Species turnover and diversity patterns along an evergreen broad-leaved forest coenocline

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Abstract. Direct gradient analysis was applied to the evergreen broad-leaved forest coenocline in the Tatera Forest Reserve, Japan. 10 quadrats of 0.1 - 0.05 ha were laid out from 140 m to 560 m above sea level at intervals of 25-70 m. Gradient analysis revealed that distributions of many species terminated or started at ca. 400 m. Community similarity, calculated in Percentage Similarity (PS) and Community Co-efficient (CC), changed abruptly below and above the 400 m contour, suggesting a change of vegetation structure at this altitude, which was also clear from population distributions.

The spatial turnover rate of species along the altitudinal gradient was calculated in two ways: as the Average turnover rate along the whole range of the gradient, and as the Zone turnover rate at individual altitudes. The overall rates calculated for five categories of populations: DBH > 10 cm, DBH >3 cm, all woody species, herb-layer, and total vegetation, were – 0.0011 to – 0.0021 for PS, and – 0.0009 to – 0.0019 for CC. The calculated rates (PS basis) indicate that a 95% change in species composition is reached at 1120 to 620 m altitude. Similarly, the rates – 0.0009 to – 0.0019 (CC) correspond to 1410 - 680 m. The altitudinal range expected here for a 95% change agrees with the actual elevation of forest zonation in northwestern Kyushu. The average rate of both PS and CC in the herb-layer population was 1.56 times higher than the rate in the woody species population, showing a more rapid change in herb-layer population than in the woody ones along the gradient.

The Zone turnover rates were higher at the 370-440 m belt than those below and above the belt. This coincided with the interchanging pattern in population distributions and the abrupt change in similarity at about 400 m above sea level. This may be due to the change in environmental conditions such as physiography and air humidity. In the diversity measurements, the species density per 100 m² showed a gradual increase in the DBH >3 cm population but a constant level in the DBH >10 cm population along the whole range of the forest coenocline studied, while index values of $S_{(100)}$ and Shannon's H' showed decreasing trends in the same gradient with a few exceptionally high and low values.

Nomenclature: Ohwi (1957, 1965).

Abbreviations: CC = Community Coefficient; PS = Percentage Similarity.

Introduction

Evergreen broad-leaved *Castanopsis* and *Quercus* (subgenus *Cyclobalanopsis*) forest is considered the climatic climax of the East Asian warm-temperate region. This forest type covered most of the lowland and foothill area of southwestern Japan in the past. At present, relict forest stands can be found only around shinto-shrines. They are small in size, usually not exceeding a few ha, and more or less disturbed. They are distributed from the Ryukyus to the north of Central Japan (Miyawaki & Sasaki 1985). The less disturbed forest stands offer opportunities to infer the original vegetation that our ancestors lived in and exploited in the remote past. On the other hand, the small size of the forest remnants makes it difficult to analyse large-scale phenomena.

The study site, the Tatera Forest Reserve, is exceptional among the remnant forest sites with regard to its size and quality (Itow 1977). It is a truly primeval evergreen broad-leaved forest, ca. 100 ha in size; it ranges without breaks and disturbances from flat, easily exploitable lowland to a mountain top (see Itow 1989 for an outline of the vegetation). The study forms part of the Tatera Vegetation Ecology Project, which encompasses every aspect of the forest vegetation: phytosociology, gradient analysis, self-maintenance mechanisms, gap dynamics, and life history and population ecology. The present paper focuses on species distribution, species turnover and diversity patterns along the altitudinal forest coenocline. It will touch upon the question on continuity or discontinuity of plant community distribution on the basis of the distribution of plant populations, and also describe the vegetation structure by means of parameters for species turnover rate and diversity.

Study area and Methods

Study area

The Tatera Forest Reserve is located in the centre of the South Island of Tsushima, at 34°25' N and 129°20' E, between the Japanese Archipelago and the Korean Peninsula. The reserve, ca. 100 ha, is situated on the north-facing slope of Mt. Tatera, ranging from 120 m to 560 m above sea level. The topography is flat and gentle in the low and middle altitudes, and rather steep at high altitudes (Fig. 1). The well-developed evergreen broad-leaved, or laurel-leaved, forest is dominated by *Castanopsis cuspidata* var. *sieboldii* or *Distylium racemosum* at low altitudes, and by *Quercus acuta* at higher altitudes. On flat and gentle slopes at low altitudes, the canopy trees are 1 m in diameter at breast height (DBH) and 28 m in height. The reserve has been free from human interference for centuries. Field studies were carried out in 1981, 1982 and 1989, but all of the data presented here are from the 1981 field season.

Field methods

10 well-developed forest stands, free of apparent recent canopy gaps, were selected. They ranged from 140 m to 560 m above sea level with altitudinal intervals of 25-70 m (Fig. 1). One big sample plot was chosen in each of the stands; plots 1 -7 were 0.1 ha (20 m × 50 m) each and situated at low to middle altitudes; plots 8-10 were 0.05 ha (10 m × 50 m) each and situated at high altitudes. Each plot was subdivided into 10 m × 10 m quadrats. Table 1 gives the physiographic features of the 10 selected stands.

Vegetation sampling was as follows: Populations of tree and shrub species were grouped into three classes:
1. DBH >10 cm;
2. DBH = 3-10 cm;
3. Juvenile (DBH <3 cm).

A fourth class was formed by herb-layer populations, including herbaceous species and dwarf shrubs that do not reach the shrub layer even at their maximum height. Plant species were identified and DBH of trees were recorded for populations of class 1 and 2; cover-abundance classes according to Braun-Blanquet (1964) were estimated for populations of class 3 and 4. Five population groups were distinguished by combining the four categories mentioned above:
a. 'Trees': DBH >10 cm population (= class 1);
b. 'Trees + subtrees': DBH >3 cm (= classes 1 + 2);
c. 'Woody species' (= classes 1 + 2 + 3);
d. 'Herb-layer' (= class 4);
e. 'All' (= classes 1 + 2 + 3 + 4).
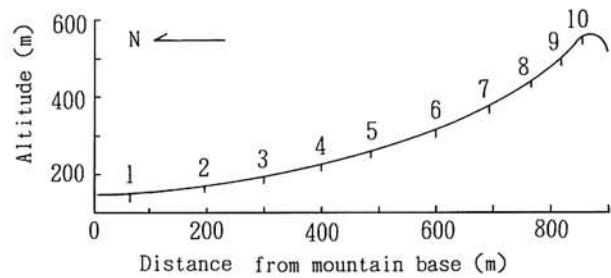
Fig. 1. Profile of the Tatera Forest Reserve showing the physiography and the positions of forest stands studied.

Stand characteristics for these five groups included 1. Percentage frequency of occurrence in quadrats; 2. Presence/ absence in the stand; 3. Actual number of trees (only for 'Trees' and 'Trees + subtrees').

Similarity calculations

Two similarity indices were calculated:
1. Percentage Similarity:

$$PS = 200w / (a + b) \qquad (1)$$

where a and b are the sums of species percentage frequency values in two plots A and B, and w is the sum of the quantitative characteristics the two plots A and B have in common (in this case percentage similarity values).
2. Community Coefficient:

$$CC = 200\, S_{ab} / (S_a + S_b) \qquad (2)$$

where S_a and S_b are the numbers of species found in plots A and B, and S_{ab} is the number of species found in both A and B (cf. Whittaker 1972; Gauch 1973). The

Table 1. Physiographic data for the 10 stands studied.

Stand	Altitude (m)	Aspect	Steepness (°)
1	140	-	0
2	165	-	0
3	190	N45W	7
4	230	N30W	7
5	260	N05W	15
6	310	N10W	15
7	370	N30W	35
8	440	N20W	35
9	500	N25W	30
10	560	N20W	20

indices were calculated between all stand pairs for each of the five population categories a - e described above.

Calculations of the spatial turnover rate of species

Species turnover rate was calculated as:
a. *Average turnover rate* along the whole altitudinal gradient ranging from 140 m to 560 m in altitude, and
b. *Zone turnover rate*, the rate within altitudinal zones.

The Average turnover rate was calculated in two steps. 1. Calculate PS and CC for every pair of plots; 2. Plot the log similarity values on the Y-axis against altitudinal difference between plots on the X-axis and calculate the regression. The slope of the regression line is the Average turnover rate of species per 1 m altitudinal difference. Extrapolation of the regression line to 0 m altitude (Wilson & Mohler 1983) gives the expected similarity value of replicate samples; that is, the internal association (IA). The calculations were done with a computer program in Wakimoto, Tarumizu & Tanaka (1984). As derived values the 50% and 95% turnover ranges were calculated as the altitudinal ranges over which the turnover is 50% and 95% respectively; these values are based on turnover rate and IA.

The calculation procedure mentioned above is basically the same as Whittaker's (1960, 1972) but differs in the use of the actual altitude as the X-axis, instead of Whittaker's 10-segmented gradient.

In addition, the Half-change value, expressed in gradient length units, was calculated according to Whittaker (1960, 1972):

$$HC = (\log IA - \log z) / \log 2 \qquad (3)$$

where IA is the Internal Association (similarity at altitudinal difference 0) and z is the similarity obtained by extrapolation of the regression line to the opposite end of the gradient.

The Zone turnover rate for an altitudinal zone was calculated by taking, for the plot in this zone and the plots at either side along the gradient, the mean of turnover rate values as (log IA-log SI) /altitudinal difference, among the three neighbouring plots. Here IA is again the internal association and SI is the similarity. This point turnover rate is calculated separately for PS and CC. Finally, the two turnover rates were calculated separately for the five population categories a - e as distinguished above.

Diversity calculations

Three diversity parameters were calculated for the a and b populations. Species richness was expressed as average number of species per quadrat of 100 m², further to be called species density. Diversity proper was calculated as $S_{(100)}$ (Itow 1984, 1988, after Hurlbert 1971), and as Shannon's H' (Pielou 1969), as follows:

$$S_{(100)} = \sum \left(1 - \binom{N-n_i}{100} / \binom{N}{100}\right) \qquad (4)$$

$$H' = -\Sigma \, p_i \log_2 p_i \qquad (5)$$

where S is the total number of species, N is the total number of individuals, $S_{(100)}$ is the expected number of species at 100 individuals, n_i is the number of individuals of the i-th species, and p_i is the proportion of i-th species (n_i/N) in the community. Correlation and regression coefficients between diversity measurements and altitude were again computed using a program in Wakimoto, Tarumizu & Tanaka (1984).

Results and Discussion

Direct gradient analysis

138 species of vascular plants were recorded in the 10 plots, on a total area of 0.85 ha. Table 2 presents the distribution of seven groups over the categories Evergreen, Summergreen and Needle-leaved. The top three plants of the above-mentioned groups were:

Trees	Shrubs
Castanopsis cuspidata var. *sieboldii*	*Aucuba japonica*
Distylium racemosum	*Skimmia japonica*
Camellia japonica	*Eucresta japonica*

Lianas	Herbaceous plants
Trachelospermum asiaticum	*Cymbidium goeringii*
Kadzura japonica	*Calanthe sieboldii*
Marsdenia tomentosa	*Panax japonica*

Ferns	Epiphytes
Dryopteris erythrosora	*Lemmapnyllum microphyllum*
Dryopteris varia	*Pleopeltis onoei*
Rumohra pseudo-aristata	*Oberonia japonica.*

Table 2. Life-forms of plants recorded in the 10 sample plots.

	Evergreen	Summergreen	Needle-leaved
Trees and subtrees	25	15	4
Shrubs	5	18	-
Dwarf shrubs	5	-	-
Liana	9	8	-
Herbs (+ graminoids)	10	16	-
Ferns and allies	13	3	-
Vascular epiphytes	7	-	-
Total	74	60	4

In the direct gradient analysis I analysed species distributions against altitude as a complex environmental axis (cf. Fig. 1 and Table 1). Fig. 2 illustrates the distributions of 45 selected species out of the 138 recorded; species performance is measured as the percentage frequency of occurrence, smoothed by a modified Curtis & McIntosh (1951) method:
$(a+2b+c)/4$, where a, b, and c are the frequencies of the species in three neighbouring plots; for the end plots I take $(2a+b)/3$; when the species was absent the value zero was taken irrespective of the occurrence in the neighbouring plots. The distribution curves (Fig. 2) are basically bell-shaped. Many curves terminated just below or above the 400 m contour.

Average turnover rate of species

Table 3 presents the matrix of PS and CC values. The lowest similarity value between neighbouring plots, 7 and 8, was PS = 47, or CC = 58. This suggests an abrupt change in species composition at about the 400 m contour; this change coincides with the discontinuity in distribution curves (Fig. 2) of many species.

The average trend in community similarity can be followed by plotting the similarity values (Table 3) against altitudinal differences (Table 1). See Fig. 3. The regression equations are:
$\log Y = 1.941 - 0.00139X$ for PS ($r = -0.94$; $p < 0.01$);
$\log Y = 1.967 - 0.00122X$ for CC ($r = -0.93$; $p < 0.01$).

The average turnover rate on the basis of PS was a little higher than that in CC. Table 4 presents the average turnover rates for the five population categories along the altitudinal gradient. The calculated rates

Table 3. Matrix of between-plot values for Percentage Similarity, PS (lower-left) and Community Coefficient, CC (upper-right) for the 10 plots studied.

CC	1	2	3	4	5	6	7	8	9	10
PS										
1	.	81	84	84	82	75	48	44	35	35
2	74	.	82	80	79	71	60	41	31	31
3	79	77	.	87	85	79	62	45	33	34
4	78	76	83	.	80	76	64	48	39	37
5	74	71	78	82	.	86	64	53	41	36
6	70	72	76	74	77	.	72	57	45	42
7	49	57	54	54	57	67	.	58	48	47
8	36	35	36	38	43	43	47	.	74	76
9	29	28	29	32	38	41	42	67	.	73
10	29	26	26	27	31	34	38	67	70	.

ranged from -0.0011 to -0.0021 on the basis of PS and from -0.0009 to -0.0019 for CC. The 50% turnover range, on the basis of PS, for the two values presented, is ca. 270 to 140 m altitudinal difference; the 95% turnover range (PS basis) varies from ca. 1180 to 620 m. On the basis of CC these values are ca. 330 to 160 m for the 50% turnover and ca. 1410 – 650 m for the 95% turnover. The 95% change means an almost complete change in species composition, which can be compared with the transition from one vegetation zone to another.

Actually, in northwestern Kyushu, in which the study site is located, the low-elevation evergreen oak forest and the high-elevation summer-green beech forest

Table 4. Beta diversity parameters on the basis of PS (above) and CC (below) similarities.

	a DBH > 10 cm	b DBH > 3cm	c Woody species	d Herb layer	e Total
PS					
Internal Association	82.4	79.5	88.3	85.7	87.2
Turnover rate	− 0.00211	− 0.00118	− 0.00112	− 0.00175	− 0.00139
Altitudinal range (m) for 50% change	143	256	268	172	21 6
Altitudinal range (m) for 95% change	617	1106	1160	743	934
Gradient length (HC)	2.94	1.64	1.56	2.44	1.94
CC					
Internal Association	84.8	84.6	92.1	92.1	92.6
Turnover rate	− 0.00192	− 0.00092	− 0.00095	− 0.00150	− 0.00122
Altitudinal range (m) for 50% change	156	326	315	201	247
Altitudinal range (m) for 95% change	676	1407	1363	870	1067
Gradient length (HC)	2.68	1.29	1.33	2.07	1.70

Fig. 2. Distributions of 45 selected plant species along the altitudinal gradient.
1-12: trees and subtrees;
13-22: shrubs;
23-33: herb-layer species (including small shrubs that do not exceed 50 cm in maximum height);
34-45: lianas and epiphytes.
e: evergreen; s: summer-green; n: evergreen needle-leaved.

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1. *Camellia japonica* (e)	2. *Castanopsis cuspidata* v. *sieboldii* (e)
3. *Distylium racemosum* (e)	4. *Michelia compressa* (e)
5. *Podocarpus macrophyllus* (n)	6. *Symplocos prunifolia* (e)
7. *Quercus acuta* (e)	8. *Torreya nucifera* (n)
9. *Symplocos coreana* (s)	10. *Abies firma* (n)
11. *Cornus kousa* (s)	12. *Ilex macropoda* (s)
13. *Aucuba japonica* (e)	14. *Euchresta japonica* (e)
15. *Daphne kiusiana* (e)	16. *Skimmia japonica* (e)
17. *Callicarpa mollis* (s)	18. *Viburnum erosum* (s)
19. *Meliosma myriantha* (s)	20. *Viburnum wrightii* (s)
21. *Pertya glabrescens* (s)	22. *Alangium platanifolium* (s)
23. *Dryopteris erythrosora* (e)	24. *Damnacanthus indicus* (e)
25. *Calanthe sieboldii* (e)	26. *Ardisia crenata* (e)
27. *Goodyera velutina* (e)	28. *Disporum smilacinum* (s)
29. *Hosta tsushimensis* (s)	30. *Goodyera schlechtendaliana* (e)
31. *Lastrea laxa* (s)	32. *Panax japonicus* (s),
33. *Polystichum tripteron* (s)	34. *Trachelospermum asiaticum* (e)
35. *Lemmaphylum microphyllum* (e)	36. *Kadzura japonica* (e)
37. *Marsdenia tomentosa* (e)	38. *Anodendron affine* (e)
39. *Gardneria nutans* (e)	40. *Rhus ambigua* (s)
41. *Schizofragma hydrangeoides* (s)	42. *Oberonia japonica* (e)
43. *Pleopeltis onoei* (e)	44. *Davallia mariesii* (s)
45. *Bulbophyllum drymoglossum* (e).	
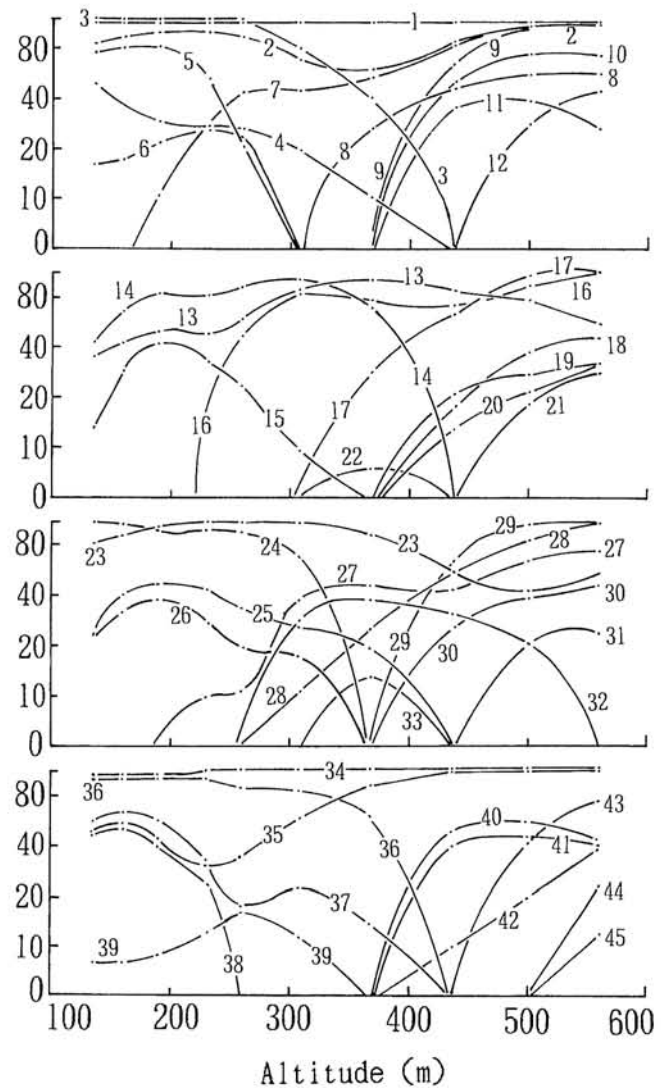
Altitude (m)

zones meet at 1000 - 1100 m altitude (Miyawaki 1981). The calculated turnover rates for woody species, -0.00112 for PS and -0.00095 for CC, fit well to this actual zonation pattern. Table 4 also shows how the half-change gradient length (Whittaker 1960) varies with high values for the bigger trees and the herbaceous species.

The turnover rate in the herb-layer population was 1.56 times higher than that in the woody-species population, both for PS and CC (Table 4). This means that the herbaceous populations change more rapidly than the tree and shrub populations along the altitudinal gradient. This result is in agreement with reports on a higher beta diversity for herbaceous species as compared with trees and shrubs in the Siskyou Mountains (Whittaker 1960), in the Great Smoky Mountains (Bratton 1975), and in Californian sage scrub (Westman 1981), and the higher beta diversity in the vascular understory species as compared with the bryophyte layer in Jasper National Park (Lee & La Roi 1979).

Zone turnover rate at different altitudes

As the direct gradient analysis (Figs. 1 and 2) already showed, species turnover rates related to altitudinal change were not even along the whole range but were abrupt at about the altitude of 400 m. Fig. 4 shows that for all five population categories, and both with PS and CC as similarity measure, the Zone turnover rates were higher at 160 - 200 m and at 370 - 440 m than at other altitudes.

The higher rates at the 160-200 m altitude were not obvious in the species distribution curves (Fig. 2), the explanation for which is not clear. At low altitudes in the study site, there were canopy gaps, both small and large, created by falling tree trunks. The apparent gaps were not sampled in the present study, but recovering phases may have been included in the plots at low altitudes. This may have caused heterogeneity within the low-altitude plots and would result in a higher rate of turnover. There were also irregularities in diversity
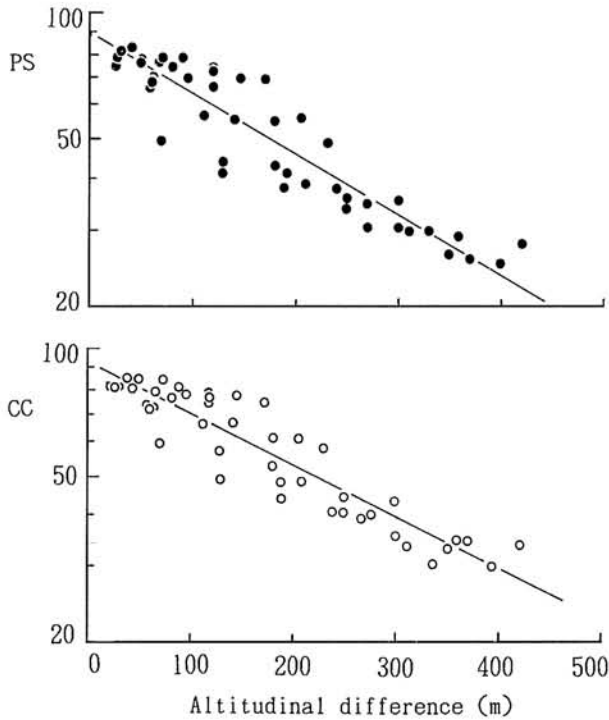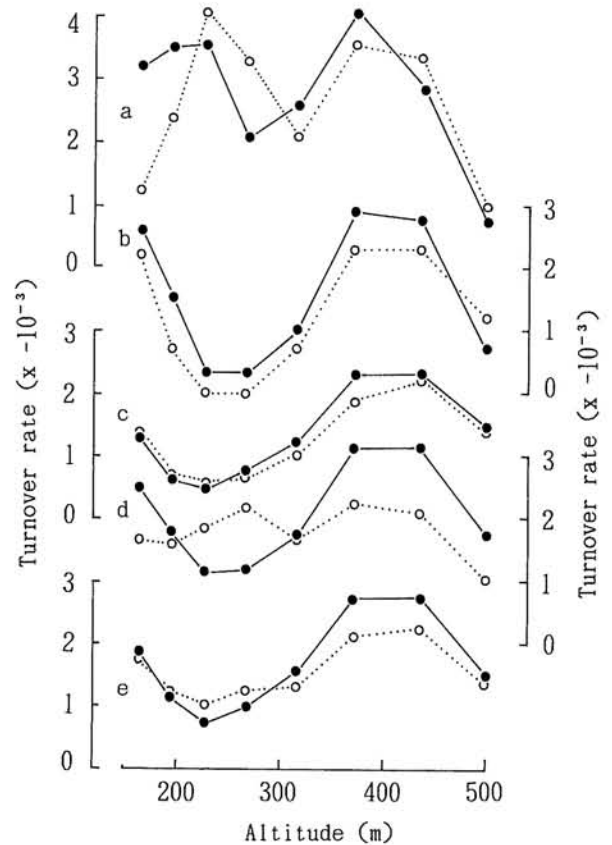
Fig. 3. Graphs showing PS and CC values for the vegetation as a whole against the altitudinal difference and regression lines. The slope of the line is the Average turnover rate of species along the altitudinal gradient, and the extrapolation down to 0 m altitude gives the expected similarity of replicate samples, the Internal Association (IA).


Fig. 4. Trends in Zone turnover rates at different altitudes in the Tatera Forest Reserve; a. DBH > 10 cm; b. DBH > 3 cm; c. Woody species; d. Herb layer; e. Vegetation as a whole.

patterns (see below).

The Zone turnover rates between 370 and 440 m were 1.5-3.5 times higher than those at higher altitudes, and 1.2-3.6 times higher than those at lower altitudes (Fig. 4). The abrupt change in this belt was particularly prominent for the populations with DBH > 3 cm (2.7-3.0 times on the basis of PS, and 1.9-3.6 times on the basis of CC).

According to Whittaker (1975) plant species are distributed continuously along an environmental gradient where the environmental changes are gradual. The present results do not entirely agree with Whittaker's hypothesis: they show synchronous change in species distribution (Fig. 2) but an abrupt change in species composition at altitudes between 370 and 440 m (Table 3 and Fig. 4). A locally high turnover rate, based on locally low similarity values, has been described for several cases and is thought of as an indication of habitat change (e.g. Beals 1969; Wilson & Mohler 1983; Ludwig & Cornelius 1987; Druitt, Enright & Ogden 1990). The abrupt change in Zone turnover rate observed at the 370-440 belt in the Tatera Forest Reserve may be such an

indication of environmental change. The mountain slope started to be steeper from the 370-440 belt onwards (Table 1). In addition, there is abundant growth of vascular epiphytes in and above this belt, which is indicative of high air humidity. The suggestion is that the belt is at the bottom level of the thick layer of clouds which develops on windy, foggy and/or rainy days through the year. So, the abrupt change in Zone turnover rate in the 370-440 m belt may be a reflection of both physiographic and meteorological conditions in the Reserve.

Species diversity pattern in tree populations

Species richness, expressed here as the average number of species found in the 100 m² quadrats within each plot, showed a slight increase in the DBH >3 cm population as compared with the other populations, with an exceptionally high value in Plot 2 (Fig. 5A: solid circles), but did not show any trend in the DBH >10 cm population (Fig. 5A: open circles). Apparently this species density pattern is independent of the changes
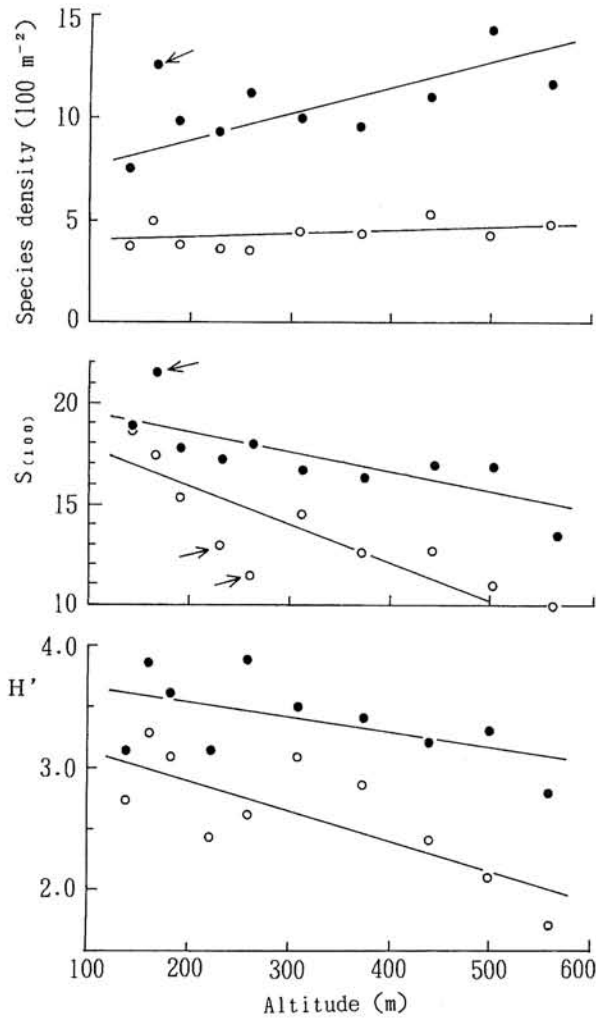
Fig. 5. Trends in diversity index values along the altitudinal gradient. Solid circles: DBH > 3 cm; open circles: DBH > 10 cm. A: Species density per 100 m²; B: Hurlbert's $S_{(100)}$; C: Shannon's H'. Arrows show unusually high or low values relative to the regression line. Regression equations are given for populations with DBH > 3 cm and > 10 cm respectively:

A: DBH > 3 cm: $Y = 7.10 + 0.0100X$ ($r = 0.74*$);
A: DBH > 10 cm: $Y = 3.90 + 0.0014X$ ($r = 0.53$);
B: DBH > 3 cm: $Y = 20.4 - 0.0097X$ ($r = -0.72*$);
B: DBH > 10 cm: $Y = 18.6 - 0.0016X$ ($r = -0.82**$);
C: DBH > 3 cm: $Y = 3.76 - 0.0012X$ ($r = -0.49$);
C: DBH > 10 cm: $Y = 3.41 - 0.0025X$ ($r = -0.73**$);
where Y is the index value and X is altitude (m).
($* p < 0.05$; $** p < 0.01$).

in species composition, whether gradual or abrupt along the altitudinal gradient (Figs. 2 and 4). The species density of the evergreen broad-leaved forest coenocline of the Tatera Reserve is stable from low to high altitudes.

The trends in the two diversity indices along the forest coenocline are different, however. Contrary to the species density trend (Fig. 5A), the index $S_{(100)}$ for the DBH > 3 cm population showed a decreasing trend with increasing altitude. On the other hand, the exceptionally high value in plot 2, coincides with the high species density for the same population category there (Fig. 5A). The anomaly of this plot may be due to its position in what is probably a regeneration stage in an old canopy gap. For the DBH > 10 cm population, index values of $S_{(100)}$ were especially low in plots 4 and 5. The reason for this is not clear. H' values also showed a decreasing trend, though somewhat irregular, with increasing altitude (Fig. 5C).

Thus, trends in species diversity along altitudinal gradients are inconsistent. Both decreasing (Hamilton & Perrott 1981) and increasing trends (Baruch 1984) have been reported. Such differences may be related to the presence or absence of a separate moisture gradient involved (Glenn-Lewin 1977; Whittaker 1977; Peet 1978; Minchin 1989) and/or a substrate gradient (Wilson, Lee & Mark 1990). In the present study of a climax forest in a humid, warm-temperate climate however, diversity indices decreased with altitude, but no trend was seen in species number per 100 m² (species density).

Before generalizations derived from this diversity trend can be made, further studies and data collection from well-developed forest communities along the wide range of forest coenoclines need to be made.

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