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Research Article

Tree Diversity and Community Composition of the Tutong White Sands, Brunei Darussalam: A Rare Tropical Heath Forest Ecosystem

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Bornean heath (*Kerangas*) forests are a unique and increasingly rare tropical forest ecosystem that remains little studied. We quantified tree floristic diversity in *Kerangas* forests in the Tutong White Sands, Brunei Darussalam, and investigated the influence of soil and environmental variables on community composition. Six 20 m × 20 m plots were established, where all trees of ≥5 cm diameter at breast height (DBH) were identified and measured to determine stem diameter and basal area. We determined pH, gravimetric water content, and concentrations of total nitrogen (N) and phosphorus (P) in topsoil, as well as litter depth and percentage canopy openness. A total of 296 trees were recorded, representing 78 species in 59 genera and 38 families. Stem diameter, basal area, species richness, and species diversity differed significantly among the six plots. The NMDS ordination revealed that differences in tree community compositions were significantly associated with total N concentrations and percentage canopy openness. Despite the small sampling area, we recorded several Bornean endemic tree species (16/78 tree species; 20.5%), including several IUCN Red List endangered and vulnerable species. Our results illustrate the potentially high conservation value of the *Kerangas* forests in the Tutong White Sands and highlight the urgent need to protect and conserve this area.

1. Introduction

Heath forests are a type of aseasonal lowland tropical rain forest that develop in dryland sites with predominantly podzolized, highly acidic, sandy soils [1, 2]. Heath forests in Borneo are known as “*Kerangas*” forests, originating from an Iban word that refers to infertile soils in which rice cannot grow [1]. *Kerangas* forests in Sarawak and Brunei have been previously studied in terms of either their ecology and plant community compositions [3–5], soil, litter, and environmental characteristics [6–8], and ecophysiology [9–11] or variations in tree leaf form and function [12–14].

Kerangas forests are distinctive in their forest structure, physiognomic features, and tree characteristics as compared with the lowland mixed dipterocarp rain forests that are more dominant throughout Borneo. *Kerangas* trees are typically shorter and unbuttressed and have stilt roots [1, 15, 16]. The plants exhibit sclerophylly with leaves that are usually small and thick [1, 12, 14, 15] and with a low nitrogen content [11]. *Kerangas* trees are often densely packed, giving the appearance of a pole forest [1, 15, 17]. Various *Kerangas* formations have been recorded in Borneo, including dryland *Kerangas* formations such as coastal and inland *Kerangas* forests and open “*Padang*” forests, as well as wetter *Kerangas* formations, known as “*Kerapah*” [2, 15, 17].

Kerangas soils derive from siliceous parent material and thus are typically low in bases and nutrients [1, 17]. Moran et al. [7] and Metali et al. [18] reported that nitrogen concentrations in soil solution and topsoils, respectively, from *Kerangas* forests in Brunei Darussalam were lower than values recorded from mixed dipterocarp forest soils. Similarly, in the Kabili-Sepilok Forest Reserve, Sabah, *Kerangas* soils were recorded as least fertile compared to alluvial and sandstone forests [19]. The free-draining sandy *Kerangas* soils allow nutrients to leach readily [17, 20]. While edaphic variation over local and landscape scales is known to drive habitat associations of Bornean tree species [21, 22], similar studies on *Kerangas* forests remain few. Floristic variation of plots in *Kerangas* forests in Sarawak and Brunei have been shown to be influenced by soil type and elevation [3], while tree species in heath forests in Central Kalimantan are known to respond to humus depth and relative elevation [6].

In Brunei Darussalam, *Kerangas* forests cover an area of approximately 3000 ha, accounting for only 1% of Brunei's forests [16, 23]. The *Kerangas* forests of the White Sands in Tutong stretch along the Tutong-Belait Highway in an area which is approximately 11.0 km long and 1.6 km wide [24]. The Tutong White Sands area has been the site of several studies on *Nepenthes* (Nepenthaceae) and other carnivorous, myrmecophytic, and parasitic plants [25–28]. As a rare ecosystem, *Kerangas* forests harbor endemic plants and animals and are therefore of high conservation value.

Here, we present the first study on the composition of the tree communities in the Tutong White Sands in Brunei Darussalam. The main aim of our study was to investigate floristic patterns in the tree communities of the *Kerangas* forests in the Tutong White Sands in response to differences in selected soil and environmental variables. We focused on three research questions: (1) Do soil and environmental variables differ among the six plots? (2) Do measures of forest structure (stem diameter and basal area) and tree floristic diversity differ among the six plots? (3) Is differentiation of tree floristic patterns associated with underlying differences in soil and environmental variables?

2. Study Sites

A total of six 20 m × 20 m plots were established in the Tutong White Sands area, which is located along the Tutong-Belait Highway (Figure 1). The Tutong White Sands area is uniquely characterized by two habitat types: (1) an open area comprised of shrubby vegetation on strikingly white silica sands and (2) intact *Kerangas* forests where the forest canopy was still intact and the trees were approximately 15–20 m tall [29]. The open habitat is located along the roadsides of the Tutong-Belait Highway and is characterized by islands of native vegetation consisting of shrubs and a few trees growing among the exposed white sands. The vegetation is mainly dominated by *Sindora* (Leguminosae-Caesalpinioideae), *Dillenia* (Dilleniaceae), and *Glochidion* (Phyllanthaceae) species [30, 31]. This open shrubby vegetation bears some similarity to "*Padang*" vegetation which is largely dominated by shrubs and trees which are up to 5 m tall over sparse grass and sedges [15–17]. The intact *Kerangas* forests lie beyond this open and shrub-dominated area, at a distance of approximately 0.5 km away from the roadsides.

Our six plots were set up in these interior *Kerangas* forests and ranged in elevation from 18 to 27 m a.s.l., with slopes ranging from 1.35° to 4.06° [29]. Plots were selected randomly and avoided areas that have been affected by severe human disturbance or fires or showed signs of *Acacia* invasion. Plot distances ranged from 0.5 to 5.0 km, with the furthest distance being between plots 2 and 6.

3. Methods

3.1. Soil Analyses and Measurements of Environmental Variables. Each 20 m × 20 m plot was subdivided into four 10 m × 10 m subplots, and soils were sampled from three random points within each subplot at a depth of 0–15 cm using a screw auger. Soils from each subplot were mixed thoroughly to form one bulk sample per subplot ($n = 24$ samples for all six plots). Soil sampling was conducted during the wet season in November 2013, during which two plots (Plots 2 and 3) were waterlogged. Soil samples for these two plots were therefore taken from a nonwaterlogged area just outside the plots.

A portion of the fresh soil samples was used to determine pH and gravimetric water content (GWC; [32]). The remaining portion of the fresh soil samples was air-dried in the shade for at least 3 weeks before further analysis. Air-dried soil samples were ground using a pestle and mortar, sieved through a 250 μm sieve, and further ground using a ball mill to obtain fine soil samples for nutrient analysis. Fine soil samples were analyzed to determine the concentrations of total phosphorus (P) and total nitrogen (N). The fine soils were acid-digested for 2 h at 360°C using a Block Digestor BD-46 (LACHAT Instruments, CO, USA) and the total P and N concentrations in the acid-digested samples were then determined using a Flow Injector Analyzer (FIAstar 5000, Hoganas, Sweden).

In addition to the soil variables, two environmental variables (litter depth and % canopy openness) were determined for each plot. Litter depth was measured using a ranging pole as described by Martin et al. [33] and percentage canopy openness was determined using a spherical densiometer (Model A, Forest Densiometers, Bartlesville, OK, USA).

3.2. Tree Census. Within each plot, all trees of ≥5 cm diameter at breast height (DBH) were tagged, measured to determine DBH, and identified. The basal area of each tree was calculated using the following equation: basal area (B.A.) = $\pi\ (\mathrm{DBH}/2)^2$, and total basal area (m^2) was then calculated for each plot. We determined the size distributions of trees according to DBH for each plot, with juvenile trees defined as all trees of <10 cm DBH, and adult trees are those of DBH >10 cm [34]. Trees with more than 50 cm DBH are classified as "large trees" [35]. Field identification of all tagged trees was conducted with the assistance of Brunei National Herbarium (BRUN) botany staff, and voucher specimens collected were further identified at BRUN.

3.3. Statistical Analyses. The significance of differences among plots in DBH and basal area was analyzed using one-way ANOVA in R 3.2.2 [36]. Both DBH and basal area data were $\log_{10}$-transformed to satisfy assumptions of normality and equal variances before one-way ANOVA. Species richness and abundance of trees for each plot were determined as the number of species and number of individuals in each plot, respectively. Three diversity indices were determined using the R vegan package version 3.2.2 [37]: Shannon's index, inverse Simpson index, and evenness. The significance of differences in species richness, abundance, and diversity indices among plots was analyzed by one-way ANOVA. The

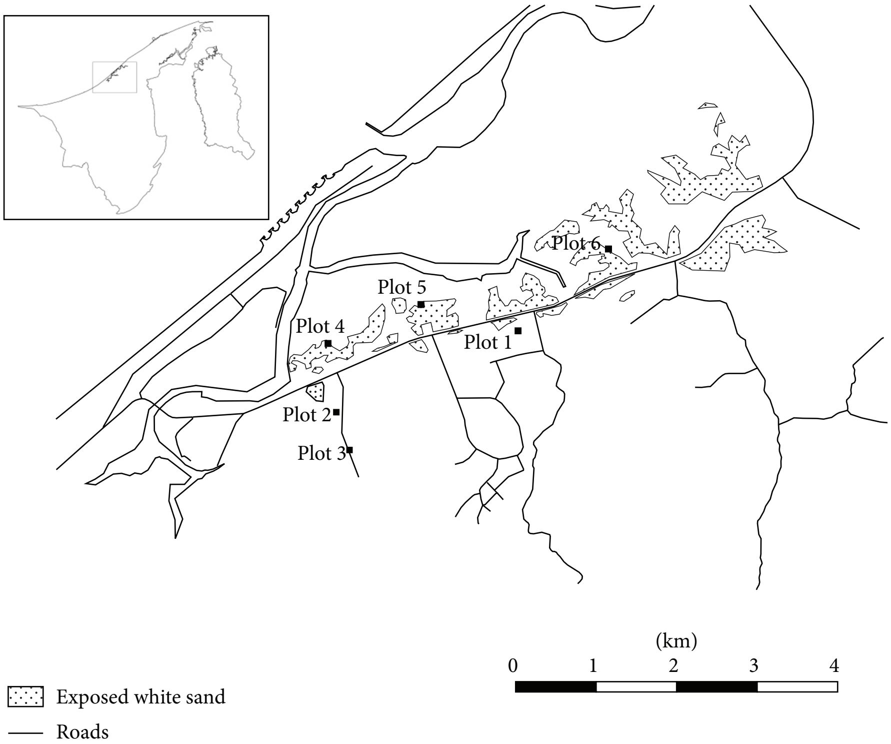

Figure 1: Location of the study sites in *Kerangas* forests of the Tutong White Sands along the Tutong–Belait Highway. Six 20 m × 20 m plots were established within intact *Kerangas* forests, and adjacent to the exposed white sands area. The location of the Tutong White Sands within Brunei Darussalam is shown in the inset.

significance of differences in soil variables (total N, total P, pH, and GWC) and environmental variables (canopy openness and litter depth) among plots was determined separately by one-way ANOVA. All data met the assumptions for these tests.

All soil and environmental variables were subjected to a principal component analysis (PCA) to determine which variable/s accounted for the most variation in the dataset. Nonmetric multidimensional scaling (NMDS) ordination was then used to map tree species in relation to soil and environmental variables using the R vegan package version 3.2.2 [37].

4. Results

4.1. Differences in Soil and Environmental Variables. Soil variables differed significantly among the six plots (Table 1). Plot 6 had the highest concentrations of both total N and P concentrations (mean total $N = 10.37 \pm 0.44\,\text{mg g}^{-1}$, mean total $\text{P} = 0.17 \pm 0.01\,\text{mg g}^{-1}$) and the lowest pH (mean pH = 3.85 ± 0.28) and soil GWC (mean GWC = 14.70 ± 1.12%). The lowest total N was in Plot 4 (mean total $N = 0.28 \pm 0.06\,\text{mg g}^{-1}$) and the lowest total P was in Plots 3 and 4 (mean total $\text{P} = 0.03 \pm 0.003\,\text{mg g}^{-1}$, $0.03 \pm 0.01\,\text{mg g}^{-1}$, resp.). The highest soil pH was in Plot 1 (mean pH = 4.70 ± 0.27), while Plot 4 had the highest soil GWC (mean GWC = 88.70 ± 1.70%).

Similarly, environmental variables differed significantly among the six plots (Table 1). The highest mean percentage canopy openness was in Plot 2 (14.1% ± 1.26%), whereas the lowest mean was in Plot 5 (0.44% ± 0.17%). Plot 5 had the deepest litter layer (mean litter depth = 0.57 ± 0.06 m) and Plot 4 had the shallowest little layer (mean litter depth = 0.15 ± 0.03 m).

Together, the first two axes of the PCA accounted for 68.3% of the variation in soil and environmental variables (Table 2). PC1 accounted for 40.0% of the variation and comprised a gradient of increasing total N and total P concentrations and decreasing soil GWC. PC2 accounted for 28.3% of the variation and represented a gradient of increasing pH. In the PCA biplot (Figure 2), the most influential variable with the longest arrow was pH. Litter depth, total P concentration, and total N concentration were inversely related to percentage canopy openness and GWC.

4.2. Variation in Stem Abundance, Diameter, Basal Area, and Size Class Distributions. A total of 296 individual trees ≥5 cm DBH were censused in the six 20 m × 20 m plots in the Tutong White Sands. Both mean DBH and the mean basal area of trees were highly significantly different among the six plots ($P < 0.001$; Table 3). The largest mean DBH and mean basal area were recorded in Plot 6 (DBH: 20.9 ± 2.2 cm and basal area: $458.14 \pm 81.45\,\text{cm}^2$). Plot 4 had the smallest mean DBH (13.0 ± 1.3 cm) and mean basal area ($209.75 \pm 52.92\,\text{cm}^2$; Table 3). The highest total basal area was recorded in Plot 5 ($2.01\,\text{m}^2$) and the lowest in Plot 3 ($0.45\,\text{m}^2$; Table 3).

Size class distributions based on DBH differed between plots. Juvenile trees with DBH < 10 cm were most abundant

TABLE 1: Soil and environmental variables (mean ± SE) in six plots in the Tutong White Sands. F and P values from one-way ANOVA are shown for each variable. Different superscript letters within a column indicate significant differences at $\alpha = 0.05$.

	Soil and environmental variables					
Plot number	Total nitrogen (mg g^{-1})	Total phosphorus (mg g^{-1})	pH (units)	GWC (%)	Canopy openness (%)	Litter depth (m)
1	3.65 ± 2.20^{bc}	0.12 ± 0.040^{bc}	4.70 ± 0.27^{a}	47.3 ± 22.70^{ab}	7.00 ± 1.15^{bc}	0.52 ± 0.01^{ac}
2	0.44 ± 0.23^{c}	0.04 ± 0.003^{ce}	4.00 ± 0.04^{ab}	66.8 ± 3.24^{a}	14.10 ± 1.26^{a}	0.39 ± 0.04^{ac}
3	0.48 ± 0.32^{c}	0.03 ± 0.003^{de}	4.00 ± 0.11^{ab}	73.1 ± 2.99^{a}	12.30 ± 3.03^{ab}	0.33 ± 0.03^{bc}
4	0.28 ± 0.06^{c}	0.03 ± 0.010^{de}	3.88 ± 0.11^{bc}	88.7 ± 1.70^{a}	6.91 ± 1.37^{bc}	0.15 ± 0.03^{b}
5	7.58 ± 1.20^{ab}	0.14 ± 0.020^{ab}	4.45 ± 0.03^{ab}	19.6 ± 3.43^{b}	0.44 ± 0.17^{c}	0.57 ± 0.06^{a}
6	10.37 ± 0.44^{a}	0.17 ± 0.009^{ab}	3.85 ± 0.28^{bc}	14.7 ± 1.12^{b}	5.25 ± 0.82^{bc}	0.56 ± 0.07^{a}
F value	20.42	10.19	4.04	9.71	9.85	14.11
P value	<0.001	<0.001	<0.05	<0.001	<0.001	<0.001

TABLE 2: Component loadings for first two principal components, PC1 and PC2, from principal component analysis of soil and environmental variables. PC1 and PC2 account for 40.0% and 28.3% of total variance, respectively. Variables with the highest loadings are indicated in bold.

Variables	PC1	PC2
Total nitrogen	**0.47**	−0.32
Total phosphorus	**0.48**	−0.14
pH	0.24	**0.91**
Gravimetric water content	**−0.47**	0.13
Canopy openness	−0.33	0.03
Litter depth	0.41	0.17

TABLE 3: Mean diameter at breast height (DBH), mean basal area, and total basal area of trees in six plots in the Tutong White Sands. Total basal area of a plot was calculated from the sum of basal areas of all trees within the plot. Different superscript letters indicate significant differences in plot mean values at $\alpha = 0.05$.

Plot number	Mean DBH (cm)	Mean basal area (cm^2)	Total basal area (m^2)
1	18.3 ± 1.7^{ad}	356.2 ± 75.8^{ad}	1.50
2	14.9 ± 1.0^{acd}	235.0 ± 37.4^{acd}	1.72
3	15.2 ± 1.7^{acd}	224.3 ± 47.7^{acd}	0.45
4	13.0 ± 1.3^{c}	209.7 ± 52.9^{c}	1.30
5	14.3 ± 1.3^{abc}	260.9 ± 56.3^{abc}	2.01
6	20.9 ± 2.2^{d}	458.1 ± 81.5^{d}	1.47

in Plot 5 (55.3% of stems, $n = 42$; Figure 3). In contrast, large trees of DBH ≥50 cm were only recorded in Plot 1 (DBH = 59.1 cm), Plot 4 (DBH = 51.4 cm and DBH = 53.9 cm), and Plot 5, the latter of which recorded the largest tree in all plots (DBH = 65.2 cm; Figure 3). All individuals in Plot 3 were of DBH less than 30 cm.

4.3. Tree Species Richness and Diversity. A total of 78 species of trees with ≥5 cm DBH were recorded in the six plots, representing 38 families and 59 genera. Of these, 69 (88.5%) of the tree species were identified to the species level and nine (11.5%) were identified to the genus level only.

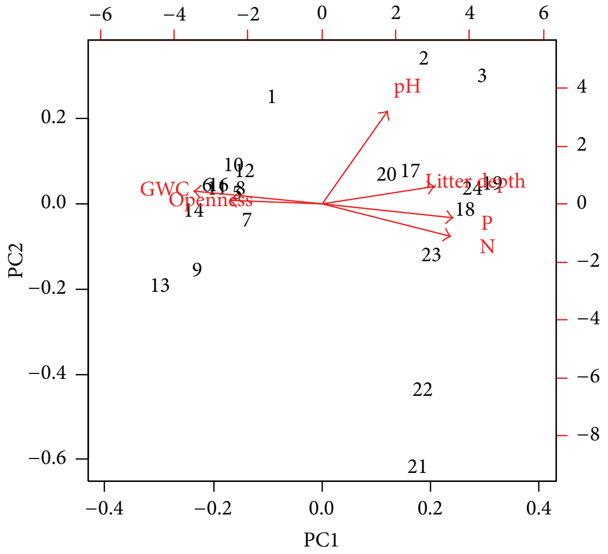

FIGURE 2: Principal component analysis biplot of soil and environmental variables in 24 subplots in the Tutong White Sands. Numbers denote 24 subplots. Variables are as follows: N: total soil N concentration, P: total soil P concentration, GWC: gravimetric water content, and openness: canopy openness.

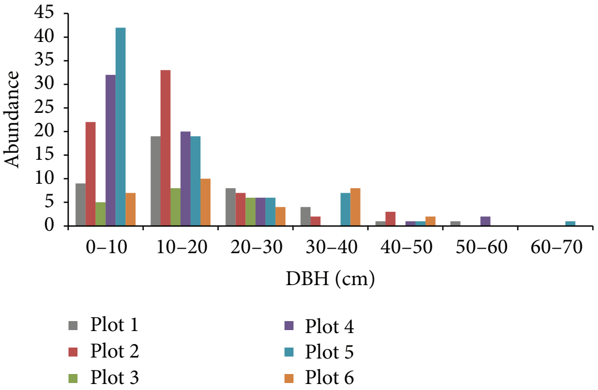

FIGURE 3: Size class distributions of trees in different DBH (cm) classes in six plots in the Tutong White Sands. Trees with DBH less than 10 cm were classified as juveniles, while trees greater than 50 cm were classified as large trees.

Table 4: Species richness, abundance, Shannon's index, evenness, and inverse Simpson's index of trees in six plots in the Tutong White Sands. Values are mean ± SE. Within each column, values followed by different letters are significantly different at $\alpha = 0.05$.

Plot number	Species richness	Abundance	Shannon's index	Evenness	Inverse Simpson's index
1	8.0 ± 0.8^{abcd}	10.5 ± 1.3^{abd}	1.99 ± 0.09^{ac}	0.96 ± 0.01^{a}	6.80 ± 0.55^{ab}
2	9.8 ± 1.4^{acd}	16.8 ± 2.4^{ab}	2.14 ± 0.14^{ab}	0.95 ± 0.01^{a}	8.00 ± 1.19^{a}
3	1.3 ± 0.3^{e}	4.8 ± 1.3^{cd}	0.13 ± 0.13^{e}	0.18 ± 0.18^{c}	1.12 ± 0.12^{c}
4	7.3 ± 1.0^{bcd}	15.3 ± 2.3^{ab}	1.70 ± 0.16^{bcd}	0.86 ± 0.03^{bc}	4.55 ± 0.88^{b}
5	12.0 ± 1.5^{a}	19.0 ± 3.1^{a}	2.28 ± 0.11^{a}	0.93 ± 0.02^{ab}	8.06 ± 0.94^{a}
6	4.5 ± 0.7^{be}	7.9 ± 2.3^{bc}	1.38 ± 0.11^{d}	0.94 ± 0.02^{ab}	3.72 ± 0.32^{bc}

The most abundant species was *Combretocarpus rotundatus* (Miq.) Danser (family Anisophylleaceae, $n = 27$). In total, 32 species were recorded as singletons, represented only by a single individual within all six plots. The family Annonaceae was the most species-rich, with eight species recorded within the six plots: *Alphonsea* sp., *Goniothalamus andersonii* J. Sinclair, *Mezzettia havilandii* (Boerl.) Ridl., *Mezzettia umbellata* Becc., *Polyalthia* sp., *Xylopia coriifolia* Ridl., *Xylopia malayana* Hook.f. & Thomson, and *Xylopia* sp.

The mean species richness (F value $= 14.32$, $P < 0.001$), abundance (F value $= 6.39$, $P < 0.01$), evenness (F value $= 9.07$, $P < 0.001$), diversity (Shannon's index: F value $= 39.38$, $P < 0.001$), and Inverse Simpson's index (F value $= 12.92$, $P < 0.001$) differed significantly among the six plots (Table 4). Plot 5 had the highest mean species richness, abundance, and diversity, whereas Plot 1 had the highest evenness value. Plot 3 had the lowest species richness, abundance, evenness, and diversity.

There was considerable variation seen in the tree community composition, with no two plots showing the exact same species composition. Plot 1 was dominated by *Dactylocladus stenostachys* Oliv., *Syzygium caryophylliflorum* (Ridl.) Merr. & L.M. Perry, and *Santiria griffithii* Engl. *Lophopetalum beccarianum* Pierre was the most abundant tree species in Plot 2, followed by *C. rotundatus* and *Madhuca curtisii* (King & Gamble) Ridl. Only two species were found in Plot 3, which was strongly dominated by *C. rotundatus* ($n = 18$). *Chionanthus ramiflorus* Roxb. ($n = 17$) was the most abundant tree species in Plot 4, followed by *Calophyllum obliquinervium* Merr. and *Ilex cymosa* Blume. Plots 5 and 6 were dominated by *Stemonurus malaccensis* (Mast.) Sleumer and *Gluta beccarii* (Engl.) Ding Hou, respectively.

4.4. Differences in Floristic Diversity in Relation to Habitat Variables. The NMDS ordinations showed a clear separation of tree species in the six plots, indicating that tree community compositions in the Tutong White Sands were highly varied (Figure 4). The two species present in Plot 3 (*Ploiarium alternifolium* (Vahl) Melchior and *C. rotundatus*) were clearly distinct and unrecorded from the other five plots. Total N concentrations and percentage canopy openness appeared to be the most influential habitat variables affecting tree community composition at the Tutong White Sands plots. In particular, total N concentrations correlated significantly with species in Plots 5 and 6 (peaty plots), while percentage canopy openness correlated significantly with species in Plot 2 (swampy plots). The effect of total N concentrations was opposite to that of percentage canopy openness. The species codes for Figure 4 and the full species checklist are provided in Supplementary Appendix 1.

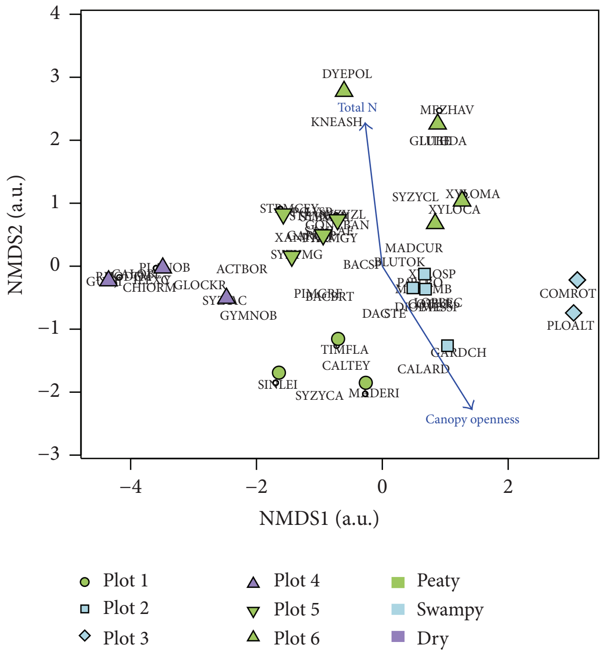

Figure 4: Nonmetric multidimensional scaling (NMDS) of tree species in relation to soil and environmental variables. Different symbols denote the six plots, while the habitat conditions of the plots are denoted by different colours. Species present in the Tutong White Sands plots are denoted by species code in the NMDS ordination space. The species code and full checklist are provided in Supplementary Appendix 1 in Supplementary Material available online at http://dx.doi.org/10.1155/2015/807876.

5. Discussion

5.1. Do Soil and Environmental Variables Differ between Plots? There was significant variation in soil physical properties (GWC and pH) and soil nutrient concentrations among the six studied plots in the Tutong White Sands. The range of GWC values in the six plots was comparable to values recorded from *Kerangas* forests in Bukit Sawat and Sungai Mau, Brunei Darussalam [38, 39], as well as those observed from *Kerangas* forests in Brunei and Sarawak [18, 40]. The range of pH values we recorded (3.85–4.7) is consistent with those from other Bornean heath forests [19, 31, 40, 41] and Amazonia *caatinga* [42, 43].

The concentrations of total N and P were low in Plots 2 and 3, but high in Plots 1, 5, and 6. The low soil nutrient concentrations in the swampy plots (Plots 2 and 3) reflected the low nutrient availability in waterlogged soils [16, 44–46]. Moran et al. [7] and Coomes and Grubb [42] reported that there were low levels of available N in the heath forests of Badas, Brunei, and Amazonia *caatinga*, respectively, because of waterlogging. Low levels of N and P were similarly recorded in another study at the intact *Kerangas* forests at the Tutong White Sands [43], as well as in *Kerangas* forests at Gunung Mulu National Park, Sarawak [41]. Conversely, the high concentrations of total N and P in Plots 1, 5, and 6 were likely because of the deeper litter layers in these plots [7, 26].

The PCA biplot revealed that both soil GWC and percentage canopy openness were inversely related to total N, total P, and litter depth. Plots with high soil moisture content (e.g., Plots 2 and 3) may have slow rates of litter decomposition and nutrient recycling [47, 48], thus resulting in low concentrations of total N and P. Areas with forest gaps (e.g., Plot 3) may have low nutrient concentrations because of the lack of canopy cover and a shallow leaf litter layer. Similar findings were recorded in exposed heath forests, or *Padang* vegetation, at the Bako National Park, Sarawak, where high canopy openness resulted in fewer litter and lower soil nutrient concentrations [20].

5.2. Do Measures of Forest Structure (Stem Diameter and Basal Area) Differ between Plots? We detected significant variation in mean basal area, and differences in total basal area, among the six plots, largely due to differences in species composition and tree abundance [1]. Plot 6 was mainly dominated by the emergent tree *G. beccarii* (Anacardiaceae) and the subcanopy tree *X. coriifolia* (Annonaceae), most of which had a DBH of 30 cm or greater. Similarly, in the 1 ha permanent forest plot in the *Kerangas* forest at Bukit Sawat, individuals of *G. beccarii* had the largest basal areas [4].

The lowest total basal area recorded in Plot 3 was due to this plot being dominated by *C. rotundatus* (family Anisophylleaceae) trees that had a DBH of ≥10 cm and a low total abundance (19 individuals). The largest tree (DBH = 65.2 cm) recorded in the study was an individual of *Gonystylus bancanus* (Miq.) Kurz (Thymelaeaceae) in Plot 5, which recorded the highest total basal area. Locally known as "*Ramin*," *G. bancanus* is a peat swamp species [49, 50]. Its presence in the swampy parts of Plot 5 may reflect its habitat preference for swampy conditions. Similarly, *Calophyllum ardens* P. F. Stevens (family Calophyllaceae) has been recorded in a peaty habitat [50] and was able to grow well in Plot 1, also a swampy plot. Large basal areas in *Kerangas* forests have been typically recorded in moist to very wet soils and in plots where one or a few species are strongly dominant [1, 3, 5].

5.3. Do Tree Diversity and Community Compositions Differ in the Tutong White Sands? Our results indicated that mean species richness, abundance, evenness, and diversity differed significantly among all six plots in the Tutong White Sands. Each plot had different tree community composition and was dominated by different species. This finding is important, as it illustrates the potentially high diversity and species turnover within this ecosystem.

C. rotundatus was the most abundant tree species in the six plots and was dominant in Plot 3. Among the six plots studied, Plot 3 was continually waterlogged but located near an open and dry area that was mainly dominated by *P. alternifolium* (family Bonnetiaceae) and *Dillenia suffruticosa* (Griff.) Martelli (Dilleniaceae). Saito et al. [51] reported that, during seed germination, both *C. rotundatus* and *P. alternifolium* were able to tolerate high soil temperature, high radiation, and drought. Additionally, *C. rotundatus* and *P. alternifolium* are peat swamp species that have been shown to thrive in flooded conditions [11, 49, 52, 53].

Most species recorded in Plot 2 were peat swamp species, such as *C. rotundatus*, *Dryobalanops rappa* Becc. (family Dipterocarpaceae), *D. stenostachys* (family Penaeaceae), *M. umbellata* (family Annonaceae), *Parishia maingayi* Hook.f. (family Anacardiaceae), and *Parastemon urophyllus* (Wall. ex A.DC.) A.DC. (family Chrysobalanaceae). The large number of peat swamp species in this part of the Tutong White Sands may indicate the presence of peaty soils, in addition to the podzolized white sands that are prevalent in this ecosystem. Davies and Becker [4] reported the presence of swampy areas in the *Kerangas* forests in Bukit Sawat and Badas, with more peat swamp tree species recorded than at Badas. Peat soils have similarly been recorded in other *Kerangas* forests of Sarawak and Brunei [1, 6, 23], with some *Kerangas* forests having a shallow peat layer (<100 cm deep), while others show deeper peat layers (>150 cm deep) [1]. The depth of the peat layer has been shown to affect plant species composition; for example, in peat swamp forest, the species composition varies between dryland and areas with deep peat layers [2, 54].

Plot 4 was the driest plot, and its topographic variation was smaller than that of the other plots. As a result, most of the species in Plot 4 were typical *Kerangas* species such as *Buchanania arborescens* (Blume) Blume and *Guioa bijuga* (Hiern) Radlk. (family Annonaceae), *Gymnostoma nobile* (Whitmore) L.A.S. Johnson (family Casuarinaceae), *Syzygium megalophyllum* Merr. & L.M. Perry, and *Rhodomyrtus tomentosa* (Aiton) Hassk. (family Myrtaceae), all of which are adapted to dry, nutrient-poor heath soils. *G. nobile* also has nitrogen-fixing root nodules that allow it to grow well in nutrient-poor *Kerangas* soils [5, 16, 55].

The low species richness in Plots 3, 4, and 6 was because of the dominance of *C. rotundatus* in Plot 3, *C. ramiflorus* and *C. obliquinervium* in Plot 4, and *G. beccarii* in Plot 6. Anderson [43] noted that dominance by a few species reduced plant species richness in *caatinga* in the New World tropics. In contrast, Plot 1 had high species richness and diversity, with 64% of the species recorded as singletons. Davies and Becker [4] similarly recorded high species richness and the absence of tree dominance in *Kerangas* forest at Bukit Sawat, compared with the same forest type in Badas.

5.4. Are Differences in Tree Community Compositions Related to Underlying Differences in Habitat Variables? Differences in species composition and dominance in the six plots of the Tutong White Sands were associated with total N concentrations in topsoil and percentage canopy openness. Total N concentrations appear to be highly influential on tree species present in Plots 5 and 6, possibly because these plots were peaty (Hazimah Din, pers. obs.). Peat, as undecomposed organic matter, contain high concentrations of total N, and the peaty soils in Plots 5 and 6 are thus able to support the presence of peat swamp species, *Dyera polyphylla* (Miq.) Steenisand *G. bancanus* [56]. Pribadi and Kusuma [57] also found that peat depth correlated significantly with basal area of *G. bancanus* trees in Riau province, Indonesia. The NMDS ordination also revealed that two species, *C. ardens* and *Gardenia chanii* Y. W. Low, appeared to be highly influenced by percentage canopy openness. This may indicate a habitat preference of more open canopy for these two species. However, no information is currently available in literature on the habitat preference of these species.

Despite the significant influence of total N concentrations and percentage canopy openness, the NMDS ordination has revealed clustering of tree species in a drier habitat (Plot 4) as well as the complete separation of Plot 3, which comprised only two species (*P. alternifolium* and *C. rotundatus*). These clusters appear to be not influenced by total N concentrations or percentage canopy openness. We suggest that other edaphic variables, such as topsoil cation concentrations, soil texture, and soil water availabilities, as well as other environmental factors, such as elevation, slope, and topography, that we did not measure in our study, may also be influential upon these tree species. Cation concentrations, soil texture, and soil water availabilities have been shown to influence tree species distributions in Borneo [21, 22], while topography is known to affect the spatial distribution of heath forest trees in Central Kalimantan [6]. Future studies at the Tutong White Sands should therefore aim to quantify other soil and environmental variables to further elucidate their effects on community structure and composition at this site.

Despite the influence of environmental factors upon tree species composition in these plots, we also acknowledge the potential effects of dispersal mechanisms in determining the distribution of trees at this site. Dispersal mechanisms have been shown to influence tree communities of White Sands forests in Peru and the upper Rio Negro [58, 59]. For example, *C. rotundatus* and *D. stenostachys* seeds are wind- and animal-dispersed, respectively [60], and this may influence their distribution patterns in the Tutong White Sands. However, the distance between plots in our study ranged only between 0.5 and 5 km, and so dispersal limitation may not exert too strong an influence on community compositions.

5.5. Conservation Value of the Tutong White Sands. Despite the low total abundance of trees recorded in the six plots, 16 of the 78 tree species (20.5%) found in this study were Bornean endemics: *Actinodaphne borneensis* Meisn., *C. ardens*, *Chionanthus crispus* Kiew, *Copaifera palustris* (Symington) De Wit, *Cotylelobium burckii* (Heim) Heim, *D. stenostachys*, *D. rappa*, *G. chanii, Glochidion kerangae* Airy Shaw, *G. andersonii*, *Knema ashtonii* J. Sinclair var. *ashtonii*, *Lithocarpus dasystachyus* (Miq.) Rehder, *Sarcotheca glauca* (Hook.f.) Hallier f., *S. caryophylliflorum*, *S. megalophyllum*, and *X. coriifolia. Ixora caudata* Bremek, also a Bornean endemic species, was found outside the plots. As Bornean endemics, these species are only found in Borneo, with habitats that are restricted to *Kerangas* or peat swamp forests, or both. Moreover, *C. burckii* is currently listed as an endangered species in the IUCN Red List [61], while *C. rotundatus, D. polyphylla*, and *G. bancanus* are listed as vulnerable species. These species are valuable sources of timber and latex (especially *D. polyphylla*, locally known as *Jelutong*) and are under increasing threat from overexploitation and deforestation [61].

When our findings are compared with the levels of endemicity recorded in other forest types in Brunei, it further indicated the potential conservation value of the Tutong White Sands. It has been estimated that Brunei's *Kerangas* forests may contain only a total of 300 tree species but account for 50% of Bornean endemism [62]. Most Brunei endemics have been recorded in Mixed Dipterocarp forest (54%), in contrast to 12% of Brunei endemics found in *Kerangas* forests [63]. It has been suggested, however, that *Kerangas* forests, including the Tutong White Sands, potentially contain more endemics than Mixed Dipterocarp Forests in Brunei Darussalam [63]. For example, a new Brunei endemic, a climbing epiphyte, *Hoya wongii* Rodda, Simonsson & L. Wanntorp, was recently discovered at the Tutong White Sands [64] and has, to date, not been recorded elsewhere in Borneo.

Additionally, many of the tree species we recorded in the Tutong White Sands are commercially valuable timber species, such as *C. palustris*, *D. stenostachys*, *D. rappa*, *S. glauca, Sindora leiocarpa* Backer ex K. Heyne & De Wit, *Strombosia ceylanica* Gardner, *M. curtisii*, and *X. malayana* [49, 65]. Other species found in the Tutong White Sands have medicinal value; for example, *G. andersonii* has anticancer properties [66] and *C. ardens* is thought to be a potential source of anti-HIV medicine [67]. Ecologically, some of the peat swamp species (*C. rotundatus*, *D. stenostachys*, and *X. coriifolia*) recorded in our study plots have been shown to significantly contribute to the regeneration and rehabilitation of disturbed peat swamp forests [51, 68, 69].

As an open and harsh habitat, the Tutong White Sands area has been mistakenly regarded by many as having low species richness and thus little conservation value. Our study has clearly shown that while the open and exposed areas of the Tutong White Sands may be species-poor, the intact *Kerangas* forests appear to be potentially species-rich, with high levels of endemism as well as species of medicinal and economic value. The Tutong White Sands area is currently under threat from land-use changes for road development and forest fires. Continued habitat fragmentation of the Tutong White Sands will also likely raise the risk of increased invasion by exotic Acacias, which are fast becoming a problem in coastal areas of Brunei Darussalam [16, 70–72] and within tropical Southeast Asia [73–75]. Thus, we strongly recommend that the Tutong White Sands area be acknowledged as an ecosystem with high conservation value and thus protected for its unique biodiversity and economic value.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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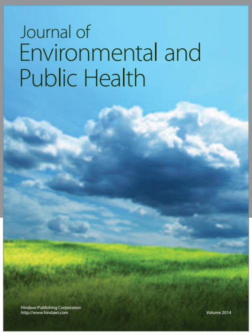
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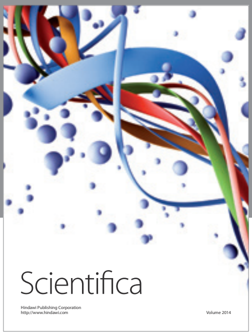
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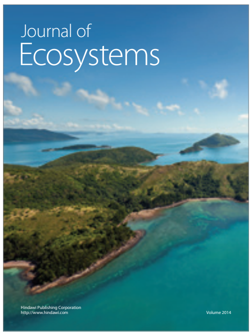
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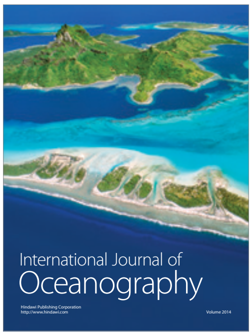
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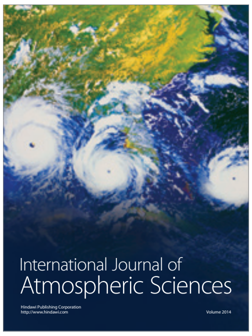
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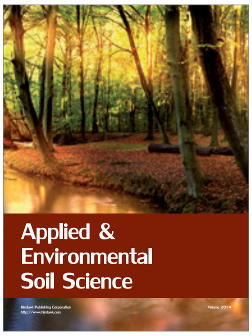
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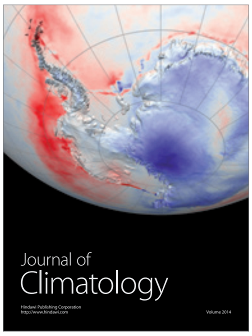
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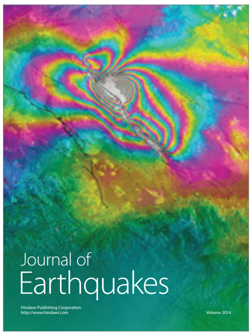
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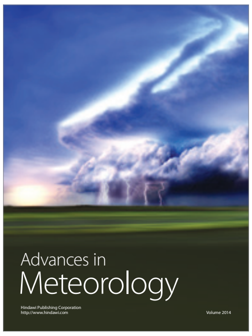
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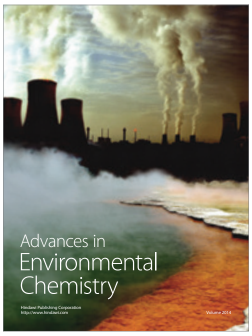
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