

Origins and Assembly of Malesian Rainforests

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great Asiatic floristic interchange, GAFI, India, Malesia, rainforest assembly, paleobotany, Sunda–Sahul

Abstract

Unraveling the origins of Malesia's once vast, hyperdiverse rainforests is a perennial challenge. Major contributions to rainforest assembly came from floristic elements carried on the Indian Plate and montane elements

from the Australian Plate (Sahul). The Sahul component is now understood to include substantial two-way exchanges with Sunda inclusive of lowland taxa. Evidence for the relative contributions of the great Asiatic floristic interchanges (GAFIs) with India and Sahul, respectively, to the flora of Malesia comes from contemporary lineage distributions, the fossil record, time-calibrated phylogenies, functional traits, and the spatial structure of genetic diversity. Functional-trait and biome conservatism are noted features of montane austral lineages from Sahul (e.g., diverse Podocarpaceae), whereas the abundance and diversity of lowland lineages, including *Syzygium* (Myrtaceae) and the Asian dipterocarps (Dipterocarpoideae), reflect a less well understood combination of dispersal, ecology, and adaptive radiations. Thus, Malesian rainforest assembly has been shaped by sharply contrasting evolutionary origins and biogeographic histories.

INTRODUCTION

The aseasonal (perhumid) rainforests of Malesia (**Figure 1**) may rival or exceed the Amazon forests in tree species richness (Slik et al. 2015). They have assembled through time from lineages with remarkably different biogeographic histories (van Steenis 1934; Morley 2003, 2018a; Slik et al. 2018) while providing habitat for a rich diversity of nonwoody plants, as well as terrestrial, arboreal, flying, gliding, and aquatic animals. Many of the region's lowland and other habitats have been cleared for settlement and agriculture on an industrial scale (Ashton 2014).

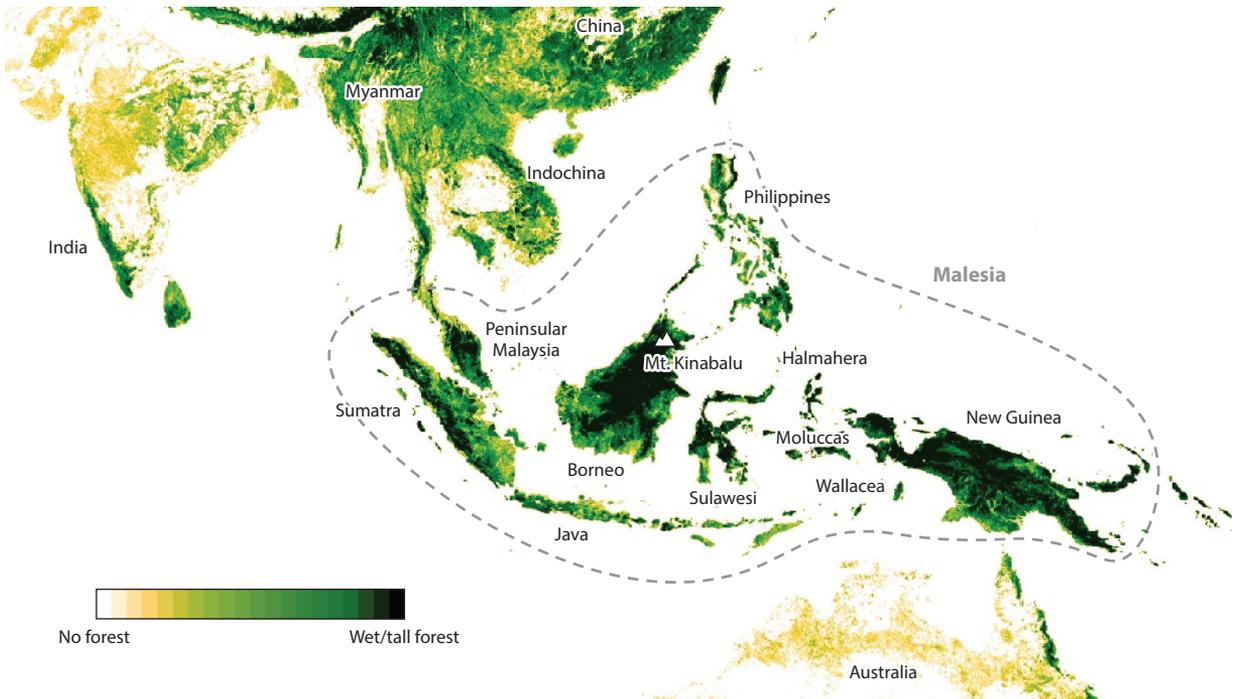


Figure 1

Vegetation map highlighting the tall, wet (perhumid) rainforests (*darkest green*) of the study area, Malesia (*dashed gray outline*) (Simard et al. 2011). The base map refers (broadly) to forest cover in 2005. Figure adapted from original map prepared by Will Cornwell.

The Malesian region is geologically dynamic and volcanically active and is assembled from multiple terranes. It straddles zones of subducting Pacific and Indian Ocean seafloor, and it currently includes more than 20,000 islands that reflect the most recent cycle of submergence and reconnection caused by eustatic sea-level variation (Wallace 1869; Hall 1996, 2009, 2012; Lohman et al. 2011; de Bruyn et al. 2014). Tectonic plate collisions have caused the rise of mountains and the formation of marine basins (Pubellier & Morley 2014), making the region one of the most geologically complex on Earth (Hall 2009).

Contact between once-isolated land masses provides opportunities for terrestrial organisms to disperse, compete, and diversify across new terranes (Schuster 1972, Morley 2000, Wilf et al. 2013). Malesia's complex physiography and perhumid tropical climate support its rich biota and several recognized biodiversity hot spots (Myers et al. 2000). On the basis of his explorations and observations as a naturalist in the region, Alfred Russel Wallace founded the science of biogeography and independently derived the theory of evolution by natural selection (Darwin & Wallace 1858; Wallace 1860, 1869). Since Wallace first visited the area, Malesia has inspired and attracted a long succession of biologists, geologists, and paleontologists determined to unravel its secrets.

Two continental plate collisions laid the foundations for the movement of vegetation into and out of the Malesian region, and thus to the origins and evolution of the perhumid rainforest. As first described by Schuster (1972), the Indian and Australian Plate collisions with Asia were postulated to have triggered substantial plant dispersals along newly formed corridors. These great Asiatic floristic interchanges (GAFIs) are central to the origins and evolution of the rainforests of Malesia and are named here in tribute to the classic, and very different, Great American Biotic Interchange (GABI) (Stehli & Webb 1985). According to Schuster (1972), these interchanges were a collection of eclectic concepts in need of evidential support. He sought to bring concordance to the theory that the exceptional biodiversity of the region was not a reflection of in situ origins alone but rather resulted from juxtaposition and interaction with several rich biotas.

GAFI 1 began with the separation of India and Madagascar from Africa and Antarctica before the end of the Albian (~110 Ma) and the subsequent Late Cretaceous separation of Madagascar from India. GAFI 1 continued with India's northward passage in some degree of isolation until activation of floristic interchange during, and probably prior to, its middle Eocene collision with South Asia (Morley 2000, 2018a; Hall 2009; Klaus et al. 2016). GAFI 2 describes the middle Eocene (~45 Ma) separation and northward trajectory of Australia (Sahul) from Antarctica, which resulted in its collision with Sunda beginning in the late Oligocene (~26 Ma; Hall 2009, 2012). The resulting collocation of Sunda and northern Sahul within the same climate zone activated an ongoing floristic interchange that included the movement of Gondwanan lineages into Malesia (see van Steenis 1934, Morley 2000, Kooyman et al. 2014, and references therein).

Although the two GAFIs and respective movements of the associated perhumid vegetation are the most widely discussed, other sources have contributed to phytogeographical patterns in Malesia (Schuster 1972, de Bruyn et al. 2014). These include in situ evolution and diversification and exchange with higher latitudes of Laurasia (Huang et al. 2015).

Plate tectonics and climate constraints have shaped the distribution of plant lineages in Malesia and the history of lineage survival and diversification through time (Slik et al. 2015). Investigations into the history of the vegetation have used palynology (Morley 2000, 2003; Moss & Kershaw 2000, 2007; Kershaw et al. 2007; Macphail & Hill 2018), microfossils (Christophel 1994, Hill 1994, Wilf 2012, Kooyman et al. 2014), time-calibrated molecular phylogenies (Muellner et al. 2008, de Bruyn et al. 2014, Crayn et al. 2015), and combinations of data sources (Sniderman & Jordan 2011, Richardson et al. 2012).

Perhumid: largely aseasonal, or with minimal seasonality such that plant growth is not affected

Malesia: the area including Peninsular Malaysia, Borneo, Sumatra, Java, Sulawesi, Moluccas, Philippines, Lesser Sundas, and New Guinea

GAFI: great Asiatic floristic interchange

Sahul: the Australian Plate inclusive of the Sahul Shelf and New Guinea

Sunda: the Sunda Shelf, as part of the Asian Plate, includes part of Indochina, Peninsular Malaysia, Borneo, Sumatra, Java, and Bali

Our goal in this review is to refocus understanding of the origins and assembly of perhumid rainforests in Malesia relative to the opportunities provided through time by the alignment of geodynamics and tropical climates. We aim to review rainforest origins based on the available and emerging empirical evidence. To update our understanding of the GAFIs and the evolutionary and biogeographic history of the living perhumid flora, we emphasize plant lineages that are widely discussed in the literature and ecologically well understood (e.g., Kooyman et al. 2014, Raes et al. 2014), and we contrast current lineage distributions with the available fossil record.

How do evolutionary history and ecological relationships interact in contributing to community composition and assembly? To address this question, we examine current biogeographic interpretations of lineage origins and the contributions of lineage diversification and adaptation versus functional-trait conservatism in shaping the living perhumid vegetation of Malesia. Using the example of the extant flora of Mount Kinabalu, which includes many of the fossil and living genera discussed throughout this review, we show how lineages with different origins are distributed in relation to edaphic and altitudinal gradients.

PALEOBOTANICAL BACKGROUND

Given the long history of biogeographic focus on the region, it is remarkable how poorly sampled Malesia's macrofossil record is, especially for terrestrial organisms (Lee 1992, van Gorsel 2014). The primary source of the intensively mined coals of Southeast Asia was terrestrial plant matter (Moore & Ferm 1992, Davis et al. 2007), yet modern paleobotanical investigations have focused almost exclusively on the Permian of Sumatra (e.g., van Waveren et al. 2018); there have been few investigations of Cretaceous or Cenozoic, especially Paleogene, paleobotany since historical Dutch surveys more than a century ago (Heer 1874, 1879; Geyley 1900). Few fossil-plant identifications from that pioneer era are likely to be accurate.

In contrast to the scarce record of plant macrofossils, there are a wealth of Cenozoic palynological data and interpretations available from Malesia (Morley 1982, 1998, 2000, 2002, 2003, 2012, 2018a; Lelono & Morley 2011; Witts et al. 2012). Palynological data represent extremely high sample sizes and stratigraphic densities, form the basis of biostratigraphic correlations, and provide evidence of numerous lineages not preserved as macrofossils, although isolated palynomorphs often do not provide sufficient information to allow unambiguous phylogenetic placement on a crown versus a stem lineage (Sauquet et al. 2009). In comparison to macrofossils, which are often patchy in time and space, are discontinuously sampled, and have greater lowland bias, dispersed palynomorph assemblages typically sample a much broader area, are considerably more time-averaged and transported, and have coarser taxonomic resolution (Behrensmeyer et al. 2000).

Reconstructions of the Cenozoic climatic and environmental history of the Sunda region are based mostly on the palynological record (Morley 2012). However, they also consider lithological indicators of climate, especially the occurrences of evaporites and coals (Morley 2018a), with the latter forming during periods of everwet (perhumid) climate (Ziegler et al. 2003). Morley (2012) discusses the regional climate record through time in relation to trends in global temperatures from the deep-sea oxygen isotope record (Zachos et al. 2001). We note that many of the samples used to reconstruct the paleoclimatic history of Southeast Asia represent unpublished palynological data gathered during the course of hydrocarbon exploration (Morley 2012, 2018a), although published primary data are increasingly becoming available. The indicator taxa used to identify perhumid climate and dispersals from India to Southeast Asia related to GAFI 1 include *Durio*-type pollen recorded as *Lakiapollis ovatus* (including *Cullenia*; Malvaceae), *Alangiium* sect. *Conostigma* (Alangiaceae) as some *Lanagiopollis* species, *Ctenolophon* (Ctenolophonaceae) as *Retistephanocolpites*

williamsii, *Gonystylus* (Thymelaeaceae) as *Cryptopolyporites cryptus*, and *Podocarpus* (Podocarpaceae) as *Podocarpidites*.

Ironically, the most complete fossil records relevant to the Malesian region are from Australia and other former Gondwanan landmasses that were the sources for the GAFI 2 interchange (Hill 1994). Paleo-Antarctic rainforest lineages (PARLs) are living plants with fossil records in the mid-high-latitude paleo-rainforests of the Cretaceous and Paleogene Southern Hemisphere (Kooyman et al. 2014). The movement of woody PARLs from Antarctica–Patagonia–Australia into Southeast Asia (GAFI 2) is represented by a notably rich record from both macrofossils and microfossils (as summarized in table 4 of Kooyman et al. 2014). Considerable fossil and nonfossil information has elucidated other aspects of the Sunda–Sahul floristic interchange. Genetically and phylogenetically informed studies have started to fill some of the gaps in the chronology of the fossil record (Sniderman & Jordan 2011, Richardson et al. 2012, Crayn et al. 2015) and bring to light the roles of plant traits and strategies that reflect dispersal and climate (Yap et al. 2018).

Woody angiosperm and especially conifer PARLs have provoked considerable discussion regarding their histories of competition and co-occurrence and their contrasting water-use physiology and life-cycle strategies (Brodribb & Feild 2010, Brodribb et al. 2012). The notable conservatism of many PARLs (e.g., most podocarp conifers) reflects ancestral, retained (plesiomorphic) physiological traits related to water balance and shade tolerance (Brodribb et al. 2012). Functional constraints related to water balance in leaves (e.g., transfusion tissue, stomatal features), stems (e.g., xylem conduits), and seeds (water content) provide compelling evidence for drought intolerance and the presence of mesic, perhumid climates when PARLs are abundant or diverse in either fossil or living floras (Brodribb & Hill 1998, Brodribb et al. 2012, Wilf 2012).

GEOLOGIC SETTING FOR FLORISTIC CHANGE

Core areas of Malesia accreted from terranes that broke off from Gondwana (which was part of Pangaea until the Late Jurassic) and moved northward through the Mesozoic (Metcalf et al. 2001). These areas represent the first involvement of Gondwanan terranes with the formation of Southeast Asia and presumably included some floristic contributions. Southwest Borneo abutted the Sunda Plate during the Early Cretaceous, and the East Java/West Sulawesi and Sumatran Woyla Terranes followed in the Late Cretaceous (Hall 2012, Hall & Sevastjanova 2012). Paleogeographic and tectonic maps supporting the following discussion are presented by Hall (2009, 2012) and Morley (2018a).

The regional flora of Malesia in the latest Cretaceous to Paleocene, immediately prior to the collision of the Indian Plate with Asia, is described by a palynological succession taken from the Kayan Formation in western Sarawak (Muller 1968; see also Morley 1998, Breitfeld et al. 2015). The latest Cretaceous to Paleocene flora of Malesia, as seen in these samples, is depauperate, with affinities to continental East Asia (Morley 2018a). The pollen assemblages included taxa with living representatives in the Malesian rainforest, such as possible Santalaceae (*Aquilapollenites*); probable Ulmaceae; *Ilex* (Aquifoliaceae); and megathermal elements such as *Anacolosa* (Olacaceae), Calamoideae, Apocynaceae, Myrtaceae, and *Nypa* (Arecaceae). The alluvial, fluvial, and shallow marine fossiliferous strata represent part of a long process of land formation and erosion that started with regional uplift during the Cretaceous collision of the East Java/Southwest Sulawesi Terrane with western Borneo. From the Late Cretaceous to the early Eocene, the core area of Sundaland, which included the present-day islands of Borneo, Sumatra, Java, and Bali, as well as the Malay Peninsula, became an elevated and emergent extension of continental Asia surrounded by inactive margins (Clements & Hall 2011). However, by the middle Eocene, most of southern Sundaland was a low-lying plain with mainly southward-flowing rivers (Witts et al. 2012).

Wallacea: the area between the Sunda and Sahul plates, east of Wallace's Line, including Sulawesi, Lombok, Sumbawa, Flores, Sumba, Timor, Halmahera, Buru, and Seram

The Eocene collision of India with Asia has been postulated as the most influential event with respect to introducing today's diverse extant rainforest lineages into Southeast Asia (GAFI 1) (Schuster 1972; Morley 1998, 2018a). Pollen records of lineages described as moving into Asia with India include Arecaceae, Alangiaceae, Ctenolophonaceae, Dipterocarpaceae, Lecythydaceae, Lythraceae, Malvaceae, Proteaceae, Sapindaceae, and Podocarpaceae (Morley 2000). Relevant fossil pollen locations include the middle to late Eocene Nanggulan Formation of Central Java (Lelono 2000) and several middle Eocene formations in the region of South Sulawesi (Morley 1998, 2018a). Overwater India–Asia dispersals are thought to have commenced at ~48 Ma or earlier, with a land connection at ~41 Ma (Klaus et al. 2016, Morley 2018a), although the literature suggests significant variation surrounding these dates. Also, during the middle Eocene (~45 Ma; Hall 2009), Australia began to separate from Antarctica and move toward Sunda (GAFI 2), carrying the PARLs (Kooyman et al. 2014). Floristic exchanges between Sunda and Sahul began in the late Oligocene to early Miocene (Hall 2009, Crayn et al. 2015). Sunda in the Oligocene apparently was seasonally dry, with lower floristic diversity than in the Eocene (Morley 2000, 2012). The presence in Sunda of Dipterocarpaceae, the dominant tree family in the Malesian lowlands today (Ashton 1982, 2014), dates at least to the Oligocene on the basis of pollen data (Muller 1981).

Elevations across Sunda diminished during the early Miocene, while marine transgression resulted in widespread shallow seas across the Sunda Shelf and intermittent submergence of much of Borneo. During the middle Miocene, most of Sunda was low-lying and included an extensive inland Malay Sea (Morley 2018a). Around the same time, widespread uplift occurred in central Borneo with the formation of the Central Kalimantan Ranges and the Crocker Range (Morley 2018b). Mount Kinabalu and the Barisan Mountains were probably uplifted to near their current elevations by the Pliocene, whereas Javanese mountains became established only within the late Pliocene and Quaternary (Morley 2018b). Borneo today retains the highest floristic diversity in Malesia, suggesting the persistence of diverse, perhumid forests through late Neogene climatic oscillations (Raes et al. 2014).

The continuing northward progress of Australia and the collision between Sunda and Sahul initiated the dramatic uplift of New Guinea. During the late Miocene, New Guinea began to transform from an arc of isolated islands, coalescing and widening from around 5 Ma with peak elevations eventually reaching ~5,000 m (Toussaint et al. 2014). Then, as now, New Guinea was in the perhumid tropics during its orogenic phase. The uplift of the large tropical island of New Guinea set the scene for the assembly of its rich rainforest diversity. The lowland rainforests of New Guinea are considered to be derived predominantly from the Sunda lowland flora (Good 1960, Hartley 1986), whereas the uplands are dominated by austral–Gondwanan lineages (Johns 1976). At higher altitudes, woody montane elements with austral origins dispersed westward from New Guinea to Sunda as soon as appropriate uplands formed across Wallacea and Sunda (van Steenis 1934, Morley 2002, Ashton 2014, Kooyman et al. 2014). In contrast, only a few high-altitude, presumably Asian lineages such as *Rhododendron* (Ericaceae) appear to have moved in the opposite direction and immigrated into Sahul (Hartley 1986, Craven et al. 2011, Shrestha et al. 2018). At lower elevations, however, pollen and genetic evidence shows that the Sunda influence in Sahul has increased over time (Sniderman & Jordan 2011, Richardson et al. 2012, Crayn et al. 2015, Yap et al. 2018).

The Philippines and Halmahera were Pacific island arcs brought together by the combination of the northward progress of the Australian Plate and the westward movement of the Pacific Plate. The present configuration of the Philippines took shape during the late Miocene and consists of a multitude of islands (Hall 2009, 2012). The Philippine lowland forests share almost identical generic diversity with lowland Borneo, including in Dipterocarpaceae, but they have much lower species diversity (Raes et al. 2014).

The late Cenozoic history of Malesia shows that its island biotas were repeatedly isolated and rejoined through eustatic sea-level changes (Morley 2000, 2012; Raes et al. 2014; Scotese et al. 2014). During Pleistocene lowstands, many of the islands of Malesia became interconnected. However, deepwater barriers maintained some separations (e.g., Sunda from Wallacea, the Philippines from areas to the south; Hall 2009, 2012). In combination, the expansion and contraction of available land area, the timing of orogenies (e.g., Mt. Kinabalu, New Guinea), climate change (Zachos et al. 2001, Ziegler et al. 2003), shifts in edaphic gradients, and barriers to interchange (Slik et al. 2011) variously constrained and facilitated the transfer of vegetation into and out of perhumid Southeast Asia (van Steenis 1934, 1979; Schuster 1972; Morley 2003). The same factors shaped the in situ evolution, diversification, and current-day distribution of Malesian lineages and their assembly into distinct vegetation communities (Ashton 2014).

VEGETATION MOVEMENTS

China and Indochina–Malesia

The collision of the Indian Plate with Asia during the Eocene resulted in dramatic changes to Asian paleogeography, including the onset of Tibetan Plateau uplift (Ding et al. 2017) and re-configuration of Indochina through compression, resulting in regional uplift and extrusion to the southeast (Tapponnier et al. 1986). Recent macrofossil discoveries from Tibet do not appear to include any tropical rainforest lineages (Jia et al. 2019, Jiang et al. 2019) or other reliable evidence for the dispersal of equatorial (perhumid) rainforest plant taxa during the Paleogene. The middle Eocene floras from coal seams on Hainan Island and in Guangdong Province, China, include palynological or macrofossil evidence of Lauraceae, *Nageia* (Podocarpaceae), Fagaceae, Myricaceae, Ulmaceae, Fabaceae, Celastraceae, and Coryphoideae (Arecaceae) (Yao et al. 2009; Jin et al. 2010, 2017). These assemblages include a mix of meso- and megathermal evergreen, temperate, and deciduous elements, suggesting a seasonal climate (Yao et al. 2009, Jin et al. 2017).

Despite the presence of some megathermal elements in the fossil floras of China (Jacques et al. 2015), there is little to no empirical evidence to suggest they originated in China or that they moved out of China into Malesia, because most parts of China were in temperate latitudes in the geological past. *Shorea* (Dipterocarpaceae) was present in southern China in the late Eocene (Feng et al. 2013), and seasonal rainforests with tropical elements including *Shorea* extended further into East Asia from Southeast Asia in the middle Miocene than at any other time, as shown by reports from southern China at 24°N (Shi et al. 2014). Other taxa identified from the middle Miocene of southern China include *Calophyllum* (Calophyllaceae), *Dipterocarpus* (Dipterocarpaceae), *Macaranga* (Euphorbiaceae), *Baubinia* (Fabaceae), *Castanopsis* (Fagaceae), Hamamelidaceae, Lauraceae, *Artocarpus* (Moraceae), *Flacourtia* (Salicaceae), and *Boehmeria* (Urticaceae), with the floristics suggesting a seasonal rather than megathermal perhumid climate (Jacques et al. 2015). Alternatively, some taxa that are now successful in Malesian rainforests, perhaps most conspicuously *Quercus* and other Fagaceae, have excellent fossil records in temperate Laurasia and Asia (Barrón et al. 2017) and in all likelihood originated in Laurasia and migrated into Malesia.

GAFI 1: India–Asia

Extant lineages with confirmed macrofossil evidence for presence on India before contact with Asia include Achariaceae, Anacardiaceae, Annonaceae, Connaraceae, Lamiaceae, Oleaceae, Phyllanthaceae, Planchoideae (Lecythidaceae), Grewioideae and Sterculioideae (Malvaceae), Castilleae (Moraceae), Myrtoideae (Myrtaceae), Salicaceae, Simaroubaceae, and Vitaceae (Manchester et al. 2013, Wheeler et al. 2017). All these taxa are represented as fossil woods and fruits/seeds in

the Deccan Traps, which straddle the Cretaceous–Paleogene boundary (Manchester et al. 2013, Wheeler et al. 2017); are present in the living rainforests of Malesia; and confirm a modern-aspect angiosperm flora. Additional lineages represented as pollen in terminal Cretaceous Deccan volcanics include Dipterocarpaceae, Arecaceae (Calamoideae), and Proteaceae (Prasad et al. 2018).

The first signals of plant dispersals from India to Southeast Asia occur in pollen records. Close to the early/middle Eocene boundary (47.8 Ma), records of what are described as Indian pollen of *Alangium* sect. *Conostigma*, and *Durio*-type pollen, occur in sediments from southern Sulawesi (Morley 1998, 2018a). The climate of southern Sunda during the early/middle Eocene has been suggested as being seasonal, on the basis of Restionaceae pollen abundance (Morley 2012). After ~45 Ma, the climate became perhumid (Morley 2012), coinciding with the appearance of *Ctenolophon* and *Gonystylus* pollen in Sulawesi and Java and as part of an overall dramatic increase in pollen diversity (Lelono 2000).

The dipterocarps (Dipterocarpaceae), with more than 500 species globally, are often the most abundant and diverse tree taxa in the low- to midaltitude perhumid as well as seasonal rainforests of modern-day Southeast Asia (Slik et al. 2009, Raes et al. 2014, Ghazoul 2016). Dipterocarpaceae are notably emphasized in biogeographic hypotheses for lineage movements from Africa or, more often, India into Southeast Asia (Ashton 1982, Morley 2003, Ghazoul 2016). Current biogeographic interpretations (Morley 2000, 2018a; Heckenhauer et al. 2017) are based on the relationship of Sarcolaenaceae to Dipterocarpaceae, the timing of clade divergence within the family, and the relationships of fossils to crown lineages of Southeast Asian dipterocarps (Dipterocarpoideae). In addition to the relatively large-seeded, mostly wind-dispersed species in the Asian subfamily Dipterocarpoideae, the Dipterocarpaceae include the subfamilies Monotoideae, with species in Africa, Madagascar, and the Colombian Amazon, and the monospecific Pakaraimaeoideae, from the Guianan Highlands of South America (Heckenhauer et al. 2017).

Because of its central importance to plant biogeography and the living Malesian rainforests, we further explore the subfamily Dipterocarpoideae as part of our evaluation of evidence for the India–Asia interchange (GAFI 1). In doing so, we acknowledge recent studies that show strong genetic differentiation and lack of contemporary gene flow between dipterocarps in proximate areas such as peninsular Malaysia and Borneo (Tnah et al. 2012, Ng et al. 2017), in contrast to the ability of some dipterocarps to disperse across marine barriers, as shown by the presence, with limited species richness, of several dipterocarp genera in Wallacea and New Guinea (Symington 1943; Ashton 1982, 1988, 2014).

Recent interpretations based on molecular data (Ducousso et al. 2004, Chase et al. 2016, Heckenhauer et al. 2017) have shown the Dipterocarpaceae to be paraphyletic. Pakaraimaeoideae resolve as sister to Cistaceae, and Sarcolaenaceae (endemic to Africa and Madagascar) are placed as sister to a pantropical clade composed of Monotoideae plus Dipterocarpoideae (Africa, Madagascar, South America, and Southeast Asia, in total). Thus, fossil Sarcolaenaceae (or Pakaraimaeoideae) could not provide a direct proxy for Dipterocarpoideae in biogeographic interpretations of lineage origins for Southeast Asia. There is also no confirmed pre-India-collision macrofossil record of any of these groups from Africa, Madagascar, or South America. However, the presence of Sarcolaenaceae and Dipterocarpaceae pollen has been suggested, but not yet verified, from the Maastrichtian of Sudan (Morley 2018a). The presence of Dipterocarpaceae in the African Paleogene macrofossil record also remains uncertain (e.g., Jacobs 2004, Jacobs et al. 2010). Although Gondwanan origins of Dipterocarpaceae (Ashton 1982) are still frequently suggested (e.g., Ghazoul 2016, Heckenhauer et al. 2017), no fossils of the group have been recorded from any part of Gondwana. The nearest example to Gondwana temporally is cf. *Pseudomonotes* wood from the late middle Eocene (~39 Ma) of Peru (Woodcock et al. 2017); although this occurrence is only ~5 Myr younger than the South America–Antarctica separation, it is ~70 Myr younger

BICADINANE BIOMARKERS

Bicadinanes, thermal decomposition products of polycadinane-rich resins, have often been used to track the history of Dipterocarpoideae (Rudra et al. 2017) because their source was assumed to be exclusively dipterocarp resins (van Aarssen et al. 1994). However, the compounds also occur in resins found in Eocene fruits of mastixioid Cornaceae (van Aarssen et al. 1994) and in Eocene sediments from southeastern Australia (Coward et al. 2018); dipterocarp fossils have never been found in Australia, despite decades of paleobotanical research (Macphail & Hill 2018). These findings suggest that bicadinanes can be derived from nondipterocarp taxa and that the presence of the biomarker cannot be used as a *prima facie* indicator of dipterocarps, including crown-group Dipterocarpoideae, without supporting evidence.

than the most recent connections of India–Madagascar and Africa to the remainder of Gondwana (Antarctica, South America, Australia, Zealandia).

On the Indian Plate, Late Cretaceous *Dipterocarpuspollenites* from the Deccan Volcanic Province in central India (Maharashtra; Prasad et al. 2018) represents the strongest current evidence for the precollision presence of the family. So far, only limited direct evidence supports this finding, including a lack of dipterocarp macrofossils in the diverse and well-preserved Deccan wood flora (Wheeler et al. 2017). Likewise, dipterocarp macrofossils and pollen are absent from the otherwise-diverse Paleocene Tura Formation flora of Meghalaya, northeast India (Saxena et al. 1996, Mehrotra 2000). The early Eocene Cambay amber deposit in Gujarat, India, includes resins, wood, and pollen with what are described as strong morphological affinities to Dipterocarpaceae (Rust et al. 2010, Dutta et al. 2011). However, Shukla et al. (2013) cautioned that the wood characters were potentially misinterpreted and that Lauraceae cannot be excluded as a possibility; additional experts whom we recently queried confirmed this opinion (E. Wheeler & C. Williams, personal communication, 2018). More generally, reference to dipterocarps based on resin (amber) spectroscopy, if not supported by direct fossil evidence, may require closer scrutiny because bicadinanes are now known to come from sources other than Dipterocarpaceae (see the sidebar titled Bicadinane Biomarkers) (van Aarssen et al. 1994, Coward et al. 2018).

By the early Eocene, the time of the Cambay deposits, the maritime distance between India and South Asia was greatly diminished (van Hinsbergen et al. 2012) and faunal similarities were increasing (see the sidebar titled Faunal Analog) (Clyde et al. 2003), making determinations about

FAUNAL ANALOG

The well-constrained mammalian fossil record of the early Eocene northwest Indian Plate (Ghazij Formation, Balochistan, Pakistan) supports an into-India, not an out-of-India, scenario for mammalian interchange with Asia, documenting a series of endemic precollision to cosmopolitan, Holarctic postcollision faunas (Clyde et al. 2003). Rose et al. (2014) revived the out-of-India scenario based on the presence of an extinct sister group to perissodactyls (cambaytheres) in the early Eocene of Gujarat (~54 Ma or 56–53 Ma per Missiaen & Gingerich 2014; Rose et al. 2014), from where Smith et al. (2016) showed the early Eocene presence of additional Holarctic elements as well as some Gondwanan lineages. Nevertheless, the oldest perissodactyls, artiodactyls, and primates are definitely Holarctic, favoring the into-India hypothesis, and date at least to the earliest Eocene (56 Ma) in Asia, where perissodactyls were already well diversified (Bai et al. 2018), as well as to the earliest Eocene in North America and Europe (Gingerich 1989, Smith et al. 2016).

the directionality of plant lineage movements difficult. Despite an apparent consensus that dipterocarp fruits cannot tolerate salt water and are poor dispersers (i.e., they often have heavy fruits that rely on gyration; Ghazoul 2016), the group clearly can cross short distances of ocean; no other circumstance can explain the distribution of several genera across Wallace's Line in Wallacea and New Guinea. Thus, confident determination of an Indian source for Asian dipterocarps (and other taxa) requires evidence of at least Paleocene age from the Indian Plate, and in this regard further investigations of recently discovered pollen from the Deccan Province (Prasad et al. 2018) and elsewhere will be critical.

The oldest macrofossils with dipterocarp affinities are fossil twigs similar to *Anisoptera* from the early Eocene London Clay (Poole 1993), although, given their relative maturity, these should be considered unconfirmed because they lack some diagnostic characters exhibited by mature wood of the family (E. Wheeler, personal communication, 2019). *Shoreoxylon* woods from the middle Eocene Pondaung Formation of Myanmar (Licht et al. 2014) display affinity to the Balau group of *Shorea* and demonstrate diversification in Dipterocarpoideae by the middle Eocene. Late Eocene winged fruits from South China (Guangdong; Feng et al. 2013) provide the oldest unequivocal macrofossil of an extant genus of Dipterocarpoideae and are referable to the White Meranti group of *Shorea* (Heckenhauer et al. 2017). The amber and the floral and faunal fossils of the Eocene–Oligocene Na Duong section in Vietnam (Böhme et al. 2013) include reference to dipterocarps on the basis of amber composition but without supporting evidence from macrofossils. No Cretaceous or Paleogene dipterocarp macrofossils are known from India; the oldest Indian record is a *Shorea kachhbhensis* winged fruit (Shukla et al. 2012) from the early Miocene. Subsequently, diverse dipterocarp wood and leaf fossils are reported from the latest middle and late Miocene Siwalik sequences (northern India) and have been referred to the genera *Anisoptera*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, and *Vatica* (Srivastava et al. 2014). Overall, dipterocarps do not become abundant in Indian macrofloras until the Neogene (Mehrotra 2003, Shukla et al. 2012, Mehrotra et al. 2014), although pollen is reported as common in the early Eocene and as present in the Maastrichtian (Prasad et al. 2018).

Synthesis

The lack of dipterocarp pollen or macrofossils in Cretaceous and Paleocene Asian samples (Muller 1968) argues against an Asian origin of the group before the Eocene. These data would be consistent with either a dispersal from elsewhere or an in situ Eocene divergence of crown Dipterocarpoideae in Asia. In the process of biogeographic hypothesis formulation for determining the origins, ancestry, and spread of the dipterocarps that dominate Asian perhumid rainforests, multiple components converge to add substantial complexity, and some uncertainty. What is clear from the pollen and macrofossil record is that evidence for the presence of megathermal lineages in India near the time of the Cretaceous–Paleogene boundary is strong (Mehrotra 2003, Wheeler et al. 2017). Macrofossil evidence of Dipterocarpoideae in both India and Southeast Asia is strongest in the Neogene (Muller 1981, Prasad 1993, Guleria 1996, Khan & Bera 2010), although continental Asian occurrences begin in the middle Eocene (Licht et al. 2014), while palynological evidence supports presence in India since the Deccan volcanics (Prasad et al. 2018). Evidence for dipterocarp lineage movement out of India or out of Africa (e.g., Ashton & Gunatilleke 1987) is not currently sufficient to dispel uncertainties about the timing of the arrival, and crown diversification, of the subfamily in Southeast Asia, or even the existence of crown Dipterocarpoideae before the collision. In order to better trace the evolutionary history of the lineage, additional data from palynology; macrofossil records from older time periods, especially the Maastrichtian and

Paleocene (Shukla et al. 2013, Morley 2018a, Prasad et al. 2018); and more fossils that document the diversification of the family's major clades are required.

GAFI 2: Australia–Southeast Asia

Opportunities for floristic interactions through direct contact between Sunda and Sahul began during the late Oligocene to early Miocene (Hall 2009) and are continuing. In contrast to the poor macrofossil record for GAFI 1 (India–Asia), an outstanding PARL macrofossil as well as palynological record from Australia, New Zealand, Antarctica, and Patagonia presents detailed information about stem and crown lineage appearances (Wilf & Escapa 2015, Escapa et al. 2018) and movements across the principal source terranes for GAFI 2 through time (Christophel 1994, Hill 1994, Wilf et al. 2013, Kooyman et al. 2014). In addition, increasingly detailed information is becoming available about the Sunda–Sahul floristic interchange from the Malesian region itself, which largely lacks published plant macrofossils, from palynology (Morley 1998, 2000, 2003; Macphail & Hill 2018) and phylogenetics (Richardson et al. 2012, Crayn et al. 2015). Whereas the PARLs occupy mostly higher elevations and indicate dominant movements out of Sahul, at lower altitudes genetic, distributional, and some fossil data indicate more transfers into than out of Sahul (Sniderman & Jordan 2011, Richardson et al. 2012, Crayn et al. 2015, Yap et al. 2018).

PARL movements into Malesia (Wilf et al. 2009, 2014; Wilf 2012; Kooyman et al. 2014) included *Dacrycarpus* (Podocarpaceae; Wells & Hill 1989, Wilf 2012), *Papuacedrus* (Cupressaceae; Hill & Carpenter 1989, Wilf et al. 2009), *Agathis* (Araucariaceae; Hill et al. 2008, Escapa et al. 2018), and *Gymnostoma* (Casuarinaceae), as well as other angiosperms (Scriven & Hill 1995, Zamalua et al. 2006; see also Christophel 1994, Hill 1994), among numerous others (Kooyman et al. 2014). Palynological evidence of Casuarinaceae (*Gymnostoma/Casuarina*) and *Dacrydium* (Podocarpaceae) from the early Oligocene of Malesia has been used to suggest precontact dispersal from Australia into Malesia (Lelono & Morley 2011). Morley (2000) and Macphail & Hill (2018) note the presence of Casuarinaceae pollen from the Paleocene–Eocene of the Bird's Head Peninsula (New Guinea) and northwestern Australia, whereas the record for *Dacrydium* pollen in Australia extends to the Santonian (Dettmann 1994). Both the timing of arrival and the path taken by these lineages into Sunda remain unresolved.

Over geologic time, PARLs have demonstrated remarkable biome and trait conservatism (Crisp et al. 2009, Wilf et al. 2009, Brodribb 2011, Sniderman & Jordan 2011, Brodribb et al. 2012, Wilf 2012, Kooyman et al. 2014). They have generally tracked the cool-wet environmental conditions in which they evolved and have shifted their ranges dramatically in response to plate movements and climatic change (Hill 1994, Wilf et al. 2013, Kooyman et al. 2014). PARL dispersal is mediated by frugivores attracted to the swollen, fleshy receptacles of podocarp seeds and the fruits of many of the angiosperms, and by wind for most of the conifers (e.g., *Agathis*).

Unraveling the timing, direction, and sequence of interchange between Sunda and Sahul for some abundant angiosperm lineages, even those with good macrofossil records, can be difficult (Sniderman & Jordan 2011, Richardson et al. 2012, Crayn et al. 2015). The fleshy-fruited family Lauraceae provides a useful example. The family is ancient, with macrofossils distributed globally, but because of the difficulty in distinguishing extant versus extinct genera among these fossils (Carpenter et al. 2010), and poor preservation of Lauraceae pollen, the biogeographic history of living genera is difficult to interpret. Particular genera co-occurring in Malesia may have Gondwanan (e.g., *Cryptocarya* and *Endiandra*; Hill 1986, Chanderbali et al. 2001, van der Merwe et al. 2016) or Laurasian (e.g., *Cinnamomum*, *Litsea*, and *Neolitsea*; Huang et al. 2016) origins. In addition, as species expanded their ranges in different directions after the collision of Sunda and Sahul, independent diversification occurred in the two areas. The resulting complexity has made

biogeographic interpretations even more difficult. Resolution will require phylogeographic analyses of genomic data sets incorporating broad and dense geographical sampling.

Other examples of potential two-way interchanges between Sunda and Sahul and subsequent diversification include families such as Elaeocarpaceae (Maynard et al. 2008, Rossetto et al. 2009), Meliaceae (Muellner et al. 2008, McPherson et al. 2013), and Myrtaceae (*Syzygium*; Biffin et al. 2010, Tarran et al. 2018). The first confidently described leaf fossils allocated to the fleshy-fruited genus *Syzygium* come from the early Miocene of Kiandra, New South Wales, Australia (Tarran et al. 2018), which aligns with molecular age estimates for the Syzygieae crown group of ~17–30 Ma (Biffin et al. 2010, Thornhill et al. 2012). This convergence of evidence raises the possibility that the genus *Syzygium* may be the most successful Sahul immigrant into Southeast Asia. We consider this scenario more likely than an Asian origin, given that there is little evidence for any Sunda genera reaching so far into Australia during the early Neogene (e.g., Sniderman & Jordan 2011). *Syzygium* provides an example of a genus that is present across the full extent of Malesia and a broad range of altitude, extends a considerable distance into mainland South Asia, and is both abundant and extensively diversified (~1,200 species; Biffin et al. 2010, Ashton 2014, Tarran et al. 2018). Phylogenomic studies are needed to shed further light on the diversification of *Syzygium* and, specifically, to resolve questions related to the direction and timing of movement events and the tempo of diversification processes.

The benefits of supplementing phylogenetic reconstructions with detailed nuclear DNA (nDNA)-based population genetics and chloroplast DNA (cpDNA)-based genomic evaluations emerge from several recent examples. Research on *Elaeocarpus* (Elaeocarpaceae) has shown contrasting patterns of population genetic structure in different species groups and provided insights into the role of phenotypic traits in mediating dispersal and persistence. For example, the bird-dispersed *Elaeocarpus angustifolius* species group, which is distributed widely in northeast and eastern Australia, exhibits spatial genetic structure consistent with recent migration from Malesia (Rossetto et al. 2007). Conversely, *Elaeocarpus sedentarius*, a congener with very restricted distribution (~100 km²), has fruits that are not readily bird-dispersed and shows genetic structure consistent with isolation and persistence in Australian mesothermal refugia in the subtropics (28°S; Rossetto et al. 2008). Despite its current restricted distribution and isolation, *E. sedentarius* retains strong morphological (Maynard et al. 2008) and genetic relationships with *Elaeocarpus blepharoceras* from equatorial New Guinea. Also in Australia, genomic methods detected low levels of cpDNA diversity (across >20° of latitude) as well as low geographic structuring in the small-seeded, wind-dispersed *Toona ciliata* (Meliaceae), suggesting recent arrival from Southeast Asia and rapid, presumably Quaternary spread (McPherson et al. 2013). In contrast, interpretations based on phylogenetic analyses of the partly bird-dispersed genus *Aglaiia* (Meliaceae), with both dehiscent and indehiscent fruits, thought to have originated in Southeast Asia, suggest that multiple founder events followed by speciation and long-distance dispersal explain its current distribution in Malesia, Australia, and the Pacific Islands (Muellner et al. 2008, Grudinski et al. 2014).

Synthesis

Floristic exchange between Sunda and Sahul is increasingly well documented and has occurred in both directions. The fossil record of many montane lineages with Gondwanan origins, in particular, is outstanding. In some cases, multiple genus- and species-level founder events and subsequent radiations in both Sunda and Sahul increased diversity while obscuring signals of origins. Sunda lineage expansions into Sahul outnumber those from Sahul to Sunda, align with the expansion-contraction dynamics of Australian rainforest, and are dispersal mediated; most Sunda immigrants into Sahul have small seeds and fleshy fruits (Sniderman & Jordan 2011, Richardson et al. 2012, Crayn et al. 2015, Yap et al. 2018). The highly diversified and abundant genus *Syzygium*

(Myrtaceae) has provided a significant contribution to lowland and midaltitude rainforest community assembly in both Malesia and Australia mediated by fleshy fruits and volant dispersal (Biffin et al. 2010). The early Miocene *Syzygium* fossils described by Tarran et al. (2018) favor Gondwanan origins and dispersal from Sahul. The subsequent timing of *Syzygium* dispersal more broadly into Asia and elsewhere remains unresolved. Overall, the dominant path out of Sahul has been via cool-wet, tropical montane New Guinea (sensu van Steenis 1934), reflecting the inherent climate conservatism and capacity of PARLs with origins in mid-high-latitude, cool-wet rainforests of Gondwana to track suitable climate conditions through time and be successful in the perhumid mountain forests of Malesia.

Environmental Filtering and Community Assembly: Mount Kinabalu

In the UNESCO World Heritage site of Gunung Kinabalu in Sabah, Malaysian Borneo, biologically diverse Mount Kinabalu, at 4,095 m, is the tallest mountain between the Himalaya and New Guinea. The mountain emerged during the late Miocene and early Pleistocene as a granitic pluton that intruded the Eocene to early Miocene sandstones of the Crocker Range (Cottam et al. 2013). Mount Kinabalu has often been referred to as a sky island and a meeting place of northern and southern lineages (Stapf 1894, van Steenis 1964). It highlights the important role of mountain building in creating topographic complexity, increasing the heterogeneity of soil types, and affecting local and regional climates. Together, those factors facilitate the establishment of immigrant genera and in situ speciation, and the resulting community assemblages later supply new species to neighboring areas (Antonelli et al. 2018).

To illustrate the influences of lineage origins, dispersal, and environmental filtering on the assembly of perhumid rainforest communities in current day Malesia, we use nine plot samples (from Aiba & Kitayama 1999; see also Kitayama & Aiba 2002) representing 189 woody plant genera and 70 families arranged along the altitudinal (~700–3,100 m) and edaphic gradients on Mount Kinabalu. Because of its location, altitudinal range, diversity of soil types, floristic diversity, and long research history (Stapf 1894, Kitayama 1992, Aiba & Kitayama 1999, Aiba 2002, Merckx et al. 2015), Mount Kinabalu provides both a window into Malesian rainforest history and an opportunity to look closely at perhumid community assembly along the elevation and soil gradients.

Many of the genera referred to in this review as indicators of GAFI 1, GAFI 2, Laurasia, and in situ sources of Malesian floras occur on Mount Kinabalu in high abundance. **Figure 2** shows the positions of the abundance-weighted community assemblages (the nine plots) in ordination space, reflecting the underlying genus-level floristic associations in relation to elevation and soil types. Abundance is represented as the square root of stem numbers for each genus. Lineage importance is measured as influence (indicated by vector length) on assemblage positions in the ordination. The pairwise comparisons of soil chemistry by plot detailed by Kitayama & Aiba (2002) showed that ultrabasic soils had lower soil phosphorus than sedimentary soils at similar elevations and that nitrogen and phosphorus values mostly declined with elevation. Pairwise vegetation community samples on each soil type align with the elevation categories (**Figure 2**) and include hill dipterocarp, lower montane, upper montane, and subalpine forests, respectively (Kitayama & Aiba 2002).

The megathermal GAFI 1 indicator lineages *Durio*, *Gonystylus*, *Ctenolophon*, and Dipterocarpoideae (*Sborea* and *Hopea*) are abundant in the lower-altitude plots and co-occur with other abundant genera, including *Canarium* (Burseraceae), *Barringtonia* (Lecythidaceae), *Polyalthia* (Annonaceae), *Diospyros* (Ebenaceae), *Calophyllum* (Calophyllaceae), *Palaquium* (Sapotaceae), and *Harpullia* (Sapindaceae). The presumably Laurasian-origin Fagaceae are abundant in plots at lower to mid altitudes; *Quercus* favors ultrabasic and sandy granitic soils, and *Castanopsis* and *Litbo-carpus* occur mostly on sedimentary-derived soils (see the sidebar titled Gondwanan Fagaceae).

Rainforest community assembly: the process of dispersal, establishment, and growth of rainforest species filtered by environmental gradients into an assemblage at a location

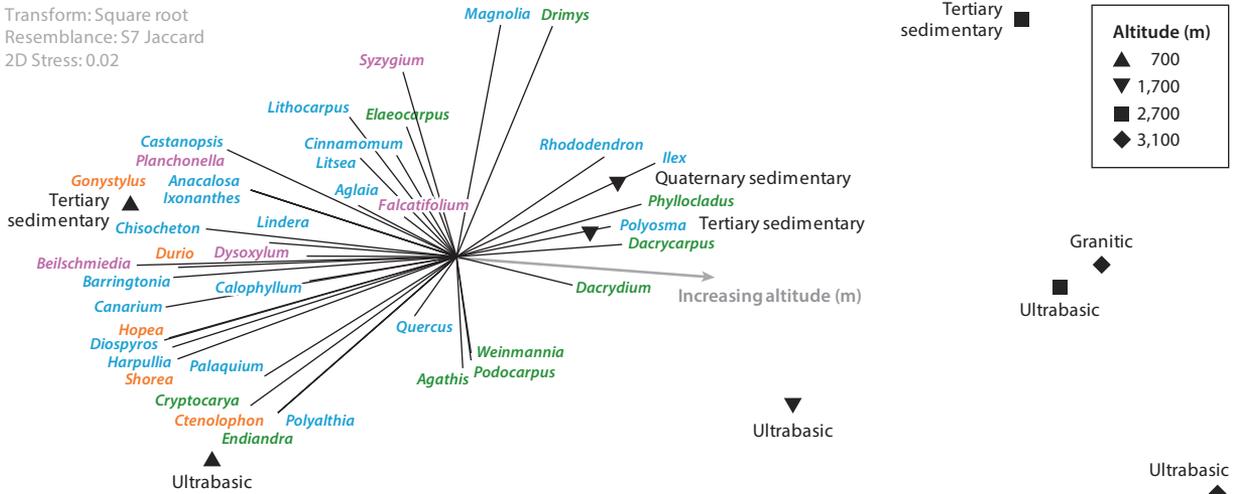


Figure 2

nMDS ordination based on full floristic abundance (stems ≥ 4.8 cm diameter at breast height over bark) of woody genera in nine plot samples on Mount Kinabalu (Sabah) (Kitayama 1992, Aiba & Kitayama 1999, Aiba 2002), showing selected upland to lowland lineages referred to in the text as vectors (*black lines*). The length of each line corresponds to the strength of contribution to the ordination, and the direction of each line represents the direction of the response to nominated gradients, in this case altitude (*gray arrow*). GAFI 1 and Laurasian lineages are shown in blue, and key tropical perhumid palynological indicators (*Durio*, *Gonystylus*, *Ctenolophon*) and genera in Dipterocarpoideae are shown in orange. GAFI 2 lineages are in green. In this case, conifer PARLs such as *Dacrycarpus*, *Dacrydium*, and *Phyllocladus* occur mostly at higher altitude, and *Agathis* and angiosperm PARLs such as *Weinmannia*, *Endiandra*, and *Cryptocarya* are more widespread. Genera with more uncertain origins are shown in purple. Abbreviations: GAFI, great Asiatic floristic interchange; nMDS, nonmetric multidimensional scaling; PARL, Paleo-Antarctic rainforest lineage.

PARLs (GAFI 2) such as *Dacrycarpus*, *Dacrydium*, *Phyllocladus*, and *Drimys* dominate the higher-altitude plots on ultrabasic and shallow granitic soils, with abundant Laurasian genera such as *Rhododendron*, *Ilex*, and *Polyosma*. Other PARLs such as *Agathis*, *Podocarpus*, and *Weinmannia* are more abundant on ultrabasic soils in mid- to lower-altitude plots, while *Elaeocarpus* and the PARL laurels *Endiandra* and *Cryptocarya* are spread more broadly. Community assembly and composition on Mount Kinabalu are structured across multiple gradients and may also reflect complex biotic interactions with regard to dispersal and competition that are not identified here.

GONDWANAN FAGACEAE

The beech–oak family Fagaceae consistently dominates forests in the northern temperate zone and tropics, including Malesia, where some genera range into the low southern latitudes. The fossil record of Fagaceae is extensive but, until recently, was entirely restricted to the Northern Hemisphere (the southern beech *Nothofagus* belongs to a separate family). Recently, Wilf et al. (2019) reported diagnostic infructescences of *Castanopsis*, a dominant and diverse living genus, in Southeast Asian and Malesian lower montane rainforests, and numerous associated fagaceous leaves from the early Eocene (52 Ma) flora of Laguna del Hunco in southern Argentina. The Patagonian fossils are the oldest record of *Castanopsis* by ~ 8 My and, remarkably, co-occur with fossils of diverse PARLs (Kooyman et al. 2014) whose living relatives characteristically associate with *Castanopsis* and *Lithocarpus* in the perhumid, lower montane (oak–laurel) rainforests of Malesia. The new fossils challenge prior biogeographic interpretations of Fagaceae by suggesting that one genus, *Castanopsis*, evolved in the Southern Hemisphere and followed the southern pathway to Malesia like the associated PARLs.

BIOGEOGRAPHY AND RAINFOREST ASSEMBLY

Community ecology links evolutionary and biogeographic history to present-day population biology (Ricklefs 2007). Trait expression in rainforest assemblages reflects species ecological strategies and fitness in the rainforest habitat, while biogeographic history delimits the species pool, filtered by environmental gradients (e.g., Westoby et al. 2002, Westoby 2006). As part of the explanation for the maintenance of high diversity in complex rainforests, competition has been suggested as operating more strongly among phylogenetically related species with more similar traits (Webb 2000). Environmental filtering is suggested when species that co-occur in specific environments are more closely related and share similar traits and environmental tolerances. Community phylogenetic structure metrics that use phylogenetic relationships to differentiate between the relative influence of environmental gradients and competition emerged from such insights. However, recent research has shown that species that are stronger competitors are also more tolerant of competition (Kunstler et al. 2016). Traits that enhance the capacity of individuals to both compete and resist competition include greater maximum height at maturity, higher wood density (Kooyman et al. 2011), and shade tolerance (Wright et al. 2004, 2017; Kunstler et al. 2016). In combination, those traits can promote coexistence and result in higher abundances of more closely related taxa with similar traits (e.g., Falster et al. 2017).

The role of Sunda and Sahul ancestry in explaining community assembly on the basis of interactions between functional traits and local, regional, and continental climates has been evaluated for a subset of tree taxa by Yap et al. (2018). Their results showed that the establishment potential of Sunda lineages in Australia was greater for species with fleshy fruits and smaller seeds, interacting with climate-induced expansion–contraction cycles (Yap et al. 2018; see also Rossetto et al. 2015). In contrast, Sahul-dominated assemblages in Australian moist refugia resisted the Sunda invasion through a combination of prior occupation of stable environments, traits that enhanced tolerance of competition, and traits that facilitated in situ persistence (Rossetto & Kooyman 2005, Rossetto et al. 2009) such as resprouting and clonality (self-replacement; Rossetto & Kooyman 2005).

The high abundance and diversity in Dipterocarpoideae provide an outstanding example of in situ success in the lowland tropics by a subfamily with identified seed dispersal constraints but high seed production and seedling survival (Ashton 1988). In contrast, the success of the genus *Syzygium* (Myrtaceae) demonstrates the influence of effective dispersal mediated by fleshy fruits with an attractive reward for volant frugivores (Biffin et al. 2010). Despite the differences in dispersal traits, both Dipterocarpoideae and *Syzygium* include canopy and subcanopy trees with shade-tolerant seedlings and saplings (Ashton 1988) that provide an advantage in the height-, light-, and competition-mediated assembly of rainforests (Falster et al. 2017). More generally, our understanding of the influence of soils on community assembly at larger scales is limited. Of particular interest is the role of sandy soils in Sunda acting as both a barrier to dispersal and a species filter for rainforest community assembly through time (Slik et al. 2011, Raes et al. 2014). Sandy soils probably played an important role in the diversification of dipterocarps in Malesia, as demonstrated by the edaphic endemism reported in relation to soil types in northwestern Borneo (Ghazoul 2016).

Synthesis

Evolutionary history and present-day ecological fitness form part of a unified account of trait variation across species that co-occur in assemblages under varying conditions (Westoby 2006, Ricklefs 2007). In the perhumid forests of Malesia, different evolutionary origins and biogeographic histories interact with contemporary functional-trait variation to influence rainforest assembly processes and structure genetic diversity across landscapes.

CONCLUDING REMARKS

Our review has emphasized that a number of factors remain to be clarified concerning the origins and assembly of the perhumid rainforests of Malesia. For example, more detailed evaluations of the fossil and other evidence supporting current hypotheses about the origins of Dipterocarpoideae, the most abundant tree lineage in Malesia, are still required. In addition, the relative contributions to Malesian rainforest assembly of floristic elements carried by India (GAFI 1) and Australia (GAFI 2), of in situ evolved lineages and of Laurasian lineages including some Fagaceae, need to be more carefully assessed.

This review has highlighted several research opportunities. For example, well-collected, stratigraphically constrained, well-identified fossil macrofloras from Malesia itself are urgently required to provide core information about plant evolution, diversity dynamics, biogeography, paleoclimate, and vegetation community composition and assembly in relation to paleoenvironments and time (as done in the Neotropics; e.g., Wing et al. 2009). Similarly, there is a need to further evaluate, verify, and voucher palynofloras from critical locations using a comprehensive range of microscopy methods (i.e., light, scanning electron, and transmission electron microscopy). In relation to Sunda and Sahul, distribution-wide, landscape-level genetic studies of representative taxa, preferably with good fossil records, have the potential to clarify both the directionality and the tempo of floristic exchanges between these floras. Lineage selections could be based on abundant and dominant tree taxa (ter Steege et al. 2013) with different dispersal characteristics and ecological strategies. In combination, these approaches could provide critical information about community assembly along environmental gradients as well as diversification processes in relation to orogenesis (Antonelli et al. 2018).

Modern methods are rapidly increasing our capacity to understand the relative contributions of evolutionary and ecological processes underlying the assembly of the Southeast Asian rainforests. Developing approaches in molecular genetics and genomics promise unprecedented insights into species relationships and a greater range of phylogenies that are more densely sampled and more accurately timescaled than has yet been possible. In turn, improved data on the timing of lineage splits and rates of diversification will advance our understanding of the origins of rainforest lineages and their biogeographic patterns, diversification dynamics, and trait evolution.

Schuster (1972) was the first to describe the potential role of major continental plate collisions in the origins and evolution of the Malesian rainforests. This review has expanded and clarified those early insights to include multiple perspectives and has examined some of the supporting evidence. We confirm the contribution of the GAFIs, Laurasia, and in situ evolution to the extraordinary diversity of the region, but in doing so we reveal many areas where more research is needed. Tectonic and climatic events facilitated interchange between floras with sharply contrasting evolutionary origins and biogeographic histories that allowed the rainforests of Malesia to assemble, diversify, and survive.

SUMMARY POINTS

1. The goal of this review is to refine understanding of the origins and assembly of perhumid rainforests in Malesia, relative to the opportunities provided through time by the convergence of plate tectonics, dynamic landscape change, and megathermal climates.
2. We describe and update how the Indian and Australian Plate collisions enabled the great Asiatic floristic interchanges (GAFI 1 and GAFI 2, respectively), which were

foundational to the origins and evolution of the perhumid rainforest and the movement of vegetation into and out of the Malesian region.

3. We highlight some of the unexplained and conflicting patterns in current biogeographic descriptions of lineage origins, including for the widely discussed Southeast Asian subfamily Dipterocarpoideae. We find that resolution of the evolutionary history of the Asian dipterocarps will require additional data from palynology; macrofossil records from older time periods, especially the Maastrichtian and Paleocene; and more fossils that document the diversification of the family's major clades.
4. More generally, geographically representative, well-collected, stratigraphically constrained, well-identified fossil macrofloras from the Malesian region are urgently required to provide core information about plant evolution, diversity dynamics, biogeography, paleoclimate, and community composition and assembly in relation to paleoenvironments.
5. In the perhumid forests of Malesia, different evolutionary origins and biogeographic histories interact with current-day functional-trait variation to influence rainforest assembly processes and to structure genetic diversity across landscapes.
6. Phylogeographical and genomic studies that track repeated patterns of diversification across multiple lineages representing the most abundant tree taxa with different dispersal characteristics and ecological strategies will provide critical information about community assembly along environmental gradients.
7. Evolutionary history and present-day ecology form part of a unified account of community assembly in Malesia under varying conditions.

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- Kooyman et al. (2014) provides extensive supplementary materials including the PARL location matrix and associated references. <https://doi.org/10.3732/ajb.1400340>
- Palaeobiology Database. <https://paleobiodb.org/#/>
- Yap et al. (2018) includes a file listing the ancestry of 1,399 Australian rain forest species with support from published data, available through DRYAD. <https://doi.org/10.5061/dryad.4pm81>