

Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India

R. Sukumar, H. S. Dattaraja, H. S. Suresh, J. Radhakrishnan, R. Vasudeva, S. Nirmala and N. V. Joshi

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

As part of an international network of large plots to study tropical vegetation dynamics on a long-term basis, a 50-hectare permanent plot was set up during 1988–89 in the deciduous forests of Mudumalai, southern India. Within this plot 25,929 living woody plants (71 species) above 1 cm DBH (diameter at breast height) were identified, measured, tagged and mapped. Species abundances corresponded to the characteristic log-normal distribution. The four most abundant species (*Kydia calycina*, *Lagerstroemia microcarpa*, *Terminalia crenulata* and *Helicteres isora*) constituted nearly 56% of total stems, while seven species were represented by only one individual each in the plot. Variance/mean ratios of density showed most species to have clumped distributions. The population declined overall by 14% during the first two years, largely due to elephant and fire-mediated damage to *Kydia calycina* and *Helicteres isora*. In this article we discuss the need for large plots to study vegetation dynamics.

RESEARCH on forests has been going on for several decades and yet we do not precisely understand their ecology. This is especially true of tropical forest ecology. It is well known that tropical forests are amongst the richest biological communities on earth. The disappearance of these forests, at an estimated rate of 1–2% per year¹, comes at a time when our knowledge of their structure and dynamics is woefully inadequate².

With a few exceptions, ecological studies of tropical forests have been largely isolated efforts, on small spatial scales and over short time periods. Notable

among the exceptions are the ongoing research on Barro Colorado Island in Panama by the Smithsonian Tropical Research Institute^{3,4} and the La Selva Biological Reserve in Costa Rica by the Organization for Tropical Studies⁵, both in the Neotropics.

Unlike in the relatively species-poor temperate forests, the study and characterization of species-rich tropical forests is a far more complex task. For one, the distribution of plant species is very heterogeneous, with most species having clumped distributions, making it necessary to study a large area in order to get an unbiased representation of the species present in the study sample. There is also a very wide variation in the relative abundance of species; a large study plot is again needed to provide sufficiently large sample sizes for the less common plants if one is to do any meaningful statistical analyses. Year to year variations in life-history phenomena of individuals and populations in response to climatic fluctuations (hurricanes, for instance, cause tremendous changes) also make long-term studies important.

Studies of tropical forests had been mostly confined to sampling trees within one or a few hectares until Hubbell and Foster^{6,7} took a bold step by setting up a 50-ha permanent plot in the tropical evergreen forests of Barro Colorado Island during 1980–82. Not only trees but also all other woody plants, excluding lianas, down to 1 cm stem DBH (diameter at breast height, in this case 1.3 m height) were enumerated and mapped. This provided an unprecedented opportunity to follow in detail the life histories of species, their interactions and the dynamics of plant communities.

This was soon followed during 1985–88 by another similar-sized plot in the equatorial rain forests of Pasoh Reserve in Peninsular Malaysia, set up by the Malaysian Forest Research Institute⁸, in collaboration with Peter Ashton of the Harvard University and Stephen Hubbell of the Princeton University.

These two 50-ha vegetation plots involved considerable effort in the field. In the Panamanian plot about 238,000 individuals from 302 species were enumerated, while in the Malaysian plot there were 340,000 individuals from 818 species.

The Indian Institute of Science has been involved since 1980 in the setting up of the Nilgiri Biosphere Reserve in southern India and had a commitment towards long-term ecological research that would contribute to the management of the reserve. Fundamental to the research programme is an understanding of the dynamics of the diverse forest types that are found here. The vegetation ranges from dry thorn forest in the low rainfall (500 mm annually) eastern regions through deciduous forest to montane stunted evergreen forest on the summit of the Nilgiri plateau to wet evergreen forests along the western slopes which enjoy copious rainfall (over 5000 mm annually) (refs. 9,10). The plant species diversity varies tremendously across these vegetation types from about 9–13 species above 10 cm DBH within 0.1 ha in the deciduous forests to 34–49 species in the montane *shola* forests and 36–41 species in the lower elevation wet evergreen forests^{9,11,12}.

When we began our research programme here, we had to make choices regarding the locations of our study sites amongst this vegetational diversity and the design of the study plots. We decided to join the international network of 50-ha plots that were being promoted by Hubbell. Considering the logistical problems in setting up such a large plot, this meant that only a single plot was possible, at least in the beginning.

We also selected the relatively species-poor deciduous forests of Mudumalai Sanctuary for our study for a number of reasons. Firstly, this would ideally complement the Panamanian (tropical semi-evergreen forest) and the Malaysian (equatorial evergreen forest) sites by its being a different vegetation type. Factors influencing the vegetation dynamics of a deciduous forest can be expected to be rather different from those driving the dynamics of rain forests. In rain forests, for instance, the size, shape, orientation and seasonal timing of canopy gaps influence the regeneration and subsequent establishment of woody species, particularly heliophilic pioneers (refs. 7, 13–15; also see the papers in *Ecology*, June 1989). On the other hand, gaps may be relatively less important in influencing the dynamics of a relatively open-canopied forest almost resembling a savanna woodland in its physiognomy. Other factors such as fire and large mammals can be expected to play major roles in the dynamics. Fire is an almost annual occurrence in

these forests and causes high mortality of saplings. Large mammals such as elephants alter the vegetation significantly by damaging or pushing over trees. The three sites in different vegetation types with their own peculiar environmental conditions would thus permit a comparative approach to the study of forest dynamics. A second reason for selecting the deciduous forest was that this had been traditionally a source of timber, and thus our study of these logged forests could potentially generate the scientific information for future sustainable management of similar forests for timber and other products. A third reason for selecting the deciduous forest was that this would complement our own ongoing research here on the large mammal populations, thus providing a more comprehensive picture of ecosystem dynamics.

In this article we merely describe the basic field methods adopted by us, present the preliminary results of the study based on static data from the first enumeration and discuss the issue of whether we were justified in setting up a single large plot of 50 ha.

The study area

Mudumalai Sanctuary extending over 321 km² is situated to the north of the Nilgiri plateau (11°32' to 11°43' N, 76°22' to 76°45' E) at an altitude of 850–1250 m above MSL in the Tamil Nadu state of southern India (Figure 1). A distinct rainfall gradient extends from west (higher rainfall, average 1800 mm per annum) to east (lower rainfall, average 800 mm per annum), with a corresponding change in vegetation type from moist deciduous forest (*Lagerstroemia-Tectona-Terminalia* series) through dry deciduous forest

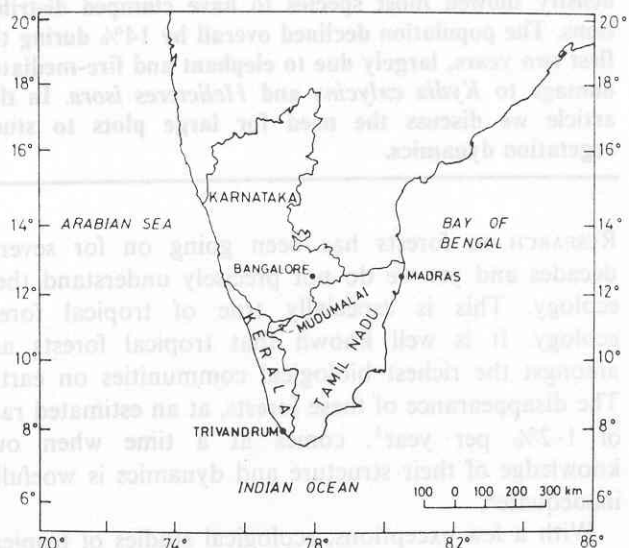


Figure 1. Map showing the location of Mudumalai Sanctuary in the Tamil Nadu state of southern India.

(*Anogeissus-Tectona-Terminalia* series) to dry thorn forest (*Acacia-Ziziphus* series) (for more details of vegetation types and floristics see Sharma *et al.*¹¹, Puri *et al.*¹⁶, Bellan¹⁷). The moister regions in the west have swampy grasslands (or *vyals*) extending through the forest. *Bambusa arundinacea* is common in the moister forests and along stream banks in the drier tract. The understory is dominated by perennial grasses, particularly of the genus *Themeda* (*T. cymbaria* and *T. triandra*). In the more disturbed areas the undergrowth also features the weeds *Chromolaena odorata*, *Lantana camara* and *Spatholobus parviflorus*.

Aims of the study

We had the following broad questions in mind while initiating this study.

The structure of a deciduous forest community

What are the patterns of abundances of different canopy trees, understory trees and shrubs? How are these species distributed in space? Do they have even, random or clumped distributions? Are there differences between the more common and rarer species in dispersion patterns? How are saplings distributed in relation to their adult conspecifics? Could species distributions be explained by topography such as degree of slope? What are the species-specific positive, neutral or negative associations?

The dynamics of the community

What are the patterns of recruitment, growth and mortality of species? Are the populations of these increasing, stable or decreasing in the plot? How does fire effect the dynamics of the community? What role do large mammals such as elephants play in the dynamics through debarking, breaking stems or even pushing over trees?

How does intra- and inter-specific competition shape the structure of a community? For instance, do saplings perform better if close to a conspecific or a heterospecific? In what direction is succession taking the community; specifically, is the community moving towards an equilibrium or is it constantly in a state of nonequilibrium over the 50-ha spatial scale?

Implications for management

One important goal of the study is to make recommendations for scientific management of such tropical forests based on the results of ecological research. What is the best strategy for harvesting timber

trees in deciduous forests? How can these forests be managed for fire to ensure optimum regeneration?

Basic field methods

After a preliminary reconnaissance of Mudumalai Sanctuary during 1987 we selected a 50-ha block of forest (11°35'41" to 11°35'57" N, 76°31'50" to 76°32'22" E) in Compartment 17 of Kargudi Range in the heart of the sanctuary. One of the important requisites of a site, namely that it should not be subject to any present or anticipated disturbance in future through felling of trees or grazing by domestic livestock, was fulfilled here.

The work began in February 1988 with survey and gridding of the plot using a theodolite. The plot running 1 km west to east and 0.5 km south to north was gridded into quadrats of 20 m × 20 m (projected in space), making appropriate corrections for slope. Due to the very hilly nature of the terrain there were considerable problems in ensuring accurate survey and gridding. Aluminium pipes with the x and y axis coordinates stamped were installed as boundary markers. The enumeration began in May 1988, proceeded concurrently with the gridding, and was completed in May 1989.

For the enumeration each 20 m × 20 m quadrat was temporarily subdivided into four 10 m × 10 m sub-quadrats with ropes. All living woody plants above 1 cm DBH were identified, measured for DBH, numbered with an aluminium tag and their locations mapped to the nearest 10 cm (in practice the accuracy was probably about 0.5 m). Individuals with multiple stems from below or above ground branches were given a single number, though all the stems were separately measured. For plants above 10 cm DBH the number tags were nailed on to the stem, while for smaller plants they were threaded through an aluminium wire which was tied around the stem to prevent any injury. We used aluminium wire which had the capacity to withstand possible melting from the fires that regularly sweep these forests. Damage to plants by mammals, insects or other causes was recorded. Bamboos were also enumerated; they were not measured but the number of culms in each clump was noted. Standing dead trees above 10 cm DBH alone were enumerated to get an idea of mortality patterns. Within each quadrat and hectare the enumeration proceeded in a clockwise direction beginning with the southwest corner, and from one hectare to another in a south to north direction.

We have tried to ensure that disturbance to the plot from enumerators is minimal. The breaking of saplings or introduction of seeds of exotic plants (such as fruits that may be eaten) are not permitted. While doing the theodolite survey it was inevitable that some

of the tall grasses or weeds such as *Chromolaena* were pushed aside when these obstructed the line of sighting. Similarly, some trampling of soil in the plot was inevitable. These were not expected to be serious disturbances, because they in any case also occur naturally through the action of the abundant elephant and other large mammal populations here.

Results

Vegetation composition and species abundances

The 50-ha plot contained 25,929 living individual woody plants above 1 cm DBH, coming from 71 species (including one bamboo species) during the first enumeration (Table 1). In addition, 955 standing dead stems above 10 cm DBH of 31 species were recorded. The most common species in the plot was *Kydia calycina*, an understorey tree, with 5175 individuals constituting 20% of the total enumerated woody plant population, while the second most abundant was *Lagerstroemia microcarpa*, a canopy tree, with 3980 individuals (15.3%). At the rare end of the scale were seven species with only one individual each in the entire 50 ha, while as many as 45 species had average densities of less than one individual per hectare. The four most common species made up 55.9%, the eight most common species made up 83.2% and the 12 most common species made up 90.6% of all individuals. A very few species thus dominate the community numerically.

The genus with the largest number of species was *Ficus* (Moraceae) with five species in the plot. *Ficus* were however among the most rare, with only 3–12 individuals per species. This was followed by the genus *Terminalia* (Combretaceae) with three species, represented by 34 (*T. bellirica*), 61 (*T. chebula*) and 2776 (*T. crenulata*) individuals. There were seven genera with two species each, while the remaining 50 genera were monospecific in the plot.

The most common family was Fabaceae (13 species), followed by Moraceae (6 species), Rubiaceae and Euphorbiaceae (5 species each).

When the species abundances are represented on a semilogarithmic scale—the abundance on a log₂ scale and the number of species on an arithmetic scale—the pattern is seen to largely correspond to the familiar log-normal distribution (Figure 2) (ref. 18). Towards the abundant end of the scale there are more than an expected number of co-dominant species with abundances of 2048–4096 individuals each. With *Kydia calycina*, the most common species reducing to below 4000 by the year 1989 itself, thus moving into this octave, the last octave became even more pronounced. This may have some biological significance in that it may be an indicator of a disturbed community.

Patterns of dispersion

Most of the species show clumped pattern of dispersion. The variance to mean ratio of density of a species is a simple yet reasonably robust measure of its dispersion pattern^{19,20}. The variance/mean ratio of 26 species with over 50 individuals in the plot (i.e. at least one individual per hectare on average) is given in Table 2 for three varying plot sizes—0.04 ha, 0.25 ha and 1.0 ha. A ratio of 1.0 indicates a random dispersion, less than 1.0 an uniform dispersion and greater than 1.0 an increasingly clumped dispersion.

The two most abundant species, *Kydia calycina* and *Lagerstroemia microcarpa*, along with *Helicteres isora* (ranked fourth) also show the highest degrees of clumping. On the other hand, no species has a variance/mean ratio below 1.0, indicating that none approaches a uniform dispersion pattern. On a 0.04-ha scale a number of species have ratios from 1.0 to 2.0, which indicates a near-random dispersion. At the larger scale of 1 ha, the ratios increase substantially for practically all species. One exception to this is *Gmelina arborea*, which still maintains a ratio suggestive of a random dispersion even at the larger plot sizes. Among the very abundant species, *Tectona grandis* shows the least clumping. It is not clear at this stage whether this is the natural pattern for this species or an artefact arising from its selective harvest in the past for timber.

Patterns of regeneration

Figure 3 gives the size class frequency distribution of all individuals in the 50-ha plot. Assuming that growth is linear and that mortality rates are monotonic across all size classes and species, it can be seen that there is a deficiency of individuals in the smallest size class. The above assumptions are, however, too simplistic.

Individual species can certainly be expected to show enormous differences in life-history patterns. The size class frequency distributions also show very different patterns in the species. Some species have few or no individuals in the smallest size class (below 5 cm DBH) compared to the larger size classes. These include *Anogeissus latifolia*, *Grewia tiliifolia*, *Eriolaena quinquelocularis*, *Diospyros montana*, *Ougeinia oojeinensis*, *Schleichera oleosa*, *Gmelina arborea*, *Terminalia chebula*, *Bridelia retusa*, *Bombax ceiba* and *Terminalia bellirica*.

The implications of this apparent 'lack of regeneration' for the future dynamics of these species are not clear. It would be fallacious to directly equate size class with age class of a species²¹. What is more relevant for population dynamics is the age distribution of a species in relation to its other demographic traits. Inferences about whether a species is increasing, stable or declining can usually be made after censuses conducted

Table 1. List of all species in order of abundance in the 50-ha plot

Species (Family)	Total no. of individuals	No. of ha of occurrence	Total (%)	Cumulative percentage
<i>Kydia calycina</i> Roxb. (Malvaceae)	5175	49	19.96	19.96
<i>Lagerstroemia microcarpa</i> Wight. (Lythraceae)	3980	49	15.35	35.31
<i>Terminalia crenulata</i> Roth. (Combretaceae)	2776	50	10.71	46.01
<i>Helicteres isora</i> L. (Sterculiaceae)	2571	43	9.91	55.93
<i>Anogeissus latifolia</i> (DC.) Wall.ex Guill. & Perr. (Combretaceae)	2280	50	8.79	64.72
<i>Tectona grandis</i> L. f. (Verbenaceae)	2143	50	8.26	72.99
<i>Cassia fistula</i> L. (Fabaceae)	1881	50	7.25	80.24
<i>Xeromphis spinosa</i> (Thunb.) Keay. (Rubiaceae)	770	46	2.97	83.21
<i>Emblica officinalis</i> Gaertner. (Euphorbiaceae)	577	49	2.22	85.44
<i>Grewia tiliifolia</i> Vahl. (Tiliaceae)	539	50	2.08	87.52
<i>Syzygium cumini</i> (L.) Skeels. (Myrtaceae)	415	46	1.60	89.12
<i>Bambusa arundinacea</i> (Retz.) Roxb. (Poaceae)	381	29	1.47	90.59
<i>Radermachera xylocarpa</i> (Roxb.) Schum. (Bignoniaceae)	357	47	1.38	91.96
<i>Eriolaena quinquelocularis</i> (Wt. & Arn.) Clegh. (Sterculiaceae)	251	46	0.97	92.93
<i>Cordia obliqua</i> Willd. (Boraginaceae)	197	44	0.76	93.69
<i>Diospyros montana</i> Roxb. (Ebenaceae)	130	32	0.50	94.19
<i>Stereospermum colias</i> (Dillw.) Mabberley. (Bignoniaceae)	123	10	0.47	94.67
<i>Ougeinia oojinensis</i> (Roxb.) Hochr. (Fabaceae)	111	10	0.43	95.09
<i>Lagerstroemia parviflora</i> Roxb. (Lythraceae)	92	18	0.35	95.45
<i>Shorea roxburghii</i> Don. (Dipterocarpaceae)	79	8	0.30	95.75
<i>Cordia wallichii</i> G. Don. (Boraginaceae)	78	27	0.30	96.05
<i>Dalbergia latifolia</i> Roxb. (Fabaceae)	76	22	0.29	96.37
<i>Schleichera oleosa</i> (Lour.) Oken. (Sapindaceae)	75	29	0.29	96.64
<i>Schrebera swietenoides</i> Roxb. (Oleaceae)	69	15	0.27	96.90
<i>Terminalia chebula</i> (Gaertn.) Retz. (Combretaceae)	61	26	0.23	97.14
<i>Gmelina arborea</i> Roxb. (Verbenaceae)	60	32	0.23	97.37
<i>Casearia esculenta</i> Roxb. (Flacourtiaceae)	47	26	0.18	97.55
<i>Bridelia retusa</i> (L.) Spreng. (Euphorbiaceae)	40	20	0.15	97.70
<i>Bombax ceiba</i> L. (Bombacaceae)	38	21	0.15	97.85
<i>Terminalia bellirica</i> (Gaertn.) Roxb. (Combretaceae)	34	23	0.13	97.98
<i>Butea monosperma</i> (Lam.) Taub. (Fabaceae)	34	9	0.13	98.11
<i>Careya arborea</i> Roxb. (Lecythidaceae)	34	21	0.13	98.24
<i>Garuga pinnata</i> Roxb. (Burseraceae)	32	15	0.12	98.37
<i>Ziziphus xylopyrus</i> Willd. (Rhamnaceae)	31	15	0.12	98.49

Table 1. Continued

<i>Cassine glauca</i> (Rottb.) Kuntze. (Celastraceae)	31	4	0.12	98.61
<i>Bauhinia malabarica</i> Roxb. (Fabaceae)	30	21	0.12	98.72
<i>Mallotus philippensis</i> (Lam.) Muell. (Euphorbiaceae)	28	6	0.11	98.83
<i>Indigofera cassioides</i> Rottler ex DC. (Fabaceae)	22	4	0.08	98.92
<i>Pterocarpus marsupium</i> Roxb. (Fabaceae)	22	13	0.08	99.00
<i>Cassia montana</i> Heyne ex Roth. (Fabaceae)	21	4	0.08	99.08
<i>Canthium dicoccum</i> (Gaert.) T. & B. (Rubiaceae)	20	12	0.08	99.16
<i>Mitragyna parvifolia</i> (Roxb.) Korth. (Rubiaceae)	20	12	0.08	99.24
<i>Allophylus cobbe</i> (L.) Raeusch. (Sapindaceae)	19	6	0.07	99.31
<i>Hymenodictyon orixense</i> (Roxb.) Mabblerley (Rubiaceae)	14	10	0.05	99.36
<i>Semecarpus anacardium</i> L. f. (Anacardiaceae)	14	12	0.05	99.42
<i>Antidesma diandrum</i> Roth. (Euphorbiaceae)	13	7	0.05	99.47
<i>Ficus virens</i> Aiton. (Moraceae)	12	10	0.05	99.51
<i>Lannea coromandelica</i> (Houtt.) Merr. (Anacardiaceae)	12	9	0.05	99.56
<i>Bauhinia racemosa</i> Lam. (Fabaceae)	11	3	0.04	99.60
<i>Ficus tsjahela</i> Burman. (Moraceae)	11	10	0.04	99.64
<i>Albizia odoratissima</i> (L. f.) Bentham. (Fabaceae)	9	6	0.03	99.68
<i>Dalbergia lanceolaria</i> L. f. (Fabaceae)	9	7	0.03	99.71
<i>Flacourtia indica</i> (N. Burm.) Merrill. (Flacourtiaceae)	8	8	0.03	99.74
<i>Wrightia tinctoria</i> R. Br. (Apocyanaceae)	8	7	0.03	99.78
<i>Ziziphus rugosa</i> Lam. (Rhamnaceae)	8	2	0.03	99.81
<i>Olea dioica</i> Roxb. (Oleaceae)	7	5	0.03	99.83
<i>Ficus religiosa</i> L. (Moraceae)	7	6	0.03	99.86
<i>Erythrina indica</i> Lam. (Fabaceae)	6	5	0.02	99.88
<i>Pavetta tomentosa</i> Roxb. ex J.E. SM. (Rubiaceae)	5	1	0.02	99.90
<i>Grewia hirsuta</i> Vahl. (Tiliaceae)	5	3	0.02	99.92
<i>Mangifera indica</i> L. (Anacardiaceae)	4	4	0.01	99.94
<i>Ficus drupacea</i> Thumb. (Roth.) Corne (Moraceae)	4	3	0.01	99.95
<i>Ficus benghalensis</i> L. (Moraceae)	3	3	0.01	99.96
<i>Premna tomentosa</i> Willd. (Verbenaceae)	2	1	0.01	99.97
<i>Artocarpus gomezianus</i> Wall. ex Trecul. (Moraceae)	1	1	0.00	99.98
<i>Chukrasia tabularis</i> A. Juss. (Meliaceae)	1	1	0.00	99.98
<i>Vitex altissima</i> L. f. (Verbenaceae)	1	1	0.00	99.98
<i>Bischofia javanica</i> Blume. (Euphorbiaceae)	1	1	0.00	99.99
<i>Crotalaria</i> sp. (Fabaceae)	1	1	0.00	99.99
<i>Buchanania axillaris</i> (Desr.) Ramam. (Anacardiaceae)	1	1	0.00	99.99
Unidentified	1	1	0.00	100.00

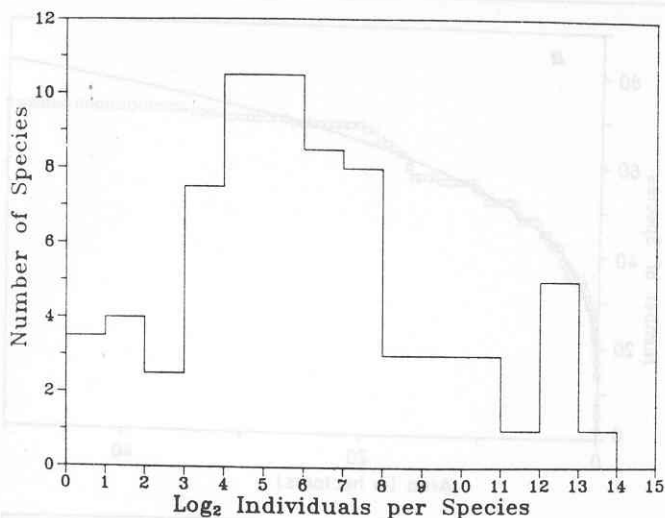


Figure 2. Species abundances for the 71 species in the 50-ha plot. Abundance categories are in octaves of abundance, shown in units of log (base 2). The log-normal distribution (for best fit curve, $\chi = 12.73$, $P > 0.05$) is given by $S_R = 8.0e^{-(0.158R)^2}$.

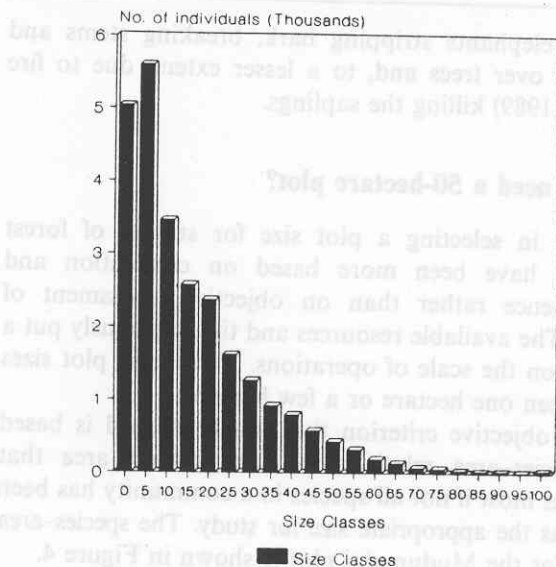


Figure 3. Size class (cm) frequency distribution of all the individuals in the plot (only the largest stem is considered for multiple-stemmed plants).

Table 2. Variance to mean ratio of density of species for varying plot sizes

Species	Plot size		
	1.00 ha	0.25 ha	0.04 ha
<i>Kydia calycina</i>	133.47	48.75	12.77
<i>Lagerstroemia microcarpa</i>	86.92	35.22	7.94
<i>Terminalia crenulata</i>	28.25	9.33	2.55
<i>Helicteres isora</i>	119.48	57.32	17.04
<i>Anogeissus latifolia</i>	39.73	14.74	3.77
<i>Tectona grandis</i>	8.50	3.40	1.44
<i>Cassia fistula</i>	17.39	7.47	3.03
<i>Xeromphis spinosa</i>	24.62	10.94	5.02
<i>Emblica officinalis</i>	4.04	2.16	1.25
<i>Grewia tiliifolia</i>	3.80	2.02	1.19
<i>Syzygium cumini</i>	6.25	2.56	1.47
<i>Shorea roxburghii</i>	28.56	9.09	3.72
<i>Bambusa arundinacea</i>	19.15	10.53	4.15
<i>Radermachera xylocarpa</i>	4.28	2.54	1.39
<i>Eriolaena quinquelocularis</i>	6.26	2.74	1.36
<i>Cordia obliqua</i>	4.61	2.43	1.33
<i>Diospyros montana</i>	4.89	2.10	1.48
<i>Stereospermum colias</i>	7.30	5.28	3.39
<i>Ougeinia oojeinensis</i>	16.92	9.04	2.95
<i>Lagerstroemia parviflora</i>	9.55	3.97	1.80
<i>Dalbergia latifolia</i>	4.16	2.51	1.70
<i>Cordia wallichii</i>	2.95	1.69	1.09
<i>Schleichera oleosa</i>	2.19	1.56	1.29
<i>Schrebera swietenoides</i>	6.61	3.12	1.58
<i>Terminalia chebula</i>	2.57	1.25	1.05
<i>Gmelina arborea</i>	1.30	1.13	1.09

Only species having 50 or more individuals in the 50-ha plot have been listed.

with a 'sufficient' time gap and not merely based on a one-time cross-sectional sampling.

Patterns of mortality

By far, the largest number of standing dead stems pertained to *Shorea roxburghii* (307 dead versus 79 living). Practically all living individuals were saplings, indicating there had been large-scale mortality of adult plants. The cause for this mortality seems to be an unidentified cerambycid beetle that is a stem borer. To investigate the population dynamics of *Shorea roxburghii*, we have also set up a one-hectare plot in Doddagatti Block of Mudumalai, where this species grows gregariously.

The data also indicated a high recent mortality of *Pterocarpus marsupium* (23 dead versus 22 living plants) and *Bridelia retusa* (17 dead, 40 living).

Patterns of species mortality should be more appropriately deduced from observing the community over a period of time and not from a one-time cross-sectional sampling. Dead stems of different species may be left standing for varying periods of time. Therefore an enumeration of standing dead stems may not reflect the true mortality pattern. Nevertheless, such an enumeration did provide useful hints as to what might have happened in the past.

The re-censuses carried out during 1989 and 1990 of the entire plot showed substantial decline in the total population. The decline was 9.1% during 1989 and 5.5% during 1990, or an overall decline of 14% from the base year. *Kydia calycina* and *Helicteres isora* showed the steepest decline, by 42% and 27% respectively, over the two-year period. This was largely

due to elephants stripping bark, breaking stems and pushing over trees and, to a lesser extent, due to fire (during 1989) killing the saplings.

Do we need a 50-hectare plot?

Criteria in selecting a plot size for studies of forest ecology have been more based on convention and convenience rather than on objective assessment of needs. The available resources and time obviously put a ceiling on the scale of operations. 'Favourite' plot sizes have been one hectare or a few hectares.

One objective criterion that has been used is based on species-area relationship. The smallest area that includes most if not all species in a community has been taken as the appropriate size for study. The species-area curve for the Mudumalai plot is shown in Figure 4.

The first hectare itself contains 31 species or 44% of the total species recorded. The range in species richness for a single hectare goes from a minimum of 19 to a maximum of 39 species. The number of species saturates by the 34th ha. In fact, with a plot size of 25 ha one would still have retained 63 or nearly 90% of the final species tally.

It is, however, obvious that given the distinctly clumped distribution of most species, a plot of one hectare would hardly be representative of the broader structure of the community. For instance, *Kydia calycina*, the most dominant species, was absent from a one-hectare subplot of the 50-ha plot, while *Lagerstroemia microcarpa*, the second most dominant, was missing from another one-hectare subplot. In many other hectares their densities vary enormously, from extremely low to extremely high, compared to their mean density over 50 ha. For instance, *Kydia calycina* has a density range of 0 to 607 individuals per hectare compared to its mean density of 104 individuals per hectare. In fact, in six hectares it is represented by only two individuals each and in 13 ha by less than 10 individuals each. In the case of *Lagerstroemia microcarpa* the range is 0–308 individuals per hectare, with a mean density of 80 ha⁻¹, and 16 ha having 20 or less individuals per hectare. It is easy then to imagine that even a plot of several hectares may not reflect the density levels of such clumped species in the community.

With a plot size of 25 ha the sample size for most species would be quite small. Only 19 species would be represented by over 50 individuals each. For the rest it would not be possible to do any kind of meaningful statistical analyses. With a 50 ha plot the situation is somewhat better with 26 out of 71 species having over 50 individuals each.

Even sample sizes of 50 would be insufficient for many kinds of statistical analyses. For instance, many species with abundances far in excess of 50 individuals are not adequately represented by different size classes,

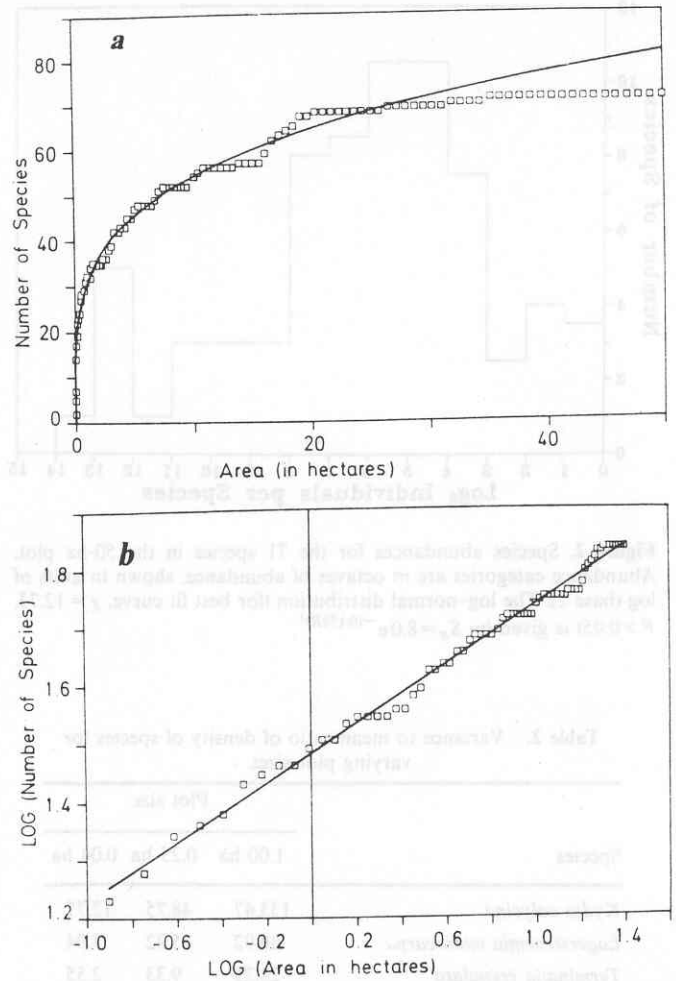


Figure 4. Species-area curve for the 50-ha plot shown on (a) a normal scale. (b) a log₁₀-log₁₀ scale. The best fit regression for the log transformed data for 67 points (from 0.1 ha to 25 ha) is given by log (number of species) = 30 A^{0.25}, where A is the area in hectares. The fitted curve for the normal data in (a) is based on the above regression. The expected number of species for the 50-ha plot is 81 species as opposed to only 71 species actually present.

that would permit a detailed insight into their life histories. From this consideration alone, we feel that a plot as large as 50 ha is justified.

Another important decision to make, while selecting plot size and shape, is whether to have a single large plot or a number of smaller plots spread over a larger tract but adding up to the same area. The answer would depend on the objectives of the study and one's definition of what constitutes an appropriate unit for studying a 'community'.

Several smaller plots distributed widely have the advantage of being able to potentially represent different 'vegetation types' and would probably encompass more species. Phenomena (say, massive mortality) that occur over a 50-ha scale may not be true when a larger spatial scale is considered; this may be better captured by studying several smaller plots. On the other hand, any individual plot may be still too small

Table 3. Number of individuals retained and species lost for different minimum stem sizes

Smallest DBH measured (cm)	No. of individuals in sample	No. of species in sample	Species lost
1.0	25,929	71	—
2.0	23,835	69	<i>Buchanania axillaris</i> , <i>Cassia montana</i> .
3.0	22,807	67	Above plus <i>Grewia hirsuta</i> , <i>Crotalaria</i> sp.
5.0	20,898	66	Above plus <i>Dalbergia lanceolaria</i> .
10.0	15,417	63	Above plus <i>Indigofera cassioides</i> , <i>Allophylus cobbe</i> , <i>Pavetta tomentosa</i>

to make firm conclusions about community dynamics on a local scale. We plan to overcome this problem partly by setting up a series of smaller plots in addition to the large 50-ha plot.

A third decision to be made concerns the minimum cut-off size of plants to be included in the enumeration. Should this be 1 cm, 2 cm, 3 cm or 10 cm DBH? Traditionally, foresters have looked at only trees above 10 cm DBH (actually 30 cm girth). The resulting total individuals enumerated and the species lost for higher cut-off sizes are given in Table 3. With a 2 cm DBH cut-off only two species and just about 8% of individuals are lost from the sample. For 10 cm DBH and above the loss is much greater with eight species and 41% of individuals. The species lost are all from the rarer segment of the original sample.

The first impression might be that one could safely increase the cut-off size to 2 cm or 3 cm DBH without any significant loss in data (number of species and individuals). However, the opposite argument could be made that with only a marginally increased effort, one is able to capture the saplings of 1–2 cm DBH in the sample. Studying the patterns of recruitment of seedlings into the 1–2 cm DBH class and tracking their fate might be important for understanding the life histories of many plant species.

Conclusions

The 50-ha vegetation plot set up in Mudumalai Sanctuary offers an opportunity, unprecedented in this region, for a host of detailed studies on tropical forest biology. The fact that the precise locations of nearly 26,000 individuals, including saplings from 71 species, are known provides baseline data that can be of tremendous advantage for a variety of investigations. This could encompass the fields of reproductive ecology, population dynamics, community ecology, population genetics, plant productivity, applied silviculture and so on. Such investigations would hopefully

provide the scientific basis for sustainable management of tropical dry forests.

1. Myers, N., in *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé, M. E.), Sinauer Associates, Sunderland, Massachusetts, 1986, p. 394.
2. Hubbell, S. P. and Foster, R. B., *Oikos*, (in press).
3. Leigh, E. G., Jr., Rand, S. A. and Windsor, D. M. (eds.), *Ecology of a Tropical Forest: Seasonal Rhythms and Long Term Changes*, Smithsonian Institution Press, Washington DC, 1982.
4. Anderson, A., *Nature*, 1991, **349**, 647.
5. Janzen, D. H. (ed.), *Costa Rican Natural History*, University of Chicago Press, Chicago, 1983.
6. Hubbell, S. P. and Foster, R. B., in *Tropical Rain Forest: Ecology and Management* (eds. Sutton, S. J., Whitmore, T. C. and Chadwick, A. C.), Blackwell Scientific, Oxford, 1983, p. 25.
7. Hubbell, S. P. and Foster, R. B., in *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé, M. E.), Sinauer Associates, Sunderland, Massachusetts, 1986, p. 205.
8. Manokaran, N. et al., Methodology for the 50 Hectare Research Plot at Pasoh Forest Reserve, Research Pamphlet No. 104, Forest Research Institute, Malaysia, 1990.
9. Blasco, F., *Vegetation of Nilgiris*, French Institute, Pondicherry, 1971.
10. von Lengerke, H. J., *The Nilgiri—Weather and Climate of a Mountain Area in South India*, Franz Steiner Verlag, Weisbaden, 1977.
11. Sharma, B. D., Shetty, B. V., Vivekanandan, K. and Rathakrishnan, N. C., *J. Bombay Nat. Hist. Soc.*, 1977, **75**, 13.
12. Puri, G. S., Meher-Homji, V. M., Gupta, R. K. and Puri S., *Forest Ecology*, vol. II, *Plant Form, Diversity, Communities and Succession*, Oxford and IBH Pub. Co., New Delhi, 1989.
13. Hartshorn, G. S., in *Tropical Trees as Living Systems* (eds. Tomlinson, P. B. and Zimmerman, M. H.), Cambridge University Press, Cambridge, 1978.
14. Denslow, J. S., *Biotropica*, 1980, **12** (suppl.), 47.
15. Brokaw, N. V. L., *Ecology*, 1985, **66**, 682.
16. Puri, G. S., Meher-Homji, V. M., Gupta, R. K. and Puri, S., *Forest Ecology*, vol. I, *Phytogeography and Forest Conservation*, Oxford and IBH Pub. Co., New Delhi, 1983.
17. Bellan, M. F., *Vegetation of Nilgiris*, Institut de la Carte Internationale de Tapis Végétal, France, 1985.
18. Preston, F. W., *Ecology*, 1962, **43**, 185, 410.
19. Greig-Smith, P., *Quantitative Plant Ecology*, 3rd edn, Blackwell Scientific, Oxford, 1983.
20. Krebs, C. J., *Ecological Methodology*, Harper and Row, New York, 1989.
21. Harper, J. L., *Population Biology of Plants*, Academic Press, London, 1977.

ACKNOWLEDGEMENTS. This study was funded by the Ministry of Environment and Forests, New Delhi, through a grant to the Centre for Ecological Sciences, and was undertaken as part of the Nilgiri Biosphere Reserve Research Programme. We thank the Forest Department of Tamil Nadu state for their interest in the project and for permission to set up the permanent vegetation plot in Mudumalai Sanctuary. In particular, we appreciate the support of John Joseph (Principal Chief Conservator of Forests), the late P. Padmanabhan (Chief Wildlife Warden), V. R. Chitrapu (Conservator of Forests, Nilgiris) and K. S. Neelakandan (Wildlife Warden, Mudumalai) while setting up the plot. We also thank Madhav Gadgil for his constant interest and support in the project and Steve Hubbell for many stimulating discussions and a gift of the numbered tags. Valuable support in the field was provided by Kirti Malhotra, K. S. Murali, M. John, B. A. Manjunath, N. M. Madhan, Shivaji, M. Bomman and the late B. Maran.

Received 16 September 1991; revised accepted 17 March 1992