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Gondwanan survivor lineages and the high-risk biogeography of Anthropocene Southeast Asia

Running title: Anthropocene biogeography in Southeast Asia

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Abstract

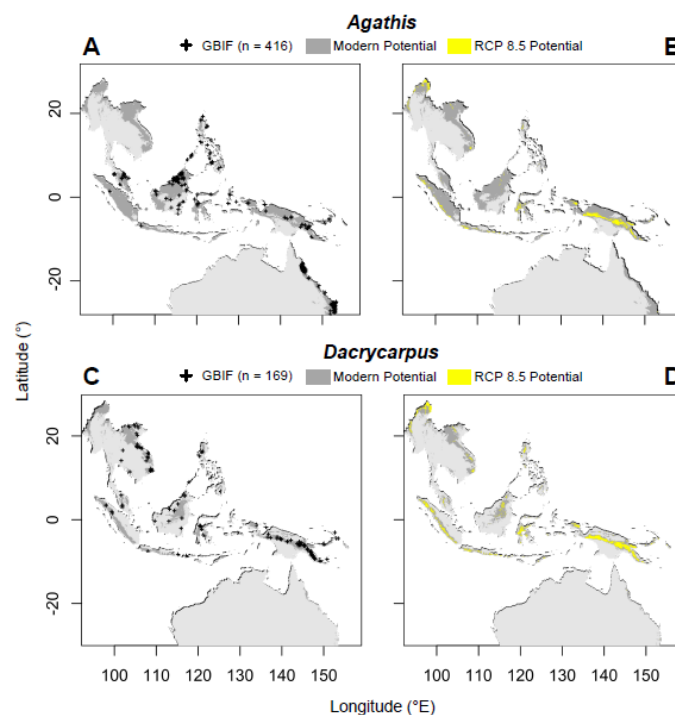
The Southeast Asian rainforest region is extremely complex and biodiverse. Fossils have shown that paleo-Antarctic rainforest lineages (PARLs) now extant in Asia tracked the ever-wet conditions needed to survive and diversify through deep time. However, the threat of future climate change to the remaining rainforest and PARLs in Southeast Asia has yet to be evaluated to set conservation priorities. We first quantified the woody-genus floristic relationships of Southeast Asian Island Groups by vetting and analyzing recent compilations of bioregional species data. We then evaluated the contributions to community assembly of woody fossil lineages and Island Group relationships to environmental gradients. To better understand climatic constraints of fossil lineage distributions and forecast distributions under projected future climate, we used exemplar living woody PARLs, including two angiosperms and two gymnosperms. Generalized linear models were used to project potential distributions under future climate pathways that assume no reduction in carbon dioxide emissions. The floristic analyses highlighted strong similarity among Island Groups in the ever-wet forest areas of Malesia, where PARLs are often concentrated. This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jse.12853.

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Ordination outliers represented more seasonal locations. Species distribution models showed that potential future distributions of ancient lineages are constrained by increasing rainfall seasonality and higher seasonal temperatures, with significant differences among exemplar genera. Notably, potential distributions often mapped onto de facto inaccessible areas, where forest clearing and the ubiquitous marine dispersal barriers that characterize the region will drastically inhibit potential relocation. These realities gravely threaten paleo-conservation values and contemporary rainforest community assembly processes in Southeast Asia.

Graphical abstract

Under the IPCC climate trajectory that is “business as usual” we compare the Modern distributions of exemplar gymnosperm genera (*Agathis*, *Araucariaceae*; and *Dacrycarpus*, *Podocarpaceae*) (Left panels) with modern potential ranges based on species distribution model output under current climate (grey), and (right panels) modern potential ranges (grey) and future potential ranges (yellow) based on species distribution model output under RCP 8.5 climate by the end of the century (2080-2100)



Key Words

Anthropocene, climate projections, Gondwana, island groups, paleo-Antarctic rainforest lineage distributions, Southeast Asia

1. Introduction

Many ancient Gondwanan lineages now inhabit Asia, showing that they tracked plate movements and the ever-wet, mesic conditions needed to survive and diversify

through deep time (e.g., Hill & Brodribb, 1999; Hermsen et al., 2010; Kooyman et al., 2019). The rich Gondwanan fossil record includes numerous paleo-Antarctic rainforest lineages (PARLs; Kooyman et al., 2014), such as *Agathis* (Araucariaceae), *Dacrycarpus* (Podocarpaceae), *Gymnostoma* (Casuarinaceae) and *Ceratopetalum* (Cunoniaceae), whose survival in Asia and elsewhere highlights their persistence in the face of major Cenozoic climate shifts, moving continents, and extinction events (Hill, 1994). The PARLs are the southern wet forest survivor lineages represented in the fossil records of Antarctica, Australia, New Zealand, and Patagonia (Kooyman et al., 2014). Contemporary distributions of PARLs include both lowland and montane refugia in the modern Asian tropics, where they continue to contribute substantially to the diversity and function of many rainforest areas (e.g., Kitayama, 1992; Aiba & Kitayama, 1999; Ashton, 2014). Those general patterns were recognized well before today's rich fossil record from Australia, Antarctica, New Zealand, and South America and the current, advanced understanding of paleoclimatology and plate tectonics (Wallace, 1869; van Steenis, 1934, 1964; Johns, 1976). However, recent history has seen the Southeast Asian rainforests devastated by clearing, fires, industrial logging, and intensive agriculture (Bryan et al., 2013; Ashton, 2014; Ashton et al., 2021; Gaveau et al., 2021; Karger et al., 2021).

The juxtaposition of the tens-of-millions-of-years timescale of plant lineage survival and the geologically instantaneous nature of human disturbances highlights a significant global challenge for conservation planning. As seen throughout the fossil record, and most famously in the instantaneous extinction of the non-avian dinosaurs and ca. 70% of other species at ~66 Ma from an asteroid strike, evolution and adaptation cannot prepare organisms for catastrophic events never before experienced in their history (Raup, 1991). Recent studies have variously quantified the evolutionary histories, sources, distributions, and concentrations of paleo-lineages in relation to key abiotic gradients at ecosystem scales, and they have provided significant insights into bio-regional vegetation history and contemporary conservation in both the Old World tropics (Manchester et al., 2009; Kooyman et al., 2019) and the Neotropics (Jaramillo et al., 2010; Carvalho et al., 2021). Many fossil lineages occur today in refugial areas characterized by high biodiversity and endemism (Rossetto & Kooyman, 2021). Predicting the likelihood of survival of known fossil lineages in contemporary environmental conditions and their future

distributions in relation to climate change remains a formidable challenge (Ivory et al., 2019; Tagliari et al., 2021).

The Southeast Asian region is geologically dynamic, with widespread volcanism. It straddles zones of subducting Pacific and Indian Ocean seafloor and was assembled from multiple tectonic plates and volcanically derived terranes, now including more than 25,000 islands and their intervening seaways. Plate collisions caused the rise of mountains and the formation of marine basins (Hall, 2017). The current configuration of islands and Asian continental connections also reflects the most recent cycle of submergence and reconnection caused by eustatic sea-level variation (Lohman et al., 2011; de Bruyn et al., 2014; Sin et al., 2021). In combination, those geological forces make the region one of the most geologically and biologically complex on Earth (Hall, 2009).

Plate movements and contacts between once-isolated land masses provide opportunities for terrestrial organisms to disperse, compete, and diversify across new terranes (Simpson, 1980; Morley, 2000, 2018; Wilf et al., 2013). The complex physiography and perhumid to seasonal tropical climate of Southeast Asia support a rich biota that includes in situ evolved and immigrant lineages, with both northern (Laurasian) and southern (Gondwanan) ancestry (van Steenis, 1934, 1964; Kooyman et al., 2019; Carta et al., 2021). The geological and biogeographic complexity of the Malay Archipelago, in combination with its omnipresent, mostly shallow-water marine barriers, highlights how different the region is from the equatorial rainforests of Amazonia and central Africa with their largely continuous land areas maintained through time (Morley, 2000; Jacobs, 2004). Although Southeast Asia's shallow marine barriers come and go over geologic time, they present formidable and growing obstacles to terrestrial species dispersal to potential refugia under rapid Anthropocene (Crutzen, 2006) warming.

The tropical forests of the Southeast Asian bioregion stretch from continental Asia and peninsular Malaysia (part of Sunda) to New Guinea and northern Australia (Sahul). These forests are postulated to rival the Amazon in terms of tree species richness and life form complexity (Slik et al., 2015), with the highest diversity found on the largest islands, Borneo (Ashton, 2014) and New Guinea (Cámara-Leret et al., 2020). In the wet forests of Malesia at the centre of the Southeast Asian bioregion, altitude has long been recognised as a significant factor influencing how historical biogeography is expressed (van Steenis, 1934, 1964, 1979). Putatively Indian- and

Asian-sourced taxa such as dipterocarps (Dipterocarpaceae) dominate the Malesian tropical lowlands, whereas conservative Gondwanan lineages such as podocarps (Podocarpaceae) are abundant at higher elevations (e.g., Ashton, 2014). In addition, novel discoveries such as fossil *Castanopsis* (Fagaceae) in Eocene Patagonia (Wilf et al., 2019a) and fossil *Syzygium* (Myrtaceae) in Miocene Australia (Tarran et al., 2018) indicate that the Gondwanan and post-Gondwanan influence at lower elevations is more significant than previously thought. However, these historical relationships have only rarely been quantified, even though the quality and quantity of relevant fossil data have grown dramatically in recent years (Sniderman & Jordan, 2011; Merkhofer et al., 2015).

Regional floristic data have previously and recently been used to analyse representation in the Island Groups of Southeast Asia (van Welzen et al., 2011; Joyce et al., 2020a,b; and see van Steenis, 1950; Balgooy, 1987). In addition, woody species composition inclusive of lineages with fossil records in the mid-high-latitude paleo-rainforests of the Cretaceous and Paleogene Southern Hemisphere, defined as paleo-Antarctic rainforest lineages (PARLs; Kooyman et al., 2014, 2019), has previously been used to track lineage distributions in both paleo- and contemporary contexts (Kooyman et al., 2014, 2019; Rossetto et al., 2015b; Yap et al., 2018). The paleo-distributions of different PARLs relative to co-occurring taxa and specific environmental variables can provide important insights into the influences of biogeographic history, edaphic constraints (Slik et al., 2011), and contemporary distributions. Australia-New Guinea and Southeast Asia represent hot spots for extinction and extant endemism, diversity, and living-fossil plant genera. These areas are positioned on either side of Wallace's Line, with Australia – New Guinea on the Sahul shelf; Peninsular Malaysia, Borneo, Sumatra, and Java on the Sunda Shelf; and the Philippines, Moluccas (Maluku), Sulawesi, and Lesser Sunda Islands representing the area referred to as Wallacea. The acknowledged signals for terrestrial fauna lineage differentiation across Wallace's Line (Wallace, 1869) contrast with the signals for plants, which generally disperse more readily across barriers (van Welzen et al., 2011; Crayn et al., 2015; Joyce, 2020b).

The focus here on southern-sourced plant lineages is topical, and reflects: 1) the dramatic recent increase in well-vetted records of survivor taxa at generic level (e.g., Kooyman et al., 2014); 2) increasing recognition of the survivors as dominant functional components of living Southeast Asian rainforests (e.g., Wilf et al., 2019a;

Kooyman et al., 2019), but with almost no quantification of their ecological roles; 3) that all these factors, and the antiquity of the southern lineages in general, are still frequently overlooked in high-profile molecular biogeographic studies (e.g., Merckx et al., 2015); and 4) the elevated conservation importance of montane tropical rainforests (Karger et al., 2021), which concentrate Gondwanan and other paleo-lineages (van Steenis, 1964; Johns, 1976; Wilf et al., 2013, 2019a; Kooyman et al., 2019) in critical watershed areas of high biodiversity and endemism.

The acknowledged importance of historical contingencies, including stochastic events, on the interplay of evolution and ecology (May, 1977; Raup, 1991; Ricklefs, 2007) highlights the potential of evolutionary history to inform contemporary ecological and conservation research at the ecosystem scale. We asked: How does the biogeographic and geologic history of living-fossil taxa in Southeast Asia correlate with their extant distributions? Can paleo-history inform assessments of extinction risk in this region in the face of projected changes in climate? At the regional scale, we expected to find some alignment between genus-level Southeast Asian Island Group assemblages, the distributions of lineages with Gondwanan history, and environmental (climate) variables (*sensu* van Welzen et al., 2011). At finer resolution, and using exemplar genera, we expected more detailed insights into the factors influencing current and projected future distributions to emerge relative to available climate space.

2. Materials and Methods

This study has two major components. First, we analyzed genus-level data for naturally occurring woody taxa from Island Groups in Southeast Asia to look at coarse-scale multivariate similarity-dissimilarity. Second, we used genus-level species distribution models to determine the finer-scale relationships of selected PARLs to contemporary and future climate variables. The rationale for including only woody genera reflects their dominant contribution to the mainframe structure of the forest, primarily as canopy trees, small trees, shrubs, and vines, and their broad range of propagule sizes and dispersal modes that influence, and in many cases constrain, contemporary distributions (Rossetto et al., 2015a; Delmas et al., 2020). In addition, and because of the acknowledged ecological differences between angiosperms and gymnosperms (e.g., Brodribb & Feild, 2010; Brodribb et al., 2012), we modeled future distributions of representatives of both these plant categories. We expected to see significant differences between current and projected distributions for exemplar

genera within the angiosperms and gymnosperms based on evaluations of inhabited modern climate spaces.

2.1 Floristics

The focus of our study was Southeast Asia, with an emphasis on Malesia plus rainforest areas in northern and eastern Australia (van Steenis, 1934, 1964, 1979; Kooyman et al., 2019). Recent compilations of the floras of specific Island Groups in Southeast Asia (Joyce et al., 2020a) and of New Guinea (Cámara-Leret et al., 2020) allowed us to create a base list of woody genera distributions. Island Groups included Australia, Borneo, Java, the Lesser Sundas, peninsular Malaysia, the Moluccas, New Guinea, Philippines, Sulawesi, and Sumatra.

We filtered the data provided in Joyce et al. (2020a) based on a caveat identified in Joyce et al. (2020b), specifically that taxonomic richness by region may be overestimated, leading to an increased likelihood for a signal of sharedness and similarity across and between Island Groups. We partly resolved this by filtering the data to include only woody genera, then reconciling genus-level distributions with occurrences available through the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>) and nomenclatural sources such as Tropicos (<https://www.tropicos.org>; also with reference to Chase et al., 2016). A total of 1095 rainforest woody genera were vetted and their verified distributions by Island Groups recorded.

2.2 Multivariate analysis

Assemblage-level data reflecting woody genus floristics for the ten Island Group areas were first entered into a site by genus rectangular matrix (S1 in Supplementary Materials). A triangular resemblance matrix was generated using the Jaccard resemblance measure (Gower, 1966; Clarke *et al.*, 2014). The relationships among sites and samples were then analysed in a non-metric multidimensional scaling ordination (NMDS; Fig. 1). The ordination locations (Island Groups) were also labelled in relation to the three major tectonic regions (Sunda, Sahul, Wallacea).

To further examine the similarity of Island Groups and the genera driving the splits and grouping relationships, we used a modified multivariate regression tree (MRT) analysis (De'Ath, 2002) referred to as the Linkage Tree procedure in PRIMER v7 (Clarke & Gorley, 2015). Groupings that emerged from the Linkage Tree analysis were further tested relative to a null hypothesis (no difference between Island Groups), using the Simprof routine and 999 permutations (Fig. 2).

2.3 Climate variables

Values for environmental variables, including climate and elevation, based on Island Group centroids were generated using R (R Core-team 2021) and Worldclim 2.1 (Fick & Hijmans, 2017). A triangular resemblance matrix of Island Group environmental variables was generated using Euclidean distance as a resemblance measure (Clarke et al., 2014). The relationships among sites and samples relative to climate variables and elevation were then analysed in a non-metric multidimensional scaling ordination (NMDS) (Fig. 3). The Island Groups were labelled in the ordination in relation to the three major tectonic regions (Sunda, Sahul, Wallacea; consistent with Fig. 1). This allowed us to compare Island Group areas relative to genus-level floristics (Fig. 1) and environmental variables (as centroid values; Fig. 3). Figure S1 (supplemental materials) provides maps of the climate variables and elevation of the study region based on the Worldclim database (Fick & Hijmans, 2017).

2.4 Selected lineages – Gondwanan

To select the taxa to be highlighted in the ordination from the full list of woody genera, we identified PARLs with validated fossil records. The identified PARLs included the 87 taxa listed in Kooyman et al. (2014: Table 4) plus *Castanopsis*. *Castanopsis* is of particular topical interest because the oldest occurrence of the genus was recently recognized from well-preserved infructescences in Eocene (Gondwanan) Patagonia, qualifying it as a PARL (Wilf et al., 2019a, 2019b). The genus was further hypothesized as having a southern origin, an idea that can be tested with additional fossil discoveries (Wilf et al., 2019a, 2019b). We then used the selected genera present in the data as vectors in a labelled floristic NMDS ordination. The length and direction of vector lines in the NMDS showed the strength of influence of genera on the position and similarity of Island Groups in ordination space (Fig. 1).

The selected genera with Gondwanan history (PARLs) highlighted in Figure 1 included the gymnosperm lineages *Araucaria* and *Agathis* (Araucariaceae: for fossil records see Hill et al., 2008; Pole, 2008; Escapa et al., 2018; Macphail et al., 2013; Macphail & Carpenter, 2014; Wilf et al., 2014), *Dacrycarpus*, *Dacrydium*, *Falcatifolium* and *Podocarpus* (Podocarpaceae: Brodribb & Hill, 1998, 2004; Hill & Brodribb, 1999; Wilf, 2012; Wu et al., 2019; Pujana et al., 2020), and *Papuacedrus* (Cupressaceae: Hill & Carpenter, 1989; Wilf et al., 2009). Angiosperm lineages included *Nothofagus* (Nothofagaceae: Hill, 1992; Hill & Jordan, 1993; Veblen et al., 1996; Sauquet et al., 2012), *Castanopsis* (Fagaceae: Wilf et al., 2019a, 2019b),

Tasmannia (Winteraceae: Brea et al., 2021), *Ackama*, *Caldcluvia*, *Weinmannia*, *Geissois* and *Ceratopetalum* (Cunoniaceae: Hill, 1991; Carpenter & Buchanan, 1993; Barnes et al., 2001; Gandolfo & Hermsen, 2017), *Quintinia* (Paracryphiaceae: Martin, 1977, 1994; Pillon & Hequet, 2019), *Allocasuarina* and *Gymnostoma* (Casuarinaceae: Scriven & Hill, 1995; Zamaloa et al., 2006; see also Christophel, 1994; Hill, 1994), *Akania* (Akaniaceae: Romero & Hickey, 1976; Gandolfo et al., 1988), and *Eucalyptus* and *Syzygium* (Myrtaceae: Biffin et al., 2010; Gandolfo et al., 2011; Hermsen et al., 2012; Thornhill & Macphail, 2012; Tarran et al., 2018). Systematic concepts of all these genera, as applied to fossils, are defined in the papers cited above.

2.5 Species distribution models

Four exemplar genera with validated Gondwanan fossil records (PARLs), representing both angiosperms and gymnosperms, were selected based on factors identified in the NMDS ordination including strength of influence as represented by the length of the vector line for each genera, direction of influence on Island Group positions, and orthogonality to minimise potential correlation (Fig. 1). The selected exemplar genera are *Gymnostoma* L.A.S.Johnson (Casuarinaceae), *Castanopsis* (D.Don) Spach (Fagaceae), *Agathis* Salisb. (Araucariaceae) and *Dacrycarpus* (Endl.) de Laub. (Podocarpaceae), comprising our selection of the most informative and interesting fossil lineages for this study. While it is the case that most PARLs occur in the cool / wet mid to higher altitude forests, both *Agathis* and *Castanopsis* have distributions that include lower elevations. In contrast, *Gymnostoma* and *Dacrycarpus* mostly occur at higher elevations (Kooyman et al., 2014, 2019).

Species distribution models (SDMs) were developed in order to estimate suitable areas for selected genera relative to climate under modern and future conditions. SDMs were constructed in BIOMOD2 in R (Thuiller et al., 2009; R Core Team, 2021) using the generalized linear model algorithm (GLM). GLMs were chosen because of their ability to minimize false presences, their decreased likelihood to overfit noise, and sensitivity tests that yielded high model evaluations statistics. The SDMs were trained on modern occurrences of selected genera. with GBIF occurrences downloaded using the R package rgbif version 3.5.2 (Chamberlain et al., 2022). Only occurrences with assigned geographic coordinates, elevation, and country label metadata were used. The coordinates of each occurrence were checked against country metadata and visually inspected to check for transcription errors. Duplicate occurrences from the same coordinates and all records south of 28°S were removed,

the latter representing cultivated / planted individuals of the target species. Distribution data recorded prior to the year 1970 were discarded so that occurrences overlapped with Worldclim climate normals used in generating the SDMs. Pseudo-absences were selected to constrain the background climate of the study area by selecting random points (5 times the number of presences for each genus) and within a geographic extent of a 2000 km radius around modern presences. These parameters were found to maximize the predictive ability of individual models based on the area under the receiver operating curve (AUC) statistic. Model evaluation was conducted using k-fold cross-validation, splitting the training and testing datasets three times (70:30% split). The final models were a total consensus ensemble of the best performing individual models (AUC > 0.80). Thresholding to designate presence-absence was based on the true skill statistic (TSS) for each model.

Modern and future potential ranges were mapped by projecting the final SDMs into geographic space using environmental variables. For modern potential ranges, the five environmental variables used in model training were mean annual precipitation (MAP), mean annual temperature (MAT), precipitation seasonality (PS), maximum temperature of warmest month (MTWM), and elevation, representing 1970-2000 conditions based on 2.5min resolution Worldclim 2.1 (Fick & Hijmans, 2017). For future potential ranges, we created an ensemble of climate model projections for years 2080-2100 under RCP8.5 boundary conditions. RCP8.5 was chosen for this study because it aligned with our intent to gauge vulnerability to an extreme climate scenario across a broad geographic region, and because it continues to track current global CO₂ emissions closely (Marcer et al., 2016; Hayes & Piaggio, 2018; Schwalm et al., 2020). The future climate ensemble integrated forecast output from four climate models used in the most recent Climate Model Intercomparison Project (CMIP5). These were CNRM-CM6-1 (Voldoire et al., 2019), MIROC6 (Tatebe et al., 2019), IPSL-CM6A-LR (Boucher et al., 2020), and CANESM5 (Swart et al., 2019). Each was downscaled to a 2.5min resolution and retrieved from the Worldclim 2.1 database.

3. Results

3.1 Island Group Signals

The proximity and location of Island Groups in the two coarse-scale NMDS ordinations and the multivariate regression tree (MRT) represent floristic (Figs. 1&2) and environmental (Fig. 3) variables. The notable positional similarity between the

Island Groups in the NMDS outputs from these independent analyses reflects strong alignment between abiotic variables, genus level distributions, and Island Group assemblage level similarity-dissimilarity.

A total of 1095 woody rainforest genera were recorded for the ten Island Group areas used in the initial floristic analyses (Fig. 1). Grouping (45% similarity) based on the underlying clustering analysis showed Australia (Sahul Plate) and the Lesser Sunda Islands (Wallacea) as outliers to the largely aseasonal “core” areas of Malesia, including large areas of peninsular Malaysia, Borneo, Sumatra, Sulawesi, and New Guinea. Java was the most distant in ordination space from the core area of Malesia and split away at 46% similarity. There were some notable alignments in Island Group areas in relation to genus level floristics and plate origins, with high similarity among Malaysia-Borneo-Sumatra in the Sunda region, the Philippines-Sulawesi-Moluccas in the Wallacea region, and between New Guinea and Australia as part of Sahul. The labelled vectors representing PARLs provided an indication of the strength (length) and direction of influence of selected genera with Gondwanan history on the position of Island Group areas in the ordination (Fig. 1). There was notable directional correlation with Australia in extant genera such as *Eucalyptus*, *Allocasuarina*, *Caldcluvia*, *Ceratopetalum*, *Akania*, and *Tasmannia*. Fossil genera historically or currently shared between Sunda and Sahul, including *Dacrycarpus*, *Dacrydium*, *Agathis*, *Castanopsis*, and *Weinmannia*, showed more orthogonality. The widely dispersed genera *Syzygium* and *Podocarpus* showed little to no signal of influence on the position of Island Groups in the ordination (Fig. 1), probably reflecting that species in both genera cumulatively have wide distributions across a broad range of habitats.

The multivariate regression tree (MRT) shows the splits and groupings between Island Groups based on the distribution of the same 1095 woody rainforest genera in more detail (Fig. 2). In the MRT, the splits are explained in relation to similarity and dissimilarity based on contributions of specific genera, with similarity profile tests (Simprof and 999 permutations) showing well-supported splits as black lines, and less well-supported splits as dotted red lines. Splits within the three Island Group pairs of Java and the Lesser Sunda Islands, Borneo and peninsular Malaysia, and New Guinea and Moluccas were not well supported, confirming that in each case, the Island Group pairs were highly similar and shared many genera. Our results largely align with the early floristic demarcations of Malesia undertaken by van

Steenis (1950), and the floristic relationships of island groups identified by Balgooy (1987) and van Welzen et al. (2011).

Island Group similarity based on values for environmental variables (Fig. 3) showed similar ordination positioning to those for genus level floristics (Fig. 1) but increasing distance between New Guinea and Australia (compared to Fig. 1) that reflects dissimilarity based on seasonality and elevation. Australia remains as an outlier to the other groupings (at 45% similarity) along the vector trajectory of increasing seasonality. The pairing of Java and the Lesser Sunda Islands confirmed their similarity based on increasing seasonality relative to the more aseasonal core area of Malesia (refer to van Welzen et al., 2011). Island group labelling relative to plates (Sunda, Sahul, Wallacea) showed less alignment than that based on genus level floristics.

3.2 Species distribution models

Occurrence density analysis (Fig. 4) and the SDMs (Figs. 5, 6) provided finer resolution insights into the signals obtained from the coarse-scale analyses (Figs. 1-3). Kernel density of occurrences for the four exemplar genera, relative to key environmental gradients for the study region (Fig. 4) showed 1) relatively strong alignment among genera for occurrence density with respect to mean annual precipitation (MAP), and 2) some major differences in relation to mean annual temperature (MAT), rainfall seasonality (PS), and maximum temperature of warmest month (MTWM) (Fig. 4). The results highlight that the currently occupied climate spaces of the exemplar genera, including niche-conservative taxa (Crisp et al. 2009), represent only part of the full range of available climate within the region. In addition, exemplar taxa sometimes occupy only the margins of the available climate space. Based on these results, some ancient lineages may already be marginalized and excluded from many areas by natural (i.e., competition) and anthropogenic factors, increasing their extinction risk. Importantly, these results highlight that the modern realized climate spaces of these exemplar genera are likely to be incomplete analogs for the past, a classic problem with using nearest-living-relative methods in paleoclimatology (e.g., Greenwood & Wing, 1995).

Future potential ranges for the exemplar genera under the RCP8.5 emissions pathway showed significant contractions by the end of the century relative to current potential distributions (Figs. 5,6). This was particularly the case for *Gymnostoma*. Both gymnosperm genera (*Agathis* and *Dacrycarpus*) showed significant potential

range contractions. Consistent with the occurrence density results (Fig. 4), *Dacrycarpus* appeared to be particularly susceptible to climate change that includes increasing temperatures and seasonality of rainfall (Fig. 6), reflecting its well-known drought intolerance (Brodribb & Hill 1998; Brodribb, 2011). The range projections for *Agathis* in response to climate changes suggest reduced occupation of lowland areas and persistence in the mountains. The probable outcome of those patterns for the genus would be low-altitude species having to move to higher elevations, and the species currently occupying higher elevations having to persist in reduced habitat areas. Extinction risk for the lowland species is thought to be particularly high because survival following extirpation in the low altitudes requires both successful dispersal and persistence in the face of high competition from populations already occupying upland areas. Somewhat in contrast, the future potential range for *Castanopsis* shows expansion and suggests that suitable climates will persist under the future climate projections, probably reflecting that it is a large, widespread genus, with many species occupying very diverse habitats (e.g., Soepadmo, 1972). However, the implications at species level for *Castanopsis* may vary, and many species presumably are at much higher risk than the genus as a whole (BGCI 2021).

Perhaps most strikingly, our results illustrate how future suitable climates will occur in locations that the genera are unlikely to be able to access because of dispersal barriers and degraded potential corridors, or will no longer be available to occupy because of forest clearing. These results signal a significantly increased risk of decline in species diversity (e.g., potential loss of the lowland *Agathis*), and an increased risk of extinction within all the exemplar genera, most notably in *Dacrycarpus* and *Gymnostoma*.

4. Discussion

Among the Earth's largest and most diverse tropical rainforest regions (Amazonia, Central Africa, and Southeast Asia), the tension between dispersal opportunities and constraints in the context of land-sea area fluctuations and climate influences are most extreme in the archipelago that is Southeast Asia. In addition to those historical factors, our results showed that the future potential ranges of exemplar genera often mapped onto areas where anthropogenic habitat loss and climate change seem likely to further inhibit the capacity of lineages to track suitable climate conditions.

Using models that facilitate forward projection relative to expected shifts in climate allows conservation planning to be informed by predictions of genus- and

species-level climate responses. Plant responses to changes in climate can be adaptive or conservative, and the PARLs and other lineages with Gondwanan history are mostly thought to exhibit trait and biome conservatism reflecting warm-wet conditions (Crisp et al., 2009; Yap et al., 2018; Delmas et al., 2020). The factors regulating the movement of such lineages into seasonally drier environments are related to physiological constraints, including vessel architecture, stomatal control, and the maintenance of xylem pressure in woody tissue (Brodribb et al., 2020). Xylem failures in trees due to seasonal and prolonged drought-induced embolisms demonstrate how increasing seasonality can act as a selection pressure and shape community assembly processes that reflect and constrain species distributions (Brodribb et al., 2020).

Although species richness was generally lower at the Last Glacial Maximum (LGM) in Southeast Asia, areas of high richness were still present (Lohman et al., 2011; Raes et al., 2014). However, these were mostly located off the current island land areas and on the emergent Sunda Shelf, indicating substantial species migration and mixing during the transitions between the Quaternary glacial maxima and warm periods such as the present (Raes et al., 2014). The geographic tensions between contemporary seaways and land area that acted as barriers and constrained dispersal in the past now differentially drive and constrain contemporary community assembly and potential species distributions, inclusive of allopatric speciation. The convergence of factors described by Raes et al. (2014) highlights that under current conditions the escape routes and habitats that previously allowed lineage movement, survival, mixing, and diversification are increasingly no longer available. The current contractions in lineage distributions as a consequence of Anthropocene impacts are happening at the worst possible point in time, a highstand in the previously existing eustatic cycle, for the survival of the ancient lineages highlighted here and the diverse ecosystems they inhabit.

The results of this study highlight the temporal disconnect between the deep-time-to-recent success of survivor fossil lineage movements representing biogeographic history and adaptation, and the limited contemporary capacity of plants to respond to the immediacy of short-term climate-change impacts. The conditions for woody rainforest plant dispersal and establishment are now more constrained by the barriers created by high-stand sea levels, recent forest clearing, and changed land-use than ever before (Gaveau et al., 2021). Sea area is currently at its largest extent, with

deep and shallow expanses of sea water both creating significant barriers to dispersal of propagules. As an example, several important Southeast Asian tree lineages, including the ecologically dominant dipterocarps, have propagules that are known to have low tolerance for exposure to salt water (Ashton, 2014; Ghazoul, 2016).

Although biogeography traditionally treats shallow shelf areas similarly to emergent land, on the short time-frame of projected anthropogenic change, currently submerged areas will remain submerged and may expand. As a consequence, shallow shelves will remain equivalent to oceanic waters as effective marine barriers to plant dispersal during the Anthropocene.

5. Conclusions

Land area expansion-contraction dynamics have historically aligned with climate fluctuations that allowed lineages to move between Island Groups, survive, establish, and diversify (Raes et al., 2014). In the modern world, land area and habitat contractions have aligned with a eustatic highstand to generate a maximum marine barrier effect, severely reducing the capacity of lineages to move between Island Groups in response to climate change. At the same time, former lowland corridors are now severely compromised from deforestation. In effect, the processes that facilitated the movement and establishment of the PARLs and other ancient plant lineages over large distances through deep time now constrain their capacity to move even short distances to survive.

To properly evaluate the potential impacts of rapid climate change in contemporary settings, we call for a new biogeography of the Anthropocene that includes fossils and their timescales of emergence and movement to contrast with the short timescales and increasing harshness of global climate and land-use changes. The highly biodiverse Southeast Asian islands provide an extreme example of how much could be lost, surrounded as they are by increasingly warm saltwater barriers to dispersal, and subject to continuing rapid decline in forest area and habitats. The consequences of those interacting factors for the paleo-lineages with Gondwanan history in this region, and the rich communities they inhabit, include decreasing dispersal potential and no suitable habitat to land in even if dispersal occurred. Diminishing opportunities for relocation, little to no time for adaptation, increasing threats, and overall low survivability seem to be the future for these ancient lineages and remarkable forests. For the species of Southeast Asia, the risky biogeography of the Anthropocene is adding a new multidimensional challenge to surviving and

evolving. Without paleo-informed conservation interventions, the evolutionary trade-offs and traits that allowed long-time-scale lineage survival in the past look set to be the drivers of extinction in the future.

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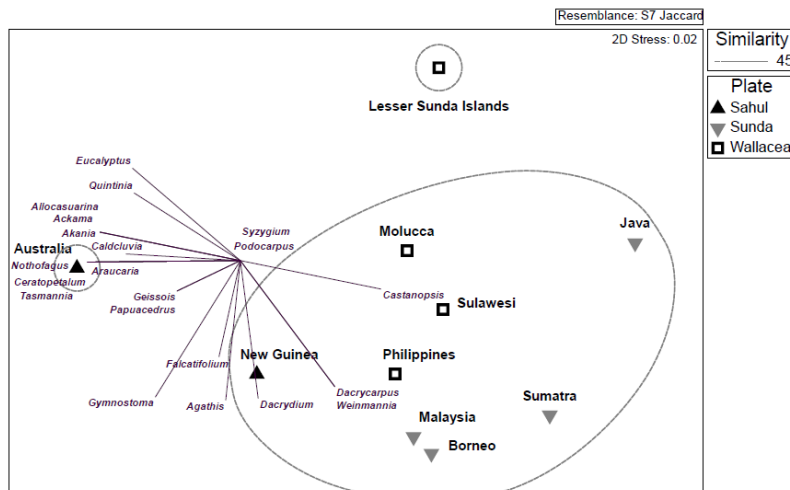


Figure 1. NMDS ordination based on presence-absence data for 1095 genera representing contemporary woody genus level floristics of ten Island Groups, with peninsular Malaysia (in this case) used to represent mainland southeast Asia. Island groups are labelled relative to plates (Sunda, Sahul, Wallacea). Similarity of the Island Groups is shown at 45% (grey dotted line) based on the underlying hierarchical clustering analysis. Vectors (as genera) are shown in grey and represent lineages with fossil evidence for Gondwanan history. The length and direction of vectors (grey lines) indicate the strength and direction of influence of the genera on the ordination (position) of Island Groups based on similarity-dissimilarity. For example, *Syzygium* and *Podocarpus* are present in all Island Groups, so they show low to no influence on the position of Island Groups in the ordination. *Dacrycarpus* and *Dacrydium* are present in Southeast Asia but absent (extinct) in Australia; *Agathis* and *Gymnostoma* are extant in parts of Southeast Asia and Australia; and *Castanopsis* is now known from the paleo-Antarctic fossil record, absent from Australia (with no fossil record), and extant elsewhere in Sahul (New Guinea) and in Asia.

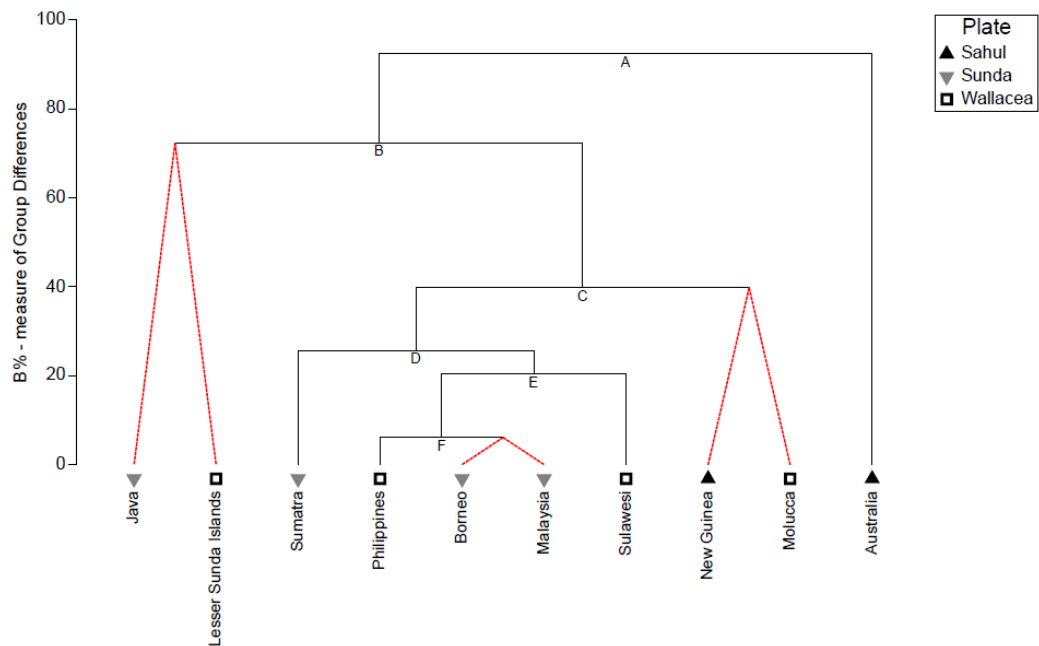


Figure 2. Linkage Tree based on assemblage (presence-absence) data for genus level floristics of Island Groups. Island groups are labelled relative to plates (Sunda, Sahul, Wallacea). Group splits (A-F) show break points based on genus level similarity - dissimilarity (Simprof tested; 999 permutations), with red lines within the major splits indicating separations between Island Groups with similar floristics that are not well supported statistically (by permutation analysis). Major splits in sequence are: A – between Australia and all other Island Groups; B – between Java + Lesser Sundas and all other Island Groups in Malesia; C – between New Guinea + Molucca and remaining Island Groups in Malesia; D – between Sumatra and remaining Island Groups in Malesia; E – between Sulawesi and remaining Island Groups in Malesia; and F – between Philippines, Borneo and Malaysia.

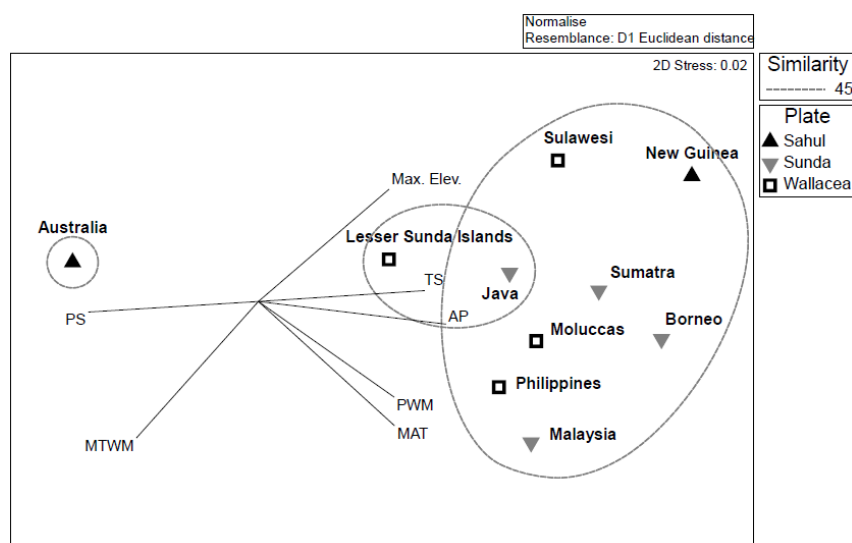


Figure 3. NMDS ordination based on values for environmental variables generated using centroids for Island Groups. Island groups are labelled relative to plates (Sunda, Sahul, Wallacea). Similarity of the Island Groups in relation to climate variables and elevation is shown at 45% (grey dotted line) based on the underlying hierarchical clustering analysis. Labelled grey lines show the relative influence of selected environmental variables, with the length of each vector line equating with strength of influence on the ordination and the direction showing influence on groupings. Orthogonality and strength of vector influence on subsequent ordinations were used to select the most informative variables to be highlighted. MAT – mean annual temperature, TS – temperature seasonality, MTWM – maximum temperature warmest month, AP – annual precipitation, PS – precipitation seasonality, PWM – precipitation wettest month, Max. elev. – maximum elevation.

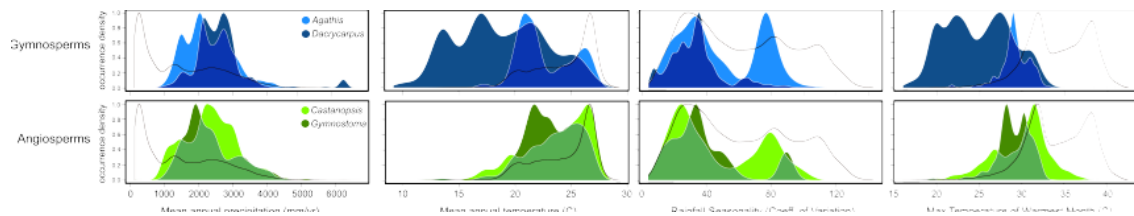


Figure 4. Currently occupied climate space of selected genus occurrences based on kernel density within the Southeast Asian study region with respect to climate. The black line indicates all available climate space for the entire study region. At top are exemplar gymnosperm genera (*Agathis*, *Dacrycarpus*), and at bottom are exemplar angiosperm genera (*Castanopsis*, *Gymnostoma*).

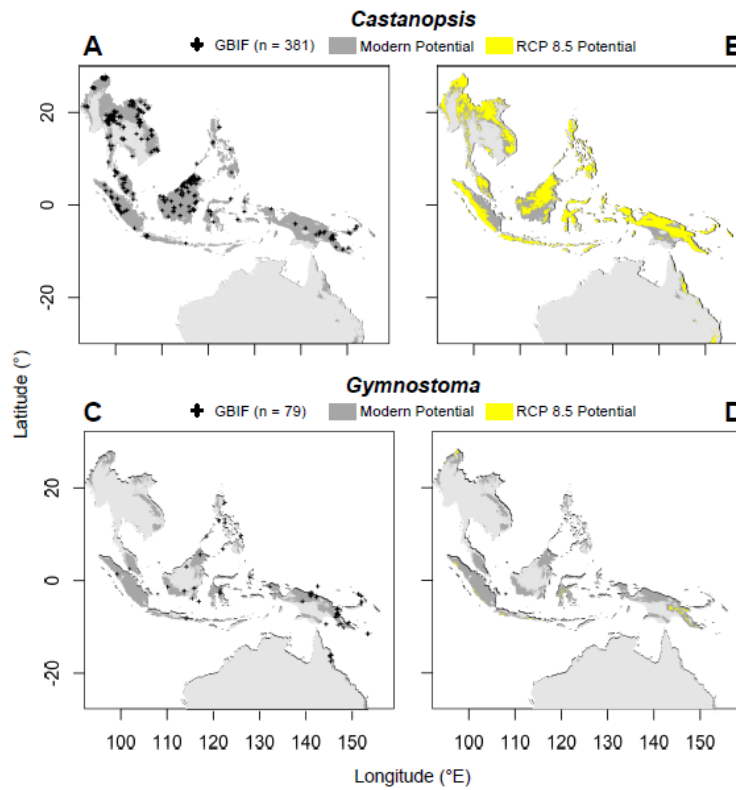


Figure 5. Modern distributions of exemplar angiosperm genera (*Castanopsis*, Fagaceae; and *Gymnostoma*, Casuarinaceae). (Left panels) Modern occurrences (post-1970) from the GBIF (black crosses), with modern potential ranges based on species distribution model output under current climate (grey), and (right panels) modern potential ranges (grey) and future potential ranges (yellow) based on species distribution model output under RCP 8.5 climate by the end of the century (2080-2100). RCP 8.5 is the IPCC climate trajectory that is “business as usual”, representing 8.5w/m² additional radiative forcing by the end of the century.

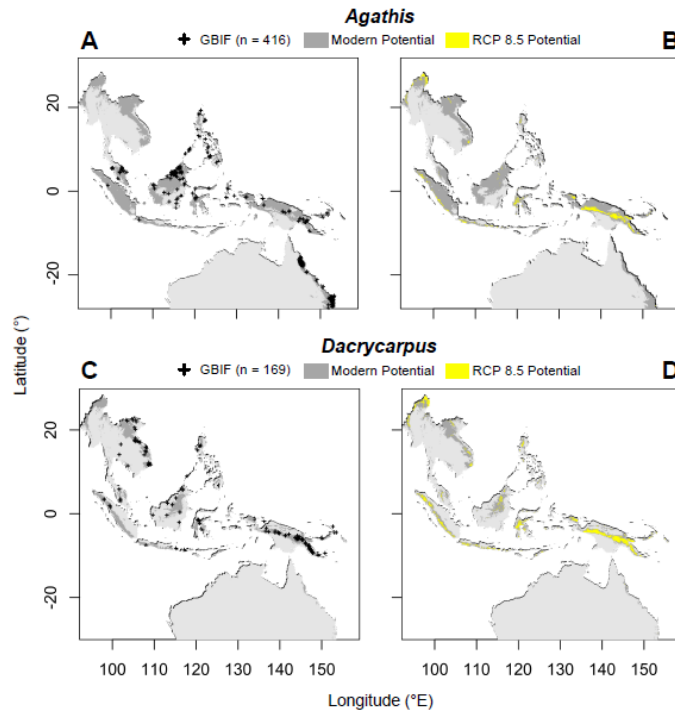


Figure 6. Modern distributions of exemplar gymnosperm genera (*Agathis*, Araucariaceae; and *Dacrycarpus*, Podocarpaceae). (Left panels) Modern occurrences (post-1970) from the GBIF (black crosses), with modern potential ranges based on species distribution model output under current climate (grey), and (right panels) modern potential ranges (grey) and future potential ranges (yellow) based on species distribution model output under RCP 8.5 climate by the end of the century (2080-2100). RCP 8.5 is the IPCC climate trajectory that is “business as usual”, representing 8.5w/m^2 additional radiative forcing by the end of the century.

Figure S1. Climate and elevation of the study region from Worldclim database 2.1 at 2.5 min resolution (1970-2000; Fick and Hijmans, 2017)