

The Nature of Ogasawara and its Conservation

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Abstract

The Ogasawara (Bonin) Islands are oceanic islands in the northwest Pacific Ocean. Their origin goes back to the Tertiary, the present islands having emerged at least several million years ago. The climate is subtropical and typhoons pass by the islands every year. The islands were first inhabited in 1830, ruled by the U.S. for 23 years after World War II, and returned to Japan in 1968 after which they were treated administratively as a new village. As oceanic islands, they are poor in flora and fauna compared with continental or mainland areas, lacking big mammals, snakes, frogs and Fagaceous trees, while the endemic ratio is high in many groups. The islands are called “the Oriental Galapagos.” The vegetation is classified into seven types according to habitat, physiognomy and dominant species. A pine wood nematode invaded the islands killing many pine trees in the early 1980s. A large typhoon hit the islands and did much damage to the forests in 1983. After this disturbance, *Bishofia javanica* (introduced sp.) invaded the natural forests rapidly taking the place of native trees. A *Bishofia* eradication project started in 2002. Feral goats which destroyed the forests of the Mukojima group were completely removed recently to restore the vegetation. Some critically endangered species were bred artificially and transplanted to the original habitats, but regeneration by itself has not been successful. An airport construction plan which was proposed by the Tokyo Metropolitan Government in 1989 was finally withdrawn in 2001.

Key words: conservation, endemic, eradication, invasion, island, Ogasawara

1. Location

The Ogasawara (Bonin) Islands are located about 1,000 km to the south of Tokyo in the northwest Pacific Ocean (Fig. 1). They consist of about 30 small islands scattered in the subtropical zone (26°40'N-27°45'N). They are divided into three island groups, the Mukojima-retto, Chichijima-retto and Hahajima-retto (retto means island group). Only two islands, Chichijima and Hahajima, are inhabited now. Chichijima (24.0 ha, 326 m) has the maximum area and Hahajima (20.8 ha, 462 m) has the highest peak in the Ogasawaras.

The Ogasawaras are oceanic islands which have been isolated since their formation. Their location defines both the northern limit of the islands of Oceania and the eastern limit of East Asia. This position is an important factor determining the nature of the Ogasawaras.

2. Geology

The Ogasawaras lie atop the ridge (400 km long, 50-70 km wide) of the Izu-Ogasawara-Mariana Arc. The base of the islands was made by submarine vol-

canoes in the Eocene (Imaizumi, 2000). Maruyama *et al.* (1989) speculated that the Ogasawaras appeared around the equator about 50 million years ago, then the islands, on the Philippine Sea plate, went north and reached their present position. In fact, they are still moving north-westward at a speed of about 4 cm a year. Taira (1994) stated that the basal rocks of the Ogasawaras (Paleo Izu-Ogasawara Arc) were formed 45 million years ago, the arc split into the Kyushu-Palao Ridge and Izu-Ogasawara Arc 15-25 million years ago, and the present Izu-Ogasawara Arc developed 15 million years ago. Though the geological history of the Ogasawaras after the formation of the arc is not clear, they may have been a landmass for at least several million years (Kaizuka, 1977).

The islands are comprised mostly of volcanic rocks including lava and tuff breccia and in part, sedimentary rocks including sandstone, mudstone and limestone (Kuroda, 1992). Outcrops of pillow lava are found everywhere in Chichijima (Fig. 2).

As the islands have been reduced by erosion since the volcanic activity stopped, the original volcanic topography, such as craters, is not recognized at present (Imaizumi, 2000). To understand the vegetational history of the Ogasawaras in total, Shimizu

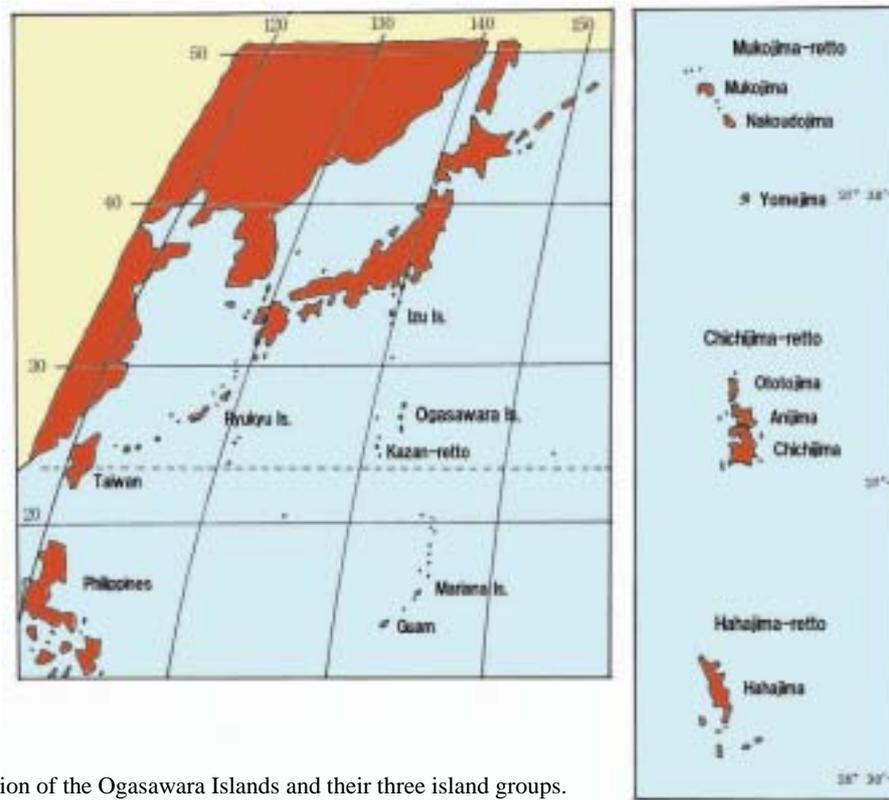


Fig. 1 Location of the Ogasawara Islands and their three island groups.

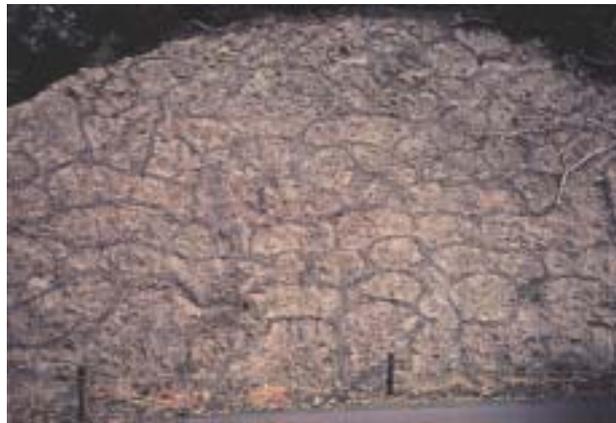


Fig. 2 Outcrop of pillow lava.

(1998) proposed a hypothesis that there once existed a huge Ogasawara Island whose height exceeded 1,000 m above sea level, then it became lower and smaller and was divided into the present three island groups.

3. Climate

The climate of the Ogasawaras is subtropical. The annual mean temperature is 22.9°C with maximum and the minimum monthly mean temperatures of 27.6°C in August and 17.6°C in February, respectively. The annual precipitation (1969-1997) is 1,268 mm at Chichijima while that of the early 20th century (1907-1939) was 1,609 mm. Though it rains throughout the year, two rainy seasons (May-June and

Oct.-Nov.) and a mid-summer drought (July-Aug.) are conspicuous. Drought years with less than 500 mm in the summer season (May-October) have increased recently (Shimizu, 1999).

The phenology of plants (seasonal rhythm of flowering, fruiting, leaf flushing and falling) shows intermediate features between tropical and temperate regions in the Ogasawaras. Flowering and fruiting occur all year round, while some deciduous plants, leaves fall in winter (Shimizu, 1994).

Several typhoons hit the islands every year doing minor damage to the nature (Shimizu, 2003). Once every several decades, a large typhoon attacks the islands making a large disturbance, which accelerates regeneration of the forests (Shimizu, 1983).

4. Flora and Fauna

The Ogasawaras are separated by a vast sea from the Asian Continent and the mainland of Japan which were the sources of the islands' creatures. Only a limited number of species reached the Ogasawaras by chance, carried by winds, ocean currents and birds, and became the ancestors of the present plants and animals (Ono & Sugawara, 1981).

The flora and fauna of the Ogasawaras are poor from the viewpoint of species diversity. There are about 330 native vascular plants, only two terrestrial vertebrates (a fox bat and a lizard), 15 land birds (four extinct), about 800 insects and about 100 land snails. No big mammals, snakes, frogs nor fresh water fish existed naturally (Shimizu, 1999).

Evergreen *Quercus* and *Castanopsis* which bear acorns, pine trees with wind-dispersed seeds and mangrove plants whose fruit germinate on the parent thrive in the Ryukyu Islands, which are the continental islands located nearly at the same latitude as the Ogasawaras, but they are completely missing in the Ogasawaras. The number of plant species in the mesic forest of the Ogasawaras is about one third that of a comparable laurel-leaved forest in the Ryukyus (personal observation). Because of the poor flora and fauna, relations among plants and animals (for example, the food web) are simple on the whole (Shimizu, 2002). The island ecosystem seems to have many vacant niches.

On the other hand, due to the long isolation of the islands, many ancestral species evolved to new endemic species within the islands. About 40% of the plants overall, 70% of trees only, are endemic to the Ogasawaras (Toyoda, 1981). *Boninia* (Rutaceae) and *Dendrocacalia* (Compositae) are endemic genera. The native fox bat is also endemic. Four land birds are classified as endemic species (*Apalopteron* is an endemic genus) and five as endemic subspecies (Chiba, 1992). About 30% of the insects and more than 90% of the land snails are endemic (Kato, 1992a; Tomiyama, 1992a).

Some species advanced to fill vacant niches and accomplished adaptive radiation. Examples of plants are four species of *Pittosporum* and three species of *Symplocos*, *Callicarpa* and *Boninia* (Shimizu & Tabata, 1991). The most remarkable example of adaptive radiation is found in a land snail genus, *Hirasea* (12 species and four subspecies) (Tomiyama, 1992b). Each species has a peculiar shell shape which is adapted to the habitat (Fig. 3).

The flora is composed mainly of SE Asian elements from the west, and in part, of Polynesian elements from the south and Japanese mainland elements from the north (Yamazaki, 1981). As for *Metrosideros boninensis*, *Clinostigma savoryana*, *Santalum boninense* and *Lobelia boninensis*, the center of these genera lies in the Polynesian region, and the Ogasawaras are the northern limit of their distribution

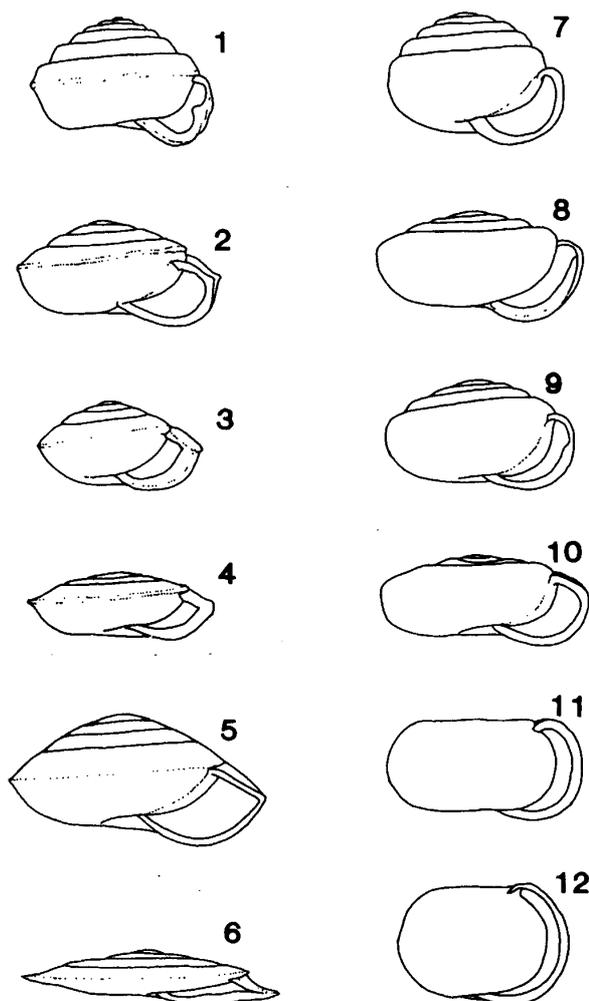


Fig. 3 Adaptive radiation of a land snail genus, *Hirasea*. (Cited from Tomiyama, 1992b)

(Tuyama, 1970). SE Asian elements compose dominant species groups in the present forests, and the degree of species differentiation among the SE Asian elements is lower than among the Polynesian elements, thus it is speculated that the Polynesian elements came to the islands first, then they were replaced by the newcomers of SE Asian origin (Yamazaki, 1981; Shimizu, 1998).

Recent research is revealing genetic relationships between Ogasawaran species and related species on the Asian continent, Oceania or the mainland of Japan (Ono, 1994). The Ogasawaran species of *Pittosporum*, *Symplocos*, *Ilex* and *Crepidiastrum* departed from relatives of mainland species millions of years ago, and they diversified within the islands relatively recently (Fig. 4). *Metrosideros boninensis* is most closely related to a Fijian species, not a Hawaiian species, and they parted from each other in the middle or late Tertiary (Wright *et al.*, 2000).

We can see many peculiarities of island biota which Carlquist (1974) termed the "island syndrome." Therefore, the Ogasawaras are called "the Oriental Galapagos" after the famous oceanic islands.

5. Vegetation

Phytosociologists classified the vegetation of the Ogasawaras into 89 communities (37 natural, 52 substitutional) and made vegetation maps of all islands (Okutomi *et al.*, 1983). Shimizu & Tabata (1991) classified the forests of the Ogasawaras into five types based on the habitat (mesic, dry), physiognomy (tall, low, dwarf) and combination of dominant species, and Shimizu (2002) revised it to seven types (Figs. 5 & 6).

A typical mesic forest (*Elaeocarpus-Ardisia* mesic f.), more than 20 m high, appears in suitable habitat with good soil, and it consists of tall trees such as *Elaeocarpus photiniaefolius*, *Pisonia umbellata*, *Pouteria obovata*, *Melia azedarach*, *Hibiscus tiliaceus*, *Celtis boninensis*, and *Ardisia sieboldii*. This type of forest had been almost completely destroyed and changed to cultivated fields in the prewar era. When the cultivated fields were abandoned after World War

II, *Pinus luchuensis* (an introduced pioneer) and *Schima mertensiana* (a native pioneer) spread over the vacant places, making a secondary mesic forest (*Pinus-Schima* mesic f.) (Shimizu & Tabata, 1985).

In the early 1980s, the all pine trees died at once from an attack of a nematode which invaded the Ogasawaras from the mainland (Fig. 7). About 80% of adult pine trees on the islands died at that time (Shimizu, 1986, 1987). The physiognomy of the *Pinus-Schima* forest changed greatly after that event.

A low, dry forest type, 4-8 m high, exists in a thin-soiled dry habitat. It consists of many shrubby trees such as *Distylium lepidotum*, *Raphiolepis umbellata*, *Syzygium buxifolium*, *Livistona chinensis* var. *boninensis*, and *Pandanus boninensis*. The physiognomy of the dry forest resembles sclerophyllous forest in a Mediterranean climate.

The dry forest type is further divided into three types according to combination of dominant species:

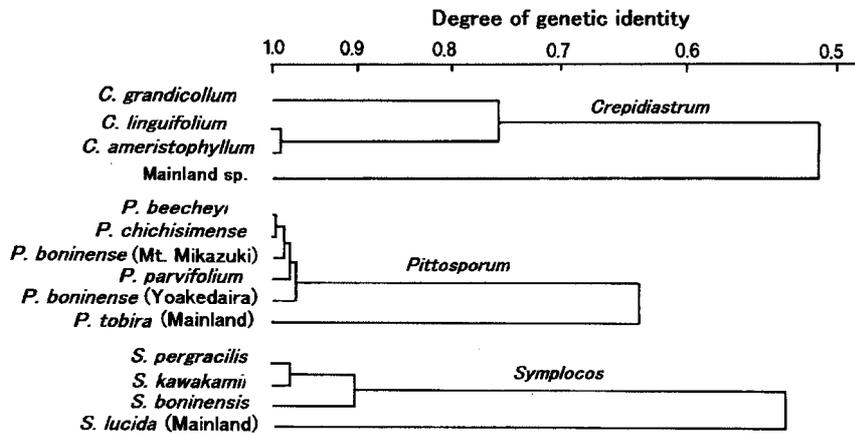


Fig. 4 Genetic relationships among congeneric species of the Ogasawaras and the mainland of Japan. (Cited from Ono, 1994)

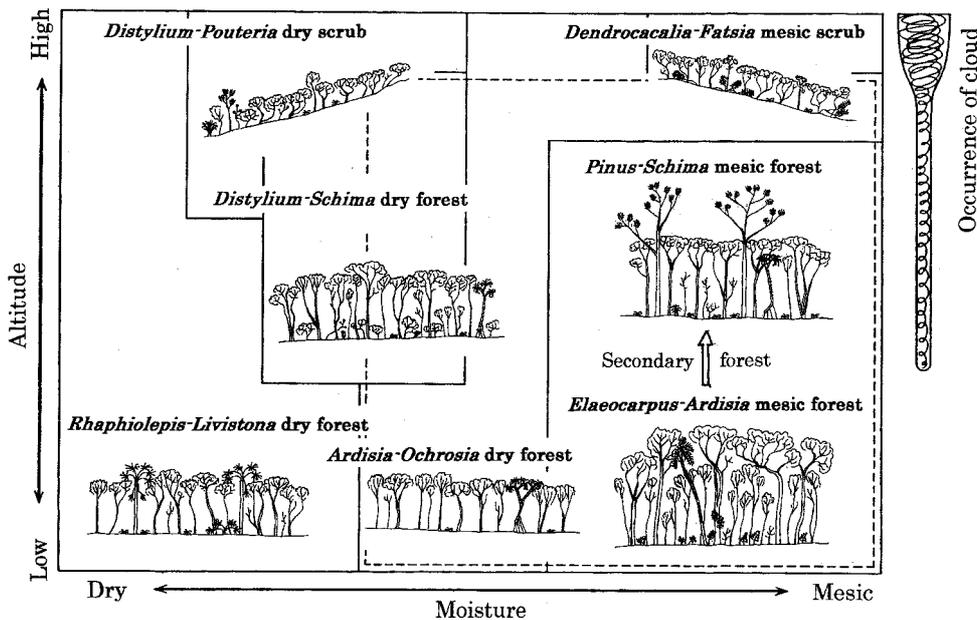


Fig. 5 Vegetation types of the Ogasawara Islands.

Distylium-Schima dry forest, *Raphiolepis-Livistona* dry forest, and *Ardisia-Ochrosia* dry forest. *Distylium-Schima* forest appears in hilly places at altitudes of 150 m or more vertically. This altitude corresponds to the cloud bottom in the rainy season. The species diversity and endemic ratio of the *Distylium-*

Schima forest is highest among the three dry type forests. A dry scrub (*Distylium-Pouteria* dry scrub), less than 2 m high, is a dwarf modification of *Distylium-Schima* forest, which is adapted to severe aridity on exposed lava.

A moist scrub (*Dendrocacalia-Fatsia* mesic scrub)



Fig. 6 Physiognomy of seven vegetation types.
The arrangement of photos coincides with that of Fig. 5.



Fig. 7 Dead crowns of *Pinus luchuensis* due to nematode attack in 1982.

dominated by *Dendrocacalia crepidifolia* is a unique vegetation. It appears only on the main ridge of Hahajima, where moist conditions are maintained all year round due to frequent cloud coverage. *Dendrocacalia crepidifolia* is thought to have originated from an herbaceous ancestor (an example of island woodiness) (Ito, 1992). *Scalesia* (Compositae), a Galapagos endemic genus, also originated from an herbaceous ancestor, and three species make up the *Scalesia* forest in the cloud zone in the Galapagos (Itow, 1983; Shimizu, 1997). So *Dendrocacalia* is comparable to *Scalesia* ecologically.

The flora of the Ogasawaras lacks real climax species (highly shade-tolerant species) such as evergreen *Quercus* and *Castanopsis* on a successional series, and both mesic and dry forests contain many light-demanding species as canopy trees. Thus, it is speculated that regeneration proceeds greatly after a large disturbance of the forests. Such a disturbance occurred in 1983. A large typhoon directly hit the Ogasawaras and did much damage not only to houses but also to the nature (Shimizu, 1984). Many trees fell down, making large canopy gaps. Crowns of evergreen trees were blown off in a mesic forest on Hahajima (Fig. 8). Typical pioneer species such as *Trema orientalis*, *Fagara boninensis* and *Sambucus javanica* var. *formosana* emerged all at once and covered the ground after the typhoon (Shimizu, 1987, 1994).

6. History of Development

The islands history goes back to 1830, when the first immigrants arrived: five western people with about 20 Polynesians. After the islands became Japanese territory in 1876, many Japanese immigrants came to settle the islands.

The islanders destroyed the Ogasawaran nature by felling useful woods, cultivating fields, collecting fuel, killing animals for food and so on. We can only imagine the virgin forest prior to human settlement

from some pictures drawn by voyagers (Kittlitz, 1844). A precious wood, *Morus boninensis*, was almost eradicated at that time and it is on the brink of extinction. An albatross (*Diomedea albatrus*) disappeared from the islands due to the feather trade. Sea turtles and whales were captured for food and greatly decreased. Introduced cats went wild and may have caused the extinction of endemic birds (Funakoshi, 1992).

All land where cultivation was possible was changed to sugarcane fields until 1910, after which they were changed to cultivated fields of vegetables and foliage plants to sell to the mainland in the days before 1945 (Kurata, 1983). The maximum population of the islands in the past was 7,711 in 1944.

The Ogasawaras were under U.S. governmental administration from the end of World War II to their return to Japan in 1968. Islanders were forced to evacuate to the mainland of Japan in 1944 and they were not allowed to come back during the reign of the U.S., so the islands almost returned to an uninhabited condition. *Pinus luchuensis* and *Schima mertensiana* invaded the abandoned fields during this period and made a vast secondary forest. *Leucaena leucocephala* (introduced sp.) also spread to vacant lots around the village area.

Construction of a new village started in 1968. The former inhabitants came back to the islands and newcomers joined them to make a village. At the same time, most of the islands were designated a national park. During the past 30 years, however, the forests were destroyed again for construction of roads, bridges, parking lots, houses and cultivated fields. Some rare plant communities were disturbed by the construction of promenades and rest stations for tourists. Fresh water creatures were also killed because riversides were lined with concrete walls.

The present population is about 2,400. A passenger ship connects Chichijima with Tokyo once a week (26 hours in each direction).



a



b

Fig. 8 Scenery of a mesic forest at Sekimon, Hahajima.
a. Just after the typhoon in 1983, b. Ordinary years.

7. Invasion of Alien Species

The creatures of oceanic islands are gentle in nature and inferior in competition compared with continental ones, because the islands are free of powerful predators or large herbivores (Carlquist, 1974). Introduced plants and animals easily go wild in such conditions, and cause serious damage to native species, which cannot be imagined on the species rich continent. Once endemic species disappear from the island, they will never recover again, because there is no refuge on a small island.

Many foreign plants and animals were introduced to the Ogasawaras from the first settlement, and many species have gone wild. Introduced trees (*Leucaena leucocephala*, *Pinus luchuensis*, *Bischofia javanica*, *Casuarina equisetifolia*, *Psidium cattleianum*), weeds (*Lantana camara*, *Stachytarpheta jamaicensis*, *Bidens pilosa*), a goat (*Capra aegarus*), a rat (*Rattus rattus*), a mouse (*Mus musculus*), a lizard (*Anolis carolinensis*), a toad (*Bufo marinus*), an African giant snail (*Achatina fulica*), a honey bee (*Apis mellifera*) and a termite (*Coptotermes formosanus*) are the main invaders to the Ogasawaras (Toyoda, 1981; Yabe, 1992; Hasegawa, 1992; Koyano & Takeuchi, 1992; Kato, 1992b).

Bischofia javanica (Euphorbiaceae) of SE Asian origin was introduced as an afforestation tree before 1905. It extended its distribution gradually from the afforestation sites, and after the large typhoon disturbance of 1983 rapidly spread to a wide range of

Hahajima.

Bischofia javanica has favorable features in competition with native species, such as rapid growth of seedlings and saplings, vigorous sprouting ability, shade-tolerant ability of juveniles, a large quantity of seeds for bird dispersal and to be buried under ground (Tanimoto & Toyada, 1996; Yamashita, 2002). Therefore, seedlings which germinate in canopy gaps grow rapidly and occupy the place securely. Native species are driven out gradually from the forest, and a pure *Bischofia* forest finally comes into being (Fig. 9) (Shimizu, 1988).

Bischofia javanica does not become a dominant tree in SE Asian forests, maybe because competition with herbivore insects, parasitic diseases and more shade-tolerant species control the number of *Bischofia* individuals.

The Forestry Agency carried out an investigation of *Bischofia*'s ecology and physiology in 1993, and then set up a test area to eradicate it on Mt. Kuwanoki of Hahajima in 1994. Large *Bischofia* trees were girdled instead of felling to avoid rapid environmental change. The trees with this treatment died after several years, though it was necessary to cut sprouts emerging from the treated portion. Juveniles of native species which were raised in a nursery on the mainland were transplanted under the canopy of dead *Bischofia* trees. The first step of the eradication project was just taken in 2002.

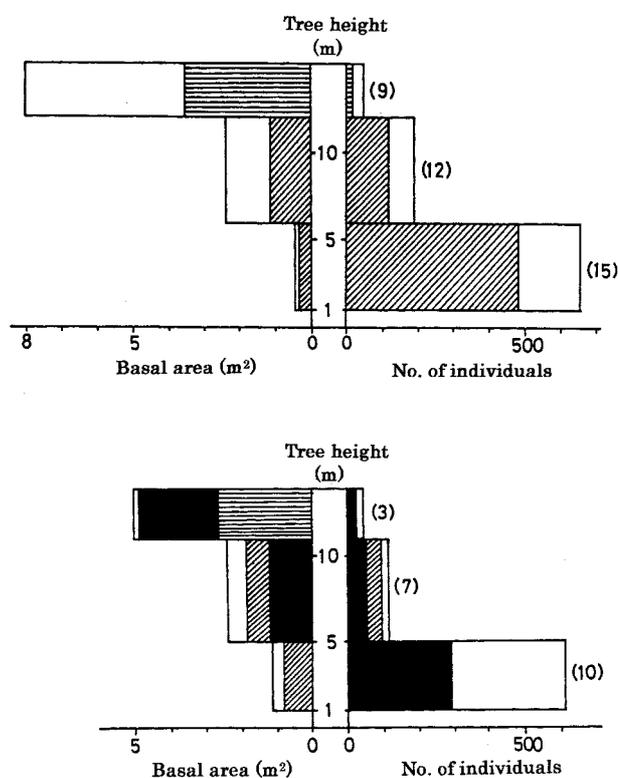


Fig. 9 Comparison of forest structure between *Bischofia*-free (upper) and *Bischofia*-invaded (lower) forests. Black part indicates *Bischofia*. (Cited from Shimizu, 1988)

8. Eradication of Feral Goats

Goats were released in the field in the early days of settlement and soon became wild. At the return of the islands in 1968, feral goats on small islets were eradicated. Vegetation recovered greatly in Minamijima after the eradication of feral goats in 1972 (Fig. 10) (Toyoda *et al.*, 1994). Feral goats were found on seven islands in the 1990s.



a



b



c

Fig. 10 Vegetation recovery at Minamijima after eradication of feral goats in 1972.
a. 13 years later, b. 22 years later, c. 30 years later.

Three islands of the Mukojima-retto (Mukojima, Nakoudojima, Yomejima) were inhabited and stock farms were run in part before 1945. After the islands became uninhabited, feral goats bred uncontrolled. The goat population counted in 1991 reached about 1,500 in total (Japanese Wildlife Research Center, 1992). According to an earlier report and vegetation map published before 1945, these islands were originally covered with dense forests, but they had changed to a vast grassland at the time of their return in 1968. In particular, soil erosion occurred and basal rock was exposed over a wide area in Nakoudojima (Fig. 11) (Japanese Wildlife Research Center, 1992; Shimizu, 1993).

Feral goats eat grasses and herbs around cliffs (their favorite habitat) and exterminate rare plant species. As their numbers increase, they eat all seedlings and saplings of tree species under the canopy of forests. Consequently, the forest floor becomes empty just like a park. When canopy trees die and fall to the ground as a result of typhoon damage, renewal does not happen, because there are no juveniles which would fill the vacant gaps. Grass invades the forest gaps and spreads gradually to make a grassland in the end. Feral goats destroy the island ecosystem completely (Shimizu, 1993).

The Environment Agency (at that time) carried out field research on feral goat influence on the vegetation in the Ogasawaras in 1991 (Japanese Wildlife Research Center, 1992), and asked the Tokyo Metropolitan Government (TMG) to eradicate feral goats and to restore the vegetation on the Mukojima-retto in 1992. The TMG started investigating how to eradicate feral goats. Actual extermination began on Nakoudojima in 1997, and ended in 1999, removing all feral goats (417 in total) (Fig. 12). Further eradication was accomplished successfully on Yomejima and Mukojima in 2000 and 2002, respectively (Natural Environment Research Center, 2002).



Fig. 11 Destruction of ecosystem by feral goats at Nakoudojima.

The TMG is conducting a project to restore the vegetation on Nakoudojima. Grasses are growing very well after the feral goats were removed, but it will take a long time for a forest like that of the old days to recover.



Fig. 12 Capture of feral goats at Nakoudojima in 1997.

9. Conservation of Endangered Species

Many endemic plants and animals of these islands are on the verge of extinction at present. The Japanese Red Data Book of Plants mentions 113 plant species from the Ogasawaras (Shimizu, 1999a). This means about 80% of the endemic species of the Ogasawaras are endangered now. Why? Shimizu (1995) proposed 10 causal factors as follows: deterioration of habitats by long-term environmental fluctuation (loss of cloud zone), logging of particular tree species, destruction and decline of habitats by humans, illegal collection by humans, unusual climate (drought and typhoon damage), attack of insects or pests, damage by introduced animals, competition with introduced plants, loss of pollinators and hybridi-

zation with introduced relatives.

According to a monitoring study in a *Distylium-Schima* dry forest, some endangered shrubby species such as *Pittosporum chichisimense* and *Callicarpa glabra* clearly decreased from 1976 to 1997 (Fig. 13). The recent dry climate (decrease of annual precipitation and frequent occurrence of drought) was speculated as the main reason, though several factors may have been involved (Shimizu, 1999b).

The Botanical Garden of the University of Tokyo has been carrying out propagation of endangered species of the Ogasawaras (Shimozono & Iwatsuki, 1986; Iwatsuki & Shimozono, 1989; Iwatsuki, Shimozono & Hirai, 1993). They succeeded in reproducing some critically endangered species in the greenhouse such as *Rhododendron boninensis*, *Melastoma tetramerum* and *Metrosideros boninensis*. Furthermore, they are planting saplings of these species in the field in the Ogasawaras. The TMG supported this propagation project financially from 1988 to 1993, and the Ministry of Environment took over the project from 1994. A local NPO is helping with the field work. Planted trees grew well in some places, but failed to grow in other places. Even if planted trees succeeded in taking root at the site, regeneration by itself has not been successful yet (Shimozono, personal communication). It is difficult to restore natural populations in their original habitats.

As for one endemic and critically endangered dove, *Columba janthina nitens*, the TMG captured three individuals in 2001 and they are kept in the Ueno Zoo to reproduce artificially. Field research for conservation is being continued for other endangered animals such as the fox bat (*Pteropus peslaphon*) and two land birds (*Buteo buteo toyoshimae* and *Apalopteron familiaris*).

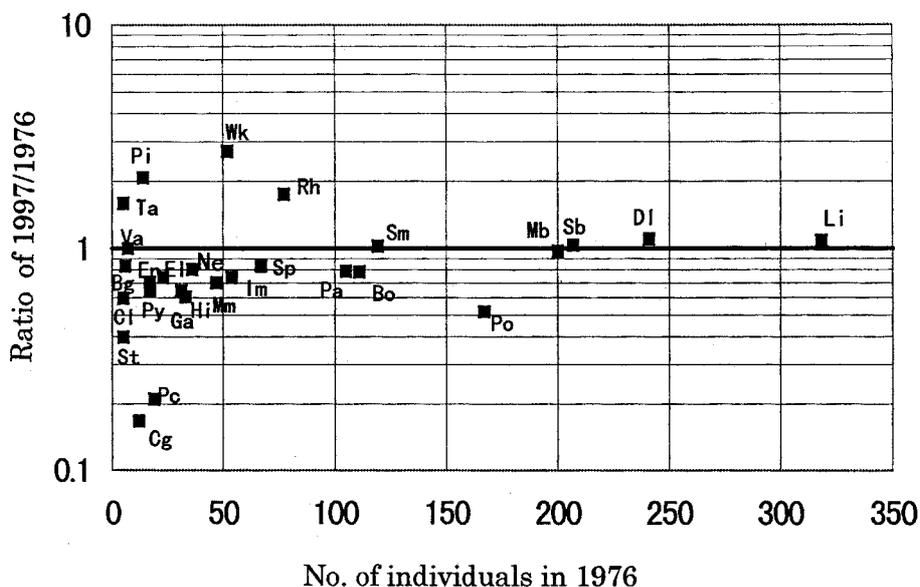


Fig. 13 Change of the number of individuals from 1976 to 1997 in a dry forest. Cg: *Callicarpa glabra*, Pc: *Pittosporum chichisimense*. (Cited from Shimizu, 1999b)

10. Withdrawal of Airport Plan

The TMG proposed an Ogasawara Airport Plan in 1989. It called for construction of a 1,500 m runway and related facilities on Anijima for medium-sized jet planes. As Anijima (a neighbor to Chichijima) is the only island which was never inhabited in the past, pristine dry forests remain all over the island.

We set up a researcher's group just after the TMG's proposal. We carried out our own assessment of Anijima's biota in 1991 and criticized the plan. Our research revealed that Anijima held many endangered plants and animals, some of which had already disappeared from other islands (see articles in *WWFJ Science Report Part1*, 1992). This means the island ecosystem remains intact on Anijima. We showed this fact using an index of wilderness (Fig. 14) (Shimizu *et al.*, 1991). The Ecological Society of Japan and Pacific Science Association made resolutions for protection of Anijima and reconsideration of the airport plan in 1991 (Ogasawara Natural Environment Study Group, 2002).

As the Environment Agency (at that time) appealed for reconsideration of the Anijima plan in 1996, the TMG set up a committee of researchers to assess proposed sites. The committee chose nine proposed sites from four islands excluding Anijima, and the TMG adopted Mt. Shigure of Chichijima as a new

airport site in 1998. An environmental assessment of the Mt. Shigure plan started in 1999, and the result (Interim Report) was announced officially in May, 2001. According to the report, many rare and important endemic species which were designated as Japanese natural monuments or endangered species in the Japanese Red Data Book dwell on Mt. Shigure and its circumference. The last single wild individual of *Rhododendron boninensis* is within the construction area. If the airport construction were put into practice, fatal damage would be brought on the Ogasawaran nature.

The TMG accepted the result and retracted the Mt. Shigure plan in November, 2001. It is expected that no large-scale airport plan will be realized for the time being. Instead of airport construction, a new type of ship, the Techno Super Liner (TSL), is scheduled to be introduced in 2005. It will connect Chichijima and Tokyo in 16-17 hours.

Oceanic islands are comparable to a "natural laboratory of evolution." Many natural experiments are going on in "the Oriental Galapagos," too. We will be able to get valuable lessons about coexistence of man and nature by observing those natural experiments carefully.

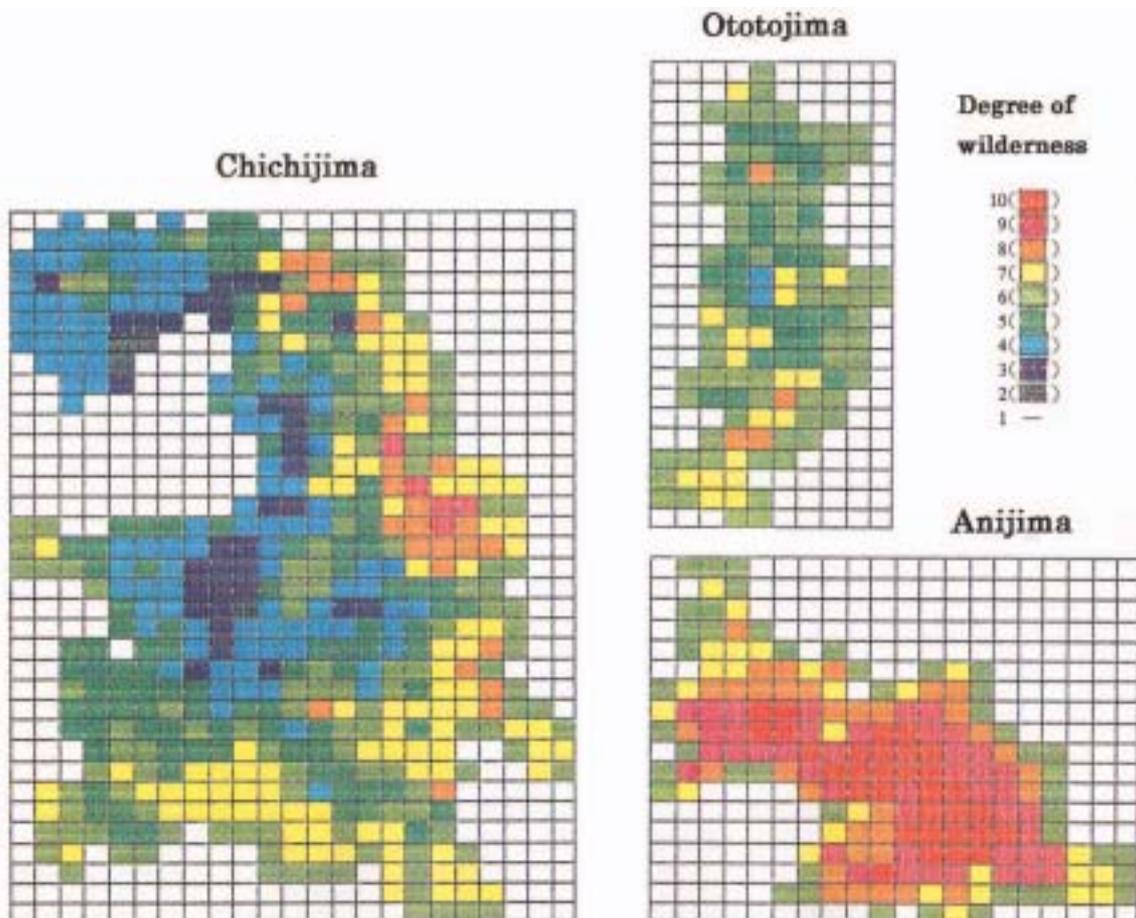


Fig. 14 Degree of wilderness on three islands of the Chichijima-retto. Grade 10 is the best. (Cited from Shimizu *et al.*, 1991)

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