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Plant diversity and ecology of ultramafic outcrops in Sabah (Malaysia)

Antony van der Ent[A,E], *Rimi Repin*[B], *John Sugau*[C] *and Khoon Meng Wong*[D]

[A]Centre for Mined Land Rehabilitation, Sustainable Minerals Institute, The University of Queensland, St Lucia, Qld 4072, Australia.
[B]Sabah Parks, KK Times Square, Coastal Highway, 88100 Kota Kinabalu, Malaysia.
[C]Forest Research Centre, Sabah Forestry Department, Malaysia.
[D]Singapore Botanic Gardens, National Parks Board, Singapore.
[E]Corresponding author. Email: a.vanderent@uq.edu.au

Abstract. Ultramafic outcrops occupy less than 1% of the land surface of the Earth and are renowned as hotspots of plant diversity and endemism. With over 3500 km^2 of ultramafic outcrops in Sabah (4.6% of the total landmass of the state) on the island of Borneo and a total of 4252 plant species recorded occurring on this substrate, Malaysia has one of the most species-rich floras occupying these outcrops globally. Over 2542 plant species have been documented on ultramafic outcrops in Kinabalu Park alone, of which a large percentage is endemic to either Kinabalu Park or Borneo. Despite the existence of this species rich flora, the full plant diversity and ecology remains largely unknown because of a lack of focussed research. Furthermore, plant diversity in many areas of Sabah is severely threatened by land-use conversion and, because many plant species occur only in a single or a few ultramafic sites, impacts on the ecosystems that support them could eventually result in their extinction.

Additional keywords: Endemism, Kinabalu Park, Mount Tambuyukon, serpentinite.

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Introduction

Ultramafic outcrops are widespread and extensive in Sabah (Malaysian Borneo), covering an area of ~3500 km^2 or 4.6% of the surface area of Sabah (Proctor *et al*. 1988; Repin 1998). The largest ultramafic outcrops are (west to east) around Mount Kinabalu (the mountain itself is a granite intrusion), Hampuan and Kulung Hill, Morou Porou, Bidu-Bidu Hills, Meliau Range, Mount Tawai and Mount Silam (Fig. 1). In Sabah, ultramafic outcrops can be found from sea level up to nearly 3000 m (on Mount Kinabalu). The flora of Sabah is very rich in plant species, with an estimated 8000 vascular plant species (Wong 1992; J. Sugau, unpubl. data), of which at least 800 species are endemic (Maycock *et al*. 2012). Compared with other renowned ultramafic floras, for example, New Caledonia (5500 km^2, 2150 species), California, United States (6000 km^2, 1100 species) and Queensland, Australia (818 km^2, 553 species) and Zimbabwe (3000 km^2, 322 species), the ultramafic flora of Sabah (3500 km^2, 4252 species) is extremely rich in plant species (Batianoff and Specht 1992; Batianoff and Singh 2001; Safford *et al*. 2005; Harrison and Grace 2007; Bostock and Holland 2010; Jaffré and L'Huillier 2010). The ultramafic floras of Indonesia and the Philippines are also very species rich, but insufficient information is known to quote exact numbers of plant species at this stage (van der Ent *et al*. 2013*a*).

Kinabalu Park is the most species-rich area on Earth in terms of species density, with over 5000 plant species in an area of <1200 km^2 (Beaman 2005). A substantial part of the Kinabalu flora is endemic to either the Park alone or to Borneo in general (van der Ent *et al*. 2014). The number of plant species occurring on ultramafic substrates in Kinabalu Park is not precisely known; however, when enumerating the plant species collected from localities that are known to be entirely ultramafic (Hampuan Hill, Bambangan River, Marai Parai, Pig Hill, Mount Tambuyukon, Panataran Valley, Lohan River, Kulung Hill; Fig. 2), added to those from other sites for which 'ultramafic' has been noted during collection, a total of 2542 plant species (vascular plants and ferns) is certainly ultramafic (data from Beaman and Beaman database, unpubl. data).

The ultramafic flora of Sabah contains a recorded 4252 plant species in 207 families and 1047 genera (vascular plants and ferns, excluding all infraspecific ranks, but including cf. and aff. notations). These numbers are based on tallying the following parks and forest reserves that are wholly ultramafic (the number of species/genera/families are given in parentheses): Kinabalu Park (2542/773/187), Bidu-Bidu Hills Forest Reserve (460/251/95), Meliau Range Forest Reserve (413/230/97), Nicola (45/39/33), Mount Silam Forest Reserve (695/331/109), Mount Tawai Forest Reserve (822/395/117), Mount Tingkar Forest Reserve (857/390/116), Hampuan Forest Reserve (701/343/123), Imbak Forest Reserve (852/371/118), Sakar Island (310/208/90) and Malawali Island (56/53/39). The numbers are likely to be an underestimate because all localities that are partly ultramafic were

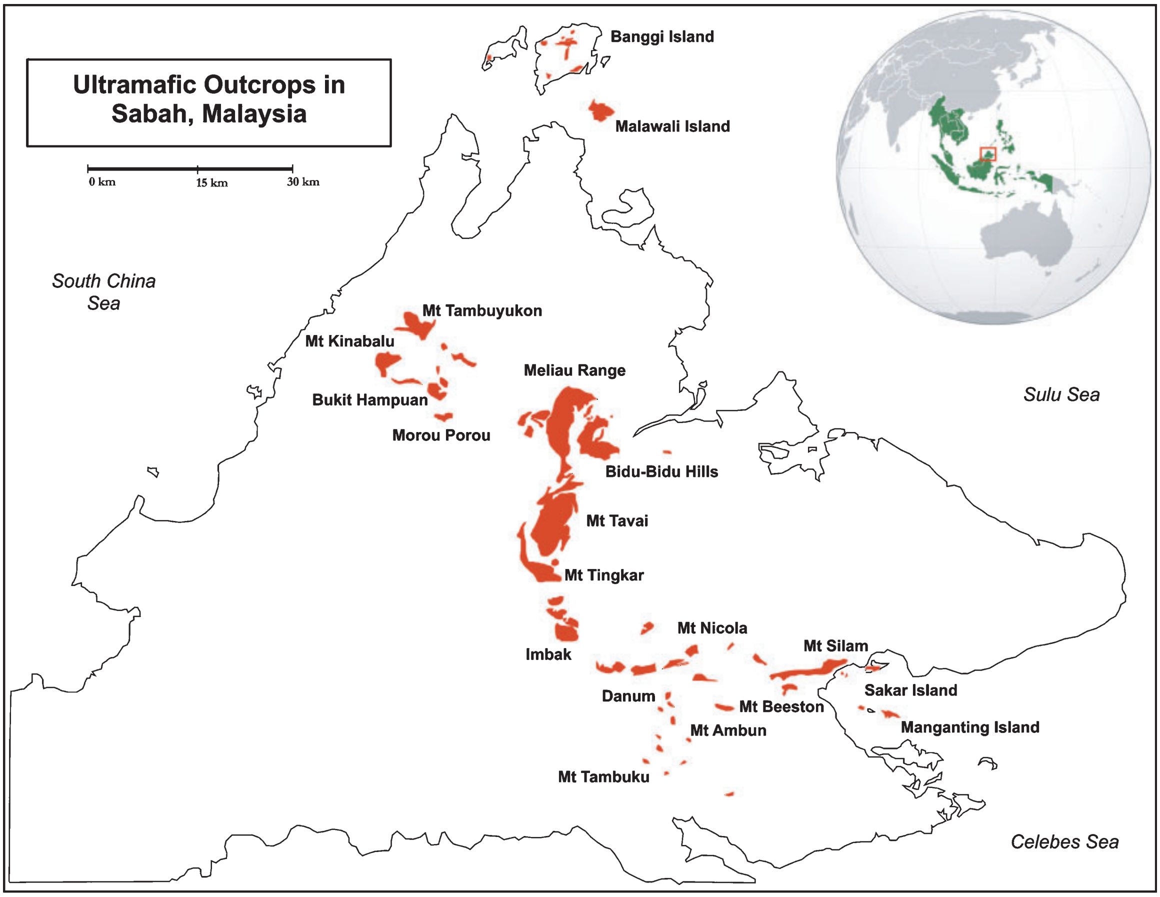

Fig. 1. Ultramafic outcrops in Sabah, Malaysia. The outcrops are marked in red and appear as an arc through the landscape of Sabah, connecting in the north to offshore islands and Palawan (in the Philippines). Outline of ultramafic outcrops from 'Igneous Rocks of Sabah, Malaysia' (Anonymous 1965), with globe insert from Wikimedia Commons (2009). Figure was reproduced from van der Ent *et al.* (2014), with permission from Natural History Publications (Borneo).

excluded from the analysis. Here, we present the current state of knowledge on the plant-diversity patterns and ecology of the ultramafic outcrops in Sabah, focussing in particular on Kinabalu Park. As such, we augment the knowledge from the literature base with the latest insights and outline research needs. We have provided a more detailed account of the plant diversity of ultramafic soils in Sabah in a recent book (van der Ent *et al.* 2014) on which this review is based.

Ultramafic rock and derived soils

Ultramafic outcrops and derived soils occur on every continent (Boyd *et al.* 2009), with the world's largest outcrops in the Southeast Asian region, including Indonesia, the Philippines and Malaysia (van der Ent *et al.* 2013*a*). Ultramafic rocks are composed of minerals high in magnesium, iron, nickel, chromium and cobalt (Proctor 2003) that originate from fragments of the upper mantle (Searle and Stevens 1984). In tropical conditions, the soil weathering leads to the formation of laterite soils, in which magnesium, manganese and nickel are leached down the soil profile and the surface soil consists mainly of iron oxide (Latham 1975; McCoy *et al.* 1999; Proctor 2003). The main ultramafic soil types in Sabah include shallow hypermagnesian soils on ridges and steep slopes (for example, in the summit region of Mount Tambuyukon and at Layang-Layang on Mount Kinabalu), brown organic soils under montane cloud-forest (particularly common in the lower and upper montane zone of Mount Kinabalu), deep iron-oxide rich laterite soils (for example, near Serinsim) and serpentinite soils (derived from fragmented strongly serpentinised bedrock (for example, in the Panataran Valley and Wuluh River in Kinabalu Park).

Soil–plant interactions on ultramafic outcrops in Sabah

Ultramafic soils have several adverse chemical properties to plant life (Brooks 1987; Rajakaruna and Baker 2004; Rajakaruna *et al.* 2009). Ultramafic soils generally have high concentrations of exchangeable magnesium (Mg) and low concentrations of exchangeable calcium (Ca), resulting in high Mg : Ca quotients (Rajakaruna and Baker 2004), while the soil is alkaline in soil rich in Mg and mildly acidic in leached laterite soils (Baillie *et al.* 2000). Table 1 presents the soil chemistry of two ultramafic outcrops in Sabah from the literature. In addition, Kitayama *et al.* (2000) and Kitayama and Aiba (2002) have shown lower phosphorus concentrations in ultramafic soils over a range of altitudes on Mount Kinabalu than non-ultramafic soils. Similarly, nitrogen concentrations are low in most ultramafic soils (Proctor *et al.* 1988), and trees in the family Casuarinaceae

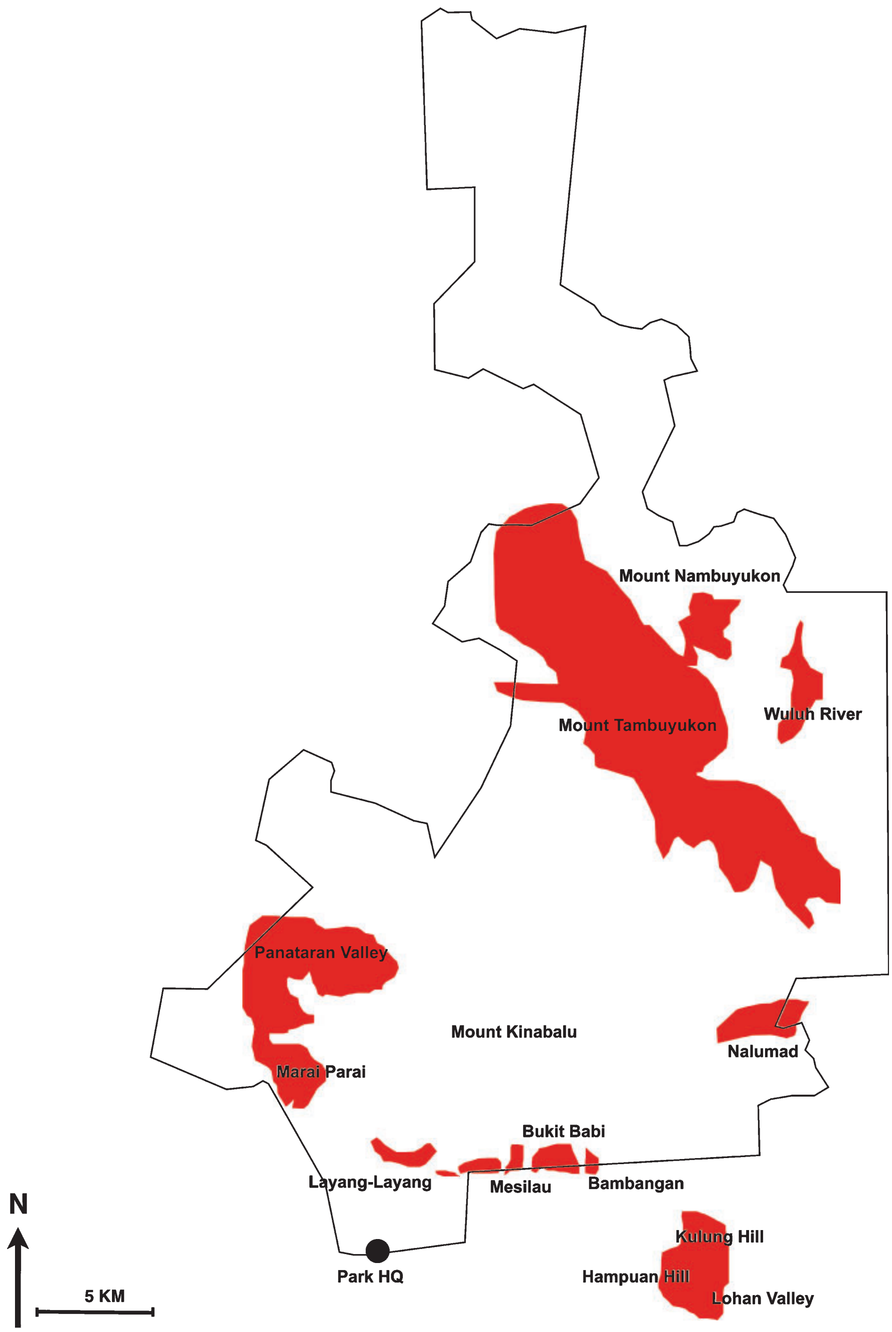

Fig. 2. Outline of ultramafic outcrops in Kinabalu Park, based on Jacobson (1970). The largest outcrops are in the north of the Park, making up Mount Tambuyukon (almost 90 km^2) and the Panataran Valley (~30 km^2).

(genera *Gymnostoma* and *Ceuthostoma*), which have nitrogen-fixing nodules, are often found on ultramafic soils in Sabah. In a growth experiment using *Dryobalanops lanceolata* (Dipterocarpaceae) it was shown that the seedlings had similar biomass production on ultramafic and non-ultramafic soils, but the concentrations of potassium in plant leaves were lower on the ultramafic soils and hence this species is probably potassium-limited (Brearley 2005, 2006). Such studies and further field observations point to nutrient deficiency as an important cause for the unusual plant communities on ultramafic soils in Sabah.

Adaptations to water stress have also been shown to be important in Kinabalu Park (Aiba and Kitayama 1999) and on Mount Silam (Bruijnzeel *et al*. 1993). The low concentrations of potassium in most ultramafic soils may also further exacerbate the effects of water stress (Pandolfini *et al*. 1992). Although nickel is an essential micronutrient for some plants (Brown *et al*. 1987), at the high concentrations found in ultramafic soils it can be toxic to plants (Chen *et al*. 2009). The low water-retention capacity of many ultramafic soils could also increase the toxicity of magnesium and nickel, by concentrating these elements in the

Table 1. Soil chemistry of two ultramafic outcrops in Sabah

Soil parameter	Unit	Malaysia (Mount Tawai)	Malaysia (Mount Silam)
Altitude asl	m	180	280–870
pH	–	5.3	4–6.1
Magnesium (Mg) : calcium (Ca)	–	1.6	0.8–6.7
Ca (exch.)	$cmol^{(+)}$ 100 g^{-1}	0.9	0.9–12
Mg (exch.)	$cmol^{(+)}$ 100 g^{-1}	1.4	5.4–25
Potassium (exch.)	$cmol^{(+)}$ 100 g^{-1}	0.2	0.1–0.5
Phosphorus (P) (pseudo-total)	µg g^{-1}	201	n.a.
P (extract.)	µg g^{-1}	0.3	1.1–17
Nickel (Ni) (pseudo-total)	µg g^{-1}	2980	n.a.
Ni (extract.)	µg g^{-1}	2.4	2–18
Chromium (Cr) (pseudo-total)	µg g^{-1}	9620	n.a.
Cr (extract.)	µg g^{-1}	n.a.	0.5–1
Cobalt (pseudo-total)	µg g^{-1}	123	n.a.
Co. (extract.)	µg g^{-1}	n.a.	2.5–8.3
References		Brearley (2005)	Proctor *et al.* (1988)

soil moisture (Proctor and Nagy 1992). Acidic soils with an accumulation of organic matter may also be toxic because nickel availability increases with decreasing pH (Proctor and Nagy 1992). The effect of magnesium is dependent on the ratio with calcium (Proctor and Nagy 1992), but in the growth experiment with *Dryobalanops lanceolata* seedlings, the addition of calcium had no significant effect on the growth of the seedlings (Brearley 2005). The effect of the magnesium to calcium ratio in ultramafic soils on the stature of the vegetation is not clear in Sabah, for example, Proctor *et al*. (1988, 1989) found a tall forest at 330 m on Mount Silam with lower calcium concentrations in the soil compared to higher slopes which had stunted forest. In contrast, Wright (1975) found similar magnesium to calcium ratios on sites near Tawau and Lahad Datu, which had small-statured forest. An extremely high magnesium to calcium ratio (265) was reported by Acres *et al*. (1975) from a site in the headwaters of Sungai Takala dominated by *Tristaniopsis grandifolia* (Myrtaceae), but such values are not uncommon in Sabah, with similar values recorded from Kinabalu Park on sites with stunted or tall forest (van der Ent and Wood 2013).

Vegetation types and ecology of ultramafic outcrops in Sabah

The vegetation on ultramafic soils in Sabah ranges from tall forests (trees >50 m) in the lowland to graminoid communities in the upper montane to sub-alpine zone. On Mount Kinabalu, Kitayama (1991) discerned three vegetation types on ultramafic soils at elevations >1700 m either typified by (1) *Tristaniopsis elliptica* (Myrtaceae), (2) *Leptospermum javanicum* and *Tristaniopsis elliptica* (Myrtaceae) or (3) *Leptospermum recurvum* (Myrtaceae) and *Dacrydium gibbsiae* (Podocarpaceae). At lower elevations, *Gymnostoma sumatranum* and *Ceuthostoma terminale* (Casuarinaceae) were characteristic (Beaman and Beaman 1990), especially on serpentinite soils. Figure 3 illustrates vegetation types on ultramafic soils in Kinabalu Park.

No plant community is dominated by ultramafic obligate species, but the forest dominated by *Leptospermum recurvum* (Myrtaceae) and *Dacrydium gibbsiae* (Podocarpaceae) at high elevation on Mount Kinabalu, may be an exception. Distinct assemblages (of species which occur facultatively on ultramafic soils) are known, however, for example the lowland forest dominated by *Agathis borneensis* (Araucariaceae), *Shorea venulosa* and *Shorea laevis* (Dipterocarpaceae). The co-occurrence of these trees may be attributed to their drought-tolerance adaptations (Aiba and Kitayama 1999). Another example is the co-occurrence of ultramafic facultative species of dipterocarps, such as *Dipterocarpus lowii*, *Shorea kunstleri*, *S. laxa*, *S. lowii*, *S. tenuiramulosa*, *S. venulosa* and *Dryobalanops beccarii* that are known elsewhere from non-ultramafic nutrient-poor soils (Acres *et al*. 1975; Ashton 1982, 2004).

On ultramafic mountains in Sabah the altitudinal sequence of vegetation zones is often compressed (van der Ent *et al*. 2014), similarly to the 'Massenerhebung effect' which relates to compression of the altitudinal zonation on isolated small mountains compared to larger mountain massifs (Grubb 1971, 1977; Bush 1986). This is further exacerbated on coastal mountains, such as Mount Silam on Sabah's east coast where the species composition and physiognomy are substantially 'pushed' down slope (Bruijnzeel *et al*. 1993). This "ultramafic compression of vegetation zones" can be observed on the main ultramafic mountains in Sabah, including Mount Meliau (1336 m) and Mount Tawai (1273 m), but the effect is most clear on Mount Tambuyukon (2579 m). Many plant species occurring also have an extended elevational range on ultramafic soils compared with non-ultramafic soils. For example, on Mount Kinabalu, a number of plant species found on high-elevation granite-derived soils occur lower downslope on ultramafic soils (Beaman and Anderson 2004). It is noteworthy in this respect that Aiba and Kitayama (1999) reported that inherent chemical differences between ultramafic and non-ultramafic soils are more strongly reflected in the vegetation with increasing altitude.

Plant diversity of ultramafic outcrops in Sabah

Kinabalu Park (excluding Mount Tambuyukon)

In total, the extent of ultramafic soils in Kinabalu Park amount to some 142 km^2 (Collenette 1964); The Park is famous for the

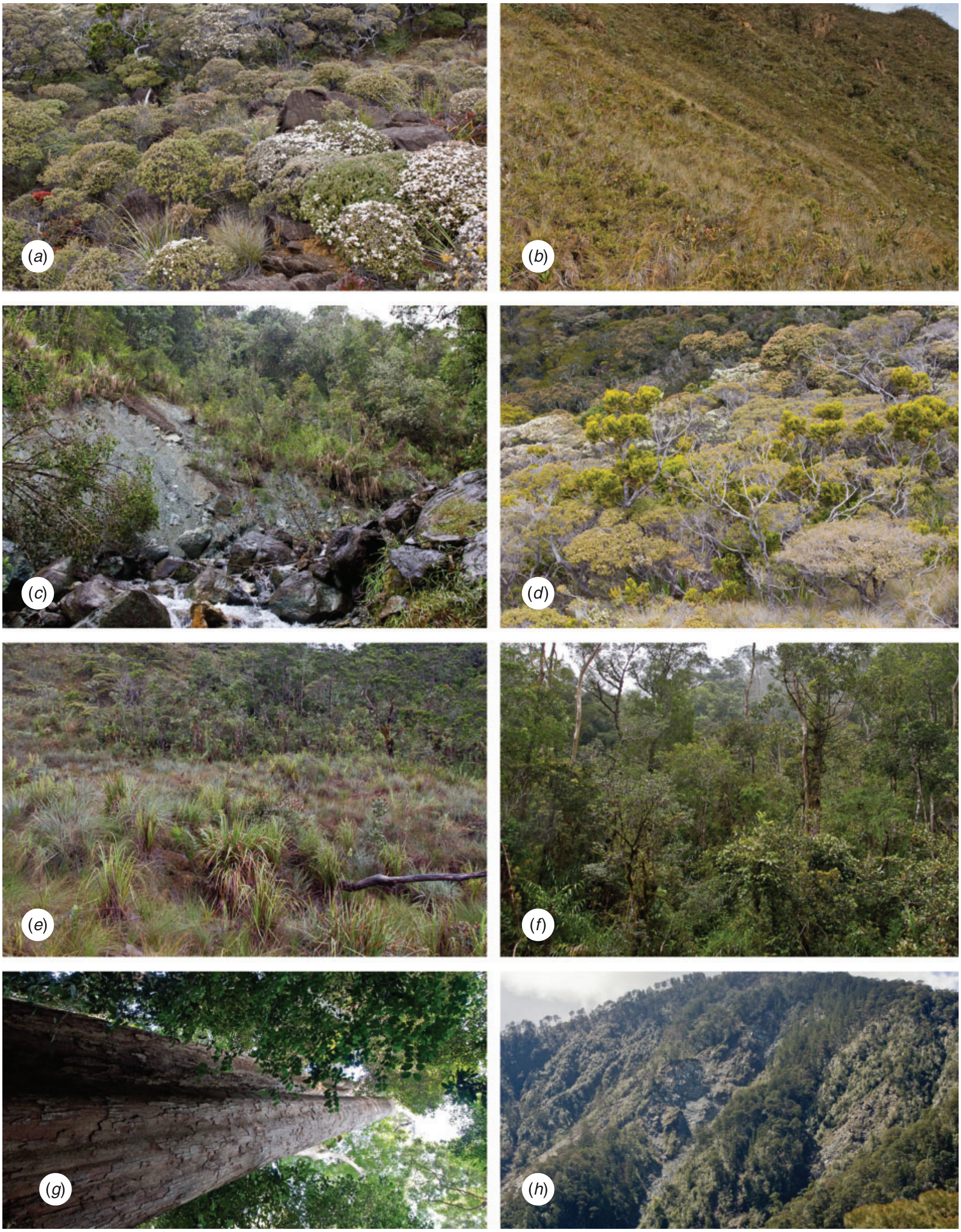

Fig. 3. Main vegetation types on ultramafic soils in Kinabalu Park. (*a*) Ericaceous high-altitude scrub, (*b*) graminoid scrub on the flanks of the summit ridge of Mount Tambuyukon, (*c*) serpentinite landslides cut through by the Wuluh River, (*d*) *Dacrydium gibbsiae*- and *Leptospermum recurvum*-dominated dwarf forest at Layang-Layang, (*e*) graminoid vegetation at Marai Parai, (*f*) tall upper montane forest in the Bambangan Valley, (*g*) *Shorea laevis* in tall mixed dipterocarp forest near Nalumad, and (*h*) cascading serpentinite landslides in various stages of succession in the Panataran Valley.

richness in plant species and the high levels of local endemism (Beaman and Beaman 1990; Beaman 2005). Numerous plants are ultramafic obligates in Kinabalu Park, for example *Syzygium dasyphyllum* (Myrtaceae), *Urophyllum subanurum*, *Hedyotis protrusa* (Rubiaceae) and *Wikstroemia indica* (Thymelaeaceae) (Beaman and Beaman 1990). Of the tropical gymnosperms (kauri and podocarps), obligate ultramafic species include *Agathis kinabaluensis* (Araucariaceae), *Dacrydium gibbsiae*, *Podocarpus brevifolius*, *P. confertus*, *P. gibbsiae* and *P. globulus* (Podocarpaceae) (Beaman and Beaman 1998). Sedges (Cyperaceae), number 18 species on ultramafic soil (some of which are facultative) including *Carex* (five species), *Cyperus* (one species), *Schoenus* (four species), *Mapania* (one species), *Machaerina* (four species), *Lepidosperma* (one species), *Scirpus* (one species) and *Costularia* (one species). Interestingly, *Costularia* spp. are also common on ultramafic outcrops in New Caledonia (Lagrange *et al*. 2011). Five species of *Calamus* (Arecaceae) occur on ultramafic soils, especially common locally is *Calamus gibbsianus*. All four species of the myco-heterotrophic *Sciaphila* (Triuridaceae) are ultramafic obligate species.

Wood *et al*. (2011) listed a total of 866 orchid taxa in 134 genera, of which 90 species are endemic to Kinabalu Park. Of those, 359 orchid species are obligate or have most populations on ultramafic soils ('preferential'), including *Appendicula tembuyukensis*, *Arachnis longisepala*, *Ceratostylis ampullacea*, *Cymbidium elongatum*, *Dendrobium spectatissisimum*, *D. patentilobum*, *Epigeneium kinabaluense* and *Neuwiedia borneensis* (Wood *et al*. 2011). Typical for ultramafic soils in Kinabalu Park are a number of strict endemics from the carnivorous Nepenthaceae family that are ultramafic obligates. These include *Nepenthes burbidgeae* and *N. rajah*, in addition to ultramafic preferential species such as *N. edwardsiana* and *N. villosa*.

The site Marai Parai, at approximately 1500 m on the west slope of Mount Kinabalu, is named after *Costularia pilisepala* (Cyperaceae) (Beaman and Beaman 1998) and has pioneer vegetation on a range of landslides with sedges such as *Scirpus subcapitatus* (Cyperaceae) common. The soils are especially nutrient-poor and waterlogged and the rare sundew *Drosera ultramafica* (Droseraceae) has been recorded from this site, and from the summit region of Mount Tambuyukon (Fleischmann *et al*. 2011).

In Kinabalu Park, the largest extent of serpentinite soils (soils derived from ultramafic bedrock which has undergone mineralogical alteration to serpentine minerals such as antigorite, lizardite, chrysotile and secondary smectite clays) occurs in the Panataran Valley, Wuluh Valley and the Lohan Valley. The vegetation on these soils is characterised by the dominance of *Gymnostoma sumatranum* at lower elevations (200–1400 m) and *Ceuthostoma terminale* at higher elevations (1400–1800 m); both belong to the Casuarinaceae. The ultramafic obligate tree *Borneodendron aenigmaticum* (Euphorbiaceae) is often found on these soils too.

Extremely species-rich vegetation types on ultramafic soils have been described from Hampuan Hill and Kulung Hill, adjacent to Kinabalu Park. *Shorea venulosa* is particularly common as well as *Dipterocarpus ochraceus* (Dipterocarpaceae), the latter being a rare obligate ultramafic species first described from this site.

Mount Tambuyukon

Mount Tambuyukon (2579 m), which lies inside Kinabalu Park, is the highest ultramafic mountain in Sabah and on the island of Borneo. The ligneous and graminoid vegetation (<1 m) on the summit is not found anywhere else in Sabah, and forms the habitat of a number of hyper-endemic plant species. These species, known only from Mount Tambuyukon, include *Rhododendron meijeri* and *R. baconii* (Ericaceae), *Begonia vaccinioides* (Begoniaceae), *Scaevola verticillata* (Goodeniaceae), and two recently described species: *Eriobotrya balgooyi* (Rosaceae) (Wong and van der Ent 2014) and *Gynura tambuyukonensis* (Asteraceae) (van der Ent and Vanijajiva 2014). Several rare terrestrial orchids occur among the grasses and sedges, including *Platanthera kinabaluensis*, *Cymbidium elongatum*, *Thrixspermum triangulare* and *Calanthe otuhanica* (van der Ent and Wood 2012) together with the carnivorous plant *Nepenthes rajah* (Nepenthaceae).

At the foothills of Mount Tambuyukon, species-rich lowland mixed dipterocarp forest occurs on deep iron-rich laterite ultramafic soils. Common trees here include *Shorea laevis*, *Shorea venulosa*, *Parashorea malaanonan* (Dipterocarpaceae) and *Agathis borneensis* (Araucariaceae), which grow up to 50 m tall with girths >4 m.

Mount Tawai

Mount Tawai (1273 m) in central Sabah is a Class 1 forest reserve surrounded by oil palm estates. The Sabah Forestry Department (2005) described the vegetation in the area as: (1) lowland ultramafic forest, (2) hill forest (above 300 m) and (3) hill and lower montane mixed dipterocarp forest. The canopy of the lowland forest is dominated by dipterocarps (*Dipterocarpus lowii*, *D. acutangulus*, *D. confertus*, *Dryobalanops lanceolata*, *Hopea beccariana*, *Shorea laevis* and *S. multiflora*). Mount Tawai has an extensive plateau at about 400m with stunted forest that resembles *kerangas* forest (otherwise known from acid, leached sandy soils). Sadly, the plateau had been logged 20–25 years ago. The Tawai Forest Reserve has four hyper-endemics: *Rhododendron sugaui* (Eriaceae), *Semecarpus angustifolius* (Anacardiaceae), *Sygyzium soepadmoi* and *Tristaniopsis merguensis* subsp. *tavaiensis* (Myrtaceae) (J. Sugau, unpubl. data). In addition, 35 endemics for Sabah and 98 endemics for Borneo are known from this site (J. Sugau, unpubl. data). Other recently described species include *Payena khoonmengiana* (Sapotaceae) and *Lithocarpus tavaiensis* (Fagaceae).

Meliau Range

The ultramafic Meliau Range lies along the Labuk River at the northern end of a large north–south ophiolite belt that stretches for ~120 km from Mount Rara to the Tungud–Labuk Rivers (Chung 2006). It is a conservation area within the Class II Commercial Forest Reserve called Ulu Tungud (active logging concession). The Meliau Reserve has several peaks, the highest of which is Mount Meliau (1336 m).

The plant diversity and ecology of the Meliau Range has been described in Chung (2006). Lowland ultramafic forest (<350-m) in the Meliau Range is dominated by dipterocarps, including *Shorea kunstleri*, *S. micans* and *Dipterocarpus lowii*. Other species are from the Gentianaceae (*Fagraea*), Leguminosae, Dilleniaceae, Euphorbiaceae and Rubiaceae families. The Sabah Forestry Department (2005) has recorded 400 plant species in the Meliau Range, of which 50 are endemic to Borneo and 16 endemic to Sabah, including recently described species such as *Adinandra longipedicellata* and *A. crassifolia* (Theaceae).

Bidu-Bidu Hills

The Bidu-Bidu Hills is also a Class 1 forest reserve close to the Meliau Range and surrounded by oil-palm estates. *Gymnostoma sumatranum* and *Tristaniopsis grandifolia* are particularly common. The vegetation along the Bangau Bangau River has a riparian aspect with *Pandanus matthewsii* (Pandanaceae), *Phyllanthus balgooyi* (a nickel hyperaccumulator) and *Dillenia luzonensis*. The Bangau Bangau River was named after the vernacular name for *Borneodendron aenigmaticum*, which is locally common here together with *Dipterocarpus lowii*.

Mount Silam

The coastal Mount Silam (884 m) is part of the ultramafic Silam–Beeston Range, which is roughly 30 km by 6 km (Leong 1974; Proctor *et al*. 1988). Mount Silam is extremely species rich with a total of 435 plant species from 252 genera recorded to date (Perumal 1994), of which 374 tree species (>10-cm dbh) were recorded in a combined plot area of just 2.6 ha (Proctor *et al*. 1989). At low elevations (280 m and 330 m), the forest is tall (up to 50 m high; Proctor *et al*. 1988) and includes large individuals of *Borneodendron aenigmaticum* (Fox 1972).

Ecological studies undertaken by Proctor *et al*. (1988, 1989) on Mount Silam revealed that ranging from 280 to 870 m (summit), three main vegetation zones may be discerned: tall lowland forest (canopy: 33–45 m), a transition zone (canopy: 20–30 m) and upper montane forest (canopy: 10–15 m) (Fox 1972; Proctor *et al*. 1988, 1989). In the dipterocarp forest at the foot of the mountain, 23 dipterocarp species have been recorded (Fox 1972; Perumal 1994), with species characteristic for ultramafic soils such as *Dipterocarpus lowii*, *Shorea kunstleri*, *S. venulosa*, *S. atrinervosa*, and *S. laxa*. The latter is, as in the Bidu-Bidu Hills, the dipterocarp with the highest elevational occurrence, and common up to 600 m. The vegetation in the summit area is similar to that found at much higher elevations (such as on Mount Kinabalu) and dominated by plants in the Myrtaceae and Ericaceae families. The rattan *Calamus microsphaerion* (Arecaceae) is known in Sabah only from Mount Silam. Other rattans recorded from the mountain include *C. laevigatus* var. *serpentinus* and *Korthalsia concolor* (Arecaceae).

Darvel Bay and Malawali Island

Coastal ultramafic areas include those on the islands in the Darvel Bay (Banggi and Sakar) on the eastern coast and Malawali on the northwestern coast of Sabah. The vegetation on these islands is dominated by *Tristaniopsis grandifolia* or *Gymnostoma nobile* (Casuarinaceae) (Fox 1972; Wright 1975). At Sakar Island, coastal forest has dipterocarp species (up to 40 m tall) such as *Shorea guiso*, *S. bracteolata*, *S. gratissima*, *Hopea nutans*, *Vatica albiramis* and *Dipterocarpus grandiflorus* (Fox 1972). Malawali Island has extensive ultramafic soils and the local vegetation was described by Sugau and Tangah (2004). Most of the island is covered by a species-poor *Gymnostoma nobile*-forest, with co-occurrence of *Alstonia macrophylla* (Apocynaceae), whereas the southeastern part has grassland from previous disturbance. The *Gymnostoma nobile*-forest is low (~10–15 m tall) with an even canopy and a shrub layer consisting of *Eurycoma longifolia* (Simaroubaceae), *Pandanus motleyanus* (Pandanaceae) and *Fagerlindia emanuelssoniana* (Rubiaceae) (Sugau and Tangah 2004). Fire sustains this vegetation, and successional gradients towards *Gymnostoma nobilis*-dominated forest or mixed forest are present. *Borneodendron aenigmaticum*, which is common on the islands in the Darvel Bay, has not been recorded from Malawali Island.

Endemism and restriction to ultramafic outcrops in Sabah

The isolation of many ultramafic outcrops may, coupled with strong edaphic and climatic stresses, promote the evolution of plant species (Kruckeberg 1986; Wong 2011). Ultramafic obligate species are, however, little documented in the flora of Sabah, with the majority of plant species known occurring facultatively on this substrate (van der Ent *et al*. 2014). Where ultramafic soils and altitude combine, hyper-endemics are sometimes found. Such species include *Rhododendron meijeri* and *R. baconii* (Ericaceae), *Begonia vaccinioides* (Begoniaceae), which are all restricted to Mount Tambuyukon in Kinabalu Park; *Rhododendron tuhanensis* (Mount Kinabalu), *R. sugaui* (Mount Tawai); and *R. monkoboense* (Mount Monkobo, Morou Porou) (Argent *et al*. 2007). Other well-known hyper-endemics include carnivorous plants, such as *Nepenthes burbidgeae. N. villosa* and *N. rajah* (Kinabalu Park). Figure 4 illustrates several ultramafic edaphic endemic species from Kinabalu Park.

Ultramafic obligate tree species include *Borneodendron aenigmaticum* (Euphorbiaceae) (a monotypic genus endemic to Sabah, which is allied to *Bertya*, *Myricanthe* and *Cocconerion* that mainly occur in Australia and New Caledonia; Radcliffe-Smith 2001), *Atuna cordata* (Chrysobalanaceae), *Quercus kinabaluensis* (Fagaceae), *Pittosporum linearifolium* and *P. silamense* (Pittosporaceae), *Weinmannia clemensiae* (Cunoniaceae), *Syzygium ultramaficum* (Myrtaceae), *Payena khoonmengiana*, *Madhuca silamensis* (Sapotaceae), *Helicia maxwelliana*, *H. symplocoides* (Proteaceae), *Ilex zygophylla* (Aquifoliaceae), and the small shrubs *Scaevola micrantha* (Goodeniaceae, also in the Philippines on Palawan), *S. chanii* (on Mount Kinabalu), and *S. verticillata* (on Mount Tambuyukon). Recently a few more species, that are hyper-endemic to a single or only a few sites, have been described, these include *Ardisia silamensis* (Primulaceae) (Utteridge *et al*. 2014), *Eriobotrya balgooyi* (Rosaceae) (Wong and van der Ent 2014) and *Gynura tambuyukonensis* (Asteraceae; van der Ent and Vanijajiva 2014).

Endemic orchids that are ultramafic obligate include the terrestrial and lithophytic slipper orchids *Paphiopedilum rothschildianum* and *P. dayanum* from Kinabalu Park, *P. hookerae* var. *volonteanum* from Kinabalu Park and the Meliau Range, the terrestrial *Calanthe otuhanica* known only from Kinabalu Park where it occurs on landslides, other terrestrial orchids such as *Coelogyne rupicola* and *Platanthera*

Fig. 4. Selection of ultramafic edaphic endemic species from Kinabalu Park. (*a*) *Begonia vaccinioides* (Begoniaceae), (*b*) *Scaevola verticillata* (Goodeniaceae), (*c*) *Rhododendron meijeri* (Ericaceae), (*d*) *Rhododendron baconii*, (*e*) *Drosera ultramafica* (Droseraceae), (*f*) *Wendlandia tambuyukensis* (Rubiaceae), (*g*) *Platanthera otuhanica* (Orchidaceae), (*h*) *Paphiopedilum hookerae* var. *volonteanum* (Orchidaceae), (*i*) *Paraphalaenopsis labukensis* (Orchidaceae), (*j*) *Nepenthes rajah* (Nepenthaceae), and (*k*) *Eriobotrya balgooyi* (Rosaceae).

Table 2. Nickel-hyperaccumulator plants described from Sabah (from literature), with maximum reported nickel concentrations in the literature
Recent discoveries of nickel hyperaccumulator plant species by van der Ent *et al*. (2013*c*, 2015) and van der Ent and Mulligan (2015) are not included in this table

Species	Ni (µg g^{-1})	Occurrence	Reference
Rinorea bengalensis	17 500	Throughout Southeast Asia	Brooks and Wither (1977)
Rinorea javanica	2170	Throughout South-east Asia	Brooks *et al*. (1977)
Phyllanthus balgooyi	16 000	Philippines and Sabah (Malaysia)	Baker *et al*. (1992); Hoffmann *et al*. (2003)
Dichapetalum gelonioides subsp. *tuberculatum*	26 600	Philippines and Sabah (Malaysia)	Baker *et al*. (1992)
Psychotria cf. *gracilis*	10 590	Sabah (Malaysia)	Reeves (2003)
Shorea tenuiramulosa	1000	Sabah (Malaysia)	Proctor *et al*. (1989)

kinabaluensis both of which are found in high-altitude ultramafic scrub, the epiphytes *Arachnis longisepala*, *Porpax borneensis*, *Paraphalaenopsis labukensis* and *Renanthera bella* all of which are known from a few populations only in lowland forests on ultramafic soils.

Nickel hyperaccumulator plants in Sabah

In total 6 nickel hyperaccumulator plants (Reeves 2003) are known from Sabah: *Rinorea bengalensis*, *R. javanica* (Violaceae), *Psychotria* cf. *gracilis* (Rubiaceae), *Phyllanthus balgooyi* (Phyllanthaceae), *Dichapetalum gelonioides* subsp. *tuberculatum* (Dichapetalaceae) and *Shorea tenuiramulosa* (Dipterocarpaceae) (Table 2). Of these species, *Phyllanthus balgooyi* (Phyllanthaceae) is relatively widespread often dominating open habitats on ridges and on riverbanks. The small tree *Shorea tenuiramulosa* is the only known nickel hyperaccumulator in the dipterocarp (Dipterocarpaceae) family (Proctor *et al*. 1989). Recent work by van der Ent *et al*. (2013*c*, 2015) and van der Ent and Mulligan (2015) revealed the further existence of a total of 19 nickel-hyperaccumulator species in Sabah, which suggests that this phenomenon may be relatively common in the local ultramafic flora.

State of knowledge of the flora of ultramafic outcrops in Sabah and threats to plant diversity

The scientific knowledge of the plant diversity and ecology of ultramafic outcrops in South-east Asia, particularly for Borneo and Sulawesi (Indonesia), is comparatively poor. Botanical collections from ultramafic outcrops in Sabah are highly biased, with many outcrops in the interior very incompletely known. So as to better understand the biogeography of plant species on ultramafic soils, it is critical that standardised georeferenced collections are made, with the aims of covering as much of Sabah as possible. This becomes more pressing because much of the existing herbarium collections originate from areas that are now cleared. The lack of knowledge puts constraints on protecting biodiversity, because Borneo is recognised for containing ~5% of all known plant species in the world and Malaysia is recognised as one of the 17 megacentres of world biodiversity (Paine 1997). In total, 15 000 species of flowering plants are estimated for Borneo (Wong 1998; Roos *et al*. 2004), of which 37% are endemic to the island (Van Welzen *et al*. 2005). Between 1995 and 2010, more than 600 species (plant and animal) have been discovered on Borneo (WWF 2013). However, biodiversity is severely threatened by deforestation, especially through large-scale plantation agriculture, particularly oil palm (Savilaakso *et al*. 2014). In ~1973, a total of 75.7% of Borneo's area was forested, but this declined by 30.2% in 2010 (Gaveau *et al*. 2014). In Sabah, 39.5% of the total forest area existing in 1973 had become non-forest in 2010 (Gaveau *et al*. 2014). Intact rain forests in protected areas amount to 8% of the land surface in Sabah (Bryan *et al*. 2013). Between 1990 and 2010, a net loss in forest cover of over 7000 km^2 occurred as a result of the clearance of forests outside of protected areas (Reynolds *et al*. 2011). The total area of oil-palm estates increased about five-fold, from 4% of land area in 1990 to ~19% in 2010 (http://econ.mpob.gov.my/economy/EID_web.htm, accessed June 2011). Sabah's population has also more than doubled, from 1.34 million in 1987 to 3.12 million in 2010 (Anonymous 2010). All these developments put severe pressure on the remaining biodiversity in Sabah and, therefore, totally protected Forest Reserves are critically important. In the period 1990–2010, the total area of Class I (total protection) Forest Reserves increased by ~3600 km^2, but unfortunately, this increase is mainly a consequence of reclassifying logged-over Class II (commercial) Forest Reserves, rather than the establishment of new protected areas (Reynolds *et al*. 2011).

In Kinabalu Park, many plant species are extremely localised, especially on ultramafic soils, so that 40% of all species recorded for the area are known only from a single collection (Beaman and Beaman 1990). The risks faced by rare plants is also illustrated by the case of the large tree *Dipterocarpus ochraceus*, known from just three populations, comprising 52 mature individuals altogether (Maycock *et al*. 2012), with most of the population outside the Kinabalu Park boundary facing clearing. This exemplifies the urgent need for detailed research on the plant diversity of ultramafic outcrops in Sabah, to assist the conservation of areas most threatened by logging and land-clearing activities. The majority of ultramafic outcrops are relatively small, and population sizes of plant species are, consequently, also small; therefore, rare plants face particular risks from the potential future effects of climate change-induced droughts and fires.

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