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Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient

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Abstract

Floristic composition, diversity, dominance and distribution pattern of species and tree population structure were studied in three stands of a sub-tropical wet hill broad-leaved forest of Meghalaya, India, along a disturbance gradient. Tree species diversity declined with increasing disturbance. Disturbed stands showed low equitability or high dominance and the undisturbed stand exhibited high equitability or low dominance. Contagious distribution among the tree species increased with increasing intensity of disturbance. Species showing regular distribution were restricted only to the undisturbed stand. Effect of disturbance on tree population structure was analysed using density-diameter curves. In the disturbed stands tree species showed reverse J-shaped and/or negative exponential curves, while those in the undisturbed stand exhibited sigmoid to bimodal mound shaped curves.

Introduction

The structure of plant and animal communities in many natural ecosystems is largely determined by the disturbances, which occur quite frequently (White 1979; Vogl 1980; Armesto & Pickett 1985). Clements (1936) viewed disturbance as a negative force that destroys climax assemblages and brings instability in the system, while Paine (1966), Lubchenco (1978) and Houston (1974) considered it as a positive force that might increase species diversity in the community by preventing competitive exclusion by dominant species. Mining activities, fire, windthrow, grazing and deforestation are main causes of disturbance in a community and each has different effects on the subsequent development of vegetation (Loucks *et al.* 1980; Pandey & Singh 1985). Species richness in the community has been attributed to natural disturbance by several workers (Grubb 1977; Connell 1978; Grime 1979; Huston 1979; Armesto & Pickett 1985), but most of their studies fail to define precisely the intensity of disturbance, pre-disturbance community structure and the effects of disturbance on the community and its microenvironment (Armesto & Pickett 1985).

The climax formation of Meghalaya ranges from moist deciduous to sub-tropical wet hill forests, which are also found on the slopes of Eastern Himalayas between 1000–2000 m (Champion & Seth 1968). Both have been exposed to various kinds of human disturbances, particularly shifting agriculture which is still prevalent among the tribals in the area. Studies on the effects of disturbance in these forests are limited to the population structure (Khan *et al.* 1987) and regeneration pattern of certain tree species (Khan *et al.* 1986). The objective of this paper is to study the community composition, species diversity and tree population structure in three stands of a sub-tropical wet hill forest along a precisely defined disturbance gradient.

In Meghalaya, major area under forest (*C* 92%) is owned by the local tribes and as such correct information about the nature and frequency of disturbance and the history of forests are not available. Since the major cause of disturbance in these forests is tree felling and burning, the ratio between basal area of cut trees and total basal area of all trees (including the felled ones) has been used to quantify the intensity of disturbance (Kanzaki & Kyoji 1986).

Study sites

Three natural forest stands (Fig. 1, Plate 1) in greater Shillong (25° 34′ N and 91° 56′ E) area were selected on the basis of varying intensities of disturbance. Although shifting cultivation is one of the major causes of deforestation in Meghalaya, the three forest stands do not have interspersed shifting agriculture farm land. The forest at Upper Shillong (altitude 1955 m), 12 km south of Shillong is highly disturbed (disturbance index – 60%), the stand at Shillong (altitude 1500 m) is mildly disturbed (disturbance index – 10%), while the forest at Mawphlang (altitude 1720 m), 30 km southwest of Shillong, represents the undisturbed stand (disturbance index – 0%). All the three stands form a part of the northern sub-tropical wet hill forest of India (Champion & Seth 1968). The undisturbed forest stand at Mawphlang is dense and evergreen with broad-leaved trees not exceeding 20 m in height. It represents the relic climax vegetation which has been left undisturbed due to religious beliefs of the local tribals. The dominant tree species are *Quercus dealbata*,

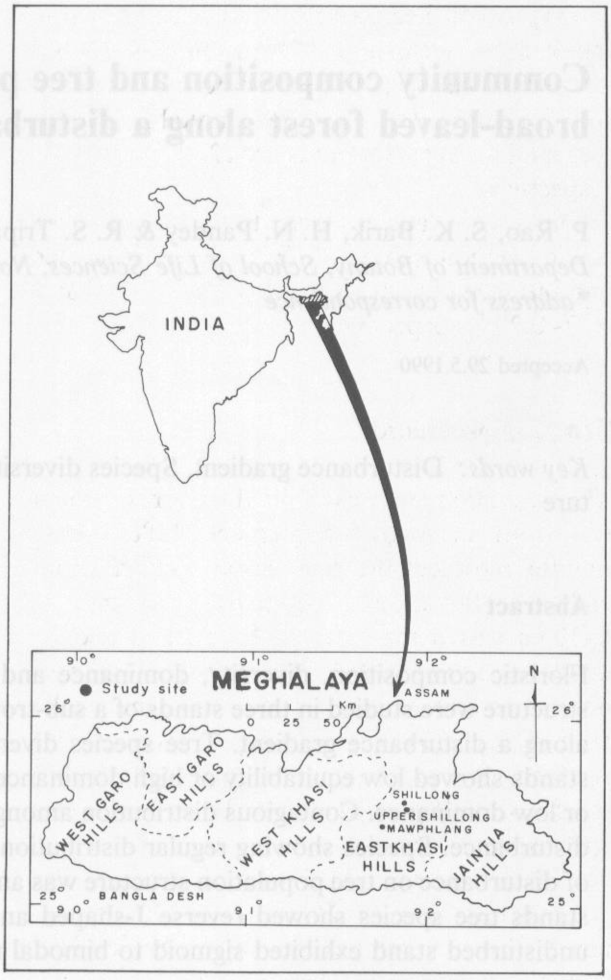


Fig. 1. Location of study site.

Quercus griffithii, Schima khasiana, Myrica esculenta, Rhododendron arboreum and *Manglietia insignis*. The understorey with *Symplocus chinensis, Daphne shillong* and *Eurya japonica* is hardly distinguishable. There is a heavy growth of epiphytic orchids, mosses, ferns and woody climbers in the forest. The dominant tree species in the disturbed stands are *Pinus kesiya* and *Q. dealbata*. These stands show poor under-canopy growth.

Climate and soil

The climate is monsoonic with an average annual rainfall of 2500 mm, 85% of which occurs between May and September. The winter season

(November to February) is characterised by low temperature (mean min. 3 °C, mean max. 16 °C) and occasional rain. The period during April-mid May is usually dry. The mean annual maximum and minimum temperatures are 22 °C and 16 °C respectively.

The soil is laterite, loam to loamy silt with acidic reaction (pH 5.0–5.7). The organic matter and nitrogen contents vary between 3.2–6.4 and 0.17–0.28% respectively.

Sampling procedures

The vegetation analysis of the three forest stands was done in August–September, 1988. These months represent the peak growth period, especially for the ground vegetation. An area of 5–10 ha was demarcated in each stand and 25 quadrats each of 10 m × 10 m size were laid randomly to study tree and shrub components, while ground vegetation (herbaceous component, tree seedlings and saplings) was studied by laying 40 quadrats of 1 m × 1 m size. In case of tree species, three categories viz., seedlings (height <20 cm) saplings (20–150 cm height & dbh <10 cm) and trees (dbh >10 cm) were recognized. The tree component was further divided into six diameter classes viz., 10–20, 21–30, 31–40, 41–50, 51–60 and 61–70 cm. Density, frequency, abundance and basal cover of all the species and canopy cover of trees were determined according to the methods given by Misra (1968). The community indices such as Sørensen's similarity index (1948), Pielou's evenness index (1966) and species richness index were computed. Spatial distribution pattern was determined using applied poisson distribution method followed by log normal (G) test for goodness of fit and also by using Whitford's index (1949). Density-diameter curves were drawn for the tree species as well as for the forest stands to depict the population structure.

The composite soil samples representing 0–10 cm depth were collected from each stand during the study period. The soil organic matter was determined by rapid titration method, nitrogen by micro-Kjeldahl method (Jackson 1962) and pH by a portable pH meter. Light intensity was measured at several places in each stand in sunny days at 12.00 h with a digital lux meter.

Results and discussion

Floristic composition

The floristic composition of the three stands is given in Table 1. The species were distributed in four distinct strata. The canopy layer (height >10 m) was mainly composed of *Q. dealbata, S. khasiana* and *M. esculenta* in all the three stands. In the undisturbed stand *Q. griffithii, Q. glauca* and *M. insignis* were also present. The sub-canopy layer (3–10 m height) was composed of *Exbucklandia populnea* and *Prunus undulata* in the undisturbed stand. This layer was dominated by the sprouts of *Q. dealbata, Q. griffithii* and *S. khasiana* in the disturbed stand. *Q. dealbata* was the dominant species in the undisturbed and mildy disturbed stands. In the undisturbed stand *R. arboreum* and *Q. griffithii* were codominant and *Q. glauca* was also present in large numbers. Secondary successional species *P. kesiya* tends to become dominant and replaces *Quercus* species in the disturbed stands. This is evident from its high density which was next to that of *Q. dealbata* in the mildly disturbed stand; highest in the highly disturbed stand and the species was completely absent in the undisturbed stand. The shrub layer was dominated by *D. shillong* in the undisturbed stand, while *S. chinensis* was dominant in the disturbed stands. The number of herbaceous species did not differ significantly among three stands. However, the density of tree saplings and seedlings did vary with disturbance (Table 2). The saplings of *Q. dealbata, Q. griffithii* and *S. khasiana* were abundant in the undisturbed stand. In the disturbed stands sapling density of *P. kesiya* was very high. The seedlings of *Q. griffithii, Q. dealbata* and *Taxus baccata* were abundant on the forest floor in the undisturbed stand, but those of *P. kesiya* and *S. khasiana* recorded a high density in the disturbed stands. The predominance of

Table 1. Density (Plants ha^{-1} ±S.E.) and importance value indices (IVI) of component species in three sub-tropical wet hill forest stands of Meghalaya along a disturbance gradient. Values in parentheses are species rating on the basis of IVI.

Species	Undisturbed		Mildly disturbed		Highly disturbed	
	Density	IVI	Density	IVI	Density	IVI
Tree species						
Castonopsis kurzii (Hance) B.	60 ± 2.2	18.43 (16)	–	–	–	–
Corylopsis himalayana Griff.	40 ± 1.0	10.97 (24)	–	–	–	–
Engelhardtia spicata Bl.	–	–	–	–	12 ± 0.3	8.66 (16)
Exbucklandia populnea (Griff.) Br.	80 ± 2.5	20.60 (15)	–	–	–	–
Ficus nerifolia Sm.	40 ± 1.6	11.80 (23)	–	–	–	–
Manglietia insignis (Wall.) Bl.	90 ± 3.5	29.04 (8)	–	–	–	–
Myrica esculenta Buch. Ham.	70 ± 1.5	25.15 (13)	33.3 ± 1.3	11.65 (9)	16 ± 0.4	15.86 (13)
Pinus kesiya Royle Ex. Gordon	–	–	173.3 ± 3.9	42.95 (5)	144 ± 0.9	114.89 (1)
Prunus undulata Buch. Ham.	90 ± 3.2	20.70 (14)	–	–	–	–
Pieris ovalifolia D. Don.	–	–	–	–	16 ± 0.4	8.83 (15)
Quercus dealbata L.	210 ± 2.8	52.27 (1)	453.3 ± 4.1	93.52 (3)	48 ± 0.7	33.25 (7)
Quercus glanca Thunb.						
Quercus griffithii Hk.	150 ± 4.5	35.12 (4)	–	–	32 ± 1.4	34.75 (6)
Rhododendron arboreum Sm.	90 ± 2.8	29.06 (7)	166.6 ± 2.5	55.89 (4)	92 ± 1.1	56.43 (3)
Schima khasiana Dyer.	90 ± 2.3	26.09 (11)	–	–	76 ± 0.4	27.32 (9)
Taxus baccata L.	40 ± 3.4	14.67 (21)	–	–	–	–
Shrub species						
Ardisia chrispa (Thumb.) DC.	40 ± 3.1	17.36 (18)	–	–	–	–
Baliospermum micrantha Muell Arg.	50 ± 2.2	39.71 (3)	–	–	–	–
Camellia caduca C.B. Cl.	20 ± 1.3	16.74 (19)	46.7 ± 1.6	25.38 (7)	56 ± 0.8	15.09 (14)
Cinamomum sp.	–	–	–	–	92 ± 1.3	25.67 (10)
Daphne bhalve Buch. Ham. exd. Don.	20 ± 1.3	14.86 (20)	–		–	
Daphne shillong Banerjee	100 ± 3.3	42.92 (2)	–	–	56 ± 0.8	20.02 (12)
Eurya japonica Thumb.	50 ± 2.2	30.93 (6)	–	–	108 ± 1.3	30.82 (8)
Iylex sp.	–	–	20.0 ± 0.7	4.88 (10)	108 ± 2.3	21.65 (11)
Lantana camara Linn.	–	–	46.7 ± 1.6	31.29 (6)	120 ± 1.4	41.44 (4)
Lindera pulcherrima Benth.	90 ± 4.8	33.58 (5)	–		–	–
Litsea elongata Wall.	–		–	–	12 ± 0.4	5.22 (17)
Mahonia pyenophylla (Fedde) Takeda	40 ± 2.8	17.66 (17)	–	–	–	–
Osbeckia sp.	–	–	233.3 ± 3.4	104.18 (1)	–	–
Symplocus chinensis	70 ± 2.6	27.98 (9)	113.3 ± 2.2	99.6 (2)	284 ± 3.5	98.69 (2)
Viburnum foetidum Wall.	30 ± 2.1	14.29 (22)	33.3 ± 1.2	17.52 (8)	172 ± 1.5	41.41 (5)
Viburnum sinensis Wall.	50 ± 2.3	25.85 (12)	–	–	–	–
Ground vegetation (density × 10^3)						
Arundinella khasiana Nees.	6 ± 0.3	15.06	–	–	–	–
Brunella vulgaris Linn.	4 ± 0.2	11.49	2.5 ± 0.7	7.69	24.2 + 0.15	21.84
Centella asiatica Linn.	–	–	–	–	10.7 + 0.11	9.90
Commelina sp.	16 ± 0.8	14.50	19.0 ± 0.3	17.94	21.0 + 0.11	12.68
Cyanotis cristata Linn.	4 ± 0.3	5.20	–	–	–	–
Cyperus rotundus Linn.	7 ± 0.2	18.22	–	–	5.0 + 0.06	6.12
Dioscoria alata Linn.	8 ± 0.3	14.14	–	–	–	–
Drymeria cordata Willd.	21 ± 0.7	21.25	10.5 ± 0.25	18.29	22.5 + 0.19	17.53
Eupatorium adenophorum Spreng	–	–	–	–	5.7 + 0.06	6.16
Eupatorium riparium Regel	–	–	4.0 ± 0.07	15.02	10.7 + 0.1	12.85
Ferns	–	–	–		8.7 + 0.09	7.42
Geranium sp.	5 ± 0.3	8.32	–	–	0.7 + 0.15	0.99

Table 1. (continued)

Species	Undisturbed		Mildly disturbed		Highly disturbed	
	Density	IVI	Density	IVI	Density	IVI
Gliechenia longissima Bl.	45 ± 2.3	25.83	23.0 ± 0.41	53.98	7.8 + 0.42	25.57
Globa sp.	–	–	11.0 ± 0.03	52.01	5.7 + 0.04	17.00
Hypocharis radicata Linn.	15 ± 0.7	15.39	3.5 ± 0.08	8.14	10.8 + 0.06	12.01
Impatiens sp.	–	–	4.5 ± 0.13	9.46	14.8 + 0.13	13.23
Lycopodium clavatum	11 ± 0.7	13.57	–	–	8.2 + 0.10	3.40
Oxalis latifolia	–	–	4.0 ± 0.13	9.32	23.5 + 0.19	19.22
Oxalis crinata	25 ± 1.3	17.71	–	–	–	–
Panicum brevefolium Linn.	–	–	19.5 ± 0.20	42.98	–	–
Plantago major Linn.	36 ± 1.7	25.45	7.0 ± 0.13	16.89	3.5 + 0.04	4.36
Polygonum sp.	6 ± 0.3	7.94	3.0 ± 0.08	6.56	14.5 + 0.15	10.18
Potentilla blanda	7 ± 0.5	17.73	2.0 ± 0.06	5.57	2.0 + 0.03	2.58
Rannunculus diffusus DC.	12 ± 0.5	15.15	2.0 ± 0.06	1.20	3.0 + 0.03	3.81
Rubia cordifolia Linn.	8 ± 0.5	11.93	–	–	–	–
Rubus sp.	9 ± 0.6	9.82	12.0 ± 0.19	29.58	–	–
Selaginella sp.	29 ± 1.8	18.74	10.0 ± 4.01	11.38	10.8 + 0.42	29.69
Spiranthus sp.	–	–	–	–	2.0 + 0.03	2.80

Dashes indicate species absence

S. khasiana seedlings in the disturbed stand could be attributed to its greater intolerance to shade, at least in juvenile stage, compared to other species (Khan *et al.* 1987).

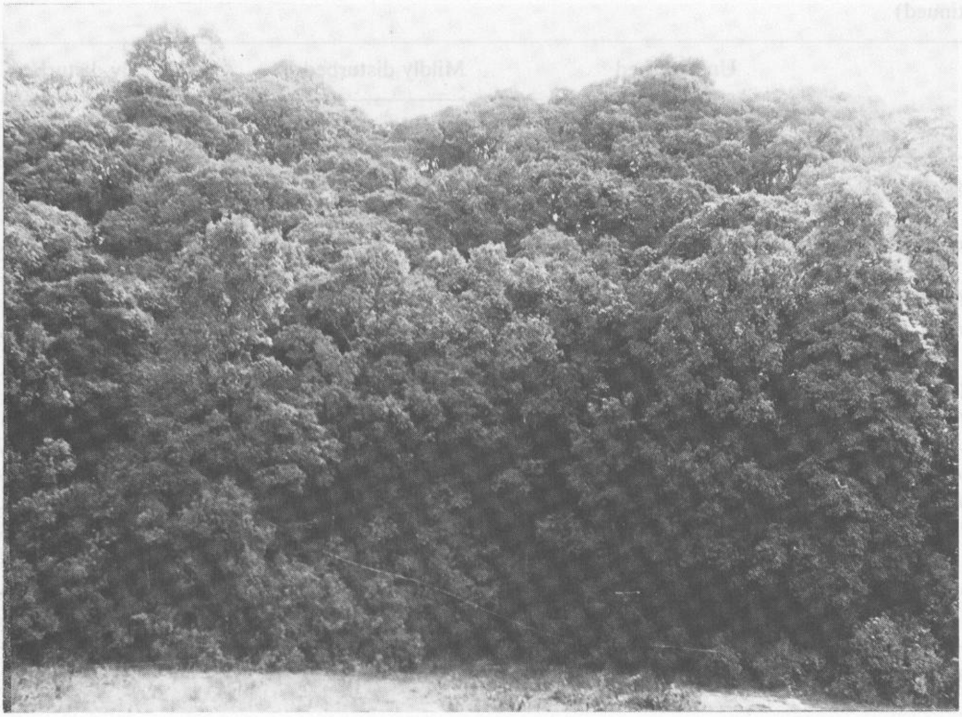
The percentage similarity of tree and shrub species among the three stands indicates that the undisturbed stand was more similar to highly disturbed stand than to mildly disturbed one (Table 3). Comparison of Sørensen's similarity index between the two disturbed stands revealed marked similarity. However, the similarity in the shrub component was more than the trees in the two stands.

The relative abundance in the undisturbed stand was distributed more or less evenly among the different species i.e. high equitability or low

Table 2. Density of tree seedlings (Plants $ha^{-1} \times 10^3 \pm$ S.E.) and saplings (Plants $ha^{-1} \pm$ S.E.) during peak growth period (August–September, 1988) in the three forest stands exposed to different degrees of disturbance.

Species	Undisturbed		Mildly disturbed		Highly disturbed	
	Seedling	Sapling	Seedling	Sapling	Seedling	Sapling
Castonopsis kurzii	–	20 ± 2.0	–	–	–	–
Exbucklandia populnea	–	20 ± 2.0	–	–	–	–
Myrica esculenta	–	–	–	13.33 ± 0.6	–	–
Pinus kesiya	–	–	1 ± 0.10	140.00 ± 2.7	7.8 ± 0.28	892 ± 4.3
Prunus undulata	–	30 ± 2.1	–	–	–	–
Quercus dealbata	32 ± 1.12	40 ± 2.2	3 ± 0.21	60 ± 1.7	2.0 ± 0.08	4 ± 0.2
Quercus griffithii	12 ± 0.8	60 ± 3.4	–	–	1.75 ± 0.11	92 ± 1.2
Rhododendron arboreum	4 ± 0.22	–	–	33.33 ± 1.1	1.5 ± 0.32	88 ± 1.1
Schima khasiana	9 ± 0.69	40 ± 3.1	7 ± 0.52		62 ± 0.32	60 ± 1.1
Taxus baccata	23 ± 1.42		–		–	–

Dashes indicate species absence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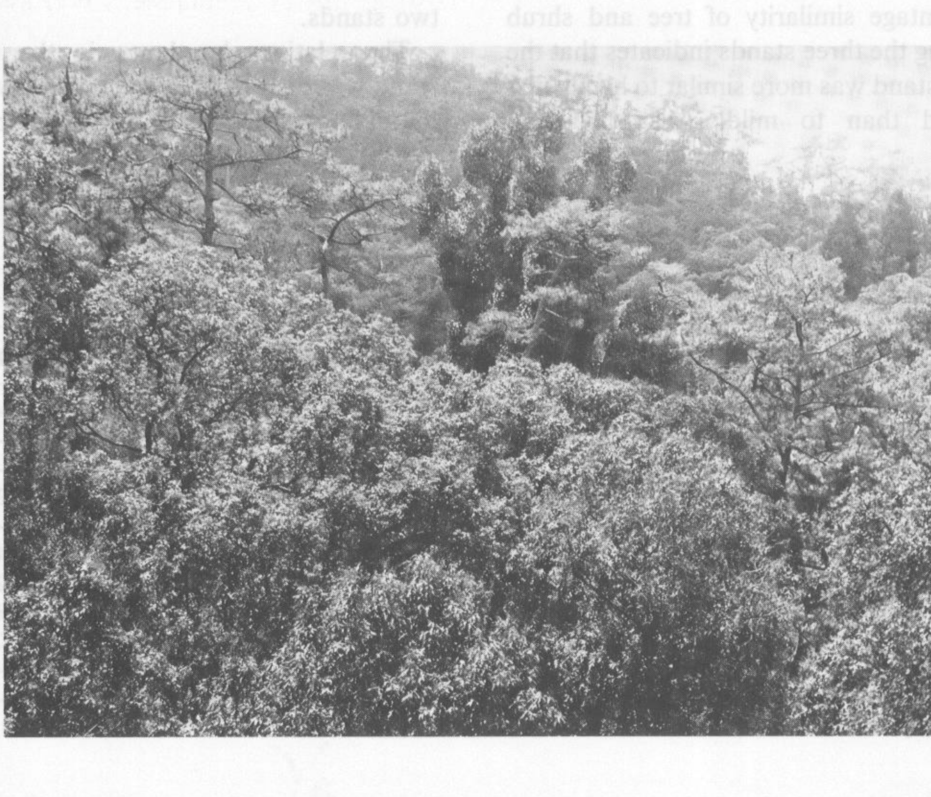
B

Plate 1. Photograph showing canopy of (A) undisturbed; – (B) Midly disturbed and; – (C) highly disturbed stands of sub-tropical broad-leaved forest at Shillong, India.

dominance (Fig. 2), while the disturbed stands presented a low equitability or high dominance

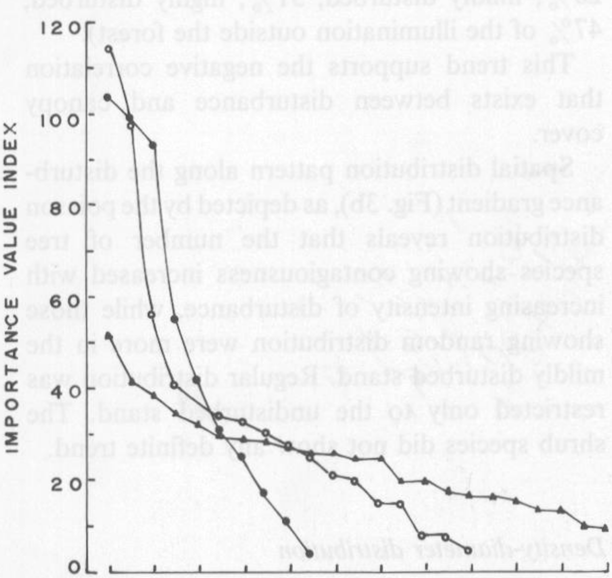

Fig. 2. IVI distribution among trees and shrubs in undisturbed (—▲—), mildly disturbed (—●—) and highly disturbed (—○—) stands.

picture. In the disturbed stands, *P. kesiya* and *Q. dealbata* were the dominant trees while all other species maintained a very low profile.

Species diversity

Fig. 3a shows the change in Pielou's index along the disturbance gradient. The species diversity

Table 3. Comparison of Sørensen's similarity index of tree and shrub components in the three forest stands.

Stand	Trees	Shrubs
Undisturbed vs highly disturbed	50	50
Undisturbed vs mildly disturbed	35.29	35.29
Highlydisturbed vs mildly disturbed	61.54	66.67

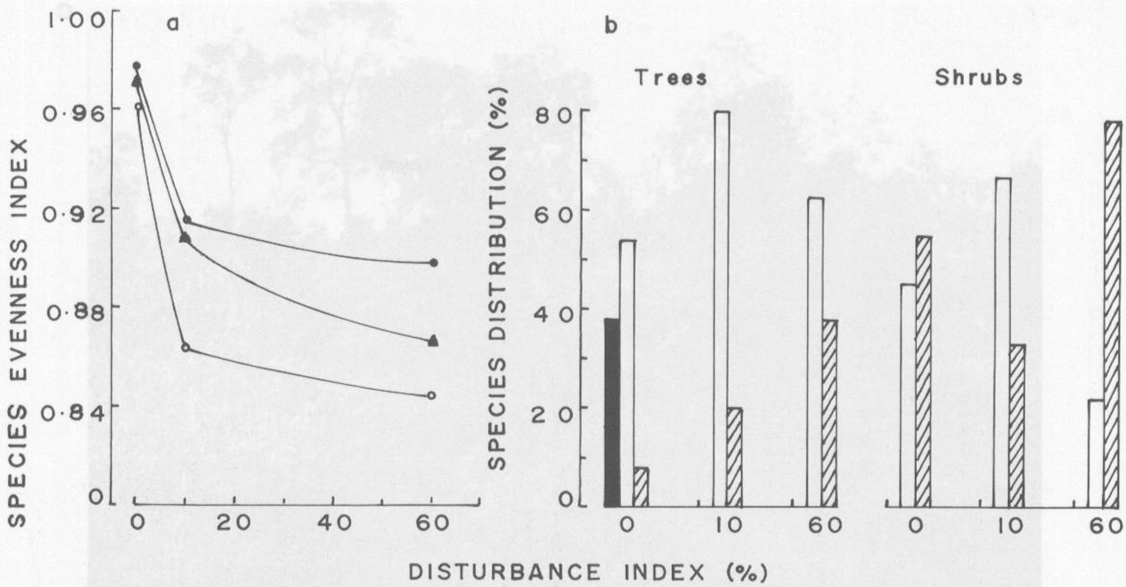

Fig. 3 (a) Species evenness as related to disturbance index. (——●——) trees, (——▲——) shrubs, (——○——) trees and shrubs; – (b) Spatial distribution pattern of trees and shrubs as related to disturbance index ■, regular; □, random and □, contagious distribution.

markedly declined from undisturbed to the disturbed stands. Similar trend was shown by Shannon's species diversity index (H) (undisturbed – 1.0, mildly disturbed – 0.6, highly disturbed – 0.8) and species richness index (d) (undisturbed – 3.6, midly disturbed – 1.3, highly disturbed – 2.2). Species richness is correlated with disturbance as shown by several authors (Grubb 1977; Connell 1978; Houston 1979; Pickett 1980; Armesto & Pickett 1985). Our observations support the concept that the more the species diversity, the more stable the community. The present study, however, does not conform with the views of Grime (1979), Huston (1979) and Armesto & Pickett (1985), who predicted a peak in species diversity at intermediate disturbance intensity or frequency. It may be argued that the characteristics of the system and type of disturbance might be responsible for this trend.

Spatial structure

The canopy cover was almost 100% in the undisturbed stand; it declined to 51.2% in the mildly disturbed stand and finally to 9.9% in the highly disturbed stand. The average light intensity on the forest floor in the three stands increased with increasing degree of disturbance (undisturbed, 20%; mildly disturbed, 31%; highly disturbed, 47% of the illumination outside the forest).

This trend supports the negative correlation that exists between disturbance and canopy cover.

Spatial distribution pattern along the disturbance gradient (Fig. 3b), as depicted by the poisson distribution reveals that the number of tree species showing contagiousness increased with increasing intensity of disturbance, while those showing random distribution were more in the mildly disturbed stand. Regular distribution was restricted only to the undisturbed stand. The shrub species did not show any definite trend.

Density-diameter distribution

The diameter distribution of trees has been often used to represent the population structure of forests (Saxena *et al.* 1984; Khan *et al.* 1987; Newton & Smith 1988). The nature of the curves

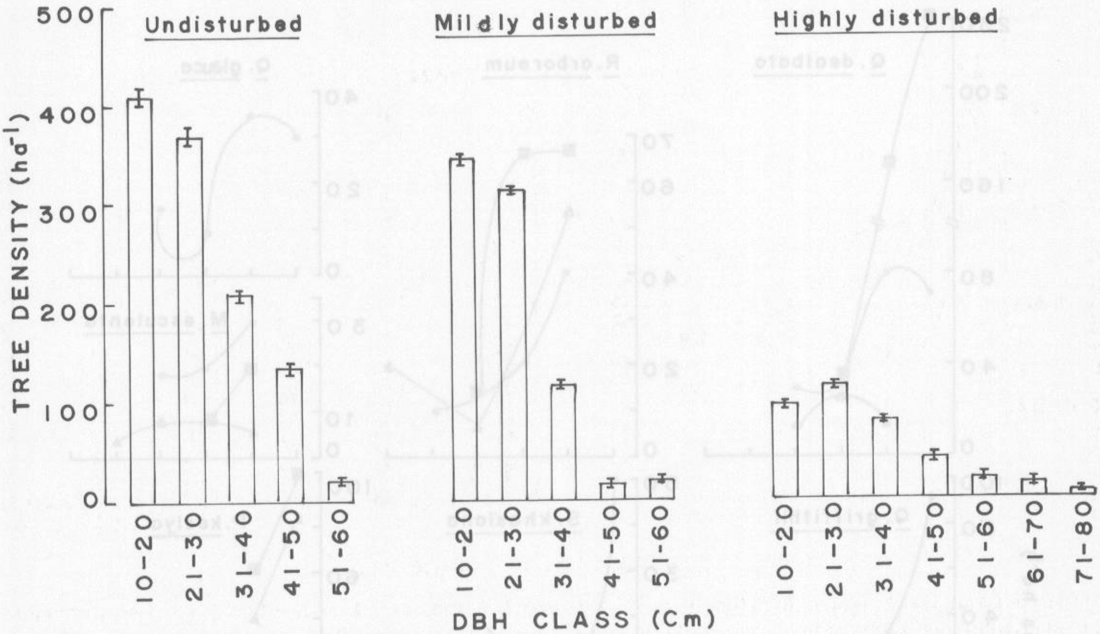

Fig. 4. Density-diameter distribution of trees in the three forest stands.

are also used to interpret the characters of vegetations. Configuration and slope of curves have been correlated with the age structure of stands, successional status of forests (Goff & West 1975; Saxena *et al.* 1984) and degree of tolerance to shade (UNESCO/UNEP/FAO 1978). The density of higher dbh classes was low in all the three stands (Fig. 4) and the forest showed an overall straight line relationship between density and diameter (negative exponential curve) confirming the observations of Schmeiz and Lindsey (1965) for uneven-aged, mixed stands and Knuchel (1953) for predominantly coniferous stands. The change in the shape of the curve at highly disturbed stand may be the result of selective felling of individuals of higher diameter classes. In the undisturbed climax forest, less tree mortality, faster growth (West *et al.* 1981) and high tree density may be the probable causes for predominance of intermediate girth classes.

Population structure of tree species

The density-diameter distribution in the population of different species (Fig. 5) indicates marked variation in the shape of the curves along the disturbance gradient. The shape of the curves for different species ranges from unimodal J-shaped to bimodal mound shaped distribution. Considering the curves from disturbance point of view, the species in the undisturbed stand showed diverse forms of curves which were simplified with increased intensity of disturbance.

The shape of density-diameter curves of *Q. dealbata*, *R. arboreum* and *M. esculenta*, common to all the three stands, exhibited a marked variation. *Q. dealbata* showed a normal distribution in the highly disturbed stand and a straight line relationship in the mildly disturbed stand. In the undisturbed stand, the species showed a rotated sigmoid curve with a plateau near the intermediate diameter region. *R. arboreum* showed a reverse J-shaped curve in the undistrubed and highly disturbed stands and a bimodal mound shaped curve in the mildly disturbed stand. *M. esculenta* showed a density-diameter distribution pattern similar to *Q. dealbata* in the two disturbed stands, while in the undisturbed stand it exhibited a reverse J-shaped curve resembling that of *R. arboreum*. *Q. griffithii* and *S. khasiana* also showed a reverse J-shaped curve

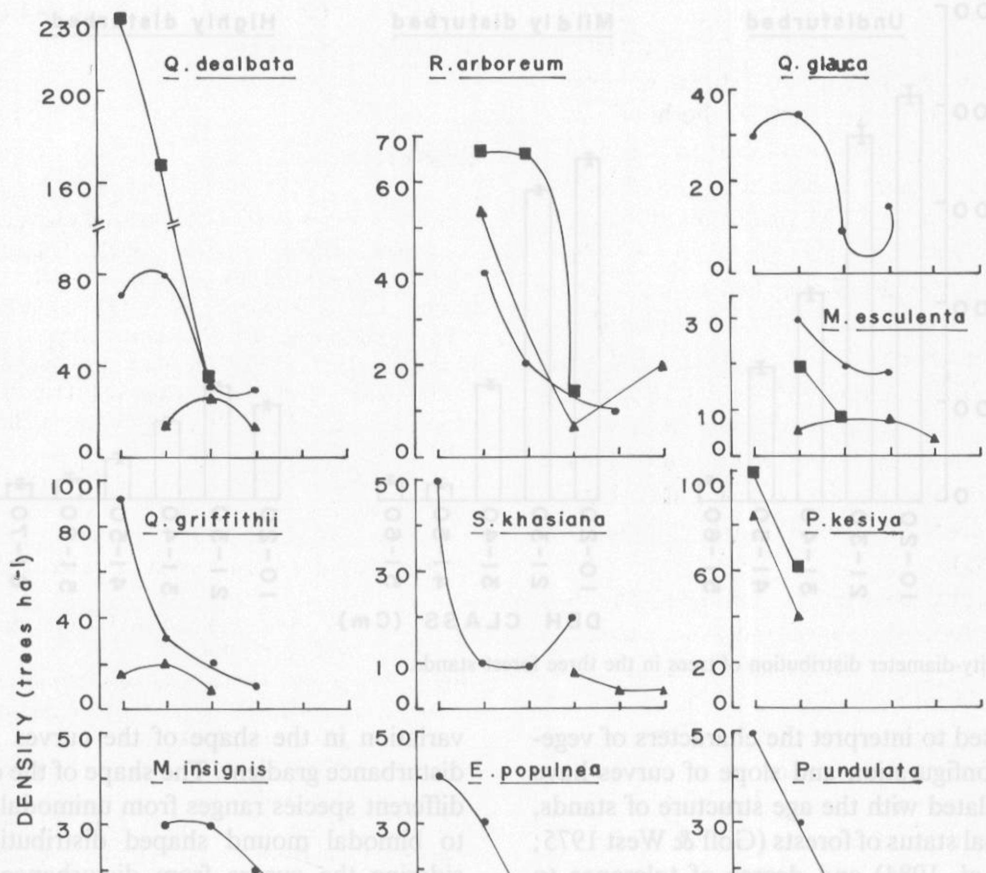

Fig. 5. Species wise density-diameter distribution curves in the undisturbed (—●—), mildly disturbed (—■—) and highly disturbed (—▲—) stands.

in the undisturbed stand. In the highly disturbed stand normal curve was obtained for *Q. griffithii* and a concave curve situated in the higher girth class region was obtained for *S. khasiana*. *P. kesiya*, exclusively present in the disturbed stands showed negative exponential curve, which is characteristic for predominantly coniferous stands (Knuchel 1953). Out of the total sixteen species, eight were present only in the undisturbed stand and two were exclusive to the highly disturbed stand. *Q. glauca* found only in the undisturbed stand showed a rotated sigmoid curve similar to that of *Q. dealbata*. However, *T. baccata, Ficus nerifolia* and *Pieris ovalifolia* showed a reverse J-shaped curve, while *M. insignis* showed a bimodal mound type of distribution. *Castonopsis kurzii* showed a J-shaped curve (peak being at intermediate diameter class) and *Corylopsis himalayana* showed normal distribution. *P. undulata, E. populnea* and *Engelhardtia spicata* had a typical mixed stand character of negative exponential type (Schmeiz & Lindsey 1965).

A normal distribution curve can be interpreted as showing preponderance of individuals in intermediate girth class, which may be due to infrequent recruitment and selective felling of trees of larger girth classes. According to Benton and Werner (1976), the population is on the way to extinction if such a trend continues. Similarly, a plateau in a rotated sigmoid curve can be explained on the basis of the lower removal rate (Saxena *et al.* 1984) across the larger diameter classes as interpreted by Wet *et al.* (1981). Occurrence of reverse J-shaped curves in the undisturbed stand indicates predominance of lower diameter classes, which may be attributed to less tree mortality and high density. In the disturbed stands, heavy exploitation in higher girth classes results in such type of curve. Occurrence of bimodal mound shaped curves in certain species in the undisturbed stand appears to be species-dependent, while in the disturbed stand it has resulted due to selective cutting of some particular girth classes which varies from species to species. J-shaped curve represents the typical behaviour of species in a climax undisturbed forest.

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