JSE Journal of Systematics and Evolution

doi: 10.1111/jse.12923

Research Article

Deep phylogeographic splits and limited mixing by sea surface currents govern genetic population structure in the mangrove genus *Lumnitzera* (Combretaceae) across the Indonesian Archipelago

Jeprianto Manurung[1,2*], Blanca M. Rojas Andrés[1†], Christopher D. Barratt[2], Jan Schnitzler[1,2], Bror F. Jönsson[3], Ruliyana Susanti[4], Walter Durka[2,5‡], and Alexandra N. Muellner-Riehl[1,2‡*]

[1]Department of Molecular Evolution and Plant Systematics & Herbarium (LZ), Institute of Biology, Leipzig University, Johannisallee 21-23, Leipzig D-04103, Germany

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, Leipzig D-04103, Germany

[3]Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

[4]Research Center for Biology, National Research and Innovation Agency, Jl. Raya Jakarta-Bogor km, 46, Bogor, Indonesia

[5]Department of Community Ecology, Helmholtz Centre for Environmental Research—UFZ, Theodor-Lieser-Str. 4, Halle D-06120, Germany

[†]Current address: Blanca M. Rojas Andrés, Departamento de Botánica y Fisiología Vegetal, University of Salamanca, Salamanca E-37007, Spain, and Biobanco de ADN Vegetal, University of Salamanca, Edificio Multiusos I+D+i, Calle Espejo s/n, Salamanca 37007, Spain

[‡]Shared last authorship.

*Authors for correspondence. Jeprianto Manurung. E-mail: jeprianto_m@apps.ipb.ac.id; Alexandra N. Muellner-Riehl. E-mail: muellner-riehl@uni-leipzig.de

Received 17 December 2021; Accepted 9 October 2022; Article first published online 17 October 2022

Abstract The Indonesian Archipelago accommodates the largest mangrove area in Southeast Asia and possesses the world's richest composition of mangrove species. The archipelago comprises areas of the biogeographic regions Sunda and Wallacea, separated by Wallace's line. Here, we used the true mangrove species *Lumnitzera littorea* and *Lumnitzera racemosa* as a study case for understanding the effects of phylogeographic history, sea surface currents, and geographical distance on genetic diversity and genetic structure. We sampled 14 populations of *L. littorea* ($N = 106$) and 21 populations of *L. racemosa* ($N = 152$) from Indonesia and used 3122 and 3048 SNP loci, respectively, genotyped using the ddRADseq approach. We assessed genetic diversity, genetic structure, and effective dispersal of the populations and related them to geographical distance and sea surface currents. Our study revealed low levels of genetic variation at the population level in *Lumnitzera*. Pronounced genetic differentiation between populations indicated two phylogroups in both species. While in *L. littorea* the two phylogroups were largely separated by Wallace's line, *L. racemosa* showed a northwest vs. southeast pattern with strong mixture in Wallacea. Our findings provide novel insights into the phylogeography of the mangrove genus *Lumnitzera* and the role of sea surface currents in the Indonesian Archipelago.

Key words: ddRADseq, genetic diversity, genetic structure, Indonesian Archipelago, isolation by distance, *Lumnitzera racemosa*, *Lumnitzera littorea*, sea surface currents.

1 Introduction

Mangroves are a diverse group of woody plants tolerant of saline water and under tidal influence in tropical and subtropical estuaries (Spalding et al., 1997; Kathiresan & Bingham, 2001; Giesen et al., 2007; Tomlinson, 2016; Saenger et al., 2019). They are part of the most productive ecosystems on Earth (Giri et al., 2011; López-Angarita et al., 2018), providing essential resources for human populations (Giri et al., 2015; Romañach et al., 2018). Increasing human pressure has led to an exploitation of mangrove biodiversity (Rands et al., 2010) and species loss (Worm et al., 2006). According to the IUCN Red List, 11 out of 75 true mangrove species are currently threatened with extinction (Polidoro et al., 2010). Land clearing for agriculture, collection of firewood, and shrimp farming have been primary forces of

mangrove destruction (Thu & Populus, 2007; Polidoro et al., 2010). In addition, unimpeded pollutants, including heavy metals from industrial activities, have severely threatened mangrove ecosystems over the past few decades (Sandilyan & Kathiresan, 2014). Moreover, sea-level rise due to global climate change may become a major threat for these ecosystems in the future (Gilman et al., 2008; Giri et al., 2011; Veettil et al., 2019; Cinco-Castro & Herrera-Silveira, 2020; Mafi-Gholami et al., 2020).

The Indonesian Archipelago comprises more than 17 500 islands and harbors 60% of the Southeast Asian mangrove area (Giesen et al., 2007), constituting 22.6% of the global area covered by mangroves (Giri et al., 2011). The archipelago accommodates 45 true mangrove species (Spalding, 2010). In his paper, Duke (1995) summarized that the Indo-Malesian coasts are the center of mangrove diversity where most mangrove species are endemic to this area. Therefore, the region of Indonesia is ideal to study the evolution and biodiversity of mangroves. After Alfred Russel Wallace's explorations to Indonesia in the 19th century, the historical biogeography of the region has increasingly attracted biologists' attention. Various studies conducted during the past two decades have shed light on the floristic diversity and underlying causes within Indonesia and beyond (e.g., Hall, 2009; Van Welzen et al., 2011; Morley, 2012; Richardson et al., 2012; De Bruyn et al., 2014; Joyce et al., 2021). Among the observed barriers for dispersal across the Indo-Australian Archipelago, Wallace's line especially has received prominent consideration. Originally defined by the faunal discontinuity across the Indo-Australian Archipelago (Wallace, 1860, 1863), resulting from deep sea conditions without any land connections between West and East throughout geological history, studies have also shown that some plant families and genera are restricted to either one or the other side of Wallace's line (Richardson et al., 2012). Wallacea, defined as the area located between Wallace's line in the West and Lydekker's line to the East, however, has been found to act as an important transition zone for both Laurasian and Gondwanan plant lineages in both directions, rather than acting as a barrier (e.g., Turner et al., 2001; Morley, 2003; Muellner et al., 2008; Van Welzen & Slik, 2009; Crayn et al., 2015). In terms of phylogeography, Wallacea is of interest, as during the last glacial period (ca. 115 kya), islands such as Sumatra, Borneo, Java, and Bali, which are located on the Sunda shelf, were connected to the Asian mainland in the West, and islands on the Sahul shelf were connected to the Australian mainland in the East. Sea levels at times (Last Glacial Maximum) were about 120 m lower than today, forming land bridges in the present shelf seas, affecting today's patterns of plant diversity (Woodruff, 2010). The islands of Wallacea were never connected to the mainland on either Sunda or Sahul, and thus could only be colonized by dispersal across the ocean. While the impact of dispersal barriers and corridors related to Wallacea has, to date, mostly concentrated on the investigation of terrestrial plants, the potential influence on mangroves still warrants further attention.

Unlike terrestrial floras, the life cycle of mangroves is mainly linked to seawater, including the distribution of their buoyant propagules (Nettel & Dodd, 2007). Therefore, the presence of land and oceanic barriers to their dispersal has been suggested as extrinsic factor determining their distribution and affecting their evolution (Duke, 2017). Recently, He et al. (2019) reported that speciation with gene flow between the Pacific and the Indian Ocean was driven by repeated cycles of mixing–isolation–mixing through the periodical opening and closing of the Malacca strait during the Pleistocene. Since then, the Indonesian seas have played an essential role as channels between the Pacific and the Indian Ocean through the Indonesian Throughflow (ITF) (Gordon, 2005; Fallon & Guilderson, 2008; Sprintall et al., 2019). Molecular studies revealed that sea currents of the ITF shape the genetic structure of various marine organisms in the Indo-West Pacific (IWP), such as coral reef species (Barber et al., 2002, 2006; Otwoma & Kochzius, 2016) and tropical marine snail (abalone) species (Imron et al., 2007). The ITF may also facilitate genetic exchange in several mangrove taxa within the IWP and between the Indian and the Pacific Ocean (Li et al., 2016; Guo et al., 2018a, 2021). Recently, a study by Guo et al. (2021) revealed a deep genetic split in each of the two ecologically important *Lumnitzera* mangrove species distributed in the IWP. However, phylogeographic patterns differed between species, with the split being located more eastward in *Lumnitzera littorea* (Jack) Voigt and more westward in *Lumnitzera racemosa* Willd. In addition, strongly differentiated subgroups in both species indicated a complex system of gene flow and genetic barriers. Moreover, while Guo et al. (2021) shed light on the large-scale patterns, the Indonesian Archipelago, including Wallacea, with its many islands and complex seawater currents, was not well covered and thus deserves further study.

The investigation of genetic variation and the role of geographic distance and sea surface currents in shaping mangrove genetic patterns specifically in the Indonesian Archipelago requires the choice of a well-suited model group, for which good baseline data on biology and distribution should ideally be available. In this study, we therefore used *L. littorea* and *L. racemosa*, the only two extant species belonging to the genus. Both species occur on the landward side of estuaries (Tomlinson, 2016). *Lumnitzera littorea* is distributed from the Pacific Ocean (the Marshall Islands and Tonga) to India, while *L. racemosa* can be found from Indo-Australia to East Africa (Tomlinson, 2016). Both, *L. littorea* and *L. racemosa*, constitute a dominant component of mangrove vegetation in the IWP (Tomlinson, 2016), including the Indonesian Archipelago (Manurung et al., 2021). In addition, because both species often occur parapatrically, hybridization appears to be rare, which eases biogeographic analysis. Besides their ecological importance, both species are of interest owing to their wealth of natural products, some of which constitute potential sources for medicinal applications (Manurung et al., 2021). All of these factors emphasize that the genus is not only of interest for basic population genetic research, but also of high importance for the Indonesian population and conservation of natural resources, making it an ideal study group.

Specifically, here, we test three hypotheses: First, we test whether a biogeographic separation of Sunda and Wallacea is reflected in a West–East intraspecific genetic structure of both species when a dense and thus representative sampling

across Indonesia is included. Guo et al. (2021) previously found a West–East genetic break in both species, but located in different areas (land barrier effect of the Malay Peninsula in *L. racemosa*; more eastward break in *L. littorea*). Second, since strong genetic structure due to present oceanic barriers has previously been reported in several mangrove taxa in the IWP (e.g., Wee et al., 2014, 2017; Yahya et al., 2014), we hypothesize a spatial pattern of genetic structure of both species reflecting the presence of contemporary sea surface currents. On the one hand, sea surface currents act as dispersal vectors, connecting populations (Van der Stocken et al., 2019). On the other hand, sea currents may act as barriers (Waters, 2008), for example, through the ITF. Third, we hypothesize to find support for a fine-scale isolation-by-distance (IBD) pattern across Indonesia, in line with the findings obtained by Guo et al. (2021) on a coarser scale across the IWP. Some mangroves have short-distance propagule dispersal ability that is limited within the same or nearby populations, while others are capable of long-distance dispersal (LDD) (Duke et al., 2002; Van der Stocken & Menemenlis, 2017). Geographical distance, sea current magnitude, and direction may play a role in gene flow and gene exchange between mangrove populations. The less isolated and the more connected a population is to the others, the higher the gene flow and genetic exchange will be between populations (Yahya et al., 2014). If LDD is common in *L. littorea* and *L. racemosa* across the Indonesian Archipelago, we expect to see no genetic differentiation across the sampled range, despite distance and habitat discontinuity between populations. If dispersal is limited merely by geographical distance, we would expect to see a pattern of broadscale IBD across the archipelago. By combining analyses of genome-wide variation with spatial distance and surface ocean connectivity analyses, here, we aim to further advance the understanding of patterns and processes in mangrove phylogeography across the Indonesian Archipelago.

2 Material and Methods

2.1 Study species

Lumnitzera (Combretaceae) consists of two non-viviparous mangrove species, *Lumnitzera littorea* and *Lumnitzera racemosa*, which occur throughout the Indonesian Archipelago; both species often occur parapatrically. Even if they co-occur, hybridization seems to be very rare, producing the sterile hybrid *L.* × *rosea* that has only been reported from particular locations in Queensland, Australia (Tomlinson et al., 1978), and Thailand (Guo et al., 2011). It was not found across the sampled regions in this study. Both species are self-compatible and superficially similar in vegetative morphology. The species differ in their flowers, axillary and white in *L. racemosa,* terminal and red in *L. littorea* (Tomlinson et al., 1978; Tomlinson, 2016). *Lumnitzera littorea* is mainly pollinated by birds, and rarely by bees and wasps. In contrast, *L. racemosa* is pollinated by day-active wasps, bees, butterflies, and moths (Solomon Raju et al., 2014, Tomlinson, 2016). Flowering of the two species occurs throughout the year, but the peak times differ across Indonesia (J.M personal observation, but see Tomlinson et al., 1978). Even though mature propagules of both species are often available throughout the year in Indonesia, low regeneration potential was observed in *L. littorea* due to the absence of embryos in mature seeds caused by insect predation and the physiological dormancy of the seed (Tomlinson, 2016; Perera et al., 2019). In *L. racemosa*, natural regeneration is also low, suggested by the abortion of embryos or predation by small grubs (Solomon Raju et al., 2014). Moreover, salinity sensitivity reduces dispersion and seedling establishment (Solomon Raju et al., 2014; Wang et al., 2019).

2.2 Sample collection and DNA isolation

We sampled 14 populations of *L. littorea* and 21 populations of *L. racemosa* across the Indonesian Archipelago (see Table 1). Fresh leaves were collected, dried, and stored in silica gel until DNA extraction. A minimum distance of 20 m was maintained between sampled individuals to prevent sampling of consanguineous individuals (except for populations with fewer than ten individuals, where material from all individuals was collected; see Table 1). Total genomic DNA was isolated from 20 mg of leaf tissue using the NucleoSpin Plant II Kit (Macherey-Nagel, Germany), with minor modifications (using PL2 and adding 20 µL of mercaptoethanol and 2% Polyvinylpyrrolidone [PVP]). Up to 40 ng/µL DNA concentration was quantified using a Qubit® 3.0 Fluorometer (Thermo Fisher Scientific, USA), and DNA quality was checked on a 1% agarose gel. Voucher specimens were deposited at Herbarium Bogoriense (BO), Indonesian Institute of Science (LIPI), in Cibinong, Indonesia. Detailed information on the voucher specimens is provided in Table 1.

2.3 Library construction, sequencing, and bioinformatics

We prepared ddRAD libraries following Peterson et al. (2012), with minor modifications, using EcoRI and MspI restriction enzymes. In total, 258 individual samples for both *L. littorea* (106 individuals from 14 populations) and *L. racemosa* (152 individuals from 21 populations) were sequenced in six ddRAD libraries. Paired-end (PE) sequencing was performed in a single run on an Illumina HiSeq 2000 Sequencing System using two lanes. Overall, we generated 469 798 646 sequences, 459 592 004 of which were of high quality and contained barcodes and RAD cut sites. Raw sequence data have been deposited in the European Nucleotide Archive (ENA) under accession number PRJEB47827 (https://www.ebi.ac.uk/ena/browser/view/PRJEB47827).

We used process_radtags from the Stacks 2.0 pipeline (Rochette et al., 2019) to demultiplex reads. The median number of reads retained per sample was 1 267 282 (Table S1). Subsequently, we used dDocent 2.7.8 (Puritz et al., 2014) to assemble reads and call SNPs first from both species combined and second, for each single species. We set the clustering similarity to 0.88, the minimum within individual coverage level to include a read for assembly (*K*1) to 5; the minimum number of individuals a read must be present to be included in the assembly (*K*2) to 6, and default values for all other parameters. We identified 230 355 (*L. littorea*) and 372 386 (*L. racemosa*) raw SNPs and filtered these following O'Leary et al. (2018). First, we used vcfallelicprimitives from the library vcflib v. 1.0.0 (Garrison et al., 2021) and vcftools v. 0.1.16 to remove indels. We kept

Table 1 Study sites and descriptors of genetic diversity of *Lumnitzera littorea* and *Lumnitzera racemosa* in the Indonesian Archipelago

Pop ID	Population	Region	Pop size estimate	Collector's no.	Voucher no.	*N*	H_o	H_e	F_{IS}	N_P
	Lumnitzera littorea									
1	North Aceh, Ladong Village	Sunda shelf	Small	J.M. 02L-02	BO1959909	8	0.097	0.065	−0.260	4
2	Northern Nias Island, Sarahili Village	Sunda shelf	Large	J. M. 03L-7	BO1959584	8	0.193	0.162	−0.101	0
3	Southern Nias Island, Istana Rakyat	Sunda shelf	Large	J.M. 03L-10	BO1959583	8	0.278	0.401	0.297	0
4	Batam Island, Cate Village	Sunda shelf	Large	J.M. 04L-3	BO1959578	10	0.124	0.095	−0.13	0
5	Batam Island, Barelang Bridge	Sunda shelf	Large			8	0.180	0.156	−0.051	0
6	West Java, Ujung Kulon National Park	Sunda shelf	Large	J.M. 16L-3	BO1959651	8	0.252	0.223	−0.099	0
7	East Borneo, Balikpapan Mangrove Center	Sunda shelf	Large	J.M. 05L-10	BO1959420	8	0.094	0.067	−0.239	4
8	East Java, Alas Purwo National Park	Sunda shelf	Small	J.M. 24L-4	BO1959653	6	0.077	0.044	−0.561	1
9	North Sulawesi, Bunaken National Park	Wallacea	Small	J.M. 08L-10	BO1959415	8	0.443	0.438	−0.016	1
10	Central Sulawesi, Luwuk, Siuna Village	Wallacea	Large	J.M. 14L-11	BO1959401	8	0.074	0.046	−0.411	0
11	Central Sulawesi, Lalong, Peleng Island	Wallacea	Large	J.M. 13L-12	BO1959404	8	0.146	0.229	0.313	0
12	Southeast Sulawesi, RAW National Park	Wallacea	Large	J.M. 07L-8	BO1959417	8	0.105	0.080	−0.204	4
13	West Halmahera Island, Tuada Beach	Wallacea	Small	J.M. 09L-15	BO1959410	8	0.069	0.040	−0.560	3
14	Ambon Island, Hila Village	Wallacea	Very small	J.M. 12L-2	BO1959407	8	0.083	0.052	−0.308	5
	Lumnitzera racemosa									
15	North Aceh, Durung Village	Sunda shelf	Small	J.M. 02R-02L	BO1959580	7	0.076	0.063	−0.098	0
16	North Sumatra, Tanjung Tiram	Sunda shelf	Large	J.M. 01-13	BO1959913	8	0.054	0.043	−0.135	0
17	West Java, Alas Purwo National Park	Sunda shelf	Large	J.M. 16R-1	BO1959655	8	0.545	0.402	−0.340	0
18	East Borneo, Tanah Merah Beach	Sunda shelf	Large	J.M. 5R-11	BO1959421	8	0.050	0.034	−0.266	0
19	East Java, Alas Purwo National Park	Sunda shelf	Large	J.M. 24R-15	BO1959640	8	0.044	0.031	−0.204	0
20	Bali Island, Tahura Park	Sunda shelf	Large	J.M. 23R-3	BO1959586	8	0.044	0.032	−0.172	0
21	Central Sulawesi, Palu, Toaya Vunta Village	Wallacea	Very small	J.M. 15R-10	BO1959650	8	0.110	0.090	−0.108	0
22	South Sulawesi, Tanakeke Island	Wallacea	Large	J.M. 06R-3	BO1959416	8	0.084	0.080	−0.014	0
23	Komodo Island, Komodo National Park	Lesser Sunda	Large	J.M. 20R-3	BO1959423	10	0.117	0.109	−0.038	0
24	Padar Island, Komodo National Park	Lesser Sunda	Large	J.M. 21R-9	BO1959591	8	0.060	0.063	0.048	0
25	Rinca Island, Komodo National Park	Lesser Sunda	Large	J.M. 22R-15	BO1959588	8	0.075	0.076	0.022	0
26	Flores Island, Labuan Bajo	Lesser Sunda	Large	J.M. 19R-15	BO1959644	9	0.058	0.052	−0.076	0
27	East Sumba Island, Watumbaka	Lesser Sunda	Large	J.M. 18R-14	BO1959641	9	0.048	0.041	−0.086	0
28	East Sumba Island, Port Waingapu	Lesser Sunda	Large	J.M. 18R-15	BO1959646	8	0.069	0.066	−0.025	0
29	Kupang Island, Kelapa Lima Beach	Lesser Sunda	Large	J.M. 17R-13	BO1959642	8	0.072	0.064	−0.069	0
30	Central Sulawesi, Tatakali, Peleng Island	Wallacea	Large	J.M. 13R-12	BO1959649	9	0.125	0.441	0.697	0
31	Central Sulawesi, Lalong, Peleng Island	Wallacea	Large			9	0.091	0.545	0.790	0
32	Southeast Sulawesi, RAW, National Park	Wallacea	Large	J.M. 07R-3	BO1959413	9	0.054	0.042	−0.138	1
33	Ternate Island, Takome Village	Wallacea	Very small	J.M. 10R-2	BO1959402	8	0.182	0.213	0.097	1
34	Ambon Island, Hila Village	Wallacea	Very small	J.M. 12R-2		8	0.082	0.539	0.816	0
35	West Seram Island, Kairatu Village	Wallacea	Large	J.M. 11R-8	BO1959776	8	0.077	0.062	−0.126	0

Population size: very small ≤ 10 individuals, small = 10–15 individuals, large ≥ 30 individuals; Number of individuals sampled (*N*) with SNP data. Rawa Aopa Watumohai (RAW); Observed heterozygosity (H_o); expected heterozygosity (H_e); fixation index (F_{IS}; significant at $P < 0.05$ deviation from Hardy–Weinberg Equilibrium [except population 25 at $P > 0.05$]); number of private alleles (N_P). Voucher specimens were deposited at Herbarium Bogoriense (BO), Indonesian Institute of Science (LIPI), in Cibinong, Indonesia.

only biallelic SNPs with a minimum allele count (mac) of 3, a minimum genotype read depth (minDP) of 3, a minimum mean sequence quality (minQ) of 30, maximum missingness across individuals (max_missing) of 50%, and skipping individuals with >75% missing values (imiss). Subsequently, using vcffilter from vcflib 1.0.0, we filtered SNPs according to allele balance (AB > 0.2 and AB < 0.8 | AB < 0.01 | AB > 0.99), strandedness (SAF/SAR > 100 and SRF/SRR > 100 | SAR/SAF > 100 and SRR/SRF > 100), mapping quality ratio of the two alleles (MQM/MQMR > 0.9 and MQM/MQMR < 1.05), and properly pairing alleles (PAIRED > 0.05 and PAIREDR > 0.05 and PAIREDR/PAIRED < 1.75 and PAIREDR/PAIRED > 0.25 | PAIRED < 0.05 and PAIREDR < 0.05). We then filtered SNPs to maximum missingness of 33% (max_missing 0.66), the minimum minor allele frequency of 0.05, the minimum mean read depth of 20, and a maximum mean depth of 1000. In the end, we retained only one single SNP per contig. After importing into R (R Core Team, 2020), we further filtered SNPs and samples in two steps to final maximum missingness of 20% using gl.filter.callrate from the *dartR* package version 1.9.9.1 (Gruber et al., 2017). The final data sets consisted of 106 samples of *L. littorea*, genotyped at 3122 biallelic SNP loci (1.62% missing data), and 152 samples of *L. racemosa*, genotyped at 3048 biallelic SNP loci (2.93% missing data). If not otherwise stated, analyses were performed on the single species data sets. The data set resulting from genotyping both species together, allowing analyses including both species, had 255 samples and 2922 SNP loci (3.91% missing data). The number of samples retained per population ranged from 6 to 10 individuals for *L. littorea* and from 5 to 9 individuals for *L. racemosa*.

2.4 Genetic diversity, population structure, and differentiation

We assessed genetic diversity at the population level as mean expected (H_e) and observed (H_o) heterozygosity and as inbreeding coefficient (F_{IS}), using the function basic.stats from the *hierfstat* package (v.0.5-7; Goudet, 2005). Heterozygote deficiency was assessed at $P < 0.05$ for deviation from Hardy–Weinberg Equilibrium. We calculated the number of private alleles per population, that is, the number of alleles observed only in this population, using the function gl.report.pa from the *DartR* package.

Population structure was analyzed using different approaches. First, we illustrated the relationships among samples by a principal component analysis (PCA) using the function glPca from package *adegenet* (v.2.1.3; Jombart et al., 2020). PCA was run with a combined data set and for each species separately. Second, we performed a discriminant analysis of principal components (DAPCs) to infer the genetic structure (Jombart et al., 2010). To assess how many clusters usefully describe the data, we ran DAPC for $K = 1$ to the number of populations. We retained all PCs in both species. We used the "elbow" method to assess the model quality and reasonable values of *K*. Third, we used an admixture model as implemented in ADMIXTURE (Alexander et al., 2009). We used a cross-validation procedure (10-fold) to choose adequate values of *K*. We aligned cluster identities among different *K* values using the CLUMPAK web server (Kopelman et al., 2015).

We also ran an analysis of molecular variance (AMOVA) using 100 permutations, discarding loci with >5% missing data using the AMOVA implementation of the package *ade4* (Dray & Dufour, 2007) within package *poppr* (Kamvar et al., 2015). Nonhierarchical and hierarchical AMOVAs were run to quantify the genetic differentiation among populations and population groups as suggested by cluster analyses.

2.5 Identifying barriers and areas of connectivity

We visualized areas of genetic connectivity and barriers using effective migration and diversity surfaces in the EEMS program (v.0.0.0.9000; Petkova et al., 2016). To identify geographic areas where genetic similarity is higher than expected by the IBD paradigm (i.e., connectivity), and conversely also areas where genetic dissimilarity is higher than expected (i.e., barriers), EEMS uses spatial and SNP data without environmental and topographic information. We converted filtered VCF files into PLINK format (.bed files, Purcell et al., 2007) and used the BED2DIFFS program within EEMS to calculate dissimilarity matrices. We ran EEMS separately for each species. Based on the size of the habitat and the number of demes required to fill that habitat, we defined a deme size (the density of populations) of 500 using the SNP version of EEMS. We ran two independent MCMC chains, each with a length of 1 000 000 generations with a burnin of 10 000. We combined results from the two MCMC chains after checking for convergence of log likelihoods using the EEMS plotting (rEEMSplot) package.

2.6 Isolation by distance and sea surface current connectivity

We tested for IBD using Mantel tests. We calculated pairwise (F_{ST}) values among sampling localities using StAMPP version 1.6.1 (Pembleton et al., 2013). Because seeds are dispersed by water, instead of using the Euclidean distance between locations, we used Distance Over Water (DOW) and Most Probable Surface Ocean Connectivity (MPSOC) based on recent sea surface current data. For DOW, we used a raster map with ~1 km^2 grid size (https://www.naturalearthdata.com/) and calculated pairwise DOW between sampling sites with the function gridDistance, omitting land grid cells, using the R packages *raster* (Hijmans & Van Etten, 2015) and *fasterize* (Ross, 2020). MPSOC was estimated by seeding virtual surface-bound particles in existing velocity fields from the Copernicus MyOcean 1/12° data-assimilated Ocean Circulation model (Lellouche et al., 2018). Particles were seeded daily for 15 days each month of 2015 and advected for 90 days using the TRACMASS off-line lagrangian particle package (Döös et al., 2017). Relative probabilities for particles to move from one study site to another in either direction were calculated by counting the number of particles starting within a 50 km zone from each study site that reached the regions within a 50 km radius from all other study sites. The 50 km zone was selected to address any potential limitations by the ocean model to resolve near-shore processes. The resulting ocean distances are presented as a probability connectivity matrix.

The directional connectivities of each pair of populations were summed up and zero values within the matrix were arbitrarily set to 0.000001, thus more than one order of magnitude lower than the lowest observed value (0.000025),

to have a full matrix. We used Mantel tests for F_{ST} as a function of log10 (DOW) and of the inverse of connectivity (−log10 (MPSOC)) with 1000 permutations. For each species, in addition to a global analysis including all populations, we performed tests separately for two subgroups of populations after classifying them into clusters (Cl1, Cl2) according to their population-level membership proportions at $K = 2$. In addition, we sought to determine whether isolation was also detected using isolation by Wallace's line. We divided populations into two main groups in each species, east and west of Wallace's line. Pairs of populations separated by the line were coded 1; pairs of populations on the same side of the line were coded 0.

3 Results

3.1 Genetic diversity

Based on our comparative analyses of biallelic SNPs' diversity, we observed that both species had high and similar levels of genetic variation at the species level ($H_T = 0.423$ and 0.432 for *Lumnitzera littorea* and *Lumnitzera racemosa*, respectively). Together with low levels of genetic variation at the population level ($H_S = 0.150$ and 0.144), this pattern indicated overall pronounced population differentiation ($F_{ST} = 0.645$ and 0.666). Descriptors of genetic diversity at the population level differed considerably among populations (Table 1), but did not differ between species (mean $H_e = 0.149$ and 0.147, $P = 0.956$; $H_o = 0.158$ and 0.101; $F_{IS} = -0.166$, $P = 0.128$ and 0.027, $P = 0.061$). In both species, a few populations showed particularly high levels of diversity ($H_e > 0.4$), while the majority had lower levels ($H_e < 0.2$). In both species, very few private alleles were observed at the population level (Table 1). In *L. littorea*, the number of private alleles ranged between 0 and 5. These alleles occurred randomly in the populations throughout the archipelago. Surprisingly, there are only two populations of *L. racemosa* with one private allele each. These two populations are from the Southeast of Sulawesi and from Ternate Island.

3.2 Population structure and differentiation

We display the general genetic relationships among samples using PCA. Since *L. littorea* and *L. racemosa* are sister species and sometimes co-occur, we first looked at the general pattern of the data using the combined data set of both species. Using this combined data set, the PCA shows a clear differentiation between *L. littorea* and *L. racemosa* individuals (Fig. 1). Separate PCAs of the species revealed significant population structure in both *L. littorea* and *L. racemosa*, with most of the genetic structure being captured by the first PC

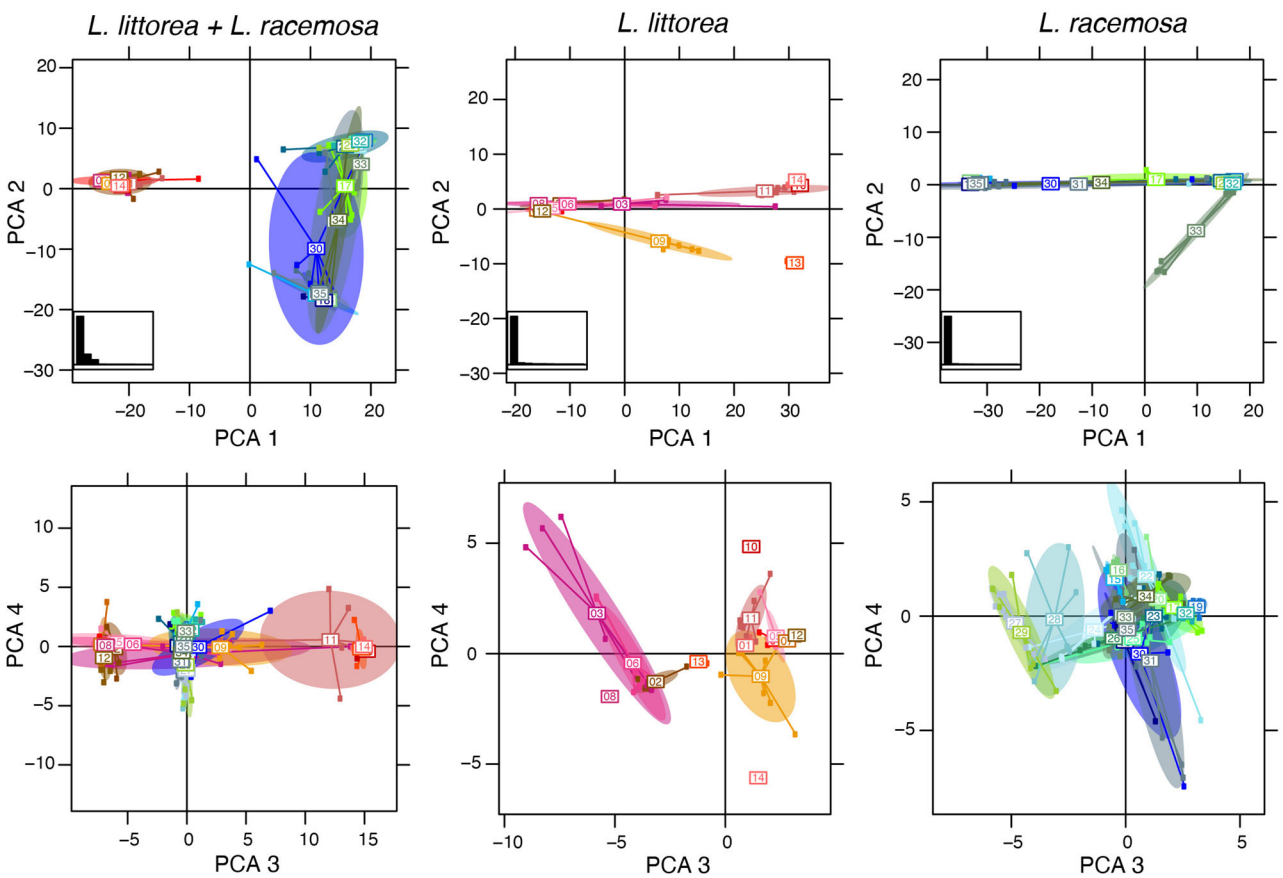

Fig. 1. Principal component analysis of *Lumnitzera littorea* (red–yellow color space) and *Lumnitzera racemosa* (green–blue color space) from Indonesia combined, and for *L. littorea* and *L. racemosa* separately. The numbers represent population IDs (see Table 1). The plots in the inset in the upper panel show eigenvalues of the first 10 principal component analysis (PCA) axes.

in *L. littorea* and *L. racemosa*. The first PCA axes had very high eigenvalues in both species compared to higher axes, indicating a pronounced hierarchical structure.

The analysis of population structure with ADMIXTURE did not reveal a definitive number of clusters. In both species, the cross-validation error strongly decreased at $K = 2$, with a minor further decrease and minima at $K = 6$ for *L. littorea* and $K = 7$ for *L. racemosa* (Fig. S1). Thus, in both species, a divergence at $K = 2$ was the most prominent, grouping the populations into two phylogroups. However, we consider $K = 3$ for *L. littorea* and $K = 5$ in *L. racemosa* further biologically plausible groupings (see Figs. 2, S2–S5 for higher values of K). In *L. littorea*, at $K = 2$, individuals belonging to the red, western cluster occur from western Indonesia to the North and Southeast of Sulawesi (Fig. S4). In contrast, individuals of the yellow, eastern cluster are confined to the eastern part of the Indonesian Archipelago (central Sulawesi and the Moluccas). On Sulawesi, both clusters occur as pure or admixed populations. At $K = 3$, the red western cluster is further separated into a southern group (pink), comprising all populations along the Indian Ocean, and a northern group, occurring along the Sumatran coastline as well as on Borneo and on Sulawesi (Fig. 2).

In *Lumnitzera racemosa* at $K = 2$, a northern phylogroup (brown cluster) ranges from the northern coast of Sumatra to Borneo, Sulawesi, and the Moluccas. A south-eastern

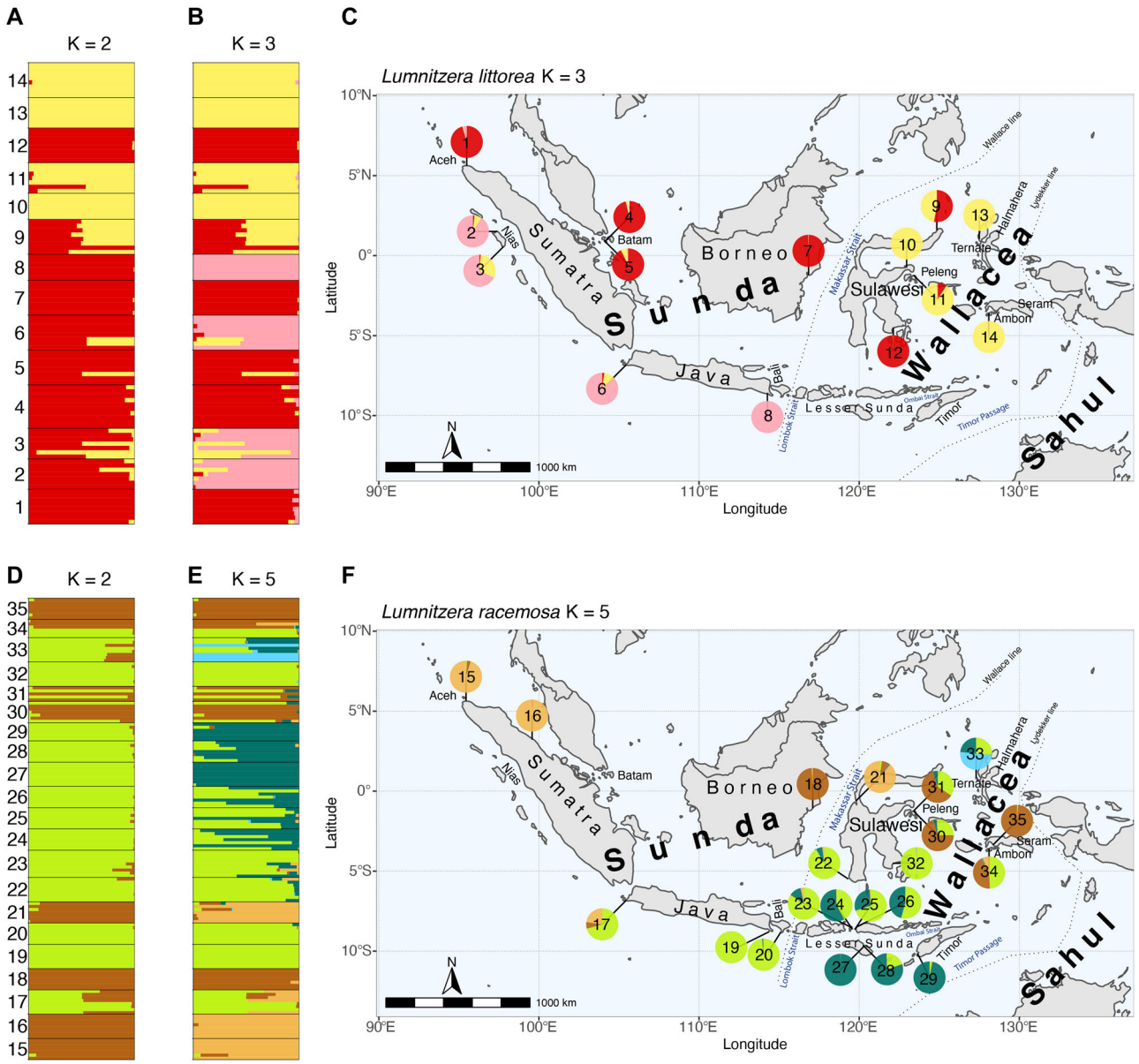

Fig. 2. ADMIXTURE analysis for $K = 2$ (**A**) and $K = 3$ (**B**) for 106 individuals of *Lumnitzera littorea*, and $K = 2$ (**D**) and $K = 5$ (**E**) for 152 individuals of *Lumnitzera racemosa*. Each color represents the proportion of the membership of a particular cluster. Maps show population-level membership proportions for *L. littorea* ($K = 3$, **C**) and *L. racemosa* ($K = 5$, **F**). Maps were created using Natural Earth Data (www.naturalearth.com).

phylogroup (green cluster) ranges from Java over the Lesser Sunda Islands to southern Sulawesi and Moluccas. Four of five populations located north-east in the Banda sea harbored a mixture of both clusters, e.g. on Peleng Island and the Moluccas. Interestingly, no admixed populations were found around the Flores Sea and the Lesser Sunda Islands (Fig. S5). At $K = 5$, both main clusters were further subdivided (Fig. 2). The northern cluster was separated into two subclusters without a clear geographic pattern. The south-eastern cluster was divided into three subclusters, a widespread cluster (light green), a cluster mainly distributed in the Lesser Sunda Islands (dark green), and a cluster (blue) restricted to Ternate Island in the north Banda Sea.

Similar to ADMIXTURE, the population structure analysis with DAPC did not identify a definitive number of clusters as BIC values decreased strongly up to $K = 3$, indicating the presence of at least three clusters in each species, but without a pronounced minimum and elbow in the curve (Fig. S1). Thus, no particular single optimal K value can be identified. Nonetheless, both DAPC and ADMIXTURE analyses show identical patterns, with a strong hierarchical clustering at $K = 2$ (see Figs. S2, S3).

We quantified genetic differentiation with non-hierarchical and hierarchical AMOVAs (Tables 2, 3). In the non-hierarchical analysis, variation between populations accounted for 65.5% and 69.6% in *L. littorea* and *L. racemosa*, respectively. In the hierarchical analysis, we compared the clustering proposed by ADMIXTURE at $K = 2$ to a grouping based on distribution on either Sunda or in Wallacea. In *L. littorea*, the clustering at $K = 2$ explained a very high proportion of variance (72.7%) and also the Sunda–Wallacea grouping had a strong explanatory power (49.2%). In contrast, the clustering at $K = 2$ in *L. racemosa* explained a similarly large proportion of variation (77.4%), but the Sunda–Wallacea separation had no significant effect, accounting only for a negligible proportion of variation (8.2%, $P = 0.17$). The different role of Wallace's line for the two species is also corroborated by Mantel tests of the effect of Wallace's line on genetic differentiation, which was stronger in *L. littorea* ($r = 0.519$, $P = 0.003$) than in *L. racemosa* ($r = 0.163$, $P = 0.053$) (Fig. S6).

3.3 Effective migration

Posterior means of effective migration rates were calculated for both species (Fig. 3). The maps show the effective migration surfaces of the species across the Indonesian Archipelago, with orange colors representing areas where effective migration is lower than expected, given geographic distance, whereas blue colors represent areas where effective migration is higher than expected, given geographic distance. For *L. littorea,* Sulawesi is a barrier separating the eastern and western populations (with another less strong barrier running through the Java Sea separating populations North–South). Similarly, for *L. racemosa,* the same barrier around Sulawesi was found, extending across the channel to Borneo and through the Java Sea, reinforcing a North–South structure in *L. racemosa*.

3.4 Isolation by distance and sea surface current connectivity

We detected a significant effect of both DOW (Figs. 4A, 4B) and sea current connectivity (Figs. 4C, 4D) on genetic differentiation in *L. littorea* and *L. racemosa* (Tables S2, S3). While the overall analysis showed a significant correlation between F_{ST} and geographical distance, an inspection of the data showed an enormous scatter of F_{ST} values that do not follow a classical IBD relationship. Instead, extremely high F_{ST} values (~0.9), representing the distance between the major clusters, were observed at distances >800 km, indicating that in both species the two major clusters represent somehow independent entities. Separate analyses within the two major clusters revealed much lower F_{ST} values and closer IBD relationships, in particular, in *L. racemosa*. In *L. littorea*, however, only the larger red cluster showed a significant IBD pattern, likely due to the low sample size of the yellow cluster. Use of sea surface currents instead of DOW as a predictor of genetic differentiation revealed similar

Table 2 Non-hierarchical and hierarchical analyses of molecular variance of *Lumnitzera littorea*

Level	*Df*	Sum sq	Mean sq	% Var	Phi	*P*-value
Non-hierarchical						
Between populations	13	16 3093.9	12 545.7	65.5	0.65	0.01
Between samples within pop	92	36 111.6	392.5	−2.5	−0.07	0.89
Within samples	106	48 084.5	453.6	37.0	0.63	0.01
Total	211	247 290.1	1172.0	100	-	-
Grouping factor K = 2						
Between admixture K2	1	129 552.2	129 552.1	72.7	0.73	0.01
Between populations within admix K2	12	33 541.9	2795.2	7.5	0.27	0.01
Between samples within populations	92	36 111.7	392.5	−1.4	−0.07	0.88
Within samples	106	48 084.5	453.6	21.4	0.79	0.01
Total	211	247 290.1	1172.0	100	-	-
Grouping factor Sunda–Wallacea						
Between Sunda–Wallacea	1	87 516.1	87 516.1	49.2	0.49	0.01
Between populations within Sunda–Wallacea	12	75 577.8	6298.1	24.4	0.48	0.01
Between samples within populations	92	36 111.7	392.5	−2.0	−0.07	0.88
Within samples	106	48 084.5	453.6	28.3	0.72	0.01
Total	211	247 290.2	1172.0	100	-	-

Table 3 Non-hierarchical and hierarchical analyses of molecular variance of *Lumnitzera racemosa*

Level	*Df*	Sum sq	Mean sq	% Var	Phi	*P*-value
Non-hierarchical						
Between populations	20	226 280.1	11 314.0	69.6	0.70	0.01
Between samples within populations	131	53 600.6	409.2	7.5	0.24	0.01
Within samples	152	37 692.8	248.0	23.9	0.78	0.01
Total	303	317 573.5	1048.1	100	-	-
Grouping factor K = 2						
Between admixture *K*2	1	192 308.9	192 308.8	77.4	0.77	0.01
Between populations within admixture *K*2	19	33 971.2	1788.0	5.8	0.22	0.01
Between samples within populations	131	53 600.6	409.2	4.3	0.24	0.01
Within samples	152	37 692.8	248.0	13.2	0.87	0.01
Total	303	317 573.5	1048.1	100	-	-
Grouping factor Sunda–Wallacea						
Between Sunda–Wallacea	1	22 843.8	22 843.8	8.2	0.08	0.17
Between populations within Sunda–Wallacea	19	203 436.3	10 707.2	62.8	0.68	0.01
Between samples within populations	131	53 600.6	409.2	7.1	0.24	0.03
Within samples	152	37 692.8	248.0	21.8	0.78	0.01
Total	303	317 573.5	1048.1	100	-	-

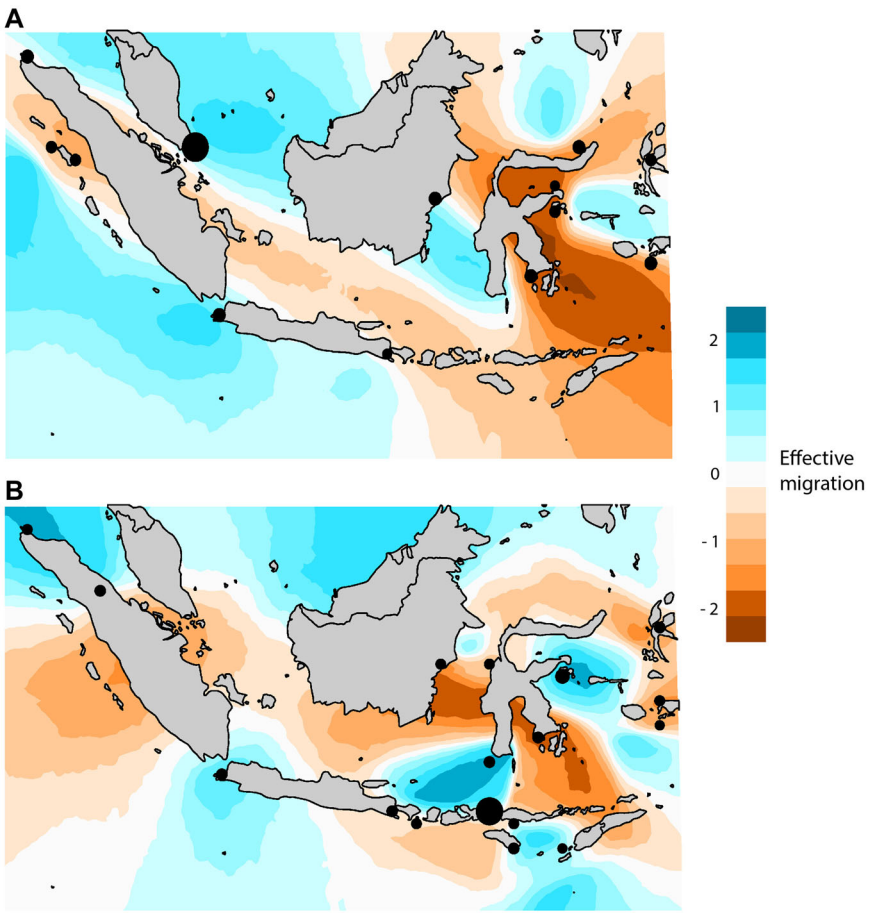

Fig. 3. Maps representing posterior means of effective migration rates m (on the log 10 scale) for *Lumnitzera littorea* (**A**) and *Lumnitzera racemosa* (**B**). The size of the dots represents the number of samples merged into a locality. Gradients of connectivity are defined based on the geo-referenced ddRAD samples, showing places where effective migration is lower (orange colors = barriers) or higher (blue colors = connectivity) than expected, given geographic distance. Maps were created using Natural Earth Data (www.naturalearth.com).

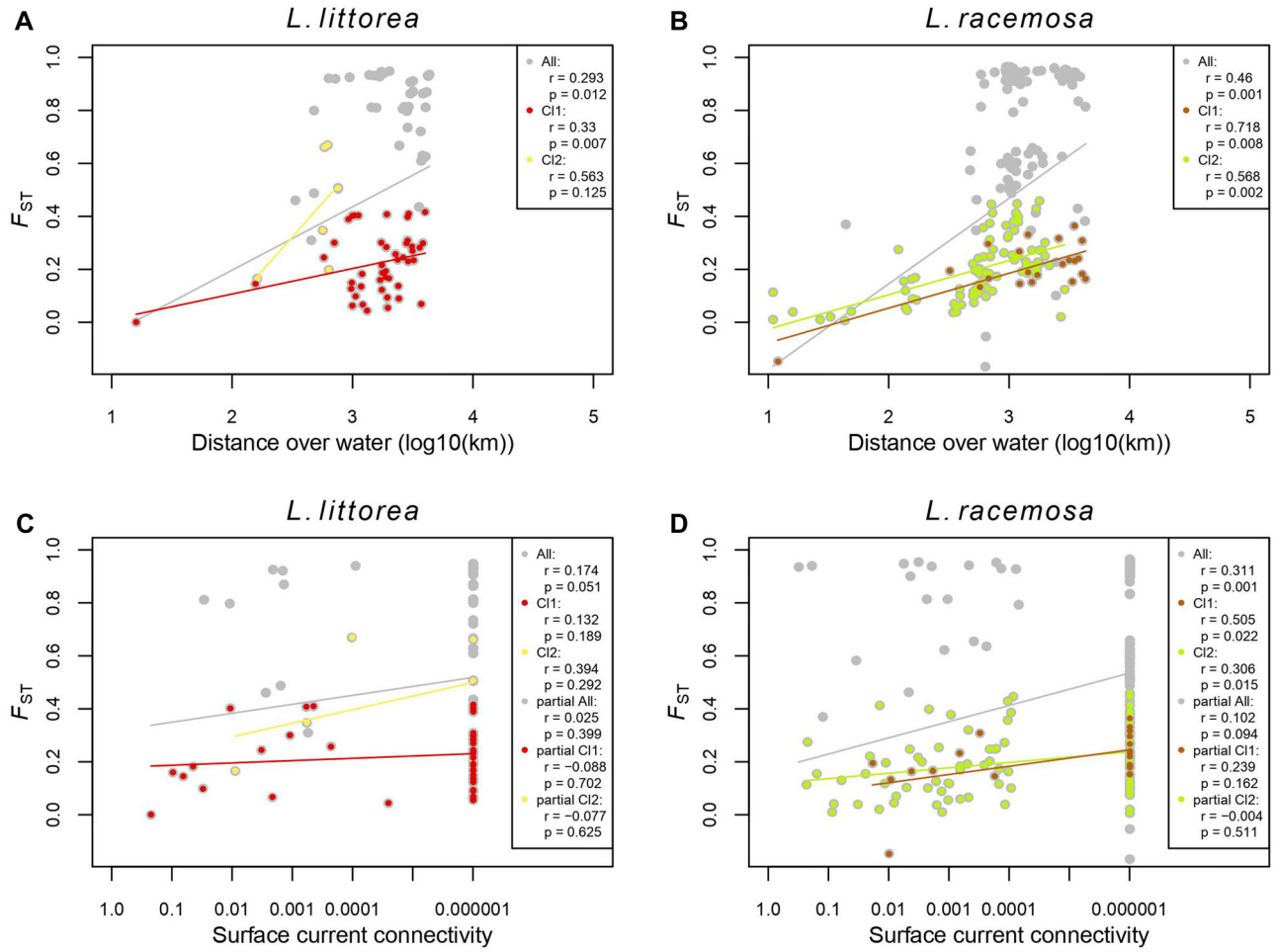

Fig. 4. Analysis of isolation by distance in *Lumnitzera littorea* and *Lumnitzera racemosa*, with pairwise genetic differentiation (F_{ST}) as a function of Distance Over Water (DOW) (**A, B**) and distance following surface current connectivity (**C, D**). For each species, we tested for IBD for all populations (All), and separately for two subsets after classifying populations into clusters (Cl1, Cl2) according to their population-level membership proportions at $K = 2$. In (**C, D**), additionally, the results for a partial Mantel test are reported, testing the effect of surface current connectivity on genetic differentiation after taking into account the effect of DOW.

results (Figs. 4C, 4D), with overall significant correlations in both species, and significant relationships within clusters only for *L. racemosa*, but not for *L. littorea*. Since sea surface currents are correlated to geographic DOW ($r = 0.311$, $P = 0.001$), a partial Mantel test was performed, which indicated that, after accounting for the effect of geographic distance, sea surface currents do not have a significant independent contribution on F_{ST}, except for a marginally significant effect in the overall analysis in *L. racemosa* (see Figs. 4B, 4D).

4 Discussion

4.1 The "genetic diversity paradox" of mangroves

Patterns of genetic variation within populations and its driving forces are well established (Hamrick & Godt, 1996). Highest values of genetic variation at the population level are generally found in long-lived woody species compared to other life forms (Schierenbeck, 2017). In contrast, true mangroves typically show low levels of variation, which has been established in many species of different families and across old and new world mangroves (e.g., Kado et al., 2004; Su et al., 2007; Pil et al., 2011; Cerón-Souza et al., 2012; Huang et al., 2012; Urashi et al., 2013; Yan et al., 2016). Thus, we may formulate a "genetic diversity paradox" of mangroves, because they are long-lived woody plants with large geographic ranges, but generally show low diversity at the population level. The two species of *Lumnitzera* in our study corroborate this pattern in that the large majority of populations had low levels of genetic diversity within the populations. A number of factors may contribute to these patterns. First, a mixed mating breeding system allowing for selfing, as has been shown for *Lumnitzera racemosa* (Solomon Raju et al., 2014), could explain low diversity. Actually, for *Lumnitzera littorea*, high inbreeding coefficients have been found, potentially indicating selfing, although Null alleles could result in a similar pattern (Guo et al., 2021).

Second, strong demographic bottlenecks due to the instability of their habitats (Kado et al., 2004), deforestation and habitat fragmentation (Basyuni et al., 2012), heavy metal pollution (Manurung et al., 2017), and first-comer effects during the founding phase of the populations can lead to low diversity at the population level. Lastly, gene flow into established populations, that is, seed and pollen dispersal, needs to be low to keep populations at a low level of diversity. Mangrove propagules encounter challenges right after getting released from their mother trees, as they quickly lose viability and tend to have low germination rates, as generally observed in most backshore species (Clarke et al., 2001), including *Lumnitzera* spp. (Yong et al., 2004; Solomon Raju et al., 2014; Perera et al., 2019). Previous studies report that the period of *L. littorea* propagule germination varies between 44 (Yang et al., 2016) and 3 days (Perera et al., 2019), with a low rate of germination due to the reduced viability of the orthodox seeds caused by seawater dispersal. Moreover, Perera et al. (2019) reported that seeds are often without embryos, and even if they bear embryos, some of them fail to germinate, suggesting that they are dormant or nonviable. Similarly, in *L. racemosa*, reduced seed viability in seawater was reported (Tomlinson et al., 1978; Yong et al., 2004). In addition, following a day of floating, the buoyancy rate of the propagules was reduced from 100% to 75% (Wang et al., 2019). Thus, limited effective seed dispersal capacity and low immigration rates into already established populations may also contribute to the low population diversity.

4.2 Phylogroups and the Sunda–Wallacea biogeographical pattern

The Indonesian Archipelago has a complex geological and biogeographical history and encompasses parts of Sunda and Wallacea. Wallacea was always isolated from Sunda mainland without any direct land connections during the last glaciations. Moreover, the ITF, one of the strongest water currents worldwide, separates Wallacea from Sunda. Together, the historical isolation and the barrier effect of strong currents have imprinted species distribution patterns and intraspecific patterns in marine organisms (e.g., Barber et al., 2002; Wainwright et al., 2018), including mangrove species (e.g., Wee et al., 2014; Guo et al., 2016, 2018a, 2018b, 2021). For both *Lumnitzera* species, here, we found a deep split into two intraspecific groups, which was shown by each of our analyses. Does this intraspecific split into phylogroups coincide with Wallace's line? For *L. littorea*, the distribution of the two groups largely matched the Sunda–Wallacea separation in that the two clusters were by far the dominant groups in either Sunda or Wallacea, the western phylogroup dominating in Sunda and the eastern phylogroup being confined to Wallacea. This pattern was corroborated by a significant AMOVA explaining about 50% of genetic variation. In contrast, in *L. racemosa*, the two phylogroups were distributed into two loosely confined northwestern and southeastern areas. Here, both phylogroups occurred West and East of Wallace's line, which had no significant explanatory power.

Recently, Guo et al. (2021) presented a phylogeographic study across the species range of both species, but sparsely covering the Indonesian Archipelago. Similar to our study, they identified two main haplogroups in both species that were distributed in the West (Indian Ocean) and the East (Pacific Ocean) of the distribution range, respectively. Using our dense sampling scheme from Indonesia, we, therefore, hypothesize that the western and eastern phylogroups of *L. littorea* could be part of the "western LL" and "eastern LL" groups, respectively, of Guo et al. (2021). Also, for *L. racemosa*, although the pattern in the Indonesian Archipelago was complex, our northern and southeastern clusters of *L. racemosa* are suggested to represent their "western LR" and "eastern LR" groups, respectively. Thus, while on the species level, both taxa are deeply divided into two phylogroups originating in Sunda and Sahul, specific patterns emerged in Wallacea as their intermediate region. In *L. littorea*, the eastern phylogroup dominates in Wallacea, while in *L. racemosa,* phylogroups were mixed. Thus, there is both evidence for (in *L. littorea*) and against (in *L. racemosa*) a match of intraspecific phylogroups and Wallace's line. Clearly, given the existence of two phylogroups, the complex geological, climatic, and hydrogeographical conditions and stochastic dispersal events may have affected population structure within and among the phylogroups in species-specific ways, even more so considering biological differences among species, for example, in seed viability and habitat.

Looking at possible reasons for the different structuring patterns of the two *Lumnitzera* species in Wallacea, the following picture emerges. In both species, an IBD pattern was found. However, in *L. littorea*, only the larger red cluster showed a significant IBD pattern. As we state in Section 3.4, this is likely due to the low sample size of the yellow cluster. Using sea surface currents (instead of DOW) as a predictor of genetic differentiation revealed similar results, with overall significant correlations in both species, and significant relationships within clusters only for *L. racemosa*, but not for *L. littorea*. While the differences found between the species could be a result of different sampling sizes (14 populations were sampled for *L. littorea*, 21 populations for *L. racemosa*), there are also some ecological differences between the species that could contribute to the different results observed, for example, through unequal chances of establishment after successful dispersal. While propagules of *L. littorea* are supposed to be capable of longer-distance traveling across the open ocean than *L. racemosa*, establishment of plants and new populations may be impeded in comparison to *L. racemosa* (Guo et al., 2021 and references therein). First, *L. littorea* prefers areas with less saline and infrequent inundation at the landward margin, which are less easily reachable by propagules floating from the sea, and second, seeds are prone to heavy embryo abortion and insect-mediated damage, reducing the change of successful germination, even if suitable habitats were found (Solomon Raju et al., 2014; Tomlinson, 2016; Perera et al., 2019).

4.3 Limited mixture among phylogroups and populations by sea surface currents

Surface sea currents play an essential role in dispersing (Van der Stocken et al., 2019) and connecting mangroves throughout the intertidal zones (Wee et al., 2014; Van der Stocken et al., 2019). In this context, complex patterns of seasonal surface sea currents need to be distinguished from

temporally stable deep-water currents, in particular, the ITF. While the latter connects the Western Pacific and the Indian Ocean and coincides with Wallace's line, seasonal, weather-driven surface currents likely are more important for dispersal of the buoyant seeds of mangroves. The well-known sea surface currents that flow during the Northwest (NW) Monsoon (January to March) and the Southeast (SE) Monsoon (May to November) have evolved over the past 35 kyr as part of the monsoon system in Indonesian seas (Liu et al., 2020) and generate dynamic seawater movements across the Indonesian Archipelago (Gordon et al., 2003; Fallon & Guilderson, 2008; Sprintall et al., 2019). In particular, they connect East and West and partly run northward into the Makassar Strait, therefore making Wallace's line permeable (Wainwright et al., 2018).

In *Lumnitzera littorea*, we found a Sunda–Wallacea biogeographical pattern, but no perfect separation of phylogroups by Wallace's line. This pattern is also nicely represented at $K = 3$. We suggest that gene flow between Sunda and Wallacea in *L. littorea* populations could potentially have erased an earlier geographical history. A recent study from Wainwright et al. (2018) reported a similar pattern, where only one of two seagrass species was genetically differentiated across Wallace's line. In *L. racemosa*, there was no clear Sunda–Wallacea pattern, indicating that whatever large-scale phylogeographical pattern may have existed in the past has been wiped out by a mixing of gene pools. In particular, at $K = 5$, a mixture of different clusters from the West (Sunda) and South (Lesser Sunda) was observed in the Banda Sea. The Banda Sea is known as a sea-water reservoir during the NW Monsoon (Fallon & Guilderson, 2008). During this time, sea currents move southward from the North Pacific, passing through Makassar Strait directly into the Banda Sea (Fig. S7), facilitating gene flow between populations in the Banda Sea. Oceanic circulation patterns are considered a vital, unseen force promoting population subdivision despite maintaining gene flow, as found in *Rhizophora mucronata* in Southeast Asia (Wee et al., 2014). In our study, genetic discontinuity in *L. racemosa* was detected between the West (North Sumatra) and the Lesser Sunda region. Although the Lesser Sunda region is the channel for the three main outflow passages, namely, Lombok Strait, Ombai Strait, and Timor Passage (Gordon, 2005; Sprintall et al., 2019), contradictory to our expectations, we did not observe more individuals from the northwestern phylogroup in this area. Populations on Lesser Sunda are distinct from most of the populations, indicating that this region has only limited genetic exchange with the northern populations, for example, southern Sulawesi.

While the two phylogroups of both species reflect evolutionarily ancient patterns, the within-group structure is affected by more recent history. In both *Lumnitzera* species, a much clearer pattern of isolation by distance was found within the phylogroups. This indicates that while mixing among the phylogroups is a highly stochastic event, within phylogroups, a gene flow–drift equilibrium is maintained (Whitlock & Mccauley, 1999). This in turn indicates that the underlying unifying and diversifying processes, such as seed dispersal and population bottlenecks, have been acting more recently. In our IBD analyses, both sea current connectivity and geographic distance explained population differentiation similarly well. This underlines the highly stochastic nature of seed dispersal even if sea currents are explicitly considered (Barber et al., 2000).

4.4 Conclusions

This study has shown that the two species of *Lumnitzera* share a pattern of two phylogroups with broadly Western and Eastern distributions in South East Asia. However, species-specific patterns emerged in the Indonesian Archipelago and particularly in Wallacea, the intermediate area between the Sunda and Sahul biogeographic domains. The species differed in the degree of mixing of phylogroups in Wallacea, with a dominance of the Eastern phylogroup and little mixing in *L. littorea*, and pronounced mixing of phylogroups in *L. racemosa*. Only in *L. racemosa* were sea surface currents strong enough to wipe out the geographical history of the Indonesian regions during the last glacial period. Thus, despite the omnipresence of seawater and complex sea surface currents, mangroves as marine plants with seawater-dependent seed dispersal have limited and species-specific seed dispersal capacity. Nevertheless, our study showed that sea surface currents have shaped the contemporary distribution of genetic diversity and population structure of *Lumnitzera* mangroves in Indonesia. Further comparative studies are needed to identify the underlying processes that lead to the different patterns of large- and small-scale distribution and of genetic structure between the two species, for example, seed viability (Perera et al., 2019; Wang et al., 2019) or habitat structure. Overall, our study contributes to a growing body of literature suggesting that both land barrier effects and ocean currents contribute to the observed genetic discontinuities found in mangrove species (Guo et al., 2016, 2018a, 2018b) and that differential limitations in dispersal capabilities may lead to contrasting phylogeographic patterns even between very closely related and equally distributed species (Guo et al., 2018a, 2021).

Acknowledgements

This research was possible through collaboration between the Research Center for Biology, the Indonesian Institute of Sciences, (RCB-LIPI), and Leipzig University, funded by the German Federal Ministry of Education and Research (BMBF project BIOHEALTH, no. 16GW0120K) to Alexandra Muellner-Riehl. We thank our Indonesian partners at RCB-LIPI, Hetty I.P. Normakristagaluh, Lina Juswara, and Witjaksono (former director of RCB-LIPI) for administrative support; in memoriam of Fajria Novari (Ministry of Environment and Forestry Republic of Indonesia) for help with plant material export permits; and all local forestry officers, national parks, and natural resources conservation units for permits and logistic support. We thank Ina Geier and Martina Herrmann (UFZ) for support in ddRAD library preparation. Jeprianto Manurung was funded by a PhD grant from the German Academic Exchange Service (DAAD project no. 91653688), hosted by Alexandra Muellner-Riehl. Jan Schnitzler and Christopher Barratt were supported by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (DFG—FZT 118). Open Access funding enabled and organized by Projekt DEAL.

Author Contributions

J.M., A.N.M.R., and J.S. conceived the study, with input on study design from W.D., C.D.B., B.M.R.A., and B.J.; J.M. collected plant material with support from R.S.; J.M., W.D., and B.M.R.A. performed lab work; J.M., W.D., C.D.B., B.M.R.A., and B.F.J. analyzed the data; and J.M., W.D., and A.N.M.R. led the writing of the manuscript, with contributions from all co-authors.

References

Alexander DH, Novembre J, Lange K. 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Research* 19: 1655–1664.

Barber PH, Erdmann MV, Palumbi SR. 2006. Comparative phylogeography of three codistributed stomatopods: Origins and timing of regional lineage diversification in the coral triangle. *Evolution* 60: 1825–1839.

Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2000. A marine Wallace's line? *Nature* 406: 692–693.

Barber PH, Palumbi SR, Erdmann MV, Moosa MK. 2002. Sharp genetic breaks among populations of *Haptosquilla pulchella* (Stomatopoda) indicate limits to larval transport: Patterns, causes, and consequences. *Molecular Ecology* 11: 659–674.

Basyuni M, Hamzah RS, Siregar UJ. 2012. Effect of anthropogenic activities on genetic variation of *Rhizophora mucronata* Lamk. in Secanggang mangrove forest, North Sumatra. *Foresta Indonesian Journal of Forestry* 1: 41–48.

De Bruyn M, Stelbrink B, Morley RJ, Hall R, Carvalho GR, Cannon CH, van den Bergh G, Meijaard E, Metcalfe I, Boitani L, Maiorano L. 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology* 63: 879–901.

Cerón-Souza I, Bermingham E, McMillan WO, Jones FA. 2012. Comparative genetic structure of two mangrove species in Caribbean and Pacific estuaries of Panama. *BMC Evolutionary Biology* 12: 1–15.

Cinco-Castro S, Herrera-Silveira J. 2020. Vulnerability of mangrove ecosystems to climate change effects: The case of the Yucatan Peninsula. *Ocean & Coastal Management* 192: 105196.

Clarke PJ, Kerrigan RA, Westphal CJ. 2001. Dispersal potential and early growth in 14 tropical mangroves: Do early life history traits correlate with patterns of adult distribution? *Journal of Ecology* 89: 648–659.

Crayn DM, Costion C, Harrington MG. 2015. The Sahul-Sunda floristic exchange: Dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography* 42: 11–24.

Döös K, Jönsson B, Kjellsson J. 2017. Evaluation of oceanic and atmospheric trajectory schemes in the TRACMASS trajectory model v6.0. *Geoscientific Model Development* 10(4): 1733–1749.

Dray S, Dufour AB. 2007. The ade4 Package: Implementing the duality diagram for ecologists. *Journal of Statistical Software* 22: 1–20.

Duke NC. 1995. Genetic diversity, distributional barriers and rafting continents—More thoughts on the evolution of mangroves. In: Wong YS, Tam NFY eds. *Asia-Pacific symposium on mangrove ecosystems*. Dordrecht: Springer. 167–181.

Duke NC. 2017. Mangrove floristics and biogeography revisited: Further deductions from biodiversity hot spots, ancestral discontinuities, and common evolutionary processes. In: Rivera-Monroy VH, Lee SY, Kristensen E, Twilley RR eds. *Mangrove ecosystems: A global biogeographic perspective*. Cham: Springer International Publishing. 17–53.

Duke NC, Lo E, Sun M. 2002. Global distribution and genetic discontinuities of mangroves—Emerging patterns in the evolution of *Rhizophora*. *Trees* 16: 65–79.

Fallon SJ, Guilderson TP. 2008. Surface water processes in the Indonesian Throughflow as documented by a high-resolution coral Δ14C record. *Journal of Geophysical Research* 113: 1–7.

Garrison E, Kronenberg ZN, Dawson ET, Pedersen BS, Prins P. 2021. *Vcflib and tools for processing the VCF variant call format*. bioRxiv. https://doi.org/10.1101/2021.05.21.445151

Giesen W, Wulffraat S, Zieren M, Scholten L. 2007. *Mangrove guidebook for Southeast Asia*. Bangkok, Thailand: FAO and Wetlands International, Dharmasarn Co. Ltd.

Gilman EL, Ellison J, Duke NC, Field C. 2008. Threats to mangroves from climate change and adaptation options: A review. *Aquatic Botany* 89: 237–250.

Giri C, Long J, Abbas S, Murali RM, Qamer FM, Pengra B, Thau D. 2015. Distribution and dynamics of mangrove forests of South Asia. *Journal of Environmental Management* 148: 101–111.

Giri C, Ochieng E, Tieszen LL, Zhu Z, Singh A, Loveland T, Masek J, Duke N. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography* 20: 154–159.

Gordon A. 2005. Oceanography of the Indonesian seas and their throughflow. *Oceanography* 18: 14–27.

Gordon AL, Susanto RD, Vranes K. 2003. Cool Indonesian Throughflow as a consequence of restricted surface layer flow. *Nature* 425: 824–828.

Goudet J. 2005. Hierfstat, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes* 5: 184–186.

Gruber B, Unmack PJ, Berry OF, Georges A. 2017. dartrR: An R package to facilitate analysis of SNP data generated from reduced representation genome sequencing. *Molecular Ecology Resources* 18: 691–699.

Guo W, Banerjee AK, Wu H, Ng WL, Feng H, Qiao S, Liu Y, Huang Y. 2021. Contrasting phylogeographic patterns in *Lumnitzera* mangroves across the Indo-West Pacific. *Frontiers in Plant Science* 12: 637009.

Guo Z, Guo W, Wu H, Fang X, Ng WL, Shi X, Liu Y, Huang Z, Li W, Gan L, He S, Zhong C, Jian S, Gong X, Shi S, Huang Y. 2018a. Differing phylogeographic patterns within the Indo-West Pacific mangrove genus *Xylocarpus* (Meliaceae). *Journal of Biogeography* 45: 676–689.

Guo Z, Huang Y, Chen Y, Duke NC, Zhong C, Shi S. 2016. Genetic discontinuities in a dominant mangrove *Rhizophora apiculata* (Rhizophoraceae) in the Indo-Malesian region. *Journal of Biogeography* 43: 1856–1868.

Guo W, Ng WL, Wu H, Li W, Zhang L, Qiao S, Yang X, Shi X, Huang Y. 2018b. Chloroplast phylogeography of a widely distributed mangrove species, *Excoecaria agallocha*, in the Indo-West Pacific region. *Hydrobiologia* 807: 333–347.

Guo M, Zhou R, Huang Y, Ouyang J, Shi S. 2011. Molecular confirmation of natural hybridization between *Lumnitzera racemosa* and *Lumnitzera littorea*. *Aquatic Botany* 95: 59–64.

Hall R. 2009. Southeast Asia's changing palaeogeography. *Blumea* 54: 148–161.

Hamrick JL, Godt MJW. 1996. Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351: 1291–1298.

He Z, Li X, Yang M, Wang X, Zhong C, Duke NC, Wu C-I, Shi S. 2019. Speciation with gene flow via cycles of isolation and migration: Insights from multiple mangrove taxa. *National Science Review* 6: 275–288.

Hijmans RJ, Van Etten J. 2015. raster: Geographic data analysis and modeling. R package version 2.3-40.

Huang Y, Zhu C, Li X, Li X, Hu L, Tan F, Zhou R, Shi S. 2012. Differentiated population structure of a genetically depauperate mangrove species *Ceriops tagal* revealed by both Sanger and deep sequencing. *Aquatic Botany* 101: 46–54.

Imron JB, Hale P, Degnan BM, Degnan SM. 2007. Pleistocene isolation and recent gene flow in *Haliotis asinina*, an Indo-Pacific vetigastropod with limited dispersal capacity. *Molecular Ecology* 16: 289–304.

Jombart T, Devillard S, Balloux F. 2010. Discriminant analysis of principal components: A new method for the analysis of genetically structured populations. *BMC Genetics* 11: 94. https://doi.org/10.1186/1471-2156-11-94

Jombart T, Kamvar ZN, Collins C, Luštrik R, Beugin M-P, Knaus BJ, Solymos P, Mikryukov V, Schliep K, Maié T, Morkovsky L, Ahmed I, Cori A, Calboli F, Ewing RJ, Michaud F, DeCamp R, Courtiol A. 2020. adegenet: Exploratory analysis of genetic and genomic data. The Comprehensive R Archive Network.

Joyce EM, Thiele KR, Ferry Slik JW, Crayn DM. 2021. Plants will cross the lines: Climate and available land mass are the major determinants of phytogeographical patterns in the Sunda–Sahul Convergence Zone. *Biological Journal of the Linnean Society* 132: 374–387.

Kado T, Fujimoto A, Giang LH, Tuan M, Hong PN, Harada KO, Tachida H. 2004. Genetic structures of natural populations of three mangrove species, *Avicennia marina*, *Kandelia candel* and *Lumnitzera racemosa*, in Vietnam revealed by maturase sequences of plastid DNA. *Plant Species Biology* 19: 91–99.

Kamvar ZN, Brooks JC, Grünwald NJ. 2015. Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. *Frontiers in Genetics* 6: 208.

Kathiresan K, Bingham BL. 2001. Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* 40: 81–251.

Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I. 2015. Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. *Molecular Ecology Resources* 15: 1179–1191.

Lellouche JM, Greiner E, Le Galloudec O, Garric G, Regnier C, Drevillon M, Benkiran M, Testut C-E, Bourdalle-Badie R, Gasparin F, Hernandez O, Levier B, Drillet Y, Remy E, Le Traon P-Y. 2018. Recent updates to the Copernicus Marine Service global ocean monitoring and forecasting real-time 1/12° high-resolution system. *Ocean Science* 14: 1093–1126.

Li J, Yang Y, Chen Q, Fang L, He Z, Guo W, Qiao S, Wang Z, Guo M, Zhong C, Zhou R, Shi S. 2016. Pronounced genetic differentiation and recent secondary contact in the mangrove tree *Lumnitzera racemosa* revealed by population genomic analyses. *Scientific Reports* 6: 1–12.

Liu S, Zhang H, Shi X, Chen M-T, Cao P, Li Z, Troa RA, Zuraida R, Triarso E, Marfasran H. 2020. Reconstruction of monsoon evolution in southernmost Sumatra over the past 35 kyr and its response to northern hemisphere climate changes. *Progress in Earth and Planetary Science* 7: 1–13.

López-Angarita J, Tilley A, Hawkins JP, Pedraza C, Roberts CM. 2018. Land use patterns and influences of protected areas on mangroves of the eastern tropical Pacific. *Biological Conservation* 227: 82–91.

Mafi-Gholami D, Zenner EK, Jaafari A. 2020. Mangrove regional feedback to sea level rise and drought intensity at the end of the 21st century. *Ecological Indicators* 110: 105972.

Manurung J, Kappen J, Schnitzler J, Frolov A, Wessjohann LA, Agusta A, Muellner-Riehl AN, Franke K. 2021. Analysis of unusual sulfated constituents and anti-infective properties of two Indonesian mangroves, *Lumnitzera littorea and Lumnitzera racemosa (Combretaceae). Separations* 8: 82.

Manurung J, Siregar IZ, Kusmana Cecep, Dwijayanti FG. 2017. Genetic variation of the mangrove species *Avicennia marina* in heavy metal polluted estuaries of Cilegon industrial area, Indonesia. *Biodiversitas Journal of Biological Diversity* 18: 1109–1115.

Morley RJ. 2003. Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 5–20.

Morley RJ. 2012. *A review of the Cenozoic palaeoclimate history of Southeast Asia. Biotic evolution and environmental change in Southeast Asia.* Cambridge, United Kingdom: Cambridge University Press.

Muellner AN, Pannell CM, Coleman A, Chase MW. 2008. The origin and evolution of Indomalesian, Australasian and Pacific island biotas: Insights from Aglaieae (Meliaceae, Sapindales). *Journal of Biogeography* 35: 1769–1789.

Nettel A, Dodd RS. 2007. Drifting propagules and receding swamps: Genetic footprints of mangrove recolonization and dispersal along tropical coasts. *Evolution: International Journal of Organic Evolution* 61: 958–971.

O'Leary SJ, Puritz JB, Willis SC, Hollenbeck CM, Portnoy DS. 2018. These aren't the loci you'e looking for: Principles of effective SNP filtering for molecular ecologists. *Molecular Ecology* 22: 3193–3206.

Otwoma LM, Kochzius M. 2016. Genetic population structure of the coral reef sea star *Linckia laevigata* in the Western Indian Ocean and Indo-West Pacific. *PLoS One* 11: 1–14.

Pembleton LW, Cogan NOI, Forster JW. 2013. StAMPP: An R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Molecular Ecology Resources* 13: 946–952.

Perera PLMM, Jayasuriya KMGG, Gunaratne AMTA, Karunaratne WAIP, Damunupola JW, Prassanna MGM. 2019. Conservation attempt of critically endangered mangrove *Lumnitzera littorea* (Jack) Voigt in Madu Ganga Ramsar Site of Sri Lanka; stand composition and seed germination. *Ceylon Journal of Science* 48: 225–234.

Peterson BK, Weber JN, Kay EH, Fisher HS, Hoekstra HE. 2012. Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One* 7: 1–11.

Petkova D, Novembre J, Stephens M. 2016. Visualizing spatial population structure with estimated effective migration surfaces. *Nature Genetics* 48: 94–100.

Pil MW, Boeger MRT, Muschner VC, Pie MR, Ostrensky A, Boeger WA. 2011. Postglacial north-south expansion of populations of *Rhizophora mangle* (Rhizophoraceae) along the Brazilian coast revealed by microsatellite analysis. *American Journal of Botany* 98: 1031–1039.

Polidoro BA, Carpenter KE, Collins L, Duke NC, Ellison AM, Ellison JC, Farnsworth EJ, Fernando ES, Kathiresan K, Koedam NE, Livingstone SR, Miyagi T, Moore GE, Ngoc Nam V, Ong JE, Primavera JH, Salmo SG, Sanciangco JC, Sukardjo S, Wang Y, Yong JWH. 2010. The loss of species: Mangrove extinction risk and geographic areas of global concern. *PLoS One* 5: 1–10.

Purcell S, Neale B, Todd-Brown K, Thomas L, Ferreira MAR, Bender D, Maller J, Sklar P, Bakker PIW, de, Daly MJ, Sham PC. 2007. PLINK: A tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics* 8: 559–575.

Puritz JB, Hollenbeck CM, Gold JR. 2014. dDocent: A RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ* 2: e431.

Rands MR, Adams WM, Bennun L, Butchart SH, Clements A, Coomes D, Entwistle A, Hodge I, Kapos V, Scharlemann JP, Sutherland WJ. 2010. Biodiversity conservation: Challenges beyond 2010. *Science* 329: 1298–1303.

R Core Team. 2020. *R: A language and environment for statistical computing [Internet]*. Vienna, Austria: R Foundation for Statistical Computing 2018.

Richardson JE, Costion CM, Muellner AN. 2012. *The Malesian floristic interchange: Plant migration patterns across Wallace's Line. Biotic evolution and environmental change in Southeast Asia*. Cambridge, United Kingdom: Cambridge University Press.

Rochette NC, Rivera-Colón AG, Catchen JM. 2019. Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology* 28: 4737–4754.

Romañach SS, DeAngelis DL, Koh HL, Li Y, Teh SY, Raja Barizan RS, Zhai L. 2018. Conservation and restoration of mangroves: Global status, perspectives, and prognosis. *Ocean & Coastal Management* 154: 72–82.

Ross N. 2020. fasterize: Fast polygon to raster conversion. R package version.

Saenger P, Ragavan P, Sheue C-R, López-Portillo J, Yong JWH, Mageswaran T. 2019. Mangrove biogeography of the Indo-Pacific. In: Gul B, Böer B, Khan MA, Clüsener-Godt M, Hameed A eds. *Sabkha ecosystems*. Cham: Springer International Publishing. 379–400.

Sandilyan S, Kathiresan K. 2014. Decline of mangroves—A threat of heavy metal poisoning in Asia. *Ocean & Coastal Management* 102: 161–168.

Schierenbeck KA. 2017. Population-level genetic variation and climate change in a biodiversity hotspot. *Annals of Botany* 119: 215–228.

Solomon Raju AJ, Kumar R, Rajesh B. 2014. Pollination ecology of *Lumnitzera racemosa* Willd. (Combretaceae), a non-viviparous mangrove tree. *TAPROBANICA: The Journal of Asian Biodiversity* 6: 100–109.

Spalding M. 2010. *World atlas of mangroves*. London: Earthscan.

Spalding M, Blasco F, Field C. 1997. *World mangrove atlas*. Okinawa, Japan: International Society for Mangrove Ecosystems.

Sprintall J, Gordon AL, Wijffels SE, Feng M, Hu S, Koch-Larrouy A, Phillips H, Nugroho D, Napitu A, Pujiana K, Susanto RD, Sloyan B, Peña-Molino B, Yuan D, Riama NF, Siswanto S, Kuswardani A, Arifin Z, Wahyudi AJ, Zhou H, Nagai T, Ansong JK, Bourdallé-Badié R, Chanut J, Lyard F, Arbic BK, Ramdhani A, Setiawan A. 2019. Detecting change in the Indonesian seas. *Frontiers in Marine Science* 6: 1–24.

Su G, Huang Y, Tan F, Ni X, Tang T, Shi S. 2007. Conservation genetics of *Lumnitzera littorea* (Combretaceae), an endangered mangrove, from the Indo-West Pacific. *Marine Biology* 150: 321–328.

Thu PM, Populus J. 2007. Status and changes of mangrove forest in Mekong Delta: Case study in Tra Vinh, Vietnam. *Estuarine, Coastal and Shelf Science* 71: 98–109.

Tomlinson PB. 2016. *The botany of mangroves*. New York: Cambridge University Press.

Tomlinson PB, Bunt JS, Primack RB, Duke NC. 1978. *Lumnitzera rosea* (Combretaceae)—Its status and floral morphology. *Journal of the Arnold Arboretum* 59: 342–351.

Turner H, Hovenkamp P, van Welzen PC. 2001. Biogeography of Southeast Asia and the West Pacific. *Journal of Biogeography* 28: 217–230.

Urashi C, Teshima KM, Minobe S, Koizumi O, Inomata N. 2013. Inferences of evolutionary history of a widely distributed mangrove species, *Bruguiera gymnorrhiza*, in the Indo-West Pacific region. *Ecology and Evolution* 3: 2251–2261.

Van der Stocken T, Carroll D, Menemenlis D, Simard M, Koedam N. 2019. Global-scale dispersal and connectivity in mangroves. *Proceedings of the National Academy of Sciences of the United States of America* 116: 915–922.

Van der Stocken T, Menemenlis D. 2017. Modelling mangrove propagule dispersal trajectories using high-resolution estimates of ocean surface winds and currents. *Biotropica* 49: 472–481.

Van der Stocken T, Wee AK, De Ryck DJ, Vanschoenwinkel B, Friess DA, Dahdouh-Guebas F, Simard M, Koedam N, Webb EL. 2019. A general framework for propagule dispersal in mangroves. *Biological Reviews of the Cambridge Philosophical Society* 94: 1547–1575.

Van Welzen PC, Parnell JAN, Ferry Slik JW. 2011. Wallace's Line and plant distributions: Two or three phytogeographical areas and where to group Java? *Biological Journal of the Linnean Society* 103: 531–545.

Van Welzen P, Slik JW. 2009. Patterns in species richness and composition of plant families in the Malay Archipelago. *Blumea* 54: 166–171.

Veettil BK, Ward RD, Quang NX, Trang NTT, Giang TH. 2019. Mangroves of Vietnam: Historical development, current state of research and future threats. *Estuarine, Coastal and Shelf Science* 218: 212–236.

Wainwright BJ, Arlyza IS, Karl SA. 2018. Population genetic subdivision of seagrasses, *Syringodium isoetifolium* and *Thalassia hemprichii*, in the Indonesian Archipelago. *Botanica Marina* 61: 235–245.

Wallace AR. 1860. On the physical geography of the Malay Archipelago. *Journal of the Royal Geographical Society* 33: 217–234.

Wallace AR. 1863. *On the zoological geography of the Malay Archipelago*. London, United Kingdom: Read Books Ltd.

Wang W, Li X, Wang M. 2019. Propagule dispersal determines mangrove zonation at intertidal and estuarine scales. *Forests* 10: 245.

Waters JM. 2008. Marine biogeographical disjunction in temperate Australia: Historical landbridge, contemporary currents, or both? *Diversity and Distributions* 14: 692–700.

Wee AKS, Takayama K, Asakawa T, Thompson B, Onrizal, Sungkaew S, Tung NX, Nazre M, Soe KK, Tan HTW, Watano Y, Baba S, Kajita T, Webb EL. 2014. Oceanic currents, not land masses, maintain the genetic structure of the mangrove *Rhizophora mucronata* Lam. (Rhizophoraceae) in Southeast Asia. *Journal of Biogeography* 41: 954–964.

Wee AKS, Teo J, Chua J, Takayama K, Asakawa T, Meenakshisundaram S, Adjie B, Ardli E, Sungkaew S, Suleiman M, Tung N, Salmo S, Yllano O, Saleh M, Soe K, Tateishi Y, Watano Y, Tsuda Y, Kajita T, Webb E. 2017. Vicariance and oceanic barriers drive contemporary genetic structure of widespread mangrove species *Sonneratia alba* J. Sm. in the Indo-West Pacific. *Forests* 8: 483.

Whitlock MC, Mccauley DE. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm+1)$. *Heredity* 82: 117–125.

Woodruff DS. 2010. Biogeography and conservation in Southeast Asia: How 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity and Conservation* 19: 919–941.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790.

Yahya AF, Hyun JO, Lee JH, Kim YY, Lee KM, Hong KN, Kim S-C. 2014. Genetic variation and population genetic structure of *Rhizophora apiculata* (Rhizophoraceae) in the greater Sunda Islands, Indonesia using microsatellite markers. *Journal of Plant Research* 127: 287–297.

Yan YB, Duke NC, Sun M. 2016. Comparative analysis of the pattern of population genetic diversity in three Indo-West Pacific *Rhizophora* mangrove species. *Frontiers in Plant Science* 7: 1–17.

Yang Y, Zhong CR, Li YH, Zhang Y. 2016. The morphological structure and germination characters of seed of endangered Mangrove *Lumnitzera littorea* (Jack.) Voigt. *Molecular. Plant Breeding* 14: 2851–2858.

Yong Y, Lu CY, Wong YS, Tam NFY. 2004. Diaspore traits and intertidal zonation of non-viviparous mangrove species. *Acta Botanica Sinica* 46: 896–906.

Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12923/suppinfo:

Fig. S1. Cross-validation error analysis of the ADMIXTURE analysis (A, C) and BIC values of k-means clustering used during DAPC (B, D) for K = 1 to 15 for *Lumnitzera littorea* and *L. racemosa*. Red dots and lines indicate the minimum values.

Fig. S2. Barplots of the ADMIXTURE (A) and the DAPC (B) analyses of 14 populations of *Lumnitzera littorea*. Each bar represents an individual, and each color is the inferred membership in each of the K groups (2 to 6).

Fig. S3. Barplots of the ADMIXTURE (A) and the DAPC (B) analyses of 21 populations of *Lumnitzera racemosa*. Each bar represents an individual, and each color is the inferred membership in each of the K groups (2 to 7).

Fig. S4. Population level membership proportions of *Lumnitzera littorea* according to the ADMIXTURE analyses for K = 1 to 6 based on 3,122 SNPs.

Fig. S5. Population level membership proportions of *Lumnitzera racemosa* according to the ADMIXTURE analyses for K = 1 to 7 based on 3,048 SNPs

Fig. S6. Test for "isolation by Wallace's line" using a Mantel test. Population pairs separated by Wallace's line had distance = 1, while pairs on the same side had distance = 0.

Fig. S7. Mean surface current movement in the study region based on Marine Copernicus GLORYS12V1 velocity fields for 2015. A. Northwest Monsoon (January to March) and B. Southeast Monsoon (May to November). The red dots on the maps represent the sampled localities. Maps were created using cartopy v0.20.1.

Table S1. Numbers of sequences obtained and numbers of SNPs.

Table S2. Nei's (1978) pairwise genetic distances (FST) between populations of *Lumnitzera littorea* in the Indonesian Archipelago. For population information see Table 1.

Table S3. Nei's (1978) pairwise genetic distances between populations of *Lumnitzera racemosa* in the Indonesian Archipelago. For population information see Table 1.