HABITAT DIFFERENCES AND SPATIAL DISTRIBUTION PATTERNS OF MARITIME STRAND FOREST AND ADJACENT INLAND FOREST ON SUBTROPICAL IRIOMOTE ISLAND, SOUTHERN JAPAN

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Abstract. The habitat differences and spatial distribution patterns of maritime strand-forest and adjacent inland-forest species were investigated on Iriomote Island, to predict future coastal-forest structure and environmental change dynamics. Forest types were classified into the following three types: beach scrub, strand forest, and adjacent inland forest. The number of co-dominant species in the three vegetation zones were significantly different from each other, based on dominance analysis. Many coastal species coexisted in adjacent inland forest as co-dominant species. Consequently, inland forest in this study might be a primary successional stage that was formed by gap creation in strand forest. Soil water content, soil texture (siltation rate), and relative light intensity (RLI) were extracted by canonical correspondence analysis (CCA) as important factors determining the species habitat differences. Small differences in elevation and soil salinity between research quadrats were not found to be a significant factor determining species distribution. As a result, we suggest that change of light and soil water conditions on the forest floor, due to catastrophic disturbances (e.g., multiple tree falls during typhoons) rather than topographic heterogeneity, decide the small-scale changes in forest structure and vegetation zonation. *Accepted 2 July 2007*.

Key words: canonical correspondence analysis, co-dominant species, habitat differences, Iriomote Island, maritime strand forest, spatial distribution, vegetation zonation.

INTRODUCTION

Tree plantation has been extensively conducted along the Japanese coastline, especially with *Pinus densiflora* Sieb. et Zucc. and *Pinus thunbergii* Parl. in the temperate zone and *Casuarina equisetifolia* Forster in the subtropical zone. The main objectives were to reduce severe coastal disturbances, such as sand movement, and to block the penetration of salt spray and strong sea wind further inland. Hence maritime forests remaining in a natural condition are currently rarely found in Japan. It is important to accumulate ecological information on the remaining natural vegetation because, as Schemske *et al.* (1994) showed, biological information on natural vegetation is necessary for developing recovery guidelines for rare species, and the information should include an assessment of the biological status of species and identification of life-history stages. Studies of maritime strand forests have

been conducted mainly for studying the relationship between vegetation changes and natural disturbances in temperate and boreal zones (e.g., Gresham *et al.* 1991, Hook *et al.* 1991, Hayden *et al.* 1995, Shao *et al.* 1995, Conner *et al.* 2005). Gardner *et al.* (1992), Bellis (1995), and Hayden *et al.* (1995) reported that the most severe impacts on vegetation types and their distribution involved hydrogeomorphological processes, such as water-table elevation and groundwater salinization due to surges. These factors may act alone or in combination with others, and each impact will be influenced by local environmental conditions. Thus differences in species composition are related to local variations in abiotic conditions (Hayasaka & Fujiwara 2005), such as seawater salinity, soil water content and texture, and beach management methods. Maekawa & Nakagoshi (1997), Rodgers & Parker (2003), and Conner *et al.* (2005) reported that increased sunlight, raised water table, and human disturbances accelerate invasion of alien species. Masaka *et al.* (2004) also described how shade-intolerant species cannot regen-
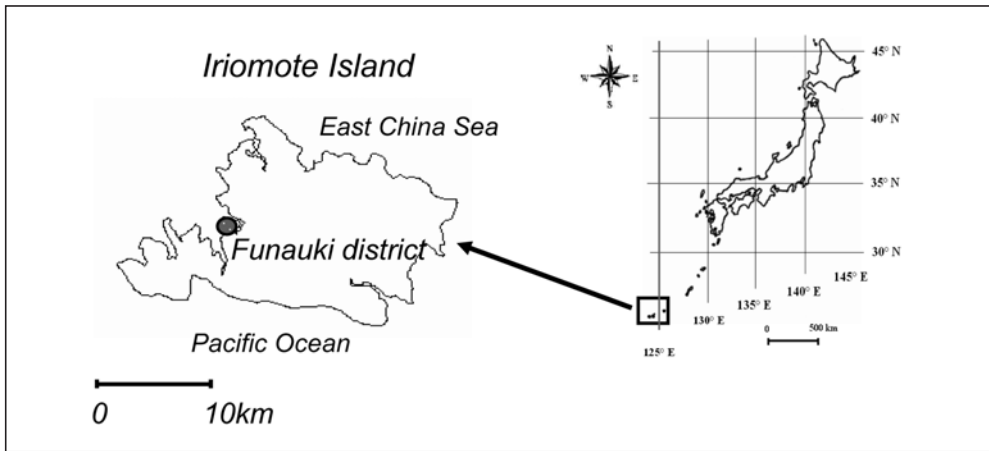
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FIG. 1. Location of the study site, in the Funauki district of Iriomote Island, Okinawa Prefecture, Japan.

erate under the canopy. There are few studies on spatial distribution patterns and coexistence mechanisms of maritime forest species. The reasons are that: 1) maritime forests are narrow; 2) many coastal forests have been planted and extensively fragmented by population pressure escalation and land use, and 3) many researchers have focused on mangrove ecology (e.g., McKee 1995, Clarke *et al.* 2001, Clarke 2004, Dahdouh-Guebas *et al.* 2005).

We studied the habitat differences and spatial distribution patterns of maritime and adjacent inland forest species on the subtropical island of Iriomote, in southern Japan. The goals of this study are to explain the spatial distribution patterns of various species in the different vegetation zones and to predict future maritime forest structure and dynamics related to environmental change.

METHODS

Study site. The study was carried out on Iriomote Island, Okinawa Prefecture, southern Japan (Fig. 1). Iriomote is located between 24°15' and 24°20'N, and 123°40' and 123°45'E; the study site faces the East China Sea. Iriomote is 322 km² in area and is the largest island in the Yaeyama Islands. Most of the islands are designated as a national park (Iriomote National Park).

The climate is subtropical, with a mean annual temperature of 23.4°C. In winter (from December to February) the average maximum temperature is 21.3°C and the average minimum is 16.1°C. In summer (from June to August) the average highest temperature is 30.9°C and average lowest is 25.3°C. Mean annual precipitation is 2342.3 mm. Kira's (1977) Warmth Index is 250.7°C. Iriomote has a monsoonal climate, with southerly winds in summer and northeasterly winds in winter (Japan Meteorological Agency 2001).

We studied a natural maritime forest on the northwestern part of the island (Funauki district: Fig. 1), which is designated as a forest reserve. Floristically, *Scaevola sericea* Vahl. and *Pandanus odoratissimus* Linn. fil., with *Messerschmidia argentea* Johnson, dominate the beach scrub. *Hernandia sonora* Linn., *Calophyllum inophyllum* Linn., *Planchonella obovata* Pierre, and *Cerbera manghas* Linn. occur in the strand forest behind the beach scrub. *Bischofia javanica* Bl., *Fraxinus griffithii* C.B.Clarke, and *Macaranga tanarius* Muell.-Arg. appear in adjacent inland forest, with shrub species such as *Antidesma pentandrum* var. *barbatum* Merr. and *Turpinia ternata* Nakai. Many of these species occur widely from subtropical to tropical regions (Nakamura & Suzuki 1984, Hayasaka & Fujiwara 2005) due to their thalassochory (Nakanishi 1988). Thalassochory is defined as species dispersed by seadrift; their disseminules have a high buoyancy and viability in sea water.

Community structure of three vegetation zones. A rectanglular plot of 0.15 ha (30 m width and 50 m length) encompassing the three vegetation zones was sur-

veyed. The plot was divided into 2 x 2 m quadrats (N = 375). Tree growth was measured based on DBH (diameter at breast height) and tree height. Tree height was used to distinguish trees from shrubs. Trees were classified as follows: seedlings (< 0.3 m), saplings (0.3 m to 1.49 m), and adults (> 1.5 m in height). Adults were measured for DBH and tree height above 1.3 m, and were plotted to ± 0.1 m on the x and y axes (taking measurements perpendicular from strip-division tapes). Where individual plants were multi-stemmed (i.e., > 1 stem of 1 cm DBH) each stem was measured separately, but for the subsequent analyses only the largest stem was used. Saplings were measured for GBH (girth at breast height), height, and position in the plot. Seedlings were measured for height and position in the plot. Shrubs were classified as follows: seedlings (< 0.3 m), saplings (0.3 m to 0.99 m), and adults (> 1.0 m in height). Determination of co-dominants in the quadrats was done using dominance analysis (Ohsawa 1984).

In a community dominated by a single species, its relative dominance should be 100 %. If two species share a habitat, the relative dominance of each should ideally be 50 %. If there are three co-dominants in a habitat, it should be 33.3 %. The number of dominant species represents the least deviation (d) between the actual relative dominance values and the expected percentage share of the corresponding co-dominant number model. The deviation (d) is calculated by the following equation:

$$d = 1/N \left\{ \sum_{i \in T} (x_i - \overline{x})^2 + \sum_{j \in U} x_j^2 \right\}$$

where x_i is the actual percentage share (here relative basal area (BA) or stem density is adopted) of the top species (T), i.e., in the one dominant of the one-dominant model, or the two dominants of the two-dominant model, and so on; $\overline{x}$ is the ideal percentage share based on the model as mentioned above; and x_j is the percentage share of the remaining species (U). N is the total number of species (Ohsawa 1984).

Abiotic factors. The following abiotic data were collected to record environmental factors that could determine species distribution and establishment: soil pH and water content, soil salinity, sand compaction, relative light intensity (RLI), leaf area index (LAI), soil texture, and micro-elevation. Soil pH was measured by an electric pH meter (Horiba, Type D-11, Japan). Soil water tester (DM-18, Takeyama electric works, Japan) was used to measure water content. Sea con-

centration meter (ATAGO, S/ Mill-E, Japan) was used to measure soil salinity 10 cm below the surface, which is the depth of average groundwater level of the three vegetation zones in this study site. Sand compaction was measured using a soil hardness tester (Yamaoka System Hardness Tester, Type A-0858, Japan). This parameter indicates sand compaction, expressed as pressure (kg/cm^2) (Matsuo 1989). Hemispherical photographs for RLI and LAI, measured using LIA for Win32 (LIA32: http://www.agr.nagoya-u.ac.jp/%7Eshinkan/LIA32/index.html), were taken at a height of 1.5 m. Soil texture was classified based on grain diameter: fine gravel above 2.0 mm; coarse sand from 2.0 to 0.2 mm; fine sand from 0.2 to 0.02 mm; and silt under 0.02 mm. Plane-table survey of the plot (30 x 50 m) was done at intervals of 1.0 m in both the x and y directions using a transit compass (Tracon LS-25, Ushikata, Japan).

Data analysis. The relationships between spatial distribution patterns and abiotic factors were analyzed using canonical correspondence analysis (CCA) (ter Braak 1986, 1994, 1995). Before the CCA was carried out, we excluded correlated factors in order to reduce multi-colinearity. The independent variable was species population size, and the dependent variables were environmental conditions of all quadrats. Habitat differences between dominant species and quadrats were tested using ANOVA corrected for multiple comparisons (Tukey-Kramer test).

RESULTS

Community structure. There were 683 adults, 1066 saplings, and 21780 seedlings of 32 tree species in this study plot. Species ecological traits are shown in Table 1. Co-dominant species of the three vegetation zones, based on BA, are shown in Table 2 (left). Five co-dominant species were defined in the beach scrub zone. *Pandanus odoratissimus* was the most abundant species (44.36 % of total BA), followed by *Scaevola sericea* (15.12 %), *Messerschmidia argentea* (10.34 %), *Hibiscus tiliaceus* L. (9.7 %), and *Guettarda speciosa* L. (7.91 %). Although co-dominance by stem density (D) showed a similar tendency (Table 2, right), the density of *Messerschmidia argentea* (3.03 %) and *Guettarda speciosa* (2.02 %) was low and *Planchonella obovata* was more abundant (10.10 %). Most of the *Planchonella obovata* population were unhealthy individuals. *Hernandia sonora*, *Calophyllum inophyllum*, and *Cerbera manghas* were co-dominant species, based on BA, in the strand forest. *Hernandia sonora* was the

TABLE 1. Numbers of individuals in each growth stage for each species in the study plot (0.14 ha), plus selected species characteristics. Asterisks show the dominant species that are studied in detail.

Nomenclature	Distribution range	Life form	Flower type	Seed size (mm)	Fruit size (mm)	Fruit type	Number of adults total	Male	Female	Unsexed	Number of saplings	Number of seedlings
Euonymus japonicus (Eu.j.)	Japan ~ Taiwan	Nanophanerophyte	Hermaphrodite	6.5±0.4	8.3±0.7	Capsule	17	–	–	–	8	13
*Rhaphiolepis umbellata (Rh.u.)	Japan	Nanophanerophyte	Hermaphrodite	7.3±0.6	10.0-	Drupe	21	–	–	–	38	168
Psychotria manillensis (Ps.m.)	southern Japan	Nanophanerophyte	Hermaphrodite	6.6±0.2	10.0-12.0	Drupe	11	–	–	–	39	145
Callicarpa japonica (Ca.j.)	southern Japan ~ Taiwan	Nanophanerophyte	Hermaphrodite	3.1±0.3	4.0-5.0	Drupe	11	–	–	–	9	18
Messerschmidia argenta (Me.a.)	Subtropical ~ Tropical	Nanophanerophyte	Hermaphrodite	3.4±0.2	4.0-	Drupe	2	–	–	–	0	0
*Scaevola sericea (Sc.s.)	Subtropical ~ Tropical	Nanophanerophyte	Hermaphrodite	5.7±0.4	8.0-10.0	Drupe	10	–	–	–	2	17
*Hibiscus tiliaceus (Hi.t.)	Subtropical ~ Tropical	Microphanerophyte	Hermaphrodite	2.8±0.2	–	Capsule	30	–	–	–	6	0
*Turpinia ternata (Tu.t.)	southern Japan ~ Taiwan	Microphanerophyte	Hermaphrodite	4.9±0.3	10.0-	Sap fruit	47	–	–	–	31	31
*Cerbera manghas (Ce.m.)	Subtropical ~ Tropical Asia	Microphanerophyte	Hermaphrodite	–	43.2±1.5	Sap fruit	45	–	–	–	95	116
Guettarda speciosa (Gu.s.)	Subtropical ~ Tropical	Microphanerophyte	Hermaphrodite	–	20.0-30.0	Drupe	2	–	–	–	0	0
Morinda citrifolia (Mo.c.)	Subtropical ~ Tropical	Microphanerophyte	Hermaphrodite	8.0-	20.0-40.0	Drupe	4	–	–	–	0	5
Premna corymbosa var. obtusifolia (Pr.c.)	Subtropical ~ Tropical	Microphanerophyte	Hermaphrodite	–	3.0-4.0	Drupe	15	–	–	–	8	2
Ficus microcarpa (Fi.m.)	Subtropical ~ Tropical	Mesophyte	Hermaphrodite	1.0±0.0	–	Achene	0	–	–	–	2	9
*Hernandia sonora (He.s.)	Subtropical ~ Tropical	Mesophyte	Hermaphrodite	–	30.0-40.0	Drupe	32	–	–	–	77	854
Persea thunbergii (Pe.t.)	Japan ~ China	Mesophyte	Hermaphrodite	9.0±0.4	10.0-	Sap fruit	0	–	–	–	16	148
*Planchonella obovata (Pl.o.)	Subtropical ~ Tropical	Mesophyte	Hermaphrodite	5.3±0.4	12.0-	Sap fruit	38	–	–	–	207	463
Pongamia pinnata (Po.p.)	Subtropical ~ Tropical	Mesophyte	Hermaphrodite	–	50.0-70.0	Capsule	2	–	–	–	0	0
*Pittosporum tobira (Pi.t.)	Japan ~ China	Nanophanerophyte	Dioecious	2.4±0.2	10.0-15.0	Capsule	13	3	5	5	30	65
*Antidesma pentandrum var. barbatum (An.p.)	Okinawa ~ Taiwan	Nanophanerophyte	Dioecious	4.1±0.2	5.0-	Drupe	162	20	16	126	104	242
Arenga tremula (Ar.t.)	Okinawa	Nanophanerophyte	Dioecious	10.0-	10.0-15.0	Drupe	32	–	–	–	0	0
Cycas revoluta (Cy.r.)	southern Japan ~ China	Nanophanerophyte	Dioecious	43.1±1.1	–	Drupe	2	–	–	–	5	8
*Diospyros maritima (Di.m.)	Subtropical ~ Tropical	Microphanerophyte	Dioecious	9.4±0.2	20.0-30.0	Sap fruit	31	5	10	16	191	267
Macaranga tanarius (Ma.t.)	Subtropical ~ Tropical	Microphanerophyte	Dioecious	5.1±0.4	10.0-12.0	Capsule	5	–	–	–	1	4
Morus australis (Mo.a.)	Okinawa ~ China	Microphanerophyte	Dioecious	–	10.0-15.0	Achene	10	–	–	–	17	19
*Pandanus odoratissimus (Pa.o.)	Subtropical ~ Tropical	Microphanerophyte	Dioecious	7.3±0.6	10.0-	Drupe	57	10	21	26	43	146
*Fraxinus griffithii (Fr.g.)	Okinawa ~ India	Mesophyte	Dioecious	8.6±0.5	27.2±1.4	Samara	18	2	6	10	44	17652
Neolitsea sericea (Ne.s.)	Japan ~ China	Mesophyte	Dioecious	9.4±0.3	10.0-	Sap fruit	0	–	–	–	1	73
*Bischofia javanica (Bi.j.)	Subtropical ~ Tropical	Mesophyte	Dioecious	4.4±0.2	10.0-15.0	Drupe	27	6	8	13	6	9
Rhus succedanea (Rh.s.)	central Japan ~ China	Mesophyte	Dioecious	5.5±0.2	8.9±0.5	Drupe	7	–	–	–	1	1
Garcinia subelliptica (Ga.s.)	Okinawa	Mesophyte	Dioecious	21.7±1.7	25.0-35.0	Drupe	11	–	–	–	7	19
*Calophyllum inophyllum (Ca.i.)	Subtropical ~ Tropical	Mesophyte	Submonoecious	28.2±1.3	30.0-40.0	Drupe	12	–	–	–	47	1243
Diospyros ferra var. buxifolia (Di.f.)	Subtropical ~ Tropical	Microphanerophyte	Polygamous	11.0±0.9	8.0-14.0	Sap fruit	9	–	–	–	31	43
Total							683				1006	21780

* Species life form was categorized into dormancy forms of Raunkiaer (1934) and Numata (1947). Seed and fruit characters were classified by Nakayama et al. (2000) and Hatsusima (1975). Plants were classified as shrub (nanophanerophyte: N), micro (microphanerophyte: M), sub-canopy tree (microphanerophyte: M), and canopy tree (mesophyte: MM).

TABLE 2. Floristic composition of the tree layer, including saplings and adults, in the three vegetation zones in the study plot. *n* indicates the number of research quadrats (2 x 2 m).

Basal Area (BA)			Stem Densitiy (*D*)			
Species name	BA (cm²) of the site	BA/ha (cm²/ha)	% of total BA	Species name	*D* of the zone	*D*/ha	% of total *D*
Beacch scrub zone (30.0 m x 8.0 m) (*n* = 60)							
Pandanus odoratissimus	2431.5	101318.6	44.36	*Pandanus odoratissimus*	43	1791.8	43.44*
Scaevola sericea	828.5	34522.0	15.12*	*Hibiscus tiliaceus*	18	750.1	18.18*
Messerschmidia argentea	566.7	23614.7	10.34*	*Scaevola sericea*	10	416.7	10.10*
Hibiscus tiliaceus	531.6	22152.6	9.70*	*Planchonella obovata*	10	416.7	10.10*
Guettarda speciosa	433.5	18062.7	7.91*	*Hernandia sonora*	4	166.7	4.04
Calophyllum inophyllum	253.0	10542.4	4.61	*Arenga tremula*	4	166.7	4.04
Planchonella obovata	172.7	7197.1	3.15	*Messerschmidia argentea*	3	125.0	3.03
Hernandia sonora	141.8	5910.9	2.59	*Euonymus japonicus*	3	125.0	3.03
Euonymus japonicus	121.6	5066.1	2.22	*Guettarda speciosa*	2	83.3	2.02
Arenga tremula	–	–	–	*Calophyllum inophyllum*	2	83.3	2.02
Strand forest zone (30.0 m x 18.0 m) (*n* = 135)							
Hernandia sonora	18245.6	347578.2	52.29*	*Antidesma pentandrum* var. *barbatum*	68	1295.4	18.00*
Calophyllum inophyllum	4815.7	91739.4	13.80*	*Cerbera manghas*	46	876.3	12.17*
Cerbera manghas	3217.0	61283.7	9.22*	*Diospyros maritima*	45	857.3	11.90*
Bischofia javanica	1976.4	37651.4	5.66	*Planchonella obovata*	43	819.2	11.38*
Hibiscus tiliaceus	1290.2	24579.3	3.70	*Pandanus odoratissimus*	32	609.6	8.47*
Pandanus odoratissimus	1115.2	21244.6	3.20	*Hernandia sonora*	31	590.6	8.20*
Pongamia pinnata	1026.1	19547.0	2.94	*Arenga tremula*	21	400.1	5.56*
Garcinia subelliptica	507.3	9664.5	1.45	*Hibiscus tiliaceus*	17	323.9	4.50*
Antidesma pentandrum var. *barbatum*	489.5	9324.6	1.40	*Euonymus japonicus*	14	266.7	3.70
Diospyros maritima	467.1	8898.1	1.34	*Garcinia subelliptica*	12	228.6	3.17
Planchonella obovata	462.6	8813.4	1.33	*Calophyllum inophyllum*	10	190.5	2.65
Euonymus japonicus	396.6	7555.8	1.14	*Diospyros ferra* var. *buxifolia*	9	171.5	2.38
Turpinia ternata	357.8	6815.2	1.03	*Bischofia javanica*	8	152.4	2.12
Premna corymbosa	257.3	4901.9	0.73	*Morus australis*	7	133.4	1.85
Morus australis	229.2	4365.4	0.65	*Turpinia ternata*	4	76.2	1.06
Diospyros ferra var. *buxifolia*	30.6	583.1	0.09	*Premna corymbosa*	3	57.2	0.79
Fraxinus griffithii	8.8	167.8	0.03	*Fraxinus griffithii*	3	57.2	0.79
Neolitsea sericea	0.3	5.4	0.00	*Pongamia pinnata*	2	38.1	0.53
Arenga tremula	–	–	–	*Cycas revoluta*	2	38.1	0.53
Cycas revoluta	–	–	–	*Neolitsea sericea*	1	19.1	0.26
Inland forest zone (30.0 m x 16.0 m) (*n* = 135)							
Fraxinus griffithii	5361.7	108307.1	32.23*	*Antidesma pentandrum* var. *barbatum*	94	1898.8	23.04*
Bischofia javanica	3865.1	78075.9	23.23*	*Turpinia ternata*	58	1171.6	14.22*
Rhus succedanea	1608.7	32496.7	9.67*	*Fraxinus griffithii*	27	545.4	6.62*
Cerbera manghas	1379.4	27863.2	8.29*	*Diospyros maritima*	26	525.2	6.37*
Macaranga tanarius	871.1	17596.7	5.24*	*Cerbera manghas*	24	484.8	5.88*
Turpinia ternata	699.7	14133.5	4.21	*Planchonella obovata*	24	484.8	5.88*
Antidesma pentandrum var. *barbatum*	624.4	12612.0	3.75	*Rhaphiolepis umbellata*	21	424.2	5.15*
Morinda citrifolia	486.4	9825.2	2.92	*Bischofia javanica*	20	404.0	4.90*
Pandanus odoratissimus	512.5	10353.1	3.08	*Premna corymbosa*	16	323.2	3.92*
Morus australis	340.0	6867.0	2.04	*Pandanus odoratissimus*	15	303.0	3.68*
Rhaphiolepis umbellata	278.6	5627.0	1.67	*Pittosporum tobira*	13	262.6	3.19*
Premna corymbosa	276.5	5584.8	1.66	*Callicarpa japonica*	11	222.2	2.70
Diospyros ferra var. *buxifolia*	128.6	2598.0	0.77	*Psychotria manilensis*	11	222.2	2.70
Callicarpa japonica	60.7	1227.0	0.37	*Diospyros ferra* var. *buxifolia*	10	202.0	2.45
Psychotria manilensis	42.3	854.4	0.25	*Morus australis*	8	161.6	1.96
Diospyros maritima	40.2	811.7	0.24	*Rhus succedanea*	7	141.4	1.72
Planchonella obovata	29.0	586.7	0.17	*Arenga tremula*	7	141.4	1.72
Pittosporum tobira	17.1	346.0	0.10	*Macaranga tanarius*	5	101.0	1.23
Calophyllum inophyllum	13.1	263.6	0.08	*Morinda citrifolia*	4	80.8	0.98
Persea thunbergii	2.4	47.7	0.02	*Calophyllum inophyllum*	4	80.8	0.98
Hibiscus tiliaceus	0.8	15.9	0.01	*Persea thunbergii*	2	40.4	0.49
Arenga tremula	–	–	–	*Hibiscus tiliaceus*	1	20.2	0.25

* Values given for each species are: cm² of basal area (BA) and stem density in each vegetational zone (*D*). Asterisks indicate dominant spec based on BA and *D* using dominance analysis (Ohsawa 1984).
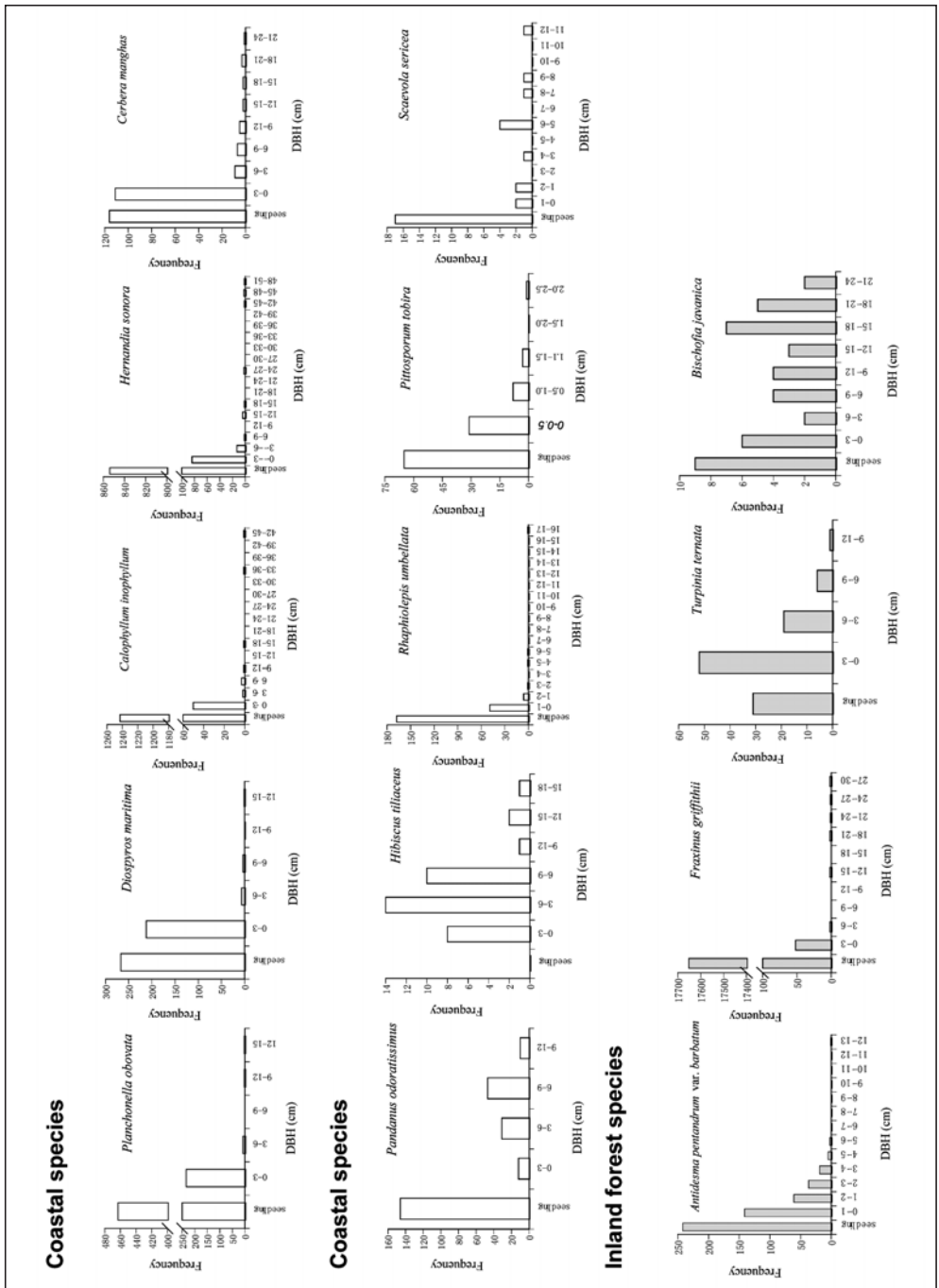
FIG. 2. DBH size-class distributions for 14 dominant species including seedlings. Coastal species are *Ca. i.*, *Ce. m.*, *Rh. u.*, *Di. m.*, *He. s.*, *Hi. t.*, *Pa. o.*, *Pi. t.*, *Pl. o.*, and *Sc. s.*. Inland species are *An. p.*, *Bi. j.*, *Fr. g.*, and *Tu. t.*. DBH distribution was measured at 3-cm intervals for tree species and at 1-cm intervals for shrubs.

most abundant species (52.29 %). On the other hand, there were eight co-dominant species based on stem density. In the adjacent inland forest, there were five co-dominant species based on BA (*Fraxinus griffithii* 32.23 %, *Bischofia javanica* 23.23 %, *Rhus succedanea* L. 9.67 %, *Cerbera manghas* 8.29 %, and *Macaranga tanarius* 5.24 %) and 11 co-dominant species based on stem density. The stem densities of *Antidesma pentandrum* var. *barbatum* (23.04 %) and *Turpinia ternata* (14.22 %) were high in the inland forest zone.

We selected the 14 most dominant species based on a combination of BA and stem density to define forest structure, habitat difference, and spatial distribution patterns. Of these, *Calophyllum inophyllum*, *Cerbera manghas*, *Diospyros maritima*, *Hernandia sonora*, *Hibiscus tiliaceus*, *Rhaphiolepis umbellata* Makino, *Pandanus odoratissimus*, *Pittosporum tobira* Ait., *Planchonella obovata*, and *Scaevola sericea* are coastal species. *Antidesma pentandrum* var. *barbatum*, *Bischofia javanica*, *Fraxinus griffithii*, and *Turpinia ternata* are inland species (Table 2). They were classified into three plant groups: Group I (G I) 'beach scrub' (*Hibiscus tiliaceus*: Hi. t., *Pandanus odoratissimus*: Pa. o., and *Scaevola sericea*: Sc. s.); Group II (G II) 'strand forest' (*Calophyllum inophyllum*: Ca. i., *Cerbera manghas*: Ce. m., *Hernandia sonora*: He. s., *Rhaphiolepis umbellata*: Rh. u., *Pittosporum tobira*: Pi. t., and *Planchonella obovata*: Pl. o.); and Group III (G III) 'inland forest' (*Antidesma pentandrum* var. *barbatum*: An. p., *Bischofia javanica*: Bi. j., *Fraxinus griffithii*: Fr. g., and *Turpinia ternata*: Tu. t.).

DBH size-class distributions including seedlings are shown in Fig. 2. The populations of *Calophyllum inophyllum*, *Hernandia sonora*, *Planchonella ovobata*, and *Fraxinus griffithii* were largely dominated by seedlings rather than young and adult individuals. *Hibiscus tiliaceus*, *Scaevola sericea*, *Bischofia javanica*, and *Turpinia ternata* had more young and adults than seedlings. *Cerbera manghas*, *Pittosporum tobira*, and *Antidesma pentandrum* var. *barbatum* had more even distributions of all sizes. Most species showed a reverse-J pattern of size-class distribution, while *Pandanus odoratissimus*, *Scaevola sericea*, and *Bischofia javanica* exhibited bimodal peaks in size. *Hibiscus tiliaceus* and *Turpinia ternata* showed a bell-shaped distribution. *Hernandia sonora* and *Calophyllum inophyllum* (coastal canopy species) reached about 50 cm DBH. *Bischofia javanica* and *Fraxinus griffithii* (inland pioneer trees) reached about 30 cm DBH.

Factors determining establishment and spatial distribution of the 14 dominant species. Effects of local environmental factors on species distribution, as suggested by CCA, are shown in Fig. 3. The following highly correlated factors were excluded from the results: soil pH, LAI, and soil texture (fine gravel, coarse sand, and fine sand rate). Relative light intensity (RLI) was not analyzed for the adult stage. The first-axis score for adult stages was positively associated with soil water content (0.972 $p < 0.01$), sand compaction (0.517 $p < 0.01$), and siltation rate (0.633 $p < 0.01$). Siltation rate (0.770 $p < 0.01$) was also positively correlated with the second axis. For sapling stages, the first-axis score was negatively associated with soil water content (-0.911 $p < 0.01$) and siltation rate (-0.520 $p < 0.01$) and positively with RLI (0.549 $p < 0.01$). Siltation rate was also positively correlated with the second axis (0.831 $p < 0.01$). For seedling stages, siltation rate was negatively correlated (-0.781 $p < 0.01$) with axis 1, and soil water content (-0.687 $p < 0.01$) was negative as well. RLI (0.493 $p < 0.01$) was positively correlated with axis 2. Small differences in elevation and soil salinity among research quadrats were not found to be significant factors determining habitat difference and spatial distribution of trees in this analysis.

Pandanus odoratissimus, *Scaevola sericea*, and *Calophyllum inophyllum* were positively correlated with RLI. Most inland species were correlated with soil water content, and also with sand compaction in the adult stage. *Cerbera manghas*, *Diospyros maritima*, and *Hernandia sonora* were positively associated with siltation rate in all stages. Most coastal species, especially beach shrubs, were negatively correlated with soil water content and sand compaction in the adult stage.

Habitat differences among the 14 dominant species. It was found that soil water content, soil texture (siltation rate), and relative light intensity (RLI) have an impact on the habitat of the 14 dominant species over the three habitat types, their growth stages, and interactions (Table 3). There was no significant difference in soil water content on the habitat among G I and G III dominant species through all the growth stages. On the other hand, there was a significant difference in soil water content on the habitat among G III species in the seedling stage and G II dominant species (Table 4). There were significant differences in siltation rate and RLI on the habitat of the 14 dominant species in all stages (Tables 5 and 6). Canopy species such as *Calophyllum inophyllum*, *Hernandia sonora*, and *Planchonella obovata* were significantly commoner on drier and less silty sites than the other G II dominant species. In addition, among these spe-
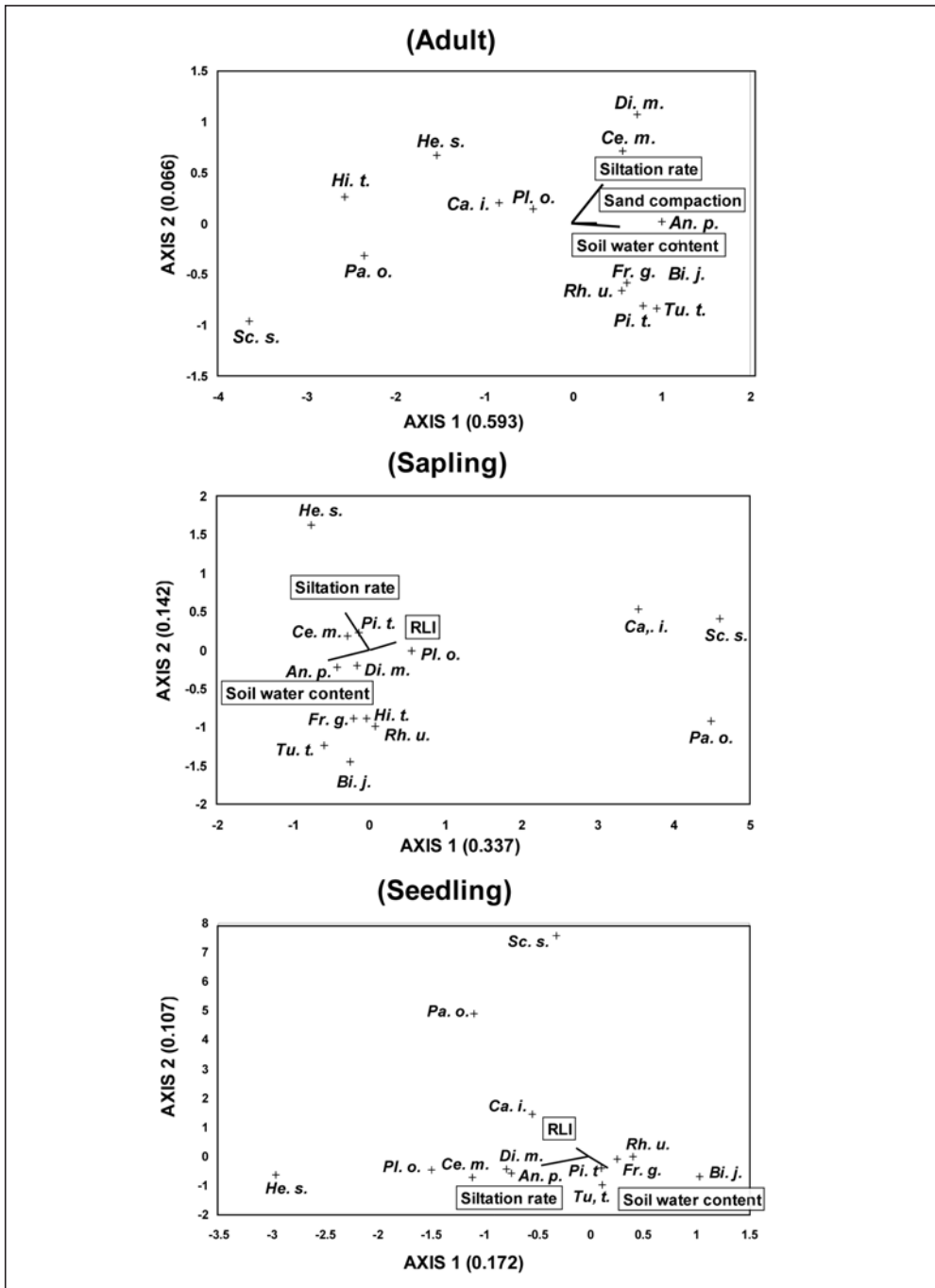
FIG. 3. The relationship between local environmental factors and establishment and spatial distribution between the 14 dominant species over the three growth stages using CCA ordination. Eigenvalues for the axes are shown in brackets.

TABLE 3. Correlation between local environmental factors (soil water content, siltation rate, relative light intensity) and habitat differences between 14 dominant species over the three habitat types, their growth stages, and interactions, using F statistics for ANOVA. The values in brackets show significance probability.

	F value (probability)					
	Species		Stage		Species x Stage	
Soil water content						
Group I (G I)	1.51	(0.223)	1.14	(0.321)	0.26	(0.856)
Group II (G II)	14.55	(0.000)	14.19	(0.000)	5.62	(0.000)
Group III (G III)	4.59	(0.003)	0.75	(0.474)	1.94	(0.071)
Siltation rate						
Group I (G I)	4.95	(0.008)	0.71	(0.491)	1.20	(0.309)
Group II (G II)	10.19	(0.000)	19.35	(0.000)	7.02	(0.000)
Group III (G III)	40.36	(0.000)	1.78	(0.168)	3.50	(0.002)
Relative light intensity						
Group I (G I)	7.07	(0.001)	5.21	(0.023)	3.57	(0.060)
Group II (G II)	4.83	(0.000)	0.02	(0.879)	0.89	(0.471)
Group III (G III)	3.78	(0.010)	0.71	(0.399)	1.33	(0.262)

cies, *Hernandia sonora* and *Planchonella obovata* occurred significantly more often on drier ($p < 0.01$) and less silty ($p < 0.05$) sites as their growth stages progressed (Tables 4 and 5), while *Cerbera manghas* and *Diospyros maritima* showed the opposite tendency (Table 5). *Scaevola sericea* occurred on lower, more silty, and sunnier sites than the other G I species through all the growth stages (Tables 5 and 6). There was no significant difference in siltation rate in the habitat among G III species in the adult stage (Table

TABLE 4. Habitat differences between 14 dominant species over the three habitat types in all growth stages in mean soil water content. Values with different letters are significantly different at the $P < 0.05$ level according to the Tukey-Kramer test. Refer to species names in Table 1.

Group	Stage Species*	Seedling Average	S.D.	P Values > 0.05	Sapling Average	S.D.	P values > 0.05	Adult Average	S.D.	P values > 0.05
	Hi. t.	–	–	–	8.27	0.27	ns	8.39	0.12	ns
G I	*S. s.*	8.46	0.14	ns	8.60	0.42	ns	7.93	0.21	ns
	Pa. o.	8.92	0.09	ns	8.57	0.17	ns	8.60	0.15	ns
	Ca. i.	10.04	0.03	a	10.06	0.16	a	9.60	0.31	ab
	He. s.	10.21	0.03	ab	10.57	0.11	b	9.01	0.17	a
	Pl. o.	10.39	0.04	bc	10.41	0.06	b	9.76	0.14	ab
G II	*Ce. m.*	10.53	0.06	c	10.46	0.07	b	10.42	0.10	c
	D. m.	10.55	0.04	c	10.50	0.05	b	10.52	0.12	c
	R. u.	10.57	0.04	c	10.46	0.09	b	10.50	0.12	c
	Pi. t.	10.67	0.08	c	10.52	0.11	b	10.69	0.17	c
	F. g.	10.49	0.00	a	10.62	0.09	ns	10.49	0.14	ns
G III	*A. p.*	10.54	0.04	a	10.53	0.06	ns	10.70	0.05	ns
	T. t.	10..86	0.11	ab	10.77	0.11	ns	10.71	0.09	ns
	B. j.	11.04	0.22	b	10.83	0.27	ns	10.64	0.13	ns

TABLE 5. Habitat difference between 14 dominant species over the three habitat types in all growth stages in mean siltation rate (soil texture). Values with different letters are significantly different at the $P < 0.05$ level according to the Tukey-Kramer test. Refer to species names in Table 1.

Group	Stage Species*	Seedling Average	S.D.	P Values > 0.05	Sapling Average	S.D.	P values > 0.05	Adult Average	S.D.	P values > 0.05
G I	Hi. t.	–	–	–	0.06	0.02	a	0.08	0.01	b
	S. s.	0.07	0.01	a	0.06	0.03	a	0.05	0.01	a
	Pa. o.	0.10	0.00	b	0.10	0.01	b	0.08	0.01	b
G II	Ca. i.	0.12	0.00	a	0.13	0.01	ab	0.11	0.01	ab
	R. u.	0.12	0.00	a	0.12	0.00	a	0.11	0.01	ab
	Pi. t.	0.12	0.00	ab	0.12	0.00	a	0.11	0.01	ab
	D. m.	0.13	0.00	bc	0.13	0.00	ab	0.14	0.01	b
	Ce. m.	0.14	0.00	c	0.14	0.00	b	0.13	0.01	ab
	Pl. o.	0.14	0.00	c	0.14	0.00	b	0.11	0.01	ab
	He. s.	0.17	0.01	d	0.16	0.00	c	0.10	0.01	a
G III	B. j.	0.11	0.01	a	0.10	0.01	a	0.12	0.00	ns
	F. g.	0.12	0.00	ab	0.12	0.00	ab	0.11	0.00	ns
	T. t.	0.12	0.00	bc	0.12	0.00	ab	0.11	0.00	ns
	A. p.	0.13	0.00	c	0.14	0.00	b	0.13	0.00	ns

5). *Antidesma pentandrum* var. *barbatum* occurred on more silty and shadier sites than did the other G III species in all stages (Tables 5 and 6). *Bischofia javanica* occurred on less silty sites in young stages (Table 5). Habitat differences in RLI among the G II species weakened with increasing age (Table 6). *Calophyllum*

TABLE 6. Habitat difference between 14 dominant species over the three habitat types through all growth stages in mean relative light intensity. Values with different letters are significantly different at the $P < 0.05$ level according to the Tukey-Kramer test. Refer to species names in Table 1.

Group	Stage Species*	Seedling Average	S.D.	P Values > 0.05	Sapling Average	S.D.	P values > 0.05
G I	Hi. t.	–	–	–	0.33	0.06	a
	S. s.	0.42	0.03	b	0.64	0.10	b
	Pa. o.	0.32	0.01	a	0.34	0.02	a
G II	Pi. t.	0.17	0.01	a	0.18	0.01	a
	Ce. m.	0.19	0.01	ab	0.19	0.01	ab
	R. u.	0.19	0.01	ab	0.19	0.01	ab
	Pl. o.	0.20	0.00	ab	0.21	0.01	ab
	D. m.	0.20	0.25	ab	0.21	0.74	ab
	He. s.	0.21	0.00	ab	0.21	0.01	ab
	Ca. i.	0.25	0.00	c	0.22	0.01	c
G III	A. p.	0.18	0.01	a	0.17	0.01	a
	F. g.	0.19	0.00	ab	0.22	0.02	b
	T. t.	0.20	0.01	ab	0.18	0.01	a
	B. j.	0.22	0.03	c	0.25	0.03	c

inophyllum is the most light-requiring species in G II during the seedling stage. *Bischofia javanica* occurred on significantly sunnier sites than did the other G III species in all the stages (Table 6).

DISCUSSION

Co-dominant species diversity. Of the 32 species in this study plot, 28 (87.5%) occur widely from subtropical to tropical regions; the exceptions are *Arenga tremula* Becc., *Garcinia subelliptica*, *Psychotria manilensis* Bartl., and *Rhaphiolepis umbellata* (Hatsusima 1975) (Table 1). Ridley (1930) suggested that the origin of plants with thalassochory is not the continental coasts of South America or Africa, but rather Asian regions where many islands exist. The diversity of co-dominant species as well as the forest structure clearly become more complex from the beach scrub zone to the inland forest (Table 2). Severe disturbances near the shoreline, such as sea wind, sand movement, and salt spray, decrease, and site conditions stabilize. Many co-dominant species of the beach scrub zone exhibited bimodal peaks in the DBH size-class distributions (Fig. 2), which suggests that most populations were damaged or killed by severe disturbances directly along the shoreline. As a result, these species might have lateral branches in order to increase their tolerance to disturbance. *Messerschmidia argentea* also showed a similar distribution pattern. Few seedlings of *Scaevola sericea* and *Hibiscus tiliaceus* were found in this study plot, although the population of *Pandanus odoratissimus* was relatively rich (Fig. 2, Table 1). It is considered that the beach scrub zone may develop into a pure *Pandanus odoratissimus* forest under stable environmental conditions as succession progresses.

Adjacent inland species did not occur as co-dominant species in the beach scrub zone, as measured by stem density. Of the eight species, two inland species co-dominated in the strand forest zone. Adjacent inland species *Bischofia javanica*, *Fraxinus griffithii*, *Rhus succedanea*, and *Macaranga tanarius* are pioneer species, and especially *Bischofia javanica* and *Macaranga tanarius* appear widely on limestone areas in the Ryukyu Islands (Miyawaki & Suzuki 1976). In contrast, of the 11 species, seven coastal species occurred in inland forest as co-dominant species (Table 2). Consequently, adjacent inland forest in this study plot might be a primary successional stage that formed in gaps created in strand forest by multiple tree falls during typhoons. It has been suggested that the adjacent inland forest plays the role of an ecotone. Many ecologists have described how species richness becomes higher in ecotonal zones than in adjacent communities (e.g., Odum 1983, Petts 1990). However some reports show species richness in ecotones not to be different from that in adjacent communities (e.g., Harper 1995, Luczaj & Sadowska 1997). Walker *et al.* (2003) also reported that characteristic ecotone features depend on particular ecological situations and the ecology of the species present, rather than being intrinsic properties of ecotones. This study showed a significant tendency for inland forest, considered as an ecotonal zone, to have more species than the adjacent strand forest. Therefore we need to compare the forest structure of ecotonal zones in this study with forests further inland to clarify the differences in biological traits between these vegetation zones.

Prediction of future forest structure and dynamics. *Hibiscus tiliaceus*, *Scaevola sericea*, *Bischofia javanica*, and *Turpinia ternata* had more adult than young individuals (Fig. 2, Table 1), which implies that they are not regenerating in situ. Regeneration of *Hibiscus tiliaceus* and *Scaevola sericea* might be restricted by the death of young individuals due to sand burial and by shifting sand damage. Most flowering or fruiting individuals of *Turpinia ternata* (7.08 cm mean dbh, 5.33 m mean height) were unhealthy; they were infected by tree diseases, or their trunks were broken by typhoons or lighting strikes. Therefore it is suggested that *Turpinia ternata* cannot produce seeds stably under current conditions. *Bischofia javanica* shows a higher degree of physiological and morphological acclimation when transferred to new light conditions in gaps (Yamashita *et al.* 2000, 2002). Denslow (1987) and Kuuluvainen & Juntunen (1998) have described the rapid seedling establishment and growth of large-gap species. *Fraxinus griffithii* adapts to disturbances well, regenerates rapidly with sprouts, and is an anemochore (wind-dispersed species) with samaras. Therefore it is very likely to establish a very high number of seedlings over various habitats given these traits compared with other species. However, we presume that the population size of *Fraxinus griffithii* in young stages was unstable due to high density-dependent mortality in seedlings (Fig. 2, Table 1), since we could not show any significant habitat traits for that species in this study (Tables 4 to 6). Seedlings and saplings of *Calophyllum inophyllum* occurred on significantly sunnier sites than other G II species (Fig. 3, Table 6). Distributions of *Hernandia sonora* were significantly defined by light and siltation rate (Fig.

3, Tables 5 and 6). *Calophyllum inophyllum* and *Hernandia sonora* showed higher survival rates under soil water stress than other G II species (Table 4). Our study also found that *Bischofia javanica* is a species with a strong light requirement (Table 6). Therefore the regeneration chances of *Bischofia javanica* are limited under the closed canopy of a stable forest. *Bischofia javanica* and *Calophyllum inophyllum* are described as colonizers after large-scale disturbance, with more shade-intolerant seedlings and saplings than other pioneer species. In contrast, the population sizes of *Cerbera manghas*, *Pittosporum tobira*, and *Antidesma pentandrum* var. *barbatum* were stable in all growth stages (Fig. 2, Table 1) and it appears strongly shade-tolerant (Table 6). These results suggest that these species keep their population stable in understory conditions.

We suggest that changes in light and soil water conditions on the forest floor, following catastrophic disturbances (e.g., multiple tree falls during typhoons), rather than topographic heterogeneity, determine the forest composition and vegetation zonation. Because topographic heterogeneity on shorelines is different from that in mountains (Hörnberg *et al.* 1997, Kubota *et al.* 2004), macro-topographic site selection in species was not clearly found. There was also no significant difference in soil salinity between research quadrats or vegetation zonation in this study, and therefore it is not a key factor in determining species habitat and vegetation zonation in a small-scale study. Connell *et al.* (1984) and He *et al.* (1997) reported that the shift in distribution pattern must be caused by higher mortality of small trees under higher density of conspecifics. On the other hand, our study indicates that spatial distribution patterns of maritime strand forest species could be explained by density-independent mortality of seedlings.

For future studies, we need to investigate the effects of other biotic and abiotic factors, such as the amount of carbohydrate storage, herbaceous cover (Maguire & Forman 1983), and soil nutrients (Kachi & Hirose 1979a,b), on the spatial distribution of dominant species and structure. Many researchers have concluded that the amount of carbohydrate storage is one of the most important factors governing the survival of seedlings in shaded conditions (e.g., Kitajima 1994, Kobe 1997, Canham *et al.* 1999). Wargo (1977) and Marson & Waring (1984) also indicated that plants with low reserves of carbohydrates are more sensitive to infection by fungal pathogens. In this study, we could not show a significant relationship between seed size and seedling survival of the 14 dominant species in understory conditions (Table 1). Masaka *et al.* (2004) also described how shade-intolerant species cannot regenerate under the canopy. However, we classified the 14 dominant species into two survival-strategy types based on life form; shade-intolerant canopy trees, such as *Calophyllum inophyllum*, *Hernandia sonora*, and *Fraxinus griffithii*, have high rates of birth and infant mortality, while shade-tolerant subcanopy and shrub species, such as *Cerbera manghas*, *Pittosporum tobira*, *Diospyros maritima*, and *Antidesma pentandrum* var. *barbatum*, have low birth and premature death rates (Table 1). Therefore, future forest structure in maritime forest could be explained by the relationship between survival-strategy types and abiotic stress tolerances of forest species.

We hope that the ecological data on natural maritime forest vegetation accumulated in this study are useful for developing restoration guidelines for disturbed or destroyed coastal vegetation in subtropical and tropical areas.

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