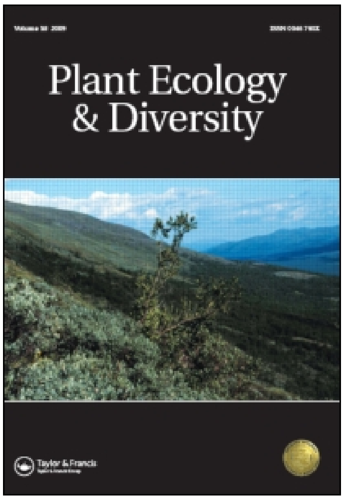
This article was downloaded by: *[Davidar, Priya]*
On: *6 August 2010*
Access details: *Access Details: [subscription number 925260886]*
Publisher *Taylor & Francis*
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



**Plant Ecology & Diversity**
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t793409773

# The relationship between area, and vegetation structure and diversity in montane forest (shola) patches in southern India

Dharmalingam Mohandass[a]; Priya Davidar
[a] Department of Ecology and Environmental Sciences, School of Life Sciences, Pondicherry University, Kalapet, Pondicherry, India

Accepted uncorrected manuscript posted online: 17 May 2010

Online publication date: 17 May 2010

**To cite this Article** Mohandass, Dharmalingam and Davidar, Priya(2010) 'The relationship between area, and vegetation structure and diversity in montane forest (shola) patches in southern India', Plant Ecology & Diversity, 3: 1, 67 — 76, doi: 10.1080/17550874.2010.492843, First posted on: 17 May 2010 (iFirst)

**To link to this Article: DOI:** 10.1080/17550874.2010.492843

**URL:** http://dx.doi.org/10.1080/17550874.2010.492843

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

*Plant Ecology & Diversity*
Vol. 3, No. 1, February 2010, 67–76

# The relationship between area, and vegetation structure and diversity in montane forest (shola) patches in southern India

Dharmalingam Mohandass and Priya Davidar*

*Department of Ecology and Environmental Sciences, School of Life Sciences, Pondicherry University, Kalapet, Pondicherry, India*

(*Received 7 May 2009; final version received 9 May 2010*)

***Background:*** The montane forests of the higher altitudes of the Western Ghats in southern India, called 'sholas', are naturally patchy and closely juxtaposed with grasslands. Palaeoclimatic studies have indicated that the sholas have expanded in warmer climatic regimes and the grasslands during colder climates. Therefore during the present post-glacial climatic regime sholas may be in the expansion phase.
***Aims:*** We aimed to test if sholas are in an expansion phase; in particular, if smaller sholas could be at earlier successional stages than larger sholas.
***Methods:*** We enumerated all non-climbing plants (≥ 1 cm dbh) in 18 shola patches ranging from 0.09 ha to 15 ha in area. We tested whether species richness, basal area, and proportion of large trees (≥ 30 and ≥ 60 cm dbh) increased with shola size, and rare and 'ecotone' species decreased with shola size.
***Results:*** As predicted, species richness, basal area and the proportion of large trees (≥ 60 cm dbh) increased with shola size, whereas the proportion of rare and 'ecotone' species decreased with shola size, and species in smaller sholas were a nested subset of those in larger sholas.
***Conclusions:*** These results suggest that shola forests are a highly structured plant community, possibly driven by succession.

**Keywords:** ecotone; India; nestedness; Nilgiris; plant succession; tropical montane forests; Western Ghats

## Introduction

Climate has played a major role in shaping tropical forests worldwide, and the responses of vegetation to climate have been well documented (Flenley 1998). The dynamics of forests that have been subject to severe climate changes during the Pleistocene could provide insights into possible responses of vegetation to climate change. The upper montane forests (≥ 1800 m above sea level, a.s.l.) of the Western Ghats of India, locally called 'sholas', naturally occur as discrete patches restricted to the folds in the hillside that are less subject to winter frost. The sholas are separated from the adjacent grasslands by a narrow ecotone (Meher-Homji 1967). The grasslands, dating back to at least 30 ky BP predate human presence in this region (Vasanthy 1988; Sukumar et al. 1995; Caner et al. 2007). Most shola plants are of tropical origin and have low tolerance to frost and fire, and do not regenerate in the open, whereas the species along the shola edges, called 'ecotone' species, are frost resistant and are temperate in origin (Ranganathan 1938; Meher-Homji 1967; Blasco 1970).

The factors that have maintained sholas and grasslands juxtaposed to each other have provoked much debate: for instance, Sukumar et al. (1993) have attributed the dynamism of the shola–grassland mosaic to moisture and $CO_2$ levels, whereas others have emphasised the role of frost and fire (Ranganathan 1938; Vasanthy 1988). The montane forests of the Western Ghats have been subject to considerable climatic changes in the Pleistocene: there was a relatively drier period from 30 to 18 ky BP, where the grasslands expanded, followed by a more humid period between 18 to 10 ky BP, associated with the expansion of forests (Caner et al. 2007). The stable carbon isotope composition ($\delta^{13}C$) of organic matter in the soil shows that the surface horizon (0–20 cm) derives from C3 plants (forests) and the deeper horizons (20–120 cm) from C4 plants (grasses), indicating the more recent origin of forests in this region (Caner and Bourgeon 2001).The extent of grasslands was highest during drier conditions since 10 ky BP, and many of the areas under grassland at that period are now under forest (Caner et al. 2007).

The vegetation changes since 18 ky BP have not been homogenous in the upper plateau of the Nilgiris (Caner et al. 2007). In the western region, where we conducted the present study, there was limited expansion of the sholas into the grasslands during warmer climates since 18 ky BP, whereas in the southern and eastern region the sholas expanded extensively and rapidly (Caner et al. 2007). The limited expansion in the west has been attributed to the severe winds prevailing in that region during the southwesterly monsoon, wherefore (Caner et al. 2007) the sholas have remained separated even during warmer periods.

Vishnu-Mittre and Gupta (1968) analysed pollen sequences since 18 ky BP in peat deposits in two swamps in the northern Nilgiri Plateau (> 2000 m a.s.l.). The resulting pollen diagram suggested that sholas were initiated by a core of frost-resistant shrubby vegetation such as

---

*Corresponding author. Email: pdavidar@pondiuni.edu.in

ISSN 1755-0874 print/ISSN 1755-1668 online

DOI: 10.1080/17550874.2010.492843
http://www.informaworld.com

*Rhododendron* that over time was replaced by taller and more shade-tolerant trees. Clements (1916) described succession as an orderly and sequential process following a chronological sequence. Facilitation, a process in which the early successional stages created conditions conducive for the establishment of later successional plants (Connell and Slatyer 1977) may have played a role in the dynamics of the shola–grassland ecosystem. The ecotone species could have facilitated the establishment of frost-intolerant forest interior species, therefore playing a role in shola expansion. Odum (1983) argued that succession necessarily proceeds towards greater diversity and biomass. Whitmore (1984) described succession in tropical rain forests as a progression where self-thinning occurs in the intermediate phases, followed by a mature phase resulting in more stable conditions. Others have regarded succession as a more stochastic process, with recurrent and small-scale disturbances causing structural variations in vegetation over the landscape (Whittaker and Levin 1977; Sousa 1984; Pickett and White 1985; Veblen 1992).

If the type of successional process in shola forests were a progression as predicted by the Clementsian model, then we would expect there to be associations between shola size and vegetation parameters such as basal area of woody plants and the proportion of large trees, because plants in smaller sholas would be smaller with higher densities and lower basal area compared with those of larger sholas. Species diversity would also increase because the expanding sholas would accumulate more species due to the area effect (MacArthur and Wilson 1967). However, larger sholas would also have a discrete boundary bordered by an ecotone (Meher-Homji 1967); therefore ecotone species would be found in all sholas, regardless of size but restricted to the margins. If so, then we could expect a nested pattern of species distributions, as seen in land-bridge islands where species in a smaller island were shown to be a subset of that of a larger island (Patterson 1987).

The reverse process could also lead to this pattern, caused by the deterioration of larger sholas. However, the mechanisms for such are not obvious, since human impact is minimal in this region and the natural causes for forest retrogression cannot be identified.

We had earlier recorded 87 species (≥ 1 cm diameter at breast height (dbh)) from 65 genera and 42 families from within 18 sholas ranging in size from 0.09–15 ha in the Korakundah and Upper Bhavani region in the south-western region of the Nilgiris (Mohandass and Davidar 2009), and 86 species in a large shola in the Palni Hills, a mountain range about 150 km south of the present study site. These two study areas shared 47% of species, and vegetation structure and diversity were similar to the Nilgiri sholas (Davidar et al. 2007). In both study areas the shola interior was dominated by the tropical families Lauraceae and Rubiaceae, whereas the shola–grassland ecotone was dominated by frost-tolerant shrubby vegetation such as *Berberis*, *Mahonia* and *Rhododendron* that are widely distributed in the Himalayas and on mountains of Asia and of subtropical latitudes (Meher-Homji 1967; Ohsawa 1991; Mohandass and Davidar 2009). In this study we assessed species richness, plant basal area ($m^2 ha^{-1}$), rarity (proportion of species represented by one individual plant), proportion of large trees (≥ 30 and ≥ 60 cm dbh), and frost-resistant plants found in the shola ecotone, termed 'edge' species in this study. We predicted that if smaller sholas were at earlier stages of succession than larger sholas, then species diversity, basal area of trees, and the proportion of larger trees would increase, whereas the proportion of edge species would decrease with increase with shola size. The proportion of forest interior species would also be rare in smaller sholas, since random dispersal events would account for their presence in smaller sholas, whereas they would be well established in larger sholas. We also predicted that species assemblages would be nested, i.e. species in smaller sholas would be a subset of those in larger sholas. We tested the null hypothesis that there would be a lack of association between shola area and vegetation structure and diversity.

## Materials and methods

### *Study area*

The study was conducted from November 2002 to September 2004 in the sholas of the Korakundah and Upper Bhavani Reserved Forest (11° 14' N; 76° 33' E) about 60 km south-west of Ootacamund, the headquarters of the Nilgiri District. These sholas are, on average, about 6 km apart, separated by a ridge (Figure 1). Reserved Forest is a category of forest that has a lower level of protection than a National Park.

The elevation in the study area ranged from 2200–2400 m a.s.l., and the climate was relatively cold and dry for this latitude and altitude with temperature ranging from 0 °C–23 °C, although mist and intermittent fog frequently covered the western slopes. Frost was prevalent from December to February. The mean annual rainfall over a period of 10 years (1994–2003) was 1887 mm at Korakundah

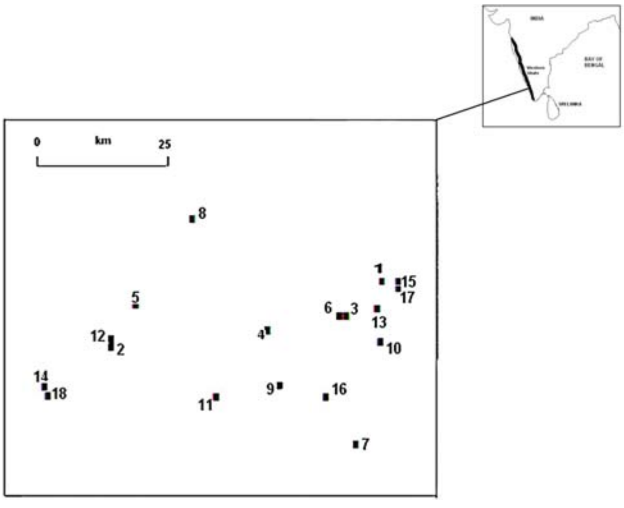


Figure 1. Map of the study area indicating location of the study site and the sholas.

Tea Estate and 2637 mm at Upper Bhavani Electricity Department (Mohandass 2007). The dry season length was about 5 months in both sites (Mohandass 2007).

We selected 18 shola forests to represent a size range from the very small (0.09 ha) to the large (15 ha), and at differing distances from each other. The median distance between sholas was 3–4 km: nine of the sholas were close together (< 1 km apart), and several sholas were more than 7 km apart (Figure 1). Ten of the sholas were from Korakundah and eight from the Upper Bhavani region (Table 1). Four sholas were near roads and small settlements (less than five households) and 14 were inaccessible by road and far from settlements. Ten sholas were adjacent to *Acacia* plantations, three were close to tea plantations and the rest were surrounded by natural grasslands and grassy swamps (Table 1). The Australian *Acacia* plantations date from the 1970s and are unlikely to have influenced the dynamics of the slow-growing shola vegetation, and the tea plantations were not juxtaposed to sholas. Anthropogenic change was minimal in the studied sholas since the local households, mostly settlers except for a small community of the Toda ethnic group, have only used electricity/gas for cooking, subsidized by the plantations and the Tamilnadu Electricity Board.

The figure for the area of larger sholas was obtained from the Nilgiri Forest Department records. The area of the smaller sholas was obtained by actual measurement of the perimeter of the shola. The geographical coordinates of each plot were determined by using a Geographical Positioning System. The areas of sholas on slopes were expressed as vertically projected areas after using a trigonometric function: $\cos \alpha \times l$ (where $\alpha$ is the measured slope angle and $l$ is the measured slope length) to correct for slope. Slope angle was measured by using a clinometer and slope length by a tape measure.

The soil profile underlying sholas is black soil, which is a superposition of a thick dark reddish-brown (60–100 cm) surface horizon rich in organic matter above a reddish ‘lateritic’ material (Blasco 1970; Caner and Bourgeon 2001). As the soils under sholas are fairly uniform, they are unlikely to influence species distribution patterns in these forests (Caner and Bourgeon 2001; Mohandass 2007). The soils on the Nilgiri Plateau today are basically relicts of a formerly much thicker soil cover that developed under pedodynamic conditions prevailing from late Jurassic to early Tertiary time (Subramanian and Murthy 1976). The black soils are acidic in nature (pH 4.5–6), containing a high percentage of iron and alumina ($Al_2O_3$) and can be classified as non-allophanic andisols, shaped by advanced weathering, with the parent material being lateritic subsoil (Caner et al. 2000).

Earlier assessments have indicated that preferences for particular habitat/topographical categories at local scales are unlikely to have significantly influenced species distribution patterns: 67% of the 60 shola plant species investigated occurred in a variety of habitats such as slopes, stream sides and valleys, 17% were mostly recorded on slopes, 15% on edges and one species was riparian (Mohandass 2007). Only two habitat categories, shola interior and edge, were distinctive, and the others such as slopes, stream sides intergraded with each other.

### Plant inventory

It was not possible to employ identical methodology for very small and large sholas because randomisation of plot

Table 1. Name, location, sampled area and floristic features of the study sholas.

| SL | Name of shola | Region | Surrounding vegetation | Area (ha) | Area sampled (ha) | Species richness | Number of plants (≥ 1 cm dbh) | Basal area ($m^2\ ha^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 1 | Goodmorsh | Korakundah | Grassland, grass swamps | 15 | 1.17 | 42 | 3069 | 77.38 |
| 2 | Paybungalow | Upper Bhavani | Acacia plantation | 9 | 1.08 | 41 | 2175 | 75.93 |
| 3 | Godown | Korakundah | Acacia plantation | 4 | 1.08 | 47 | 3177 | 85.39 |
| 4 | Korakundah Estate | Korakundah | Tea plantation | 3 | 1.08 | 37 | 2350 | 35.72 |
| 5 | Kolimund | Upper Bhavani | Grassland, grassy swamps | 2 | 0.9 | 36 | 2012 | 49.37 |
| 6 | Forest camp | Korakundah | Acacia plantation | 1.26 | 1.26 | 47 | 4238 | 86.7 |
| 7 | East Varagapalam | Korakundah | Acacia plantation | 0.9 | 0.9 | 47 | 1946 | 62.5 |
| 8 | Narkulimund | Upper Bhavani | Grassland, grassy swamps, Acacia plantation | 0.82 | 0.82 | 37 | 1915 | 46.43 |
| 9 | Tunnel | Korakundah | Tea plantation | 0.72 | 0.72 | 38 | 2012 | 44.14 |
| 10 | Mandu | Korakundah | Grassland, Acacia plantation | 0.5 | 0.5 | 42 | 1062 | 34.51 |
| 11 | Kutkoor | Upper Bhavani | Grassland, grassy swamps, Acacia plantation | 0.4 | 0.4 | 36 | 895 | 22.3 |
| 12 | Siege | Upper Bhavani | Acacia plantation | 0.4 | 0.4 | 31 | 1303 | 13.11 |
| 13 | Doddabeta | Korakundah | Tea plantation | 0.3 | 0.3 | 29 | 622 | 9.75 |
| 14 | Thurawadkoor | Upper Bhavani | Acacia plantation | 0.24 | 0.24 | 25 | 547 | 12.7 |
| 15 | Kershnkoor | Korakundah | Acacia plantation | 0.18 | 0.18 | 31 | 542 | 9.23 |
| 16 | Peautikoor | Korakundah | Acacia plantation | 0.12 | 0.12 | 31 | 415 | 8.93 |
| 17 | Mesrshnkoor | Korakundah | Acacia plantation | 0.1 | 0.1 | 24 | 236 | 4.61 |
| 18 | Nununkoor | Upper Bhavani | Acacia plantation | 0.09 | 0.09 | 21 | 223 | 2.94 |

locations was not possible in the small sholas. Therefore all non-climbing plants were enumerated in the 12 smaller sholas of an area ≤ 1.26 ha using 10 m × 10 m subplots laid sequentially from one end to the other until the entire patch was covered. In the six sholas greater than 1.26 ha, plots of 30 m × 30 m (0.09 ha) in size were laid randomly within each shola. Each plot was divided into 10 m × 10 m subplots. All individuals of at least 1 cm dbh were enumerated, identified and tagged with sequentially numbered aluminium tags. The habitat in which each plant was found was classified as 'edge', gradual slope (< 40 °), steep slope (≥ 40 °), flat area (< 10 °) and streamside. The sampling in the larger sholas was terminated when the species accumulation curve reached an asymptote. The total area sampled was 11.36 ha.

All plant specimens were identified to species level using floras (Fyson 1932; Gamble and Fischer 1915–1936; Matthew 1999) and identification of sample specimens was confirmed at the Botanical Survey of India, Coimbatore and the French Institute of Pondicherry. Herbarium specimens were deposited in the Department of Ecology and Environmental Sciences, Pondicherry University. Nomenclature follows the Flora of Tamilnadu and Flora of the Palni Hills (Nair and Henry 1983; Henry et al. 1987; Henry et al. 1989; Matthew 1999).

### *Floristic analyses*

Since sholas are isolated from each other, we assessed if the log number of species would increase linearly with log area, as predicted by the theory of island biogeography (MacArthur and Wilson 1967). To establish if larger sholas were at a more mature phase with larger trees, we examined the relationship between basal area and the proportion of large trees of at least 30 and at least 60 cm dbh. The proportion of large trees in each shola was obtained by dividing the number of large trees by the total number of plants recorded (≥ 1 cm dbh). We also assessed if very large trees (≥ 100 cm dbh) tended to be restricted to larger sholas by looking at the total number of very large trees per shola and the proportion confined to the larger sholas. To rule out the effect of topographic limitations on shola size, we obtained an indirect measure of the proportion of different habitat types available within each shola by summing the number of plants recorded on that particular habitat. Therefore, in order to see whether smaller sholas were disproportionately located on steep slopes which could be a constraint on their size, we then summed the proportion of plants that were recorded on steep slopes (> 40 ° gradient) and divided this over the total number of plants in that shola, as an indirect estimate of the availability of that habitat type within the shola. We correlated the arcsine-transformed proportion of plants recorded on steep slopes with the log-transformed area of the shola.

If smaller sholas were at an earlier stage of succession, then the proportion of edge species and rare species should decrease with increasing shola size. The edge species were those that have already been identified as 'ecotone' species by Meher-Homji (1967) and belong to genera such as *Rhododendron*, *Gaultheria*, *Mahonia*, *Photonia*, *Rubus* and *Rosa*, which are of temperate affinity and occur in the tropical mountains of East Asia (Ohsawa 1991). These species appear to be more adapted to the cold frosty conditions prevalent in the grasslands (Meher-Homji 1967), and had probably migrated southwards from the Himalayas during the glaciations (Blasco 1970). Of the 15 species with temperate affinity reported in the study area, nine species (56%) were predominantly found on edges, and six species (38%) such as *Ilex* spp. (Aquifoliaceae), *Vaccinium neilgherrense* (Ericaceae) and *Mahonia leschenaultii* (Berberidaceae) were habitat generalists (Mohandass 2007). We selected the above nine temperate 'edge' species and included another species, *Berberis tinctoria*, for which the habitat analysis had not been conducted but which occurred along edges (Mohandass 2007), and assessed the proportion of these species over the total plants recorded for each shola. We looked at the proportion of these species over the total number of plants in each shola. The analysis was conducted using all 18 sholas, and then to correct for the sampling effect, a subset of the 12 sholas (< 1 ha) where the entire shola, both interior and edge, was sampled.

The proportion of edge species may be related to the shape of the shola. We classified sholas as rectangular/triangular or oval/round and using Fisher's exact test, and tested whether larger (≥ 0.9 ha) or smaller sholas (< 0.9 ha) differed significantly between these two shape categories. We tested whether there were significant differences in the number of smaller sholas (< 0.9 ha) in the two shape categories.

Rare species were those represented by single plants, and using the $\chi^2$ test we assessed if rare plants in the smaller sholas tended to be species of the forest interior rather than the edge. We then regressed the proportion of edge species on shola size. The analysis was conducted using all 18 sholas, and then to correct for the sampling effect, a subset of the 12 sholas (< 1.26 ha) where the entire shola, both interior and edge was sampled.

We evaluated whether, collectively, small sholas had more species and stems ha$^{-1}$ than medium and larger sholas, because as succession progresses, the thinning effect would reduce plant density in the larger sholas, and if small sholas differed from each other in species composition due to random colonisation processes, then collectively, smaller sholas may have more species than a single large shola (Cook and Quinn 1995). We designated sholas less than 0.9 ha as small, sholas of at least 0.9 but less than 5 ha as medium and those greater than 5 ha as large. We pooled data from all sholas of each size class and estimated the total number of species in each size class, and densities of plants ha$^{-1}$ for three different lower dbh classes: at most 10 cm dbh, from 15 to at most 25 cm dbh and greater than 30 cm dbh.

We assessed the relationship between species richness, basal area, rarity, the proportion of large trees and edge species with shola size with regression analysis. Species richness and shola area were transformed into their natural logarithms, and all proportionate values were arcsine transformed for the analysis. Statistical tests were conducted using Systat version 10 (SPSS Inc 2000).

### *Nestedness*

We used the nestedness analysis, which may provide insights into whether the assemblage was randomly assembled or was an outcome of deterministic processes (Atmar and Patterson 1993). Nestedness occurs when species in a smaller isolate is a subset of that of a larger isolate. The nestedness of species assemblage can be measured by the matrix temperature $T$ developed by Atmar and Patterson (1993, 1995). Nestedness arises due to structuring mechanisms (Cook et al. 2004) and can be due to selective extinction, as species disappear when the isolate becomes smaller (Patterson 1987; Atmar and Patterson 1993), or due to colonisation, when the differential dispersal abilities of species results in a nested pattern (Cook and Quinn 1995; Loo et al. 2002).

The plant assemblage was tested for nestedness using the nestedness calculator (Atmar and Patterson 1995). A presence–absence matrix, with the species in columns in decreasing order of abundance, and sholas in rows in decreasing order of size, was assembled. The nestedness calculator maximally packs the matrix, reordering rows and columns so as to concentrate presences in the upper left-hand corner of the matrix (Wright et al. 1998). The packed matrix is then compared with randomly generated matrices using Monte Carlo simulations. The matrix temperature $T$ gives a standardised measure of matrix disorder by assessing the deviation of an ordered matrix from one of the same rank and fill that is perfectly nested. The $T$ ranges from 0 for a perfectly nested matrix to 100 for one that is completely disordered. We used Monte Carlo simulations of 100 randomly generated matrices, the $T$ value of which could be statistically compared with that of the species assemblage.

## Results

### *General patterns*

There were a total of 69 species and 28,648 individuals enumerated in the 18 sholas. Trees accounted for 54 of the species, and there were 11 shrubs and four large herbs. Only one species, *Cestrum elegans*, was non-native but was uncommon (comprising 0.13% of plants) and restricted to the edge (Mohandass 2007). Over one-third of species (27, 36%) were recorded on more than 75% of the sholas. Forty-nine species (63%) were common to the Korakundah and Upper Bhavani sholas. Dominant species in both regions were *Psychotria nilgiriensis*, *Lasianthus venulosus* and *Litsea wightiana*. These three species comprised 38% of the plants in Korakundah and 37% in Upper Bhavani. Species that were rare (< 10 plants) in both sites were a bamboo *Arundinaria wightiana* var. *wightiana* and a small tree *Schefflera capitata*.

### *Effect of shola size*

The total area of the 18 sholas was 39.03 ha, of which 11.34 ha was the sampled area. Of the sampled area, 3.87 ha were sampled in the 11 small sholas (< 0.9 ha), 4.32 ha in the five medium-sized sholas (≥ 0.9 to < 5 ha) and 2.25 ha in the two large (> 5 ha) sholas. The number of smaller or larger sholas in the two shape categories round/oval or triangle/rectangle did not significantly differ (Fisher's exact test two tailed = 0.35, ns), and there were similar numbers of smaller sholas (< 0.9 ha) in both shape categories, therefore we did not consider shape of the shola in the analysis (Wilcoxon signed-rank test = 1.62, ns).

There was no correlation between the proportion of plants on steep slopes and log shola size (Pearson's correlation coefficient $r = 0.09$, $n = 18$, ns), indicating that smaller sholas tended not to be differentially located on steeper slopes. When small sholas less than 0.5 ha were considered, the proportion of plants on steep slopes ranged from 0–40%, which further indicates that smaller sholas were not located on steeper topography than larger sholas. In fact, when five larger sholas of at least 3 ha were considered, two of them had more than 25% of plants growing on steep slopes.

The number of species ($\log_n$ species richness) in a shola increased significantly with increase in shola size ($\log_n$ ha). However, the polynomial function gave a better fit than the linear function, indicating that intermediate-sized sholas could have more species, although this is probably because there were only two large sholas in the sample (Table 2, Figure 2). Basal area of trees ($m^2$ $ha^{-1}$) and the proportion of large trees at least 60 cm dbh increased significantly with increasing shola size ($r = 0.60$), whereas the proportion of trees at least 30 cm dbh increased marginally with shola size (Table 2, Figure 2). About 83% of the largest trees in the assemblage (≥ 100 cm dbh) were

Table 2. The effect of shola size (ha) on various vegetation parameters.

| Dependent variable | Equation | Number of sholas | R-square | $P$ value |
|---|---|---|---|---|
| Ln species (linear) | $y = 38.53 + 3.97x$ | 18 | 0.54 | 0.0004 |
| Ln species (polynomial) | $y = 41.46 + 3.87x – 1.26x^2$ | 18 | 0.70 | 0.0001 |
| Basal area ($m^2$ $ha–^1$) | $y = 43.54 + 16.96x$ | 18 | 0.74 | <0.0001 |
| Trees ≥ 30 cm dbh (arc sin prop) | $y = 0.07 + 0.006x$ | 18 | 0.16 | 0.09 |
| Trees ≥ 60 cm dbh (arc sin prop) | $y = 0.013 + 0.0015x$ | 18 | 0.36 | 0.008 |
| Rarity index (arc sin prop) | $y = 11.17 – 2.97x$ | 18 | 0.37 | 0.007 |
| Ecotone species (all sholas) (arc sin prop) | $y = 0.15 – 0.02x$ | 18 | 0.24 | 0.04 |
| Ecotone species (< 1 ha) (arc sin prop) | $y = 0.16– 0.014x$ | 12 | 0.03 | ns |

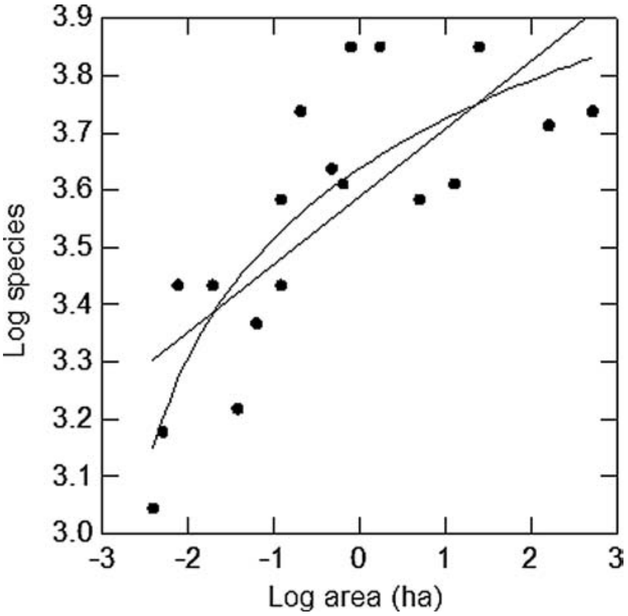


Figure 2. The relationship between ln shola size (ha) and ln species richness: linear (solid line) and polynomial (dashed line) models.

found in eight larger sholas (≥ 0.8 ha in area) totalling a sampled area of 3.47 ha, whereas 17% were found in the 10 smaller sholas of total area 3.05 ha; therefore the larger sholas had proportionately twice the number of very large trees as the smaller sholas per unit area.

Shola shape may influence the proportion of edge plants, since linear sholas (rectangular/triangular) have a larger edge proportionate to interior than circular sholas. The number of smaller or larger sholas in the two shape categories round/oval or triangle/rectangle did not significantly differ (Fisher's exact test two tailed = 0.35, ns), and there were similar numbers of smaller sholas (< 0.9 ha) in both shape categories (Wilcoxon signed-rank test = 1.62, ns).

Overall there were 16 species (23%) that were of temperate affinity. These belonged to the families Ericaceae, Rosaceae, Theaceae and Berberidaceae. Among the trees at least 60 cm dbh, temperate families comprised 36% of the trees in sholas less than 0.5 ha, and 22% in the larger sholas ($\chi 2$ = 3.84, df = 1, $P$ = 0.05). Two species, *Ilex denticulata* and *I. wightiana* were found in all except the smallest shola (0.09 ha), and may be more resistant to low temperatures than the other species.

The arcsine-transformed proportion of edge species declined significantly with increase in shola size, but there was no relationship when only sholas < 1 ha were considered (Table 2, Figure 3). The rarity index also declined significantly with increase in shola size, indicating that larger sholas had fewer rare species (Table 2, Figure 3). The number of rare (i.e. single individuals) species belonging to the forest interior/edge did not differ between the large/medium and

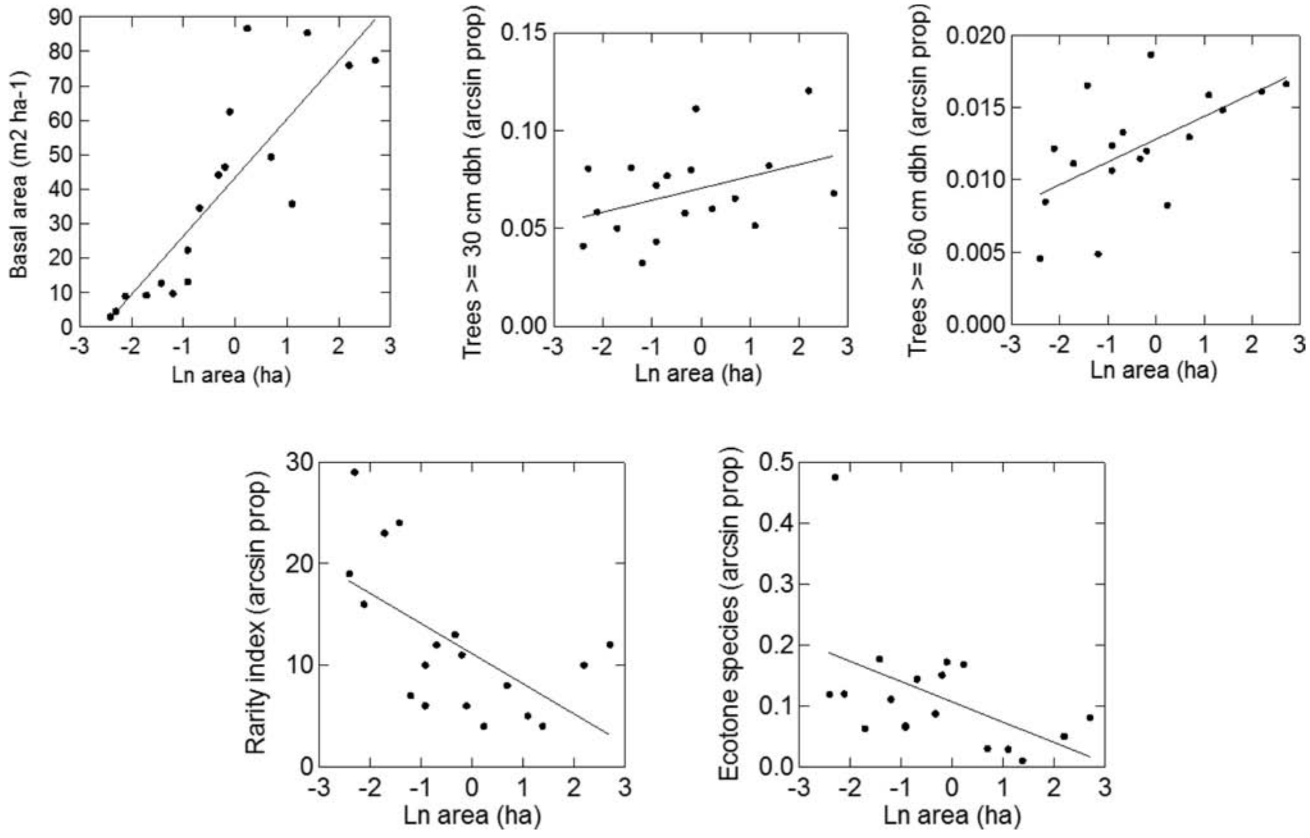


Figure 3. The relationship between ln shola size (ha) and basal area ($m^2$ $ha^{-1}$), rarity (proportion of species represented by single plants, arcsine transformed), proportion of large trees (≥ 30 and ≥ 60 cm dbh) arcsine transformed, and ecotone species (proportion of temperate species, arcsine transformed).

Table 3. Differences in species richness and tree densities $ha^{-1}$ across different lower dbh classes in small (< 0.9 ha), medium (≥ 0.9 to < 5 ha) and large (> 5 ha). Percentage values of species numbers are those of total recorded across all sholas (species = 69); tree numbers across dbh classes total 100%.

| | Small < 0.9 ha (%) | | Medium ≥ 0.9 to < 5 ha (%) | | Large > 5 ha (%) | |
|---|---|---|---|---|---|---|
| DBH Class | Species | Trees $ha^{-1}$ | Species | Trees $ha^{-1}$ | Species | Trees $ha^{-1}$ |
| ≤ 10 | 50 (86) | 1683 (78) | 55 (96) | 874 (69) | 45 (85) | 1014 (74) |
| > 15 to ≤ 25 | 44 (75) | 299 (14) | 51 (89) | 235 (19) | 43 (81) | 185 (14) |
| ≥ 30 | 41 (71) | 184 (8) | 38 (67) | 158 (12) | 36 (68) | 157 (12) |
| Total | 58 | 2166 | 57 | 1267 | 53 | 1356 |

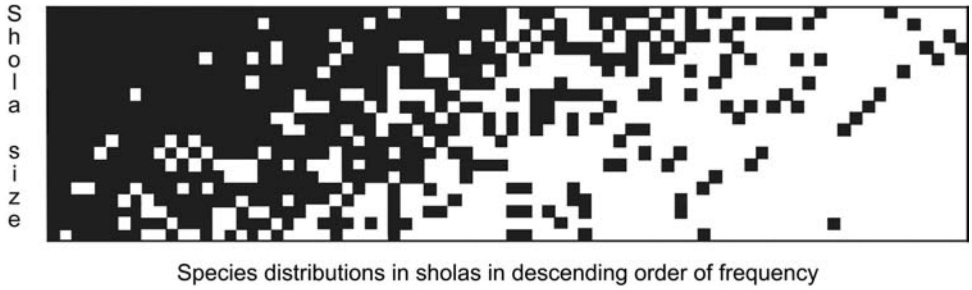


Figure 4. Distribution of tree species (≥ 1 cm dbh) among sholas of different sizes, with species in columns, in descending order of abundance, and sholas in rows in descending order of size. Matrix fill = 43.9. The nestedness index temperature $T = 26.1°$ differed significantly from the mean temperature $T$ of 67.75° generated randomly by 100 Monte Carlo simulations ($T = –3.07$, $P < 0.0001$).

small sholas ($\chi^2 = 0.12$, df = 1, ns), suggesting that rare species were represented in both the interior and edge.

Species richness was similar across different lower dbh classes in small, medium and large sholas (Table 3). Tree densities were higher in the smaller sholas and were lower in the larger dbh classes, i.e. smaller sholas had higher densities of small plants compared with larger sholas. Plant densities also decreased with increase in shola size, indicating a thinning effect (Table 3). The number of large trees at least 30 cm dbh remained the same in all three size classes of sholas, whereas the proportion differed, since tree densities were higher in the smaller sholas (Table 3).

Tree distributions on sholas of different sizes were significantly nested (matrix fill of 43.9%), with the species in smaller sholas being a subset of that of larger sholas but with a number of species having idiosyncratic distributions (Figure 4). The $T$ of the sholas was 26.1° which differed significantly from the mean $T$ of 67.75°, generated randomly by 100 Monte Carlo simulations ($T < 26.1° = –3.07$, $P < 0.0001$).

## Discussion

### *General patterns*

Our study demonstrates that area is the key variable structuring plant assemblages in shola forests: in most of the vegetation features, particularly species richness and basal area, the proportion of large trees was positively associated with shola size, whereas the proportion of edge species was negatively associated with shola size. The plant assemblages were significantly nested, indicating a structured pattern of species distribution, where the species in the smaller sholas were a subset of those of larger sholas. It is unlikely that soils and microclimatic features have shaped this assemblage, since soils beneath sholas have been found to be similar (Caner and Bourgeon 2001), and the majority of shola plants are habitat generalists (Mohandass 2007). The homogeneity of the shola vegetation across different regions suggests that local microclimatic and topographical factors may not play a major role in structuring the vegetation (Davidar et al. 2007; Mohandass and Davidar 2009).

### *The dynamics of shola–grassland vegetation: the role of succession?*

The plant species assemblage in the sholas was highly structured, indicating that plant succession, described by Clements (1916) as a deterministic process, could have played an important role in shola dynamics. The larger number of small-stemmed plants, the lower basal areas, and the higher proportion of edge species in the smaller sholas suggests that these could be at earlier successional stages than the larger sholas. Larger sholas had a higher proportion of very large trees, which indicates that they are older and have had the time to accumulate very old and large trees. This could happen if the early successional stages created conditions that facilitated the establishment of frost-intolerant forest interior plants (Connell and Slatyer 1977). Small sholas also have large trees, a higher proportion of which belong to montane/lower montane families such as the Aquifoliaceace that might be more frost resistant and able to survive the more exposed conditions within small sholas. This pattern of succession differs from that described for tropical rain forests, where gap-related processes create mosaics of different vegetations in the landscape (Brokaw 1985).

Pollen analysis indicated that shola vegetation invaded the grassland about 35 ky BP through a nucleus of frost and fire-tolerant shrubby vegetation comprising species of genera such as *Impatiens*, *Strobilanthes* and *Berberis* (Vishnu-Mittre and Gupta 1968). Gradually the vegetation changed to a more arboreal type, with pollen profiles dominated by more temperate species such as *Rhododendron* and *Ilex*. Around 25 ky BP, during the interglacial period, mature forest trees such as *Elaeocarpus* and *Euonymus* became more abundant. Our study also shows that smaller sholas have a higher proportion of shrubby frost-resistant edge species such as *Berberis*, *Rhodomyrtus* and *Rhododendron* that could function as pioneers in the ecotones and grasslands, paving the way for species of the forest interior. This pattern of succession has been described for a montane forest in Kinabalu, where shade-intolerant trees of later successional stages established under heliophilic shrubs (Aiba et al. 2004).

The collective species richness of small sholas was similar to that of larger sholas. There was a higher proportion of species represented by single plants in the smaller sholas, suggesting that seed dispersal into smaller sholas consisted of random events; therefore smaller sholas would have different sets of rare species, all of which would occur in larger sholas since the species pool in these forests is limited (Mohandass 2007; Davidar et al. 2007). Thus, stochastic processes related to dispersal may be more important in early successional stages (del Moral et al. 1995). Although we probably underestimated the edges in the larger sholas, other data such as decrease in plant density and increase in basal area and the proportion of large trees with shola size does suggest that smaller sholas have a higher proportion of smaller plants. Shola vegetation has to be monitored over a long period to assess the dynamics and see whether the ecotone facilitates expansion of shola vegetation into grasslands.

Of course, the reverse is also possible, where small sholas are a result of deterioration processes of much larger forest patches through retrogressive succession (Blasco 1971). This could happen if large trees had higher levels of mortality in small sholas because of greater vulnerability to high-speed winds prevailing during the south-westerly monsoon (Meher-Homji 1967; Vishnu-Mittre and Gupta 1968; Jayasuriya and Pemadasa 1983; Caner et al. 2007). The closed, well-integrated canopy characteristic of the larger sholas might reduce wind turbulence and thereby protect shola trees from the ravages of severe wind (Lawton 1982; Leigh 1983, 1999). Studies have indicated that strong winds have been a consistent factor in this region, even during the colder epochs of the Pleistocene that resulted in drier climates in South Asia but did not diminish the wind strengths of the south-westerly monsoon (Beaufort 1996). It is well known that tree stature in tropical forests is lower in regions with frequent cyclones (Webb 1958; de Gouvenain and Silander 2003). High-speed winds were the major cause for tree mortality in a Mexican cloud forest (Arraiga 2000), and strong winds could have shaped shola forests over time and may have been more detrimental to plants in smaller sholas. Therefore smaller sholas could have remained small due to exposure to severe winds and this may be unrelated to succession. In the Bangitappal/Sispara region in Upper Bhavani, where extremely severe winds prevail during the monsoon, the sholas remain small (Blasco 1971). However, in our study area both small and large sholas occur within short distances of each other (Table 1, Figure 1), and have been exposed to similar climatic conditions. Our study also indicates that there were no topographical constraints on shola size.

Palaeoclimatic and vegetation records, and our study, do favour the hypothesis that sholas are in the expansion phase in the present epoch (Caner et al. 2007). Long-term monitoring and experimental research is needed to fully understand the mechanisms underlying these observed patterns.

### *Nestedness and species distribution patterns*

The successional processes in sholas seem similar to those of low-elevation rain forest expansion into grasslands. Rain forest plants regenerate in the forest ecotone and in thorny thickets in the grasslands, where they are protected against fire and grazing livestock (Puyravaud et al. 1994; 2003). Studies of these vegetation thickets have shown that the species assemblage in undisturbed thickets was nested, i.e. the species in a smaller thicket was a subset of that of a larger thicket. This was apparently caused by selective colonisation due to seed dispersal by birds, since bird-dispersed species were disproportionately represented in the thickets. The young thickets were dominated by species of open, dry habitats, and the older thickets had a higher proportion of rainforest species (Puyravaud et al. 1994).

In general, a nested pattern could be a result of colonisation or extinction processes (Atmar and Patterson 1993; Cook and Quinn 1995). Biotas driven by colonisation have been found to be less structured than those driven by extinction because colonisation is generally more of a random process (Loo et al. 2002). The degree of nestedness in shola forests was found to be similar to that in the low-elevation vegetation thickets in the Western Ghats that seemed to be colonisation-dominated ($T \approx 20°$, Puyravaud et al. 2003). Extinction-dominated systems such as avifaunal assemblages in the Andaman Islands in the Bay of Bengal were found strongly nested ($T \approx 6°$), probably because they are undergoing faunal relaxation due to post-glacial rise in sea levels (Davidar et al. 2002).

### *History of the shola–grassland vegetation in the Nilgiris*

This study provides additional support for historical reconstruction of the shola–grassland vegetation during climatic shifts in the Pleistocene and Holocene (Vasanthy 1988; Sukumar et al. 1995; Caner et al. 2007), and provides a mechanism to explain the process of shola expansion into grasslands. Caner et al. (2007), in a study using carbon isotopes, have noted that the sholas in the western part of the Nilgiris, where our study was conducted, faced severe south-westerly monsoon winds and the sholas have never completely covered the hillsides since 18 ky BP to present, whereas sholas in the southern and eastern parts of the Nilgiris, where the monsoon has not been so severe, expanded rapidly during warmer past climates. Therefore the sholas in our study area have probably remained isolated for a longer time due to the adverse climatic conditions.

Our study is the first attempt to describe patterns of plant distribution in sholas and suggest that succession might be the mechanism by which sholas have expanded into grasslands during warmer climates, though further experimental studies are required. If succession is the major process regulating shola expansion, it can be used as a process to restore shola forests where they have been damaged and destroyed. Species of montane/lower montane origin could be used to initiate the succession process and provide a conducive environment for the establishment of the forest interior species. Sholas are now restricted to a very limited area in the upper montane regions of the Western Ghats of India, and need stringent protection and restoration in order to survive.

## Acknowledgements

This study was partially supported by a small grant from the Center for Tropical Forest Science and assistance from Dr Egbert G Leigh Jr. We thank Mr Hegde and staff of UNITEA Pvt. Ltd., the Tamilnadu Forest Department and Electricity Board for logistical help and support. We gratefully appreciate the critical comments and suggestions by Dr JP Puyravaud, Dr Peter Ashton, Dr Egbert G Leigh Jr, and the anonymous reviewers that helped considerably in improving the quality of the manuscript.

## Notes on contributors

Dharmalingam Mohandass conducted his doctoral research on the dynamics of the shola forests of the Nilgiris. He is currently a scientist at the Edhkwehlynawd Botanical Refuge and is undertaking the restoration of shola forests.

Priya Davidar is a Professor at Pondicherry University, India, and a Research Associate at the Smithsonian Tropical Research Institute, Panama. She conducts biodiversity assessments in the Western Ghats and Andaman Islands of India.

## References

Aiba S, Kitayama K, Takyu M. 2004. Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. Plant Ecology 174:147–161.

Arraiga L. 2000. Types and causes of tree mortality in a tropical montane cloud forest of Tamaulipas, Mexico. Journal of Tropical Ecology 16:623–636.

Atmar W, Patterson BD. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96:373–382.

Atmar W, Patterson BD. 1995. The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. AICS Res., Inc., University Park, New Mexico, and The Field Museum, Chicago.

Beaufort L. 1996. Dynamics of the monsoon in the equatorial Indian Ocean over the last 260,000 years. Quaternary International 31:13–18.

Blasco F. 1970. Aspects of the flora and ecology of savannas of the south Indian Hills. Journal of Bombay Natural History Society 67:522–534.

Blasco F. 1971. Montagnes du Sud de l'Inde. Forêt, Savanes, Écologie. Pondichéry: Institut Français de Pondichéry Travaux de la Section Scientifique et Technique X, 1–436.

Brokaw NVL. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682–687.

Caner L, Bourgeon G. 2001. Andisols of the Nilgiri highlands: new insight into their classification, age and genesis. In: Gunnell Y, Radhakrishna, BP, editors. Sahyadri: the great escarpment of the Indian subcontinent (patterns of landscape development in the Western Ghats). Bangalore: Memoirs Geological Society of India. p. 905–918.

Caner L, Bourgeon G, Toutain F, Herbillon AJ. 2000. Characteristics of non-allophanic andisols derived from low activity clay regoliths in Nilgiri Hills (Southern India). European Journal of Soil Science 51:553–563.

Caner L, Lo Seen D, Gunnell Y, Ramesh BR, Bourgeon G. 2007. Spatial heterogeneity of land cover response to climatic change in the Nilgiri highlands (southern India) since the last glacial maximum. Holocene 17:195–205.

Clements FE. 1916. Plant succession. Washington: Carnegie Institute. 512 pp.

Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 1877:1118–1114.

Cook RR, Angermeier PL, Finn DS, LeRoy Poff N, Krueger KL. 2004. Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia. Oecologia 140:639–649.

Cook RR, Quinn JF. 1995. The influence of colonization in nested species subsets. Oecologia 102:413–424.

Davidar P, Mohandass D, Vijayan L. 2007. Floristic analysis of tropical montane evergreen forest in Kukkal, Palni Hills. Tropical Ecology 48:15–25.

Davidar P, Yoganand T, Ganesh T, Devy MS. 2002. Distribution of forest birds and butterflies in the Andaman Islands, Bay of Bengal: nested patterns and processes. Ecography 25:5–17.

De Gouvenain RC, Silander Jr JA. 2003. Do tropical storm regimes influence the structure of tropical lowland rain forests? Biotropica 35:166–180.

del Moral R, Titus JH, Cook AM. 1995. Early primary succession on Mount St. Helens, Washington, USA. Journal of Vegetation Science 6:107–120.

Flenley JR. 1998. Tropical forests under the climates of the last 30,000 years. Climatic Change 39:177–197.

Fyson PF. 1932. The flora of Nilgiri and Palni hill tops. Madras: Govt. Press. 3 vols.

Gamble JS, Fischer CEC. 1915–1936. Flora of the Presidency of Madras, Vols 1–111. London: Adlard and Son Ltd.

Henry AN, Chitra V, Balakrishnan NP. 1989. Flora of Tamil Nadu, India, Ser I. Analysis. Vol 3. Coimbatore: Botanical Survey of India.

Henry AN, Kumari GR, Chitra V. 1987. Flora of Tamil Nadu, India, Ser I. Analysis. Vol 2. Coimbatore: Botanical Survey of India.

Jayasuriya AHM, Pemadasa MA. 1983. Factors affecting the distribution of tree species in a dry zone montane forest in Sri Lanka. Journal of Ecology 71:571–583.

Lawton RO. 1982. Wind stress and elfin structure in a montane rain forest tree: an adaptive explanation. American Journal of Botany 69:1224–1230.

Leigh EG Jr. 1983. Tree shape and leaf arrangement: a quantitative comparison of montane forests, with emphasis on Malaysia and south India. In: Daniel JC, Serrao JS, editors. Conservation in developing countries: problems and prospects. Bombay and Oxford: Oxford University Press. p. 119–174.

Leigh EG Jr. 1999. Tropical forest ecology: a view from Barro Colorado Island. New York: Oxford University Press.

Loo SE, MacNally R, Quinn GP. 2002. An experimental examination of colonization as a generator of biotic nestedness. Oecologia 132:118–124.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, New Jersey: Princeton University Press. 203 pp.

Matthew KM. 1999. The flora of the Palni Hills, South India. The Rapinat Herbarium, India (3 volumes).

Meher-Homji VM. 1967. Phytogeography of the South Indian Hill stations. Bulletin of the Torrey Botanical Club 94:230–242.

Mohandass D. 2007. Plant diversity and forest dynamics in montane evergreen forest (shola) of the Nilgiri mountains, southern India. [PhD thesis]. Pondicherry University, India.

Mohandass, D, Davidar, P. 2009. Floristic structure and diversity of a tropical montane evergreen forest (shola) of the Nilgiri Mountains, southern India. Tropical Ecology 50:219–229.

Nair NC, Henry AN. 1983. Flora of Tamilnadu, India, Ser 1, Vol 1. Coimbatore: Botanical Survey of India.

Odum HT, 1983. Systems ecology: an introduction. New York: John Wiley and Sons.

Ohsawa M. 1991. Structural comparison of tropical montane rain forests along latitudinal and altitudinal gradients in South and East Asia. Vegetatio 97:1–10.

Patterson BD. 1987. The principle of nested subsets and its implications for biological conservation. Conservation Biology 1:323–334.

Pickett STA, White PS, editors. 1985. The ecology of natural disturbance and patch dynamics. New York: Academic Press.

Puyravaud JP, Dufour C, Aravajy S. 2003. Rain forest expansion mediated by successional processes in vegetation thickets in the Western Ghats of India, Journal of Biogeography 30:1067–1080.

Puyravaud JP, Pascal JP, Dufour C. 1994. Ecotone structure as an indicator of changing forest-savanna boundaries (Linganamakki region, southern India). Journal of Biogeography 21:581–593.

Ranganathan CR. 1938. Studies in the ecology of the shola grassland vegetation of the Nilgiri Plateau. Indian Forester 64:523–541.

Sousa WP. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65:1918-1935.

SPSS Inc. 2000. Systat, version 10, SPSS Inc. Chicago, IL.

Subramanian KS, Murthy MVN. 1976. Bauxite and hematite cappings in the Nilgiri – Study from geomorphologic angle. Journal of the Geological Society of India 17:353–358.

Sukumar R, Ramesh R, Pant RK, Rajagopalan G. 1993. A $\delta\,^{13}$C record of late Quaternary climate change from tropical peats in southern India. Nature 364:703–706.

Sukumar R, Suresh HS, Ramesh R. 1995. Climate change and its impact on tropical montane ecosystems in southern India. Journal of Biogeography 22:533–536.

Vasanthy G. 1988. Pollen analysis of late Quaternary sediments: evolution of upland savanna in Sandynallah (Nilgiris, south India). Review of Palaeobotany & Palynology 55:175–192.

Veblen TT. 1992. Regeneration dynamics. In: Glenn-Lewin DC, Peet RK, Veblen TT, editors. Plant succession: theory and prediction. London: Chapman and Hall. p. 152–187.

Vishnu-Mittre, Gupta HP. 1968. A living fossil plant community in south Indian hills. Current Science 37:671–672.

Webb LJ. 1958. Cyclones as an ecological factor in tropical lowland rain-forest, North Queensland. Australian Journal of Botany 6:220–228.

Whitmore TC. 1984. Tropical rain forests of the Far East. 2nd edition. Oxford: Oxford University Press.

Whittaker RH, Levin SA. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12:117–139.

Wright DH, Patterson BD, Mikkelson GM, Cutler A, Atmar W. 1998. A comparative analysis of nested subset patterns of species composition. Oecologia 113:1–20.