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AN INVESTIGATION OF SOIL PHYSICO-CHEMICAL VARIABLES ACROSS DIFFERENT LOWLAND FOREST ECOSYSTEMS OF BRUNEI DARUSSALAM

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ABSTRACT Tropical forests undisputedly harbor the largest share of global plant diversity, but the mechanisms of maintenance for this diversity cannot be well understood without good data on environmental variables, primarily soil characteristics. This study investigates differences in soil physico-chemical properties in various tropical lowland forest types in Brunei Darussalam, in the Northwest Borneo plant diversity hotspot. Nine different vegetation types were investigated: intact primary mixed-dipterocarp forest, old disturbed secondary forest, young disturbed secondary forest (partly invaded by alien Acacias), heath (Kerangas) forest, peat swamp forest, swampy heath (Kerapah) forest, core mangrove, fringe mangrove and island mangrove forests. Nine 60 x 20 m plots were set up, and sampled for soils at topsoil (0-15 cm depth) and subsoil (15-30 cm depth) layers. Soil gravimetric water and organic matter content, texture, nutrient concentrations, pH, and salinity were determined. The peat swamp and core mangrove forests recorded highest soil nutrient concentrations. Peat swamp forest had the highest GWC, OM content, total N, and total Ca recorded, whereas the soil in core mangrove forest had higher total P, total Mg, total K, exchangeable Mg, exchangeable Ca, exchangeable K and salinity compared to the other habitat types. These results were also highlighted by the principal component analysis for the soil parameters measured. The most nutrient-poor soils were found in the Kerapah and heath forest sites. The difference between topsoil and subsoil for soil variables were generally not significantly different from each other. The present study has shown that soil physico-chemical properties differ significantly between the nine vegetation types studied, and this may have important implications upon differences seen in plant community compositions in these vegetation types.

Keywords: Heath forest, Mangrove forest, Mixed Dipterocarp forest, Peat swamps, Edaphic

INTRODUCTION

Rain forests occur over a wide range of soils, with some occurring on nutrient-poor soils, others on nutrient-rich soils (Proctor 1987).

These soils are diverse in terms of their physical, chemical and biological properties, thus making any generalization about rain forest soils difficult (Richards 1996). The most diverse tropical rain forest soils are typically found in the lowlands, which receive continuous rainfall affecting the nutrients input, organic matter decomposition, erosion and weathering (Ghazoul & Sheil 2010).

This study focuses specifically on Brunei Darussalam, located in the Northwest Borneo plant diversity hotspot. The lowland Bornean forests are considered as the most diverse amongst the tropical rain forests in South-East Asia. The stable climatic conditions have given rise to the world's richest assemblage of plant species, as it houses high diversity of trees, approximately 10,000 species of plants, including about 267 species of Dipterocarpaceae of which 155 species are endemic to Borneo (Ashton 1989).

The underlying geology and climatic conditions of this island influence the occurrence of various soil types (Ashton 2004). The thick sedimentary rocks underlying Borneo were laid down during the Miocene and Pliocene eras (Ashton *et al.* 2003) and underwent rapid erosion continuously due to the wet climate. These rocks have been uplifted and eroded to create the topography which gives Brunei its distinctive landscape. The resulting weathered materials vary in composition, from sand to clay. This contributes to the great diversity of drainage and soil fertility to be found across Brunei, which results in different floras and vegetation types, characteristic to each soil type (Ashton *et al*. 2003, Grealish & Fitzpatrick 2013).

The present study is the first attempt to quantify variation in soil chemical and physical properties across almost all of the lowland forest types in Brunei Darussalam. The main primary forest type in Brunei lowlands is the mixed-dipterocarp forest (Ashton *et al*. 2003) whereas, peat swamp forests are the second most dominant forest type (Wong & Kamariah 1999) and followed by mangrove forests and heath (Kerangas) forest (Forestry Department 2011). Data gathered during this project will be crucial for future studies on the influence of soil properties upon the distribution of different vegetation types in Brunei, despite experiencing the same climate throughout.

The main aim of this study was to quantify and describe differences in soil physico-chemical properties across nine different vegetation types: intact primary mixed-dipterocarp forest (PMDF), old disturbed secondary forest (OSF), young disturbed secondary forest (partly invaded by alien Acacias; YSF), heath (Kerangas) forest (HF), peat swamp forest (PSF), swampy heath (Kerapah) forest (KF), core mangrove (CM), fringe mangrove (FM) and island mangrove forests (IM). We analysed selected physical and chemical soil properties to determine their differences across the nine study sites, as well as differences in these soil physico-chemical properties between the topsoil (0-15 cm depth) and subsoil (15-30 cm depth) layers at each vegetation types. We also determined which soil properties explain most of the variation between the nine different vegetation types.

MATERIALS AND METHODS

The study was conducted at nine different lowland forest sites located in Brunei Darussalam, Northwest Borneo. Five of the study sites were located in Brunei-Muara District: the fringe mangrove (FM) site at Pantai Serasa, the island mangrove (IM) site at Pulau Bedukang, core mangrove (CM) site at Jalan Batu Marang, a young disturbed secondary forest (YSF) site at Jalan Kebangsaan, and old-growth secondary forest (OSF) site at Sungai Akar. The other study sites, located in the Belait

District, were the intact primary mixed dipterocarp forest (PMDF) site at compartment 7 and heath (Kerangas) forest (HF) site at compartment 8 of the Andulau Forest Reserve in Sungai Liang, as well as the peat swamp forest (PSF) site at Badas, and swampy heath (Kerapah) forest (KF) site at Lumut (Figure 1). Field work was carried out in March 2014 within three weeks during the dry season.

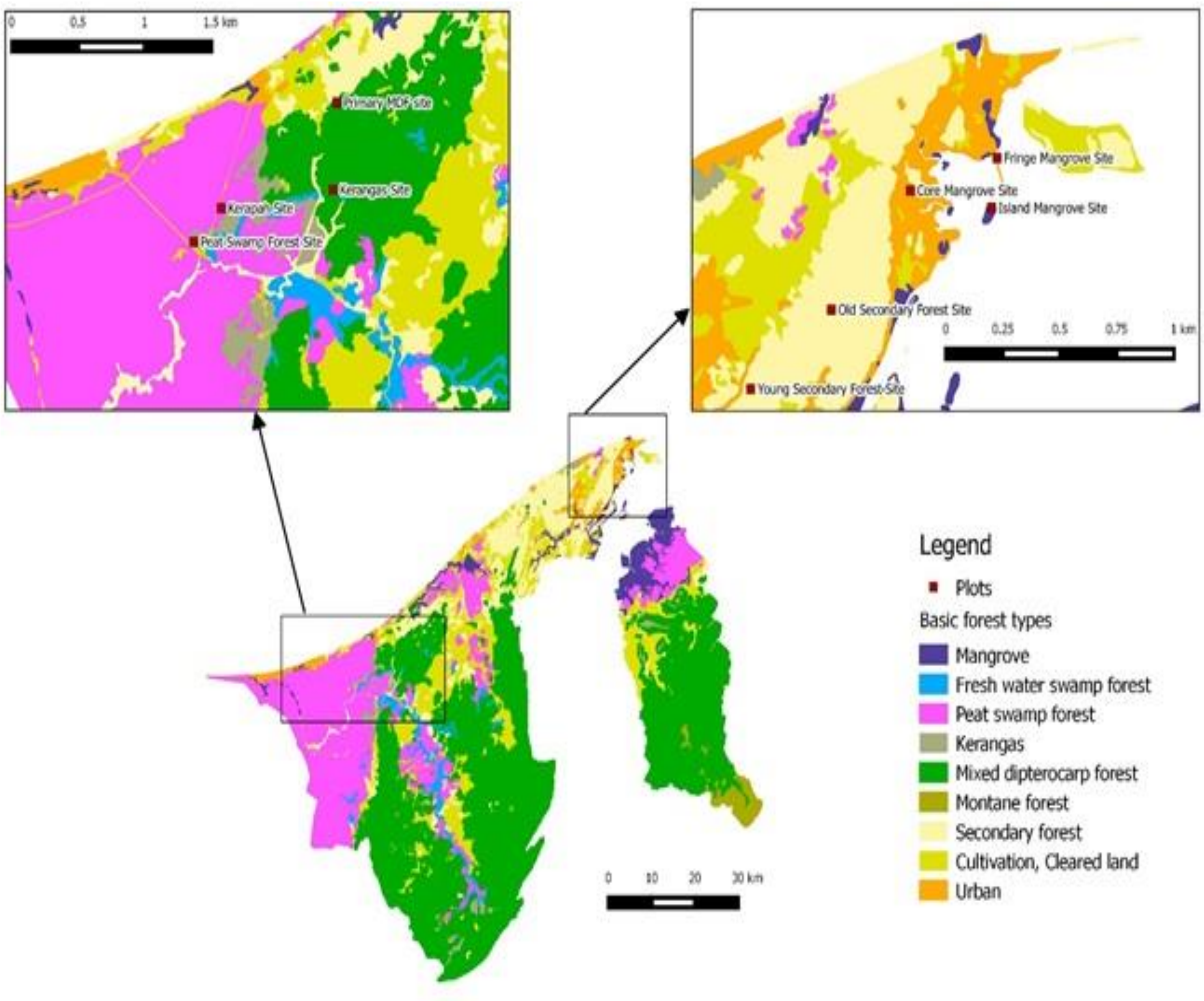

Figure 1 Map of Brunei Darussalam showing different forest types, and indicating the sites studied (Adapted from Anderson & Marsden 1984)

Soil sampling

At each study site, a 60 m x 20 m plot was randomly selected within accessible forest area, and subdivided into three 20 m x 20 m subplots, giving a total of 27 subplots for the entire study. In each 20 m x 20 m subplot, five soil cores were sampled using a soil auger. Soil samples were collected from the topsoil (0 – 15 cm depth) and subsoil (15 – 30 cm depth). In each subplot, four soil cores were collected close to each corner, and one in the center. The five samples were then mixed together as a composite bulk for each subplot. A total of 54 soil samples were collected (n = 27 subplots x 2 depths).

Soil analyses

Gravimetric water content and pH in distilled water were determined using fresh soil samples (Allen *et al*. 1989), whereas the salinity of the soil in distilled water were determined by measuring its electrical conductivity (expressed as deci-Siemens per meter; dS/m). The electrical conductivity was measured using a YSI 63 pH, conductivity, temperature, and salinity multimeter (Rickly Hydrological Company, Columbus, Ohio, USA). The remaining samples were air-dried to constant weight, ground and sieved, and used for macronutrient analysis. Organic matter (OM) content was determined using a muffle furnace (Gallenkamp Size 2, Apeldoorn, Netherland) set at 550°C for two hours (Allen *et al*. 1989). Soil texture was determined using a modified pipette method, following the procedures of the Brunei Department of Agriculture (2006).

Total N and P concentrations were determined using the Kjeldahl method by digesting each soil sample in concentrated sulphuric acid (conc. H_2SO_4), and were analysed using the Flow Injector Analyser (FIAstar 5000, Hoganas, Sweden). For analysis of total Mg, Ca and K, air-dried soil samples were acid-digested using a microwave digestor (Multiwave 3000 Anton Paar, Austria) following the procedures of Allen *et al*. (1989). Exchangeable Mg, Ca and K were extracted using 1N Neutral ammonium acetate (Chapman 1965). Total and exchangeable Mg, Ca and K concentrations were measured using a Flame Atomic Absorption Spectrophotometer (AAS; Thermo Scientific iCE 3300, Sydney, Australia).

Soil available P concentrations were extracted using Bray's solution (0.03 N ammonium fluoride in 0.025 N HCl) and mixed with ascorbic acid and molybdate reagent (Brunei Department of Agriculture 2006). The absorbance of each solution was read at 880 nm wavelength using UV-spectrophotometer (UV-1800, Shimadzu, Kyoto, Japan).

Data analysis

All statistical analyses were conducted in R 3.1.1 (R Core Team, 2014). Between-site differences in soil properties were determined using one-way ANOVA and significant results further analysed using Tukey's HSD test. Variables for soil nutrient concentrations (total N, P, Mg, Ca and K, exchangeable Mg, Ca and K, Available P) were ln-transformed, pH and salinity were $\log_{10}$-transformed, and GWC and OM content were arcsine-transformed. All 13 soil variables between different sites and depth were then subjected to a principal component analysis (PCA) to determine which variables account for most of the variation in the data set.

RESULTS

Between-site differences in soil physico-chemical variables

Soil physico-chemical variables did not differ significantly between the topsoil and subsoil depths for the sites studied, except for GWC which showed significant differences at topsoil and subsoil between sites ($F = 44.3$, $p < 0.001$ and $F = 55.0$, $p < 0.001$, respectively; Table 1 and Table 2). Soil GWC at PSF was consistently significantly higher than the other forest types at both sampling depths (0 – 15 cm and 15 – 30 cm), and the lowest mean GWC values were found in KF and HF soils at both sampling depths.

Soil pH in both the topsoil and subsoil were significantly different between sites ($F = 17.9$, $p = < 0.001$; $F = 18.1$, $p = < 0.001$, respectively). Soil pH at two mangroves sites, FM and CM were the highest and close to neutral pH values, whereas KF and HF soils were the most acidic at both depths (Table 1 and Table 2). Salinity in the topsoil and subsoil were significantly different between sites ($F = 170.2$, $p = < 0.001$; $F = 229.6$, $p = < 0.001$, respectively). The highest mean salinity was recorded in CM and the lowest was in HF soils.

OM content in the topsoil and subsoil also showed significant differences between sites ($F = 370.7$, $p = < 0.001$; $F = 542.1$, $p = < 0.001$, respectively; Table 1 and Table 2). PSF soils recorded the highest mean OM content, while the lowest mean OM content were found in both IM and KF soils.

Soil texture at topsoil and subsoil depths varied between plots (see Jaafar, 2014), with some classified as sandy (FM, IM, KF and HF), while the rest were classified as loamy sand (PMDF and OSF), sandy loam (PSF and CSF) or loam (CM). Sand content ranged from 34.2 % to 97.3 % in all the sites studied.

At both sampling depths, CM and PSF soils were found to have the highest concentrations of nutrients, significantly higher than the other forest types. CM soils had the highest total P, total Mg, total K, exchangeable Mg, exchangeable Ca, and exchangeable K concentrations recorded, whereas PSF soils had the highest total N and total Ca concentrations (Table 1 and Table 2). Total N, P, Mg, Ca, K, exchangeable Mg, Ca and K and available P concentrations in both the topsoil and subsoil showed significant differences between sites.

Table 1 Measurements of topsoil (0 – 15 cm depth) variables in lowland forest ecosystems of Brunei across 27 subplots from nine different sites. Soils were sampled from each 20 x 20 m subplot. Gravimetric water content (GWC) and OM content are expressed in percentage (%). Data for GWC and OM content were arcsine-transformed prior to statistical analysis. Soil nutrient concentrations are expressed as mg g^{-1} for total N, total Mg, total Ca, total K, exchangeable Mg, exchangeable Ca, exchangeable K and available P and were ln-transformed. pH is expressed as unit pH whereas salinity is expressed in dS/m. Data for pH and salinity were log-transformed in statistical analyses.

Soil variables	**FM**	**IM**	**CM**	**PSF**	**KF**	**HF**	**PMDF**	**OSF**	**YSF**	
GWC	34.7 ± 1.1	19.4 ± 1.9	51.9 ± 7.8	80.5 ± 1.5	17.4 ± 3.1	15.8 ± 4.6	18.0 ± 0.8	18.8 ± 2.6	17.4 ± 3.1	***
OM content	2.1 ± 0.3	1.9 ± 0.2	14.9 ± 4.1	85.9 ± 1.4	2.5 ± 0.5	4.2 ± 1.3	3.0 ± 0.4	3.8 ± 0.3	2.5 ± 0.5	***
Total N	0.5 ± 0.08	0.45 ± 0.07	2.5 ± 0.45	7.8 ± 2.5	0.42 ± 0.07	0.69 ± 0.15	0.75 ± 0.12	0.9 ± 0.07	0.42 ± 0.07	***
Total P	0.07 ± 0.01	0.05 ± 0.003	0.24 ± 0.02	0.20 ± 0.03	0.04 ± 0.001	0.03 ± 0.002	0.08 ± 0.01	0.09 ± 0.01	0.04 ± 0.001	***
Total Mg	0.3 ± 0.05	0.15 ± 0.03	0.61 ± 0.23	0.49 ± 0.04	0.03 ± 0.01	0.03 ± 0.004	0.08 ± 0.01	0.07 ± 0.004	0.03 ± 0.01	***
Total Ca	0.05 ± 0.01	0.07 ± 0.02	0.03 ± 0.02	0.20 ± 0.06	0.11 ± 0.02	0.09 ± 0.01	0.01 ± 0.001	0.002 ± 0.002	0.11 ± 0.02	***
Total K	1.4 ± 0.15	0.73 ± 0.15	7.7 ± 1.1	0.12 ± 0.02	0.04 ± 0.01	0.01 ± 0.004	2.7 ± 0.6	3.3 ± 0.9	0.04 ± 0.01	***
Exchangeable Mg	0.7 ± 0.11	0.34 ± 0.07	1.32 ± 0.35	0.17 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.01 ± 0.002	0.01 ± 0.001	0.03 ± 0.01	***
Exchangeable Ca	0.35 ± 0.03	0.2 ± 0.04	0.58 ± 0.18	0.01 ± 0.003	0.01 ± 0.003	0.02 ± 0.003	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.003	***
Exchangeable K	0.05 ± 0.04	0.1 ± 0.01	0.35 ± 0.16	0.07 ± 0.01	0.02 ± 0.001	0.04 ± 0.004	0.08 ± 0.001	0.05 ± 0.01	0.02 ± 0.001	*
Available P	0.02 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.02 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	*
pH	7.2 ± 0.14	5.3 ± 0.47	5.58 ± 0.82	3.11 ± 0.08	3.1 ± 0.1	3.8 ± 0.18	4.2 ± 0.09	4.4 ± 0.02	3.1 ± 0.1	***
Salinity	2.1 ± 0.25	0.73 ± 0.08	3.85 ± 1.67	0.07 ± 0.01	0.01 ± 0.001	0.01 ± 0.001	0.02 ± 0.003	0.01 ± 0.001	0.01 ± 0.001	***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

FM: Fringe Mangrove , IM: Island Mangrove, CM: Core Mangrove, PSF: Peat Swamp Forest, KF: Kerapah Forest, HF: Heath Forest, PMDF: Primary Mixed-Dipterocarp Forest, OSF: Old Secondary Forest, YSF: Young Secondary Forest

Table 2 Measurements of subsoil (15 – 30 cm depth) variables in lowland forest ecosystems of Brunei across 27 subplots from nine different sites. Soils were sampled from each 20 x 20 m subplot. Gravimetric water content (GWC) and OM content are expressed in percentage (%).Data for GWC and OM content were arcsine-transformed prior to statistical analysis. Soil nutrient concentrations are expressed as mg g^{-1} for total N, total Mg, total Ca, total K, exchangeable Mg, exchangeable Ca, exchangeable K and available P and were ln-transformed. pH is expressed as unit pH whereas salinity is expressed in dS/m. Data for pH and salinity were log-transformed in statistical analyses.

Soil variables	**FM**	**IM**	**CM**	**PSF**	**KF**	**HF**	**PMDF**	**OSF**	**YSF**	
GWC	35.5 ± 0.5	23.5 ± 3.0	50.0 ± 8.9	87.1 ± 1.2	14.9 ± 1.4	9.7 ± 4.6	16.2 ± 0.6	18.4 ± 2.2	12.9 ± 0.6	***
OM content	2.4 ± 0.2	2.4 ± 0.3	13.2 ± 3.8	86.7 ± 1.0	1.2 ± 0.2	1.9 ± 0.7	2.1 ± 0.3	2.6 ± 0.02	2.2 ± 0.1	***
Total N	0.5 ± 0.04	0.50 ± 0.09	2.4 ± 0.50	8.1 ± 2.7	0.17 ± 0.04	0.33 ± 0.12	0.52 ± 0.08	0.6 ± 0.01	0.48 ± 0.04	***
Total P	0.06 ± 0.002	0.07 ± 0.01	0.23 ± 0.03	0.18 ± 0.01	0.03 ± 0.004	0.03 ± 0.003	0.08 ± 0.01	0.08 ± 0.01	0.11 ± 0.01	***
Total Mg	0.4 ± 0.03	0.22 ± 0.03	0.60 ± 0.18	0.42 ± 0.02	0.04 ± 0.01	0.04 ± 0.003	0.06 ± 0.02	0.08 ± 0.03	0.17 ± 0.01	***
Total Ca	0.06 ± 0.01	0.06 ± 0.01	0.03 ± 0.01	0.15 ± 0.01	0.13 ± 0.02	0.12 ± 0.02	0.03 ± 0.02	0.01 ± 0.005	0.003 ± 0.001	***
Total K	1.8 ± 0.17	0.84 ± 0.13	6.7 ± 0.9	0.10 ± 0.01	0.04 ± 0.004	0.02 ± 0.01	2.7 ± 0.7	2.7 ± 1.3	4.8 ± 0.7	***
Exchangeable Mg	0.8 ± 0.05	0.42 ± 0.08	1.66 ± 0.13	0.18 ± 0.01	0.02 ± 0.002	0.01 ± 0.004	0.01 ± 0.002	0.01 ± 0.001	0.02 ± 0.004	***
Exchangeable Ca	0.40 ± 0.01	0.2 ± 0.04	0.57 ± 0.19	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.002	0.01 ± 0.001	0.01 ± 0.002	0.01 ± 0.002	***
Exchangeable K	0.08 ± 0.05	0.11 ± 0.01	0.48 ± 0.21	0.06 ± 0.004	0.01 ± 0.002	0.04 ± 0.002	0.07 ± 0.003	0.04 ± 0.003	0.07 ± 0.002	***
Available P	0.02 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.001	*
pH	7.1 ± 0.10	5.3 ± 0.44	5.90 ± 0.82	3.24 ± 0.03	3.4 ± 0.1	4.1 ± 0.16	4.2 ± 0.07	4.7 ± 0.04	4.0 ± 0.1	***
Salinity	2.2 ± 0.03	0.98 ± 0.12	3.95 ± 1.68	0.05 ± 0.004	0.01 ± 0.001	0.01 ± 0.001	0.02 ± 0.001	0.01 ± 0.001	0.04 ± 0.001	***

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

FM: Fringe Mangrove , IM: Island Mangrove, CM: Core Mangrove, PSF: Peat Swamp Forest, KF: Kerapah Forest, HF: Heath Forest, PMDF: Primary Mixed-Dipterocarp Forest, OSF: Old Secondary Forest, YSF: Young Secondary Forest

Variation in soil physico-chemical properties between vegetation types

In the principal component analysis (PCA) for the 13 topsoil parameters measured (GWC, OM content, total N, total P, total Mg, total Ca, total K, exchangeable Mg, exchangeable Ca, exchangeable K, Available P, pH, and Salinity), the first three axes accounted for 86.6% of the variation in soil properties between the nine vegetation types (Table 3). The first (PC1), second (PC2), and third (PC3) axes explained 46.3%, 29.3% and 11.0% of the variation seen in topsoil variables, respectively. Topsoil concentrations of total Mg, exchangeable Mg, exchangeable Ca, exchangeable K and salinity were strongly positively associated with PC1. PC2 represented a gradient of decreasing GWC and OM content, as well as decreasing concentrations of total N and total Ca in the topsoil. PC3 represented a gradient of increasing concentrations of total P and total K, but decreasing concentrations of available P and decreasing pH in the topsoil.

Table 3 Variations from principal component analysis (PCA) of one topsoil physical parameter (GWC) and twelve topsoil chemical variables (Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K, Available P, pH, Salinity and OM content) across all 27 subplots from nine different sites, and percentage of total variation explained by each principal component axis. Loadings and signs of the correlation coefficient (trait loadings) of each property for the first three principal component axes are presented. Variables with the highest loadings are indicated in bold.

Parameters	Principal component axes		
	1	2	3
% of total variation explained	46.3	29.3	11.0
Cumulative % variation explained	46.3	75.6	86.6
Loadings of soil physical and chemical properties			
GWC	0.29	**-0.34**	-0.03
OM content	0.16	**-0.46**	0.06
Total N	0.18	**-0.40**	0.16
Total P	0.33	-0.16	**0.34**
Total Mg	**0.39**	-0.10	-0.003
Total Ca	0.05	**-0.38**	-0.28
Total K	0.24	0.24	**0.43**
Exchangeable Mg	**0.35**	0.17	-0.16
Exchangeable Ca	**0.35**	0.21	-0.20
Exchangeable K	**0.33**	0.15	0.20
Available P	0.06	-0.22	**-0.54**
pH	0.21	0.30	**-0.42**
Salinity	**0.36**	0.19	-0.14

The 27 subplots of the nine sites sampled were partitioned in ordination space and differentiated on the basis of topsoil nutrient concentrations (Figure 2). For the PSF subplots, GWC, total N, OM, available P, and total Ca were the most influential set of variables. CM subplots were mostly influenced by exchangeable cation concentrations (exchangeable Ca, Mg and K), and also by salinity. FM subplots were influenced mostly by pH and total K concentration. The rest of the subplots (IM, KF, HF, PMDF, OSF and YSF) were not clearly distinguishable from each other based on topsoil parameters (Figure 2). The PCA for subsoil samples showed a very similar pattern with the topsoil PCA, indicating no differences in soil variation between the sampling depths (Table 4; Figure 3).

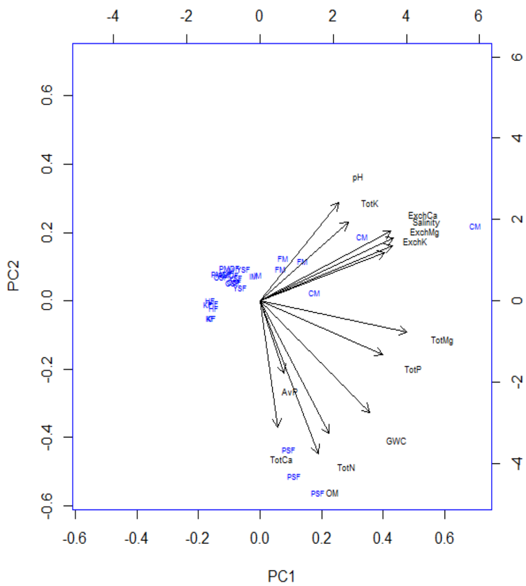

Figure 2 Biplot of principal component (PC) axes 1 and 2 from principal component analysis (PCA) of two topsoil physical properties (GWC and OM) and eleven topsoil chemical variables (Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K, Available P, pH and Salinity) across all 27 subplots from nine different sites.s Abbreviations denote the 27 subplots censused; FM, IM, CM, PSF, KF, HF, PMDF, OSF and YSF. GWC, OM, TotN, TotP, TotMg, TotCa, TotK, ExchMg, ExchCa, ExchK, and AvP represents gravimetric water content, organic matter content, concentrations of Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K and and Available P, respectively

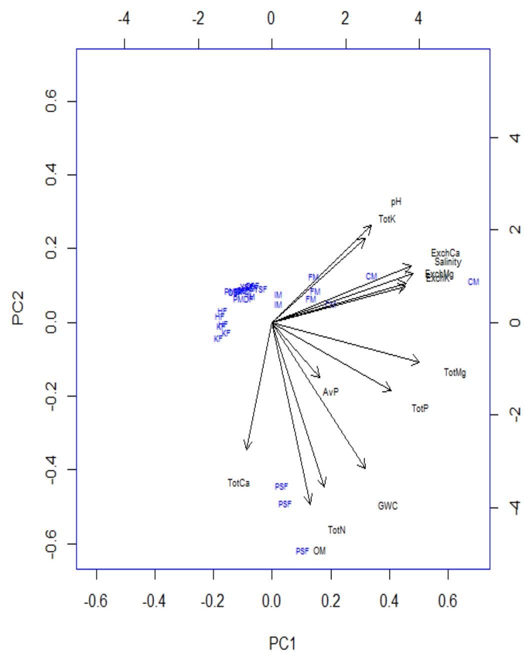

Figure 3 Biplot of principal component (PC) axes 1 and 2 from principal component analysis (PCA) of two subsoil physical properties (GWC and OM) and eleven subsoil chemical variables (Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K, Available P, pH and Salinity) across all 27 subplots from nine different sites. Abbreviations denote the 27 subplots censused; GWC, OM, TotN, TotP, TotMg, TotCa, TotK, ExchMg, ExchCa, ExchK, and AvP represents gravimetric water content, organic matter content, concentrations of Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K and and Available P, respectively

Table 4 Variations from principal component analysis (PCA) of one subsoil physical parameter (GWC) and twelve subsoil chemical variables (Total N, Total P, Total Mg, Total Ca, Total K, Exchangeable Mg, Exchangeable Ca, Exchangeable K, Available P, pH, Salinity and OM content) across all 27 subplots from nine different sites and percentage of total variation explained by each principal component axis. Loadings and signs of the correlation coefficient (trait loadings) of each property for the first three principal component axes are presented. Variables with the highest loadings are indicated in bold.

Parameters	Principal component axes		
	1	2	3
% of total variation explained	47.6	27.4	12.1
Cumulative % variation explained	47.6	75.0	87.1
Loadings of soil physical and chemical properties			
GWC	0.24	**-0.40**	-0.009
OM content	0.10	**-0.50**	-0.10
Total N	0.14	**-0.45**	-0.12
Total P	0.31	-0.19	**-0.39**
Total Mg	**0.39**	-0.11	0.05
Total Ca	-0.07	**-0.35**	**0.37**
Total K	0.24	0.23	**-0.44**
Exchangeable Mg	**0.35**	0.11	0.08
Exchangeable Ca	**0.37**	0.16	0.21
Exchangeable K	**0.35**	0.10	-0.13
Available P	0.12	-0.15	**0.53**
pH	0.26	0.27	**0.35**
Salinity	**0.37**	0.14	0.12

DISCUSSION

Soil variation in Brunei's lowland forests

Our study has revealed considerable variation in soil physical and chemical properties between the nine different lowland vegetation types in Brunei. Overall, all soils sampled were acidic, except for the fringe mangrove (FM) and core mangrove (CM) soils which were close to neutral pH values. Soils generally showed low OM content, except for PSF soils which showed very high values exceeding 80%. Soil nutrient concentrations also varied between vegetation types.

Some of the most remarkable results obtained here were relevant to peat swamp forests. The high OM content in PSF soils recorded indicates OM production exceeded its decomposition rate (Page *et al*. 2006, Whitten *et al*. 2000). The acidic conditions of PSF soils also slow down the decomposition rates further (Baillie 1996, Tie 1990, Whitten *et al*. 2000). In addition, PSF had significantly higher mean GWC than the other forest types, and this is also visible in the PCA biplots (Figure 2 and Figure 3). The high water content in PSF soil is derived mainly from precipitation (Rieley *et al*. 1996, Yule 2010), which could also be the cause of high OM content on its peat layer. The very slow decomposition in PSF seems to immobilize nutrients, and these nutrients can reside in OM for many years rather than being released into soil (Baillie 1996, Tie 1990). The accumulation of OM directly affects the retention of water in the soil, and thus increases GWC. The availability of nutrients for plants is also dependent on soil GWC (Morris *et al*. 2011). High soil GWC typically increase nutrient availability in the soil, because nutrients become labile in the presence of water and are more easily absorbed by plant roots (Hager *et al*. 1991, Yule & Gomez 2009).

The highest concentrations of total N and Ca were also recorded in the PSF plots. The PCA biplots (Figure 2 and Figure 3) clearly show a separation of the PSF subplots from the other subplots due to a high influence of total N and Ca, and to a lesser extent, available P concentrations. This may be partly due to sampling of peat, rather than mineral soil, at the PSF site. Soil sampling procedures in this study were standardized at 0 – 15 cm for topsoil and 15 – 30 cm for subsoil samples. As peat depth can range from 0.5 m to in excess of 10 m (Anderson *et al*. 1983, Hooijer 2006, Whitten *et al.* 2000, Yule & Gomez 2009, Yule 2010), it is possible that soil samples from the PSF site were mainly comprised of peat. This is not necessarily a drawback though, as most of the PSF plants directly access nutrients from the thick OM accumulating in the peat rather than directly from the soil (Jackson *et al.* 2008, Page *et al*. 2006, Rieley *et al*. 1996).

In the PCA, all the three mangrove sites were found to be different from each other. The island mangrove (IM) was indistinguishable from the rest of the forest types, except for the CM, FM and PSF. Core mangrove (CM) plots had the highest mean of total P, Mg, K, exchangeable Mg, Ca and K concentrations recorded. This may be due to its location near the urban areas in Jalan Batu Marang, very closely located to the nearby river, Sungai Batu Marang. Nutrient availability may be increased due to the continuous flushing down of nutrients from neighbouring rivers and streams (Hogarth 1996, Morgany *et al*. 1999).

Another possible reason, not involving anthropogenic effects, could be that the permanently waterlogged condition at the CM site causes accumulation of OM made up of underground portions of mangrove root systems on the soil (Arianto *et al*. 2015, Tomlinson 1986), creating higher cation concentrations as the nutrients can also be derived directly from the accumulation of OM (Thomas 1970, Clark *et al*. 2001). In this way, CM ecosystem could be considered as a nearly closed system, which only continuously receives nutrient input via OM accumulation and decomposition, but has little or no nutrient leakage, thus retains a high concentration of nutrients (Whitmore 1984).

One of the mangrove sites studied, the FM, could be seen clearly in the PCA biplot as being highly influenced by pH and total K concentrations. Due to its high concentration of total K ions, the pH was also recorded as the highest, close to neutral. The K ions were likely mainly supplied by the neighbouring seawater residing in the soil of the FM. We also recorded low pH in all of our sites, except for the mangrove sites. Grealish and Fitzpatrick (2013) determined that acid sulphate soils in Brunei Darussalam are generally of low pH and strongly suggested that sulphur is present in the soils of Brunei’s forests. Thus, most forest soils in Brunei are acid sulphate soils with low pH, as detected in our study. In contrast, CM soils are not acid sulphate soils (Kathiresan & Bingham 2001) and so their pH values tend to be higher.

The most nutrient-limited soils appeared to occur at the HF, KF and to a lesser extent, PMDF sites. Although low levels of N were recorded previously from HF soil solutions (Moran *et al*. 2000), higher levels of N in soils have been recorded in HF at Bukit Sawat, Brunei (Metali *et al.* 2015). In our study, the low levels of total N in the HF and KF soils was probably due to the rapid uptake of N into the plant biomass in order to sustain the production of sclerophyllous leaves that are typical of KF and HF vegetation (Turner *et al*. 2000). The plant communities of KF and HF are closer in composition compared to PMDF (Forestry Department 2011), and so it is possible that they utilize similar nutrients, thus both may have similar requirements for N. The low pH recorded on both HF and KF soils increased their acidity and therefore caused lower total and available P. Nutrient retention tend to be low in heath forests (Becker & Wong 1993) due to intense leaching and the soils' inability to retain cations (Proctor 1999), resulting in soil acidification due to increased hydrogen ions (Metali *et al.* 2015).

Patterns in available phosphorus (P) concentrations in the soils sampled here were particularly interesting. High available P concentrations were recorded in all sites except for PMDF, which recorded the lowest available P concentrations at both depths. Tropical forests are most often limited by P (Sollins 1998) and P has been shown to be an important nutrient for Bornean tropical soils (Paoli *et al.* 2006, Sukri *et al,* 2012). The low available P concentration detected here may mean that the plant roots in the PMDF site take up available P in the soils effectively because available P is the form that is more accessible to plants than total P (Sollins 1998). The low available P concentrations in the soil possibly indicates that it is a nutrient that is in high demand by plants and therefore it is absorbed very quickly by the plants in PMDF. Available P concentrations in Andulau and another PMDF site in Brunei, Belalong, were also recorded as very low (Metali *et al.* 2015, Sukri *et al.* 2012).

Kerapah forest (KF) was the forest type that was least investigated prior to our study. We found that both KF and HF have significantly low total N, P, Mg, K, exchangeable Mg, Ca, and K concentrations for both depths, as well as low GWC values. The low GWC in KF and HF soils could mean that there is very little water retention in these soils due to their porous and sandy nature (Brunig 1974, Katagiri *et al*., 1991, Proctor *et al*. 1983, Proctor 1999, Whitmore 1984), and therefore this could be an indication of nutrient leaching (Davies & Becker 1996, Moran *et al*. 2000). HF by nature is located on sandy soils (Whitmore 1984) and, in general, sandy soils do not contain a lot of nutrients (Proctor *et al*. 1983). The amount of nutrients and salts are dependent upon the amount of water present in the soil (Biswas & Mukherjee 1994). Thus, sandy soils with low water content tend to lose nutrients more easily than other soil types. As only three plots were each sampled in HF and KF, the results from this study should not be generalized to all HF and KF in Brunei and in Borneo. Nevertheless, the low water availability in both HF (Richards 1996, Whitmore 1984) and KF soils are known to limit the decomposition rates, thus reducing nutrient release into the soil (Proctor 1999, Villela & Proctor 2002).

A comparison of this current study and other soil studies based in Brunei's forests in terms of differences in nutrient concentrations is limited due to differences in methodologies used (Moran *et al*. 2000, Sukri *et al*. 2012) or because most previous studies in Brunei did not measure all soil nutrient concentrations, pH, salinity or soil physical properties investigated in this study (Ashton & Hall 1992, Austin *et al*. 1972). In addition, most of these previous studies were conducted in PMDF (Ashton & Hall 1992, Austin *et al*. 1972, Moran *et al*. 2000, Sukri *et al*. 2012). Moran *et al*. (2000) measured soil nutrient concentrations in a 1 ha permanent plot at Andulau, but measurements were made from soil solution rather than from the bulk soil, and so are not directly comparable to the results obtained in this present study. Nevertheless, Moran *et al*. (2000) found similar patterns of low N concentrations in their HF site at Badas Forest Reserve (4^{o}34', 114^{o}25'E; 11-16 m elevation a. s. l.). Additionally, the data recorded for this study are comparable with the data from Matali & Metali (2015) for HF soils, conducted at the same locality in compartment 8 of the Andulau Forest Reserve and with the data from Metali *et al.* (2015) for MDF soils, conducted at the same compartment 7 of the Andulau Forest Reserve in Sungai Liang.

Regarding the dearth of soil depth differences, subsoil samples in our study were only taken at 15 – 30 cm depth, and were not as deep as in other studies (see Sukri *et al*. 2012); thus, most nutrient concentrations were not significantly different between topsoil and subsoil. It is likely that increasing sampling depth to 30 – 50 cm for subsoil samples similar to that of Sukri *et al.* (2012) would result in significant differences in soil properties between depths. Nevertheless, most nutrient uptake occur at the topsoil where most of the plant roots are concentrated (Jobbagy & Jackson 2001) and where the biological recycling of cations is most active (Baillie 1996), or nutrients may be supplied directly from the weathering of parent rocks (Proctor 1987). Therefore, an attempt was made here to determine whether differences could be noted between closer soil layers. The general failure to detect one suggests that, for most purposes, future studies can simply focus on topsoil properties.

CONCLUSION

The present study has explored a number of forest types for which information was previously lacking, in particular swampy heath (Kerapah) forest, which was found to be largely similar to heath (Kerangas) forest in terms of the physico-chemical properties of the soil. The inclusion of mangrove forest types here is also viewed as an innovative contribution, as these are often treated as a marine system, and comparison with fully terrestrial forest types are limited. Indeed, insofar as the adaptations of mangrove trees belonging to the same lineages as fully terrestrial ones are to be understood, such standardized approaches are needed. The analyses conducted here confirm the distinctness of these ecosystems, but also highlight major differences between mangrove forest sites at different locations.

The data set assembled here is one of the most comprehensive data sets covering a variety of tropical forest types, and thus provides an opportunity for understanding the factors filtering major plant lineages across soil types in a climatically homogeneous environment. At the same time, the breadth of the system types covered here had to be compensated by limited sampling in each type, and so the thorough characterization of those forest types first analysed here will require further replication.

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