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Structure of tree communities and their association with soil properties in two fan-palm dominated forests of east coast Peninsular Malaysia

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Abstract: Structure of tree communities and their association with soil properties were investigated in two fan-palm dominated forests at Pahang and Terengganu States of Peninsular Malaysia. Tree species inventory was conducted in one-hectare plots at Endau Rompin State Park (ERSP), Pahang, and at Bukit Bauk Forest Reserve (BBFR), Terengganu, whilst soil sampling was made in 25 selected subplots within 1-ha plot. A total of 1,644 trees of ≥ 5 cm in diameter were enumerated in the 1-ha plot at the ERSP site, while 1,320 trees were surveyed at BBFR site. Enumerated trees at the ERSP comprised 334 species representing 150 genera from 55 families whilst BBFR recorded 100 tree species in 71 genera and 37 families. The most speciose family at ERSP was Myrtaceae (26 species) and at BBFR, Guttiferae and Euphorbiaceae (8 species) were the most species-rich families. At ERSP, the most important species based on the highest importance value (*IVI*) was *Elateriospermum tapos* (Euphorbiaceae) with *IVI* of 1.98 %, while in BBFR *Parishia paucijuga* (Anacardiaceae) was the most important species with *IVI* of 12.13 %. Soil analyses of both study sites showed substantial variation in soil properties. A floristic compositional pattern was observed among all surveyed subplots which were correlated to the edaphic variables as revealed by canonical correspondence analysis. The results indicate that soil factors may play an important role in distribution and beta diversity of plants at the study sites.

Resumen: Se investigó la estructura de las comunidades de árboles y su asociación con propiedades del suelo en dos bosques dominados por palmas de hojas de abanico en los estados Pahang y Terengganu de la porción peninsular de Malasia. Se llevó a cabo el inventario de especies arbóreas en parcelas de 1 ha en el Parque Estatal Endau Rompin (ERSP, siglas en inglés), Pahang, y en la Reserva Forestal Bukit Bauk (BBFR, siglas en inglés), Terengganu; el suelo fue muestreado en 25 subcuadros seleccionados dentro de la parcela de 1 ha. En total se enumeraron 1,644 árboles con diámetro ≥ 5 cm en la parcela de 1 ha en el sitio ERSP, y 1,320 árboles en el sitio BBFR. Los árboles registrados en el ERSP abarcaron 334 especies que representaron 150 géneros y 55 familias, mientras que en BBFR se registraron 100 especies de árboles distribuidos en 71 géneros y 37 familias. La familia con mayor riqueza de especies en el ERSP fue Myrtaceae (26 especies), y en BBFR Guttiferae y Euphorbiaceae (8 especies) fueron las familias con más especies. En el ERSP, la especie más importante de acuerdo con el valor de importancia (*IVI*) fue *Elateriospermum tapos* (Euphorbiaceae), con un *IVI* de 1.98 %, mientras que en BBFR P*arishia paucijuga* (Anacardiaceae) fue la especie más importante con un *IVI* de 12.13 %. Los análisis del suelo de los dos sitios de estudio mostraron una variación sustancial en las propiedades edáficas. Se observó un patrón en la composición florística entre todos los subcuadros muestreados, los cuales estuvieron correlacionados con las variables edáficas, cono lo mistró el análisis canónico de correspondencias. Los resultados indican que los factores del suelo pueden jugar un papel importante en la distribución y la diversidad beta de las plantas en los sitios de estudio.

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Resumo: Investigou-se a estrutura das comunidades arbóreas e a sua associação com as propriedades do solo em duas florestas dominadas pela palmeira de leque nos estados de Pahang e Terengganu na península da Malásia. Conduziu-se um inventário das espécies arbóreas em talhões de um hectare no Parque Estatal de Endau Rompim (ERSP), Pahang e na Reserva Florestal de Bukit Bauk (BBFR), Terengganu, enquanto que as amostras de solo foram recolhidas em 25 sub-talhões selecionados nos talhões de 1 ha. No talhão de 1 ha em ERSP foram enumeradas um total de 1.644 árvores com diâmetro ≥ a 5 cm, enquanto que em BBFR foram inventariadas 1.320. As árvores enumeradas em ERSP compreenderam 334 espécies representando 150 géneros de 50 famílias enquanto que em BBFR se registaram 100 espécies arbóreas em 71 géneros e 37 famílias. As Myrtaceae (26 espécies) eram a família mais representativa em ERSP sendo as Guttiferae e Euphorbiaceae (8 espécies) as famílias com as espécies mais abundantes em BBFR. Em ERSP, a espécie mais importante na base das que apresentam o maior valor (*IVI*) foi a *Elateriospermum tapos* (Euphorbiaceae) com *IVI* de 1,98 % enquanto que em BBFR a *Parishia paucijuga* (Anacardiaceae) foi espécie mais importante com um *IVI* de 12,13 %. As análises de solos de ambas as estações mostraram um variação substancial nas propriedades dos solos. Entre todas as sub-parcelas amostradas observou-se um padrão de composição florística o qual estava correlacionado com as variáveis edáficas, tal como se evidenciou por uma análise de correspondências canónicas. Os resultados indicam que os factores de solo podem desempenhar um papel importante na distribuição e diversidade beta das plantas nas estações estudadas.

Key words: Canonical correspondence analysis, edaphic factors, floristic pattern, species composition, vegetation-environment relationship.

Introduction

Tree species diversity in tropical forest varies greatly from place to place mainly due to variation in biogeography, habitat and disturbance (Whitmore 1998). The variation in terms of floristic and environmental properties that contributes to the structural pattern and characteristics of tropical forests has been reported in many studies (e.g. Jose *et al.* 1996; Poulsen *et al.* 2006; Tripathi & Singh 2009). Many studies conducted in different parts of the tropics stressed the importance of environmental factors, especially soil properties, for plant species distributions. For instance, edaphic gradients were found to be important for the distribution of trees at large scale (Baillie *et al.* 1987; Phillips *et al.* 2003; Pyke *et al.* 2001), whilst at smaller scales (< 1 km^2), occurrence and distribution of tree species clearly indicate the influence of soil and topography (Lieberman *et al.* 1985; Webb & Peart 2000) Moreover, an extensive survey by Baillie *et al.* (1987) in Sarawak, East Malaysia, suggested the role of edaphic factors, particularly reserve nutrients, in determining the distribution of Dipterocarpaceae. Prior to Baillie *et al.* (1987) survey, Newbery & Proctor (1984) looked at differences in floristic composition within four 1-ha plots in Mulu, Sarawak, which might be related to changing edaphic conditions within each plot. They reported that differences were found for the alluvial and heath forest plots, but not for the dipterocarp and limestone plots. Their study revealed that differences in soil chemistry were associated with floristic changes. Information on such relationships of tree species and its soil properties is necessary for understanding the response of rain forest ecosystems to natural and anthropogenic perturbations, for the selection of suitable native species for reforestation of degraded areas, and for sustainable forest management.

The forests at Bukit Bauk FR (BBFR) and Endau Rompin State Park (ERSP) are situated in the east coast states of Terengganu and Pahang, respectively, that are comprised of lowland to hill dipterocarp forests. These forests are unique because of the abundance of fan-palm species of *Livistona endauensis* and *Johannesteijsmannia altifrons* on the forest floor, as such the forests are called as fan-palm forests. The *L. endauensis* which is known locally as Serdang, is a gregarious fan-palm to 15 m tall while *J. altifrons,* known as

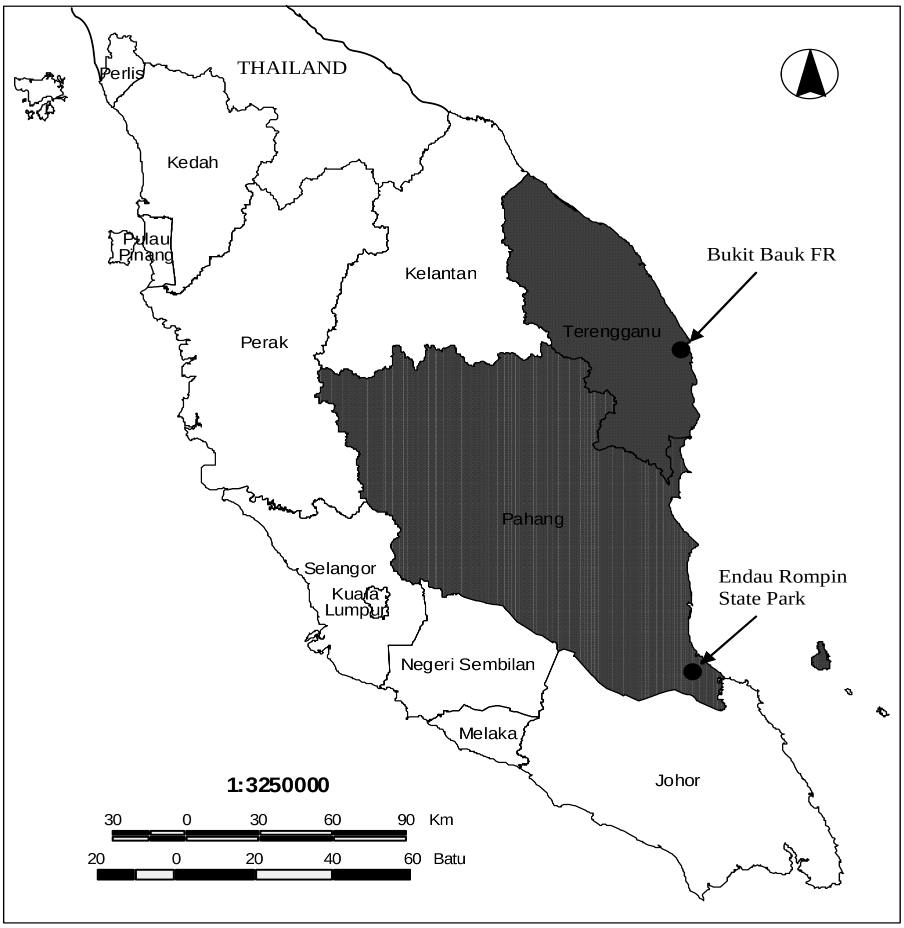


Fig. 1. Map of Peninsular Malaysia showing the location of Bukit Bauk Forest Reserve (BBFR), Terengganu and Endau Rompin State Park (ERSP), Pahang.

Daun Payong, can reach 6 m tall. Both the species occur abundantly at both sites (Jeffri 2005). As both study areas are characteristically abundant in palm communities, we hypothesized that the characteristics of its soil environment are perhaps similar, which would also reflect in terms of its tree communities. Thus, this paper attempts to describe structure of tree communities of the forests and also to assess the variability in soil properties between the areas, subsequently to look at associations of tree communities with soil properties.

Material and methods

Study area and tree community survey

The first study area was at Endau Rompin State Park (ERSP), Pahang, which covers a total area of 31797 ha (Fig. 1). A 1-ha study plot (250 m x 40 m) was established at 350 m above sea level (a.s.l.), and positioned at latitude of 02° 37' 16" N to 02° 37' 22" N and longitude 103° 21' 31" E to 103° 21' 38" E. The second study area was at Bukit Bauk Forest Reserve (BBFR), Terengganu, which is located at the south end of the East Coast Range that covers a total area of 7596 ha. At the BBFR, compartment 11A was chosen as the study site, and a one-hectare plot was established at an altitude of 325 m a.s.l, and positioned at 04° 42'11" to 04° 42'17" N and 103° 24' 6' to 103° 24' 13" E. The topography of the plot indicates that slopes ranged from 0°- 60°.

In the one-hectare plot at each study site, 100 subplots of 10 m x 10 m were constructed to enable systematic tree sampling. In each subplot, all trees with diameter at breast height (dbh) of 5.0 cm and above were tagged and manually measured using the diameter tape at approximately 1.3 m above the ground. All specimens of each measured tree were collected for the preparation of voucher specimens and species identification. The identification of the specimens was made possible using keys in the *Tree Flora of Malaya* (Ng 1978, 1989; Whitmore 1972, 1973). The voucher specimens are deposited in the Universiti Kebangsaan Malaysia Herbarium (UKMB).

Soil sampling and analysis

Twenty-five subplots of 10 m x 10 m within each one-hectare plot were selected randomly for determination of soil physical and chemical properties. The selection of these subplots is sufficient to represent the characteristics of soils in the study plot. Three topsoil samples (0 - 20 cm depth) were taken randomly in the selected subplots and the samples were air-dried in the field and stored in polythene bags until they were analysed in the laboratory for analyses of physical and chemical properties.

Prior to analyses, three soil samples of each subplot were bulked together to represent soil sample for the subplot. The soil analyses involved determination of particle size distribution following pipette method together with dry sieving (Abdulla 1966). Organic matter content was determined by loss-on-ignition method, igniting soils for 16 h at 400 °C (Avery & Bascomb 1982), whilst soil pH was measured using pH meter in soil : water ratio of 1:2.5 (Metson 1956). Soils were extracted with 1 M KCl for exchangeable acidic cations (Al^{3+} and H^+), which were determined by titration. As for exchangeable base cations (K^+, Na^+, Ca^{2+} and Mg^{2+}), the soil samples were extracted in 1 M ammonium acetate, and the extract was determined by Atomic Absorption Spectrophotometer (FAAS) Model 3300 Perkin-Elmer. Available macronutrients and micronutrients in soil were extracted using 1 M ammonium acetate-acetic acid; the extract was run under the UV spectro-photometer for determination of phosphorus, whilst the availability of K, Mg, Cu, Fe, Mn and Zn in the extracts was determined using Atomic Absorption Spectrophotometer (AAS) Model 3300 Perkin Elmer. Differences in soil parameters between study plots were tested statistically using *t*-test.

Data analysis

All trees enumerated in the 1-ha plots were identified, and basal area, density and frequency of occurrence of each species were calculated. Tree basal area (BA) was calculated using the equation as follows:

$$BA = [\pi \times (d^2)/40000] \text{ (unit: m}^2\text{)},$$

where, d is the diameter at breast height and π=3.142.

Shannon-Wiener Diversity Index (*H'*) (Shannon & Weaver 1949) and Importance Value Index (*IVI*) were calculated to determine species diversity and species importance, respectively, of the study areas. The *IVI* was calculated by summing up the values of relative density (R_D), relative dominance (based on basal area) (R_B), and relative frequency (R_F) of each species or family [$IVI = (R_D + R_B + R_F)/3$] (Brower *et al.* 1997); whilst the Shannon-Wiener Diversity Index (*H'*) was calculated using formula:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where, s = the number of species; p_i = the proportion of the total number of individuals that belong to species i ($p_i = \frac{n_i}{N}$; where, n_i is the number of individuals of species i; N is the total number of all individuals); ln = log base e. Community similarity between the two study areas was determined using the Sörensen's Similarity Index (S_s) as follows:

Sörensen's Similarity Index, $S_s = \frac{2a}{2a+b+c} \times 100$ (Kent & Coker 1992),

where, a - Number of species common to Site ERSP and BBFR

b - Number of species occurring in Site ERSP only

c - Number of species occurring in Site BBFR only

Patterns of tree species composition in relation to the measured soil variables were analysed using canonical correspondence analysis (CCA) (ter Braak & Prentice 1988; ter Braak 1992), which were performed using CANOCO version 4.0 (ter Braak & Šmilauer 1998). The use of CCA, which is a direct gradient analysis method, is appropriate because the data had been tested with Detrended Correspondence Analysis (DCA) to confirm that the data were unimodal with gradient length of 3.566, that is greater than 3.0 (Leps & Smilaeur 2003). Data on tree species composition of the 25 selected subplots from where soil samples were collected at each site, were used together with the soil data obtained in the subplots. Species with only one entry in the data matrix were deleted to increase the reliability of the results (Baruch 2005). Analyses were performed on the matrix of the selected species by seven environmental variables, namely, slope, soil pH, potassium (K) content, available phosphorus (P), organic matter content, ammonium-N and nitrate-N. The significance of each edaphic variable in determining the species compositional changes was assessed through a Monte Carlo permutation test based on 499 random trials at 0.05 significance level (ter Braak 1990).

Results and discussion

Tree species composition

A total of 1,644 trees with dbh of 5 cm and above, representing 334 species in 150 genera from 55 families, were enumerated in the 1-ha plot at the ERSP site, while 1,320 trees representing 100 species in 71 genera from 37 families were enumerated at the BBFR study site. Both study sites showed domination of palm species of *Livistona endauensis* and *Johannesteijsmannia altifrons* whereby in the 1-ha plot at the ERSP, 319 individuals of *L. endauensis* and 83 individuals of *J. altifrons* were recorded. At BBFR, a large number of 1,430 individuals of *L. endauensis* were recorded, however, no individual of *J. altifrons* was present.

Table 1 lists all tree families, number of genera and species that occurred at both sites. It is apparent that out of 56 families listed, 36 families were represented at both study areas, 19 families present at the ERSP plot, whilst only one family, i.e. Podocarpaceae, was exclusively present at the BBFR study site. This indicates a high similarity in terms of family composition between the study areas with Sörensen similarity index (S_s) of 78.3 %. However, further similarity analysis on the species composition of both sites revealed that the similarity of tree species composition between the sites was low with S_s value of 30.2 %. This is because the ERSP contained more than three fold of species richness compared to the BBFR, and majority of species occurred only at the ERSP. Nevertheless, both sites indicate high species number per hectare and the results agree with reports of Clark & Clark (1996) and Gentry (1990) who stated that the number of tree species in the tropical forests is extremely high, commonly passing 100 species per hectare. Zakaria *et al.* (2009), reported high diversity of woody plant species (359 species) at Penang Forest Reserve, Malaysia. The most speciose family at ERSP was Myrtaceae with 26 species i.e 7.8 % of the total number of species occurred in the plot (Table 1). The second most speciose family was Dipterocarpaceae with 24 species (7.2 %) followed by Anacardiaceae of 22 species (6.6 %). The most speciose family at the BBFR site was Guttiferae and Euphorbiaceae, which comprised eight species each (8 %). The next largest families were Myrtaceae and Ebenaceae both represented by seven species (7 %).

Abundance

Study plot at the ERSP had high tree density of 1,644 individuals ha^{-1}, compared to 1,320 individuals ha^{-1} at the BBFR plot. Both the forest areas contained high density of trees ha^{-1} and this is not surprising because it is a characteristic feature of tropical rain forests as also reported in several previous studies (Huang *et al.* 2003; Swaine *et al.* 1987). It is apparent that density of trees in tropical forests shows high variation which depends on various factors. Richards (1952) recognized the factors that control tree density to be the effects of natural and anthropogenic disturbance and soil condition of the forests.

At family level, the highest tree density of the ERSP plot was represented by the Dipterocarpaceae of 262 trees ha^{-1}, followed by Guttiferae and Euphorbiaceae of 143 trees ha^{-1} and 129 trees ha^{-1}, respectively (Table 1). As for the BBFR site, Anacardiaceae was the most dense with 295 trees in the 1-ha plot, whilst Guttiferae (216 trees ha^{-1}) and Dipterocarpaceae (108 trees ha^{-1}) scored the second and third highest density, respectively. Species-wise, *Dryobalanops aromatica* (Dipterocarpaceae) was the highest density at the ERSP with 51 trees ha^{-1} and represented 3.1 % of total trees in the study plot. Dipterocarpaceae had the highest density at the ERSP, thus the species from this family obviously dominated the tree stratum where the second and the third most abundant species of the area were from this family, i.e. *Cotylelobium lanceolatum* occurred with 44 trees ha^{-1} whilst the *Shorea blumutensis* with 40 trees ha^{-1} (Table 2). At the BBFR, *Parishia paucijuga* (Anacardiaceae) had the highest density with 290 trees ha^{-1} (22.0 % of the total stand) followed by *Hopea pubescens* (Dipterocarpaceae) and *Calophyllum symingtonianum* (Guttiferae) with 85 and 81 trees ha^{-1}, respectively (Table 2).

Total basal area (BA) for all trees in the ERSP study plot was 48.6 m^2 ha^{-1}. Conversely, the BA for trees in BBFR study plot is very much lower with just 25.3 m^2 ha^{-1}. The low value of basal area at BBFR is because trees in this study area were mainly small in size and none of the trees was

Table 1. List of families, number of genera, species and density of trees ≥ 5 cm in 1-ha study plot at Endau Rompin State Park (ERSP), Pahang, and Bukit Bauk Forest Reserve (BBFR), Terengganu, Malaysia.

Family	ERSP			BBFR		
	No. Genus	No. Species	No. Stems	No. Genus	No. Species	No. Stems
Actinidiaceae	1	1	9	-	-	-
Anacardiaceae	8	22	97	4	5	295
Anisophylleaceae	1	3	10	-	-	-
Annonaceae	8	14	54	3	3	23
Apocynaceae	1	1	4	-	-	-
Bignoniaceae	1	1	1	-	-	-
Bombacaceae	2	4	10	-	-	-
Burseraceae	3	12	77	2	2	14
Caprifoliaceae	1	1	1	-	-	-
Celastraceae	4	6	46	-	-	-
Chrysobalanaceae	2	2	15	3	3	30
Cornaceae	1	2	4	1	1	1
Crypteroniaceae	1	1	1	-	-	-
Ctenolophonaceae	1	1	6	1	1	11
Dilleniaceae	1	3	4	-	-	-
Dipterocarpaceae	9	24	262	3	4	108
Ebenaceae	1	15	57	1	7	47
Elaeocarpaceae	1	5	8	-	-	-
Euphorbiaceae	15	21	129	8	8	49
Fagaceae	2	8	12	2	2	69
Flacourtiaceae	3	6	41	1	1	5
Guttiferae	4	20	143	3	8	216
Icacinaceae	1	2	9	1	2	5
Irvingiaceae	1	1	2	-	-	-
Ixonanthaceae	1	1	1	1	2	3
Lauraceae	9	15	63	4	5	41
Lecythidaceae	1	1	30	1	2	23
Leguminosae	8	9	31	2	2	5
Magnoliaceae	1	2	3	-	-	-
Melastomataceae	2	8	62	2	3	13
Meliaceae	5	10	17	1	1	8
Moraceae	1	4	10	2	3	27
Myristicaceae	3	9	46	3	6	30
Myrsinaceae	1	2	10	1	1	12
Myrtaceae	2	26	119	2	7	69
Ochnaceae	1	1	2	1	1	9
Olacaceae	3	3	6	1	1	1
Oxalidaceae	1	2	10	-	-	-
Podocarpaceae	-	-	-	1	1	21
Polygalaceae	1	5	34	1	1	5

Contd...

Table 1. Continued.

Family	ERSP			BBFR		
	No. Genus	No. Species	No. Stems	No. Genus	No. Species	No. Stems
Proteaceae	1	1	1	-	-	-
Rhizophoraceae	3	3	21	-	-	-
Rosaceae	1	4	12	1	1	1
Rubiaceae	9	11	24	2	2	29
Rutaceae	1	1	3	-	-	-
Santalaceae	1	1	1	-	-	-
Sapindaceae	4	4	10	1	1	9
Sapotaceae	3	10	67	3	4	33
Simaroubaceae	1	1	1	1	1	7
Sterculiaceae	3	6	13	2	2	8
Symplocaceae	1	4	13	1	2	22
Theaceae	2	4	9	2	2	38
Thymelaeaceae	1	1	1	1	1	11
Tiliaceae	3	5	14	-	-	-
Ulmaceae	1	2	5	1	1	22
Verbenaceae	2	2	3	-	-	-
TOTAL	150	334	1644	71	100	1320

recorded above 65 cm diameter. Family-wise, the Dipterocarpaceae scored the largest basal area at ERSP of 17.5 m^2 ha^{-1} (36.0 %), whilst the second and the third largest BA was from Myrtaceae (4.22 m^2 ha^{-1}) and Guttiferae (3.41 m^2 ha^{-1}) (Table 2). Subsequently, the BBFR study area indicates Anacardiaceae with largest BA of 4.85 m^2 ha^{-1} (19.2 %), followed by Guttiferae (3.91 m^2 ha^{-1}) and Myrtaceae (2.0 m^2 ha^{-1}). At species level, the *Dryobalanops aromatica* (Dipterocarpaceae) had highest basal area at ERSP with an area of 4.71 m^2 ha^{-1}. Two dipterocarp species contributed to the second and third largest basal area in the study plot with *Shorea curtisii* and *Cotylelobium lanceolatum* scoring basal areas of 3.41 m^2 ha^{-1} and 3.34 m^2 ha^{-1}, respectively. In BBFR, *Parishia paucijuga* (Anacardiaceae) has the largest basal area of 4.73 m^2 ha^{-1} followed by *Mesua kochummeniana* (Guttiferae) and *Castanopsis schefferiana* (Fagaceae) with basal area of 1.74 m^2 ha^{-1} and 1.71 m^2 ha^{-1}, respectively (Table 2).

Comparing the results of this study with previous reports on lowland forests in Peninsular Malaysia, the BA of both study sites are within those reports at various lowland forests of the Peninsular Malaysia. For instance, Nizam *et al.* (2010) reported a total tree BA of 48.59 m^2 ha^{-1} at Bintang Hijau Forest Reserve, Perak, in which the tree communities were dominated by the dipterocarps; whilst Manokaran & Kochummen (1990) reported a total BA of trees in lowland forest at Pasoh of 29.13 m^2 ha^{-1}. It is apparent that the previous and current studies share a common feature wherein the dipterocarps contribute to the high BA values, because the dipterocarps commonly reach diameters more than 55 cm.

Diversity and Importance Value

Diversity of tree species in the study plots calculated using the Shannon-Weiner Diversity Index (H') showed values of 5.15 (H'_{max} = 5.79) and 3.57 (H'_{max} = 4.58) for the plots at ERSP and BBFR, respectively. The values of the diversity index were significantly different between the study areas (t-test; $P < 0.05$). The highest diversity at ERSP was mainly contributed by the highest species number in the study plot that contained 334 tree species ha^{-1}, whereas the low value of H' at BBFR is because of the low species richness. As the H' value contains the species richness (species number) and species evenness components (Magurran 1988), the Evennes Index (H'/H'_{max}) of the tree communities at both ERSP and BBFR

Table 2. Summary of tree density and basal area (BA) of five leading families and species at both study plots of ERSP and BBFR.

	ERSP		BBFR	
	Family		Family	
	Dipterocarpaceae	262	Anacardiaceae	295
	Guttiferae	143	Guttiferae	216
	Euphorbiaceae	129	Dipterocarpaceae	108
	Myrtaceae	119	Fagaceae	69
	Anacardiaceae	97	Myrtaceae	69
DENSITY	Species		Species	
(stems ha^{-1})	*Dryobalanops aromatica*	51	*Parishia paucijuga*	290
	Cotylelobium lanceolatum	44	*Hopea pubescens*	85
	Shorea blumutensis	40	*Calophyllum symingtonianum*	81
	Shorea curtisii ssp. *curtisii*	37	*Mesua kochummeniana*	70
	Dacryodes rostrata	37	*Castanopsis schefferiana*	64
	Family		Family	
	Dipterocarpaceae	17.50	Anacardiaceae	4.85
	Myrtaceae	4.22	Guttiferae	3.91
	Guttiferae	3.41	Myrtaceae	2.00
	Anacardiaceae	3.09	Fagaceae	1.83
	Euphorbiaceae	2.39	Dipterocarpaceae	1.63
BASAL AREA				
(m^2 ha^{-1})	Species		Species	
	Dryobalanops aromatica	4.71	*Parishia paucijuga*	4.73
	Shorea curtisii	3.41	*Mesua kochummeniana*	1.74
	Calophyllum lanceolatum	3.34	*Castanopsis schefferiana*	1.71
	Shorea blumutensis	1.60	*Podocarpus neriifolius*	1.52
	Elateriospermum tapos	1.26	*Calophyllum symingtonianum*	1.22

sites showed high evenness value of 0.89 and 0.78, respectively, thus reflecting that the *H'* value mainly depends on the species richness (species number) of the study areas. Nevertheless, the diversity index values computed in this study reflects high tree species diversity of Malaysian tropical forests, as also reported in previous studies, such as at Krau Wildlife Reserve, Pahang (*H'* = 5.19; Nizam *et al.* 2006) and at Panti Forest Reserve, Johore (*H'* = 4.94; Nizam *et al.* 2009).

Importance value index (*IVI*) of ten leading species at both study sites is shown in Table 3. At ERSP, the predominant species based on the highest *IVI* was *Elateriospermum tapos* (Euphorbiaaceae) with *IVI* of 1.98 %, followed by *Melanochyla auriculata* (Anacardiaceae) and *Dryobalanops aromatica* (Dipterocarpaceae) with *IVI* values of 1.7 % and 1.57 %, respectively. Obviously, no species could be considered as having absolute dominance in the tree community of the study plot. At BBFR site, the most dominant species was *Parishia paucijuga* (Anacardiaceae) with index value of 12.13 %. According to Curtis & MacIntosh (1951), a species that has *IVI* of more than 10 % is considered as having an absolute dominance in its community. Thus *P. paucijuga* exhibits absolute dominance among tree species at BBFR. The second and third dominants at BBFR include two species of Guttiferae, *Mesua kochummeniana* and *Calophyllum symingtonianum* contributing 6.00 % and 5.72 % respectively.

Soil characteristics

Soil characteristics of the two sites varied. The texture of the soil at ERSP was sandy loam-clay, whilst the soil at BBFR was a loam. As for chemical properties, soil pH of both study areas showed low values- 3.36 ± 0.03 at ERSP, whilst the soil pH at BBFR was significantly higher than the ERSP with mean pH value of 3.79 ± 0.02 ($P < 0.05$; *t*-test). The acidic soil of the study areas is in

Table 3. Ten leading important species at ERSP and BBFR study areas in descending order of its Importance Value Index (*IVI*).

ERSP	*IVI* (%)	BBFR	*IVI* (%)
Elateriospermum tapos	1.98	*Parishia paucijuga*	12.13
Melanochyla auriculata	1.70	*Mesua kochummeniana*	6.00
Dryobalanops aromatica	1.57	*Calophyllum symingtonianum*	5.72
Lophopetalum pachyphyllum	1.56	*Castanopsis schefferiana*	5.09
Dacryodes rostrata	1.44	*Hopea pubescens*	4.12
Shorea curtisii	1.43	*Podocarpus neriifolius*	3.46
Shorea blumutensis	1.42	*Tristaniopsis obovata*	2.80
Gluta curtisii	1.38	*Atuna racemosa*	2.57
Cotylelobium lanceolatum	1.31	*Diospyros subrhomboidea*	2.57
Saurauia pentapetala	1.25	*Gonystylus brunnescens*	2.20

line with a report by Othman & Shamshuddin (1982) who mentioned that most soils in the tropical rainforests of Peninsular Malaysia were acidic with pH between 3.5 and 5.5. This common scenario in the wet tropical region has resulted in soil becoming so weathered and leached (Lal & Greenland 1979); base cations are leached and being replaced by H^+ and Al^{3+} ions that caused the high acidity in soil. Organic matter (OM) content in soil at both ERSP and BBFR was low with mean value of 5.10 ± 0.17 % and 5.58 ± 0.05 % respectively. The low content is perhaps due to the climate factor of tropical rainforest where the hot and wet climate increases the decomposition rate of organic residue in soil (Longman & Jenik 1987).

Concentration of available macronutrients, i.e. magnesium (Mg), potassium (K), phosphorus (P) and soluble nutrients of ammonium-N and nitrate-N varied between areas (Table 4). Mg level at BBFR study plot is significantly higher than the concentration at ERSP, with mean concentrations of 15.54 ± 0.58 µg g^{-1} and 13.07 ± 0.32 µg g^{-1}, respectively ($P < 0.05$). Available phosphorus (P) indicated mean concentration of 20.94 ± 0.72 µg g^{-1} at ERSP and 21.81 ± 0.47 µg g^{-1} at BBFR, and these values did not differ significantly. The concentrations of soluble nutrients of nitrate-N and ammonium-N showed a consistent trend where the latter was at lower concentration compared to the former, at both the sites. The mean concentration of nitrate-N at ERSP was 14.05 ± 1.01 µg g^{-1} and 10.72 ± 0.99 µg g^{-1} in BBFR and the values were significantly different ($P < 0.01$). Further, the concentration of ammonium-N showed no significant difference between study areas with values of at ERSP 6.03 ± 0.30 µg g^{-1} and 6.06 ± 0.34 µg g^{-1} at BBFR. Apparently the differences in soil properties between the two study sites are quite notable, suggesting that other environmental factors determine soil nutrient availability, where leaching may influence the availability of more mobile nutrients (Schuur & Matson 2001).

Association between tree species and soil variables

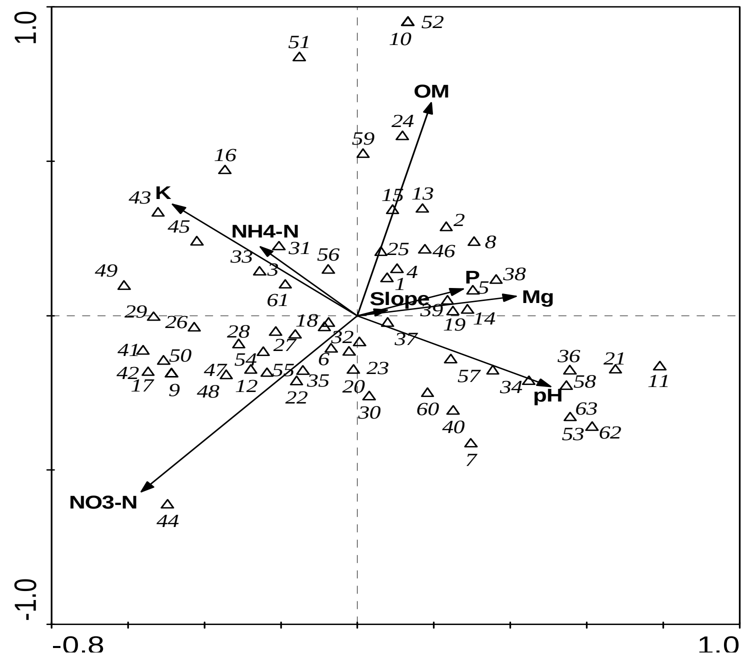
Fig. 2 illustrates the canonical correspondence analysis (CCA) ordination of tree species at ERSP site, wherein 63 tree species (after deletion of one occurrence from data matrix) figured in the direct gradient analysis of CCA. The CCA outputs include a set of vectors that visually represent the strength and directionality of the relationship between the environmental variables and ordination axes (ter Braak 1990). The output of vegetation and environment data at ERSP site is summarized in Table 5, which shows that the species-environment correlations were high, with eigenvalues (a measure of the strength of an axis or the amount of variation along an axis) of 0.539 for the first axis and 0.372 for the second axis. The Monte-Carlo permutation test indicates that there was a significant difference between the eigenvalues of the ordination axes ($P = 0.003$). At BBFR site, a total of 41 tree species was selected for CCA, and the output of CCA indicates the eigenvalues of the first and second axes are 0.390 and 0.242 respectively (Table 5). The Monte-Carlo permutation test also revealed significant difference of eigenvalues between the ordination axes ($P = 0.008$).

From Fig. 2, it is apparent that the species did not cluster into well-defined groups; nevertheless loose arrangement of species can be identified associated with the environmental variables. The figure illustrates the influence of soil variables on canonical axes wherein vectors indicate not only the direction but also the magnitude of influence of each variable. The soil factors that have long arrows are more closely correlated in the ordination than those with short arrows and are

Table 4. Summary of soil properties for at ERSP and BBFR study plots.

Soil parameters	ERSP Mean ± S.E.	BBFR Mean ± S.E.	
pH	3.36 ± 0.03	3.79 ±0.02	*
Exchangeable cations (meq 100 g^{-1})			
Ca^{2+}	0.011 ± 0.002	0.012 ± 0.001	NS
Mg^{2+}	0.023 ± 0.001	0.025 ± 0.001	NS
Na^{+}	0.119 ± 0.004	0.143 ± 0.003	*
K^{+}	0.120 ± 0.006	0.115 ± 0.005	NS
Total Cation Exchange Capacity	0.273 ± 0.010	0.294 ± 0.006	*
Available nutrients (μg g^{-1})			
Phosphorus (P)	20.94 ± 0.72	21.81 ± 0.47	NS
Nitrate-N (NO_3-N)	14.05 ± 1.01	10.72 ± 0.99	**
Ammonium-N (NH_4-N)	6.03 ± 0.30	6.06 ± 0.34	NS
Magnesium (Mg)	13.07 ± 0.32	15.54 ± 0.58	*
Potassium (P)	67.21 ± 5.33	72.11 ± 4.10	NS
Organic Matter Content, OM (%)	5.10 ± 0.17	5.58 ± 0.05	**

Note : n = 25 ; NS – not significant ; * P < 0.05 ; * P < 0.01 .

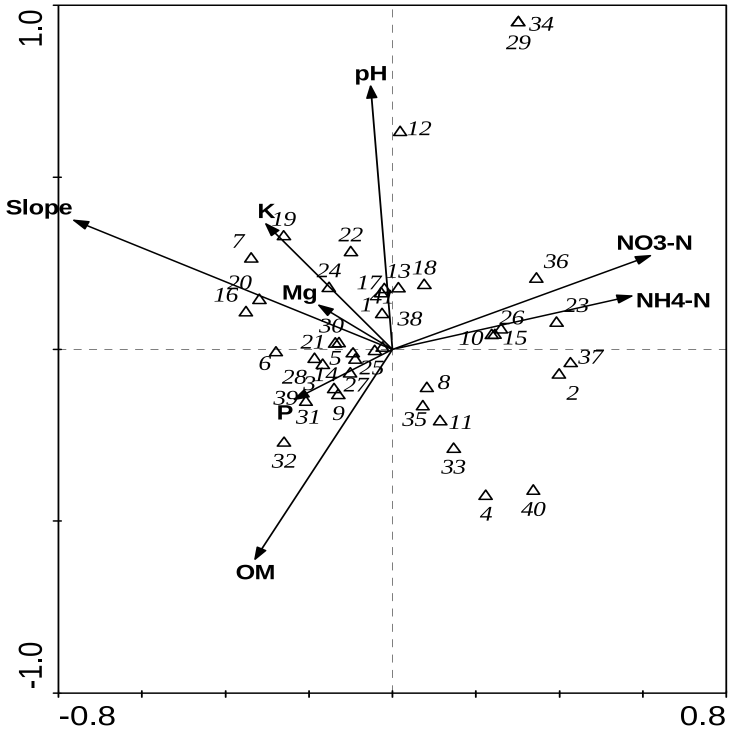


1-*Actinodaphne sesquipedalis;* 2-*Agrostistachys longifolia*; 3-*Alphonsea elliptica*; 4-*Antidesma neurocarpum*; 5-*Aporosa falcifera*; 6-*Ardisia crassa*; 7-*Atuna racemosa*; 8-*Barringtonia macrostachya*; 9-*Buchanania sessifolia*; 10-*Calophyllum alboramulum*; 11-*C. symingtonianum*; 12-*C. teysmannii* var. *inophylloide*; 13- *C. wallichianum* var. *incrassatum*; 14- *C. patentinervium*; 15-*Cotylelobium lanceolatum*; 16-*Cratoxylum arborescens* var. *arborescens*; 17-*Dacryodes laxa*; 18-*D. rostrata*; 19-*Diospyros pendula*; 20-*D. rigida*; 21-*Dipterocarpus costulatus*; 22-*Dryobalanops aromatica*; 23-*Elateriospermum tapos*; 24-*Garcinia eugeniifolia*; 25-*G. rostrata*; 26-*G. scortechinii*; 27-*Gynotroches axillaris*; 28-*Horsfieldia superba*; 29-*Hydnocarpus filipes*; 30-*H. kunstleri* var. *kunstleri*; 31-*H. woodii*; 32-*Knema intermedia*; 33-*Litsea lancifolia* var. *lancifolia*; 34-*Lophopetalum pachyphyllum*; 35-*Mallotus penangensis*; 36-*Melanochyla auriculata*; 37-*Mesua kochummeniana*; 38-*Palaquium microphyllum*; 39-*P. rostratum*; 40-*Parishia maingayi*; 41-*Pentace triptera*; 42-*Pimelodendron griffithianum*; 43-*Pternandra echinata*; 44-*Santiria laevigata*; 45-*Saurauia pentapetala*; 46-*Shorea blumutensis*; 47-*S. curtisii* ssp. *curtisii*; 48-*S. macroptera*; 49-*S. multiflora*; 50-*S. pauciflora*; 51-*Swintonia schwenkii*; 52-*Symplocos adenophylla*; 53-*Syzygium campanulatum*; 54-*S. dyerianum*; 55-*S. fastigiatum*; 56-*S. griffithii*; 57-*S. palembanicum*; 58-*S. subdecussatum* var. *subdecussatum*; 59-*Vatica cuspidata*; 60-*Xanthophyllum eurhynchum* ssp. *maingayi*; 61-*Xanthophyllum rufum*; 62-*Xerospermum noronhianum*; 63-*Xylopia caudata*.

Fig. 2. Canonical correspondense analysis (CCA) biplot of species and soil variables showing species occurrence in relation to soil variables at ERSP study site. Numbers denote species that occurred in the subplots. (NH_4-N: ammonium nitrogen; NO_3-N: nitrate-nitrogen; P: phosphorus; K: potassium; OM: organic matter).

Table 5. Summary of CCA of vegetation and environment data in the selected subplots at ERSP and BBFR sites.

Axes	ERSP				BBFR			
	1	2	3	4	1	2	3	4
Eigenvalues	0.539	0.372	0.331	0.278	0.390	0.242	0.227	0.170
Species-environment correlations	0.956	0.931	0.954	0.959	0.958	0.878	0.891	0.851
Cumulative percentage variance of species data	8.7	14.7	20.0	24.4	9.3	15.1	20.6	24.6
Species-environment relation	23.4	39.6	53.9	66.0	26.2	42.5	57.7	69.1



1-*Actinodaphne pruinosa*; 2-*Agrostistachys longifolia* var. *leptostachya*; 3-*Ardisia elliptica*; 4-*Artocarpus nitidus* ssp. *griffithii*; 5-*Atuna racemosa* ssp. *racemosa*; 6-*Barringtonia macrostachya*; 7-*B. scortechinii*; 8-*Brackenridgea hookeri*; 9- *Calophyllum symingtonianum*; 10-*Calophyllum wallichianum* var. *incrassatum*; 11-*Castanopsis schefferiana*; 12-*Ctenolophon parvifolius*; 13-*Cynometra malaccensis*; 14-*Dacryodes rostrata*; 15-*Diospyros subrhomboidea*; 16- *Dysoxylum dumosum*; 17-*Endiandra rubescens*; 18-*Garcinia bancana* var. *bancana*; 19-*G. rostrata*; 20-*Gonystylus brunnescens*; 21-*Gordonia maingayi*; 22-*Heritiera borneensis*; 23-*Hopea pubescens*; 24-*Knema intermedia*; 25-*Litsea grandis*; 26-*Madhuca tomentosa*; 27-*Madhuca utilis*; 28-*Mesua kochummeniana*; 29-*Parinari costata* ssp. *costata*; 30-*Parishia paucijuga*; 31-*Podocarpus neriifolius*; 32-*Pternandra echinata*; 33-*Streblus elongatus*; 34-*Swintonia floribunda*; 35-*Symplocos adenophylla*; 36-*Syzygium cinereum*; 37-*S. subdecussatum* var. *subdecussatum*; 38-*Timonius wrayi*; 39-*Tristaniopsis obovata*; 40-*Xerospermum noronhianum*; 41-*Xylopia malayana* var. *malayana*

Fig. 3. Canonical correspondense analysis (CCA) biplot of species and soil variables showing species occurrence in relation to soil variables at BBFR study site. Numbers denote species that occurred in the subplots. (NH_4-N: ammonium nitrogen; NO_3-N: nitrate-nitrogen; P: phosphorus; K: potassium; OM: organic matter).

much more important in influencing community variation. The slope vector at the ERSP site was at low magnitude, thus the influence of this factor on the community variation is low. Several species such as *Lophopetalum pachyphyllum* (34), *Syzygium palembanicum* (57), *S. subdecussatum* var. *subdecussatum* (58) and *Xylopia caudata* (63) are strongly associated with soil pH. Further, the soil vectors of potassium (K) and ammonium-N are seemed strongly correlated with the occurrence of species such as *Hydnocarpus woodii* (31), *Litsea lancifolia* var. *lancifolia* (33), *Pternandra echinata*

(43) and *Saurauia pentapetala* (45).

At BBFR study site, a slightly different scenario was observed on species ordination (Fig. 3) compared to ERSP site. Fig. 3 illustrates the strong influence of slope factor at the study site which was in contrast to ERSP site that shows low magnitude of slope vector. Several study plots at the BBFR indicate that slope ranged between 30° - 35°. Further, vectors of soil pH, organic matter content (OM) and inorganic soluble nitrogen (nitrate-N and ammonium-N) also indicate strong influence of the gradients on study sites. The species biplot illustrates that several species such as *Barringtonia scortechinii* (7), *Dysoxylum dumosum* (16) and *Gonystylus brunnescens* were closely associated with slope factor. Moreover, species of *Hopea pubescens* (23), *Madhuca tomentosa* (26) and *Syzygium cinereum* (36) seem to be influenced by the inorganic soluble nitrogen concentration (nitrate-N and ammonium-N). Clumping of species, for instance *Ardisia elliptica* (3), *Mesua kochummeniana* (28), *Podocarpus neriifolius* (31) and *Tristaniopsis obovata* (39), are associated with phosphorus level.

The results of ordination analyses for each forest site revealed a close relationship between soil factors and tree species distribution. It is apparent that different habitats display varied spatial distribution among tree species in relation to soil properties. Several researchers have reported variation in species composition and forest structure in relation to edaphic and topographic gradients (Davies & Becker 1996; Newbery & Proctor 1984). As the results from this study indicate the influence of soil nutrients on species distribution and this observation is in accordance with reports of Potts *et al.* (2002) and Baillie *et al.* (1987) who suggested that soil nutrient availability particularly phosphorus (P) and magnesium (Mg), directly influences species distributions and community composition in mixed dipterocarp forest in Borneo. Although there are many studies that reported significant soil-plant associations (Clark *et al.* 1998; Harms *et al.* 2001; Phillips *et al.* 2003), only some have specifically reported correlations with soil characteristics (John *et al.* 2007; Swaine 1996) whilst many others did not propose a mechanism to explain the association.

Conclusions

This study demonstrated that differences existed were between the two forest areas in terms of tree species composition, diversity and dominance. It also revealed the variation in soil characteristics between the sites, which perhaps influence the distribution of tree communities in the forests. It appears that the distribution of tree species in ERSP and BBFR is determined by soil factors such as pH, potassium, inorganic nitrogen, phosphorus and magnesium. Nevertheless, experimental manipulations on plant responses on the variation in soil characteristics would perhaps reveal the mechanisms that determine species distribution and beta-diversity in tropical forests.

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