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Predominant colonization of Malesian mountains by Australian tree lineages

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Abstract

Aim: Massive biota mixing due to plate-tectonic movement has shaped the biogeography of Malesia and during the colonization process, Asian plant lineages have presumably been more successful than their Australian counterparts. We aim to gain a deeper understanding of this colonization asymmetry and its underlying mechanisms by analysing how species richness and abundance of Asian versus Australian tree lineages in three Malesian subregions change along environmental gradients. We hypothesize that differing environmental histories of Asia and Australia, and their relation to habitats in Malesia, have been important factors driving assembly patterns of the Malesian flora.

Location: Malesia, particularly Sundaland, the Philippines and Wallacea.

Taxon: Seed plants (trees).

Methods: We compiled plot-level data of environmental variables and tree abundances from three Malesian subregions. For each species, we inferred its geographical ancestry (Asian or Australian) based on published phylogenetic studies and the fossil record. We used proportions of Australian versus Asian species and individuals per plot to test how they are related to environmental parameters and geographical position using logistic regression models.

Results: Proportionally more Australian (and fewer Asian) tree species and individuals occurred (a) at higher elevations, (b) on sites over ultramafic parent material and (c) closer to their source region Australia with a significant increase of Australian elements east of Wallace's line. The trend was stronger for individuals than for species.

Main conclusions: Long-term environmental similarities between source and sink habitats have shaped the assembly of the Malesian flora: Tree lineages from tropical Southeast Asia predominantly colonized the Malesian lowlands and rich soils, whereas trees from montane refuges in Australia were more successful in the newly emerging Malesian mountains and on poorer soils. The biogeographical patterns caused by the Malesian Floristic Interchange point to the importance of phylogenetic biome conservatism in biotic interchanges and resemble those resulting from the Great American Biotic Interchange in the Neotropics.

KEYWORDS
Australia, biogeography, biotic interchange, Malesian Floristic Interchange, rain forest, Sundaland, tropical mountains, Wallacea

1 | INTRODUCTION

The distribution of terrestrial life on earth is spatially structured into biogeographical regions with more or less homogeneous biota, separated by biogeographical boundaries (Cox, 2001; Holt et al., 2012; Wallace, 1876). Long-term geographical isolation has shaped the deepest boundaries between these regions (Ficetola, Mazel, & Thuiller, 2017) by limiting dispersal to and from other land masses, thus leading to the independent evolution of biotas (e.g. Madagascar, Australia) for millions of years. Rare but frequent long-distance dispersal events followed by successful establishment can lead to the exchange of organisms even between distant landmasses (Crisp et al., 2009). Events where landmasses approach each other due to sea-level changes and/or collision of moving tectonic plates are much less frequent than long-distance dispersal, but cause massive biotic exchange with profound impacts on biotas (Antonelli et al., 2018; Vermeij, 1991). Examples include the collision of the Indian continent with Asia in the Eocene (Dutta et al., 2011) and the repeated presence of the Bering Land Bridge between East Asia and North America during the Tertiary (Donoghue & Smith, 2004; Graham, 2018). Much more recently, transport of organisms by humans has been accelerating the mixing of biotas, causing massive environmental and economic impacts (van Kleunen et al., 2015). Understanding the patterns of past biotic exchanges and their underlying processes can help predict future impacts due to anthropogenic biotic interchange (Heberling, Jo, Kozhevnikov, Lee, & Fridley, 2017; Vermeij, 1991).

One of the best-studied of such events was the successive establishment of the Central American land bridge (Graham, 2018; Montes et al., 2015), which culminated in the Great American Biotic Interchange (GABI; Marshall, Webb, Sepkoski, & Raup, 1982; Wallace, 1876), the extensive mixing of South American and North American faunas and floras in the late Miocene to Pliocene. Much of our current understanding of tropical biotic exchange resulting from geological processes stems from the intense study of the GABI. The past isolation of landmasses, availability of different habitats in space and time and taxon-specific traits like dispersal capability have all had an influence on the interchange patterns, but their relative importance is debated (Faurby & Svenning, 2016; Marshall et al., 1982; Simpson, 1980; Webb, 2006; Woodburne, 2010). Furthermore, it remains unclear whether the mechanisms of biota mixing unravelled from the study of the GABI are of universal validity throughout the tropics or largely specific to the Neotropical realm.

Another striking example of geology-driven biota mixing in the tropics is the Indo-Australian or Malay Archipelago. This part of the Palaeotropics encompasses the insular region between Asia and Australia (plus the Malay Peninsula) and is usually referred to as Malesia in botanical research (Raes & van Welzen, 2009; Zollinger, 1857). Similar to the situation in Central America before the closure of the Central American land bridge, the extensions of the Asian continent on the Sunda shelf and of the Australian continent on the Sahul shelf have never had a continuous land bridge connecting them. Today, they are separated by narrow stretches of ocean and the islands referred to as Wallacea (Hall, 2017). Already in the Palaeogene, when the continents were still far apart from each other, sporadic long-distance dispersal events by plants occurred from Asia to Australia and vice versa. However, biotic interchange, termed the Malesian Floristic Interchange (MFI) or Sahul-Sunda floristic exchange, sharply intensified in the Early Neogene when the two land masses approached each other and the Wallacean islands emerged in between (25–20 Ma; Crayn, Costion, & Harrington, 2014; Lohman et al., 2011; Richardson, Costion, & Muellner, 2012; Sniderman & Jordan, 2011). Hence, we can generally assume that the species present today in Malesia belong to lineages that were present on either of the two continents before the Neogene but did not occur on both of them.

Today, the fauna of Malesia shows strong geographical structure and includes numerous taxa endemic to the region's diverse subregions. This pattern, known since the initial observations by Wallace (1860) and consistent with relatively low dispersal capabilities in many animal taxa, indicates dispersal filters from Asia to Australia and vice versa. The situation in plants, however, is different: Malesia is a well-defined floristic region, albeit with internal geographical structuring (Culmsee & Leuschner, 2013; Raes & van Welzen, 2009). Among the most diverse floras worldwide (Slik et al., 2015), the Malesian flora is furthermore said to be derived predominantly from Asian ancestors, indicating asymmetric colonization (Richardson et al., 2012). This assumption is mainly based on the fast-growing number of phylogeographical studies of single plant taxa (e.g. Grudinski, Wanntorp, Pannell, & Muellner-Riehl, 2014; Thomas et al., 2012). These studies have proven highly valuable to understand the evolutionary history and biogeography of numerous Malesian taxa and have allowed insights into more general patterns of colonization (summarized in Crayn et al., 2014).

While the available information suggests that overall, Asian lineages dominate the Malesian flora today (e.g. Richardson et al., 2012), detailed phylogeographical studies are still lacking for many species-rich taxa and the mechanisms of the MFI are generally much less understood than those of its Neotropical counterpart GABI. In particular, the colonization patterns of plants since the onset of the MFI under different environmental conditions have not received sufficient attention (but see Yap et al., 2018). Earlier phytogeographical research has highlighted the abundance of Australian elements in certain Malesian forest habitats, such as in mountains and areas with ultramafic parent material (van Steenis, 1935b). Attempts to quantify the contribution of plant lineages of different origins to habitat-wise floral assembly have so far been limited to case studies using few forest plots available on a regional level (Aiba et al., 2015; Culmsee, Pitopang, Mangopo,

& Sabir, 2011). Furthermore, previous studies have predominantly used species richness as a measure for evolutionary success (e.g. Richardson et al., 2012) neglecting other quantitative measures like abundance or biomass due to lack of adequate data (but see Culmsee, Leuschner, Moser, & Pitopang, 2010). These other parameters are needed, however, to comprehensively describe patterns of colonization and dominance. Tropical mountain forests are well suited to study colonization processes in the distant geological past: They possess bioclimatic belts with a steep turnover in tree community composition (Körner, Paulsen, & Spehn, 2011), are typically less affected by anthropogenic disturbance and their tree floras are often more natural than those of remaining lowland forests (Cannon, Summers, Harting, & Kessler, 2007).

Malesia and the MFI can serve as an independent model to test hypotheses resulting from decades of research on the GABI. If long isolation leads to lower competitiveness (Faurby & Svenning, 2016; Simpson, 1980), then Australian lineages should be less successful in the colonization of Malesia than their Asian counterparts, regardless of habitat suitability (in the following we speak of Asia and Australia instead of Sunda shelf and Sahul shelf, as Asian species dispersed into Malesia not only from Sundaland, but also via the Philippines; see van Steenis, 1935a). Alternatively, if colonization depends strongly on the available habitat (Cody, Richardson, Rull, Ellis, & Pennington, 2010; Woodburne, 2010), colonization asymmetry will vary between habitats and relate to the environmental history of the source and sink regions. Trees with ancestors in continental Southeast Asia and Sundaland, where rainforest has been present since at least the mid-Eocene (Hall, 2013; Morley, 2012), may possess adaptations to hotter and moister climates than taxa from clades that originated on the Australian continent. The latter underwent strong aridification in the Neogene after its separation from Antarctica when mesic biomes remained confined to mountain areas along the eastern coast of Australia and in parts of New Guinea (Byrne et al., 2011; Kooyman et al., 2014; Quarles van Ufford & Cloos, 2005; Sniderman & Jordan, 2011). Furthermore, the large extent of nutrient-poor soils on the Australian continent could have favoured plant lineages adapted to these soils (Hill, 2004; van Steenis, 1979).

Dispersal filters such as stretches of ocean between suitable terrestrial habitats limit biotic exchange (Bacon et al., 2015; Graham, 2018; Woodburne, 2010). However, plants have comparatively high dispersal capabilities, so that the filter function of ocean barriers may be less-important to them than to many animal taxa, as exemplified by the relative commonness of long-distance dispersal in plants (Bacon et al., 2015; Donoghue & Smith, 2004; Sanmartín, Ronquist, & Cunningham, 2004). During the MFI, newly emerging islands in Wallacea likely facilitated stepping-stone dispersal, so that the occurrence of plant lineages in Malesia may be only weakly dependent on distance from their host region, that is, the land masses of Asia and Australia, whereas suitable habitat may play a larger role.

In this study, we attempt to close the knowledge gap about colonization asymmetry in the MFI. More specifically, we try to quantify the proportion of tree species and individuals with Asian versus Australian ancestry in Malesian forests by adopting a mixed approach. First, we compiled plot-level data of trees from the three major Malesian subregions and biodiversity hotspots Sundaland, the Philippines and Wallacea, to establish a dataset with >15,800 tree individuals of c. 1,640 species from a wide phylogenetic range (c. 35% of all seed plant families containing trees). The dataset further contains information on species abundances and environmental variables for each plot. Second, we inferred the geographical ancestry (Asian or Australian) for each species by building on the wealth of phylogenetic information that has become available in the last three decades supplemented by relevant fossil records. This allows us to quantify for the first time the contribution of Asian versus Australian lineages to community composition in Malesian forests under different environmental conditions and to test the following hypotheses regarding biotic interchanges:

1. The contribution of Asian versus Australian tree lineages to community composition in Malesian forests differs between habitats.
2. Asian lineages are more dominant in lowland rain forests, whereas Australian lineages strive better in mountains and on nutrient-poor soils.
3. Habitat, rather than distance to the source region (Asia or Australia), drives the differences in community composition.

2 | MATERIALS AND METHODS

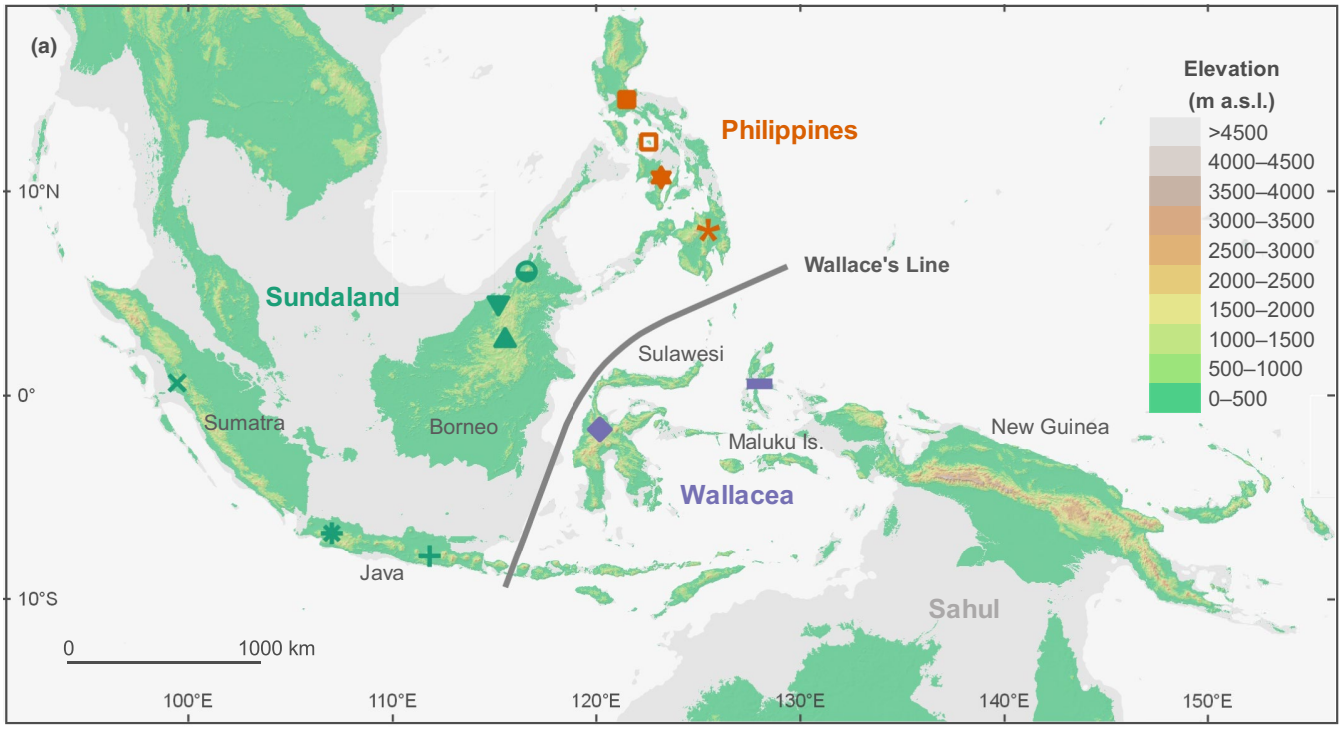
2.1 | Malesian tree inventory data

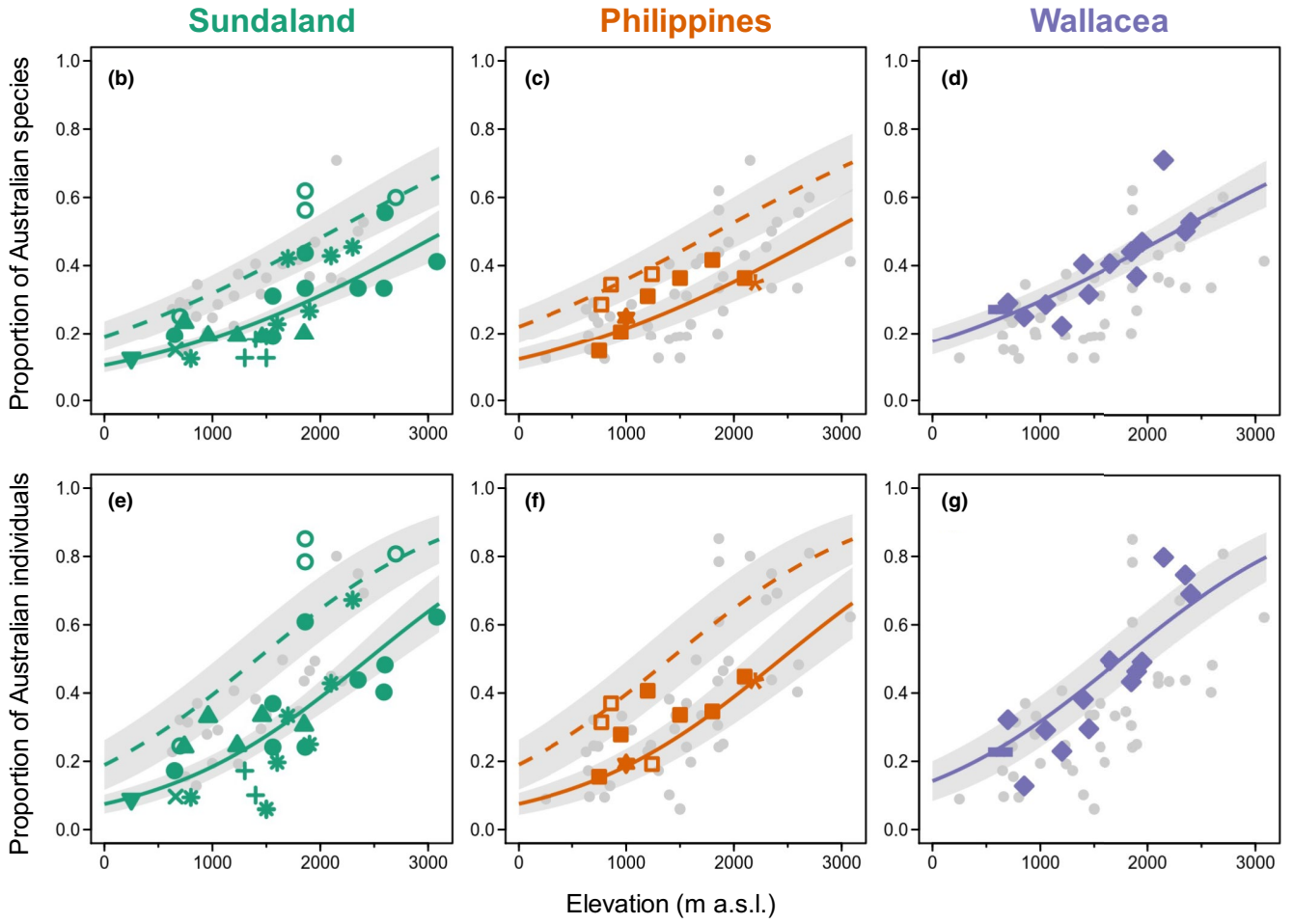
We compiled a dataset of 55 tree inventory plots (all trees with diameter at breast height ≥10 cm) in old-growth forests (Figure 1), including 42 plots from published studies and 13 plots from our own work on Sulawesi, Indonesia (Table 1, Appendix 1). We classified the western and central parts of Malesia covered by our dataset into three phytogeographical areas, Sundaland, the Philippines and Wallacea, following the nomenclature of biodiversity hotspots of Myers, Mittermeier, Mittermeier, da Fonseca, and Kent (2000). Sundaland was represented by plots in Sumatra (n = 1), Borneo (n = 19) and Java (n = 10) spanning an elevational gradient from 250–3080 m a.s.l., the Philippines by plots on four islands (n = 11) from 750–2,200 m, and Wallacea by two areas, each one in the subregions Sulawesi (n = 13) and Maluku Islands (n = 1) from 630–2,400 m. Plot size varied within and among the studies (0.1–1.0 ha; Table 1, data sources in Appendix 1).

We selected only such studies that provided species identification to genus or species level with a high taxonomic standard, including the deposition of voucher specimens in herbaria and a full list of the recorded species per plot with their abundances, that is, the per-plot number of individuals per species.

2.2 | Assignment of biogeographical origin

We checked the inventory lists of the original studies and excluded tree ferns (208 individuals from 10 species) because we were not





sure whether all original studies had included them in their inventories; we also removed non-tree taxa (24 individuals from four species). Then we combined the lists of species and their abundances from all plots (16,131 individuals in total) and standardized the plant names with the help of taxonomic literature and web tools (IPNI, 2019; Soepadmo, Wong, Saw, Chung, & Kiew, 1995; van Steenis et

FIGURE 1 Diversity and abundance of Australian tree lineages in Malesian forest plots are higher at higher elevations, on ultramafic soils, and east of Wallace's line. Shown are the locations of 55 old-growth forest plots in 12 Malesian areas in the phytoregions Sundaland, the Philippines and Wallacea (a) and the per-plot proportions of tree species (b–d) and individuals (e–g) with Australian ancestry in relation to elevation, parent material and phytoregion. Regression lines show significant results based on multiple logistic regression models (model 1 for b–d, model 3 for e–g; see Table 2 for details). Symbols represent the 12 studied Malesian areas (a), each with 1–16 forest plots (b–g). Plots on non-ultramafic parent material are represented by closed symbols and continuous regression lines and plots on ultramafic parent material by open symbols and dashed regression lines (the Mt Kinabalu site in N Borneo contains plots with both types of parent material). Grey dots show plots of other phytoregions for comparison and light grey shadows indicate the 95% CI of the regression models. Map in WGS1984, Mercator projection, created with QGIS 3.4.9 (www.qgis.org) showing shelf areas in grey (200-m bathymetric contours from Natural Earth: www.naturalearthdata.com)

TABLE 1 Dataset of 55 tree inventory plots from 12 Malesian areas in the three phytogeographical regions of Sundaland, the Philippines and Wallacea with physiographical information (geographical coordinates, distance from the Sahul Shelf and elevation), geological substrate, plot sizes and numbers and original sources

Location	Sahul dist. (km)	Data source	Parent material	Elevation (m a.s.l.)	Plot size (ha)	Plots (*n*)
Sundaland						
Batang Gadis NP, N Sumatra (N 0.6°, E 99.5°)	3,050	Kartawinata et al. (2004)	Sedimentary	660	1.00	1
Batu Apoi NP, Brunei, Borneo (N 4.5°, E 115.2°)	1,760	Poulsen et al. (1996)	Sedimentary	250	1.00	1
Apo Kayan FR, E Kalimantan, Borneo (N 2.7°, E 115.5°)	1,640	Bratawinata (1986)	Sedimentary	740–1,850	0.80	5
Mt Kinabalu, Sabah, Borneo (N 6.1°, E 116.6°)	1,690	Aiba et al. (2002)	Sedimentary	650–3,080	0.20–1.00	5
			Ultramafic	700–2,700	0.20–1.00	3
		Takyu et al. (2002)	Sedimentary	1,560–1,860	0.10	2
			Ultramafic	1,860	0.10	1
		Kitayama (1995)	Sedimentary	2,350–2,600	0.14–0.17	2
Mt. Wilis, E Java (S 7.9°, E 111.8°)	1,410	Purwaningsih et al. (2017)	Volcanic	1,300–1,500	0.25	3
Mt Gede-Pangrango NP, W Java (S 6.8°, E 107.0°)	1,960	Helmi et al. (2009)	Volcanic	800	1.00	1
		Meijer (1959)	Volcanic	1,500	1.00	1
		Yamada (1975)	Volcanic	1,600	1.00	1
		Yamada (1977)	Volcanic	1,700–2,300	0.10	4
Philippines						
Mt Banahao, Luzon (N 14.5°, E 121.5°)	1,980	Aragones (1991)	Volcanic	750–2,100	0.42	6
Mt Giting-Giting, Sibuyan (N 12.4°, E 122.6°)	1,730	Proctor et al. (1998)	Ultramafic	770–1,240	0.25	3
Mt Mandalagan, Negros (N 10.7°, E 123.2°)	1,530	Hamann et al. (1999)	Volcanic	1,000	1.00	1
Mt Kinasalapi, Mindanao (N 8.0°, E 125.5°)	1,140	Pipoly & Madulid (1998)	Volcanic	2,200	1.00	1
Wallacea						
Lore Lindu NP, Central Sulawesi (S 1.5°, E 120.2°)	1,040	Brambach et al. (2017)	Acid plutonic	700–2,400	0.24	13
Tapayo, Halmahera, Maluku Islands (N 0.8°, E 128.0°)	330	Whitmore et al. (1987)	Sedimentary	630	0.50	1

Note: All data sources are listed in Appendix 1.
Abbreviations: FR, Forest Reserve; NP, National Park; Sahul dist., Distance from Sahul Shelf.

al., 1948–2019; The Plant List, 2019; WCSP, 2019). We pruned the original names to species level and manually corrected spelling errors. We removed cf.- and aff.-qualifiers but retained the following epithets unless the purportedly similar species did not occur naturally in the respective biogeographical region (in that case we used 'sp.'). We treated morphospecies as different species when they were clearly distinguished as such in the original sources (e.g. as sp.1, sp.2, etc., see Appendix 1). In addition, we assumed that morphospecies in the same genus but from different original studies represented different species. The total number of species in our dataset (see Appendix S2) is thus probably inflated and should be seen as an estimate. However, since our main results are based on calculated percentages on a plot basis, this possible bias does not affect our analyses. Assuming that each species or its ancestor was present in only one continent—Asia or Australia—before the intensification of the MFI in the early Neogene (see Crayn et al., 2014), we separated the species into two groups: those with Asian ancestry (hereafter: Asian species) versus those with Australian origin (Australian species). To compile this information, we carried out an exhaustive literature search for phylogeographical studies (e.g. phylogenetic studies including direct reconstruction of ancestral areas), other dated and undated phylogenetic studies, relevant fossil data and taxonomic literature, using in total c. 300 published sources (see references in Appendix S1 in the Supplementary Information). As most phylogenetic studies use incomplete taxon sampling, many of our species were not directly represented in the references. We therefore assumed that all species of a genus shared the same biogeographical ancestry (Asian or Australian) unless the results of studies indicated otherwise. In the latter cases (e.g. *Macaranga*, *Ficus*), we attempted to match our species to infrageneric clades, mostly based on systematic studies and morphological characters. Likewise, we attempted to assign species of polyphyletic genera to the correct clades in the phylogenetic studies. When phylogeographical studies were not available, we resorted to other phylogenetic sources. These often did not explicitly contain information on biogeographical history, but with the distribution of sampled species taken from floristic accounts and databases, we could usually infer the geographical ancestry nonetheless, especially when the phylogenies were dated. Tree individuals which could not be assigned to one of these ancestry groups were excluded from further analyses (n = 245). The majority of those ambiguous individuals belonged to morphospecies which did not have sufficient taxonomic resolution to infer their geographical origin, but we also included alien species here (11 individuals in four species), as they do not convey any meaningful biogeographical information in the context or our study. The percentages of individuals with ambiguous ancestry per plot ranged from 0% to 11.8% (median 0%, mean 1.3%). Plots on ultramafic parent material contained a significantly higher proportion of individuals with unknown geographical origin than plots on other substrates (logistic regression model with quasi-binomial error structure: D^2 = 0.16, p < .0001), possibly highlighting the high number of insufficiently known endemics expected to occur there; the other variables did not have any significant effects (Appendix S1: Figure S1.1). Most of the trees that lack information on their geographical origin do so because of insufficient taxonomic resolution (i.e. completely unidentified or identified to family level only). We consider it unlikely that species with Australian ancestry are generally more difficult to identify than those from Asia or vice versa. Therefore, despite the unequal representation of trees with ambiguous geographical origin per plot, deleting these records prior to the main analyses is unlikely to add a significant bias to our results.

The final dataset contained 15,886 individuals assigned to 1,636 species and morphospecies. We were able to classify the majority of individuals (73%) using phylogeographical studies or a combination of these with information on fossils. For most of the rest, we found dated (17%) or undated phylogenies (9%) without direct inference of geographical origin and combined these with information on the fossil record and/or distribution data to infer the respective ancestral regions from other sources. Only for the remaining 2% of individuals, we used fossil record and/or distribution data alone. Details regarding the methods, references and specifications of species' assignation to their geographical ancestry are summarized in Appendix S1. A list of all species with their respective inferred origin is given in Appendix S2. Finally, we calculated the proportion of Australian species per plot and the proportion of individuals belonging to these species (Australian individuals) per plot. The Australian and Asian proportions per plot amount to 100%.

2.3 | Data analysis

To link the occurrence of Australian versus Asian lineages in Malesia to geography and environmental factors, we employed the per-plot proportions of Australian species and individuals as response variables in multiple logistic regression models (LRM) using the *glm* function in RStudio (RStudio Team, 2016, based on R, R Core Team, 2017). To select suitable explanatory variables, we extracted plot elevation, geological parent material and (approximate) geographical position from the original studies (Table 1). We followed two strategies to account for the geographical position: first, we calculated the distance of each plot to the nearest border of the Sahul Shelf (displayed in Figure 1a) using the ruler tool in QGIS (QGIS Development Team, 2018). Second, we used the three phytogeographical regions Sundaland, the Philippines and Wallacea to define the plots' regional affiliations.

We then tested for correlation between the environmental parameters elevation, parent material (geology), distance from the Sahul Shelf (Sahul distance) and phytogeographical region (phytoregion). Geology was strongly correlated with phytoregion (χ^2 test: χ^2 = 62.5, p < .00001) and with Sahul distance (Kruskal–Wallis test: χ^2 = 31.5, p < .00001). We explain this by the uneven distribution of different parent materials between the studied locations, e.g. volcanic material only occurred on Java, whereas acid plutonic rock was exclusively found on Sulawesi (Table 1). We therefore simplified the geology classification to have only two categories: ultramafic versus non-ultramafic. The resulting binary geology showed no significant correlation with phytoregion (χ^2 test: χ^2 = 4.1, p = .13) or Sahul distance (Kruskal–Wallis test: χ^2 = 1.3, p = .25) and was used for all further analyses. Phytoregion and Sahul distance were also highly correlated

(Kruskal–Wallis test: χ^2 = 34.5, p < .00001), whereas elevation was independent of all other parameters. We decided to start the model selection with two separate models for each response variable, one employing elevation, geology and phytoregion (hereafter referred to as phytoregion model), the other using elevation, geology and Sahul distance (hereafter: distance model) as explanatory variables. Hence, we computed four different models: A phytoregion model for Australian species (model 1), a distance model for Australian species (model 2), a phytoregion model for Australian individuals (model 3) and a distance model for Australian individuals (model 4).

For the proportion of Australian species, we started with a full model with binomial error structure and logit link function containing all three explanatory variables and their interaction effects. Using the *dredge* function of the *MuMIn* package (Bartoń, 2018), we then computed all possible nested models and sorted them according to their Bayesian information criterion (BIC) to select the best model. BIC penalizes model complexity more strongly than the commonly used Akaike information criterion (AIC). We chose BIC because we wanted to avoid multiple interaction effects, which would be difficult to interpret ecologically. We discarded all models with ΔBIC ≥ 2 compared to the model with the lowest BIC. Among the remaining ones, we successively discarded those with the most parameters. For both the phytoregion model and the distance model, the best model included all three independent variables but no interaction effects. For the proportion of Australian individuals, we employed a similar model selection process, but due to large data overdispersion, here we used the LRM with a quasi-binomial error structure and performed the model selection based on quasi-BIC (qBIC). The resulting best models also included all three independent variables without interaction effects. To test whether spatial autocorrelation between plots played a role beyond the tested parameters, we calculated Moran's *I* for the residuals of all four best models (models 1–4, see Table 2) using the *lm.morantest* function of the *spdep* package (Bivand et al., 2019). All models contained non-spatially correlated residuals (Moran's *I* = 0.45–0.60, p = .27–.33).

3 | RESULTS

3.1 | Biogeographical patterns in the Malesian subregions

In the 12 analysed Malesian areas taken together, Asian lineages strongly dominated, representing 76% of all investigated tree species and 67% of all tree individuals. The dominance decreased from Sundaland in the west (80% of species, 69% of individuals) over the Philippines (75%, 68%) to Wallacea in the east (64%, 53%). Asian lineages were more dominant on sites over non-ultramafic (78% of species, 69% of individuals) than on those with ultramafic parent material (65%, 54%).

TABLE 2 Elevation, geology and geographical position determine the proportion of tree species and individuals with Australian ancestry in Malesian forest plots

	Proportion of							
	Australian species plot^{-1}				Australian individuals plot^{-1}			
	Model 1 (Phytoregion)		Model 2 (Sahul distance)		Model 3 (Phytoregion)		Model 4 (Sahul distance)	
BIC/qBIC	285.28		298.48		103.89		105.63	
D^2_{adj}	0.71***		0.66***		0.69***		0.67***	
Variable	D^2	**Coefficient**	D^2	**Coefficient**	D^2	**Coefficient**	D^2	**Coefficient**
Elevation	0.42	0.0007***	0.47	0.0007***	0.51	0.0010***	0.51	0.0009***
Geology (ultramafic)	0.12	0.7133***	0.12	0.6625***	0.12	1.0595***	0.12	0.9942***
Sahul distance	—	—	0.08	−0.0004***	—	—	0.06	−0.0006***
Phytoregion	0.16		—	—	0.06		—	—
Sundaland		−0.1814				−0.0065		
Philippines		0				0		
Wallacea		0.4246**				0.7102**		

Note: Results of multiple logistic regression models (LRM) of the per-plot (n = 55) proportion of Australian tree species and individuals in 12 Malesian areas. Models include the independent environmental factors elevation, geology (ultramafic vs. non-ultramafic) and geographical location. Geographical location (see Table 1) was included as the position in one of three phytoregions (Sundaland, the Philippines and Wallacea; models 1 and 3) or the distance to the Sahul shelf (models 2 and 4). Error structure is binomial in models 1 and 2 and quasi-binomial due to overdispersion in models 3 and 4.

Abbreviations: BIC, Bayesian information criterion (models 1 and 2); D^2 = proportion of deviance explained. D^2_{adj} = adjusted D^2 (Guisan & Zimmermann, 2000); qBIC = quasi-BIC based on a quasi-binomial error structure (models 3 and 4); Sahul distance = Distance from Sahul Shelf.

**p < .01,

***p < .001.

Correspondingly, the mean per-plot percentage of Australian tree species was higher in Wallacea (39%, n = 14) than in the Philippines (31%, n = 11) and Sundaland (30%, n = 30). Similarly, Wallacean plots had the highest mean number of Australian individuals (43%) compared to the Philippines (32%) and Sundaland (34%). Plots on ultramafic parent material on average had more Australian species (43%, n = 7) and individuals (51%) than non-ultramafic plots (31% of species and 34% of individuals, n = 48).

3.2 | Environmental conditions driving biogeographical patterns

Multiple logistic regression models (LRM) uncovered significant differences in the proportion of both Australian species and Australian individuals between the 55 plots from 12 Malesian areas in relation to all investigated environmental variables (Table 2). For the proportion of Australian species per plot, the model with elevation, parent material and phytogeographical region as independent variables (model 1, D^2_{adj} = 0.71***) performed better than the one using elevation, parent material and distance from the Sahul shelf (model 2, D^2_{adj} = 0.66***). In both models, plots at higher elevation had higher percentages of Australian species and this factor accounted for about half of the deviance. Australian species were also better represented on plots with ultramafic parent material compared to non-ultramafic localities but the explanatory power of the parent material was much lower (D^2 = 0.12***) compared to elevation. In the phytoregion model (model 1), phytoregion was the second most explanatory variable (D^2_{adj} = 0.16). Here, Wallacean plots had significantly more Australian species than those from the Philippines and Sundaland. In the distance model (model 2), the explanatory power of distance to the Sahul shelf (D^2_{adj} = 0.08**) was lower than that of parent material (Table 2, Figure 1b–d).

For the proportion of Australian tree individuals in a plot, differences between phytoregion model (model 3, D^2_{adj} = 0.69***) and the distance model (model 4, D^2_{adj} = 0.67***) were negligible. Again, elevation explained more than half of the deviance (D^2_{adj} = 0.54***) with an increasing proportion of trees from Australian lineages towards higher elevations. The patterns of higher proportions of Australian trees in ultramafic than in non-ultramafic parent materials remained constant (models 3 and 4, D^2_{adj} = 0.12***). Phytoregion (model 3) and the distance to the Sahul shelf (model 4) both explained a similar proportion of the respective model deviance, and in model 3, there was again a significant difference between the Wallacean plots with more and those from Sundaland and the Philippines with fewer Australian tree individuals (Table 2, Figure 1e–g).

The patterns retrieved for the elevational distribution of Australian species and tree individuals were remarkably similar but the increase with elevation was stronger for individuals than species. Likewise, the increase of Australian individuals from non-ultramafic to ultramafic plots was larger than that of Australian species (Table 2, Figure 1b–g).

On non-ultramafic parent materials, our models predicted c. 35%–55% Australian species at an elevation of 2,500 m in the three phytoregions (Figure 1b–d), whereas the proportion of Australian

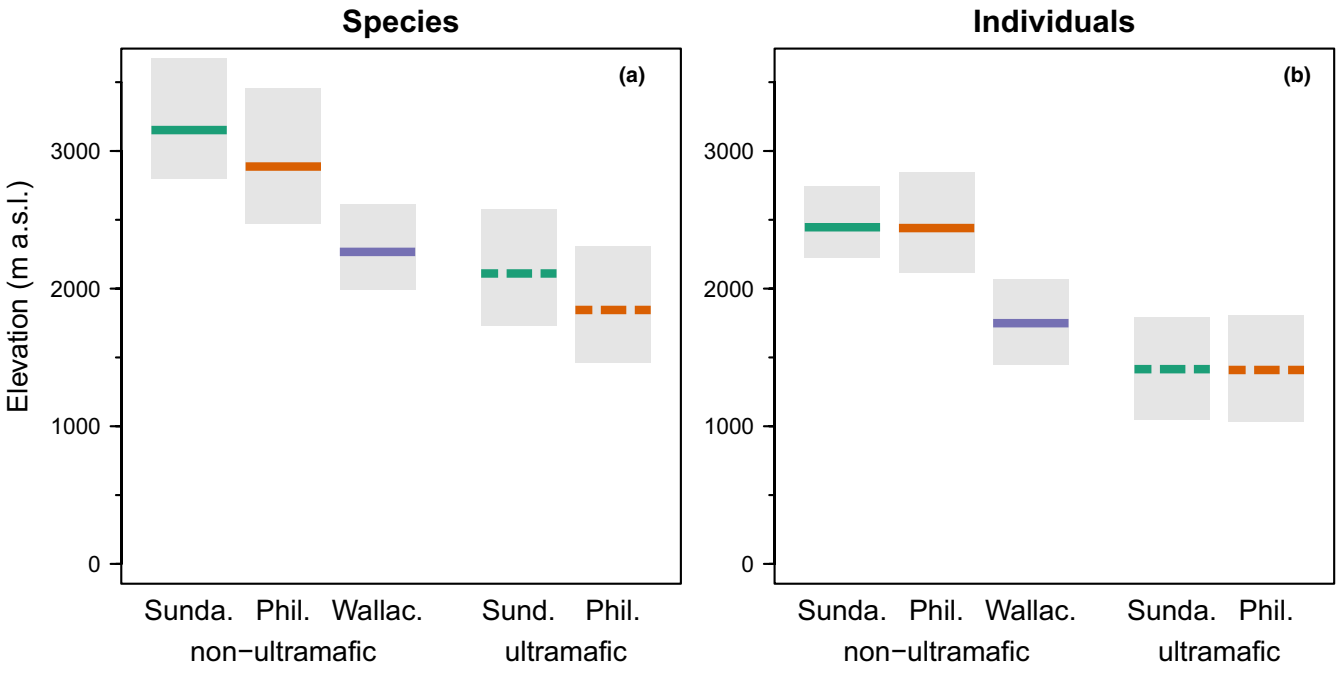


FIGURE 2 Elevational tipping points with a 50%-share of Australian tree species showing the transition from Asian-dominated forests below the coloured lines to Australian-dominated forests above them. Data show the 50%-tipping points for species (a) and individuals (b) in forests of the Malesian phytoregions Sundaland (Sunda.), the Philippines (Phil.) and Wallacea (Wallac.) on non-ultramafic (solid lines) and ultramafic (dashed lines) parent materials. Values from multiple logistic regression models with elevation, parent material and phytoregion as independent variables (model 1 for a, model 3 for b; see Table 2 for details), based on 55 old-growth forest plots in 12 Malesian areas. Grey boxes correspond to the elevational range of the 95%-CI at a 50%-proportion of Australian trees/individuals

individuals at the same elevation varied between 50% and 75% (Figure 1e–g).

3.3 | Elevational tipping points

On non-ultramafic substrates, the elevational tipping point with a 50%-share of Australian species was reached at 2,270 m in Wallacea (Figure 2a), but at 2,890 m and 3,150 m in the Philippines and Sundaland, respectively, according to model 1. On ultramafic soils, the 50%-tipping points occurred at much lower elevations: 1,850 m in the Philippines and 2,110 m in Sundaland (Figure 2a).

In all areas, elevational tipping points with half of the individuals having Australian ancestry according to model 3 were much lower than those based on species, but patterns between phytoregions and parent materials were similar: the 50%-individuals tipping point was reached at the lowest elevations on ultramafics (1,410 m in the Philippines, 1,420 in Sundaland) followed by non-ultramafic areas in Wallacea (1,750 m), the Philippines (2,440 m) and Sundaland (2,450 m, Figure 2b).

3.4 | Dominant Australian taxa in Malesian forests

Four taxa largely drove the proportion of Australian individuals: Myrtaceae, southern hemisphere conifers (Podocarpaceae and Araucariaceae), *Polyosma* (Escalloniaceae) and *Elaeocarpus* (Elaeocarpaceae) accounted for 70% of all recorded Australian individuals. They provided at least half of the individuals in 44 (80%) and two-thirds or more in 28 (51%) of all 55 plots. While Myrtaceae were present in most plots (although less so in Java), conifers attained high dominances at higher elevations and over ultramafic parent material. *Elaeocarpus*, on the other hand, was absent from ultramafic soils and rather poorly represented in the Philippines. Compared to the other subregions, Java stood out in the low percentages of Myrtaceae and conifers at higher elevations; instead *Polyosma* and *Elaeocarpus* were more dominant there (Figure 3).

4 | DISCUSSION

4.1 | Contrasting biogeographical patterns in Malesia

Our results demonstrate that in Malesia, proportionally more Australian (and conversely fewer Asian) tree species and individuals occur (a) at higher elevations, (b) in forests over ultramafic parent material and (c) closer to their source region Australia with a significant increase east of Wallace's line, that is the boundary between Sundaland plus the Philippines and Wallacea. The trend is stronger for tree individuals than for species. Our estimates for the overall contribution of Asian species to the floras of Malesian subregions are generally lower than in previous studies, especially for Wallacea. This is unsurprising, since we focused on tree inventory plots along environmental gradients, giving more weight to azonal and less-diverse habitats like montane forests and those over ultramafic soils and less to lowland rain forest, the most widespread and diverse

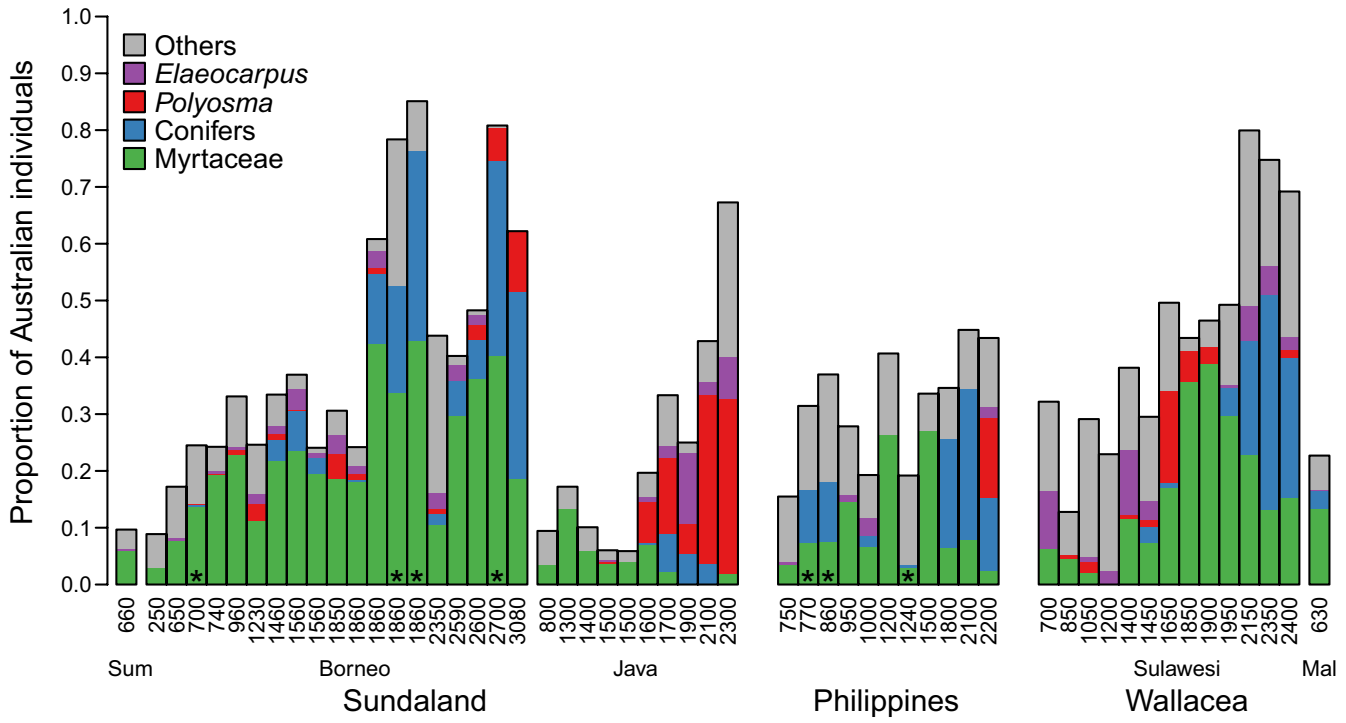


FIGURE 3 Four taxa drive the proportion of tree individuals with Australian ancestry in most of 55 Malesian forest plots. Plots are grouped by their geographical location and sorted by ascending elevation (m.a.s.l). Conifers include the Gondwanan families Podocarpaceae and Araucariaceae but not the Laurasian Taxaceae. Plots with ultramafic parent material are marked with an asterisk. Proportions of Australian and Asian trees per plot amount to 1. Sum = Sumatra, Mal = Maluku Islands

habitat. In contrast, previous results were based on flora treatments and checklists (Richardson et al., 2012), which rely on collected herbarium specimens. Especially in the underexplored areas of Wallacea, there may be a strong collection bias towards more accessible lowland sites (Cannon et al., 2007).

Due to lack of available data, we did not include plots from New Guinea in our study. However, previous studies have suggested that even in New Guinea and tropical northern Australia, Asian lineages contribute more to regional floras than their Australian counterparts (Richardson et al., 2012; Yap et al., 2018). Thus, the available information indicates that Asian lineages generally dominate the Malesian flora today. However, the picture changes, if one considers different habitats in a similar way as has been done in tropical northern Australia (Yap et al., 2018). Our results indicate that above a certain elevational tipping point, Australian lineages dominate Malesian forests. The exact elevation of the tipping point varied strongly (c. 1,700 m elevation distance); it occurred at lower elevations over ultramafic bedrock than over other parent materials. In Wallacea, east of Wallace's line, where only non-ultramafic sites were included, the proportions of Australian species and individuals per plot were comparable to those on ultramafic soils in the other two regions. The dominance of plants with Australian origin in montane areas and on poor soils in Malesia has long been acknowledged (Aiba et al., 2015; Culmsee & Leuschner, 2013; Culmsee et al., 2011; Morley, 1998; van Steenis, 1935b; Wallace, 1869) but here, we show for the first time that this pattern is consistent throughout western and central Malesia based on a large dataset of 55 plots including all major woody seed plant clades.

4.2 | Plate tectonics, climate and the Malesian Floristic Interchange

We used a dataset of tree inventory plots in three Malesian biodiversity hotspots in combination with the phylogeographical affinities of the present tree species from an extensive literature review to demonstrate that environmental conditions and—to a lesser degree—geographical position must have had a strong effect on biota mixing during the MFI. We explain patterns of contrasting colonization trajectories of Asian and Australian tree lineages in the context of the complex geological and climatic history of Malesia and its adjacent regions Southeast Asia and Australia: Southeast Asia including Sundaland was assembled by the accretion of different continental fragments to the Asian plate in the Late Triassic and Cretaceous. Today, Sundaland consists of the Malay Peninsula and the islands Sumatra, Borneo and Java, but only shallow seas over the continental Sunda Shelf separate these land areas. They formed a more or less continuous land mass connected to Eurasia during most of the Cenozoic and throughout that period, Sundaland remained near the equator (Hall, 2013, 2017). Despite intervals of strong climatic oscillations, since the middle Eocene tropical rain forests have covered parts of Sundaland, especially in what today is the island of Borneo. Hence, since the large-scale onset of the MFI c. 23 Ma, there has been a large source population of plants adapted to tropical rainforest habitats in Sundaland (Hall, 2013; Morley, 2012). On the other hand, Australia, together with the southern portion of present-day New Guinea, separated from Antarctica in the late Eocene to early Oligocene (40–33 Ma; Lawver, Gahagan, & Dalziel, 2013) and started rafting north towards Asia. It also supported extensive tropical rain forest until the end of the separation at the Eocene-Oligocene-boundary when temperatures dropped, leading to a shift to temperate rain forests and widespread extinction of warm-adapted lineages. After c. 10 My of isolation, the Australian plate started to collide with the Southeast Asian plate and island arcs from several Pacific plates around the Oligocene-Miocene boundary (c. 25–20 Ma). The exact geological processes involved were complex both in time and space but, together, caused extensive uplifting at the northern margin of the Sahul Shelf in what is today New Guinea, and shaped the young islands comprising Wallacea (Sulawesi, Maluku Islands, Lesser Sunda Islands) including some of the largest areas of ultramafic bedrock worldwide (Galey, van der Ent, Iqbal, & Rajakaruna, 2017; Hall, 2013, 2017). At the same time, temperatures rose again and moist tropical habitats expanded in Australia until the mid-Miocene climatic optimum. Global cooling since the mid-Miocene (c. 14 Ma) was offset in Australia by the continued rafting towards the equator, at least in the north but intensive aridification occurred, leading to an overall contraction of mesic biomes, which remained mostly in montane refugial areas along the eastern coast of the continent and in eastern New Guinea, where mountains had been present since the early Oligocene (Bryant & Krosch, 2016; Byrne et al., 2011; Macphail, 2007; Martin, 2006; Quarles van Ufford & Cloos, 2005).

The emergence of Wallacea greatly reduced the distances of open sea between Asia and Australia and coincided with the dramatic intensification of the MFI (Crayn et al., 2014) likely due to the facilitation of stepping-stone dispersal between the continents (Richardson et al., 2012; van Welzen, Parnell, & Slik, 2011). The dominance of plants with Asian ancestors observed today in most of Malesia derives from the high colonization success of these lineages in the newly emerging nutrient-rich and moist tropical habitats. The colonization success can be explained by the large and diverse source populations adapted to similar climatic and edaphic conditions that existed in Sundaland. Conversely, the Australian wet tropics have been a sink for Southeast Asian rain forest plants migrating through Malesia (Sniderman & Jordan, 2011; Yap et al., 2018). Because the Australian flora had suffered widespread extinction of typical tropical rain forest taxa before the intensification of the MFI, source populations for the colonization of Malesian lowlands were probably small, when rain forest habitats expanded in the early Miocene (Byrne et al., 2011; Richardson et al., 2012; Sniderman & Jordan, 2011).

Nevertheless, our results show that some Australian lineages were highly successful in colonizing Malesia from the east, especially in azonal habitats with poor soils including ultramafics and on mountains. Taxa adapted to poor soils and/or colder upland habitats were

widely present in Australia at the onset of the MFI (Bryant & Krosch, 2016; Hill, 2004; van Steenis, 1979) and were presumably able to colonize the newly emerging extensive ultramafic areas in New Guinea and Wallacea in due time (Galey et al., 2017). Malesian mountain building has mainly occurred in the last 10 My but the highest ranges like the New Guinea Highlands, Central Sulawesi Mountains, Barisan Mountains in Sumatra, or Mt. Kinabalu in Borneo were only formed in the Plio-Pleistocene (Baldwin, Fitzgerald, & Webb, 2012; Hall, 2013; Merckx et al., 2015; Nugraha & Hall, 2017). As montane habitats in Malesia were formed and aridification intensified in Australia, species spread from refugia along the eastern Australian coast and in already existing mountain ranges of New Guinea to the large emerging mountains in New Guinea, Wallacea and Sundaland (Hill, 2004; Kooyman et al., 2014; Morley, 1998; Sniderman & Jordan, 2011). This scenario is consistent with the retrieved recent timing of disjunction between Australian and Malesian montane taxa for most lineages we assessed, including the dominant Australian lineages in Malesia today (see below and Appendix S1). The late influx of Australian plants to Malesian mountains had a profound impact, essentially providing today's dominant components of the tree assemblages there (Figure 1e–g, 3).

4.3 | Dominant Australian taxa differ in their history and ecology

Four taxa mostly drove the dominance of Australian elements in montane and ultramafic areas: Myrtaceae, southern-hemisphere conifers (Podocarpaceae and Araucariaceae), *Polyosma* (Escalloniaceae) and *Elaeocarpus* (Elaeocarpaceae). The myrtle genus *Syzygium* started to diversify in the mid-Oligocene in eastern Australia, presumably in the prevalent temperate rain forests there, and dispersed into Malesia at least four times between 12.4 and 6.8 Ma. The genus underwent a spectacular radiation, possibly linked to the key innovation of fleshy fruits (Biffin et al., 2010). Today it is the most species-rich genus of Malesian trees, occurring in a variety of moist forest ecosystems, especially dominant on nutrient-poor soils and in montane areas (Aiba et al., 2015). *Elaeocarpus* shows a similar spatial and temporal pattern of diversification (crown age c. 30 Ma, dispersal into Malesia c. 14 Ma; Crayn, Rossetto, & Maynard, 2006) and is widespread geographically and ecologically in Malesia. In contrast, southern conifers are old Gondwanan lineages that, however, mostly reached Wallacea and Sundaland only in the Plio-Pleistocene and remained largely confined to upland areas (Kooyman et al., 2014; Morley, 1998). Notably, conifers with Asian affinities (Pinaceae) were common in mountains of Borneo until the Miocene, but Podocarpaceae apparently replaced them afterwards (Muller, 1966). In upper montane forest throughout Malesia, podocarps are often extremely dominant, although not particularly species-rich (Aiba et al., 2015; Brambach, Leuschner, Tjoa, & Culmsee, 2017). An exception is Java with its seasonal climate, where far fewer of the particularly drought-sensitive southern conifers occur (van Welzen et al., 2011). Instead, *Polyosma* and *Elaeocarpus* as well as Asian lineages like Fagaceae and Ericales dominate Javanese montane forests (Figure 3).

4.4 | Habitat-suitability is more important than distance

We found evidence that Asian species predominantly colonized lowland habitats and medium to rich soils during the MFI, whereas Australian species were more successful in the colonization of montane areas and poorer (ultramafic) soils. This pattern across Malesia, one of the major tropical regions of the world, is remarkable given the region's large extension and archipelagic nature.

Geographical distance from the source regions (Asia and Australia) only had a minor influence on the colonization success compared to habitat. This influence was best explained using Malesian subregions as categorical variables, indicating a nonlinear relationship (Table 2).

Newly emerging tropical lowland habitats in Malesia were predominantly colonized by lineages from Sundaland, where similar ecological conditions prevailed and large source populations existed (Richardson et al., 2012; Zobel, 2016). The nature of habitats containing the lineages that came to colonize Malesian mountains and nutrient-poor soils, is more obscure because of the complex plate-tectonic and climatic history of Australia since the Oligocene that caused recurrent expansions and contractions of different forest types. Nevertheless, there are indications that moist habitats were mostly present in colder upland areas, a least since the middle Miocene (Bryant & Krosch, 2016; Byrne et al., 2011; Martin, 2006), providing the nearest source population of plants adapted to Malesian mountain habitats.

We therefore interpret the colonization pattern found here in the light of similar ecological conditions between source and sink areas, Sundaland as a source area for lowland Malesia on the one hand and Australia as a source area for montane Malesia on the other. This likely points to the importance of phylogenetic biome conservatism (Crisp et al., 2009; Crisp & Cook, 2012), that is the tendency of lineages to retain their ancestral ecology over long time spans and continental scales, in the assembly of the Malesian vegetation (Grudinski et al., 2014; Kooyman et al., 2014). Notably, Asian immigrants have also been relatively successful in the colonization of tropical lowland habitats in northern Australia but not in temperate habitats further south due to environmental filtering (Yap et al., 2018). However, speciation events including biome shifts between montane and lowland forest and vice versa must have occurred in numerous clades, as indicated by species-rich genera spanning wide environmental gradients today like *Syzygium*, *Lithocarpus* (Fagaceae), *Litsea* (Lauraceae), *Elaeocarpus* and *Symplocos* (Symplocaceae). Biome shifts between tropical lowland and montane forests have received relatively little attention, possibly due to the blurred boundaries and close spatial interconnectedness between the two (Antonelli et al., 2018; Donoghue & Edwards, 2014). Nevertheless, tropical mountain areas with their close proximity of widely differing habitats are known to be

cradles of diversity with strong species turnover along the elevational gradient, facilitating speciation and associated niche evolution (Merckx et al., 2015; Sanín et al., 2016). The dynamic history of Malesia since the onset of the MFI together with two ecologically and geographically different source regions may thus have contributed to the exceptionally high plant diversity in Malesia today (Slik et al., 2015). Malesian montane forests, while less species-rich than their lowland counterparts, today harbour many survivors of dramatic extinction events in Australia during the Tertiary (Kooyman et al., 2014) as well as elements of originally tropical Asian families. Their unique evolutionary history and associated higher phylogenetic diversity (Culmsee & Leuschner, 2013; Slik et al., 2009) attest to their exceptional conservation value.

4.5 | Patterns resembling the Great American Biotic Interchange

The patterns uncovered in this study allow the assessment of several hypotheses regarding biota mixing that have been postulated based on studies of the GABI, the mixing of North American and South American biotas during the Neogene and Quaternary. Malesia presents an independent model system, which has similarities to the Neotropics but also shows some differences. In both regions, tectonic movement and climatic changes have led to the mixing of biotas between Gondwanan fragments that had long been isolated before (Australia and South America) and Laurasian regions, which had repeatedly been connected to each other during the Tertiary (Eurasia and North America; Donoghue & Smith, 2004; Lawver et al., 2013). No land bridge connects Asia and Australia, which is similar to the situation before the closure of the Central American land bridge in the Americas, but the absence of a land connection is less important to plants, which have relatively high dispersal capabilities compared to many animal groups (Bacon et al., 2015; Sanmartín et al., 2004). More importantly, before the GABI began, the largest source population of lowland rainforest plants was located in the Amazon basin, that is on the formerly isolated continent of South America. In contrast, Australia, had not only undergone a 10 My-long isolation before the onset of the MFI, but also large-scale extinction of rainforest plants due to continent-wide cooling and aridification (Byrne et al., 2011), whereas large tropical rainforests persisted in Sundaland.

The dominance of Australian plants in Malesian mountain habitats today adds to the growing evidence against the isolation hypothesis (Antonelli et al., 2018; Bacon et al., 2015; Cody et al., 2010), which states that biotas are less successful in events of biotic interchange after long isolation due to lower competitiveness or higher susceptibility to predators (Faurby & Svenning, 2016; Simpson, 1980). Instead, our results are in line with studies that have highlighted the importance of habitat similarities between source and sink areas during the GABI and, hence, phylogenetic biome conservatism in biotic interchanges. During the MFI, tropical Asian tree lineages spread through Malesia to tropical Australia in a similar manner as Amazonian lineages colonized tropical Central America. Conversely, Australian plants, adapted to upland habitats, had great colonization success in Malesian mountains as Nearctic lineages had in the Andes (Antonelli et al., 2018; Bacon et al., 2015; Cody et al., 2010; Graham, 2018; Woodburne, 2010). While our results have to be viewed with caution due to the persisting lack of data from a key area, New Guinea, the congruence of scenarios from the MFI and the GABI shown here provide support to the idea that patterns and mechanisms that have been found through decades of studying the GABI are not specific to the Neotropics but have more universal validity.

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DATA AVAILABILITY STATEMENT

The tree inventory data are available from the original studies (see Table 1, Appendix 1).

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BIOSKETCH

The authors, based at Goettingen University, Germany and Tadulako University, Indonesia, are interested in patterns of plant diversity and composition in relation to ecological and evolutionary processes, especially in tropical montane habitats.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX 1

Data sources

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