RESEARCH ARTICLE

# Naturalizations have led to homogenization of the Malesian flora in the Anthropocene

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## Abstract

**Aim:** Worldwide, floras are becoming homogenized at global scales, but regional patterns vary. Here, we present the first assessment for the Malesian phytogeographical region in terms of the timing of introductions, direction, magnitude and drivers of floristic change due to alien plant naturalizations.

**Location:** Malesian phytogeographic region, including Southeast Asia and the Pacific.

**Taxon:** Tracheophyta (vascular plants).

**Methods:** We compiled data on first records of naturalized plants in Malesia to investigate temporal trends in the rate and origin of introductions. We then calculated β-diversity (including turnover and nestedness) for the native, naturalized and Anthropocene (native + naturalized) floras for each pair of island groups (36 pairs), and a homogenization index for the native and Anthropocene floras, using presence/absence data for 31,580 plant species. Mantel tests were used to investigate the geographic, climatic and anthropogenic correlates of dissimilarity and homogenization.

**Results:** Around 75% of all naturalized species documented to date were already reported for the first time within Malesia prior to 1950. This has led to homogenization between the historic (native) and contemporary (Anthropocene) floras for all island group pairs. Turnover was the most important process for driving compositional dissimilarity between island groups in Malesia in the native and Anthropocene floras, but homogenization resulted from decreases in nestedness and turnover. Differences in average taxonomic homogenization for island groups were associated with differences in their level of anthropogenic modification.

**Main Conclusions:** This study improves current understanding of the direction and drivers of floristic homogenization in one of the world's most diverse tropical regions. Alien plant introductions carry a long historical legacy in Malesia, and naturalizations of these plants have led to overall taxonomic homogenization of the region's flora. Expected increases in the magnitude of human modification, without appropriate policy, will likely lead to further reductions in the floristic uniqueness of island groups.

## 1 | INTRODUCTION

Anthropogenic translocation of species beyond their native range has occurred for thousands of years (Pyšek et al., 2020; Seebens et al., 2022). When these species form self-sustaining populations, they are defined as naturalized (Blackburn et al., 2011). Worldwide, at least 13,939 vascular plant species have become naturalized because of intentional or unintentional anthropogenic action (van Kleunen et al., 2019), contributing to increased similarity among biogeographic regions through biotic homogenization (Baiser et al., 2012; Daru et al., 2021; Olden et al., 2016; Yang et al., 2021). While evidence in the geological record shows significant movement of species into previously disparate regions over deep time (Stigall, 2019), the rapidity and scale of historical and contemporary naturalizations are novel, serving as key evidence for researchers pursuing a formalization of the Anthropocene epoch (Barnosky, 2014; Williams et al., 2022).

The impacts of naturalizations on patterns of plant diversity vary at different spatial scales (Vellend et al., 2017). Generally, naturalizations lead to increased species richness and alpha diversity within areas and a decrease in beta diversity between areas (i.e. homogenization, see Table S1). This is because many introduced species that naturalize or become invasive (i.e. a subset of naturalized species rapidly spread over a substantial range of habitats and spatial areas; Blackburn et al., 2011) are likely to become naturalized elsewhere (Olden et al., 2016). Additionally, naturalizations may lead to extirpations of endemic species, further increasing the similarity between regions. Alternatively, introductions can increase beta diversity (i.e. differentiation) when distinct species naturalize in only a few areas (Olden & Poff, 2003; Winter et al., 2009).

The wider impacts of homogenization on people and the environment are diverse. Taxonomic homogenization can affect cultural services by reducing the individuality of areas, which is important for developing a sense of 'place' and deriving income from activities such as ecotourism (Olden et al., 2005). Homogenization also influences the diversity of functional traits within an area, which could reduce the ability of ecosystems to compensate for essential traits lost through native extirpations (Dar & Reshi, 2020; Hautier et al., 2018; Olden et al., 2004).

Several factors have been reported to be significantly associated with homogenization (Cassey et al., 2007; Daru et al., 2021; Devictor et al., 2008; Petsch, 2016; Yang et al., 2021), but the importance of these drivers varies between studies due to differences in spatial scale, taxonomic focus and dissimilarity measures. Potential drivers should be evaluated within the context of the focus region and taxonomic group, or groups. For plants, research often finds that more geographically and climatically disparate floras increase in similarity, and floras with similar anthropogenic legacies, such as similar land use or shared trading history, tend to experience comparable levels of homogenization (e.g. Daru et al., 2021; Kramer et al., 2023; Qian & Qian, 2022; Yang et al., 2021).

With increasing evidence of the homogenizing impact of naturalized species distributions on discrete biogeographic areas at global scales (Capinha et al., 2015; Daru et al., 2021; Yang et al., 2021), there is a need to investigate if these introductions have had similar effects at regional scales. It is particularly important to generate data for Southeast Asia and tropical Africa because these are not currently available for global studies (Olden et al., 2018; Yang et al., 2021). This is particularly important in phytogeographic regions where biogeographic barriers are hypothesized to have led to highly unique and diverse taxonomic assemblages, making them potential 'homogenization hotspots' (Yang et al., 2021). One such region at the intersection of several biogeographic boundaries is the Southeast Asian

phytogeographic region of Malesia. Malesia is bounded in the west by the Thai–Malay peninsula at the Kangar Pattani line and in the east by New Guinea and the Bismarck Archipelago (Ali & Heaney, 2021) (Figure 1; Table S2). The complex and diverse geological and biogeographical history of Malesia, which is an archipelago consisting of a peninsula and islands of different sizes, topographies, climates and ages; underpins its floral diversity with an estimated 45,000 native vascular plant species (see Appendix S1 in Supporting Information; Corlett & Primack, 2011; Hall, 2009). Malesia has traditionally been divided into three floristic sub-regions: Sunda, Wallacea and Sahul (van Steenis, 1950; van Welzen et al., 2011). However, our understanding of the relationships between these sub-regions continues to develop through new analysis using larger datasets (Joyce et al., 2021; van Welzen et al., 2011; van Welzen & Raes, 2011).

The earliest known anthropogenic species translocation within Malesia occurred as early as ~20,000 years ago with the introduction of the northern common cuscus (*Phalanger orientalis*) (Flannery & White, 1991; Heinsohn, 2001). Although that was an animal translocation, this suggests the capacity for human-mediated plant introductions at least since the late Pleistocene in the region. Although early introductions of some alien crop species are well known, for example, from the Philippines (Amano et al., 2021), most early introductions of naturalized plant species are poorly quantified due to preservation and recovery bias (Castillo & Fuller, 2010). Major trading networks were established throughout the Holocene and into the historic period of Hindu and Islamic kingdom building in the archipelago, leading to the development of the Indian Ocean Corridor and eventually the Maritime silk road, where plant species were one type of goods transported between regions (Bellina, 2022; Fuller et al., 2011). During the colonial era, species were introduced directly due to expanding trade networks and land-use change (Barnard, 2021). In the pursuit of commodifying plants of economic value within their new territories through botanic gardens and later forestry departments, colonial regimes actively introduced alien plants and facilitated their growth and

spread in Malesia (Barnard, 2021). Post-1950, expansion of monocultural plantations, urbanization and globalization (Zhao et al., 2006) further opened up new areas for naturalized taxa to establish within Malesia and improved access to novel source pools for new aliens to be introduced (Seebens et al., 2018). Malesia now hosts over a thousand alien naturalized plant species (Holmes et al., 2023).

To understand phytogeographic patterns of Malesia's extant flora, we must investigate spatial and temporal patterns of floristic change, including native and naturalized species. Global introductions of alien species have increased since the 1800s (Seebens et al., 2017). However, patterns vary between regions and taxonomic groups (Seebens et al., 2022). The first records of introduced vascular plants in Asia have a distinct regional pattern, with peaks in introductions in the early and late 1900s (Seebens et al., 2017), but it is unclear whether the introduction of plants now naturalized in Malesia followed the same temporal trends as the rest of Asia, and if rates of first reports are still increasing.

Here, we use the 'Malesian Naturalized Alien Flora database' (MalNAF) alongside a checklist of the native flora for Malesia (see Appendix S2) to provide the first assessment of the timing, magnitude and drivers of homogenization in the region by answering the following questions: (i) Has there been an increase in introductions over time? (ii) Has the naturalization of introduced plant species led to taxonomic homogenization or differentiation of the Malesian flora? and iii) What are the key factors driving changes in similarity?

## 2 | MATERIALS AND METHODS

### 2.1 | Compilation of island group species checklists

The analysis utilized two checklists for terrestrial and freshwater vascular plants. The first is the Malesian Naturalized Alien Flora database (MalNAF) (Holmes et al., 2023), and the second
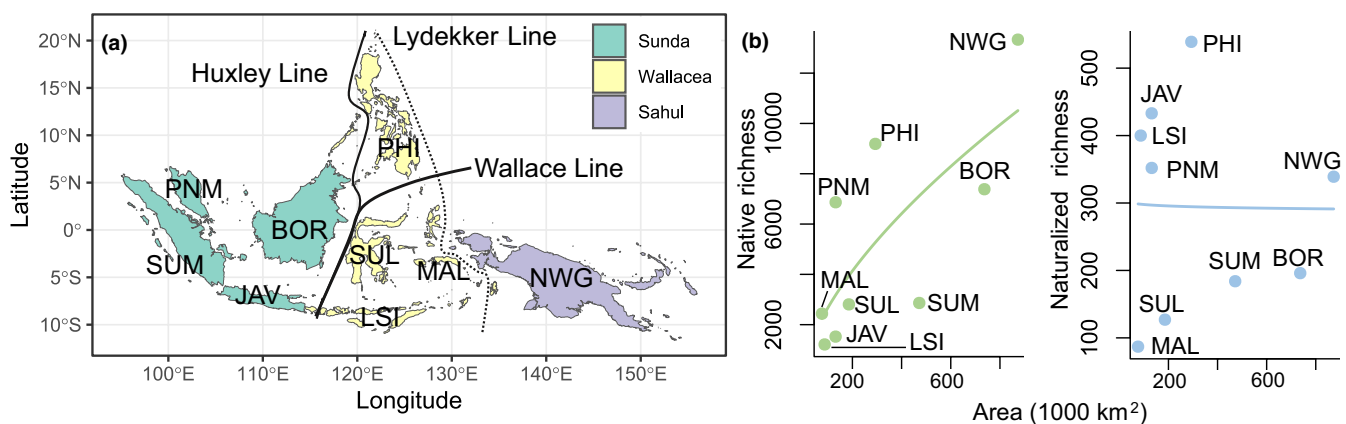


**FIGURE 1** (a) Study area with selected phytogeographic boundaries for the region: Sunda in the west bounded by the Huxley Line, Wallacea is a transitional zone bounded in the west by the Huxley Line and the east most commonly by Lydekker Line (although various boundaries exist), and Sahul traditionally lies to the east of the Lydekker Line; (b) Species area relationship for native and naturalized plant species as represented by the Arrhenius (power law) model (Arrhenius, 1921). Key for island group names: BOR, Borneo; JAV, Java; LSI, Lesser Sunda Islands; MAL, Maluku; NWG, New Guinea; PHI, Philippines; PNM, Peninsular Malaysia; SUM, Sumatra; SUL, Sulawesi.

is a native species checklist for Malesia based on published data. The MalNAF database includes distribution information (presence/absence) for 1177 naturalized plant species at the level of islands or island groups for Malesia, covering 10 biogeographic units (Holmes et al., 2023). We excluded distribution information for native and naturalized plant species for Thailand south of the Kangar Pattani line because data were not available at suitable spatial resolution. We subsumed Singapore within the biogeographic unit of Peninsular Malaysia, resulting in distribution information for 1138 naturalized species across nine biogeographic units or 'island groups' (Figure 1; Table S2). The native checklist was produced by compiling records from four key sources: Pelser et al. (2011 Onwards) for the Philippines; Cámara-Leret et al. (2020) for New Guinea; and Joyce et al. (2020) for the islands/island groups of the Indonesian archipelago (Sumatra, Borneo, Java, Sulawesi, Lesser Sunda Islands and the Maluku Islands) and in combination with Lindsay et al. (2022) for Peninsular Malaysia. Before inclusion in the checklist, the Joyce et al. (2020) dataset was edited to remove alien and cryptogenic species (data deficient with unknown native origin) erroneously included as native.

The taxonomy and binomial species names of all native checklists were standardized in R 4.2.1 (R Studio Team, 2020), following the Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020) using version 1 of their 'LCVP' and 'lcvplants' R package, allowing for three-character fuzzy matching of the species and genus names. To identify and address potential conflicts between the native and naturalized plant species checklists, both datasets were directly compared. When the status of a species conflicted and this could not be resolved, both records were ascribed a new designation: 'cryptogenic' (Essl et al., 2018). The cryptogenic taxa were not included in the analysis.

The native checklist compiled for this study is not considered a comprehensive account of the Malesian flora but seeks to use species lists from the published literature as a baseline with which to investigate floristic change in the region. As such, true species richness in Malesia and that of individual island groups would be expected to be higher than presented here and extant distributions of species may be overrepresented where extirpations have occurred. We made no attempt to account for extinctions and local extirpations in each island group, as comprehensive data are currently only available for Singapore (Kristensen et al., 2020; Lindsay et al., 2022). This omission is likely to lead to a small overestimate of homogenization, as species that are now extirpated from individual island groups may not have disappeared from all, and therefore, removing extirpated taxa could lead to differentiation between the 'native flora' and 'Anthropocene flora' (native + naturalized) (Olden & Rooney, 2006). However, as naturalization of alien species is usually more important than extirpations and extinctions for driving changes in floristic dissimilarity between floras (Castro et al., 2010; Daru et al., 2021; Winter et al., 2009), it is unlikely that the overall direction of floristic change would be different if data on extirpated taxa were available for our study.

With these limitations in mind, the native flora used in this analysis is comprised of 30,724 species. This is, therefore, representative of around 68% of recent estimates for the region's flora of 45,000 species (Corlett & Primack, 2011), whereas the Anthropocene vascular flora of Malesia is composed of at least 31,580 species. Around 2.7% (856) of these species are alien to the region and naturalized, and <1% (282 species) are native to some but alien and naturalized on other island groups within Malesia.

## 2.2 | Minimum residence time

A minimum residence time (Rejmánek, 2000; Richardson & Pyšek, 2006) for each naturalized species was obtained for Malesia by integrating published dates with those extracted from the first herbarium collection of the species within its alien range in Malesia, sourced from the Global Biodiversity Information Facility (GBIF, 2020). Searches were conducted in R using the 'rgbif' package (Chamberlain, 2017) following a four-stage process (obtaining taxon keys, searching by country, cleaning the data and combining datasets), which was adapted after Waller and Grosjean (2019). The dates may represent collection from an individual under cultivation, growing sporadically or fully naturalized, so they are not always a true approximation for either the first arrival of the species or when the species first naturalized but it is a useful proxy when published introduction dates are not available. When a time range was provided for species introductions, the method of Seebens et al. (2017) was used to standardize minimum residence times to a single year for each taxon in a biogeographic unit; this involved using a random number generator to attribute a single year to a species when only a decadal time window was provided for the first introduction. This avoids spikes around attributing them to the beginning, middle or end of the decade. The earliest date from either the published literature or the GBIF-hosted herbarium data was used. Where the literature suggested prehistoric introduction with little consensus on timing, it was labelled as 'likely prehistoric', and the taxon was not included in the temporal analysis. A minimum residence time for Malesia was attained for 902 (=79%) of 1138 naturalized plant species. The majority of first record dates came from herbarium specimen sheets accessed via GBIF ($n = 820$), while minimum residence times for a further 82 species were obtained from the literature.

We created a generalized additive model (GAM) using the mgcv package in R (Wood, 2017) to identify rapid periods of change for the first reports of now naturalized plant species over time (Burge et al., 2023). A non-zero first derivative (slope) of the fitted GAM indicates a rapid change (Burge et al., 2023). As collection effort has varied significantly since the 1700s, potentially influencing detection timing, we included the total number of first reports for all plant species in Malesia as an offset in the model. Data for the first reports of all plant species are only a proxy for collection effort and were also based on GBIF-hosted herbarium data (GBIF. Org, 2023) and are therefore biased by the inclusion of only digitized records.

## 2.3 | Quantifying changes in species composition

Pairwise compositional dissimilarity was quantified using the Sørensen family of dissimilarities: Sørensen ($\beta_{sor}$), beta Simpson ($\beta_{sim}$) and the nestedness-resultant ($\beta_{nes}$) dissimilarity between island groups. Formulas as follows (Baselga, 2010):

$$\beta_{sor} = \frac{b+c}{2a+b+C}, \beta_{sim} = \frac{\min(b,c)}{\min(b,c)+a}$$

$$\text{and } \beta_{nes} = \frac{\max(b,c)-\min(b,c)}{2a+\min(b,c)+\max(b,c)} \times \frac{a}{a+\min(b,c)}$$

where $a$ is the number of shared species between a pair of island groups, $b$ is the number of unique species for the first island group and $c$ is the number of unique species for the second island group (Baselga, 2010). Sørensen pairwise dissimilarity ($\beta_{sor}$) provides a measure of the overall compositional dissimilarity between two island groups but can be partitioned into its constituent components (i.e. $\beta_{sor} = \beta_{sim} + \beta_{nes}$, Figure 2). $\beta_{sim}$ is the spatial turnover (= replacement) component of Sørensen, more independent of species richness than some other dissimilarity indices (Baselga et al., 2007), and therefore, a useful measure due to the large differences in species richness between island groups in this study (Table 1). $\beta_{nes}$, however, quantifies dissimilarity due to differences in richness if floras are nested (Murray & Baselga, 2015), that is, if less species-rich island groups represent a sub-set of floras on more species-rich island groups. Partitioning out beta diversity patterns is useful for disentangling the underlying processes associated with compositional change across space and through time due to naturalizations (Baeten et al., 2012; Baselga, 2010; Castro et al., 2020).

Pairwise dissimilarity was calculated in R using the package 'betapart' (Baselga & Orme, 2012). We produced a dissimilarity matrix where 0 suggests that all species of a pair of island groups are present on both island groups and 1 indicates that there are no species shared. Dissimilarity was quantified for the native, naturalized and Anthropocene (native + naturalized) floras. To quantify the degree of taxonomic homogenization or differentiation, a homogenization index ($H$) (Rahel, 2000) was then calculated as the change between the native and Anthropocene

total dissimilarity for an island group pair, which represents compositional change between the past and present, that is, $H_{sor} = \text{Anthropocene}(\beta_{sor}) - \text{native}(\beta_{sor})$. A negative $H$ value indicates homogenization, and a positive value indicates differentiation. We calculated the homogenization index for turnover ($H_{sim}$) and nestedness resultant dissimilarity ($H_{nes}$) in the same way to identify which was a bigger contributor to $H_{sor}$. Additionally, we quantified and partitioned total dissimilarity across all island groups for the native, naturalized and Anthropocene floras as well as a homogenization index again using the complimentary multi-site dissimilarity of Baselga (2010):

$$\beta_{sor} = \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}, \beta_{sim} = \frac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$

$$\text{and } \beta_{nes} = \frac{\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]-\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]} \times \frac{\sum_i S_i - S_T}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}.$$

Here, $S_i$ is the number of species in island $i$; $S_T$, total species richness for all islands; and $b_{ij}$ and $b_{ji}$ are unique species to $i$ and $j$ (Baselga, 2010).

To test whether observed patterns of floristic change could be due to stochastic process, we compared mean homogenization index values across all island pairs with a null model, following Padullés Cubino et al. (2019). This involved using the Picante package in R (Kembel et al., 2010) to generate 999 random permutations of the species community data using the independent swap algorithm (Gotelli, 2000), calculating dissimilarity and $H$ for each permutation and then identifying if observed values appear in the null model at 95%, 99% and 99.9% confidence intervals (Figure S3). If significant, this suggests that observed patterns of floristic change are not due to chance alone and are likely a consequence of human-mediated introductions.

Lastly, hierarchical cluster analysis employing the unweighted pair group method using arithmetic averages (UPGMA) was used to identify clusters of similar floras for all dissimilarity matrices. These steps were also performed as part of an additional analysis at the genus and family level (Appendix S1). Exploring the degree of floristic change across taxonomic rank allows for an exploration of the evolutionary depth of native biogeographic patterns and how these have been influenced by naturalizations.

We present results based on Baselga's approach for partitioning beta diversity (Baselga, 2010), the most widely used (Baselga & Leprieur, 2015). Criticism (Carvalho et al., 2012; Chen & Schmera, 2015; Podani & Schmera, 2016; Schmera et al., 2020) has led to alternative approaches, including the Podani family (Podani & Schmera, 2011) used here in a supplementary analysis
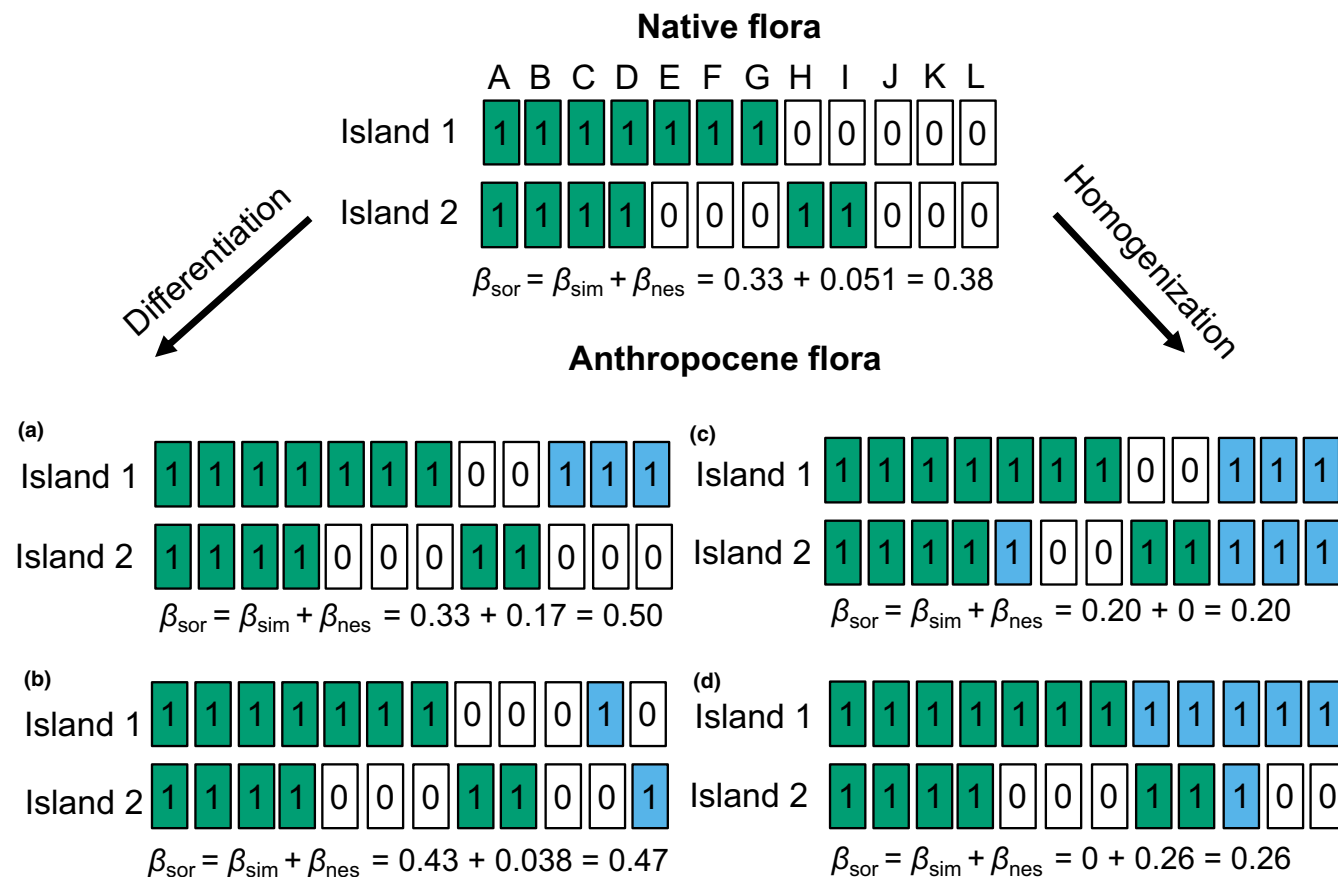
**FIGURE 2** Hypothetical examples using presence (1)/absence (0) data for 12 species (A–L) showing compositional change based on the Sørensen family of dissimilarities between the native and Anthropocene floras due to naturalizations (adapted after Baeten et al., 2012, p. 1401). Green indicates the species is native and blue are naturalized species. The native floras share four species and have three and two unique species, respectively, reflecting dissimilarity ($\beta_{sor}$) due to both turnover ($\beta_{sim}$) and nestedness resultant dissimilarity ($\beta_{nes}$). In examples (a) and (b), differentiation has occurred due to naturalizations only occurring on the more species-rich island (i.e. $H_{sor} = 0.50 - 0.38 = +0.12$); and due to naturalization of different species to each island ($H_{sor} = +0.09$), respectively. For (c) and (d), homogenization has occurred due to naturalization of widespread species in both islands and naturalization of a species native to Island 1 to Island 2 ($H_{sor} = -0.18$); and in (d), the richer island has become richer through naturalizations perfectly nesting Island 2 ($H_{sor} = +0.12$). Values are rounded to two decimal places (adapted after Baeten et al., 2012 p. 1401).

**TABLE 1** Summary of average dissimilarity (mean ± SD) of the Malesian flora, the degree of floristic change ($H$ mean), across all unique pairs of island groups ($n = 36$ pairs) and multi-island group dissimilarity ($n = 9$ island groups).

| Comparison | Dissimilarity | Native flora | Naturalized flora | Anthropocene flora | $H$ mean |
|---|---|---|---|---|---|
| Pair | $\beta_{sor}$ | 0.770 ± 0.10 | 0.590 ± 0.11 | 0.752 ± 0.10 | −0.018 ± 0.01 |
| Pair | $\beta_{sim}$ | 0.572 ± 0.13 | 0.358 ± 0.15 | 0.565 ± 0.12 | −0.007 ± 0.03 |
| Pair | $\beta_{nes}$ | 0.198 ± 0.13 | 0.230 ± 0.17 | 0.187 ± 0.13 | −0.011 ± 0.03 |
| Multi | $\beta_{sor}$ | 0.899 | 0.807 | 0.893 | −0.006 |
| Multi | $\beta_{sim}$ | 0.795 | 0.668 | 0.790 | −0.006 |
| Multi | $\beta_{nes}$ | 0.104 | 0.140 | 0.103 | −0.001 |

*Note*: Mean $H$ values were all significantly different against the null model ($p < 0.001$).

to identify differences in partitioning. We found high correlations (native Mantel's $r = 0.72$, naturalized $r = 0.94$, Anthropocene $r = 0.78$ and $H$ $r = 0.77$) between the turnover component of both metrics as well as for the nestedness and richness differences (native Mantel's $r = 0.94$, naturalized $r = 0.97$, Anthropocene $r = 0.93$ and $H$ $r = 0.85$). An overview of the results is included in Appendix S1; the full code and outputs are at the end of Appendix S5.

## 2.4 | Exploring drivers of dissimilarity and floristic change

We explored the relationship between floristic dissimilarity ($\beta_{sor}$, $\beta_{sim}$ and $\beta_{nes}$) of the native and naturalized floras of island pairs, and absolute differences in the average degree of homogenization (or differentiation) ($H_{sor}$, $H_{sim}$, $H_{nes}$) for island groups, with climatic, geographic

and anthropogenic variables through Mantel tests using Spearman's method due to non-normality in some variables. Calculations were conducted in QGIS 3.14, and R 4.2.1 with the package 'ecodist' for Mantel tests (Goslee & Urban, 2007).

Global climate data at 2.5-min spatial resolution were downloaded from WorldClim 2.1 (Fick & 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 were then extracted for PC1 (59.4%), PC2 (27%) and PC3 (10.4%), which together explain ~96.8% of climatic variation across the Malesia region (Figure S1). PC1 increases with increasing seasonality of precipitation (bio15) and decreases with precipitation in the driest month (bio14), whereas PC2 and PC3 largely reflect differences in temperature, that is, PC2 increases with average annual temperature (bio1), and PC3 decreases with increasing seasonality of temperature (bio4). To produce one variable to represent differences in climate (i.e. climate dissimilarity), we used the Euclidean distance between the first three PCA axes for each pair of island groups (calculated as the square root of the sum of the squares of the differences between paired PC scores) (Qian & Shimono, 2012).

To get a single variable to represent differences in the levels of anthropogenic impact, we calculated the absolute value of the difference in the mean of the Human Modification Index (HMI) (Kennedy et al., 2020) for each unique pair of island groups. The HMI is a modelled index (0=not modified; 1=highly modified) based on 13 anthropogenic environmental stressors: human settlement (population density and built-up areas), agriculture (cropland and livestock), transportation (major roads, minor roads, two tracks and railroads), mining and energy production (mining, oil wells and wind turbines) and lastly electrical infrastructure (powerlines and night-time lights) (Kennedy et al., 2019).

Geographic distance was calculated as the distance between the estimated centroids of polygons for each unique pair of island groups (see Appendix S3).

An R Markdown pdf of the code and output used for analysis can be found in Appendix S5.

## 3 | RESULTS

### 3.1 | Temporal trends in introductions

In Malesia, the introduction of naturalized plant species began in prehistory, and first reports accelerated since the 1800s, peaking between the 1860s and the 1920s (Figure 3a). The average rate of introductions is 4.85 species per year since 1750. Our records suggest that the rate of introductions increased from 1800 to 1950, with around six species introduced per year. Around 75% of the naturalized plant species now present across Malesia had already been introduced by 1925, with 50% being introduced during a 58-year period from 1867 to 1925. The rate of introductions has slowed but continued into the 21st century. The GAM of naturalized plant species introductions explained 36% of the variation in the rate of introductions overtime (p<0.001) and identified two short periods of rapid increase followed by a decrease, around the 1900s and 1950s (Figure 3b). Current rates
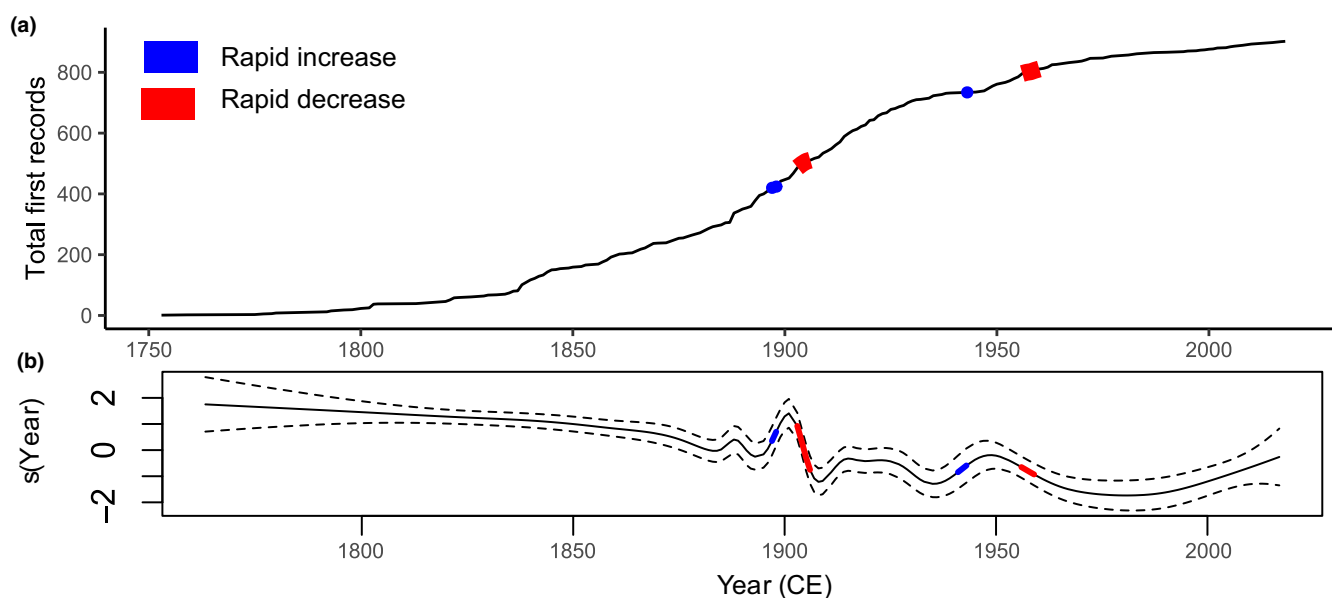


**FIGURE 3** Minimum residence time of naturalized plant species in Malesia: (a) cumulative number of naturalized plant species first records (n=904); (b) smooth plot showing the non-linear relationship between first records of naturalized plant species (n=892) over time when accounting for changes in sampling effort using an offset with a generalized additive model (GAM, adj. R=0.36, p<0.001). Where the first derivative (slope) of the fitted GAM is different from 0, this indicates a rapid period of change. Therefore, blue indicates a period of rapid increase in introductions, and red, a rapid decrease.

of introductions are not significantly different compared with the general trend in introductions since 1750 (Figure 3b). Species likely introduced during prehistory had a native range that included tropical Asia, temperate Asia and Australasia (Figure S2). From the 1750s, native ranges of the introduced species diversified, with species from Southern and Northern America, Africa, the Pacific and Europe being introduced (Figure S2). Between 1800 and 1850, most naturalized species had a native range that included Southern America. As overall first reports decrease from 1950 until recently, introductions from Southern America remain high, and those from Asia fall below Africa.

## 3.2 | Floristic change in the Anthropocene

Average species richness per island group was much higher for native species (5291 ± 4149 SD) compared with naturalized species (295 ± 153 SD). Conversely, average frequency was higher for naturalized plants, which occur on 2.33 ± 2.09 SD island groups, compared with only 1.55 ± 1.31 SD island groups for native plant species. Orchidaceae, Rubiaceae, Apocynaceae, Arecaceae and Myrtaceae represent the plant families with the highest numbers of native species, whereas Fabaceae, Asteraceae, Acanthaceae and Solanaceae rank among the families with the highest numbers of naturalized species. Orchidaceae, Rubiaceae, Fabaceae, Apocynaceae and Areceae possess the highest numbers of species when considering the whole Anthropocene flora (Figure S3).

Values for $\beta_{sor}$ for both the native (Figure 4a) and Anthropocene (Figure 4c) floras were comparable, ranging from 0.56 to 0.92 for the former and 0.56 to 0.90 for the latter (Table 1). In the native flora, Peninsular Malaysia and Borneo were the most similar and Java and New Guinea were the most dissimilar (Figure 4a), whereas New Guinea and Sumatra were the most dissimilar in the Anthropocene flora (Figure 4c). All pairs of island groups demonstrated taxonomic homogenization (Figure 4b) with the level of floristic change (H) ranging from −0.0032 to −0.056 and averaged −0.018 or a ~2% increase in similarity (Table 1). Homogenization (−0.0063) also occurred for changes in dissimilarity when comparing all island groups in the multi-site analysis (Table 1). However, this decrease is much smaller than the change in dissimilarity between island pairs. The flora of Java and the Lesser Sunda Islands increased in similarity the most (Figure 3b). Turnover ($\beta_{sim}$) was the most important for explaining compositional differences between island groups in Malesia in the native and Anthropocene floras (Figure S2). Mean values for $H_{sim}$ and $H_{nes}$ were significantly different from the null model ($p < 0.001$), suggesting that both contributed to pairwise homogenization of the flora (Table 1; Figures S4 and S6). However, mean decreases in nestedness ($\beta_{nes}$) between the native and Anthropocene floras ($H_{nes} = −0.011$) were larger than decreases in turnover ($H_{sim} = −0.0069$) in our pairwise comparison (Table 1; Figure S6). This suggests that richness differences became less important for the dissimilarity between island pairs in the Anthropocene flora (Table 1), while turnover became less important for dissimilarity in our multi-island comparison (Table 1).

Based on the UPGMA analysis of $\beta_{sor}$, the native flora can be split into two groups (Figure 4a): (1) New Guinea; and (2) all other islands that traditionally comprise Sunda and Wallacea. These and all other UPGMA clusters based on $\beta_{sor}$ values for the Anthropocene are identical (Figure 4c), suggesting that the introduction of naturalized plant species has not led to a shift in phytogeographic groups.

For the naturalized flora, the $\beta_{sor}$ dissimilarity between island groups ranged from 0.32 to 0.83 (Figure 4d). Here, Sulawesi and Sumatra were the most similar of all island groups and the Philippines had the most dissimilar naturalized flora with the Maluku Islands. Two clusters were identified from the UPGMA analysis of $\beta_{sor}$ for the naturalized flora: (1) Borneo, Maluku, Sulawesi and Sumatra; and (2) Peninsular Malaysia, the Philippines, Java, the Lesser Sunda Islands and New Guinea (Figure 4d). The mean dissimilarity of the naturalized flora across island groups ($\beta_{sor} = 0.59 \pm 0.12$ SD) was lower than for the native flora at the species level (Table 1). Therefore, the naturalized flora is around 23% more similar than the native flora on average.

Data for the pairwise dissimilarity values and changes can be found in Appendix S6.

In our analysis of the broad potential drivers (geographic distance, climate and anthropogenic modification) of dissimilarity ($\beta_{sor}$) among the native flora, we found significant positive relationships between increasing geographic (Mantel's $r = 0.70$, $p < 0.001$; Figure S9a) and climatic (Mantel's $r = 0.49$, $p < 0.05$; Figure S9b) distance and increasing dissimilarity (Table 2; Table S3). For the naturalized flora, there was only a significant relationship between geographic distance and species turnover ($\beta_{sim}$; Mantel's $r = 0.42$, $p < 0.05$, one-tailed; Figure S9c; Table S5). Island pairs with similar levels of human impact, as measured by the HMI, have experienced similar levels of homogenization on average (Mantel's $r = 0.48$, $p < 0.05$; Figure S9d; Table S6).

## 4 | DISCUSSION

Our results support most previous studies at regional and global scales in showing an increase in the cumulative number of naturalized plant species introduced during at least the last few centuries (Egawa & Koyama, 2023; Ni & Deane, 2022; Seebens et al., 2017, 2022), demonstrating that this has led to a loss of taxonomic beta diversity (Baiser et al., 2012; Daru et al., 2021; Yang et al., 2021). Our focus on Malesia resulted in filling a crucial geographic data gap for homogenization research in tropical regions (Olden et al., 2018).

### 4.1 | Accumulation of naturalized plant species in Malesia

First reports of naturalized plant species in Malesia did not increase linearly over time (Figure 3a). Our data suggest introductions peaked around the 1900s in Malesia, with an additional smaller peak around the 1950s (Figure 3b). Our results differ from Seebens et al. (2017)
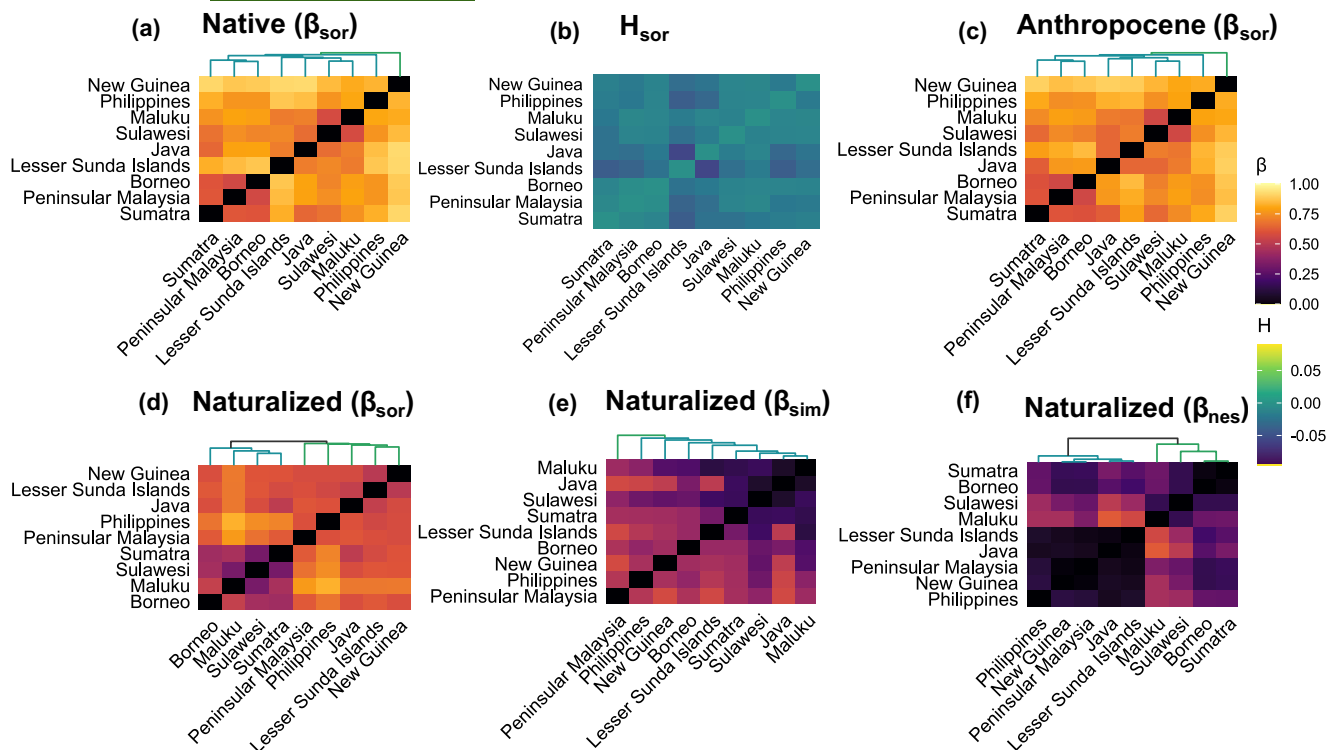
**FIGURE 4** Species-level dissimilarity as inverse matrices for the native (a), naturalized (d–f) and Anthropocene floras (c) and changes in dissimilarity between the native and Anthropocene floras based on the homogenization index (H) values for $\beta_{sor}$ (b). For $\beta_{sor}$, 0 suggests flora on both islands are the same (black) and 1 indicates there are no species shared (yellow). For $\beta_{sim}$, 0 suggests there is no dissimilarity due to turnover and 1 indicates that all dissimilarity is due to turnover. $\beta_{nes}$ would have a value of 0 if there was no nestedness between pairs regardless of whether there are other dissimilarities due to turnover. Therefore, for $\beta_{nes}$, values above 0 largely reflect dissimilarity due to richness differences for nested pairs. Dendrograms are based on hierarchical cluster analysis of the dissimilarity matrix which are coloured by group. For H, negative values indicate homogenization (black), and positive values indicate differentiation (yellow).

**TABLE 2** Results of two-tailed Mantel tests using Spearman's correlation among geographic, climatic and anthropogenic (human modification index: HMI) distances with floristic dissimilarity ($\beta_{sor}$) of the native and naturalized flora and differences in the average degree of floristic homogenization ($H_{sor}$) for unique pairs of island groups in Malesia.

| Variable | Geographic distance | | Climatic distance | | Dif. Mean HMI | |
|---|---|---|---|---|---|---|
| | r | p-value | r | p-value | r | p-value |
| Native | 0.702 | **<0.001** | 0.488 | **0.023** | 0.097 | 0.676 |
| Naturalized | 0.014 | 0.938 | 0.0221 | 0.906 | 0.001 | 1.000 |
| $H_{sor}$ | −0.248 | 0.283 | 0.338 | 0.158 | 0.479 | **0.049** |

*Note*: Significant values (p<0.05) are in bold. See Appendix S1 for full results.

reporting peaks around the 1920s and 2000s for the Asian continent. This suggests introductions of alien plant species in Malesia preceded those in the rest of Asia. Seebens et al. (2017) and similar studies do not account for fluctuations in collection effort over time and this may lead to differences in the timing of peaks and trends in introduction rates between studies. The 19th and 20th centuries saw a worldwide expansion of botanical collections (Penn et al., 2018), although notable declines have occurred, for example, during the Second World War (Seebens et al., 2022). We recommend using a proxy for collection effort as an offset in temporal analysis, as we have used here, to account for such changes in future studies. When accounting for collection effort (Figure 3b), the first period of

introductions, around the 1900s, coincided with the dominance of European colonial empires across the archipelago (Barnard, 2021), mirroring the legacy of European colonialism elsewhere in the world (Lenzner et al., 2022). This led to the introduction of important invasive species (such as *Vachellia nilotica* and *Eichhornia crassipes* [Tjitrosoedirdjo et al., 2016]) with significant economic impacts (Nghiem et al., 2013). After a short rapid increase, the rate of introductions declined after 1950, stabilizing at an average of 2.6 species per year until 2018. Most countries in Malesia now have policies and legislation in place to prevent further introductions and curb the spread of naturalized plants (e.g. Aruga et al., 2020; Department of Environment and Natural Resources-Biodiversity Management

Bureau, 2021; Plant Biosecurity Division, 2021; Radiansyah et al., 2015). However, introduction rates in the 21st century have not significantly decreased from the modelled trend since 1750 in Malesia; and rates may increase in the future. The prediction of an increase in alien plant species in tropical Asia and Australasia (10% and 28%, respectively; Seebens et al., 2021) calls for more effective legislation to reduce future introductions (Latombe et al., 2023).

## 4.2 | Homogenization of the Malesian flora

Through the first assessment of the direction and magnitude of floristic change due to naturalizations in Malesia, we have shown that significant but modest taxonomic homogenization has occurred between all island pairs (Figure 4b). Total similarity increased by around 2% on average (i.e. $H$ mean −0.0179; Table 2). Accordingly, the overall level of homogenization in Malesia is similar to that reported for plants in analyses for other tropical, subtropical and temperate regions (Castro et al., 2010; Qian & Qian, 2022; Qian & Ricklefs, 2006; Wani et al., 2023; Winter et al., 2009) and the global average ($H_{sor}=0.022\pm0.033$) (Yang et al., 2021). However, because these studies used a range of dissimilarity measures, and some included species extirpations, they are not entirely comparable. Additionally, the native Malesian flora has high species richness and, therefore, significantly more naturalizations need to occur to be able to identify taxonomic homogenization.

Reductions in turnover and nestedness both contributed to homogenization to varying degrees heterogeneously across Malesia (Figure 4b,c). Declines in turnover are partly caused by the 15% of naturalized plant species that are now widespread throughout the archipelago (Holmes et al., 2023), increasing the total shared taxa among all island groups and some island pairs. Many of these taxa are the same 'superinvaders' (Daehler, 2003; Stohlgren et al., 2011) that have had a substantial influence on homogenization globally (Daru et al., 2021) and are therefore likely to also increase the similarity of the Malesian flora with geographically disparate floras, especially those with similar climates (Yang et al., 2021). The mean decrease in nestedness was highly influenced by changes in only a few island group pairs (Figure 4c). The biggest decrease in nestedness of ~7% occurred between Java and Borneo (Figure S8). For these islands, the dissimilarity of their native floras was equally due to turnover and nestedness ($\beta_{sim}$ and $\beta_{nes}=0.40$) but a different suite of naturalized species was introduced to both islands, as well as more species native to Borneo but not to Java, thus increasing spatial turnover and reducing the dissimilarity due to nestedness. Most regional studies of floristic compositional change in plants have only investigated changes in either total dissimilarity or turnover dissimilarity (e.g. Castro & Jaksic, 2008; Qian & Qian, 2022; Qian & Ricklefs, 2006; Wani et al., 2023; Winter et al., 2009), which limits available comparative data. This omission risks masking the different processes associated with homogenization, within and between regions, that are provided through partitioning of turnover and nestedness (Baeten et al., 2012) and should be a focus for future work.

Geographic and climatic distance were associated with dissimilarity between native island floras but not with naturalized floras, suggesting dispersal is less limiting for the latter and that naturalized plants tend to have a broader climate tolerance—which is unsurprising and has previously been shown (e.g. Yang et al., 2021). Additionally, the link between human impact and homogenization that we found for Malesia tracks other studies across several different taxonomic groups and regions (Gossner et al., 2016; McKinney, 2006; Olden et al., 2005, 2006; Petsch, 2016), and even for global species interactions (Fricke & Svenning, 2020), reinforcing the critical role of people and economic systems in driving homogenization. As human modification increases as predicted, for example, for cropland in Malesia (Molotoks et al., 2018), taxonomic homogenization is likely to increase in the future. Additionally, the Chinese Government's 'Belt and Road' initiative, which expands road, rail, air and sea networks, increases Malesia's risk of invasion through increased connectivity, further threatening native floristic biodiversity (Chapman et al., 2017; Liu et al., 2019; Seebens, 2019) unless adequate policies are in place to prevent and control new naturalizations.

Notably, the increase in similarity that we observed has not resulted in a shift of phytogeographic groupings, and the estimate of homogenization resulting from the multi-island comparison was small. Therefore, based on currently available data, the blurring of globally significant biogeographic boundaries that has been a proven feature of the Anthropocene for some taxonomic groups and regions (Capinha et al., 2015; Williams et al., 2022) has yet to occur for plants within Malesia. However, our results likely underestimate the magnitude of floristic change that has resulted from naturalizations due to our focus on taxonomic homogenization using presence/absence data. La Sorte and McKinney (2007) have argued that it is important to provide a quantitative assessment of real-world patterns of floristic change. Currently, there is limited information on the abundance of native and naturalized plant species in our study region. However, floristic surveys undertaken within Malesia provide an indication that many naturalized and especially invasive species are widespread and abundant at the local level (Hashim et al., 2010; Padmanaba et al., 2017). For example, Rembold et al. (2017) conducted floristic surveys along a land-use intensity gradient from native forest to monoculture forest (rubber and oil palm) in lowland Sumatra and found that overall species numbers decreased, and the proportion of alien species increased with increasing intensity of land use. Within the oil palm plantations they surveyed, 25% of species were alien, and these made up 62% of abundance in the community; oil palm and rubber plantations (both alien crop species) were floristically similar. It is therefore important for future research to improve data on measures of abundance and area covered by naturalized species with geo-referenced distribution information, which is currently at low resolution for much of the Malesian region and confined to a subset of species (Shrestha et al., 2022). Developments in methods like remote sensing for mapping native and alien plant species (Huang & Asner, 2009; Walsh, 2018) will be crucial for obtaining these data in Malesia, where botanical collection effort has highly varied between islands (Middleton et al., 2019). Collating this

information would improve our ability to assess the true direction and magnitude of floristic compositional change at a range of spatial scales, and ultimately this needs to be combined with an assessment of phylogenetic and functional homogenization (Olden et al., 2018).

## 5 | CONCLUSION

Malesia's island groups have become more homogenized due to alien plant species naturalization, although no phytogeographic shift has occurred when considering total dissimilarity. Early introductions came mostly from Asia and Australasia, but South America quickly became a major source of introduced plants as source pools diversified alongside expanding trade routes and land-use change associated with colonialism and globalization. Between the 1860s and 1925, around 50% of naturalized plant species were reported and over 75% by the 1950s. Differences in the level of human modification were significantly correlated with differences in the magnitude of floristic change. Although current first report rates of introductions are lower than during the colonial era, further human modification (e.g. in urban and agricultural areas) may lead to more homogenization; but future patterns will depend on the establishment of new trade networks and the implementation of effective biosecurity policies.

### CONFLICT OF INTEREST STATEMENT
The authors have no relevant financial or non-financial interests to disclose.

### DATA AVAILABILITY STATEMENT
The MalNAF dataset is accessible here: https://link.springer.com/article/10.1007/s10530-022-02989-y, the native checklist is included in Appendix S2 in Supporting Information. Data on climate variables are available here: https://www.worldclim.org/data/bioclim.html, on the Human Modification Index here: https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems. Herbarium collection data for Malesia can be downloaded from GBIF (GBIF.Org, 2023). The clipped and transformed environmental data are available as a shape file with an attribute table in Appendix S3. Minimum residence time data used in this analysis are in Appendix S4. An R Markdown pdf of the code and output used for analysis can be found in Appendix S5. Appendix S6 is an xlsx file including the pairwise island dissimilarity data.

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**BIOSKETCH**

**Rachael Holmes** is interested in anthropogenic dimensions of tropical environmental change. This work represents a component of her PhD work at the University of Leicester on human impacts on the biosphere in Island Southeast Asia over the Holocene and into the Anthropocene. She and the other authors collaborate on questions of invasion biology, botanical biodiversity and the Anthropocene.

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## SUPPORTING INFORMATION

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