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Origin of *Distylium* Dry Forest and Occurrence of Endangered Species in the Bonin Islands[1]

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ABSTRACT: The *Distylium* dry forest is a low-stature forest or scrub, 0.5–8 m high, growing in dry habitats with shallow soils in the Bonin Islands. The forest, dominated by *Distylium lepidotum*, has the highest species diversity and proportion of endemics of all vegetation types in the Bonins, and it includes many endangered species. Distribution and species composition of the *Distylium* dry forest and distribution patterns of 25 endangered species were studied in Chichijima-retto, a cluster of islands in the Bonins. The relationship between the distribution of forest and fog occurrence was investigated. Also analyzed were damage caused by the severe drought in 1980 and the habitats of congeneric species of the three islands at different altitudes. A hypothesis is proposed to explain the origin of the *Distylium* dry forest and the occurrence of endangered species: *Distylium* dry forest originated from a mesic forest similar to a cloud forest when the Islands were once higher than they are at present; it has been declining in area and species composition with the sinking of the Islands and the tendency toward increasing aridity over time, producing many endangered species. This trend has been accelerated by a rise of sea level of about 100 m after the last Ice Age, during which the total area of the Islands decreased to one-third of the former area.

THE BONIN ISLANDS (Ogasawara-gunto in Japanese) are located about 1000 km south of Tokyo in the Pacific Ocean. The islands are divided into three clusters, Mukojima, Chichijima, and Hahajima-rettos (island groups) from north to south (Figure 1). The head administrative office of Ogasawara Village is located at Chichijima, the largest of the Bonin Islands. This paper is focused on the vegetation of Chichijima-retto.

The basal rocks of the Islands were formed by submarine volcanic activity in the Tertiary. Boninite, a kind of andesite characterized by rich MgO, Cr, and SiO_2 content, is spread widely. Volcanic breccia covers the boninite lava in some places (Kuroda 1979).

The Islands are almost completely surrounded by sea cliffs 50–100 m high. Land with low relief (hilly land) occurs on higher regions above the sea cliffs (Tamura and Imaizumi 1981).

The climate is subtropical and maritime (Figure 2). The annual mean temperature is 22.9°C. The annual range of temperature is small compared with that of Okinawa Island, a continental island located at nearly the same latitude. It rains throughout the year to some extent, although annual precipitation (about 1200 mm) is not high. Rainfall centers around the rainy seasons of May–June and October–November. Water deficits occur in places with shallow soils in midsummer.

Vegetation

I classified the natural forests (except the coastal ones) of the Bonin Islands on the basis of forest structure and dominant species (Shimizu 1989). Six vegetation types were recognized; they are grouped into mesic types and dry types (Figure 3).

Elaeocarpus–Ardisia mesic forest (E–A m.f.) is the tallest forest in the Bonin Islands.

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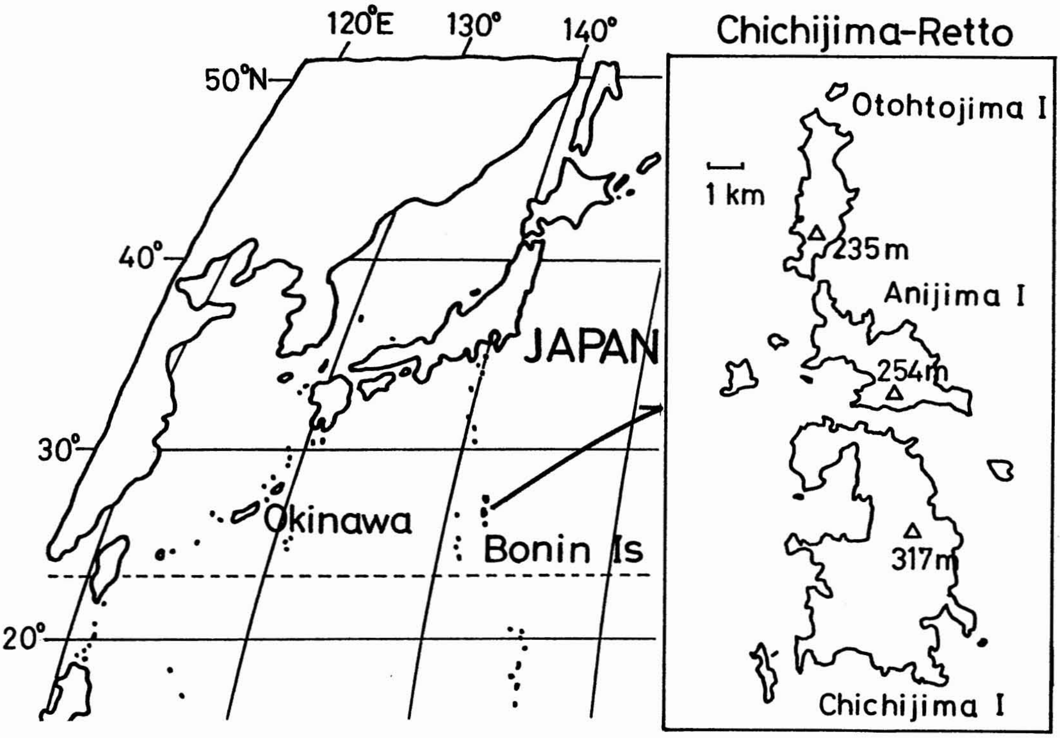


FIGURE 1. Location of the Bonin Islands with inset showing the three main islands of Chichijima-retto.

FIGURE 2. Climate diagram of Chichijima Island based on monthly mean temperatures and precipitation recorded from 1969 to 1989.

It consists of large trees of *Elaeocarpus photiniaefolius*, *Pisonia umbellifera*, *Pouteria obovata*, and others in the crown layer and is dominated by *Ardisia sieboldii* trees in the lower layers. It once dominated at low altitude on flat places and gentle slopes with thick soils, but it was destroyed almost completely when these habitats became cultivated fields before 1945.

Pinus–Schima mesic forest (P–S m.f.), a secondary forest composed of *Pinus lutchuensis* (introduced pine) and *Schima mertensiana* (native pioneer), is presently replacing the *Elaeocarpus–Ardisia* mesic forest (Figure 4).

Dendrocacalia–Fatsia mesic scrub (D–F m.s.) occurs only on the mesic ridges above 400 m on Hahajima, the main island in Hahajima-retto. It consists of an endemic woody composite, *Dendrocacalia crepidifolia*, and some other shrubs preferring moist conditions.

Distylium–Schima dry forest (D–S d.f.)

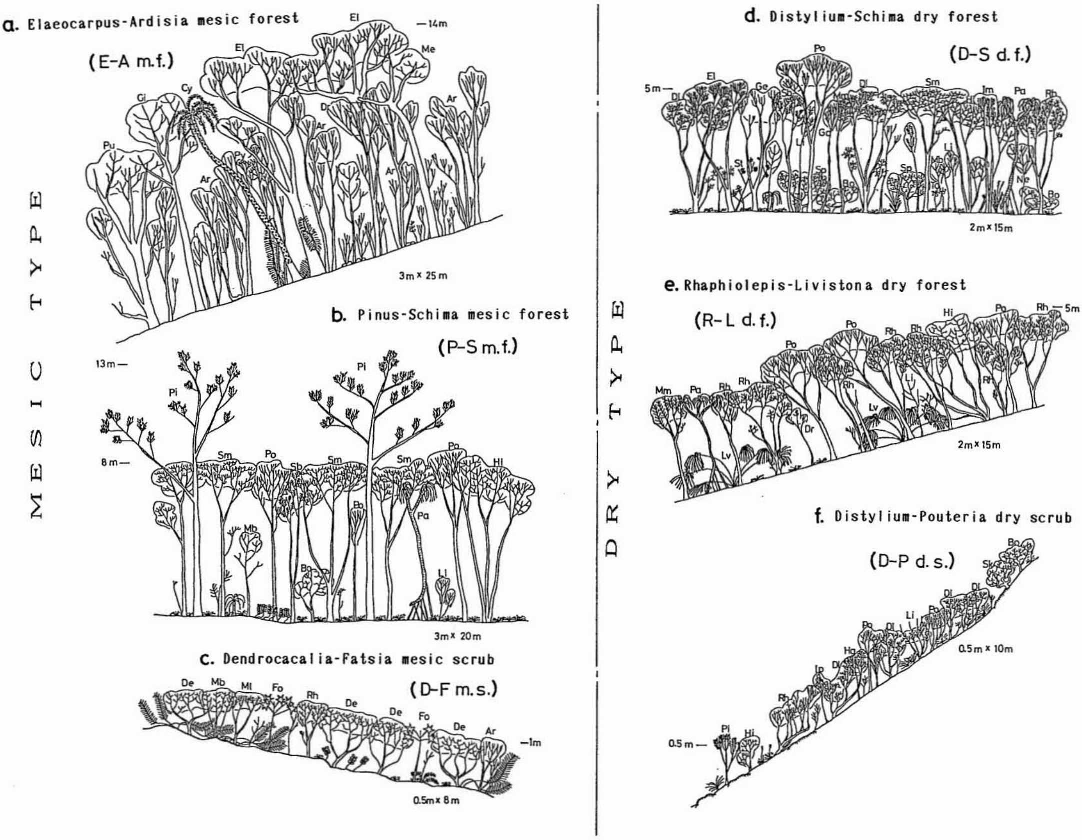


FIGURE 3. Profile diagrams of the six vegetation types. Key to abbreviations: Ar, *Ardisia sieboldii*; Bo, *Boninia glabra*; Ci, *Cinnamomum insularimontanum*; Cy, *Cyathea mertensiana*; De, *Dendrocacalia crepidifolia*; Dl, *Distylium lepidotum*; Dr, *Drypetes integerrima*; El, *Elaeocarpus photiniaefolius*; Fo, *Fatsia oligocarpela*; Ga, *Gardenia boninensis*; Ge, *Geniostoma glabrum*; Hg, *Hedyotis grayi*; Hi, *Hibiscus glaber*; Im, *Ilex matanoana*; Ip, *Ilex percoriacea*; Li, *Ligustrum micranthum*; Lv, *Livistona chinensis* v. *boninensis*; Mb, *Machilus boninensis*; Me, *Melia azedarach*; Ml, *Melastoma tetramerum* v. *pentapetalum*; Mm, *Myrsine maximowiczii*; Ne, *Neolitsea sericea*; Pa, *Pandanus boninensis*; Pi, *Pinus lutchuensis*; Po, *Pouteria obovata*; Pu, *Pisonia umbellifera*; Py, *Psychotria homalosperma*; Rh, *Rhaphiolepis indica* v. *integerrima*; Sb, *Syzygium buxifolium*; Sk, *Symplocos kawakamii*; Sm, *Schima mertensiana*; Sp, *Symplocos pergracilis*; St, *Stachyurus macrocarpus*; Ta, *Tarenna subsessilis*.

characterizes the dry-type vegetation of the Bonin Islands. It is distributed mainly in higher areas on Chichijima-retto (Figure 3). *Distylium lepidotum* is the most dominant species. *Schima mertensiana*, *Pouteria obovata*, *Syzygium buxifolium*, and *Pandanus boninensis* are subdominant (Table 1). The forest has the highest species diversity of all forest types in the Bonins. It contains many endemics, most of which are rare and endangered species in a broad sense.

Distylium–Pouteria dry scrub (D–P d.s.) is a dwarf type of *Distylium–Schima* dry forest. *Distylium lepidotum*, *Pouteria obovata*, *Syzygium buxifolium*, and *Pandanus boninensis* are also common in this forest type. It differs from the preceding forest type in that tree species preferring mesic habitats disappear and some arid-tolerant species such as *Juniperus taxifolia* and *Dodonaea viscosa* appear in the scrub. It is distributed over shallow soils on main ridges and in peripheral parts of higher areas (Figure 5). Forest structure and species composition change gradually be-

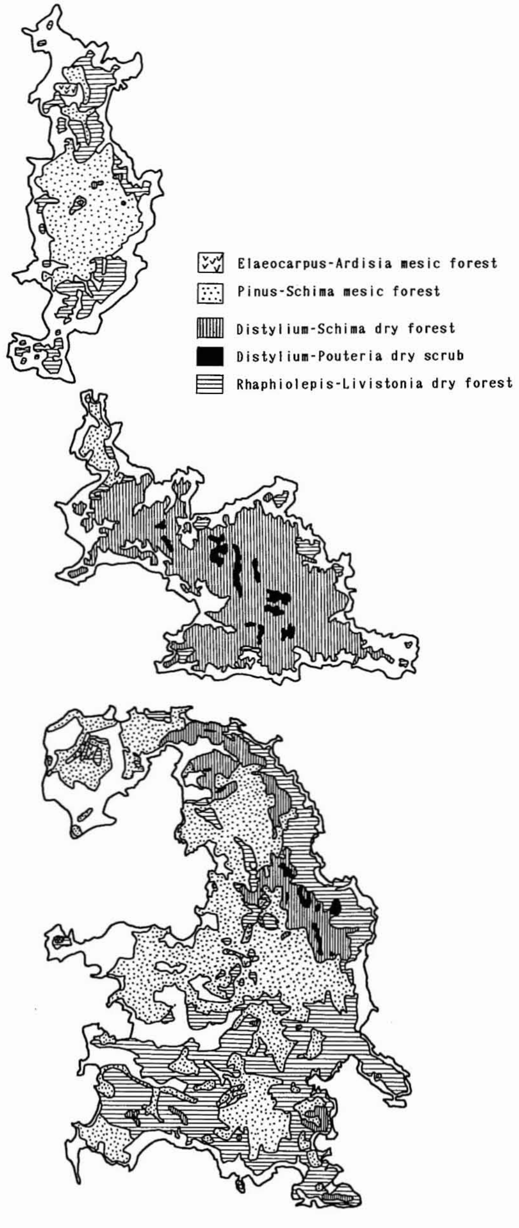


FIGURE 4. Vegetation map of Chichijima-retto. Blank spaces denote exposed basal rocks, village areas, cultivated fields, coastal forests, and secondary vegetation such as *Leucaena leucocephala* scrub and *Stachytarpheta jamaicensis* grassland.

tween *Distylium–Schima* dry forest and *Distylium–Pouteria* dry scrub, so I call these two types *Distylium* dry forest collectively in this paper.

Rhaphiolepis–Livistona dry forest (R–L d.f.) is mainly distributed on dry rocky slopes below the higher areas (Figure 5). *Rhapiolepis indica* v. *integerrima*, *Livistona chinensis* v. *boninensis*, *Pandanus boninensis*, and *Ochrosia nakaiana* are dominant species, but the dominance of each species varies greatly from place to place. I call this forest *Rhaphiolepis* dry forest to distinguish it from *Distylium* dry forest in this paper.

Endangered Species

Many plants and animals have become extinct on oceanic islands because of direct or indirect human activities (see Elton 1958, Carlquist 1965). Protection of endangered species is a worldwide problem.

Ono et al. (1986) pointed out 85 endangered plant taxa classified into two categories (group A: 21 endangered species; group B: 64 rare and/or vulnerable species) in the Bonin Islands. The Japanese Red Data Book (Nature Conservation Society of Japan and World Wildlife Fund Japan 1989) recognizes three extinct, 20 endangered, and 39 vulnerable species of vascular plants in the Bonin Islands. Shimizu (1990) categorized seven causal factors that have made these species endangered, as follows: (1) Felling of particular tree species in the past (e.g., *Morus boninensis*, *Clinostigma savoryana*); (2) reduction of habitat by deforestation (e.g., *Claoxylon centinarium*, *Ficus iidaiana*); (3) collection for commercial use (e.g., *Calanthe hattorii*, *Cirrhopetalum boninense*); (4) damage by introduced animals (goats, land snails) (e.g., *Cirsium boninense*, *Lobelia boninensis*); (5) competition with introduced plants (e.g., species of *Elaeocarpus–Ardisia* mesic forest); (6) damage by drought and typhoon (e.g., *Symplocos kawakamii*, *Procris boninensis*); (7) fluctuation of environments (and a long-term trend of aridity) (e.g., species of *Distylium* dry forest).

Figure 6 shows that woody species with small numbers of individuals (less than 10,000) are concentrated in the *Distylium* dry

TABLE 1

SPECIES COMPOSITION OF THE *Distylium–Schima* DRY FOREST

HEIGHT CLASSES / SPECIES NAME	NO. OF INDIVIDUALS (900 m²)				
	I (4–6 m)	II (2–4 m)	III (0.7–2 m)	IV (0.2–0.7 m)	V (<0.2 m)
Bischofia javanica°					1
*Boninia glabra**		31	69	5	51
*Boninia grisea**		6	1	1	
*Callicarpa glabra**		2	9	60	102
Cinnamomum insularimontanum⁺				1	1
*Clinostigma savoryana**		3	2	3	
*Distylium lepidotum**	108	83	42	396	639
*Elaeocarpus photiniaefolius**	5	10	9	20	50
*Evodia nishimurae**	13	3			12
*Fagara boninensis**					5
*Ficus boninsimae**		1	3	9	6
*Gardenia boninensis**	2	19	9	1	2
*Geniostoma glabrum**	6	1	1	6	32
*Hibiscus glaber**	7	16	10	3	9
*Ilex matanoana**	33	9	13	32	225
*Juniperus taxifolia**	1				
*Ligustrum micranthum**	10	91	198	1,626	1,727
*Machilus boninensis**	3	36	163	137	78
*Machilus kobu**	1		1		
*Myrsine maximowiczii**	41	2	4	4	18
Neolitsea sericea⁺		5	28	3	
Osmanthus insularis⁺				1	7
*Osteomeles boninensis**		1			8
*Pandanus boninensis**	37	15	51	70	3
Photinia wrightiana⁺			1		6
Pinus lutchuensis°	2	5	7	16	81
*Pittosporum chichisimense**		5	15	37	
Pouteria obovata⁺	82	39	54	114	13,416
*Psychotria homalosperma**	12		2		3
Rhaphiolepis indica v. *integerrima*⁺	14	32	37	319	716
*Schima mertensiana**	79	18	21	17	430
*Stachyurus macrocarpus**		1	3	4	4
*Symplocos pergracilis**		8	58	11	
Syzygium buxifolium⁺	57	68	76	319	579
*Tarenna subsessilis**		1	4	62	229
*Vaccinium boninense**	1	2	3		1
Viburnum japonicum v. *boninsimense**				1	
*Wikstroemia pseudoretusa**	6	5	39	86	325
Total	520	518	933	3,364	18,766

* Endemics of the Bonin Islands.
⁺ Indigenous species.
° Exotics.

forest (D–S d.f. and D–P d.s.) on Chichijima. Most of the rare and endangered species have only small numbers of seedlings and saplings relative to the number of mature trees of the same species (Figure 7). This situation is true all over the Bonin Islands (field observation). It seems that regeneration of individuals is not going well for these species. Therefore, they will probably become extinct in the future, though the possibility of some unknown regeneration mechanism such as highly episodic reproduction cannot be ruled out. I selected

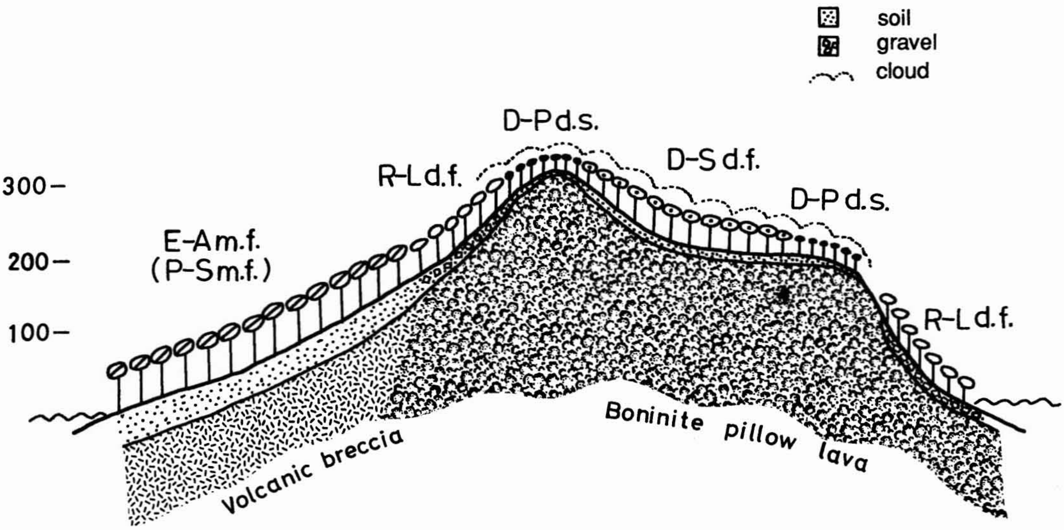


FIGURE 5. Diagramatic presentation of an east-west transect through the center of Chichijima Island, showing depth of soils, kinds of basal rocks, and vegetation types.

25 woody species (see Figure 14) that have small numbers of mature trees and whose individuals occur mainly in the *Distylium* dry forest in Chichijima-retto. I call these "endangered species" in a broad sense in this paper.

Elaeocarpus–Ardisia mesic forest also has some rare and endangered species (Figure 6), but this is because the present distribution of this forest is confined to a very narrow area on Chichijima-retto (Figure 4) because of nearly complete destruction in the past (category 2 above). More individuals of species in this type of mesic forest may be found in Hahajima, where this type of forest is preserved more widely.

Because the dry habitat of *Distylium* dry forest was not suitable for cultivation, there was less human impact on this forest in the past, and more of its original distribution remained than that of the mesic forest. Most of the endangered species in the *Distylium* dry forest have little value for practical use. Thus, the reduction of density of these species should be attributed first to natural causes. I ascribe it to the fluctuation of the environment during a long range of time (category 7).

In this paper I analyze the distribution and species composition of *Distylium* dry forest and the distribution patterns of the endangered species on Chichijima-retto. I propose a hypothesis connected with the origin of the *Distylium* dry forest to explain why many endangered species occur there.

METHODS

Figure 8 presents the route of field observation and the location of plots surveyed in this study. Plots (10 × 10 m–20 × 20 m) were located in dry forests. The number of plots was as follows: Chichijima, 70; Anijima, 74; Otohtojima, 15. I categorized woody individuals as trees in the canopy and subcanopy layers, as saplings in the shrub layer, and as seedlings in the herb layer (less than 0.2 m high). The survey of plots included three potential methods, as follows: (1) Recording names of all vascular plants; (2) counting the number of trees for woody species and checking names for herbaceous species; or (3) measuring dbh (diameter at breast height) of all stems of trees, counting the number of saplings and seedlings of woody species, and checking the names of herbaceous species in 20 quadrats (1 × 1 m) in a plot. For any given plot I chose one of these methods according to the time and assistance available.

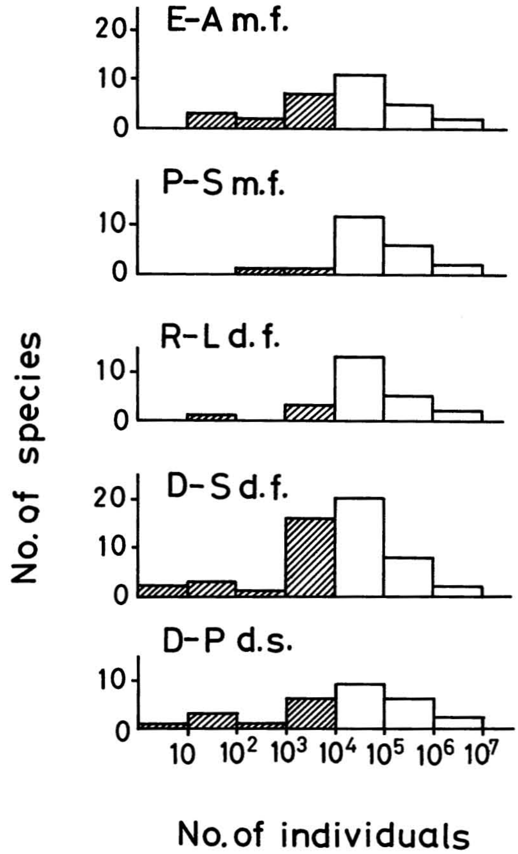


FIGURE 6. Estimated number of mature individuals of all woody species of six different vegetation types on Chichijima Island. Hatching shows species with less than 10,000 individuals. Calculated from Shimizu (1981).

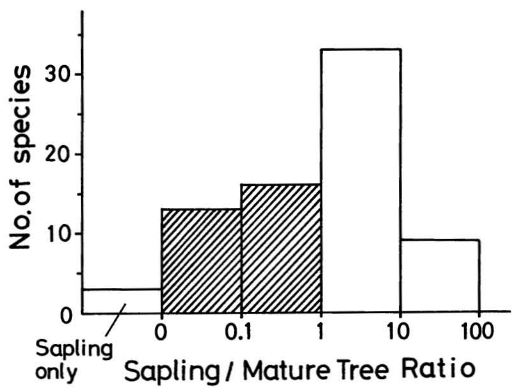


FIGURE 7. Ratio of number of saplings to number of mature individuals in the 95 plots on Chichijima Island. Hatching shows species with a ratio between 0 and 1. Calculated from Shimizu (1982*a*).

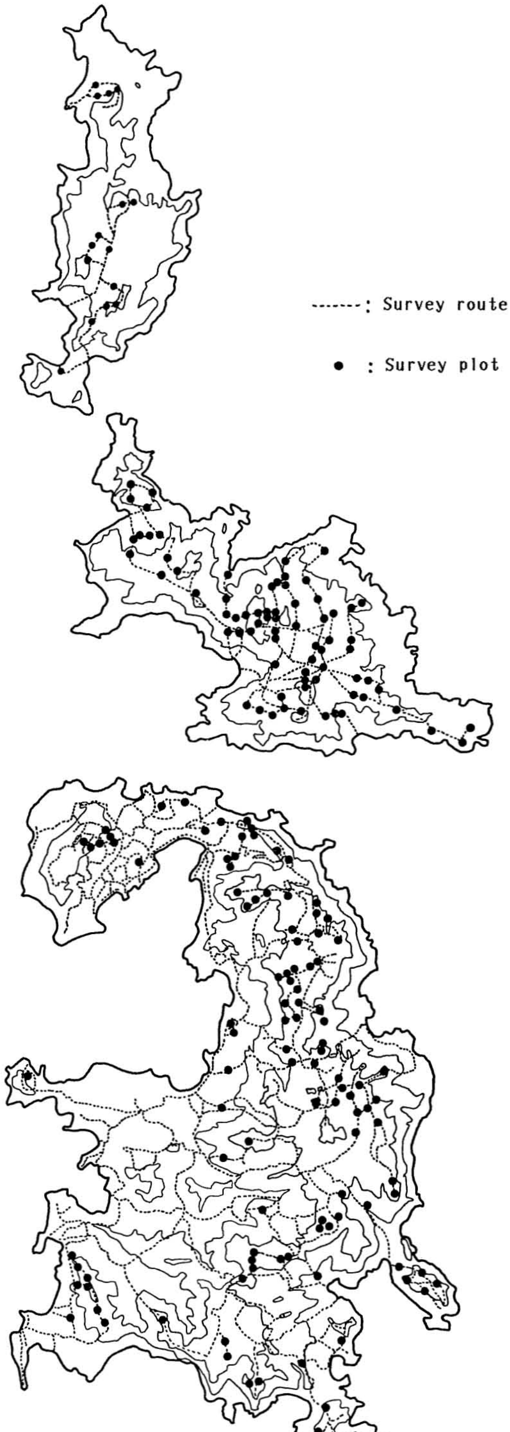


FIGURE 8. Survey route and plots in Chichijima-retto.

RESULTS

Distribution of Distylium *Dry Forest*

Figure 9 shows the distribution of *Distylium* dry forest on Chichijima, Anijima, and Otohtojima in Chichijima-retto. The configuration of these islands and the adjacent sea bottom is also presented. The distribution of *Distylium* dry forest roughly coincides with areas above 100 m on Chichijima and Anijima, with densest distribution in areas above 200 m. Small patches of this forest are dispersed on ridges and mountaintops and surrounded by *Rhaphiolepis* dry forest on the southern half of Chichijima and on Otohtojima. Flat areas and gentle slopes with deep soils are covered with mesic forests instead of *Distylium* dry forest, even though located at altitudes above 200 m (Figure 4).

FIGURE 9. Distribution of the *Distylium* dry forest (stippled area) and configuration of the three islands and adjacent sea bottom in Chichijima-retto. Contour lines are drawn every 100 m on land and every 20 m at sea.

Sea level was at least 100 m lower in the last Ice Age (ca. 20,000 yr B.P.) than at present (Ohta and Yonekura 1987). All islands belonging to Chichijima-retto were united as a larger island (Figure 9). It is estimated that this single, large island was about three times as large in area as the present area of Chichijima-retto. In those days, the present patches of *Distylium* dry forest might have been connected with each other, resulting in a wide continuous distribution on the large island.

Relationship with Fog Occurrence

The higher areas of Chichijima are sometimes shrouded by fog (Figure 10). The distribution of *Distylium* dry forest seems to be related to fog occurrence (altitude of cloud bottom). The frequency of fog is greatest during the rainy season (May–June and October–November) (Figure 11), especially for fog occurring at altitudes lower than 270 m.

The frequency of fog has two peaks: 270–330 m and 450–600 m (Figure 12). These altitudes are nearly equivalent to the highest points on Chichijima and Hahajima, respectively. The frequency is very low at altitudes less than 210 m (Figure 12). This means that the *Distylium* dry forest at altitudes less than 200 m gets scarcely any fog.

When the islands were united into a single larger and higher island in the last Ice Age, the whole area of *Distylium* dry forest might have been shrouded in fog more frequently.

Species Composition

Figure 13 shows the proportion of canopy trees in the three dominant species (*Distylium lepidotum*, *Schima mertensiana*, and *Rhaphiolepis indica* v. *integerrima*) that characterize the dry forests on Chichijima-retto. *Distylium lepidotum* and *Shima mertensiana* dominate in the *Distylium–Schima* dry forest located on higher areas on Chichijima and Anijima. The

FIGURE 10. Fog occurrence in higher areas (Chuosan-higashi-daira) on Chichijima Island.

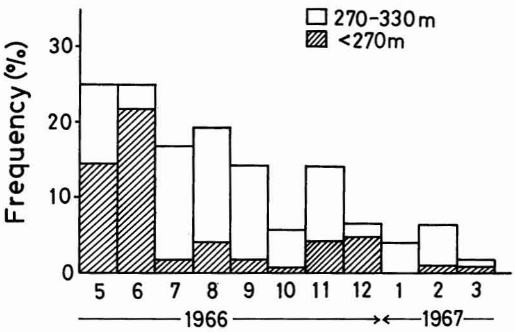


FIGURE 11. Monthly frequency of fog occurrence. Calculated from data from Ministry of Transport (1969), which was recorded by the U.S. Army from May 1966 to March 1967 on Chichijima Island.

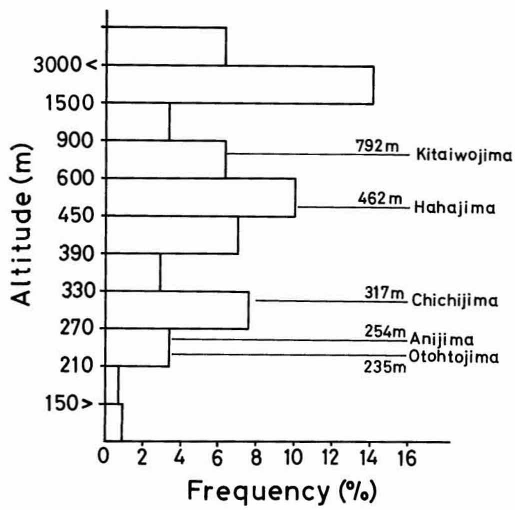


FIGURE 12. Altitudinal frequency of fog occurrence. Calculated from data from Ministry of Transport (1969), which was recorded by the U. S. Army from May 1966 to March 1967 on Chichijima Island.

dominance of *Distylium lepidotum* increases and *Schima mertensiana* disappears in *Distylium–Pouteria* dry scrub. In contrast, the *Rhaphiolepis–Livistona* dry forest is characterized by a high proportion of *Rhaphiolepis indica* v. *integerrima* and a lack of *Distylium lepidotum* and *Schima mertensiana.*

Table 2 presents the species composition of the *Distylium–Schima* dry forest and the *Rhaphiolepis–Livistona* dry forest. As mentioned previously, the *Distylium–Schima* dry forest includes many endemic and endangered species, especially shrub species. In contrast,

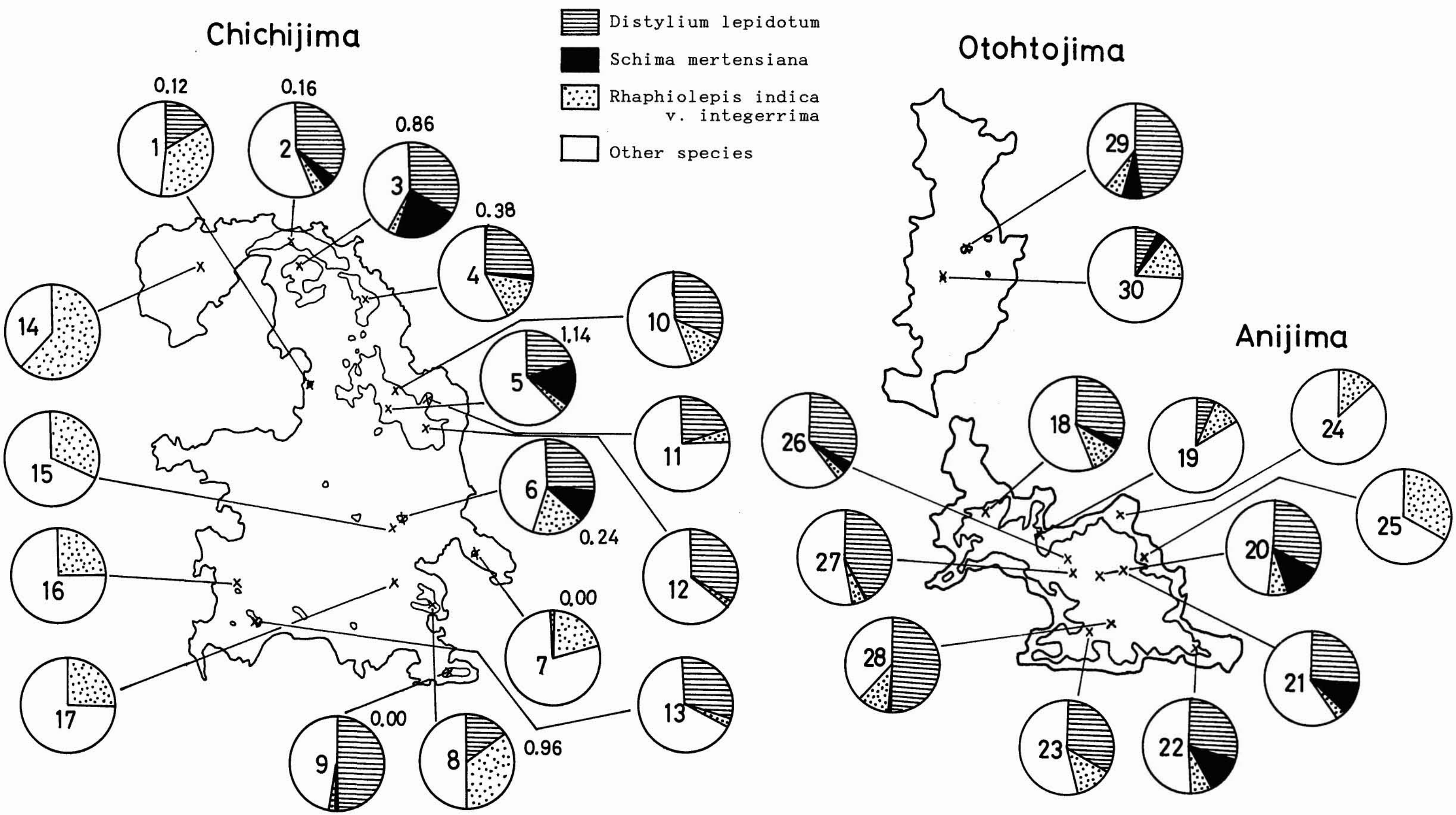


FIGURE 13. Proportion of three dominant species based on the density of canopy trees in dry-type vegetation in Chichijima-retto. Numbers above the circles numbered 1–9 show the seedling density (no./m^2) of *Distylium lepidotum*. Key to numbered circles: 1–9, 18–23, 29–30: *Distylium–Schima* dry forest; 10–13, 26–28: *Distylium–Pouteria* dry scrub; 14–17, 24–25: *Rhaphiolepis–Livistona* dry forest.

TABLE 2

COMPARISON OF THE SPECIES COMPOSITION OF *Distylium–Schima* DRY FOREST AND *Rhaphiolepis–Livistona* DRY FOREST

Distylium–Schima DRY FOREST ← TRANSITIONAL → *Rhaphiolepis–Livistona* DRY FOREST

<table>
<tr><td colspan="2">Distylium lepidotum, Schima mertensiana
Elaeocarpus photiniaefolius
Gardenia boninensis, Myrsine maximowiczii
Geniostoma glabrum, Psychotria homalosperma
Pouteria boninensis, Juniperus taxifolia
Machilus boninensis, Machilus kobu
Metrosideros boninensis
Boninia glabra*, Vaccinium boninense*
Photinia wrightiana*, Tarenna subsessilis*
Viburnum japonicum v. boninsimense*
Osteomeles boninensis*</td><td></td></tr>
<tr><td>Evodia nishimurae
Ilex matanoana
Callicarpa glabra*
Symplocos pergracilis*
Pittosporum chichisimense*
Stachyurus macrocarpus*
Eurya boninensis*
Melastoma tetramerum*</td><td colspan="2">Boninia grisea, Drypetes integerrima
Ilex mertensii, Ochrosia nakaiana
Livistona chinensis v. boninensis
Osmanthus insularis, Ardisia sieboldii
Pittosporum boninense^{+}
Callicarpa subpubescens^{+}
Celtis boninensis^{+}
Melia azedarach^{+}, Trema orientalis^{+}
Fagara boninensis^{+}, Morus australis^{+}
Elaeagnus rotundata^{+}
Boehmeria boninensis^{+}</td></tr>
<tr><td colspan="3">Pouteria obovata, Syzygium buxifolium, Neolitsea sericea
Hibiscus glaber, Rhaphiolepis indica v. integerrima
Ilex percoriacea, Ficus boninensis, Ligustrum micranthum
Cinnamomum insularimontanum, Wikstroemia pseudoretusa</td></tr>
</table>

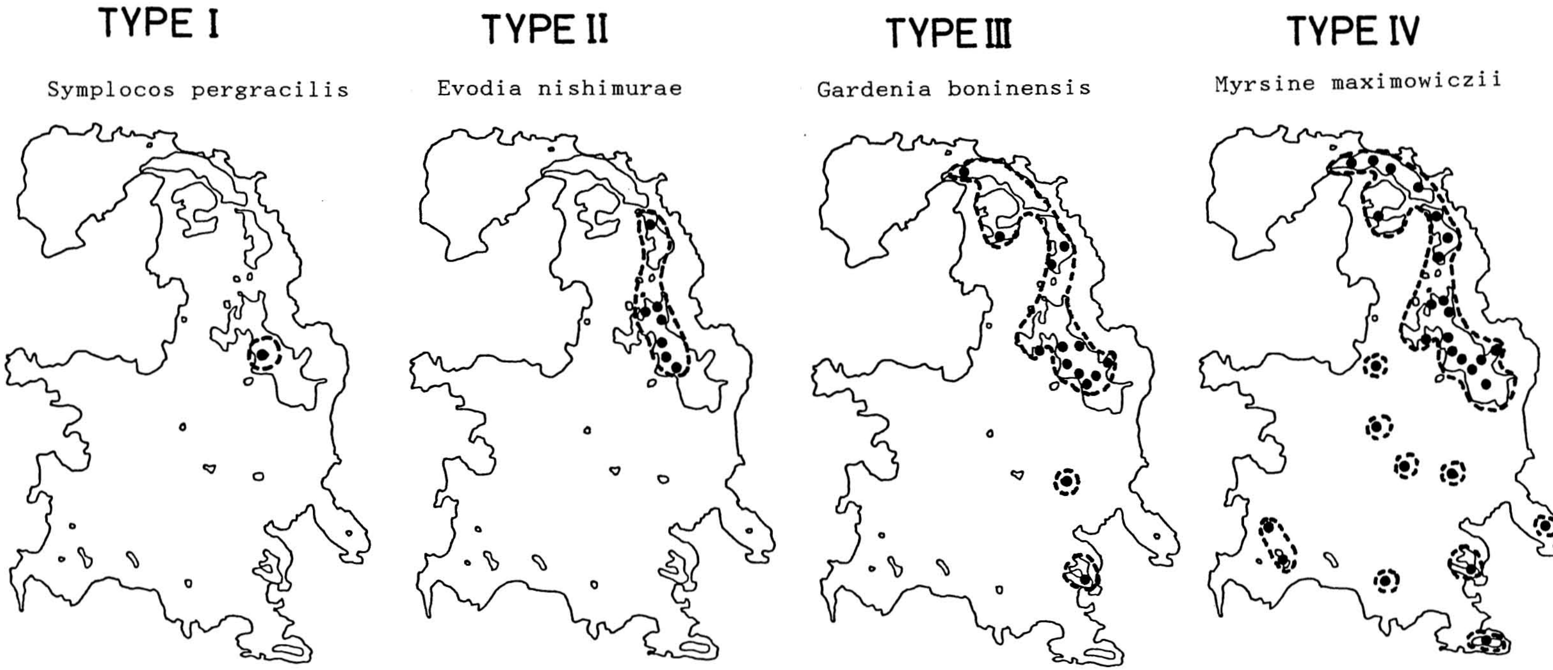
NOTE: Width of dissected blocks shows the distribution range of the species enclosed.
* Undergrowth shrub species.
$^{+}$ Pioneer or light-demanding species.

the *Rhaphiolepis–Livistona* dry forest has no such endangered shrub species. Instead, many light-demanding species, including some pioneer trees, are mixed in the *Rhaphiolepis–Livistona* dry forest. In contrast to the *Distylium–Schima* dry forest, which occurs in higher areas, the *Rhaphiolepis–Livistona* dry forest is situated on rocky slopes at lower altitudes (Figure 5). Judging from species composition and habitat condition, the *Rhapiolepis–Livistona* dry forest is drier and more unstable than the *Distylium–Schima* dry forest.

There are some plots where the species composition is intermediate between *Distylium–Schima* and *Rhaphiolepis–Livistona* dry forests (Figure 13). These plots occur at pheripheral areas in the distribution range of the *Distylium* dry forest; almost all of them are located at altitudes below 100 m (Figure 9). Seedlings and saplings of *Distylium lepidotum* are not abundant in these plots. I found some dead trees of *D. lepidotum* in the marginal part of this forest. It seems that this intermediate forest is changing from a *Distylium* dry forest to a *Rhaphiolepis* dry forest.

Types of Distribution Patterns of Endangered Species

Figure 14 shows four distribution patterns of 25 endangered woody species that are members of the *Distylium* dry forest on



Symplocos pergracilis
Pittosporum chichisimense*
Eurya boninensis
Stachyurus macrocarpus
Melastoma tetramerum*
Myrsine okabeana
Callicarpa nishimurae
Boninia crassifolia

Evodia nishimurae
Callicarpa glabra
Ilex matanoana
Psychotria homalosperma
Metrosideros boninensis
Pittosporum parvifolium

Gardenia boninensis
Viburnum japonicum
v. boninsimense
Boninia glabra
Pouteria boninensis
Geniostoma glabrum
Fatsia oligocarpella
Symplocos kawakamii*
Santalum boninense

Myrsine maximowiczii
Photinia wrightiana
Vaccinium boninense

FIGURE 14. Distribution patterns of 25 endangered woody species on Chichijima Island classified into four distribution types. Each type is represented by a typical species. Species with similar distribution patterns are listed below the figure. Asterisks indicate species endemic to Chichijima.

Chichijima-retto. All of these species occur at the highest altitude on Chichijima-retto, called Chuosan-higashi-daira, lying at the eastern side of the main ridge in the center of Chichijima (Figure 10), where fog occurrence is probably more frequent than at other places.

The distribution of eight of the 25 endangered species (type 1) is confined to a small area of Chuosan-higashi-daira. The other species (types 2–4) are distributed more or less widely in the *Distylium* dry forest on Chichijima (Figure 14). But even in types 2–4, the density of individuals of each species is highest at Chuosan-higashi-daira and it decreases gradually with distance from that area (Figure 15). Thus, species composition is richest in the *Distylium* dry forest of Chuosan-higashi-daira.

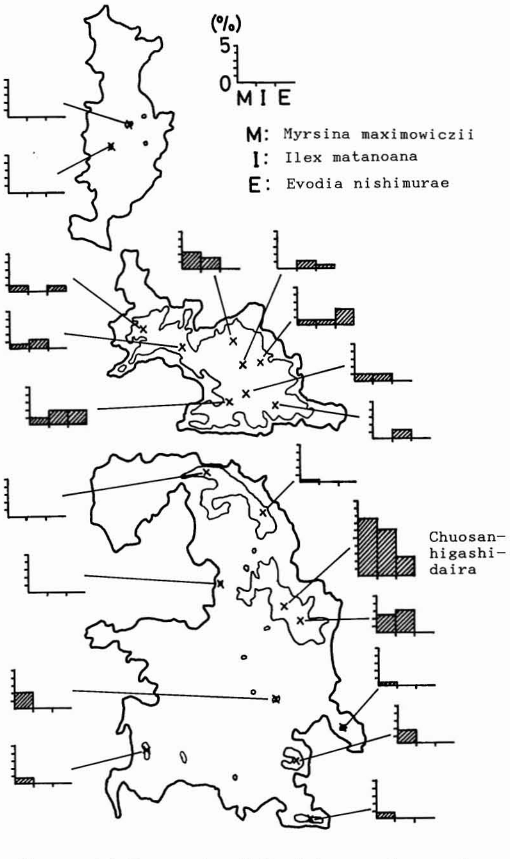


FIGURE 15. Proportion (%) of three endangered species based on density of canopy trees in some plots in Chichijima-retto, showing the concentrated distribution in Chuosan-higashi-daira on Chichijima.

Almost all the endangered species listed in Figure 14 also occur in Anijima (Figure 16). Only three species (*Symplocos kawakamii*, *Pittosporum chichisimense*, and *Melastoma tetramerum*) out of the 25 are not found on Anijima. The distribution patterns of the 22 endangered species on Anijima are classified into two types: widespread type and restricted type (Figure 16). Species composition in the distribution patterns on Anijima does not necessarily coincide with that on Chichijima (Figure 16). For example, *Ilex matanoana*, *Callicarpa glabra*, and *Evodia nishimurae* are distributed more widely on Anijima than on Chichijima, though the density of these species on Anijima is as low as that in the peripheral areas on Chichijima (Figure 15).

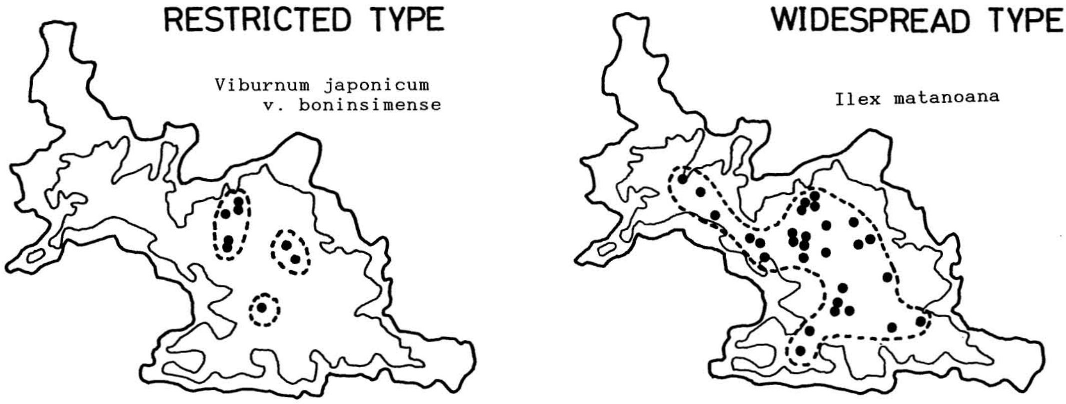
It seems that the distribution of the restricted-type species on Anijima is centered on the ridges and valleys located in the central, highest part of the island (Figure 9). But in Anijima, there is no such place as Chuosan-higashi-daira of Chichijima where all endangered species occur together with high density. This is probably because the highest areas of Anijima are about 50–100 m lower in altitude than those of Chichijima, thus the habitat conditions offered by Chuosan-higashi-daira do not occur on Anijima.

The species composition of the *Distylium* dry forest is poor on Otohtojima. Only a few of the 25 endangered species appear there.

Damage of Drought in 1980

A severe drought hit Chichijima-retto in the summer of 1980 (Shimizu 1982*b*). The total precipitation in May–October 1980 was only 18% of normal. This kind of severe drought seems to happen occasionally, about every 20 yr, in the Bonin Islands. Many plants were killed or damaged by the drought in 1980, especially in the *Distylium–Pouteria* dry scrub, which grows on shallow soils (Table 3).

Strangely, *Distylium lepidotum*, the most dominant species in the *Distylium–Pouteria* dry scrub, was damaged the most. About 70% of the total *Distylium lepidotum* individuals studied in the plots were dead (Table 3). Some



Viburnum japonicum
v. boninsimense
Eurya boninensis
Stachyurus macrocarpus
Fatsia oligocarpella
Metrosideros boniensis
Pittosporum parvifolium
Santalum boninense
Symplocos pergracilis

Ilex matanoana
Geniostoma glabrum
Psychotria homalosperma
Pouteria boninensis
Callicarpa glabra
Callicarpa nishimurae
Photinia wrightiana
Evodia nishimurae
Gardenia boninensis
Myrsine maximowiczii
Myrsine okabeana
Boninia glara
Boninia crassifolia
Vaccinium boninense

FIGURE 16. Distribution patterns of 21 endangered woody species on Anijima Island. Each type is represented by a typical species, and species with similar distribution patterns are listed below the figure.

endangered species, such as *Symplocos pergracilis*, *Callicarpa nishimurae*, and *Pittosporum parvifolium*, were also killed or damaged to some degree. Thus, this type of scrub has degenerated to grass vegetation in some places.

Most of the species in the *Distylium–Pouteria* dry scrub have drought-tolerant features such as multistem growth forms and small, thick, hairy leaves. They survive the usual droughts in midsummer, but they cannot endure occasional severe drought. This phenomenon indicates that *Distylium lepidotum* and other members of the *Distylium–Pouteria* dry scrub are not truly resistant against severe drought.

Comparison of Congeneric Species on Other Islands

Another cluster of islands, called Iwo-retto (Volcano Islands), exists about 150 km to the south of the Bonin Islands. Iwo-retto, which is composed of three main islands, was produced by volcanic activity in the Quaternary (Fukuyama 1983). Its flora has been formed basically from colonization by the species of the Bonin Islands, together with some elements from mainland Japan and the Micronesian islands (Tuyama 1970, Ohba 1983). Minami-Iwojima (highest altitude 916 m) and Kita-Iwojima (highest altitude 792 m) islands have a true fog zone above 500 m (Kaji and Takiguchi 1983, Kawakubo 1986).

Hahajima (highest altitude 462 m) in the Bonin Islands is located about 50 km south of Chichijima. The main ridge, above 400 m, is frequently shrouded by fog (Figure 12). *Dendrocacalia–Fatsia* mesic scrub (see Figure 3) occurs on the ridge together with dense thickets of *Freycinetia boninensis* in places.

Figure 17 shows a comparison of habitats of congeneric species found in Kita-Iwojima, Hahajima, and Chichijima. *Eurya*, *Fatsia*, *Viburnum*, and *Melastoma* species grow in the cloud forest on Kita-Iwojima; *Fatsia*,

TABLE 3

DAMAGE FROM DROUGHT IN 1980 IN *Distylium–Pouteria* DRY SCRUB

SPECIES NAME	NO. OF INDIV. STUDIED	RATIO (%) OF INDIVIDUALS DEAD	DAMAGED	HEALTHY
Distylium lepidotum	91	69.2	25.3	5.5
Ligustrum micranthum	65	7.7	89.2	3.1
Pouteria obovata	48	0	75.0	25.0
Osteomeles boninensis	32	0	56.3	43.7
Rhaphiolepis indica v. *integerrima*	14	0	14.3	85.7
Syzygium buxifolium	13	7.7	53.8	38.7
Dodonaea viscosa	13	7.7	15.4	76.9
Hibiscus glaber	10	0	40.0	60.0
Hedyotis grayi	8	50.0	50.0	0
Ilex percoriacea	7	0	71.4	28.6
Pinus lutchuensis	6	100	0	0
Boninia glabra	5	0	100	0
Vaccinium boninense	4	0	25.0	75.0
Wikstroemia pseudoretusa	4	0	75.0	25.0
Juniperus taxifolia	4	0	100	0
Gardenia boninensis	3	0	33.3	66.7
Pandanus boninensis	3	0	0	100
Photinia wrightiana	2	0	50.0	50.0
Pittosporum parvifolium	2	50.0	50.0	0
Schima mertensiana	1	0	100	0
Symplocos kawakamii	1	0	100	0
Myrsine okabeana	1	0	100	0
Callicarpa nishimurae	1	0	100	0

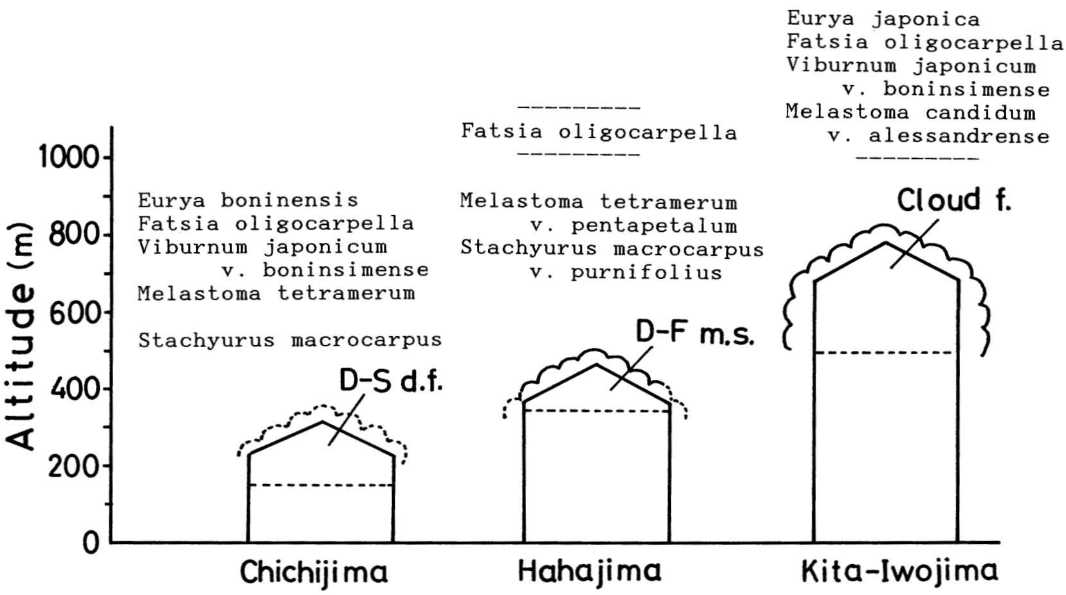


FIGURE 17. Comparison of habitats of congeneric species in five genera among Chichijima, Hahajima, and Kita-Iwojima islands.

Melastoma, and *Stachyurus* species occur in the mesic scrub on Hahajima. Species of these genera are found also in the *Distylium* dry forest on Chichijima. *Hydrangea macraphylla* f. *normalis* on Kita-Iwojima and *Dendrocacalia crepidifolia* on Hahajima, both of which require mesic conditions, do not occur on Chichijima, probably because the true fog zone that favors these species is now absent on Chichijima.

DISCUSSION AND CONCLUSIONS

The results given above offer some clues regarding the origin of the *Distylium* dry forest and the occurrence of so many endangered species in this type of forest in Chichijima-retto: *Distylium* dry forest is distributed widely over the central parts of Chichijima and Anijima, with scattered patches in the peripheral areas. Small patches of *Distylium* dry forest are poor in species composition because of the absence of many endangered species. All of the 25 endangered species selected in this study are preserved in the highest area on Chichijima, called Chuosan-higashi-daira. The three islands of Chichijima-retto were united into a large island (about three times as large as the present area) during the last Ice Age, when sea level was at least 100 m lower than at present. The present distribution of the *Distylium* dry forest seems to be related to the frequency of fog occurrence. *Distylium lepidotum* and many other members of the *Distylium* dry forest are not resistant to severe drought. The *Distylium* dry forest located below 100 m altitude seems to be changing to a *Rhaphiolepis* dry forest, the drier vegetation type. Mesic-type forests take the place of *Distylium* dry forest in deep soils, irrespective of altitude.

In general, the geological history of oceanic islands begins as submarine volcanic activity. A large, high mountainous island with simple topography is formed first. After volcanic activity ceases, the island becomes lower and smaller because of subsidence of the basal landmass and continuous erosive action, which makes for an intricate topography. The island finally becomes flat and low and covered by the sea. This historical trend of oceanic islands should be applicable to the Bonin Islands, but there is no direct geological evidence.

Clouds are usually generated by an ascending air current around oceanic islands. Thus, high islands always have a cloud zone (fog zone) in their mountainous areas above some altitude (usually about 500 m and above). Here one usually finds cloud forests (Kaji and Takiguchi 1983). It can be said that the higher and larger an island, the more frequent and abundant is its cloud cover.

Large trees in mesic-type forests (*Elaeocarpus–Ardisia* mesic forest) in the Bonin Islands were selectively cut. The forests on deep soils were almost completely cleared for sugarcane fields by the 1900s (Katahira 1981). But the dry-type forests on shallow soils were less damaged, probably because the dry habitat conditions were not suitable for agriculture. (This assumption is supported by the fact that Anijima, where *Distylium* dry forest spreads over almost all the island, has never been inhabited by humans [Yasui 1988].) As a result, most of the *Distylium* dry forest areas have been preserved in rather natural condition in Chichijima-retto. Thus the presence of endangered species in the *Distylium* dry forest seems to be a natural pattern that still exists at present in the Bonin Islands.

Based on the results and assumptions mentioned above, I propose a hypothesis to explain the origin of the *Distylium* dry forest and the occurrence of endangered species in Chichijima-retto (Figure 18):

STAGE 1: A large, high island was formed. The environment was simple and the vegetation was not so diversified. A mesic scrub existed in the fog zone on the upper part of the island.

STAGE 2: The island began to shrink after volcanic activity ceased. Vegetation diversified into several types according to the habitats formed by erosion. *Distylium–Schima* dry forest occurred at the lower part of the fog zone or just below the fog zone. This forest grew on shallow soils in habitats characterized by both frequent fog occurrence and periodic aridity. Mesic-type forest was established on deep soils.

STAGE 3 (Present): The island decreased in

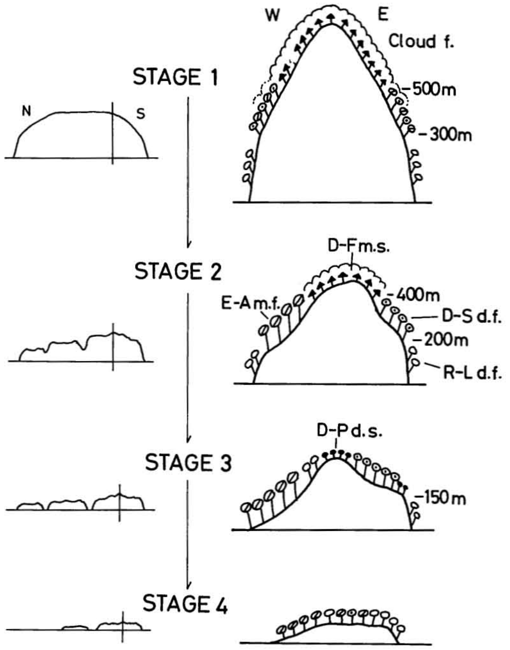


FIGURE 18. The hypothetical process of the origin of *Distylium* dry forest and the occurrence of endangered species in Chichijima-retto.

altitude below the usual fog zone and the true mesic scrub disappeared. Some members of the mesic scrub survived in the *Distylium–Schima* dry forest and became endangered species. The island was dissected into three islands by the rise in sea level and the opening of two straits. The *Distylium* dry forest became fragmented into several patches. Some species, sensitive to reduced fog frequency, disappeared from small pheripheral patches of this forest. These sensitive species survive now only in the highest areas on Chichijima and in the central part of Anijima, where they are endangered species. The *Distylium* dry forest is changing to a *Rhaphiolepis* dry forest at low altitude. The *Distylium–Pouteria* dry scrub has diversified from the *Distylium–Schima* dry forest in dry habitats, which first appeared earlier in this stage. Some species endemic to Chichijima-retto (*Pittosporum parvifolium*, *Callicarpa nishimurae*, *Myrsine okabeana*, *Symplocos kawakamii*, *Boninia crassifolia*) speciated in the dry scrub from the congeneric species in the *Distylium–Schima* dry forest. This trend of aridification has been accelerated by the roughly 100-m rise of sea level after the last Ice Age. The trend must have been interrupted during several Ice Ages in the Quaternary.

STAGE 4: As subsidence of the islands continues, the *Distylium* dry forest will almost disappear on the flat, low islands. Most of the endangered species will become extinct when stage 4 is reached. Flat land with deep soils will be covered with a dwarfed mesic-type forest with simple species composition. Only a few members of the *Distylium* dry forest will survive in the *Rhaphiolepis* dry forest that will have displaced the *Distylium* dry forest on shallow soils.

Pollen analysis might support this hypothesis, but there is no bog with sediments suitable for pollen analysis. Germination experiments with some species of the *Distylium* dry forest and investigations of similar dry forests on islands other than Chichijima-retto are planned for future research.

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