

## **MICROSITES AND DIVERSITY OF UNDERSTOREY SHRUBS IN SOUTHERN WESTERN GHATS, INDIA**

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**KRISHNAN, R. M. 2001. Microsites and diversity of understorey shrubs in southern Western Ghats, India.** This study examines the diversity of understorey shrubs in their microhabitats in a primary wet evergreen forest of south India. A matrix of environmental factors and the species distribution across quadrats were analysed using correspondence analysis to identify the microhabitats of understorey shrubs. Slope of the terrain, level of light, soil cover and tree density were important parameters that defined the microhabitats of the shrubs. Most shrub species (85%) were clumped in their dispersion patterns. Moderate overstorey cover supported greater diversity of understorey shrubs. Capturing diversity and increasing density were not operationally similar for shrubs. While shaded conditions tended to increase the density and dominance of certain species, disturbance-mediated light regimes increased species diversity. The narrow-endemic species had greater richness in tree fall gap, while broad-endemic and non-endemic species maximised richness in openings. For all groups, high densities were observed in shade.

Key words: Understorey - evergreen forests - Western Ghats - microhabitat - endemic

**KRISHNAN, R. M. 2001. Mikrosit dan kepelbagaian pokok renek tingkat bawah di selatan Ghats Barat, India.** Kajian ini memeriksa kepelbagaian mikrohabitat pokok renek tingkat bawah di hutan malar hijau lembap primer di selatan India. Matriks faktor persekitaran dan taburan spesies dalam semua kuadrat dianalisis menggunakan analisis kesamaan untuk mengenal pasti mikrohabitat pokok renek tingkat bawah. Cerun permukaan, tahap cahaya, penutup tanah dan kepadatan pokok merupakan parameter penting yang dapat menentukan mikrohabitat bagi pokok renek tersebut. Kebanyakan spesies pokok renek (85%) mempunyai corak penyerakan berumpun. Penutup tingkat atas yang sederhana menyokong kepelbagaian yang lebih besar bagi spesies pokok renek tingkat bawah. Kepelbagaian dan peningkatan kepadatan adalah tidak sama bagi pokok renek. Keadaan naung cenderung untuk meningkatkan kepadatan dan kedominanan spesies tertentu manakala regim cahaya terganggu pula meningkatkan kepelbagaian spesies. Spesies endemik yang sempit mempunyai kekayaan ruang jatuhan pokok, manakala spesies endemik yang lebar dan spesies tak endemik memaksimumkan kekayaan pembukaannya. Bagi kesemua spesies, kepadatan yang tinggi diceraap dalam naung.

### **Introduction**

Several contrasting features characterise the understorey conditions of a tropical rain forest. The ground vegetation gets poor light (Evans *et al.* 1960, Yoda 1974, Chazdon & Fetcher 1984), but a large number of species co-exists here, tolerating varied degrees of shade and stress. Several studies show that response to various environmental factors such as levels of light, nutrient availability and temperature influences the diversity of the assemblages in the understorey plant community (Denslow *et al.* 1990, Newell

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*et al.* 1993, Laska 1997). Some studies also reported the correlation of precipitation and soil fertility with species richness (Gentry & Emmons 1987, Tuomisto & Ruokolainen 1994) and understorey diversity (Gentry 1982, 1988). It is now known that plants in the understorey are adapted to deep shaded conditions and are affected by very small differences in levels of light (Chazdon & Fetcher 1984, Denslow 1987). Tree or branch falls are the principal disturbances that lead to openings in forest canopy (Denslow 1987). These episodes also facilitate regeneration, due to which, species diversity increases depending upon the disturbance regimes and temporal heterogeneity (Grubb 1977). Thus, a group of species can be loosely defined by a set of similar environmental preferences, for instance, shade-tolerant and drought-intolerant.

Studies in the understorey of old world tropical forests focus mainly on phenology or species richness (Wong 1983, Kiew 1986). However, seedlings and saplings predominantly constitute understorey in the low elevation dipterocarp forests, as compared to shrubs in some forests of Western Ghats. Our understanding of forest dynamics in Western Ghats is mostly derived from trees (Pascal & Pelissier 1996). A significant number of studies are available on the tree strata (e.g. Ganesh *et al.* 1996, Ayappan & Parthasarathy 1999, Parthasarathy 1999) compared to the understorey strata along the Ghats (e.g. Rajavanshi 1987, Krishnan 1996). This is despite the fact that evergreen forests of Western Ghats have the highest diversity of understorey shrubs compared to the other tropical regions (Krishnan & Davidar 1996).

The main objectives of this study were to:

- (1) distinguish the kinds of microhabitats available for the understorey shrubs,
- (2) determine the influence of the overstorey layer, and
- (3) examine the microhabitat preferences of the endemic species.

### Study area

The study site, Kakkachi, is located in the core area of Kalakkad-Mundanthurai Tiger Reserve in the Agastyamalai region, Tirunelveli district, Tamil Nadu. The site is at an altitude of 1400 m. Kakkachi receives rain from the south-west monsoon (June till August) and north-east monsoon (November till January). The annual rainfall is between 1500 mm to 3400 mm (BBTC rain gauge, Nalmukku, approximately 2 km from Kakkachi). The peak rainfall is during the north-east monsoon. The major dry season is between March and May.

The primary evergreen forests are floristically classified as *Cullenia exarillata*-*Mesua ferrea*-*Palaquium ellipticum*-*Gluta travancorica*-*Nageia wallichiana* type (Ganesh *et al.* 1996, Ramesh *et al.* 1998). The area is rich in endemic species (Ahamedullah & Nayar 1986, Ramesh & Pascal 1997). The common trees in the area are *Cullenia exarillata* and *Palaquium ellipticum*. The forest has a closed canopy with no emergents, the average canopy height being 30 m. Some canopy trees are *Calophyllum austroindicum*, *Cullenia exarillata*, *Ormosia travancorica*, *Nageia wallichiana* and *Palaquium ellipticum*. Tress like *Myristica dactyloides*, *Canarium strictum*, *Diospyros malabarica*, *Tricalysia apiocarpa* and *Vepris bilocularis* form the subcanopy. The understorey trees include *Cinnamomum travancoricum*, *Agrostistachys borneensis* and *Milusa wightiana*. Some small trees in the area are *Antidesma menasu*, *Murraya paniculata*, *Mallotus beddomeii* and *Vernonia travancorica*. The common shrubs here are *Diotacanthus grandis*, *Lasianthus cinereus*,

and *Saprosma corymbosum*. The understorey shrubs and herbs in the area are *Impatiens grandis*, *Justicia indica*, *Pepromia* sp. and *Phyllanthus fimbriatus*.

### Materials and methods

Nine transects, each measuring 105 m long, were laid irregularly in the study area. At every alternate 5 m, a quadrat measuring 5 × 5 m was laid. In each quadrat, all shrubs, trees and herbs were recorded. Spatial dispersion for shrub species was estimated using variance-to-mean ratio (Krebs 1989). A total of 99 quadrats were laid in the study area. The total area assessed was 2475 m<sup>2</sup>. Data on the following parameters were recorded in every quadrat: canopy cover as an indicator of levels of light, slope, soil cover by leaf litter, presence of rocks, proximity to a stream, tree density, number of dead trees, herb richness and shrub density.

Due to lack of information on the frequency and nature of canopy openings for the study area, and because size of the quadrats and the scale of the study were small, standard canopy cover classifications were not applied. Thus, a quadrat with (1) greater than 75% canopy cover was considered to be in shade, (2) greater than 50–75% canopy cover was classified as light gap, (3) greater than 25–50% canopy cover was grouped as opening, and (4) 0–25% canopy cover was classified as tree fall. To estimate the soil type, quadrats were grouped under six categories depending upon the percentage of rocky area prevailing in them. A minimum of 0% indicated no rocks, while values greater than 80% indicated extreme rockiness. Other categories included 1–19%, 20–39%, 40–59% and 60–80% of rockiness in quadrats. The per cent area of a quadrat covered by leaf litter was classified into three classes to indicate the percentage of soil covered: (1) greater than 80–100% indicated good leaf litter cover with no exposed soil, (2) greater than 50–80% indicated quadrats with partial leaf litter, and (3) 0–50% indicated poor leaf cover. Four slope categories were included: (1) flat, (2) mild slope (> 25°), (3) gentle slope (> 50°), and (4) steep slope (> 70°).

The data on variables from all parameters were quantified for further analysis in the following manner:

Variable	Data type	No. of classes	Parameter estimated per quadrat
Light intensity	Ordered multistate	4	% canopy open
Soil type	Nominal multistate	6	% rockiness
Soil cover	Nominal multistate	3	% leaf litter cover
Slope	Ordered multistate	4	Estimation of slope
Moisture availability	Presence/absence	2	Proximity to stream
Shrub density	# per quadrat		
Dead trees	# per quadrat		
Herb density	# per quadrat		
Tree density	# per quadrat		

To identify microhabitats, correspondence analysis using ADE (Thioulouse *et al.* 1997) was performed independently on the following matrices: environmental factors and quadrats (9 factors × 99 quadrats), abundance of tree species and quadrats (38 species × 99 quadrats), and shrub species and quadrats (35 species × 99 quadrats). In the correspondence analysis, adult and juvenile trees were not distinguished. Since

quadrats were common for all the analyses, the scatter diagrams obtained for the environmental factors were then superimposed on the shrub and tree scatters. The resulting scatter diagrams were interpreted visually for clusters that explained the closest approximation to the kinds of microhabitat in which the understorey shrubs thrived. The details of the species and factors used in the study are listed in Appendix 1. To estimate the density and richness of the understorey shrub community across varied light regimes, data from quadrats with similar light regimes were pooled and richness was estimated using Menhinick's index. Changes in diversity and dominance of understorey shrubs across different light regimes were compared using the Berger-Parker index of dominance ( $N_{\max}/N$ ) and diversity ( $1/D$ ). These measurements also allow interpretation of evenness, as it increases when dominance is lowest. Similarity was determined using Jaccard's index (Magurran 1988). Per cent relative dominance of species in different light regimes was calculated using the formula:

$$\frac{\text{Number of species in a single light regime}}{\text{Total number of species in all groups}} \times 100$$

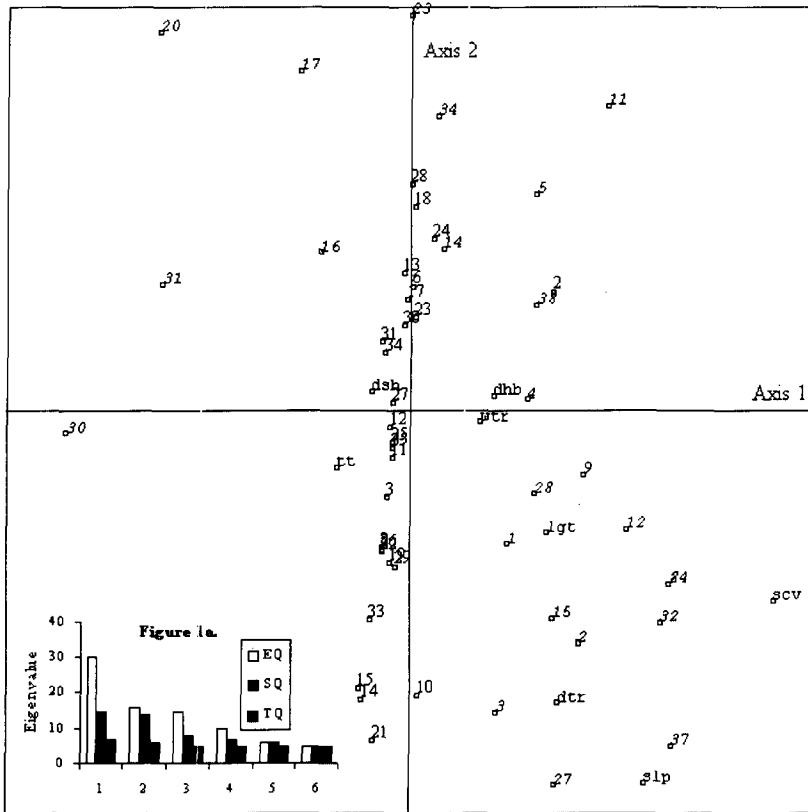
The endemic species were further grouped into broad- (endemic to the entire Western Ghats) and narrow- (restricted to Agastyamalai region) endemic species. Under different overstorey densities, richness was measured using Menhinick's index, and dominance and diversity were measured using Berger-Parker index. The independence of the density of shrub from the density of the overstorey species was examined using chi-square. Changes in dispersion patterns of most common and abundant understorey shrubs under varying overstorey densities were measured using variance to mean ( $v/m$ ) ratio. If  $v/m$  was equal to 1, the species was randomly dispersed as described by Poisson distribution. Uniform distribution patterns were inferred if values were close to 0, and clumping was inferred if values were  $> 1$  (Krebs 1989).

## Results

### *Microhabitats*

#### Quadrats and factors

The non-overlap of the environmental factors indicates that a single factor or a combination of factors could be important in delineating microhabitats. The first axis is defined solely by soil type and the second axis by the slope, with simultaneous contributions by soil type, levels of light and leaf litter cover. The principal factor delineating the third axis is tree density, with significant contributions by factors like leaf litter, slope of the terrain, and levels of light. The cumulative variance accounted for by the first four axes of the environmental factors was 72%, while that for shrubs and trees was 45% and 24% respectively (Figure 1a). The continuum of quadrats along the second axis indicates the significance of the combination of levels of light, soil cover and tree density in defining the species-specific microhabitat (Figure 1b).



**Figure 1b.** Microhabitats of understorey shrubs

The inset (Figure 1a) depicts the eigenvalues obtained for the first six axes of the matrices analysed: environmental factors & quadrats (EQ), shrubs & quadrats (SQ), and trees & quadrats (TQ). The overlay of three analyses (Figure 1b): environmental factors (letters), tree species (numbers in italics) and shrub species (numbers in regular). The distinct separation between tree species and shrub species can be observed.

### Shrub species and environmental factors

The scatter of the shrub species and the environmental factors indicate that the preference of the understorey shrub species was within the extremes of the microhabitat, as defined by factors like soil type and slope. The contributions of *Canthium travancoricum* (62%) and *Coffea robusta* (33%) were important in defining the first axis. The major contributors for the grouping of species along the second axis were *Agrostistachys indica* (46%) and *Diotacanthus grandis* (12%). The third axis indicated the importance of *Nilgirianthus* sp. (68%).

*Aglaia simplicifolia* could tolerate extremely sparse, rocky soil, falling away from most of the shrub species in the scatter plot. All the other shrub species varied in their tolerance to soil type and slope, although more species were aligned towards sloping terrain. When the relative distances of individual species from slope were considered, preference for sloping terrain seemed possible (Figure 1b). The tolerance of 32% of

the shrub species for higher light regimes was also observed when the overlay of environmental factors and shrub species were made. Shade-loving species were located farther to the right of the first axis, while those tolerating higher light regimes were found to the left of the axis.

Another significant trait that determined the grouping of the understorey shrubs in the community was the tolerance for co-existence with other shrub species. This trait could be inferred by the clustering of the species along axis 1 and 2 towards shrub density when environmental factors and shrub species were overlaid. Tolerance to greater density indicated the capability of the species to co-exist, even when local dominance of other species was high. Shrub species that were intolerant to the presence of other species were located farther away from this cluster. Eleven species could co-exist, although their individual relative degree of tolerance varied. Species like *Erythroxylum obtusifolium*, *Cinnamomum filipedicellatum*, *Aglaia simplicifolia*, *Microtropis stocksii*, *Symplocos wyanadense*, *Chassalia ophioxylodes* and *Micrococca beddomei* fell under this category. Several other shrub species could persist in deeply shaded microhabitats and co-existed with trees, rather than shrubs. Some of these species were *Psychotria annamalayana*, *Euonymus crenulatus*, *Lasianthus cinereus*, *Maesa* sp. and *Tarenna asiatica*. Located at the other end of the axis were species that had no tolerance for co-existence. Shrubs like *Glyptopetalum zeylanicum*, *Melastoma malabathricum*, *Saprosma corymbosum* and *Nilgirianthus foliosus* fell into this category.

#### Influence of the overstorey

The overstorey influenced the understorey shrub community in two ways. First, light penetration was reduced considerably by the successive layering of the canopy and overtopping trees. Second, the dispersion of understorey shrubs was not independent of tree density, as indicated by the chi square test ( $\chi^2 = 235.318$ ,  $df = 14$ ,  $p < 0.005$ ). Of the four light regimes, shade supported greater density of understorey shrubs. Common and dominant shrub species like *Lasianthus cinereus*, *Micrococca beddomei*, *Chassalia ophioxylodes*, *Saprosma corymbosum*, *Symplocos wyanadense*, *Agrostistachys indica* and *Psychotria annamalayana* had more than 50% of individuals in shade compared to other light regimes. Although the maximum shrub density was seen in shade, richness was highest in low density situation, as observed for tree fall gap (Table 1). The difference in diversity and dominance across different light regimes was determined using Berger-Parker index. The maximum diversity was captured in light gap followed by tree fall gap, opening and shade (Table 2). Poor evenness was observed in shaded microsites as they had the highest dominance. Light gap and tree fall gap supported greater evenness in the community due to low dominance. However, the relative dominance of species was higher in tree fall gap compared to

**Table 1.** Richness of understorey shrubs under varied light regimes

Shrub density	Light regimes			
	Shade	Light gap	Opening	Tree fall gap
0-50	1.98	2.54	2.54	2.82
> 50-100	0.70	0.60	0.40	0.30
> 100-500	0.31	0.13	0	0.35
> 500-1000	0.63	0	0	0

**Table 2.** Comparison of richness and diversity estimates across different light regimes

Parameters	Light regimes			
	Shade	Light gap	Opening	Tree fall gap
Number individuals	4406	1030	492	1720
Number species	30	27	22	31
Number quadrats	52	15	9	23
Relative dominance (% species)	85.71	77.14	62.85	88.57
Diversity	5.24	6.51	5.59	6.46
Dominance	0.19	0.15	0.17	0.15
Richness (overall)	0.45	0.84	0.99	0.74
Richness (NE)	0.39	0.49	0.44	0.76
Richness (BE)	0.24	0.46	0.72	0.36
Richness (NnE)	0.26	0.56	0.83	0.38

NE: narrow-endemic species, BE: broad-endemic species, NnE: non-endemic species

in shade. Overall richness was highest in opening, while relative species dominance was highest in tree fall gap followed by shade. Similarity values indicate that opening and tree fall gap were the closest (Jaccard = 0.20), while shade and tree fall gap had the poorest similarity (Jaccard = 0.01). Opening had many common species with light gap (Jaccard = 0.11) and shade (Jaccard = 0.16), but not with tree fall gap (Jaccard = 0.07). Shade and light gap also had poor similarity (Jaccard = 0.05).

The influence of tree density in determining the density and diversity of shrubs is summarised in Table 3. Despite the maximum diversity occurring under high tree density, low tree density provided the best balance between diversity and density for this understorey shrub community. High tree density supported high richness compared to low tree density. High dominance was observed under low, medium and high tree densities. A combination of conditions that encouraged richness, diversity and dominance in the understorey community was found under low tree density.

A clumped dispersion pattern was observed in 85% of shrub species, and the pattern of dispersion carried across all tree densities. Most species were uniformly distributed at moderate tree density, followed by at high tree density (Table 4). At lower tree densities, random distribution of most understorey shrub species was observed. Most of the common species aggregated under low tree densities, although the degree of clumping varied. For example, *Micrococca beddomei*, *Chassalia ophioxylloides* and *Psychotria annamalayana*, showed maximum clumping at very low tree density, and on the other hand, *Saprosma corymbosum*, *Lasianthus cinereus* and *Diotacanthus grandis*

**Table 3.** Patterns of species richness, diversity and dominance over varied overstorey densities

Parameters	Tree density				
	0-2	3-5	6-8	9-11	12-14
Shrub density	2296	3007	1573	276	496
Richness	0.64	0.54	0.65	1.46	0.97
Diversity	4.81	5.67	4.96	5.86	4.76
Dominance	0.20	0.17	0.20	0.17	0.20
Diversity NE	3.64	3.25	3.03	3.39	2.84
Dominance NE	0.27	0.30	0.32	0.29	0.35
Diversity BE	1.75	1.66	1.36	1.08	1.50
Dominance BE	0.57	0.60	0.73	0.92	0.66

Abbreviations follow Table 2

**Table 4.** Dispersion patterns for common and dominant shrub species across different tree densities

Parameters	Tree density				
	0–2	3–5	6–8	9–11	12–14
<i>Saprosma corymbosum</i>	6.14	2.57	4.10	13.65	5.87
<i>Diotacanthus grandis</i>	5.62	6.60	5.34	3.60	9.72
<i>Micrococca beddomei</i>	11.86	6.41	3.37	7.79	3.05
<i>Chassalia ophioxylodes</i>	11.53	6.86	7.10	4.15	10.91
<i>Psychotria annamalayana</i>	7.47	2.61	2.97	4.81	3.71
<i>Lasianthus cinnerus</i>	6.71	6.76	7.21	8.37	4.56
<i>Nilgirianthus sp.</i>	8.75	8.75	22.93	6.88	2.63

The species listed are common and dominant understorey shrubs

(all narrow-endemics) dispersed in a highly clumped manner in microsites with high tree density. Only *Nilgirianthus sp.* favoured sites with moderate tree density. Thus, the clumped dispersion pattern of the individual species varied only in relative intensity.

#### Microhabitat of the endemic species

The endemic understorey shrub species accounted for 55% of the total species studied. Richness for broad and narrow-endemic species indicated differential capacity for tolerating disturbances (Table 2). Richness of narrow-endemic species was highest in tree fall gaps (Mn = 0.76), and was considerable in other light regimes. Even in shaded microhabitat, the richness of narrow-endemic species was high (Mn = 0.39) compared to broad-endemic species (Mn = 0.24) and non-endemic species (Mn = 0.26). However, there was very little difference between the richness for broad-endemic and non-endemic under various light regimes. The highest richness in both broad-endemic species and non-endemic species was observed in opening.

The Berger-Parker index used to determine changes in the dominance of the endemic species under varied tree densities indicated that the greatest dominance of narrow-endemic species was attained in high tree density, while diversity was highest under low tree density (Table 3). Greater evenness was observed for narrow-endemic species as their dominance values were always small (range 0.27–0.35) compared to the broad-endemic species (range 0.57–0.92). Narrow-endemic species had greater diversity than the broad-endemic species under all tree densities.

Under low shrub density conditions, richness of broad- and narrow-endemic species was highest in the openings (Mn = 1.55) (Table 5). However, the broad-endemic species did not seem to be abundant and adaptive as the narrow-endemic species since

**Table 5.** Density and richness of endemic shrub species

Shrub density	Light regimes			
	Shade	Light gap	Opening	Tree fall gap
0–50	0.28 (1.27)	0.84 (1.41)	1.55 (1.55)	0.84 (1.41)
> 50–100	0.50 (0.10)	0.50 (0.10)	0.10 (0)	0.20 (0)
> 100–500	0.17 (0.04)	0.04 (0)	0 (0)	0.17 (0.04)
> 500–1000	0.03 (0)	0 (0)	0 (0)	0 (0)
Overall	0.39 (0.24)	0.49 (0.46)	0.44 (0.72)	0.76 (0.36)

Richness values of NE and BE (values in parentheses)



they were absent in opening and tree fall gap under moderate shrub densities. Unlike shade, light intense microsites such as light gap, opening and tree fall gap, supported lower density of shrubs.

The understory shrubs can be classified into three groups based on their preference to light regimes and tolerance for other shrub species:

- Group 1 Those that prefer dense shade and co-exist with other shrub species. These include *Meiogyne pannosa*, *Psychotria annamalayana*, *Euonymus crenulatus* (all endemic species, two narrow-endemic species).
- Group 2 Those that prefer moderate shade and co-exist with other shrub species that are in low density. These include *Xenacanthus pulneyensis*, *Erythroxylum obtusifolium*, *Cinnamomum filipedicellatum*, *Microtropis wallichiana*, *Chassalia ophioxyloides*, *Phyllanthus fimbriatus* and *Micrococca beddomei* (77% endemic species, four narrow-endemic species).
- Group 3 Those that prefer light and are intolerant to other shrub species. These include *Melastoma malabathricum*, *Diotacanthus grandis*, *Glyptopetalum zeylanicum* and *Nilgirianthus foliosus* (67% of the species are endemic, all narrow-endemic species).

### Discussion

The principal environmental factors that had significant influence on the understory community were soil type, slope and tree density. At the scale of study, shaded microhabitat supported greater shrub density than other light regimes, but had poor diversity and greater dominance of some species. No microsite was favourable for all the species, and values of relative dominance and similarity indicated that certain microsites were favoured by some species. Tree fall gaps had greater diversity and richness, but were poor in density and dominance. Low tree densities encouraged the establishment of greater shrub diversity without allowing for dominance by any single species. The diversity, richness and dominance of the understory shrubs were maintained in low tree density. In this study, the effects of the overstorey on the understory shrub diversity were viewed in a relative manner, wherein, one-to-one interference was not inferred. The effects were largely due to the regulation of light regimes, litter cover and the density of trees as physical attributes of the microsites. The narrow-endemic species had greater richness in tree fall gap, higher density in shade and clumped dispersion pattern. The broad-endemic species had greater richness in openings, but less evenness than narrow endemic species and tended to be dispersed in a uniform manner. The richness of non-endemic species was however in openings. Several studies showed that understory plants can be less gap dependent than the canopy trees, and thus adapted to disturbances that vary the amount of light available (Denslow 1980, Hartshorn 1980, Whitmore 1980). This study indicates that capturing diversity and increasing density were not operationally similar for understory shrubs. Greater diversity was captured in the openings than in the shade. This can be due to the differences observed among species with respect to the number of adults that can occupy a light gap or that part of the light gap that is opened for colonisation by the species (Richards & Williamson 1975). Gap regimes also enabled colonising species, such as *Nilgirianthus*, to establish and thrive in different light regimes. Although the establishment of most understory shrubs favoured some form

of disturbance, shading by the overstorey facilitated the increase in density for most species. This ability of understorey plants to survive in low light conditions is not attributed to their adaptation, but to their tolerance for varied light regimes (Beatty 1984).

The plurality of the response of the shrubs was also observed with their dispersion pattern. Although clumped pattern was the most dominant dispersion pattern, some species showed a shift in the density patterns across the various overstorey assemblages, leading to expansion of their distribution ranges. The understorey conditions seemed to be a continuum of a narrow set of environmental parameters in which the overstorey played a significant role in defining the microhabitats. The predictions of the hypotheses of species co-existence (Connell 1978) and availability of regeneration niche (Grubb 1977), emphasise the occurrence of some form of disturbance to reduce the dominance of a species, thereby allowing the establishment of a new species by colonisation or growth of new individuals. These hypotheses can serve well to explain the diversity of the understorey shrubs, although they may not be mutually exclusive. Shrubs, in the understorey conditions, establish themselves across varied microhabitats by adaptation to the minor disturbance regimes.

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## Appendix 1

## Environmental factors

lgt	Light intensity
st	Soil type
scv	Soil cover
slp	Slope of terrain
wtr	Moisture availability
dsh	Shrub density
dtr	Dead trees
dhb	Herb density
tt	Tree density

Tree species	Family	Legend for Figure 1b
<i>Acronychia pedunculata</i>	Ru	1
<i>Actinodaphne tudulingami</i>	La	2
<i>Agalia jainii</i>	Me	3
<i>Agalia elaeagnhoidea</i> var. <i>bourdillonii</i>	Me	4
<i>Agrostistachys borneensis</i>	Eu	5
Annonaceae		6
<i>Antidesma menasu</i>	Eu	7
<i>Ardisia pauciflora</i>	My	8
<i>Artocarpus heterophyllus</i>	Mo	9
<i>Bentinckia coddapenna</i>	Pa	10
<i>Calophyllum austroindicum</i>	Cl	11
<i>Cinnamomum travancoricum</i>	La	12
<i>Clerodendrum viscosum</i>	Ve	13
<i>Cullenia exarillata</i>	Bo	14
<i>Cinnamomum verum</i>	La	15
<i>Diospyros malabarica</i>	Eb	16
<i>Epiphrinus mallotiformis</i>	Eu	17
<i>Garcinia travancorica</i>	Cl	18
<i>Gomphandra coriacea</i>	Lc	19
<i>Hologarna nigra</i>	An	20
<i>Litsea insignis</i>	La	21
<i>Litsea ligustrina</i>	La	22
<i>Litsea wightiana</i>	La	25
<i>Maesa indica</i>	My	24
<i>Millettia wightiana</i>	An	25
<i>Myristica dactyloides</i>	Mr	26
<i>Notopegia travancorica</i>	An	27
<i>Ocrotropis travancorica</i>	Rb	28
<i>Olea dioica</i>	Ol	29
<i>Ormosia travancorica</i>	Pp	30
<i>Palaequium ellipticum</i>	Sa	31
<i>Persea macarantha</i>	La	32
<i>Nageia wallichiana</i>	Po	33
Unidentified		34
<i>Scolopia crenata</i>	Fl	35
<i>Syzygium gartneri</i>	Mt	36
<i>Tricalysia apiocarpa</i>	Ru	37
<i>Veprip bilocularis</i>	Ru	38

Shrub species	Family	Legend for Figure 1b
<i>Agrostictachys indica</i>	Eu	1
<i>Aglia simplicifolia</i>	Me	2
<i>Meiogyne pinnosa</i>	An	3
<i>Sauropus androgynus</i>	Eu	4
<i>Canthium travancoricum</i>	Ru	5
<i>Cinnamomum filipedicellatum</i>	La	6
<i>Saccandra chloranthoides</i>	Ch	7
<i>Chionanthus malabarica</i>	Ol	8
<i>Coffea robusta</i>	Ru	9
<i>Saprosma corymbosum</i>	Ru	10
<i>Diotacanthus grandis</i>	Ac	11
<i>Euonymus crenulatus</i>	Ce	12
<i>Erythroxylum obtusifolium</i>	Er	13
Unidentified		14
<i>Glyptopetalum zeylanicum</i>	Ce	15
<i>Barleria involucratavar. elata</i>	Ac	16
<i>Microtropis stocksii</i>	Ce	17
<i>Micrococca beddomei</i>	Eu	18
<i>Maesa</i> sp.	My	19
<i>Murraya paniculata</i>	Ru	20
<i>Melastoma malabathricum</i>	Me	21
<i>Memecylon flavescens</i>	Me	22
<i>Chassalia ophioxylodes</i>	Ru	23
<i>Phyllanthus fimbriatus</i>	Eu	24
<i>Psychotria annamalayana</i>	Ru	25
<i>Lasianthus cinereus</i>	Ru	26
<i>Symplocos wyanadense</i>	Sy	27
<i>Solanum ferox</i>	So	28
<i>Tarenna asiatica</i>	Rb	29
<i>Toddalia asiatica</i>	Ru	30
<i>Uvaria narum</i>	An	31
<i>Delmegeasia longifolia</i>	Ur	32
<i>Nilgiranthus foliosus</i>	Ac	33
<i>Xemacanthus pulneyensis</i>	Ac	34
<i>Nilgiranthus</i> sp.	Ac	35

Ac = Acanthaceae, An = Anacardiaceae,  
 An = Annonaceae, Bo = Bombacaceae,  
 Ce = Celastraceae, Ch = Chloranthaceae,  
 Cl = Clusiaceae, Eb = Ebenaceae,  
 Er = Erythroxylaceae, Eu = Euphorbiaceae,  
 Fl = Flacourtiaceae, Ic = Icacinaceae  
 La = Lauraceae, Me = Melastomataceae,  
 Me = Meliaceae, Mo = Moraceae,  
 Mr = Myristicaceae, Mt = Myrtaceae,  
 My = Myrsinaceae, Ol = Oleaceae,  
 Pa = Palmae, Po = Podocarpaceae,  
 Pp = Papilionaceae, Rb = Rubiaceae,  
 Ru = Rutaceae, Sa = Sapotaceae,  
 So = Solonaceae, Sy = Symplocaceae,  
 Ur = Urticaceae, Ve = Verbenaceae