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REGULAR ARTICLE

Vegetation on ultramafic edaphic 'islands' in Kinabalu Park (Sabah, Malaysia) in relation to soil chemistry and elevation

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Abstract
Background and aims Kinabalu Park is the world's most species-rich hotspot with over 5000 plant species recorded for an area 1200 km^2. The aim of this study was to characterise the vegetation on ultramafic edaphic 'islands' in relation to soil chemistry and elevation.
Methods In total 87 non-permanent vegetation plots were established covering 12 ultramafic edaphic 'islands' from 474 to 2950 m asl in which 2854 plant species in 742 genera and 188 families were recorded from 14 662 collections.
Results The results show that plant diversity decreases with elevation, but a mid-elevation (circum 1500 m asl) 'hump' occurs for some plant groups (orchids, pteridophytes) as a result of the presence of cloud forests. Six main vegetation classes with associated soil types were discerned: (i) Sub-Alpine Scrub; and (ii) Graminoid Scrub, both associated with Hypermagnesic Cambisols ('hypermagnesian soils'); (iii) Montane Cloud Forest, associated with Cambisols often with accumulation of humus; (iv) Mixed Dipterocarp Forest, associated with deep Ferralsols ('laterites'); (v) Pioneer Casuarina Scrub; (vi) Mature Mixed Casuarina Forest, both associated with Hypermagnesic Leptosols.
Conclusions We hypothesised that 'adverse' soil chemistry would exacerbate vegetation stunting, and the results confirmed that stunted vegetation and elevational floristic compression occurs on chemically adverse soils (mainly hypermagnesian soils). However, no clear correlation with plant diversity was found, as some of the most 'adverse' soils on the summit of Mount Tambuyukon had up to 132 species per 250 m^2.

Keywords Edaphic factor · Floristic zonation · Serpentinite · Vegetation physiognomy

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Introduction

Ultramafic rocks consist of ferromagnesian minerals obducted at continental margins (Guillot and Hattori 2013). Soils derived from ultramafic bedrock are characterised by relatively high concentrations of trace elements (Ni, Co, Cr, Mn), major cations imbalances (high Mg:Ca molar quotients) and nutrient deficiencies (K, P) (Baillie et al. 2000; Proctor 1999, 2003). The 'edaphic factor' relates to the influence of the soil physical and chemical properties on the ecology and distribution of plants (Rajakaruna 2004). In the case of ultramafic soils, the edaphic factor and its cumulative interactions with biophysical, climatic and chemical constituents cause what has been called the 'serpentine syndrome' on the vegetation (Jenny 1980; Brady et al. 2005). Therefore, the vegetation on ultramafic soils, though immensely varied, has several traits that are universally recognised when contrasted with vegetation on surrounding non-ultramafic soils: (i) lower stature and lower biomass; (ii) higher levels of endemism; and (iii) distinct species composition (Whittaker 1954a, b; Brooks 1987; Proctor 2003; Harrison and Rajakaruna 2011). Elevation is an over-arching factor influencing the distribution of plant species but within an elevational range, the edaphic factor can 'filter' the local distribution of plant species (Jenny 1941; Kruckeberg 1986, 1991; Harrison and Rajakaruna 2011). In this study, ultramafic outcrops were conceptualised as edaphic 'islands' of contrasting soil chemistry (viz. Rajakaruna and Boyd 2008; O'Dell and Rajakaruna 2011). These edaphic 'islands' are not truly insular, but recruit plant species from the surrounding vegetation over ecological and evolutionary time when species adapt to the prevailing edaphic conditions (Harrison and Inouye 2002).

Some of the world's largest ultramafic exposures occur in Southeast Asia and occur as prominent geological features in the landscape of Sabah (Malaysia, on the island of Borneo) totalling approximately 3500 km^2 (Proctor et al. 1988; Repin 1998). Sabah has an estimated 8000 plant species of which over half are known to occur on ultramafic soils (Van der Ent et al. 2015a). Mount Kinabalu is located in the northeastern part of Sabah (at 6°5′N 116°33′E) inside Kinabalu Park, which has an area of 754 km^2, and also includes Mount Tambuyukon (2579 m asl). The Park is recognised as a major centre of plant diversity with more than 5000 species in 1000 genera and 200 families recorded to date (Beaman and Beaman 1990; Beaman 2005) of which 2542 plant species have been found on the ultramafic soils inside the Park (Van der Ent et al. 2015a). Several characteristics are thought to be the primary precursors for this exceptional plant diversity: (i) different climatic zones present from lowland to sub-alpine; (ii) recent mountain-formation during the late Pliocene-Pleistocene; (iii) high geodiversity, particularly ultramafic soils; (iv) precipitous morphology causing isolation; (v) proximity of ancient mountain ranges forming a 'species dispersion base'; (vi) geographic isolation from other high-elevation tropical regions; and (vii) climatic instability caused by periods of glaciation and frequent catastrophic climatic oscillations (El Niño events) (Beaman and Beaman 1990; Wong and Phillipps 1996; Beaman 2005). It has been proposed that isolated ultramafic outcrops in conjunction with elevation may have stimulated the evolution of localized edaphic endemic plant taxa (Beaman and Beaman 1990). Of the 18 most important localities for plant diversity in Kinabalu Park that Beaman and Beaman (1990) list, 11 are wholly or largely ultramafic and three localities have 30 % of their species known only from that locality, pointing to the importance of ultramafic soils in plant diversification and the extreme localisation of the plant diversity. In total ultramafic outcrops cover 151 km^2 in Kinabalu Park, and occur like a collar around the granite Kinabalu massif and forms Mount Tambuyukon, which is entirely ultramafic (Repin 1998; Van der Ent et al. 2014). The ultramafic outcrops range in size from 0.6 km^2 (Mesilau) to 89 km^2 (Mount Tambuyukon) (Table 1).

Kinabalu Park has a humid tropical climate with a relatively weak influence from the Asiatic monsoon, with a mean monthly air temperature of 20 °C throughout the year at 1680 m asl, and a daily fluctuation of 7–9 °C (Kitayama 1991). The temperature decreases with elevation with a lapse rate of 0.55 °C per 100 m (Aiba and Kitayama 1999). Precipitation patterns are complex because of a mid-elevation cloud-zone, but differs little with elevation with mean annual rainfall of 2380 mm at 1560 m and 2253 mm at 2700 m asl (Kitayama 1991; Kitayama et al. 1998; Kitayama and Aiba 2002). The elevational demarcation of vegetation zones differs on Mount Kinabalu from other mountains in the region (Kitayama 1991) as a result of its greater overall height and associated climatic effects. On Mount Kinabalu this could be (partly) explained by the 'Massenerhebung Effect' (or 'mountain mass elevation') in which vegetation zonation is further shifted upwards on larger mountain massifs (Grubb 1971, 1977). At the same elevation on Mount Kinabalu, the vegetation on ultramafic soils is often shorter than on non-ultramafic soils. This is particularly evident across geological boundaries as, for example, occurs on the boundary between ultramafic and granite bedrock on Kinabalu's south slope. Such differences between ultramafic and non-ultramafic soils are not evident everywhere in tropical regions, for example in New Caledonia, the forest on ultramafic and non-ultramafic soils has roughly 30 %

Table 1 Overview of ultramafic edaphic ‘islands’ and plot locations and sizes with soil types, and vegetation classes

Site	Ultramafic island	‘Island’ size (km^2)	Number of plots	Plot size (m^2)	Altitude (m asl)	Soil type	Vegetation classes	Canopy height (m)
1	Mount Tambuyukon (*summit*)	89.09	11	250	2359–2534	Eutric Hypermagnesic Cambisol	Graminoid Scrub	<2
	Mount Tambuyukon (*slopes*)		13		1466–2491	Dystric Folic Magnesic Cambisol	Montane Cloud Forest	<20
2	Wuluh River	3.04	5	250 *[4]* 500 *[1]*	750–820	Mollic Hypermagnesic Leptosol	Pioneer Casuarina Scrub, Mature Mixed Casuarina Forest	2–20
3	Serinsim	1.48	3	2000 *[2]* 500 *[1]*	474–671	Plinthic Geric Rhodic Ferralsol	Mixed Dipterocarp Forest	>40
4	Mount Nambuyukon	5.29	2	250	1495–1839	Dystric Ferralic Cambisol	Montane Cloud Forest, Mature Mixed Casuarina Forest	<20
5	Panataran Valley	29.66	7	250	588–781	Mollic Hypermagnesic Leptosol	Pioneer Casuarina Scrub, Mature Mixed Casuarina Forest	2–20
6	Marai Parai	3.99	11	250	1606–1753	Dystric Leptic Cambisol	Graminoid Scrub, Montane Cloud Forest	<2
7	Layang–Layang	2.08	10	250	2822–2950	Eutric Hypermagnesic cambisol	Sub-Alpine Scrub, Montane Cloud Forest	2–8
8	Mesilau	0.63	5	250	1909–2067	Folic Hypermagnesic Hypereutric Cambisol	Montane Cloud Forest, Graminoid Scrub	<20
9	Bukit Babi	2.28	4	250	1877–2286	Dystric Folic Magnesic Cambisol	Montane Cloud Forest	<20
10	Bambangan	1.12	4	250	1683–2077	Mollic Hypermagnesic Leptosol	Montane Cloud Forest	<10
11	Bukit Hampuan	5.56	4	500	963–1336	Mollic Hypermagnesic Leptosol	Montane Cloud Forest	<20
12	Nalumad	1.65	4	500	754–836	Plinthic Rhodic Magnesic Ferralsol	Mixed Dipterocarp Forest	>40

species difference (Jaffré 1980), and there are often no obvious physiognomic differences except in the lower and denser canopy on the boundary between ultramafics and schist (Proctor 2003).

During 2010–2014 an extensive ecological study was conducted in Kinabalu Park. The research was wide-ranging, but focussed on the "plant-soil relationships" of the vegetation on ultramafic soils within the Park (Van der Ent et al. 2014, 2015a, b; Van der Ent and Mulligan 2015). The main aim of the work described in this paper was to characterise the vegetation on ultramafic edaphic 'islands' in Kinabalu Park in relation to soil chemistry and elevation. Specifically, we hypothesised that: (i) overall plant diversity per unit area decreases with elevation and with more chemically adverse soils; and that (ii) adverse soil chemistry would compress elevational floristic zonation.

Materials and methods

Plot census and collection of plant specimens

In total, 87 non-permanent vegetation plots were established covering all major 12 ultramafic edaphic 'islands' known in Kinabalu Park. Within each 'island' several plots were laid out (Fig. 1). The elevation ranged from 474 to 2950 m above sea level (asl). Plots were of different sizes to account for increasing tree density but decreasing diversity with elevation: 400–1000 m asl: 20 × 100 m, 1000–1600 m asl: 20 × 25 m and 1600–3000 m asl: 10 × 25 m. The plots aimed at capturing the variability within each 'island'. The total aggregate plot area was 34 250 m^2. In each plot, samples of all vascular plants (monocots, dicots, gymnosperms, and pteridophytes), including epiphytes, were collected and processed as herbarium specimens and vouchers kept at the Sabah Parks Herbarium (SNP). It was not possible to collect all epiphytes in the Mixed Dipterocarp Forest due to the very tall (>40 m) habit of the host trees. Plant specimens were also collected outside the plots if additional flowering material was required to aid identification, as well as to obtain a more complete inventory of plant species within each 'island' (but these collections were not included in the data analysis). In total, 28 897 plant specimens (14 662 unique collections) were collected from all the plots. All trees ≥4.8 cm dbh (=15 cm circumference) were enumerated and voucher specimens collected for identification purposes. The fieldwork was undertaken between January 2011 and September 2012. At each plot bedrock samples ($n = 1$), soil samples ($n = 3$), leaf litter samples ($n = 1$) and foliar samples ($n = 4–6$) were collected, as detailed separately below.

Identification of plant specimens

Plant and voucher specimens were identified at the Sabah Parks Herbarium (SNP) and the Herbarium of the Sabah Forestry Department (SAN), and by specialists from the Kew (K), Leiden (L) and Singapore (SING) herbaria. Unidentified specimens were collated as 'morpho-species' and numbered. However, virtually all (≥95 %) specimens were identified to family level and the majority (≥80 %) to genus level or species level (≥70 %). The identifications were checked against the enumeration of the flora of Mount Kinabalu (Parris et al. 1992; Wood et al. 2011; Beaman and Beaman 1998; Beaman et al. 2001; Beaman and Anderson 2004), and updated using name conventions provided on The Plant List (http://www.theplantlist.org) and family classifications following APG III (Angiosperm Phylogeny Group 2009). All data on plant collections were compiled in a database system for management.

Collection and analysis of bedrock and soil samples

In each (ultramafic) plot, three soil samples were collected at a depth of 10–20 cm from the surface. In addition, a non-ultramafic "reference dataset' was collected from around Kinabalu Park HQ and from the nearby non-ultramafic Mount Trus Madi. Samples were brought to the local field station, air-dried at room temperature to constant weight, sieved to <2 mm, shipped to Australia, and gamma irradiated at Steritech Pty. Ltd. in Brisbane following Australian quarantine regulations. The soil classification was based on World Reference Base (WRB) classification system (IUSS Working Group WRB 2015). Sub-samples of 300 mg were digested using freshly prepared 'reverse' Aqua Regia (9 mL 70 % nitric acid and 3 mL 37 % hydrochloric acid per sample) in a digestion block for 2 h and diluted to 45 mL with ultra-pure water before analysis with ICP-AES (see below) to give 'pseudo-total' concentrations (hereafter 'total' concentrations). Soil pH and electrical conductivity (EC) were obtained in a 1:2.5 soil: water mixture. Phytoavailable Ni, Co, Cr and Mn were extracted with Diethylene triamine pentaacetic acid (DTPA) according to Lindsay and

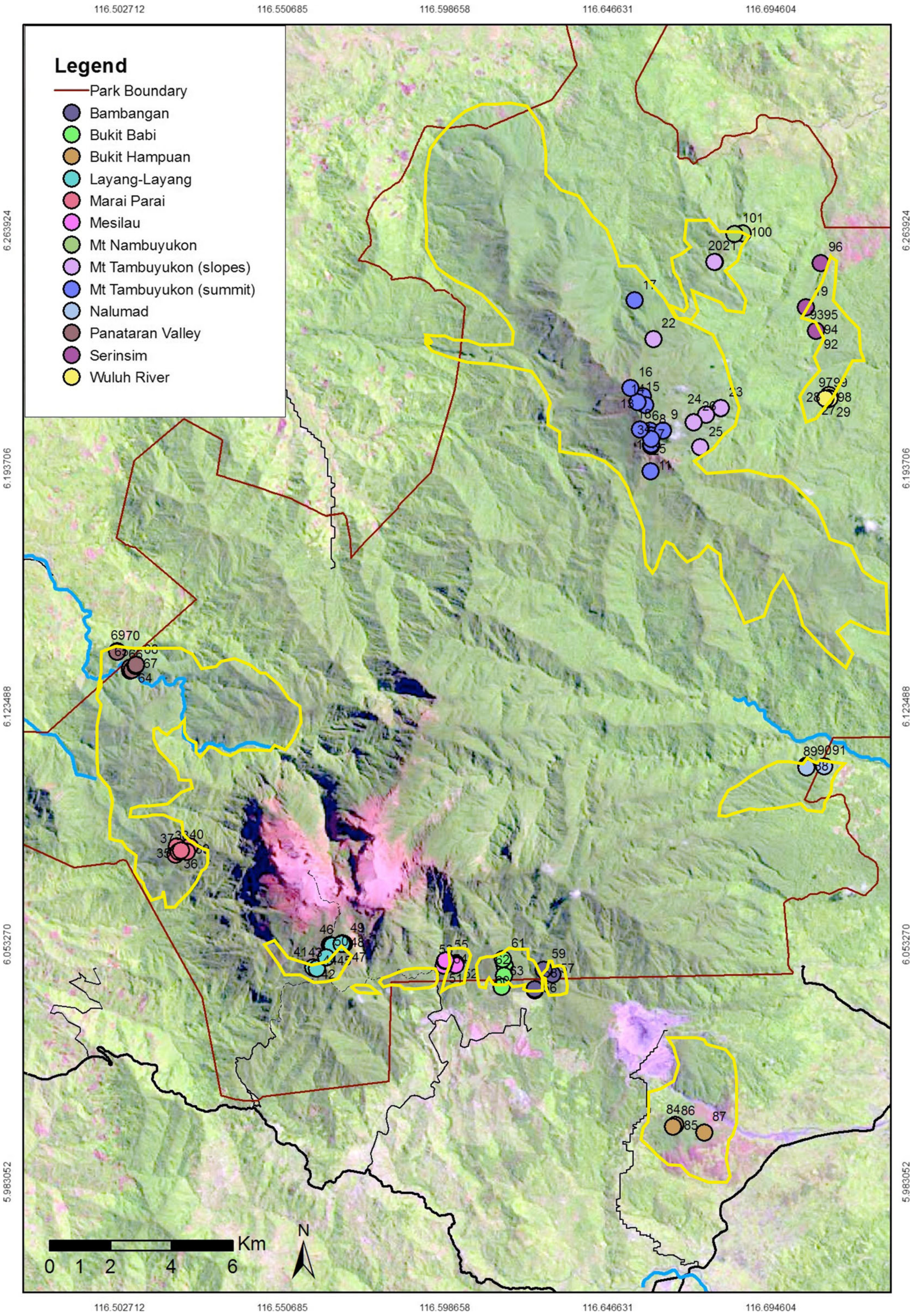

Fig. 1 Map of the study area with the ultramafic edaphic 'islands'. Plots are indicated by coloured closed *circles*. The boundary of Kinabalu Park is outlined with a *red line* whereas *yellow lines* demarcate approximate outlines of ultramafic geology

Norvell (1978), but with modifications from Bequer et al. (1995) (excluding TEA, adjusted to pH 5.3, soil:solution 5 g:25 mL). Plant-available phosphorus was extracted with the Mehlich-3 method (Mehlich 1984) and the Olsen-P method (Olsen et al. 1954). Bicarbonate-extractable K (Colwell-K) was extracted following Rayment and Higginson (1992). Exchangeable cations were extracted with silver-thiorea (Dohrmann 2006) over 16 h in the dark. Samples were agitated for method-specific times using an end-over-end shaker at 60 rpm and subsequently centrifuged (10 min at 4000 rpm). The supernatants were collected in 10 mL polyethylene tubes and aliquots analysed with ICP-AES (Varian Vista Pro II) wherein the analytical package consisted of Al, Ca, Co, Cu, Cr, Fe, K, Mg, Mn, Na, Ni, P, S and Zn. The quality controls included National Institute of Standards and Technology (NIST) and Australasian Soil and Plant Analysis Council (ASPAC) standards. Total soil carbon and nitrogen were analysed on a subset of samples from the plots. Approximately 150 mg of finely-ground (<100 μm) soil was weighed into tin foil boats and analysed on a LECO TruSpec CHN combustion analyser.

Ultramafic bedrock samples were collected from soil pits in each plot and also from around Kinabalu Park HQ/Mount Trus Madi (non-ultramafic reference). The rock samples were crushed and ground in a ball-mill to a <100-μm powder. Total elemental concentrations in rock samples (100 mg) were obtained by digestion with a mix of 4 mL 70 % nitric acid, 3 mL 37 % hydrochloric acid and 2 mL 48 % hydrofluoric acid for 2 h in a microwave, diluted to 45 mL with ultra-pure water before analysis with ICP-AES (Varian Vista Pro II) for Al, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, P, S, Si and Zn.

Collection and analysis of leaf litter and foliar samples

Leaf litter samples were collected from each plot by carefully removing un-decomposed plant material and partly-decomposed organic matter (O horizon) from a 1-m^2 area (and avoiding inclusion of any adhered mineral soil particles). Samples of leaf litter from non-ultramafic soil areas were also collected (around Kinabalu Park HQ/Mount Trus Madi) to serve as a reference. The samples were dried (60 °C for 5 days in a dehydrating oven), finely ground in an electric ring-mill with cutting blades, sieved to < 1 mm and analysed similarly to the foliar samples as detailed below.

Fully-grown leaves were collected from the five most dominant tree species (defined as those species constituting the highest combined basal area or highest total cover) in each plot. Similarly, non-ultramafic reference samples were collected from trees growing on non-ultramafic soils (around Kinabalu Park HQ/Mount Trus Madi). All foliar samples were thoroughly washed with de-mineralized water following collection to remove potential soil dust contamination and then dried at 60 °C for 5 days in a dehydrating oven and packed for transport to Australia. All samples were then crushed, and a 300 mg subsample was digested in 4 mL 70 % nitric acid and 1 mL 30 % hydrogen peroxide in a digestion microwave. Digests were diluted to 30 mL with ultra-pure water and analysed with ICP-AES (Varian Vista Pro II). The analytical package consisted of Al, Ca, Co, Cu, Cr, Fe, K, Mg, Mn, Na, Ni, P, S and Zn. The quality controls included National Institute of Standards and Technology (NIST) and Australasian Soil and Plant Analysis Council (ASPAC) standards.

Statistical analyses

The statistical analyses of plant diversity and associated environmental data were performed in Plymouth Routines In Multivariate Ecological Research (PRIMER, version 6) (Clarke and Gorley 2006), and in Canonical Community Ordination by Correspondence Analysis (CANOCO, version 5) (Šmilauer and Lepš 2014). The vegetation was classified by performing an analysis of similarity (Bray-Curtis distance) followed by hierarchical clustering, and non-metric multidimensional scaling (NMDS) ordination of the species labelled either by edaphic 'island' or vegetation class. The SIMPER function was then used to calculate individual contributions of species to the similarity and dissimilarity between groups (i.e. vegetation classes) to derive 'indicator species'. This process was undertaken separately for the presence/absence data (all occurring species) and for the quantitative tree data (using tree volume). *k*-Dominance curves were produced on the basis of quantitative tree data from the plots. These analyses were performed using PRIMER (v. 6.0). For the tree species abundance, the volume was used (calculated using the simple FAO-formula, Magnussen and Reed 2015) as: Volume = 0.42 * basal area * height) because it takes into account both diameter at breast height and the height of the trees, hence correcting for the bias because of the lower stature of trees with increasing elevation. The different plot sizes were not normalised for surface area (i.e. to 1 ha) in the vegetation classification but rather taken as single samples. Relationships between species data and environmental and soil data were analysed using Canonical Correspondence Analysis (CCA) in CANOCO (v. 5). The demarcation of altitudinal intervals of the occurrence of characteristic plant groups was calculated on the basis of the number of plots by elevation (which does not show a regular interval between circa 400–2900 m asl). Finally, a map was produced in ArcGIS 10 with Landsat (USGS EROS Data Center, NASA Landsat Program, scene LT51180561991165AAA03) data.

Results

Bedrock chemistry

Analysis of the elemental composition of bedrock samples collected from each plot (see Supplementary Table 1) confirm the ultramafic origin of the 'islands' bedrock as they showed high contents of mafic minerals: Fe (up to 14 %) and Mg (up to 39 %). When comparing overall ultramafic bedrock contents with the reference non-ultramafic bedrock samples, Al, K, Na, P and Si are significantly ($p = <0.01$) lower, whereas Co, Cr, Fe, Mn and Ni are significantly higher. Comparing the elemental contents in bedrock of the different 'islands' shows that Co is rather uniform, but Cr varies greatly, with mean concentrations ranging from 812 ± 258 μg g^{-1} (Nalumad) to 3616 ± 1719 μg g^{-1} (Bukit Babi). Nickel is also variable with means ranging from 650 ± 194 μg g^{-1} (Mount Tambuyukon slopes) to 2172 ± 900 μg g^{-1} (Nalumad). Compared to the bedrock, the soils (Table 2) are strongly enriched in most elements; for example, mean Co is 8.4 ± 0.5 μg g^{-1} in bedrock, and 249 ± 16 μg g^{-1} in soil.

Soil chemistry

Contrasting the ultramafic soil chemistry with non-ultramafic reference data from similar localities is useful because ultramafic soils are purported to pose edaphic constraints to plants. Table 2 (and Supplementary Table 2) show the soil chemistry of the vegetation classes and the edaphic 'islands'. Of the total elemental concentrations, only K is significantly ($p = <0.01$) lower, while pH, and total concentrations of Ca, Co, Cr, Fe, Mg and Mn are all significantly higher in the ultramafic soils, and total P is not significantly different. DTPA-extractable concentrations of Co, Mn and Ni are all significantly higher in the ultramafic soils. Exchangeable Al is higher in non-ultramafic soils, exchangeable Mg and Na are higher in ultramafic soils, and exchangeable Ca and K are not significantly different. The higher exchangeable Al in non-ultramafic soils could be explained by the significantly lower pH of non-ultramafic soils. Although total P does not significantly differ between ultramafic soils and non-ultramafic soils, Mehlich-3 and Olsen-P are significantly lower in ultramafic soils (overall means of 2.1 ± 0.15 μg g^{-1} versus 3.5 ± 0.80 μg g^{-1}, and 2.8 ± 0.4 μg g^{-1} versus 8.3 ± 1.3 μg g^{-1}, respectively). This might be explained by the extremely high Fe concentrations in ultramafic soils, which can reduce P-availability by occlusion in Fe-oxides (Sanchez 1976; Reed et al. 2011). It is clear from the overall comparison of ultramafic and non-ultramafic soils that the ultramafic soils are more nutrient-deficient. However, low nutrient concentrations are not just typical of tropical lowland ultramafic soils, but for most weathered tropical soils in Kinabalu Park (Aiba and Kitayama 1999).

Total soil N concentrations were universally low (0.1–0.3 % dry wt) in all 'islands' with C:N ratios of 13–19. However, these values are in the same range as in non-ultramafic soils supporting rainforest in Sarawak (0.19 ± 0.003 %N and C:N of 19.9 ± 0.9 in Read et al. 2006) and in ultramafic soils supporting *Nothofagus* -forest in New Caledonia (0.13 ± 0.005 %N and C:N 14.6 ± 0.94 in Palmiotto et al. 2008). The exception were the soils at Wuluh River that had extremely low N (0.03 ± 0.02) and a high C:N ratio (85).

Cation imbalances towards Mg are a special feature of ultramafic soils, and the overall mean Mg:Ca molar quotient in the ultramafic soils is 7 ± 1.0 whereas it is 0.3 ± 0.03 in the non-ultramafic soils. Locally, the Mg:Ca molar quotient can reach up to 136, and exchangeable Mg can be as high as 43 $cmol^{(+)}$ kg^{-1} in the ultramafic soils. However, absolute Ca concentrations are not low (overall mean of 1.17 ± 0.1 $cmol^{(+)}$ kg^{-1}), and generally at higher concentrations than in non-ultramafic soils. In addition to cation imbalances, phytotoxicity may also contribute to the edaphic factor of ultramafic soils and in particular the high concentrations of Ni, with total concentrations at an overall mean of 1436 ± 73 μg g^{-1} in ultramafic soils, and 28 ± 7 μg

Table 2 Soil chemistry associated with main vegetation classes (elemental concentrations in μg g^{-1} or cmol$^{(+)}$ kg^{-1} as means and standard error of means)

Vegetation class	Graminoid Scrub	Mature Mixed Casuarina Forest	Mixed Dipterocarp Forest	Montane Cloud Forest	Pioneer Casuarina Scrub	Sub-Alpine Scrub
Altitude (m asl)	1606–2534	718–1584	474–1504	1466–2928	586–790	2628–2950
n	17	11	12	34	6	6
pH	5.74 ± 0.11	6.25 ± 0.20	4.77 ± 0.12	5.58 ± 0.11	7.17 ± 0.21	5.28 ± 0.12
Al exch. cmol$^{(+)}$ kg^{-1}	0.03 ± 0.01	0.02 ± 0.01	0.8 ± 0.4	0.1 ± 0.02	0.01 ± 0.002	0.1 ± 0.03
Ca exch. cmol$^{(+)}$ kg^{-1}	0.6 ± 0.1	3.1 ± 0.9	0.4 ± 0.1	0.9 ± 0.1	2.0 ± 1.2	0.6 ± 0.2
K exch. cmol$^{(+)}$ kg^{-1}	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.01	0.1 ± 0.02	0.1 ± 0.01
K bicarb. μg g^{-1}	34 ± 3.3	54 ± 3.6	63 ± 5.3	42 ± 2.3	45 ± 6.6	31 ± 5.6
Mg exch. cmol$^{(+)}$ kg^{-1}	2.5 ± 0.5	11 ± 1.7	0.6 ± 0.4	2.9 ± 0.6	10 ± 2.9	2.2 ± 0.7
Mg:Ca	4.5 ± 0.8	11 ± 4.4	0.9 ± 0.4	6.1 ± 2.8	14 ± 7.1	6.3 ± 2.9
CEC	3.9 ± 0.6	15 ± 1.9	2.2 ± 0.6	4.7 ± 0.6	13 ± 3.9	3.4 ± 0.7
P ML-3 μg g^{-1}	1.3 ± 0.1	2.4 ± 0.3	1.9 ± 0.2	2.5 ± 0.6	2.9 ± 0.9	1.6 ± 0.2
Olsen-P μg g^{-1}	1.5 ± 0.2	2.2 ± 0.3	3.5 ± 0.4	3.5 ± 0.9	2.7 ± 1.1	2.9 ± 0.7
Co DTPA μg g^{-1}	23 ± 4.6	17 ± 4.1	8.2 ± 4.5	23 ± 3.9	2.9 ± 1.0	14 ± 2.3
Mn DTPA μg g^{-1}	266 ± 50	164 ± 27	57 ± 29	240 ± 31	42 ± 17	204 ± 43
Ni DTPA μg g^{-1}	75 ± 15	103 ± 18	12 ± 8	41 ± 8	35 ± 12	51 ± 15

Abbreviations: 'ML-3' is Mehlich-3 extractable P, 'DTPA' are DTPA-extractable trace elements, 'bicarb.' is $NaHCO_3$-extractable K, and 'exch.' are major cations exchangeable with silver-thiorea

g^{-1} in non-ultramafic soils, with DTPA-extractable Ni of 50 ± 4 μg g^{-1} and 0.3 ± 0.1 μg g^{-1}, respectively. Similarly Mn concentrations could contribute to phytotoxicity, with an overall mean of 3275 ± 219 μg g^{-1} for ultramafic soils and 107 ± 35 μg g^{-1} for non-ultramafic soils, and overall mean DTPA-extractable Mn of 194 ± 12 μg g^{-1} and 3.6 ± 1.1 μg g^{-1}, respectively. The soil chemistry of these main soil types in relation to the ultramafic 'islands' is discussed in more detail below.

The two 'islands' that have deep soils (Plinthic Geric Rhodic Ferralsols, Plinthic Rhodic Magnesic Ferralsols) are Serinsim and Nalumad. These 'laterite soils' consist mainly of Fe-Cr sesquioxides (total Fe 369 ± 28 mg g^{-1} and Cr 15 ± 1.2 mg g^{-1} at Serinsim), with low CEC (1.56 ± 0.3 cmol$^{(+)}$ kg^{-1}), acidic pH (~pH 4.8 ± 0.2 for Serinsim) and low exchangeable Mg (0.9 ± 0.7 cmol$^{(+)}$ kg^{-1} for Serinsim). The Mg:Ca molar quotient is also low at both locations (1.3 ± 0.5 for Serinsim) and not likely to have any major effects on the vegetation which is very tall dipterocarp forest. Despite very low concentrations of (exchangeable and extractable) nutrients, including Ca, K and P (at Serinsim Ca 0.4 ± 0.08 cmol$^{(+)}$ kg^{-1}, K 0.08 ± 0.01 cmol$^{(+)}$ kg^{-1}, P 1.4 ± 0.1 μg g^{-1}), these soils support very high biomass ecosystems. Most nutrients are likely contained in the living biomass, and recycling from leaf litter mass is fast (as evidenced by the absence of leaf litter accumulation) and efficient (as indicated by the high density of surface roots).

Soils in the montane zone (Dystric Folic Magnesic Cambisols, Mollic Hypermagnesic Leptosols), usually with build-up of mor humus, are common and widespread in Kinabalu Park, and occur in the 'islands' Bukit Babi, Marai Parai, Mount Tambuyukon (slopes), Mesilau, Bambangan, Bukit Hampuan and Mount Nambuyukon. The latter four sites, however, are derived from strongly serpentinised bedrock, and are therefore less acidic (pH 5.5–5.9) and have higher exchangeable bases (in the case of Bukit Hampuan, extremely high exchangeable Mg at 10.1 ± 3.2 cmol$^{(+)}$ kg^{-1}). In general, the montane soils are acidic (pH <6), and have an intermediate to high CEC (3–6 cmol$^{(+)}$ kg^{-1}).

The sub-alpine zone on the summit ridge of Mount Tambuyukon has shallow soils (Eutric Hypermagnesic Cambisols) that are characterised by high total and exchangeable Mg (14 ± 3.8 and 4.2 ± 0.7 cmol$^{(+)}$ kg^{-1} respectively), high but variable Mg:Ca molar quotients (6.5 ± 1.7), low CEC (6.1 ± 0.7 cmol$^{(+)}$ kg^{-1}), very high DTPA-extractable Ni (Ni 120 ± 11 μg g^{-1}), DTPA-extractable Co (35 ± 3.2 μg g^{-1}) and DTPA-extractable Mn (403 ± 29 μg g^{-1}), and are mildly acidic (pH 6.1

±0.1). DTPA-extractable Mn can reach up to 779 μg g^{-1} and may cause phytotoxicity. Similar soils occur at Layang-Layang, but these are more acidic (pH 5.1 ± 0.1), have similar Mg:Ca molar quotients (6.3 ± 2.6), but higher exchangeable Al (0.1 ± 0.04 $cmol^{(+)}$ kg^{-1}).

The soils developed over serpentinite bedrock (Mollic Hypermagnesic Leptosols) that occur in the Panataran Valley and Wuluh River have extremely high total and exchangeable Mg (Mg:Ca molar quotients of 27 ± 8.7 at Wuluh River), very low exchangeable K (0.05 ± 0.01 $cmol^{(+)}$ kg^{-1} at Wuluh River), very high CEC (16.8 ± 2.4 $cmol^{(+)}$ kg^{-1} at Panataran Valley), high extractable Ni (97 ± 13 μg g^{-1} DTPA-extractable Ni at Panataran Valley) and circum-neutral pH (pH 7.3 ± 0.2 at Wuluh River) near the surface and highly alkaline at depth (up to pH 9.8). Locally, DTPA-extractable Ni can be up to 274 μg g^{-1} at Wuluh River and 254 μg g^{-1} at Panataran Valley. The occurrences of these soils are where rivers cut through serpentinite bedrock formations, and occur mainly on the steep sides of the valleys. These soils support a highly distinctive vegetation dominated by Casuarinas (genera *Gymnostoma* and *Ceuthostoma*).

Vegetation physiognomy and altitudinal floristic zonation

Plots physiognomic and diversity features of the ultramafic edaphic 'islands' are given in Tables 3 and 4. Serinsim and Nalumad have multi-layered tall forests with three strata, whereas the lower and upper montane forest has only one stratum, and ligneous and Graminoid Scrub at Layang-Layang and Mount Tambuyukon (summit) has no closed canopy. Dominant leaf size classes range from macrophyll (lowland forest) to microphyll (upper montane forests) to nanophyll (sub-alpine zone). Epiphytes are most abundant in the upper montane (cloud) forest, a consequence of favourable climatic conditions (high humidity and precipitation) and dense vegetation structure of host trees. The lowland forests are the tallest (mean canopy height >40 m) and have a high basal area (up to 118 m^2 ha^{-1}), but a low density (with 1525 and 1718 trees ha^{-1} respectively, for Nalumad and Serinsim). The highest tree density (up to 4618 trees ha^{-1} on the slopes of Mount Tambuyukon) occurs in the upper montane forest (where the mean canopy is <10 m). Although vegetation stunting on tropical ultramafic soils is well documented, especially in conjunction with elevation (Proctor et al. 1988; Bruijnzeel et al. 1993; Proctor 2003), it is less well known that tropical ultramafic soils can also host very tall stature forest in lowland areas. Nalumad, where trees are up to 50 m tall and with a tree volume of 1989 m^3 ha^{-1}, shows that despite the low-nutrient status of the soils, these forests can be highly productive. This may be explained by the relatively benign soil chemical characteristics of deep Ferralsols (compared to, for example, Hypermagnesic Cambisols), not unlike many non-ultramafic soils derived from sedimentary bedrock. This is in contrast with the lowest tree volume in the Graminoid Scrub at Mount Tambuyukon (summit) with just 10 m^3 ha^{-1}, and several nearby plots with no trees at all. There are weak correlations between elevation and tree density ($r = 0.20$, p 0.09) and elevation and basal area ($r = -0.30$, p 0.008).

Figure 2 is an ordination incorporating all 'islands' with elevation, tree density, tree volume ha^{-1} and number of tree genera as vectors. There is an overall opposite trend between elevation and tree volume, with the highest values for the lowland forest (Serinsim and Nalumad). Further, the number of tree genera increases with tree density in many (but not all) plots. Tree density is highest at mid-elevation, whereas basal area largely follows the same trend as tree density, except at low elevation (Serinsim, Nalumad, Wuluh River and Panataran Valley) where density is low but basal area high. Figure 3 shows the frequency distribution over elevation for different plant groups. Overall, plant diversity decreases with increasing elevation; this also applies to trees-ligneous shrub species diversity and palms-rattan species diversity. However, the number of pteridophytes, orchids, grasses-cyperoids and ground herbs, which are indicative of the 'cloud-zone' in the upper montane forest, have a maximum taxon diversity in the 1332–1753 m asl zone. These results confirm earlier reports for maximum diversity of pteridophytes and orchids around 1500 m asl in Kinabalu Park (Beaman and Beaman 1990). The greatest numbers of orchid and pteridophyte species are found at Mount Tambuyukon (slopes), Mesilau and Bambangan, whereas they are almost absent at Nalumad and Serinsim (lowland forest), and also sparse at Panataran Valley and Wuluh River (due to the locally xeric conditions). The gymnosperms are most diverse between 1332 and 2534 m asl, whereas the maximum number of species of carnivorous plants (*Nepenthes*, *Drosera*, *Utricularia*) occurs in the 2206–2534 m asl zone; a result of the combination of favourable climate (very high precipitation) and low competition (stunted open vegetation).

Table 3 Plant structural and composition (density, tree basal area and volume, and major floristic groups) attributes of the ultramafic edaphic 'islands'

Site	Bambangan	Bukit Babi	Bukit Hampuan	Layang-Layang	Marai Parai	Mesilau	Mount Nambuyukon	Mount Tambuyukon (slopes)	Mount Tambuyukon (summit)	Nalumad	Panataran Valley	Serinsim	Wuluh River
Number of samples (plots)	4	4	4	10	11	5	2	13	11	4	7	3	6
Aggregate plot area (ha)	0.1	0.1	0.2	0.25	0.28	0.13	0.05	0.33	0.28	0.2	0.18	0.45	0.2
Density (trees/ha)	2940 ± 1470	3520 ± 1760	1785 ± 893	2452 ± 775	1713 ± 516	2264 ± 1012	2840 ± 2008	4618 ± 1281	1105 ± 333	1525 ± 763	1754 ± 663	1718 ± 992	1770 ± 723
Basal area m^2/plot/ha	49 ± 25	28 ± 14	35 ± 18	24 ± 8	13 ± 4	23 ± 10	85 ± 60	88 ± 24	7 ± 2	118 ± 59	26 ± 10	115 ± 67	29 ± 12
Volume m^3/plot/ha	145 ± 73	79 ± 39	229 ± 115	58 ± 18	40 ± 12	105 ± 47	603 ± 426	285 ± 79	10 ± 3	1989 ± 995	172 ± 65	1153 ± 666	129 ± 53
Casuarinas (% of total volume)	15 ± 7	0	30 ± 15	0	5 ± 2	0	22 ± 16	0	0	6 ± 3	45 ± 17	0	41 ± 17
Dipterocarps (% of total volume)	0	0	0	0	0	0	0	0	0	68 ± 34	0	47 ± 27	0
Fagaceae + Lauraceae (% of total volume)	6 ± 3	14 ± 7	6 ± 3	0	8 ± 3	12 ± 5	18 ± 13	7 ± 2	1 ± 0	0	0	5 ± 3	7 ± 3
Gymnosperms (% of total volume)	27 ± 13	16 ± 8	26 ± 13	33 ± 10	36 ± 12	26 ± 12	4 ± 3	24 ± 7	61 ± 21	11 ± 6	1 ± 0	4 ± 2	0
Myrtaceae + Ericaceae (% of total volume)	38 ± 19	64 ± 32	14 ± 7	64 ± 20	42 ± 14	23 ± 10	41 ± 29	50 ± 14	32 ± 11	4 ± 2	0	7 ± 4	5 ± 2
Other angiosperms (% of total volume)	14 ± 7	6 ± 3	24 ± 12	3 ± 1	8 ± 3	39 ± 17	15 ± 11	19 ± 5	6 ± 2	10 ± 5	54 ± 20	37 ± 22	46 ± 19

Table 4 Plant diversity (number of families/genera/species, number of orchid and pteridophyte species, number of tree species and individuals) attributes of the ultramafic edaphic 'islands'

Site	Bambangan	Bukit Babi	Bukit Hampuan	Layang-Layang	Marai Parai	Mesilau	Mount Nambuyukon	Mount Tambuyukon (slopes)	Mount Tambuyukon (summit)	Nalumad	Panataran Valley	Serinsim	Wuluh River
Families (total for 'island')	76	48	88	50	66	71	68	92	67	69	75	100	77
Families (plots)	44 ± 22	30 ± 15	50 ± 25	20 ± 6	27 ± 8	39 ± 18	41 ± 29	41 ± 11	35 ± 11	38 ± 19	32 ± 12	63 ± 36	35 ± 14
Genera (total for 'island')	155	95	178	99	128	157	136	214	125	142	150	248	163
Genera (plots)	76 ± 38	54 ± 27	77 ± 38	32 ± 10	43 ± 13	69 ± 31	65 ± 46	70 ± 19	59 ± 17	58 ± 29	46 ± 17	123 ± 71	53 ± 21
Species (total for 'island')	312	177	283	199	272	368	180	610	285	238	232	505	268
Species (plots)	114 ± 57	76 ± 38	98 ± 49	40 ± 13	56 ± 17	100 ± 45	82 ± 58	103 ± 28	72 ± 22	78 ± 39	54 ± 20	209 ± 120	68 ± 28
Orchid species (total for 'island')	75	54	5	40	51	101	13	104	47	1	11	22	23
Pteridophyte species (total for 'island')	30	12	14	44	24	51	4	58	20	8	23	19	21
Total number of tree species	27	25	70	14	23	44	22	108	20	75	30	147	25
Total number of tree individuals	265	340	350	593	369	282	116	1322	301	294	263	680	281

Figure 4 shows the relative proportions (normalised as % of total volume) of major ecological tree groups. These groups are: Casuarinas (indicative for the lowland and lower montane zone on Hypermagnesic Leptosols), Dipterocarps (typical for lowland to lower montane zone on Ferralsols), Fagaceae and Lauraceae (characteristic for the lower and upper montane zone), Gymnosperms (characteristic for the upper montane forest and sub-alpine zone), Myrtaceae and Ericaceae (characteristic for the sub-alpine zone), versus other angiosperms. Casuarinas (*Gymnostoma sumatranum*, *G. nobile* and *Ceuthostoma terminale*) are local obligate ultramafic species in Kinabalu Park, occurring only on Hypermagnesic Leptosols, mainly at Panataran Valley and Wuluh River. Elsewhere (Bambangan, Bukit Hampuan, Mount Nambuyukon), the occasional occurrence of Casuarinas is indicative of localised outcrops of strongly serpentinised bedrock. Dipterocarps are nearly absent from all 'islands' but Nalumad and Serinsim where they dominate. The Fagaceae and Lauraceae are common elements of the lower and upper montane forest (cloud forests). In total, 26 species of gymnosperms occur in Kinabalu Park, of which eight occur predominantly ('preferential') or exclusively ('obligate') on ultramafic soils (Beaman 2005). Gymnosperms become dominant with increasing elevation, although this differs slightly for the genera, with *Agathis* (Araucariaceae) typical for lower and upper montane forest zone (and one species, *A. borneensis*, occurring only in lowland forest), *Phyllocladus*, *Podocarpus*, *Dacrycarpus* are elements of upper montane forest, and *Dacrydium* is dominant in the sub-alpine zone. Finally, the Myrtaceae and Ericaceae are typical of the extremely stunted forest in the sub-alpine zone, mainly at Layang-Layang.

Vegetation classification

The vegetation was classified by hierarchical clustering (Fig. 5) and plotted in a NMDS (Fig. 6) for the total number of vascular plant species (presence/absence) at the taxonomic level of species and genera, respectively. The classification supports the distinction of six main vegetation classes: (i) Sub-Alpine Scrub; (ii) Graminoid Scrub; (iii) Montane Cloud Forest; (iv) Mixed Dipterocarp Forest; (v) Pioneer Casuarina Scrub; and (vi) Mature Mixed Casuarina Forest. Figure 7 shows typical examples of these six main vegetation classes. The demarcation of the vegetation classes is similar

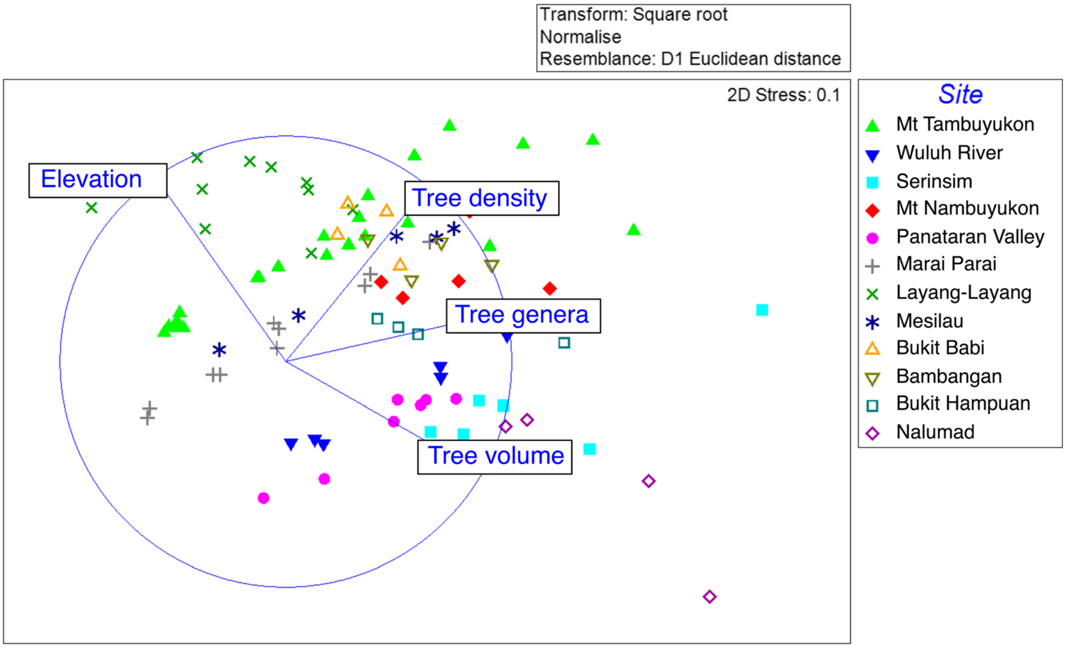

Fig. 2 NMDS of the ultramafic edaphic 'islands' with elevation (m asl), tree density (number of trees/ha), tree genera (number) and tree volume (m^3/plot/ha)

using the taxonomical ranks of both genera and species (presence/absence data), as well as by using quantitative tree data (data not shown, but see CCA-analyses further on). The NMDS graphs display a large 'montane plane' at the centre of the NMDS. This cluster encompasses lower montane and upper montane forest at Mesilau, Bukit Babi, Bambangan and Mount Tambuyukon (slopes), and mainly encloses the 'Montane Cloud Forest' vegetation class. Another 'plane' runs alongside the main 'montane plane' (e.g. of higher elevation vegetation classes) in the NMDS; that of Marai Parai and Mount Tambuyukon (summit). Marai Parai, a locality with a mosaic of landslides, has a Graminoid Scrub, that although similar in appearance to Mount Tambuyukon (summit) has floristic affinities with Casuarina-forest, and upper montane forest (older landslides) to Graminoid Scrub (young landslides). In the Graminoid Scrub, the local abundance of pitcher plants *Nepenthes rajah* and *N. villosa* (Nepenthaceae) is typical. Many of the dwarf shrubs of the graminoid vegetation occur as larger trees on lower elevations, for example, *Leptospermum javanicum*, *Dacrydium gibbsiae*, *Schima brevifolia* and *Tristaniopsis elliptica* can be stunted shrubs barely 30 cm tall, but grow as trees up to 10 m on the lower slopes. The graminoid vegetation of Mount Tambuyukon (summit) and Marai Parai is enclosed in the 'Graminoid Scrub' vegetation class. The extension of the 'montane plane' in the NMDS consists of plots at Layang-Layang with vegetation that ranges for stunted upper montane forest to species-poor short forest (with virtually only *Leptospermum recurvum* and *Dacrydium gibbsiae*), and at the highest elevations graminoid vegetation and herbaceous tufts. The latter is nested in the 'Sub-Alpine Scrub' vegetation class.

The NMDS further shows a 'lowland plane' from tall multi-layered forest (Nalumad, Serinsim) to Casuarina forest (Panataran Valley, Wuluh River), enclosing the 'Mixed Dipterocarp Forest', 'Pioneer Casuarina Scrub', and 'Mature Mixed Casuarina Forest' vegetation classes. The vegetation on Hypermagnesic Leptosols (Panataran Valley, Wuluh River) is distinctly xeric and dominated by Casuarinas and has a high frequency of myrmecophytes ('ant plants' in the genera *Hydnophytum*, *Myrmecodia*, *Dischidia*).

Supplementary Tables 6 and 7 show the results of a SIMPER-analysis using presence/absence and quantitative tree data for six vegetation classes, respectively. The result from Table 6, using all vascular plant species, because it is based on presence/absence data, is in effect a measure of fidelity (as it analyses individual occurrences per plot). Each species has therefore similar

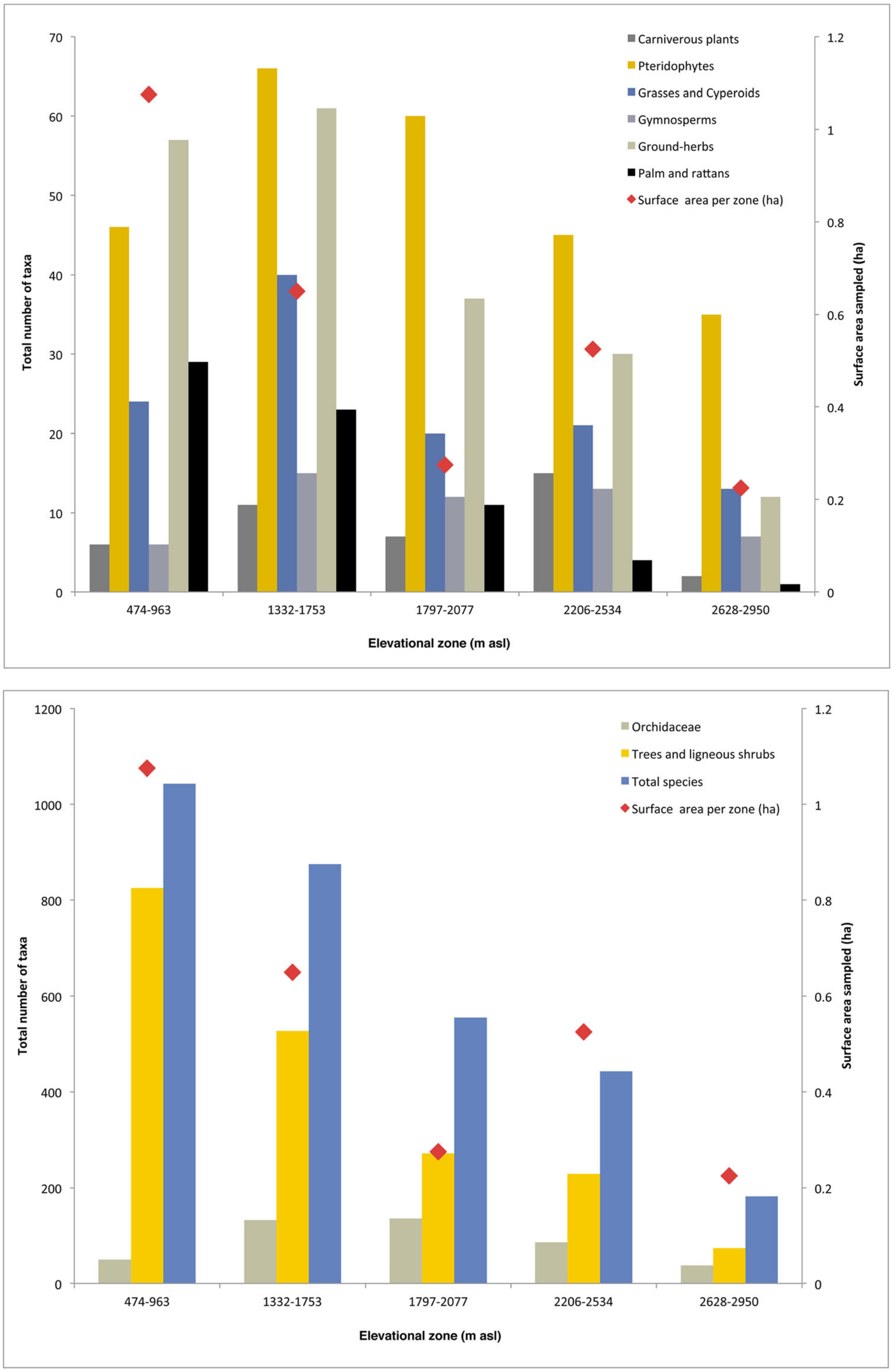

Fig. 3 Frequency distribution of plant groups over elevation. Frequency bins were determined by the elevational sequence of the plots. Carnivorous plants *n* = 126 records, Pteridophytes *n* = 424 records, Grasses and Cyperoids *n* = 289 records, Gymnosperms *n* = 233 records, Ground-herbs *n* = 439 records, Orchidaceae *n* = 843 records, Palm and rattans *n* = 142 records, Trees and ligneous shrubs *n* = 4432 records and Total species *n* = 6928. The top graph shows Carnivorous plants, Pteridophytes, Grasses and Cyperoids, Gymnosperms, Ground-herbs and Palm and rattans. The bottom graph shows Trees and ligneous shrubs, Orchidaceae, and Total species

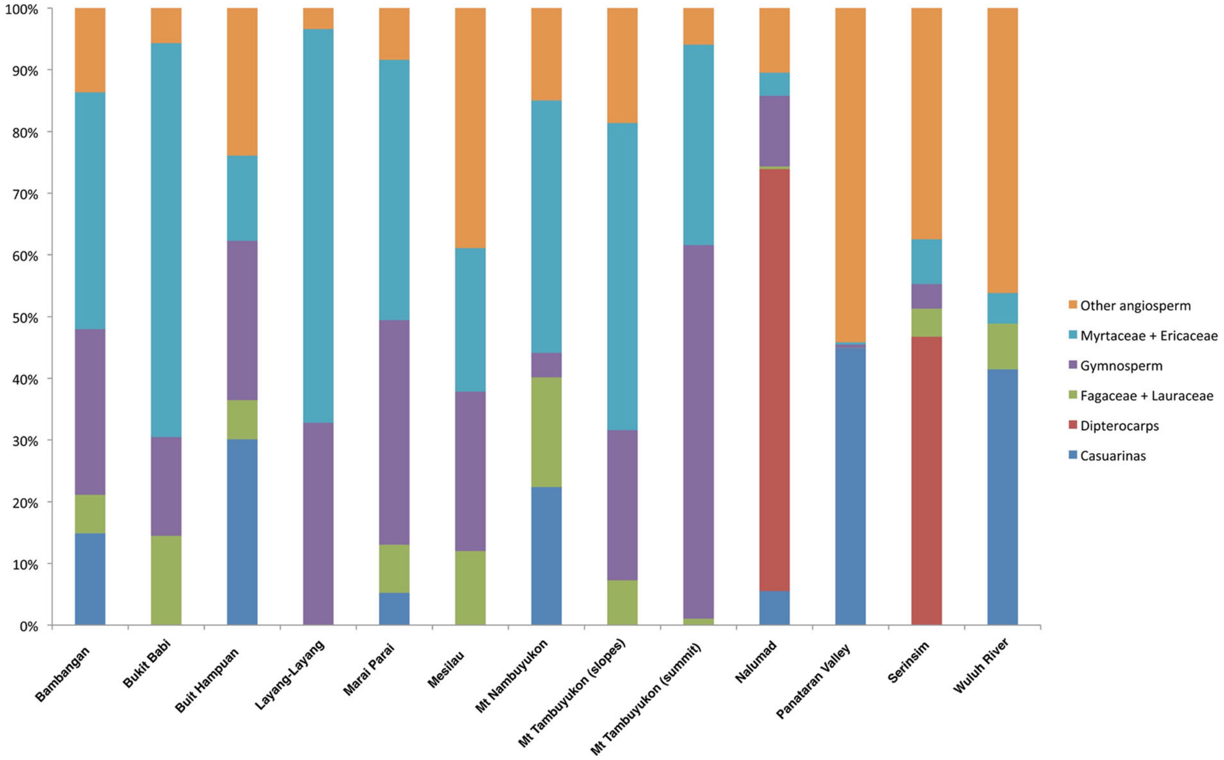

Fig. 4 Percentual composition (normalised to 100 %) for important structural and diagnostic groups of trees: Casuarinas, Dipterocarps, Fagaceae + Lauraceae, Gymnosperms, Myrtaceae + Ericaceae and other angiosperms using quantitative tree data (tree volume in m^3)

ranking (regardless of abundance in the plots), as opposed to the analysis of tree and woody shrub species using quantitative tree data i.e. based on diameter and height measures of trees in the plots (Table 7) which are ranked according to their dominance. This results in apparent differences; for example, in 'Graminoid Scrub' and 'Sub-Alpine Scrub' with the locally very common *Dacrydium gibbsiae* and *Leptospermum recurvum*, and in the 'Mixed Dipterocarp Forest' by the presence of very large individuals of *Shorea laevis* and *Shorea venulosa*. However, in the 'Pioneer Casuarina Scrub' *Macaranga kinabaluensis* and *Ceuthostoma terminale* are indicative in both SIMPER-analyses. Mixed types also occur; for example, Bukit Hampuan (963–1336 m asl) on Magnesic Cambisols is intermediate to tall multi-layered forest and Casuarina forest, and similar to Mount Nambuyukon (1495–1839 m asl). At Bukit Hampuan and Mount Nambuyukon, *Gymnostoma sumatranum* is replaced by *Ceuthostoma terminale* (Casuarinaceae) and a similar situation occurs at Bambangan (1683–2077 m asl).

Plant diversity attributes of the edaphic 'islands'

Figure 8 shows *k*-Dominance curves for the edaphic 'islands' (based on the quantitative tree data) illustrating the differences in tree dominance relative to species richness. The highest richness is present in the Mixed Dipterocarp Forest at Serinsim (whereas other low elevation 'islands' such as Wuluh River and Panataran Valley are species-poor). There is a correlation between species richness and basal area per plot ($r = 0.55$, $p < 0.001$) that might be explained because an increase in abundance generally accompanies an increase in the number of species. Bambangan and Mesilau stand out as having relatively high plant diversity. Figure 9 shows two species-area curves of plots at Mount Tambuyukon (2450 m asl) and Serinsim (700 m asl). It is remarkable that high elevation plots on ultramafic soils (Mount Tambuyukon) have such high diversity per unit area, with neither of the two sites reaching an asymptote for species richness in the plots captured.

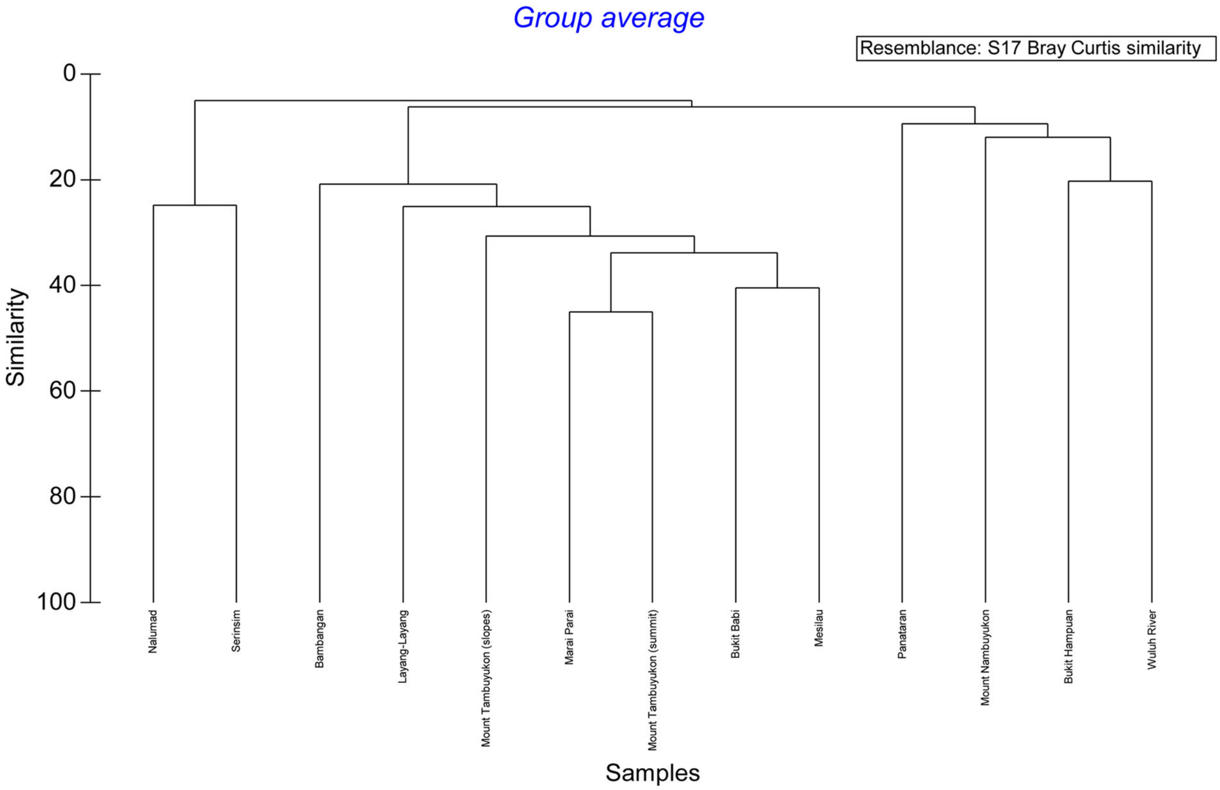

Fig. 5 Hierarchical cluster analysis (Bray-Curtis similarity) of the vegetation at the rank of species by edaphic 'islands' in PRIMER

The most species-rich vegetation in this study, in the lowland zone (Serinsim and Nalumad with up to 285 species per 0.2 ha), in upper montane forest (Bambangan up to 168 species per 0.025 ha) and in the sub-alpine shrub of Mount Tambuyukon (up to 132 species per 0.025 ha), are compared with global plant diversity maxima for tropical forests in Table 5.

Links between environment/soil and vegetation classes

Canonical Correspondence Analysis (CCA) was performed on quantitative tree genera (using tree volume) for the plots, and the explanatory variables (elevation and soil chemistry) accounted for an explained variation of 29.4 % (permutation tests show that all canonical axis are significant with a pseudo-F ratio of 2.8 $p = 0.002$), and the graph is shown in Fig. 10. This graph resembles the NMDS graphs in Fig. 6, with the Graminoid Scrub clustered within the Montane Cloud Forest class, and the Sub-Alpine Scrub forming a narrow extension from that class, whereas Pioneer Casuarina Scrub forms part of the Mature Mixed Casuarina Forest, and the Mixed Dipterocarp Forest aligns, but departs from that class. The CCA made it possible to link elevation and soil chemistry to the vegetation classes and to infer indictor genera. This demonstrates that Montane Cloud Forest - Graminoid Scrub - Sub-Alpine Scrub have generally similar soil chemistries, and that their occurrence is primarily elevation driven (*Dacrycarpus*, *Phyllocladus* and *Tristaniopsis* at the lower altitudinal end and *Leptospermum* and *Dacrydium* at the higher elevational end). Opposite the elevational vector (lower end) are Mixed Dipterocarp Forest and Pioneer Casuarina Scrub - Mixed Mature Casuarina forest, which depart in different directions under the influence of soil chemistry: towards the Fe and Ni (total) and Al and K (exchangeable) vectors for Mixed Dipterocarp Forest, and towards the Ca and Mg (exchangeable), Ni (DTPA-extractable) and pH vectors for Mixed Mature Casuarina forest. In the former the genera *Beilschmiedia*, *Shorea* and *Aquilaria* are indicative, whereas in the latter *Buchanania*, *Rhaphiolepis* and *Ceuthostoma* are indicative.

Similar to quantitative tree genera data, a CCA was also performed on all vascular plant species data

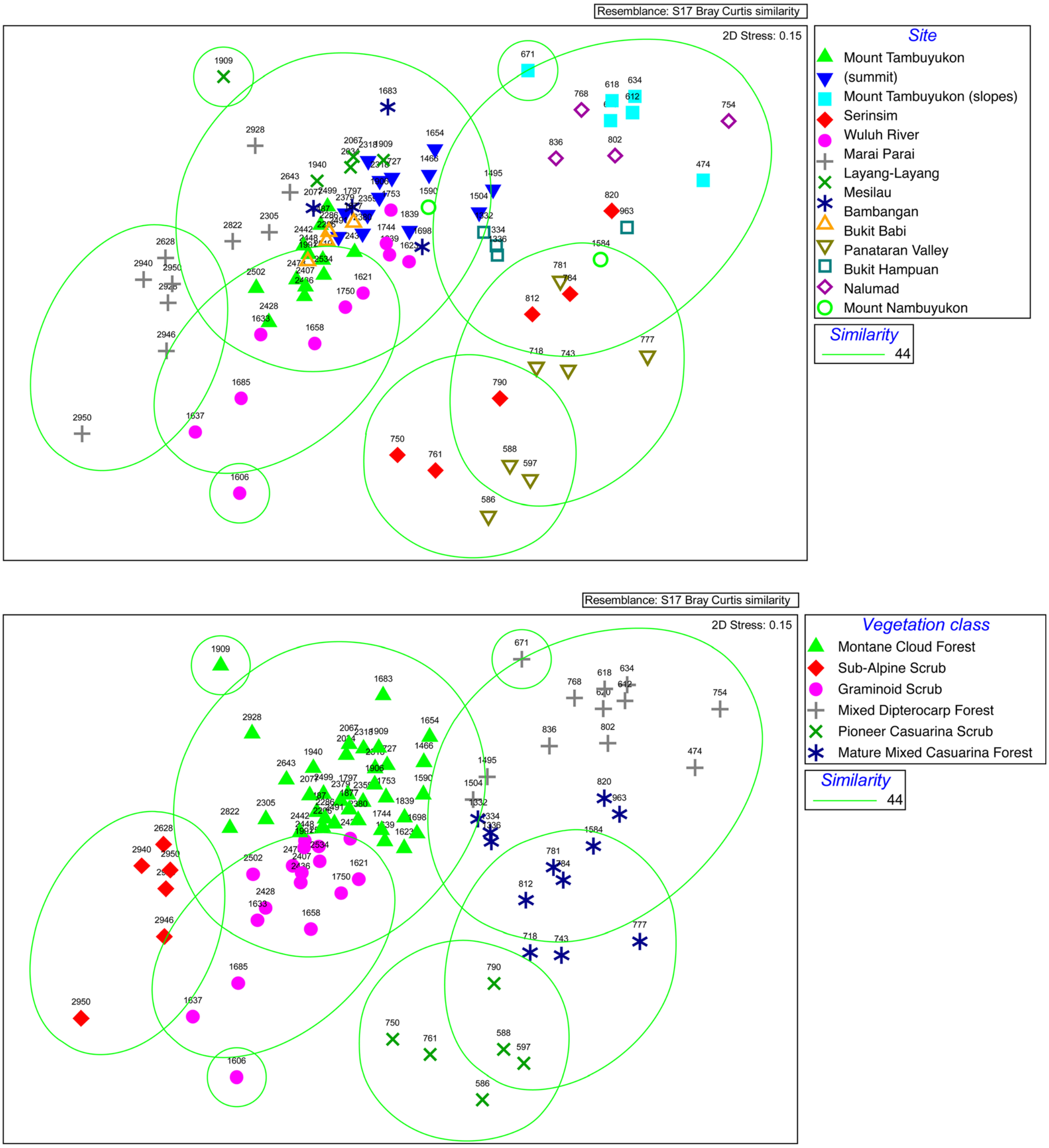

Fig. 6 NMDS of plant species (taxonomic rank of genera) of all the ultramafic edaphic 'islands' using presence/absence data. The markings in the top graph show plots in the ultramafic edaphic 'islands' whereas the bottom graph shows identical plots, but marked as main vegetation classes. At each plot the elevation (m asl) is indicated. The *green circles* depict Bray-Curtis similarity at the 44 % interval

(presence/absence) and environmental factors (elevation and soil chemistry), and the total adjusted explained variation was 10.3 % (permutation test results yielded a pseudo-F value of 1.5 $p = 0.002$), see Fig. 11. These results closely match those of the previous CCA in Fig. 10, and the classifications remain largely unchanged. These results suggest that, for the purpose of vegetation classification and understanding associated

Sub-Alpine Scrub

Graminoid Scrub

Mature Mixed Casuarina Forest

Pioneer Casuarina Scrub

Montane Cloud Forest

Mixed Dipterocarp Forest

Fig. 7 Typical characteristics of the six main vegetation classes on ultramafic soils in Kinabalu Park showing: (top-left) Sub-Alpine Scrub; (top-right) Graminoid Scrub; (middle-left) Mature Mixed Casuarina Forest; (middle-right) Pioneer Casuarina Scrub; (bottom-left) Montane Cloud Forest; (bottom-right) Mixed Dipterocarp Forest

edaphic and environmental interactions, a census of only tree genera is sufficient.

Two types of soils (Hypermagnesic Cambisols and Hypermagnesic Leptosols) are the most adverse in their chemical properties. Hypermagnesian Cambisols occur at Layang-Layang and in the summit zone of Mount Tambuyukon, whereas Hypermagnesic Leptosols occur in the Panataran Valley and at Wuluh River. The Cambisols are characterised by extremely high phytoavailable Ni and Mn, high exchangeable Mg and slightly acidic pH (5.5–6.5), and occur in the upper montane and sub-alpine zone (2400–3150 m asl). Although potentially adverse in terms of potential phytotoxic effects and contributes to the extreme stunting of the vegetation stature ('Graminoid Scrub'), the vegetation is exceptionally species-rich at Mount Tambuyukon. However, at Layang-Layang, the 'Sub-Alpine Scrub' is species-poor and dominated by

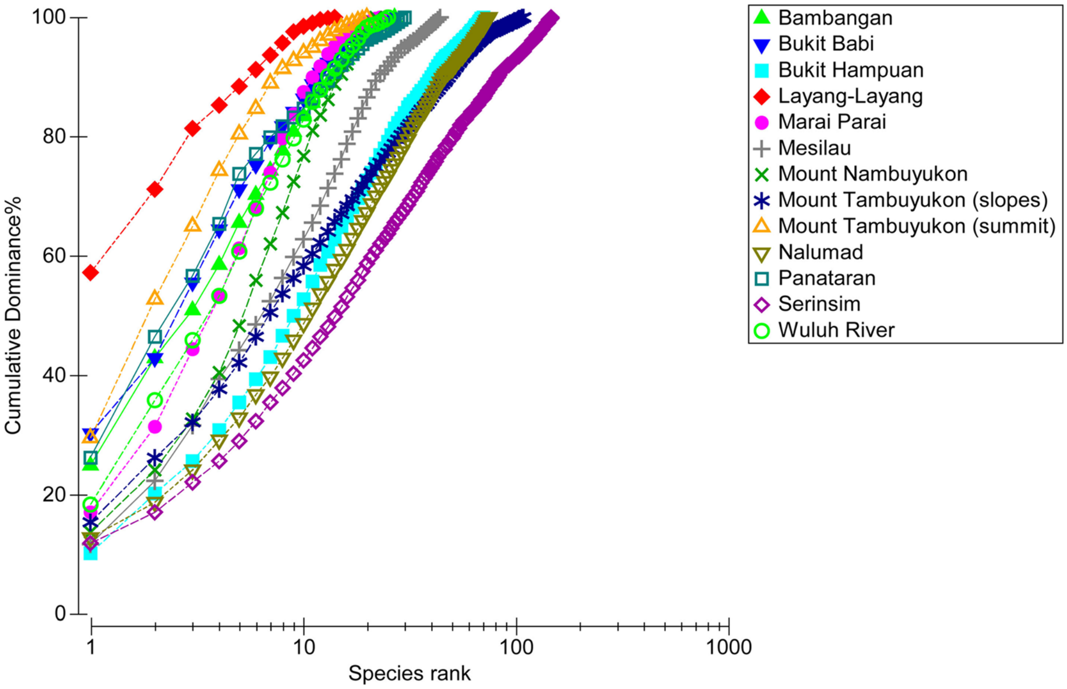

Fig. 8 *k*-Dominance curves for the edaphic 'islands'. Each curve is based on the quantitative tree data (basal area) from the plots

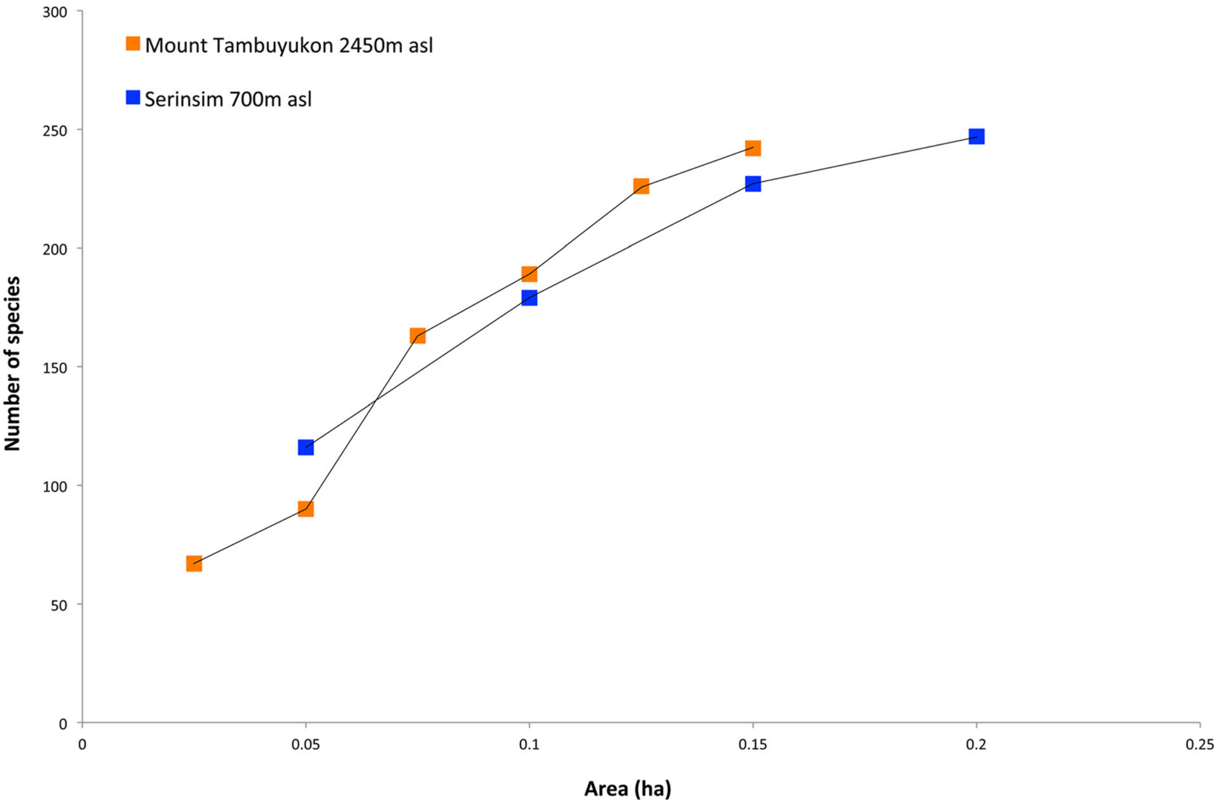

Fig. 9 Species area-curve of plots at Mount Tambuyukon (6 sub-plots of 10 × 25 m each) in the summit zone (2450 m asl) and Serinsim (4 contiguous plots at 20 × 25 m each) in the lowland zone (700 m asl)

Table 5 Global species richness records of selected tropical forests from around the world reported in the literature, including data from this study

Site	Reference	Substrate	Census	Altitude (m asl)	Area (ha)	Species
Horquetas, Costa Rica	Whitmore et al. 1985	Non-ultramafic	All vascular species	100	0.01	233
Mt. Pangasugan, Philippines	Langenberger et al. 2006	Non-ultramafic	All vascular species (excluding crown epiphytes)	100	0.01	80
Bambangan, Malaysia	This study	Ultramafic	All vascular species	1680	0.025	168
Sinamary River, French Guiana	Bordenave et al. 1998	Non-ultramafic	All vascular species	50	0.05	203
Bukit Hampuan, Malaysia	This study	Ultramafic	All vascular species	960	0.05	134
Caquetá, Colombia	Duivenvoorden 1994	Non-ultramafic	All vascular species	160	0.1	313
Serinsim, Malaysia	This study	Ultramafic	All vascular species	670	0.2	285
Mount Giting-Giting, Philippines	Proctor et al. 1998	Ultramafic	All vascular species	860	0.25	111
Mount Silam, Malaysia	Proctor et al. 1988	Ultramafic	All vascular species	480	0.4	104
Cuyabeno, Ecuador	Balslev et al. 1998	Non-ultramafic	All vascular species	<100	1	942
Tjibodas, Indonesia	Meijer 1959	Non-ultramafic	All vascular species	1450	1	333
Mount Kinabalu, Malaysia	Aiba and Kitayama 1999	Non-ultramafic	Only trees dbh >4.8 cm	650	1	163

Dacrydium gibbsiae and *Leptospermum recurvum*. The Leptosols are characterised by very high Mg:Ca molar quotients (mean 27 ± 8.7, locally up to 136) and alkaline pH (7.5–9.5), and occur in the lowland zone (300–800 m asl). In areas of low to moderate relief, deep soils develop over serpentinite bedrock, but where rivers cut through serpentinite outcrops (such as at the Panataran Valley and Wuluh River), cascading landslides continuously set back vegetation succession (ranging from 'Pioneer Casuarina Scrub' to 'Mature Mixed Casuarina Forest'). The vegetation on such soils is readily recognizable by the dominance of *Gymnostoma sumatranum* and *G. nobile*. At higher elevation (1200–1800 m asl), a montane variant (Magnesic Cambisols) occur at Bambangan and Mesilau with strongly serpentinised bedrock and here, another Casuarina (*Ceuthostoma terminale*) is frequent. Total C and N analysis was undertaken on a subset of samples and showed that the Hypermagnesic Leptosols (Wuluh River) have extremely low N concentrations (0.03 ± 0.02 % dry wt. versus 0.22 ± 0.01 % dry wt. for all plots), which could explain the dominance of Casuarinaceae that have nitrogen-fixing nodules (Dommergues et al. 1990).

Magnesic Cambisols and Hypermagnesic Leptosols are widespread soils associated with 'Montane Cloud Forests' on ultramafic geology in Kinabalu Park. The tree density is generally high and these ecosystems have high species diversity, particularly in epiphytes such as orchids. The vegetation typical for this altitudinal zone is dominated by trees in the families Myrtaceae, Fagaceae, Podocarpaceae and Rubiaceae. This vegetation differs little from soils derived from non-ultramafic bedrock in the same area, although the physiognomy is often more stunted on ultramafic soils for reasons not fully understood. The soils derived from strongly serpentinized bedrock at high elevation (Bukit Hampuan, Bambangan, Mesilau) are much more base-rich (CEC, pH) and have higher Mg:Ca molar quotients compared to soil derived from peridotite or non-ultramafic soils. These localities host extremely species-rich vegetation, suggesting that the more base-rich conditions may somehow ameliorate adverse soils conditions (limit peat formation, reduce acidification, increase N-mineralisation) and are hence more conducive to supporting diverse plant-assemblages.

Leaf litter and foliar chemistry

The motivation for analysing elemental concentrations in leaf litter were to gain insight into strategies around nutrient cycling (Ca, K, Na, P) and shedding of toxins (Ni, Mn, Co, Cr). In a previous study on Mount Silam, it was shown that Ni was up to 13-fold higher in leaf litter compared to living leaves, whereas in senescing leaves Ca was lower relative to Mg, which could suggest excretion of toxins (Ni, Mg) and preservation of nutrients (Ca) (Proctor et

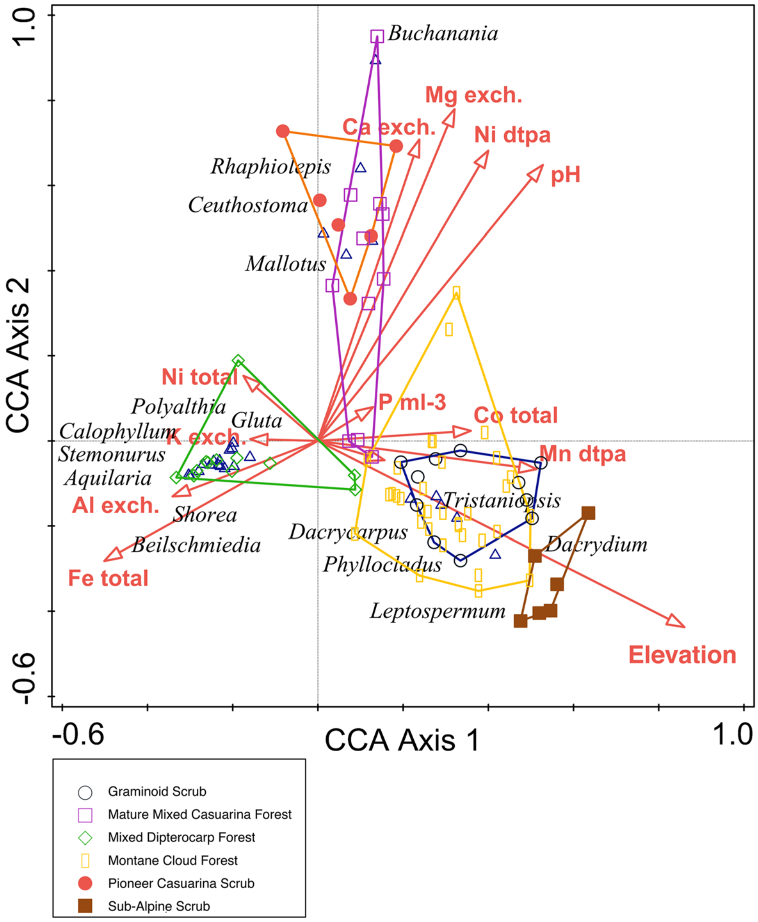

Fig. 10 Canonical Correspondence Analysis (CCA) using quantitative tree genera (tree volume in m^3) and environmental factors (elevation and soil chemistry). Indicative tree genera (as 'best fitting' explanatory variables) are marked. The main vegetation classes are marked with coloured lines (based on classified plots). Abbreviations: 'total' are elements after acid digest, 'ml-3' is Mehlich-3 extractable P, 'dtpa' are DTPA-extractable trace elements, and 'exch.' are major cations exchangeable with silver-thiorea

al. 1988). The results in the current study show that of the elemental concentrations in leaf litter, only K is significantly lower from the ultramafic soils whereas concentrations of Mn and Ni are higher. Supplementary Table 3 shows the leaf litter chemistry of the edaphic 'islands'.

When comparing overall foliar elemental concentrations from ultramafic soils with the reference from non-

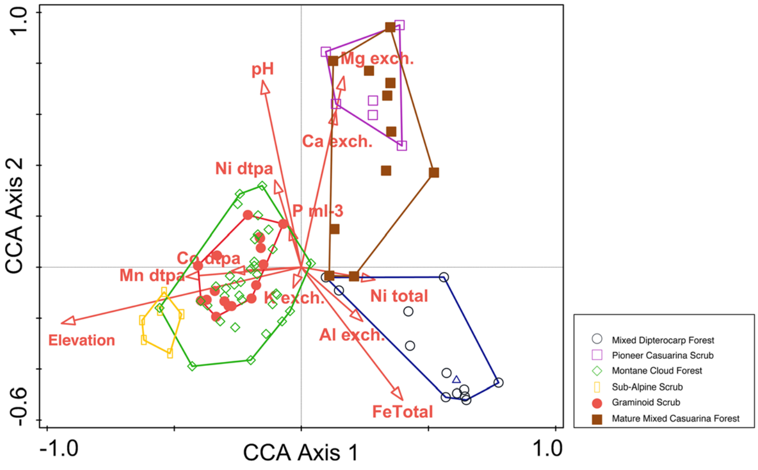

Fig. 11 Canonical Correspondence Analysis (CCA) using all vascular species (presence/absence data) and environmental factors (elevation and soil chemistry). The main vegetation classes are marked with coloured lines (based on classified plots). Abbreviations: 'total' are elements after acid digest, 'ml-3' is Mehlich-3 extractable P, 'dtpa' are DTPA-extractable trace elements, and 'exch.' are major cations exchangeable with silver-thiorea

ultramafic soils (Supplementary Table 4), it is evident that foliar Ca, Fe, Mn and Na are significantly higher in ultramafic soils, Co, K and P are lower, while Al, Cr, Mg and Ni are not significantly different. As soil K is lower in ultramafic soils, the lower foliar concentrations on ultramafic soils are to be expected. However, soil Al is much higher in non-ultramafic soils (as extractable Al), but foliar Al concentrations are not significantly different. The foliar elemental concentrations vary widely between the 'islands'. However, overall mean foliar concentrations of Fe (34 ± 1.6 μg g^{-1}), Ni (50 ± 17 μg g^{-1}), Cr (4.4 ± 0.3 μg g^{-1}) and Co (2.7 ± 0.2 μg g^{-1}) are universally low in the ultramafic flora. Foliar Ni concentrations are higher at Bukit Hampuan (because of the inclusion of a single Ni hyperaccumulator, *Phyllanthus balgooyi* with 4787 μg g^{-1} which is a local canopy tree). A similar situation applies to Panataran Valley and Wuluh River (with the occurrence of a single Ni hyperaccumulator species in the canopy). Foliar Mn is highest in the lowland forest at Nalumad (1141 ± 296 μg g^{-1}) and Serinsim (933 ± 346 μg g^{-1}). The foliar concentrations of K and P are remarkably high when compared to the soil concentrations of these elements, which are very low (K is approximately 40-fold higher in foliage than in the soil). The growth of plants in tropical lowland rainforests is generally P-limited (Vitousek and Sanford 1986) and the foliar concentrations of P are relatively uniform with an overall mean of 308 ± 6 μg g^{-1} for all 'islands', which is marginally lower compared with foliar concentrations from non-ultramafic soils (471 ± 22 μg g^{-1}). Finally, foliar Al, Na and Ca concentrations are highly variable between the 'islands' (mean Al ranging from 13 to 1620 μg g^{-1}, mean Na ranging from 349 to 1902 μg g^{-1}, mean Ca ranging from 2315 to 11 060 μg g^{-1}), whereas foliar K ranges from 1969 to 5680 μg g^{-1} with no obvious patterns.

Pair-wise correlations between foliar elemental concentrations and exchangeable and extractable soil metal concentrations are given in Supplementary Table 5. These values are derived from the extractable or exchangeable elemental concentrations in the soil (three samples per plot) versus mean foliar elemental concentrations (4–6 samples per plot). Foliar Cu and Mn are significant ($p = <0.05$) but weakly correlated with soil pH, whereas foliar concentrations of all other elements are not correlated with soil concentrations (although cross-correlations for different elements does occur).

Discussion

On the outset we hypothesized that: (i) overall plant diversity per unit area decreases with elevation and with more chemically adverse soils; (ii) adverse soil chemistry compresses elevational floristic zonation. We discuss these hypotheses in light of the results separately below.

The edaphic filter: plant diversity and chemically adverse soils (hypothesis 1)

The complex geodiversity, morphology, elevation and local climate all contribute to the mosaic of vegetation classes in Kinabalu Park. The flora of the area, as a result, is extremely localised, and many species occur only at one location. The results show that ultramafic soils support extreme plant diversity with 2854 plant species in 742 genera and 188 families recorded (14 662 unique collections). This represents over 50 % of the total flora of the area in the 87 vegetation plots studied. Edaphic filters locally have a major impact on plant diversity. Comparing plots within the same altitudinal range, but with radically different soil chemistries, shows that in the lowland range, the Mixed Dipterocarp Forest on Ferralsols differs radically from the Mature Mixed Casuarina Forest on Hypermagnesic Leptosols in species composition, diversity metrics and physiognomy. For example, comparing Serinsim (Ferralsols) with nearby Wuluh River (Hypermagnesic Leptosols), at roughly the same elevation (range for both sites 474–820 m asl) showed a similar tree density (1718 and 1770 trees ha^{-1}), but almost a 10-fold tree volume at Serinsim (1153 and 129 m^3 ha^{-1} respectively). The flora has very little overlap in species (29 % at the level of genera and 10 % at the level of species), and diversity figures are also very different with 100/248/505 and 77/163/268 families/genera/species for Serinsim and Wuluh River, respectively. Elsewhere, for example on Bukit Hampuan, the unusual geology (strongly serpentinised bedrock) has stimulated the occurrence of a unique mixture of lowland, lower montane and upper montane floristic elements, with high diversity and numerous plants species known only from that site.

The plots with the highest total plant diversity are at Serinsim with 80/173/285 and Bambangan with 55/100/162 families/genera/species respectively. Note that the plot at Serinsim (0.2 ha) is nearly 10-fold larger than the plot at Bambangan (0.025 ha); the latter is also at higher elevation (1680 m asl versus 670 m asl). It is well known that the Mixed Dipterocarp Forest in Borneo is extremely species-rich (Palmiotto et al. 2008; Ashton 2004, 2010), as illustrated by the 52 ha plot at Lambir Hills (Sarawak) with a total of 1182 trees species (Lee et al. 2013), the most species-rich forest globally. Global comparisons of plant diversity richness have been made elsewhere (Wilson et al. 2012), and included all synusiae and both temperate and tropical ecosystems, but in this study we made a comparison that was restricted to tropical forests alone. Somewhat confounding such a direct comparison is the fact that most censuses have included only trees (usually >4.8 or >10 cm dbh), but a few have included all vascular plants (for example, Whitmore et al. 1985; Duivenvoorden 1994) as does our study. Indeed, the diversity figures for the Mixed Dipterocarp Forest (Serinsim and Nalumad), are likely conservative because only a fraction of the epiphytes could be collected due to the stature of the host trees (>40 m). Nevertheless, it is clear that some of the ultramafic plots from this study rank among the most species-rich globally.

Through ordination, we distinguish six main vegetation classes on ultramafic soils, along an elevational gradient: (i) Sub-Alpine Scrub; and (ii) Graminoid Scrub, both associated with Hypermagnesic Cambisols; (iii) Montane Cloud Forest, associated with Cambisols often with accumulation of humus; (iv) Mixed Dipterocarp Forest, associated with deep Ferralsols ('laterites'); (v) Pioneer Casuarina Scrub; (vi) Mature Mixed Casuarina Forest, both associated with Hypermagnesic Leptosols.

The elevational filter: compression of elevational floristic zonation (hypothesis 2)

Altitudinal vegetation zonation on tropical mountains, expressed through a decrease in species richness and vegetation stature with increasing elevation, and concomitant changes in floristics and physiognomic features, is primarily linked to a temperature gradient (Kitayama 1992; Pendry and Proctor 1996) but influenced by a wider spectrum of environmental factors, mainly the incidence of cloud cover (Grubb and Whitmore 1966). The results from this study show that plant diversity (especially tree species) decreases with elevation, but a mid-elevation (circum 1500 m asl) 'hump' occurs for some plant groups (orchids, pteridophytes) as a result of the presence of cloud forests. The high diversity of pteridophytes, orchids, grasses-cyperoids and ground herbs are indicative of this 'cloud-zone' at 1332–1753 m asl. This finds support in records of plant collections with 661 genera and 1925 species and infras pecific taxa recorded from circum 1500 m asl on Mount Kinabalu by Beaman and Beaman (1990) and Grytnes and Beaman (2006).

Plant-soil chemistry relationships

Although ultramafic soils are universally regarded as 'adverse' by ecologists (Brooks 1987; Proctor 2003; Brady et al. 2005), and often considered as one unit in topographical mapping, generalisations are hard to make because the chemistry of the tropical ultramafic soils at Kinabalu Park varies greatly. Analysis of soil total elemental concentrations showed that K is lower, while pH, and total concentrations of Ca, Co, Cr, Fe, Mg and Mn are all higher in the ultramafic soils relative to non-ultramafic soils. Leaf litter was analysed with the aims of gaining insight in nutrient cycling and shedding of toxins. The fact that K is much higher in foliage compared to leaf litter could indicate K retention before shedding, but could also be explained by the high mobility and hence leachability from freshly deposited leaf litter. There are no indications of shedding of toxins (for example Ni), as foliar and leaf litter concentrations are similar. Foliar elemental concentrations from plants growing on ultramafic soils were compared with a reference dataset from plant growing on non-ultramafic soils. This showed that some foliar elements (Ca, Fe, Mn and Na) were higher in plants growing on ultramafic soils, whereas nutrient concentrations were lower (K and P). Although Co and Ni are substantially higher in ultramafic soils; the foliar concentrations for these elements were not significantly different in comparison with non-ultramafic soils, indicating effective ecophysiological exclusion mechanisms for most plants.

The lack of correlations between foliar elemental and soil elemental concentrations might be explained by: (i) different ecophysiological behaviour in elemental uptake by plants; (ii) the presence of micro-gradients in the soil chemistry over the plots; and/or (iii) the inadequacy of extractable and exchangeable soil extraction methods for predicting long-term plant uptake.

Conclusions

Vegetation classification is immensely challenging in tropical regions because of the levels of plant diversity and complexity (>5000 plant species in 1200 km^2 in Kinabalu Park). This necessitates exceedingly large sample sizes (very large plots and many replicates), conditions that are practically impossible to realise in the field. This is further complicated by the fact that the flora of Kinabalu Park is extremely localised, and many plant species occur only at one location (Beaman and Beaman 1990). Montane forests in particular differ greatly in stature as a function of local exposure, cloud-incidence, slope gradient and soil depth. Some generalisations can be made about major vegetation classes, however, and this study defined six main vegetation classes in the study area on ultramafic soils in Kinabalu Park. These classes represent the 'extreme' ends, for example, the Mixed Dipterocarp Forest on Ferralsols on the one hand, and Mature Mixed Casuarina Forest on hypermagnesic Leptosols on the other. These forests have contrasting species composition with little overlap, but occur in the same elevation range, but on different types of (ultramafic) soils; hence the effect of the 'edaphic filter' is clearly evident. In reality, many intermediate vegetation classes exist, and in some cases such 'mixed' occurrences have the highest plant diversity locally as, for example, on Bukit Hampuan. This is hardly surprising as environmental gradients, often promote plant diversity by increasing beta-diversity (Grime 1979; Austin 1987; Ashton 1989; Pausas and Austin 2001).

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