Contents lists available at ScienceDirect

Plant Diversity

journal homepage: http://www.keaipublishing.com/en/journals/plant-diversity/
http://journal.kib.ac.cn

Rainforests north of the Tropic of Cancer: Physiognomy, floristics and diversity in 'lowland rainforests' of Meghalaya, India

Uma Shankar[*], Amit Kumar Tripathi

Department of Botany, North-Eastern Hill University, Shillong 793 022, India

ARTICLE INFO

ABSTRACT

The lowland rainforests of Meghalaya, India represent the westernmost limit of the rainforests north of the Tropic of Cancer. These forests, on the Shillong plateau, are akin to Whitmore's 'tropical lowland evergreen rainforest' formation and exhibit striking similarities and conspicuous differences with the equatorial rainforests in Asia-Pacific as well as tropical seasonal rainforests in southwestern China near the Tropic of Cancer. We found these common attributes of the rainforests in Meghalaya: familial composition with predominance of Euphorbiaceae, Lauraceae, Meliaceae, Moraceae, Myrsiticaceae, Myrtaceae and Rubiaceae; deciduousness in evergreen physiognomy; dominance of mega- and meso-phanerophytic life-forms; abundance of species with low frequency of occurrence (rare and aggregated species); low proportional abundance of the abundant species; and truncated lognormal abundance distribution. The levels of stand density and stand basal area were comparable with seasonal rainforests in southwestern China, but were lower than equatorial rainforests. Tropical Asian species predominated flora, commanding 95% of the abundance. The differences include overall low stature (height) of the forest, inconspicuous stratification in canopy, fewer species and individuals of liana, thicker understory, higher proportion of rare species, absence of locally endemic species and relatively greater dominance of Fagaceae and Theaceae. The richness of species per hectare (S) was considerably lower at higher latitudes in Meghalaya than in equatorial rainforests, but was comparable with seasonal rainforests. Shannon's diversity index ($H' = 4.40$ *nats* for ≥ 10 cm gbh and 4.25 *nats* for ≥ 30 cm gbh) was lower on higher latitudes in Meghalaya in comparison to species-rich equatorial rainforests, but it was the highest among all lowland rainforests near the Tropic of Cancer.

Copyright © 2016 Kunming Institute of Botany, Chinese Academy of Sciences. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co., Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Globally, 'tropical lowland evergreen rainforests' are regarded as the most diverse terrestrial ecosystems, having both high species richness per unit area and high equitability in abundance sharing (Whitmore, 1984). These forests occur around the equator and extend between the Tropic of Cancer and the Tropic of Capricorn in three major chunks, namely, the Amazon basin of South America, the Congo River basin of Central Africa, and the ever-wet peninsula and islands of Southeast Asia (*cf.* figures 1.1 and 1.4 in Corlett and Primack, 2011). In addition, there are two smaller and very distinctive rainforest regions on the giant islands of Madagascar and New Guinea (Corlett and Primack, 2011). In northeastern India, northern Myanmar and southwestern China, 'tropical lowland evergreen rainforests' occur around the Tropic of Cancer (Corlett, 2009). In southwestern China, the climate is extreme for tropical rainforests, with a mean annual rainfall between 1200 and 1800 mm and a mean annual temperature of about 21—22.8 °C (Zhu, 1997). Northeastern India has a relatively wetter climate (rainfall 2000—12,000 mm) than southwestern China, and is therefore more conducive for the growth of lowland rainforests.

The available information on the structure and floristics of lowland rainforests north of the Tropic of Cancer (around 27°30′N) stems mainly from Arunachal Pradesh in northeastern India (Proctor et al., 1998; Bhuyan et al., 2003; Nath et al., 2005; Deb et al., 2009), and near the Tropic of Cancer (around 21—22°N) from Xishuangbanna in southern Yunnan province (Zhu, 1997; Shanmughavel et al., 2001; Lü et al., 2010; Lan et al., 2012) and from Hainan Island in China (Meng et al., 2011). The State of

* Corresponding author.
  E-mail address: arshuma@yahoo.com (U. Shankar).
  Peer review under responsibility of Editorial Office of Plant Diversity.

Meghalaya represents the westernmost limit of the lowland rainforests north of the Tropic of Cancer. These scarcely known rainforests patchily occupy rolling hills on the southern slopes of the Shillong plateau (also referred to as the Meghalaya plateau since 1971), below 1000 m altitude, where the world's heaviest rainfall is received, especially in the Cherrapunji-Mawsynram sector. This region has been virtually ignored on world maps of rainforests.

According to the seminal work of Champion and Seth (1968), the lowland rainforests of Meghalaya would closely correspond to 'Cachar tropical evergreen forests'. Indeed, Champion and Seth considered this vegetation as 'climatic climax' with fewer giant trees and infrequent climbers. They remarked that: "… after shifting cultivation on hill slopes, fallows are restocked with the deciduous species and if protected from slashing-and-burning, will revert to a closed evergreen type". Champion and Seth (1968) further remarked that the natural regeneration of evergreen species was better in these forests than in dipterocarpus lowland evergreen rainforests in the Deomali Division of Assam. While forest types, such as the lowland 'Khasi hill sal' forests (Tripathi and Shankar, 2014), montane evergreen rainforests (Khiewtam and Ramakrishnan, 1993; Jamir and Pandey, 2003; Upadhaya et al., 2003) and subtropical pine forests (Tripathi et al., 2003) have been extensively investigated, the floristics, structure and regeneration of the lowland rainforests of Meghalaya have yet to be studied.

In order to generate a dataset from the western edge of lowland rainforests north of the Tropic of Cancer, we initiated a study of the rainforests of Meghalaya. The data shall not only fill the gap in understanding of rainforests in northern limits, but also facilitate fine cross-continental comparisons. We examined: (1) if lowland rainforests of Meghalaya exhibit the characteristic physiognomy, life-form spectrum and floristic composition typical of equatorial and tropical seasonal rainforests; (2) if diversity of woody species declines moving away from the equator towards the northern edges of rainforests, corroborating the globally recognized latitudinal diversity gradient (Brown, 2014); (3) if floristic richness of landscape (gamma diversity) and of samples (alpha diversity) as well as compositional heterogeneity of samples (beta diversity) are competitive with those of other rainforests; and (4) if equitability of species abundances follows a lognormal distribution, shaping a high value of Shannon's diversity index (H').

We supplement our results by comparing them with the equatorial lowland rainforests predominated by dipterocarps, and lowland seasonal rainforests near the Tropic of Cancer in Xishuangbanna in southwestern China (Zhu, 1997; Lü et al., 2010), as this region belongs to the same biogeographical entity. Finally, we compare our results with lowland rainforests in extreme northern limits in the world, which occur in Namdapha National Park in Arunachal Pradesh (Proctor et al., 1998; Nath et al., 2005; Deb et al., 2009) and Deomali Forest Division in Assam (Bhuyan et al., 2003) in northeastern India. The comparisons affirm that the lowland rainforests of Meghalaya yield the highest value of H' among the rainforests north of the Tropic of Cancer, even while these values are lower than the equatorial lowland rainforests.

2. Materials and methods

2.1. Study area

The hilly State of Meghalaya abounds between 24°02′ and 26°07′N latitude and 89°48′ and 92°51′E longitude and covers a geographical area of 22,429 km² (Fig. 1a). Meghalaya is included in the 'Indo-Burma' global biodiversity hotspot (Myers, 2003). The east-west series of mountains ascends from 100 m in the north to about 1965 m towards the south, attaining the highest peak at

Upper Shillong and a second peak at Tura before descending further south to nearly 50 m, carving an archway (*cf.* figure 1 in Shankar et al., 1993). The low elevations all along the periphery of Meghalaya plateau experience fairly high temperature, whereas the higher elevations in the centre of the plateau benefit from moderate temperatures. The minimum temperature (°C) in the coldest month, (January), mean annual temperature (°C) and annual rainfall (mm) at some sites on southern slopes are: 10.2, 22.0 and 5011 at Mawlynnong (517 m), 7.8, 17.6 and 9963 at Cherrapunji (1274 m), 11.7, 24.4 and 3704 at Dawki (82 m), 10.2, 21.7 and 5629 at Ranikor (602 m) and 12.0, 24.2 and 3127 at Tura (246 m) (www.climate-data.org). Frost may occur at the table land of Cherrapunji, but is unrecorded for our study sites below 900 m.

The Cherrapunji-Mawsynram sector on the southern slopes of Meghalaya receives exceptionally high levels of rainfall (Fig. 1b). Cherrapunji holds two world records: (1) greatest 48-hour rainfall (2493 mm) during June 15—16, 1995; and (2) greatest 12-month rainfall (26,470 mm) during August, 1860 and July, 1861 (WMO, 2014). The southwest monsoon moving from the Bay of Bengal causes heavy rainfall on abruptly rising southern slopes of the Shillong plateau and rapidly diminishes northward, creating a steep gradient in rainfall (*ca.* 10,000 mm) within a distance of only 100 km. About 80% of rain falls during the rainy season and most of the remainder falls in spring, rendering the winter cool and dry (Shankar et al., 1991). The climate is controlled by the Asia-Pacific monsoon with the following distinct seasons: spring (March—April), rainy (May—September), autumn (October—mid-November) and winter (mid-November—February).

The rainforests of Meghalaya occur mainly on lateritic soil developed from siliceous rocks, such as gneisses, schists and granite rocks of Archaean age. The surface of the highest rainfall area of the Shillong plateau is largely flat and dissected by canyons up to 1000 m deep. The steep slopes of the canyons harbour stunted evergreen vegetation. The plateau is composed of thick horizontally bedded sandstones and siltstones passing south into limestone facies that support patches of the rainforest. The landscape is characterized by either exposed bedrock or the remains of lateritic cover, armoured by a surface layer of coarse gravely residual debris with very sparse grass cover (Shankar et al., 1991). The underlying, weathered regolith permits very low infiltration and subsurface runoff, but speeds up overland flow and soil erosion (Soja and Starkel, 2006). Long-term human intervention in these globally extreme pluvial conditions has destroyed a dense vegetation cover and thick soil of the primary ecosystem (Ramakrishnan, 2001). Soil pH ranges between 4.6 and 6.1 and soil texture is predominantly sandy loam.

2.2. Field sampling

Six patches of tropical lowland evergreen rainforest were sampled in Meghalaya. The sampled transects were 10 m wide and up to 500 m in length. To determine species frequency, transects encompassed contiguous subplots of 50 m in length. In all, 2.45 ha were sampled. All stems ≥10 cm girth at breast height (1.37 m above ground level) were included in enumeration. Each stem was measured for girth (cm), height (m), phenophase (leaf flush, flowering, fruiting) and damage (top broken, lopping, disease) following Murali et al. (1996). The voucher specimens of species were put up on herbarium sheets for identification. The plant species were identified and their habits verified from the regional floras (Hooker, 1872—1897; Kanjilal et al., 1934—1940; Balakrishnan, 1981—1983; Haridasan and Rao, 1985—1987). The herbarium of the Botanical Survey of India, Shillong was consulted for identification. The accepted botanical names were adopted from The Plant List (2013) and the plant families follow APG III (2009).
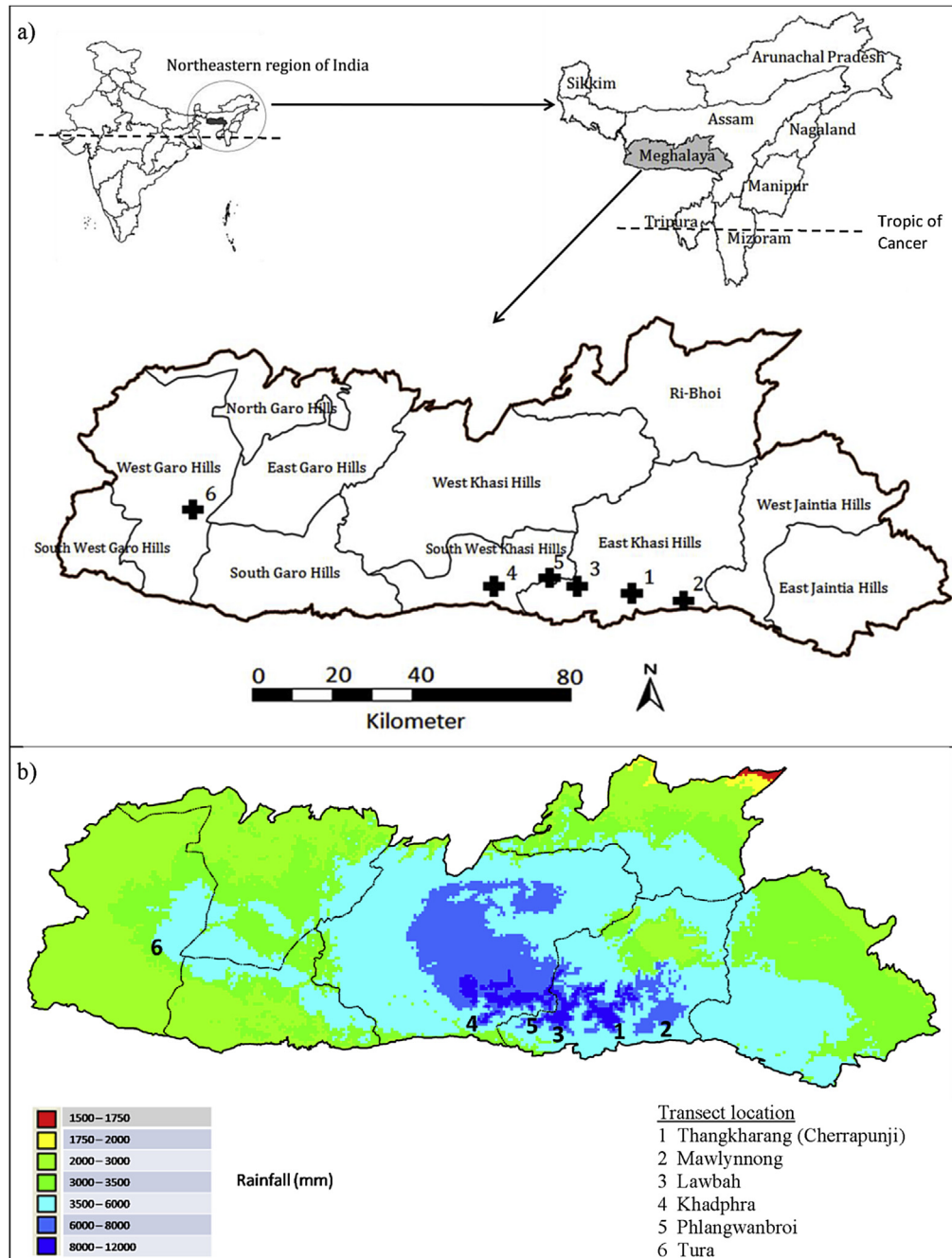
Fig. 1. a) Geographical location of sampled sites in the State of Meghalaya in India; and b) map of rainfall distribution. The horizontal dashed line indicates the Tropic of Cancer.

The species were classified into the following growth forms: large tree, medium tree, small tree, shrub, scandent shrub and liana following Shankar (2001). The tree species which occupy the upper-canopy ($\geq$20–<25 m height) and emergent strata ($\geq$25 m height) were large trees; the species which occur in middle-canopy ($\geq$10–<20 m) were medium-trees; and the species which restrict themselves to understory (<10 m) were small trees. Multi-stemmed species predominant in understory were considered shrub, and the species climbing on the trunks of other trees were designated as liana. The stragglers were classified as scandent shrubs. In some tables, the data for scandent shrubs and liana were considered together as 'liana' because of the negligible presence of the latter. We assigned a phanerophytic life-form (Raunkiaer, 1934) to each species following measurements of maximum height: megaphanerophyte (>20 m), mesophanerophyte (>10–20 m), microphaerophyte (5–<10 m), nanophanerophyte (<5 m) and liana (all heights).

2.3. Data analysis

The phytosociological dataset was analysed individually for six sites and as an assemblage by pooling all six samples. The occurrences of species in contiguous subplots of 500 m² were taken into account for calculation of frequency (Mueller-Dombois and

Ellenberg, 1974). A frequency distribution was developed in five frequency classes of Raunkiaer (1934). The density of a species in a hectare was determined by dividing the count of individuals in all samples by the total area sampled. The stand density was found by summing the densities of all species in the assemblage. The basal area of each individual was calculated from its respective girth and, in multi-stemmed individuals, basal area of each stem was calculated separately (Shankar, 2001). The basal areas of all individuals of a species were summed to arrive at the total basal area of the species. The stand basal area was found by summing the basal areas of all species. For each species, the frequency, density and basal area were converted into relative values by dividing respectively by the sums of frequencies, densities and basal areas of all species. The Importance Value Index (IVI) of a species was computed by summing relative density, relative frequency and relative basal area of the respective species (Curtis and McIntosh, 1950). Here we refer to the sums of individuals, basal areas and importance values of all species belonging to the respective family as the numbers of individuals, basal area and importance value of a family (FIV).

PAST software Version 3.14 (Hammer et al., 2001) was used for clustering of samples, ordination of species and abundance modelling for plotting species abundances in descending rank order. Unweighted pair-group average (UPGMA) algorithm and Bray−Curtis similarity measure based on abundance data were selected for clustering samples. An ordination of species was performed, using counts of individuals of species in samples, in PCA module of PAST software and the locations of species in PCA space were recognized from consequential PCA scores. A scree plot of eigenvalues was examined for significance of the principal components.

Four classical models of rank-abundance plots described by Whittaker (1972) and Magurran (1988) were fitted to species abundances (importance values): (1) the geometric series (Motomura's niche pre-emption hypothesis), (2) Fisher's logarithmic series, (3) the broken-stick series (MacArthur's random niche boundary hypothesis), and (4) May's truncated lognormal distribution which is modified from Preston's octave frequency distribution. Here, we include results on lognormal distribution.

The alpha diversity ($\overline{\alpha}$) is the mean number of species in samples and the gamma diversity (γ) is the total number of species in all samples (Whittaker, 1972). The beta diversity (β_W), which refers to compositional heterogeneity among sampling units, was calculated following Whittaker (1972), as follows:

$$\beta_W = (\gamma/\overline{\alpha}) - 1$$

where, γ is total species diversity at regional or landscape level and $\overline{\alpha}$ = the mean species diversity at the local or within-habitat scale. The beta diversity is zero if all species in all samples are the same and it is maximum (number of samples − 1) if there is no overlap of species among all samples. To allow comparisons among sites, Harrison's beta-one index (β_{-1}) was computed as follows (Harrison et al., 1992):

$$\beta_{-1} = 100 \frac{(\gamma/\overline{\alpha}) - 1}{N - 1}$$

where, N is the number of samples. Beta-one ranges from 0 (complete similarity) to 100 (complete dissimilarity).

The Shannon's diversity index was calculated following Shannon (1948) as:

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} \log_e \frac{n_i}{N}$$

The Simpson's index of dominance was calculated following Simpson (1949) as:

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

The Pielou's index of evenness was calculated following Pielou (1975) as:

$$E = \frac{H'}{H'_{max}}$$

Where, n_i = importance value of ith species, N = sum of importance values of all species, S = number of species in the assemblage and H'_{max} is $\log_e S$.

3. Results

Of 2408 individuals sampled, 99% were live and 1% dead (Table 1). About 0.5% of live individuals were partially damaged by wind throws. The coefficient of variation for the count of individuals per sample was 27.8%. About 7.6% of live individuals were multi-stemmed. Hence, 2385 live individuals were of ≥10 cm girth, 1145 individuals were of ≥30 cm girth, and 262 individuals were of ≥90 cm girth. The live individuals comprised 184 taxa (species) in 142 genera and 66 families (Table 2). Of these, 173 taxa could be identified up to the species level with certainty. Seven taxa were identified up to the genus level, one taxon up to the family level and three taxa remained unidentified.

3.1. Familial dominance

The identified species belonged to 65 families and the three unidentified species were placed in an 'indeterminate' family (Table 2). Thirty-two families had a single species each, 13 families had two species each, seven families had three species each, and 14 families had four or more species each. The most speciose families were Lauraceae (16 species), Moraceae (11), Leguminosae (10), Rubiaceae (10), Euphorbiaceae (8) and Phyllanthaceae (8). At the generic level, Leguminosae and Rubiaceae topped the list with nine genera each and Lauraceae followed with eight genera (Table 3).

Individually, no single family was incredibly dominant in count of individuals (Table 3). The top seven families accounted for <10% of individuals each: Urticaceae (9.5%), Lauraceae (9.1%), Fagaceae (8.5%), Araliaceae (8%), Euphorbiaceae (6.2%), Theaceae (4.5%) and Myrtaceae (4.2%). The next 20 families, each with ≥1% but <4% of individuals, contributed 37% of the individuals. The remaining 39 families, each with <1% of individuals, shared only 13% of individuals. Five families (Berberidaceae, Cannabaceae,

Table 1
Structural attributes of six sample sites in lowland rainforests of Meghalaya.

Attribute	Sample sites						All samples
	T1	T2	T3	T4	T5	T6	
Altitude (m)	863	531	812	319	750	577	642 ± 205
Transect							
Width (m)	10	10	10	10	10	10	10
Length (m)	500	300	400	350	400	500	2450
Area (ha)	0.5	0.3	0.4	0.35	0.4	0.5	2.45
Count of species	40	41	48	51	61	51	184
Count of individuals							
Live	349	344	606	314	428	344	2385
Dead	5	3	10	4	1	0	23
Total (live + dead)	354	347	616	318	429	344	2408
Multi-stemmed	29	25	33	25	57	13	182

Table 2

Floristic composition and phytosociology of woody layer (girth ≥10 cm) of lowland rainforests of Meghalaya. The species arrangement is in descending order of importance value index (IVI). The growth forms are: LT, large tree; MT, medium tree; ST, small tree; SH, shrub; SS, scandent shrub; LI, liana.

Species	Family	Growth form	Occurrence	Density (ha^{-1})	Basal area (cm^2 ha^{-1})	IVI
1. *Schima wallichii* Choisy	Theaceae	LT	21	40.0	32,277	18.7
2. *Macropanax undulatus* (Wall. ex G. Don) Seem.	Araliaceae	ST	20	58.8	19,960	16.0
3. *Cinnamomum tamala* (Buch.-Ham.) T. Nees & Eberm.	Lauraceae	MT	15	38.8	13,889	11.0
4. *Castanopsis armata* (Roxb.) Spach	Fagaceae	MT	7	22.4	18,655	10.0
5. *Boehmeria glomerulifera* Miq.	Urticaceae	SH	16	61.2	1989	9.1
6. *Syzygium tetragonum* (Wight) Wall. ex Walp.	Myrtaceae	MT	17	34.7	1988	6.5
7. *Persea odoratissima* (Nees) Kosterm.	Lauraceae	MT	7	9.0	12,046	6.2
8. *Oreocnide integrifolia* (Gaudich.) Miq.	Urticaceae	ST	17	30.2	2249	6.1
9. *Itea macrophylla* Wall.	Iteaceae	ST	16	26.5	2965	5.9
10. *Toona ciliata* M. Roem.	Meliaceae	LT	6	11.0	10,816	5.9
11. *Stereospermum chelonoides* (L. f.) DC.	Bignoniaceae	LT	5	6.9	11,247	5.5
12. *Sarcosperma griffithii* Hook. f. ex C.B. Clarke	Sapotaceae	MT	14	23.3	3393	5.5
13. *Castanopsis lanceifolia* (Oerst.) Hickel & A. Camus	Fagaceae	LT	13	23.3	3579	5.4
14. *Xanthophyllum flavescens* Roxb.	Polygalaceae	LT	6	10.6	9595	5.4
15. *Helicia nilagirica* Bedd.	Proteaceae	MT	13	20.0	2915	4.8
16. *Macaranga indica* Wight	Euphorbiaceae	MT	17	14.3	3050	4.8
17. *Symplocos sumuntia* Buch.-Ham. ex D. Don	Symplocaceae	ST	14	25.3	496	4.6
18. *Castanopsis indica* (Roxb. ex Lindl.) A. DC.	Fagaceae	LT	10	11.0	5879	4.6
19. *Magnolia hodgsonii* (Hook. f. & Thomson) H. Keng	Magnoliaceae	LT	6	5.3	6312	3.6
20. *Claoxylon longipetiolatum* Kurz	Euphorbiaceae	ST	7	18.4	2241	3.6
21. *Ostodes paniculata* Blume	Euphorbiaceae	MT	12	12.2	1799	3.5
22. *Cinnamomum bejolghota* (Buch.-Ham.) Sweet	Lauraceae	LT	9	15.9	1796	3.5
23. *Garcinia elliptica* Wall. ex Wight	Clusiaceae	ST	6	20.0	1567	3.4
24. *Aidia cochinchinensis* Lour.	Rubiaceae	MT	8	7.3	4040	3.3
25. *Mallotus tetracoccus* (Roxb.) Kurz	Euphorbiaceae	MT	6	5.3	4459	3.0
26. *Saurauia roxburghii* Wall.	Actinidiaceae	ST	5	12.7	2166	2.7
27. *Calamus erectus* Roxb.	Arecaceae	SH	5	17.6	245	2.5
28. *Caryota urens* L.	Arecaceae	MT	7	5.3	2852	2.5
29. *Bischofia javanica* Blume	Phyllanthaceae	LT	5	3.7	3962	2.5
30. *Aporosa octandra* (Buch.-Ham. ex D. Don) Vickery	Phyllanthaceae	ST	3	9.8	2837	2.4
31. *Trevesia palmata* (Roxb. ex Lindl.) Vis.	Araliaceae	ST	10	10.2	191	2.4
32. *Garuga pinnata* Roxb.	Burseraceae	LT	2	0.8	5682	2.4
33. *Dillenia indica* L.	Dilleniaceae	LT	6	3.3	3469	2.4
34. *Hydnocarpus kurzii* (King) Warb.	Achariaceae	MT	5	9.0	2215	2.4
35. *Lithocarpus elegans* (Blume) Hatus. ex Soepadmo	Fagaceae	LT	9	9.8	516	2.4
36. *Eriobotrya bengalensis* (Roxb.) Hook. f.	Rosaceae	LT	5	7.8	2506	2.4
37. *Leea indica* (Burm. f.) Merr.	Vitaceae	ST	10	8.6	347	2.3
38. *Engelhardtia spicata* Lechen ex Blume	Juglandaceae	LT	8	4.9	1853	2.2
39. *Callicarpa arborea* Roxb.	Lamiaceae	MT	7	5.7	1817	2.2
40. *Macaranga denticulata* (Blume) Müll.Arg.	Euphorbiaceae	MT	7	5.3	1875	2.1
41. *Artocarpus lakoocha* Roxb.	Moraceae	LT	5	4.1	2726	2.1
42. *Duabanga grandiflora* (DC.) Walp.	Lythraceae	LT	7	4.5	1849	2.1
43. *Styrax serrulatus* Roxb.	Styracaceae	ST	7	9.4	443	2.0
44. *Syzygium diospyrifolium* (Wall. ex Duthie) S.N. Mitra	Myrtaceae	ST	10	6.1	169	2.0
45. *Wendlandia ligustrina* Wall. ex G. Don	Rubiaceae	ST	9	6.1	194	1.9
46. *Ficus hirta* Vahl	Moraceae	ST	8	6.9	258	1.9
47. *Alangium chinense* (Lour.) Harms	Cornaceae	ST	7	7.3	481	1.8
48. *Castanopsis tribuloides* (Sm.) A. DC.	Fagaceae	MT	7	5.3	770	1.7
49. *Xerospermum glabratum* Radlk.	Sapindaceae	MT	2	4.1	2900	1.7
50. *Crypteronia paniculata* Blume	Crypteroniaceae	LT	2	0.8	3640	1.7
51. *Litsea laeta* (Nees) Hook. f.	Lauraceae	ST	7	5.3	532	1.7
52. *Antidesma montanum* Blume	Phyllanthaceae	ST	4	9.0	422	1.6
53. *Lithocarpus thomsonii* (Miq.) Rehder	Fagaceae	MT	3	5.3	1692	1.6
54. *Phoebe lanceolata* (Nees) Nees	Lauraceae	ST	7	3.7	490	1.5
55. *Quercus glauca* Thunb.	Fagaceae	LT	4	5.7	972	1.5
56. *Drimycarpus racemosus* (Roxb.) Hook. f. ex Marchand.	Anacardiaceae	LT	6	3.7	729	1.4
57. *Polyalthia simiarum* (Buch.-Ham. ex Hook. f. & Thomson) Benth.	Annonaceae	LT	3	3.7	1796	1.4
58. *Litsea salicifolia* (Roxburgh ex Nees) Hook. f.	Lauraceae	ST	6	5.3	197	1.4
59. *Euonymus attenuatus* Wall. ex M.A. Lawson	Celastraceae	ST	5	6.5	203	1.4
60. *Terminalia myriocarpa* Van Heurck & Mull. Arg.	Combretaceae	LT	1	0.4	3304	1.4
61. *Turpinia pomifera* (Roxb.) DC.	Staphyleaceae	MT	1	1.2	3073	1.4
62. *Gmelina arborea* Roxb.	Lamiaceae	MT	4	2.9	1462	1.4
63. *Mallotus paniculatus* (Lam.) Müll.Arg.	Euphorbiaceae	ST	7	2.9	337	1.3
64. *Ficus cyrtophylla* (Wall. ex Miq.) Miq.	Moraceae	ST	5	4.5	586	1.3
65. *Pterospermum acerifolium* (L.) Willd.	Malvaceae	LT	4	3.3	1010	1.2
66. *Ardisia thomsonii* Mez	Primulaceae	SH	5	5.3	64	1.2
67. *Viburnum odoratissimum* Ker Gawl.	Adoxaceae	ST	4	5.7	305	1.2
68. *Myristica* sp.	Myristicaceae	ST	3	6.9	311	1.2
69. *Artocarpus chaplasha* Roxb.	Moraceae	LT	4	2.9	1094	1.2
70. *Eurya acuminata* DC.	Pentaphylacaceae	ST	5	4.9	157	1.2
71. *Elaeocarpus lanceifolius* Roxb.	Elaeocarpaceae	MT	5	3.7	334	1.2

(continued on next page)

Table 2 (continued)

Species	Family	Growth form	Occurrence	Density (ha^{-1})	Basal area (cm^2 ha^{-1})	IVI
72. *Knema linifolia* (Roxb.) Warb.	Myristicaceae	LT	5	4.1	120	1.1
73. *Lepisanthes rubiginosa* (Roxb.) Leenh.	Sapindaceae	ST	3	1.6	1507	1.1
74. *Morinda angustifolia* Roxb.	Rubiaceae	SH	5	4.1	58	1.1
75. *Amblyanthus glandulosus* (Roxb.) A. DC.	Primulaceae	SH	5	4.1	41	1.1
76. *Archidendron clypearia* (Jack) I.C. Nielsen	Leguminosae	ST	5	3.3	159	1.0
77. *Macropanax dispermus* (Blume) Kuntze	Araliaceae	ST	4	3.7	399	1.0
78. ML081T32	Indeterminate	LT	1	1.2	1895	0.9
79. *Saraca indica* L.	Leguminosae	MT	4	3.7	93	0.9
80. *Camellia kissi* Wall.	Theaceae	SH	4	3.7	42	0.9
81. *Ficus benjamina* L.	Moraceae	LT	1	0.4	2029	0.9
82. *Lasianthus hookeri* C.B. Clarke ex Hook. f.	Rubiaceae	SH	4	3.7	38	0.9
83. *Schoepfia* sp.	Schoepfiaceae	ST	4	2.0	486	0.9
84. *Artocarpus heterophyllus* Lam.	Moraceae	MT	2	3.3	836	0.9
85. *Photinia integrifolia* Lindl.	Rosaceae	ST	3	2.0	785	0.9
86. *Melia dubia* Cav.	Meliaceae	LT	1	0.4	1763	0.8
87. *Cyathea khasyana* Domin	Cyatheaceae	ST	3	3.3	224	0.8
88. *Pterygota alata* (Roxb.) R.Br.	Malvaceae	LT	4	2.4	66	0.8
89. *Actinodaphne obovata* (Nees) Blume	Lauraceae	MT	3	2.4	353	0.8
90. *Ficus hispida* L. f.	Moraceae	ST	4	2.0	96	0.8
91. *Gynocardia odorata* R.Br.	Achariaceae	LT	3	1.6	557	0.8
92. ML081T48	Lauraceae	LT	3	1.6	557	0.8
93. *Tarenna asiatica* (L.) Kuntze ex K. Schum.	Rubiaceae	ST	4	2.0	59	0.8
94. *Ligustrum robustum* (Roxb.) Blume	Oleaceae	SH	3	1.2	646	0.8
95. *Goniothalamus sesquipedalis* (Wall.) Hook. f. & Thomson	Annonaceae	SH	3	2.9	158	0.7
96. *Psychotria symplocifolia* Kurz	Rubiaceae	SH	3	3.3	31	0.7
97. *Pandanus furcatus* Roxb.	Pandanaceae	ST	3	2.0	355	0.7
98. *Protium serratum* (Wall. ex Colebr.) Engl.	Burseraceae	LT	3	2.4	231	0.7
99. *Xylosma controversa* Clos	Salicaceae	ST	3	2.9	43	0.7
100. *Carallia brachiata* (Lour.) Merr.	Rhizophoraceae	ST	4	1.6	30	0.7
101. *Mallotus philippensis* (Lam.) Müll.Arg.	Euphorbiaceae	ST	4	1.6	20	0.7
102. *Eurya japonica* Thunb.	Pentaphylacaceae	SH	3	2.9	25	0.7
103. *Lindera melastomacea* Fern.-Vill.	Lauraceae	ST	2	3.7	114	0.7
104. *Magnolia champaca* (L.) Baill. ex Pierre	Magnoliaceae	LT	3	1.2	393	0.7
105. *Microcos paniculata* L.	Malvaceae	ST	2	2.0	474	0.6
106. *Brassaiopsis glomerulata* (Blume) Regel	Araliaceae	ST	2	3.3	129	0.6
107. *Careya arborea* Roxb.	Lecythidaceae	MT	1	0.4	1260	0.6
108. *Fagraea ceilanica* Thunb.	Gentianaceae	SH	3	1.2	281	0.6
109. *Bridelia glauca* Blume	Phyllanthaceae	MT	3	1.6	141	0.6
110. *Albizia chinensis* (Osbeck) Merr.	Leguminosae	LT	2	0.8	685	0.6
111. *Schefflera pueckleri* (K. Koch) Frodin	Araliaceae	SS	2	2.0	336	0.6
112. *Tetrameles nudiflora* R. Br.	Tetramelaceae	LT	1	0.4	1135	0.6
113. *Ficus auriculata* Lour.	Moraceae	SS	2	1.2	534	0.6
114. *Ficus heteropleura* Blume	Moraceae	SS	3	1.2	158	0.6
115. *Mesua ferrea* L.	Calophyllaceae	LT	2	2.0	281	0.6
116. *Ceriscoides campanulata* (Roxb.) Tirveng.	Rubiaceae	ST	2	2.9	42	0.6
117. *Ulmus lanceifolia* Roxb. ex Wall.	Ulmaceae	LT	2	1.6	383	0.6
118. *Kayea floribunda* Wall.	Calophyllaceae	MT	3	1.2	138	0.6
119. *Sapindus attenuatus* Wall.	Sapindaceae	ST	3	1.6	20	0.6
120. *Vitex quinata* (Lour.) F.N. Williams	Lamiaceae	LT	1	0.8	906	0.5
121. *Dalbergia assamica* Benth.	Leguminosae	MT	2	2.4	54	0.5
122. *Plectocomia himalayana* Griff.	Arecaceae	SS	2	2.4	26	0.5
123. *Magnolia insignis* Wall.	Magnoliaceae	LT	1	0.4	927	0.5
124. *Parkia timoriana* (DC.) Merr.	Leguminosae	LT	2	1.2	335	0.5
125. *Firmiana colorata* (Roxb.) R.Br.	Malvaceae	ST	2	1.6	171	0.5
126. *Phoebe attenuata* (Nees) Nees	Lauraceae	LT	2	0.8	374	0.5
127. *Vitex pinnata* L.	Lamiaceae	LT	2	1.6	110	0.5
128. *Aglaia elaeagnoidea* (A. Juss.) Benth.	Meliaceae	ST	2	0.8	291	0.5
129. *Trema orientalis* (L.) Blume	Cannabaceae	MT	1	0.4	760	0.5
130. *Micromelum integerrimum* (Buch.-Ham. ex DC.) Wight & Arn. ex M. Roem.	Rutaceae	ST	2	1.6	22	0.4
131. *Maesa indica* (Roxb.) A. DC.	Primulaceae	ST	2	1.6	21	0.4
132. *Heritiera macrophylla* Wall. ex Kurz	Malvaceae	LT	2	1.6	19	0.4
133. *Dasymaschalon longiflorum* (Roxb.) Finet & Gagnep.	Annonaceae	ST	2	1.6	18	0.4
134. *Toddalia asiatica* (L.) Lam.	Rutaceae	SS	2	1.6	16	0.4
135. *Antidesma* sp.	Phyllanthaceae	ST	2	1.2	85	0.4
136. *Alstonia scholaris* (L.) R. Br.	Apocynaceae	LT	1	0.4	636	0.4
137. *Syzygium cumini* (L.) Skeels	Myrtaceae	LT	1	0.4	618	0.4
138. *Xantolis assamica* (C. B. Clarke) P. Royen	Sapotaceae	ST	2	1.2	24	0.4
139. *Olax acuminata* Wall. ex Benth.	Olacaceae	ST	2	1.2	24	0.4
140. *Symplocos pyrifolia* Wall. ex G. Don	Symplocaceae	ST	1	2.4	31	0.4
141. *Cinnamomum* sp.	Lauraceae	LT	1	0.4	583	0.4
142. *Memecylon cerasiforme* Kurz	Melastomataceae	ST	2	0.8	90	0.4
143. *Randia* sp.	Rubiaceae	MT	1	0.4	503	0.4
144. *Bauhinia variegata* L.	Leguminosae	ST	2	0.8	28	0.4

Table 2 (continued)

Species	Family	Growth form	Occurrence	Density (ha^{-1})	Basal area (cm^2 ha^{-1})	IVI
145. *Sterculia hamiltonii* (Kuntze) Adelb.	Malvaceae	ST	2	0.8	16	0.4
146. *Gomphandra tetrandra* (Wall.) Sleumer	Stemonuraceae	SH	2	0.8	14	0.4
147. *Reevesia wallichii* R.Br.	Malvaceae	MT	1	1.6	107	0.3
148. *Zanthoxylum ovalifolium* Wight	Rutaceae	ST	1	1.2	72	0.3
149. *Elaeocarpus* sp.	Elaeocarpaceae	LT	1	0.4	293	0.3
150. ML071T37	Indeterminate	MT	1	0.4	257	0.3
151. *Clerodendrum hastatum* (Roxb.) Lindl.	Lamiaceae	SH	1	1.2	26	0.3
152. *Tectona grandis* L. f.	Lamiaceae	LT	1	0.4	240	0.3
153. ML081T18	Indeterminate	LT	1	0.4	218	0.3
154. *Litsea monopetala* (Roxb.) Pers.	Lauraceae	MT	1	0.4	198	0.2
155. *Dracaena elliptica* Thunb. & Dalm.	Asparagaceae	SH	1	0.8	70	0.2
156. *Cinnamomum glaucescens* (Nees) Hand.-Mazz.	Lauraceae	LT	1	0.4	150	0.2
157. *Glochidion lanceolarium* (Roxb.) Voigt	Phyllanthaceae	ST	1	0.8	19	0.2
158. *Nerium oleander* L.	Apocynaceae	SH	1	0.8	16	0.2
159. *Benkara griffithii* (Hook. f.) Ridsdale	Rubiaceae	SH	1	0.8	15	0.2
160. *Ficus pyriformis* Hook. & Arn.	Moraceae	SH	1	0.8	15	0.2
161. *Clerodendrum bracteatum* Wall. ex Walp.	Lamiaceae	SH	1	0.8	12	0.2
162. *Psychotria adenophylla* Wall.	Rubiaceae	SH	1	0.8	11	0.2
163. *Hiptage acuminata* Wall. ex A. Juss.	Malpighiaceae	SS	1	0.8	8	0.2
164. *Ardisia pedunculosa* Wall.	Primulaceae	SH	1	0.8	6	0.2
165. *Baccaurea ramiflora* Lour.	Phyllanthaceae	MT	1	0.4	115	0.2
166. *Erythrina stricta* Roxb.	Leguminosae	MT	1	0.4	81	0.2
167. *Dendrocnide sinuata* (Blume) Chew	Urticaceae	SH	1	0.4	48	0.2
168. *Cynometra ramiflora* L.	Leguminosae	SH	1	0.4	32	0.2
169. *Ficus* sp.1	Moraceae	MT	1	0.4	31	0.2
170. *Oroxylum indicum* (L.) Kurz	Bignoniaceae	ST	1	0.4	30	0.2
171. *Calliandra umbrosa* (Wall.) Benth.	Leguminosae	ST	1	0.4	29	0.2
172. *Elaeocarpus prunifolius* Wall. ex Müll.Berol.	Elaeocarpaceae	ST	1	0.4	27	0.2
173. *Actinodaphne angustifolia* Nees	Lauraceae	MT	1	0.4	25	0.2
174. *Olea salicifolia* Wall. ex G. Don	Oleaceae	ST	1	0.4	17	0.2
175. *Garcinia lanceifolia* var. *oxyphylla* (Planch. & Triana) Laness.	Clusiaceae	SH	1	0.4	13	0.2
176. *Alchornea tiliifolia* (Benth.) Müll.Arg.	Euphorbiaceae	ST	1	0.4	9	0.2
177. *Litsea lancifolia* (Roxb. ex Nees) Benth. & Hook. f. ex Villar	Lauraceae	ST	1	0.4	9	0.2
178. *Machilus gamblei* King ex Hook. f.	Lauraceae	MT	1	0.4	8	0.2
179. *Bauhinia rufa* (Bong.) Steud.	Leguminosae	LI	1	0.4	7	0.2
180. *Flueggea virosa* (Roxb. ex Willd.) Royle	Phyllanthaceae	SH	1	0.4	5	0.2
181. *Areca catechu* L.	Arecaceae	MT	1	0.4	5	0.2
182. *Sapindus erectus* Hiern	Sapindaceae	ST	1	0.4	5	0.2
183. *Boehmeria macrophylla* Hornem.	Urticaceae	SH	1	0.4	3	0.2
184. *Mahonia napaulensis* DC.	Berberidaceae	SH	1	0.4	3	0.2
Total for all species			49	973.5	273,378	300.0

Combretaceae, Lecythidaceae and Tetramelaceae) had only one individual each and another five families (Asparagaceae, Crypteroniaceae, Malpighiaceae, Melastomataceae and Stemonuraceae) had only two individuals each.

In terms of basal area, no single family was exceedingly dominant as the top seven families, each with <12% basal area, accounted for 56.5% of the basal area: Theaceae (11.8%), Fagaceae (11.7%), Lauraceae (11.5%), Araliaceae (7.7%), Euphorbiaceae (5%), Meliaceae (4.7%) and Bignoniaceae (4.1%). The next 20 families, each with ≥1% but <4% of the basal area, contributed to 33.7% basal area. The remaining 39 families, each with <1% of the basal area, shared only 9.7% of the basal area.

In terms of the importance value index (IVI), no single family was dominant as the top eight families, each with <10% of IVI, accounted for 50.7% of IVI: Lauraceae (9.8%), Fagaceae (9.1%), Araliaceae (6.9%), Theaceae (6.5%), Euphorbiaceae (6.4%), Urticaceae (5.2%), Moraceae (3.5%) and Rubiaceae (3.3%). The next 19 families, each with ≥1% but <3% of the importance value, contributed 32.8% importance value. The remaining 39 families, each with <1% of the importance value, shared 16.4% of the importance value.

3.2. Physiognomy and life-form spectrum

The height of the canopy is low, i.e., below 30 m. The emergent trees occur between 25 and 30 m, upper-canopy between 20 and 25 m, middle-canopy between 10 and 20 m and understory below 10 m. The forest exhibits a pyramidal packing of species and individuals in rather inconspicuous vertical stratification. The general physiognomy of the forest is evergreen. The overall deciduousness in the assemblage was only 16.3%, i.e., only 30 out of 184 species were deciduous. These species accounted for only 7.5% of individuals, 17.7% of the basal area and 12.1% of the IVI. Some species were facultative deciduous (retaining leaves in rainforests, but not in dry forests during winter season) and these were considered as evergreen. Among deciduous species, 26 were trees, three were shrubs and one was a liana.

Partitioning of deciduous species among canopy strata showed that the deciduousness was minimum in the understory (girth <30 cm), which increased through lower and middle-canopy (girth ≥30 cm, but <90 cm) and was maximum in upper-canopy and emergent strata (girth ≥90 cm) in count of species (Fig. 2a), count of individuals (Fig. 2b), accumulation of basal area (Fig. 2c) and importance value index (Fig. 2d). Leguminosae, Lamiaceae (with inclusion of Verbenaceae vide APG III), Malvaceae (with inclusion of Sterculiaceae vide APG III), Meliaceae and Rubiaceae were the principal families contributing to deciduousness in Meghalaya. All species with an IVI ≥3 were distinctively evergreen with the exception of *Stereospermum chelonoides* and *Toona ciliata*. Some other deciduous species include the following: *Bischofia javanica*, *Garuga pinnata*, *Engelhardita spicata*, *Artocarpus lakoocha*, *Alangium chinense*, *Gmelina arborea* and *Pterygota alata*.

Table 3
Familial composition of lowland rainforests of Meghalaya. The count of individuals and of species (as superscript if more than one species) with girth ≥10 cm in different plant families is from 2.45 ha sampled area. The family importance value (FIV) is in percentage.

Plant family	Growth form					Total	FIV
	Large tree	Medium tree	Small tree	Shrub	Liana[a]		
1. Achariaceae	4	22				26^2	1.0
2. Actinidiaceae			31			31	0.9
3. Adoxaceae			14			14	0.4
4. Anacardiaceae	9					9	0.5
5. Annonaceae	9		4	7		20^3	0.9
6. Apocynaceae	1			2		3^2	0.2
7. Araliaceae			186^4		5	191^5	6.9
8. Arecaceae		14^2		43	6	63^4	1.9
9. Asparagaceae				2		2	0.1
10. Berberidaceae				1		1	0.1
11. Bignoniaceae	17		1			18^2	1.9
12. Burseraceae	8^2					8^2	1.1
13. Calophyllaceae	5	3				8^2	0.4
14. Cannabaceae		1				1	0.2
15. Celastraceae			16			16	0.5
16. Clusiaceae			49	1		50^2	1.2
17. Combretaceae	1					1	0.5
18. Cornaceae			18			18	0.6
19. Crypteroniaceae	2					2	0.6
20. Cyatheaceae			8			8	0.3
21. Dilleniaceae	8					8	0.8
22. Elaeocarpaceae	1	9	1			11^3	0.5
23. Euphorbiaceae		91^4	57^4			148^8	6.4
24. Fagaceae	122^4	81^3				203^7	9.1
25. Gentianaceae				3		3	0.2
26. Iteaceae			65			65	2.0
27. Juglandaceae	12					12	0.7
28. Lamiaceae	7^3	21^2		5^2		33^7	1.8
29. Lauraceae	47^5	126^6	45^5			218^{16}	9.8
30. Lecythidaceae		1				1	0.2
31. Leguminosae	5^2	16^3	11^3	1	1	34^{10}	1.6
32. Lythraceae	11					11	0.7
33. Magnoliaceae	17^3					17^3	1.6
34. Malpighiaceae					2	2	0.1
35. Malvaceae	18^3	4	11^3			33^7	1.4
36. Melastomataceae			2			2	0.1
37. Meliaceae	28^2		2			30^3	2.4
38. Moraceae	18^3	9^2	33^3	2	6^2	68^{11}	3.5
39. Myristicaceae	10		17			27^2	0.8
40. Myrtaceae	1	85	15			101^3	3.0
41. Olacaceae			3			3	0.1
42. Oleaceae			1	3		4^2	0.3
43. Pandanaceae			5			5	0.2
44. Pentaphylacaceae			12	7		19^2	0.6
45. Phyllanthaceae	9	5^2	51^4	1		66^8	2.7
46. Polygalaceae	26					26	1.8
47. Primulaceae			4	25^3		29^4	1.0
48. Proteaceae		49				49	1.6
49. Rhizophoraceae			4			4	0.2
50. Rosaceae	19		5			24^2	1.1
51. Rubiaceae		19^2	27^3	31^5		77^{10}	3.3
52. Rutaceae			7^2		4	11^3	0.4
53. Salicaceae			7			7	0.2
54. Sapindaceae		10	9^3			19^4	1.2
55. Sapotaceae		57	3			60^2	2.0
56. Schoepfiaceae			5			5	0.3
57. Staphyleaceae		3				3	0.5
58. Stemonuraceae				2		2	0.1
59. Styracaceae			23			23	0.7
60. Symplocaceae			68^2			68^2	1.7
61. Tetramelaceae	1					1	0.2
62. Theaceae	98			9		107^2	6.5
63. Ulmaceae	4					4	0.2
64. Urticaceae			74	152^3		226^4	5.2
65. Vitaceae			21			21	0.8
66. Indeterminate family	4^2	1				5^3	0.5
Total	522^{49}	627^{38}	915^{63}	297^{27}	24^7	2385^{184}	100

[a] liana include scandent shrubs.
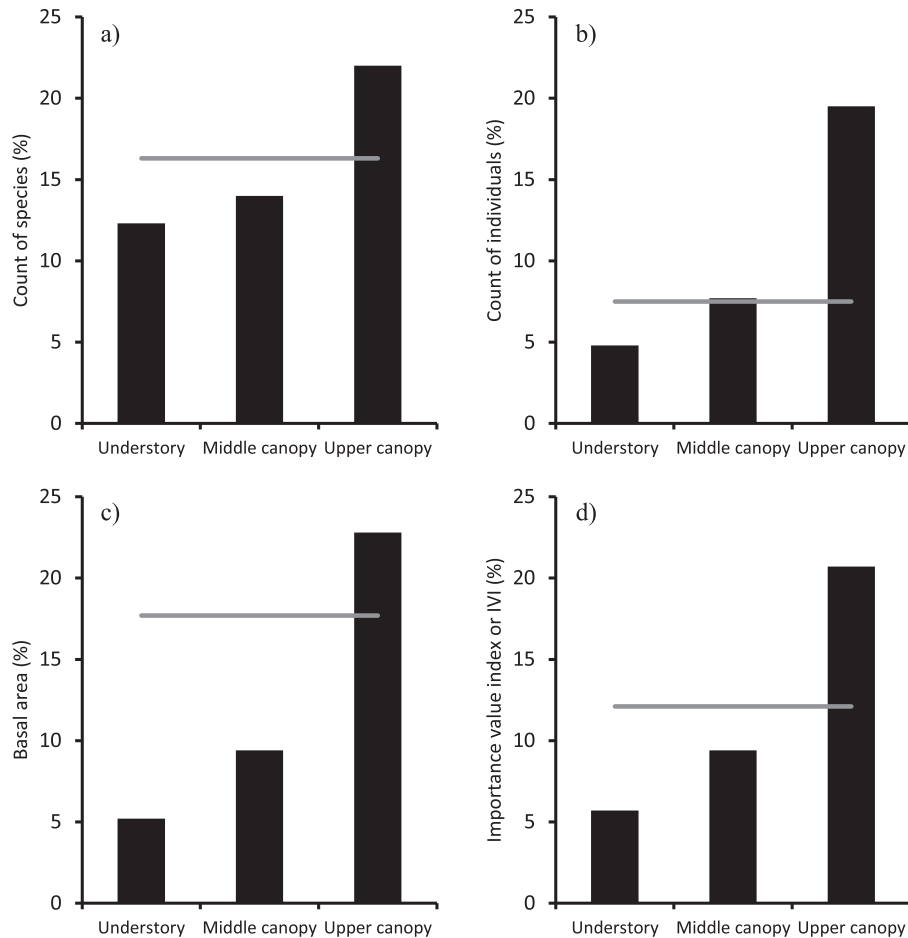
Fig. 2. Deciduousness in canopy of lowland rainforest of Meghalaya. The black bars depict proportions of deciduous species in different strata and grey horizontal line depicts the average value for entire canopy.

The majority of species were 'small tree', followed by 'large tree', 'medium tree', 'shrub', 'scandent shrub' and 'liana' (Table 4). Small trees included a single tree fern, *Cyathea khasyana* (Table 2). The count of individuals was maximum for 'small tree' followed by 'medium tree', 'large tree', 'shrub', 'scandent shrub' and 'liana' (Table 4). In terms of accumulation of basal area, 'large tree' ranked at the top followed by 'medium tree', 'small tree', 'shrub', 'scandent shrub' and 'liana' (Table 4). In terms of IVI, the 'tree' was the most dominant growth form in the assemblage with competitive proportions of 'large tree', 'medium tree' and 'small tree'. The IVI for shrubs was small, while for scandent shrubs and liana it was almost negligible (Table 4).

The rainforests of Meghalaya exhibited a phanerophytic life-form spectrum. Mega and mesophanerophytes were dominant in the species count (Fig. 3a), count of individuals (Fig. 3b), basal area (Fig. 3c) and importance value index (Fig. 3d). Micro- and nano-phanerophytes were more prominent in species count and in count of individuals as compared to accumulation of basal area and IVI. There were few liana phanerophytes. The proportion of deciduous species was much smaller than the proportion of evergreen species in all life forms.

3.3. Frequency of species and cluster analysis

The variation in count of species among samples was low, between 40 and 61 with a mean of 48.6 and a coefficient of variation of 15.8% (Table 1). The most species common to any two samples was 23, between T4 and T5, and the least was four, between T1 and

Table 4
Species richness, density, basal area and importance value index (IVI) of different growth forms of species, based on the count of individuals with girth ≥10 cm in lowland rainforests of Meghalaya.

Growth form	Species		Density		Basal area		IVI	
	(#)	(%)	(ha^{-1})	(%)	(m^2 ha^{-1})	(%)	Out of 300	(%)
Large trees	49	26.6	213.1	21.9	13.21	48.3	95.7	31.9
Medium trees	38	20.7	255.9	26.3	9.02	33.0	84.5	28.2
Small trees	63	34.2	373.5	38.4	4.61	16.9	93.0	31.0
Shrubs	27	14.7	121.2	12.4	0.38	1.4	23.7	7.9
Liana including scandent shrubs	7	3.8	9.8	1.0	0.11	0.4	3.1	1.0
All species	184	100	973.5	100	27.33	100	300	100
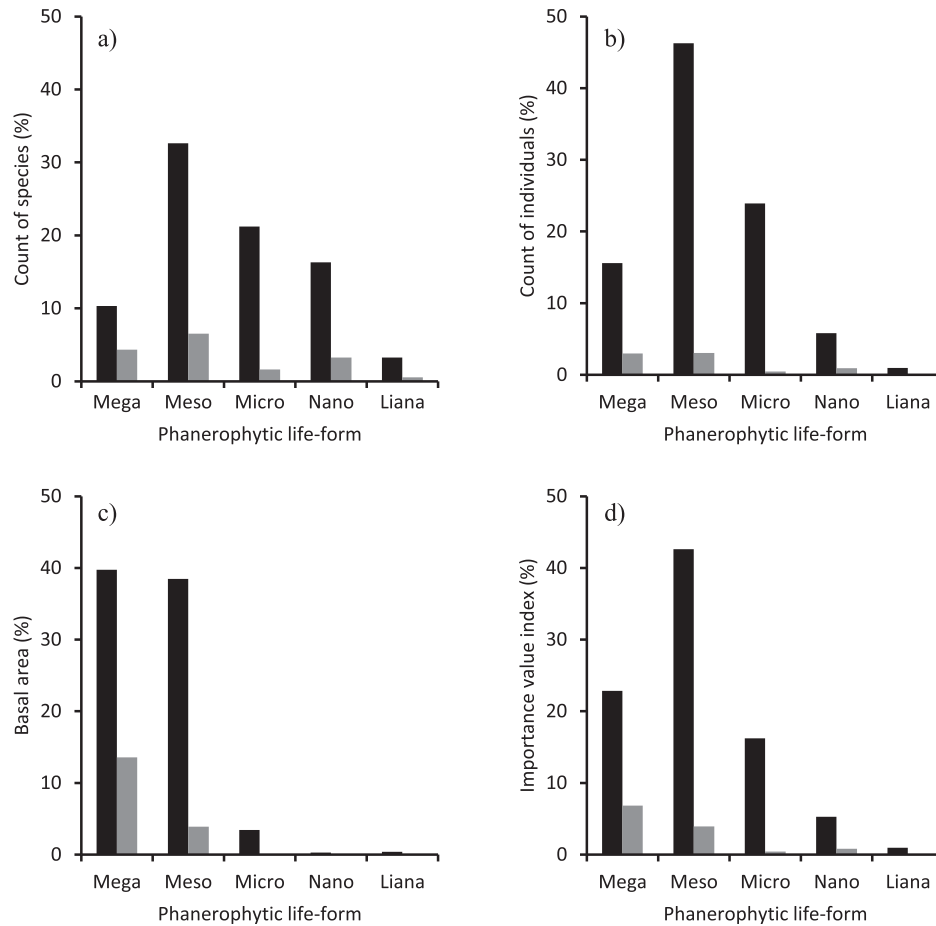
Fig. 3. Life-form spectrum of lowland rainforest of Meghalaya. The woody species were categorized into five phanerophytic classes: megaphanerophyte, mesophanerophyte, microphanerophyte, nanophanerophyte and liana. The black bars indicate evergreen species and grey bars indicate deciduous species.

T6. Nearly 63% of species occurred in a single sample, 22.3% of species in two samples, 8.2% of species in three samples, 6% of species in four samples and 0.5% of species in five samples (Fig. 4). No single species occurred in all six samples.

Furthermore, 53 species (28%) appeared in a single subplot (500 m²) out of 49 subplots of six samples. Of these, 37 species were singletons (with one individual). Another 16 species with more than one individual also tended to aggregate within one subplot: 10 species with two individuals each, four species with three individuals each (*Clerodendrum hastatum*, *Turpinia pomifera*,
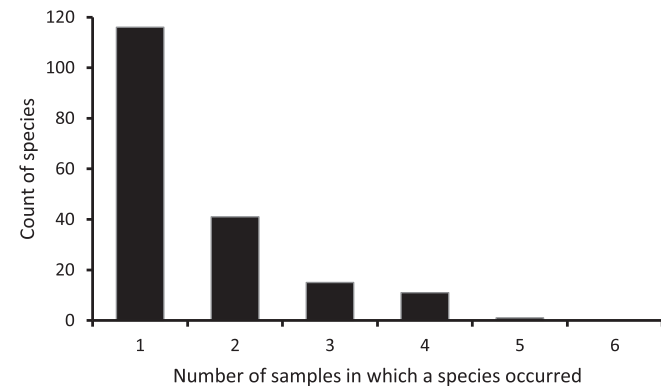
Fig. 4. Frequency of occurrences of species in samples of lowland rainforest of Meghalaya.

Zanthoxylum ovalifolium, ML081T32), one species with four individuals (*Reevesia wallichii*) and another one species with six individuals (*Symplocos pyrifolia*). Altogether, 32 species appeared in two subplots with a range of 2−10 individuals, and 23 species appeared in three subplots with a range of 3−24 individuals. In terms of Raunkiaer's frequency spectrum, 91% of species belonged to class 'A' with ≤20% frequency of occurrence (Fig. 5). Only 8.2% species belonged to class 'B' (>20−≤40% frequency) and 1.1% of species belonged to class 'C' (>40−≤60% frequency). No single species occurred in class 'D' (>60≤80% frequency) or class 'E' (>80−100% frequency).

Paired-group cluster analysis based on Bray−Curtis similarity showed a principal cluster of five samples with the T4 sample the most distinct at <50% similarity to all other samples (Fig. 6). The Cophenetic correlation was 0.9203. Altitudinal location had an influence on clustering of samples. The T4 sample at the lowest altitude (319 m) exhibited the least similarity (33.9%−48.5%) to other samples. The T1 and T3 samples, both between 800 and 900 m, clustered with maximum similarity (72.4%). The T2 and T6 samples, between 500 and 600 m, clustered with 61.1% similarity. The T5 sample, at 750 m, was closer to the sub-cluster of T1 and T3 (66.8%) as compared to the sub-cluster of T2 and T6 (59.7%).

3.4. Abundances (stand density, basal area and importance value)

Stand density was 973.5 ha⁻¹ and stand basal area was 27.34 m² ha⁻¹ for girth ≥10 cm (Table 2). These values were 467.3 ha⁻¹ and 26.06 m² ha⁻¹, respectively, for girth ≥30 cm. The

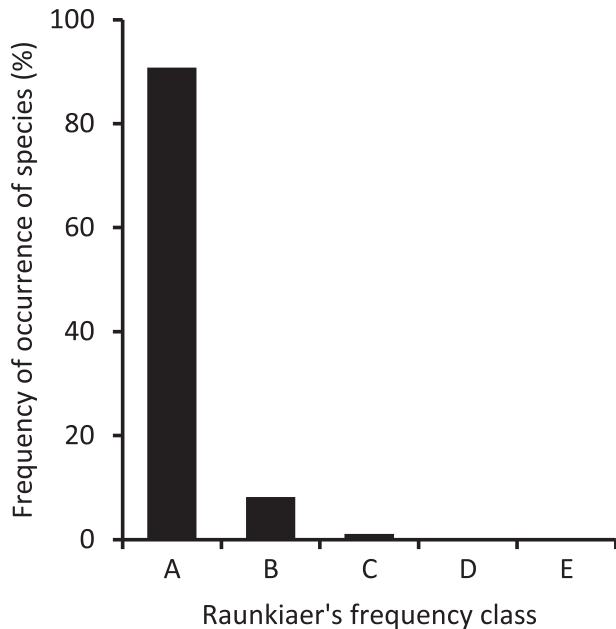**Fig. 5.** Frequency of occurrence of species in subplots of 500 m² size, modelled on Raunkiaer's frequency classes, lowland rainforest of Meghalaya.
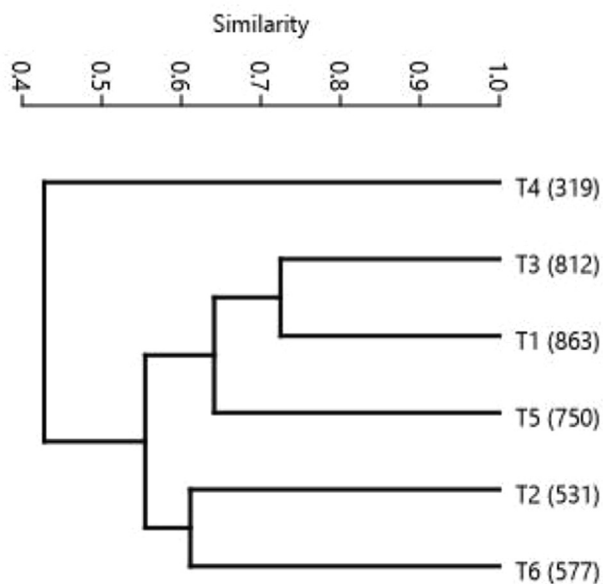

Fig. 6. A cluster analysis of six samples of lowland rainforests of Meghalaya. The sample names are indicted as T1, T2, T3, T4, T5 and T6. The values of elevation (m) of the sites are given in parentheses.

basal area of an average individual was 280.8 cm² (= 59.4 cm girth) for girth ≥10 cm and 557.6 cm² (= 83.7 cm girth) for girth ≥30 cm.

Eleven species with ≥50 individuals each, accounted for 39.5% of the individuals: *Boehmeria glomerulifera* (150 individuals), *Macropanax undulatus* (144), *Schima wallichii* (98), *Cinnamomum tamala* (95), *Syzygium tetragonum* (85), *Oreocnide integrifolia* (74), *Itea macrophylla* (65), *Symplocos sumuntia* (62), *Sarcosperma griffithii* (57), *Castanopsis lanceifolia* (57) and *Castanopsis armata* (55). The next 49 species, with ≥10 but <50 individuals each, accounted for 41.5% of individuals. The remaining 124 species, with <10 individuals each, accounted for 19% of individuals. Most species were

rare: 159 species with <1% of total individuals, 94 species with two or less than two individuals ha⁻¹ and 36 species with one or less than one individual ha⁻¹ (Table 2). No single species endemic to Meghalaya made the list, but *Kayea floribunda* of Calophyllaceae (arising out of Clusiaceae in APG III) is possibly endemic to northeast India.

Twelve species, each with at least 1 m² basal area, constituted 55.2% of the total basal area: *S. wallichii* (7.91 m²), *M. undulatus* (4.89 m²), *C. armata* (4.57 m²), *C. tamala* (3.40 m²), *Persea odoratissima* (2.95 m²), *S. chelonoides* (2.76 m²), *T. ciliata* (2.65 m²), *Xanthophyllum flavescens* (2.35 m²), *Magnolia hodgsonii* (1.55 m²), *Castanopsis indica* (1.44 m²), *G. pinnata* (1.39 m²) and *Mallotus tetracoccus* (1.09 m²). The next 67 species, each with basal area between ≥0.1 and <1 m², comprised 40.3% of the basal area. The remaining 105 species, each with basal area <0.1 m², accounted for 4.5% basal area (Table 2).

Fourteen species, each with IVI ≥5, represented 39.1% of total IVI: *S. wallichii* (18.7), *M. undulatus* (16), *C. tamala* (11), *C. armata* (10), *B. glomerulifera* (9.1), *S. tetragonum* (6.5), *P. odoratissima* (6.2), *O. integrifolia* (6.1), *I. macrophylla* (5.9), *T. ciliata* (5.9), *S. chelonoides* (5.5), *S. griffithii* (5.5), *C. lanceifolia* (5.4) and *X. flavescens* (5.4). The next 63 species, each with IVI between ≥1 and <5, constituted 44.2% IVI. The remaining 107 species, each with IVI <1, shared 16.7% IVI (Table 2).

3.5. Species diversity, abundance modelling and ordination

The gamma diversity (γ) was 184 species in 2.45 ha. The Whittaker's alpha diversity ($\overline{\alpha}$) was 30.7 species per sample. The compositional heterogeneity among samples, in terms of Whittaker's beta diversity (β_w), was 2.79 and Harrison's beta-one value was 55.8%. Shannon's diversity (H'), based on the count of individuals with ≥10 cm girth, was 4.402 *nats* (= 6.351 *bits*). The maximum diversity (H'_{max}) was 5.215 *nats*, Pielou's evenness or homogeneity index (E) was 0.844 and Simpson's dominance index (D) was 0.021. For individuals with ≥30 cm girth, H' was 4.254, E was 0.869 and D was 0.029, and for individuals ≥90 cm girth, H' was 3.549, E was 0.870 and D was 0.051.

Four classical models of species abundance distribution were applied to rank-abundance data. The observed pattern followed a truncated lognormal distribution in Preston's octaves of abundance (black bars in Fig. 7). The truncation point, or veil line, occurred at 0.125 octave (red line). An expected distribution in octaves of abundance (green bars) was close to the observed abundance distribution ($\chi^2 = 17.48$, df = 4, p = 0.00016). An estimate of hidden species behind the truncation point, or veil line, yielded 22 species (blue bar).

The PCA ordination revealed that the first two principal components were important and none of them were exceedingly overriding (Fig. 8a). Nine of the top ten dominant species in upper and middle canopies successfully separated along Component 1, between PCA score 20 and 80 (Fig. 8b). The most dominant species in the understory, *B. glomerulifera*, distinctly separated along Component 2 (Fig. 8b). Nearly 94% of species concentrated near the centroid in PCA space of Components 1 and 2, indicating that all these species required similar habitat and environmental conditions for growth.

4. Discussion

Aerial views of 'tropical lowland evergreen rainforests' appear alike across regions due to striking similarity in physiognomy, but are dissimilar in floristic composition and patterns of tree diversity (Whitmore, 1984; Corlett and Primack, 2011). While an appreciable number of phytosociological studies are available from rainforests
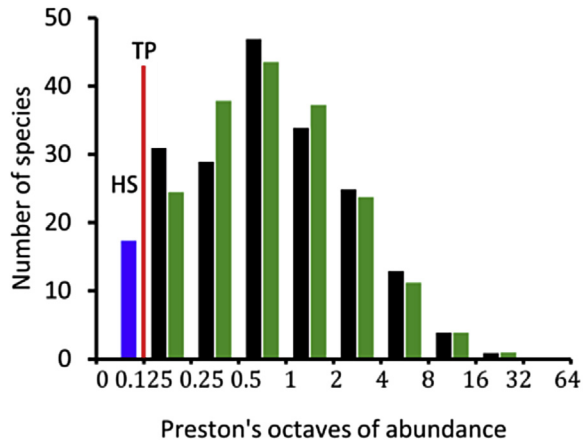
Fig. 7. A plot of truncated lognormal distribution of species abundances in Preston's octaves (abundance classes) following Pielou's (1975) method of fitting. The observed frequencies of species in octaves are shown in black bars, expected frequencies in green bars and the frequency of hidden species in the blue bar (HS). The red line marked with TP indicates the truncation point.

in the equatorial region of Asia-Pacific, there are a limited number of studies which examine the northern limits of rainforests around the Tropic of Cancer. The known lowland rainforests north of the Tropic of Cancer are situated up to 27°40′N in Namdapha National Park in northeastern India (Kaul and Haridasan, 1987; Proctor et al., 1998; Deb et al., 2009) and up to 27°20′N in Myanmar (Kingdon-Ward, 1945; Davis, 1960). In China, tropical areas near the Tropic of Cancer are situated disjunctively in southeastern Xizang (Tibet), southern parts of Yunnan, Gunangxi, Guangdong, Taiwan and Hainan Island (Corlett, 2014). The largest tropical area is in Yunnan province, which occupies a transitional position between northeastern India at the junction of the Indian and Burmese plates of Gondwanaland and the Eurasian plate of Laurasia (Audely-Charles, 1987). A vegetation map of China depicts rainforests up to 28°28′N in the eastern vicinity of Namdapha National Park, presumably with the same biogeographical formation (Hou, 1979; Wu, 1980), but phytosociological studies from these forests are not available (Proctor et al., 1998; Corlett, 2014). The westernmost limit of the lowland rainforests north of the Tropic of Cancer occurs in Khasi and Garo hills of Meghalaya, and this paper presents the first dataset on lowland rainforests from this region. The lowland rainforests situated at the northern limits, especially in Meghalaya around 24°00′N, are restricted mainly to moist depressions in rolling mountains below 1000 m in altitude, primarily in patches

experiencing tropical climate governed by the Asia-Pacific monsoon. During his visit to Khasi Hills in 1850, J. D. Hooker noticed these rainforests (Hooker, 1854). The rainforests in Khasi Hills tend to grade gradually into 'tropical montane evergreen rainforests' at higher altitudes, between 1200 and 1800 m, and tend to degrade as 'tropical lowland semievergreen forests' following clear-cutting for shifting agriculture (Tripathi and Shankar, 2016).

4.1. Physiognomy, life-form spectrum and frequency of species

Display of an evergreen physiognomy is the characteristic of rainforests despite modest shrinkage of foliage during winter. Deciduous species principally contribute to the reduction in foliage. However, these species flush newer leaves shortly after senescence in spring to sustain an evergreen appearance. Hence, species with long periods of leaflessness (>2 months), as is common in temperate forests, do not occur in tropical rainforests. At our sites, deciduousness increased from the sapling layer through understory and middle-canopy strata and reached a maximum in upper-canopy and emergent strata. Previous research has recorded the distinctive presence of deciduous trees in the canopy of rainforests near the Tropic of Cancer. Notably, at Xishuangbanna, deciduous trees account for one-half of the individuals in the canopy and one-third of the species in the emergent layer (Zhu, 1997). While we found that Xishuangbanna and Meghalaya shared some deciduous trees in common (*B. javanica*, *Tetrameles nudiflora*, *Ulmus lanceifolia*), the levels of deciduousness were lower in Meghalaya compared to Xishuangbanna despite the former being at higher latitudes compared to the latter. In rainforests near the equator, deciduousness is insignificant (Poore, 1968). Increasing deciduousness in rainforests, from the equator towards the Tropic of Cancer, is attributed to distinctively seasonal climate. The levels of deciduousness are presumably governed by annual quantities of rainfall and the period and intensity of dryness during winter.

The rainforests of Meghalaya exhibited a phanerophytic life-form spectrum. Species richness can be principally ascribed to tree diversity as there are few species of shrubs or liana. Among woody life-forms, mega- and mesophanerophytes are predominant, commanding up to three-fourths of IVI. The micro- and nanophanerophytes contribute more to species richness than to IVI, and the contribution of liana phanerophytes is negligible. These patterns substantiate the observations of Champion and Seth (1968), and Whitmore (1984) that the dominance of trees over other growth forms is common in lowland forests in India. Notably, similar proportions of trees, shrubs and liana have been recorded in sal-dominated lowland forests in Darjeeling (Shankar, 2001) and in Meghalaya (Tripathi and Shankar, 2014). The dominance of
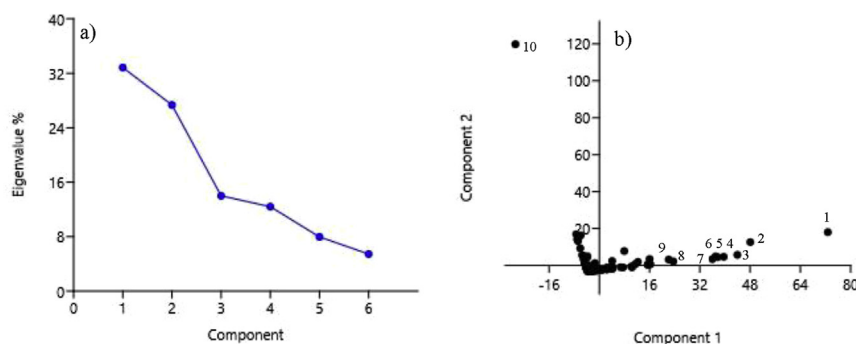

Fig. 8. A PCA ordination of species in lowland rainforest of Meghalaya: a) the scree plot of eigenvalues of the principal components, and b) the dispersion of species in two dimensional space of component 1 and component 2. The top ten species are numbered as: 1) *Macropanax undulatus*, 2) *Schima wallichii*, 3) *Castanopsis armata*, 4) *Symplocos sumuntia*, 5) *Castanopsis lanceifolia*, 6) *Itea macrophylla*, 7) *Syzygium tetragonum*, 8) *Helicia nilagirica*, 9) *Sarcosperma griffithii* and 10) *Boehmeria glomerulifera*.

phanerophytes in Meghalaya also conforms to findings in the equatorial rainforests of Malaya (Poore, 1968; Lee et al., 2002). However, Zhu (1997) found that liana phanerophytes attained higher proportions (up to one-fourth) in rainforests of Xishuangbanna. Although the seasonality of climate in Meghalaya is quite similar with that in Xishuangbanna, the quantity of annual rainfall is greater in the former than in the latter, which most likely promotes the dominance of mega- and mesophanerophytes.

Tropical rainforests are usually teeming with an abundance of species with a low frequency of occurrence (Pitman et al., 1999; Small et al., 2004). Previous research at Jengka revealed that certain species, including the most abundant ones, exhibited aggregation (Poore, 1968). For instance, all individuals of *Hopea griffithii* occurred within 100 m of each other. Many species are distributed nearly at random, and probably no species are uniformly dispersed. We found that in the rainforests of Meghalaya a large number of species showed aggregation. Abundance of species with high aggregation testifies to the fact that the rainforests contain plenty of rare species, which remain confined to specific microhabitats (subplots). Only a few species show moderate levels of dispersion in the forest. This is one of the reasons why 'rainforests appear similar in physiognomy, but differ in floristic composition'. This is also the reason why 'individuals-to-species ratio' is low in rainforests, which means the frequency of newer species added with increasing count of individuals is very high. In other words, beta diversity is high.

4.2. Familial dominance

The basic framework of the lowland rainforests of Meghalaya is strikingly similar to those near the equator (Poore, 1968; Proctor et al., 1983; Lee et al., 2004; Manokaran et al., 2004) and in Xishuangbanna (Zhu, 1997; Lan et al., 2012). The familial composition is predominantly tropical and many top-ranked families are similar, viz., Euphorbiaceae, Lauraceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae and Rubiaceae (Table 5). However, some conspicuous differences prevail. Dipterocarpaceae was predominant near the equator and in the Mengla plot in Xishuangbanna (Lan et al., 2012), but was absent in Meghalaya and in other plots in Xishuangbanna (Zhu, 1997; Lü et al., 2010). Dipterocarpaceae is present in some (Deb et al., 2009; Nath et al., 2005), but is absent in many patches of rainforests, both in northeastern India and in southwestern China.

Fagaceae occurs in most rainforests from the equator to the northern limits, but it was far more important (with third rank) in Meghalaya than in Xishuangbanna as well as near the equator. Fagaceae is absent from peninsular India, Islands of Andaman and Sri Lanka and appears east of Wallace's line principally in Indo-Burma, southern China and western Malesia (Ashton, 1988). The flora of Meghalaya is rich in Fagaceae with 15 species predominating in lower and upper montane forests between 1000 and 2000 m, although some species have previously been found to occur between 400 and 1000 m (Tripathi and Shankar, 2014).

The occurrence of Araliaceae, Theaceae, Urticaceae and Iteaceae, which rank 4, 5, 6, and 11, respectively, was distinct in Meghalaya. These families were probably absent or occurred in meagre quantities in both Xishuangbanna and in many other forests near the equator, including Jengka (Table 5), Batang Gadis (Kartawinata et al., 2004) and Wanariset (Kartawinata et al., 2008). In Meghalaya, Araliaceae is predominant in middle-canopy and Urticaceae in understory. This is not surprising as Theaceae (*S. wallichii*) has been known to predominate in upper-canopy and emergent strata in almost all forests of Meghalaya (Tripathi and Shankar, 2014, 2016) and other locations in northeastern India (Shankar et al., 1998). Theaceae may occur near the equator, but in meagre quantities. The

rainforests of Meghalaya also differed with rainforests of Jengka as well as Xishuangbanna in having much lesser importance of Annonaceae, Lecythidaceae (absent at Jengka), Burseraceae (absent at Xishuangbanna), Clusiaceae, Leguminosae, Sapindaceae and Ulmaceae (Table 5).

4.3. Patterns of species richness, stand density and basal area

The records of maximum species count emanate from the richest known equatorial lowland rainforests of Malaya Peninsula, Sumatra and Borneo between latitudes 0° and 4° N. Long-term vegetation dynamics studies in large-sized plots (up to 52 ha) as well as individual one-hectare plots of primary rainforests have revealed several instances of more than 200 tree species of ≥10 cm dbh in a hectare (Corlett, 2014). Lee et al. (2002) claimed the rainforests of Lambir Hills in Sarawak, Malaysia were the most diverse with 247 tree species per hectare (Table 6). However, Sukardjo et al. (1990) recorded 276 tree species in just a hectare from Sebulu, Indonesia. From studies in East Kalimantan, Indonesia, Kartawinata et al. (2008) claimed the rainforests of Malinau were the most species-rich and those of Wanariset Samboja the second highest species-rich in the world. Future exploration will likely provide ample opportunity for the revision of these records. The rainforests of Meghalaya exhibit only moderate levels of species richness in comparison to species-rich equatorial rainforests. Nonetheless, it is amply clear from Table 6 that: (1) the Islands of Sumatra and Borneo harbour the most species-rich equatorial dipterocarpus rainforests in the world; (2) moving away from the equator towards the Tropic of Cancer and beyond, richness of tree species declines in lowland rainforests; (3) the richness of tree species varies within a narrow range around the Tropic of Cancer and it is comparable between southwestern China and northeastern India; and (4) the maximum richness of large tree species (≥30 cm dbh) does probably occur in Lambir Hills and is followed by Jengka Forest Reserve, Malaysia with 375 species in 23 ha.

Among the most species-rich equatorial rainforests, stand density (ha^{-1}) of trees ≥10 cm dbh ranges between 422 and 778 (Table 6). In seasonal rainforests of southwestern China, the range is lower, from 386 to 617, and it varies from 478 to 858 for trees ≥5 cm dbh (Table 6). North of the Tropic of Cancer, lowland rainforests in northeastern India exhibit a range of 333−610, excluding a study from Deomali, which included individuals of smaller diameter (Table 6). A density of 467 trees ha^{-1} in rainforests of Meghalaya is lower in comparison to equatorial rainforests, but it is intermediate in the range for rainforests around the Tropic of Cancer. Interestingly, among all rainforests, the density of trees ≥10 cm dbh varies by less than two-fold only. Although limited datasets are available, the range of density of trees ≥30 cm dbh is also narrow, i.e., from 76 to 120 per hectare and the sites from Meghalaya crop up at the upper end of this range (Table 6).

The basal area (m^2 ha^{-1}) of trees ≥10 cm dbh ranges between 25.7 and 57 in equatorial rainforests, between 30 and 39 in seasonal rainforests of southwestern China, and between 26.1 and 49.7 in northeastern India (Table 6). Broadly, the basal area of trees ≥10 cm dbh varies by nearly two-fold. The basal area in rainforests of Meghalaya is on the lower side of the range of all rainforests. The exceptionally high values of basal area, reported from Deomali by Bhuyan et al. (2003) and from Namdapha by Nath et al. (2005) remain difficult to interpret, as the sampling methods of these studies appear to be unorthodox and inconsistent. Future studies should resolve these unrealistic figures. For large diameter trees (≥30 cm dbh), basal area ranges from 15.9 to 26.3 m^2 ha^{-1} and the sites from Meghalaya occur at the lower end of this range (Table 6). The large trees (≥30 cm dbh) contribute around two-thirds of the

Table 5
A comparison of top fifteen dominant families in lowland rainforest of Meghalaya with those of Xishuangbanna near the Tropic of Cancer and Jengka near the equator. The count of individuals ranked families at Jengka, because IVI values are not available for this site.

Family	Meghalaya, India (this study)		Xishuangbanna, China (Zhu, 1997)		Jengka, Malaysia (Poore, 1968)	
	IVI	Rank	IVI	Rank	Individuals	Rank
1. Lauraceae	29.4	1	39.1	1	43	16
2. Euphorbiaceae	27.4	2	23.3	5	155	4
3. Fagaceae	27.2	3	*present*	<20	41	18
4. Araliaceae	20.7	4	*	*	*absent*	*absent*
5. Theaceae	19.6	5	*	*	*absent*	*absent*
6. Urticaceae	15.6	6	*	*	*absent*	*absent*
7. Moraceae	10.6	7	26.4	2	82	9
8. Rubiaceae	10.0	8	11.6	9	13	<20
9. Myrtaceae	8.9	9	7.0	14	113	6
10. Meliaceae	7.1	10	16.9	6	18	<20
11. Iteaceae	5.9	11	*	*	*absent*	*absent*
12. Sapotaceae	5.9	12	*	*	56	12
13. Arecaceae	5.7	13	*	*	*absent*	*absent*
14. Bignoniaceae	5.7	14	*	*	4	<20
15. Polygalaceae	5.4	15	*	*	52	13
16. Leguminosae (Fabaceae)	*4.7*	*21*	7.7	13	174	3
17. Sapindaceae	*3.6*	*23*	15.0	7	44	15
18. Clusiaceae (Guttiferae)	*3.6*	*24*	11.3	10	33	<20
19. Burseraceae	*3.2*	*26*	*	*	370	2
20. Annonaceae	*2.6*	*30*	24.3	4	89	7
21. Myristicaceae	*2.3*	*32*	10.8	11	84	8
22. Rutaceae	*1.2*	*47*	5.0	15	*absent*	*absent*
23. Ulmaceae	*0.6*	*59*	26.1	3	1	<20
24. Lecythidaceae[#]	*absent*	*absent*	11.9[#]	8[#]	*absent*	*absent*
25. Datiscaceae	*absent*	*absent*	8.1	12	*absent*	*absent*
26. Dipterocarpaceae	*absent*	*absent*	*	*	771	1
27. Sterculiaceae	*absent*	*absent*	*	*	132	5

The * indicates 'probably absent or in meagre quantities'. #Includes Barringtoniaceae at Xishuangbanna.

basal area to the basal area of all trees ≥10 cm dbh. The proportional contribution of the basal area of large trees was comparable between Meghalaya (67.8%), Mengla (67.8%) and Lambir (69.6%), although it was slightly smaller at Pasoh (61.9%).

4.4. Patterns of diversity and equitability of abundances

A pattern of diversity, in terms of Shannon's entropy (H'), is visible along a gradient in latitude, from the equator to the northern limits (Table 6). The value of H' combines both species richness and equitability of abundance and it is not on a linear scale. For trees ≥10 cm dbh, equatorial rainforests exhibited maximum H' from Lambir Hills (5.96), which is followed by Pasoh (5.64). The value of H' declines towards northern limits and ranges between 3.5 and 4.0 in rainforests of southwestern China and northeastern India. In this study, H' was 4.25, which is maximum among all rainforests around the Tropic of Cancer, although values for some sites are not available (Table 6). A declining gradient in annual rainfall (5000 to 1500 mm) from the equator to the northern limits probably shapes the patterns of diversity, but excessively high quantity of rainfall (>5000 mm) in Meghalaya appears unutilized, as it does not contribute to enhance diversity and productivity of vegetation (Shankar et al., 1993).

The high value of H' for rainforests of Meghalaya is due to high equitability of species abundances. Clearly, low abundance of the most abundant species and nearly comparable abundance of the top four species distinguishes rainforests of Meghalaya from those in southwestern China wherein a single species is clearly dominant (Lü et al., 2010; Lan et al., 2012). The value of H' is also sensitive to the quantum of sampling area, as with an increase in area, the number of species increases and adds to the value of H'. The high values of H' from Lambir and Pasoh result from large plots (nearly 50 ha) and these values from the rainforests around Tropic of

Cancer result from nearly 1 to 2 ha only. Hence, these comparisons should be applied with prudence. For large trees ≥30 cm dbh, H' is smaller for Meghalaya compared to equatorial rainforests (Table 6).

The equitability of species abundances was marginally higher (Pielou's $E = 0.876$) in Meghalaya than at Jengka ($E = 0.850$). A comparison of rank-abundance plot between Meghalaya and Jengka exhibited striking similarity and followed a closely matching lognormal pattern of abundance distribution (Fig. 9). Presumably, with increased sampling efforts more species would be added to the list, resulting in a relatively moderate slope at the intermediate-to-tail region of the curve for Meghalaya, which would be in accord with the Jengka curve. Neither curve exhibits a 'tail off' phenomenon in the abundances of rare species that is common in tropical dry forest in Costa Rica, but not in tropical wet forest in Brazil (Hubbell, 1979). The lognormal abundance distributions prevail in closed, stable and undisturbed assemblages with a high proportion of species with intermediate abundances, i.e., an assemblage of 'a truly middle class' (Magurran and Henderson, 2003). The lognormal distributions indicate that an increasingly greater number of species is getting packed into the assemblage, with the result that more species inevitably random walk to rarity, increasing the risk of local extinction due to stochastic disturbance events (Hubbell, 1979).

For all individuals ≥10 cm in girth, compositional heterogeneity (β_w) of the rainforests of Meghalaya is 'high' and nearly 55.8% of species indicate a very high horizontal patchiness or turnover within the assemblage. The heterogeneity of a landscape is a function of the differentiation in species composition across samples and of the distances among the samples. Due to the lack of data from sites shown in Table 6, it is difficult to make comparisons. By Simpson's measure of D, the probability that the two trees drawn at random from the sample population belong to the same species is smaller at Jengka (1.2%) than in Meghalaya (5.1%).

Table 6
A comparison of phytosociological attributes of rainforests of Meghalaya with rainforests north of the Tropic of Cancer, rainforests near the Tropic of Cancer and equatorial rainforests.
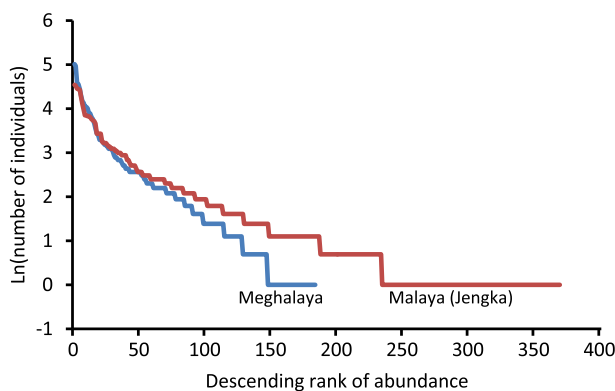
Site	DBH class (cm)	Area sampled (ha)	Species sampled (S)	Shannon's diversity index (H′)	Average per hectare		
					N	S	BA
North of the Tropic of Cancer (Northeastern India)							
Meghalaya, this study	≥10	2.45	133	4.25	467	89	26.1
Namdapha[1]	≥10	1	116	?	333	116	29.6
Namdapha[2]	≥10	2.4	77	3.36	610	?	98.6
Namdapha-Hornbill[3]	≥10	1.2	98	3.85	418	88	45.5
Namdapha-Gibbonland[3]	≥10	1	54	3.55	390	54	49.7
Deomali[4]	≥3.1	0.9	47	2.02	5452	?	104.6
Near the Tropic of Cancer (Southwestern China)							
Jinghong SRF[5]	≥10	1.04	125	?	386	120	30.03
Menglum[6]	≥10	1	106	4.08	393	106	30.2
Mengla[6]	≥10	1	94	3.93	423	94	39.7
Manyang[6]	≥10	1	84	3.45	467	84	31.3
Mengla[7]	≥10	20	339	?	617	123	36.6
Xishuangbanna SRF[8]	≥5	1.25	131	?	763	?	?
Xishuangbanna MRF[8]	≥5	1.46	140	?	478	?	?
Xishuangbanna DRF[8]	≥5	1.04	125	?	858	?	?
Tietahe[9]	≥5	1	145	?	730	145	31.3
Caiyanghe[9]	≥5	1	86	?	489	86	32.8
Equatorial rainforests of Asia-Pacific							
Sarawak Alluvial[10]	≥10	1	223	?	615	223	28.0
Sarawak Dipterocarp[10]	≥10	1	214	?	778	214	57.0
Sarawak Heath[10]	≥10	1	123	?	708	123	43.0
Sarawak Limestone[10]	≥10	1	73	?	644	74	37.0
Sarawak Lambir Hill[11]	≥10	52	1003	5.96	637	247	37.8
Pasoh, Malaysia[12]	≥10	50	678	5.64	531	206	25.7
Sebulu, Indonesia[13]	≥10	1	276	?	592	276	37.3
Bukit Lawang,Indonesia[14]	≥10	1	216	?	453	216	?
Kalimantan, Indonesia[15]	≥10	15	1298	?	584	218	?
Batang Gadis, Indonesia[16]	≥10	1	184	?	583	184	40.6
Wanariset, Indonesia[17]	≥10	10.5	553	?	557	?	33.3
Temburong, Brunei[18]	≥10	1	231	?	550	231	?
Kuala Belalong, Brunei[19]	≥10	1	197	?	422	197	31.4
Comparison of large diameter trees (≥30 cm dbh)							
Meghalaya, this study	≥30	2.45	59	3.55	107	44	17.7
Mengla, Xishuangbanna[9]	≥30	20	215	?	112	43	24.8
Lambir Hill, Sarawak[11]	≥30	52	574	5.25	119	67	26.3
Pasoh, Malaysia[12]	≥30	50	375	4.90	76	47	15.9
Jengka, Malaysia[20]	≥30	23	375	5.04	120	?	24.2
Jengka, Malaysia[21]	≥30	11.7	261	4.72	104	?	23.3

N is number of individuals, S is number of species, BA is basal area in m² ha⁻¹, H′ is Shannon's diversity index in *nats*, Some values of H′ were converted from *decs* to *nats* by multiplying with 2.302585,? means that the value cannot be deduced from the source study.
Sources: [1] Proctor et al. (1998), [2] Nath et al. (2005), [3] Deb et al. (2009), [4] Bhuyan et al. (2003), [5] Shanmughavel et al. (2001), [6] Lü et al. (2010), [7] Lan et al. (2012), [8] Zhu (1997), [9] Zheng et al. (2006),[10] Proctor et al. (1983), [11] Lee et al. (2004), [12] Manokaran et al. (2004), [13] Sukardjo et al. (1990), [14] Polosakan (2001), [15] Wilkie et al. (2004), [16] Kartawinata et al. (2004), [17] Kartawinata et al. (2008), [18] Poulsen et al. (1996), [19] Small et al. (2004), [20] Poore (1968), [21] Ho et al. (1987).

Fig. 9. A comparison of rank-abundance plots of lowland rainforest of Meghalaya (blue) with equatorial rainforest of Jengka (red). Both the curves are based on the count of individuals per species. For Jengka, data were obtained from Poore (1968).

5. Conclusions

This study reveals phytosociological attributes of lowland rainforests of Meghalaya, which are situated in the westernmost limits north of the Tropic of Cancer. The rainforests of Meghalaya differ with equatorial rainforests in low stature restricted to 30 m height, inconspicuous multi-layering in vertical stratification, paucity of lianas, absence of Dipterocarpaceae, prominence of Fagaceae and Theaceae, smaller basal area, and lower levels of alpha and gamma diversities. Although the floristic composition is largely native to the Indo-Malaya biogeographical realm, there are a negligible number of species endemic to the local geography. These differences are most likely due to increased seasonality of climate and relatively lower annual mean temperature. Exceptionally high quantities of rainfall do not add to the vigour of the rainforests of Meghalaya, presumably due to poor substratum and impoverished soils. Nonetheless, the rainforests of Meghalaya exhibit striking similarities to seasonal rainforests in southwestern China, exhibiting evergreen physiognomy interspersed by deciduous emergent trees, life-form spectrum, familial composition and levels of stem

densities and beta diversity. The equitability of species abundances appears greater in Meghalaya than in southwestern China, resulting in higher *H'*. These similarities are generally due to seasonal climate, which is broadly similar, i.e. Asia-Pacific monsoon-dependent around the Tropic of Cancer. The rainforests in Namdapha and Deomali in northeastern India differ from the rainforests of Meghalaya in harbouring Dipterocarpaceae, larger basal area and lower equitability of species abundances. The rainforests of Meghalaya survive largely due to community-based conservation practices. The local tribes have a rich culture of preserving forests as 'sacred groves' not only in inaccessible pockets, but also in the vicinity of hamlets. Enquiries with locals reveal that the rainforests have remained free from grazing, fire and commercial logging, and strong anecdotal religious beliefs and taboos continue to remain popular among the tribes. Government control of forest landholding is minimal and hence legal intervention is not possible. As long as anthropogenic disturbances are under control, the rainforests of Meghalaya shall survive.

Acknowledgements

References

APG III, 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants, APG III. Bot. J. Linn. Soc. 161 (2), 105–121. http://dx.doi.org/10.1111/j.1095-8339.2009.00996.x.

Ashton, P.S., 1988. Dipterocarp biology as a window to the understanding of tropical forest structure. Ann. Rev. Ecol. Syst. 19, 347–370.

Audley-Charles, M.G., 1987. Dispersal of Gondwanaland, relevance to evolution of the angiosperms. In: Whitmore, T.C. (Ed.), Biogeographical Evolution of the Malay Archipelago. Clarendon Press, Oxford, pp. 5–21.

Balakrishnan, N.P., 1981-1983. Flora of Jowai and Vicinity, Meghalaya, vols. I & II. Botanical Survey of India, Howrah, India.

Bhuyan, P., Khan, M.L., Tripathi, R.S., 2003. Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas, India. Biodivers. Conserv. 12, 1753–1773.

Brown, J.H., 2014. Why are there so many species in the tropics? J. Biogeogr. 41, 8–22.

Champion, H.G., Seth, S.K., 1968. A Revised Survey of the Forest Types of India. Government of India, New Delhi.

Corlett, R.T., 2009. The Ecology of Tropical East Asia. Oxford University Press, Oxford, UK.

Corlett, R.T., 2014. The Ecology of Tropical East Asia, second ed. Oxford U.P., UK, p. 336.

Corlett, R.T., Primack, R.B., 2011. Tropical Rain Forests, an Ecological and Biogeographical Comparison, second ed. Wiley-Blackwell, USA, p. 336.

Curtis, J.T., McIntosh, R.P., 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31, 435–455.

Davis, J., 1960. The forests of Burma. Department of Botany, University of Florida, p. 23.

Deb, P., Sundriyal, R.C., Shankar, Uma, 2009. Tree diversity and population structure in a lowland tropical rainforest in the eastern Himalayas, India. Ind. For 135, 1526–1544.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST, paleontological statistics software package for education and data analysis. Palaeontola Electron 41, 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Haridasan, K., Rao, R.R., 1985-1987. Forest flora of Meghalaya, vols. I & II. Bishen Singh Mahendra Pal Singh, Dehra Dun, India.

Harrison, S., Ross, S.J., Lawton, J.H., 1992. Beta diversity on geographic gradients in Britain. J. Anim. Ecol. 61, 151–158.

Ho, C.C., Newbery, McC., Poore, M.E.D., 1987. Forest composition and inferred dynamics in Jengka forest Reserve, Malaysia. J. Trop. For. Sci. 3, 25–56.

Hooker, J.D., 1854. The Himalayan Journals, Notes of a Naturalist in Bengal, the Sikkim and Nepal Himalayas, the Khasia Mountains etc, vol. 2. John Murray, Albemarle Street, London.

Hooker, J.D., 1872-1897. Flora of British India, vols. I–VII. L. Reeve and Company, London.

Hou, H.Y., 1979. The Vegetation Map of China. Chinese Academy of Sciences, Institute of Botany, Peking.

Hubbell, S.P., 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203, 1299–1309.

Jamir, S.A., Pandey, H.N., 2003. Vascular plant diversity in the sacred groves of Jaintia Hills in northeast India. Biodivers. Conserv. 12, 1497–1510.

Kanjilal, U.N., Kanjilal, P.C., Das, A., 1934-1940. Flora of Assam, vols. I–IV. Government of Assam, India.

Kartawinata, K., Samsoedin, I., Heriyanto, M., Afriastini, J.J., 2004. A tree species inventory in a one-hectare plot at the Batang Gadis National Park, North Sumatra, Indonesia. Reinwardtia 12, 129–204.

Kartawinata, K., Purwaningsih, Partomihardjo T., Yusuf, R., Abdulhadi, R., Riswan, S., 2008. Floristics and structure of a lowland dipterocarp forest at Wanariset Samboja, East Kalimantan, Indonesia. Reinwardtia 12 (4), 301–323.

Kaul, R.N., Haridasan, K., 1987. Forest types of Arunachal Pradesh – a preliminary study. J. Econ. Taxon. Bot. 9, 379–389.

Khiewtam, R.S., Ramakrishnan, P.S., 1993. Litter and fine root dynamics of relic sacred grove forest of Cherrapunjee in northeastern India. For. Ecol. Manage 60, 327–344.

Kingdon-Ward, F., 1945. A sketch of the botany and geography of north Burma. J. Bombay Nat. Hist. Soc. 45, 16–30.

Lan, G., Zhu, H., Cao, M., 2012. Tree species diversity of a 20-ha plot in a tropical seasonal rainforest in Xishuangbanna, Southwest China. J. For. Res. 17, 432–439.

Lee, H.S., Davies, S.J., Lafrankie, J.V., Tan, S., Yamakura, T., Itoh, A., Ohkubo, T., Ashton, P.S., 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir hills National Park, Sarawak, Malaysia. J. Trop. For. Sci. 14, 379–400.

Lee, H.S., Sylvester, T., Davies, S.J., Lafrankie, J.V., Ashton, P.S., Yamakura, T., Itoh, A., Ohkubo, T., Harrison, R., 2004. In: Losos, E.C., Leigh, E.G. (Eds.), Lambir Forest Dynamics Plot, Sarawak, Malaysia. Tropical Forest Diversity and Dynamism: Findings from a Large-scale Plot Network. University of Chicago Press, Chicago, pp. 527–539.

Lü, X.T., Yin, J.X., Tang, J.W., 2010. Structure, tree species diversity and composition of tropical seasonal rainforests in Xishuangbanna, South-west China. J. Trop. For. Sci. 22, 260–270.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, New Jersey, USA.

Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422 (6933), 714–716. http://dx.doi.org/10.1038/nature01547.

Manokaran, N., Seng, Q.E., Ashton, P.S., et al., 2004. Pasoh forest dynamics Plot, Peninsular Malaysia. In: Losos, E.C., Leigh, E.G. (Eds.), Lambir Forest Dynamics Plot, Sarawak, Malaysia. Tropical Forest Diversity and Dynamism: Findings from a Large-scale Plot Network. University of Chicago Press, Chicago, pp. 585–598.

Meng, J., Lu, Y., Lei, X., Liu, G., 2011. Structure and floristics of tropical forests and their implications for restoration of degraded forests of China's Hainan Island. Trop. Ecol. 52, 177–191.

Muller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, Inc.

Murali, K.S., Shankar, Uma, Uma Shaanker, R., Ganeshaiah, K.N., Bawa, K.S., 1996. Extraction of non-timber forest products in the forest of Biligiri Rangan Hills, India. 2. Impact of NTFP extraction on regeneration, population structure and species composition. Econ. Bot. 50, 252–269.

Myers, N., 2003. Biodiversity hotspots revisited. BioScience 53, 916–917.

Nath, P.C., Arunachalam, A., Khan, M.L., Arunachalam, K., Barbhuiya, A.R., 2005. Vegetation analysis and tree population structure of tropical wet evergreen forests in and around Namdapha National Park, Northeast India. Biodivers. Conserv. 14, 2109–2136.

Pielou, E.C., 1975. Ecological Diversity. Wiley, New York.

Pitman, N.C.A., Terbirgh, J., Silman, M.R., Nunez, V.P., 1999. Tree species distribution in an upper Amazonian forest. Ecology 80, 2651–2661.

Polosakan, R., 2001. Komposisi jenis pohon di hutan kawasan Taman Nasional Bukit Tigapuluh, Propinsi Riau. In: Sunaryo, et al. (Eds.), Laporan Teknik 2001. LIPI, Bogor, pp. 31–40. Proyek Inventarisasi Dan Karakterisasi Sumberdaya Hayati, Pusat Penelitian Biologi.

Poore, M.E.D., 1968. Studies in Malaysian rain forest, I. The forest on Triassic Sediments in Jengka forest Reserve. J. Ecol. 56, 143–196.

Poulsen, A.D., Neilsen, I.C., Tan, S., Balslev, H., 1996. A quantitative inventory of trees in one hectare of mixed dipterocarp forest in Temburong, Brunei Darussalam.

In: Edwards, D.S., Booth, W.E., Choy, S. (Eds.), Tropical Rainforest Research: Current Issues. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 139–150.

Proctor, J., Anderson, J.M., Chai, P., Vallack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: I. Forest environment, structure and floristics. J. Ecol. 71, 237–260.

Proctor, J., Haridasan, K., Smith, G.W., 1998. How far north does lowland evergreen tropical rain forest go? Glob. Ecol. Biogeogr. Lett. 7, 141–146.

Ramakrishnan, P.S., 2001. Ecology and Sustainable Development. National Book Trust, India, p. 198.

Raunkiaer, C., 1934. The Life Forms of Plants and Statistical Plant Geography. Clarendon Press, Oxford.

Shankar, Uma, 2001. A case of high tree diversity in sal (*Shorea robusta*-dominated lowland forest of eastern Himalaya, floristic composition, regeneration and conservation. Curr. Sci. 81, 776–786.

Shankar, Uma, Tripathi, R.S., Pandey, H.N., 1991. Structure and seasonal dynamics of humid tropical grasslands in Meghalaya, India. J. Veg. Sci. 2, 711–714.

Shankar, Uma, Pandey, H.N., Tripathi, R.S., 1993. Phytomass dynamics and primary productivity in humid grasslands along altitudinal and rainfall gradients. Acta Oecol 14, 197–209.

Shankar, Uma, Lama, S.D., Bawa, K.S., 1998. Ecosystem reconstruction through 'taungya' plantations following commercial logging of a dry, mixed deciduous forest in Darjeeling Himalaya. For. Ecol. Manage. 102, 131–142.

Shanmughavel, P., Zheng, Z., Liqing, S., Min, C., 2001. Floristic structure and biomass distribution of a tropical seasonal rain forest in Xishuangbanna, southwest China. Biomass Bioenergy 21, 165–175.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423 and 623–656.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Small, A., Martin, T.G., Kitching, R.L., Wong, K.M., 2004. Contribution of tree species to the biodiversity of a 1 ha Old World rainforest in Brunei, Borneo. Biodivers. Conserv. 13, 2067–2088.

Soja, R., Starkel, L., 2006. Extreme rainfalls in Eastern Himalaya and southern slope of Meghalaya Plateau and their geomorphologic impacts. Geomorphology 84, 170–180.

Sukardjo, S., Hagihara, A., Yamakura, T., Ogawa, H., 1990. Floristic composition of a tropical rain forest in Indonesian Borneo. Bull. Nogoya Univ. For. 10, 1–44.

The Plant List 2013. Version 1.1. Published on the Internet; http//www.theplantlist.org/(Accessed 10 July 2014).

Tripathi, A.K., Shankar, Uma, 2014. Patterns of species dominance, diversity and dispersion in 'Khasi hill sal' forest ecosystem in northeast India. For. Ecosyst. 1, 23. http://dx.doi.org/10.1186/s40663-014-0023-2.

Tripathi, A.K., Shankar, Uma, 2016. Rainforests North of the Tropic of Cancer: Recovery Patterns 40-years after Shifting Cultivation in Lowland Rainforests of Meghalaya In Review.

Tripathi, O.P., Pandey, H.N., Tripathi, R.S., 2003. Distribution, community characteristics and tree population structure of subtropical pine forest of Meghalaya, northeast India. Int. J. Ecol. Env. Sci. 29, 207–214.

Upadhaya, K., Pandey, H.N., Law, P.S., Tripathi, R.S., 2003. Tree diversity in sacred groves of Jaintia Hills in Meghalaya, northeast India. Biodivers. Conserv. 12, 583–597.

Whitmore, T.C., 1984. Tropical Rain Forests of the Far East, second ed. Clarendon Press, Oxford, p. 352.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.

Wilkie, P., Argent, G.C.G., Campbell, E.J.F., Saridan, A., 2004. The diversity of 15 ha of lowland mixed dipterocarp forest, Central Kalimantan. Biodivers. Conserv. 13, 695–708.

WMO, 2014. Cherrapunji, India, Holds New Record for 48-hour Rainfall. Press Release No. 988. World Meteorological Organization, Switzerland. http://www.wmo.int/pages/mediacentre/news/index_en.html.

Wu, C.Y., 1980. Vegetation of China. Beijing Science Press, Beijing, pp. 363–379 in Chinese.

Zheng, Z., Feng, Z., Cao, M., Li, Z., Zhang, J., 2006. Forest structure and biomass of a tropical seasonal rain forest in Xishuangbanna, southwest China. Biotropica 38, 318–327.

Zhu, H., 1997. Ecological and biogeographical studies on the tropical rain forest of south Yunnan, SW China with a special reference to its relation with rain forests of tropical Asia. J. Biogeogr. 24, 647–662.