditions. The variation on axis 2, which seems to separate the two types of dry forest, is not attributable to any one environmental variable. The relation between vegetation and edaphic conditions needs further study.

Structure and Composition

Table 1 shows the average density of individuals for all woody species in each vegetation type.

Elaeocarpus-Ardisia MESIC FOREST. The *Elaeocarpus-Ardisia* mesic forest consists of four layers (Figure 5A). The T1 layer is composed of several tall trees such as *Elaeocarpus photinaefolius*, *Pisonia umbellifera*, *Pouteria obovata*, and *Sapindus boninensis* (Table 1). *Ardisia sieboldii*, with suckering ability, overwhelmingly dominates the lower layers (Table 1). Some mature trees of light-demanding species such as *Fagara boninensis*, *Celtis boninensis*, *Melia azedarach*, and *Schima mertensiana* are found without any seedlings and saplings (Table 1). These trees may have invaded earlier canopy gaps and survived in the forest. Most of the canopy trees have large leaves compared with those of the other vegetation types (Figure 6).

Stumps of *Morus boninensis* more than 1 m in diameter are sometimes found in the forest. *M. boninensis* was a member of the canopy species, but almost all trees of this species were selectively cut before 1945 because of their timber value (Toyoda 1981). *Morus australis*, an escaped species, has replaced the endemic species.

Because of the close upper-forest strata and the dominance of *Ardisia sieboldii* in the lower

layers, the forest is relatively dark (Table 2). Few understory shrub species indigenous to *Elaeocarpus-Ardisia* mesic forest are found on Chichijima (Table 3), and seedling density of woody and herbaceous species is low in the H layer (Table 1). On Hahajima, the second largest island, where this type of forest has been preserved in better condition, some small undergrowth trees (*Claoxylon centinarium*, *Ficus iidaiana*), herbaceous plants (*Piper postelsianum*, *Corymborchis subdensa*, *Goodyera boninensis*, *Bolbitis boninensis*), and epiphytes (*Cirrhoptalum boninense*, *Peperomia boninsimensis*, *Asplenium nidus*) are found. Thus, the *Elaeocarpus-Ardisia* mesic forest on Chichijima may have had a richer flora of understory shrubs, herbaceous plants, and epiphytes before destruction of the forest by man.

The *Elaeocarpus-Ardisia* mesic forest was seriously damaged by the exceptionally severe typhoon that hit the Bonins on 6–7 November 1983 (Shimizu 1984b). Regeneration of this forest following large-scale canopy gap formation by typhoons is being investigated (Shimizu, in preparation).

Pinus-Schima MESIC FOREST. There are four forest layers in the *Pinus-Schima* mesic forest. The top layer, which consists of *Pinus lutchuensis* together with *Casuarina equisetifolia* in some plots, forms an emergent layer (Figure 5B). The T layer is densely occupied by *Schima mertensiana* and, to some extent, by other native tree species.

Density of stems and individuals is lowest of all the vegetation types (Table 4), and the forest is rather dark (Table 3) because of the closed canopy of *Schima mertensiana*. Seedlings of canopy trees are not abundant (Figures 3B, 5B). No trees, shrubs, or herbs are unique to *Pinus-Schima* mesic forest (Tables 1, 3) because it is a secondary forest derived from cultivated fields abandoned about 1945 (Shimizu 1983).

Pinus lutchuensis in this forest has been attacked by the pine wood nematode since 1979. Many mature pine trees in the emergent layer are dead, and the physiognomy of the *Pinus-Schima* mesic forest has been greatly changed (Shimizu 1986, 1987).

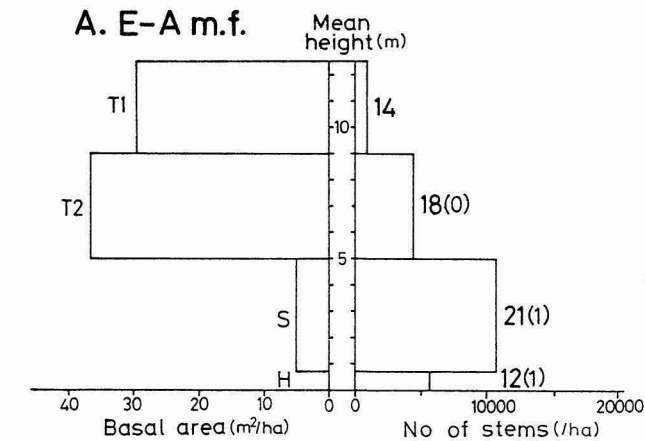
TABLE 1

MEAN NUMBER OF INDIVIDUALS (ha⁻¹) OF ALL WOODY SPECIES SURVEYED IN EACH VEGETATION TYPE

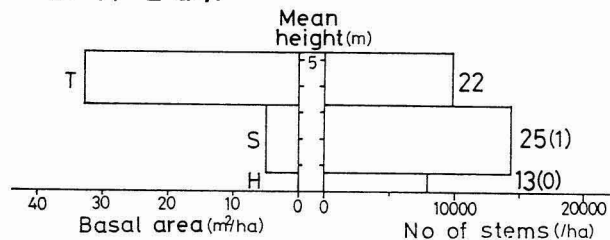
SPECIES	<i>Elaeocarpus-Ardisia</i> MESIC FOREST				<i>Raphiolepis-Livistonia</i> DRY FOREST			<i>Distylium-Schima</i> DRY FOREST			<i>Distylium-Pouteria</i> DRY SCRUB		<i>Pinus-Schima</i> MESIC FOREST				
	T1	T2	S	H	T	S	H	T	S	H	T	H	E	T	S	H	
1. <i>Pouteria obovata</i>	12	48	221	1,086	752	574	3,426	554	515	3,821	2,599	1,509		127	211	3,920	
2. <i>Raphiolepis indica</i> v. <i>integerrima</i>	6	389	1,334	829	2,148	2,645	3,977	631	418	2,161	791	349		292	683	2,045	
3. <i>Cinnamomum insularimontanum</i>	3	55	174	203	190	554	458	24	161	238	155	230		7	69	442	
4. <i>Pandanus boninensis</i>	3	41	137	67	184	222	36	394	230	339	773	240		83	97	157	
5. <i>Syzygium buxifolium</i>		50	40	10	87	75	1,267	290	408	1,177	1,158	642		7	220	277	
6. <i>Ficus boninsimae</i>		17	44				9	6	16	74	5	20			36	9	
7. <i>Ligustrum micranthum</i>		14	223	520	838	2,281	6,063	237	1,612	4,780	4,305	2,473		91	286	1,394	
8. <i>Osmanthus insularis</i>		7	84	46	147	192	369	55	143	143	234	38		19	50	164	
9. <i>Hibiscus glaber</i>		6				256	46	13	164	98	7	337	172		121	63	11
10. (<i>Archontophoenix alexandrae</i>)	6	22	54	32													
11. <i>Sapindus boninensis</i>	10	86	55														
12. <i>Pisonia umbellifera</i>	7	28	10														
13. (<i>Morus australis</i>)	6	31	17														
14. <i>Celtis boninensis</i>	6	25		94	8	7											
15. <i>Melia azedarach</i>	3	17			4												
16. <i>Fatsia oligocarpela</i>			13											3	3		
17. <i>Elaeocarpus photiniaefolius</i>	14	7	8		21		7	101	26	135				165	37	114	
18. <i>Livistonia chinensis</i> v. <i>boninensis</i>	10	128	242	276	201	358	106	94	145	191		20		9	49	32	
19. <i>Machilus boninensis</i>	7	76	251	168		7	58	41	342	528	5			38	200	190	
20. <i>Schima mertensiana</i>	3	16			98	83	96	392	108	637		96		1,133	493	232	
21. <i>Fagara boninensis</i>	3	26	4					3		2		36		4		32	
22. <i>Ardisia sieboldii</i>		856	2,377	688	22	16	18	18	31	20				73	236	57	
23. <i>Ochrosia nakaiana</i>		72	101	13	38	138		37	41	12				9	2		
24. <i>Boninia grisea</i>		30	30	13	52	19		18	17	1				9	37	5	
25. <i>Drypetes integerrima</i>		26	4	4	92	19		36	22	8							
26. <i>Machilus kobu</i>		25	14		29	50	41	108	68	92				48	86	47	
27. <i>Ilex mertensii</i>		16	25	16	27	13	54	44	42	22				6	1	25	
28. <i>Neolitsea sericea</i>		14	31	10	45	65	44	29	164	131	5	45		42	96	95	
29. <i>Psychotria homalosperma</i>		11	4					29	2					4	7		
30. (<i>Leucaena leucocephala</i>)		4	18	85	71	137	440							4	17	11	
31. <i>Cyathea mertensiana</i>		3						3							9		
32. <i>Tarenna subsessilis</i> *			54	48		15			15	211		172			16	59	
33. <i>Callicarpa subpubescens</i> *			37						26	10		40			186	32	
34. <i>Pittosporum boninense</i>			6		85	33	9	5	1	2		51		11	20	86	
35. <i>Trema orientalis</i>			4	57		10	30			1							

36. (<i>Casuarina equisetifolia</i>)	60	7	10	13	7	2			24	9	38	7	
37. <i>Myrsine maximowiczii</i>	26	4		69	7	4							
38. <i>Pouteria boninensis</i>	9	9		7	14						3		
39. (<i>Rhus secundanea</i>)	7												
40. (<i>Psidium cattleianum</i>)		20	20									5	
41. <i>Clinostigma savoryana</i>		18	10		9	3							
42. <i>Ilex matanoana</i>				76	34	46						3	5
43. <i>Evodia nishimurae</i>				21	4	50				9			
44. <i>Geniostoma glabra</i>				16	12	20				11	13	17	
45. <i>Symplocos pergracilis*</i>					73	12							
46. <i>Callicarpa glabra*</i>					43	151						43	39
47. <i>Pittosporum chichisimense*</i>					23	125	40	52				6	82
48. <i>Stachyurus praecox</i> v. <i>matsuzakii*</i>					4	7							
49. <i>Viburnum japonicum</i> v. <i>boninsimense*</i>					2	1						4	4
50. <i>Eurya boninensis*</i>					2								
51. <i>Wikstroemia pseudoretusa</i>	76	470	297	29	148	1,082	799	751					92
52. (<i>Pinus lutchuensis</i>)	66	31	47	3	14	62	278	39	278	46	16		
53. <i>Ilex percoriacea</i>	13	5	9	5	16	19	166	60				7	
54. <i>Gardenia boninensis</i>	3	24		23	31	2	414	20				5	
55. <i>Osteomeles boninensis*</i>		118	491		24	5	2,526	508					
56. <i>Hedyotis grayi*</i>			19		4	10	417	247					
57. <i>Photinia wrightiana*</i>		14	26	1	28	23	496	58				23	6
58. <i>Distylium lepidotum</i>				723	777	1,224	9,968	1,689					
59. <i>Boninia glabra*</i>					340	52	777	269		23	287	85	
60. <i>Vaccinium boninense*</i>					14	1	5				3	14	
61. <i>Dodonaea viscosa*</i>					11		549	56					7
62. <i>Juniperus taxifolia*</i>				1		1	443	140					
63. <i>Pittosporum parvifolium*</i>							80	75					
64. <i>Symplocos kawakamii*</i>							41						
65. <i>Myrsine okabeana*</i>							40						
66. <i>Callicarpa nishimurae*</i>							28	11					
67. <i>Hedyotis mexicana*</i>								80					
68. <i>Zanthoxylum arnottianum*</i>								11					
69. <i>Boehmeria boninensis*</i>								3					

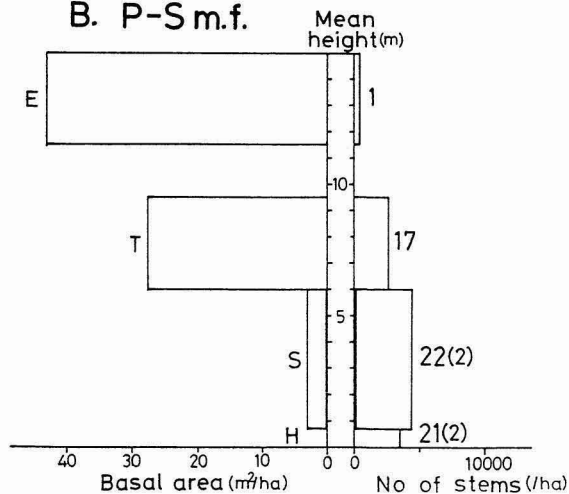
NOTE: An asterisk denotes shrubby species. Introduced and escaped species are presented in parentheses. Species with similar distribution patterns are enclosed within dashed lines.



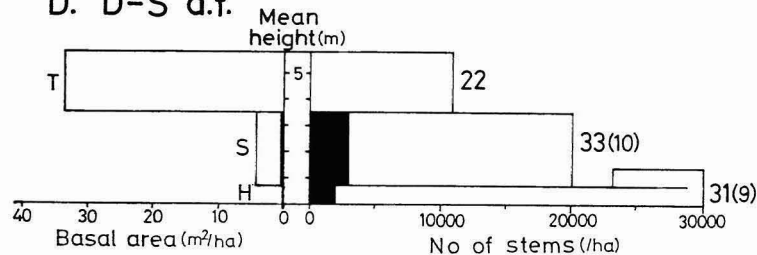
C. R-L d.f.



B. P-S m.f.



D. D-S d.f.



E. D-P d.s.

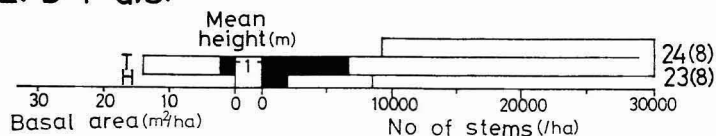


FIGURE 5. Basal area and stem density of woody species in the five vegetation types, presented at the average height of each forest layer. The black part denotes the share of intrinsically shrub species (see Table 1). Numerals on the right show the total number of woody species and the number of intrinsically shrub species (in parentheses) in each forest layer.

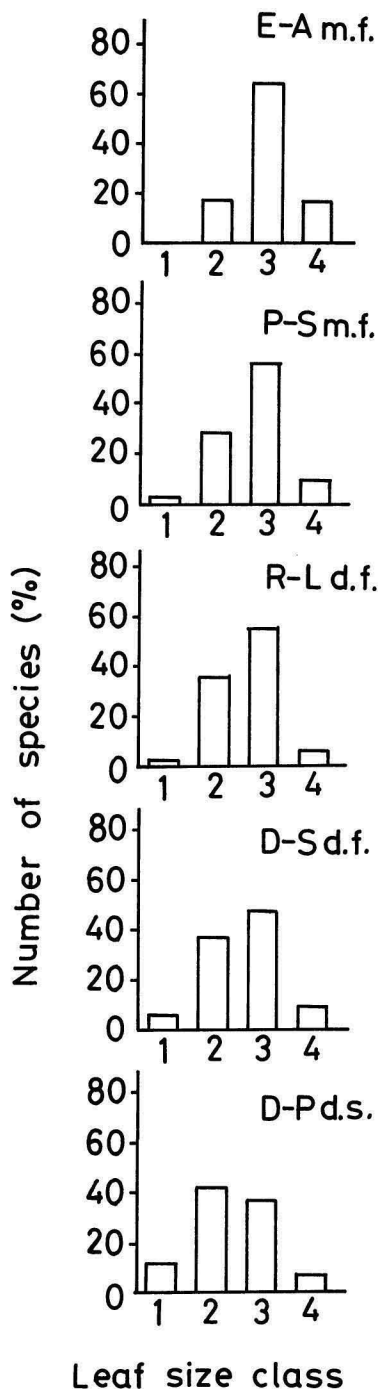


FIGURE 6. Diagrams of leaf size classes for each vegetation type. Classification of leaf size was based on Raunkiaer (1934): 1, <0.25 cm²; 2, 0.25-2.25 cm²; 3, 2.25-20.25 cm²; 4, >20.25 cm².

TABLE 2

RELATIVE LIGHT INTENSITY IN TYPICAL PLOTS OF FIVE VEGETATION TYPES (AVERAGE OF 50 SAMPLING SPOTS)

VEGETATION TYPE	RELATIVE LIGHT INTENSITY (%)
E-A m.f.	0.5 ± 0.2
P-S m.f.	3.6 ± 0.8
R-L d.f.	7.9 ± 2.9
D-S d.f.	11.2 ± 6.3
D-P d.s.	15.9 ± 11.7

Rhaphiolepis-Livistonia DRY FOREST. *Rhaphiolepis-Livistonia* dry forest includes all dry forests that lack *Distylium lepidotum* as a canopy-forming species. *Rhaphiolepis indica* v. *integerrima*, *Pouteria obovata*, *Hibiscus glaber*, *Syzygium buxifolium*, *Pandanus boninensis*, and *Ligustrum micranthum* are dominant or subdominant canopy trees that are also found in *Distylium-Schima* dry forest. *Livistonia chinensis* v. *boninensis*, *Boninia grisea*, *Drypetes integerrima*, and *Pittosporum boninense* characterize *Rhaphiolepis-Livistonia* dry forest, though they sometimes appear in *Distylium-Schima* dry forest.

Rhaphiolepis indica v. *integerrima* is usually predominant in every forest layer in this forest (Table 1). Other species, for example *Pouteria obovata*, *Syzygium buxifolium*, *Pandanus boninensis*, and *Livistonia chinensis* v. *boninensis*, become dominant in some places instead of *Rhaphiolepis indica* v. *integerrima*.

The canopy is almost closed in the typical forest of this type, and relative light intensity on the forest floor is intermediate between that in the *Elaeocarpus-Ardisia* mesic forest and the *Distylium-Schima* dry forest (Table 3). The understory of the forest is exclusively composed of juveniles of the canopy trees, and shrub species are absent (Figure 5C). Seedlings in the H layer are not abundant.

Distylium-Schima DRY FOREST. The *Distylium-Schima* dry forest is dominated by *Distylium lepidotum* and other species common to the *Rhaphiolepis-Livistonia* dry forest including *R. indica* v. *integerrima* (Table 1). *Schima mertensiana* and *Elaeocarpus photiniaefolius* are also abundant, but they are uncommon in the *Rhaphiolepis-Livistonia* dry forest. The occurrence of *Geniostoma gla-*

TABLE 3

MEAN FREQUENCY (%) OF OCCURRENCES OF ALL HERBACEOUS PLANTS INCLUDING WOODY VINES ON THE GROUND

SPECIES	<i>Elaeocarpus- Ardisia</i>	<i>Rhaphiolepis- Livistonia</i>	<i>Distylium- Schima</i>	<i>Distylium- Pouteria</i>	<i>Pinus- Schima</i>
	MESIC FOREST	DRY FOREST	DRY FOREST	DRY SCRUB	MESIC FOREST
1. <i>Morinda boninensis</i>	1.2	0.5	9.5(v)	5.9(v)	2.3(v)
2. <i>Tracherospermum foetidum</i>	6.1(v)	37.0(v)	17.0(v)	55.6(v)	11.3(v)
3. <i>Oplismenus compositus</i>	9.4	4.5	2.7	0.6	2.1
4. <i>Nephrolepis cordifolia</i>	8.1	13.7	3.5(e)	0.3	31.2
5. <i>Psychotria boninensis</i>	1.1	7.3(v)	23.6(v)	2.5	28.2(v)
6. <i>Carex oahuensis</i>	6.1(v)	16.6	17.7	43.1	11.2
7. <i>Carex hattoriana</i>	1.2	31.1	72.3	65.3	27.1
8. <i>Smilax china</i> v. <i>yanagitata</i>	0.6	1.4(v)	12.5(v)	3.8(v)	5.5(v)
9. <i>Gahnia aspera</i>	2.7	15.1	12.7	20.7	3.6
10. <i>Dianella ensifolia</i>	0.5	7.7	0.8	2.5	0.8
11. <i>Platanthera boninensis</i>	0.5			3.8	1.5
12. <i>Korthalsella japonica</i>	(p)		(p)	(p)	
13. <i>Goodyera boninensis</i>	3.3				
14. <i>Cyrtomium falcatum</i>	1.1				
15. <i>Caesalpinia crista</i>	0.6				
16. <i>Jasminum hemsleyi</i>	(v)				
17. <i>Thelypteris parasitica</i>	1.1	1.4	0.8		6.3
18. <i>Asplenium nidus</i>	1.5		(e)		1.5(e)
19. <i>Microlepia strigosa</i>	0.2		0.2		1.5
20. <i>Pteris quadriaurita</i>	13.9		0.01		4.0
21. <i>Luisia boninensis</i>	2.0		0.1(e)		
22. <i>Freycinetia boninensis</i>	2.3(v)		6.8(v)		0.4(v)
23. <i>Pleopeltis boninensis</i>	14.5(v)		1.5(e)		0.5
24. <i>Cirrhopetalum boninense</i>	0.5		0.1		
25. <i>Thelypteris boninensis</i>	8.3(v)		0.03		
26. <i>Scutellaria longituba</i>		1.4	6.8		
27. <i>Calanthe hattorii</i>			1.0		
28. <i>Machaerina rubiginosa</i>			0.8		0.4
29. <i>Lindsaea repanda</i>			0.3		1.1
30. <i>Selaginella tamariscina</i>			0.5		
31. <i>Sciaphila boninensis</i>			0.01		
32. <i>Orobanche boninsimae</i>			0.2		
33. <i>Vittaria elongata</i>			0.2(e)		
34. <i>Nephrolepis hirsutula</i>			0.02		
35. <i>Sphenomeris chinensis</i>			3.1		
36. <i>Schizaea boninensis</i>		3.4	16.5	4.7	5.6
37. <i>Stachytarpheta jamaicensis</i>		2.7	0.1	1.7	
38. <i>Fimbristylis dichotoma</i>			4.0	17.2	
39. <i>Oxalis corniculata</i>			0.3	2.5	
40. <i>Selaginella boninensis</i>			0.5	5.0	
41. <i>Rhynchospora rubra</i>			2.5	0.6	
42. <i>Machaerina glomerata</i>			12.0	6.3	
43. <i>Paspalum orbiculare</i>			4.5	4.4	
44. <i>Eleusine indica</i>			0.5	3.1	
45. <i>Cymbopogon tortilis</i>			0.3	6.0	
46. <i>Psilotum nudum</i>			2.0	0.3(e)	1.1
47. <i>Ageratum conyzoides</i>			0.3	2.3	

TABLE 3 (continued)

SPECIES	<i>Elaeocarpus-Ardisia</i> MESIC FOREST	<i>Rhaphiolepis-Livistonia</i> DRY FOREST	<i>Distylium-Schima</i> DRY FOREST	<i>Distylium-Pouteria</i> DRY SCRUB	<i>Pinus-Schima</i> MESIC FOREST
48. <i>Miscanthus condensatus</i> v. <i>boninensis</i>				3.4	3.5
49. <i>Lysimachia mauritiana</i>				0.3	
50. <i>Digitaria platycarpa</i>				0.6	
51. <i>Vernonia cinerea</i>				1.6	
52. <i>Euphorbia hirta</i>				0.9	
53. <i>Dactyloctenium aegyptium</i>				0.9	
54. <i>Sedum boninense</i>				0.9	
55. <i>Lantana camara</i>				0.9	
56. <i>Kalanchoe pinnata</i>				0.3	
57. <i>Paspalum dilatatum</i>				0.3	
58. <i>Youngia japonica</i>				0.3	
59. <i>Blechnum orientale</i>					0.3
60. <i>Cyperus cyperinus</i>					0.04
61. <i>Clematis terniflora</i>					2.6(v)
62. <i>Derris elliptica</i>					0.7(v)

NOTE: Occurrences as epiphytes, parasites, and vines or climbers are indicated as (e), (p), and (v), respectively. Species with similar distribution patterns are enclosed with dashed lines.

TABLE 4

SUMMARY OF SOME CHARACTERISTICS OF FORESTS AND SCRUB ON CHICHIJIMA ISLAND

VEGETATION TYPE	<i>Elaeocarpus-Ardisia</i> MESIC FOREST	<i>Rhaphiolepis-Livistonia</i> DRY FOREST	<i>Distylium-Schima</i> DRY FOREST	<i>Distylium-Pouteria</i> DRY SCRUB	<i>Pinus-Schima</i> MESIC FOREST
No. of plots surveyed	7	10	10	10	13
Mean species no. per plot (Total species no. in all plots)					
Trees and shrubs	17.3 (35)	15.7 (37)	22.4 (51)	15.8 (28)	17.1 (43)
Herbs and vines	6.4 (24)	6.6 (14)	11.6 (42)	12.5 (35)	8.3 (28)
Mean crown height (m) (Height of <i>Pinus lutchuensis</i>)	12.8	5.5	6.1	1.3	9.3 (14.9)
Mean no. of individuals (E-S layers, ha ⁻¹)	7,861	13,934	10,592	27,434	6,378
Mean no. of stems (E-S layers, ha ⁻¹)	13,863	21,951	15,710	57,453	9,864
Stem no. per individual	1.76	1.58	1.48	2.09	1.55
Basal area (m ² ha ⁻¹)	6.04	3.69	4.78	1.75	5.37
Diversity index (Fisher's α)	4.1	4.3	6.6	4.1	4.8

brum, *Evodia nishimurae*, and *Ilex matanoana* is unique to the *Distylium-Schima* dry forest (Table 1), though they sometimes appear in the secondary forests formed near this type of forest.

The understory of this dry forest mainly consists of juveniles of canopy species (Figure 5D), but it is also represented by several

undergrowth species such as *Boninia glabra*, *Callicarpa glabra*, *Eurya boninensis*, *Symplocos pergracilis*, *Stachyurus praecox* v. *matsuzakii*, *Pittosporum chichisimense*, and *Viburnum japonicum* v. *boninsimense*, most of which are peculiar to the *Distylium-Schima* dry forest (Table 1) and are designated as endangered species (Ono et al. 1986).

The H layer of this forest contains not only many seedlings of woody species (Figure 5D), but also a rich flora of herbaceous species including *Calanthe hattorii*, *Scutellaria longituba*, and *Schizaea boninensis*, which are also found mainly in the *Distylium-Schima* dry forest (Table 3).

A high relative light intensity in this forest (Table 2), attributable to the many small canopy gaps, enables both shrub species and seedlings of shade-intolerant trees, like *Schima mertensiana* and *Pinus lutchuensis*, to grow in the forest (Table 1). The *Distylium-Schima* dry forest is, therefore, characterized by the highest number of species and highest diversity index of all the vegetation types (Table 4).

Distylium-Pouteria DRY SCRUB. Canopy height decreases from *Distylium-Schima* dry forest to *Distylium-Pouteria* dry scrub without change in the dominant or subdominant canopy species (Table 1). The lowest height is only 0.3 m (field observation). *Distylium lepidotum* is the dominant species here, too, and *Pouteria obovata*, *Syzygium buxifolium*, *Pandanus boninensis*, *Ligustrum micranthum*, and *Rhaphiolepis indica* v. *integerrima* are common subdominant species in both the dry forest and the dry scrub (Table 1).

Many species of the *Distylium-Schima* dry forest, for example, *Schima mertensiana*, *Elaeocarpus photiniaefolius*, *Ilex matanoana*, *Myrsine maximowiczii*, and *Machilus boninensis*, cease to exist at the ecotone between the dry forest and the dry scrub because of the arid condition imposed by the shallow soil (Table 1). Two shrubs, *Juniperus taxifolia* and *Dodonaea viscosa*, which thrive in dry scrub, begin to appear at the ecotone. Several rare and endangered shrubs such as *Pittosporum parvifolium*, *Callicarpa nishimurae*, *Symplocos kawakamii*, and *Myrsine okabeana* are also found in the dry scrub (Table 1). The total number of woody species in this scrub is about half that in the neighboring *Distylium-Schima* dry forest (Table 4).

Almost all species have features that indicate drought resistance: stunted growth forms with two or more stems per individual (Figure 3E) and small, thick, and sometimes hairy leaves (Figure 6). Density of individuals is

highest and total basal area smallest of all the vegetation types.

Relative light intensity in the dry scrub is rather high (Table 2) because of small outcrops of lava that result in a partially open canopy of stunted shrubs. Seedlings of canopy species are not so numerous as in the *Distylium-Schima* forest (Figure 5D, E), perhaps because of the arid habitat. Several weedy herbs, most of which are alien species in the Bonins, are found in the canopy gaps, and the number of herbaceous species is comparatively large (Table 3).

The scrub was severely damaged in places with shallow soil (that is, around lava outcrops) during an unusually long drought in 1980. Many individuals of *Distylium lepidotum* died in the drought, and many new canopy gaps were produced (Shimizu 1982). Because there is no pioneer species such as *Schima mertensiana*, *Fagaria boninensis*, or *Trema orientalis*, which occur in mesic or dry forests, all stages of succession are occupied by the same members of the *Distylium-Pouteria* scrub.

Distribution

Figure 7 shows a vegetation map of Chichijima and Figure 8 a schematic transect profile through the center of the island. *Elaeocarpus-Ardisia* mesic forest occurs in rather mesic habitats with deep soils (Figure 8). It occupies only 0.9% of Chichijima (Figure 7) and is now confined to a slope of Mt. Mikazuki and other small inland areas composed of volcanic breccia. The limited distribution of the forest habitat was caused by its selective cutting for crop cultivation until 1945. Copperplate drawings by Kittlitz (1844) and some statements in old documents (Ogasawara-Tocho 1914, Fukuda 1920) suggest that dense forests occupied much of Chichijima before the 1830s, when humans first settled the Bonins.

Pinus-Schima mesic forest covers 36.9% of the island and occupies almost all flat land and gentle slopes with fairly deep soil of volcanic breccia (Figures 7, 8). These places were once used as cultivated fields but were abandoned after World War II (Katahira 1981).

Species composition of the *Pinus-Schima*

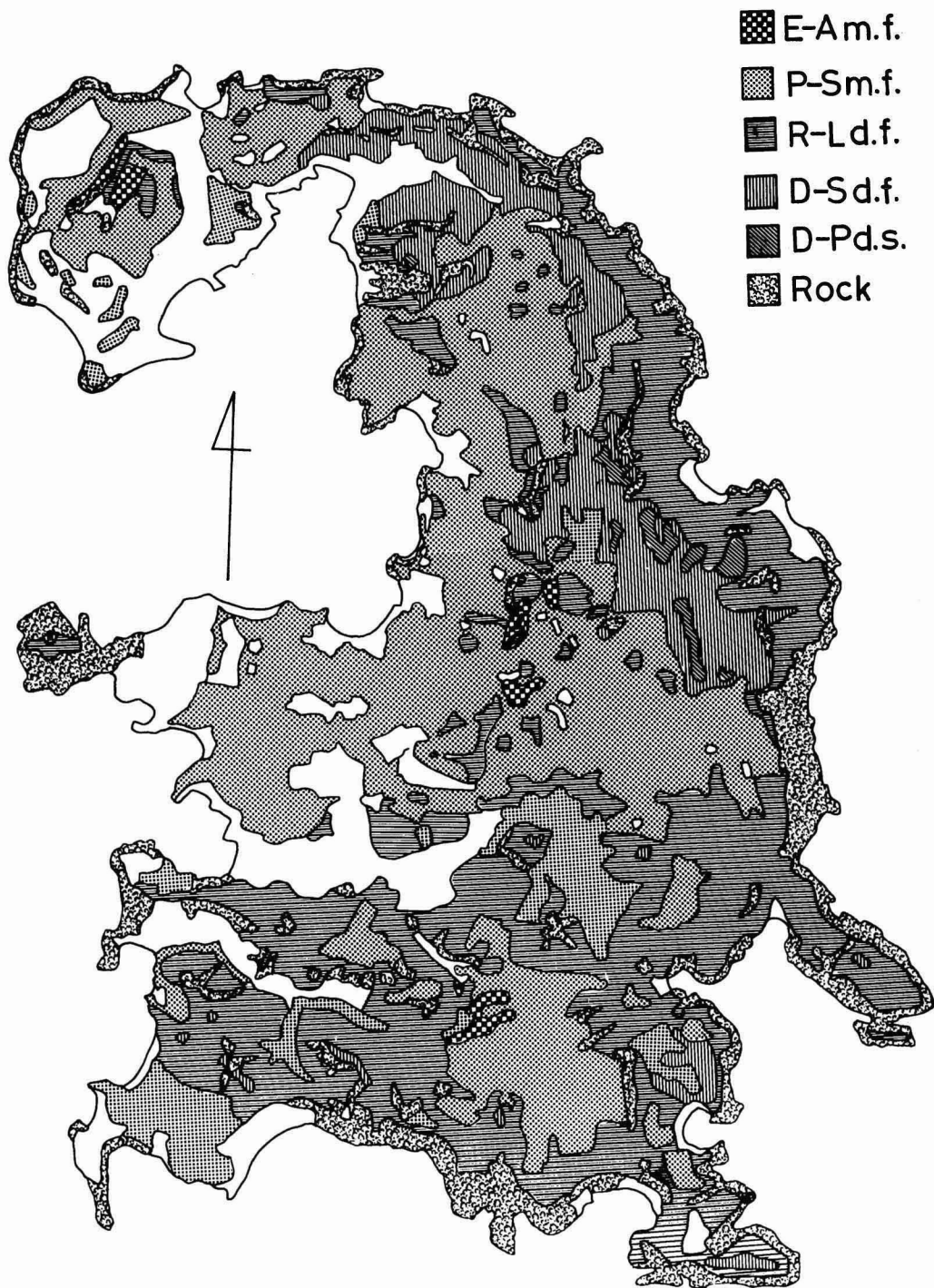


FIGURE 7. Vegetation map of Chichijima Island. Blank space denotes village area, cultivated fields, coastal forests, and secondary vegetation such as *Leucaena leucocephala* scrub and *Stachytarpheta jamaicensis* grassland.

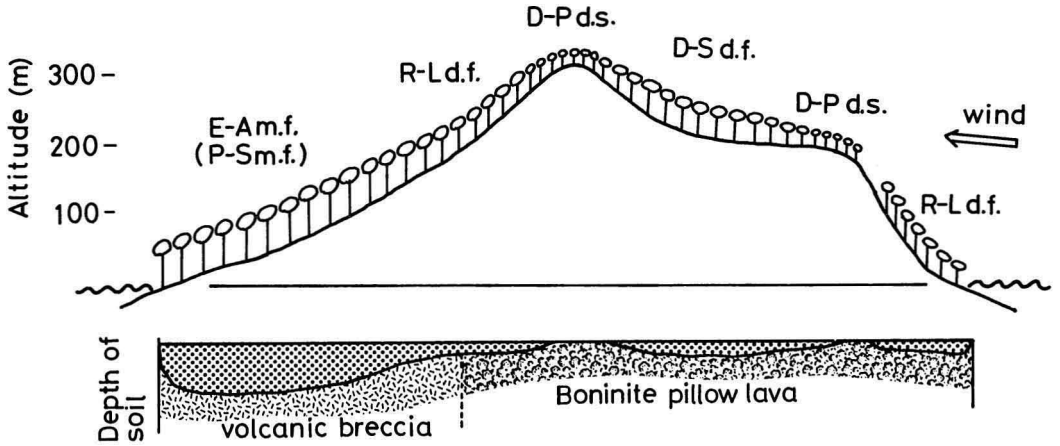


FIGURE 8. Diagrammatic representation of an east-west transection through the center of Chichijima Island, showing depth of soils, kinds of basal rocks, direction of prevailing wind, and vegetation types.

mesic forest is different from that of the *Elaeocarpus-Ardisia* mesic forest (Figure 4), probably because the area of *Pinus-Schima* mesic forest was once cultivated, so that habitat conditions shifted toward dryness—conditions in which the *Raphiolepis-Liviston* dry forest and *Distylium-Schima* dry forest are now supported. Most of the area now occupied by *Pinus-Schima* mesic forest was once covered by the dense *Elaeocarpus-Ardisia* mesic forest.

Raphiolepis-Liviston dry forest, now occupying 26.4% of the island area, is distributed widely throughout the island (Figure 7). It covers rocky ridges on boninite pillow lava, steep slopes with thin gravelly soils, and is found along valleys or sea cliffs irrespective of basal rocks (Figure 8). Habitat conditions in this forest appear to be unstable compared with those of *Distylium-Schima* dry forest.

Distylium-Schima dry forest, which now occupies 7.6% of the total area of the island, occurs on rather flat places with thin soils of boninite pillow lava. It is found mainly at altitudes above 150 m in the northeastern part of the island (Figure 7). The most typical forest is found on the flat area called Chuosanhigashi-daira, located at the east side of Mt. Chuo (Figure 1). This flat is thought to be one of the oldest landforms on Chichijima (Tamura and Imaizumi 1981), and the habitat is apparently quite stable. Small patches of

Distylium-Schima dry forest are scattered on mountain tops and ridges above 150 m over the rest of the island and are surrounded below by *Raphiolepis-Liviston* dry forest (Figure 7). These small patches are thought to be remnants of the former *Distylium-Schima* dry forest, which once covered these areas more widely than they do now (Shimizu, in preparation).

Distylium-Pouteria dry scrub, now occupying 0.7% of the island, occurs on mountain ridges and edges of sea cliffs of boninite pillow lava above 150 m, where thin soil with occasional lava outcrops and the prevailing wind produce arid conditions (Figures 7, 8). *Distylium-Pouteria* dry scrub, with a wide ecotonal zone (Figure 8), is usually continuous with *Distylium-Schima* dry forest.

Speciation

Representatives of some genera that seem to have speciated in the Bonins were arranged in three groups based on differences in their habitats: (1) those occurring in mesic and dry forests or forest margins, (2) those composing the understory of *Distylium-Schima* dry forest, and (3) those composing the canopy of *Distylium-Pouteria* dry scrub (Table 5).

Four species of *Pittosporum* represent the most prominent example of speciation in the Bonins (Figure 9). *P. boninense* is a small

TABLE 5
SIMILARITY TREND OF SPECIATION IN SIX GENERA ON CHICHIJIMA ISLAND

GENUS	HABITATS OF CONGENERIC SPECIES		
	MESIC AND DRY FOREST OR FOREST MARGIN	UNDERSTORY OF D-S d.f.	CANOPY OF D-P d.s.
<i>Bonina</i>	<i>B. grisea</i>	<i>B. glabra</i>	<i>B. glabra</i>
<i>Callicarpa</i>	<i>C. subpubescens</i>	<i>C. glabra</i>	<i>C. nishimurae</i>
<i>Ilex</i>	<i>I. mertensii</i>		<i>I. percoriacea</i>
<i>Myrsine</i>	<i>M. maximowiczii</i>		<i>M. okabeana</i>
<i>Pittosporum</i>	<i>P. boninense</i>	<i>P. chichisimense</i>	<i>P. parvifolium</i>
<i>Symplocos</i>		<i>S. pergracilis</i>	<i>S. kawakamii</i>

tree (1–6 m high) producing relatively large amounts of fruit dispersed by birds. It occurs in a wide range of habitats on the island, but especially in sunny margins of mesic and dry forests. *P. boninense* is morphologically plastic compared with its congeners. It varies widely in growth form and leaf size in response to habitat conditions. *P. chichisimense* and *P. parvifolium*, both endemic to Chichijima, are rare species with distributions restricted to small areas of the island. *P. chichisimense* is found in the understory of *Distylium-Schima* dry forest as a shade-tolerant shrub (1–2 m high); *P. parvifolium* grows in the canopy of *Distylium-Pouteria* dry scrub, where it assumes a stunted growth form (0.3–1.5 m high). Individuals of these two species, which produce only one fruit per inflorescence, are sparsely distributed now that fertile seeds are rare.

P. beechyi is absent from Chichijima and confined to a small area on Hahajima. It occurs in dry forest and scrub comparable to the *Distylium-Schima* dry forest and *Distylium-Pouteria* dry scrub of Chichijima, varying in growth form from stunted shrubs (0.5 m high) to low-stature trees (3 m high). Taxonomic features of this species are intermediate between those of *P. chichisimense* and *P. parvifolium*.

Similar trends in congeneric distribution were observed in several other genera (Table 5). *Symplocos* and *Callicarpa* especially show extreme convergence with *Pittosporum* in external appearance, habit, and ecology, although *Symplocos* lacks a species correspond-

ing to *P. boninense*, and *Callicarpa* lacks one comparable to *P. beechyi*.

DISCUSSION

Ecological Release

It has been suggested that the biota of oceanic islands extends its habit and habitat range to the extremes of physical and morphological ability because competitive pressure in the species-poor flora and fauna of an island is less than on the adjacent mainland (Carlquist 1974). This phenomenon is known among zoologists as ecological release (Grant 1966, Williams 1969). Diamond (1970) showed that birds living on a mainland were often confined to narrow areas, while on neighboring islands they occurred more widely, and explained the distribution in terms of release from competition. Similar examples are known in other island birds (Keast 1970, Lack 1976) and in lizards (Schoener 1975, Lister 1976).

Some phenomena in plants may also represent "ecological release." *Metrosideros collina* subsp. *polymorpha* in Hawaii has long been known to show a wide range of adaptations, spanning edaphic conditions from new lava to mature soils, and representing some of the tallest island trees in wet forests, miniature shrubs in bogs, and short, scrubby trees on windy ridges (Carlquist 1974). *Croton scouleri* in the Galápagos Islands is another example that is widely distributed from arid to moist



FIGURE 9. Four species of the genus *Pittosporum*, the most diversified woody species in the Bonin Islands. A, *P. boninense*; B, *P. chichisimense*; C, *P. parvifolium*; D, *P. beechyi*.

habitats and is extremely variable in leaf size (Hamann 1979a).

On Chichijima nine species, *Pouteria obovata*, *Hibiscus glaber*, *Syzygium buxifolium*, *Rhaphiolepis indica* v. *integerrima*, *Pandanus boninensis*, *Cinnamomum insularimontanum*, *Ligustrum micranthum*, *Osmanthus insularis*, and *Ficus boninensis*, occur in all vegetation types (i.e., the mesic forests composed of tall trees, the dry forest with low-stature trees, and the dry scrub with stunted shrubs). *Pouteria obovata* and *Hibiscus glaber*, especially, change their growth forms in the different types of vegetation. They are intrinsically large trees more than 15 m in height and nearly 1 m in girth in *Elaeocarpus-Ardisia* mesic forest, but individuals of the same species are stunted shrubs only 0.3 m high in *Distylium-Pouteria* dry scrub.

Most of the nine species make a group of subdominant species with a mix of other species (i.e., *Elaeocarpus photiniaefolius* and *Ardisia sieboldii* in *Elaeocarpus-Ardisia* mesic forest, *Pinus lutchuensis* and *Schima mertensiana* in *Pinus-Schima* mesic forest, *Livistonia chinensis* v. *boninensis* in *Rhaphiolepis-Livistonia* dry forest, *Distylium lepidotum* and *Schima mertensiana* in *Distylium-Schima* dry forest, *Distylium lepidotum* in *Distylium-Pouteria* dry scrub). Egler (1947) described dwarf scrub on the dry ridges of Oahu in the Hawaiian Islands as of nearly the same species composition as that of the forests on the neighboring slope, and Mueller-Dombois (1981) showed that 33% of native plants recorded along a transect on the island of Hawaii were wide-ranging species that occurred from montane rainforest to subalpine conditions. That not only a single tree but a group of dominant species occurs throughout an environmental gradient may be a phenomenon unique to oceanic islands.

Schima mertensiana is one of the endemic pioneer species in the Bonins (Shimizu and Tabata 1985). It also occurs in the climax forest (*Elaeocarpus-Ardisia* mesic forest, *Rhaphiolepis-Livistonia* dry forest, *Distylium-Schima* dry forest) as well as in secondary forest (*Pinus-Schima* mesic forest) as a dominant species. *Schima mertensiana* is actually a light-demanding species, but its seedlings

and saplings can survive in the forests more frequently than those of other pioneer trees such as *Fagara boninensis* and *Trema orientalis*. Once it establishes itself, it is able to exist for a long time because of its coppicing ability. Shimizu (1987) suggested that *Pinus-Schima* mesic forest would change into *Schima mertensiana* forest after the nematode-caused death of pine trees and that most individuals of *Schima mertensiana* would continue to exist as dominant trees until reaching natural senescence.

The phenomenon of a light-demanding species assuming a pioneer role as well as that of a climax function seems to be another of the characteristics of oceanic island vegetation. *Scalesia pedunculata*, a light-demanding tree in the Galápagos, forms a climax *Scalesia* forest (Hamann 1979b, Eliasson 1984, Itow and Mueller-Dombois 1988). Two light-demanding pioneer trees, *Metrosideros collina* subsp. *polymorpha* and *Acacia koa* v. *hawaiiensis*, assume the role of a climax tree in Hawaii's rainforests (Mueller-Dombois and Howarth 1981). After analyzing the death of 'ohi'a trees (*Metrosideros polymorpha*) in the Hawaiian Islands (the 'ohi'a dieback phenomenon), Mueller-Dombois (1983, 1986) proposed the "cohort senescence theory," which includes the phenomenon of "replacement dieback" in which 'ohi'a trees grow up in gaps under dieback canopy. Subsequently the 'ohi'a saplings form a new cohort stand. These later begin to die synchronously as a result of an environmental trigger when the cohort stands reach a senescing life stage.

Speciation

Adaptive radiation is one of the fascinating themes in island ecology. Prominent examples are the lobelioids of the Hawaiian Islands (Rock 1919, Carlquist 1970) and *Scalesia* in the Galápagos Islands (Carlquist 1965, Wiggins and Porter 1971, Eliasson 1984, Porter 1979). Although considerable attention has been paid to adaptive radiation, comparatively little is known of relationships between speciation and the characteristics of island vegetation in which speciation has occurred.

The Bonins lack many taxonomic groups compared with the Ryukyu Islands, the continental islands located nearly in the same latitude as the Bonins (see Figure 1). The flora of the Bonins is especially poor in undergrowth shrub species (Shimizu 1984a). Thus the shrub layer of the forests of Chichijima is usually composed on juveniles of canopy tree species. The only exception is in the *Distylium-Schima* dry forest, where several shrub species including *Callicarpa glabra*, *Pittosporum chichisimense*, and *Symplocos pergracilis* occur under the canopy. The canopy in the *Distylium-Schima* dry forest is not fully closed, perhaps because crowns of canopy trees have been damaged repeatedly by typhoons that occur every several decades. Thus, a number of seedlings and samplings not only of shade-tolerant but also of light-demanding species like *Schima mertensiana* can grow together in the forest. Even an introduced pioneer tree, *Pinus lutchuensis*, invaded the forest naturally (Shimizu and Tabata 1985).

After an exceptionally large typhoon in 1983, we observed that the crowns of many canopy trees were blown off and that many small canopy gaps had formed, although complete tree falls were seldom found in the plot area (unpublished data). Because large-scale damage by typhoons had not been observed in this type of forest, Shimizu (1984c) concluded that a series of tree-by-tree replacements in conjunction with small gap formation by a single dead tree is the usual mechanism of regeneration. Speciation in the *Distylium-Schima* dry forest thus seems associated with stable habitat conditions on a flat of ancient origin, mechanisms that permit moderate regeneration and canopy opening by occasional typhoons.

In contrast, there are no endemic undergrowth shrubs in the *Elaeocarpus-Ardisia* mesic forest or the *Rhaphiolepis-Livistonia* dry forest on Chichijima. Juveniles of canopy trees are not abundant in these forests. The same regeneration mechanism as in the *Distylium-Schima* dry forest may also operate in the *Rhaphiolepis-Livistonia* dry forest. But the habitat conditions of the *Rhaphiolepis-Livistonia* dry forest, which grows on rocky ridges and steep gravelly slopes, seem to

be unstable compared with those of the *Distylium-Schima* dry forest. Because the *Rhaphiolepis-Livistonia* dry forest is seemingly more tolerant to typhoon attacks than the *Distylium-Schima* dry forest, the canopy of this forest is not so damaged as in the *Distylium-Schima* dry forest.

The *Elaeocarpus-Ardisia* mesic forest is a very dark forest because of the development of several layers. This forest type regenerates as a result of large-scale disturbances accompanying many tree falls resulting from occasional typhoons. Once the canopy is opened, thousands of seedlings of *Fagara boninensis* or *Sambucus javanica* germinate at once and cover the forest floor completely for the first two years (Shimizu, in preparation). It is difficult for some species to invade *Elaeocarpus-Ardisia* mesic forest before it breaks down. These unfavorable situations for invasion may have prevented new species from establishing in the *Elaeocarpus-Ardisia* mesic and the *Rhaphiolepis-Livistonia* dry forests.

Because the habitat of *Distylium-Pouteria* dry scrub is very dry, many species occurring in the mesic and dry forests are absent from the dry scrub; only a few species are associated with this scrub. The number of component woody species is less than half that of the neighboring *Distylium-Schima* dry forest. Outcrops of lava in the *Distylium-Pouteria* dry scrub create canopy gaps of various sizes. *Callicarpa nishimurae*, *Symplocos kawakamii*, and *Pittosporum parvifolium*, which are all rare and now endangered, seem to be distributed mainly on the periphery of these canopy gaps. They all have drought-resistance features such as small, thick, or hairy leaves. *Pinus lutchuensis* has also invaded *Distylium-Pouteria* dry scrub, especially in the canopy gaps caused by exposed lava (Shimizu 1983).

Many individuals of the *Distylium-Pouteria* dry scrub died as the result of an unusually serious drought in 1980 (Shimizu 1982). Occasional severe droughts probably occur only once every several decades, when canopy gaps are enlarged and the chances for new species to become established in the dry scrub result.

Speciation seems to have occurred in those communities in which particular conditions favoring formation of new species persist (i.e., a comparatively small number of original

component species; historically stable habitats; means of regeneration without large-scale disturbance; and occasional, small canopy gaps). The origin of the genera shown in Table 5 and the relationships among the congeners have been studied (Kanai 1977, Ono 1980, Kobayashi 1982, Kawakubo 1987, Nagamasu 1987), but the ancestral species and the process of speciation remain uncertain.

It seems that only species with high colonizing ability were able to become successfully established in the early island habitats. Among the congeners, the species found along forest margins seem to show ecological behavior similar to that of their ancestors. Thus some populations of the ancestral species with habits and habitats similar to those of the present species occurring along the forest margins shifted to the understory of *Distylium-Schima* dry forest and the *Distylium-Pouteria* dry scrub, respectively, and speciated as they adapted to the new environments. Parallel trends in speciation in several genera support this assumption.

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