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Floristic exchange between Southeast Asia and northern Australia: molecular phylogeography reveals two geographically and temporally separated exchange tracks

Running title: Floristic exchange tracks between Southeast Asia and Australia

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Abstract

Aim

Exchanges of plant lineages between Australia and Southeast Asia have had a substantial impact on the evolution of Australia's northern, tropical flora, with important ramifications for its conservation and biosecurity. Despite this, floristic exchange tracks between northern

Australia and Southeast Asia remain poorly understood. To address this, we conducted a molecular phylogeographic case study to identify exchange tracks between Australia and Southeast Asia.

Location

India, Southeast Asia, Australia and the Pacific Islands.

Taxon

The widespread and morphologically variable tree species *Aglaia elaeagnoidea* (Meliaceae).

Methods

We conducted a phylogeographic study using DArT-seq analysis of 141 herbarium and silica-dried samples sourced from across the range of *A. elaeagnoidea*. We identified 176,331 single nucleotide polymorphisms (SNPs) across 90,456 loci which we analysed using multivariate, admixture, genetic differentiation and coalescent methods to characterise phylogeographic and phylogenetic patterns. An environmental niche model for the last glacial maximum was also elucidated.

Results

Two exchange tracks were identified, one between New Guinea and the Cape York Peninsula in north-east Australia, the other between Timor-Leste and the Kimberley region of north-west Australia. The Cape York Peninsula track is contemporary, characterised by ongoing genetic exchange, whereas the Kimberley track is historic, facilitated by multiple past exposures of the Arafura Shelf during the Pleistocene. Overall, we suggest the phylogeographic patterns of *A. elaeagnoidea* have resulted from a combination of repeated range expansion-contraction cycles concurrent with Quaternary climate fluctuations, and stochastic dispersal events.

Main conclusions

This study provides the first detailed evidence for two floristic exchange tracks between northern Australia and Southeast Asia, providing new insights into the biogeography and evolution of Australia's tropical flora.

Keywords

Exchange, Asia, Australia, Sunda, Sahul, Wallacea, *Aglaia elaeagnoidea*, Meliaceae, Phylogeography

Introduction

Joseph Hooker was the first to note affinites between the northern Australian and Asian floras, postulating that Indian and Malesian flora "continued […] with great force over the whole of tropical Australia" (Hooker 1859). More recently, palaeobotanical, phytogeographic and phylogeographic studies have confirmed that floristic exchanges commencing at least 30 Mya between Australia and Southeast Asia have had a substantial impact on the composition of Australia's contemporary flora (Joyce et al. In review; Sniderman and Jordan 2011; Crayn

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et al. 2015; Murphy et al. 2017; Yap et al. 2018, 2020). This exchange was facilitated by increased connectivity between Australia and Asia from approximately 25 Mya, as the continental shelf on which Australia is situated (the Sahul Shelf) collided with the south-east Asian Sunda Shelf and formed the complex conglomerate of intervening terranes known as Wallacea (Hall 2011, 2017; McLoughlin 2001). More than 2300 vascular plant species are shared between Southeast Asia (including New Guinea) and Australia (Joyce et al. 2020).

Despite the importance of Asian lineages in the Australian flora, particularly in northern Australia (Joyce et al. In review; Yap et al. 2018), floristic exchange tracks between Southeast Asia and northern Australia have been little-studied. It is generally assumed that the major floristic exchange track between Australia and Southeast Asia lies between New Guinea and the Cape York Peninsula, partly because the seaway between them – the Torres Strait – is the narrowest between the two regions (c. 150 km at its narrowest, with intervening islands). Van Steenis (1934) postulated that tropical montane flora was exchanged through a "Papuan track" via Borneo, New Guinea and Australia. Similarly, rainforest lineages are known to exchange between New Guinea and Cape York, and along the east coast of Australia (Burbidge 1960; Specht 1981; Sniderman and Jordan 2011). Crisp et al. (1995) was the first to suggest, based on a cladistic biogeographic analysis of 11 plant clades, that there may be a second floristic exchange track between New Guinea and the monsoon tropics of Australia (in the Northern Territory and Western Australia). More recently, a phytogeographic study including all known species of vascular plants in the region showed that the floristic composition of the Australian monsoonal tropics has a high similarity to that of the Lesser Sunda Islands and Timor (Joyce et al. In review). Examination of the phylogeography of shared lineages is needed to test the presence of a second floristic exchange route between the monsoonal tropics of Australia and Southeast Asia.

More broadly, little is known about phylogeographic patterns in Southeast Asia, with the few studies conducted mostly focussing on fauna and covering a restricted geographic range (Cannon 2001; Liao et al. 2007; Ueda et al. 2010; Tnah et al. 2012; Pedersen et al. 2018; Jusoh et al. 2019; Grismer et al. 2019; Husson et al. 2020; Lim et al. 2020). In Australia, phylogeographic studies of rainforest plants have revealed varied expansion-contraction responses to the climatic fluctuations of the Quaternary (Rossetto et al. 2004; Mellick et al. 2012, 2013; Fahey et al. 2019); however, responses of the Southeast Asian flora are yet to be studied in detail. Elucidation of Southeast Asian phylogeography, and identification of floristic exchange routes between northern Australia and Southeast Asia, is critical for understanding past evolutionary processes and present phytogeographic patterns and for managing the biosecurity and conservation of the region's biota.

To investigate exchange tracks between northern Australia and Southeast Asia and Southeast Asian phylotgeography, we conducted a phylogeographic case study using *Aglaia elaeagnoidea* (A.Juss.) Benth. *Aglaia* Lour. is one of the most widespread and species-rich genera in Meliaceae, comprising c. 120 species widely distributed in India, China, southeast Asia, Australia and the Pacific Islands (Pannell 1992, 2018; Grudinski et al. 2014). Previous genus-wide phylogenetic work has reconstructed Sunda as the ancestral area for the genus (Grudinski et al. 2014). Plants of *Aglaia elaeagnoidea* are small trees usually found in secondary forest and beach forest (Pannell 1992). The species is morphologically variable across its wide range which extends from India in the west to Wallis and Futuna Islands at its eastern-most limit (Pannell 1992), and including much of Southeast Asia. Within Australia, *A. elaeagnoidea* has a discontinuous distribution, with populations in the Kimberley region (Western Australia) and Cape York Peninsula (Queensland, eastern Australia), and no

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records between (Pannell 2008). This disjunct distribution (Asia-Kimberley-Cape York) has been observed in many other species (R. Barrett, pers. comm., B. Maslin, pers. comm., Joyce et al. 2020).

Here we report the results of a study which used genome-wide DArT-derived SNP data to characterise the phylogeography of *A. elaeagnoidea* throughout Southeast Asia, Australia and the Pacific islands. We aimed to use the phylogeographic data to evaluate four historical biogeographical scenarios that can explain the current Australian distribution of *A. elaeagnoidea*: 1) one exchange track between Australia and Asia, with *A. elaeagnoidea* once widespread across northern Australia and subsequently vicariant into two widely disparate populations; 2) one exchange track between Australia and Asia with a second disjunct population established within Australia via long-distance intra-continental dispersal; 3) two exchange tracks between Australia and Asia, with both Australian populations established from the same source area in Asia, and 4) two exchange tracks between Australia and Asia, with different source areas in Asia. The first three scenarios predict that all Australian populations would form a single genetic group, while the fourth scenario would predict that each Australian population would be more similar to different Asian populations that to each other.

Materials and methods

Sampling

Samples for this study were obtained predominantly from herbarium specimens, augmented by field-collected silica-dried material. The most recent phylogenetic study of *Aglaia* suggested (albeit with weak support) that *A. elaeagnoidea* is not monophyletic (Grudinski et al. 2014). To account for additional potential genetic variation within the complex, samples were taken from all species currently thought to be closely related to *A. elaeagnoidea*, i.e. *A. elliptica* Blume, *A. chittagonga* Miq., *A. simplicifolia* (Bedd.) Harms, *A. malabarica* Sasidh., *A. apiocarpa* (Thwaites) Hiern, *A. leucophylla* King and *A. korthalsii* Miq. (Grudinski et al. 2014). In addition, samples were taken from species morphologically similar to, but thought to be more distantly related to, *A. elaeagnoidea*, including *A. smithii* Koord., *A. edulis* (Roxb.) Wall., *A. odoratissima* Blume and *A. scortechinii* King. *Aglaia lawii* (Wight) C.J. Saldanha ex Ramamoorthy and *A. spectabilis* (Miq.) S.S. Jain & Bennet were chosen as outgroup species due to their clear morphological and genetic distinction from *A. elaeagnoidea*. In total, 254 samples were obtained from these species, including 247 herbarium specimens and seven samples (all Australian) from silica-dried material. Details of all samples used are provided in Supplementary Material 1.

Dried leaf tissue was sampled from herbarium specimens from 14 herbaria (see Supplementary Material 2 for list) following institutional destructive sampling guidelines. Species identity of all sheets was confirmed by CMP (monographer of *Aglaia*) or EMJ. Notes on morphology and locality were made and a photograph taken of every sheet.

A field trip to the Kimberley region, Western Australia was undertaken in April-May 2018 where silica-dried tissue was obtained from one population of *A. elaeagnoidea*. Vouchers for these samples are accessioned at PERTH. Silica-dried tissue for CNS accessions was obtained from Dr Wendy Cooper.

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DNA extraction

For each sample, 15 mg of leaf material was ground with a TissueLyser (Qiagen; Hilden, Germany). DNA was extracted with a DNeasy Plant Mini Kit (Qiagen; Hilden, Germany) using a modified protocol as follows. At step two, where Buffer AP1 is added, 30 µl of β-mercaptoethanol and 6 µl of 20 mg/ml Proteinase K were added to denature proteins and remove tannins and polyphenols. RNase A was not added as recommended in the manufacturer's protocol at this step as yield was slightly improved without it, likely due to the prevention of RNase A-DNA complex formation (Donà and Houseley 2014). Samples were incubated for 2 hours at 65°C instead of the recommended 10 minutes, and eluted in a total volume of 120 µl. DNA quantity and quality were ascertained with a Qubit fluorometer (Thermo Fisher Scientific, Invitrogen; Waltham, MA, USA) and Nanodrop spectrophotometer (Thermo Fisher Scientific; Waltham, MA, USA). For samples with low DNA concentrations, extractions were replicated and the products combined and concentrated.

Of 254 specimens sampled, 131 yielded > 2 ng/ul DNA, while 22 samples yielded < 1ng/ul DNA, of good quality. Samples with successful extractions were from *A. elaeagnoidea*, *A. korthalsii*, *A. chittagonga*, *A. edulis*, *A. elliptica*, *A. lawii*, *A. leucophylla*, *A. spectabilis* and *A. scortechinii*. Following optimisation, all successful samples were sent for sequencing.

Sequencing

Samples were sent to Diversity Arrays Technology Pty Ltd (DArT; www.diversityarrays.com/) for library preparation and sequencing. The proprietary DArT library preparation method is similar to that described by Kilian *et al*. (2012) and Cruz *et al*. (2013). In plants, DArT is thought to retrieve single or low copy homologous sequences distributed throughout the genome within or close to genes (Garavito et al. 2016; Rossetto et al. 2019). DArT proprietary analysis pipelines were used to remove poor-quality sequences, correct low-quality bases, call SNPs, BLAST search sequences to eliminate matches with microbial contaminants, and generate genotype data.

Resultant genotypes were initially processed in R using a pipeline described in Rossetto et al. (2019). Descriptive statistics for the genotype data were generated and SNP loci of poor quality filtered out to retain loci with a minimum reproducibility of 0.96 and with <20% of genotypes missing. Data were filtered to retain one randomly selected SNP per locus. Poor quality samples of *A. elaeagnoidea* (>20% missing loci) were identified and removed if they presented as outliers in subsequent analyses. Outgroup samples with more than 20% missing loci were retained, as the relatively high degree of missing loci could be due to differences in restriction enzyme site locations in taxa more distantly related to *A. elaeagnoidea*.

Identification of genetic structure in the A. elaeagnoidea *complex*

For the purposes of this study, a "population" refers to individuals from the same island, or in the case of Australia, on either side of the continent. Although it is unknown how prevalent interbreeding is between individuals occupying an island, our definition makes the assumption that interbreeding is more common within an island than between islands.

Relationships between *A. elaeagnoidea* and outgroup species were initially explored using Principal Components Analysis (PCA) of SNP data using the R package adegenet v 2.1.0 (Jombart et al. 2020). NeighbourNet analysis (Bryant and Moulton 2004) was conducted in

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SplitsTree4 v.4.15.1 (Huson and Bryant 2006) to visualise a distance-based phylogenetic network. Phylogenetic relationships under a coalescence model were estimated using the SVDquartets (Chifman and Kubatko 2014) method as implemented in PAUP* v4.0a (Swofford 2003) with individuals assigned to island group populations as identified from PCA clusters. 100,000 quartets were sampled at random and assembled using the QFM quartet assembly method. Confidence in resultant bipartitions was assessed with 100 bootstrap replicates.

Phylogeographic analysis of eastern A. elaeagnoidea *populations*

Because *A. eleaegnoidea* samples were clearly differentiated into groups from the eastern and western parts of the species' geographical range (see results), further analyses were conducted on the subset of eastern *A. elaeagnoidea* samples to focus on identifying exchange tracks with Australia.

Pairwise Fst statistics and geographic distances were calculated for each population using the R package SNPrelate (Zheng et al. 2012). Fst values were plotted against geographic distances to test for isolation by distance, and a Mantel test conducted with 999 permutations in the R package vegan (Oksanen et al. 2019).

TreeMix (Pickrell and Pritchard 2012) was used to characterise patterns of population splitting and mixing from allele frequencies among eastern *A. elaeagnoidea* populations. A Maximum Likelihood tree was generated, with Taiwan designated as the root population and SNPs partitioned into blocks of 1000 to account for linkage disequilibrium. Taiwan was chosen as the root because the SVDquartets analysis suggested that Taiwan is the earliest-diverging population among our sampled eastern *A. elaeagnoidea*. Trees were generated by incorporating zero to ten migration events with five iterations under each model. The optimum number of migration events to model population splitting and mixing was determined using the Evanno method (Evanno et al. 2005) as implemented in the OptM package (Fitak Submitted) in R. This process was repeated with adjacent populations merged, to assess whether differences in tree topology occurred when the number of individuals per population was more even.

Admixture analysis of populations was conducted using sparse non-negative matrix factorisation (snmf) as implemented in the snmf function in the R package LEA (Frichot and François 2015). The number of ancestral populations (K) was determined using the entropy criterion (Alexander and Lange 2011; Frichot and François 2015). Ancestry coefficients were visualised by plotting the Q-values of each individual in a bar plot, and average Q-values for each population on a map.

Environmental niche modelling

Records for *Aglaia elaeagnoidea* were downloaded from GBIF (https://www.gbif.org) and filtered to only include those from the east of the distribution to specifically investigate exchange tracks between Australia and Southeast Asia and to avoid conflation of the multiple taxa in the *A. elaeagnoidea* complex as identified in this study. Records were further filtered to only include herbarium records collected after 1960 with coordinates without geospatial issues. Records were manually checked and those with obvious errors in coordinates (e.g. records in the ocean) removed. Eastern samples included for sequencing in this study were added to the dataset; many of these have not been digitised or the localities were manually determined from locality information provided on the specimen. Duplicate records were

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removed. This resulted in 344 occurrence records for eastern *A. elaeagnoidea* (Supplementary Material 4).

Environmental variables used for modelling the distribution of *A. elaeagnoidea* were selected from the standard 19 bioclimatic variables (Booth *et al*. 2014); we used the global downscaled climate dataset (Karger *et al*. 2017a; Karger *et al*. 2017b). An initial model was run in MaxEnt with all environmental variables to ascertain the relative importance of each variable in determining the presence of *A. elaeagnoidea*. Autocorrelation between environmental variables was assessed using the corr function in R, and variables with a high degree of correlation (R>0.7; Supplementary Material 5) were removed, with the variable that explained the least variation eliminated first. The resultant set of variables was then evaluated for biological significance and to ensure that variables thought to be important for determining the distribution of *A. elaeagnoidea*, such as seasonality, were included. A final set of eight environmental variables was included in the model: Bio03 (isothermality), Bio07 (annual temperature range), Bio08 (mean temperature of wettest quarter), Bio11 (mean temperature of coldest quarter), Bio13 (precipitation of wettest quarter), Bio15 (precipitation seasonality), Bio18 (precipitation of warmest quarter) and Bio19 (precipitation of coldest quarter).

The species distribution model was trained in MaxEnt v.3.4.0 (Phillips et al. 2006) allowing only linear, quadratic and product features to minimise the risk of overfitting. A maximum of 100,000 background points were modelled and restricted to a 100km radius of presences. Ten cross-validation replicates were run.

The model was projected onto paleoclimatic data for the Last Glacial Maximum (LGM) approximately 21,000 years ago. The LGM was chosen to model distribution differences under the most extreme climatic conditions within the time that a species may have evolved. To account for climate model variation, we caculated mean climate rasters for each bioclimatic variable from nine available paleoclimatic datasets within the CHELSA dataset (Karger et al. 2017a; Karger et al. 2017b).

We considered ensemble methods for generating our ENM; however, there is much evidence that well-fitted and thoughtfully interpreted MaxEnt models perform well. Furthermore, a recent paper by Hao et al. (2019) supports the view that ensemble modelling can be helpful but has many of the same short-comings, constraints, trade-offs and subjective choices of any approach to modelling. Here, we have carefully considered and chosen the parameters to generate a model that makes good biological and statistical sense, and have interpreted the results conservatively.

Results

DArT data

This study is one of the first to use DArT-seq on herbarium material for a phylogeographic study, recovering 176,331 SNPs from 90,456 loci in 141 of 153 samples (Besnard et al. 2018). Notable successes include genotype data from a nearly 200 year old specimen from NY (*Wight 140*, DNA no. G08438), and specimens treated with mercury (e.g. some US specimens) and gamma irradiation (e.g. DNA no. G08724). Yield of extracted DNA was the main factor limiting successful sequencing; most samples that yielded >2 ng/µl of high-quality DNA were successfully sequenced. No specimens sampled from SING or BO were successful; observations made when sampling suggested that specimens kept in tropical

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conditions were generally browner in colour and were more difficult to extract adequate DNA yield from (see also Brewer et al., 2019).

The final dataset, after removal of SNPs from poor quality loci or samples, comprised 22,834 loci with one SNP per locus for 136 samples (Table 1). Of these, 129 samples were *A. elaeagnoidea* from across its distribution (Figure 1) and the remaining seven samples were from the outgroup species *A. edulis* (two samples), *A. spectabilis* (two samples), *A. korthalsii*, *A. leucophylla* and *A. chittagonga*.

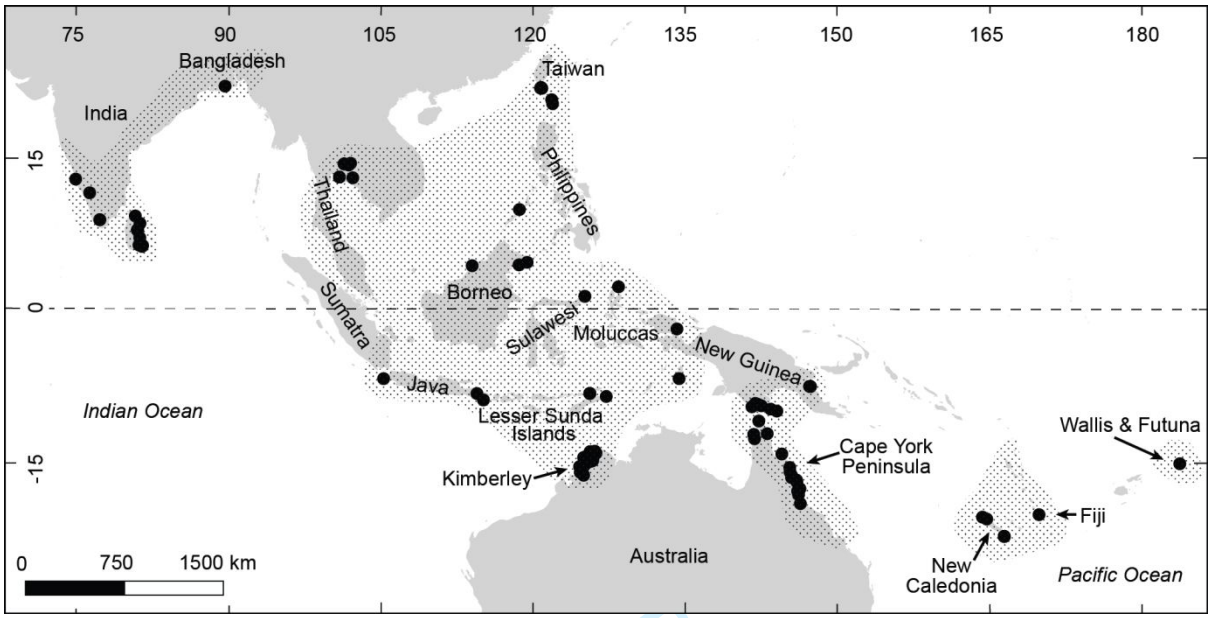


Figure 1 Map of localities of the 129 *Aglaia elaeagnoidea* samples included in this study. Shaded area represents the known distribution of *A. elaeagnoidea* according to Pannell (1992).

Lineage divergence in the A. elaeagnoidea *complex*

PCA (Figure 2a) and NeighbourNet analysis (Figure 2b) both showed substantial genetic structure in the *A. elaeagnoidea* complex, with a clear east-west divide. Individuals from the eastern part of the species' distribution (Borneo, Sulawesi, Philippines, Taiwan, the Moluccas, New Guinea, Australia, Timor-Leste, Pacific Islands and some individuals from Java and the Lesser Sunda Islands) clustered together, while specimens from the western part (India, Sri Lanka, Bangladesh, Thailand and some individuals from Java and the Lesser Sunda Islands), clustered separately. Within the western group, Indian (including Sri Lankan) individuals appear to be genetically distinct from individuals from Bangladesh, Thailand, Java and the Lesser Sunda Islands. Outgroup species clustered separately from *A. elaeagnoidea*, but the NeighbourNet analysis suggests that *A. edulis* is most closely related to the western *A. elaeagnoidea* groups.

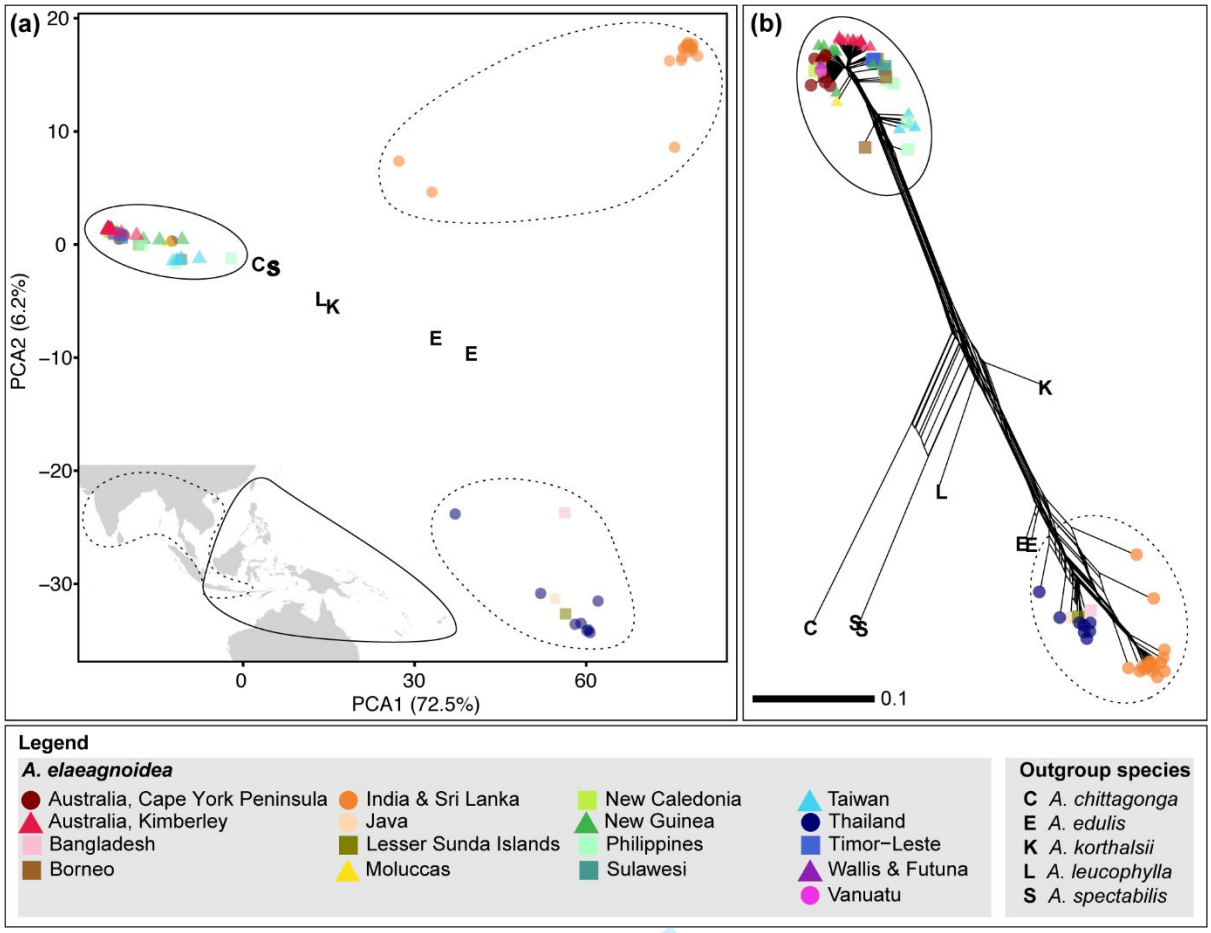


Figure 2 a) Principal Component Analysis (PCA) and b) NeighbourNet network of all *Aglaia* samples included in the study. Letter symbols represent outgroup samples, while coloured shapes represent *A. elaeagnoidea* samples from different populations. Points circled in dashed line represent samples from the west of the distribution of *A. elaeagnoidea* (India, Sri Lanka, Bangladesh, Thailand, Lesser Sunda Islands and Java), while samples circled in solid line are *A. elaeagnoidea* samples from the eastern end of the distribution (Australia, New Guinea, Pacific islands, Moluccas, Lesser Sunda Islands, Timor-Leste, Java, Sulawesi, Borneo, Philippines and Taiwan), as shown in inset map.

The SVDquartets analysis sampled 17.84% of the total number of distinct quartets, 90.9% of which were compatible in quartet assembly. The resultant 50% majority rule consensus tree recovered eastern and western populations of *A. elaeagnoidea* in separate clades (Figure 3). Western *A. elaeagnoidea* populations were recovered with maximum (100%) support in a clade including *A. edulis*. Eastern populations of *A. elaeagnoidea* were recovered in a clade with maximum (100%) support, which included *A. korthalsii* with weak (54%) support.

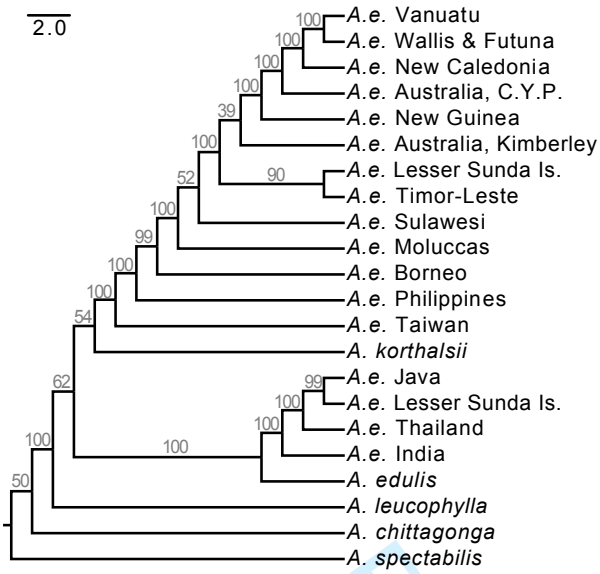


Figure 3 SVDquartets 50% majority rule consensus tree of *Aglaia elaeagnoidea* ("*A.e.*") populations and sampled outgroup species under a coalescence model. 17.84% of the total number of distinct quartets were sampled, 90.9% of which were compatible in quartet assembly. "C.Y.P." refers to Cape York Peninsula.

Analysis of eastern A. elaeagnoidea *phylogeography*

Given the clear genetic disjunction between eastern and western *A. elaeagnoidea*, all further analyses were conducted on the eastern *A. elaeagnoidea* group. This was to investigate exchange tracks between Australia and Southeast Asia, and to avoid analysis across what likely represents separate species.

Principal Components Analysis showed substantial genetic structure in eastern *A. elaeagnoidea* (Figure 4a). Individuals from Taiwan, Philippines, Borneo and Sulawesi had a high degree of variation that was mostly captured by PCA1 (31.2%), while PCA2 (18.1%) largely represented variation among individuals from the Pacific Islands, Australia and New Guinea. Individuals from the Kimberley clustered separately from Cape York Peninsula individuals, which clustered with individuals from New Guinea and the Pacific Islands. These patterns, including the strong differentiation of the Australian populations, were also found in the NeighbourNet analysis (Figure 4b).

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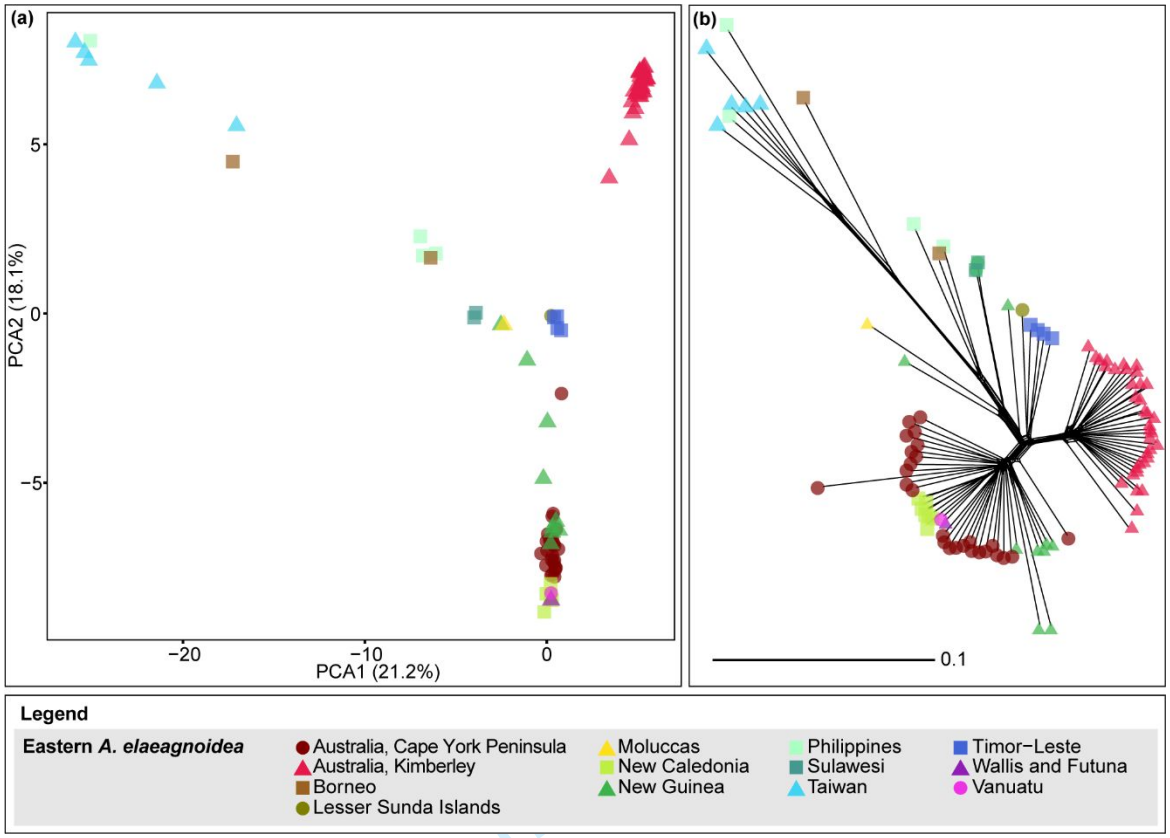


Figure 4 a) PCA and b) NeighbourNet network of the eastern *A. elaeagnoidea* group SNP data. Different symbols represent the different populations in the eastern *A. elaeagnoidea* group.

Fst statistics indicated that there is significant isolation by distance, with geographically close populations having lower pairwise Fst (r = 0.42, Mantel P = 0.004; Table 1, Supplementary Material 3). Particularly high Fst values (>0.4) were calculated between Taiwan and all other populations except Philippines, between Sulawesi and all other populations, and between the Moluccas and all other populations (Supplementary Material 3). The lowest Fst values were found between Cape York Peninsula and New Guinea (Fst = 0.094), Philippines and Borneo (Fst = 0.085), and between New Caledonia, Wallis and Futuna, and Vanuatu (Fst = 0.17–0.20) (Table 1).

Table 1 Pairwise Fst of eastern *A. elaeagnoidea* populations

	C.Y.P.	Kimberley	Borneo	Lesser Sunda Is.	Moluccas	New Caledonia	New Guinea	Sulawesi	Philippines	Taiwan	Timor-Leste	Vanuatu
Kimberley	0.50											
Borneo	0.36	0.37										
Lesser Sunda Is.	0.32	0.34	0.47									
Moluccas	0.48	0.48	0.53	0.54								
New Caledonia	0.20	0.49	0.68	0.34	0.49							
New Guinea	0.09	0.39	0.50	0.33	0.55	0.32						
Sulawesi	0.43	0.43	0.43	0.65	0.70	0.75	0.54					
Philippines	0.35	0.36	0.08	0.41	0.48	0.66	0.48	0.43				
Taiwan	0.56	0.48	0.53	0.60	0.68	0.84	0.79	0.80	0.35			
Timor-Leste	0.29	0.30	0.58	0.27	0.67	0.51	0.31	0.59	0.45	0.78		
Vanuatu	0.24	0.45	0.58	0.48	0.67	0.19	0.32	0.74	0.52	0.66	0.52	
Wallis & Futuna	0.23	0.40	0.58	0.46	0.68	0.20	0.31	0.75	0.53	0.65	0.52	0.17

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The topology of the TreeMix maximum likelihood tree suggests that the Philippines population is sister to the Taiwan population, with a high drift parameter (Figure 5; Supplementary Material 6). Sulawesi, the Moluccas and Borneo form a clade, and Lesser Sunda Islands is sister to a clade including Australian, Pacific Island, and New Guinea populations (Figure 5). Within this clade, the best model retrieved the Kimberley population as sister to the Timor-Leste population, and the Pacific Island populations as sister to the Cape York Peninsula populations, which are sister to New Guinea (Figure 5). The OptM analysis indicated that allowing for four migration events yielded the most likely tree, increasing the likelihood from 458.001 with no migration events to 535.407. The migration event with the strongest migration weight was from Philippines to Borneo, resulting in an estimated 51% shared alleles. A second migration event was modelled from Sulawesi, Borneo and the Moluccas to Philippines, contributing 33% of alleles to the Philippines population. A third migration event was modelled from Borneo to an ancestor of the Australia, New Guinea and Pacific Island populations, and the fourth event from an ancestor of the Borneo and Moluccas populations to New Guinea, both contributing 8% of alleles to their respective sink populations.

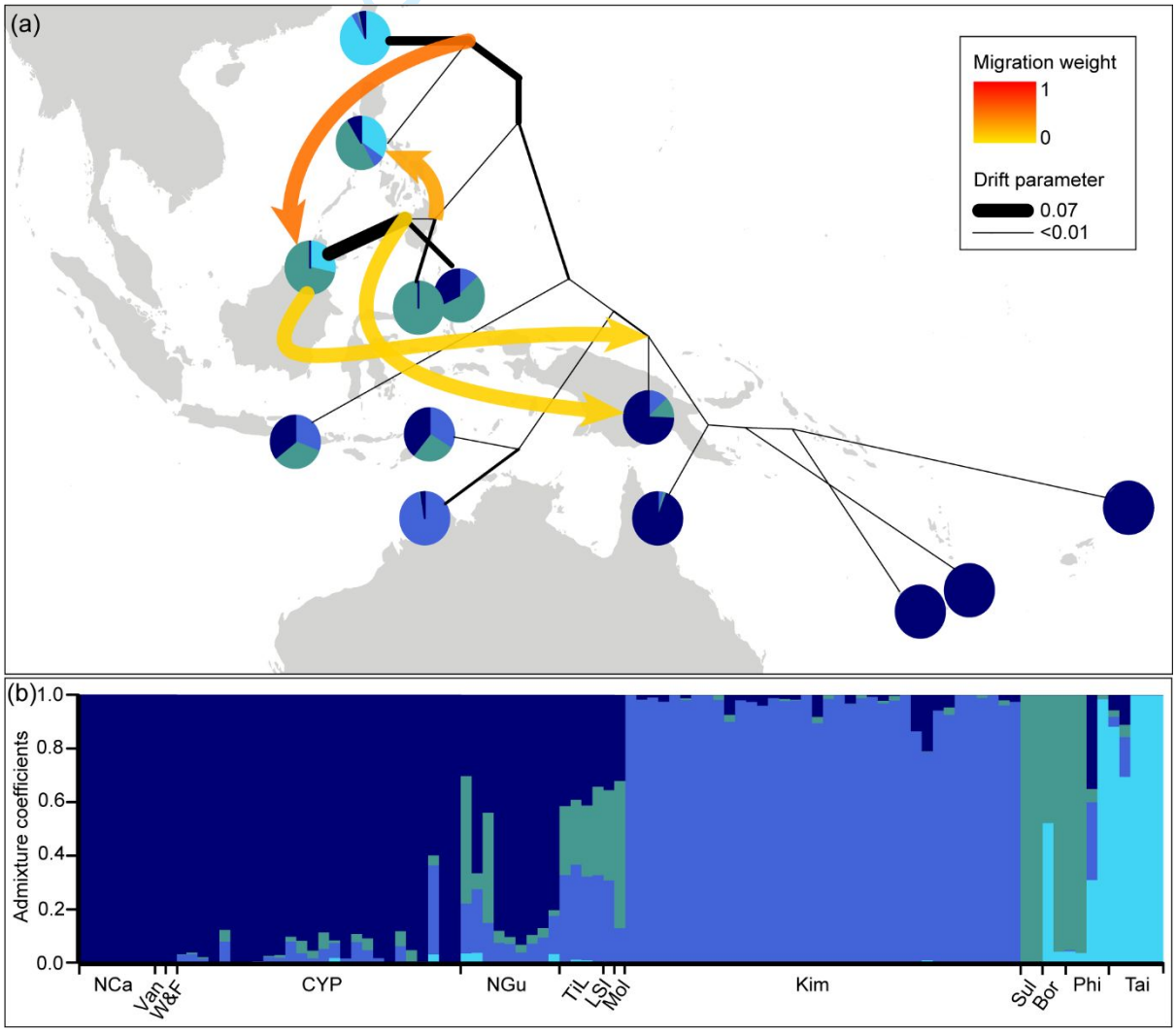


Figure 5 Results of LEA and TreeMix analysis showing genetic structure across the distribution of eastern *A. elaeagnoidea*. Map shows mean Q-values for each population in pie

charts, with Q-values for each individual represented in bar plot below (k=4). Pie charts for each population are connected by the results of the TreeMix analysis, with line thickness proportional to the drift parameter, and coloured arrows showing migration events with colour representative of migration weight. See Supplementary Material 6 for original TreeMix tree.

The results of the LEA analysis suggest that the genetic structure in eastern *A. elaeagnoidea* is best explained by four ancestral populations (Figure 5). It revealed that Australian populations have little shared ancestry. Populations with the highest degree of admixture were from New Guinea, Timor-Leste, the Moluccas and Philippines.

Environmental niche modelling

The mean environmental niche models (ENMs) based on eight climatic variables predicted climate suitability maps that broadly reflect the present-day distribution of eastern *A. elaeagnoidea* (mean AUC = 0.978, standard deviation = 0.008; Figure 6a). Bio07 (annual temperature range) and Bio03 (isothermality) explained most of the variation, contributing 38.5% and 35.2% to the model respectively. Interestingly, the model indicated high suitability in the Northern Territory of Australia, but *A. elaeagnoidea* has not been recorded there. The model also predicted that much of the landmass at equatorial latitude is currently unsuitable for *A. elaeagnoidea*, while Cape York, the Pacific Islands and Taiwan are some of the most climatically suitable areas for the species.

The projection of the model onto the LGM data predicted a much expanded distribution of climatic conditions associated with the distribution of eastern *A. elaeagnoidea*; suitable conditions were predicted south along the coast of eastern Australia into subtropical latitudes, into northern New Guinea and the Bird's Head Peninsula, across equatorial islands and around the coast of Sundaland (Figure 6b,c). Further, the Lesser Sunda Islands were suitable for *A. elaeagnoidea*, but most of the west coast of the Arafura Shelf (Figure 6c) was unsuitable, with the exception of the land-masses along the Sahul Banks and Ashmore Reef in close proximity to Timor-Leste

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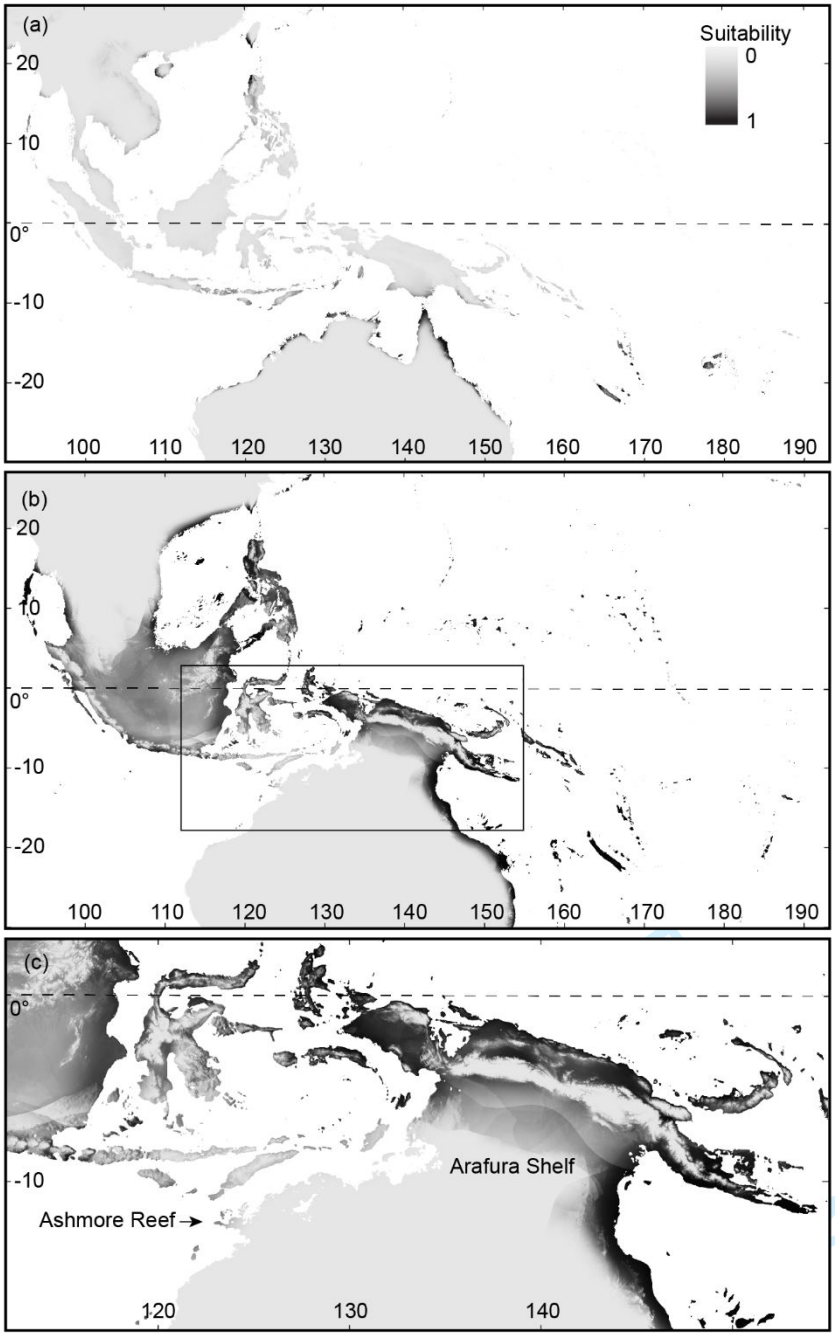


Figure 6 Results of Maxent species distribution modelling, predicting suitable climatic conditions for eastern *A. elaeagnoidea* from eight environmental variables (a) at present, and (b-c) during the last LGM, 22 ka. Relatively suitable habitat of Ashmore Reef visible in (c).

Discussion

This is the one of the first studies to examine phylogeographic patterns within a widely-distributed plant species (or species complex) that occurs from Southeast Asia to Australia and the Pacific Islands. With few exceptions (e.g. Guo et al. 2016), phylogeographic studies to date have been restricted to species across subsets of islands in Southeast Asia, and have focussed on vertebrate fauna (e.g. Liao et al. 2007; Ueda et al. 2010; Jusoh et al. 2019; Grismer et al. 2019; see Husson et al. 2020). Our study strongly suggests the presence of two exchange tracks between northern Australia and Southeast Asia. Identification of floristic exchange routes between northern Australia and Southeast Asia gives new insights into the biogeography and evolution of Australia's tropical flora, and is important for biosecurity and for planning for conservation of the region's biota.

Genetic structure in A. elaeagnoidea

Our results strongly suggest that *A. elaeagnoidea* as currently circumscribed comprises multiple genetic entities that are likely to represent different species. The NeighbourNet analysis showed a clear genetic distinction between western individuals (India, Sri Lanka, Bangladesh, Thailand, Java and Lesser Sunda Islands) and eastern individuals (Lesser Sunda Islands, Timor-Leste, Sulawesi, Borneo, Philippines, Taiwan, New Guinea, Moluccas, Australia and Pacific Islands). Moreover, the SVDquartets analysis indicates that these two groups are not monophyletic: *A. korthalsii* is sister to the eastern *A. elaeagnoidea* group whereas *A. edulis* is sister to the western *A. elaeagnoidea* group.

These findings are congruent with those of Muellner et al. (2009), who observed strong genetic differentiation between samples from eastern and western extremes of the range of *A. elaeagnoidea* based on 13 samples and one nuclear marker (internal transcribed spacer of nrDNA - ITS). Grudinski et al. (2014) included two samples of *A. elaeagnoidea* in their ITS phylogeny, which were not retrieved as monophyletic. Furthermore, observations of herbarium specimens indicates that the observed genetic disjunction coincides with morphological differences. As such, we recommend that the taxonomy of *A. elaeagnoidea* is reviewed.

Phylogeography of eastern A. elaeagnoidea *and Australian-Asian exchange tracks*

This paper is the first phylogeographic study to identify floristic exchange tracks between Southeast Asia and Australia. We posited four historical biogeographical scenarios that could explain the current Australian distribution of *A. elaeagnoidea*: 1) a single exchange track between Australia and Asia with vicariance within Australia; 2) a single exchange track between Australia and Asia with long-distance dispersal within Australia; 3) two exchange tracks between Australia and Asia from the same source regions in Asia, and 4) two exchange tracks between Australia and Asia from different source regions in Asia. Our admixture analysis and Fst statistics indicate that the Cape York Peninsula and Kimberley populations are highly genetically distinct from each other (Fst = 0.5). Furthermore, our SVDquartets and TreeMix analysis indicates that the Cape York Peninsula and Kimberley populations have greater genetic connectivity with New Guinea and Timor, respectively, than they do with each other. Finally, our ENM does not support a scenario of continuous availability of suitable habitat between the Cape York Peninsula and Kimberley populations at the LGM, precluding scenario 1. Moreover, it suggests that there is currently suitable habitat connecting the Cape York Peninsula and Kimberley populations even though *A. elaeagnoidea* has not been recorded from those areas, supporting the idea that these populations were established

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from two separate exchange tracks. Our results therefore support scenario 4, positing two exchange tracks for *A. elaeagnoidea* in Australia: one between Timor and the Kimberley region, and one between New Guinea and Cape York Peninsula.

Our results suggest the exchange track between New Guinea and Cape York Peninsula is contemporary; an extremely low Fst (Fst = 0.09; Table 1) indicates ongoing gene flow between these areas. Phylogeographic studies on birds (Roshier et al. 2012; Marki et al. 2018; Lamb et al. 2019; Joseph et al. 2019; Dorrington et al. 2019) and reptiles (Pepper et al. 2017; Natusch et al. 2020) have found shallow to no genetic divergence between Australian and New Guinean lineages. This was attributed to recent repeated geneflow between New Guinea and Cape York Peninsula populations during low glacial sea levels until c. 17 Ka ago (Voris 2000). Contemporary gene flow has been inferred for highly mobile fauna species such as the Palm Cockatoo (Keighley et al. 2019). The dispersal ecology of *A. elaeagnoidea* is largely unknown; however, Pied Imperial Pigeons (*Ducculus bicolor*), which migrate annually between Cape York Peninsula and New Guinea, have been observed eating the fruit (Pannell, 1992). Furthermore, there are approximately 40 species of birds (not including waterbirds) that migrate annually between Cape York Peninsula and the Trans-Fly of New Guinea. Of these, two are predominantly frugivorous and the small size of *A. elaeagnoidea* fruit means it is highly likely to be dispersed between New Guinea and Australia by one or more of these species (Mees 1982; Bishop 2005; Rossetto et al. 2015; Corlett 2017; Joseph et al. 2019), maintaining geneflow between these *A. elaeagnoidea* populations.

Our TreeMix and SVDquartets analyses show that the Timor-Leste and Kimberley populations are sister groups, suggesting a second exchange track is present in Australia between Timor-Leste and northwestern Australia. A track between Asia and northwestern Australia has been previously reported for fauna (e.g. Williams et al. (2008); Toon et al. (2017); Dorrington et al. (2019)), and humans (Bird *et al*. 2018) but not for plants.

The Kimberley population was likely established by over-water dispersal from Timor-Leste during a previous glacial maximum. We interpret the high genetic divergence between the Kimberley and Timor-Leste populations as being a consequence of a founder event followed by isolation and genetic drift. This interpretation is supported by the results of our TreeMix analysis that retrieved a high drift parameter for the Kimberley. Furthermore, the ENM suggests that the most likely time for dispersal between the Kimberley and Timor-Leste was during the last or a previous glacial maximum, when habitat availability and geographic proximity between the two land masses was greatest. Global sea levels dropped to as low as -120 m (below current sea level) at c. 20 Ka (Brooke et al. 2017) and -85 m prior to 60 Ka (Lambeck and Chappell 2001). Although Timor-Leste has never had a dryland connection to Australia, at sea levels of -75 m, land now represented by the Ashmore Reef and the "Sahul Banks" islands were exposed along the Arafura Shelf, with the closest island being 87 km away from Roti (Bird et al. 2018). These proximal landmasses correspond with the only areas of suitable climate for *A. elaeagnoidea* during the last LGM according to our ENM. Subsequent sea level rising at c. 17 Ka may have isolated the Kimberley populations from Timor-Leste and other *A. elaeagnoidea* populations. Pied Imperial Pigeons (a likely dispersal vector of *A. elaeagnoidea*) occur in the Kimberley region but are sedentary; they are isolated from Cape York Peninsula populations, and do not migrate to Asian islands like the Cape York Peninsula and Northern Territory Pied Imperial Pigeon populations (Johnstone 1981; Forshaw 2015).

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Cycles of expansion and contraction of suitable habitat impacted dispersal and connectivity throughout the range of eastern *A. elaeagnoidea*. Our ENM suggests that the availability of suitable habitat expanded during cooler, drier glacial peaks into equatorial Southeast Asia and contracted during interglacials to peripheral islands. This agrees with the results of our LEA that shows greatest admixture in equatorial populations, and greatest genetic differentiation in peripheral populations. In other Australian rainforest taxa repeated range expansions and contractions coeval with Quaternary climatic fluctuations have been shown to reinforce a pattern of low genetic diversity and high genetic differentiation in peripheral populations (Rossetto et al. 2012; Mellick et al. 2012, 2013; Fahey et al. 2019). This appears particularly relevant for the Kimberley and Taiwan populations of *A. elaeagnoidea*, where the TreeMix analysis modelled a high drift parameter, suggesting pronounced genetic drift following population isolation. However, the Pacific Island populations (New Caledonia, Vanuatu and Wallis and Futuna) have a low drift parameter and have little genetic differentiation between islands. This could be explained by more recent or ongoing stochastic dispersal events. Pied Imperial Pigeons are highly mobile and may be capable of dispersing *A. elaeagnoidea* seeds such distances. Although it is difficult to unequivocally identify the processes underlying geographic variation based on current sampling, our results strongly suggest that a combination of climate-induced expansion and contraction cycles and stochastic dispersal events have lead to the phylogeographic patterns observed in eastern *A. elaeagnoidea*.

Conclusion: Implications for the phytogeography of northern Australia and Southeast Asia

Our results support the broader idea that north-western Australian monsoon tropics and the north-eastern wet tropics have a separate biogeographic history (Crisp et al. 1995; Bowman et al. 2010). However, we suggest that this was not only driven by the restriction of exchange across northern Australia by biogeographic barriers (Gonzalez-Orozco et al. 2014; Edwards et al. 2017), but also by the presence of multiple exchange tracks between Asia and northern Australia. Multiple exchange tracks may also have had an influence on phytogeography in southern Australia; Brown et al. (2011) identified a phylogenetic link between south-west Western Australia and the Lesser Sunda Islands in *Paraserianthes* I.C.Nelson (Fabaceae). Our results suggest that this pattern may be explained by colonisation of northern Australia via the western Arafura Shelf and expansion into southern Australia at a deeper time-scale.

Detailed phylogeographic studies such as this are needed to understand links between Asia and Australia and the influence of multiple exchange tracks on continental phytogeography over time. Comparing the phylogenetic and phylogeographic history of Asian lineages in Australia to that of autochthonous lineages provides an exciting opportunity to gain new insight into the evolution of modern Australian phytogeographic patterns.

Biosketch

EMJ is a PhD candidate at the Australian Tropical Herbarium and James Cook University, whose research focusses on understanding the Sunda-Sahul Flroistic Exchange using floristic, phylogenetic and phylogeographic data. EMJ conceived the ideas with DMC and KRT; EMJ and CMP collected the data; EMJ conducted the lab work; EMJ, SY, MR and PDW conducted or facilitated data analysis; EMJ, SY, MR, KRT and DMC interpreted the results and EMJ led the writing.

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Supplementary Material 1 List of samples included in this study. CYP locality stands for Cape York Peninsula.

DNA no.	Species	Collector	Collection number	Collection date	Herbarium or field	Herbarium code	Locality	Latitude	Longitude
G08343	*A. elaeagnoidea*	A. Ford	5776	15/9/2010	Herbarium	CNS	CYP, Australia	-17.74	146.16
G08344	*A. elaeagnoidea*	A. Ford	6502	14/12/2015	Herbarium	CNS	CYP, Australia	-18.18	146.17
G08345	*A. elaeagnoidea*	B.M. Waterhouse	4846	27/3/1998	Herbarium	CNS	CYP, Australia	-9.75	143.42
G08346	*A. elaeagnoidea*	B. Hyland	16029	6/5/1998	Herbarium	CNS	CYP, Australia	-17.67	146.17
G08347	*A. elaeagnoidea*	J.R. Croft & Y. Lelean	LAE68526	28/7/1976	Herbarium	CNS	New Guinea	-7.52	147.35
G08348	*A. elaeagnoidea*	D.I. Nicholson	AFO04853	5/5/1975	Herbarium	CNS	CYP, Australia	-16.50	145.48
G08349	*A. elaeagnoidea*	B. Hyland	1204RFK	20/10/1967	Herbarium	CNS	CYP, Australia	-17.83	146.08
G08351	*A. elaeagnoidea*	L.J. Webb	13773	1/7/1973	Herbarium	CNS	Kimberley, Australia	-14.53	125.82
G08352	*A. elaeagnoidea*	J.G. Tracey	15234	26/5/1981	Herbarium	CNS	Kimberley, Australia	-14.88	125.77
G08353	*A. elaeagnoidea*	J.G. Tracey	15124	25/5/1981	Herbarium	CNS	Kimberley, Australia	-14.65	125.70
G08354	*A. elaeagnoidea*	J.G. Tracey	15064	27/5/1981	Herbarium	CNS	Kimberley, Australia	-14.80	125.70
G08356	*A. elaeagnoidea*	Greger	HG753	25/11/2000	Herbarium	FHO	Bangladesh	22.11	89.63
G08357	*A. elaeagnoidea*	Greger	HG502	15/2/1998	Herbarium	FHO	Thailand	13.07	102.22
G08359	*A. elaeagnoidea*	Kenneally & Hyland	10853	26/01/1989	Herbarium	FHO	Kimberley, Australia	-14.60	125.30
G08360	*A. elaeagnoidea*	Greger	HG650	3/2/1999	Herbarium	FHO	CYP, Australia	-17.60	146.30
G08361	*A. elaeagnoidea*	Pennington	8130	18/2/1964	Herbarium	FHO	New Caledonia	-20.40	164.30
G08362	*A. elaeagnoidea*	Mabberley	2012	25/8/1984	Herbarium	FHO	New Caledonia	-20.59	164.72
G08363	*A. elaeagnoidea*	K.M. Matthew	RHT27482	11/4/1980	Herbarium	GH/A	India	12.94	74.90
G08364	*A. elaeagnoidea*	McDonald & Ismail	4976	8/2/1994	Herbarium	GH/A	Bali	-8.84	115.10
G08365	*A. elaeagnoidea*	W. Takeuchi	16203	26/4/2001	Herbarium	GH/A	New Guinea	-7.51	147.30
G08366	*A. elaeagnoidea*	W. Takeuchi	16205	26/4/2001	Herbarium	GH/A	New Guinea	-7.51	147.30
G08367	*A. elaeagnoidea*	W. Takeuchi	16208	26/4/2001	Herbarium	GH/A	New Guinea	-7.51	147.30
G08368	*A. elaeagnoidea*	W. Takeuchi	16210A	26/4/2001	Herbarium	GH/A	New Guinea	-7.51	147.30
G08438	*A. elaeagnoidea*	Wight	140	April 1835	Herbarium	NY	India	8.93	77.28
G08441	*A. elaeagnoidea*	Wight	418	-	Herbarium	NY	India	11.59	76.28
G08442	*A. elaeagnoidea*	E. M. Joyce, R. Butcher & K.R. Thiele	EMJ011	9/5/2018	Field	PERTH	Kimberley, Australia	-14.66	125.76
G08443	*A. elaeagnoidea*	E. M. Joyce, R. Butcher & K.R. Thiele	EMJ012	9/5/2018	Field	PERTH	Kimberley, Australia	-14.74	125.80
G08444	*A. elaeagnoidea*	Ambriansyah *et al.*	AA 2634	Nov 2003	Herbarium	L	Sulawesi	1.38	125.10
G08445	*A. elaeagnoidea*	B. Hyland	3725RFK	12/7/1978	Herbarium	CNS	CYP, Australia	-16.75	145.97
G08446	*A. elaeagnoidea*	B. Hyland	15784	5/5/1998	Herbarium	CNS	CYP, Australia	-17.74	146.16
G08447	*A. elaeagnoidea*	J. Le Cussan	767	31/10/1997	Herbarium	CNS	CYP, Australia	-16.93	146.00
G08448	*A. elaeagnoidea*	K. Freebody	105	20/10/1999	Herbarium	CNS	CYP, Australia	-9.52	141.57

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G08449	*A. elaeagnoidea*	P.I. Forster	6432	1/3/1990	Herbarium	CNS	CYP, Australia	-10.92	142.25
G08450	*A. elaeagnoidea*	E. Cameron	2338	31/7/1975	Herbarium	CNS	CYP, Australia	-9.42	142.50
G08453	*A. elaeagnoidea*	B. Hyland	7431	12/9/1974	Herbarium	CNS	CYP, Australia	-12.17	143.08
G08455	*A. elaeagnoidea*	H. Heatwole & E. Cameron	787	29/7/1974	Herbarium	CNS	CYP, Australia	-9.94	144.03
G08456	*A. elaeagnoidea*	R. Mazlin	s.n.	5/5/1969	Herbarium	CNS	CYP, Australia	-16.33	145.50
G08457	*A. elaeagnoidea*	D.G. Fell	2869	25/2/1993	Herbarium	CNS	CYP, Australia	-15.50	145.30
G08458	*A. elaeagnoidea*	B.M. Waterhouse	2797B	26/3/1993	Herbarium	CNS	CYP, Australia	-9.28	142.18
G08459	*A. elaeagnoidea*	Fell, D.G.	2999	29/3/1993	Herbarium	CNS	CYP, Australia	-14.17	144.52
G08461	*A. elaeagnoidea*	A. Ford, P. Green. & P. Williams	4213	8/12/2003	Herbarium	CNS	CYP, Australia	-19.07	146.35
G08462	*A. elaeagnoidea*	Hyland, B.	13814	26/1/1989	Herbarium	CNS	Kimberley, Australia	-14.38	125.95
G08463	*A. elaeagnoidea*	Hyland, B.	25486RFK	10/6/1988	Herbarium	CNS	Kimberley, Australia	-14.38	125.95
G08464	*A. elaeagnoidea*	K.F. Kenneally	10175	5/6/1987	Herbarium	CNS	Kimberley, Australia	-14.62	125.25
G08465	*A. elaeagnoidea*	Volck, H.E.	AFO04304		Herbarium	CNS	CYP, Australia	-15.95	145.33
G08466	*A. elaeagnoidea*	M.R. O'Reilly	470	5/12/1989	Herbarium	CNS	CYP, Australia	-12.67	141.83
G08467	*A. elaeagnoidea*	B. Hyland	15865	5/5/1998	Herbarium	CNS	CYP, Australia	-17.75	146.16
G08468	*A. elaeagnoidea*	B. Hyland	15916	6/5/1998	Herbarium	CNS	CYP, Australia	-17.68	146.18
G08469	*A. elaeagnoidea*	Anonymous	s.n.	-	Herbarium	PERTH	Kimberley, Australia	-14.09	126.20
G08470	*A. elaeagnoidea*	J.S. Beard	7006	8/6/1974	Herbarium	PERTH	Kimberley, Australia	-14.49	125.83
G08471	*A. elaeagnoidea*	G.J. Keighery	10149	8/6/1988	Herbarium	PERTH	Kimberley, Australia	-13.90	126.08
G08472	*A. elaeagnoidea*	E.A. Chesterfield	388	28/5/1984	Herbarium	PERTH	Kimberley, Australia	-14.09	126.20
G08473	*A. elaeagnoidea*	P.G. Wilson	11401	6/7/1973	Herbarium	PERTH	Kimberley, Australia	-15.08	125.17
G08474	*A. elaeagnoidea*	P.G. Wilson	10662	12/5/1972	Herbarium	PERTH	Kimberley, Australia	-15.42	124.58
G08475	*A. elaeagnoidea*	K.F. Kenneally	5099	17/6/1976	Herbarium	PERTH	Kimberley, Australia	-14.67	125.75
G08476	*A. elaeagnoidea*	F. Lullfitz	L 6116	16/6/1968	Herbarium	PERTH	Kimberley, Australia	-13.97	126.05
G08477	*A. elaeagnoidea*	K.F. Kenneally	5234	21/6/1976	Herbarium	PERTH	Kimberley, Australia	-14.61	125.80
G08478	*A. elaeagnoidea*	K.F. Kenneally	8969	10/6/1984	Herbarium	PERTH	Kimberley, Australia	-15.03	125.35
G08479	*A. elaeagnoidea*	K.F. Kenneally	7946	24/1/1982	Herbarium	PERTH	Kimberley, Australia	-14.83	125.84
G08480	*A. elaeagnoidea*	K.F. Kenneally	9671	16/5/1986	Herbarium	PERTH	Kimberley, Australia	-15.98	124.65
G08481	*A. elaeagnoidea*	K.F. Kenneally	8147	27/4/1982	Herbarium	PERTH	Kimberley, Australia	-14.81	125.88
G08482	*A. elaeagnoidea*	K.F. Kenneally & B.P.M. Hyland	s.n.	10/6/1988	Herbarium	PERTH	Kimberley, Australia	-14.38	125.95
G08483	*A. elaeagnoidea*	K.F. Kenneally	8128	25/4/1982	Herbarium	PERTH	Kimberley, Australia	-14.59	125.76
G08484	*A. elaeagnoidea*	A.V. Milewski	102	22/5/1983	Herbarium	PERTH	Kimberley, Australia	-16.27	124.98
G08485	*A. elaeagnoidea*	K.F. Kenneally & B.P.M. Hyland	KFK10175	5/6/1987	Herbarium	PERTH	Kimberley, Australia	-14.62	125.25
G08486	*A. elaeagnoidea*	N.G. Marchant	72/379	14/6/1972	Herbarium	PERTH	Kimberley, Australia	-14.25	126.00
G08487	*A. elaeagnoidea*	T. Handasyde	TH 3494	26/5/2008	Herbarium	PERTH	Kimberley, Australia	-15.36	125.00

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G08488	*A. elaeagnoidea*	T. Handasyde	TH 3488	26/5/2008	Herbarium	PERTH	Kimberley, Australia	-15.36	125.00
G08489	*A. elaeagnoidea*	T. Willing	321	5/4/1991	Herbarium	PERTH	Kimberley, Australia	-14.38	125.95
G08490	*A. elaeagnoidea*	T. Willing	386	23/5/1991	Herbarium	PERTH	Kimberley, Australia	-14.67	125.85
G08491	*A. elaeagnoidea*	A.A. Mitchell	5428	18/5/1998	Herbarium	PERTH	Kimberley, Australia	-13.94	125.63
G08492	*A. elaeagnoidea*	A.A. Mitchell & A.J. Williams	7392	25/2/2003	Herbarium	PERTH	Kimberley, Australia	-13.94	125.63
G08493	*A. elaeagnoidea*	A.A. Mitchell	7128	21/3/2002	Herbarium	PERTH	Kimberley, Australia	-14.48	125.86
G08494	*A. elaeagnoidea*	R.P.S. - BBG consultants	356	18/4/2007	Herbarium	PERTH	Kimberley, Australia	-14.52	124.98
G08495	*A. elaeagnoidea*	P.L. Comanor	1165	28/3/1968	Herbarium	GH/A	India	6.32	81.43
G08496	*A. elaeagnoidea*	D.D. Soejarto et al.	6026	22/4/1987	Herbarium	GH/A	Thailand	14.50	102.00
G08498	*A. elaeagnoidea*	Kostermans	24392	2/6/1971	Herbarium	GH/A	India	7.16	81.22
G08500	*A. elaeagnoidea*	D.D. Soejarto & F.C. Ho	6688	6/12/1989	Herbarium	GH/A	Taiwan	21.95	120.78
G08501	*A. elaeagnoidea*	C.C. Chuang	2210	3/5/1962	Herbarium	GH/A	Taiwan	21.94	120.79
G08502	*A. elaeagnoidea*	T. Tanaka	10329	9/9/1930	Herbarium	GH/A	Taiwan	21.90	120.86
G08504	*A. elaeagnoidea*	G. Murata et al.	37072	2/10/1984	Herbarium	GH/A	Thailand	14.33	101.82
G08508	*A. elaeagnoidea*	D.D. Soejarto & E. Reynoso	6302	1/8/1988	Herbarium	GH/A	Philippines	9.94	118.65
G08514	*A. elaeagnoidea*	J.T. Buchholz	1403	20/11/1947	Herbarium	GH/A	New Caledonia	-22.31	166.46
G08515	*A. elaeagnoidea*	J.H. Taylor	35	3/2/1946	Herbarium	GH/A	New Caledonia	-22.30	166.44
G08516	*A. elaeagnoidea*	M.G. Baumann-Bodenheim	5222	8/8/1950	Herbarium	GH/A	New Caledonia	-22.30	166.44
G08518	*A. elaeagnoidea*	J.F. Maxwell	01-359	3/9/2001	Herbarium	GH/A	Thailand	14.44	101.37
G08519	*A. elaeagnoidea*	O. Petrmitr	516	22/5/2002	Herbarium	GH/A	Thailand	14.44	101.37
G08521	*A. elaeagnoidea*	Madulid, Gaerlan, *et al*.	23751	21/4/1996	Herbarium	GH/A	Philippines	20.38	121.92
G08522	*A. elaeagnoidea*	Ambriansyah *et al*.	AA 2634	Nov 2003	Herbarium	GH/A	Sulawesi	1.38	125.10
G08527	*A. elaeagnoidea*	D. Mueller-Dombois & R.G. Cooray	67120614	6/12/1967	Herbarium	US	India	6.32	81.43
G08528	*A. elaeagnoidea*	D. Mueller-Dombois & R.G. Cooray	68013012A	30/1/1968	Herbarium	US	India	6.32	81.43
G08530	*A. elaeagnoidea*	S. Ripley	469	22/11/1971	Herbarium	US	India	8.58	81.24
G08532	*A. elaeagnoidea*	J.W. Nowicke & M. Jayasuriya	392	18/7/1973	Herbarium	US	India	6.34	81.47
G08536	*A. elaeagnoidea*	F.R. Fosberg	39687	18/12/1958	Herbarium	US	Java	-6.74	105.26
G08537	*A. elaeagnoidea*	H.S. McKee	3317	23/10/1955	Herbarium	US	New Caledonia	-22.30	166.44
G08538	*A. elaeagnoidea*	J.T. Buchholz	1402	20/11/1947	Herbarium	US	New Caledonia	-22.31	166.45
G08540	*A. elaeagnoidea*	R.G. Cooray	69111624R	16/11/1969	Herbarium	US	India	6.40	81.49
G08541	*A. elaeagnoidea*	Kostermans	26000	5/6/1976	Herbarium	US	India	8.94	77.28
G08542	*A. elaeagnoidea*	W. Meijer	188	28/6/1970	Herbarium	US	India	6.44	81.14
G08544	*A. elaeagnoidea*	S. Ripley	151	14/4/1969	Herbarium	US	India	7.91	80.99

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G08545	*A. elaeagnoidea*	S. Ripley	259	31/1/1969	Herbarium	US	India	7.91	80.99
G08550	*A. elaeagnoidea*	W. Dittus	WD71090303	3/9/1971	Herbarium	US	India	7.95	81.01
G08551	*A. elaeagnoidea*	W. Meijer	766	8/7/1971	Herbarium	US	India	9.31	80.78
G08560	*A. elaeagnoidea*	D.J. Collins	1132	11/3/1926	Herbarium	US	Thailand	13.14	100.90
G08561	*A. elaeagnoidea*	D.J. Collins	802	Apr 1922	Herbarium	US	Thailand	13.14	100.90
G08562	*A. elaeagnoidea*	S. Ripley	232	24/9/1968	Herbarium	US	India	7.95	81.00
G08563	*A. elaeagnoidea*	P.L. Comanor	674	10/12/1967	Herbarium	US	India	6.32	81.43
G08564	*A. elaeagnoidea*	H. Streimann and A. Kairo	NGF 39426	-	Herbarium	BRI	New Guinea	-7.50	147.25
G08566	*A. elaeagnoidea*	B.M. Waterhouse	BMW 4148	16/2/1997	Herbarium	BRI	New Guinea	-9.18	141.91
G08568	*A. elaeagnoidea*	R.T.	T12	13/3/1991	Herbarium	BRI	Wallis and Futuna	-14.30	-178.11
G08569	*A. elaeagnoidea*	W. Cooper	WWC2559	1/11/2018	Field	CNS	CYP, Australia	-12.25	141.75
G08570	*A. elaeagnoidea*	W. Cooper	WWC2564	1/11/2018	Field	CNS	CYP, Australia	-12.25	141.75
G08609	*A. elaeagnoidea*	C.G.G.J. van Steenis	7573	1/4/1936	Herbarium	NY	Lesser Sunda Islands	-8.21	114.46
G08613	*A. elaeagnoidea*	J.A.R. Anderson	S16032	5/6/1962	Herbarium	GH/A	Borneo	4.40	113.99
G08614	*A. elaeagnoidea*	M. bin Samsudin	A169	15/12/1950	Herbarium	GH/A	Borneo	4.48	118.61
G08625	*A. elaeagnoidea*	A. Kostermans	1567	20/6/1949	Herbarium	GH/A	Moluccas	2.32	128.42
G08638	*A. elaeagnoidea*	Kostermans	24308	30/5/1971	Herbarium	GH/A	India	7.93	81.00
G08646	*A. elaeagnoidea*	M.T. Kao	9719	12/5/1982	Herbarium	GH/A	Taiwan	21.92	120.73
G08648	*A. elaeagnoidea*	A. Boonkongchart	206	12/5/2003	Herbarium	GH/A	Thailand	14.44	101.37
G08651	*A. elaeagnoidea*	A.W. Herre	1240	6/8/1931	Herbarium	GH/A	Philippines	4.73	119.41
G08652	*A. elaeagnoidea*	M. van Balgooy & J. Mamesah	6348	17/4/1993	Herbarium	GH/A	New Guinea	-6.74	134.39
G08653	*A. elaeagnoidea*	R. Kanehira & S. Hatusima	13317	31/3/1940	Herbarium	GH/A	New Guinea	-1.84	134.18
G08657	*A. elaeagnoidea*	Madulid, Gaerlan, *et al*.	23848	27/4/1996	Herbarium	GH/A	Philippines	20.77	121.83
G08662	*A. elaeagnoidea*	J.P. Wilson	987	Sep 1929	Herbarium	US	Vanuatu	-20.16	169.88
G08665	*A. elaeagnoidea*	H. Keng	s.n.	31/10/1950	Herbarium	US	Taiwan	21.98	120.78
G08723	*A. elaeagnoidea*	I.D. Cowie	IDC11230	19/10/2006	Herbarium	DNA	Timor-Leste	-8.50	127.21
G08724	*A. elaeagnoidea*	I.D. Cowie	IDC13853	6/5/2015	Herbarium	DNA	Timor-Leste	-8.20	125.59
G08726	*A. elaeagnoidea*	I.D. Cowie	IDC14565	16/5/2015	Herbarium	DNA	Timor-Leste	-8.20	125.59
G08727	*A. elaeagnoidea*	I.D. Cowie	IDC14566	17/5/2015	Herbarium	DNA	Timor-Leste	-8.20	125.59
G08523	*A. chittagonga*	A.F.G. Kerr	18931	11/4/1930	Herbarium	GH/A	Thailand		
G08525	*A. korthalsii*	E.L. Bynum	7023	23/10/1990	Herbarium	GH/A	Sulawesi		
G08555	*A. edulis*	S.K. Lau	58	10/6/1932	Herbarium	US	Hainan		
G08556	*A. edulis*	N.K. Chun.& C.L. Tso	44404	Dec 1932-33	Herbarium	US	Hainan		
G08558	*A. leucophylla*	J.H. Beaman	10643	9/7/1984	Herbarium	US	Borneo		
G08721	*A. spectabilis*	W. Cooper & C.M. Pannell	WWC2351	8/10/2016	Field	CNS	Australia		
G08722	*A. spectabilis*	W. Cooper & C.M. Pannell	WWC2356	8/10/2016	Field	CNS	Australia		

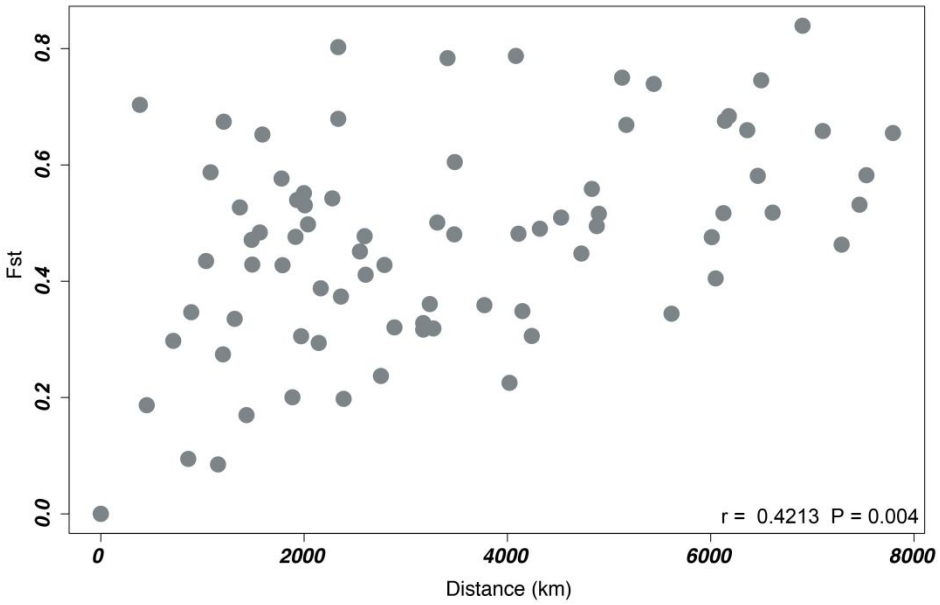
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Supplementary Material 2 List of herbaria from which *Aglaia* specimens were sampled

Herbarium Code	Herbarium Name	Institution	Country
A	Arnold Arboretum Herbarium	Harvard University	USA
BO	Herbarium Bogoriense	Research Centre for Biology, LIPI	Indonesia
BRI	Queensland Herbarium	Queensland Government	Australia
CNS	Australian Tropical Herbarium	James Cook University, Queensland Government and CSIRO	Australia
DNA	Northern Territory Herbarium	Department of Environment and Natural Resources	Australia
FHO	Daubeny Herbarium	Oxford University	UK
GH	Gray Herbarium	Harvard University	USA
K	Kew Herbarium	Royal Botanic Gardens, Kew	UK
L	Nationaal Herbarium Nederland	Naturalis Biodiversity Center	The Netherlands
MICH	University of Michigan Herbarium	University of Michigan	USA
NY	William and Lynda Steere Herbarium	The New York Botanic Garden	USA
PERTH	Western Australian Herbarium	Department of Biodiversity, Conservation and Attractions	Australia
SING	Singapore Herbarium	Singapore Botanic Gardens	Singapore
US	United States National Herbarium	Smithsonian Institute	USA

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Supplementary Material 3 Fst of *A. elaeagnoidea* populations by distance. Mantel statistical results (correlation test for significant isolation by distance) is indicated in the bottom right corner of the plot.

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species	lat	long
Aglaia elae	-6.75	105.2
Aglaia elae	-15.9236	145.3758
Aglaia elae	-6.73333	105.25
Aglaia elae	3.8	113.8
Aglaia elae	-10.8403	142.4092
Aglaia elae	-22.2667	166.4497
Aglaia elae	-22.3053	166.4383
Aglaia elae	-22.1667	166.3833
Aglaia elae	-20.3333	164.5
Aglaia elae	-10.845	142.3708
Aglaia elae	-20.2736	148.8425
Aglaia elae	-20.2486	148.7508
Aglaia elae	-20.4917	164.3047
Aglaia elae	-17.8333	146.0833
Aglaia elae	-17.8403	146.0925
Aglaia elae	21.96528	120.8044
Aglaia elae	-20.8333	167.2167
Aglaia elae	-13.9683	126.045
Aglaia elae	21.9025	120.8458
Aglaia elae	-20.7039	167.1706
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Aglaia elae	-16.3	145.5
Aglaia elae	-15.95	145.3333
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Aglaia elae	-15.9214	145.3528
Aglaia elae	-7.41667	147.1667
Aglaia elae	-22.2511	167.0294
Aglaia elae	-9.75698	143.4259
Aglaia elae	-6.01639	106.1931
Aglaia elae	-22.25	166.4833
Aglaia elae	-6.7333	105.25
Aglaia elae	-15.4167	124.5833
Aglaia elae	-14.25	126
Aglaia elae	-16.5	145.4667
Aglaia elae	-15.1167	145.2833
Aglaia elae	-15.0167	145.45
Aglaia elae	-15.0833	145.3833
Aglaia elae	-14.5333	125.8167
Aglaia elae	-15.0833	125.1667
Aglaia elae	-15.1236	145.2925
Aglaia elae	-15.6322	145.2639
Aglaia elae	-14.7403	145.1925
Aglaia elae	-15.0236	145.4425
Aglaia elae	-15.0939	145.3794
Aglaia elae	-15.02	145.45
Aglaia elae	-14.73	145.18
Aglaia elae	-15.12	145.28
Aglaia elae	-15.08	145.38
Aglaia elae	-12.1667	143.0833
Aglaia elae	-14.5819	125.8846
Aglaia elae	-14.7819	125.8346
Aglaia elae	-14.4947	125.8297
Aglaia elae	-10.2081	142.8244
Aglaia elae	-9.9433	144.0261
Aglaia elae	-14.6114	125.8014

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Aglaia elae	-16.7236	145.6425
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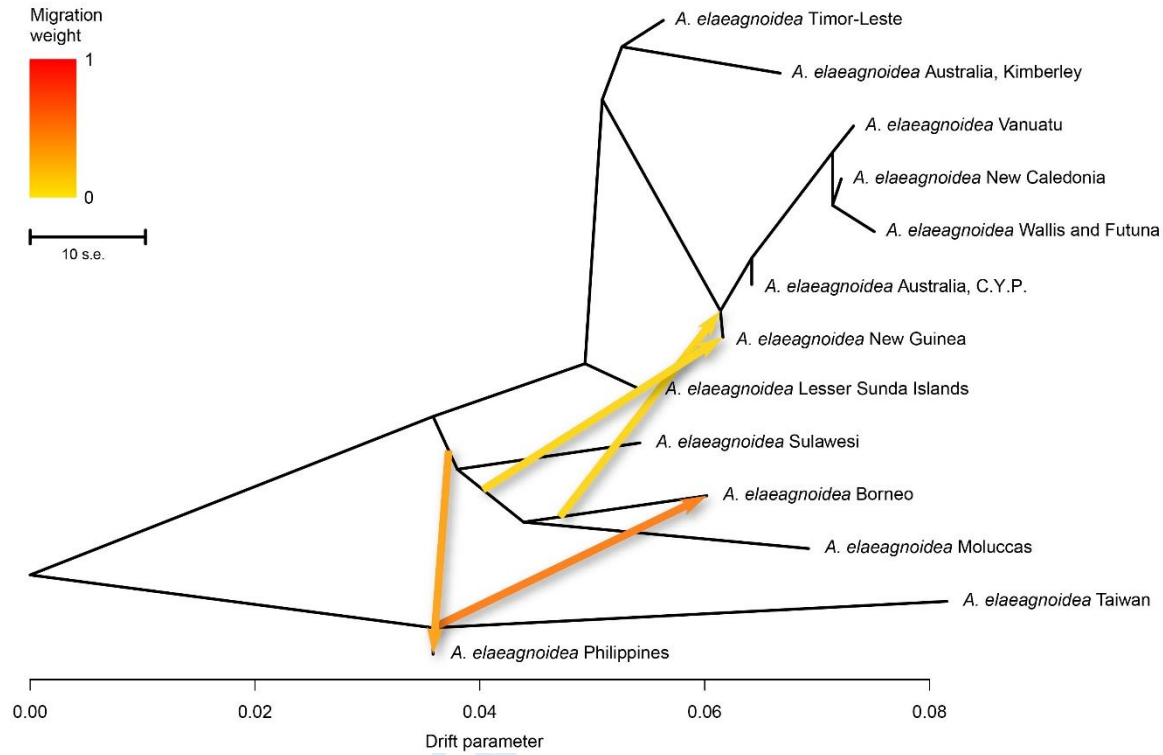
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	bio19	bio18	bio17	bio16	bio15	bio14	bio13	bio12	bio11	bio10
bio19		r= 0.24 p= <0.01	r= 0.79 p= <0.01	r= 0.14 p= 0.018	r= −0.67 p= <0.01	r= 0.79 p= <0.01	r= 0.14 p= 0.016	r= 0.66 p= <0.01	r= 0.14 p= 0.015	r= −0.33 p= <0.01
bio18	r= 0.31 p= <0.01		r= 0.65 p= <0.01	r= −0.26 p= <0.01	r= 0.32 p= <0.01	r= 0.62 p= <0.01	r= 0.71 p= <0.01	r= −0.58 p= <0.01	r= −0.36 p= <0.01	r= −0.47 p= <0.01
bio17	r= 0.025 p= 0.67	r= −0.85 p= <0.01		r= 1.00 p= <0.01	r= 0.0087 p= 0.88	r= 0.70 p= <0.01	r= 0.054 p= 0.35	r= −0.50 p= <0.01	r= 0.10 p= 0.077	r= −0.49 p= <0.01
bio16	r= 0.27 p= <0.01	r= 0.041 p= 0.48	r= 0.99 p= <0.01		r= 0.69 p= <0.01	r= −0.11 p= 0.056	r= 0.13 p= 0.025	r= −0.046 p= 0.43	r= 0.14 p= 0.014	r= 0.19 p= <0.01
bio15	r= −0.84 p= <0.01	r= 0.30 p= <0.01	r= −0.48 p= <0.01	r= 0.11 p= 0.049		r= 0.69 p= <0.01	r= 0.081 p= 0.17	r= 0.64 p= <0.01	r= 0.54 p= <0.01	r= −0.19 p= <0.01
bio14	r= 0.024 p= 0.68	r= 0.71 p= <0.01	r= 0.054 p= 0.35	r= −0.49 p= <0.01	r= 0.11 p= 0.064		r= −0.49 p= <0.01	r= −0.44 p= <0.01	r= 0.22 p= <0.01	r= −0.47 p= <0.01
bio13	r= 0.67 p= <0.01	r= −0.092 p= 0.11	r= 0.16 p= <0.01	r= −0.019 p= 0.74	r= 0.18 p= <0.01	r= 0.19 p= <0.01		r= −0.13 p= 0.022	r= 0.15 p= <0.01	r= 0.22 p= <0.01
bio12	r= −0.055 p= 0.34	r= −0.31 p= <0.01	r= 0.036 p= 0.53	r= −0.29 p= <0.01	r= −0.26 p= <0.01	r= 0.10 p= 0.075	r= −0.33 p= <0.01		r= −0.068 p= 0.24	r= 0.059 p= 0.31
bio11	r= 0.54 p= <0.01	r= 0.94 p= <0.01	r= 0.36 p= <0.01	r= −0.53 p= <0.01	r= 0.89 p= <0.01	r= 0.40 p= <0.01	r= −0.89 p= <0.01	r= 0.67 p= <0.01		r= 0.02 p= 0.73
bio10	r= 0.55 p= <0.01	r= 0.93 p= <0.01	r= 0.26 p= <0.01	r= 0.24 p= <0.01	r= 0.87 p= <0.01	r= −0.10 p= 0.081	r= 0.25 p= <0.01	r= 0.42 p= <0.01	r= 0.82 p= <0.01	
bio09	r= 0.38 p= <0.01	r= −0.48 p= <0.01	r= 0.83 p= <0.01	r= 0.41 p= <0.01	r= −0.81 p= <0.01	r= 0.62 p= <0.01	r= 0.031 p= 0.59	r= 0.88 p= <0.01		
bio08	r= 0.25 p= <0.01	r= 0.15 p= <0.01	r= 0.72 p= <0.01	r= 0.088 p= 0.13	r= 0.012 p= 0.84	r= 0.25 p= <0.01	r= 0.67 p= <0.01			
bio07	r= −0.85 p= <0.01	r= 0.55 p= <0.01	r= 0.74 p= <0.01	r= −0.10 p= 0.079	r= 0.79 p= <0.01	r= −0.22 p= <0.01				
bio06	r= −0.025 p= 0.67	r= −0.90 p= <0.01	r= 0.41 p= <0.01	r= −0.43 p= <0.01	r= 0.69 p= <0.01					
bio05	r= −0.033 p= 0.57	r= 0.46 p= <0.01	r= 0.80 p= <0.01	r= 0.69 p= <0.01						
bio04	r= −0.67 p= <0.01	r= 0.17 p= <0.01	r= −0.64 p= <0.01							
bio03	r= 0.50 p= <0.01	r= 0.58 p= <0.01								
bio02	r= 0.24 p= <0.01									
bio01										



Supplementary Material 6 Original tree output from TreeMix analysis. Drift parameter is represented along the x axis, and coloured arrows showing migration events with colour representative of migration weight.

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