The Naturalized Vascular Flora of Malesia

Rachael Holmes (rh419@leicester.ac.uk)
University of Leicester College of Science and Engineering https://orcid.org/0000-0002-6045-8705

Pieter Pelser
University of Canterbury

Julie Barcelona
University of Canterbury

Sri Sudarmiyati Tjitrosoedirdjo
Southeast Asian Regional Centre for Tropical Biology: SEAMEO BIOTROP

Indah Wahyuni
Southeast Asian Regional Centre for Tropical Biology: SEAMEO BIOTROP

Mark van Kleunen
University of Konstanz: Universitat Konstanz

Petr Pyšek
Institute of Botany Czech Academy of Sciences: Botanicky Ustav Akademie Ved Ceske Republiky

Franz Essl
University of Vienna: Universitat Wien

Holger Kreft
University of Gottingen: Georg-August-Universitat Gottingen

Wayne Dawson
Durham University

Lahiru Wijedasa
Birdlife International

Alessandra Kortz
Institute of Botany Czech Academy of Sciences: Botanicky Ustav Akademie Ved Ceske Republiky

Martin Hejda
Institute of Botany Czech Academy of Sciences: Botanicky Ustav Akademie Ved Ceske Republiky

Juan Carlos Berrio
University of Leicester College of Science and Engineering

Iskandar Siregar
Institut Pertanian Bogor

Mark Williams
University of Leicester College of Science and Engineering

Research Article

Keywords: Southeast Asia, alien, invasive, checklist, biogeography, naturalised

Posted Date: June 8th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1666818/v1

Version of Record: A version of this preprint was published at Biological Invasions on January 18th, 2023. See the published version at https://doi.org/10.1007/s10530-022-02989-y.

Abstract

Major regional gaps exist in the reporting and accessibility of naturalized plant species distribution data, especially within Asia. Here, we present the Malesian Naturalized Alien Flora database (MalNAF), the first standardized island-group level checklist of naturalized vascular plant species for the Malesian phytogeographical region. We used MalNAF to investigate the composition, origins, and habitat preferences of the naturalized flora, as well as potential drivers of taxonomic species richness across the archipelago. The naturalized vascular flora of Malesia consists of at least 1,345 species. Richness is highest in Singapore (569 spp.) and lowest in the Maluku Islands (87 spp.). Across the archipelago, 32 species are widespread, occurring in every island group, but the majority have a limited distribution of 2.3 ± 2.2 island groups per naturalized species. The naturalized plant species are representatives of 163 families, twenty of which are newly introduced to the region. Families richest in naturalized plant species in Malesia were Fabaceae (= Leguminosae) (171 spp.), Poaceae (= Gramineae) (160 spp.), and Asteraceae (= Compositae) (103 spp.). Overall, most of these have a native range that includes tropical Asia, closely followed by those with a range in Southern America, although at the island-group level, most have a higher proportion with a Southern American native range. Most naturalized species occur in anthropogenic habitats, but a few occur in specialised habitats. Human population density was the most significant driver of naturalized richness in Malesia. MalNAF provides a baseline for future studies of naturalized plant species distributions in the region.

Introduction

The establishment of global alien species databases and compendia (CABI 2015; ISSG 2015) and the publication of the Global Naturalized Alien Flora database (GloNAF) (van Kleunen et al. 2015; 2019) has led to an increasing body of research quantifying differences in the accumulation, origin, and distribution of naturalized plant species among countries worldwide (e.g., van Kleunen et al. 2015; Pyšek et al. 2017; Essl et al. 2019). Naturalized species are defined here as those introduced outside of their native range by anthropogenic activities and able to form self-sustaining populations (Richardson et al. 2000; Pyšek et al. 2004; Blackburn et al. 2011). Whilst these databases are a significant advancement in the study of naturalized plant species, they also reveal considerable geographic biases, particularly with regards to under-representation in parts of Asia.

Scarce data availability on alien species distributions in Southeast Asia translates into insufficient knowledge about their impacts (Peh *et al.* 2010). No estimates as to the total economic impact of naturalized plant species in Southeast Asia have been conducted, but as of 2013, the negative economic impact of alien species in Southeast Asia (e.g., impacts on agricultural systems, human health, and ecosystem function) was estimated at around US $33.5 billion annually (Nghiem et al. 2013). More recent research by Haubrock et al. (2021) based on the InvaCost dataset (Diagne *et al.* 2020) argues that the figure may be lower, at around US $16.89 billion in total since the 1960s. However, as Haubrock et al. (2021) acknowledge and Novoa et al. (2021) demonstrate, these values are likely to significantly underestimate the true economic costs of alien plant species due to bias in survey efforts between plants and other taxonomic groups in the initial version of this dataset. Therefore, whilst the regional negative economic impact of alien plant species is not yet known, the actual cost is expected to exceed current estimates. The increasing need for more standardized data on the distribution and status of naturalized plant species in the region is discussed by Witt (2017) in the 'Guide to Naturalized and Invasive Plants of Southeast Asia.' Standardization of nomenclature and taxonomy as well as application of standardized definitions of invasion status is particularly important to allow comparison of trends across the region based on a range of species checklists that vary in spatial scope and age. Understanding how anthropogenic factors are influencing the distribution and accumulation of alien species in Southeast Asia and determining to what extent these introductions have blurred the distinction between phytogeographic units of the archipelago is of utmost importance for the conservation of native floral diversity and the maintenance of vital ecosystem services (Vilà and Hulme 2017).

In Southeast Asia, projects recording the native flora continue to progress but remain unfinished for much of the region due, in part, to its high levels of floristic diversity (Middleton et al. 2019). Here, we focus on the phytogeographical region of Malesia (Fig. 1), which begins at the Kangar-Pattani line (Van Steenis 1950) and stretches from Peninsular Malaysia to the Bismarck Archipelago (van Welzen et al. 2011; Turner et al. 2001). This region contains over 10% of the native global vascular floral biodiversity (RGB Kew 2016). Spanning ~ 20,000 islands, Malesia possesses high levels of biodiversity and endemism, hosting four of the world's megadiverse countries (Malaysia, Indonesia, Philippines, and Papua New Guinea) (Mittermeier et al. 1997) some of which are at substantial risk of habitat loss, being declared global biodiversity hotspots (Myers et al. 2000).

Figure 1 Malesian biogeographic units used in this analysis. Basemap from ESRI (2019).

Alien species checklists and summaries for naturalized and invasive plant species have been curated for some parts of the region, for example, Singapore (Chong et al. 2009); Indonesia (e.g., Kementerian Lingkungan Hidup and SEAMEO BIOTROP 2003), with several books focussing only on subsets of taxa, such as invasive species (Tjitrosoedirdjo et al. 2016) or agricultural weeds (inclusive of native weed species) (e.g., Soerjani et al. 1987). Timor-Leste has a checklist of naturalized flora based on recent ecological surveys (Westaway 2018), the Philippines has Co's Digital Flora of the Philippines (Pelser et al. 2011 onwards) in which also naturalized species are listed, and for Papua New Guinea, the most comprehensive publication (Henty and Pritchard 1975) is several decades old but still relevant (Allison et al. 2015). Many records of naturalized species in Malesia, however, remain distributed across several published, unpublished, governmental, and non-governmental platforms, do not always use standardized terminology to describe the establishment status of a species, and mostly focus on a small subset of known highly invasive species. Thus, the usability of the data for recognizing the occurrence and spread of potential future alien species to neighbouring island groups is limited.

Here, we present the Malesian Naturalized Alien Flora database (MalNAF), Malesia's first standardized checklist of naturalized plant species at the level of islands/island groups. This checklist was produced by consolidating records of naturalized species resulting from an extensive search of literature, checklists and recent ecological surveys (< 10 years). We combined these with data from global databases such as GloNAF (van Kleunen et al. 2019) in addition to unpublished data. We use this novel dataset to answer the following questions: (i) what is the composition of naturalized vascular flora? (ii) where did the naturalized species originate? (iii) what environments do they invade within Malesia? (iv) how does naturalized species richness differ between island groups? and (v) what are the drivers of naturalized plant species richness between islands/island groups?

Methods

Study area

Malesia has high levels of plant biodiversity with an estimated total of ~ 45,000 native species of vascular plants (Corlett and Primack 2011). Across Malesia, the natural vegetation is comprised of three main types: ever-wet tropical rainforest, monsoon forest and montane forest (Richardson *et al.* 2012), as well as several edaphic and human-modified variants (Gillieson 2005; Clements et al. 2006; Giesen et al. 2007; Page et al. 2009; Posa et al. 2011; Corlett 2014; Galey et al. 2017). There are also areas of seasonal vegetation including savannahs and grasslands, which may have natural origins (e.g., in Sulawesi and the Lesser Sunda Islands) but have likely been maintained through grazing and controlled burning (Corlett 2014). Mean surface temperatures across Malesia rarely reach below 18°C in the lowland regions. Mean annual rainfall and its seasonal distribution vary spatially across the archipelago with patterns of interannual variation significantly influenced by the El Niño Southern Oscillation (ENSO), the Indian Ocean Dipole (IOD), the Pacific Decadal Oscillation (PDO) and the interactions between the Asian monsoon system and the inter-tropical convergence zone (ITCZ) (Corlett 2014).

The countries comprising the phytogeographic region of Malesia are Thailand (south of the Kangar-Pattani line (Parnell 2013), Malaysia, Singapore, Brunei Darussalam, Indonesia, Philippines, Timor-Leste, and Papua New Guinea. For most species, the spatial resolution of naturalized plant species data for Thailand was not available at the resolution required to separate species naturalized south of the Kangar-Pattani line from those only naturalized to the north. Therefore, this study sets the western limit of Malesia on the Malaysian side of the border between Thailand and Peninsular Malaysia, excluding naturalized species in Thailand (Fig. 1).

Malesian Naturalized Alien Flora database (MalNAF)

Compilation of the naturalized species dataset followed the approach of the Global Naturalized Alien Flora database (van Kleunen et al. 2019). Distribution data for alien plant species were gathered from an extensive literature and internet search, mostly in English but also in Bahasa Indonesia, of national floras and online databases of alien species in Malesia (see Supplementary file 1). The focus of this database is on naturalized species, and therefore cultivars and casuals were not included in the final version. Definitions of naturalized followed those outlined by Richardson (2000), Pyšek et al. (2004), and Blackburn et al. (2011), where the term refers to alien plant species that were introduced into a region because of anthropogenic activities (intentional or unintentional) and form self-sustaining populations in the new region. The checklist includes only species identified as naturalized within the given region, but if the taxon was reported in the original source as invasive, a subcategory of naturalized, then this was retained in the database as the original status, because this more detailed information could be useful for future studies on impact. However, we did not discriminate in our analyses between invasive and non-invasive naturalized species.

The literature search was conducted in two rounds. First, we sought checklists of alien naturalized plant species at the level of countries, islands, and island groups. These primarily came from existing databases (van Kleunen et al. 2019; CABI 2020; SEAMEO BIOTROP 2019; Pelser et al. 2011 onwards, etc.), scientific journals and books. Second, we attempted to fill potential gaps in distribution information presented in these resources by using species-specific literature searches for distribution information. Contributors of large datasets were invited to verify the compiled lists and contribute as authors. In place of a coded data quality designation for the sources used, as provided by GloNAF (van Kleunen 2019), a short qualitative description is provided for the key sources used, that highlights their attributes and limitations (see Supplementary file 2). However, the quality and availability of the data differed across the region. Sumatra and the Maluku Islands would particularly benefit from targeted collecting focused on improving knowledge of the number and distribution of naturalized species.

Definitions of invasion status differ between sources. Therefore, taxa have been included that are both explicitly listed as naturalized in the original source, when the authors' definitions matched those outlined above, as well as those that have been inferred as such based on associated information, following the decision tree approach used by Pagad et al. (2018). Taxa listed in the source material as naturalized within a biogeographic unit were omitted from MalNAF, if multiple additional sources (i.e., POWO 2021; USDA 2015; WCSP 2020) suggested that the taxon is, in fact, native to any island of the biogeographic unit. If there were multiple conflicting sources attesting to both native and naturalized status within a biogeographic unit and the status was unresolvable, these taxa were designated as cryptogenic (*sensu* Essl et al. 2018), which is similar to the category of 'weeds of unknown origin' in Chong et al. (2009). These cryptogenic taxa need further research to ascertain their true status, i.e., through archaeobotanical, genetic and linguistic studies, which are beyond the scope of this publication.

We report naturalized plant species at the level of islands/island groups (except for Peninsular Malaysia, which is, of course, a peninsula) and the biogeographical units were separated into 10 non-overlapping areas, covering most of the phytogeographical region of Malesia and including Peninsular Malaysia, Singapore, Sumatra, Java, Borneo, the Lesser Sunda Islands, the Philippines, Sulawesi, Maluku Islands and New Guinea (after Van Steenis 1950 and van Welzen et al. 2011) (Fig. 1). Island and island-group level biogeographical units were delimited as to (i) best represent isolated geological units of floristically similar composition; (ii) correspond to units used in Flora Malesiana and by van Welzen et al. (2011) and therefore make the comparison of biogeographic data of naturalized flora with native species easier, and (iii) because of the practical consideration that it was not possible to identify the presence of most taxa in the dataset to a spatial resolution below the island-group level. Analyzing the distribution data by island group does bring some limitations, as data regarding the presence of a given species, for example, in the Philippines would be attributed to that biogeographic unit, whereas for Malaysia or Indonesia, there would be a need for information with a higher spatial resolution. As a result, information about the heterogeneity of naturalized plant species richness and distribution within diverse island archipelagos such as the Philippines cannot be retrieved from our data set.

One deviation from the biogeographical units of van Steenis (1950) and van Welzen et al. (2011) is the segregation of Singapore from Peninsular Malaysia. The deviation is based on three factors: (i) as an island city-state, Singapore has a recently divergent socioeconomic history from Peninsular Malaysia; (ii) Singapore has the highest national plant specimen collection density in the world in comparison to most of Malesia, which has a relatively low collection density (Niisalo *et al.* 2014) and (iii) because Singapore is the only country in the region that is known to host more alien plant species than native (Chong et al. 2009), so this may have led to the number of naturalized plant species recorded being overestimated for Peninsular Malaysia.

Taxonomic harmonization of the checklists was conducted using the Leipzig Catalogue of Vascular Plants (LCVP) as the most up-to-date and comprehensive reference dataset currently available for vascular plants (Freiberg et al. 2020). This was done using version 1 of the associated "LCVP" and the "lcvplants" packages (https://github.com/idiv-biodiversity/lcvplants) in RStudio, for taxonomic name resolution. Fuzzy matching of three characters in both the species and genus name was allowed for each search to account for spelling deviations in the original name, and these were subsequently manually checked for mismatches. Naturalized plant species that were initially reported with no authority associated with the binomial name (e.g., in CABI 2015) were matched to the most likely correct authority. When species names were not included in the LCVP list, then Kew's Plants of the World Online (WCVP 2021) was followed. If the name remained unresolved, then the original binomial and authority from the source were retained. All original species names and authors (when provided) were retained in the MalNAF dataset so that source information can be more easily verified for species that are included under different names in the original data source and MalNAF.

Once compiled, the MalNAF checklist was verified by regional botanical specialists, and taxa flagged as problematic at this stage were removed. MalNAF version 1 is available in Supplementary file 1 and any update will be held with the first author.

Family naturalization index

Typically, families contributing the highest number of naturalized species in a region are those that are the most species-rich globally. To be able to identify which families may be overrepresented in the naturalized flora relative to their global number of species and to determine differences in family representation between island groups, we therefore calculated a family naturalization index (FN) (after Rejmánek et al. 1991 and Jiménez et al. 2008):
$FN = \frac{\text{no.naturalizedspeciesinthefamily}}{\text{totalspeciesinfamily} \times \text{totalspeciesnaturalizedinislandgroup}} \times 100.$

This index corrects for differences among families in species numbers worldwide and for differences among island groups in their overall naturalized richness, allowing more meaningful comparison of invasion success between families and island groups.

Habitat occurrence

For each species, information on the habitats in which they occur was recorded. Unfortunately, these data remain patchy - spatially and across taxa. Therefore, data availability limited the analysis to investigating patterns at the country level for four countries: Indonesia, Timor-Leste, the Philippines, and Papua New Guinea. Habitat classification followed Hejda et al. (2015), recognizing the following classes: 1. Forests, 2. Open forests, 3. Scrub, 4. Grasslands (split into 4a. natural grassland and 4b. human-maintained grasslands), 5. Sandy, 6. Rocky, 7. Dryland, 8. Saline, 9. Riparian, 10. Wetland, 11. Aquatic, 12. Anthropogenic (split into 12a. ruderal/urban habitats and 12b. agricultural habitats). Using the available literature (and annotations from herbarium sheets accessed via the Global Biodiversity Information Facility (GBIF) for the Philippines), plants were assigned to one or more habitat classes. This was done separately for each country in which each species has been recorded. Patterns of habitat association and species composition were then compared between countries.

Native ranges of naturalized species

Information regarding the native range of each species in the checklist was obtained by matching the accepted species names with native range data that was compiled using the World Checklist of Selected Plant Families (WCSP 2020), the Germplasm Resources Information Network (GRIN) (USDA 2015) and Kew's Plants of the World Online (POWO 2020) also following the World Geographical Scheme for Recording Plant Distributions (WGSRPD) (Taxonomic Database Working Group – TDWG; Brummit 2001) at the continent level (TDWG level 1), which included records for 1,341, out of the total 1,345 species plant species in MalNAF (see Supplementary file 1). To allow for future analysis using the botanical categorization of regions, we followed the WGSRPD when coding the areas to which the naturalized species in Malesia are native. As part of the WGSRPD, it is important to note that the Americas are split into two geographic areas, Northern (inclusive of Mexico) and Southern America, and Antarctica includes all sub-Antarctic islands.

When a direct match was not found, manual searches were done for synonyms of a given taxon as the different lists adhere to a variety of taxonomies. MalNAF also includes taxa that are native to parts of Malesia but naturalized somewhere else within the region. To ensure only alien species were included in the dataset, all of those identified as native somewhere within Malesia were labelled, checked against a native species checklist at the same biogeographical unit level as of this study (Holmes *et al.* in prep) and conflicting results were removed. Artificial hybrids were listed as hybrid in place of a native range and those with unknown or highly obscure native ranges were reported as 'obscure'.

Drivers of richness

To assess the drivers of naturalized species richness (total naturalized plant species per island group), geographic, climatic and anthropogenic data were collated. Global climate data at 2.5-minute spatial resolution were downloaded from WorldClim v.2.1 (Fick and Hijmans 2017) and the mean value of each of the 19 climate variables (each variable is an average value for the years 1970–2000) was obtained per island group. To produce uncorrelated climate variables for use in the analysis, a Principal Components Analysis (PCA) was conducted on all 19 bioclimatic variables (Dupin et al. 2011). PCA scores where then extracted for PC1 (45.9%), PC2 (28.8%) and PC3 (17.6%), which together explain ~ 92% of climatic variation across the region (Supplementary file 3). PC1 was mostly driven by differences in the minimum temperature during the coldest months (bio6 and bio11), whereas PC2 and PC3 largely reflect differences in rainfall, i.e., annual precipitation (bio12) and precipitation in the wettest month (bio13), respectively. The altitudinal range was calculated as the range in elevation for each island group from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) dataset (Danielson and Gesch 2011). The percentage of urban area for each island group was calculated taking the proportion of land classes as "urban area" from the European Space Agency (ESA) Climate Change Initiative (CCI) Global Land Cover Map v2.1.1 at 300m spatial resolution for the year 2020, relative to the area of the island group polygons.

The proportion of agricultural land was calculated in the same way by combining values for the "cropland" classes ("Cropland rainfed", "Cropland irrigated or post-flooding" and "Mosaic cropland (> 50%) / natural vegetation (< 50%)"). Calculating agricultural area this way is likely to under-represent pastureland, so it would likely be an underestimate for the area covered by some forms of animal agriculture. Human population density per island was extracted from a globally gridded dataset of population estimates for 2020 (Global High Resolution Population Denominators Project 2018) at 30 arcsecs by clipping the data by island group and then dividing the total by island group area. Island level data on Gross Domestic Product (GDP) were obtained from a globally gridded dataset at 5 arc-min resolution for the year 2015 and are presented in the original dataset as their equivalent in USD for the year 2011 (Kummu et al. 2020).

Spearman's rank correlation was conducted between all pairs of variables (Supplementary file 3) (independent variables that were not normally distributed were transformed) to identify the most important drivers of naturalized plant species richness (n = 9): human population density (p/km2) (log 10 transformed), proportion of agricultural area (%), proportion of urban area ("built environment") (%), GDP (USD $) (square root transformed), altitudinal range (m), area (square root transformed) and climatic data (as PC1, PC2, PC3). Based on the results of the correlation tests, variables that were highly correlated with naturalized richness and had low collinearity with each other were selected for input into a multiple linear regression.

Results

Composition of the naturalized flora

The naturalized vascular flora of Malesia is composed of at least 1,363 distinct taxa when infraspecific taxa are included, dropping to 1,345 at the species level (see Supplementary file 1). Of these, 878 species are not native to any island group in Malesia, and 467 species are naturalized intra-regionally. Additionally, a total of 88 taxa were labelled as cryptogenic due to conflicting reports on invasion status. All further results presented here focus on the naturalized taxa and are reported at the level of the species.

The naturalized species belong to 161 families and 707 genera (Table 1). In total, 20 families are novel to Malesia, having been introduced mostly from the Americas (Table 2). Across the archipelago, at least 32 species have become naturalized in every island/island group, and ~ 13% are widespread (occurring in > 5 islands/island groups), suggesting that most species occur in less than half of the island groups in Malesia with 56% reported in only one biogeographic unit (Fig. 2). The average frequency is 2.3 ± 2.2 island groups per naturalized species (mean ± SD). However, the distributions presented in the dataset are likely an underestimate of true distributions of naturalized taxa in the region, as species perceived to be common are less likely to be collected and reported by botanists during surveys and this is even more likely if the focus of the survey is on the native flora.

The 32 frequently occurring species are representatives of 14 families, with Asteraceae and Poaceae each contributing six species (Fig. 2). The average naturalized plant species richness per island/island group was 311 ± 171 (mean ± SD). Naturalized plant species richness was highest in Singapore (569 spp.), closely followed by the Philippines (539 spp.), and was lowest in the Maluku Islands (87 spp.) (Fig. 3). Naturalized plant species richness relative to native species richness was also highest in Singapore (0.4) but was instead closely followed by the Lesser Sunda Islands and Java (both 0.3), rather than the Philippines (0.06) (Fig. 3c, Table 3).

Table 1
Top ten families with the largest number of naturalized species

Family	No. genera	No. species
Fabaceae	77	171
Poaceae	66	160
Asteraceae	70	103
Cyperaceae	11	57
Acanthaceae	22	46
Lamiaceae	21	41
Solanaceae	9	38
Rubiaceae	20	34
Malvaceae	13	33
Euphorbiaceae	15	32

Table 2

Alien families with species now naturalized within Malesia. Native range adapted from Christenhusz et al. 2017[1], Thiede 2001[2], Arbo 2007[3], Stevens 2001[4], Airy-Shaw 1968[5] to fit the WGSRPD.

Family	No. genera	No. species	Family Native range
Cactaceae	4	7	Northern and Southern America; a single species occurs in Africa and tropical Asia[1]
Agavaceae	1	4	Northern and Southern America[2]
Phytolaccaceae	1	4	Northern and Southern America, Africa, temperate and tropical Asia[1]
Turneraceae	2	3	Northern and Southern America, and Africa[3]
Cabombaceae	1	2	Northern and Southern America, Africa, temperate and tropical Asia, and Australasia[1]
Cannaceae	1	2	Northern and Southern America[1]
Martyniaceae	2	2	Northern and Southern America[1]
Papaveraceae	2	2	Northern and Southern America, Africa, Europe and temperate Asia[1]
Petiveriaceae	2	2	Northern and Southern America; a single species occurs in Australasia[1]
Talinaceae	1	2	Northern and Southern America, and Africa[1]
Asphodelaceae	1	1	Southern America, Africa, Europe, temperate and tropical Asia, and Australasia[1]
Bixaceae	1	1	Northern and Southern America, Africa, temperate and tropical Asia, and Australasia[1]
Bromeliaceae	1	1	Northern and Southern America; a single species occurs in Africa[1]
Calceolariaceae	1	1	Northern and Southern America, and two species occur in Australasia[4]
Hyacinthaceae	1	1	Africa, Europe, temperate and tropical Asia[4]
Moringaceae	1	1	Africa, tropical Asia[1]
Muntingiaceae	1	1	Northern and Southern America[1]
Polemoniaceae	1	1	Northern and Southern America, Europe, temperate Asia[1]
Sphenocleaceae	1	1	Africa[5]
Tropaeolaceae	1	1	Northern and Southern America[1]

Figure 2 Naturalized plant species that have been reported from every island/island group in Malesia: **Amaranthaceae**; 1) *Amaranthus spinosus**, 2) *Celosia argentea*, **Asteraceae**; 3) *Chromolaena odorata** (R Holmes 2022), 4) *Crassocephalum crepidioides**, 5) *Eclipta prostrata*, 6) *Elephantopus scaber* (Vinod 2014, CC BY), 7) *Mikania micrantha**, 8) *Synedrella nodiflora*, **Cleomaceae**; 9) *Cleome rutidosperma**, **Convolvulaceae**; 10) *Ipomoea cairica**, 11) *Ipomoea triloba*, **Euphorbiaceae**; 12) *Euphorbia hirta*, 13) *Ricinus communis*, **Fabaceae**; 14) *Leucaena leucocephala**, 15) *Mimosa diplotricha** (Gassah 2020, CC BY), 16) *Mimosa pudica**, 17) *Senna occidentalis*, **Lamiaceae**; 18) *Hyptis capitata*, 19) *Mesosphaerum suaveolens** (Gonsalves 2020, CC BY), **Muntingiaceae**; 20) *Muntingia calabura**, **Piperaceae**; 21) *Piper aduncum**, **Plantaginaceae**; 22) *Scoparia dulcis*, **Poaceae**; 23) *Eleusine indica**, 24) *Melinis repens*, 25) *Panicum maximum*, 26) *Paspalum conjugatum**, 27) *Pennisetum polystachion**, 28) *Pennisetum purpureum**, **Pontederiaceae**; 29) *Eichhornia crassipes**, **Salviniaceae**; 30) *Salvinia adnata**, **Verbenaceae**; 31) *Lantana camara** (R Holmes 2022), 32) *Stachytarpheta jamaicensis*. The asterisk (*) indicates species reported as invasive within Malesia in the Invasive Species Compendium (CABI 2022). Images 1:2,4:5,7:14,16:18,20:30 and 31 are 'research grade' and CC0 licensed photos from iNaturalist (2021).

Table 3

Overview of naturalized plant species richness across Malesia with climatic, geographic and socioeconomic differences between island groups. Percentage of island group ((naturalized richness/total richness) * 100). Native species richness follows dataset by Holmes et al. (in prep). Relative naturalized species rich calculated against native species richness.

Island groups	**Area (km^2)**	**Native richness**	**Naturalized richness**	**Relative naturalized richness**	**Total flora naturalized (%)**	**Annual mean temp. (°C)**	**Min temp. coldest month (°C)**	**Annual precip. (mm)**	**Precip. of wettest month (mm)**	**Altitudinal range (m)**	**Urban area (%)**	**Agricultu area (%)**
Singapore	511	1,488	569	0.4	28	26.8	22.9	2,320	296	95	56.1	28.2
Philippines	293,238	9,186	539	0.06	6	25. 8	21.1	2,546	384	2,063	2.6	47.1
Java	131,697	1,524	435	0.3	22	24.6	19.5	2,419	369	3,419	8.4	61.4
Lesser Sunda Islands	87,138	1,213	400	0.3	25	24.8	19.1	1,581	296	3,439	1.2	61.2
New Guinea	873,068	13,331	338	0.03	2	24.1	19.1	3,044	348	4,872	0.1	9.7
Peninsular Malaysia	131,395	6,554	231	0.04	3	25.7	20.2	2,526	393	2,806	0.8	61.1
Borneo	736,746	7,384	194	0.03	3	26	21.5	3,028	336	3,993	0.2	32.5
Sumatra	471,869	2,860	183	0.06	6	25.1	20.6	2,671	324	3,519	0.5	56.3
Sulawesi	185,728	2,805	129	0.05	4	24.3	19.6	2,165	277	3,258	0.9	33.0
Maluku	76,224	2,436	87	0.04	3	25.6	21.2	2,291	314	2,802	0.1	12.4

Family Naturalization Index

Fabaceae (171 spp.), Poaceae (160 spp.), and Asteraceae (103 spp.), were the most species-rich families in the naturalized flora (Table 1), which is unsurprising as these are amongst the largest plant families globally. Whilst these three families are very species-rich in some island groups (represented by > 10 naturalized species), the FN index suggests that, with the exception of Poaceae, this is expected given the large size of the families (Fig. 4a). Verbenaceae, however, is not amongst the top 10 largest families in the region but is common on all island groups and has the highest FN value amongst families with at least 10 naturalized plant species in one island group in Malesia, suggesting that this family is overrepresented in the naturalized flora, containing more successful pioneering species than would be expected given the family's size. Amaranthaceae, Poaceae and Convolvulaceae, scored similarly, had at least 10 species on one island group and were also overrepresented in the naturalized flora. Despite differences in FN score between families possibly highlighting phylogenetic patterns, there was little variation within island groups (Fig. 4b).

Figure 4 (**a**) Family naturalization index showing only families with at least 10 naturalized plant species in one island group in Malesia; (**b**) family naturalization index for those same families plotted by island group.

Geographic origin

The native range was identified for 1,341 out of the total 1,345 species, as four species are considered of unknown origin. The majority of species naturalized within Malesia have a native range that includes tropical Asia (739 spp., ~ 21%). This was followed by Southern America (610 spp., ~ 17%), temperate Asia (596 spp., ~ 17%), Northern America (496 spp., ~ 14%), Africa (446 spp., ~ 13%), Australasia (281 spp., ~ 8%), the Pacific (171 spp., ~ 5%), with Europe (140 spp., ~ 4%) and lastly Antarctica (5 spp., > 1%) contributing the least. Three species were listed as of hybrid origin. It is important to note that a pantropical species may be represented in counts for tropical Asia, Southern America, and Africa, for example, which makes it difficult to determine its exact area of origin.

At the island-group level, all except Singapore had the highest proportion of their naturalized species from Southern America, followed by Northern America (Fig. 5). Singapore is an outlier with a high proportion of its naturalized species originating in tropical Asia and Australasia.

Figure 5 The proportion of naturalized species in each island group by their native range.

Habitats

We were able to obtain habitat data at the country level for 581 species within their naturalized range (Table 4, Supplementary file 1). The majority of habitat data are from the Philippines (72%, 474 spp.). Across the region, naturalized species occur in all habitat types, and most species occur in anthropogenic habitats (23% in ruderal/urban areas and 20% in agricultural areas), followed by open forests (14%), which include forests with canopy openings and clearings caused by environmental stress or disturbance. Forest, scrub, grassland (natural and anthropogenic) and riparian habitats each harbour between 6–8% of naturalized species. Only *Dalea cliffortiana* and *Leucaena leucocephala* were reported as naturalized in dryland habitats that are exposed to drought stress.

Table 4
Number of naturalized species in Indonesia (n = 132 spp.), Papua New Guinea (n = 64 spp.), Philippines (n = 474 spp.) and Timor Leste (n = 84 spp.), in each habitat type for which these data were available. The habitat classification was adapted from Hejda et al. (2015).

Habitat type	Indonesia	Papua New Guinea	Philippines	Timor Leste
Agricultural	77	26	220	45
Aquatic	2	1	10	3
Dryland			2	
Forest	68	6	47	1
Grasslands		2	92	1
Human maintained grassland	2	20	27	13
Natural grassland	4	5	6	1
Open forest	7	2	200	1
Riparian	3	5	92	4
Rocky			19	
Ruderal/Urban	51	47	262	48
Saline			49	1
Sandy		1	29	2
Scrub			95	1
Wetland			31	1

At the country level, some clear differences emerged (Fig. 6). In all except the Philippines, over 50% of the naturalized species occur in anthropogenic habitats. This increases to over 75% for Timor Leste. Indonesia has the highest proportion of naturalized species occurring in closed-canopy forests (32%), but this is most likely explained by the fact that this category can include forest plantations such as oil palm, and Indonesia is the highest global exporter of this crop. In Papua New Guinea and Timor Leste, natural and anthropogenic grasslands are a more commonly invaded habitat type.

Figure 6 (**a**) The proportion of species occurring in different habitat types in their naturalized range within Malesia; (**b**) The proportion of naturalized species occurring in different habitat types in each country; (**c**) Comparison of the proportion of widespread (≥ 5 island groups) and rare (< 5 island groups) naturalized species occurring in different habitats across Malesia.

Drivers of richness

Human population density (people/km2) (log10 transformed) and PC3, which is strongly correlated with precipitation during the wettest month (mm), were selected in the multiple regression model as the highest positively and negatively correlated variables with low collinearity. Using these explanatory variables, the model (F (2, 7) = 8.1, p = 0.015) was robust, met all assumptions (normality of residuals (Shapiro-Wilk test, W = 0.96, p = 0.8), multicollinearity (average VIF 1), homoscedasticity (Breusch-Pagan test, BP = 1.6, p = 0.45) and independence (Durbin-Watson test, DW = 2.63, p = 0.79)) and accounted for 61% (adj. R^2 = 0.61) of the variation in the naturalized richness data. Only population density had a significant relationship and was positively correlated with naturalized richness (β = 0.76, p = 0.008). PC3 was also close to the threshold of significance (β = -0.43, p = 0.076), suggesting that island groups that have, on average, higher precipitation during their wettest months may typically have a higher naturalized richness, though this relationship is weaker. Whilst no outliers were identified in the regression, New Guinea and Singapore were close to the threshold of the Cook's distance. With such a small dataset of only ten points, individual island groups can have an impact on the perceived drivers. For example, based on the Spearman's rank correlation tests, the percentage of agricultural area was not significantly correlated with naturalized plant species richness (p = 0.35), but when Singapore and New Guinea were excluded from the analysis, then the relationship became significant (p = 0.022). This attests to the importance of agricultural area in the accumulation of naturalized plant species in the rest of the region.

Discussion

Naturalized flora

The naturalized vascular flora is comprised of 1,345 species and therefore represents around 4.3% of the total vascular flora of Malesia (total flora 31,530 spp. based on Holmes *et al.* in prep). Though it should be noted that some of the naturalized taxa within Malesia are also native to some island groups (467 spp.), representing intra-regional naturalizations and would therefore appear in both lists.

Naturalized richness in Malesia is much lower when compared with other tropical and subtropical island regions, particularly oceanic islands. Malesia has ~ 50% lower naturalized plant species richness compared to the Pacific islands (2,672 spp.) (Wohlwend et al. 2021), and at 4.3% (range from 3% – 28% for individual island groups), Malesia has a lower proportion of the total flora naturalized, compared with the global average for islands (~ 48%) (Essl et al. 2019) and for example, less than the Galapagos Islands (61%) (Guézou et al. 2017). This is despite Malesia having a larger total land mass than both the Pacific

Islands and the Galapagos Islands. It is instead more similar to islands closer to the mainland, such as Madagascar (5%) (Kull et al. 2012). This is likely due to the comparatively low native plant species richness of oceanic islands because of their ontogeny and geological origins, compared with diverse and more biotically resistant continental island groups (Moser et al. 2018), such as those in Malesia. Malesian naturalized plant species richness is typically higher when compared with tropical mainland regions, such as India (471 spp.) (Inderjit et al. 2018), Ghana (291 spp.) (Ansong et al. 2019) and French Guiana (165 spp.) (Delnatte and Meyer 2012). This fits with the pattern described elsewhere (see Pyšek and Richardson 2006) that islands are typically more invaded than mainland regions. The differences in richness between Malesia and the Pacific may be partially explained by the larger geographic area covered by the Pacific Island groups, which would therefore include a wider range of climatic conditions and niches for species to naturalize. Additionally, the difference is likely influenced by the Hawaiian Islands, which alone harbour more naturalized plant species (1,776 spp.) than the whole of Malesia (Wohlwend et al. 2021). In this regard, the Hawaiian Islands are an outlier in general, likely because they are some of the best-monitored for alien species introductions globally, are densely populated, and have a relatively high GDP compared with similarly sized islands (Wohlwend et al. 2021). This may also be an indication that overall naturalized richness is much higher for Malesia than reported here and that analyses of the currently available data presented in the MalNAF database therefore underestimate naturalized plant diversity.

Of the most species-rich families in the naturalized flora (Fabaceae, Poaceae and Asteraceae), only Poaceae was overrepresented. These families are also dominant in naturalized floras of other tropical regions (e.g., Zeni 2015; Inderjit et al. 2018; Wohlwend et al. 2021). Additionally, families with a small number of species were present in the naturalized flora, such as Sphenocloeaceae with only two species, of which *Sphenoclea zeylanica* is naturalized across Malesia, commonly invading rice paddies (Holm et al. 1977; Ghosh and Ganguly 1993). For families with at least 10 naturalized species in an island group, Verbenaceae, Amaranthaceae and Convolvulaceae were overrepresented. Verbenaceae is typically a tropical and subtropical family, whereas Amaranthaceae and Convolvulaceae have cosmopolitan distributions that include the tropics, though they prefer drier (Christenhusz et al. 2017, p. 449) and wetter climates, respectively (Christenhusz et al. 2017, p. 534). Some of the most invasive and widespread naturalized species in the tropics are members of Verbenaceae (e.g., *Lantana camara*, *Stachytarpheta cayennensis*, and *Stachytarpheta jamaicensis*).

Of the ~ 20 families that have naturalized and have no native species in the region (Table 2), Cactaceae has the most species (7 spp.). The naturalized Cactaceae species are members of four genera (*Cereus*, *Epiphyllum*, *Nopalea* and *Opuntia*), which were all reported within Malesia for the first time between 1900 and 1950 (RGB Kew 2021; Meise Botanic Garden 2022; Bijmoer et al. 2022a; Bijmoer et al. 2022b) and are currently restricted to Peninsular Malaysia (1 sp.), Java (2 spp.), the Lesser Sunda Islands (1 sp.) and the Philippines (4 spp.). Most of the novel families have a native range that is not inclusive of tropical Asia and therefore their introduction for the first time potentially in Earth history has led to an increase in familial richness within the Malesian flora and an increase in similarity at the taxonomic level, with the floras of distinct phytogeographic regions globally, such as those in the neotropics.

In Malesia, 32 species are widespread and reported from all 10 island groups (Table 3). Around 60% of these widespread species are considered invasive within their globally introduced range. As elsewhere, some of the widespread and invasive taxa have both positive and negative socioeconomic and ecological impacts within Malesia, making management complex. For example, in West Java within the Cibodas Biosphere Reserve, three of the 32 species which are naturalized on every island group, *Lantana camara*, *Piper aduncum* and *Stachytarpheta jamaicensis*, are also amongst the top 15 species that are significantly important to local communities culturally and economically (Handayani and Hidayati 2020) but remain ecologically damaging (Handayani et al. 2021). For species such as these, which are already resident in every island group and have mixed cultural, economic and ecological roles, it is more important to understand how to manage populations effectively (e.g. through harvest and containment in the case of the Cibodas Biosphere Reserve (Handayani et al. 2021)), and to prevent their introduction in smaller satellite islands where they may not yet have spread, rather than focusing solely on eradicating established populations.

Other widespread species, i.e., those occurring in five or more island groups (181 spp.) (Supplementary file 1) but not yet present on every island group, should be candidates for a watch list, as they are likely the most capable of expanding their naturalized range within Malesia if introduced or if sufficient management is not taken to deal with casual populations. The proportion of widespread and less frequently occurring species, was similar across a range of habitat types (Fig. 6c). But a larger proportion of widespread naturalized species occur in closed forests (11% vs. 6%) and grasslands (13% vs. 10%), when compared with less frequently occurring species, which are more likely to be naturalized in ruderal/urban habitats (24% vs. 20%). This suggests that the widespread species have traits that make them more generalist and able to be successful across many habitat types with both an ecological and anthropogenic modification gradient.

By island group, excluding Singapore, most species have a native range that includes the Americas, likely reflecting the role of European colonialism in driving many introductions within the region as well as the importance of similar climates for the establishment of alien plants. Whilst the colonial history of Malesia is incredibly complex and heterogeneous both between and within island groups, involving the Dutch, British, Spanish, and Portuguese empires, some key factors were likely important for the establishment of taxa from the Americas, such as the establishment of botanical gardens (e.g. Kebun Raya Bogor, Kebun Raya Cibodas and Singapore Botanic Gardens), new agricultural systems including expansive monocultures, increased international trade with the Americas, and the construction of European-style parks (Abendroth et al. 2012).

Spatial patterns and drivers of richness

Singapore has the highest naturalized species richness of all island groups, and this remains true in proportion to its native flora and its area. In Malesia, Singapore is an outlier for its high human population density (~ 8214/km^2), urban area (~ 56%), and GDP (when relative to its size), which are all previously reported as important drivers of naturalized species richness (Essl et al. 2019). However, Singapore's naturalized richness may be overrepresented because of the inclusion of potentially native species in its naturalized checklists. Corlett (1988) noted in one of the first inventories focusing on naturalized plant species in Singapore that distinguishing between native and alien plants that are of Southeast Asian origin is particularly difficult in Singapore as major botanical surveys were only conducted following the deforestation of 95% of the terrestrial vegetation at the end of the 19th century. Therefore, species once native to the island may have been locally extirpated (Turner et al. 1994; Kristensen et al. 2020) and reintroduced, for example from Peninsular Malaysia (Brook et al. 2003), but be considered naturalized and vice versa. In comparison with a native checklist of flora for Malesia that follows the same taxonomy and nomenclature as MalNAF, Holmes *et al.* (in prep) suggest that 312 species that are part of the naturalized flora of Singapore are currently considered native to Peninsular Malaysia (Supplementary file 1). This may also explain why a greater proportion of naturalized species in Singapore have a native range that includes tropical Asia, in contrast to Peninsular Malaysia and the rest of Malesia. Due to Peninsular Malaysia`s size, its higher number of vegetation types and wider range in elevation, it is impossible for Singapore to harbour the same species richness as Peninsular Malaysia, so it is likely that many of these species are aliens, but some caution should be placed on the true status of these taxa. It will likely never be possible to know for certain the true status of these plants, but future palaeoecological work may provide insights into taxa with distinct pollen or seed morphology.

Conversely, the Maluku Islands had the lowest naturalized plant species richness. Partially, this can be explained by its low GDP and population density (Table 4), but this is also likely a result of under-collection in the Maluku Islands. When considering relative naturalized richness or the percentage of the total flora which is naturalized, the Maluku Islands are not the lowest and are tied with Peninsular Malaysia. New Guinea, however, has the lowest percentage of its total flora naturalized at just 2%. This island group is one of the largest in the analysis by area and has the lowest human population density as well as having the world's richest island flora (Camara-Leret et al. 2020). As this metric only covers relative taxonomic richness, the impact of naturalized plant species on large floras, such as those in New Guinea, are likely underestimated due to the high numbers of endemics amongst the native flora.

Based on United Nations (UN) global population projections (2019), human population density in Malesia is set to increase by ~ 25% by 2050 to 180/km^2. This increase in human population density could lead to future increases in the accumulation of naturalized plant species across Malesia as population density drives propagule pressure and increases the area of urban and ruderal environments.

Conclusion

There are at least 1,345 vascular plant species naturalized within Malesia though this is likely an underestimate when compared with similar island archipelagos. Twenty novel families have now naturalized in the region leading to an increase in the familial diversity of the Malesian flora. Whilst 32 species have already naturalized throughout the entire archipelago, 181 species have naturalized in at least half of the island groups and should be closely monitored in case of range expansion. Human population density was found to be the most significant driver of naturalized plant species richness across Malesia, and this could lead to further gains in naturalized species for some island groups over the next 30 years.

Declarations

The data supporting the results reported in the article can be found in supplementary files.

Acknowledgements We are thankful to Allen Allison (Bishop Museum, USA) for providing access to out-of-print resources and information on naturalized plant species in New Guinea and to Stefano de Sabbata (University of Leicester, UK) for guidance on analysing the drivers of richness.

Authors contributions RH, MW and JCB conceived of the initial study and all authors contributed to developing the studies aims and design. RH assembled, analysed the data, and wrote the first draft of the manuscript. PPe and JB, gathered habitat affiliation data for the Philippines. PPe, JB, SST and IW helped to revise species status and inclusion in the dataset. MH, AK and PPy contributed to the analysis of species' habitat affiliations. All authors commented on previous versions of the manuscript, then read and approved the final manuscript.

Funding RH was supported by the UKRI through a NERC CENTA DTP (grant no. NE/S007350/1). PPy, MH, and AK were supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). MvK was supported by the German Research Foundation DFG (grant no. 26474062). HK and SST acknowledge funding from the German Research Foundation DFG (CRC990 EFForTS).

Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

Availability of data and material (data transparency) The MalNAF dataset, additional datasets used in this study, and the R code used for analysis can be found in the published article and Supplementary file 1 and 3.

References

Abendroth S, Kowarik I, Müller N and Von der Lippe M, (2012) The green colonial heritage: Woody plants in parks of Bandung, Indonesia. Landscape and Urban Planning, 106(1): 12-22. https://doi.org/10.1016/j.landurbplan.2011.12.006

Airy-Shaw HK (1968) Sphenocleaceae in Milne-Redhead and Polhill, Flora of Tropical East Africa. Crown Agents for Overseas Governments and Administration, London.

Allison A, Pratt L, Pratt T and Imada C (2015) Exotic Species Survey of the Kokoda Track, Papua New Guinea. Bishop Museum Technical Report 67; PNG Conservation and Environmental Protection Authority (CEPA), Port Moresby, Papua New Guinea.

Ansong M, Pergl J, Essl F, Hejda M, van Kleunen M, Randall R and Pyšek P (2019) Naturalized and invasive alien flora of Ghana. Biol Invasions, 21(3):669-683. https://doi.org/10.1007/s10530-018-1860-7

Arbo MM (2007) Turneraceae. In: Kubitzki, K (eds) Flowering Plants · Eudicots. Springer, Berlin, Heidelberg, pp 458-466

Bijmoer R, Scherrenberg M, Creuwels J (2022a) Naturalis Biodiversity Center (NL) - Botany. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/ib5ypt accessed via GBIF.org on 2022-04-14. https://www.gbif.org/occurrence/2514408226

Bijmoer R, Scherrenberg M, Creuwels J (2022b). Naturalis Biodiversity Center (NL) - Botany. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/ib5ypt accessed via GBIF.org on 2022-04-14. https://www.gbif.org/occurrence/2516415065

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR and Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol, 26(7):333-339. https://doi.org/10.1016/j.tree.2011.03.023

Brook BW, Sodhi NS and Ng PK (2003) Catastrophic extinctions follow deforestation in Singapore. Nature, 424(6947): 420-423. https://doi.org/10.1038/nature01795

Brummitt RK (2001) World Geographical Scheme for Recording Plant Distributions, Edition 2. Biodiversity Information Standards (TDWG) http://www.tdwg.org/standards/109

CABI (2015) Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

CABI (2022) Invasive Species Compendium. Wallingford, UK: CAB International. www.cabi.org/isc.

Camara-Leret R, Frodin DG, Adema, F, Anderson C, Appelhans MS, Argent G, Arias Guerrero S, Ashton P, Baker WJ, Barfod AS and Barrington D (2020) New Guinea has the world's richest island flora. Nature, *584*(7822): 579-583. https://doi.org/10.1038/s41586-020-2549-5

Chamberlain S, Barve V, Mcglinn D, Oldoni D, Desmet P, Geffert L, Ram K (2022) rgbif: Interface to the Global Biodiversity Information Facility API. R package version 3.7.2, https://CRAN.R-project.org/package=rgbif.

Chong KY, Tan HTW and Corlett RT (2009) A Checklist of the Total Vascular Plant Flora of Singapore: Native, Naturalised and Cultivated Species. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.

Clements R, Sodhi NS, Schilthuizen M and Ng PK (2006). Limestone karsts of Southeast Asia: imperilled arks of biodiversity. Bioscience, 56(9): 733-742. https://doi.org/10.1641/0006-3568(2006)56[733:LKOSAI]2.0.CO;2

Corlett RT (1988) The naturalized flora of Singapore. J Biogeogr: 657-663. https://doi.org/10.2307/2845443

Corlett R (2014) The ecology of tropical East Asia. USA; Oxford University Press.

Corlett RT and Primack, RB (2011) Tropical rain forests: an ecological and biogeographical comparison. John Wiley & Sons.

Christenhusz MJ, Fay MF and Chase MW (2017) Plants of the world: an illustrated encyclopedia of vascular plants. University of Chicago Press.

Delnatte C and Meyer JY (2012) Plant introduction, naturalization, and invasion in French Guiana (South America). Biol Invasions, 14(5): 915-927. https://doi.org/10.1007/s10530-011-0129-1

Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature 592: 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dupin M, Reynaud P, Jarošík V, Baker R, Brunel S, Eyre D, Pergl J, Makowski D (2011) Effects of the training dataset, characteristics on the performance of nine species distribution models: application to Diabrotica virgifera virgifer. PLoS ONE 6:e20957. https://doi.org/10.1371/journal.pone.0020957

Essl F, Bacher S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kowarik I, Kühn I, Pyšek P, Rabitsch W, Schindler S (2018) Which taxa are alien? Criteria, applications, and uncertainties. BioScience, 68: 496-509. https://doi.org/10.1093/biosci/biy057

Essl F, Dawson W, Kreft W, Pergl J, Pyšek P, van Kleunen M, Weigelt P, Mang T, Dullinger St, Lenzner B, Moser D, Maurel N, Seebens H, Stein A, Weber E, Chatelain C, Inderjit Genovesi P, Kartesz J, Morozova O, Nishino M, Nowak PM, Pagad S, Wen-Sheng S, Winter M (2019). Drivers of the relative richness of naturalized and invasive plant species on Earth. AoB Plants, 11 (5): lz051. https://doi.org/10.1093/aobpla/plz051

European Space Agency (ESA) Climate Change Initiative (CCI) (2019) Global Land Cover Map v2.1.1. https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-land-cover?tab=form. Accessed 14 December 2021

Esri (2019) "Physical" [basemap]. https://www.arcgis.com/home/item.html?id=c4ec722a1cd34cf0a23904aadf8923a0 Accessed 25 April 2022

Fick SE and Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. https://worldclim.org/data/worldclim21.html Accessed 14 December 2021

Freiberg M, Winter M, Gentile A, Zizka A, Muellner-Riehl AN, Weigelt A and Wirth C (2020) LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. Scientific data, 7(1): 1-7. https://doi.org/10.1038/s41597-020-00702-z

Galey ML, Van Der Ent A, Iqbal MCM and Rajakaruna N (2017) Ultramafic geoecology of south and Southeast Asia. Bot Stud, 58(1): 18. https://doi.org/10.1186/s40529-017-0167-9

Gassah R (2020) Mimosa diplotricha (Photo 102583147, CC BY). https://www.inaturalist.org/photos/102583147

Ghosh DC and Ganguly S (1993) Cultural factors affecting weed infestation and crop productivity in wetland transplanted rice. In Integrated weed management for sustainable agriculture. Proceedings of an Indian Society of Weed Science International Symposium, Hisar, India, 18-20 November 1993. Indian Society of Weed Science, (3): 30-33.

Giesen W, Wulffraat S, Zieren M and Scholten L (2007) Mangrove guidebook for Southeast Asia. FAO and Wetlands International; Dharmasarn Co., Ltd.

Gillieson D (2005) Karst in southeast Asia. In: Gupta A (eds), The physical geography of Southeast Asia (vol. 4). Oxford University Press, Oxford, pp 157-176.

Global High Resolution Population Denominators Project (2018) WorldPop. School of Geography and Environmental Science, University of Southampton; Department of Geography and Geosciences, University of Louisville; Departement de Geographie, Universite de Namur) and Center for International Earth Science Information Network (CIESIN), Columbia University, www.worldpop.org. https://dx.doi.org/10.5258/SOTON/WP00647

Gonsalves C (2020) Mesosphaerum suaveolens (Photo 99022365, CC BY 4.0). https://inaturalist.ca/photos/99022365

Guézou A, Chamorro S, Pozo P, Guerrero M, Atkinson R, Buddenhagen C, Jaramillo Dı´az P, Gardener M., 2017. CDF checklist of Gala´pagos introduced plants. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jime´nez-Uzca´tegui G, Ruiz D, Guézou A, Ziemmeck F (eds) Charles Darwin Foundation Gala´pagos species checklist—Charles Darwin Foundation, Puerto Ayora, Gala´pagos. http://darwinfoundation.org/datazone/checklists/introduced-species/introduced-plants/

Handayani A, Hidayati S (2020) Utilization of Invasive Alien Species (IAS) by communities around Cibodas Biosphere Reserve (CBR): a recommendation for invasive alien species management and policy. In: IOP Conference Series: Earth and Environmental Science 2020 Aug 1, (533): 012017. IOP Publishing. https://doi:10.1088/1755-1315/533/1/012017

Handayani A, Zuhud EA, Junaedi DI (2021) Assessing the utilization of naturalized alien plant species by community to inform its management strategy: A case study in Cibodas Biosphere Reserve, West Java, Indonesia. Biodiversitas Journal of Biological Diversity, 22(7): 1-10. https://doi:10.1088/1755-1315/914/1/012035

Haubrock PJ, Cuthbert RN, Yeo DC, Banerjee AK, Liu C, Diagne C and Courchamp F (2021) Biological invasions in Singapore and Southeast Asia: data gaps fail to mask potentially massive economic costs. NeoBiota, 67: 131-152. https://doi.org/10.3897/neobiota.67.64560

Hejda M, Chytrý M, Pergl J and Pyšek P, (2015) Native-range habitats of invasive plants: are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? Diversity and Distributions, 21(3): 312-321. https://doi.org/10.1111/ddi.12269

Henty EE and Pritchard GH (1975) Weeds of New Guinea and their Control. Lae, Papua New Guinea: Department of Forests, Division of Botany. Botany Bulletin, (7).

Holm LG, Plucknett DL, Pancho JV and Herberger JP (1977) The world's worst weeds. Distribution and biology. University press of Hawaii.

iNaturalist (2021). Available from https://www.inaturalist.org Accessed 2 September 2021

Inderjit, Pergl J, van Kleunen M, Hejda M, Babu CR, Majumdar S, Singh P, Singh SP, Salamma S, Rao BRP and Pyšek P (2018) Naturalized alien flora of the Indian states: biogeographic patterns, taxonomic structure and drivers of species richness. Biol Invasions, 20(6): 1625-1638. https://doi.org/10.1007/s10530-017-1622-y

Invasive Species Specialist Group (ISSG) (2015) The Global Invasive Species Database, Version 2015.1. http://www.iucngisd.org/gisd/. Accessed 16 July 2020.

Jiménez A, Pauchard A, Cavieres LA, Marticorena A and Bustamante RO (2008) Do climatically similar regions contain similar alien floras? A comparison between the mediterranean areas of central Chile and California. J Biogeography, 35(4): 614-624. https://doi.org/10.1111/j.1365-2699.2007.01799.x

Kementerian Lingkungan Hidup and SEAMEO BIOTROP (2003) Penyebaran jenis tumbuhan asing di Indonesia. Kementerian Lingkungan Hidup Indonesia - SEAMEO BIOTROP.

Kristensen NP, Seah WW, Chong KY, Yeoh YS, Fung T, Berman LM, Tan HZ and Chisholm RA (2020) Extinction rate of discovered and undiscovered plants in Singapore. Conserv Biol, 34(5): 1229-1240. https://doi.org/10.1111/cobi.13499

Kull CA, Tassin J, Moreau S, Rakoto Ramiarantsoa H, Blanc-Pamard C and Carrière SM (2012) The introduced flora of Madagascar. Biol Invasions, 14(4): 875-888. https://doi.org/10.1007/s10530-011-0124-6

Kummu M, Taka M, Guillaume JHA (2020) Data from: Gridded global datasets for Gross Domestic Product and Human Development Index over 1990-2015. Dryad, Dataset, https://doi.org/10.5061/dryad.dk1j0

Meise Botanic Garden (2022). Meise Botanic Garden Herbarium (BR). Version 1.27. Meise Botanic Garden. Occurrence dataset https://doi.org/10.15468/wrthhx accessed via GBIF.org on 2022-04-14. https://www.gbif.org/occurrence/2243309430

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA and Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403: 853–858. https://doi.org/10.1038/35002501

Middleton DJ, Armstrong K, Baba Y, Balslev H, Chayamarit K, Chung RCK, Conn BJ, Fernando ES, Fujikawa K, Kiew R and Luu HT (2019) Progress on Southeast Asia's Flora projects. Garden Bulletin Singapore, 71(2): 267–319.

Mittermeier RA, Robles Gil P and Mittermeier CG (1997). Megadiversity: Earth's biologically wealthiest nations. CEMEX. Mexico; Mexico City.

Moser D, Lenzner B, Weigelt P, Dawson W, Kreft H, Pergl J, Pyšek P, van Kleunen M, Winter M, Capinha C, Cassey P, Dullinger S, Economo EP, García-Diaz P, Guénard B, Hofhansl F, Mang T, Seebens H, and Essl F (2018) Remoteness promotes the worldwide invasion of islands. Proceedings of the National Academy of Sciences (115):9270–9275.

Novoa A, Moodley D, Catford J, Golivets M, Bufford J, Essl F, Lenzner B, Pattison Z and Pyšek P (2021) Global costs of plant invasions must not be underestimated. NeoBiota 69: 75–78. https://doi:10.3897/neobiota.69.74121

Nghiem LT, Soliman T, Yeo DC, Tan HT, Evans TA, Mumford JD, Keller RP, Baker RH, Corlett RT and Carrasco LR, (2013) Economic and environmental impacts of harmful non-indigenous species in Southeast Asia. PLoS One, 8(8): e71255. https://doi.org/10.1371/journal.pone.0071255

Pagad S, Genovesi P, Carnevali L, Schigel D and McGeoch MA (2018) Introducing the global register of introduced and invasive species. Scientific Data, 5(1), 1-12. https://doi.org/10.1038/sdata.2017.202

Page S, Hosciło A, Wösten H, Jauhiainen J, Silvius M, Rieley J, Ritzema H, Tansey K, Graham L, Vasander H and Limin S (2009) Restoration ecology of lowland tropical peatlands in Southeast Asia: current knowledge and future research directions. Ecosystems, 12(6): 888-905. https://doi.org/10.1007/s10021-008-9216-2

Parnell J (2013) The biogeography of the Isthmus of Kra region: a review. Nordic Journal of Botany 31:1-15. https://doi.org/10.1111/j.1756-1051.2012.00121.x

Peh KSH (2010) Invasive species in Southeast Asia: the knowledge so far. Biodivers Conserv, 19(4): 1083-1099. https://doi.org/10.1007/s10531-009-9755-7

Pelser PB, Barcelona JF and Nickrent DL (2011 onwards) Co's Digital Flora of the Philippines. www.philippineplants.org

POWO (2021) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/.

Posa MRC, Wijedas, LS and Corlett RT (2011) Biodiversity and conservation of tropical peat swamp forests. BioScience, 61(1): 49-57. https://doi.org/10.1525/bio.2011.61.1.10

Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M and Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon, 53(1):131-143. https://doi.org/10.2307/4135498

Pyšek P and Richardson DM (2006) The biogeography of naturalization in alien plants. J Biogeogr, 33(12): 2040-2050. https://doi.org/10.1111/j.1365-2699.2006.01578.x

Pyšek P, Pergl J, Essl F, Lenzner B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Dullinger S, Ebel AL, Figueiredo E, Fuentes N, Genovesi P, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Maurel N, Meerman J, Morozova O, Moser D, Nickrent D, Nowak PM, Pagad S, Patzelt A, Pelser PB, Seebens H, Shu W, Thomas J, Velayos M, Weber E, Wieringa JJ, Baptiste MP and van Kleunen M (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia, 89: 203-274. https://doi.org/10.23855/preslia.2017.203

Rejmánek M, Thomsen CD and Peters ID (1991) Invasive vascular plants of California. In: Groves RH and di Castri F (eds) Biogeography of mediterranean invasions. Cambridge University Press, Cambridge. pp 81–101

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD and West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and distributions, 6(2): 93-107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Royal Botanic Gardens (RGB) Kew (2016) The state of the world's plants report–2016. Royal Botanic Gardens, Kew.

Royal Botanic Gardens (RGB), Kew (2021). Royal Botanic Gardens, Kew - Herbarium Specimens. Occurrence dataset https://doi.org/10.15468/ly60bx accessed via GBIF.org on 2022-04-14. https://www.gbif.org/occurrence/912146657

SEAMEO BIOTROP 2019. Invasive Alien Plant Species Database. http://kmtb.biotrop.org/collections/spias/detail/159. Accessed 10 December 2019

Soerjani M, Kostermans AJG and Tjitrosoepomo G (1987) Weeds of rice in Indonesia. Balai Pustaka.

Stevens PF (2001 onwards). Angiosperm Phylogeny Website. Version 14, July 2017 [and more or less continuously updated since], http://www.mobot.org/MOBOT/research/APweb/. Accessed 10 February 2022

Thiede J (2001) Agavaceae. In: Arroyo-Leuenberger S, Bayer MB, Bogner J, Eggli U, Forster PI, Hunt DR, van Jaarsveld EJ, Meyer NL, Newton LE, Rowley GD, Smith GF (eds) Illustrated handbook of succulent plants: Monocotyledons. Springer, Berlin, Heidelberg. pp. 5-102

Tjitrosoedirdjo SS, Mawardi I, Tjitrosoedirdjo S (2016) 75 Important Invasive Plant Species in Indonesia. Southeast Asian Regional Centre for Tropical Biology; Bogor.

Turner IM, Tan HTW, Wee YC, Ibrahim AB, Chew PT and Corlett RT (1994) A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. Conservation Biology, 8(3): 705-712.

Turner H, Hovenkamp P and Van Welzen PC (2001) Biogeography of Southeast Asia and the west Pacific. J Biogeogr, 28(2): 217-230. https://doi.org/10.1046/j.1365-2699.2001.00526.x

United Nations, Department of Economic and Social Affairs, Population Division (2019) World Population Prospects 2019, Volume I: Comprehensive Tables (ST/ESA/SER.A/426): 26 - 27

USDA Agricultural Research Service (2015) Germplasm Resources Information Network (GRIN). https://doi.org/10.15482/USDA.ADC/1212393 Accessed 9 November 2020

Danielson JJ and Gesch DB (2011). Global multi-resolution terrain elevation data 2010 (GMTED2010). https://doi.org/10.3133/ofr20111073

van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelser PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu W, Thomas J, Velayos M, Wieringa JJ and Pyšek P (2015) Global exchange and accumulation of alien plants. Nature, 525 (7567): 100-103. https://doi.org/10.1038/nature14910

van Kleunen M, Pyšek P, Dawson W, Essl F, Kreft H, Pergl J, Weigelt P, Stein A, Dullinger S, König C, Lenzner B, Maurel N, Moser D, Seebens H, Kartesz J, Nishino M, Aleksanyan A, Ansong M, Antonova LA, Barcelona JF, Breckle SW, Brundu G, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Conn B, de Sá Dechoum M, Dufour-Dror J-M., Ebel A-L, Figueiredo E, Fragman-Sapir O, Fuentes N, Groom QJ, Henderson L, Inderjit, Jogan N, Krestov P, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Nickrent D, Nowak A, Patzelt A, Pelser PB, Shu W-S, Thomas J, Uludag A, Velayos M, Verkhosina A, Villaseñor JL, Weber E, Wieringa J, Yazlık A, Zeddam A, Zykova E and Winter M (2019) The Global Naturalized Alien Flora (Glo NAF) database. Ecology, 100(1): p.e02542. https://doi.org/10.1002/ecy.2542

Van Steenis CGGJ (1950) The delimitation of Malaysia and its main plant geographical divisions. In: Van Steenis CGGJ (eds) Flora Malesiana Ser. 1, 1. Djakarta: Noordhoff Kolff n.v., lxx–lxxv.

van Welzen PC, Parnell JA and Slik JF (2011) Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? Biol J Linn Soc, 103(3): 531-545. https://doi.org/10.1111/j.1095-8312.2011.01647.x

van Welzen PC and Raes N (2011) The floristic position of Java. Gardens’ Bulletin Singapore, 63(1&2): 329-339.

Vilà M and Hulme PE (2017) Impact of biological invasions on ecosystem services (Vol. 12). Cham: Springer.

Vinod P (2014) Elephantopus scaber (Photo 140126166, CC BY). https://www.inaturalist.org/photos/140126166

Westaway J, Quintao V and de Jesus Marcal S (2018) Preliminary checklist of the naturalised and pest plants of Timor-Leste. Blumea-Biodiversity, Evolution and Biogeography of Plants, 63(2):157-166. https://doi.org/10.3767/blumea.2018.63.02.13

Wohlwend MR, Craven, D, Weigelt P, Seebens H, Winter M, Kreft H, Zurell D, Sarmento Cabral J, Essl F, van Kleunen M and Pergl J (2021) Anthropogenic and environmental drivers shape diversity of naturalized plants across the Pacific. Divers Distrib, 27(6): 1120-1133. https://doi.org/10.1111/ddi.13260

World Checklist of Selected Plant Families (WCSP) (2020) World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. http://wcsp.science.kew.org/.

World Checklist of Vascular Plants (WCVP) (2021) World Checklist of Vascular Plants, version 2.0. Facilitated by the Royal Botanic Gardens, Kew. http://wcvp.science.kew.org/

Witt A (2017) Guide to the naturalized and invasive plants of Southeast Asia. CABI.

Zenni RD (2015) The naturalized flora of Brazil: a step towards identifying future invasive non-native species. Rodriguésia, 66: 1137-1144. https://doi.org/10.1590/2175-7860201566413

Figures

Figure 1

Malesian biogeographic units used in this analysis. Basemap from ESRI (2019).

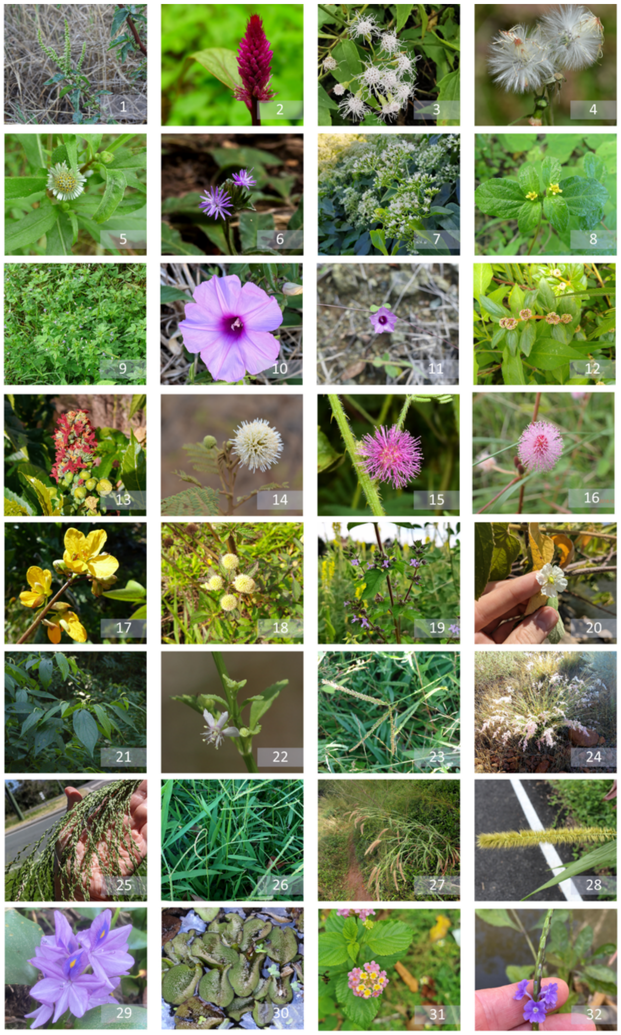

Figure 2

Naturalized plant species that have been reported from every island/island group in Malesia: **Amaranthaceae**; 1) Amaranthus spinosus*, 2) Celosia argentea, **Asteraceae**; 3) Chromolaena odorata* (R Holmes 2022), 4) Crassocephalum crepidioides*, 5) Eclipta prostrata, 6) Elephantopus scaber (Vinod 2014, CC BY), 7) Mikania micrantha*, 8) Synedrella nodiflora, **Cleomaceae**; 9) Cleome rutidosperma*, **Convolvulaceae**; 10) Ipomoea cairica*, 11) Ipomoea triloba, **Euphorbiaceae**; 12) Euphorbia hirta, 13) Ricinus communis, **Fabaceae**; 14) Leucaena leucocephala*, 15) Mimosa diplotricha* (Gassah 2020, CC BY), 16) Mimosa pudica*, 17) Senna occidentalis, **Lamiaceae**; 18) Hyptis capitata, 19) Mesosphaerum suaveolens* (Gonsalves 2020, CC BY), **Muntingiaceae**; 20) Muntingia calabura*, **Piperaceae**; 21) Piper aduncum*, **Plantaginaceae**; 22) Scoparia dulcis, **Poaceae**; 23) Eleusine indica*, 24) Melinis repens, 25) Panicum maximum, 26) Paspalum conjugatum*, 27) Pennisetum polystachion*, 28) Pennisetum purpureum*, **Pontederiaceae**; 29) Eichhornia crassipes*, **Salviniaceae**; 30) Salvinia adnata*, **Verbenaceae**; 31) Lantana camara* (R Holmes 2022), 32) Stachytarpheta jamaicensis. The asterisk (*) indicates species reported as invasive within Malesia in the Invasive Species Compendium (CABI 2022). Images 1:2,4:5,7:14,16:18,20:30 and 31 are 'research grade' and CC0 licensed photos from iNaturalist (2021).

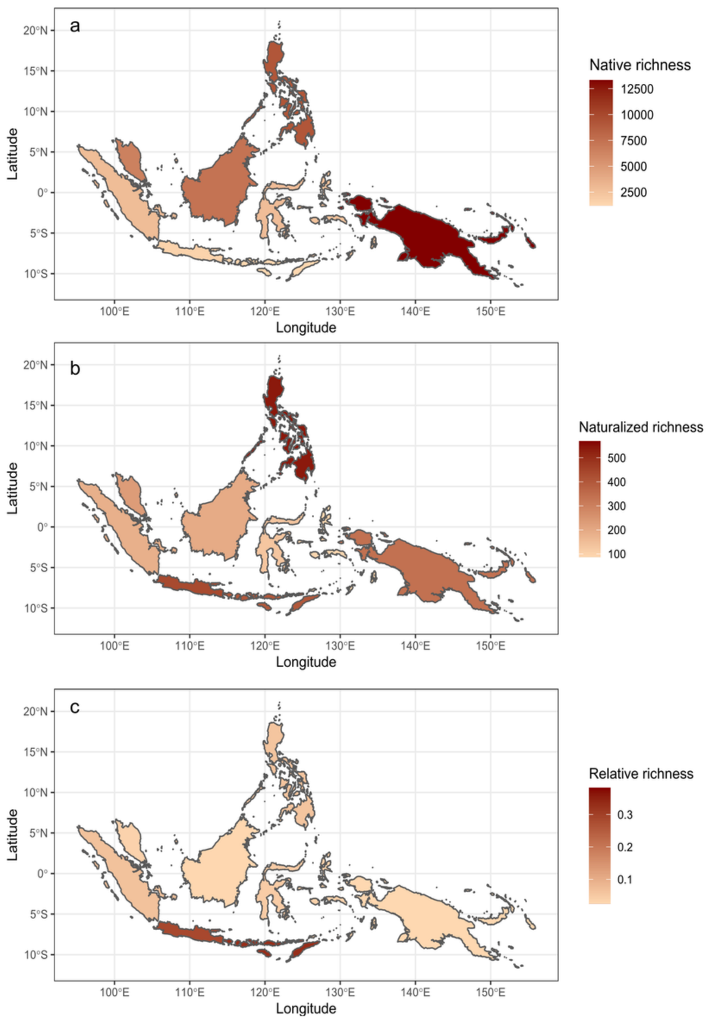

Figure 3

Plant species richness across the archipelago: (a) native richness (no. native species), (b) naturalized richness (no. naturalized species), (c) relative richness (naturalized richness/native richness)

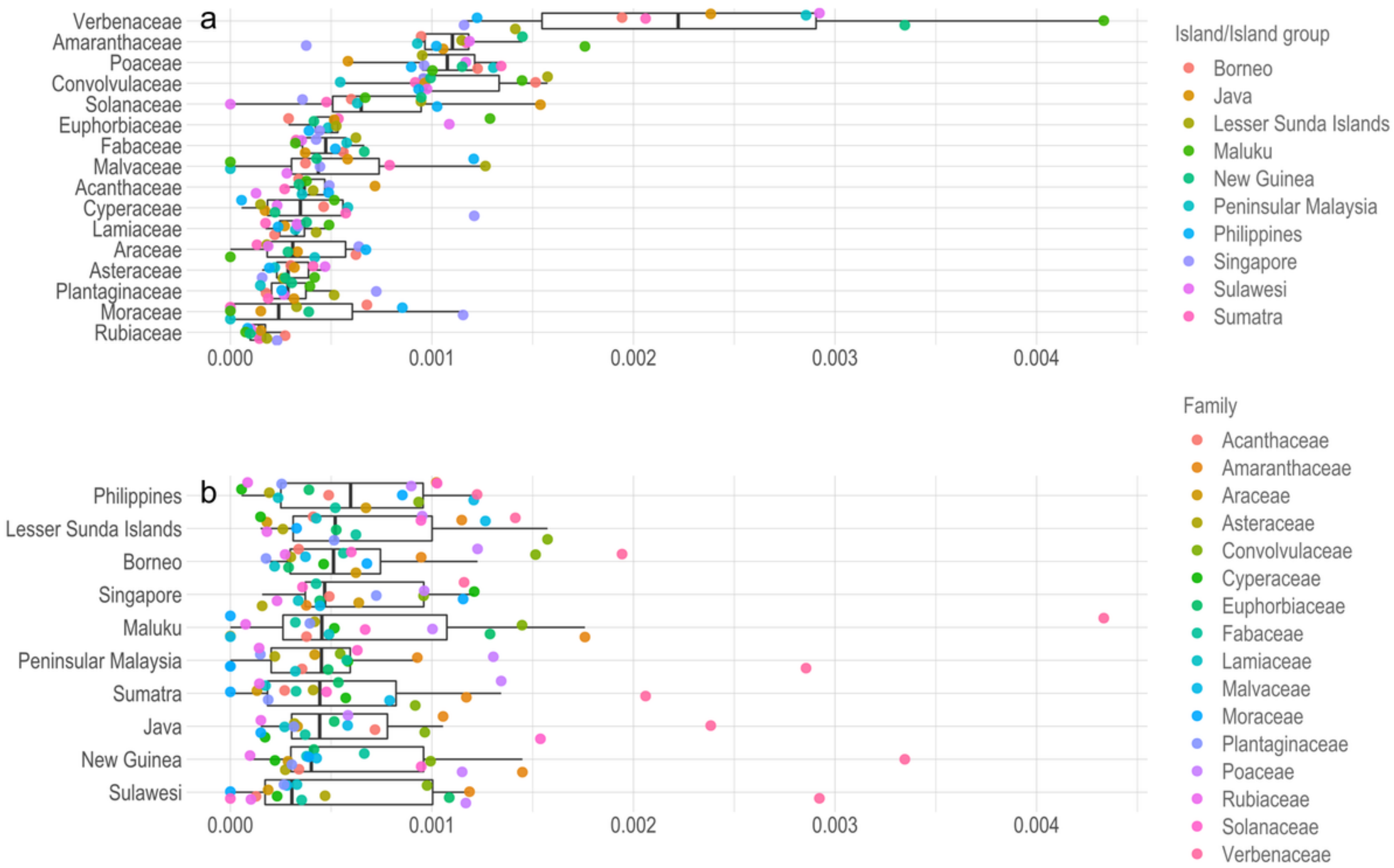

Figure 4

(**a**) Family naturalization index showing only families with at least 10 naturalized plant species in one island group in Malesia; (**b**) family naturalization index for those same families plotted by island group.

Geographic origin

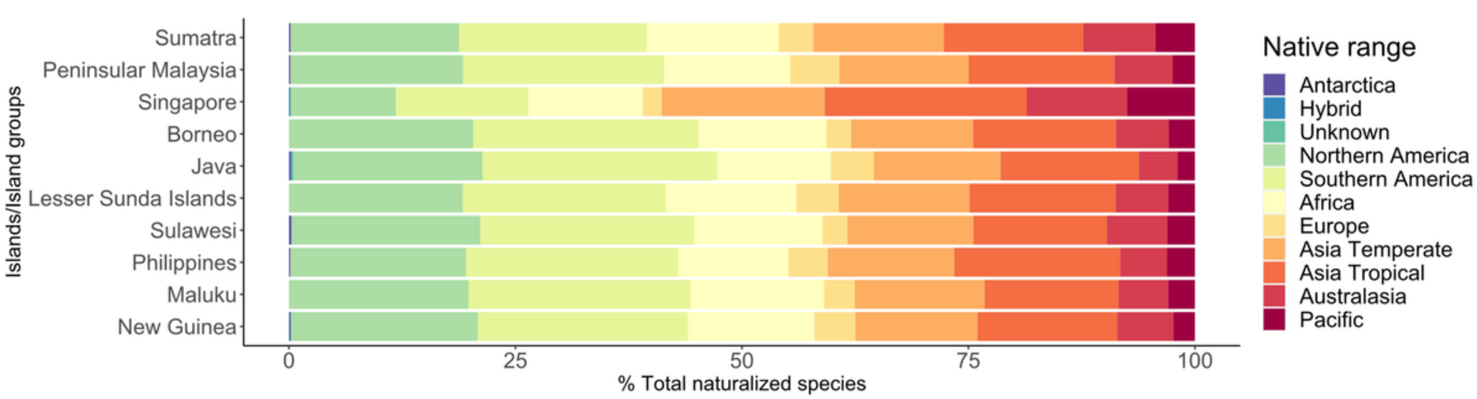

Figure 5

The proportion of naturalized species in each island group by their native range.

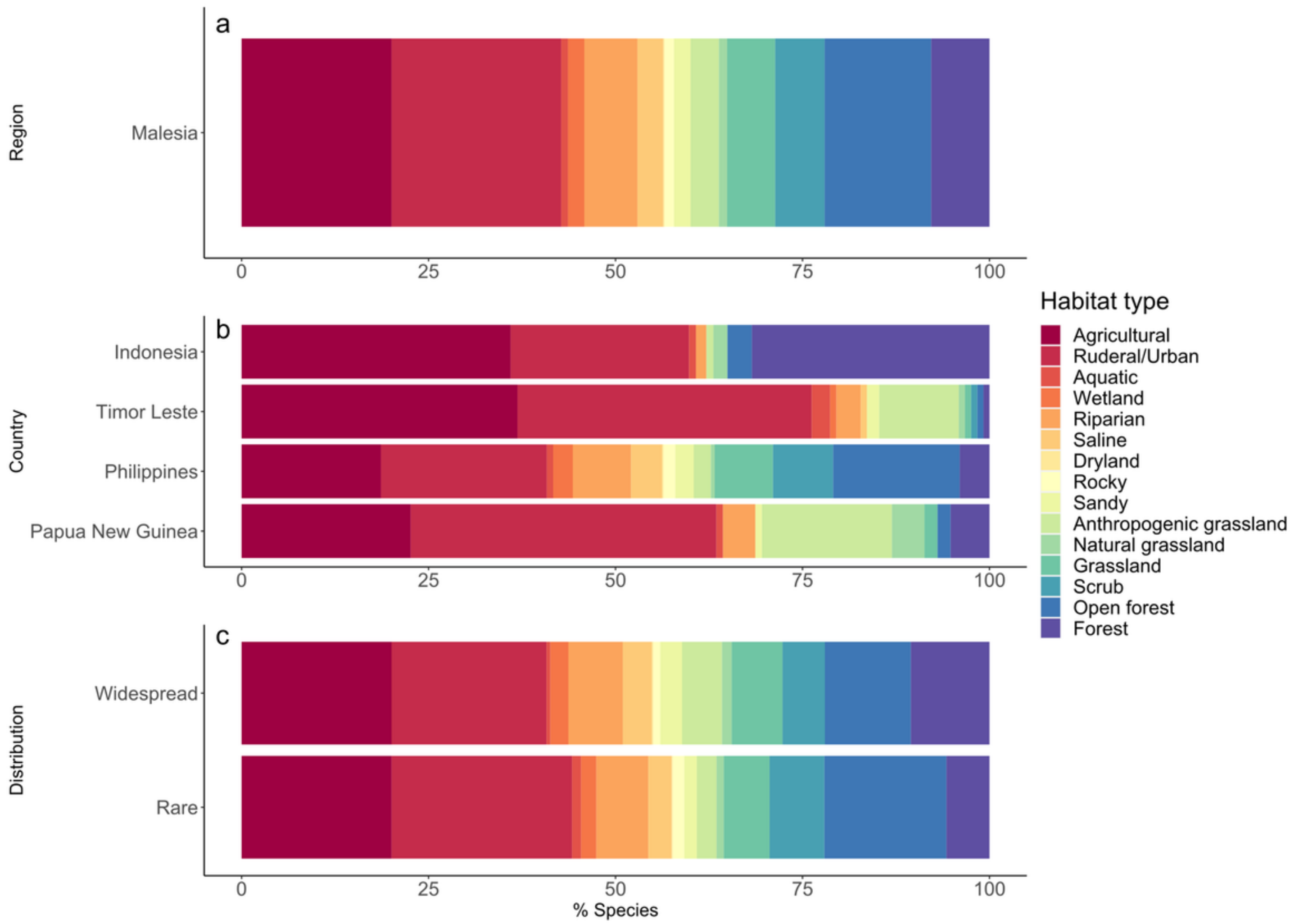

Figure 6

(**a**) The proportion of species occurring in different habitat types in their naturalized range within Malesia; (**b**) The proportion of naturalized species occurring in different habitat types in each country; (**c**) Comparison of the proportion of widespread (≥ 5 island groups) and rare (< 5 island groups) naturalized species occurring in different habitats across Malesia.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- MalNAFMalesiawatchlist.csv
- MalNAFNativerange.csv
- MalNAFNaturalized.csv
- MalNAFSynHab.csv
- MalNAFallversion1.xlsx
- MalNAFanalysis.r
- MalNAFpart1.pdf
- MalNAFpart2.pdf
- MalNAFqualitativesourcedescription.docx
- Malesiaenvironmentaldata.csv
- Nativerichness.csv
- SGPnaturalizednativePenM.csv
- SupplementaryInformationOverview.docx