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

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


Abstract. Ikbal IM, Din HHM, Tua 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 km² 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 bona in Venezuela (Adeney et al. 2016; Daly et al. 2016; Garcia-Vilacorta 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
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 podzolized 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 (Anisophyllaceae; Nafiah et al. 2022), and where soils are extremely dry with low humidity (Ashton 2013; Zolletto 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,

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1999; Ghazoul and Sheil 2010; Fine and Baraloto 2016; Zolletto 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; Zolletto 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 in 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 Wiatowitaya 2014; Taing and Sriddith 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 (Pentaphyllaceae) 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.
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; Kerfah et al. 2019). In-situ weathering of quartzite sandstone, deposition of alluvial sands by rivers or sea (Syuhada et al. 2014; Kerfah 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; Adney 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 km² 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 on 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; Brunei 2016; Coones et al. 2017). Heath forest tree roots are typically stilt-rooted and unbucktressed 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 sclerencymatous 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 Kartawnata 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), Sarcothera glauca (Hook.fil.) Hallier fil. (Oxalidaceae), Syzygium caryophylliflorum (Ridl.) Merr. & Perry and Syzygium megaphyllan 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 havelandi 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, Lindemaeaceae, Orchidaceae, Pandanaeae, Rubioaceae, Schizaceae, and Zingibereae (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 Hydrophytum spp. (Rubioaceae), have a symbiotic relationship with ants as an adaptation to the nutrient-limiting environment of heath forests (Whitmore 1984; Low et al. 2016; Zolletto and Cicuzzo 2022). Both Hydrophytum 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 (Zolletto and Cicuzzo 2022).

Epiphytic plants commonly found in Bornean heath forests include orchids, climbing ferns, and the Araceae (Ashton 2014; Cicuzzo 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; Suettsug et al. 2017, 2018; Juling et al. 2020). Epiphytic ferns in Bornean heath forests are represented by Drynaria and Platycurium (Polypodiaceae) and Haplopteris (Pteridaceae) (Chen et al. 2019; Cicuzzo et al. 2020; Zolletto and Cicuzzo 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; Cicuzzo et al. 2020). Climbers from the Araceae are represented by a few genera such as Pothis, 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 Clusiaeae (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 Clusiaeae and Myrtaceae, with basal areas of 17% and 11%, respectively (Proctor et al. 1983). The low basal area recorded for the Clusiaeae 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 Chrysobulaceae, 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 junguahumiana (Rubiaceae), with a total stem density of 12.74%, followed by Diospyros fusiformis Koster. (Ebenaceae; 7.45% total stem density) and Syzygium caudatilimum (Merr.) Merr. & Perry (Myrtaceae; 6.07% total stem density). The Myrtaceae had the highest basal area (31%), followed by the Dipterocarpaceae (19%), Clusiaeae (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 subtypes of heath forest. They also found that the two subtypes 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. Neocortexchnia kingii (Hook.f.) Pax & K.Hofm. (Euphorbiaceae), *Elaeocarpus mastersii* King (Elaeocarpaceae), and *Nepheleium 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 burchii* (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 Symlocaceae 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 *Symlocos polystylosa* (Blanco) Brand (Symlocaceae; 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. polyantha*, *Timonius flavescentis* (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* Mull.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.
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 Peradayang, 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 (Whittmore 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 Zamanulalama 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 dieri F.Heim (Dipterocarpaceae), Lithocarpus andersonii Soepadmo (Fagaceae), Sterculia rhoidifolia Stapf ex Ridl. (Malvaceae), C. burckii, and S. albida (Din et al. 2015; Pengiran Zamanulalama 2020).
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 cinnamnata* 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

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

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