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PATTERNS OF TREE DIVERSITY WITHIN A LARGE-SCALE PERMANENT PLOT OF TROPICAL EVERGREEN FOREST, WESTERN GHATS, INDIA

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Abstract. Alpha diversity of a tree community spectrum was analyzed by hectares to address the extent of variation in tree diversity between thirty adjacent 1-ha subplots within a 30-ha permanent plot of tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. Three pairs of adjacent subplors had an equal number of species and for one pair tree density matched. In the others the difference in species richness ranged from one to 23 species ha^{-1}, while tree density ranged from 2 to 192 trees ha^{-1}. In the majority of subplots the observed variation in tree species richness, density, and basal area (in all the subplots) exhibited a random pattern at a $100m^2$ scale. A total of 67% to 86% of species in each 1-ha subplot showed a random distributional pattern. There was no significant difference in species and family diversity indices between the thirty 1-ha subplots. The species-area curve did not stabilize in any of the 30 subplots at the 1-ha scale. Of the total species obtained in each subplot, 50% were captured within a 0.2 ha and 80% within a 0.5 ha scale. Principal component analysis, using the abundance of the 20 top-ranked species of each 1-ha subplot, categorized the subplots into three clusters excluding ha 4 and 5. Spearman coefficient of rank correlation analysis displayed the variation in species richness between subplots, which could partially be explained by the dominance of a few species. The size class frequency distribution of each subplot showed the classic, nearly negative exponential pattern. Being a permanent plot, as the studies on spatio-temporal changes in species diversity and density of trees continue in subsequent years, they will yield additional data useful for understanding biodiversity, forest management, and conservation. *Accepted 28 August 2001.*

Key words: Alpha diversity, India, permanent plot, trees, tropical forests, Western Ghats.

INTRODUCTION

Tropical wet forests are rapidly undergoing clear-felling, and are being either replanred wirh commercial monocultures or converted ro differenr land-uses (Parthasarathy 1999, Jha *et al.* 2000, Rennolls & Laumonier 2000). The diversity of trees is fundamental to total rainforest biodiversity, because rrees provide resources and habitat structure for all other rainforest species (Cannon *et al.* 1998). Understanding the variation in diversity is a requisite for making sound decisions about protecting and managing forests (Condit *et al.* 1998).

Much recent literature has analyzed the extent of variation in tree diversity of widely separated forests either along altitudinal (Heaney & Proctor 1990; Kitayama 1992; Lieberman *et al.* 1996; Aiba & Kitayama 1999; Parthasarathy 1999, 2001; Srinivas & Parthasarathy 2000) or latitudinal gradients (Phillips *et al.* 1994, Ghate *et al.* 1998), in mixed and monodominant forest types (Martijena & Bullock 1994, Cao & Zhang 1997, Makana *et al.* 1998) or between distanr forest plots represenring particular geographic locations (Thorington *et al.* 1982, Proctor *et al.* 1983, Campbell *et al.* 1992, Newbery *et al.* 1992, Duivenvoorden 1994, Johnston & Gillman 1995, Pascal & Pelissier 1996, Kadavul & Parthasarathy 1999a,b). However, there are marked variations in stand structure and species composition within rhe same forest type (Condit *et al.* 1996, He *et al.* 1997) and studies on within-plot variation are few (Campbell *et al.* 1986, Newbery *et al.* 1996). Replicated permanent plots within a forest type might provide insight into the nature of variation within the forest type and thus foster a better understanding of its dynamics and composition (Bunyavejchewin 1999). To decipher the variation between adjacent (contiguous) 1-ha subplots, the data from a 30-ha (600 m × 500 m) permanent plot established during 1997–98 (Ayyappan & Parthasarathy 1999) in the tropical evergreen forest of India have been adopted.

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species was included in this analysis. Spearman coefficients of rank correlation were computed for pairwise association of abundance of five dominant species in each hectare (which are represented by more than 500 individuals in the entire 30-ha area), treating subplot (i.e., 1-ha area) density, subplot species richness, and number of individuals in the lower girth class limit (30–60 cm gbh) separately. Similarly, for number of individuals ha^{-1} in the lower girth limit vs. subplot density and vs. subplot species richness. This is to elucidate the possible reason for variation in species richness among the thirty 1-ha subplots. Species importance value index (as per Cottom & Curtis 1956) and family importance value (based on Mori *et al.* 1983) were calculated.

RESULTS

Tree diversity. The 30-ha plot as a whole contained 153 tree species in 50 families. The mean species richness was 66 ha^{-1} with an 11% coefficient of variation. On a hectare scale, there was a wide variation in species richness among the thirty 1-ha subplots, ranging from 52 species in the species-poor subplot ha 5 to 79 species in the species-rich ha 11 and 20 (Table 1). Only in three pairs of adjacent subplots

TABLE 1. Species richness, stand density, diversity indices, and basal area details of trees (≥30 cm gbh) by hectares in the 30-ha permanent plot.

Hectare	Number of		Diversity indices		Basal area
	Species	Individuals	Shannon	Simpson	(m^2)
1	58	273	3.54	0.04	37.5
2	56	360	3.39	0.05	41.1
3	73	348	3.74	0.03	35.6
4	73	422	3.78	0.03	33.7
5	52	275	3.34	0.05	27.2
6	75	406	3.93	0.02	34.4
7	71	422	3.24	0.06	33.3
8	58	473	3.24	0.06	35.6
9	61	363	3.50	0.04	31.7
10	68	328	3.53	0.05	33.3
11	79	343	3.95	0.02	28.6
12	73	430	3.64	0.04	34.7
13	62	495	3.37	0.05	40.7
14	61	493	3.27	0.06	45.3
15	65	544	3.46	0.05	37.5
16	55	548	3.26	0.06	46.6
17	61	528	3.35	0.05	37.7
18	72	414	3.72	0.03	25.9
19	69	454	3.63	0.04	36.0
20	79	341	3.95	0.02	32.1
21	71	356	3.75	0.03	33.1
22	73	422	3.70	0.03	35.1
23	69	501	3.53	0.05	37.6
24	77	588	3.51	0.05	39.9
25	60	629	3.30	0.06	44.8
26	55	606	2.89	0.12	33.1
27	63	674	3.30	0.07	37.1
28	61	598	3.33	0.06	41.7
29	67	406	3.57	0.04	35.1
30	65	375	3.63	0.04	48.0

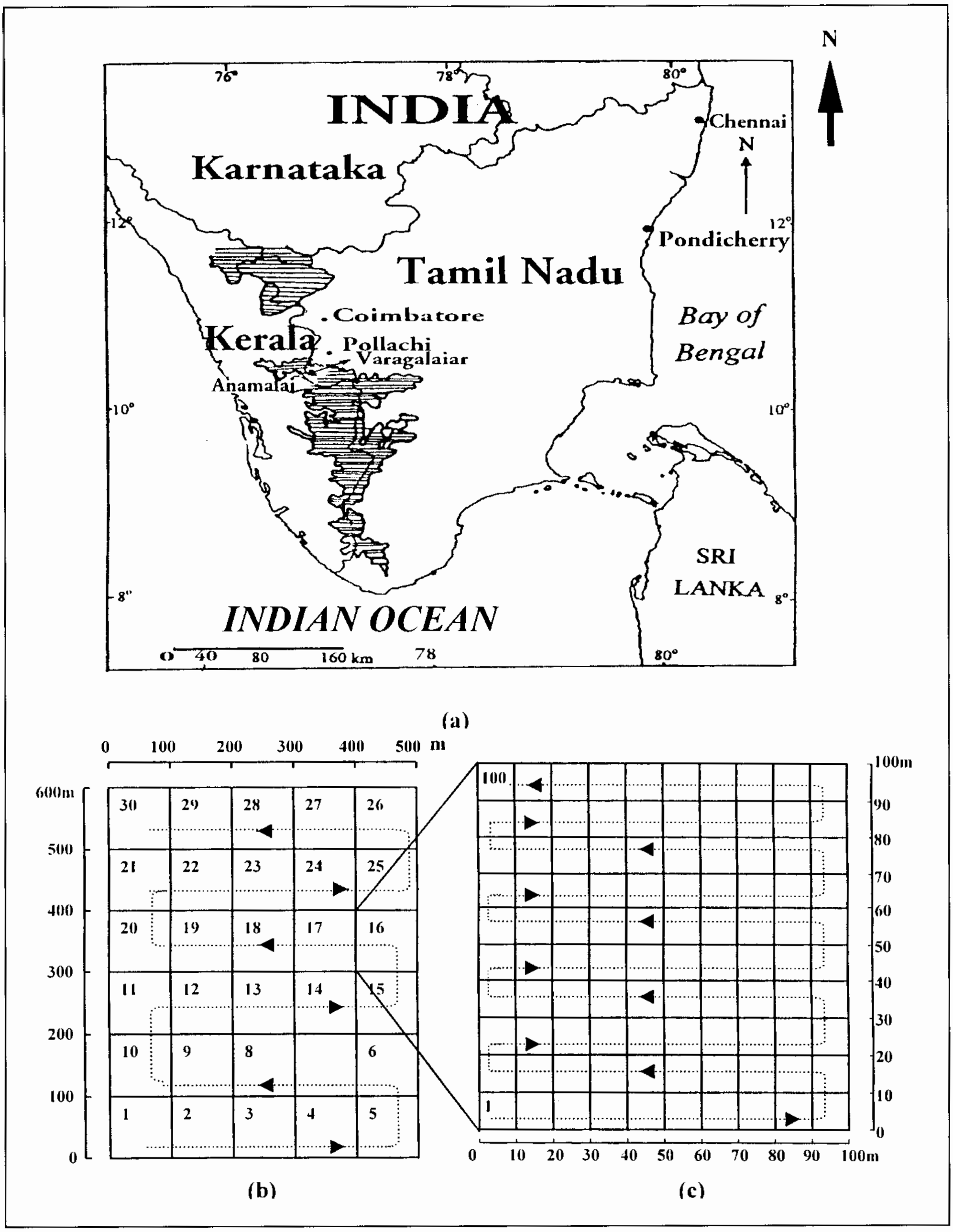

FIG. 1. Map showing the study site Varagalaiar in the Anamalais, Western Ghats, south India (a) and the layout of the 30-ha (600 m × 500 m) plot (b), with a hectare enlarged (c) showing one hundred 10 m × 10 m quadrats. The arrows indicate the sequence by which the census was made in the 30 ha plot and in each 1-ha subplot.

species was included in this analysis. Spearman coefficients of rank correlation were computed for pairwise association of abundance of five dominant species in each hectare (which are represented by more than 500 individuals in the entire 30-ha area), treating subplot (i.e., 1-ha area) density, subplot species richness, and number of individuals in the lower girth class limit (30–60 cm gbh) separately. Similarly, for number of individuals ha^{-1} in the lower girth limit vs. subplot density and vs. subplot species richness. This is to elucidate the possible reason for variation in species richness among the thirty 1-ha subplots. Species importance value index (as per Cottom & Curtis 1956) and family importance value (based on Mori *et al.* 1983) were calculated.

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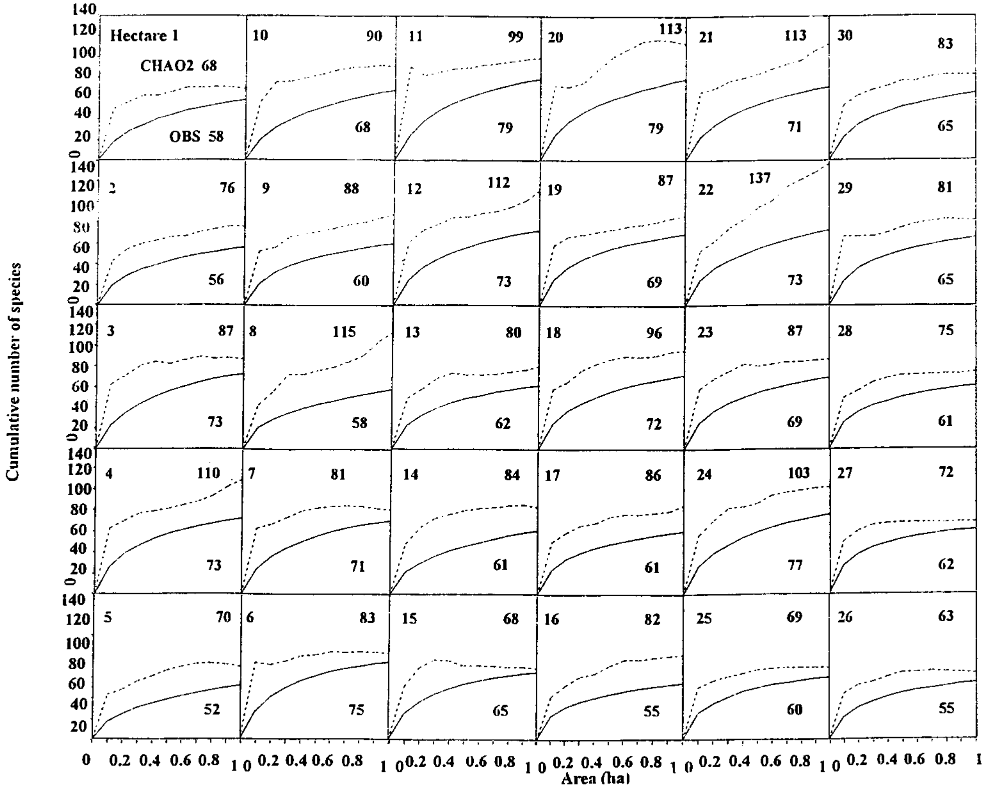

FIG. 2. Observed and estimated (Chao 2) species-atea curves for the thirty 1-ha subplots. At the top left hectare order is given; at the top right Chao 2 and bottom right observed (OBS) species richness are provided.

(ha 3 and 4, 11 and 20, 14 and 17) was tree species richness similar, while in the other subplots the difference in species richness varied from 1 to 23 species (Table 1 and Fig. 2). Mean tree species richness pet 100 m² of each 1-ha subplot varied significantly for trees ≥ 30 cm gbh (Table 2). Similarly, for the subsample area of 400 m², mean species richness of trees ≥ 30 cm gbh, ≥ 60 cm gbh, and ≥ 120 cm gbh varied significantly between the subplots (Table 2), but for trees ≥ 240 cm gbh mean species richness between 1-ha subplots was significant. For the subsample area of 2500 m², mean species richness for tbe minimum girth threshold of trees ≥ 30 cm, ≥ 60 cm, ≥ 120 cm, and ≥ 240 cm did not vary significantly between subplots. The coefficient of variation in species richness of 100 m² of each 1-ha subplot varied from 33% to 67%. At the scale of 400 m² it ranged from 12% to 46% and for 2500 m² it varied between 4% to 38%. A chi-square test for random variability of species richness revealed that in twenty eight (1-ha) subplots species richness is dispersed randomly (χ^2 ranged from 56 to 112, df = 99, $P < 0.05$), while in the remaining 2 subplots ha 20 and 21 it displayed a non-random pattern (χ^2 128, df = 99, $P < 0.05$). Individual species distribution in each 1-ha subplot, based on the ratio of observed to expected density of each and every species (Fig. 3), revealed that 67% to 86% of species scored the index value of 1, indicating a random distribution. One to 14% of the species in each hectare scored < 1 (0.8 or 0.9), displaying a slight tendency towards a uniform pattern, while the remaining 10% to 31% of species (ratio > 1 to 2) were clumped.

The Shannon diversity index was highest for ha 11 and 20 and lowest for ha 26. Except for ha 26, the Shannon index showed a narrow range of variation (3.24 to 3.95) between the other subplots (Table

1). The Simpson index showed the reverse of the Shannon index, i.e., it was highest (0.12) for ha 26 and lowest (0.02) for ha 6, 11 and 20. The Simpson index (indicating the proportion of 100 pairs taken at random composed of two different species) was as low as 88 pairs for ha 26 and for the remaining hectares it varied from 93 to 98 pairs.

The mean Sorensen similarity index percentage (100% indicates identical subplots) for species between 1-ha subplots was 81%, varying from 70% to 87% for various subplots. By the exclusion of species with just 1, 2, 3, and 4 individuals in each 1-ha subplot, the mean Sorensen similarity index between subplots was 80%, 79%, 79%, and 78%. Further, by exclusion of tree species with 5 and 6 individuals the mean index value remained the same (78%).

Tree density and basal area. The mean tree density per hectare was 447 with a 24% coefficient of variation. The mean stem density for trees ≥ 30 cm gbh per 100 m^2 of each subplot differed significantly (Table 2). The mean tree density of trees ≥ 240 cm gbh did not differ for the subsample areas of 400 m^2 and 2500 m^2 between subplots, while for the other tree girth classes (≥ 30 cm, ≥ 60 cm, and ≥ 120 cm gbh) it differed significantly (Table 2). Coefficient of variation in tree density of each 1-ha subplot ranged from 35% to 72% at the 100 m^2 scale, 18% to 48% at 400 m^2, and 4% to 38% at the 2500 m^2 scale. The χ^2-test revealed that in 25 subplots tree density was dispersed randomly (χ^2-value ranged from 75 to 123, df = 99, $P < 0.05$) and in the remaining five 1-ha subplots (ha 5, 18, 19, 20, and 21) it showed non-randomness. There is a wide 2.5-fold difference between the subplots with greatest density (ha 27) and lowest density (ha 1) (Table 1). Only one pair of juxtaposed subplots (ha 4 and 7) contained a similar density of trees (422 trees ha^{-1}), while in the others the difference in stem density varied from 2 to 192 trees. The mean basal area per 100 m^2 of each subplot varied significantly (F = 2.7, $P < 0.05$). Coefficient of variation in basal area at 100 m^2 of each 1-ha subplot varied from 69% to 120%. The χ^2 test for the random variability of basal area per 100 m^2 of each 1-ha subplot demonstrated that the dispersion was random in all subplots, with χ^2 values ranging from 18 to 50, df = 99, $P < 0.05$. Stand basal area of the thirty 1-ha subplots ranged from 25 m^2 ha^{-1} (ha 18) to 47 m^2 ha^{-1} (ha 16 and 30) (Table 1).

Species-area curve. The observed species accumulation and incidence-based richness estimator (Chao 2) curves for the thirty 1-ha subplots are compared in Fig. 2. The observed species accumulation curve of each 1-ha subplot captured about 50% of the species on the 0.2-ha scale and 80% on the 0.5-ha scale, increasing gradually (an addition of 2 to 3 species for every 0.1 ha) towards an asymptote, but it did not reach a stable value. The rate of increase of the observed species accumulation curve was lowest (2.6) for the species-poor ha 5 and highest (7.4) for one of the species-rich subplots (ha 11). The Chao 2 species

TABLE 2. Range of mean tree species richness and tree density (for the different minimum girth classes) for the sample size of 100 m^2 (10 m × 10 m), 400 m^2 (20 m × 20 m) and 2500 m^2 (50 m × 50 m) with F value (one-way analysis of variance) of thirty 1-ha adjacent subplots. Degrees of freedom: 29, 2970 for 100 m^2; 29, 720 for 400 m^2 and 29, 30 for 2500 m^2.

Sample size m	Minimum gbh (cm)	Range of mean species richness (F)		Range of mean tree density (F)	
10 × 10	≥ 30	3–5	(18.59)NS	3–7	(25.27) NS
20 × 20	≥ 30	8–15	(7.85) NS	11–27	(19.76) NS
20 × 20	≥ 60	4–9	(5.32) NS	5–12	(7.33) NS
20 × 20	≥ 120	2–4	(2.05) NS	2–5	(3.20) NS
20 × 20	≥ 240	0.12–0.92	(1.84)***	0.12–1	(1.93)***
50 × 50	≥ 30	27–44	(1.63)**	68–168	(10.23) NS
50 × 50	≥ 60	17–31	(1.95)***	33–77	(5.37) NS
50 × 50	≥ 120	8–17	(1.98)***	15–30	(2.59) NS
50 × 50	≥ 240	0.25–5	(1.56)**	0.75–7	(1.81)**

NS –Not significant at $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$.

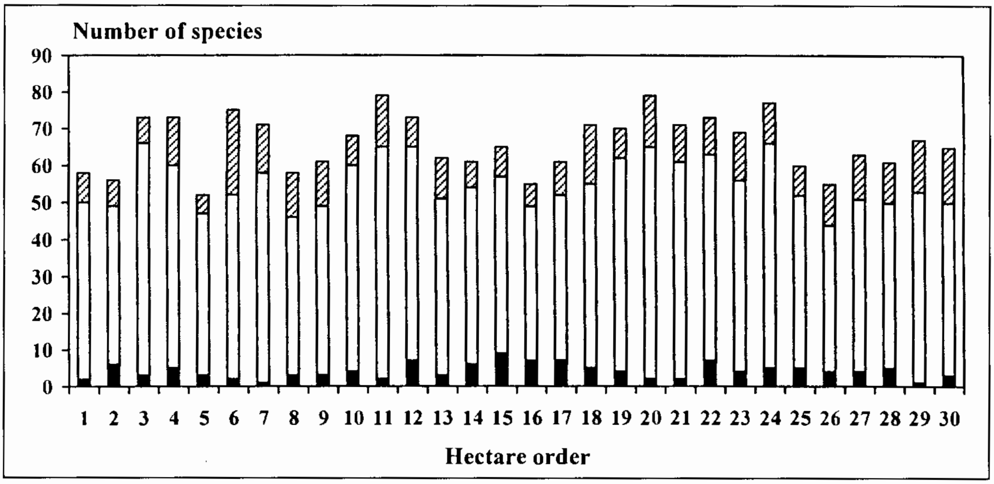

FIG. 3. Tree species distribution in the thirty 1-ha subplots based on the ratio of observed and expected tree species density. Filled bar ratio < 1, open bar ratio = 1, thatched bar ratio > 1. Ratio 1 indicates that species distribution is random, < 1 indicates species departure towards uniform and > 1 towards clumped.

richness curve yielded an overestimate (of 3 [ha 15] to 54 species ha^{-1} [ha 22]), but the curve is more or less parallel to the observed species accumulation curve and reached a stable value for 15 subplots (Fig. 2).

Principal component analysis. The principal component analysis employing species abundance displayed a total of 28 subplots that are positively correlated with both factors (Eigenvalue of Factors I and II are 16.17 and 3.69 respectively). These accounted for 66.23% of the variation and formed three distinct clusters (Fig. 4). Of the remaining two subplots, ha 5 was negatively correlated with both factors, while ha 4 was negatively correlated with Factor I.

Spearman coefficient of rank correlation. The abundance of the five dominant species (*Drypetes longifolia*, *Reinwardtiodendron anamallayanum*, *Poeciloneuron indicum*, *Fahrenheitia zeylanica*, and *Dipterocarpus indicus*) was positively correlated with total tree density of the subplots (Spearman r (r_s) = 0.89, P = 0.00) and also with the number of individuals in the lower girth class (30–60 cm gbh) (r_s = 0.88, P = 0.00). Similarly, density of stems in the 30–60 cm girth class was positively correlated with density of stems per hectare (r_s = 0.96, P = 0.00). The abundance of the five dominant species and density of stems in the 30–60 cm girth class were negatively correlated with species richness of the subplots (r_s = –0.36, P = 0.05 and r_s = -0.19, P = 0.29 respectively).

Importance value index - species dominance. Of the 153 species encountered in the 30-ha plot, 10 species dominated in terms of IVI (Table 3). *Drypetes longifolia* dominated in 9 subplots, *Dipterocarpus indicus* in 7 subplots, followed by *Fahrenheitia zeylanica* and *Poeciloneuron indicum* (in 3 subplots each), *Reinwardtiodendron anamallayanum* and *Vitex altissima* (in 2 subplots each), and *Bischofia javanica*, *Cleidion spiciflorum*, *Palaquium ellipticum*, and *Terminalia crenulata* in one subplot each (Table 3).

Families. The number of families encountered in the thirty 1-ha subplots varied from 21 (in the species-poor ha 26) to 36 families (in the species-rich ha 11 and 20) (Table 4) and the mean number of families per hectare is 28. The Shannon diversity index for families displayed a trend similar to that of species diversity. It was highest (index value 3.0) for ha 20 and lowest (2.1) for ha 26 (Table 4). Mean number of species per family in each subplot was three for 6 subplots (ha 15, 23, 26, 27, 28, and 29); the others invariably had two species per family (Table 4). Mean family richness per 100 m^2 quadrat differed significantly between subplots (F = 13.16, $P < 0.05$).

Of the 50 families encountered in the thirty hectare plor, four families were predominant (based on the family importance value). Combretaceae and Meliaceae were dominant in one subplot each (ha 5 and 9), Dipterocarpaceae in 3 subplots (ha 21, 22 and 29), and the remaining 25 subplots were dominated by Euphorbiaceae (Table 4). Invariably, Euphorbiaceae was the top-ranked family in terms of species richness in all thirty subplots, represented by 7 to 12 species per hectare.

Tree size-class distribution. Tree size-class frequency distribution of stem density of the thirty subplots followed a more-or-less negative exponential pattern (Fig. 5). The stem density of the lowest girth class (30–60 cm gbh) conrribured ≥ 50% of the total forest stand density in all subplots, except in three subplots (42, 45 and 46% for ha 1, 10, and 21 respectively). Invariably, ten peripheral subplots (ha 1 to 5 and 10, 11, 20, 21, and 30) contained a low density of the lowest girth class when compared to their adjacent interior subplots. In the subsequent higher girth classes, the stem density of all the subplots were more or less similar in proportion. The mean per cent contribution of the 60-90 cm gbh class was less than 17%, followed by 120 cm contributing 10%, 150 cm 8%, and the 180 cm class 5%. The remaining higher girth classes (210 to 330 cm) contributed less than 8% of the srand density in all the subplots.

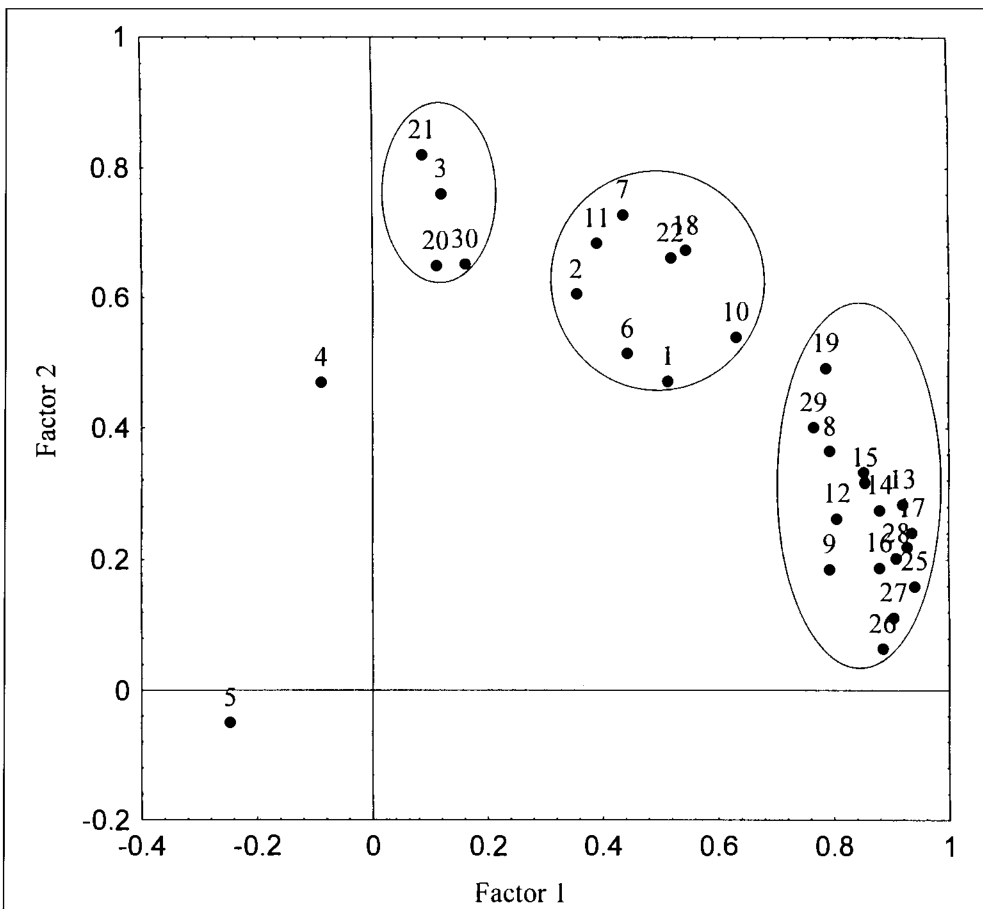

FIG. 4. Principal component analysis, using the abundance data of 20 top-ranked tree species in each 1-ha subplot.

DISCUSSION

The idea that there is a limit to the number of species in communities is pervasive in ecology (e.g., MacArthur & Levins 1967, Lowlor 1980, Giller 1984, Case 1991, Pimm 1991, Sheil 1996). The question "why do areas vary in species richness?" is difficult to answer definitively. In general, there are two main ways in which more species can co-exist in an area: (1) if there are no dominants, i.e., if all species are equal competitors with rheir continued existence depending on stochastic factors, and/or (2) if there are many micro-niches (spatially and temporally) with different dominants in each (Tilman & Pacala 1993).

This study documented no single species dominance in the stand (the first-ranked species accounted for < 20% of the IVI of each subplot) and most of the species were distributed randomly in each 1-ha subplot. In the majority of the 1-ha subplots (28 out of 30 hectares) the observed variation in species richness and tree density (in 25 subplots) at the 100 m^2 scale followed a normal random pattern. The topography of these subplots varied from flat terrain to gentle to moderate slopes with or without streams (width < 4 m) traversing the area. The non-random distribution of species richness in two subplots (ha 20 and 21) can be attributed to the presence of a stream (whose width

TABLE 3. Top-ranked species (based on their IVI score) along with their density and basal area contribution in the respective hectares in the thirty 1-ha subplots at Varagalaiar.

Hectare	Species (family)	Density	Basal area (m^2)	IVI
1	*Palaquium ellipticum* (Dalz.) Baillon (Sapotaceae)	17	4.2	25
2	*Fahrenheitia zeylanica* (Thw.) Airy Shaw (Euphorbiaceae)	34	2.9	26
3	*Fahrenheitia zeylanica*	36	2.4	26
4	*Vitex altissima* L.f. (Verbenaceae)	22	4.5	24
5	*Terminalia crenulata* Roth (Combretaceae)	25	6.6	42
6	*Poeciloneuron indicum* Bedd. (Clusiaceae)	25	1.9	18
7	*Fahrenheitia zeylanica*	42	3.2	29
8	*Poeciloneuron indicum*	38	4.8	29
9	*Reinwardtiodendron anamallayanum* (Bedd.) Saldanha (Meliaceae)	48	1.0	28
10	*Reinwardtiodendron anamallayanum*	49	1.0	32
11	*Dipterocarpus indicus* Bedd.(Dipterocarpaceae)	15	2.9	19
12	*Dipterocarpus indicus*	24	6.2	31
13	*Drypetes longifolia* (Blume)Pax & Hoffm. (Euphorbiaceae)	66	2.0	30
14	*Dipterocarpus indicus*	25	11.4	36
15	*Poeciloneuron indicum*	44	6.8	34
16	*Drypetes longifolia*	76	1.9	29
17	*Drypetes longifolia*	74	2.0	31
18	*Cleidion spiciflorum* (Burm.f.) Merr. (Euphorbiaceae)	30	0.9	16
19	*Drypetes longifolia*	45	1.1	21
20	*Vitex altissima*	13	2.3	15
21	*Dipterocarpus indicus*	18	3.3	19
22	*Dipterocarpus indicus*	33	6.0	32
23	*Drypetes longifolia*	73	1.9	31
24	*Drypetes longifolia*	93	1.9	31
25	*Drypetes longifolia*	112	2.4	36
26	*Drypetes longifolia*	181	3.1	59
27	*Drypetes longifolia*	136	2.9	42
28	*Dipterocarpus indicus*	52	8.5	37
29	*Dipterocarpus indicus*	32	8.3	39
30	*Bischofia javanica* Blume (Bischofiaceae)	23	7.5	29

varied from 8 to 10 m) traversing both the subplots. This renders a pottion of these subplots devoid of trees. The subplots ha 5, 18, and 19 also contained streams (width 8 to 10 m), in addition to the above two subplots. The ptesence of streams in these five subplots would have tesulted in non-random dispetsion of ttee individuals. Among these subplots, ha 5 tecorded the lowest species richness (Table 1) probably due to its well-drained, sloping and exposed terrain with many bouldets.

Possible mechanisms that determine and maintain species diversity in tropical forests have been extensively reviewed. It is likely that density-dependent processes during seedling/sapling rectuitment are critical in determining both species divetsity and tegulation of tree populations in both species-rich and species-poot forest types (Connell *et al.* 1984, Hubbell & Foster 1990, Weldon *et al.* 1991, Condit *et al.* 1992). According to Kohyama (1997), the canopy atchitecture of vegetation creates a spatial heterogeneity of microenvironments and resources (autogenic engineers) and thus promotes stable coexistence among plant species. Our study also at least pattially points to density-dependent ptocesses being a factot

TABLE 4. Family tichness and diversity, mean number of species and individuals, and predominant family, with its family importance value (FIV) in the thirty 1-ha subplots of tropical evergreen forest at Varagalaiar.

Hectare	Family richness	Shannon diversity	Mean species per family	Predominant family	FIV
1	26	2.5	2	Euphorbiaceae	65
2	27	2.4	2	Euphorbiaceae	73
3	30	2.7	2	Euphorbiaceae	59
4	33	2.9	2	Euphorbiaceae	47
5	27	2.6	2	Combretaceae	74
6	33	2.7	2	Euphorbiaceae	60
7	30	2.5	2	Euphorbiaceae	71
8	28	2.3	2	Euphorbiaceae	68
9	28	2.5	2	Meliaceae	59
10	30	2.5	2	Euphorbiaceae	62
11	36	2.9	2	Euphorbiaceae	56
12	30	2.6	2	Euphorbiaceae	55
13	26	2.3	2	Euphorbiaceae	73
14	26	2.3	2	Euphorbiaceae	66
15	24	2.3	3	Euphorbiaceae	68
16	24	2.3	2	Euphorbiaceae	65
17	27	2.3	2	Euphorbiaceae	76
18	32	2.7	2	Euphorbiaceae	65
19	32	2.7	2	Euphorbiaceae	55
20	36	3.0	2	Euphorbiaceae	44
21	31	2.8	2	Dipterocarpaceae	48
22	32	2.8	2	Dipterocarpaceae	52
23	26	2.4	3	Euphorbiaceae	61
24	31	2.5	2	Euphorbiaceae	59
25	25	2.4	2	Euphorbiaceae	65
26	21	2.1	3	Euphorbiaceae	84
27	23	2.4	3	Euphorbiaceae	66
28	23	2.3	3	Euphorbiaceae	65
29	26	2.4	3	Dipterocarpaceae	54
30	28	2.7	2	Euphorbiaceae	51

in the species diversity of an area. Even though the Varagalaiar forest belongs physiognomically to the same community, the observed variation in species richness between 1-ha subplots could possibly be due to the dominance by fewer species, as is evident from the present static tree inventory data. In our site, the dominance of 5 ahundant species is positively correlated with density of stems ha^{-1}, and with the number of trees in the lower girth class (30–60 cm gbh), and negatively correlated with species richness. In addition, the dominant species occupy different strata in the forest: *Drypetes longifolia* is a lower srory component of the forest, *Reinwardtiodendron anamallayanum* and *Fahrenheitia zeylanica* occupy the midstory, and *Poeciloneuron indicum* and *Dipterocarpus indicus* forms the upper story.

The narrow range of variation in the diversity indices observed between the subplots could be attributable to the variation in the proportional abundance of various species in each subplot, which is not so high. Hubbell *et al.* (1999) demonstrated that there is a high degree of constancy in relative species abundance despite large changes in stem density during the gap regeneration process, which may be due to a random thinning process and performance of individuals. Probably such constancy would also be expected in the established canopy trees. The subplots ha 11 and 20 accounted for the highest Shannon and the lowest Simpson values due to high species richness and low abundance of component species. By contrast, ha 26 had a high abundance of *Drypetes longifolia* (181 trees) resulting in a high Simpson index and a low Shannon value, as well as a low species richness (55 species). The Sorensen similarity index demonstrated that the thirty 1-ha subplots differed from each other by 13% to 30% of species, which could probably be attributed to the rarity of species in terms of their density and spatial distribution. The mean Sorensen similariry index of 30 subplots, after sequential removal of rare species, was nearly the same, indicating that the percentage similarity index is also maintained between the common species (in terms of density), and this in turn is evidence for the concept of the spatial rarity of species.

Although the richness estimators plateaued the curves, the empirical 1-ha site data did not exhibit this trend. The species-area curve did not stabilize at the 1-ha scale, which is in conformity with other tropical evergreen forests (Wattenberg & Breckle 1995, Lieberman *et al.* 1996, Parthasarathy & Karthikeyan 1997, Wright *et al.* 1997, Milliken 1998, Kadavul & Parthasarathy 1999a, b).

The presence of *Drypetes longifolia*, a shade-loving lower story species, greatly contributed to subplot segregation in the principal components of factor analysis. The subplots ha 4 and 5 shared 9 species, but differed from the other clusters by the absence of *Drypetes longifolia*. In addition, the absence of *Poeciloneuron indicum* and *Fahrenheitia zeylanica* segregated ha 5. Characteristically these subplots are situated in well drained firm terrain, where the upper story is dominated by the deciduous species *Vitex altissima* and *Terminalia paniculata*, and the lower story by the light-demanding species *Aporusa lindleyana* (40 and 31 trees in ha 4 and 5 respectively). Subplots ha 3, 20, 21, and 30 shared 10 species, with poor representation of *Drypetes longifolia*, but dominated by the mid-story species *Fahrenheitia zeylanica*, *Flacourtia montana*, and *Dimocarpus longan*. Eight subplots (ha 1, 2, etc.......18, and 22) formed a single cluster, and these had 6 species in common. *Drypetes longifolia* was moderately denser in these subplots. The remaining cluster contained 16 subplots and had 5 species in common. This group was characterized by the abundance of *Drypetes longifolia* (33 to 182 trees ha-1) followed by *Reinwardtiodendron anamallayanum*, *Poeciloneuron indicum*, and *Dipterocarpus indicus*.

The importance value index of species measures indirectly the reproducibility, spatial dispersal ability, and growth potential of a species spectrum in the community based on the static data of relative species density, frequency, and basal area. Relatively few trees (10 species) take advantage of space and nutrients and dominate the forest stand (Table 3). Of these, 6 species were dominant in 2 to 9 subplots, indicating the similarity in species dominance between the subplots. According to Tilman (1988), species dominance in a community may be achieved by reducing resources to the lowest rate of supply to exclude all other species utilizing that resource.

The size class frequency distribution reveals a greater number of stems in the lowest size class (30–60 cm gbh), reflecting the regeneration potential of the subplots and the forest, and also showing that there was no severe site disturbance in the pasr. In the past decade Varagalaiar forest has been used to sustain the tame elephant population of more than twenty that were used for log transportation from the nearby teak plantations. Over 200 tribals resided there and depended on the forest to supply their hamlet with fuel, edible fruits, and other minor forest produce. These activities were mostly confined to the easily approachable outskirts (fringe subplots) of the evergreen forest. This could be the reason for the low density of stems in the outer subplots (Fig. 5). Presently, to minimize the disturbance level, the forest department has shifted the tame elephants, and the tribals engaged in their taming, to the nearby camp site (Kozhikamuthy, 10 km away), retaining just five elephants and about 50 residents at Varagalaiar.

The data of tropical tree inventories in square plots of 1-ha (100 m × 100 m) in area are compared with our study in Table 5. Rectangular plots (narrow or wide) of comparable scale consistently include more species than square plots (Condit *et al.* 1996, Laurance *et al.* 1998), hence they were excluded. The species richness of 66 species ha^{-1} of our site is moderate when compared to the range of 26 species ha^{-1} (Kolli hills, Indian Eastern Ghats, Chittibabu & Parthasarathy 2000) to 307 ha^{-1} (Amazonian Ecuador, Valencia *et al.* 1994) (Table 5). The results of tree inventories within the evergreen forests of peninsular India revealed that most Western Ghats sites harbor greater species richness than those of the Eastern Ghats (Table 5). The Varagalaiar forest appears to be a mosaic of tree species assemblages, as illustrated by the number of species with a wider range of species richness (52–79 ha^{-1}) contained in various 1-ha subplots of the 30-ha area, and thus it ranks as one of the most diverse forests of peninsular India, next only to the tropical wet evergreen forest around Sengaltheri, south Western Ghats (Parthasarathy 1999, 2001) (Table 5).

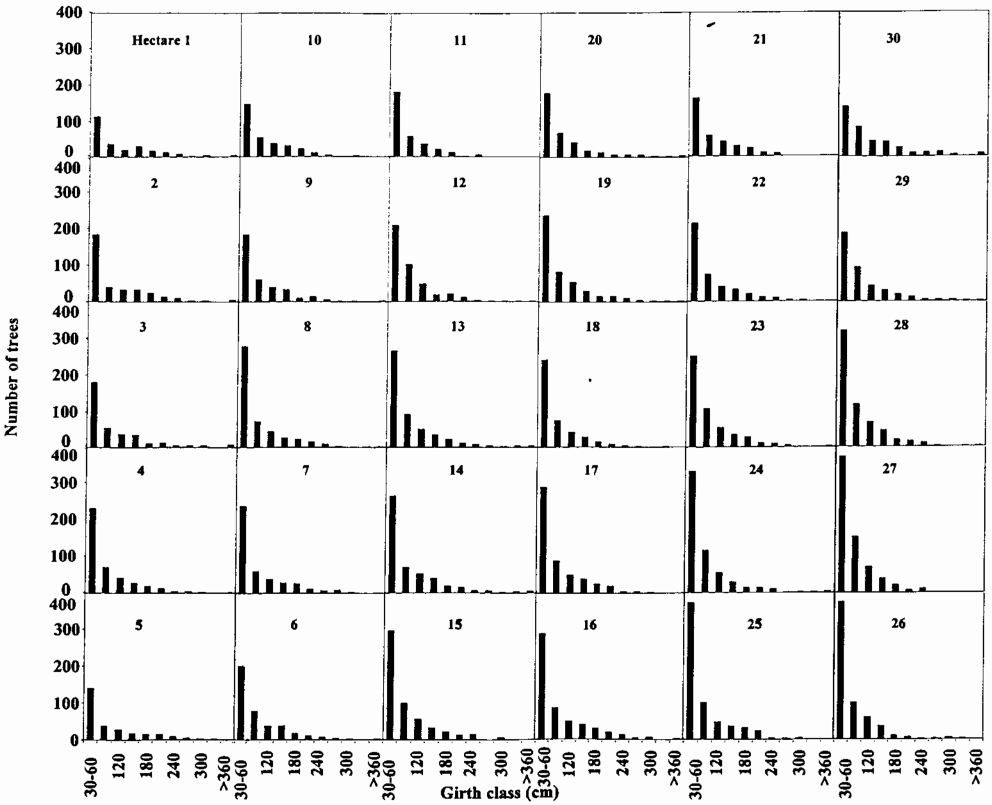

FIG. 5. Population structure of trees ≥ 30 cm gbh for the thirty 1-ha subplots of tropical evergreen forest at Varagalaiar, Western Ghats. Number of trees in each girth class (30–60 cm, 60–90, etc.) are plotted with 30 cm girth interval from minimum gbh of 30 cm to maximum of ≥ 360 cm.

TABLE 5. Density, species and family richness, and basal area ($m^2\ ha^{-1}$) of trees ≥ 30 cm gbh in the present study site at Varagalaiar forest of Anamalais, Indian Western Ghats, compared with other tropical tree inventories (≥ *c.* 30 cm gbh) at the 1-ha (100 m × 100 m) scale.

Location	Sample size	Number of			Basal	Source
		Trees	Species	Families	area (m^2)	
India						
Varagalaiar, Western Ghats	Range for thirty 1-ha plots	273–674	52–79	21–36	25–47	Present study
Courtallum, Western Ghats	1 ha	482	57	32	42.6	Parthasarathy & Karthikeyan 1997
Agumbe, Western Ghats	Three 1-ha plots (Range)	304–605	47–61	19–30	33.2–37.6	Srinivas 1997
Shervarayan hills, Eastern Ghats	Four 1-ha plots (Range)	640–986	33–50	26–35	21.6–44	Kadavul & Parthasarathy 1999a
Kalrayan hills, Eastern Ghats	Four 1-ha plots (Range)	367–667	42–47		25.8–41.6	Kadavul & Parthasarathy 1999b
Kalakad, Western Ghats	Three 1-ha plots (Range)	575–855	80–85	33–35	62–95	Parthasarathy 1999
Kolli hills, Eastern Ghats	Eight1-ha plots (Range)	266–632	26–54	–	23–53	Chittibabu & Parthasarathy 2000
Kalakad, Western Ghats	Three1-ha plots (Range)	852–965	64–82	–	55–87	Parthasarathy 2001
Other tropical areas						
Moraballi Creek, Guyana	Five1-ha plots (Range)	460–919	56–93	23–30	–	Davis & Richards 1934
Brazil	1 ha	423	87	31	–	Black *et al.* 1950
Belem, Para	1 ha	564	60	28	–	Black *et al.* 1950
Venezuela	1 ha	744	83	–	–	Uhl & Murphy 1981
Manu Park, Peru	1 ha	673	210	43	–	Gentry 1985
Costa Rica	Eleven 1-ha plots (Range)	425–654	29–149	19–55	23–43	Lieberman *et al.* 1985
Mexico	1-ha	359	88	–	–	Bongers *et al.* 1988
La Selva Biological station, Volcan Barvo	Six 1-ha plots (Range)	391–617	35–135	14–31	22.7–51.2	Heaney & Proctor 1990
Amazonian Ecuador	1 ha	734	153	46	–	Korning & Balslev 1994
Amazonian Ecuador	1 ha	693	307	46	–	Valencia *et al.* 1994
Kurupukari, Guyana	Four1-ha plots (Range)	357–742	50–71	23	32.29–34.63	Johnston & Gillman 1995
Cordillera Tilaran, Costa Rica	1 ha	436	90	40	41.67	Wattenberg & Breckle 1995
Brunei Darussalam	1 ha	550	231	43	40.79	Poulsen *et al.* 1996
Papua New Guinea	1 ha	693	228	58	37.1	Wright *et al.*1997
Central Amazonian Brazil	Three 1-ha plots (Range)	618–654	280–285	44–48	–	Oliveira & Mori 1999

Results of tropical tree density on a per hectare basis ranged from 304 trees in Agumbe, Western Ghats (Srinivas 1997) to 986 ha^{-1} trees in the Shervarayan hills, Eastern Ghats (Kadavul & Parthasarathy 1999a) (Table 5). Tree density per hectare on the Varagalaiar site recorded a still lower limit 273 trees ha-1, while the upper limit was 674 trees ha^{-1} (Table 5). The basal area per hectare of Varagalaiar forest (25.9 to 48) is well within the range of 21.6 m^2 ha-1 in the Shervarayan hills (Kadavul & Parthasarathy 1999a) to 95 m^2 ha^{-1} in Kalakad (Parthasarathy 1999). The range of family richness of 21 to 36 families per hectare of our study site is well within the range of 14 families ha^{-1} in Volcan Barva (Heaney & Proctor 1990) to 58 ha^{-1} in Papua New Guinea (Wright *et al.* 1997).

This study has depicted the extent of variation in tree diversity assemblages in a relatively "homogeneous" forest (for the sample size considered), under the same prevailing climatic and soil conditions, except for the minimal topographic variations of with or without streams. The spatio-temporal distribution of tree species assemblages in the forest stand is possibly governed by a multitude of factors (including the prime stochastic factor), and being a permanent plot, where studies will continue in subsequent years, will begin to offer detailed information on the ecology of individual species and tree communities that will provide further insight on patterns of tree species diversity and a database for forest management and conservation.

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