BIODIVERSITAS
Volume 24, Number 5, May 2023
Pages: 2814-2829

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d240535

Review: Diversity, structure, and community composition of Bornean heath forest with a focus on Brunei Darussalam

IRSALINA M. IKBAL[1], HAZIMAH H.M. DIN[2], WARDAH H. TUAH[2], SALWANA M. JAAFAR[2], NORHAYATI AHMAD[1,2], RAHAYU S. SUKRI[2,♥]

[1]Program of Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam. Jl. Tungku Link BE 1410, Bandar Seri Begawan, Brunei Darussalam

[2]Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam. Jl. Tungku Link BE 1410, Bandar Seri Begawan, Brunei Darussalam. Tel: +673 246 0923, ♥email: rahayu.sukri@ubd.edu.bn

Manuscript received: 19 December 2023. Revision accepted: 23 May 2023.

Abstract. *Ikbal IM, Din HHM, Tuah WH, Jaafar SM, Ahmad N, Sukri RS. 2023. Review: Diversity, structure, and community composition of Bornean heath forest with a focus on Brunei Darussalam. Biodiversitas 24: 2814-2829.* Tropical heath forests, a unique lowland forest ecosystem with high conservation value, are increasingly threatened by disturbances. Heath forests are characterized by trees of short stature and the presence of highly acidic, sandy soils with poor nutrient content. Bornean heath forests are widely studied for their diversity, structure, and community composition and are known to support endemics of high conservation value. Environmental factors and soil properties, such as topography, water availability, and nutrient status, are known to influence tree species diversity and forest structure of Bornean forests. However, factors influencing their community composition, including the role of seedling communities in influencing heath forest communities, are still not well understood. In particular, studies of tree diversity and community composition of heath forests in Brunei Darussalam have revealed high endemism and the presence of species with high conservation value. Anthropogenic threats to Bornean heath forests highlight the urgent need for an increased understanding of these forests and prioritization of their conservation. Increased insights into the ecological preferences of heath forest species are crucial for the successful restoration of degraded heath forests. The intact forest ecosystems of Brunei could provide opportunities for further ecological research on the plant communities found in these unique forests.

Keywords: Endemism, environmental factors, forest conservation, *kerangas* forest, tree diversity

INTRODUCTION

Tropical heath forests, a type of lowland forest formation with unique structure and physiognomic features, are characterized by trees of short stature and sclerophyllous leaves and are found on nutrient-poor soils (Whitmore 1984; Metali et al. 2014; Pereira 2016). They remain understudied and are considered to be low-diversity habitats because of their nutrient-deficient sandy soils (Sellan et al. 2019; Oktavia et al. 2021). However, they provide many ecosystem services, such as carbon storage (Kenzo et al. 2015; Hattori et al. 2016) as tropical podzols can store large quantities of carbon in both their upper and deeper horizons (Montes et al. 2011), and often harbor high numbers of endemic species (Din et al. 2015; Kueh et al. 2017; Suzana et al. 2018; Maimunah et al. 2019; Pesiu 2019). Consequently, the degradation of these rare forest ecosystems could have an impact on carbon emissions (Miyamoto et al. 2016; Hattori et al. 2019). Additionally, high rates of atmospheric nitrogen deposition can disrupt N-limited heath forests (Sellan et al. 2023), leading to soil acidification (Lu et al. 2014). Taken together, these ecosystem-level disruptions can eventually result in the loss of invaluable biodiversity and especially the loss of species endemic to heath forests (Raes et al. 2009; Ashton 2010).

Heath forests are found extensively in the flooded lowlands of the upper Rio Negro and Rio Orinoco basins in South America, including Brazil, Columbia, Peru, and Venezuela and the Guyanas where they extend over 900,000 km^2 and are referred to as white sand forests (Adeney et al. 2016; Fine and Bruna 2016; Mendonça et al. 2017). Owing to the distinct physiognomies and floristic compositions of the white sand forests across the Amazon, coupled with their patchy distribution, heath forests in the Neotropics are often known by several local terms, such as Amazonian *caatinga*, *campina*, and *campinarana* in Brazil, *wallaba* forest and *muri bush* in Guyana, French Guiana, and Suriname, *varillal* and *chamizal* in Peru and Colombia, and *caatinga* and *bana* in Venezuela (Adeney et al. 2016; Daly et al. 2016; Garcia-Villacorta et al. 2016). Patches of heath forests are also found in Amazonian Ecuador, French Guiana, Suriname, and Guyana, as well as on the Serra do Cachimbo on the Pará-Mato Grosso boundary, the Atlantic coast near the mouth of the Amazon, the Parecis plateau in Rondônia, and in Maranhão, while in Africa, they are found on the coastal sands of the Gulf of Guinea, Gabon, Cameroon, and the Ivory Coast (Whitmore 1998; Proctor

1999; Ghazoul and Sheil 2010; Fine and Baraloto 2016; Zoletto and Cicuzza 2022).

In Southeast Asia, the most extensive areas of heath forest are found on Borneo, representing 3.3% of the island's total forest cover (Brunig 1974; Kartawinata 1980; Harrison et al. 2012; MacKinnon et al. 2013; Sellan et al. 2019; Zoletto and Cicuzza 2022). Kalimantan (Indonesian Borneo) has the largest area of heath forest, which occupies around 11% of its total area (approximately 2,475,000 ha) (MacKinnon et al. 2013; Maimunah et al. 2019). Small patches of coastal heath forest are also found on the Bangka Belitung Islands and Singkep Island of Sumatra (Oktavia et al. 2021). In Peninsular Malaysia, heath forests grow in a narrow strip parallel to the east coast and extend down through Terengganu and Pahang. They also occur along the coastal plains of Kelantan and on the part of the coast of Johor (Wong et al. 1987; Musa et al. 2014). In addition, heath forests are also found on the summit of the sandstone plateau of Gunung Keriong on the southern border of Pahang and Sibu Island (Chua et al. 1995; Syuharni et al. 2014; Jani et al. 2019). They are known to occur at the foot of the central Maoke Range of Irian Jaya (Ashton 2014) and are also found in the Songkhla Lake Basin in the southern part of Thailand and the coastal foothills of the Cardamom mountains and on sandstone soils on the Bokor Plateau of the Elephant mountains in southern Cambodia (Hozumi et al. 1969; Whitmore 1984; Peeters and Wiwatwitaya 2014; Taing and Sridith 2016; Rundel and Middleton 2017; Rundel et al. 2019; Ashton and Lee 2022). In Singapore and Peninsular Malaysia, the type of secondary forest known as *Adinandra* belukar has also been identified as heath forest as its physiognomic features and floristic composition are similar to those of heath forest formations (Sim et al. 1992). This forest is dominated by the tree species *Adinandra dumosa* Jack (Pentaphyllacaceae) and was formed by plant succession after the original forest was cleared for plantation agriculture, which was later abandoned because of soil exhaustion (Sim et al. 1992).

This review examines the distributions, key characteristics and plant communities of Bornean heath forests, and discusses the present knowledge gaps on tree and seedling communities of these increasingly threatened forests. We focus on Brunei Darussalam's heath forests where tree and seedling community studies have revealed high endemism and the presence of species with high conservation values. Information synthesized in this review highlights essential areas for further ecological research in Brunei Darussalam's heath forests, as well as for Bornean heath forests, and is important as a reference for increased conservation efforts and forest restoration programs in these rare ecosystems.

HEATH FOREST FORMATIONS IN BORNEO

The tropical coastal heath forests of Borneo are distributed along the coastline on raised Pleistocene sea beaches with a podzolic profile (Whitmore 1984; Jusoh and Aziz 2014; Nugroho et al. 2022). Lowland heath forests (< 1000 m above sea level) are found inland on sandstone plateaus and cuesta formations on the hillsides of Kalimantan, Sarawak, Sabah, and Brunei (Brunig 1964; Miyamoto et al. 2003; Ashton 2014; Langner et al. 2015). On mountains (> 1000 m above sea level), lower montane heath forests (lower montane kerangas; Ashton 2014) occur on sandstone ridges, on podozolized soils, and over ultrabasic rocks (Ashton 2014; Van der Ent et al. 2015; Aiba and Kitayama 2020). In Central Kalimantan, heath forest fragments occur diagonally throughout the region as isolated patches within mixed dipterocarp forests (MDFs) or as stunted lower montane forests (Ashton 2014). In Sabah and Sarawak, lower montane heath forests are found from 800 to 1,800 m above sea level, for example on the sandstone ridge on Gunung Mulu (Sarawak) and the summit zone of Imbak Canyon (Sabah) (Proctor et al. 1983; Suratman et al. 2014). Heath forests can also occur at the center of Bornean peat swamp forest domes (Anderson 1963), which are often dominated by *Combretocarpus rotundatus* (Miq.) Danser (Anisophylleaceae; Nafiah et al. 2022), and where soils are extremely dry with low humidity (Ashton 2013; Zoletto and Cicuzza 2022).

Two heath forest formations occur in the lowlands of Borneo, comprising the dryland heath forests commonly referred to as *kerangas* forests and the waterlogged heath forests known as *kerapah* forests (Brunig 1974; Whitmore 1984; Wong et al. 2015a). The term *kerangas*, derived from the language of the local Iban community, refers to the infertile nature of the soil that prevents rice from growing (Brunig 1974; Whitmore 1984). *Kerangas* forests occur on weathered coastal alluvium and sandstone which give rise to nutrient-poor and acidic soils (Wong and Kamariah 1999; Wong et al. 2015a; Sellan 2019). The sandy soils are porous and have high permeability which results in well-drained soils (Brunig 1974; Ghazoul and Sheil 2010; Jaafar et al. 2016; Adanan et al. 2020). The inherently infertile, highly acidic soils (< pH 4) are usually overlain by a thin peaty soil or covered with a superficial thick fibrous raw humus layer, formed through the accumulation of organic matter, as well as thick litter layers with slow decomposition rates, rendering the soils unsuitable for cultivation of agricultural crops (Joffre and Shahri 2011; Ashton 2013; Wong et al. 2015a; Jaafar et al. 2016).

Kerapah forests are a sub-type of *Kerangas* forests and occur when heath soils experience waterlogging and poor soil drainage due to the presence of an impermeable hardpan, a distinct soil layer made up of humic colloids and quartz that is impervious to water (Proctor 1999; Wong and Kamariah 1999; MacKinnon et al. 2013; Wong et al. 2015a; Sellan 2019). *Kerapah* forests are recognized as one of the rarest and most unique forest formations in Borneo (Proctor 1999; Wong and Kamariah 1999; Nafiah et al. 2022). They are confined to the central regions of peatlands in Sarawak and Brunei but have not been described for Kalimantan (Osaki and Tsuji 2016). *Kerapah* forests can also occur next to heath forests, often displaying a similar physiognomy and floristic composition (Proctor 1999). They are characterized by their nutrient-poor soils, which are comparable to well-drained heath forest soils in acidity, but with lower soil nutrients, gravimetric water content, and organic matter content (Jaafar et al. 2016). *Kerapah* peat is typically rich in non-hydrolysable polyphenols (tannins) and allelopathic compounds (Brunig 2016).

Soil characteristics of Bornean heath forests

A distinguishing feature of Bornean heath forests is their soils, which are characterized by the presence of podzolized white sands (Figure 1A), marked with a white, often spodic, horizon (Whitmore 1984; Proctor 1999; Miyamoto et al. 2015). These white sand soils are primarily fine quartz lacking in brown, red, or yellow color due to the absence of iron oxides that are commonly associated with tropical soils (Syuhada et al. 2014; Kerfahi et al. 2019). In-situ weathering of quartzite sandstone, deposition of alluvial sands by rivers or sea (Syuhada et al. 2014; Kerfahi et al. 2019; Sellan 2019), or the podzolization of Oxisols which leaches organic matter and clay constituents into deeper soil layers while sands remained on the upper parts of the soil profile (Anderson 1981; Adeney et al. 2016; Sellan 2019), are thought to be the main origins of the sandy, podzolized Bornean heath soils. In Borneo, the drought-prone white sand podzols are confined to ridges, plateaus, and raised Pleistocene marine terraces, forming "islands" not greater than 50 km^2 in area (Ashton and Lee 2022).

Sandy soils are free-draining in nature and do not retain water, which, instead, percolates deep into the soil (Ashton 1992). Under these conditions, the soils lie directly over a sandstone substrate on a raised plateau or ridge (Zoletto and Cicuzza 2022). Sandy soil drainage can be impeded on such topographies, leaving stagnant water on the soil surface (Proctor 1999; Takada et al. 2016). The dark-colored water (Figure 1B) is due to the presence of humic acids caused by the lack of clay to adsorb them (Janzen 1974; Becker 2006). The highly acidic water carries iron sesquioxides and aluminum that precipitate at depth, forming a hardpan layer impermeable to water, which consequently inhibits water drainage (Becker 2006). Heath soils are typically shallow, with their dominant texture being sand or silty sand atop an interbedded sandstone with a moderate to high sand content (Davies and Becker 1996). The sand content increases with increasing soil depth; therefore, removal of aboveground vegetation from heath soils causes soil degradation and replacement of the area with bare sand and patches of shrubs and trees over a sparse grass called *padang* in Malay (Davies and Becker 1996; Whitmore 1998).

The strongly acidic (< pH 4) heath soils contain toxic concentrations of hydrogen ions (Proctor 1999; Sellan et al. 2022). For example, studies of Bornean heath forests have recorded a mean pH of 3.80-3.90 in Kalimantan, Indonesia (Vernimmen et al. 2013), 3.80 (± 0.18 SE) in Brunei (Jaafar et al. 2016), and 4.08 (± 0.04 SE) in Sabah, Malaysia (Sellan et al. 2021). Nutrients are leached quickly from heath forest soils due to their sandy texture (Ho et al. 2019). Moran et al. (2000) showed that nitrogen, carbon, and exchangeable calcium and magnesium concentrations decreased with depth, while phosphorus and exchangeable potassium concentrations remained relatively constant. The low cation concentration due to the intense leaching of heath forest soils increases hydrogen ion concentrations, lowering the soil pH and making the soil highly acidic (Proctor 1999; Metali et al. 2015). The low soil pH of heath forests can hinder organic matter decomposition, which further slows down nutrient cycling and affects forest productivity (Xu et al. 2013; Sellan et al. 2020). Heath forests often experience closed nutrient cycling due to the presence of deep organic layers (Moran et al. 2000; Jaafar et al. 2022b). The infertility of sandy heath soils has been linked to low pH, water shortage, and nutrient deficiency, particularly, in nitrogen and phosphorus (Whitmore 1984; Proctor 1999; Atikah 2014; Din et al. 2015). Soil solutions from heath forests in Brunei contain lower concentrations of nitrogen compared to those from MDF (Moran et al. 2000; Jaafar et al. 2016).

Figure 1. A. White sandy soils of the Bukit Sawat heath forest in Brunei Darussalam*;* B. Dark colored water due to the presence of humic acids found in the heath forests

Structure and physiognomy of Bornean heath forests

Bornean heath forests have a distinctive forest structure and tree characteristics compared to other lowlands Bornean tropical forests, such as the more widely distributed MDFs (Davies and Becker; 1996; Moran et al. 2000). Heath forests are characterized by smaller pole-sized trees (Figure 2) and large saplings that result in a densely packed and difficult to penetrate forest interior (MacKinnon et al. 2013; Atikah 2014; Brunig 2016; Coomes et al. 2017). Heath forest tree roots are typically stilt-rooted and unbuttressed and are mostly confined to the surface organic humus (Ashton 2014). The tree roots tend to be fine, intertwined, dense rooting that resists windthrow (Ashton and Lee 2022). Emergent dipterocarps are either lacking or restricted to isolated clumps within the heath forests where they rarely reach above the main canopy (Ashton and Lee 2022). The low tree species diversity of heath forests is related to the absence or poor representation of emergent species and few light hardwood successional species (Ashton 2014). *Kerangas* forests often lack pioneer species and are mainly dominated by slow-growing, shade-tolerant heavy hardwoods (Proctor et al. 1983; Ashton 2014).

In heath forests, tree canopy heights vary between 18 and 50 m and tree stand basal area is usually lower compared to trees in MDFs (Ashton and Hall 1992; Davies and Becker 1996; Miyamoto et al. 2007). Heath forests have low, densely packed, and even canopy surfaces with little vertical stratification (Jucker et al. 2018). The forest ground is well illuminated because of the smaller leaves that allow higher light penetration, resulting in high juvenile survivorship of shade-tolerant species and light-demanding climax species, dense undergrowth, and high abundances of bryophytes, myrmecophytes, and insectivorous plants (Whitmore 1984; Proctor 1999; Ashton 2014; Chua and Suleiman 2015; Aiba and Kitayama 2020; Mansur et al. 2021).

Another unique characteristic of heath forests is the usually vertically oriented, sclerophyllous, coriaceous (leathery) leaves, which are smaller in size, with higher density near twig ends, compared to leaves in corresponding MDFs because of greater leaf longevity and shorter internodes (Whitmore 1984; Ghazoul and Sheil 2010; Ashton 2014; Pereira 2016). For example, in Brunei's heath forests, Ashton and Lee (2022) found the dominant leaf size class to be notophylls (<12.5 cm long), borne by 37% of the trees sampled, followed by mesophylls (32%) and microphylls (26%). Leaves of heath forests are characterized by their narrow shapes; thicker epidermis, lamina, and cuticle layers; small leaf area relative to leaf mass; a well-developed palisade mesophyll; lower stomatal density; abundant sclerenchymatous tissue; and trichomes (Miyamoto et al. 2007; Ashton 2014; Ibrahim et al. 2021; Bartholomew et al. 2022; Ordway et al. 2022; Rodda and Rahayu 2022; Zoletto and Cicuzza 2022).

The low rate of decomposition of organic matter in heath forests is attributed to the thicker, tougher, and long-lived nature of leaves in heath forests (Moran et al. 2000; Miyamoto et al. 2016). Plants growing in highly infertile environments exhibit greater nutrient-use efficiency (NUE) (Vernimmen et al. 2013). The long-lived nature of leaves in heath forests is a typical trait associated with high NUE and slow decomposition rates (Vernimmen et al. 2013). This results in a feedback mechanism, whereby at sites where nutrients are limited, the nutrient-poor litter produced by plants decomposes at a slower rate, intensifying the nutrient limitation at these sites (Vernimmen et al. 2013). In addition, leaf litterfall in heath forests contains higher polyphenol (tannin) concentrations compared to litterfall in neighboring MDFs (Proctor 1999; Dent et al. 2006). High phenolic concentrations are a defense mechanism against herbivory, particularly in nutrient-poor habitats where the nutritional cost of leaf replacement is high (Janzen 1974; Vernimmen et al. 2013; Zoletto and Cicuzza 2022).

Figure 2. The smaller, pole-sized trees give the stunted appearance of the heath forests at: A. Badas Forest Reserve and; B. Bukit Sawat Forest Reserve, Brunei Darussalam

In addition to their low nitrogen and phosphorus concentrations (Ordway et al. 2022), leaves in heath forests have xeromorphic features that serve as oligotrophic adaptations that reduce transpiration and conserve water (Whitmore 1984; Ashton 2014). The xeromorphic structures and vertically orientated leaves may also be adaptations to drought because they reduce water loss, heat loads, and irradiance, making plants less susceptible to photoinhibition and protecting leaves from irreversible photodamage during droughts and excessive radiation levels (Zoletto and Cicuzza 2022). Miyamoto et al. (2016) showed that heath forests could maintain moderately high productivity under stressful conditions, such as low water or nutrient availability, probably due to the adaptive leaf features.

Plant communities in Bornean heath forests

The floristic composition of Bornean heath forests varies widely but the most common and species-rich families are from the families Myrtaceae, Clusiaceae and Rubiaceae (Davies and Becker 1996; Ikbal 2021). Other tree species that can also be commonly found in the heath forests include those in the families Burseraceae, Dipterocarpaceae, Malvaceae and Sapotaceae (Brunig 1974; Wong and Kamariah 1999; Culverhouse 2013). In contrast, the Polygalaceae, Sapindaceae, and Meliaceae are represented by fewer species (Davies and Becker 1996; Syuharni et al. 2014; Din et al. 2015; Ashton 2016; Purwaningsih and Kartawinata 2018; Maimunah et al. 2019). Tree species characteristic of Bornean heath forests include the tropical conifers *Agathis borneensis* Warb. (Araucariaceae), *Dacrydium* spp. (Podocarpaceae) and *Gymnostoma nobile* (Whitmore) L.A.S.Johnson (Casuarinaceae) (Brunig 1974; Farjon and Filer 2013; Wong et al. 2015a; Stalin and Franco 2020; Maimunah et al. 2022) and canopy tree species such as *Calophyllum ferrugineum* Ridl. (Calophyllaceae), *Copaifera palustris* (Symington) de Wit (Fabaceae), *Dipterocarpus borneensis* Slooten (Dipterocarpaceae), *Gluta beccarii* (Engl.) Ding Hou (Anacardiaceae), and *Shorea multiflora* (Burck) Symington (Dipterocarpaceae) (Davies and Becker 1996; Ashton 2014) (Figure 3). Other tree species found in heath forests are *Shorea* spp. (Dipterocarpaceae), *Lithocarpus* spp. (Fagaceae), *Syzygium* spp. (Myrtaceae), and *Cratoxylum* spp. (Hypericaceae) (Whitmore 1990; Purwaningsih and Kintamani 2018).

Heath forests show lower plant diversity compared to other lowland forest types (Davies and Becker 1996; Vernimmen et al. 2013; Tjiu et al. 2021) but support higher numbers of rare and endemic tree species with high conservation value (Pengiran Kamsani and Slik 2018). Studies in Brunei's heath forests have recorded several of these, such as *Chionanthus crispus* Kiew (Oleaceae), *Calophyllum ardens* P.F.Stevens (Calophyllaceae), *Glochidion kerangae* Airy Shaw (Phyllanthaceae), *Knema ashtonii* J.Sinclair (Myristicaceae), *Sarcotheca glauca* (Hook.fil.) Hallier fil. (Oxalidaceae), *Syzygium caryophylliflorum* (Ridl.) Merr. & Perry and *Syzygium megalophyllum* Merr. & Perry (Myrtaceae), and *Ternstroemia gymnanthera* var. *gymnanthera* (Pentaphylacaceae) (Din et al. 2015; Tuah et al. 2020; Ikbal 2021). Furthermore, *K. ashtonii* and *S. caryophylliflorum* were registered as vulnerable species while all the other tree species listed are not yet assessed under the IUCN Red List (IUCN 2022).

In the heath forests of Sarawak and Brunei, heavier hardwood species that are shade and drought-tolerant, such as *Shorea* and *Hopea* (Dipterocarpaceae), are prominent and can be found in abundance (Whitmore 1984; Wong and Kamariah 1999). These dense, hardwood tree species typically grow in well-drained soils, where drought can increase the risk of cavitation (Ashton and Lee 2022). The high wood density reflects anatomical structures that reduce cavitation and increase transport (Ashton and Lee 2022). Trees with highly dense wood have a higher carbon investment that reduces their overall growth rates; therefore, *kerangas* tree species typically have slow growth rates (Ashton and Lee 2022). In addition, the slow organic matter decomposition rate, which results in lower available soil nitrogen, further limits tree growth (Miyamoto et al. 2016). Heath forests on well-drained lowland podzols show the lowest maximum individual growth rates (Ashton 2014). The soil nutrient limitation of Bornean heath forests has a strong influence on the adaptations of many tree species, which have developed functional traits to survive in their environment. For example, *Gymnostoma nobile* (Whitmore) L.A.S.Johnson has nitrogen-fixing actinomycetes residing in its root nodules, allowing it to grow well on nutrient-deficient soil (Proctor 1999; Wong et al. 2015a; Idhamsah and Yusop 2019).

Figure 3. Some of the tree saplings found in Brunei Darussalam's heath forests: A. *Hopea pentanervia* Symington (Dipterocarpaceae); B. *Shorea multiflora* (Burck) Symington (Dipterocarpaceae); C. *Shorea havilandii* Brandis (Dipterocarpaceae) and; D. the tropical conifer, *Agathis borneensis* Warb. (Araucariaceae)

In addition, coniferous species in heath forests take up nutrients via their mycorrhizal associates and their leaves show high nutrient-use efficiency (Miyamoto et al. 2016). The species richness of the herbaceous layer of Bornean heath forests is comparable to that of MDFs, with abundance and density being significantly higher in the former (Shabdin et al. 2013; Zaini and Sukri 2014; Noor Ain et al. 2015). This difference may be due to the more open canopy of heath forests, which allows higher light penetration than the closed canopy of MDFs (Zaini and Sukri 2014). Some of the most abundant herbaceous species include plants from Araceae, Lindsaeaceae, Orchidaceae, Pandanaceae, Rubiaceae, Schizaeaceae, and Zingiberaceae (Zaini and Sukri 2014). Specialist plants that are adapted to survive on highly infertile soils by trapping and digesting insects for additional nutrition, such as carnivorous pitcher plants (*Nepenthes* spp.), sundews (*Drosera* spp.), and bladderworts (*Utricularia* spp.), are commonly associated with Bornean heath forests (Latiff et al. 2014; Bazile et al. 2015; Clarke and Moran 2016; Osunkoya and Muntassir 2017; Setiawan et al. 2018; Mansur et al. 2020; Kang et al. 2021). Other specialist plants such as the myrmecophytic epiphytic fern, *Lecanopteris sinuosa* (Wall. ex Hook.) Copel. (Polypodiaceae), and epiphytic ant-plants, *Myrmecodia* spp. and *Hydnophytum* spp. (Rubiaceae), have a symbiotic relationship with ants as an adaptation to the nutrient-limited environment of heath forests (Whitmore 1984; Low et al. 2016; Zoletto and Cicuzza 2022). Both *Hydnophytum* spp. and *Myrmecodia* spp. possess an enlarged stem with chambers that act as shelter for ants, in exchange for which the ants provide the plants with essential nutrients by bringing them into the chambers where the plants will then break down and absorb the nitrogen-rich debris brought by the ants through their wall linings or adventitious roots (Low et al. 2016). *L. sinuosa* has a mutualistic association with stingless shelter ants from the genera *Crematogaster*, *Technomyrmex* or *Iridomyrmex*, sheltering the latter in exchange for protection against herbivory, as well as nutrients derived from the feces of ant colonies (Zoletto and Cicuzza 2022).

Epiphytic plants commonly found in Bornean heath forests include orchids, climbing ferns, and the Araceae (Ashton 2014; Cicuzza et al. 2020; Wong et al. 2020; Yudistira et al. 2022). Epiphytic orchids that anchor themselves to tree trunks are more diverse than terrestrial orchids growing on the ground, mainly because the nutrient-deficient, acidic, sandy heath forest soils are not favorable to the growth of terrestrial orchids (Wood and van der Ent 2012; Suetsugu et al. 2017, 2018; Juiling et al. 2020). Epiphytic ferns in Bornean heath forests are represented by *Drynaria* and *Platycerium* (Polypodiaceae) and *Haplopteris* (Pteridaceae) (Chen et al. 2019; Cicuzza et al. 2020; Zoletto and Cicuzza 2022). Climbing ferns are mostly represented by *Stenochlaena* (Blechnaceae), while the woody climbers, *Uncaria* and *Smilax* species usually form sparse canopies and are low in number (Ashton 2014; Cicuzza et al. 2020). Climbers from the Araceae are represented by a few genera such as *Pothos*, *Raphidophora*, and *Scindapsus* (Saibeh et al. 2015; Wong and Boyce 2019).

STUDIES ON TREE DIVERSITY AND COMMUNITY COMPOSITION OF BORNEAN HEATH FORESTS

Previous studies of Bornean tropical heath forests focused on describing and documenting their tree diversity and communities (Brunig 1974; Proctor et al. 1983; Kartawinata 1980; Newbery and Proctor 1984; Vernimmen et al. 2013; Din et al. 2015; Purwaningsih and Kartawinata 2018; Maimunah et al. 2019; Sellan et al. 2019; Tuah et al. 2020). Heath forests in Sarawak, Sabah and Brunei were among the first Bornean heath forests to be studied (Brunig 1974; Proctor et al. 1983; Newbery and Proctor 1984) and continue to be well investigated (Suratman et al. 2011, 2015; Din et al., 2015; Miyamoto et al. 2016; Kueh et al. 2017; Takeuchi et al. 2017; Sellan et al. 2019; Suis et al. 2019; Miyamoto et al. 2021; Bukhori et al. 2022). Proctor et al.'s (1983) study of the community composition and structure of four types of lowland forest formation in Gunung Mulu National Park in Sarawak recorded a total of 113 tree species, of which the Clusiaceae (Guttiferae) was the most abundant (n = 170 individuals) within the 1.0-ha heath forest study area, followed by the Dipterocarpaceae (n = 92 individuals) and Myrtaceae (n = 74 individuals). The Dipterocarpaceae had the highest basal area (42.9%), followed by the Clusiaceae and Myrtaceae, with basal areas of 17% and 11%, respectively (Proctor et al. 1983). The low basal area recorded for the Clusiaceae and Myrtaceae was because both families consisted of only small-sized individuals (Proctor et al. 1983). In the case of forest structure, the Gunung Mulu National Park heath forest was dominated by pole-sized trees (62.0%), with a stem diameter of 10-20 cm (Proctor et al. 1983). The tallest individual tree recorded within the study area was *Shorea albida* Symington ex A.V.Thomas (Dipterocarpaceae), with a height not exceeding 50 m.

Sellan et al. (2019) investigated the species composition and forest structure of heath forests in the Kabili-Sepilok Forest Reserve in Sabah and recorded 124 species in 48 families, of which the Myrtaceae (19%) and Rubiaceae (14%) were the most abundant within a 0.36-ha area. They also noted that their site lacked the Myrsinaceae, Annonaceae, and Chrysobalanaceae, which are commonly found in Bornean tropical heath forests, most likely due to their small study area (0.36 ha). The most common tree species recorded were understory specialists and included *Gaertnera junghuhniana* (Rubiaceae), with a total stem density of 12.74%, followed by *Diospyros fusiformis* Kosterm. (Ebenaceae; 7.45% total stem density) and *Syzygium caudatilimbum* (Merr.) Merr. & Perry (Myrtaceae; 6.07% total stem density). The Myrtaceae had the highest basal area (31%), followed by the Dipterocarpaceae (19%), Clusiaceae (11%), and Euphorbiaceae (10%). In the case of forest structure, trees with a diameter at breast height (DBH) of < 2 cm were the most abundant, with 1,413 individuals, followed by trees with a DBH of 2-5 cm (n = 1,087 individuals). The plot studied was a typical short-statured heath forest with a canopy height of approximately 28 m. Several edaphic factors were shown to have different influences on tree size classes in the heath forest. For example, soil depth, soil pH, and soil nutrients (cation exchange capacity and available aluminum concentration) had a strong influence on species composition and distribution of trees of 5 cm ≤ DBH < 10 cm, whereas small trees were less influenced by edaphic factors and topography (Sellan et al. 2019).

Maimunah et al. (2019) investigated the tree diversity and forest composition of two types of heath forest in south-central Kalimantan: white sand heath forest and black sand heath forest. The two types of heath forests differed in their soil type with the white sand heath forest characterized by white sands with a thin layer of peat on top of the soil while the black sand heath forest has high organic material contented in the upper layer of the soil, which gives the appearance of the *black sand* (Maimunah et al. 2019). They recorded a total of 1,007 trees, representing 87 species in 40 families from the two sub-types of heath forest. They also found that the two sub-types of heath forest were dominated by different tree families (Maimunah et al. 2019). The black sand heath forest was dominated by three families, the Dipterocarpaceae (19.5%), Myrtaceae (19.2%), and Sapotaceae (13.0%), while the white sand heath forest was largely dominated by tree species from the Dipterocarpaceae (43.4%), i.e., *D. borneensis* and *Shorea teysmanniana* Dyer ex Brandis. *Neoscortechinia kingii* (Hook.f.) Pax & K.Hoffm. (Euphorbiaceae), *Elaeocarpus mastersii* King (Elaeocarpaceae), and *Nephelium maingayi* Hiern (Sapindaceae), present in the black sand heath forest, were absent in the white sand heath forest. Likewise, several tree species, such as *Ilex cymosa* Blume (Aquifoliaceae), present in the white sand heath forest, were absent in the black sand heath forest. Trees with a DBH of 10-20 cm were the most abundant, with 710 individuals recorded from both heath forest sites. The variation in tree community composition in the two heath forests was significantly influenced by the organic layer depth and soil moisture (Maimunah et al. 2019). Purwaningsih and Kartawinata (2018) examined the species composition and structure of four forest types in the Muara Kendawangan Nature Reserve in West Kalimantan and found the lowest species richness in the heath forest, with only eight species recorded within a 0.3-ha area, the dominant family being the Myrtaceae, with species including *Baeckea frutescens* L., *Syzygium griffithii* (Duthie) Merr. & Perry, and *Tristaniopsis whiteana* (Griff.) Paul G.Wilson & J.T.Waterh. The structure of the heath forest plot was dominated by small trees (98.7%) with a stem diameter of 10-14 cm and a height of < 10 m, with the average height being 6 m.

Several tree diversity and community studies have been conducted in the heath forests of Brunei Darussalam (Davies and Becker 1996; Din et al. 2015; Haji Saman 2015; Jambul et al. 2020; Pengiran Zamanulalam 2020; Tuah et al. 2020; Ikbal 2021). Species richness of trees ≥ 5cm DBH were higher in a 0.96-ha plot in the Bukit Sawat heath forest compared to a similar-sized area in the heath forest of Badas Forest Reserve, with 171 and 113 species, respectively (Davies and Becker 1996). The heath forest in Badas was heavily dominated by *A. borneensis*, which contributed 64.5% of the basal area and 16.2% (n = 217 individuals) of the total number of trees recorded (Davies and Becker 1996). In Bukit Sawat, *D. borneensis* was the most abundant tree species, accounting for 6.1% of the total number of trees and 6.8% of the basal area (Davies and Becker 1996). The lack of dominance of *A. borneensis* in the Bukit Sawat heath forest might have led to greater evenness in species composition and, consequently, higher species richness (Davies and Becker 1996). Floristic variation appeared to be related to the drainage gradient, with *A. borneensis* dominating in well-drained areas and *G. beccarii* (Anacardiaceae) in areas with impeded drainage (Davies and Becker 1996). Similarly, Pengiran Zamanulalam (2020) recorded higher abundance, species richness, and diversity of trees ≥ 5 cm DBH within six 0.04 ha plots in the Bukit Sawat heath forest than in six 0.04 ha plots in Sungai Kargu heath forest, with 126 and 113 species, respectively, with both study sites being dominated by the Dipterocarpaceae.

In the Tutong White Sands (TWC) heath forest within six 0.04 ha plots, 296 trees ≥ 5 cm DBH have been recorded, representing 78 species in 38 families (Din et al. 2015). The most abundant tree species was *Combretocarpus rotundatus* (Miq.) Danser, with 27 individuals, while the most species-rich family was the Annonaceae, with eight species recorded. The tree species recorded in peaty plots of the heath forest at TWC were peat swamp specialists, while common *kerangas* species, such as *Buchanania arborescens* (Blume) Blume (Anacardiaceae) and *G. nobile*, were found in drier heath forest areas, possibly due to differences in topsoil nitrogen concentrations and canopy openness. Despite the small size of the study area, 16 of the 78 tree species (20.5%) recorded were Bornean endemics, such as *Actinodaphne borneensis* Meisn. (Lauraceae), *C. ardens* (Calophyllaceae), *Chionanthus crispus* (Oleaceae), *Cotylelobium burckii* (F.Heim) F.Heim (Dipterocarpaceae), and *Lithocarpus dasystachyus* (Miq.) Rehder (Fagaceae).

Within the 1-ha intact coastal *kerangas* forest of the Universiti Brunei Darussalam (UBD) Botanical Research Centre, Ikbal (2021) recorded 825 trees of ≥ 1 cm DBH, representing 61 species in 34 families, seven of which were Bornean endemics: *Calophyllum woodii* P.F.Stevens (Calophyllaceae), *Picrophloeus belukar* (K.M.Wong & Sugau) K.M.Wong (Gentianaceae), *Syzygium incarnatum* (Elmer) Merr. & Perry (Myrtaceae), and *S. glauca* (Oxalidaceae). The Symplocaceae was the most abundant family (n = 188 individuals), followed by the Myrtaceae (n = 112 individuals) and Rubiaceae (n = 110 individuals), while the Calophyllaceae was the most species-rich, with a total of six species. The species importance value (SIV) measures the dominance of a species in a particular area (Musa et al. 2014). In this case, the most important species was *Symplocos polyandra* (Blanco) Brand (Symplocaceae; species importance value (SIV) = 69.1), followed by *Tristaniopsis obovata* (Benn.) Paul G.Wilson & J.T.Waterh. (Myrtaceae; SIV = 17.5) and *Calophyllum obliquinervium* Merr. (Calophyllaceae; SIV = 17.0) within the 1-ha UBD BRC *kerangas* area. With regards to forest structure, trees with a DBH of 1-10 cm were the most abundant, comprising 68.2% of stems (n = 563 individuals). The heath forests on the UBD campus appear to contain remnants of intact old-growth forest (Jambul et al. 2019; Tuah et al. 2020; Ikbal 2021), indicated by the presence of species such as *S. polyandra*, *Timonius flavescens* (Jacq.) Baker (Rubiaceae), and *T. obovata*.

KNOWLEDGE GAPS ON BORNEAN HEATH FORESTS

Vegetation succession and regeneration in Bornean heath forests

While most studies of Bornean heath forests have focused on tree communities, the determination of seedling community diversity may better inform the findings on tree communities. To date, few studies have investigated woody seedling diversity and morphology, and the influence of environmental and soil properties on seedling diversity and communities in heath forests (Nishimura and Suzuki 2001; Tuah 2017; Ya'akub 2020; Nafiah et al. 2022). Nafiah et al. (2022) compared woody seedling diversity, composition, and abundance between four different forest types in Brunei Darussalam, including dry *kerangas* forest and waterlogged *kerapah* forest. The most abundant tree seedlings in the dry *kerangas* forest were from the Dipterocarpaceae (mainly *C. burckii* individuals), followed by the Sapotaceae (mainly *Madhuca curtisii* (King & Gamble) Ridl. individuals), Myrtaceae, and Euphorbiaceae; the Dipterocarpaceae, Euphorbiaceae, and Lauraceae were the most species-rich, with a total of four species recorded for each family. In the waterlogged *kerapah* forest, the Myrtaceae was the most abundant (n = 62 individuals), followed by the Rubiaceae and Sapotaceae, with a total of 12 individuals recorded for each family, while the Myrtaceae and Rubiaceae were the most species-rich, with a total of three species in each family. In addition, four high-conservation-value species were documented in the dry *kerangas* and waterlogged *kerapah* plots: *A. borneensis*, *C. burckii*, *Dryobalanops rappa* Becc. (Dipterocarpaceae), and *M. curtisii*. Nafiah et al. (2020) concluded that these two heath forest formations are floristically related, sharing nine families, such as the Anacardiaceae, Annonaceae, and Elaeocarpaceae, possibly due to similarities in their soil characteristics (Jaafar et al. 2016). Ya'akub (2020) compared woody seedling diversity, survival, and growth in *kerangas* and *kerapah* forests in Lumut, Brunei, and found that the Myrtaceae was the dominant family in both heath forest formations, followed by the Dipterocarpaceae and Sapotaceae, while the Dipterocarpaceae and Lauraceae were the most species-rich families with a total of four species each. Of the 28 families recorded, 11 were common to both heath forest formations, including the Fagaceae, Phyllanthaceae, and Polygalaceae (Ya'akub 2020).

Forest tree community composition and seedling distribution are interrelated, therefore, research findings on woody seedling diversity and communities can improve the understanding of the role of seedling communities in influencing tree community composition, as well as being a useful reference that can aid the success of rehabilitation programs and restoration of degraded heath forests. For example, *D. rappa* is a light-demanding tree species commonly found in heath forests (Ashton et al. 2003). It is well adapted to the dry, nutrient-deficient, and acidic soils of heath forests and performs well under the open canopy (Ashton et al. 2003). *D. rappa* is well recorded in both *kerangas* and *kerapah* forests in Brunei (Coode et al. 1996; Din et al. 2015; Haji Saman 2015; Tuah 2017; Nafiah et al. 2020; Pengiran Zamanulalam 2020; Ya'akob 2020). The percentage survival of *D. rappa* has been shown to be higher at the seedling and sapling stages compared to that of seedlings or saplings of other species (Tuah 2017; Din et al. 2018). A rehabilitation study by Tuah (2017) in the degraded *kerapah* forest in Brunei showed that, of the five species studied, *D. rappa* saplings had a higher growth and survival rate (89.71%). Tuah's (2017) finding of *D. rappa*'s ability to perform well within the revegetation plots with open canopies coincides with Ashton et al.'s (2003) report of this light-demanding species growing well under high light exposure. Therefore, understanding the ecological preferences of the selected species and effective species-site matching is crucial, as they play a substantial role in sapling performance (Manson et al. 2013), for the successful restoration of degraded heath forests.

Abiotic factors influencing tree diversity and community composition in tropical heath forests

The roles of environmental factors and soil properties in influencing heath forest tree communities are still poorly understood. The patterns of distribution and diversity of tree species, community composition, and structure of heath forests are known to be influenced by various environmental factors and soil characteristics, such as variability in water and nutrient status, topography, humus depth, soil depth, and drainage (Proctor et al. 1983; Davies and Becker 1996; Miyamoto et al. 2003, Sellan et al. 2019). These factors may allow different species to establish themselves in different heath forest sites.

Soil properties, such as high acidity, low soil fertility, and low concentrations of cations, e.g., aluminum, phosphorus, potassium, calcium, and magnesium, have been shown to influence species composition and forest structure of Bornean heath forests (Moran et al. 2000; Metali et al. 2015; Sellan et al. 2019). Tree species distributions within heath forests of Gunung Mulu in Sarawak are associated with differences in soil organic carbon and cation exchange capacity (Newbery and Proctor 1984). In this site, *Calophyllum teysmannii* Miq. (Calophyllaceae), *Kayea calophylloides* Ridl. (Calophyllaceae), and *Lophopetalum rigidum* Ridl. (Celastraceae) are commonly found on soil containing higher organic matter and nutrients, while *Baccaurea bracteata* Müll.Arg. (Phyllanthaceae), *Calophyllum andersonii* P.F.Stevens, *H. pentanervia* (Dipterocarpaceae), and *S. scabrida* (Dipterocarpaceae) are common on heath forest plots at Gunung Mulu, which have less organic matter. Furthermore, the basal area of *S. albida*, *C. teysmannii*, and *L. rigidum* is greater on soils with higher organic matter content than on soils with less organic matter and nutrients

(Newbery and Proctor 1984). Sellan et al. (2019) showed that heath forest tree species distribution and forest structure in the Kabili-Sepilok Forest Reserve, Sabah were influenced by available aluminum concentration, soil acidity, and soil depth. They found that the overall floristic variation through their parcels of trees with a DBH of <10 cm was strongly influenced by soil depth and available aluminum concentration, while that of trees with a DBH of 5-10 cm was also affected by cation exchange capacity and total soil phosphorus. Sellan et al. (2019) concluded that soil acidity was the main factor influencing floristic variation and forest structure in their study area (Sellan et al. 2019). In addition, differences in species composition and dominance at the Tutong White Sands heath forest in Brunei are associated with total nitrogen concentrations in the topsoil (Din et al. 2015). For example, Din et al. (2015) reported that the heath forest plots with poor drainage in their study had lower soil nutrient concentrations, resulting in trees with smaller basal areas compared to the trees in well-drained heath forest plots.

Topography is recognized as a key driver of tropical forest composition and structure (Sukri et al. 2012; Limin et al. 2021) as topographic gradients typically translate to gradients in soil resources, which can then affect the conditions for tree growth (Davies and Becker 1996; Moeslund et al. 2013; Jucker et al. 2018; Sellan et al. 2019). Topographic features of the terrain, such as relief and slope, have a strong influence on soil chemistry (Chadwick and Asner 2016; Bittencourt 2022). Gradients in nutrient concentrations and water availability on ridges, slopes, and valleys (Sukri et al. 2012) can result in habitat-specific adaptations in species (Jucker et al. 2018). Jucker et al. (2018) investigated different lowland tropical forest types (alluvial dipterocarp forests, sandstone dipterocarp forests, and heath forests) in the Sepilok Forest Reserve, Sabah, with topography being the strongest driver of differences seen in forest structure and composition. In addition, the vertical structure of the canopy decreased progressively with increasing elevation, and tree species composition changed with topographic variation (Jucker et al. 2018). Topographic variables are some of the factors shaping species diversity, distribution, and forest structure of the Kabili-Sepilok heath forest ecosystem in Sabah, and account for 76% of the floristic variation observed (Sellan et al. 2019). Tree species abundance in the heath forest in Central Kalimantan, Indonesia appears to be affected by topographic variables, in particular relative elevation and edaphic factors (Miyamoto et al. 2003). In Brunei's heath forests, topographic relief and drainage gradient have been shown to influence species abundance (Davies and Becker 1996).

HEATH FORESTS OF BRUNEI DARUSSALAM: DISTRIBUTION, CONSERVATION VALUE, AND CURRENT THREATS

Brunei Darussalam is recognized as a floristically rich region and is one of the few tropical Asian nations to remain well forested (Henrot et al. 2013; Ashton 2014; Wong et al. 2015b, 2015c; Neo et al. 2020), with 54% of its land area still covered by unlogged, pristine forest (Bryan et al. 2013). With a land area of about 576,532 ha, Brunei Darussalam is one of the countries with the highest percentage of forest cover, with approximately 76% (438,000 ha) of the land remaining heavily forested (Haji Ahmat and Haji Tongkat 2010). Coode et al. (1996) listed 3451 plant species occurring in Brunei, with a total of 1902 tree species. The actual number of tree species is thought to be higher; Ashton and Lee (2022) estimated a total of 3,000 tree species occurring in the different forests in Brunei, accounting for ca. 12% of tree species in all of tropical Asia, with 38% of them endemic to Borneo. A total of 65 angiosperm species have been recorded as Brunei endemics, with seven being trees belonging to the Elaeocarpaceae, Menispermaceae, Myristicaceae, Polygalaceae, and Rubiaceae (Henrot et al. 2013).

Brunei Darussalam's heath forests comprise an estimated 3455 ha and cover around 0.6% of its forests (Wong and Kamariah 1999; Haji Ahmat and Haji Tongkat 2010; Wong et al. 2015a, Figure 4). They occur in patches on ancient white-sand terraces and along the coastal region, the Tutong-Belait highway area known as Tutong White Sands in Tutong District. They also occur as inland heath forests on thick sand deposits associated with peat swamp complexes, such as those in the Badas Forest Reserve, Anduki Forest Reserve, and Bukit Sawat in Belait District, in some parts of Brunei-Muara District, e.g., the intact coastal *kerangas* in the UBD Botanical Research Centre and its surrounding area, and montane *kerangas* on the sandstone plateaus of Bukit Patoi, Gunong Pagon Priok, and on the hills and ridges of Bukit Peradayan, Bukit Biang, Bukit Telugong, and Bukit Gelagas of Temburong District (Davies and Becker 1996; Wong and Kamariah 1999; Joffre and Shahri 2011; Din et al. 2015; Ibrahim et al. 2021; Ikbal 2021; Ashton and Lee 2022; Ibrahim et al. 2022). Three types of heath forests occur in Brunei: lowland *kerangas*, hill *kerangas*, and permanently waterlogged or *kerapah* forests (Whitmore 1984).

Previous studies on tree diversity and forest structure of heath forests in Brunei (Davies and Becker 1996; Din et al. 2015; Haji Saman 2015; Pengiran Zamanulalam 2020; Ikbal 2021) found high species endemism, as well as species with high conservation value, in these rare and fragile tropical forest ecosystems (Brunig 1974; Din et al. 2015; Pengiran Kamsani and Slik 2018; Nafiah et al. 2022). These studies have collectively recorded several tree species endemic to Borneo, as well as species of high conservation value listed as endangered in the IUCN Red List, for example *A. borneensis* (Lauraceae), *C. palustris* (Fabaceae), *Syzygium grande* (Wight) N.P.Balakr. (Myrtaceae), *Hopea dyeri* F.Heim (Dipterocarpaceae), *Lithocarpus andersonii* Soepadmo (Fagaceae), *Sterculia rhoidifolia* Stapf ex Ridl. (Malvaceae), *C.burckii*, and *S. albida* (Din et al. 2015; Pengiran Zamanulalam 2020).

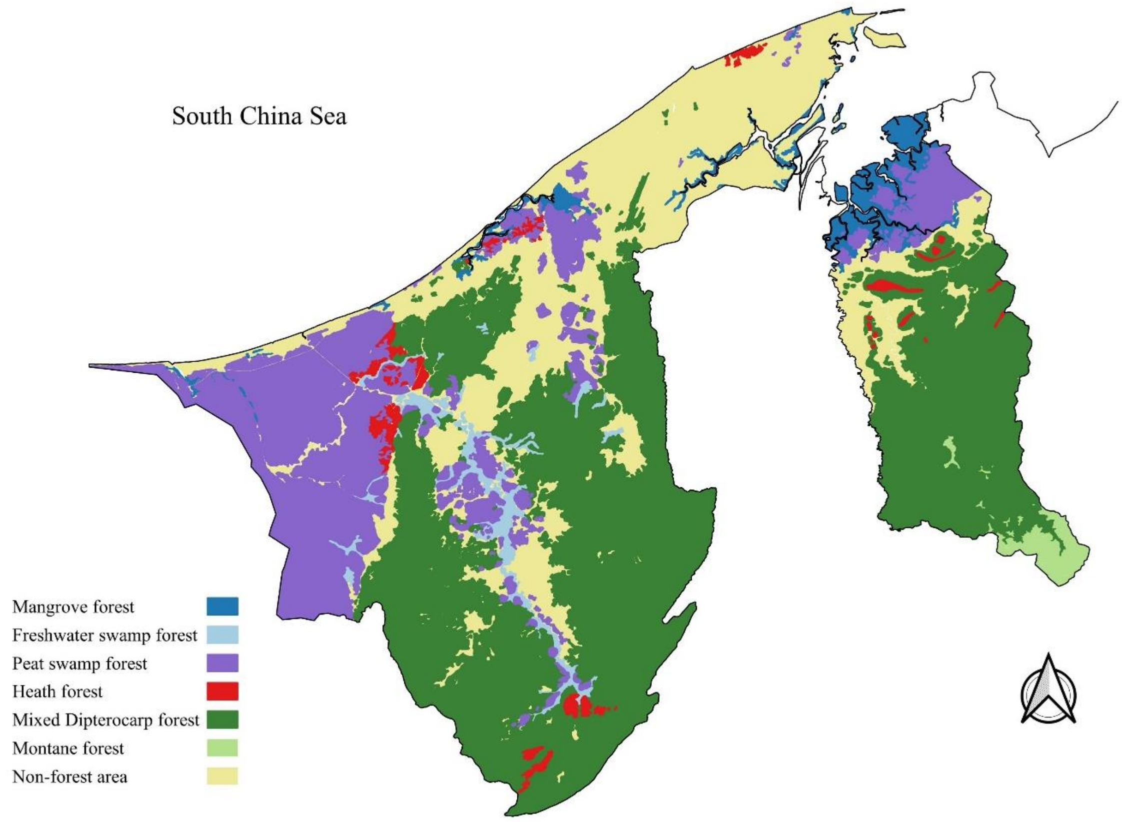

Figure 4. The distribution of different forest types in Brunei Darussalam, with heath forests shown in red

At present, the heath forests of Brunei Darussalam are under threat due to increasing disturbances such as fire events, alien species invasion, and deforestation (Din et al. 2015; Jambul et al. 2020; Tuah et al. 2020; Ibrahim et al. 2021). Heath forests of Brunei are highly vulnerable and prone to fires during droughts and dry periods due to the inherently dry nature of the sandy, porous soil, which is poor at retaining water; their more open canopy, which increases light penetration; and high accumulation of dry leaves on the forest floor, forming a combustible layer during dry periods (Tuah et al. 2020). Most native *kerangas* species are not adapted to high-intensity fires, and repeated forest fires increase the mortality of native plant species, decrease native tree species diversity and richness, and cause the eventual displacement of native trees with *Acacia* (Jambul et al. 2020; Tuah et al. 2020). Following these fire disturbances, invasive *Acacia* species often successfully spread within natural habitats in Brunei, most notably in the coastal areas where most heath forests are found (Islam et al. 2019; Tuah et al. 2020, Figure 5). Presently, there are four exotic *Acacia* spp. in Brunei, the most abundant being *Acacia mangium* Willd., followed by *Acacia auriculiformis* A.Cunn. ex Benth., *Acacia cincinnata* F.Muell., and the less common *Acacia holosericea* A.Cunn. ex G.Don (Quong-Vuong et al. 2018; Islam et al. 2019; Ibrahim et al. 2022). *A. mangium* (Figure 5C), in particular, is an urgent threat to Brunei's coastal heath forests, because it affects native tree species diversity (Suhaili et al. 2015; Tuah et al. 2020) and modifies soil and leaf litter properties (Yusoff et al. 2019; Ibrahim et al. 2021; Jaafar et al. 2022a), ion deposition (Ibrahim et al. 2022), and nutrient cycling of invaded heath forests (Jaafar et al. 2022b). It is shade-intolerant and performs well in disturbed areas with high light exposure, and its successful invasion is partly attributed to its ability to form an extensive soil seed bank in the areas it occupies (Suhaili et al. 2015). In addition, *Acacia* spp. invasion has increased the risk of forest fires in invaded areas and the coastal forest of Brunei due to their high litter production (Yusoff et al. 2019; Jambul et al. 2020). *Acacia* individuals are known to shed high amounts of litter due to their rapid growth rate, producing a thick litter layer that may be flammable during dry seasons (Boudiaf et al. 2013; Jambul et al. 2020; Nafiah et al. 2022).

Although invasive *Acacia* spp. are a major threat to heath forest biodiversity and have caused significant losses of native plant diversity in Brunei's coastal *kerangas* forests (Islam et al. 2019; Jambul et al. 2020; Tuah et al. 2020), successful recovery of heavily degraded heath forests is possible. In the absence of disturbance events, such as fires, and provided that the spread of invasive *Acacia* spp. is mitigated, heath forests can naturally regenerate within two to three decades (Islam et al. 2019; Jambul et al. 2020). Thus, forest management policies that limit disturbance events and eliminate or reduce the dominance of invasive *Acacia* spp. are crucial to the recovery of degraded heath forests. As *Acacia* spp. are shade-intolerant, once natural forest regeneration restores canopy cover, the shaded understory conditions hinder *Acacia* seed germination, which is stimulated by heat, thereby reducing the rate of successful germination over time (Suhaili et al. 2015; Jambul et al. 2020).

Forest clearance and selective logging are a potential threat to heath forests, although there has been less forest exploitation in Brunei compared to other parts of Southeast Asia, mainly due to its oil and gas economy and the low population size (Haji Ahmat and Haji Tongkat 2010). Although Brunei's heath forests and its tropical forests in general, are less threatened by deforestation, these forests are under constant threat of destruction elsewhere in Borneo (Bryan et al. 2013; Gaveau et al. 2014, 2016; Riswan 2014; Adrianto et al. 2019; Estoque et al. 2019; Milodowski et al. 2021). To safeguard Brunei's forests, the Forestry Department of Brunei Darussalam has implemented various initiatives, programs, policies, and strategies to conserve and sustainably manage the country's remaining pristine forest (Haji Ahmat and Haji Tongkat 2010). The Heart of Borneo (HoB) is one of the largest initiatives of Brunei, in partnership with Malaysia and Indonesia, aiming to conserve Borneo's remaining tropical rainforests (Haji Ahmat and Haji Tongkat 2010; Wulffraat and Morrison 2013). Many small areas of tropical heath forest (of < 500 ha) are scattered throughout the HoB region, and this initiative further strengthens the efforts to protect and sustainably manage these rare forests and their associated biodiversity (Wulffraat and Morrison 2013). To date, 40% of Brunei's land area (235,520 ha) has been gazetted as forest reserves, with an additional 15% of the land area currently being earmarked for forest management purposes; patches of the fragile tropical heath forests are mostly included within these gazetted areas (Haji Ahmat and Haji Tongkat 2010; Joffre and Shahri 2011).

The Forestry Department has also limited the issuance of logging permits or licenses as a conservation strategy (Haji Ahmat and Haji Tongkat 2010; Joffre and Shahri 2011). This is especially crucial to the conservation of the fragile tropical heath forests as logging will rapidly degrade their soil, turning them into open, savanna-like grassland within a few years (Whitmore 1998; Hattori et al. 2019). Moreover, the turnover of heath forests is slow due to the slow growth of their valuable timber species, such as the tropical conifer, *A. borneensis*, which requires centuries for it to grow and develop into productive timber (Stalin and Franco 2020; Zoletto and Cicuzza 2022). In addition, increased biomass within Borneo can significantly impact atmospheric nutrient redistribution, resulting in acidifying effects on nutrient-limited ecosystems (Ponette-González et al. 2016) such as heath forests. Such excessive deposition of atmospheric nitrogen may lead to several environmental issues including soil acidification and consequently a decline in biodiversity (Lu et al. 2014; Midolo et al. 2019)

Between 1980 and 2000, an estimated 24% of Brunei's heath forests were cleared and lost due to increasing human activity (Becek and Odihi 2008). However, much of Brunei Darussalam is still covered in undisturbed forests and intact forest ecosystems, which provide opportunities for education and further research on the plant communities found in these forests. The unique biodiversity of Bornean heath forests, which support many important endemic and specialist species, makes this habitat particularly fragile and highly vulnerable to natural and anthropogenic threats, such as forest fires and habitat degradation (Proctor et al. 1983; Brunig 2016; Garcia-Villacorta et al. 2016; Miyamoto et al. 2021). Given the high conservation value of this fragile and unique forest type, careful management and protection of Brunei's heath forests are crucial and studies focusing on the factors influencing their diversity and community composition are essential.

Figure 5. *Acacia*-invaded heath forests in Brunei Darussalam, showing: A. The monodominance of invasive *Acacia* trees; B. the change in forest structure from *Acacia* invasion; and C. leaves and flowers of *A. mangium*

CONCLUDING REMARK

Our literature survey confirmed the high plant diversity of Bornean lowland heath forests and their high conservation value as habitats. The species diversity, composition, and distribution patterns and forest structure of these nutrient-poor heath forests are influenced by soil physicochemical properties and environmental conditions. Although several attempts have been made to investigate the impacts of these factors, further studies are essential to clarify their importance in influencing the tree communities and structure of heath forests. The presence of numerous rare and endemic species of high conservation value in the heath forests of Brunei, as well as in Bornean heath forests in general, emphasizes the importance of protecting and managing these increasingly rare forests, as well as the critical need to study their biodiversity to inform conservation planning strategies.

ACKNOWLEDGEMENTS

The authors would like to thank Universiti Brunei Darussalam for research funding (grant reference number: UBD/RSCH/1.13/FICBF(b)/2022/033) and the Ministry of Education, Brunei Darussalam for the lead author's graduate scholarship. We thank the Brunei Forestry Department for field and herbarium support for heath forest studies in Brunei Darussalam. We thank Rodzay Hj Abd Wahab for assistance with the Brunei forest map.

REFERENCES

Adanan IC, Wasli ME, Perumal M, Ho SY. 2020. Characterization of soil properties in relation to *Shorea macrophylla* growth performance under sandy soils at Sabal Forest Reserve, Sarawak, Malaysia. Biodiversitas 21 (4): 1467-1475. DOI: 10.13057/biodiv/d210426

Adeney JM, Christensen NL, Vicentini A, Cohn-Haft M. 2016. White-sand ecosystems in Amazonia. Biotropica 48 (1): 7-23. DOI: 10.1111/btp.12293

Adrianto HA, Spracklen DV, Arnold SR, Sitanggang IS, Syaufina L. 2019. Forest and land fires are mainly associated with deforestation in Riau province, Indonesia. Remote Sens 12 (1): 3. DOI: 10.3390/rs12010003

Aiba SI, Kitayama K. 2020. Light and nutrient limitations for tree growth on young versus old soils in a Bornean tropical montane forest. J Plant Res 133 (5): 665-679. DOI: 10.1007/s10265-020-01217-9

Anderson BA. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13: 199-210. DOI:10.2307/2388125

Anderson JAR. 1963. The flora of the peat swamp forests of Sarawak and Brunei, including a catalogue of all recorded species of flowering plants, ferns and allies. Gardens Bull Singap 20: 31-228.

Ashton MS. 1998. Seedling ecology of mixed-dipterocarp forest. In: Appanah, S, Turnbull, JM (eds). A Review of Dipterocarps: Taxonomy, Ecology and Silviculture. Center for International Forestry Research, Bogor.

Ashton P. 2016. Notes on northern Borneo Myrtaceae. Sandakania (22): 55-75.

Ashton PS, Hall P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. J Ecol 80: 459-81. DOI: 10.2307/2260691

Ashton PS, Kamariah AS, Said IM. 2003. Field guide to the forest trees of Brunei Darussalam and the Northwest Borneo hotspot. Universiti of Brunei Darussalam in association with Brunei Forestry Department, Brunei Shell Petroleum and Sultan Haji Hassanal Bolkiah Foundation, Bandar Seri Begawan, Brunei Darussalam.

Ashton PS, Lee D. 2022. Trees and Forests of Tropical Asia: Exploring Tapovan. University of Chicago Press, Chicago. DOI: 10.7208/chicago/9780226535722.001.0001.

Ashton PS. 2010. Conservation of Borneo biodiversity: do small lowland parks have a role, or are big inland sanctuaries sufficient? Brunei as an example. Biodivers Conserv 19: 343-356. DOI: 10.1007/s10531-009-9717-0.

Ashton PS. 2013. A view from the trees. Raffles Bull Zool S29: 41-47.

Ashton PS. 2014. On the Forests of Tropical Asia: Lest the Memory Fade. Kew Publishing, London.

Atikah TD. 2014. Differentiation in Architecture and Demographic Properties across Forest Types and Species in Tropical Lowland Kalimantan. [Dissertation]. Hokkaido University, Sapporo. DOI: 10.14943/doctoral.k11350.

Bartholomew DC, Banin LF, Bittencourt PR, Suis MAF, Mercado LM, Nilus R, Burslem, DFRP, Rowland L. 2022. Differential nutrient limitation and tree height control leaf physiology, supporting niche partitioning in tropical dipterocarp forests. Funct Ecol 36 (8): 2084-2103. DOI: 10.1111/1365-2435.14094.

Bazile V, Le Moguédec G, Marshall DJ, Gaume L. 2015. Fluid physico-chemical properties influence capture and diet in *Nepenthes* pitcher plants. Ann Bot 115 (4): 705-716. DOI: 10.1093/aob/mcu266.

Becek K, Odihi JO. 2008. Identification and assessment of factors affecting forest depletion in Brunei Darussalam. Intl Arch Photogram Remote Sens Spat Inf Sci 37 (B2): 209-214.

Becker P. 2006. Special features of tropical heath forest: facts and myths. Tropics 15: 267-270. DOI: 10.3759/tropics.15.267

Bittencourt PRDL, Bartholomew DC, Banin LF, Bin Suis, MAF, Nilus R, Burslem DF, Rowland L. 2022. Divergence of hydraulic traits among tropical forest trees across topographic and vertical environment gradients in Borneo. New Phytol 235 (6): 2183-2198. DOI: 10.1111/nph.18280

Boudiaf I, Baudoin E, Sanguin H, Beddiar A, Thioulouse J, Galiana A, Prin Y, Le Roux C, Lebrun M, Duponnois R. 2013. The exotic legume tree species, *Acacia mearnsii*, alters microbial soil functionalities and the early development of a native tree species, *Quercus suber*, in North Africa. Soil Biol Chem 65: 172-179. DOI: 10.1016/j.soilbio.2013.05.003

Brunig EF. 1974. Ecological Studies in the Kerangas Forests of Sarawak and Brunei. Borneo Literature Bureau, Kuching.

Brunig EF. 2016. Conservation and Management of Tropical Rainforests: An Integrated Approach to Sustainability. CABI, Oxfordshire, England. DOI: 10.1079/9781780641409.0000.

Bryan JE, Shearman PL, Asner GP, Knapp DE, Aoro G, Lokes B. 2013. Extreme differences in forest degradation in Borneo: Comparing practices in Sarawak, Sabah, and Brunei. PloS ONE 8 (7): e69679. DOI: 10.1371/journal.pone.0069679.

Bukhori MFM, Daud R, Gintoron CS, Othman MR, Idris MI, Tingga RCT, Mustapha MA, Goh MBL. 2022. Brief documentation of ecosystem in Kubah, Bako, and Santubong National Park, Sarawak. Trends Undergrad Res 5 (2): a1-16. DOI: 10.33736/tur.4354.2022.

Chadwick KD, Asner GP. 2016. Tropical soil nutrient distributions determined by biotic and hillslope processes. Biogeochemistry 127 (2): 273-289. DOI: 10.1007/s10533-015-0179-z.

Chen CW, Lindsay S, Yong KT, Mustapeng, AMA, Amoroso VB, Dang VD, Huang YM. 2019. Clarification of two poorly known vittarioid ferns (Pteridaceae): *Haplopteris angustissima* and *H. capillaris*. Syst Bot 44 (3): 483-493. DOI: 10.1600/036364419X15620113920545 .

Chua GLS, Koh BL, Lau L, Lee SC, Mathias M, Turner IM, Yong, JWH. 1995. The nutrient status of the plateau heath forest of Gunung Keriong, Pahang, Peninsular Malaysia. J Trop For Sci 8: 240-246.

Chua MS, Suleiman M. 2015. Additions to the moss flora of Imbak Canyon Conservation Area, Malaysian Borneo. Bryophyte Divers Evol 37 (2): 23-30. DOI: 10.11646/bde.37.2.1

Cicuzza D, Ahmad MAH, Jipli AR, Pg Sapudin DNS, Hj Ismail NSA. 2020. Fern diversity and distribution in the UBD campus. Sci Bruneiana 19 (1): 1-18. DOI: 10.46537/scibru.v19i1.114

Clarke C, Moran JA. 2016. Climate, soils and vicariance - their roles in shaping the diversity and distribution of *Nepenthes* in Southeast Asia. Plant Soil 403 (1): 37-51. DOI: 10.1007/s11104-015-2696-x

Coode M, Dransfield J, Forman L, Kirkup D, Said I. 1996. A checklist of the flowering plants and gymnosperms of Brunei Darussalam. Ministry of Industry and Primary Resources, Brunei Darussalam.

Coomes DA, Dalponte M, Jucker T, Asner GP, Banin LF, Burslem DF, Lewis SM, Nilus R, Phillips OL, Phua MH, Qie L. 2017. Area-based vs tree-centric approaches to mapping forest carbon in Southeast

Asian forests from airborne laser scanning data. Remote Sens Environ 194: 77-88. DOI: 10.1016/j.rse.2017.03.017

Culverhouse F. 2013. The Taxonomy and Conservation of *Palaquium* in Brunei [MSc Dissertation]. The University of Edinburgh, Scotland.

Daly DC, Silveira M, Medeiros H, Castro W, Obermüller FA. 2016. The white-sand vegetation of Acre, Brazil. Biotropica 48 (1): 81-89. DOI:10.1111/btp.12307.

Davies SJ, Becker P. 1996. Floristic composition and stand structure of mixed dipterocarp and heath forests in Brunei Darussalam. J Trop For Sci 8 (4): 542-569.

Dent DH, Bagchi R, Robinson D, Majalap-Lee N, Burslem, DF. 2006. Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest. Plant Soil 288 (1): 197-215. DOI:10.1007/s11104-006-9108-1.

Din H, Bakiri NB, Sukri RS, Metali FH. 2018. Assessment of seedling abundance, survival and growth of two dipterocarp species in peat swamp forests of Brunei Darussalam. Biotropia 25 (2): 148-154. DOI: 10.11598/btb.2018.25.2.805.

Din H, Metali F, Sukri RS. 2015. Tree diversity and community composition of the Tutong White Sands, Brunei Darussalam: A rare tropical heath forest ecosystem. Intl J Ecol 2015 (4): 1-11. DOI:10.1155/2015/807876.

Estoque RC, Ooba M, Avitabile V, Hijioka Y, DasGupta R, Togawa T, Murayama Y. 2019. The future of Southeast Asia's forests. Nat Commun 10 (1): 1-12. DOI: 10.1038/s41467-019-09646-4.

Farjon A, Filer D. 2013. An Atlas of the World's Conifers: An Analysis of Their Distribution, Biogeography, Diversity and Conservation Status. Brill, Netherlands. DOI: 10.1163/9789004211810.

Fine PVA, Baraloto C. 2016. Habitat endemism in white-sand forests: Insights into the mechanisms of lineage diversification and community assembly of the Neotropical flora. Biotropica 48 (1): 24-33. DOI: 10.1111/btp.12301.

Fine PVA, Bruna EM. 2016. Neotropical white-sand forests: Origins, ecology and conservation of a unique rain forest environment. Biotropica 48: 5-6. DOI:10.1111/btp.12305.

Garcia-Villacorta R, Dexter KG, Pennington T. 2016. Amazonian white-sand forests show strong floristic links with surrounding oligotrophic habitats and the Guiana shield. Biotropica 48: 47-57. DOI:10.1111/btp.12302.

Gaveau DL, Sheil D, Salim MA, Arjasakusuma S, Ancrenaz M, Pacheco P, Meijaard E. 2016. Rapid conversions and avoided deforestation: Examining four decades of industrial plantation expansion in Borneo. Sci Rep 6 (1): 1-13. DOI: 10.1038/srep32017.

Gaveau DL, Sloan S, Molidena E, Yaen H, Sheil D, Abram NK, Ancrenaz M, Nasi R, Quinones M, Wielaard N, Meijaard E. 2014. Four decades of forest persistence, clearance and logging on Borneo. PloS ONE 9 (7): e101654. DOI: 10.1371/journal.pone.0101654.

Ghazoul J, Sheil D (eds). 2010. Tropical Rain Forest Ecology, Diversity, and Conservation. Oxford University Press, Oxford, UK.

Haji Ahmat M, Haji Tongkat R. 2010. The management of forest resources and land in Brunei Darussalam. In: McConnell, LuQian and WangQian (eds). Participants Reports on Forest Resources Management; Proceedings of APFNet Workshop on Forest Resources Management. Kunming, China, 8-19 November 2010.

Haji Saman F. 2015. A Comparison of the Tree Flora Diversity in the Heath Forest at Bukit Sawat and the Tutong White Sands. [BSc Dissertation]. Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam.

Harrison ME, Cheyne SM, Husson SJ, Jeffers KA, Smallcombe JV, Ehlers Smith DA. 2012. Preliminary Assessment of the Biodiversity and Conservation Value of the Bawan Forest, Central Kalimantan, Indonesia. Orangutan Tropical Peatland Project Report. Palangka Raya, Indonesia.

Hattori D, Kenzo T, Shirahama T, Harada Y, Kendawang, JJ, Ninomiya I, Sakurai K. 2019. Degradation of soil nutrients and slow recovery of biomass following shifting cultivation in the heath forests of Sarawak, Malaysia. For Ecol Manag 432: 467-477. DOI: 10.1016/j.foreco.2018.09.051.

Henrot J, Ahmed JA, Wong KM. 2013. The Flowering Plants Endemic to Brunei Darussalam. Forestry Department, Ministry of Primary Resources, Brunei Darussalam.

Ho SY, Wasli MEB, Perumal M. 2019. Evaluation of physicochemical properties of sandy-textured soils under smallholder agricultural land use practices in Sarawak, East Malaysia. Appl Environ Soil Sci 2019 (2): 1-14. DOI: 10.1155/2019/7685451.

Hozumi K, Yoda K, Kokawa S, Kira T. 1969. Production ecology of tropical rain forests in southwestern Cambodia I. Plant Biomass. Nat Life Southeast Asia 6: 1-51.

Ibrahim MH, Metali F, Tennakoon KU, Sukri RS. 2022. Impacts of invasive Acacias on ion deposition in a coastal Bornean tropical heath forest. J For Res 27 (1): 20-27. DOI: 10.1080/13416979.2021.1965700.

Ibrahim MH, Sukri RS, Tennakoon KU, Le QV, Metali F. 2021. Photosynthetic responses of invasive *Acacia mangium* and co-existing native heath forest species to elevated temperature and CO_2 concentrations. J Sustain For 40 (6): 573-593. DOI: 10.1080/10549811.2020.1792317.

Idhamsah D, Yusop H. 2019. Preliminary Results of Rooting *Gymnostoma nobile* Cuttings Using the Simple Water Method. Conf.: 18th Malay Forest Conference.

Ikbal IS. 2021. Community Composition and Diversity of Trees in the 1-ha Kerangas Forest at UBD Botanical Research Centre. [BSc Dissertation]. Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam.

Islam SN, Haji Mohamad SM, Azad AK. 2019. *Acacia* spp.: Invasive trees along the Brunei coast, Borneo. In: Makowski C, Finkl C (eds). Impacts of Invasive Species on Coastal Environments. Springer, Cham. DOI: 10.1007/978-3-319-91382-7_14.

IUCN (International Union for Conservation of Nature). 2022. IUCN Red List of Threatened Species. www.iucnredlist.org.

Jaafar S, Metali F, Sukri R. 2022a. *Acacia* invasion differentially impacts soil properties of two contrasting tropical lowland forests in Brunei Darussalam. J Trop Ecol 38 (5): 259-266. DOI: 10.1017/s0266467422000141.

Jaafar SM, Metali F, Nafiah SNS, Supri NE, Ahmad N, Burslem DFRP, Sukri RS. 2022b. Differential impacts of *Acacia* invasion on nutrient fluxes in two distinct Bornean lowland tropical rain forests. Forests 13 (12): 2101. DOI: 10.3390/f13122101.

Jaafar SM, Sukri RS, Proches S. 2016. An investigation of soil physicochemical variables across different lowland forest ecosystems of Brunei Darussalam. Malaysian J Sci 35 (2): 148-166. DOI: 10.22452/mjs.vol35no2.6.

Jambul R, Limin A, Ali AN, Slik F. 2020. Invasive *Acacia mangium* dominance as an indicator for heath forest disturbance. Environ Sustain Indic 8: 100059. DOI: 10.1016/j.indic.2020.100059.

Jani JM, Shahrudin R, Chan AA, Ismail M, Bahrin B, Jamaludin S. 2019. Pulau Sibu scientific expedition: Connecting the land and the sea for biodiversity management of a Marine Park island. Malay Nat J 71 (3): 277-284.

Janzen DH. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6: 69-103. DOI: 10.2307/2989823.

Joffre AA, Shahri HH. (eds). 2011. Proceeding of the 5th Workshop on Sustainable Resource Management 2011: Sustainable Forest Resource Management in Brunei Darussalam. Asia-Pacific Network for Sustainable Forest Management and Rehabilitation, Kunming, China, October 2011.

Jucker T, Bongalov B, Burslem DF, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L, Coomes DA. 2018. Topography shapes the structure, composition and function of tropical forest landscapes. Ecol Lett 21 (7): 989-1000. DOI: 10.1111/ele.12964.

Juiling S, Leon SK, Jumian J, Tsen S, Lee YL, Khoo E, Sugau JB, Nilus R, Pereira JT, Damit A, Tanggaraju S, O'Byrne P, Sumail S, Mujih H, Maycock CR. 2020. Conservation assessment and spatial distribution of endemic orchids in Sabah, Borneo. Nat Conserv Res 5 (1): 136-144. DOI: 10.24189/ncr.2020.053.

Jusoh I, Aziz MA. 2014. Species composition and stand structure of an exploited mangrove forest. Kuroshio Sci 8 (1): 63-67.

Kang V, Isermann H, Sharma S, Wilson DI, Federle W. 2021. How a sticky fluid facilitates prey retention in a carnivorous pitcher plant (*Nepenthes rafflesiana*). Acta Biomaterialia 128: 357-369. DOI: 10.1016/j.actbio.2021.04.002.

Kartawinata K. 1980. A note on a Kerangas (heath) forest at Sebulu, East Kalimantan. Reinwardtia 9 (4): 429-447. DOI: 10.14203/REINWARDTIA.V9I4.925.

Kenzo T, Furutani R, Hattori D, Tanaka S, Sakurai K, Ninomiya I, Kendawang JJ. 2015. Aboveground and belowground biomass in logged-over tropical rain forests under different soil conditions in Borneo. J For Res 20 (1): 197-205. DOI: 10.1016/j.foreco.2018.09.051.

Kerfahi D, Tripathi BM, Slik, JWF, Sukri RS, Jaafar S, Dong K, Ogwu MC, Kim H, Adams, JM. 2019. Soil metagenome of tropical white sand heath forests in Borneo: What functional traits are associated with an extreme environment within the tropical rainforest? Pedosphere 29 (1): 12-23. DOI: 10.1016/S1002-0160(18)60054-2.

Kueh RJH, Mang NG, Huat OK, Sait M, Sam S, Empin, GB, Rajanoran T. 2017. Tree diversity at Payeh Maga Montane Forest, Sarawak, Borneo. J Trop Biol Conserv 14: 125-150. DOI: 10.51200/jtbc.v14i0.903.

Langner A, Achard F, Vancutsem C, Pekel JF, Simonetti D, Grassi G, Kitayama K. Nakayama M. 2015. Assessment of above-ground biomass of Borneo forests through a new data-fusion approach combining two pan-tropical biomass maps. Land 4 (3): 656-669. DOI: 10.3390/land4030656.

Latiff NA, Sukri RS, Metali F. 2014. *Nepenthes* diversity and abundance in five habitats in Brunei Darussalam. Reinwardtia 14 (1): 67-71. DOI: 10.14203/reinwardtia.v14i1.396.

Limin A, Slik F, Sukri RS, Chen SB, Ahmad JA. 2021. Large tree species composition, not growth rates, is affected by topography in a Bornean tropical forest. Biotropica 53 (5): 1290-1300. DOI: 10.1111/btp.12969.

Low YW, Sugau JB, Wong KM. 2016. *Hydnophytum puffii* (Rubiaceae: Psychotrieae), a new ant-plant from Sabah, Malaysian Borneo. Plant Ecol Evol 149 (1): 123-130. DOI: 10.5091/plecevo.2016.1102.

Lu X, Mao Q, Gilliam FS, Luo Y, Mo J. 2014. Nitrogen deposition contributes to soil acidification in tropical ecosystems. Glob Chang Biol 20 (12): 3790-3801. DOI: 10.1111/gcb.12665.

MacKinnon K, Hatta G, Halim H, Mangalik A. 2013. The Ecology of Kalimantan: Indonesian Borneo. Tuttle Publishing, New York, USA.

Maimunah S, Capilla BR, Harrison ME. 2019. Tree diversity and forest composition of a Bornean heath forest, Indonesia. IOP Conf Ser: Earth Environ Sci 270 (1): 012028. DOI: 10.1088/1755-1315/270/1/012028.

Maimunah S, Kessler PJ, Indrioko S, Naiem M. 2022. Natural distribution of the genus *Dacrydium* Lamb. (Podocarpaceae) in Central Kalimantan, Indonesia. Biodiversitas 23 (6): 2816-2822. DOI: 10.13057/biodiv/d230605.

Manson DG, Schmidt S, Bristow M, Erskine PD, Vanclay JK. 2013. Species-site matching in mixed species plantations of native trees in tropical Australia. Agrofor Syst 87 (1): 223-250. DOI: 10.1007/s10457-012-9538-0.

Mansur M, Brearley F, Haq JR. 2020. Diversity, abundance and ethnobotany of *Nepenthes* in Mandor Nature Reserve, West Kalimantan, Indonesia. Planta Carniv 41 (1): 12-6.

Mansur M, Brearley FQ, Esseen PJ, Rode-Margono EJ, Tarigan MRM. 2021. Ecology of *Nepenthes clipeata* on Gunung Kelam, Indonesian Borneo. Plant Ecol Divers 14 (3-4): 195-204. DOI: 10.1080/17550874.2021.1984602.

Mendonça BAD, Filho EIF, Schaefer CEGR, Mendonça, JGD, Vasconcelos BN. 2017. Soil-vegetation relationships and community structure in a "terra-firme"-white-sand vegetation gradient in Viruá National Park, northern Amazon, Brazil. An Acad Bras Ciênc 89: 1269-1293. DOI: 10.1590/0001-3765201720160666.

Metali F, Abu Salim K, Tennakoon K, Burslem DF. 2015. Controls on foliar nutrient and aluminium concentrations in a tropical tree flora: Phylogeny, soil chemistry and interactions among elements. New Phytol 205 (1): 280-292. DOI: 10.1111/nph.12987.

Midolo G, Alkemade R, Schipper AM, Benítez-López A, Perring MP, De Vries W. 2019. Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis. Glob Ecol Biogeogr 28 (3): 398-413. DOI: 10.1111/geb.12856.

Milodowski DT, Coomes DA, Swinfield T, Jucker T, Riutta T, Malhi Y, Svatek M, Kvasnica J, Burslem DFRP, Ewers RM, Teh YA, Williams M. 2021. The impact of logging on vertical canopy structure across a gradient of tropical forest degradation intensity in Borneo. J Appl Ecol 58 (8): 1764-1775. DOI: 10.1111/1365-2664.13895.

Miyamoto K, Aiba SI, Aoyagi R, Nilus R. 2021. Effects of El Niño drought on tree mortality and growth across forest types at different elevations in Borneo. For Ecol Manag 490: 119096. DOI: 10.1016/j.foreco.2021.119096.

Miyamoto K, Kohyama TS, Rahajoe JS, Mirmanto E, Simbolon H. 2016. Forest structure and productivity of tropical heath and peatland forests. In: Osaki M, Tsuji N (eds) Tropical Peatland Ecosystems. Springer, Tokyo. DOI: 10.1007/978-4-431-55681-7_10.

Miyamoto K, Rahojoe JS, Kohyama T, Mirmanto E. 2007. Forest structure and primary productivity in a Bornean heath forest. Biotropica 39: 35-42. DOI: 10.1111/j.1744-7429.2006.00231.x.

Miyamoto K, Suzuki E, Kohyama T, Seino T, Mirmanto E, Simbolon H. 2003. Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical heath forest of Central Kalimantan, Indonesia. J Trop Ecol 19 (1): 43-54. DOI: 10.1017/s0266467403003067.

Miyamoto K, Wagai R, Aiba SI, Nilus R. 2016. Variation in the aboveground stand structure and fine-root biomass of Bornean heath (kerangas) forests in relation to altitude and soil nitrogen availability. Trees 30 (2): 385-394. DOI: 10.1007/s00468-015-1210-7.

Moeslund JE, Arge L, Bøcher PK, Dalgaard T, Svenning JC. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. Nord J Bot 31 (2): 129-144. DOI:10.1111/j.1756-1051.2013.00082.x.

Montes CR, Lucas Y, Pereira OJR, Achard R, Grimaldi M, Melfi AJ. 2011. Deep plant-derived carbon storage in Amazonian podzols. Biogeosciences 8 (1): 113-120. DOI: 10.5194/bg-8-113-2011, 2011.

Moran JA, Barker MG, Moran AJ, Becker P, Ross SM. 2000. A comparison of the soil water, nutrient status, and litterfall characteristics of tropical heath and mixed-dipterocarp forest sites in Brunei. Biotropica 32: 2-13. DOI: 10.1111/j.1744-7429.2000.tb00442.x.

Musa NLW, Nawi L, Isa NNM, Adam J. 2014. Study on the floristic composition and forest structure of heath forest at Dungun Area in Terengganu. In: Proceedings of the International Conference on Science, Technology and Social Sciences (ICSTSS), 2012, Springer, Singapore. DOI: 10.1007/978-981-287-077-3_80.

Nafiah NS, Sukri RS, Md Ya'akub MYS, Metali F. 2022. Contrasting patterns of woody seedlings diversity, abundance and community composition in unique Bornean heath and peat swamp forests. Mires Peat 28 (10): 1-18. DOI: 10.19189/MaP.2021.MEH.StA.2160.

Newbery D, Proctor J. 1984. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. IV. Associations between tree distribution and soil factors. J Ecol 72: 475-493. DOI: 10.2307/2260060.

Nishimura TB, Suzuki E. 2001. Allometric differentiation among tropical tree seedlings in heath and peat swamp forests. J Trop Ecol 17: 667-681. DOI: 10.1017/S0266467401001493.

Noor Ain C, Tawan C, Meekong K. 2015. Two new *Zingiber* species from Sarawak, Malaysia. Folia Malay 16 (1): 23-30.

Nugroho Y, Suyanto S, Makinudin D, Aditia S, Yulimasita DD, Afandi AY, Harahap MM, Matatula J, Wirabuana PYAP. 2022. Vegetation diversity, structure and composition of three forest ecosystems in Angsana coastal area, South Kalimantan, Indonesia. Biodiversitas 23 (5): 2640-2647 DOI: 10.13057/biodiv/d230547.

Oktavia D, Pratiwi SD, Munawaroh S, Hikmat A, Hilwan I. 2021. Floristic composition and species diversity in three habitat types of heath forest in Belitung Island, Indonesia. Biodiversitas 22 (12). 5555-5563. DOI: 10.13057/biodiv/d221240.

Ordway EM, Asner GP, Burslem DF, Lewis SL, Nilus R, Martin RE, O'Brien MJ, Phillips OL, Qie L, Vaughn NR, Moorcroft PR. 2022. Mapping tropical forest functional variation at satellite remote sensing resolutions depends on key traits. Commun Earth Environ 3 (1): 1-11. DOI: 10.1038/s43247-022-00564-w.

Osaki M, Tsuji N. 2016. Tropical peatland ecosystems. Springer, Tokyo. DOI: 10.1007/978-4-431-55681-7.

Osunkoya OO, Muntassir NA. 2017. Comparative anatomy of the assimilatory organs of *Nepenthes* species. Aust J Bot 65 (1): 67-79. DOI: 10.1071/BT16157.

Peeters C, Wiwatwitaya D. 2014. *Philidris* ants living inside *Dischidia* epiphytes from Thailand. Asian Myrmecol 6: 49-61. DOI: 10.20362/am.006004.

Pengiran Kamsani DK, Slik JWF. 2018. Medicinal Plants of UBD Botanical Research Centre. Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam.

Pengiran Zamanulalam AA. 2020. A Comparative Study of Tree Diversity in Heath forests of Brunei. [BSc Dissertation]. Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei Darussalam.

Pereira JT. 2016. Four new species of *Ridsdalea* (Rubiaceae: Gardenieae) from Borneo, Wallacea and New Guinea. Sandakania 22: 77-95.

Pesiu E. 2019. Taxanomic Composition and Conservation Status of Plants in Imbak Canyon, Sabah, Malaysia. J Biol Conserv 16: 79â-100. DOI: 10.51200/jtbc.v16i0.2029.

Ponette-González AG, Curran LM, Pittman AM, Carlson KM, Steele BG, Ratnasari D, Weathers KC. 2016. Biomass burning drives atmospheric nutrient redistribution within forested peatlands in Borneo. Environ Res Lett 11 (8): 085003. DOI: 10.1088/1748-9326/11/8/085003.

Proctor J, Anderson JM, Vallack HW. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: I. Forest environment, structure and floristics. J Ecol 71 (1): 237-260. DOI: 10.2307/2259975.

Proctor J. 1999. Heath forests and acid soils. Bot J Scotl 51 (1): 1-14. DOI: 10.1080/03746609908684920.

Purwaningsih, Kartawinata K. 2018. Species composition and structure of forests in the Muara Kendawangan Nature Reserve, West-Kalimantan, Indonesia. IOP Conf Ser: Earth Environ Sci 166 (1): 012005. DOI: 10.1088/1755-1315/166/1/012005.

Purwaningsih, Kintamani E. 2018. The diversity of *Shorea* spp. (meranti) at some habitats in Indonesia. IOP Conf Ser: Earth Environ Sci 197 (1): 012034. DOI: 10.1088/1755-1315/197/1/012034.

Quong-Vuong L, Tennakoon KU, Metali F, Sukri RS. 2019. Photosynthesis in co-occurring invasive *Acacia* spp. and native Bornean heath forest trees at the post-establishment invasion stage. J Sustain For 38 (3): 230-243. DOI: 10.1080/10549811.2018.1530602.

Raes N, Roos MC, Slik JWF, van Loon EE, ter Steege H. 2009. Botanical richness and endemicity patterns of Borneo derived from species distribution models. Ecography 32: 180-192. DOI: 10.1111/j.1600-0587.2009.05800.x.

Riswan S. 2014. Nitrogen content of topsoil in lowland tropical forest in east Kalimantan (Indonesia), before and after clear-cutting and burning. Reinwardtia 10 (2): 131-138. DOI: 10.14203/reinwardtia.v10i2.267.

Rodda M, Rahayu S. 2022. Nine new species and one new subspecies of *Hoya* (Apocynaceae: Asclepiadoideae) from Borneo. Gard Bull Singapore 74 (1): 101-129. DOI: 10.26492/gbs74(1).2022-08.

Rundel PW, Middleton DJ. 2017. The flora of the Bokor Plateau, southeastern Cambodia: A homage to Pauline Dy. Cambodian J Nat Hist 1: 17-37.

Rundel PW, Sharifi MR, King-Rundel J, Middleton DJ. 2019. Leaf traits in the dwarf montane heathland of the Bokor Plateau, Cambodia. Cambodian J Nat Hist 2: 77-84.

Saibeh K, A/P Batumale SR, Boyce PC. 2015. Studies on Monstereae (Araceae) of Borneo. II: Furtado's *Rhaphidophora kinabaluensis* elucidated and transferred to *Scindapsus*. Willdenowia 45 (3): 409-413. DOI: 10.3372/wi.45.45305.

Sellan G, Brearley FQ, Nilus R, Titin J, Majalap-Lee N. 2021. Differences in soil properties among contrasting soil types in Northern Borneo. J Trop For Sci 33 (2): 191-202. DOI: 10.26525/jtfs2021.33.2.191.

Sellan G, Majalap N, Thompson J, Dise NB, Field CD, Pappalardo SE, Codato D, Robert R, Brearley FQ. 2023. Assessment of Wet Inorganic Nitrogen Deposition in an Oil Palm Plantation-Forest Matrix Environment in Borneo. Atmosphere 14 (2): 297. DOI: 10.3390/atmos14020297.

Sellan G, Thompson J, Majalap N, Brearley FQ. 2019. Soil characteristics influence species composition and forest structure differentially among tree size classes in a Bornean heath forest. Plant Soil 438 (1): 173-185. DOI:10.1007/s11104-019-04000-5.

Sellan G, Thompson J, Majalap N, Brearley FQ. 2022. Influence of species functional strategy on leaf stoichiometric responses to fertilizer in a Bornean heath forest. J Ecol 110 (6): 1247-1258. DOI: 10.1111/1365-2745.13865.

Sellan G, Thompson J, Majalap N, Robert R, Brearley FQ. 2020. Impact of soil nitrogen availability and pH on tropical heath forest organic matter decomposition and decomposer activity. Pedobiologia 80: 150645. DOI:10.1016/j.pedobi.2020.150645

Sellan G. 2019. Ecological Responses of A Bornean Heath Forest (Kerangas) to Experimental Lime and Nitrogen Addition. [Doctoral Dissertation]. Manchester Metropolitan University, Manchester.

Setiawan H, Wardhani HAK, Kamaludin K, Hutagaol RR, Afriani R. 2018. The diversity of *Nepenthes* at the post-mining area in Sintang District, West Kalimantan, Indonesia. Biodiversitas 19 (5): 1820-1827. DOI: 10.13057/biodiv/d190532.

Shabdin Z, Culham A, Simpson DA, Meekiong K. 2013. *Mapania multiflora*, a distinctive new species of Cyperaceae (Mapanioideae) from Borneo. Kew Bull 68 (4): 673-678. DOI: 10.1007/s12225-013-9474-9.

Sim JWS, Tan HTW, Turner LM. 1992. *Adinandra* belukar: An anthropogenic heath forest in Singapore. Vegetatio 102 (2): 125-137. DOI: 10.1007/BF00044729.

Stalin A, Franco FM. 2020. *Agathis borneensis* Warb. Araucariaceae. In: Franco FM (ed). Ethnobotany of the Mountain Regions of Southeast Asia. Springer, Cham. DOI: 10.1007/978-3-030-14116-5.

Suetsugu K, Kikuchi ABIS, Suleiman M, Tsukaya H. 2017. New distributional records for the mycoheterotrophic orchid *Kalimantanorchis nagamasui* from Sabah, Borneo, Malaysia. Acta Phytotax Geobot 68 (2): 117-121. DOI: 10.18942/apg.201621.

Suetsugu K, Suleiman M, Anthony F, Tsukaya H. 2018. *Aphyllorchis maliauensis* (Orchidaceae), a new species from the Maliau Basin, Sabah, Borneo. Phytotaxa 367 (1): 85-90. DOI: 10.11646/phytotaxa.367.1.10.

Suhaili ALR, Tennakoon K, Sukri RS. 2015. Soil seed bank of an exotic *Acacia* sp. plantation and an adjacent tropical heath forest in Brunei Darussalam. Biotropia 22 (2): 140-150. DOI: 10.11598/btb.2015.22.2.487.

Suis MAF, Sugau JB, Esther DKM, Nilus R. 2019. Forest ecosystem assessment of Sungai Rawog Conservation Area in Segaliud Lokan Forest Reserve, Sabah. Seminar on Sungai Rawog Conservation Area Scientific Expedition. Kota Kinabalu, Sabah.

Sukri RS, Wahab RA, Salim KA, Burslem DF. 2012. Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. Biotropica 44 (5): 595-605. DOI: 10.1111/j.1744-7429.2011.00837.x.

Suratman MN, Abd. Hamid NH, Md. Sabri MD, Yamani SAK. 2015. Changes in tree species distribution along altitudinal gradient of montane forests in Malaysia. In: Ozturk M, Hakeem KR, Faridah-Hanum I, Efe R (eds). Climate Change Impacts on High Altitude Ecosystems. Springer International Publishing, Switzerland. DOI: 10.1007/978-3-319-12859-7_19.

Suratman MN, Hamid NH, Daim MS, Malim IMS, Sabri MDM. 2014. Beyond Biodiversity Conservation. UiTM Press, Shah Alam.

Suzana S, Pereira JT, Jumian J, Damit A, Suleiman M. 2018. A brief note on *Ternstroemia* (Pentaphylacaceae) of Tama Abu PF, Ulu Baram, Sarawak, Malaysia. Sepilok Bull 27 (1): 51-58.

Syuhada AB, Shamshuddin J, Fauziah CI, Arifin A, Rosenani AB. 2014. Formation and characteristics of Spodosols formed on sandstone in the extremely high rainfall area of Sarawak, Malaysia. Asian J Agric Food Sci 2 (2): 115-128.

Syuharni AW, Hakeem KR, Faridah-Hanum I, Alias MS, Ozturk M. 2014. Ecology of the coastal heath forest flora: A case study from Terengganu, Malaysia. Emir J Food Agric 26 (12): 1114-1123. DOI: 10.9755/ejfa.v26i12.19122.

Taing L, Sridith K. 2016. The vegetation structure of the Songkhla Lake Area through the woody plants architectural models. Thai J Bot 8 (1): 7-29.

Takada M, Shimada S, Takahashi H. 2016. Tropical peat formation. In: Osaki M, Tsuji N (eds). Tropical Peatland Ecosystems. Springer, Tokyo. DOI: 10.1007/978-4-431-55681-7_8.

Takeuchi Y, Soda R, Diway B, Kuda TA, Nakagawa M, Nagamasu H, Nakashizuka T. 2017. Biodiversity conservation values of fragmented communally reserved forests, managed by indigenous people, in a human-modified landscape in Borneo. PLoS One 12 (11): e0187273. DOI: 10.1371/journal.pone.0187273.

Tjiu A, Meididit A, Iswinanto I, Ginanjar A, Atut Y, Agusti R. 2021. Plant diversity in logged over forest in Mahakam Ulu, East Kalimantan, Indonesia. Biodiversitas 22 (11): 4829-4838. DOI: 10.13057/biodiv/d221115.

Tuah W. 2017. Rehabilitation Study at A Degraded Kerapah Forest in Lumut, Brunei Darussalam. [MSc Thesis]. Universiti Brunei Darussalam, Brunei.

Tuah WH, Tennakoon KU, Jaafar SM, Sukri, RS. 2020. Post-fire impacts on tree diversity in coastal heath forests of Brunei Darussalam. Sci Bruneiana 19 (1): 19-32. DOI: 10.46537/scibru.v19i1.109.

Turnbull JW. 2017. Australian Acacias in developing countries. In: Turnbull JW (ed). Proceedings of an International Workshop at Forestry Training Centre, Gympie, Qld. Victoria, Australia, 4-7 August 1986.

van der Ent A, Repin R, Sugau J, Wong KM. 2015. Plant diversity and ecology of ultramafic outcrops in Sabah (Malaysia). Austr J Bot 63 (4): 204-215. DOI: 10.1071/BT14214.

Vernimmen RRE, Bruijnzeel LA, Proctor J, Verhoef HA, Klomp NS. 2013. Does water stress, nutrient limitation, or H-toxicity explain the differential stature among heath forest types in Central Kalimantan,

Indonesia? Biogeochemistry 113 (1): 385-408. DOI:10.1007/s10533-012-9766-4.
Whitmore TC. 1984. Tropical Rain Forest of the Far East. Oxford University Press, Oxford, UK.
Whitmore TC. 1988. Forest types and forest zonation. In: Cranbrook, E (ed). Key Environments: Malaysia. Pergamon Press, Oxford, UK. DOI: 10.1016/B978-0-08-028866-6.50008-8.
Whitmore TC. 1998. An Introduction to Tropical Rain Forests. Oxford University Press, Oxford, UK.
Wong KM, Ahmad JA, Low YW, Kalat MAA. 2015a. Rainforest Plants and Flowers of Brunei Darussalam. Forestry Department, Ministry of Industry and Primary Resources, Bandar Seri Begawan, Brunei Darussalam.
Wong KM, Kamariah, AS. 1999. Forests and Trees of Brunei Darussalam. Universiti Brunei Darussalam, Forestry Department & Brunei Shell Petroleum Co. Sdn. Bhd, Brunei Darussalam.
Wong KM, Low YW, Ariffin AM, Joffre A. 2015b. Novitates Bruneienses, 4. New records in the Araliaceae, Araucariaceae, Arecaceae, Fagaceae, Musaceae and Thymelaeaceae. Gard Bull (Singapore) 67 (2): 275-287. DOI: 10.3850/S238258121500023X.
Wong KM, Low YW. 2015c. Novitates Bruneienses, 3. Eight new woody plants in the Brunei flora, including five new species. Gard Bull Singapore 67: 69-84. DOI: 10.3850/S2382581215000083.
Wong KM, Saw LG, Kochummen KM. 1987. A survey of the forests of the Endau-Rompin area, Peninsular Malaysia: Principal forest types and floristic notes. Malay Nat J 41: 125-144.
Wong KM. 1998. Patterns of plant endemism and rarity in Borneo and the Malay Peninsula. In: Peng CI, Lowry PP 2nd (eds). Rare, Threatened and Endangered Floras of Asia and the Pacific Rim, Monograph Series No. 16. Institute of Botany, Academia Sinica, Taipei.
Wong SY, Boyce PC. 2019. Studies on Potheae of Borneo I: *Pothos pugnax*, a new species of *Pothos* (Allopothos: *Pothos barberianus* grou) from Kuching Division, Sarawak, Malaysian Borneo. Webbia 74 (2): 259-264. DOI: 10.1080/00837792.2019.1639107.
Wong SY, Jyloerica J, Boyce PC. 2020. Studies on the Homalomeneae (Araceae) of Borneo XXV: A remarkable new kerangas-associated *Homalomena* (Chamaecladon Clade) from Sabah. Feddes Repertorium 131 (3): 188-195. DOI: 10.1002/fedr.202000008.
Wood JJ, van der Ent A. 2012. Mount Tambuyukon: An intriguing mountain and its orchids. Malesian Orchid J 10: 103-122.
Wulffraat S, Morrison J. 2013. Measuring biological indicators for status assessment of the Heart of Borneo. Environ Conserv 40 (3): 277-286. DOI: 10.1017/S0376892913000064.
Xu S, Liu LL, Sayer EJ. 2013. Variability of above-ground litter inputs alters soil physicochemical and biological processes: A meta-analysis of litterfall-manipulation experiments. Biogeosciences 10 (11): 7423-7433. DOI: 10.5194/bg-10-7423-2013, 2013.
Ya'akub MYS. 2020. Seedling Growth and Diversity in Two Contrasting Heath Forest Formation in Brunei Darussalam. [BSc Dissertation]. Universiti Brunei Darussalam, Bandar Seri Begawan, Brunei.
Yudistira YR, Kurniawan FH, Mustaqim WA. 2022. *Bulbophyllum* (Orchidaceae: Epidendroideae) of Indonesian Borneo: A new species and first record for *B. lyriforme*. Taiwania 67 (4): 544-551. DOI: 10.6165/tai.2022.67.544.
Yusoff A, Tennakoon KU, Jaafar SM, Pg Zaman DNAN, Sukri RS (2019). Effects of *Acacia* invasion on leaf litter nutrient and soil properties of coastal Kerangas forests in Brunei Darussalam. Sci Bruneiana 18 (1): 1-10. DOI:10.46537/scibru.v18i1.87.
Zaini NH, Sukri RS. 2014. The diversity and abundance of ground herbs in lowland mixed dipterocarp forest and heath forest in Brunei Darussalam. Reinwardtia 14 (1): 73-78. DOI: 10.14203/reinwardtia.v14i1.397.
Zanchi FB, Dolman AJ, Groenendijk M, Kesselmeier J, Kruijt B, Bolson MA, Luizão FJ, Manzi AO. 2011. Influence of drainage status on soil and water chemistry, litter decomposition and soil respiration in central Amazonian forests on sandy soils. Rev Ambient Água 6 (1): 6-29. DOI: 10.4136/ambi-agua.170.
Zoletto B, Cicuzza D. 2022. Heath forest in tropical Southeast Asia, its ecology and conservation risk. In: DellaSala DA, Goldstein MI (eds). Imperiled: The Encyclopedia of Conservation. Elsevier, Amsterdam. DOI: 10.1016/B978-0-12-821139-7.00235-X.