

4. THE PLANT DIVERSITY OF SINGAPORE

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The position of Singapore on the Sunda continental shelf is a special one, with the principal island originally about 540 km² in size, together with some 60 smaller islands at the southern exit to the Malacca Strait and near the confluence of the South China Sea and Karimata Strait just west of Borneo. Geographically at the equatorial extremity of the Malay Peninsula, Singapore is separated from the Riau Islands to its south (principally the Karimata Islands, Batam and Bintan) by the Singapore Strait which includes the deeply scoured 204 m ‘Singapore Deeps’, a likely subsidence basin resulting from tectonic movements (Bird et al., 2006). While this Strait may seem able to restrict the dispersal of some organisms with interglacial and post-Pleistocene high sea levels, it probably was not an effective dispersal barrier during episodes of lowest sea levels, such as during the Last Glacial Maximum (LGM) at 18,000 years ago. Then, it must have been in the path of a key land bridge between mainland Southeast Asia further north and likewise exposed links to Java and other areas to the south (Ho, 1960; Morley & Flenley, 1987; Heaney, 1991; Voris, 2000; Bird et al., 2005). By contrast, the Johor Strait that separates Singapore from south Peninsular Malaysia is just about 10 m deep and 600 m wide at its narrowest.

The Sundaland region on the Sunda continental shelf has seen climate shifts since even before the Pleistocene, sometimes associated with tectonic events. Although the late Oligocene (c. 27–23 Ma) probably had more pronounced seasonal climates and open forests or savanna (Morley, 2012), by the beginning of the Miocene (23–5.3 Ma), with the closure of the Indonesian throughflow and the establishment of the East Asian monsoon (Wang et al., 2003), the region transitioned to a perhumid climate. The warmer climates after the Early Miocene (c. 20 Ma) allowed a greater extent of tropical lowland rain forests in Southeast Asia, and it was at this time that a diverse and distinctively regional (‘Malesian’: see later) flora (including Dipterocarpaceae or ‘dipterocarp’ taxa related to *Anisoptera* Korth., *Dipterocarpus* C.F.Gaertn., *Hopea* Roxb., or *Shorea* Roxb. ex C.F.Gaertn.) could have developed from ancestral forms that crossed over from the Indian plate that drifted and juxtaposed against south Asia in the Eocene (Morley, 2000, 2024; Bansal et al., 2022). Mid-Miocene (16–11.5 Ma) dipterocarp fossils, suggesting wetter regimes than presently, are known from as far north as southern China (Shi et al., 2014). The late Miocene (11.5–5.3 Ma) and Pliocene (5.3–1.95 Ma) shift back to cooler, drier climates probably allowed the establishment of more open forest and grasslands across South and Southeast Asia (Morley, 2018). Drastic sea-level fluctuations at the start of the Quaternary (0–1.95 Ma) corresponded to glacial episodes in the northern hemisphere (Zachos et al., 2001).

The now-disputed interpretation of a Pliocene-Pleistocene continuous ‘savanna corridor’ having extended from more seasonal mainland Southeast Asia southwards to the Javan region (Medway, 1972; Heaney, 1991; van den Bergh et al., 2001) was invoked to explain present-day distribution of plant taxa between more seasonal mainland Southeast Asia and Java and

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the Lesser Sunda Islands (the ‘Asian/South Malesian drought disjunction’; Jacobs, 1974), as well as the distribution of essentially open-woodland fauna into Java, where their fossils are not older than 2.4 Ma (Medway, 1972; Heaney, 1991; Cranbrook, 2000; van den Bergh et al., 2001). An abundance of pine (36%), grass (19%), and Asteraceae (2%) found in a pollen core near Kuala Lumpur seemed to suggest mid-Pleistocene pine savanna (Morley & Flenley, 1987; Morley, 1998) but the possibility that this could have been an ecological island cannot be ruled out (Ashton, 2014); also, dry-adapted grassland or vegetation was inferred further south and southeast from the Malay Peninsula (Morley, 2000). However, vegetation modelling (Cannon et al., 2009) and species distribution modelling using the region’s Dipterocarpaceae dataset (Raes et al., 2014) suggest that dipterocarp forest, posited as representative of humid tropical conditions, was likely present throughout the LGM in central Sundaland. Indeed, such forest contiguity would allow the dispersal of the agile gibbon, the three-coloured Prevost’s squirrel, and ruddy tree shrew from Sumatra across the Karimata Strait to Borneo (Cranbrook & Piper, 2007). Ashton (2014) has summarised evidence that suggests a Pleistocene savanna corridor enabling dispersal of seasonal-climate elements was unlikely across Sundaland, especially considering that comparatively few deciduous forest elements from mainland Southeast Asia are present in East Java, and the strong floristic similarity between east Sumatra and Peninsular Malaysia, indicating little historical segregation. Instead, a drier climate corridor, supporting increased frequency of patches of more seasonal vegetation types such as semi-evergreen and deciduous forests, was thought more feasible at times of lowest Quaternary sea level, and possibly extended down the western flank of the Malay Peninsula, east and south Sumatra, to the Javan region (Ashton, 2014; Morley, 2018).

Ashton (2014) suggested that the mammalian dispersal from north to south could also have followed seasonally flooded riverine grasslands that served as a key open habitat. But, additionally, vegetation patchiness throughout a landscape, where different rock or soil types (e.g., granitic vs sedimentary soils) and physiographic features (flats, slopes of different aspect, ridges) can sustain different vegetation variants from closed canopy forest to more open vegetation (Whitmore, 1984; Wong et al., 1987), permits opportunities for dispersal of different ecologically adapted taxa. Disturbance events, including fires and the possibility of landscape-level changes following the late-Pleistocene eruption of Toba in north Sumatra (Chesner et al., 1991), may have sustained disruptions to vegetation continuity, creating more open or pioneer-type environments; ash horizons up to 90 cm thick around Kuala Lumpur (Stauffer, 1971, 1973; Stauffer & Batchelor, 1978) can be correlated to the youngest Toba tuff (explosion) of 74 ± 2 ka, some 350 km away (Chesner et al., 1991). A continuous corridor of enabling vegetation is not necessary for dispersal, as evident from the present-day distribution of the wind-dispersed and annually deciduous *Tetrameles nudiflora* R.Br. (Tetramelaceae) (India, continental Southeast Asia, partway south into the Malay Peninsula, as well as seasonal parts of south and eastern Indonesia), transcending quite different climatic regimes, with the Malay Peninsula localities well buffered by thick moist evergreen forests not found further north; presently the species persists on Gunung Datuk (2.54°N) in Negri Sembilan, southwest Peninsular Malaysia (pers. obs.). This probably applies to large mammals as well, which are able to survive through tracts of less favourable vegetation.

During glacial maxima the Sunda region probably had double the land area of interglacial episodes, such as at the present interglacial with the extent of the flora much diminished and considered to be in a state of refuge (Cannon et al., 2009). Fluctuations in climatic and vegetation character throughout this history, and the colonisation of newly available habitat and niches,

likely added stress and selective pressure and acted as a ‘speciation pump’, spearheading the evolution of novel genotypes and taxa. Into this context, our modern scholars, including the indefatigable Henry Nicholas Ridley, the foremost collector and writer on the botany of the Malay Peninsula, came to Singapore. What is now documented about Singapore’s flora and how does it relate to that of the surrounding region? Singapore, like its region, has seen its landscape change, in part drastically owing to anthropogenically driven pressures. What features of the flora might be important to retain in conservation measures?

The Sunda and Malayan floras

For most of its extent, the Sunda continental shelf connects the Malay Peninsula, of which Singapore is a part, continental Southeast Asia and Peninsular Thailand, Sumatra, Java and Borneo. Most of this is considered the western flank of the Indo-Malayan rainforest region (Whitmore, 1984, 1989, 1998) that spans the Malay Archipelago (Whitmore, 1984) and extends northward, as pockets, into parts of Myanmar, Thailand, Cambodia, Laos, Vietnam, the Xishuangbanna area in southwest China, as well as southward into northern Queensland in Australia and the southwest Pacific (Corlett & Primack, 2011; Whitmore, 1998). Across this distribution, seasonality, rainfall, physiography and geology play key roles in determining the characteristics (particularly physiognomy and floristics) and classification of the forests (Money, 1972; Ashton, 2014). The ever-wet core of this region has been distinguished as a coherent plant geographical region called Malesia, stretching from Sumatra to Papua New Guinea and including the Philippines, with hundreds of seed plant and fern genera that do not occur in surrounding regions and similar suites that are absent from it (van Steenis, 1950). The Sunda Shelf therefore defines much of Western Malesia and its landmasses can be expected to have much floristic similarity (Corner, 1960; Whitmore, 1984), engendered by intermittent land contiguity throughout the millennia and maintained by the currently shared generally perhumid climate, except for a more significantly seasonal Java (van Welzen et al., 2005) and perhaps southern Sumatra.

Vascular plant diversity is highest in tropical evergreen rain forest (the typical vegetation type of wet tropical areas of the earth with a precipitation/evapotranspiration (P/E) index of 128 or higher), which includes the lowland evergreen rain forest, tropical montane forests, mangrove and brackish water vegetation, tropical heath forest, forest on limestone and ultramafic substrates, peat swamp forest, and freshwater swamp forest, and beach vegetation (Whitmore, 1984; Richards, 1998). This vegetation is largely evergreen, luxuriant, lofty, and rich in life forms (Holtum, 1954a), including herbs (terrestrial or aquatic), shrubs, treelets, sizeable trees, epiphytes (Fig. 1), creepers, lianas, strangling hemi-epiphytes, mycotrophic heterotrophs (e.g., the leafless terrestrial orchids (Orchidaceae) *Galeola nudifolia* Lour. and *Gastrodia javanica* (Blume) Lindl.), and parasitic plants, as well as rich in species. In Singapore, life form distribution was assessed at 25.9% herbs, 9.8% shrubs, 37.2% trees, 13% epiphytes and 14% climbers; an overwhelming 73.5% of the species are lowland forest species (Turner, 1994). Most herbs belonged to Poaceae, Cyperaceae (in more open habitats), and ferns and lycophytes (more so in the forest understorey); climbers were mostly Rubiaceae, rattans in the Arecaceae, and Annonaceae; whereas trees were principally Rubiaceae and Euphorbiaceae (Turner, 1994). Since Turner (1994), changes in family delimitation have led

to some changes in the distribution of the various life forms amongst families. For example, an expanded Apocynaceae is one of the largest families of climbers and the Euphorbiaceae sensu Turner has now been split into various different families, particularly the Phyllanthaceae (see Lindsay et al., 2022), and it is no longer one of the largest families of tree species. The distinctive feature that sets Sunda forests apart from those of other regions of the world is the dominance of one family, the dipterocarps (Whitmore, 1998; Corlett & Primack, 2011; Ashton, 2014). Dipterocarps became more diverse in Southeast Asia during the Oligocene–Pleistocene (Morley, 2000). Ashton (2014) calls the region's main lowland vegetation the Sunda mixed dipterocarp forest, of which two variants occur in Singapore, principally the red meranti-keruing mixed dipterocarp forest (most of the remaining primary forest patches in the Central Catchment Nature Reserve), and also the coastal hill dipterocarp forest (of which Bukit Timah Nature Reserve has a semblance). These were forest types recognised by foresters in Malaya (Wyatt-Smith, 1995). Wong et al. (1995) found the Central Catchment forests to have much floristic similarity to those on Bukit Timah.

In general, three vertical floristic strata or synusia can be recognised for tropical evergreen forests: subcanopy or understorey species (trees with mature crowns and which flower within or beneath the main canopy), main canopy species, and emergent species (Ashton, 2003) reaching 35 m in Bukit Timah (Murphy, 1973). The Dipterocarpaceae are often the emergents, along with some Fabaceae (Leguminosae), Sapotaceae and others. The main canopy includes families like Annonaceae, Apocynaceae, Fagaceae, Malvaceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae, Olacaceae, Pentaphylacaceae, Rubiaceae and Theaceae. Understorey plants include those from the Ebenaceae, Euphorbiaceae, Phyllanthaceae, Rubiaceae, Sapindaceae and Urticaceae. The forest floor flora predominantly belong to Araceae, Arecaceae, Marantaceae, Piperaceae and Zingiberaceae, as well as tree and liane seedlings, and ferns, often patchily so.

Like tropical forests elsewhere, the Sunda forests are characterised by intense species richness, high endemism, a predominance of species rare by frequency, significant numbers of co-occurring congeners (as in *Aglaia* Lour. (Meliaceae), *Aporosa* Blume (Phyllanthaceae), *Ardisia* Sw. (Primulaceae), *Asplenium* L. (Aspleniaceae), *Baccaurea* Lour. (Phyllanthaceae), *Bulbophyllum* Thouars (Orchidaceae), *Calamus* L. (Arecaceae), *Calophyllum* L. (Calophyllaceae), *Dendrobium* Sw. (Orchidaceae), *Diospyros* L. (Ebenaceae), *Elaeocarpus* L. (Elaeocarpaceae), *Ficus* L. (Moraceae), *Horsfieldia* Willd. (Myristicaceae), *Knema* Lour. (Myristicaceae), *Lasianthus* Jack (Rubiaceae), *Lithocarpus* Blume (Fagaceae), *Litsea* Lam. (Lauraceae), *Macaranga* Thouars (Euphorbiaceae), *Memecylon* L. (Melastomataceae), *Psychotria* L. (Rubiaceae), *Syzygium* P.Browne ex Gaertn. (Myrtaceae), *Tectaria* Cav. (Tectariaceae) and *Urophyllum* Wall. (Rubiaceae) in Singapore forests), and unique species assemblages in special sites, where floristic differences are often associated with edaphic characteristics. In a 2 ha plot studying long-term forest dynamics of trees 1 cm diameter at breast height (DBH) or larger in Bukit Timah Nature Reserve, 347 species in 71 families were recorded; whereas this is more tree species than found in the United Kingdom, this diversity is only about half that of more central forest sites in Peninsular Malaysia or Borneo (LaFrankie et al., 2005). This has been attributed to the relatively isolated geographical position of Singapore as well as Bukit Timah Nature Reserve being a small fragment of the original forested area (LaFrankie et al., 2005).

In the analysis by Turner (1997a), 2310 of 8059 native species of vascular plants in the entire Malayan flora (Peninsular Malaysia and Singapore) (28.7%) are endemic. Included were

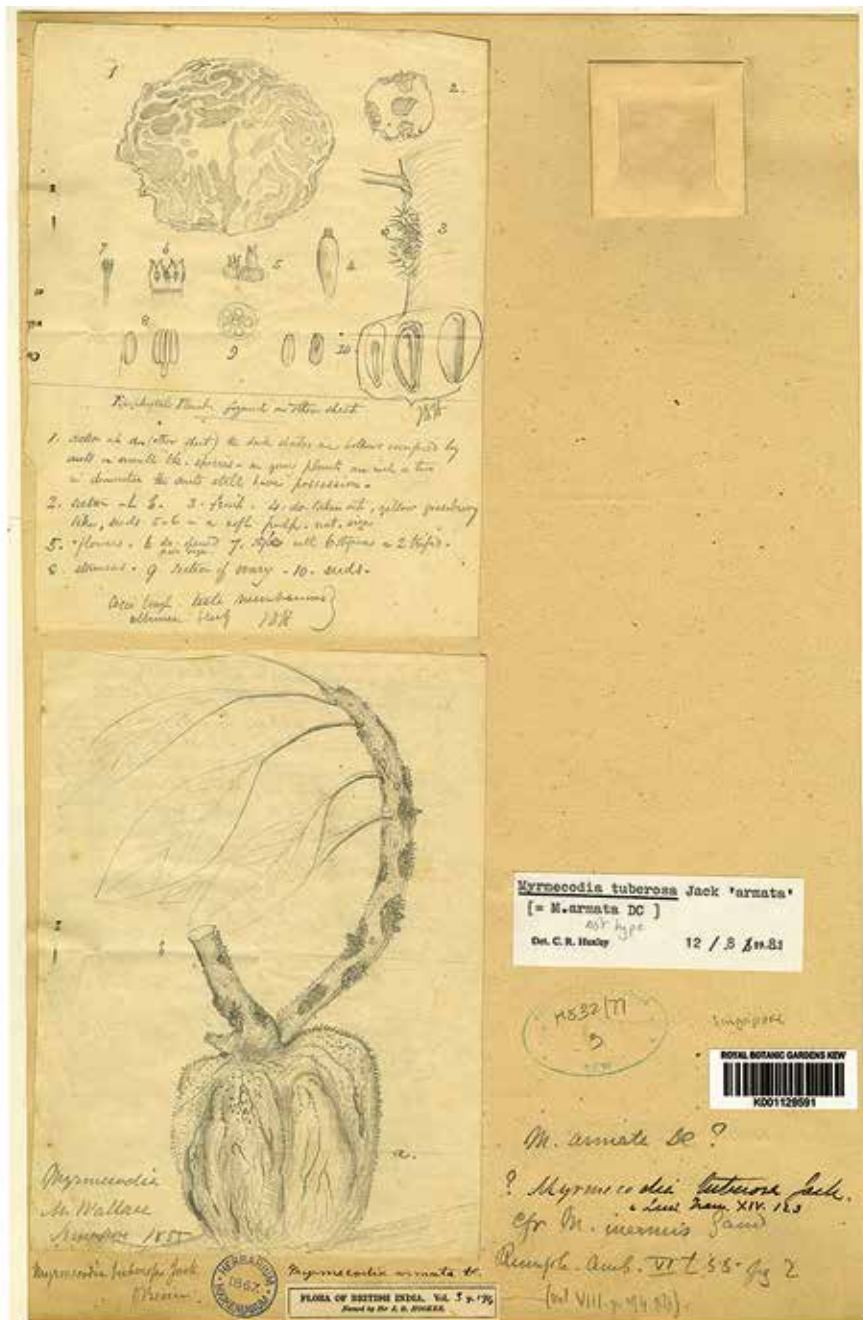


Figure 1. Sketches of the epiphytic ant-plant *Myrmecodia tuberosa* Jack (Rubiaceae), made by the ardent naturalist Alfred Russel Wallace in Singapore in 1854 at the start of his sojourn in the Malay Archipelago, and sent to the Royal Botanic Gardens, Kew in 1854–1855, where they were studied by Sir Joseph Dalton Hooker for his *Flora of British India*. (Reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew).

7623 species of seed plants, compared to 6766 species enumerated by Ridley (Keng, 1970). In Turner (1997a) the largest family is the Orchidaceae (853 species), followed by the Rubiaceae (562 species) and Euphorbiaceae (368 species), and the largest genera are *Syzygium* (195 species), *Bulbophyllum* (110 species) and *Ficus* (102 species). For Singapore (Turner & Tan, 1994; Turner, 1994), the three largest families using the traditional family delimitations were the same as that for the Malayan flora. With modern family delimitations the Fabaceae replaces Euphorbiaceae as the third largest family in Singapore with Poaceae close behind as the fourth largest (see Lindsay et al., 2022). The largest genera with native species in Singapore, using the data in Middleton et al. (2024), are *Syzygium* (50 species), *Ficus* (49 species), *Dendrobium* (37 species), *Bulbophyllum* (37 species) and *Cyperus* L. (Cyperaceae) (35 species). Turner (1994) tallied 2277 species of native Singapore vascular plant species in 868 genera and 158 families, of which 7.6% were ferns and lycophytes, 0.4 % were gymnosperms, 25.9% monocots, and 66.1% dicots. In Middleton et al. (2024), 2382 native vascular plant taxa are enumerated of which 7.3% are ferns and lycophytes, 0.3% are gymnosperms and 92.4% are angiosperms, with the distinction between monocots and dicots no longer considered relevant. Unsurprisingly, the flora of Singapore is very much a subset of the Malay Peninsula flora, and also related to that of Sumatra and Borneo (Corner, 1960; Keng, 1970). Singapore's small land area (42 km east to west, 23 km north to south), comparative isolation by interglacial sea levels, and lack of physiographic diversification (the highest point is 163 m at the summit of Bukit Timah), possibly sustains a lower biodiversity compared to larger land masses, as can be expected (Hawksworth & Kalin-Arroyo, 1995; Mutke & Barthlott, 2005).

Of the native plant species of Singapore, eight species of vascular plants are considered endemic. These are *Dendrobium lacinosum* Ridl., *Hanguana triangulata* Škorničk. & P.C.Boyce (Hanguanaceae), *Homalomena nathanielii* S.Y.Wong & P.C.Boyce (Araceae), *Litsea ridleyi* Gamble (Lauraceae), *Neonauclea kranjiensis* K.M.Wong & W.W.Seah (Rubiaceae), *Nervilia singaporensis* Niissalo (Orchidaceae), *Strychnos ridleyi* King & Gamble (Loganiaceae) and *Zingiber singaporense* Škorničk. (Zingiberaceae) (Lindsay et al., 2022; Wong & Boyce, 2022; de Kok & Thomas, 2026). Of these, the following three species are most likely extinct: *Dendrobium lacinosum*, *Neonauclea kranjiensis* and *Strychnos ridleyi*. Unlike previous compilations, the *Flora of Singapore* now includes bryophytes and the following four bryophytes are most likely endemics: *Gaolejeunea hoi* W.Ye & Y.M.Wei (Lejeuneaceae), *Riccardia latifrondoides* Schiffn. (Aneuraceae), *Calohypnum singaporense* (Dixon) S.He & B.C.Ho (Hypnaceae) and *Splachnobryum temasekense* B.C.Tan et al. (Pottiaceae) (Lindsay et al., 2022). Of these, one, *Riccardia latifrondoides* is likely extinct.

A more realistic consideration of how special Singapore's flora might really be is to take it in the context of the south Malayan flora, or the southeast Sumatran flora, so that near-endemics, such as *Hanguana neglecta* Škorničk. & Niissalo, *H. nitens* Siti Nurfazilah et al., *Utania austromalayensis* Sugumaran, *U. nervosa* K.M.Wong & Sugumaran (Gentianaceae), *Vatica ridleyana* Brandis (Dipterocarpaceae), and others, are considered. This makes more practical sense given the geological and evolutionary relatedness, as well as proximity of these places. More importantly, the region's flora has been greatly impacted by land use changes, so that any surviving populations of such native plants should be specially noted.

For there to be significant endemism in the Singapore flora, a sufficient period of isolation preventing gene flow between populations in Singapore and that of surrounding areas would be necessary. This is manifestly not the case as the main island of Singapore was connected by land to southern Peninsular Malaysia as recently as about 10,000 years ago.

Also, during the LGM, Singapore was part of the emerged Sunda continental shelf. Singapore also does not possess edaphic habitat islands such as ultramafic or limestone outcrops that contribute to much of the endemism in the Sunda region.

LaFrankie et al. (2005) noted that no species of large tree is endemic to Singapore; the few examples of endemic Singapore taxa being either herbs, climber or treelets, with faster generation turnover times and growth to maturity, generally better buffered by the canopy vegetation than are taller or emergent trees. It has, however, recently been confirmed that *Litsea ridleyi* Gamble, with trees up to 25 m tall, is only known from Singapore (de Kok & Thomas, 2026). Also, Singapore contains some local Riau Pocket tree endemics like *Anisoptera marginata* Korth. (Dipterocarpaceae) (now extinct in Singapore), *Vatica ridleyana* and the strangler *Ficus microsyce* Ridl.

The Riau Pocket and Singapore

Based on floristic affinities between geographical areas that are now separated by shallow seas, the Riau ('Riouw') Pocket was first identified by Corner (1958). Through his study of the distribution of *Ficus*, Corner (1958) frequently found that species abundant in surrounding countries were absent in this pocket. Also, there were species found in this pocket that were apparently not found outside. Initially, Corner (1958) defined the Riau Pocket as consisting of the Riau Islands, Bangka, Singapore, southeastern Johore and southwestern Borneo. Corner (1958) was uncertain whether any part of Sumatra should be included. Later, Corner (1960) suggested the possibility of including southeastern Sumatra in the Riau Pocket. Ashton (1992), based on his study of the distribution of dipterocarps, suggested an expanded Riau Pocket that included the whole east coast of Peninsular Malaysia. Later, Ashton (2005) suggested another expansion of the Riau Pocket to include the coastal hills of Perak State and Pulau Simeulue off the northeast Sumatra coast. Our current understanding is that the Riau Pocket consists of the following: parts of northwestern Borneo, eastern coastal Peninsular Malaysia and its west coast from the mouth of the Perak River north to the seasonal zone, Singapore, and the Lingga and Riau archipelagos, central-east Sumatra and Pulau Simeulue (Ashton, 2014). The rationale for the Riau Pocket floristic relatedness is that during the LGM, the shallow seas separating the above geographical areas receded, exposing a 'maritime' continent. During this period there existed land connections or close proximities between these geographical areas enabling the dispersal of plants, including a suite that was special to the connected areas.

Singapore was included as part of the Riau Pocket in Corner (1958) and Corner (1960), but subsequent authors did not make specific mention of Singapore nor include it in maps showing the extent of the Riau Pocket (e.g., Ashton, 1992, 2005, 2014; Wong, 1998). A possible explanation is that the Singapore flora is essentially a subset of the southern Malay Peninsula flora. The main island of Singapore is extremely close to southern Peninsular Malaysia. Moreover, the separating Johor Strait is of relatively recent origin from the early Holocene (Bird et al., 2005). However, it is clear that Riau Pocket elements figure prominently in the Singapore flora. For instance, 19 of the provisional list of 36 species of Dipterocarpaceae found in Singapore also occur in West Borneo and/or Sumatra. It is also noteworthy, with the recent completion of the Dipterocarpaceae account for the *Flora of Thailand* (Pooma et al., 2017), that some dipterocarp species occurring in Singapore have been found to extend

even into Peninsular Thailand. These include *Cotylelobium lanceolatum* Craib, *Rubroshorea macroptera* (Dyer) P.S.Ashton & J.Heck. subsp. *macroptera* and *S. sumatrana* (Slooten ex Thorenaar) Desch., which were cited as Riau Pocket taxa by Ashton (2001). These occurrences in Peninsular Thailand may be considered outliers presently, but nevertheless suggest a past connectivity. Like the extent of the Riau Pocket in Sumatra (Laumonier, 1990), the boundaries of the Riau Pocket in the Malay Peninsula and the Gulf of Siam area lack clarity.

The Riau Pocket flora is mostly recorded on freely drained humult ultisols, deep podsols and in peat swamps (Wong, 1998). Allopatric variation in the Riau Pocket especially between Borneo and the Malay Peninsula / Sumatra is well known. One example is *Rubroshorea macroptera* which occurs in Singapore. In this species, the geographical subspecies, *Rubroshorea macroptera* subsp. *macroptera*, occurs in the Malay Peninsula (including Singapore) and Sumatra, whereas another three subspecies occur in Borneo (Ashton, 2001). *Shorea sumatrana*, recently recorded for Singapore (Ganesan & Ali Ibrahim, 2018), may provide another example of allopatric variation within the Riau Pocket, with *S. sumatrana* occurring in the Malay Peninsula and its closely related sister species, *S. seminis* (de Vriese) Slooten, occurring across the South China sea in Borneo.

Insights from the swamps

Swamp forests have a lower overall diversity than dryland forests (Whitmore, 1984). The swamp forests of Singapore include freshwater swamps and mangrove forests. Whereas freshwater swamps derive water from rainfall and streams, mangroves experience a daily tidal routine of saltwater inundation. In Singapore, freshwater swamps probably existed mostly along the Kallang and Singapore river basins and areas flanking the Jurong and Pandan rivers, but those at Jurong and elsewhere are now mostly transformed, with the remaining Nee Soon remnant (part of the Seletar drainage) now protected (Davison et al., 2018).

Pristine features such as trees bearing stilt-roots (e.g., *Palaquium xanthochymum* (de Vriese) Pierre ex Burck (Sapotaceae) and *Xylopius fusca* Maingay ex Hook.f. & Thomson (Annonaceae)) and vertically ascending peg- or columnar pneumatophores (e.g., *Lophopetalum multinervium* Ridl. (Celastraceae)) can still be seen at Nee Soon. The aquatic *Barclaya motleyi* Hook.f. (Nymphaeaceae) is probably no longer in Nee Soon and survives only through populations in Bukit Timah (Lok et al., 2009) and Upper Peirce (Kiew, 2026). The Nee Soon swamp flora includes at least 672 species of vascular plants from 117 families, including 288 trees of 5 cm DBH or larger from 60 families (Chong et al., 2018). A swamp forest is necessarily highly specialised in comparison to more widespread terrestrial types, in that it is quite strictly bound by its environmental parameters, so that many of its species may not stand disturbance as weedy species rapidly colonise the newly available space. Once its hydrological regime is altered, there is almost certainly no way of regaining what would be lost. The fact that new records continue to be found underscores how little we have documented these forests, and the potential losses with disturbance. Regionally, few swamp forest fragments remain and even fewer are protected. This is likely because most swamps have a coastal occurrence, and most landscape-changing activities radiate from human settlements along coastlines.

Most mangrove forests in the region are secondary, the disturbances continuing even when proper regrowth has not been attained. Consequently, tall mangroves in the region (as

in Brunei) are rather rare. For Singapore, Ng & Sivasothi (1999), using their terminology, recorded 19 major mangrove species (in 6 families) and nine other minor species (7 families). An additional two species, *Bruguiera hainesii* C.G.Rogers (Rhizophoraceae) (Sheue et al., 2005) and *Ceriops zippeliana* Blume (Rhizophoraceae) (Sheue et al., 2010), were later added. *Ceriops zippeliana* is close to *C. tagal* (Perr.) C.B.Rob., with which it had been confused, demonstrating the need for detailed taxonomic study. *Ceriops decandra* (Griff.) W.Theob. and *C. zippeliana* occupy distinct ranges: *C. decandra* around the Bay of Bengal and Andaman Sea and *C. zippeliana* along sea margins of west and central Malesia (Sheue et al., 2009).

More recently, *Bruguiera hainesii* was shown to be a hybrid between *B. cylindrica* (L.) Blume and *B. gymnorhiza* (L.) Lam. ex Savigny (Ono et al., 2016). While this could be expected between species whose distributions overlap, Sundaland, especially the Malay Peninsula, could also present a barrier between populations in the Indian Ocean and South China Sea. This impediment to free-flow inter-oceanic connectivity between the Indian and Southwest Pacific regions has been called the Indonesian or Southeast Asian Gateway, with the marine passages forming the so-called Indonesian throughflow (Hall, 2009). This gateway has not only influenced throughflow and ocean/atmospheric phenomena affecting distribution of temperature–moisture regimes (Kuhnt et al., 2004), but presents a barrier effect that may cause biogeographic differentiation. Thus, sharply differentiated chloroplast DNA traits between east and west coast populations of *Ceriops tagal* in the Malay Peninsula (Liao et al., 2007), and the significantly different haplotype compositions across the South China Sea between a west Sabah population of this species and east Malay Peninsula populations, may be explained by barriers to genetic exchange (Liao et al., 2007). Singapore, in the midst of this gateway and due to its size, may, however, not see a significant effect of this. Or, it may witness more complex scenarios.

New, endemic or rare

In the period 2009–2023, when taxonomic botany in Singapore picked up in pace, 155 new native vascular plant records for Singapore were published (Neo et al., 2024). This represents an increase of about 7% compared to the enumeration by Chong et al. (2009). It is significant in that these new records also include taxa of large trees, including in the Dipterocarpaceae and in *Mangifera* L. (Anacardiaceae) (e.g., Ganesan et al., 2018; Ganesan, 2019).

Plant families with the highest new native records are Rubiaceae (8 species), Euphorbiaceae (8 species) and Orchidaceae (8 species). No doubt, members of these three families and others treated for the *Flora of Singapore* have benefitted from the attention of specialists and this, together with increased field collection in Singapore, have contributed to the increase in species number. As of 2023 there have also been around 173 rediscoveries of vascular plant species previously presumed to be nationally extinct (Neo et al., 2024), a significant number, by any serious reckoning. If this is possible in the already well-botanised island of Singapore, we can only begin to contemplate how much more awaits us in the rich but heavily disturbed habitats of this region. It is, however, conceivable that plants are going extinct even before they become known to science (Seah & Wong, 2018).

Endpoints

Singapore's lowland flora is part of the West Malesian or central Sundaland flora, and clearly a subset of the Malayan lowland evergreen rainforest flora. Its affinities are clearly with the south Malayan, east Sumatran and west Bornean floras, and Corner's Riau floristic elements point to an association with southeast Sumatra, coastal Perak in Peninsular Malaysia, eastern and southeastern Peninsular Malaysia, and coastal portions of western and northwestern Borneo, areas previously linked through a larger land continuity in the Pleistocene ice ages. In that respect, while native plant conservation programmes should continue to give priority to Singapore genotypes (see Chapter 7), enrichment or reforestation programmes that would benefit from plant material of rare or extinct taxa which can still be obtained from adjacent regions, should first look to these regions.

The intactness of the 3-dimensional structure of the rain forest as well as large-enough or well-buffered tracts are fundamental to shaping and maintaining microenvironments and niches (Richards, 1998; Terborgh, 1992; Whitmore, 1998; Solé et al., 2005). If forest areas are not carefully preserved, or persist only as relatively small and thinly buffered fragments, the overall diversity is affected and is likely to decline (Turner, 1997b). There could be a need to create buffers around small and thinly buffered fragments. Plantings need to be considered as stands rather than specimens, with a species mix to approximate the floristic composition of the climax vegetation. However, a shelterwood system may be used with pioneer tree species initially in exposed sites and/or areas where soils have been heavily degraded.

Only some 0.28 % of the land area of Singapore is still under primary forest (Yee et al., 2011), with lowland forests much restricted to Bukit Timah Nature Reserve (the largest contiguous area of primary forest, about half of Singapore's native vascular plant flora on less than 0.2% of Singapore's land surface – Ho et al., 2019) and fragments in the Central Catchment Nature Reserves. Notwithstanding the drastic reduction in natural vegetation, there has not been as steep a reduction in the numbers of native species. In the Rubiaceae (Wong et al., 2019), Singapore's second largest plant family, 66% of the native species are still extant. In the Apocynaceae (Middleton & Rodda, 2019), 72% of the native species are still extant. Similar proportions of extant species also occur in families with very different habits and habitat preferences such as the Cyperaceae (Simpson, 2019) with 69% of the native species still extant and Poaceae (Veldkamp et al., 2019) with 80% still extant. Conversely, however, the epiphytes, in particular the epiphytic Orchidaceae (the largest vascular plant family in the flora), have fared much more poorly (Turner, 1994).). There are preliminary indications that families that are composed entirely of or mostly of trees in Singapore have a high proportion of species that are still extant. These include the Anacardiaceae (Ganesan, in prep.) with 90% of native species extant and Dipterocarpaceae (Ganesan & Ashton, in prep.) with 95% of native species extant. The longer lifespan of trees may mask extinction debt. Several species of trees in the abovesaid plant families are represented by 1–2 mature individuals only.

Different substrates support different plant assemblages and even species. Singapore also has sandstone sequences, notably in its southwestern parts such as at Kent Ridge and the Southern Ridges/Mount Faber area, on which disturbance seems more degradative, the ensuing secondary growth such as *Adinandra belukar* much more open in nature (Holtum, 1954b; Sim

et al., 1992). These sites should be allowed to regenerate without further degradation. Aside from dryland lowland forests, the Nee Soon Swamp Forest also takes special pride of place in considering what special diversity remains to be protected. If the Southeast Asian flora is in a refugial state, then the current biological accounting and conservation initiatives are all the more relevant.