International Journal of Biological, Life and Agricultural Sciences
ISSN: 2415-6612
Vol:4, No:10, 2010

Comparative Studies on Vertical Stratification, Floristic Composition, and Woody Species Diversity of Subtropical Evergreen Broadleaf Forests Between the Ryukyu Archipelago, Japan, and South China

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Abstract**—**In order to compare vertical stratification, floristic composition, and woody species diversity of subtropical evergreen broadleaf forests between the Ryukyu Archipelago, Japan, and South China, tree censuses in a 400 m^2 plot in Ishigaki Island and a 1225 m^2 plot in Dinghushan Nature Reserve were performed. Both of the subtropical forests consisted of five vertical strata. The floristic composition of the Ishigaki forest was quite different from that of the Dinghushan forest in terms of similarity on a species level (Kuno's similarity index r_0 = 0.05). The values of Shannon's index H' and Pielou's index J' tended to increase from the bottom stratum upward in both forests, except H' for the top stratum in the Ishigaki forest and the upper two strata in the Dinghushan forest. The woody species diversity in the Dinghushan forest (H'= 3.01 bit) was much lower than that in the Ishigaki forest (H'= 4.36 bit).

Keywords**—**floristic similarity, subtropical evergreen broadleaf forest, vertical stratification, woody species diversity.

I. Introduction

OWING to the Asiatic monsoon associated with the Tibeto-Himalayan Highland, the east- and southeast-coastal zone of the Asian continent lacks the subtropical dry belt [1]. Instead, a small part (including the chain of islands from Okinawa to Taiwan and South China) is sufficiently moist for the development of subtropical forests [2]. Therefore, subtropical forests in the zone have attracted considerable phytogeographic interest. In Ishigaki Island of the Ryukyu Archipelago, Japan, and Dinghushan Nature Reserve of South China, which respectively have the subtropical maritime and the subtropical monsoon climate, the subtropical evergreen broadleaf forests are characterized by high woody species diversity. Owing to the effect of different climates, woody species diversity, floristic composition, and stand structure of subtropical evergreen broadleaf forests between them might be different.

Tree species composition is considered a biodiversity indicator and an important attribute of forest ecosystems e.g. [3], because trees provide resources and habitats for almost all other organisms [4]–[9]. Structural diversity measured as variation across vertical stand profile (vertical stratification) also appears to be a good indicator index of the conservation of woody species diversity [10]–[12]. There were lots of studies on species composition and biodiversity of subtropical forests in South China e.g. [13]–[14], and researches on biodiversity of subtropical evergreen broadleaf forests in the Ryukyu Archipelago are also carried out e.g. [15]–[16]. However, there were no studies reporting the effect of the vertical stratification on floristic composition and woody species diversity in the subtropical evergreen broadleaf forests in the Ryukyu Archipelago and South China, and the comparison between the two locations. The purposes of this study are, therefore, to distinguish vertical stratification, to quantify woody species diversity and floristic composition on the basis of the vertical stratification and to compare the above parameters between the Ryukyu Archipelago and South China which have similar latitude but different climatic environments.

II. Materials And Methods

A. Study sites and sampling

Two study sites were respectively selected in Ishigaki Island of the Ryukyus Archipelago, Japan, and Dinghushan Nature Reserve of South China. The former is located in a subtropical evergreen broadleaf forest at Mt. Omoto (24º25′03″N and 124º11′17″E), the central part of Ishigaki Island. The latter is located in a subtropical evergreen broadleaf forest in Dinghushan Nature Reserve (23º10′26″N and 112º32′17″E), South China.

This study was financed in part by a Grant-in-Aid for Scientific Research (No. 20510011) from the Ministry of Education, Culture, Sports, Science, and Technology, Japan.

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In the Ishigaki site, a sampling plot of area 400 m^2 (20 m × 20 m) was established and divided into 64 quadrats (2.5 m × 2.5 m); slope, altitude, and slope orientation were respectively 21.4º, 200 m above sea level, and southwest; bedrock is composed of silicate having soil pH of 4.55. In the Dinghushan site, a sampling plot of area 1225 m^2 (35 m × 35 m) was established and divided into 196 quadrats (2.5 m × 2.5 m); slope, altitude, and slope orientation were respectively 23º, 291 m above sea level, and south; soil is mainly lateritic with a pH of 4.18.

All woody plants in the two plots were numbered and identified to species according to nomenclators [17]–[18]. Tree height *H* (m) and stem diameter at a height of *H*/10 $D_{0.1H}$ (cm) were measured.

B. Climate

The climatic data from Maezato Meteorological Observatory for the central part of Ishigaki Island and from Dinghushan Weather Station for Dinghushan Nature Reserve were collected. The warmth index is 227.2 ± 1.3 (SE) ºC month in Ishigaki Island and 207.0 ± 1.6 (SE) ºC month in Dinghushan Nature Reserve, whose values are within the range of 180 to 240 ºC month of the subtropical region defined by Kira [19]. Mean annual rainfall is 1942 ± 159 (SE) mm yr^{-1} (2003–2007) in Ishigaki Island and 1587 ± 129 (SE) mm yr^{-1} (1998–2007) in Dinghushan Nature Reserve.

C. Vertical stratification

The *M*–*w* diagram proposed by Hozumi [20] was used to identify the vertical strata of the forest stands. Tree weight *w* was assumed to be proportional to $D_{0.1\mathrm{H}}^2 H$ whose unit is cm^2 m. In this paper, $D_{0.1\mathrm{H}}^2 H$ was used as a surrogate for *w*. In order to draw the *M*–*w* diagram, the *w* values were arranged in descending order. Average tree weight M_n from the maximum tree weight w_1 to the *n*th tree weight was calculated using the form of $M_n = \sum_{i=1}^{n} w_i \big/ n$ (*n* = 1,…, total number of trees *N*). If the *M*–*w* diagram is constructed by plotting the values of *M* against the corresponding values of *w* on logarithmic coordinates, then some segments on the *M*–*w* diagram are formed. Each segment is related to the stratum with the specific characteristics of the beta–type distribution designated by Hozumi [20]. He pointed out that the segments on the *M*–*w* diagram can be written by either of the following equations:

$$M = A\,w + B \quad (1)$$

$$M = C\,w^b \quad (2)$$

where *A*, *B*, *C*, and *b* are coefficients.

D. Species dominance

Dominance of a species was defined by importance value IV (%) of the species:

$$\mathrm{IV} = \left(\frac{n_i}{\sum_{i=1}^{S} n_i} \times 100 + \frac{a_i}{\sum_{i=1}^{S} a_i} \times 100 + \frac{f_i}{\sum_{i=1}^{S} f_i} \times 100 \right) \Big/ 3 \quad (3)$$

where n_i is the number of individuals of the *i*th species, a_i is the basal area at a height of *H*/10 of trees belonging to the *i*th species, f_i is the number of quadrats in which the *i*th species appeared, and *S* is the total number of species.

E. Species–area relationship

The expected number of species S_q appeared within the number of quadrats *q* selected at random from the total number of quadrats *Q* was calculated from the equation proposed by Shinozaki [21] (cf. [22]):

$$S_q = \sum_{i=1}^{s} \left[1 - \binom{Q - q_i}{q} \Big/ \binom{Q}{q} \right] \quad (4)$$

where q_i is the number of quadrats in which the *i*th species occurred. The S_q-values were obtained for *q*-values of 1, 2, 4, 8, 16, 32, and 64 for the forest in Ishigaki Island, and 1, 2, 4, 7, 14, 28, 49, 98, and 196 for the forest in Dinghushan Nature Reserve.

F. Floristic similarity

The similarity of floristic composition between two forests was calculated using the following index r_0 [23]:

$$r_0 = \frac{\sum_{i=1}^{S_p} n_{\mathrm{A}i} n_{\mathrm{B}i}}{\sqrt{\sum_{i=1}^{S_p} n_{\mathrm{A}i}^2 \sum_{i=1}^{S_p} n_{\mathrm{B}i}^2}} \quad (5)$$

where S_p is the total number of species in the two forests, and $n_{\mathrm{A}i}$ and $n_{\mathrm{B}i}$ are the number of individuals of the *i*th species respectively belonging to the Ishigaki forest and the Dinghushan forest. The value of r_0 is 1.0 when the number of individuals belonging to a species is the same between the two forests for all species, i.e. floristic composition is completely the same between the forests, and is 0.0 when no common species is found between them.

G. Species diversity

The following two indices of Shannon's index H' (bit) and Pielou's index J' were used to measure woody species diversity and equitability (evenness), respectively:

$$H' = \sum_{i=1}^{S} \frac{n_i}{N} \log_2 \frac{N}{n_i} \quad (6)$$

$$J' = \frac{H'}{H'_{\max}} \quad (H'_{\max} = \log_2 S) \quad (7)$$

where *N* is the total number of individuals.

H. Regression analysis

The coefficients for nonlinear equations were determined with statistical analysis software (KaleidaGraph V. 4.0, Synergy Software, USA). On the other hand, the coefficients for linear and curvilinear equations were determined with the least-squares method.

III. Results

A. Vertical stratification

The *M*–*w* diagrams of the Ishigaki forest and the Dinghushan forest both show five phases (Fig. 1). In the Ishigaki forest (Fig. 1a), all phases have the property of (1). In the Dinghushan forest (Fig. 1b), the fifth, the second, and the first phases possess a property of (1), whereas the fourth and the third phases possess a property of (2). Therefore, both forests consisted of five strata.

Relationships between tree height H and tree weight w of the Ishigaki forest and the Dinghushan forest were respectively formulated (cf. [24]) as follows:

$$\frac{1}{H}=\frac{1}{1.06w^{0.368}}+\frac{1}{21.0} \tag{8}$$

$$\frac{1}{H}=\frac{1}{1.16w^{0.380}}+\frac{1}{28.1} \tag{9}$$

The estimated maximum tree heights in the Ishigaki and the Dinghushan forests were respectively 21.0 m and 28.1 m. The boundary tree heights were determined as 0.21, 0.87, 2.70, and 7.60 m in the Ishigaki forest and 0.66, 1.27, 4.80, and 11.43 m in the Dinghushan forest by substituting the tree weights at boundaries obtained from Fig. 1 for w respectively in (8) and (9).

B. Species dominance

In the Ishigaki forest, a total of 34 families, 52 genera, 77 species, and 4157 individuals were recorded. Aquifoliaceae was the most species-rich family in this forest and it contained six species which entirely belong to the genus of *Ilex*. *Ardisia quinquegona* Blume was the most dominant species at the total stand level in terms of the highest IV (Table I, upper). It was a small climax species because of its disappearance in the top stratum but higher IV in the lower four strata.

In the Dinghushan forest, a total of 35 families, 55 genera, 75 species, and 14680 individuals were recorded. The most species rich family was Lauraceae, which contained 15 species.

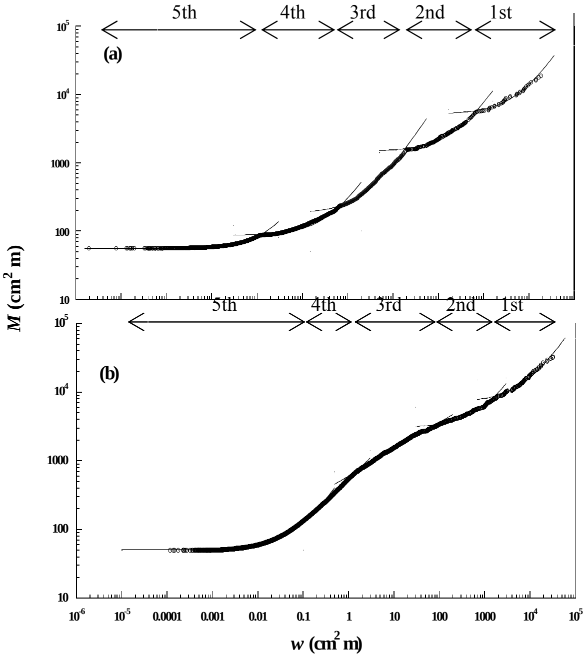

Fig. 1 Relationships between mean tree weight M and tree weight w in the Ishigaki forest (a) and the Dinghushan forest (b). In the M–w diagram (a), the regression curves for all strata were given by (1) (R^2 = 0.96 for the bottom, 0.88 for the fourth, 0.90 for the third, 0.92 for the second, and 0.98 for the top). In the M–w diagram (b), the regression curves of the bottom, the second, and the top strata are given by (1) (R^2 = 0.98 for the bottom, 0.97 for the second, and 0.97 for the top). The regression curves of the fourth and the third strata are given by (2) (R^2 = 0.99 for the fourth and 0.99 for the third)

TABLE I
TEN DOMINANT SPECIES IN ORDER OF SPECIES RANK DETERMINED BY IMPORTANCE VALUE IV IN THE TOTAL STAND OF THE ISHIGAKI FOREST (UPPER) AND THE DINGHUSHAN FOREST (LOWER)

Rank	**Species**	**IV (%)**					
		Top	**2nd**	**3rd**	**4th**	**Bottom**	**Total**
1	*Ardisia quinquegona* Blume	0.0	9.2	24.7	10.5	24.7	15.4
2	*Lasianthus plagiophyllus* Hance	0.0	0.0	8.5	19.1	9.5	7.9
3	*Psychotria marillensis* Bartl.	0.0	0.0	9.3	6.9	6.9	6.5
4	*Sarcandra glabra* (Thunb.) Nakai	0.0	0.8	0.8	11.0	3.2	6.2
5	*Camellia sasanqua* Thunb. Ex Murray	0.0	7.6	1.7	6.8	6.7	5.5
6	*Lasianthus cyanocarpus* jack	0.0	0.0	5.4	4.0	3.0	3.9
7	*Antidesma japonicum* Sieb. & Zucc.	0.0	0.0	5.6	3.4	1.6	3.4
8	*Machilus thunbergii* Sieb. & Zucc.	6.4	0.8	0.6	1.6	5.7	2.8
9	*Daphniphyllum teijsmannii* Zoll. ex Kurz	2.6	2.5	0.5	1.9	1.1	2.5
10	*Neolitsea aciculata* (B1.) Koidz.	10.5	0.8	1.3	1.5	4.1	2.4

Rank	**Species**	**IV (%)**					
		Top	**2nd**	**3rd**	**4th**	**Bottom**	**Total**
1	*Cryptocarya concinna* Hance	1.2	0.0	15.6	40.5	40.4	20.7
2	*Ormosia glaberrima* Wu	7.7	23.3	12.3	10.5	8.5	9.1
3	*Syzygium rehderianum* Merr. & Perry	8.6	30.1	4.4	4.3	7.3	7.8
4	*Cryptocarya chinensis* (Hance) Hemsl.	15.9	20.0	5.2	2.6	2.1	6.5
5	*Schima superba* Gardn. & Champ.	25.5	0.7	0.0	0.0	0.03	6.0
6	*Engelhardtia roxburghiana* Wall.	11.4	0.0	0.0	0.0	0.02	5.5
7	*Castanopsis fissa* (Champ.) R. & W.	1.3	0.0	1.8	7.8	9.0	5.4
8	*Castanopsis chinensis* Hance	16.7	1.0	1.1	0.2	0.1	5.4
9	*Ardisia quinquegona* Bl.	0.0	0.6	16.3	3.8	4.2	3.9
10	*Calophyllum membranaceum* Gardn. &	0.0	0.0	0.0	0.4	5.8	3.5

Machilus (Lauraceae) was the most species rich genus and contained five species. *Cryptocarya concinna* Hance was the most dominant species in terms of the highest IV in the total stand (Table I, lower). However, this species concentrated only in the lower strata. *Ormosia glaberrima* Wu, *Syzygium rehderianum* Merr. & Perry, and *C. chinensis* (Hance) Hemsl. appeared in all strata with high importance values in each stratum. *Schima superba* Gardn. & Champ. had the highest IV in the top stratum and extremely low IV in the bottom stratum, and it did not appear in the third and the fourth strata.

C. Species–area relationship

The expected number of species increased with increasing number of quadrats in the Ishigaki forest and the Dinghushan forest as shown in Fig. 2. The relationship of the expected number of species S_q to the number of quadrats q in each stratum and the total stand was well approximated by the following equation [25] (cf. [26]):

$$\frac{1}{S_q} = \frac{1}{cq^d} + \frac{1}{S_{\max}} \qquad (10)$$

where c and d are coefficients, and $S_{\max}$ is the expected maximum number of species.

In the Ishigaki forest, the expected maximum number of species was estimated to be 92 in the total stand. The $S_{\max}$ increased from 88 in the bottom stratum to 90 in the fourth stratum, then decreased through 77 in the third stratum and 55 in the second stratum to 44 in the top stratum. Therefore, the fourth stratum contained the highest expected number of species. However, in the Dinghushan forest, the bottom stratum had the highest potential number of species 126, which was almost the same as 127 in the total stand. The expected maximum numbers of species in the fourth stratum and the third stratum were respectively estimated to be 57 and 56, which were lower than the potential number of species 74 in the second stratum. The top stratum in the Dinghushan forest contained the lowest expected maximum number of species 15.

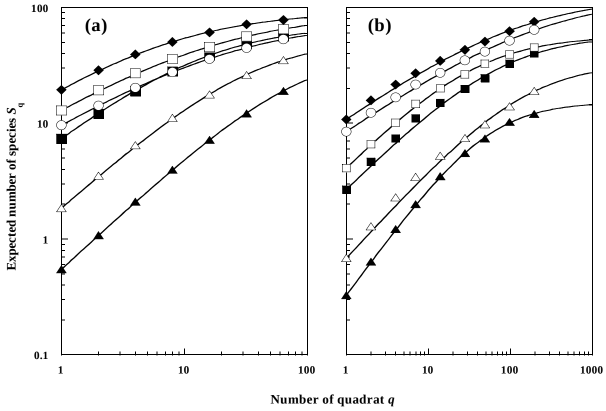

Fig. 2 Species–area curves (quadrat dimensions: 2.5 m × 2.5 m). Solid diamonds, total stand; open circles, bottom stratum; open squares, fourth stratum; solid squares, third stratum; open triangles, second stratum; solid triangles, top stratum. The species–area curves were fit with (10), where in the Ishigaki forest (a) $S_{\max}$ = 92 ($R^2 \cong$ 1.0) for the total stand, and $S_{\max}$ = 88 ($R^2 \cong 1.0$), 90 ($R^2 \cong 1.0$), 77 ($R^2 \cong 1.0$), 55 ($R^2 \cong 1.0$), and 44 ($R^2 \cong 1.0$) for the bottom through the top stratum, respectively, and in the Dinghushan forest (b) $S_{\max}$ = 127 ($R^2 \cong 1.0$) for the total stand, and $S_{\max}$ = 126 ($R^2 \cong 1.0$), 56 ($R^2 \cong 1.0$), 57 ($R^2 \cong 1.0$), 74 ($R^2 \cong 1.0$), and 15 ($R^2 \cong 1.0$) for the bottom through the top stratum, respectively

TABLE II
DIVERSITY INDICES AMONG STRATA IN THE ISHIGAKI FOREST (UPPER) AND THE DINGHUSHAN FOREST (LOWER)

Stratum / Tree size	Height range (m)	No. of trees (ha^{-1})	Basal area ($m^2 ha^{-1}$)	No. of species (sample-area^{-1})	H' (bit)	J'
Top	$7.60 < H \le 14.1$	1050	36.4	19	3.84	0.90
Second	$2.70 < H \le 7.60$	3250	7.7	35	4.49	0.87
Third	$0.87 < H \le 2.70$	22875	4.1	56	4.29	0.71
Fourth	$0.21 < H \le 0.87$	45150	1.1	65	4.21	0.70
Bottom	$0.0 < H \le 0.21$	31600	0.08	52	3.73	0.65
All trees	$0.0 < H \le 14.1$	103925	49.4	77	4.36	0.69
Large trees	$H \ge 1.30$ m	17450	46.9	64	4.58	0.76

Stratum / Tree size	Height range (m)	No. of trees (ha^{-1})	Basal area ($m^2 ha^{-1}$)	No. of species (sample-area^{-1})	H' (bit)	J'
Top	$11.4 < H \le 19.1$	644	25.6	12	3.05	0.85
Second	$4.80 < H \le 11.4$	1265	5.6	19	2.90	0.68
Third	$1.30 < H \le 4.80$	6946	1.9	40	3.66	0.69
Fourth	$0.66 < H \le 1.30$	18587	0.9	44	3.00	0.55
Bottom	$0.0 < H \le 0.66$	92391	1.0	64	2.73	0.46
All trees	$0.0 < H \le 19.1$	119836	35.0	75	3.01	0.48
Large trees	$H \ge 1.30$ m	9534	33.1	48	4.15	0.74

D. Floristic similarity

As shown in Fig. 3, the floristic composition of the Ishigaki forest was quite different from that of the Dinghushan forest in terms of similarity on a species level (r_0 = 0.05). However, the floristic composition of the two forests was similar on a genus level (r_0 = 0.47) and quite similar on a family level (r_0 = 0.74). This is mainly due to the low number of the common species rate which was just 4.1%. The floristic composition of the two forests on a genus level and a family level was similar because of the higher common genus and family rates which were 22% and 35%, respectively.

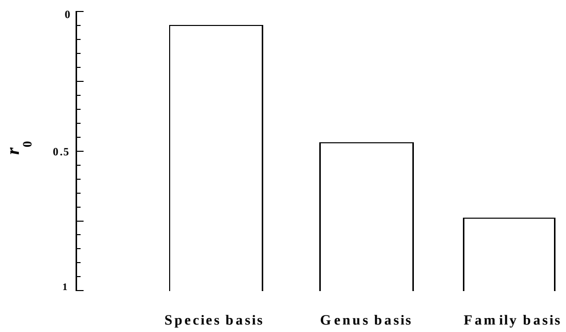

Fig. 3 Dendrograms of the similarity r_0 in the composition of species, genera, and families between the Ishigaki forest and the Dinghushan forest

E. Woody species diversity in the stratified forest stands

Woody species diversity in the stratified forest stands in the Ishigaki forest and the Dinghushan forest was shown in Table II. The values of diversity indices H' and J' tended to increase from the bottom stratum upward except H'-value for the top stratum in the Ishigaki forest and the upper two strata in the Dinghushan forest. It follows that high woody species diversity depended on the large trees in the two forests. The woody species diversity in the Dinghushan forest (H'= 3.01 bit) was much lower than that in the Ishigaki forest (H'= 4.36 bit).

IV. Discussion

In the Ishigaki forest, the top-six dominant species did not appear in the top stratum, but they had high IV in the lower strata (Table I, upper). Therefore, they were not typically facultative shade species (light-tolerant under high light conditions and shade-tolerant under low light conditions) and mainly shade-tolerant, growing from the bottom stratum to the subcanopy stratum (or the second stratum). The other four species from the top-ten dominant species grew to the top stratum and also had high IV in the lower strata. As a result, these four species were likely to be typically facultative shade species and provided a suitable shade environment for the top-six dominant species.

In the Dinghushan forest, *Cryptocarya concinna* was the most dominant species which occupied almost half individuals of the total stand and mainly appeared in the lower three strata with high IV (Table I, lower). The species has a higher photosynthesis rate and can develop rapidly [27]. In Dinghushan Nature Reserve, however, this species is highly susceptible to herbivory damage caused by the insect *Thalassodes quadraia* Guenee [28]–[29], which is a strong impediment to maturation in this species. *Ormosia glaberrima*, *Syzygium rehderianum*, *Castanopsis chinensis* Hance, and *Cryptocarya chinensis* are typically facultative shade species, becasue they appeared in all strata in the Dinghushan forest.

The diversity of a community depends on species richness and evenness, as was shown for patterns in Shannon’s and Pielou’s indices across vegetation strata in the present results. The lower strata contained many species relative to their smaller height ranges (Table II). Therefore, these strata obviously support high species richness of the forests. For example, 67% of the total species and 30% of the total individuals in the Ishigaki forest, and 85% of the total species and 77% of the total individuals in the Dinghushan forest were respectively packed within thin bottom strata of 21 cm and 66 cm deep.

In the Ishigaki forest, the value of H' for the large trees ($H \geq$ 1.3 m) was higher than that of H' for the total stand (Table II, upper). This is mainly caused by a higher value of J' for large trees, whose increase could surpass a decrease of the H'-value caused by a low species richness for large trees. The diversity tended to increase up to the second stratum and then decreased downward. These results may represent that the large trees have an important role in maintaining high woody species diversity. Similarly, the value of H' in the Dinghushan forest for the large trees ($H \geq$ 1.3 m) was also much higher than that of H' for the total stand (Table II, lower). It is apparent that high woody species diversity in this forest depends on large trees, because the values of H' and J' tended to increase from the bottom stratum upward, except H' for the upper two strata. In addition, the lowest diversity was in the bottom stratum, though the total number of species of the bottom stratum was much higher than those of the upper strata. This is because almost half of individuals in the bottom stratum were occupied by *Cryptocarya concinna*. Woody species diversity was higher in the Ishigaki forest than in the Dinghushan forest, because the values of H' and J' for the total stand and the large trees in the Ishigaki forest were higher than those in the Dinghushan forest (Table II).

Acknowledgment

We are grateful to Drs. R. Suwa, K. Nakamura, and K. Analuddin, Messrs. S. Sharma and A. T. M. R. Hoque, and Ms. Y. Li for their cooperation and active participation in the fieldwork. Special thanks go to Profs. H. Ota, M. Yokota, and M. Izawa, and Accos. Prof. T. Denda for their kind cooperation and valuable suggestions.

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