Okinawa Institute of Science and Technology Graduate School

Thesis submitted for the degree **Doctor of Philosophy**

Role of Island Systems in Mangrove Biogeography

by

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November 14th, 2022

Declaration of Original and Sole Authorship

I, Maki Kohata Thomas, declare that this thesis entitled, "Role of Island Systems in Mangrove Biogeography", and the data presented in it are original and my own work.

I confirm that:

- No part of this work has previously been submitted for a degree at this or any other university.
- References to the work of others have been clearly acknowledged. Quotations from the work of others have been clearly indicated, and attributed to them.
- In cases where others have contributed to part of this work, such contribution has been clearly acknowledged and distinguished from my own work.
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Thesis Abstract

Island mangrove populations are connected by hydrochory (dispersal via water) in space and time. Yet connectivity studies focusing on island mangroves are still scarce compared to those addressing continental mangroves. There are two distinct mangrove biogeographic regions, the Indo-West Pacific (IWP) and the Atlantic-East Pacific (AEP). In the IWP, both taxonomic and degradation hotspots are located in archipelagos, and more than half of mangrove habitat occurs on islands. As habitat loss and fragmentation continue, understanding of recruitment and population connectivity of island mangroves is critical for mangrove conservation. Moreover, long-distance dispersal and local retention of mangrove propagules depend on species dispersal abilities and land/seascape characteristics. However, demographic rates and historical population changes of island mangrove systems are still largely unknown, especially at a local scale. Thus, this thesis examined island mangrove connectivity in the IWP and focused on one archipelago as a model site to quantify local-scale measures of mangrove connectivity. First, I investigated biogeographic roles of island mangroves in regional mangrove distribution. Using the graph-theoretical method on presence-absence data, I reconstructed the biogeographic structure of the IWP and identified biogeographic roles of species and mangrove sites, which provided insights into how distant mangrove islands are connected, e.g., transoceanic dispersal or stepping-stones. Outputs were then qualitatively compared with paleogeographic studies, population genetic studies, and oceanographic studies to explore which characteristics affect island biogeographic structure and roles. The results showed 4 biogeographic modules (areas with similar floral composition) in the IWP. The distribution of each module was influenced differently by geological events and dispersal parameters, depending on their locations. Furthermore, site biogeographical roles showed intricate networks of stepping stones that constructed ambiguous modules in the region. Individual islands showed heterogeneous species compositions, even within modules, and no area appeared to serve as a biogeographic hub in the IWP. Secondly, I sought to identify localscale population connectivity, focusing on detecting the spatiotemporal scale of propagule dispersal using a multi-disciplinary approach, including population genetic and oceanographic methods. The model site included four islands of the Ryukyu Archipelago in southwestern Japan. Population genetic analyses based on microsatellite markers detected a few contemporary migrations among islands, with overall infrequent genetic exchange among and within islands. In-situ release-recapture experiments employing GPS drifters produced a subset of successful beaching probabilities and supported genetic results that population connectivity was too stochastic and rare to homogenize the genetic structure in the archipelago. To conclude, islands serve as stepping-stones, facilitating species exchange across the IWP. This may create regional biogeography resilient to habitat loss, but also suggests the potential for site losses to become critical gaps that restrict connectivity. Networks of stepping stones are complex and depend on local population connectivity that determines the role of island groups as meta-communities. Moreover, despite competent dispersal abilities, the spatiotemporal scale of mangrove dispersal among islands must be locally quantified using a multi-disciplinary approach. The results from all methods, scales, and resolutions tested in this study to evaluate island mangrove population connectivity suggest that dispersal is primarily localized, and that rare, inter-island dispersal events may maintain regional connectivity.

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List of Abbreviation

IWP	Indo-West Pacific	5
AEP	Atlantic-East Pacific	8
l	Within-module degree	15
r	Between-module degree	15
M	Modularity	15
UP	Ultra-peripheral	16
Р	Peripheral	23
С	Connectors	23
NHub	Network hub	25
MHub	Module hub	25
IRM	Iriomote island	36
ISG	Ishigaki island	36
MYK	Miyako island	36
OKI	Okinawa mainland	36
NM	North Miyako Island	42
OKN	Okinawa cluster	42
WI	West Iriomote Cluster	42
m	Migration rate	37

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Chapter One Thesis Introduction

Studies of mangrove population connectivity have focused primarily on global to regional scales, and some have also explored the potential for long-distance dispersal and suggested that archipelagos may serve as stepping stones for trans-oceanic dispersal (Van der Stocken et al., 2019b). However, the contribution of propagule dispersal to connectivity is still largely unknown, especially at local scales. Studies of island roles in species distributions and mangrove population connectivity, particularly the spatiotemporal scale of propagule dispersal, are scarce compared to continental coastal mangrove studies (Vannucci, 2002). Thus, identifying fine-scale propagule dispersal patterns unique to individual island systems is essential to understanding island contributions to global species distributions and to selecting appropriate sizes and locations for mangrove conservation in archipelagos.

In addition to land barriers, coastal population connectivity is influenced by oceanic barriers because of hydrochory (dispersal of propagules by water). Coastal species often establish source-sink relationships with distant populations, and as a result, develop a meta-community that supports biodiversity and increases resilience to threats as an ecological assemblage. Thus, hydrochory is essential to connectivity of different populations in terms of expansion of species distributions, migration between populations, colonization of unoccupied niches, and assembling local communities from the metacommunity (Levin et al., 2003; Levine and Murrell, 2003). However, quantifying the spatiotemporal scale of oceanic dispersal to identify oceanic barriers is difficult, not only for mangrove species, but also for other coastal species such as corals and sea grasses, especially in island systems where coastlines are discrete within the meta-community (Edmunds et al., 2018). As it is generally understood that ocean currents are the most important natural driving force for dispersal (Nathan et al., 2008), dispersal has been studied extensively in relation to larvae of high-value coastal species such as corals and fish, using individual or combinations of genetic methods, network theory, remote sensing, and numerical ocean circulation modeling (Treml et al., 2008; Erftemeijer et al., 2009; Mitarai et al., 2009; Fujimura et al., 2014).

This study sought to illuminate island mangrove population connectivity, about which little is yet known. Using a multi-disciplinary approach, including graph-theoretical, population genetic, and oceanographic methods, the objective, which was to identify island biogeographical roles in regional mangrove distribution and to quantify the spatiotemporal scale of propagule dispersal and population connectivity on a local scale. This is critical to understand how mangrove species distributions are maintained and how habitat loss may affect other mangrove areas on local and regional scales. The latter may provide particularly valuable information to design conservation and monitoring plans. Moreover, due to the characteristics of mangrove propagules, i.e., buoyancy and duration of viability, mangroves could be proxies to better understand hydrochory in island systems (Van der Stocken et al., 2019b) applicable to other species whose propagules are more difficult to study, such as corals.

Mangroves exhibit many unique ecological attributes and construct spatially, biologically, and hydrologically diverse ecosystems, including trees, shrubs, palms, and ground ferns. However, mangrove species are still not clearly defined because experts still disagree on which plant species can be considered mangroves (Mukherjee et al., 2014; Dahdouh-Guebas et al., 2021). A recent study on mangrove ecosystems offered a consensus definition that mangroves are woody plants that grow normally in tropical and subtropical latitudes at the land-sea interface, such as bays, estuaries, lagoons, and backwaters. These plants and associated organisms constitute the "mangrove forest community" or "mangal", and the mangal and its associated abiotic factors constitute the "mangrove ecosystem" (Mukherjee et al., 2014). They generally exceed one-half meter in height and grow above mean sea level in brackish water at the intertidal zone of coastal marine environments or estuarine edges. The northernmost mangroves are located in Bermuda (32 '20 N), and the southernmost are in New Zealand (38 '59 S) (Tomlinson, 2016; Duke, 1992; Spalding et al., 2010) (Figure 1.1). Mangrove species are uniquely adapted to survive under challenging conditions in which water height and salinity in the soil and water column fluctuate daily and seasonally due to changing tides, seasonal precipitation, and river out-flows (Duke, 1992). Those environmental conditions regulate species diversity in mangrove ecosystems (Duke et al., 1998). Local expansion of this niche is regulated by the amount of terrestrial material input, including soil and nutrients from rivers (Woodroffe et al., 2016). Therefore, mangroves thrive in soft sediments away from strong, direct wave action and on protected rocky shores.



Figure 1.1. Global distribution of mangroves. The colors indicate species counts in the area (Saenger et al., 2019).

On the other hand, mangroves exposed to flushing tides and waves are often limited in population size and tree mass because they cannot obtain as many nutrients, or as much organic matter and sediment as riverine mangroves (Spalding et al., 2010; Fu et al., 2014). These are called fringing or overwashed mangroves, and are often found on island coastlines. Despite such harsh environmental conditions with limited areas and species richness, mangrove plants have evolved to fulfill a multitude of ecological functions for which many plant species in temperate forests may be required (Mukherjee et al., 2014). However, as mangrove areas diminish or become fragmented, their long-term survival is at significant risk, and essential ecosystem services may be lost or compromised (Duke et al., 2007; Bryan-Brown et al., 2020). A recent study has shown that mangrove deforestation is not always associated with high levels of mangrove fragmentation. At the same time, >50% of conversion to rice patties resulted in fragmentation and loss of mangroves, and >15% of conversion to palm oil plantation was just weakly correlated with fragmentation.

However, reconnection of once-fragmented patches is rare without mangrove expansion (Bryan-Brown et al., 2020). While how much migration corridors can be secured to maintain patch residency depends on the distance to the nearest neighbor and

patch size, a study showed that land use is one of the significant determinants of the correlation between deforestation and fragmentation (Bryan-Brown et al., 2020). Species distributions, population connectivity, life-history traits, and global threats have been studied for specific species to understand the effects of mangrove area loss on individual mangrove species and populations at different spatial scales (Polidoro et al., 2010). Moreover, how species abundance responds to habitat fragmentation may also be influenced by propagule dispersal, which is one of the essential traits for persistence in fragmented landscapes (Hagen et al., 2012). Therefore, understanding how propagule traits and environmental parameters affect dispersal is also essential, particularly when habitat loss threatens biodiversity (Fahrig, 2003). The most significant cause of mangrove area loss has been the destruction of mangrove forests for aquaculture/agriculture for food and social security (Thomas et al., 2017). On the other hand, Mukherjee et al. (2014) argued that degradation of mangroves due to development has a major impact on mangrove ecosystems across all countries and will take a long time to restore.

Until the 2010s, the loss of mangrove areas was observed globally ; however, with increasing awareness of mangrove ecological and economic services, mangrove ecosystems became a high priority for several recent large international conservation initiatives, including the International Blue Carbon Initiative (https://www.thebluecarboninitiative.org/) and the Global Mangrove Alliance (https://www.mangrovealliance.org/). Mangroves are also now being discussed in international policy circles. They are increasingly incorporated into national pledges associated with the Paris Agreement of the United Nations Framework Convention on Climate Change (Friess et al., 2020). Although global mangrove coverage represents only about 0.013% of all terrestrial ecosystems, on an equal-area basis, mangrove forests, on average, store more soil carbon than most other ecosystems; 361 Mg C ha⁻¹ of CO₂ fixed in just 1 m of topsoil in mangroves (Sanderman et al., 2018), with an additional contribution to benthic biodiversity. The contribution of mangroves per unit area to combat climate change has caught the attention of the greater public and governments, leading to increased investment and on-the-ground action. (Friess et al., 2020).

Moreover, the global economic value of mangrove ecosystem services has also been estimated at US\$194,000 ha-1y-1 including tourism, fishery, fuels, aqua farming, and lumber(Costanza et al., 2014; Zu Ermgassen et al., 2020). For example, one study identified over 3,000 mangrove attractions in 93 countries, some of which include bird watching and boating in a multi-billion dollar industry (Spalding and Parette, 2019). The indirect economic contribution of mangroves includes natural coastal protection via mitigation of storm surges and tsunamis (Yanagisawa et al., 2009). Lastly, the importance of mangroves as nursery habitat for juvenile fish has been long recognized. Mangroves in the Caribbean strongly influence the community structure of fish in neighboring coral reefs, and the biomass of several commercially important fish species is more than double when adult habitat is connected to mangroves (Mumby et al., 2004). These ecosystem services have become better understood during the last two decades, leading to implementation of monitoring systems, improved data access, changes in industrial practices, expanded management and protection, and increased protection of remaining mangrove forests. As a result, the global rate of mangrove area decline has decreased from 2% to <0.4% in the last two decades (Friess et al., 2020).

On the other hand, the threat of mangrove area loss has shifted from global to regional concerns, which can revert to global again if continuous effort in every region is not maintained (Friess et al., 2020). Some recent hotspots of mangrove destruction exist in Myanmar due to rice cultivation, in Malaysia due to oil palm plantations, and in SE Asia, Papua New Guinea, and West Africa due to deforestation (Friess et al., 2020). Aside from

such direct negative impacts, climate change as an indirect effect of anthropogenic activities has resulted in poleward mangrove distributional shifts, which can have cascade effects on associated ecosystems. Potential loss of island mangroves due to rapid sea-level rise caused by climate change may also be added to the list (Mafi-Gholami et al., 2020), as mangrove ecosystems are sensitive to rapid inundation (Horstman et al., 2015). Although the rate of mangrove area loss is subsiding globally, effects of habitat loss on local and regional population connectivity, biodiversity, and genetic diversity are not yet known.

Although restoration efforts have been implemented as global initiatives in many areas, earlier studies examined the effects of restoration. They reported that mangrove restoration often did not yield expected results because of a lack of species- and site-specific knowledge of mangroves, such as topography, hydrology, appropriate inundation for propagules to ground themselves successfully and salinity, along with fundamental difficulties in restoring damaged environments (Friess et al., 2020; Kodikara et al., 2017). Because successful cases require a long-term commitment to local efforts, including continuous management and monitoring of hydrology and salinity, many restoration efforts are unsuccessful (Zimmer et al., 2022; Friess et al., 2020). While conserving existing mangroves has been given increasing attention in recent years, it is critical to better understand island mangrove connectivity so as to implement mangrove conservation, in the hope of determining the necessary spatiotemporal scale of mangrove conservation and monitoring plans.

Recent mangrove biogeography has mainly focused on understanding evolutionary processes of mangroves. For example, the land connection due to sea-level drop during the last glacial maximum caused mangrove ranges to expand along the Malay Peninsula, Sumatra, Borneo, Java, as well as between Australia and Papua New Guinea (Lo et al., 2014). These findings suggest large-scale connectivity that could lead us to hypothesize island-scale connectivity and major genetic barriers (Triest, 2008). Considering that reduced biodiversity and genetic diversity enhance vulnerability to environmental changes (Beger et al., 2014), ecological and physical dispersal barriers that prevent recruitment from distant populations can negatively affect the resilience of populations. Land and oceanic barriers to mangrove population connectivity have been identified using genetic and taxonomic methods (Abeysinghe et al., 1999; Arbeláez-Cortis et al., 2007; Ge et al., 2001; Giang et al., 2006; Takayama et al., 2013). Examples include the coastal ocean corridor separating populations in Cameroon from Bioko Island (Ngeve et al., 2016), and ocean currents separating populations on either side of the Malay peninsula (Inomata et al., 2010, Wee et al., 2014). Moreover, Wallace's Line also marks a major, well-known discontinuity for mangroves from SE Asia to Australia (Lo et al., 2014). Although they are geographically close, this genetic discontinuity has been maintained over millions of years, and it is hypothesized that local ocean currents are responsible (Lo et al., 2014).

To further understand key mechanisms that shift distributions in response to environmental change and habitat loss, oceanographic methods have been used to estimate potential dispersal. Establishment of population connectivity involves various spatiotemporal scales of dispersal, for which species- and site-specific characteristics of mangrove dispersal are critical (Van der Stocken et al., 2019a; Triest and Van der Stocken, 2021). For example, species-specific traits include propagule size, buoyancy, floating orientation, and floating period, while site-specific attributes include landscape, hydrodynamics, wind vectors, and niche availability. These parameters and their interactions determine the spatiotemporal scale of dispersal (Van der Stocken et al., 2019a). Island nations like the Philippines, Indonesia, Maldives and Papua New Guinea have been stepping stone sites for transoceanic dispersal under conditions where propagules from continental coastlines reach those island habitats, according to global numerical ocean models (Van der Stocken et al., 2019b; Cumick et al., 2019) while dispersal range is strongly sensitive to propagule floating periods.

Additionally, propagule dispersal of coastal species is facilitated by along-coast currents, which have been validated by genetic methods (Wee et al., 2014; Van der Stocken et al., 2019b; Geng et al., 2021). For example, poleward distributional shifts have been documented along the Florida coastline apparently due to increased winter temperatures (Kennedy et al., 2017). Additionally, south-to-north dispersal has consistently occurred over a historical timescale without successful settlement until global warming increased the annual lowest temperature to enable northward colonization by mangrove species (Cavanaugh et al., 2014). The recent poleward shift in northeast Florida could be permanent, based on climate projections suggested by historical accounts showing climate changes and mangrove and salt marsh shifts during the last 300 years (Cavanaugh et al., 2019). A population genetic study on the Rhizophoraceae in south China showed expansion of species distributions from south to north along the coast with a trend of declining genetic diversity in more polar habitats (Geng et al., 2021).

The number of population connectivity studies of island systems must be increased to obtain comprehensive understanding of regional biogeography and dispersal. So far, the general understanding of island mangrove population connectivity is based on only a few studies. Most of these suggest low genetic variation and limited genetic connectivity (Islam et al., 2012; Islam et al., 2014; Yahya et al., 2014; Al-Qthanin and Alharbi, 2020). Except for the study of Yahya et al. (2014), in the Sunda Islands of Indonesia, archipelagos investigated in previous studies are located near distributional edges of the studied species, where they are subject to more genetic drift and environmental selection compared to those in central regions of the species ranges (Arnaud-Haond et al., 2006). Those studies also suggest that the discreteness of island coastlines potentially limits genetic variation, regardless of distributional area. However, because of the paucity of studies in island systems and the specificity of studies on species and sites, more island studies with various species are needed to understand demographic connectivity in archipelagos.

This study, therefore, sought to document critical aspects of island mangrove connectivity in the IWP, including defining biogeographic modules (clusters of areas with similar species composition), determining the biogeographical roles of islands, and the spatiotemporal scale of island mangrove demography. A multi-disciplinary approach employing graph-theoretical, biological, and oceanographic methods was utilized to address each subject. In Chapter Two, the biogeographic patterns and roles of island mangroves were evaluated in the context of mangrove distribution networks, using graph theory, a novel method for studying ecological networks such as food-webs, and symbiotic microbial community networks, neural networks, etc. On the regional scale, species distributions have been shaped not only by dispersal among distant sites, but also by natural selection and bottlenecks induced by geological events, climatic shifts, and sealevel changes. In Chapter Three, the focus of the evaluation is narrowed to one archipelago as a model site to evaluate fine-scale population connectivity and to document the spatiotemporal scale of propagule dispersal among islands.

While evaluating roles of locally vs. distantly-sourced propagules remains challenging, earlier studies suggest that progress in understanding island connectivity is impeded by the limited breadth, details, and spatiotemporal concordance of existing research (Edmunds et al., 2018). Although population genetic connectivity has been studied for several mangrove species, focusing on evolutionary connectivity for each species (Saenger et al., 2019), processes driving the assembly of meta-communities, especially island communities are not well known. Therefore, my objective was to improve our understanding of the function of different island mangroves in creating regional and bioregional mangrove distribution patterns and to document propagule dispersal and population connectivity among islands, which are also critical information to conserve existing mangrove habitats.

Chapter Two identifies contributions of island mangroves in constructing regional scale biogeographic modules in the IWP, using the graph-theoretical method on species presence data (Carstensen et al., 2012; Guimera and Amaral, 2005). Biogeographical roles of each site in the IWP were defined by two parameters, within- and between-module connectivity (Guimera and Amaral, 2005; Olesen et al., 2007), and the simulated annealing method was used to demonstrate regional and bioregional mangrove distributional units in the IWP, called modules. These modules were grouped together with highly linked mangrove sites based on similarity in species compositions. The graph-theoretical method is not entirely new to mangrove studies. One of the oldest studies using this method described the relationship between freshwater input and floristic richness (Bunt et al., 1982). The graph theoretical method has also been used to study ecological networks of mangrove microbial communities (Lin et al., 2019), benthic food webs of mangrove forests (Ray, 2008), as well as social networks around mangroves (Orchard et al., 2015). Furthermore, D'acampora et al. (2018) used a graph theoretical method to identify potential connectivity of mangrove species between fragmented habitats in Brazil. However, I am not aware that this method has been used to understand mangrove biogeography, even though genetic methods have been used extensively with the rapid development of molecular techniques. Saenger et al. (2019) documented restricted gene flow in the IWP based on molecular studies of 6 mangrove species, demonstrating 8 areas in the IWP. Although many questions are best answered with data on genetic connectivity, such as the degree to which gene flow affects evolutionary processes within populations, genetic data alone provide little information on demographic connectivity, especially when information on local demographics and historical changes are lacking (Lowe and Allendorf, 2010).

The graph-theoretical method determines the degree of compositional connectedness based on species distributions. It identifies the degree of local vs. regional topological linkage using null models to assess the significance of the links, which helps determine how best to define module membership and inter-connectedness from biogeographic perspectives (Whittaker et al., 2018). Assuming that the dataset used for the analyses provided complete species composition at each site, the hypothesis was that the delineated modules would overlap with results of previous population genetic studies, taxonomic studies, and oceanographic roles of mangroves were expected, especially island mangroves, to improve our understanding of dispersal patterns, including networks of stepping-stones and long-distance dispersal (LDD).

Although the graph theoretical method is appropriate to detect biogeographic patterns, it cannot identify what drives establishment of modules and their communities. In the last decade, a multi-disciplinary approach considering oceanographic and genetic methods has suggested several oceanographic barriers to population connectivity, such as the Malacca Strait and the South China Sea, in addition to previously known land barriers. For island mangroves, information about population connectivity is scarce. Demographics and shifting distributions of island mangrove systems are still largely unknown, especially at local scale. Thus, in Chapter Three, the spatiotemporal scale of dispersal and population connectivity with quantifiable measures were reported using population genetic and oceanographic methods. Since the potential for long-distance dispersal and local retention of mangrove propagules depends on species dispersal abilities and land/seascape characteristic, propagules retention rates contribute significantly to mangrove connectivity. This study focused on the Ryukyu Archipelago in southwestern Japan, on the northern edge of the IWP (Spalding et al., 2010). The study was conducted both around and among four islands. Since biodiversity often declines at distributional boundaries, this region appeared suitable for identifying distinct genetic and oceanographic discontinuities across the archipelago. The Ryukyu Archipelago currently is not suffering ongoing degradation. Iriomote Island is registered as a Japanese National Monument and has been protected since 1972. Monitoring and conservation strategies of the Ryukyu Archipelago have protected these mangroves for over 50 years, and these methods may be applied to other coastal habitats such as corals and seagrasses. Data acquired with *in-situ* Lagrangian experiments using GPS drifting buoys are compared with population genetic results, including contemporary migration rates. As this study was motivated by conservation of mangroves, the thesis concludes with suggestions for future conservation plans.

Chapter Two

Islands' biogeographical roles in the Indo-West Pacific region

2.1. Introduction

Species compositions of bioregions can reveal ecological processes affecting plant communities, such as interactions between functional traits and landscape parameters (Aggemyr et al., 2018). Understanding such interactions in mangrove ecology requires site- and species-specific studies because mangrove forest types range from dense riverine forests to patchy and small fringing or island mangroves, interactions of which vary greatly. However, such studies require resources and access to each site, which often are obstacles for mangrove research. While much of global mangrove species distribution is understood, biogeographic boundaries, especially involving islands and archipelagos, require further definition despite the high abundance of mangroves on islands compared to continental mangrove sites. It is crucial to gain an understanding of island roles in maintaining mangrove area loss is focused on southeast Asia, where many islands reside. Thus, in this chapter, the goal was to build biogeographic modules based on similar species compositions and to identify the roles of mangrove sites in maintaining those modules.

Mangrove forests are ecosystems that comprise many plants and animals, that evolved specifically in unique coastal environments and mangrove-associated species that are not specific to the inter-tidal environment but receive benefits from the ecosystem. Plant species specifically adapted to subtropical and tropical coastal environments are widely known as "true mangroves" (Tomlinson 2016), and previous taxonomic studies have delineated two separate distributional regions based on true mangrove species distributions. One is the Indo-West Pacific region (IWP, often referred to as the Old World), which comprises about 57% of the global mangrove forest area, with 62 species, and the other is the Atlantic-East Pacific region (AEP, referred to as the New World), with only 12 species constituting 43% of global mangrove coverage (Spalding et al., 2010). Biogeographic barriers within and between those regions have been identified on the basis of archeology, biogeography, ecology, taxonomy, and genetics (Duke et al., 2002).

Locally, limited knowledge of spatial ecology and disregard for hydrological conditions of habitats has resulted in ineffective conservation policies in many areas (Van Loon et al., 2016). Previous review papers about global mangrove conservation efforts claim that site-specific designs to protect existing mangroves rather than generalized restoration methods may be the most effective approach (López-Portillo et al., 2017). However, there have been few studies on island mangroves, even though more than half of all mangroves are located in island systems; thus, a better understanding of island mangroves is critical. Moreover, while more than half of mangrove habitat occurs on islands in the IWP, both global species hotspots and degradation hotspots occur in the IWP. Thus, this chapter reviews how island mangroves may contribute to regional mangrove biogeography in the IWP.

The spatial scale of mangrove distribution networks, distributional patterns, and biogeographic contributions of islands differ depending on their locations. These are evaluated using the graph-theoretical method. The first objective was to identify subgroups

of mangrove sites and species in the IWP based on the species composition of each site, and the second goal was to determine the biogeographical roles of sites and species. To identify subgroups (modules hereafter) of mangroves, a simulated annealing algorithm was used to detect modules (Guimera and Amaral, 2005) in a bipartite network comprised of two types of nodes (site nodes and species nodes). Links are established between site nodes and species nodes based on species presence information at each mangrove site. Hence, a module comprises a cluster of closely linked nodes. The simulated annealing method of defining modules also provides a convenient framework for summarizing functions of sites and species in the network and assigning them to biogeographical roles (Economo et al., 2015). Two parameters define the biogeographical roles of sites and species. The first is a within-module degree "r", which indicates how well nodes are linked to other nodes within their modules relative to nodes in other modules. The second parameter is a between-module degree "r", which indicates how a node within its module is positioned relative to other modules (Figure 2.2, 2.3).

This method identifies how individual site and species nodes contribute to biogeographic networks both within modules and across the studied region. There are typically four biogeographical roles that can be assigned for each node in a network: (i) network hubs, possessing many local and many shared species across the region; (ii) module hubs, possessing many local species, but few regional species; (iii) connectors, possessing few local species, but many shared across the region; and (iv) peripherals, possessing few local and few regionally shared species (Figure 2.2). These roles help to interpret complex spatial patterns among distant mangroves and may help to determine which islands serve as stepping-stones and which are isolated.

Graph theory has been applied in many fields, including physics, neurosciences, mathematics, and social sciences (Watts 2004), and has been used to analyze complex ecological interactions (Gomez et al., 2010), such as landscape connectivity to design conservation plans (Saura and Rubio, 2010). Moreover, between 2000 and 2014, 42 publications conducted studies of human impacts on population connectivity in marine and freshwater systems using graph theory (Saunders et al., 2016). Its capacity to handle large, complex network topologies is also helpful in analyzing population connectivity and exploring conservation options for threatened nearshore environments (Treml et al., 2008; Watson et al., 2011). For example, Treml et al. (2008) applied graph-theory to investigate coral larval dispersal in the South Pacific islands. With this approach, nodes were set to different scales, such as habitat patches, populations, islands, or reef sites, and links were geographic distance, gene flow, and dispersal probabilities between every pair of nodes in a domain with weight difference representing strength of connectedness. Graph representation of population or habitat connectivity can reveal similarities across different systems and may suggest common strategies for conservation management (Saunders et al., 2016). Thus, these methods are suited for estimating seascape connectivity as a way to overcome the difficulty of obtaining empirical data (Engelhard et al., 2017) so as to design



Figure 2.1

Illustration of modules and roles. Yellow circles are sites, and each tree is a different species. Blue background partitioning represents modules. Links only connect sites with species. conservation plans for ecologically valuable organisms (Treml et al., 2008; Ospina-Alvarez et al., 2020). The biophysical model and graph-theoretic approach provide a more detailed and flexible framework for analyzing population connectivity in the marine environment and implementing practical marine protected areas (Treml et al., 2008).

Previously for mangrove research, graph-theoretical methods were used to study ecological networks of microbial communities in mangroves (Lin et al., 2019), benthic food webs in mangroves (Ray, 2008), mangrove social networks with aquacultures and coastal communities (Orchard et al., 2015), ecological connectivity among fragmented mangrove landscapes (d'Acampora et al., 2018), and ecological relations between freshwater input and floristic richness (Bunt et al., 1982). However, to our knowledge, this is one of a few studies of regional mangrove biogeography to which graph-theory has been applied. Identifying biogeographic patterns and roles assigned for each site and species will contribute to designing effective, long-term conservation plans. Particularly for mangroves, recent studies have shown that protecting healthy existing mangroves is more effective conservation than repairing or reforesting other areas (Saenger et al., 2019).





Site modularity roles diagram The x-axis shows the between-module (=regional) network, and the y-axis indicates within module (=local) networks of site nodes.

The algorithm used in this chapter has been used in metabolic (Guimera and Amaral, 2005) and ecological studies, including plant networks (Olesen et al., 2007; Dupont and Olesen, 2009; Gomez et al., 2010; Kougioumoutzis et al., 2014). It provides an approach free of a priori assumptions, which is better than classical pairwise interaction analyses for assessing interactions within a complex dataset (Kougioumoutzis et al., 2014). Biophysical connectivity data such as the dispersal model (Van der Stocken et al., 2019a) has been obtained regionally for mangroves, but not incorporated in the current study in order to use only empirical data to a coarse-grained, simplified description of the network among sites and modules. Identifying networks among islands will help delineate inter-connectedness from a biogeographic perspective (Whittaker et al., 2019). Current findings are expected to clarify the roles of specific islands in maintaining species biogeography.

2.1.1. Paleogeography of mangroves in the IWP

Since the simulated annealing method is based on shared species among sites, it is vital to consider biogeographic shifts at geological timescales, including differences in local species richness that arise from site-specific historical and biogeographic events

(Ricklefs and Latham, 1993). First, species richness may be strongly influenced by origins of mangrove distributions, which date back to the late Cretaceous. Fossil records of mangrove pollen show that mangrove species first appeared in non-marine environments about 60 million years ago (mya), shortly after flowering plants appeared (Duke, 1995). They then entered the intertidal environment along the coastline of the Tethys Sea (Ellison et al., 1999), outcompeting terrestrial plants by developing physiological mechanisms to remove salt and to be able to respire even when inundated (Ball, 1988). Thus, mangroves colonized unoccupied niches and minimized interspecific competition (Tomlinson, 2016).

Modern species distributions are almost entirely based on vicariance events (Ellison et al., 1999), including historical tectonic movements, and multiple sea-level changes due to glaciers, and climate shifts (Lo et al., 2014). According to fossil records, many modern mangrove taxa have persisted since the late Cretaceous, with Rhizophora, Pelliciera, and the Sonneratiaceae known from the early Eocene, at least 30 mya (Muller, 1981). Furthermore, the presence of mangrove genera in Tethyan and European deposits of the Eocene era indicates that the Tethyan region contained a suitable environment for mangrove habitat. The Tethys Sea closed 30–35 mva, establishing the IWP and AEP. After closure of the Tethys Sea, palynological and geological evidence suggests that most of the African and New World tropics were dry during the late Cretaceous. In contrast, Southeast Asia and Malaysia have been wet since the Cretaceous. Because a wet climate maintains a gradual transition in soil salinity, whereas dry areas induce high soil salinity (Hutchings and Saenger, 1987), it has been suggested that modern mangroves originated in the IWP, especially in southeast Asia. On the other hand, the AEP has fewer species. The Tethys Sea was subdivided into smaller oceans by the northward continental drift of India and Africa.





Species modularity roles diagram The x-axis shows the between-module (=regional) network, and the y-axis indicates within module (=local) networks of species nodes.

With regard to the vicariance events mentioned above, physical and environmental variables are assumed to affect distribution and propagule dispersal range. For example, dense forests limit access to open water, which limits propagule dispersal (Triest and Van der Stocken, 2021). In addition, salinity variations influence both morphology and types of mangroves that can become established and survive (Duke, 1992). While true mangrove species, including hybrids and subspecies, have complex biogeography, genetic methods have revealed population connectivity and genetic barriers over evolutionary time scales and trans-oceanic spatial scales (Triest, 2008). For example, using haplotype differentiation, it is clear that the American continent acts as a dispersal barrier

for *Rhizophora* species and South America for *Avicennia* species (Takayama et al., 2013; Mori et al., 2015).

We assume that vicariance events established initial regional distributions followed by influences from local ecological parameters, such that contemporary species compositions and ecological conditions in the IWP became site-specific. However, understanding of complex mangrove dispersal dynamics is far from complete. Assuming that species compositions of bioregions and sites reflect local environmental and physical conditions, network analysis may shed light on bioregions of mangroves.

2.1.2. Extant Mangroves in the Indo-West Pacific region

The IWP is the focus of this study, where more than 80% of mangrove species reside (Chapman, 1976; Hadac, 1976; Barth, 1982; Tomlinson, 2016; Duke, 1993). Species diversity is maximal in Southeast Asia, in an area known as the Coral Triangle, which has incomparable diversity of corals. These common diversity patterns among unrelated taxa indicate the importance of geophysical events (Duke 2017). In the IWP, 20 of 25 mangrove genera are common across the region, and the other five genera are restricted to specific areas: Aglaia and Brownlowia in south and southeast Asia, Camptostemon and Osbornia in southeast Asia and Australasia, and Diospyros limited to Australasia. Maximal species richness occurs along the shorelines of Makassar Strait between Borneo and Sulawesi in Indonesia (Saenger et al., 2019), supported by high rainfall, relatively low salinity, and establishment at least as early as the Holocene (Saenger et al., 2019). During sea-level changes in the late Pliocene and Pleistocene glacial intervals, this area maintained a moderately direct connection between the tropical Pacific and Indian oceans via Makassar Straight. Opening and closing of oceanic passages and fluctuating salinities resulted in bottlenecks and founder effects in mangrove populations in the region, inducing rapid speciation (Saenger et al., 2019).

Many mangrove species recolonized oceanic islands during the Holocene, and their present distribution is in part a result of successful trans-oceanic dispersal to those islands (Woodroffe and Grindrod, 1991). Mangrove species distributions show limitations of expansion for each species, while overlapping distributions extend differently depending on the species. For example, Lo et al. (2014) conducted an extensive genetic study combined with fossil records to unravel evolutionary lineages of Rhizophora species and their dispersal history. Distributions of *Rhizophora stylosa* and *Rhizophora mucronata* overlap in the coral triangle. However, R. stylosa does not extend as far westward as R. mucronata, despite their taxonomic and genetic similarities (Lo et al., 2014). Their data revealed at least three major transoceanic dispersals within the IWP, including Southeast Asia to Sri Lanka, Australia to the NW Pacific, and Australia to East Africa. Genetic associations among *R. apiculata* and *R. mucronata* in Southeast Asia and Sri Lanka suggest the dispersal of *Rhizophora* propagules from southeast Asian lineages to Sri Lanka across the Bay of Bengal. Based on species presence information, Duke (1972) delineated three sub-groups within the IWP: i) eastern Africa, ii) Indo-Malaysia, and iii) Australia. In this chapter, the regional taxonomic delineations were compared with the results of network modularity analysis.

2.2. Methods

2.2.1 Species and location data collection and organization

Mangrove plant species distributional data in the IWP were collected from the World Atlas of Mangrove (Spalding et al., 2010), Mangrove Reference Database, and Herbarium (Dahdouh-Guebas., 2021, Massó i Alemán et al., 2010), Plants of the World Online (POWO, 2021), and Poedjirahajoe et al. (2019). Species data include true mangrove species, which only grow in brackish water, non-true mangrove species, which grow in terrestrial areas, and mangrove subspecies. Data were compiled and organized into a presence-absence dataset (1, present; 0, absent) based on locations using Excel (Supplementary 2.1). Each site was provided with latitudinal and longitudinal information, which were retrieved from the databases and used as sampling locations. Google Map searches for location names were used when source datasets did not provide coordinates. A dataset was then created, based on three area resolutions (N-resolution, G-resolution, and R-resolution). The coarsest resolution is N-resolution delineated by political regions or countries (66 site nodes and 72 species nodes), which provided enough species counts per location for the analyses. N-resolution was for a preliminary test of the method since each site was politically partitioned. The finest resolution is *R*-resolution, including 224 nodes for mangrove sites and 73 species nodes. Site nodes included every site record from our database, discretely separating island sites from continental coastal mangroves. Many sites have few species per site (< 3). To compensate for small species counts to obtain a sufficient species count per site for the analysis, those island sites in *R*-resolution with low species counts (< 3) were grouped with the nearest island sites until each group had at least 3 species (Figure 2.4). G-resolution included 102 site nodes and 73 species nodes. Those three resolutions were formatted into a network dataset discarding all missing data using R. A network consists of species nodes and site nodes, and network connectivity was based on shared species occurrences between sites (Carstensen and Olesen, 2009; Carstensen et al., 2012). In this study, we excluded data that mangrove species were introduced as far as our source provided the information. As mangrove species are sometimes considered invasive species harmful to the local ecosystem, (i.e. Manko Estuary in Okinawa, as well as along the Florida coast), exotic species must be assessed thoroughly based on how they are adopted by indigenous ecosystems. It would be out of our scope this time to assess how introduced species are serving the local and regional populations and ecosystems.



Figure 2.4 Study sites based on *G*-resolution. Filled circles on the map show every raw site data points (*R*-resolution). Polygons indicate grouping, and the names of all groups are listed below the map. Every site with low (< 3) species counts was grouped with their nearest sites to obtain species counts >3 per site (group).

2.2.2. Modularity analysis

Nodes of the bipartite network (sites and species) were assigned to modules using *rnetcarto* in R (Dulcimer and Stouffeer 2022) based on the algorithm described in Guimerà and Amaral (2005a;b). Modules were identified by partitioning nodes using the simulated annealing method to obtain the optimal delineation of modules of a network based on direct maximization of modularity (M). The simulated annealing method maximized within-module links while minimizing between-module links to obtain the most discrete partitions (Guimera and Amaral, 2005). This algorithm assigned each node to a module, in which all site and species nodes have most of their links inside their module with an accuracy of 90% (Guimerà and Amaral, 2005b). Thus, some nodes may change their module affinity if running a simulated annealing analysis several times. Maximization of modularity (M) is

$$M \equiv \sum_{s=0}^{N_{M}} \left[\frac{l_{s}}{L} - \left(\frac{d_{s}}{2L} \right)^{2} \right]$$
(1)

where N_M is the number of modules, L is the number of links in the network, l_s is the number of links between modules, and d_s is the sum of the degrees of nodes in the module s (Guimera and Amaral, 2005). M is a measure between 0 and 1 to which the network is organized into clearly delimited modules. As M approaches 1, modules become more distinct, and as it approaches 0, the network becomes more homogeneous. For species, the analysis delineates species modules based on the distribution of occurrences in a network (Carstensen et al., 2013). This analysis was conducted for each R, G, and N data resolution.

2.2.3. Biogeographic roles

Topological roles of nodes, both for species and sites, were calculated based on the following two parameters. First, between-module degree (r), is given by the formula:

$$r_i = 1 - \sum_{s=u1}^{N_M} \left(\frac{\kappa_{is}}{\kappa_i}\right)^2 \tag{2}$$

where κ_{is} is the number of links of node *i* to nodes in module *s*, which represents non-local modules, and κ_i is the total degree of node *i*. If the between-module degree of a node is close to one, that node is uniformly distributed among all modules. A between-module degree of zero would indicate that the node is wholly confined to a single module (Guimerà and Amaral, 2005).

The second parameter is the within-module degree (l), which represents the connectivity of nodes within modules. It is defined as

$$l_i = \frac{\kappa_i - \overline{\kappa_s}}{SD\kappa_s} \tag{3}$$

in which κ_i is the number of links of node *i* to other nodes of the same module *s*, $\overline{\kappa_s}$ and SD_{κ_s} are the mean and standard deviation of values within the module *s*, respectively. Within-module degree (*l*) is also known as a Z-score, i.e., standard score, which ranges between -3 and +3, and which represents the distance and position of a data point from the mean value within its module. When "*l*" is negative, the data point is below the mean value in its module. Within-module degree of below 2.5 indicates that the data point is

considered as a non-hub node with a limited number of within-module links, and a node would be a hub with a number of links significantly higher than average if above 2.5. Hub and non-hub nodes are further categorized into finer biogeographic roles based on their between-module degree (r).

Mathematically, when a non-hub node has no between-module degree (r = 0), it is an *ultra-peripheral role* (Figure 2.2, 2.3). When a hub node has at least 60% of its links within its module, then for a modularity degree of < 4, a within-module degree would be <0.625, which assigns a *peripheral role*. Finally, when a non-hub node, has half or fewer of its links within the module, the node is assigned as a non-hub connector (0.625 < l <0.8). Similarly, when a hub node has at least half of its links within the module (0.625 < l), it is considered a *module-hub role*, and if fewer than half of its links within the module (l >0.625), it is considered *network-hub role* (Figure 2.2, 2.3). These are also validated with real-world networks to confirm the thresholds (Guimerà and Amaral, 2005). Species with high between-module degree (r) are considered more ecologically general and widespread, and sites with high within-module degree (l) include a mix of taxa with different ecological and biogeographic characteristics. Those values were obtained for all three data resolutions (R, G, N). Visualization of output data was also done in R.

2.3. Results

2.3.1. Site modules and roles

The network of locations and species in the IWP was significant, but not clearly defined. Each modularity was M = 0.187, M = 0.187, and M = 0.281 for R-, G-, and Nresolutions, respectively. All resolutions exhibited four modules (R: RA~RD, G: GA~GD, N: NA~ND). Geographic patterns of modules were generally similar among resolutions. Modules RD, GD, and ND comprised the greatest numbers of sites (Table 2.1) and cover East Africa and along the edges of the IWP with the lowest average species count (Figure 2.5). Modules RC, GC, and NC clustered in Northern Australia and the Coral Triangle, consisting of Indonesia, Malaysia, Papua New Guinea, the Philippines, the Solomon Islands, and Timor-Leste (Figure 2.5). They included a higher proportion of continental mangroves compared to other modules (Table 2.1). Modules RB, GB, and NB run along the India-Papua New Guinea line in the central IWP and contain the fewest sites and the smallest proportions of islands, but maximum and average species counts per site were higher compared to other modules (Figure 2.5). Modules RA, GA, and NA are distributed on the eastern side of the IWP, but their clustering patterns differed among resolutions and had more geographic outliers than other modules at each resolution (Figure 2.5, Figure 2.1). Their mean species counts per site were also small compared to other modules, but represented the highest proportion of islands in the module (Table 2.1).

Island-continental evaluations were highlighted from the results of *R*- and *G*-resolutions. In order to examine biogeographical roles of individual islands and metacommunities, islands were evaluated individually at *R-resolution*, whereas some islands were grouped in *G-resolution*. In all modules, more than 60% of sites are islands in both resolutions. Modules RD, GD, and ND appeared on the edges of the IWP resulting in about 70% island sites. These modules had the lowest proportion of islands, and islands in these modules are mainly located furthest from continental coastlines (Seychelles, Mauritius, Maldives, Fiji, etc.). Furthermore, species counts per site were lower than other modules (Table 2.1). In contrast, modules RB, GB, and NB had the highest average species counts per site among modules while the proportion of island sites was the lowest. Modules RA, GA, and NA comprised mostly western Pacific islands at all resolutions.

Of the four roles mentioned in the Introduction, module hubs and network hubs were consistently absent at all resolutions (between-module degree (r) < 0.75 and (l) < 1) (Figure 2.6). Ultra-peripheral sites (UP) were found in East Africa and the Middle East (Figure 2.7), within which the Sevchelles, Djibouti, Yemen, Eritrea, Sudan were common to all resolutions, and Egypt, Iran, Saudi Arabia, Nauru, Oman, Qatar, and the United Arab Emirates were common to R- and N- resolutions (Figure 2.6). UP appeared as the least common role at G-resolution (Figure 2.8). The proportion of islands in UP and peripherals varied among resolutions; 90% and 43% in *R*- and *G*- resolutions, respectively. On the other hand, connectors were similarly found in all modules (Figure 2.8). The connector was identified as the second most common role following UP in *R*-resolution, but as the most common role in G-resolution (Table 2.1). More than half of all site nodes in Gresolution were assigned to connector roles, of which 75% were island sites (Table 2.1). Most connector nodes are clustered in areas east of India and are extremely scarce in East Africa for all resolutions (Figure 2.7). On the other hand, the peripheral role was found in all modules distributed throughout the IWP. The proportion of island sites with peripheral roles exceeded 80% for both *R*- and *G*-resolutions (Table 2.1).

Ultra-peripheral sites appeared to be the least common at *G*-resolution. The proportion of islands in UP varied between the *R*- and *G*-resolutions, at 90% and 33%, respectively, due to the absence of UP in three of four modules at *G*-resolution. On the other hand, the island proportions in connectors and peripherals did not vary between resolutions (Figure 2.8). The connector was identified as the second most common module role following UP in *R*-resolution. In contrast, it was the most common role at *G*-resolution due to the drastic decline of UP sites. More than half of all site nodes at *G*-resolution were assigned to the connector role, of which 73% were island sites (Table 2.1).

Analyses			max	ava	% ofModularity role						
resolution	Site	Module	species	species	site no.	islands	Ultra			Module	Network
(modularity)	count		no./site	no./site	/module	/module	peripheral	Peripheral	Connector	Hub	Hub
		RA	29	5	62	86.9	19	23	19	0	0
R	223	RB	44	21	35	77.8	12	1	23	0	0
<i>(M =</i> 0.187)		RC	43	13	37	83.8	9	12	17	0	0
		RD	26	4	89	77.5	49	27	13	0	0
	island: 184				Total site counts		89	63	72	0	0
	cont: 39				% o	f islands	89.9	84.1	72.2	0	0
		GA	27	13	21	95.2	0	6	15	0	0
G <i>(M =</i> 0.187)	102	GB	44	31	21	61.9	0	2	19	0	0
		GC	48	26	18	72.2	0	2	16	0	0
		GD	29	9	42	73.8	6	25	10	0	0
	island: 75				Total site counts		6	35	60	0	0
	cont: 39				% of islands		33.3	80.0	73.3	0	0
		NA	25	8	20	-	3	9	8	0	0
N (M = 0.218)	66	NB	45	33	6	-	0	0	6	0	0
		NC	28	7	29	-	11	12	6	0	0
		ND	42	30	11	-	0	2	9	0	0
					Total site counts		14	23	29	0	0

Table 2.1 For each resolution (*R*, *G*, *N*), four modules were detected. In each module for all resolutions, max and average species counts per site, and site counts in each module and proportion of island sites in each module was shown. Total site numbers are also shown, (is): number of island sites, (cnt): number of continental sites. No source sites (hubs) were detected in the IWP mangrove biogeography. The majority were stepping-stone sites, but island-wide assessment shows a high number (one-third) of ultra-peripheral sites, which indicates significant isolation.



Figure 2.5 Modules were overlaid on the IWP map, showing that the delineation of modules was mostly consistent among all three resolutions, suggesting a meta-community at archipelago scale and regional scale. In contrast, the pink module is the most variable, suggesting islands that are strongly peripheral in terms of species composition. Colors are applied to each module. A) *R*-resolution, **B**) *G*-resolution, **C**) *N*-resolution.

2.3.2. Species modules and biogeographical roles

Four species modules were detected at all resolutions: ra~rd, ga~gd, and na~nd (Table 2.2). Similarity in species compositions of modules was found among the three resolutions with >70% shared species among modules, which include 1) ra-gb-na, 2) rbgd-nd, 3) rc-ga-nb, and 4) rd-gc-nc (Figure 2.9). While the modularity hub represents species that appear more locally than regionally, consistently, no species was assigned to the module hub among resolutions. In contrast, a few species were consistently assigned to the network hub among resolutions: Avicennia marina among all resolutions, Rhizophora *mucronata* in *R*- and *G*-resolutions, and *Bruguiera gymnorrhiza* in *R*- and *N*-resolutions (Figure 2.8). The network hub represents higher regional species occurrence than local. In addition to the species in the network hub mentioned above, 8 more species (A. marina subsp. marina, Ceriops tagal, Excoecaria agallocha,, Heritiera littoralis, Lumnitzera littorea, Pemphis acidula, R. apiculata, and Sonneratia alba) were assigned to the network hub just in *R*-resolution (Figure 2.8). Ten and more species were assigned to the ultraperipheral role, locally restricted species, in all analyses; Camptostemon schultzii, Camptostemon philippinenss, Heritiera fomes, Avicennia integra, Sonneratia apetala, and Sonneratia × hainanensis were shared among all resolutions. Generally, the majority of species were assigned to peripheral and connector roles.

2.4. Discussion

Maintaining recruitment from distant populations is essential to facilitate genetic diversity and to avoid harmful effects of genetic monomorphism (Lowe and Allendorf, 2010). The frequency of recruitment that is sufficient to obtain enough genetic diversity is species-specific, and how recruitment is achieved can also be site-specific. While global distribution patterns alone cannot explain how the hydrochory of mangrove species contributes to contemporary habitat shifts and zonation within populations (Lowe and Allendorf, 2010), it is clear that present species distribution is a product of multidimensional interactions among ecological, environmental, and physical processes. Studies of population connectivity among islands and within archipelagos are scarce compared to those of continental mangrove sites.

To shed light on island roles in mangrove population connectivity, in this chapter, the simulated annealing approach enabled the depiction of mangrove bioregions in the IWP and identified biogeographic roles of both sites and species using species presence data. The network of links among sites was successfully optimized based on the presence of shared species, and the IWP region was partitioned into four optimally distinct modules with modularity < 0.2, which may represent high similarity among modules with respect to half of the species in the region widely spreading across modules (Figure 2.10). Regardless of data resolution (N-, G-, R-), the number and distribution of modules and the modularity were consistent, which suggests the robustness of the analysis and the dataset. It is important to note that this method ignores all processes that shape mangrove populations and establish population connectivity. It is the coarse and simplified description of networks, identifying key sites and species represented by the number of links between nodes.



Figure 2.6 Site roles showed the absence of hubs. This indicates that species exchanges are not frequent enough to establish site connectivity. Connectors and Peripherals are major roles, and African sites tend to be UP consisting mainly of endemic species. *R*-resolution (A) and *G*-resolution (B), *N*-resolution (C); circles show site nodes, and colors indicate modules of the site. Between-module participation coefficient is shown on the x-axis, and the within-module connectivity coefficient is shown on the y-axis.

From a conservation point of view, the least linked sites (ultra-peripheral sites) that contain the fewest linked species (ultra-peripheral species) must be considered a priority for conservation, because those sites are most isolated in the site-species network. In R-resolution, those sites included Keriri Is., Moa Is., and Marchinbar Is. in Australia, Parama Is. in Papua New Guinea, and Trangan Is. in India. On the other hand, sites with the highest within-module degree should also be considered a priority for conservation because those sites are the key to establishing a network that shapes local bioregions. Those sites include Thailand (India-Sunda module), NT Australia (PHL-AUS module), New Caledonia (IWP.edge module), and Hainan Is. (West-Pacific module). All modules consist of >70% island sites, which suggests that islands are abundant in every bioregion, and maintaining species compositions on those area-limited distant mangroves on islands is important to mangrove biogeography. The spatial range of recruitment from distant islands is identified based on those four modules consistently at all resolutions (Table 2.1). As discussed below, the borders of these modules correspond well to previous studies on population genetic connectivity and contemporary dispersal factors, including geographic position, island characteristics, propagule dispersal characteristics, and area sizes.

One of the salient biogeographic characteristics is that mangrove biogeography in the IWP consists only of connectors, peripherals, and ultra-peripherals. There are no module hubs or network hubs assigned to any site nodes. Although the eastern IWP (Indonesia and Malaysia) are considered the most species-rich sites, the network analysis did not identify them as hubs. Instead, they were assigned as peripherals or connectors. Connectors are considered stepping-stones, receiving species from sites outside their modules (Carstensen et al., 2012). Peripherals, however, are linked with sites primarily within their module. The higher number of connector sites indicates that mangrove distribution in the IWP is based on a network of sites linked via geological events or dispersal, and the latter may have fewer impacts. Moreover, the absence of hubs and relatively homogeneous modules may suggest that widely distributed stepping-stone sites are crucial for species distributions in the IWP. It is important to note that in the current study, we did not assess whether those stepping stones are biogeographic or dispersal. It is important to further assess this with more site-specific analyses among islands, which is addressed in Chapter 3.

Moreover, the absence of hubs indicates that links between connectors and peripherals form a complex network of mangrove sites that facilitates an inter-module network within the IWP, instead of having a designated site or meta-community as a source. This may correspond to mangrove dispersal characteristics defined by parameters such as propagule floating period, conservative fecundity, salt tolerance, and site-specific factors such as micro-climate, tidal inundation, oceanography, and wind effects. Each module has unique modular characteristics, as described below.

2.4.1. The *IWP.edge* module (*blue*): pattern and roles

Each resolution (R, G, N) showed a module that extended along the regional edge, dominating east African continental sites and the western Indian Ocean (Figure 2.5 - 2.7). East Africa and the Middle East have no reported endemic species, and species compositions are a subset of other areas of the IWP (Duke et al., 1998). This module is the most spatially expanded module, indicating potential transoceanic dispersal, or the effects of geological events with minor contemporary dispersal.

Site nodes in Eastern South Africa, the Red Sea, and the Arabian sea are assigned ultra-peripheral (UP) or peripheral biogeographic roles, except for Madagascar+Europa (in R and G resolutions), which is assigned as a connector (Figure 2.2, 2.7), indicating limited

local and between-module species counts per site. Species roles in those UP sites are often connectors or hub species (Table 2.2; res. R and G), that are cross-regionally distributed species. Two regionally distributed species, Avicennia marina and Rhizophora mucronata, were particularly common in all modules, regardless of resolution. Both R. mucronata and A. marina were found in the network hub or connector role (depending on the analysis resolution), which indicates higher links in its module as well as a higher number of intermodule participation (r > 0.62) (Figure 2.9). According to previous studies, these two species exhibit a different form of colonization suggested by differences in genetic connectivity patterns. A. marina, a widely distributed species in the IWP, showed a high number of unique alleles in South Africa, the United Arab Emirates, India, and Malaysia-Australasia, indicating little genetic connectivity among those areas (Maguire et al., 2000). R. mucronata, of the western Indo-Pacific area, including Madagascar and the Seychelles, along with coastal mangroves, also showed localized heterogeneity in genetic structures (Triest et al., 2021), while the Kenvan population nested in the Australian population (Lo et al., 2014), which suggests connectivity of these two distant areas in the module. Moreover, R. mucronata and R. stvlosa in the SE Asia clade were grouped with the Pacific Islands clade (Duke et al., 2002). Furthermore, *B. gymnorrhiza* is also the most widely distributed longitudinally. However, as *B.gymnorrhiza* was found to be either connector or network hub, the species may not be as common within its module as A. marina and R. *mucronata* are in theirs.

Propagule dispersal has a vital role in colonization of new environments; thus, dispersal ability strongly influences the structure and distribution of a species (Pil et al., 2011). One well-known difference between *A. marina* and *R. mucronata* is their dispersal ability. Propagules of *Rhizophora* are generally buoyant for several months in seawater (Rabinowitz, 1978a), and viable up to a year (Van der Stocken et al., 2019). Propagules of *A. marina*, on the other hand, sink within a few days, but the species propagules could be viable for several months if they do not touch sediment (Clarke 1993; Triest et al., 2021a). They are often found within a few km, although observations of propagule beaching have shown that they can travel over 50 km (Clarke 1993).

A recent study of global-scale mangrove dispersal, using numerical ocean modeling, demonstrated the potential for direct connectivity between Java Transitional and Western Indian Ocean coastal areas via the Indian South Equatorial Current, if the propagule floating period exceeds six months (Van der Stocken et al., 2019b). Moreover, the western Indian Ocean, the Red Sea, and the Somali/Arabian sea are well connected by propagules having a floating period >1 month. However, when the floating period is <1 month, the study showed a drastic decline in dispersal potential for this range. This further supports the wider-range in genetic connectivity of *R. mucronata* and more localized connectivity of *A. marina* between eastern Africa and the western Indian Ocean.

Islands in the mid-Indian Ocean and east African sites are either ultra-peripheral or peripheral sites (Figure 2.8), suggesting that those islands are in inter-module isolation (Carstensen et al., 2012; Carstensen et al., 2013), meaning that no species exchange with sites in other modules leads to successful establishment. Islands with those roles tend to be limited in area with lower habitat diversity, and they tend to be geographically isolated (Torre et al., 2019). This may lead to bottlenecks and vulnerability to environmental changes, including sea-level rise and climate change. Peripheral and ultra-peripheral sites of this area correlate well with earlier genetic studies in this area. They found genetically impoverished populations and suggested that these are caused by the rarity of long-distance dispersal, followed by inbreeding and dispersal limitations due to coastal geomorphology and availability of suitable habitats (De Ryck et al., 2016).



Figure 2.7 Map of Biogeographical roles. Regardless of analysis resolution, peripherals (P) and connectors (C) were the majority, and islands and sites in eastern Africa were ultra-peripherals (UP), while hubs were completely absent from the IWP region. The colors indicate the four modules each role belongs to. A) *R*-resolution, (B) *G*-resolution, C) *N*-resolution. Each color represents modules that share similar geographical patterns.

Madagascar, on the other hand, was a connector, corresponding to findings related to *R. mucronata* in the western IWP. Triest et al. (2021b) found that this species colonized the region recently, compared to those in the eastern IWP, and showed transboundary connectivity despite the distance between sites, via ocean currents between continental sites and offshore islands in the region. Because Madagascar is a larger island compared to ultra-peripheral and peripheral islands in the same module, such as the Seychelles and Mauritius, it may act as a connector site. Surrounded by peripheral and ultra-peripheral sites in the western IWP, Madagascar may be critical as a stepping stone for transoceanic dispersal on the regional edge.



Figure 2.8. Site counts for Ultra-peripherals [up] and peripherals[p] varied the most among modules (blue, green, pink, purple), as well as between resolutions (G and R). Only *G*-resolution connectors [c]consisted of a higher proportion of continental sites than islands.

Moreover, connector sites, such as some islands in the Western Pacific (Norfolk Is., Fiji, Tuvalu, Vanuatu, Marianas) and a few sites along continental coastlines east of Pakistan (Figure 2.8), may also be transboundary stepping-stones. West India, the Maldives, and Pakistan may be stepping-stones between the West Indian Ocean and other IWP sites, as suggested by earlier studies. An oceanographic estimate for mangrove dispersal demonstrated a higher frequency of dispersal in those areas (Van der Stocken et al., 2019b). A genetic study showed potential reciprocal gene exchange via the Arabian Sea and Gulf of Bengal (Duke et al., 2002) facilitated by the seasonally reversing monsoon currents south of India and Sri Lanka and the eastern and central Arabian Sea (Tomizawa et al., 2017).

Overall module attributes, including low hub species counts, were found at many sites in *the IWP.edge* module. Most individual sites in the module were ultra-peripherals or peripherals. In contrast, the proportion of ultra-peripheral sites drastically decreased in the module when islands were grouped. Thus, we suggest that individual islands have limited capability to recruit new species, and they are fragmented in the island system. This further indicates that losing more island or small mangrove populations in the module may create additional barriers to species movement and dispersal, as suggested by Curnick et al. (2019). To further understand the spatiotemporal network of mangroves among neighboring islands in the module, more local-scale population connectivity studies are

needed.

Resolution	Module	Spc.Cnt. /module	Modularity role					
			UP	Р	С	MHub	NHub	
R	W.Pacific	11	1	3	1	0	6	
	India-Sunda	27	4	15	8	0	0	
	PHL-AUS	22	4	10	8	0	0	
	IWP.edge	13	1	3	4	0	5	
	Total	73	10	31	21	0	11	
G	W.Pacific	20	3	11	6	0	0	
	India-Sunda	13	0	2	9	0	2	
	PHL-AUS	14	2	3	9	0	0	
	IWP.edge	26	5	11	10	0	0	
	Total	73	10	27	34	0	2	
N	W.Pacific	11	4	0	6	0	1	
	India-Sunda	24	7	13	4	0	0	
	PHL-AUS	10	0	2	7	0	1	
	IWP.edge	27	5	15	7	0	0	
	Total	72	16	30	24	0	2	

Table 2.2 Species modularity roles are listed. Four modules were found in all resolutions. Module hubs (MHub) is absent from the IWP, and species of Network Hub (NHub) are widely distributed species in the IWP. Peripherals (P) and connectors (C) are shared about one-third of species. Ultraperipherals (UP) are about the same count among resolutions.

2.4.2. The East India-Sunda (green) module: patterns and roles

Modules RB, GB, and NB, the East India-Sunda (green) module, stretch from East India to the western Coral Triangle, including northern Australia (Figure 2.5). This module contains the fewest sites and the largest proportion of islands, but average species counts per site were higher than in other modules. The high species richness of this area is well known not only for mangroves, but also for other tropical coastal species. Moreover, this module and the Philippines-Northern Australia (purple) module both had a lower proportion of UP sites, despite the >60% island ratio in the modules. In contrast, connector sites were dominant in this module, which suggests that stepping-stone sites facilitating species exchange between modules may support species richness. This pattern was consistent with estimated potential southeastward dispersal (Van der Stocken et al., 2019b) from the Bay of Bengal to the Eastern Coral Triangle (Papua New Guinea and the Solomon Islands), which reside in both green and purple modules, and also down to Western Australia, which belongs in the *purple* module. Moreover, from the Nansei Islands in Japan and Taiwan, potential dispersal reached the northern Philippines, the green module, to support a connector role. Estimated dispersal between modules was high, especially from the western Coral Triangle to the eastern Coral Triangle, the blue and West Pacific (pink) modules.

Islands in the eastern Coral Triangle that were ultra-peripheral at *R*-resolution were detected as connectors at *G*-resolution (Figure 2.8). This may indicate that the species diversity of those smaller islands is limited due to their reduced areas, but species diversity is conserved. Considering that this module was relatively homogeneous, the results suggest that between-module species exchange may be more active in this area. Still, in the western Coral Triangle, a clear module boundary was observed with the *purple* module, which compared well with previous findings.



Figure 2.9 Species modularity roles showed the absence of Module Hub, and that many are either peripherals or connectors. The network patterns of species nodes are consistent throughout resolutions. *R*-resolution(A),*G*-resolution (B), and *N*-resolution (C); circles show species nodes, and colors indicate their modules. Module participation coefficient is shown on the x-axis, and the within-module connectivity coefficient is shown on the y-axis.

For example, Yahya et al. (2014) showed that genetic differentiation of *R. appiculata* among Sunda islands in Indonesia was higher than of populations along the coastline outside the archipelago in northern Sumatra (Fst >0.381). They also suggested that local hydrodynamics influence connectivity among populations in the area. Another genetic study concluded that the genetic break among populations of *R. apiculata* in the South China Sea (including the eastern side of the Philippines) and Australasia (including West Papua and Indonesia) support Wallace's Line (Guo et al., 2016). Carstensen et al. (2012) found that biogeographic modules of terrestrial breeding birds (excluding seabirds and non-breeding migratory species) in Indonesia also reflected Wallace's Line.



Figure 2.10 Bipartite network of R-resolution with site nodes contracted by module group, connected by species nodes. Node colors represent module groups, and edge colors represent module of site node linked to species nodes. Species nodes are identified by numbers, indicated in Figure 2.9A. More than half of the species in the IWP are shared among all modules. IWP.edge module has no indicative species.

For continental mangrove sites, connector sites were consistently found at all resolutions (Figure 2.7). Bangladesh, Cambodia, East India, Myanmar, Thailand, and Vietnam are connectors, serving as regional stepping-stones (Torre et al., 2019). They may facilitate broader dispersal since along-coast dispersal was the dominant transport in many areas (Van der Stocken et al., 2019b; Triest et al., 2021b). Continental mangroves in East India, for example, are geomorphologically different from those of west India. While none of the species on the west coast are unique, several species, such as *Scyphiphora hydrophylacea, Acrostichum speciosum, Aegialitis rotundifolia, Aglaia cucullata,* and *Heritiera fomes*, etc., are restricted to the east coast of India. In this case, geomorphological differences may affect module partitions between west and east India (*blue* and *green*, respectively), in which river deltas are responsible for the greater species richness on the east coast (Saenger et al., 2019).

2.4.3. The Philippines-Northern Australia (purple) module: pattern and roles

Australia, Indonesia, the Philippines, and Papua New Guinea were mainly clustered in the *Philippines-Northern Australia (purple)* module (module RC, GC, and NC). Australian sites serve as connectors, and potential dispersal was reported from the Sunda Shelf and the Northeast Australian shelf (Van der Stocken et al., 2019b), reflected in the current study by inter-module links between the *green* and *purple* modules, and a high number of connectors in both modules.

Mangrove species distribution and diversity in the IWP region have been influenced evolutionarily by movements of Gondwanan southern land mass fragments, including Africa, India, and Australia, which migrated dramatically northward to join with Asia (Duke, 2017). The collision of the Australian and Asian plates 20 mya, resulted in 21 common mangrove genera (Duke et al., 2002). The biogeographic distribution barrier of *Lumnitzera littorea*, a non-viviparous mangrove species, was also detected, particularly along Huxley's Line (Guo et al., 2021), which runs through the Lombok Strait in the south and northward between Sulawesi and Borneo, stretching between the Palawan Islands and the rest of the Philippines (Simpson, 1977). Both *L. littorea* and *R. apiculata* demonstrated higher between-module degree (*r*) (Figure 2.9), indicating that the *purple* and *green* modules also support Huxley's Line with many connector sites through *L. littorea* and *R. apiculata*.

This eastward dispersal appears more plausible than westward migration (Van Welzen et al., 2011), because those islands in this module east of Huxley's Line have never formed a single land mass or been connected to the Sunda or Sahul shelves (O'Connor et al., 2017). This further emphasizes that in this region it is critical to identify stepping-stones to avoid amplification of area loss to regional loss.

2.4.4. The West Pacific (pink) module: pattern and roles

The West Pacific (pink) module (Figure 2.5) in the western Pacific and southern China, including Hainan Island, demonstrated more variability among resolutions and identified geographical outliers at various resolutions (Figure 2.5). At G-resolution with low species counts, which increased minimum species counts per site, compared to Rresolution, the proportion of ultra-peripherals and increased connectors in the pink module was drastically reduced (Figure 2.8). However, modularity (M = 0.187) was the same at Rand G-resolutions. This suggests that the species composition of each site varied more among resolutions due to the higher proportion of islands in this module (Table 2.1).

In contrast, species richness of sites in this module was generally low (Table 2.1). Two factors could explain this, the distance from other mangrove habitats in the IWP and the small sizes of the islands. For example, a much greater eastward extent of *Rhizophora*
than *Avicennia* across the Western Pacific was suggested because propagules of *Rhizophora* have considerable longevity and buoyancy at sea of over a few months, while those of *Avicennia* are viable for only a few weeks (Rabinowitz, 1978b; Duke et al., 2002). *Rhizophora apiculata* and *R. stylosa* were found at 14 and 12 grouped sites (*G*-resolution), respectively. In comparison, *Avicennia alba* and *A. marina* were located at only 5 and 6 grouped sites, respectively (*G*-resolution), consistent with the argument that dispersal ability limits westerly dispersal (Osland et al., 2017). This module had a higher proportion of islands with lower species richness, regardless of resolution (Table 2.1). This was explained by earlier studies of islands or atolls (Woodroffe, 1987).

Although propagule dispersal ability may filter out species that could reach the western Pacific islands, more than half the grouped sites were connectors, whereas 95% of the sites in the module were islands. Consistently for this module, most island habitats are stepping-stones to other modules, primarily to western Australia and New Zealand, as well as to the northwest Pacific and the coral triangle. A previous numerical model supports pathways of stepping-stone dispersal identified in the current results and a 1-month floating period allows particle exchange with western Australia and the western Coral Triangle, while an extended 6-month floating duration allows further easterly dispersal from the southern part of the *pink* module and further northerly dispersal from the northern part (Van der Stocken et al., 2019b).

Although southern China is connected biologically with Malaysia and the coral triangle, it is separated from the *green* and *blue* modules. The unexpectedly greater separation of biota in the Indian Ocean and the South China Sea has been mentioned previously. Duke (2017) suggested that partial submergence of the ancient Sunda Peninsula, which now forms the Indonesian Archipelago, may be the cause of the isolation and that the submergence event was the result of the massive collision between the Australian and Asian land masses (Duke 2017). Hence, geological events seem to have had a greater effect on species compositions in this area than dispersal.

2.5. Chapter Conclusion

Biogeographic patterns of island mangroves have been understudied compared to species-specific genetic population connectivity. The simulated annealing approach revealed species network patterns of mangroves at regional scale, and more importantly, identified island biogeographic roles in regional species distributions, showing that mangroves in the IWP are linked in a network largely sustained by stepping stone sites. Areas with higher species richness showed their roles as regional stepping stones, and areas further away from the species hotspot triangle tended to be local stepping stones.

While the simulated annealing method does not provide spatiotemporal information about population connectivity that constructs biogeographic patterns, it added compelling results to previous studies on mangrove biogeography. Of four modules defined in the IWP, two modules in the species hotspot triangle aligned with Wallace's and Huxley's lines. Those biogeographical lines were also highlighted in previous population genetic studies on several species that in the current study were found to perform connector and network-hub roles. On the contrary, the other two modules showed meager species richness. Their module boundaries aligned with previous studies on the population genetic disconnect shown among widely distributed species, and with species dispersal abilities and oceanographical effects.

In this chapter, geographic, biological, and physical dispersal parameters were reflected in species composition, which affected the delineation of biogeographical

modules. We identified critical sites for conservation based on biogeographic roles as stepping stones and as isolated sinks. Overall, the biogeographic network of mangrove sites consists of more inter-module linkages than intra-module linkages. Additionally, we found that non-continental sites include all connectors, peripherals, and ultra-peripherals. These imply a complex network of mangrove sites even within each module and that the effects of historical events rather than contemporary dispersal may determine the biogeographic roles of modules in the region. Furthermore, effects of local habitat loss may not be immediately reflected in species loss due to the low modularity. Since mangrove degradation has become a more regional concern, the current findings can be used to understand island membership in the meta-community.

Chapter Three

Island Roles evaluated by genetics and physical oceanography

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3.1. Introduction

Based on results from Chapter Two, islands with mangrove populations are predominantly stepping stones that facilitate species exchange between modules. Biogeographicly, many islands act as ultra-peripherals, and many island groups act as connector and peripheral sites, indicating intra- and inter-module species exchanges. Thus, the need for site-specific conservation plans at archipelago/regional scale is apparent. However, the method does not distinguish contemporary from historical dispersal; thus, we posed the following questions. What is the spatiotemporal scale (range limits and frequencies) of successful propagule dispersal within and between modules? Although nearly half of the mangrove sites in the IWP are connectors that have served as stepping stones, are they currently doing so, or are these historical remnants with little to no contemporary exchange?

The possibility of long-distance dispersal (LDD), especially trans-oceanic LDD, was examined with several methods. Genetic methods have been used to evaluate how closely related mangroves populations are. For example, a close genetic relationship of *Avicennia germinans* in the AEP between populations from West Africa and South America was detected as evidence for LDD (Nettel and Dodd, 2007). As another example, *R. stylosa*'s historical genetic lineages suggest an association of habitats on Iriomote (southern Ryukyu Archipelago of Japan) and Taiwan with Australian lineages (Lo et al., 2014). After those islands were established during the Miocene, mangrove distribution moved northward following clockwise ocean circulation from the Pacific islands. Other plant species also suggest the possibility of LDD (Lo et al., 2014).

Genetic methods have been useful not only to support transoceanic connectivity, but have also helped to identify bioregions, indicating genetic discontinuities among distant populations (Takayama et al., 2013, Lo et al., 2014, Dodd et al., 2002). Spatial patterns of genetic discontinuity have been compared with ocean currents, prevailing winds, landscapes, and seascapes to understand mechanisms of dispersal. For example, the Central American Isthmus was suggested as a land barrier for dispersal of *Rhizophora mangle* and *Rhizophora racemosa* (Takayama et al., 2013), as was the Mexican coast for *Avicenna germinans* and *Rhizophora mangle* (Sandoval-Castro et al., 2012). Other studies have shown that mangrove connectivity is related to oceanic currents, particularly their direction along coastlines and that migration routes follow major oceanic and coastal currents (Triest et al., 2021a).



Figure 3.1 The Ryukyu Archipelago is located in southwestern Japan, spanning 545 km (A). Okinawa, Iriomote, Ishigaki, and Miyako Islands served as study sites. Each filled circle shows sampling sites with their location IDs. All sampling sites were natural, non-riverine coastal habitats (B), except for site OKI (C) which is located in a river mouth, and is the most northern site for R. stylosa. * shows the location of a deployment site for drifting buoys with the number of buoys deployed for *in-situ* experiments. KCC (Kuroshio Counter Current).

In contrast to coastal studies, mangrove propagule dispersal in island systems has received less attention. Earlier studies on mangrove genetic connectivity in island systems have suggested low genetic variation and limited genetic connectivity (Islam et al., 2012, 2014, Al-Qthanin et al., 2020, Yahya et al., 2014). Except for Yahya et al. (2014), a study in the Sunda Islands in Indonesia, previous studies of archipelagos were executed near the distributional edges of studied species. At distributional margins, species are subject to more genetic drift and environmental selection compared to areas in distribution centers (Arnaud-Haond et al., 2006). Those studies also suggest that the discreteness of island coastlines is a potential cause of limited genetic variation, regardless of distributional area. However, because of the paucity of island studies with various species are needed to understand demographic connectivity in archipelagos. Although genetic methods can detect outcomes of connectivity interference caused by physical phenomena such as the influence of ocean currents on hydrochory, genetic information alone is insufficient to estimate spatiotemporal scales of connectivity (Lowe and Allendorf, 2010).

Thus, numerical ocean modeling methods have been employed to validate population genetic connectivity for marine and coastal organisms in recent decades, (Van der Stocken et al., 2019). Knowledge of propagule immigration revealed by genetic data, combined with physical oceanographic information obtained from ocean modeling and/or empirical release-recapture methods, has been used to investigate demographic connectivity (Nathan et al., 2000, 2008, Ngeve et al., 2017). In the past decade, with advances in computational power and modeling processes, ocean modeling has been extensively incorporated into dispersal and connectivity studies (Fox-Kemper et al., 2019), including mangrove connectivity studies, to interpret genetic results at regional and global scales (Wee et al., 2014, Ngeve et al., 2016, Pil et al., 2011, Geng et al., 2021). For example, a previous biophysical approach suggested an oceanic barrier between the Andaman Sea and the Malacca Strait around the Malay Peninsula for dispersal of *R. mucronata* by interpreting genetic outcomes with simulated ocean currents (Wee et al., 2014). Ngeve et al. (2016) identified an oceanic barrier at an oceanic conversion zone near the Cameroon Estuary Complex for dispersal of *R. racemosa* using a genetic approach with particle tracking models. Van der Stocken et al. (2019) quantified potential for long-distance propagule dispersal on a global scale using a Lagrangian particle tracking model. They found along-coast transport dominant over many continental coastlines, as well as stepping-stone dispersal via several Pacific island systems (the Galapagos Islands, Polynesia, Micronesia, and Melanesia) that allow for trans-oceanic dispersal. Their findings suggested potential effects of minimum and maximum floating periods of propagules in determining the extent of dispersal. However, detailed spatiotemporal dispersal using this method has not yet been employed for island systems.

The spatiotemporal scale of dispersal is the foundation for understanding demographic connectivity among islands that support fragmented, fringing mangrove populations. However, such island studies are scarce. Demographic connectivity is defined as the relative contribution of propagule dispersal to the population growth rate in comparison to local recruitment, and it is an important concept for conservation, especially when changes in propagule translocation result in a negative shift from stable and/or positive population growth (Lowe and Allendorf, 2010). Although mangrove habitats are protected by several international agreements and have shown diminishing annual rates of loss (>2% down to <0.4%) on average since the late 20th century (Friess et al., 2020), conversion and degradation of mangroves are continuing, especially for smaller mangrove forests (Curnick et al., 2019), even among hotspots of mangrove distribution. They have suffered in Malaysia due to oil palm plantation, in Papua New Guinea due to deforestation, and in Myanmar for rice cultivation (Friess et al., 2020). Thus, loss of small mangrove habitats on islands may impact the global distribution of mangroves in the long run, if not sooner. While demographic connectivity is essential to sustain population sizes, to colonize unoccupied niches, and to assemble local communities from the meta-community (Levin et al., 2003, Levine and Murrell, 2003), effects of population loss or degradation on other populations in the same island system are not well understood. Thus, understanding the spatiotemporal scale of propagule dispersal should help estimate demographic connectivity among islands, thereby helping to design functional protected areas.

Fragmented mangrove populations are particularly susceptible to environmental changes. Changing climatic conditions have resulted in distributional shifts in a diverse range of marine and terrestrial taxa, including mangroves, typically to higher latitudes and elevations (Cavanaugh et al., 2014). Identifying physical and biological factors that contribute to dispersal processes is essential to understanding distributional responses of species under ongoing climate change. This is particularly true for mangrove populations at the edges of their distributions, commonly exhibiting low genetic diversity, which puts them at higher risk of adverse effects compared to mangrove habitats in the center of the species range. Therefore, this study investigated the spatiotemporal scale of propagule transport among islands located on the polar edge of mangrove distributions. We used seven microsatellite markers for 354 samples collected from 16 populations on four islands. We also obtained spatial information regarding genetic connectivity and migration rates to quantify the potential for propagule transport between every site pair over several generations. To determine the temporal scale of dispersal trajectories and to quantify the potential for direct dispersal within the archipelago, we used a release-recapture method

employing GPS tracking-drifting buoys. These buoys float along the surface and provide spatiotemporal information about their geographic positions until they beach or turn off due to battery exhaustion. Using ocean current data combined with genetic data and propagule ecological information, we estimated demographic connectivity among islands with detailed information about propagule dispersal.

3.1.1 Study sites: physical characteristics and geological history

The model site was the southern half of the Ryukyu Archipelago (Figure 3.1A), a northern peripheral region of *Rhizophora stylosa (Rhizophoraceae)* in the northern hemisphere. The total mangrove area of Japan is about 553 ha, from the Ryukyu Archipelago to Kagoshima Prefecture (31'20'N), of which 80% occurs on Iriomote island (Figure 3.1C) with 7 - 19 species (Minagawa, 2000). According to radiocarbon studies on one of the largest rivers on Iriomote Island (Urauchi River; 7.45 km), the present mangrove forests were established over 1,000 years ago (Fujimoto et al., 2015). Depending on locations in the archipelago, development of mangrove habitats varies between 400 years BP (Before Present) and 3,500 years BP (Fujimoto et al., 2015, Fujimoto and Ohnuki, 1995), which is relatively recent compared to global mangrove establishment. During the establishment period, the sea level was the highest between 5,100 and 1,700 years BP and declined to the current level in the southern part of the archipelago about 1,000 years BP (Yamano et al., 2019). The archipelago is located 150~200 km east of the western boundary of the Kuroshio Current which flows northeastward (Figure 3.1A). A previous oceanographic study regarding coral larval dispersal around the archipelago showed that most particles are carried southward by the Kuroshio Countercurrent (Figure 3.1A) from spring to fall, and eastward transport of particles from the Kuroshio toward the western coast of Okinawa Island occurs primarily in warm seasons (Uchiyama et al., 2018).

Additionally, the probability of long-distance dispersal (LDD) may be primarily influenced by oceanic conditions south of the archipelago, indicating complex surface hydrodynamics in the region (Uchiyama et al., 2018). Sampling sites for the current study focused on fringing, non-riverine mangrove habitats (Figure 3.1B). We predicted that non-riverine sites proximal to the open ocean would facilitate island-to-island propagule transport, based on previous studies (Kadoya and Inoue, 2015, Triest et al., 2021a).

3.1.2. Study species: ecological traits

Rhizophora stylosa was chosen as the model species for this study based on the suitability of its propagules for the study. *Rhizophora stylosa* propagules have higher dispersal capacity than other mangrove species in the Ryukyu Archipelago, e.g., *Bruguiera gymnorhiza* and *Kandelia obovata*, which is determined mainly by positive buoyancy upon detaching from parent trees, the length of the viable period while submerged in water, and root initiation time while floating (Kadoya and Inoue, 2015, Wang et al., 2019). By comparing those dispersal properties, *Rhizophora* appears to have great potential for LDD, especially *R. mangle* and *R. stylosa*, because of their long floating periods (over 100 days in the laboratory) (Rabinowitz, 1978a). They also tolerate high salinity and dryness (Clarke et al., 2001, Kadoya and Inoue, 2015, respectively) and maintain a vertical orientation that is favorable for dispersal between roots of mangrove forests than a horizontal orientation (Van der Stocken et al., 2015b).

However, reproduction via propagules is significantly lower than that of other tropical and subtropical coastal taxa, such as seagrasses and corals. The fecundity of mangrove species depends on the reproductive stage. Coupland et al. (2006) studied 20 reproductive shoots and 222 young buds from 10 trees. They showed a poor rate of

pollination (0.5%), accomplished by wind (Yan et al., 2016), as well as a poor conversion rate (< 3%) from flowers to mature propagules, which resulted in a meager propagule fertility rate. Such a low conversion rate was also found in a study of litter in mangrove forests on Okinawa Island (Sharma et al., 2011). Producing large propagules, like those of *R. stylosa,* is metabolically expensive. Restricted pollination and resource limitation interfere with propagule reproduction (Coupland et al., 2006). Hence, species fecundity appears quite low. However, it is still understudied. It has also been argued that wind pollination efficiency is low in fragmented habitats (Ngeve et al., 2016). Hence, the primary method for mangrove gene exchange seems to be propagule dispersal.

3.2 Materials and Methods

3.2.1. Study sites and collection of mangrove specimens

Sampling involved 16 sites on four islands spanning 545 km (Figure 3.1A). The area of individual sites ranged from 0.04 ha to 8 ha, smaller than coastal mangrove populations. According to local records, all sample sites were natural habitats where no mangrove reforestation had occurred. Okinawa Island (Figure 3.1) is R. stylosa's most northern habitat (Spalding et al., 2010) and has been protected by the Ministry of the Environment in Japan. Iriomote Island (Figure 3.1C) has been protected since 1972 as a Japanese National Monument. All sampling sites, except for one riverine habitat on Okinawa Island, are fringing habitats with tree heights from 1.5 m to 5m. Sampling took place over three years. The first sampling occurred from May to July of 2017 in the Sakishima region (Iriomote, Ishigaki, Miyako Islands). Sampling on Okinawa Island was done in January 2018, and we returned to the same sampling sites in the Sakishima region between May and June 2019. We collected 538 leaf samples from 20 to 40 trees, 5 to 10 m apart to avoid sampling overlap. We cut leaves from their petioles, cleaned the surfaces with Kimwipes[®], and immediately preserved them individually in sealable bags with silica gel to dehydrate them. To completely dehydrate the leaves within 24 h, we discarded the main veins of leaves and cut the leaves into smaller pieces within 12 h after collection. After samples were brought back to the lab, they were kept in plastic bags with silica gel, sealed in a container, and kept at 25 °C until DNA extraction.

3.2.2. DNA Extraction and Microsatellite Analysis

I extracted DNA from all 538 samples. For genomic DNA extraction, 0.03–0.05 g of each leaf was homogenized with zirconia beads using a cell disrupter (Tomy Micro Smash MS-100) at 2,500 rpm for two cycles of 29 s to achieve evenly homogenized specimens. Then, we used a QIAGEN DNeasy Plant Kit to extract DNA and quantified the collected DNA with a NanoDrop. 1000 Spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) before storing it at -20 °C until use. We analyzed it with 11 nuclear microsatellite markers (ncSSR), of which eight ncSSR markers (Rhst01, Rhst02, Rhst13, Rhst15, Rhst16, Rhst19, Rhst20, Rhst27) were developed by Islam et al. (2004), and the other three ncSSR (RM110, RM107, RM121) were developed by Shinmura et al. (2012). Seven loci (Rhst01, Rhst15, Rhst19, Rhst20, Rhst27, RM107, RM121) were successfully amplified and showed polymorphisms under the following conditions. Of 538 samples, only 354 were successfully amplified to show polymorphisms for the loci. While the theoretical guideline is to use 30 loci, six were suggested to be the most used number of loci due to limited resources for isolating and analyzing microsatellites (Koskinen et al., 2004). Drawbacks related to the low number of loci were evidenced by the substantial increase in the standard deviation of interpolated genetic distances, although how many loci should be employed for optimal statistical power is still a matter of debate (Koskinen

et al., 2004). Another study showed that 95% of *Drosophila nigrosparsa* specimens could be assigned correctly when using eight loci and a sample size of 248 (Arthofer et al., 2018). Additionally, with a sample size of 25 or more, variability in allele frequency and expected heterozygosity among replicates decreased with a minimum rate between different population sizes despite differences in taxa (insects, birds, mammals) and several loci from 5 to 9 (Hale et al., 2012). Thus, utilizing seven polymorphic loci to obtain accurate allele frequencies and accurate estimates of genetic diversity in Okinawa is statistically acceptable.

Polymerase chain reactions (PCR) were performed in 10- μ L volumes containing 10 ng/ μ L DNA template, QIAGEN Multiplex Master Mix, 0.2 μ M of each primer pair, 0.2 μ M of each fluorescence-labeled probe, and RNAse-free water. PCR cycle conditions were 15 min at 94 °C, followed by 35 cycles of 30 s at 94 °C, 90 s at 60 °C for annealing, and 60 s at 72 °C in the final cycle. Each locus was amplified individually for samples that failed to amplify with the method above. PCR solution, in this case, was 10 μ L consisting of 1 μ L DNA template, 5 μ L of QIAGEN Amplitaq Gold 360 Master Mix, 1.5 μ L MilliQ water, and 0.2 mol primer pair and fluorescent-labeled probe. PCR cycle conditions for Amplitaq included 5 min at 90°C initially, followed by 35 cycles of 30 s at 95 °C, 30 s at 50 °C for annealing, and 60 s at 72 °C in the final cycle with a final extension at 72 °C for 10 min. PCR products were then diluted 5x with MilliQ water and applied to a 3130 xl Genetic Analyzer (Applied Biosystems) to analyze allelic variation. Fragment sizes were analyzed with Geneious 11.0.3 (Biomatters Ltd., Auckland, New Zealand) relative to internal lane size standards using a GeneScan. 600 LIZ® (Thermo Fisher Scientific).

3.2.3. Genetic Data Quality Check

Prior to population genetic analysis, we tested the probability of identity (PI) and linkage disequilibrium of genetic data. PI was tested to determine whether any two individuals accidentally shared an identical multilocus genotype, to derive a cumulative probability of identity for all polymorphic loci in each population using GenAlEX 6.5 (Peakall and Smouse, 2012), and gave a total value of 2.9 x 10 to 5.4 x 10 for all polymorphic loci in each site. Linkage disequilibrium for each locus pair across all populations was tested using Fisher's method on GENEPOP on the web (Rousset, 2008, Raymond and Rousset, 1995), and detected significant linkage disequilibrium (P < 0.01) for Rhst15 & Rhst20 (MYKc, ISGa, IRMe), Rhst01 & Rhst15 (IRMa, IRMc), Rhst01 & Rhst19 (MYKd), Rhst15 & Rhst27 (IRMd), Rhst20 & Rhst27 (IRMd), Rhst20 & RM107 (ISGa), and Rhst27 & RM107 (IRMc). In the majority of populations, paired loci with significant linkage disequilibrium were not observed.

3.2.4. Genetic Diversity

To analyze genetic diversity, we computed expected heterozygosity (H), observed heterozygosity (H), and pairwise population genetic differentiation ($F_{ST}P$) using GenAlEx (Peakall and Smouse, 2012). $F_{ST}P < 0.05$ was set as the threshold for insignificant genetic differentiation between paired sites (Frankham et al., 2010). The number of alleles (A) per locus and per population and the inbreeding coefficient (F_{is}) for each population were analyzed using FSTAT 2.9.3 (Goudet, J. 2001). Allelic richness was rarefied to the smallest population size of 9 (MYKb) based on a rarefaction method (Hurlbert, 1971). To evaluate population differentiation, an analysis of molecular variance (AMOVA) was conducted within and among populations using GenAlEx 6.5 (Peakall and Smouse, 2012).

3.2.5. Genetic Structure

To identify genetic structures of individual samples, we used a Bayesian clustering model, STRUCTURE 2.3 (Hubisz et al., 2009, Pritchard et al., 2000). Each run assigned K (1 to 18) clusters to each sample. All parameters were set to default. With a Bayesian Markov chain Monte Carlo resampling method, each run underwent 500,000 iterations after discarding 80,000 as burn-in for 20 replicates. The optimal K for this dataset was determined with Structure Harvester (Earl and Holdt, 2012) using results from STRUCTURE, and the likelihood of multiple values of K was tested using the Evanno method (Evanno et al., 2005). With CLUMPAK (Kopelman et al., 2015), the entire set of runs obtained from STRUCTURE was merged for each K value, based on similarity matrices, and visualized. Additionally, as preliminary information, we compared the obtained heterozygosity and inbreeding coefficient values with those of coral species in the Ryukyu archipelagos, including a brooding coral, Seriatopora spp. (Nakajima et al., 2017), broadcast spawning corals Acropora tenuis (Zavasu et al., 2016) and Galaxea fascicularis (Nakajima et al., 2016). Similarly, we compared heterozygosity and relatedness from our samples with the previous study of *R. stylosa* in riverine habitats in the Sakishima Islands (Islam et al., 2014).

3.2.6. Isolation by Distance

To test the effect of geographic distance on genetic connectivity, we compared pairwise genetic differentiation ($F_{ST}P$) and geographic distance between every population pair using Mantel's test in GenAlEx 6.5 (Peakall and Smouse, 2012). All $F_{ST}P$ values were linearized (Lin $F_{ST} = F_{ST}P/1-F_{ST}P$), and we measured the Euclidean distance between populations using Google Earth Pro.

3.2.7. Bayesian Assignment Tests

To identify differences in contemporary patterns of migration (several generations) from historic patterns of population connectivity, we estimated recent migration rates between site pairs with BayesAss 3.0.4 (Wilson and Rannala, 2003), which uses a Bayesian method and Markov chain Monte Carlo (MCMC) resampling method. BayesAss assumes that migration does not change allelic frequencies over two generations, and it assumes that output migration rates reflect the most recent several generations. We computed five replicates with different random starting seeds for an MCMC run with 10,000,000 iterations, discarding the first 1,000,000 as burn-in for each run. Samples were collected every 100 observations with default parameter settings. Sample site MYKb was excluded from this analysis due to its inadequate sample size. We examined posterior mean migration rates (m) for gene flows between sites. We followed (Faubet et al., 2007) for performance analysis of the test.

3.2.8. In-situ Drifting Buoy Experiments

Thirty-one drifting buoys were deployed to estimate ocean hydrodynamic effects on propagule dispersal. Drifter deployment was carried out with one drifter per day for 31 consecutive days (except when weather or sea conditions made it unsafe to conduct fieldwork) starting on August 7, 2018, which is the middle of the fruiting season on Okinawa Island (Sharma et al., 2011), and a little after its peak in July for Iriomote Island (Kadoya and Inoue, 2015). August was also a reasonable time of the year for deployment to avoid major typhoons. Buoys were deployed from just off the reef of IRMg on Iriomote Island (Figure 3.1C), where genetic isolation was detected despite the proximity of neighboring populations (< 5km to the closest population). To obtain ocean surface current vector information, we used Microstar drifters developed by Pacific Gyre (Figure 3.2). A)





Figure 3.2 Microstar drifters floating at the deployment site (A), schematic of the floating bouy and drogue (B).

Microstar drifters have two parts, a surface float (20 cm in diameter) and an underwater corner-radar-reflector-type drogue (Ohlmann et al., 2005). The float maintains its drogue at a depth of 1 m below the surface to capture the surface current subjected to Ekman transport and to minimize direct effects of wind and surface waves with its spherical shape. Drogues were calibrated to provide about < 2 cm/s velocity difference from the "tagged" water parcel's horizontal motion under calm wind (< 12 m); however, direct effects of high wind on Microstar drifters are not yet well understood (Ohlmann et al., 2005; Ohlmann et al., 2011). Significant direct effects of wind on propagule dispersal can be expected when propagules are floating in a horizontal position, based on studies of wind effects on *R. mucronata* (Van der Stocken et al., 2013; Van der Stocken et al., 2015a), as dispersal characteristics of *R. stylosa*'s propagules resemble those of *R. mucronata*'s. However, the effects of wind on propagules when floating in vertical positions are still unknown.

Although the drifter shape differs significantly from that of propagules, it is designed to capture the surface current, which may diverge from the current in speed, direction, or both, due to local winds that can change hourly. Hence, drifters captured a range of eddies and current energies at a local scale (Heupel, 2011). Drifter positions were determined by GPS in near-real-time, using the Iridium satellite data network with user-specified up-linking intervals. This allowed us to collect spatiotemporal information on dispersal trajectories from all deployed buoys. We set the intervals so that positioning information with higher resolution would be obtained near the coast. Intervals were set from 5 min to 12 h depending on the distance from the nearest coast. Drifters can be positioned with an accuracy of < 7m (Ohlmann et al., 2005). Collected spatiotemporal data were analyzed using MATLAB.

3.2.9. Gene-Flow Comparisons with Potential Dispersal Estimates

Potential dispersal from coastal areas in the Yaeyama region was estimated from biophysical models of Uchiyama et al. (2018). The newly developed ROMS-L2 model output local ocean currents with 1-km horizontal resolution and 32 layers (nested from the parent ROMS-L1 model with 3-km resolution) for the whole Nansei Archipelago from the northeastern part of Taiwan to the southern tip of Kyushu (Uchiyama et al., 2018). The

computational period for L2 was about 6 years from Dec. 27th, 2010 to November 2nd, 2015, and the baroclinic time step was set for 40s, and configuration for L2 included tides and boundary, and initial conditions were based on the output of ROMS-L1 (Uchiyama et al., 2018). Output was validated with satellite and *in-situ* observations and the assimilative JCOPE2 reanalysis (Uchiyama et al. 2018). Simulated probability densities of water parcel displacement were estimated with 280,000 particles released daily from 145 reef patches with a 2-km diameter along the Yaeyama coast with an advection time of 21 days for four years. We used MATLAB to manipulate datasets into a compatible format for mangrove study areas. All data were averaged over four years and consolidated into five areas (Figure 3.3). To investigate the effect of ocean currents on gene flow, migration rates were calculated using BayesAss with the same settings as previously explained, according to areas defined in Figure 3.3, followed by comparison of derived migration rates with dispersal predictions based on regional ocean circulation simulations for the Yaeyama region (Uchiyama et al., 2018) using Pearson's correlation test in R.



Figure 3.3 Area map of Yaeyama region showing current study sites within sites delineated for the numerical modeling study by Uchiyama et al. (2018). The current study sites are shown in black, e.g., IRMe, and model sites are indicated in white, e.g. a) with each area indicated in blue.

3.3. Results

3.3.1. Genetic Diversity

The average number of alleles (allelic richness) per population varied from 1.2 (OKI) to 2.7 (IRMc), depending on the site (Table 3.1). This study showed little to no heterozygosity (H_o) in any population at any locus, and expected heterozygosity (H.) consistently exceeded H_o for all sampling sites. The inbreeding coefficient (F_{IS}) exceeded 0.8 (p < 0.01) for all sites, while pairwise genetic differentiation (F_{ST}P) varied depending on sites ranging from 0.017 (IRMe-IRMf) to 0.828 (IRMg-OKI) (Figure 3.4A). We found four site pairs (three neighboring pairs, IRMf-IRMe, ISGa-ISGc, MYKb-MYKd, and one inter-island pair, IRMd-MYKc) with insignificant pairwise genetic differentiation (F_{ST}P < 0.05) (Figure 3.4B). Hierarchical analysis of molecular variance (AMOVA) (Excoffier et al., 1992) showed that 78% of genetic variation occurred among individuals within sites, 12% of variation occurred among sites on the same island, and 10% of variation occurred among islands (p < 0.01) (Table 3.2).

Compared with other coastal species in the same region, brooder corals *Seriatopora* spp. (Nakajima et al., 2017), broadcast spawning corals *Acropora tenuis* (Zayasu et al., 2016) and *Galaxea fascicularis* (Nakajima et al., 2016), as well as the previous study of *R*. *stylosa* in riverine habitats in Sakishima Islands (Islam et al., 2014), we found that the genetic diversity of *R*. *stylosa* samples was comparatively lower. Species comparisons showed that *R*. *stylosa* had higher inbreeding coefficients and higher genetic differentiation than corals (Figure 3.5A & B). Both observed and expected genetic heterozygosity of *R*. *stylosa* were comparatively lower than those of corals (Figure 3.5C). Furthermore, between non-riverine and riverine *R*. *stylosa*, non-riverine mangroves showed lower genetic

heterozygosity and higher inbreeding coefficients. We found that H_e was higher than H_o for all studies in this area regardless of species and landscape (Figure 3.5C).

Island	Population	Lat	Lon	Area (ha)	Geographical traits	Ν	Ar	Na	Но	He	Fis
Okinawa	OKI	26.604	128.143	7,712	River mouth	13	1.21	1.286	0.000	0.022	1.000
Miyako	MYKa	24.879	125.286	8.133	Inlet Bay	19	2.00	2.143	0.008	0.389	0.982
	MYKb	24.763	125.282	0.317	Inner Bay	9	1.69	1.714	0.000	0.238	1.000
	MYKc	24.752	125.268	0.294	Sandy Beach	21	2.50	2.857	0.000	0.437	1.000
	MYKd	24.731	125.296	3.787	Sandy Beach/Bay	26	2.21	2.571	0.013	0.329	0.962
Ishigaki	ISGa	24.542	124.296	0.096	Sandy Beach	27	2.24	3.143	0.005	0.277	1.000
	ISGb	24.510	124.279	0.191	Inlet Beach	21	2.36	3.000	0.014	0.399	0.967
	ISGc	24.456	124.149	0.044	Inlet	21	2.03	2.571	0.007	0.275	0.977
	ISGd	24.467	124.125	1.024	Inlet	30	2.58	3.000	0.034	0.452	0.926
Iriomote	IRMa	24.403	123.830	3.688	Sandy Tidal Flat	26	2.54	3.000	0.000	0.433	1.000
	IRMb*	24.344	123.934	7.218	Sandy Tidal Flat	18	2.06	2.286	0.008	0.349	0.979
	IRMc *	24.344	123.928	1.776	Rocky Tidal Flat	28	2.66	3.000	0.005	0.482	0.990
	IRMd*	24.279	123.904	9.560	Inner Bay	27	2.53	2.857	0.000	0.477	1.000
	IRMe**	24.334	123.728	2.580	Inner Bay	12	2.34	2.571	0.036	0.325	0.899
	IRMf ^{**}	24.331	123.714	2.584	Inner Bay	30	2.54	3.571	0.058	0.282	0.839
	IRMg**	24.309	123.683	0.206	Inner Bay	26	1.40	1.857	0.016	0.091	0.826
						1054 1	0.04		0.010	0.000	0.050

Total 354 Avg 2.84 2.589 0.013 0.328 0.959

Table 3.1 Sampling site information and genetic variability of each site. We found rather high inbreeding coefficients (FIS), and low observed heterozygosity (H₀) at all sites, compared to similar island mangrove population connectivity studies, including that of Islam et al. (2014). Results indicate extremely rare gene exchange occurring among sites in the Archipelago. * sites are the East Coast of Iriomote Island (ECI), and ** are its West coast (WCI).



Figure 3.4 (A) Pairwise genetic differentiation values ($F_{ST}P$) revealed that strong connectivity exists among islands < 200km apart in the Ryukyu Archipelago. Of 25 site pairs with $F_{ST}P < 0.1$ (bold grids), 8 pairs exhibited intra-island connectivity, whereas OKI and IRMg are almost completely isolated. Xand Yaxes show site names, and the figure shows no directionality. P-values < 0.01for all pairs, except for grids with *, ** and NS ndicating p > 0.1, 0.05 **(B)** Population pairs with $F_{ST}P < 0.1$ are projected over the map, and bold lines indicate pairs with $F_{ST}P < 0.05$, a threshold value indicating significant connectivity.

Source of variation	df	Sum of Square	Variance Components	% of variation	Fixatio	on index	P-value
Among Regions	4	133.631	0.17	10	Frt	0.097	0.0001
Among populations	11	120.6	0.22	12	Fst	0.138	0.0001
Among individuals within populations	692	936.6	1.35	78	Fsr	0.222	0.0001
Total	707	1190.8	1.74				

Table 3.2 AMOVA summary shows that genetic variation is highest among individuals within opulations, and that fixation indices are all significant with a tendency toward genetic isolation.





Figure 3.5 Comparison among coastal species in the Ryukyu Archipelago. Overall, this study showed the highest signal for genetic isolation based on inbreeding coefficient **(A)**, genetic differentiation **(B)**, and genetic heterogeneity **(C)** comparison.

3.3.2. Isolation by Euclidian Distance

Mantel tests revealed that distance accounts for < 5% of genetic differentiation between sites in the Yaeyama region (R^2 = 0.045, p < 0.1), < 10% in the Sakishima region (R^2 = 0.076, p < 0.05), and > 30% in the entire archipelago (R^2 = 0.341, p < 0.01), which indicates isolation-by-distance over the archipelago, but not at a given island. We also found that the westernmost site in the archipelago, IRMg, revealed linearized F_{ST}P values (LinF_{ST}P), which are consistently above average regardless of the Euclidean distance between IRMg and other sites (Figure 3.6A–C). However, according to the sensitivity analysis, IRMg was not the cause of the poorer fit.



Figure 3.6 The tendency of IBD (isolation by distance) was apparent over the Sakishima region (B) and over the entire Ryukyu Archipelago (A), which indicates decreasing gene flow affected by the absence of coastline over a certain distance. Within the Yaeyama region (C), Euclidean and genetic distance did not show a correlation. All outliers in the plots are associated with IRMg indicating that the site is isolated by other environmental factors beside geographic distance or ocean connectivity. The Y-axis shows linearized genetic differentiation values, and the X-axis shows the Euclidean distance between paired sites. All filled markers in (B, C) are paired sites with IRMg.

3.3.3. Structure Analysis

Bayesian analyses suggested 3 genetically homogeneous groups of individuals (genetic clusters) in the Ryukyu Archipelago (Figure 3.7): western Iriomote Island (WI), North Miyako Island (NM), and Okinawa Island (OKN). The majority of individuals (> 75%) on the west coast of Iriomote Island (WCI) had > 90% inferred ancestry from a local genetic cluster (WI), particularly at the westernmost site, IRMg, (>95%). Site IRMf in the WCI area showed one individual with > 90% inferred ancestry from OKN. Most individuals (> 92%) at site OKI had > 90% inferred ancestry from a local cluster (OKN). OKI and IRMg exhibited homogeneous population genetic structures, highlighting the lack of common inferred ancestry between them. On the other hand, the remaining sampling sites showed heterogeneous genetic structures within each site. On Miyako, Ishigaki, and the east coast of Iriomote Island (ECI) (Figure 3.7), some specimens had > 80% inferred ancestry from NM admixed with individuals having inferred ancestry from OKN and WI. For example, 27 individuals from northern Iriomote Island (IRMa) included two individuals with inferred ancestry (> 80% hereafter) from OKN, four individuals with inferred ancestry from NM, and nine individuals with inferred ancestry from WI, and the remaining 12 individuals with mixed ancestries. We also found that very few inferred ancestries were shared within an island, particularly between WCI and ECI.

3.3.4. Contemporary Migration Rates

Contemporary migration rates (*m*) represent the frequency of genetic immigration in the last few generations between all pairs of sites in the archipelago, which ranged from m = 0.008 to m = 0.154 (m = 0.01 implies that, on average, one individual among a sample of 100 per generation would be a migrant). The highest migration rate (m = 0.154) was found at Ishigaki Island (ISGa), east of Iriomote Island (IRMb), followed by pairs among neighboring sites along the west coast of Iriomote Island, i.e., m = 0.149 from IRMg to IRMf, and m = 0.114 from IRMg to IRMe. However, migration rates in the opposite direction were substantially lower (Figure 3.8A). The analysis also identified ISGa as the site with the highest frequency of emigrants to other sites ($\Sigma m_{ISGa(Source)} = 0.489$). Furthermore, the analysis identified the potential for long-distance (> 200 km) propagule immigration from Okinawa Island (OKI) to Iriomote Island (IRMc) with relatively higher migration rates (m = 0.052) (Figure 3.8B). The majority of migration rates were too low (m < 0.05) (Meirmans, 2014) to confirm genetic exchange between sites.



Figure 3.7 The optimal number of genetic clusters was 3 (K= 3); clustered on the basis of inferred ancestry from the west coast of Iriomote Island (WCI) (purple), from Miyako Island (orange), from Okinawa mainland (blue). Each bar represents an individual sample. The cluster from OKI was distributed throughout the Archipelago, but its ratio drastically declined at WCI. The cluster from WCI revealed very limited distribution even among neighboring sites on Iriomote Island. Heterogeneous genetic structures were found at most sampling sites, except for IRMg and OKI. This structure patterns were consistent among various Ks.



Figure 3.8 Bayesian assignment test identified contemporary migration patterns in the Ryukyu Archipelago with posterior mean migration rates (m = 0.01 implying that 1 individual among a sample of 100 per generation is a migrant). The majority of site pairs showed lower m values (x-axis: target sites, y-axis: origin sites), and a few with higher, sporadic migration rates.(A) All migration patterns with m > 0.05 were projected over a map with arrows pointing at target sites. The higher migration rates (m > 0.1) for R. stylosa in the Ryukyu Archipelago were unidirectional (bold arrows). The majority of site pairs with m > 0.05 were found between Iriomote and Ishigaki Islands, and site ISGa was identified as the strongest source population for gene flows among study sites. Black arrows have higher accuracy ($F_{ST} > 0.25$). (B)

3.3.5. Comparison between migration rates and potential dispersal estimates

The highest estimated potential dispersal values were for self-recruitment in all areas (grids in diagonal, Figure 3.9A). The subsequent highest estimate for potential dispersal was found between two areas on the east coast of Ishigaki Island (areas a and b), and from the western to northern coast of Iriomote Island (areas c to e), demonstrating that they are an order of magnitude lower than estimated self-recruitment (Figure 3.9A). The smallest potential dispersal estimates were associated with area d (Figure 3.9A). It is important to emphasize that connectivity gradients do not depend on the distance between areas. When comparing spatial patterns of strong connectivity with those of genetic migration among areas, we did not detect clear correlations between potential dispersal estimates and genetic connectivity (Figure 3.9).

On the other hand, migration rates identified substantial recruitment from the northeast coast of Iriomote Island (area d) to all other areas. However, the dispersal model did not predict any of the corresponding connectivity. Moreover, the Bayesian assignment analysis did not identify strong potential dispersal between neighboring areas on Ishigaki Island (between areas a and b). Despite differences in spatial connectivity patterns and migrations, the correlation test showed a proportional trend of connectivity values to genetic migration values (Figure 3.9C). However, potential dispersal patterns did not reveal stochastic gene flow patterns outside of WCI.



Figure 3.9 The potential dispersal estimates in Yaeyama region (Iriomote & Ishigaki islands) were analyzed based on the output of numerical ocean model conducted by Uchiyama et al. (2018).**(A)** The source sites are shown on the x-axes, and destination sites are on the y-axes. The area-base self recruitement displayed the high potential in all areas, and potentials were unrelated to the geographic distance **(A)**. The correlation test between pairwise genetic differentiation and potential connectivity between areas did not show clear correlation **(B)**.

3.3.6. In-situ drifter experiments

Of 31 GPS drifting buoys released from a location just off the west coast of Iriomote Island, six drifters beached on the same island after an average of 23 days with high retention rates around the release points for the first 20 days (Figure 3.10A); however, one drifter took > 130 days to return to the Iriomote island coastline (Figure 3.10B, Table 3.3). We confirmed four island-to-island dispersal beaching events, including one each on the coasts of Ishigaki Island (58 km in 12 days), Kuroshima Island (35 km in 9 days), Miyako Island (183 km in 58 days), and Yakabi Island (414 km in 109 days). We found



FIGURE 3.10 Drifter trajectories around the archipelago displayed differences in density of trajectories between west and east ends of the archipelago. Drifters deployed from western Iriomote Island tend to stay on the west side of the archipelago, but showed frequent mixing in the Yaeyama region (A). 9 out of 30 buoys beached in the Sakishima region, one of which drifted for over 100 days while others beached < 60 days, identifying a subset of temporal scale of the trajectories. Beaching locations are shown in red. Local beaching events highlighted the absence of trajectories within Sekisei Lagoon, between Iriomote and Ishigaki Islands. The color bar shows the duration in days since the deployment. (B)

that drifter movements were predominantly northeast of the Yaeyama region (Figure 3.9A). We also found that 60% of drifters were carried by the strong western boundary current, the Kuroshio Current, of which 76% were carried out into the mid-Pacific Ocean and were eventually lost due to battery failure (Figure 3.11). We also observed sporadic counter-current drifting southwestward with various trajectories. Frequent local eddies were also observed in the archipelago, causing dispersal periods unrelated to Euclidean



Figure 3.11

Trajectories of 31 GPS drifting buoys over 250 days are shown. The retention period of buoys in the Ryukyu Archipelago is < 100 days on average and only a few stayed as long as 200 days. The Kuroshio Current is involved in transport of particles released from western Iriomote Island. Potential to travel as far as the mid Pacific Ocean was confirmed. The color bar shows temporal data in days for each position of buoys, and a red point shows the deployment location.

distance from the deployment site. For example, one drifter traveled > 1,000 km in 50 days while another traveled 183 km in 59 days.

ID	Deployment Time	Tide at deployment Incoming = 1 Outgoing = 0	Closest Distance to Shore (km)	Beached coordinates (Lat Lon)	Eucledian Distance (km)	Dispersal duration (days)	Notes
IRM-353-1	2018/08/07 9:08	0	0.5	-	-	-	
IRM-342-1	2018/08/08 7:10	0	0	24.3102, 123.6627	4.8	0.82	
IRM-343-1	2018/08/09 11:40	0	0	24.3422, 123.7293	4.6	0.94	
IRM-344-1	2018/08/13 10:45	0	0.02	-	-	-	
IRM-343-2	2018/08/14 11:05	0	-	-	-	-	
IRM-345-1	2018/08/14 11:05	0	0	24.3975, 123.8560	18.36	131.96	
IRM-346-1	2018/08/15 13:30	0	0.19	-	-	-	
IRM-347-1	2018/08/16 11:40	0	0.57	-	-		
IRM-348-1	2018/08/18 10:05	1	1.17	-	-	-	
IRM-349-1	2018/08/19 12:55	1	0.54	-	-	-	
IRM-350-1	2018/08/20 13:30	1	0	20.7030, 110.4308	1421	226.27	Guangdong, China
IRM-351-1	2018/08/21 10:45	1	0.92	-	-	-	
IRM-352-1	2018/08/22 10:35	1	0.81	-	-	-	
IRM-354-1	2018/08/25 14:00	1 spring	0	26.2179, 127.2397	413.8	108.7	Yakabi island
IRM-355-1	2018/08/26 10:30	0 spring	0.57	-	-	-	
IRM-356-1	2018/08/27 13:40	0 spring	1.19	-	-	-	
IRM-357-1	2018/08/28 10:30	0	0.15	-	-	-	
IRM-358-1	2018/08/29 11:50	0	0.67	-	-	-	
IRM-359-1	2018/08/30 11:20	0	0	24.7645, 125.4220	182.8	58.79	Miyako
IRM-360-1	2018/08/31 7:00	1	0.37	-	-	-	
IRM-361-1	2018/09/01 17:21	1	0	24.3723, 124.2526	58	12.07	Ishigaki
IRM-362-1	2018/09/02 10:55	1	0	24.2813, 123.7498	9.8	5.45	
IRM-363-1	2018/09/03 17:20	0	1.13	-	-	-	
IRM-364-1	2018/09/04 7:30	0	0	24.2505, 124.0110	34.9	8.56	Kuroshima
IRM-365-1	2018/09/05 9:35	0	0.7	-	-	-	
IRM-366-1	2018/09/06 15:55	1	0	33.2343, 126.3539	1018	49.89	Jeju, Korea
IRM-367-1	2018/09/07 10:20	0	0	24.3384, 123.7010	1.98	1.35	
IRM-368-1	2018/09/08 10:35	0	-	-	-	-	
IRM-369-1	2018/09/09 10:50	0 spring	0	24.4031, 123.8435	17.8	5.47	
IRM-370-1	2018/09/11 11:00	0 spring	0.53	-	-	-	
IRM-371-1	2018/09/12 10:40	0	1.12	-	-	-	

Table 3.3 In-situ drifter experiments showed about 30% of local beaching (Bold letters) with a wide range of temporal variation from 0 to 132 days.

3.4. Discussion

3.4.1. Genetic diversity in island systems

Genetic disequilibrium found in this study may be due to high monomorphism caused by a high rate of inbreeding, which is expected in a naturally fragmented population (Provan et al., 2008) or/and by selfing due to pollinator limitation (Bawa, 1990), both of which are common to *Rhizophora* species. The genetic variance (Na), inbreeding coefficient (F_{IS}), and limited area of fringing mangroves all exhibited characteristics of habitats at species range limits.

The Ryukyu Archipelago is located at the northern edge of mangrove global distribution, and site OKI, which showed the lowest genetic variance in the study (A=1.2), is the northernmost habitat of *R. stylosa*. Compared to a genetic connectivity study of *R. stylosa* in South China (Geng et al., 2021), reduction of genetic diversity in this study area was apparent. Hence, *R. stylosa* in the Ryukyu Archipelago may be subject to genetic drift and environmental selection due to population sizes limited by extreme and/or variable environments (Brown et al., 1996) at the edge of the species distribution. Based on genetic structures indicating infrequent gene flow among sites (Figure 3.7), we suggest that genetic variation may already have been limited at the time of establishment in the archipelago.

Lack of riverine inputs may also promote low genetic variation. Samples were collected at fringing mangrove habitats in proximity to the open ocean, where there were no inputs from rivers. On the other hand, samples used by Islam et al. (2014) were collected from river basins located further inland than our sampling sites. Overall, the F_{IS} of this study was substantially higher, and H_0 was also significantly lower than the values reported by Islam et al. (2014) (Table 3.1). Proximity to the open ocean has been suggested to influence inbreeding and genetic diversity of mangrove populations, in that most seaward habitats should have a higher likelihood of propagule dispersal and should exhibit higher genetic diversity (Triest et al., 2021a). However, genetic comparisons with those of Islam et al. (2014) revealed the opposite pattern. Our data suggested a very low likelihood of propagule dispersal among fringing mangroves in the island system via ocean currents, despite being directly exposed to ocean hydrodynamics. In general, riverine systems provide more suitable habitats for mangroves because the constant sediment supply from upstream expands available habitat areas for new propagules (Kadoya and Inoue, 2015). This, in turn, supports larger population sizes resulting in greater genetic variation within habitats (Kadoya and Inoue, 2015). Additionally, gene flow in riverine systems may be bidirectional because of interacting river flows with tidal fluxes, coastal currents, and wind, factors that support genetic diversity within fluvial systems (Ngeve et al., 2017).

On the other hand, fringing habitats lack terrestrial input and fluvial interactions with rivers. Thus, habitat areas are often limited, and demographic connectivity must rely predominantly on ocean currents, which limits genetic diversity due to a lack of dispersal connectivity among populations in island systems. Overall, genetic heterozygosity ($H_e > H_o$) and inbreeding coefficients (F_{is}) in the current study indicated inbreeding/selfing as the dominant method to sustain population sizes, which suggests that propagule dispersal in the archipelago is restricted to local scale. Genetic variation revealed that fringing habitats of the Ryukyu Archipelago are naturally fragmented with a higher potential for genetic isolation within the island system, making them vulnerable to environmental changes.

Compared to genetic structures of coral species in this region, *R. stylosa* showed more restricted gene flow among sites in the Ryukyu Archipelago, much lower heterozygosity, and substantially higher inbreeding coefficients than those of corals. *Seriatopora* (brooding corals) showed similar genetic clusters to our results in the Ryukyu Archipelago with three inferred ancestries. However, spatial patterns of the clusters were

different, and their ancestral compositions had much less heterogeneity than our study (Nakajima et al., 2017). This difference in genetic structure indicates that *Seriatopora* apparently has consistently higher gene flow among sites through larval transport, a conclusion supported by the low inbreeding coefficient and high genetic heterozygosity compared to those of *R. stylosa* (Figure 3.5A). Compared to brooding corals, broadcast spawning corals showed more homogeneous genetic structure across different geographic distances, especially *Galaxea fascicularis* (Zayasu et al., 2016, Nakajima et al., 2016).

This may be due to their pelagic larval duration (PLD). Brooding corals have short (1 to 5 day) PLDs, which promote local settlement (Ayre and Hughes, 2000) resulting in three distinguishable bioregions of *Seriatopora* (Nakajima et al., 2017). In contrast, broadcast spawning corals have longer PLDs (5 to 50 days) (Nakajima et al., 2017, Nishikawa and Sakai, 2005); thus, they disperse considerable distances, resulting in lower genetic differentiation among sites in the Okinawa Islands (Zayasu et al., 2016).

Directionality and spatial range of historic genetic connectivity were interpreted based on shared inferred ancestries in populations. With > 80% of OKN inferred ancestry in individuals throughout the Ryukyu Archipelago, genetic exchange southwestward is suggested. On the other hand, inferred ancestry of WI is absent in Miyako and Okinawa islands, which suggests that northeastward genetic exchange declines drastically beyond Ishigaki Island (Figure 3.7). The decline of genetic exchange was correlated with distance between islands, according to the Mantel test between genetic differentiation and Euclidean distance (Figure 3.6). Hence, in the Ryukyu Archipelago, a spatial range of >100 km between islands in a northeastward direction is identified as the threshold for genetic discontinuity, and no population connectivity among islands was frequent enough to homogenize genetic structure within the archipelago.

However, significantly high inbreeding coefficients from all study sites must be carefully considered since significant F_{IS} may cause additional populations to be inferred (Falush et al., 2003). Additionally, high F_{IS} and estimated selfing rates in the studied populations have been explained for *R. mucronata* (Triest et al., 2021a). The optimal K was 3 in this study, based on the Evanno method (Evanno et al., 2005), but according to genetic structure with K=2, all islands are well admixed within the archipelago; however, not enough genetic connectivity among islands was found to homogenize the genetic structure (Figure 3.7). On the other hand, at the edges of the archipelago, both OKI and IRMg exhibited genetic structure with one dominant inferred ancestry (OKN and WI, respectively), indicating their genetic isolation. Overall, genetic structures and F_{IS} showed that inbreeding/selfing has consistently been the major reproductive method, and population connectivity even within islands is limited.

Reliable migrant ancestry assignment values (m > 0.05) of the last few generations between populations were found between 14 site pairs, mostly from Ishigaki to Iriomote Island, representing an influx of immigrant alleles among populations via propagule dispersal. This southwestward pattern of propagule immigration from Ishigaki Island to ECI was also found in a locally abundant broadcast-spawning coral species, *Acropora tenuis* (Nakajima et al., 2016). A low frequency of allele influx in recent generations was suggested over the archipelago, and inter-island influx was only found in a southwestward direction, indicated by genetic structure. However, our results remain tentative since they are derived from only seven loci, which is the lower sample size limit suitable for BayesAss assignment (Wilson and Rannala, 2003). With a small number of loci (5 in Wilson and Rannala, 2003), the accuracy of assignments is reasonable if migration is low (m < 0.2) and genetic differentiation is high (F_{ST}> 0.25) (Wilson and Rannala, 2003). Hence, migration ancestries with higher accuracy in this study were found only between 6 population pairs (Figure 3.8B). The high F_{IS} values in the archipelago suggest that the influx of propagules from other populations is extremely low, but still contributes to maintain genetic diversity within populations.

Overall, in this study, contemporary gene flow patterns with higher migration rates (m > 0.05) seem to correspond well to the results of STRUCTURE, indicating that those sites with m > 0.05 have undergone consistent, sporadic gene flow over a historical timescale (Faucet et al., 2007, Wilson and Rannala, 2003, respectively). Based on the "one-migrant-per-generation" rule (Mills et al.,1996), one immigrant per generation is enough to avoid the harmful effects of local inbreeding in a population (Lowe and Allendorf, 2010). Thus, populations with m > 0.05 and population size > 20 in the archipelago indicate that those populations may avoid harmful effects of local inbreeding/selfing, despite low genetic variation and limited genetic heterozygosity.

3.4.2. Sporadic propagule transport throughout the Ryukyu Archipelago

Considering ecological characteristics of propagules that contribute to LDD and direct ocean access at each sampling site, we hypothesized a uniform level of population genetic connectivity throughout the archipelago. However, contrary to our hypothesis, genetic structures indicated limited connectivity. The majority of sites in the Sakishima region (Iriomote, Ishigaki, and Miyako Islands) displayed heterogeneous genetic structures in each population with inferred ancestries from all three bioregions (OKN, NM, WI) (Figure 3.7). Since the wind-pollination success rate of *R. stylosa* is low, structural heterogeneity may indicate that propagule immigration from other sites is sporadic but consistent over many generations and that the frequency of inbreeding/selfing is too high to achieve homogeneity. On the other hand, at the edges of the archipelago, both OKI and IRMg exhibited genetic structure with one dominant inferred ancestry (OKN and WI, respectively), indicating their genetic isolation. Overall, genetic structures and F_{1S} showed that inbreeding/selfing has consistently been the primary reproductive method, and population genetic connectivity even within islands is extremely limited.

3.4.3. Spatiotemporal interpretation of propagule immigration based on ocean currents

As a preliminary investigation of the effects of ocean current on population genetic connectivity, we compared our genetic data to previous ocean modeling data and dispersal predictions based on regional ocean circulation simulations for the Yaeyama region (Uchiyama et al., 2018). The dispersal model specific to the Yaeyama region showed a high tendency for particles to stay in local areas for the first 21 days, which was the tracking period in numerical modeling. This could be supporting evidence for homogeneous genetic structures in WCI, and the isolation of IRMg revealed in genetic analyses. Furthermore, the high genetic differentiation and the lack of shared inferred genetic ancestry between the west and east coasts of Iriomote Island were also suggested in the dispersal model, since the potential dispersal value was one to two orders of magnitude lower.

However, potential dispersal patterns did not reveal stochastic gene flow patterns outside of WCI. This may be due to differences in temporal scales between the genetic and oceanographic analyses. Since ocean current patterns are seasonal and highly variable year by year (Uchiyama et al., 2018, Takeda et al., 2021), we then ran the numerical model for the entire propagule dispersal period in the Yaeyama region. The numerical model did not have sufficient resolution to capture such fine-scale particle dispersal and lacked wave-current interactions to estimate coastal processes accurately. Thus, the dispersal model with higher resolution and wave-current interactions is crucial for understanding coastal dispersal connectivity.

Considering that ecological and mathematical improvement is needed to estimate the probability of dispersal more accurately, numerical ocean modeling and Lagrangian particle tracking methods have been widely accepted to estimate larvae dispersal of marine organisms. A previous mangrove study utilizing a numerical modeling method identified predominant coastal propagule transport along several continental coastlines and island systems that facilitate trans-Pacific population connectivity for mangrove species (Van der Stocken et al., 2019b). However, detachment and settlement in nearshore areas before and after dispersal have not yet been examined. Despite lower statistical power compared to numerical ocean modeling, our release-recapture method utilizing drifting buoys shows beaching events as part of settlement. Rhizophora stylosa propagules are about 23 cm in length, weigh about 35 grams, and tend to maintain an efficient vertical floating orientation in sea water while fully submerged at the surface (Clarke et al., 2001). Hence, drifting buoys are suitable surrogates for mangrove propagules to simulate dispersal trajectories to estimate potential dispersal connectivity via propagule dispersal. Of 31 drifters deployed from just outside the reef at WCI, four trajectories revealed the potential for inter-island dispersal with various destinations in the archipelago (Ishigaki, Kuroshima, Mivako, and Yakabi Islands), and six trajectories showed within-island dispersal (Table 3).

Mangrove sites that are < 100 km apart were indicated as neighboring sites based on genetic analyses; thus, we suggest that beaching events on Ishigaki Island (~58km in 12 days) and Kuroshima Island (~35 km in 9 days) represent the local dispersal potential, and those on Miyako Island (~180 km in 59 days) and Yakabi Island (~ 400 km in 109 days) represent potential for LDD. Those potentials for dispersal are further supported by the estimated minimum and maximum floating periods of propagules (Van der Stocken et al., 2019a).

Although we are unaware of any studies on *R. stylosa's* maximum floating and viability periods, we assume that it shares propagule traits with *Rhizophora mucronata, the* morphology of which is almost indistinguishable from that of *R. stylosa* (Spalding et al., 2010). Therefore, the potential for northeastward LDD among islands is supported by *R. stylosa*'s maximum dispersal viability (150 days; median, 70 days), even though propagule survival is thought to decrease as the dispersal period increases (Drexler, 2001). However, no genetic result has confirmed long-distance connectivity from WCI to other islands. Hence, northeastward LDD in the archipelago was not documented by this study. On the other hand, retention of buoys in the Yaeyama region was less than the maximum floating period (Figure 3.11), which may increase the potential for beaching at local scale and may explain admixed genetic structures in this region (Figure 3.7).

The genetic isolation of OKI is probably influenced by the Kuroshio Current. The Kuroshio flows northeastward about 150~200 km west of the Ryukyu Archipelago, and the current velocity and location are seasonal and highly variable year by year (Uchiyama et al., 2018, Takeda et al., 2021). The majority of observed trajectories beyond Ishigaki Island following the Kuroshio current confirmed a tendency for fast, long-distance (< 100 days) northeastward dispersal without reaching any coast in the archipelago (Table 3). The limited distribution of the WI cluster on Miyako and Okinawa Islands may be due to the Kuroshio current, with a temporal limitation imposed by propagule viability. In a previous study on the Ryukyu Archipelago, these limited trajectories were also found with numerical ocean modeling (Uchiyama et al., 2018).

Local beaching events within six days on Iriomote Island were confirmed, except for one drifter that took > 131 days to beach on the coast 18 km from its deployment site. Drifter experiments highlighted the wide variability in dispersal affected by local eddies. The higher migration rate in WCI (IRMg-IRMf, IRMg-IRMe) and homogeneous genetic structure in the area (Figure 3.7) may be explained by the higher retention rate around the deployment site along the reef at WCI during the first 20 days (Figure 3.10A). A previous ocean-modeling study for coral dispersal in the archipelago also hypothesized retention by currents in WCI and a high proportion of self-recruitment (Uchiyama et al. 2018). Moreover, the absence of a trajectory from WCI to ECI indicated a potential local oceanic barrier, which may explain the genetic discontinuities we found between those areas. Using a numerical model, Uchiyama et al. (2018) also indicated lower particle density reaching ECI from WCI, which suggests a consistent local oceanic pattern.

Difficulties of propagule dispersal among sites were further suggested by observed alongshore currents. More than half the drifters (19) failed to beach during our experiments, and their closest approaches to coastlines while drifting ranged from 20 m to \sim 1 km (Table 3). Most drifters reached reef edges and drifted with alongshore currents without entering the reefs. Even shallow reefs interfere with genetic exchange between close sites for coral species such as *Pocillopora damicornis* (Miller and Ayre, 2004) despite their floating capacities and the higher abundance of coral larvae compared to mangrove propagules. Hence, we suggest that a tendency for localized dispersal of *R. stylosa* is mainly due to its low fecundity, despite the long floating and viable periods of propagules. Stokes drift, contrary to alongshore currents, also affects onshore transport (Monismith et al., 2018). However, these drifters were designed to eliminate the effects of waves (Stokes drift); thus, the representation of propagules. It is also worth noting that the present *in-situ* results represent a subset of entire dispersal trajectories that are specific to seasons and release locations.

3.5. Chapter Conclusions

Using population genetic methods and a release-recapture method employing GPS drifting buoys, we investigated the spatiotemporal scale of island-to-island propagule dispersal of *R. stylosa*, one of the widely distributed mangrove species in the Indo-West Pacific region. With a single empirical dataset with genetic results, how ocean currents may affect fine-scale population connectivity among islands was discussed. Three genetic populations were identified, indicating distinct genetic structures comprising three distinguishable bioregions (genetic clusters). The western end of the archipelago receives relatively frequent migration (m > 0.1), but is genetically isolated from other sites. Based on genetic migration rates, we found that the central area of the archipelago serves as a stepping stone for southwestward, but not northeastward dispersal.

On the other hand, with *in-situ* drifting buoys, we did not confirm prevailing dispersal directionality within the archipelago, but instead confirmed local eddies. Some buoys trapped in those eddies demonstrated potential for successful beaching on another island. A large portion of buoys was carried predominantly northeastward by the Kuroshio Current and drifted away from coastal areas into the Pacific. We found that the spatiotemporal scale of propagule dispersal may be limited by the distance between islands (< 200km), propagule viability duration, and fecundity. Overall, we showed that propagule dispersal of *R. stylosa* in the Ryukyu Archipelago is possible even without stepping stones, although in reality, it is not frequent enough to unify population genetic structure. We also found that the archipelago is isolated from global distribution. Our findings are based on mangrove habitats with little or no human destruction, which should serve as a warning for habitats on island systems that are subject to ongoing threats from deforestation and environmental changes. Identifying the spatiotemporal scale of propagule movement specific to each island system is essential for accurately understanding demographic connectivity among populations.

We interpreted genetic discontinuities within and among islands with current patterns, the distance between islands, and propagule characteristics such as fecundity and floating periods; however, further statistical approaches are needed for a more robust understanding of genetic discontinuities in the archipelago. Fine-scale numerical models may be suitable to estimate tidal amplitude affecting inundation of mangrove habitats and cross-shore currents at the reef edge to predict propagule dispersal from distant habitats. However, including wave-current interactions and obtaining the right combination of environmental parameters, such as topological factors as parameters for the model to achieve a finer-scale evaluation for near-shore currents is difficult (Kamidaira et al., 2017, Uchiyama et al., 2018).

Lastly, the Ryukyu Archipelago was identified as a peripheral site in the *IWP.edge* module in Chapter Two, which corresponded well to the present results. This further indicated that the contribution of propagule dispersal to population connectivity is specific to each archipelago. Thus, in addition to ecological limitations on population connectivity and recruitment, including limited reproductive output and restricted settlement success, identifying fine-scale propagule dispersal patterns unique to individual island systems is essential to understanding their contribution to global species distributions and selecting appropriate sizes and locations of territories for mangrove conservation in archipelagos.

Chapter Four Thesis Conclusion

Mangroves on islands are connected in space and time by ocean currents that transport propagules between coastlines. An earlier study suggested that advances in island connectivity knowledge are impeded by the limited scope, details, and spatiotemporal concordance of existing research (Edmunds et al., 2018). Mangrove island connectivity is no exception. Although most mangroves are found on island systems, processes driving the biogeography, such as propagule dispersal range, are still a puzzle since studies of island mangrove connectivity remain scarce, and quantifying dispersal and estimating recruitment from distant populations is challenging.

Thus, this study sought to better understand island mangrove population connectivity. The first goal was to determine how island mangrove populations, individually and collectively, contribute to regional mangrove biogeography. The simulated annealing algorithm (Guimera and Amaral, 2005) was used on a network of >200 site nodes and 73 species nodes in the IWP region. This analysis yielded two main conclusions. First, although individual islands demonstrated independent, heterogeneous species compositions, most island groups in the IWP are stepping stones regardless of the modules in which they occur. A large number of stepping stone sites across the region contribute to a wide network of mangrove sites within the IWP, which helped to explain less well-defined modules (M < 0.5). Overall, the *l-r* space (*l*: within-module degree, *r*: between-module degree) demonstrated that all island mangrove sites share a smaller number of locally restricted species and some widely distributed species. As collective island groups, the number of widely distributed species per island group increased. Hence, each island group increased in between-module degree. This implied an overall tendency of individual islands to act as local stepping stones, while island groups, which comprise mangrove meta-communities, support a network of broader population connectivity. Hence, stepping stones at different spatial scales create a network of ecological assemblages that and increase resilience to environmental changes.

Second, the distribution of each module compared well with previous paleogeographic studies, population genetic studies, and oceanographic studies to show that the delineation of each module is influenced by past geological events and dispersal parameters, though differently depending on the location. For example, module distributions suggest that the LGM and closure of the Tethys Sea constituted the biogeographic blueprint. Modular species compositions have been persistent, especially for modules in the Coral Triangle (the East India-Sunda and Philippines-North Australia modules), despite rapid habitat degradation due to anthropogenic activities, most of which have been thoroughly discussed in phylogeographic studies. Those modules around the Coral Triangle also aligned well with Wallace's and Huxley's Lines. Those lines are also supported by previous studies on mangrove genera (Duke et al., 2002; Lo et al., 2014; Guo et al., 2016) and a distribution study of Lumnitzera littorea (Guo et al., 2021). Locations and species compositions of the Regional-edge module and the West-Pacific module correspond well to studies of widely distributed species, including A. marina and R. mucronata (Rabinowitz, 1978a; Duke et al., 2002; Saenger et al., 2019). Moreover, a lobal numerical oceanographic analysis with a dispersal condition, which propagule floating period is >1 month or >6 month, demonstrated potential dispersal among many areas identified as stepping stones in the current study (Van der Stocken et al., 2019b).

Overall, in Chapter Two, the simulated annealing algorithm successfully partitioned the IWP region into four bioregions. Those bioregions can be considered biogeographic units within the IWP influenced by geographic features, and biological and physical dispersal parameters. The results implied a complex network of mangrove sites even within individual modules and that effects of historical events rather than contemporary dispersal may be more important in determining biogeographic patterns in the region.

Next, finer-scale population connectivity was studied to understand the network of stepping stones, further considering processes that shape mangrove biogeography. Propagule dispersal distance is essential to understand island mangrove population connectivity, but quantifying the spatiotemporal scale of dispersal has been challenging because not only it is highly species- and site specific, but also physical oceanography around archipelago with the scale of 1 - 10 km is arguably the most difficult scale to quantify (Edmunds et al., 2018). Retention rates of propagules also play a significant part in mangrove connectivity. Within each island system, fine-scale dispersal range and frequency for most mangrove species remain largely unknown. Thus, I sought to address these issues in Chapter Three, using the genetic and oceanographic methods to conduct a fine-scale population connectivity study focusing on one archipelago.

In the current study, population genetic and *in-situ* oceanographic methods revealed the stochastic nature of dispersal of *R. stylosa* in the Ryukyu Archipelago, located at the edge of the species distribution. Considering genetic drift and environmental selection due to population sizes limited by extreme and variable environments (Brown et al., 1996), both migration rates and genetic structures showed that population genetic connectivity among distant sites in this archipelago is not frequent enough to unify the genetic structure, despite the high dispersal ability of this species and the minimal distance between islands (<5 km). The current genetic results are supported by the results of the simulated annealing method. The Ryukyu Archipelago was assigned to the northern end of *IWP.edge* module, further confirming that the Ryukyu Archipelago is comparatively isolated from the rest of the IWP. This was also supported by *in-situ* buoy experiments, demonstrating no connectivity to eastern Pacific sites, despite the Kuroshio Current.

Population genetic and oceanographic methods have been the dominant approaches in studying population connectivity and dispersal patterns. However, both methods have their shortcomings for regional scale studies. Genetic methods require extensive sampling to achieve adequate statistical power, and cannot reveal population demographic connectivity (Lowe and Allendorf, 2010), while oceanographic methods need biological validation of comparable spatiotemporal scale. Earlier studies emphasized the importance of species- and site-specific approaches to understand propagule dispersal and survival (Van der Stocken et al., 2015; Ward et al., 2016) mainly because dispersal ability, including fecundity, is particular to species, but settling patterns are specific to sites, primarily due to rainfall, overland runoff, and tidal regimes (Rabinowitz, 1978a; Sousa et al., 2007).

This thesis enhanced our understanding of island mangrove connectivity, identifying biogeographic roles of each island and island group. A complex network of local and regional stepping-stones shapes mangrove biogeography in the IWP, which in turn supports regional resilience of species against habitat loss and fragmentation. For species preservation and site preservation, network theory identified the most isolated and vulnerable sites, which should be prioritized for conservation. However, local preservation of the genetic diversity of some species may be a losing battle, due to their restricted distributions on small islands and limited dispersal abilities, in the face of rising sea levels, which may negate all efforts to preserve them.

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G -resolution	Species R-resolution Location	Aconthus ebrocteatus	Aconthus ilcifolius	Aconthus volubilis Wall	Acrostichun cureum *	n Arostichum danaeifalium	Aarostichum spedosum	Acrostichum urvillei (Fée)	Aegialitis) annulata	Aegialtis rotundifolia	Aegiæras corniculatum	Aegiæra floridun	s Aglaia a cucultata	Avitennia alba	Avicennia integra	Avitennia marina	Avicennia marina subsp. eucolyptifolia	Aviænnia marina subsp. marina	Avicennia marina subsp. Rumphiana	Avicennia officinalis	Barringtonia racemosa (L.) Spreng.	Barringtonia asiatica (L.) Kurz - c	Barringtonia conoidea Griff.	Bruguiera cylindrica	Bruguiera exaristata	Bruguiera gym norrhiza	Bruguiera 2 × hainesi	Bruguiera parvifiora (Raxb.)	Brugulera sexangula (Lour.)
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Total Saudi Arabia	Saudi Arabia Saudi Arabia Red Sea	0	0	0))	1	0	0	0 0		1	0	0 0	o o o o	0	1	0))	1 (0 (o o o o	0	0			. 0) 0		0 0 0 0	0	0
Djibouti+Yemen	Djibouti Yemen	0	0	0))	0	0	0	0 0) (0	0 0	o o o o	0	1	0))	1 (o a o a	0	0			. o		1 0 0 0	0	0
Total Fritrea	Yemen Socotra Eritrea	0	0	0	0	0	0	0	0 0) (1	0	0 0	o o o o	0	0	0	0	1 0	o o o o	0	0	0	D 0	0		0 0 0 0	0	0
Sudan	Eritrea Green Isalnd Sudan	0	0	0)	0	0	0	0 0) (1	0	0 0	o o o o	0	1	0)	0 0	o o o o	0	0		D 0	0		0 0	0	0
	Bahrain Qatar	0	0	0))	0	0	0	0 0	0 0		0	0 0	o o o o	0	1	0		0 0	o a o a	0	0	0	р с р с	, o		0 0 0 0	0	0
Parsian Sea	Oman United Arab Emirates	0	0	0	5	0	0	0	o 0) (0	o 0	o o o o	0	1	0		1 (0 (o a o a	0	0	0	0 0 0 0	0 1 0 0	, .	0 0 0 0	0	0
Egypt	Iran Egypt	0	0	0))	0	0	0	0 0) (1	0	0 0	o o o o	0	1	0))	1 0	o a	0	0	0	D 0	0 0		0 0 0 0	0	0
Red sea nation	Egypt Abu Minqar Islands Saudi Arabia Persian Gulf	0	0	0	5	0	0	0	0 0 0 0) (5	0 0	0 0 0 0	0 0 0 0	0	1	0	0	0 I	o 0 0 0	0	0	0	D 0	, o		0 0 0 0	0	0
Somalia	Somalia	0	0	0	1	0	0	0	0 0)	0	0 0	0 1	0	1	0)	1 1	0 0	1	0			0		1 0	0	0
Total Tonga	Tonga	0	0	0)	1	1	0	0 0) ()	0	0 0	0 0	0	0	0)	0 1	0 0	0	1			, o		1 0	0	0
AmericanSamoa+Toke	American Samoa	0	0	0)	0	0	0	0 0) ()	0	0 0	0 0	0	0	0)	0 1	0 0	0	0			, o		1 0	0	0
lau	NewZealand Tokelau	0	0	0	,	0	0	0	0 0			0	0 0	0 0	0	0	0	,	0 1	0 0	0	0			, o		0 0	0	0
Wallis&Futuna Islands Samoa	Walksp-utura i sanos Samoa	0	0	0)	1	1	0	0 0) ()	0	0 0	0 0	0	0	0)	0 1	0 0	1	1	0	D 0	0		1 0	0	0
Total Kiribati	Kiribati Phoenix I slands Kiribati Gilbert I slands	0	0	0	5	0	0	0	0 0) (0	0 0	o o o o	0	0	0	0	o i o i	o o o o	0	0	0		. o		0 0	0	0
Total Palau	Kiribati Line Islands Palau	0	0	0)	0	0	0	0 0) ()	0	0 0	0 0	0	0	0)	0 1	o o o o	0	1	0		0		0 0	0	0
Micronesia Kosrae	Palau Peleliu I sland	0	0	0		0	0	1	0 0			0	0 0	0 0	0	0	0		• •	0 0	0	0					0 0	0	0
Island Micronesia Pohnpei	wik romesia Kosrae Island Mic ronesia Pohnoeli	0	0	0		-	-	- 0	0 0			-	0 0	- 0 0 0	0	0	0		- 1	- 0 0 0	0	0		- c	0		- 0 1 0	0	0
Micronesia caroline	Micronesia caroline islands	1	0	0	0	1	0	1	0 0			0	0 0	0 1	0	0	0)	o 1	o 0	1	1		o 0) O		1 0	0	0
Micronesia Wonei	Micronesia Wonei	0	0	0)	0	0	0	0 0) (0	0 0	0 1	0	0	0)	0 1	0 0	0	0	(o c	0		1 0	0	0
Myanmar Philippines	Myanmar Philippines	0	1	0)	1	1	1	0 0	, 1 , (0	1 1	. 1 1 1	0	1	0	, I	1	0 1 1 1	1	0	:	. 1 0 1	0		1 1 1 0	1	1
Philippines Luzon Island	Philippines Luzon I sland	0	0	0		0	0	0	0 0			0	0 0	0 0	0	1	0		1 (0 1	0	0		0 1	. 0		1 0	1	0
Philippines islands1	Philippines Alabat I sland Philippines Polilio I sland	0	0	0	0	0	0	0	o 0) ()	1	o 0	o o o o	0	0	0	0	o i	o a o a	0	0	0	0 0 0 0	0 1 0 0		0 0 0 0	0	0
Philippines islands2	Philippines Samar Island Philippines Cullon I dawl	0	0	0	0	0	0	0	0 0) () (1	1	1 0	0 0 0 n	0	1	0	0	o :	1 1 0 n	0	0	0	0 1 0 1	. 0) n		1 0	1	1
	Philippines Palawan Island Philippines BASILAN ISLAND	0	0	0	0	0	0	0	0 0	0 0		0	0 0	0 0 0 1	0	0	0		0 0	0 0	0	0	0	0 0	i 0		1 0	0	0 0
Philippines islands3	Philippines Jolo I sland	0	0	0	5	0	0	0	0 0) (0	0 0	0 0 0 ^	0	0	0		o i	o 0	0	0			, o		0 0	0	0
	Philippines Tawi Tawi		0	-		0	0	0	0 0			0	0 0				-		n 1	o 0				- -	, , ,		1 0	0	

G-resolution	Species R-resolution L.c. ation	Aconthus ebracteatus	Acanthus ilcifolus	Aconth volubi Woll	us Acrostichur lis aureum *	n Aarostidhum donaeifalium	Acrostichum speciosum	Acrostichum urvillei (Fée)	Aegialitis annulata	Aegialītis ratundīfolia	Aegiaeras corniculatur	Aegiæn n fibridur	os Aglaia n aucullati	Avicenn a alba	nia Avicenn integro	ia Avicennia a marina	Avicennia marina subsp. eucalyptifalia	Aviarnnia marina subsp. marina	Avicennia marina subsp. Rumphiana	Avicennia officinalis	Barringtonia racemasa (L.) Spreng.	Borringtonia osiatica (L.) Kur.	Barringtonia conoidea Griff.	Bruguiera cylindrica	Bruguiera exaristata	Brugulera gymnorrhiza	Bruguiera ×hainesi	Bruguiera parvițiora (Raxb.)	Bruguiera sexonguib (Lour.)
Philippines Mindanao	Philippines Mindanao I sland	0		0	0	0	0	D	0 0	. 0		0	0	0	0	0 0	0 0		D (0		D	D :	1 (D 1	0	1	0
Philippines Guimaras	Philippines Guimaras I sland	0		0	0	0	0	D	0 0			0	0	0	0	0 :	1 () I			. 0		D 1		1 (D 0	0	0	0
Island Philippines Negros	Bhilinging Names Island				0	0		0				1	0	0	1	0	1 (n 1		0	1
Island Philippines Panay]
Island	Pheppines Panay I sand	1		1	1	1	1	1	1 0			1	1	0	0	0	1 0		1 1		. 0		1		1 0	1	0	0	1
New Caledonia	New Caledonia Grand Terre Island (Main	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0				0		D 1		0 (D 0	0	0	0
islands1	New Caledonia Kotomo Island (Ile des Pins)	0		0	0	0	0	D	o 0			0	0	0	0	0 0	o (0		D (o 0	0	0	0
	Solomon islands Naunonga island (Santa	0		0	0	0	0	D	0 0			0	0	0	0	0 0	0 0				0		D	D 1	0 0	D 0	0	0	
Solmon islands1	c ruz i sland) Solomon islands Nendo Island (Santa c ruz			,		0		n				0																	
	Islands) Solom on Islands Ula wa Islands	0		0	0	0	0	- D	o o			0	0	0	0	0 1	- ·		- ·		0		D 1		- ·	 D C	0	0	0
Vanuatu	Vanuatu Vanuatu Aniwa Island	0		1	0	1	0	D D	0 0 0 0			0	0	0	0	0 :	1 1 0 0		o (1		1 I		o (0 1 0 0	0	1	0
	Vanuatu Banksisland	0		0	0	0	0	D	0 0			0	0	0	0	0 0	0 0				0				• •	0 1	0	0	0
Vaguatu islandst	Vanuatu Erromango Island	0		0	0	0	0	- D	0 0			0	0	0	0	0 1	- ·				0				0 0	0 1	0	0	0
Validatu Islandsi	Vanuatu Malekua Island	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0		, . , .		0		D 1		0 0		0	0	0
	Vanuatu Maskiyne Island Vanuatu Tanna Island	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0				1		0		0 0	o c	0	0	0
	Vanuatu Tegua Island Indonesia Aru Islands	0		0	0	0	0	D D	0 0 0 0			0	0	0	0	0 1	o (o (0		D 1		0 0	o c o c	0	0	0
Indonesia islands1	Indonesia Aun Island Indonesia Trangan Island	0		0	0	0	0	1 D	o o o o			0	0	0	0	0 0	o () I			0		D 1		o (0	0	0
	Indonesia Misool Island Indonesia Papua	0		0	0	0	0	D D	o o o o			0	0	0 0	0 0	0 1	0 0 0 1) I	D (0		D 1		o (0	0	0
Independent in the	Indonesia Babar Island Indonesia Larat Island	0	1	0	0	0	0	0	0 0 0 0			0 0	0 0	0 0	0 0	0 0	o (o (0 0	0		D 1		0 0	0 0 0 0	0	0	0
Indonesia Islandsz	Indonesia Tanimbar Island Indonesia Yamdena Island	0		0	0 0	0 0	o 1	D D	o o o o			0 0	0	0 0	0 0	0 1	0 (0 ())	5 (5 (0		D 1		o (D 0	0	0	0
Indonesia islands3	Indonesia Kalimantan Island Indonesia Panaitan Island	0		0	0	0 0	0	D D	0 0			0 0	0 0	0 0	1	0	1 0		1 () () () (0		D 1	D :	1 (0 (D 1	0	0	1
Indennia Inco	Indonesia Sumatra Islands	0		1	0	0	0	D	0 0			0	0	1	1	0	1 0		1 0		1		1	1	1 0	D 1	0	1	1
Indonesia Java	Indonesia Maluku Islands	0		1	0	0	0	1	0 1			1	1	0	0	0 :	1 0	, .	1 0		. 0		1 1		1 0	0 1	0	0	0
Islands	Indonesia sulawesi	0				1	1	1	0 0	. 0		1	0	0	1	0	1 () :	1 0		1		1	0 :	1 (0 1	0	0	1
Indonesia Lesser	Indonesia	1		1	0	1	0	1	0 1	. 1		1	1	0	1	0	1 (0		D 1		1 :	1 1	0	1	1
Sunda islands	Indonesa Lesser Sunda islands Sevri helles	1		1	0	1	0	1	0 1			1	1	0	1	0	1 1		1 (1		1		1 1	1 1 0 1	0	0	1
Jeyenenes	Seychelles Aldabra	0		0	0	0	0	- D	0 0			0	0	0	0	0	1 ()	1 0		0		0	D 1	0 0	0 0	0	0	0
Seychells islands1	Seychelles Menailsland	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0				0				0 0	D 0	0	0	0
	Seychelles Cosmoledo island Seychelles astove island	0		0	0	0	0	D D	0 0 0 0			0	0	0	0	0 0	o ()) (o (0		D 1		o (o c o c	0	0	0
	Seychelles Benjamin Island Seychelles Coetivy	0		0	0	0	0	D D	o o o o			0	0	0	0	0 1	o (5 G		0				o (0	0	0
Seychelles islands2	Seychelles Mahe Island (Main) Seychelles Polvre Island	0		0	0	0	0	D D	o o o o			0	0	0	0	0 1	o (o (1		D 1		o (0	0	0
	Seychelles Praslin I sland Seychelles Sihouette I sland	0		0	0	0	0	D D	o o o o			0 0	0	0 0	0 0	0 : 0 i	1 (0 (D (0		D 1		o (0	0	0
Singapore	Singapore Mozambique	1		0	0	1	1	1 D	0 0 0 0			1	0	0	1	0	1 0) i) 1 1 (0		D 1	D :	1 (0 (D 1 D 1	0	1	1
Mozambique islands1	Mozambique Benguerra Island Mozambique Ibo Island	0		0	0 0	0	0	D D	o o o o			0 0	0	0 0	0 0	o :	1 0))	5 C		0		D 1		o (D 1 D 0	0	0	0
	Mozambique inhac a island Mozambique Tambuze island	0		0	0 0	0	0	D D	o o o o			0	0 0	0 0	0 0	o :	1 (0 (D (0		D 1		o (0	0	0
Mauritius islands1	Pakistan Mauritius	0		0	0	0	0	D	0 0			1	0	0	0	0	1 0		1 0		0		D 1	D 1	0 0	0 1	0	0	0
	Mauritus Rodrigues	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0				0		D 1		0 0		0	0	0
Madagascar+Europa	France Europa I sland	0		0	0	0	0	D	0 0			0	0	0	0	0 1	0 0	, ,			0		0	0 1	0 0	0 0	0	0	0
Island	Malaysia Borneo I sland	1		1	0	1	0	1	0 0	. 0		1	1	1	1	0	1 0		1 (1	1		1	1	1 0	0 1	0	1	1
Total Malay peninsula	Malaysia Malay peninsula Malaysia Pangkor Island	0		0 0	0	0	0	1 D	0 0 0 0			1	0	1	1	0	1 (0 () :) I	1 (D (0		1 ·		1 (0 (0 1 0 C	1	1	0
Chagos+Maldives	Mauritius Chagos Archipelago Maldives	0		0	0	1	0	D D	0 0 0 0			0	0	0	0	0	0 0 1 0				0		1		0 0		0	0	0
Marianas	Marianas Marshallislands	0		0	0	0	0	D D	0 0			0	0	0	1	0 0	o (5 G) (1		1		0 0	D 1	0	0	0
Bangladesh	Rep. of Nauru Bangladesh	0		0	0	0	0	D D	o o	1		0	0	0	0	0	0 0) i	0 (1 () (0		1 I		0 0	D 1 D 1	0	0	0
Total Cambodia	Cambodia Cambodia Kaoh Tonsav Island	1		1	0	1	0	D D	0 0 0 n			1	0 0	1	0	0 0	0 (0 () () () () (1		1 I	D :	1 0	0 1 0 0	0	1	1
Brunei	Cambodia Koh Rong Island Brunei	0		0	0	0	0	D 1	o o			0	0	0	0	0	0 0		o (0		D 1	D 1	0 0	0 0 0 1	0	0	0
China China Haissa Islav	China	1		1	0	1	0	1	0 0	0		1	0	0	0	0	1 ()	1 0) (0		D	D :	1 (D 1	0	0	1
crima naiñan Island	Crima Hainan Island Comoros	1		0	0	1	0	• 0	0 0 0 0			0	0	0	0	0	. (1 (. (1 (, () (1		1	0 I	. (0 (0 1 0 1	0	0	0
Total Comoros	Comoros A nj ouan island Comoros GRANDE COMORES	0		0	0	0	0	D	0 0			0	0	0	0	0	1 (D (, (0		0	u 1	0 (u a	0	0	0
	Comoros Mwalii sland (Comorol slands)	0		0	0	0	0	D	0 0			0	0	0	0	0	1 (1		D	0	• •	D 0	0	0	0
Fiji	Fiji France Mayotte	0		0	0	1	0	1 D	0 0 0 0			0	0	0	0	0	0 0		o () (1		1 D		0 0	D 1	0	0	0
Total Mayotte	France Mayotte Grand-Terre Island (main)	0		0	0	0	0	D	o 0			0	0	0	0	0	0 0				0		D		• •	D 1	0	0	0
Guam	France Mayotte Pamanai Island Guam	0		0	0	0	0	D	o o			0	0	0	0	0 1	0 0 1) (0		D 1		0 0	D 0	0	0	0
India East	India East	1		1	0	1	0	D	0 0			1	0	1	1	0	1 0		1 0		1		1	D :	1 0	0 1	0	1	1
Total India West	India West	0		1	0	1	0	- D	- 0 0 0			1	0	0	1	0 :	- 0		- 0 1 0	. (1		1	- D :	- 0	_ c 0 1	0	0 1	0
Total India Andaman island	tndia Andaman Islands India Middle Andaman island	0		0	0	0	0	D	0 0 0 0	1 0		0	0	0	0	0	1 (1		. (, 1 , 1	1			0 i	. (0 (, 1 D C	0	1	1
India Nicobar Islands	India South Andaman Island India Nicobar Islands	0		U 1	0	0 1	1	U 1	υ 0 0 0	0		0	ป 0	0	0	0	1 () (1 () (0		1	ו ט ו ס	υ (Ο (υ 0 0 1	0	0	0
Japan Nansei-Shoto Kenya	Japan Nansei-Shoto Kenya	0		0	0	1	0	D	0 0 0 0			0	0	0	0	0	1 0		1 0) (1		0		0 0	0 1	0	0	0
South Africa Sri Lanka	South A frica	0		0	0	1	0	D	0 0	. 0		0	0	0	0	0	1 0		1 () ') (1		D 1	D 1	0 0	0 1 0 °	0	0	0
Taiwan	Taiwan	1		1	0	1	1	1	0 0			1	0	0	0	0	1 (1 (1		1	0 :	1 (0 1	0	0	1
Tanzania	Tanzania Tanzania Mafia Island	0		0	0	1	0	D	u 0 0 0			0	0	0	0	0	1 0		1 C) (1		1 D	u 1	u (u 1 D 0	0	0	0
Tanzania islands	Tanzania Pemba Island Tanzania Zanzibar Island	0		0	0	0	0	D	0 0 0 0			0 0	0 0	0 0	0	o 1	0 0 1 0		0 0 0 0	1 (1 0 (1)	0		D		0 (0 (o c	0	0	0
Total Thailand	Thailand East Thailand	0		0	0	0	1	1	0 0	. 1		0	0	0	0	0 0	0 0		0 0 1 0	1	0		1	D :	1 (D 1	0	1	0
Tuvalu	Thailand West Tuvalu	0		0	0	0	0	D D	o o			0	0	0	0	0 0	o () (0		1	D :	1 0	0 1 0 0	0	1	0
Vietnam	Vietnam	1		1	0	1	1	1	0 0	0		1	1	1	1	0	1 0) :	1 0		1		1	1	1 (0 1	0	1	1

G-resolution	Species R-resolution Location	Bruguiera × rhynchopetala	Camptosteman philippinensis (Vidal) Beac	Camptostemon schultzi Most.	Ceriops australis	Ceriops decandra	Ceriops tagal	Cynametra iripa Kostel.	Diospyros Ittorea	Dolithandron spathaara	e Excoecaria agailacha L.	Excoecoria indica (Shirakiopsi Indica)	Heritiera 5 fames	Heritiera globosa Kasterm.	Heritiera ^H Kankensö ⁱ	eritiera Ittorals m Alton	Heritiera nacroptera Kasterm	Kondella candel	Kandelia obovata	Lumnitæra Ittorea	Lumnitzera Lumni raa:mosa ×ros	tzera Nyp iea frutio Wurn	po Os 2015 oct 11b.	sbornia Per todonta ac	nphis Rhia Idulo ap B	ophora _{Rh} Iculato mi Bume	sizophora iucronata	Rhizophora samoensis	Rhizophora stylosa	Rhžophora× lamaraki Montrouz.
AUS NW AUS SW	AUS SW	0	1	0 0	1 1) (0 0	1	. c		0	0	1 D	0 0	o c o c	0 0 0 0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
AUS NT	AUS NT AUS NT Bathurst Island	0	0	0 1		1 1 0 0	1	. 1		1	0	1	o (0 (0 (0 0 0 0	0	0	0	0	1	1	0	1	1	1	1	1	0	1	0
AUS Islands1	A US NT Malville Island	0	c c) 0) 0		0 0	0 0			0	0	D	o (D (0 0 0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS islands2	AUS QLD Moreton Bay (Moreton, North Stradbroke, Bribie I sland) AUS QLD North Stradbroke I sland	0	0) 0) 0		0 0 0 0	0 1	. c		0	0	0	o (0 0 0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SE AUS	AUS NSW AUS Tasmania AUS SA	0	0			0 0 0 0	, , , , , , , , , , , , , , , , , , ,			0	0	1 D D	0 0		2 0 2 0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
AUS NE	AUSVIC	0	c) 0) 0) (0 0 0 0	0 0			0	0	D	o (D (0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS QLD	AUS QLD	1	0	1		1	1	. 1		1	1	1	0 0		0	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0
A03 EA31	AUS QLD Keriri Island	0	0	0 1		0 0	0 0			0	0	0	0 0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	- 0	0
	AUS QLD Lizard Island AUS QLD Bewick Island	0	c c) 0) 0		o o o o) 0) 0			0	0	D D	o (o 0 0 0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
AUS islands3	AUS QLD Hammond Island AUS QLD HICKS ISLAND	0	c c) a) (0 0 0 0) 0) 0			0	0	D D	0 (0 (0 C	0	0	0	0	0	0	0	0	0	0	0	0	0	0 C	0
	AUS QLD Moa Island	0	0) 1)		0				0	0	D	• •		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	AUS QLD Low Wodded Island	0	0	0 0		0 0	1	0		0	0	D	0 0	D (0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS islands4	AUS QLD Daydream Island AUS QLD Daydream Island AUS QLD Keswick Island	0	c 0			, , , , , ,	, , , , , , , , , , , , , , , , , , ,			0	0	D D	0 (0 (, , , ,	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AUS OLD Hinchinbrook	AUS QLD Woody Island AUS OLD Hinchinbrook island	0	0) 0) 0		0	1			0	0	D	0 0		0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
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PNG Main	Papua New Guinea East Main Island Papua New Guinea North Main Island	0	c	, 0	, c	, 0 , 0	, 1 , 1	. c		0	1	1	1 (u (, o	1	0 0	0	0	1	1	0	1	1	1	1	0	0	1	1
	Papua New Guinea South main island	0	c) 1) 1	1			D	1	1	1 (D (0	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1
PNG Daru Island	Papua New Guinea Daru Island Papua New Guinea Haidana Island	0	0	0 1		0 1	1	. 0		0	0	D	o (0 (0 (0 0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0
	Papua New Guinea Motupore Island (SouthMainIsland)	0	c	o 0		0 0	1			D	0	D	• •	D (0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	. 0
PNG islands4	Papua New Guinea Parama Island	0	0			0 0				0	0	D	0 0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	Papua New Guinea Yule Island	0	0			0 0	0			0	0	0	0 0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PNG islands1	Papua New Guinea Los Negros Island	0	0	, o	, . , .	, o	1			0	1	1	1 (, o	1	0	0	0	1	0	0	1	0	1	1	1	0	1	1
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PNG islands2	Papua New Guinea New Britain Island	0		, . 	, . , .	, , , , , , , , , , , , , , , , , , ,				D	1	1	1 0		, , , ,	1		0	0	1	0	0	1	0	1	1	0	0	1	1
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PNG Bougainville	Papua New Guinea Bougainville Island	0	0	0 0		0 0	0 0			0	1	1	1 (0 0	1	0	0	0	1	0	0	1	0	1	1	0	0	1	1
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islands Micronesia Wonei	Micronesia Wonei	0	0	0 0		0	1	. 0		D	0	1	0 0	0 0	0 0	1	0	0	0	1	0	0	1	0	0	0	1			0
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Second 1 1 <td< th=""><th>Carrolation</th><th>Species R-resolution Location</th><th>Brugulera × rhynchopetala</th><th>Camptosteman philippinensis (Vidai) Bea:</th><th>Camptostemon schultzi Mast.</th><th>Ceriops australis</th><th>Ceriops decandra</th><th>Ceriops tagal</th><th>Cynametra iripa Kostel.</th><th>Diospyros Ittorea</th><th>Dolidhandrone spathaara</th><th>Excoecaria agailocha L.</th><th>Ex coecaria indica (Shirakiopsis Indica)</th><th>Heritiera fames</th><th>Heritiera globosa Kasterm.</th><th>Heritiera Kanikensis</th><th>leritiera littoralis Alton</th><th>Heritiera macroptera Kosterm</th><th>Kandella candel</th><th>Kandelia obovata</th><th>Lumnitaero Ittoreo</th><th>Lumnitzera Li racemosa</th><th>mnitzera ×rosea f</th><th>Nypo ruticons Vurmb.</th><th>Osbornia octodonta</th><th>Pemphis acidula</th><th>Rhizophora apiculata Blume</th><th>Rhàophora mucronata</th><th>Rhizophora samoensis</th><th>Rhizophor stylosa</th><th>a Rhèophora× Iamarakii Montrouz</th></td<>	Carrolation	Species R-resolution Location	Brugulera × rhynchopetala	Camptosteman philippinensis (Vidai) Bea:	Camptostemon schultzi Mast.	Ceriops australis	Ceriops decandra	Ceriops tagal	Cynametra iripa Kostel.	Diospyros Ittorea	Dolidhandrone spathaara	Excoecaria agailocha L.	Ex coecaria indica (Shirakiopsis Indica)	Heritiera fames	Heritiera globosa Kasterm.	Heritiera Kanikensis	leritiera littoralis Alton	Heritiera macroptera Kosterm	Kandella candel	Kandelia obovata	Lumnitaero Ittoreo	Lumnitzera Li racemosa	mnitzera ×rosea f	Nypo ruticons Vurmb.	Osbornia octodonta	Pemphis acidula	Rhizophora apiculata Blume	Rhàophora mucronata	Rhizophora samoensis	Rhizophor stylosa	a Rhèophora× Iamarakii Montrouz
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G-resolution	Species R-resolution Location	Rhizophora × selala	Scyphiphora hydrophylaœa	Shirakiapsis indico (Wilid.) Esser	sonneratia Ionceolata Blume	Sonneratio alba Sm.	Sonneratio opetolo Banks	Sonneratia caseolaris	Sonneratia griffithii Kurz	Sonneratia Ianceolata Blume	Sonneratio ovata Backer	Sonneratia× guhgai	Sonneratia × hainanensis	Sonneratia × urama	Xyibcarpus granatum	Xyibca Xyibcarpus rumj molucarnsis (Kost Mat	rpus shi Lat sl.)	Lon	Total Species Cnt.
AUS NW AUS SW	AUS SW	0) (o (0 1	1			0 0	1	0	0	0	1	0	1	0 -15.626	124.5650 115.8750	32
AUS NT	AUS NT AUS NT Bathurst Island	0) I	0 0	0 1	1			L 0 D 0	1	0	0	0	3	. 1	1	0 -11.821	133.1655 1 130.4324	38
AUS Islands1	A US NT Malville Island	0 0) I	0 (0 (0 1	1) 0) 0	0	0	0	0	0		0	0 -13.757 0 -11.468	i 136.2329 1 131.0520	2
AUS islands2	AUS QLD Moreton Bay (Moreton, North Stradbroke, Brible Island)	a		0 0	0 0	0			0 0	0	0	0	0	c	0	0	0 -27.248	3 153.2506	4
	AUS QLD North Stradbroke Island AUS NSW	0	<u> </u>	o c	0 0	0		5 (0 0	0	0	0	0	c	0	0	0 -27.521	153.4616 3 152.0203	2
SE AUS	AUS Tasmania AUS SA	0		0 () 0) 0	0) 0) 0	0	0	0	0	0	0	0	0 -42.003	146.5321 137.8589	1
AUS NE	AUS VIC	0		0 (0 (0 0	0			0 0	0	0	0	0	c	0	0	0 -38.664	146.6375 145.5690	2
AUS QLD AUS EAST	AUS QLD AUS EAST	0		1 0	1	1			L 0	1	0	1	0	0	1	1	1 -10.545	142.2225	44
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AUS islands3	AUS QLD Bewick Island AUS QLD Hammond Island	0	, i	0 (0 0 0 0	0) 0) 0	0	0	0	0	c	0	0	0 -10.166	142.2500 142.2070	1
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AUS islands4	AUS QLD Coomera Island AUS QLD Daydream Island	0		0 C	0 0	0		5 G) 0) 0	0	0	0	0	0	0	0	0 -15.093	145.3790 148.8140	1
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AUS QLD Hindhinbrook AUS Norfolk Island	AUS QLD Hinchinbrook island AUS Norfolk Island	a) I	o (0 0	1		D (0 0	0	0	0	0	c	0	1	0 -18.326	146.2290 167.9505	18
AUS Cocos Island AUS Christmas Island	AUS Cocos Island AUS Christmas Island	0) i	0 (0 (0 0	0) 0) 0	0	0	0	0	c	0	0	0 -12.172	96.8795 105.6365	4
Tuamotu&N7	French Polynesia Tuamotu Island New Zealand	0 0		0 () 0) 0	0) 0) 0	0	0	0	0	0	0	0	0 -37.980 0 -4.361	5 177.7009 5 141.4732	2
	New Zealand North I sland New Zealand South I sland	0 0		0 (0 (0 0	0) 0) 0	0	0	0	0	c c	0	0	0 -37.614	176.0060 169.8800	1
Cook.Moorea.Society.	Cook I slands French Polynesia Moorea I sland	0 0		0 C	0 0	0) 0) 0	0	0	0	0	0	0	0	0 -20.417	·159.8772 ·149.8315	2
Tubai	French Polynesia Society islands French Polynesia Tubuai island	0		0 0 0 0	0 0	0			0 0	0	0	0	0	c	0	0	0 -16.752	-151.4436 3 -150.0000	5
	Papua New Guinea Papua New Guinea East Main Island	0) i	0 1 1 1	1 1	1			L 0 L 0	1	1	1	0	1	1	0	0 -7.522	144.0012 147.6381	26 33
PNG Main	Papua New Guinea North Main Island	a		1 1	. 0	1			. 0	0	0	0	0	c	1	1	1 -3.259	142.4838	26
PNG Daru Island	Papua New Guinea South main island Papua New Guinea Daru Island	0)	1 1	0	1			0 0	0	0	0	0	c	1	1	1 -9.149 0 -9.083	142.6310 143.2015	34
	Papua New Guinea Haidana Island Papua New Guinea Motupore Island	a a		o () 0) 0	0		5 (5 () 0) 0	0	0	0	0	c		0	0 -9.445	147.0367 0 147.2851	2
PNG islands4	(SouthWhare saind) Papua New Guinea Parama Island	a		0 0		0				0	0	0	0	0	0	0	0 -8.991	143.4226	2
	Papua New Guinea Uramu Island Papua New Guinea Yule Island	0		0 1	0	1			0 0	0	1	0	0	0	0	1	0 -7.589	144.6216	11
PNG islands1	Papua New Guinea Los Negros Island Papua New Guinea Manus Island	0				1				0	0	0	0	0	1	1	1 -2.069	147.4236	24
	papua New Guinea Duke of York Island			0 0	, 0 , 0	0			, o	0	0	0	0			0	0 -4.162	5 152.4615	3
PNG islands2	Papua New Guinea New Britain Island	a		1 1	. 0	1			. 0	0	0	o	0	c	1	1	1 -6.135	149.0620	28
	Papua New Guinea New I reland I sland Papua New Guinea Umboi island	0		1 1 0 (. o	1		2 C	1 0 0 0	0	0	0	0	c c	1	1	1 -3.329 0 -5.615	152.0001 147.9638	25
	Papua New Guinea Goodenough Island	a		0 0	0 0	0			0 0	0	0	0	0	c	0		-9.373	5 150.2203	1
	Papua New Guinea Misima Island Papua New Guinea Motorina Island	0	, i	0 (0 0 0 0	0) 0) 0	0	0	0	0	c	0	0	0 -10.661	152.7210 152.5917	1
PNG islands3	Papua New Guinea Normanby Island Papua New Guinea Rossel Island	0 0		0 () 0) 0	0) 0) 0	0	0	0	0	0	0	0	0 -10.048 0 -11.348	151.1082	3
	Papua New Guinea Sideia Island Papua New Guinea Sudest Island	0		0 C	0 0	0) 0) 0	0	0	0	0	0	0	0	0 -10.578	150.8564 3 153.4662	2
	Papua New Guinea Watts Island Papua New Guinea	0		o () 0) 0	0		5 (5 () 0) 0	0	0	0	0	c c		0	0 -10.620	9 152.7842	1
PNG Bougainville	Papua New Guinea Bougainville Island	0		1 1	0	1			. 0	0	0	0	0	c	1	1	1 -6.326	5 155.3960	24
	Solomon islands Solom on islands Guadalc anal I sland			1 1 D (0				0	0	0	0	0	0	0	0 -9.551	158.4089 160.1930	39
Total Solomon islands	Solomon islands New Georgia Island					0				0	0	0	0	0		0	0 -8.102	157.5148	1
	Solomon islands San Christobal I sland	0			0	0			0 0	0	0	0	0	0	0	0	0 -0.853	+ -89.4319 5 39.0043	3
Total Saudi Arabia	Saudi Arabia Red Sea	0			0	0			0 0	0	0	0	0	0	0	0	0 20.934	39.4308	2
Djibouti+Yemen	Yemen Yemen			 0 (0	0			, , , , , , , , , , , , , , , , , , ,	0	0	0	0	0	0	0	0 15.919	5 42.8560 5 53.8427	3
Total Eritrea	Eritrea Eritrea Green Isaind	0		o (0 0	0) 0) 0	0	0	0	0	- - -	0	0	0 13.187	2 42.5332 2 39.4790	4
Sudan	Sudan Bahrain	0) I	0 0	0 0	0)))) 0) 0	0	0	0	0	0	0	0	0 18.192	38.3525 9 50.5125	4
Parsian Sea	Qatar Oman	a a) i	0 (0 (0 0 0 0	0		5 (5 () 0) 0	0	0	0	0	0	· •	0	0 25.751	51.5351 5 58.4788	1
	United Arab Emirates Iran	a a) i	0 (0 () 0) 0	0		5 (5 () 0) 0	0	0	0	0	c c	· •	0	0 24.652	54.6462 55.6802	1
Egypt	Egypt Egypt Abu Mingar I slands	0) i	0 (0 (0 0	0)))) 0) 0	0	0	0	0	0	0	0	0 24.153	35.4532 33.8762	3
Red sea nation Somalia	Saudi Arabia Persian Gulf Somalia	0))	0 (0 (0 0	0)))	0 0	0	0	0	0	c	0	0	0 26.968	51.6186 43.8190	2
Niue	Niue	0		0 0 0 0	0 0	0)))	0 0	0	0	0	0	0	0	0	0 -19.094	3 -169.8100 5 -175.1973	5
Total Tonga	Tonga Pangaimotu Island American Samoa	0		o c	0 0	0) 0) 0	0	0	0	0	0	1	0	0 -21.123	·175.1589	2
AmericanSamoa+Toke lau	American Samoa Tutulla Island New Zealand Tokelau	0) i	0 (0 (0 0 0 0	0		5 (5 () 0) 0	0	0	0	0	0	· •	0	0 -14.188	·170.4277 2 ·171.8312	2
Wallis&Futuna Islands Samoa	Walls&Futura Islands Samoa	0) I	o (0 0	0) () (0 0 0 0	0	0	0	0	c c	· 0	0	-13.303 0 -13.727	·176.2354 2 ·172.3118	6 10
Total Kiribati	Kiribati Phoenix I slands Kiribati Gilbert I slands	0		o () 0) 0	0		D () 0) 0	0	0	0	0	c	0	0	0 -3.589	5 171.5132 0 172.5000	1
	Kiribati Line I slands Palau	0	<u> </u>	0 0 1 0	0 0	0)))) 0) 0	0	0	0	0	c c	0	0	0 2.088	4 -157.1222 4 134.5169	2
Micronesia Kosrae	Palau Peleliu Island	a		o (0 0	0				0	0	0	0	c	0	0	0 7.005	134.2427	1
Island Micronesia Pohnpei	Mic ronesia Kosrae I sland Mic ronesia Pohnpei	0 0		- c	, o	1			, o) o	0	0	0	0	c	1	0	0 5.293	102.9835 6 158.2073	4
Micronesia caroline islands	Micronesia caroline islands	a		1 1	0	1		D (0 0	0	0	0	0	c	1	1	0 8.159	147.6068	22
Micronesia Wonei	Micronesia Wonel	0		1 0	0 0	1		D (0 0	0	0	0	0	0	1	1	0 7.356	7 151.6247	13
Philippines	Philippines	0		1 0	0 0	0			1 0	0	0	0	0	0	1	0	1 13.418	122.0285	35
Philippines Luzon Island	Philippines Euzon I sland	a		o (0	0			0 0	0	0	0	0	c	0	0	0 16.804	121.2344	10
Philippines islands1	Philippines Alabat I sland Philippines Polilio I sland	a a			, 0) 0	0			, 0) 0	0	0	0	0	c	0	0	0 14.121	1/2.0544	3
Philippines islands2	Philippines Samar I sland Philippines Culion I sland	a -			, 0) 0	0 0			. 0 0 0	0	0	0 0 -	0	c -	1	0	0 12.278	119.9588	21
	Philippines BASILAN ISLAND Philippines BASILAN ISLAND	0			0 0	0) () (0 0	0	0	0	0	0	0	0	0 6.573	122.0233 4 121.1340	1
Philippines islands3	Philippines Pangutaran island Philippines Tawi Tawi	a a		0 0 0 0) 0) 0	0		, , , , , , , , , , , , , , , , , , ,) 0) 0	0	0	0	0	c c	0	0	0 6.317	120.5647 119.8281	1

G-resolution	Species R-resolution Location	Rhizophora × selala	Scyphiphora hydrophylaata	Shirakiopsis Indica (Wilid.) Esser	sonneratia Ionceolata Blume	Sonneratio alba Sm.	Sonneratio opetolo Banks	Sonneratia caseolaris	Sonneratia griffithii Kurz	Sonneratio lanceolata Blume	Sonnerati ovata Backer	a Sanneratia× guihgai	Sanneratia × hainanensis	Sonneratia × urama	Xylocarpus granotum	Xylocarpus molucænsis	Xyibcarpus rumphii (Kostel) Mabb.	Lat	Lon	Total Species Cnt.
Philippines Mindanao Island	Philippines Minda nao Island	0		L (0 0	0) (0	0	0 0	0	c) (0	0	8.4632	123.4904	. 6
Philippines Guimaras	Philippines Guimaras I sland	0			0 0	0) (1	0	0 0	0	c) (0	0	10.5788	122.6103	e
Philippines Negros	Philippines Negros I sland	0				1		. 1		D	0	0 0	0	c		0	0	9.7916	122.9273	21
Island Philippines Panay	Philippines Panay I sland	0				1) (0	0	0 0	0	c) (1	. 0	11.3851	122.5178	25
Island New Caledonia	New Caledonia	1		L (0 0	0) 1	. 1	0	0	0 0	0	c) 1	. 0	1	-21.8425	165.7846	27
New Caledonia	New Caledonia Grand Terre Island (Main Island)	0			0 0	1		0 0		0	0	0 0	0	c	0 0	0	0	-21.1958	165.4041	5
islands1	New Caledonia Kotomo Island (I le des Pins)	0			0 0	0) a		D	0	0 0	0	c) a	0	0	-22.6565	167.5333	1
	Solomon islands Naunonga island (Santa cruz I sland)	0			0	0) (D	0	0 0	0	c	9 1	. 0	0	-11.6474	166.8516	1
Solmon islands1	Solomon islands Nendo Island (Santa cruz Islands)	0				0) c		D	0	0 0	0	c) c	0	0	-10.7068	165.9255	6
Vanuatu	Solomon islands Ula wa Islands Vanuatu	0			0	0) (0	0	0 0	0	0) (0	0	-9.7539 -16.5113	161.9652 167.7511	25
	Vanuatu Aniwa Island Vanuatu Banksi dand	0			0	0				D D	0	0 0	0	0		0	0	-19.2509	169.6006	1
	Vanuatu Efate Island Vanuatu Fromaneo Island	0		 		0				- D	- 0 0	0 0	0	0		. 0	0	-17.6431	168.4345	2
Vanuatu islands1	Vanuatu Espiritu Santo (Main Island)	0				0				0	- 0	0 0	0	-		0	0	-15.2747	166.9307	1
	Vanuatu Maskiyne Island	0				0				0	0	0 0	0	0				-16.5308	167.8461	1
	Vanuatu Tegua Island	0			0	0				0	0	0 0	0	0		0	0	-19.5046	169.3649	1
	Indonesia Aru I stands Indonesia Aun I stand	0			, u	0		, . , .		0	0	0 0	0	0	, . , .	. 0		-6.4813	134.5395	2
Indonesia islands1	Indonesia Trangan Island Indonesia Misool Island	0) () 0) 0	0) c		0	0	o o o o	0	0) c	0	0	-6.5009	134.3521 130.1010	1
	Indonesia Papua Indonesia Babar Island	0) 0	1) c		0	0	0 0	0	c) c	0	0	-4.4649 -7.8911	137.7694 129.6964	3
Indonesia islands2	Indonesia Larat Island Indonesia Tanimbar Island	0) () () 0) 0	0				0	0	0 0 0 0	0	0		0	0	-7.1444 -7.4694	131.9032 131.5010	1
	Indonesia Yamdena Island Indonesia Kalimantan Island	0) () 0) 0	0) 0) 1		0	0	0 0 0 0	0	0) 0) 1	. 0	0	-7.5342 -0.7630	131.3594 117.0725	17
Indonesia islands3	Indonesia Panaitan Island Indonesia Sumatra Islands	0) 0 . 0	0) ()) 1		0	0 0	0 0 0 0	0	c c) ()) 1	0	0	-6.5802 -1.1096	105.2075 101.3974	33
Indonesia Java Indonesia Maluku	Indonesia Java	0		1	. 0	1) 1	. 1	0	0	1 0	0	c) 1	1	1	-7.4802	110.7471	33
Islands	Indonesia Maluku Islands	0				1				0	0	1 0	0	0		1	1	-6.5033	134.2300	25
Indonesia islands4	Indonesia	0			1	1) 1		0	1	1 1	0	1	. 1	1	0	-2.5408	120.5956	41
Sunda islands	Indonesia Lesser Sunda islands	0			. 0	1) 1	. 1	0	0	0 0	0	1	. 1	1	1	-8.9991	120.0000	38
Seychelles	Seychelles Seychelles Aldabra	0) () 0) 0	1) (0	0	0 0	0	0) 1) (0	0	-4.6458 -9.4154	55.3899 46.3384	14 6
Seychells islands1	Seychelles Assomption I sland Seychelles Menai I sland	0) () 0) 0	0) a		0	0	o o o o	0	0) a	0	0	-9.7356 -9.7084	46.5103 47.5153	1
	Seychelles Cosmoledo island Seychelles astove island	0) () 0) 0	0) (0	0 0	0 0 0 0	0	0) (0	· · ·	-9.7045 -10.0644	47.5173 47.7403	1
	Seychelles Benjamin island Seychelles Coetivy	0) () () 0) 0	0) (0	0 0	0 0 0 0	0	c) (· 0	· 0	-5.4415 -7.1303	53.3465 56.2787	1
Seychelles islands2	Seychelles Mahe Island (Main) Seychelles Poivre Island	0) () () 0) 0	0) a		0	0 0	o o o o	0	c c) a	· 0	· •	-4.4610 -5.7464	55.4959 53.3057	5
	Seychelles Prasiin I sland Seychelles Silhouette I sland	0) () a	0) a		0	o 0	o o o o	0	0) a	· •		-4.3312	55.7474 55.2370	2
Singapore	Singapore	0		1 1) (. 0	1				0	0	1 0	0	0) 1	1	. 0	1.4419	103.7183 34.7596	30
Mozambique islands1	Mozambique Benguerra Island	0				0				o n	0	0 0	0	0		. 0	0	-21.8628	35.4416	5
	Mozambique inhac a island	0				0				0	- 0	0 0	0	-		0	0	-26.0162	32.9564	3
Mauritius islands1	Pakitan	0			0	0				0	0	0 0	0	0		0	0	24.4043	67.3119	
Mauricius Islandsi	Mauntius Mauritius Rodrigues	0			0	0				0	0	0 0	0	0		0	0	-20.3882	63.4261	1
Madagascar+Europa	Madagascar France Europa Island	0				1) (0	0	0 0	0	6	, , , ,	0	0	-16.1940	44.4685 40.3528	15
Malaysia Borneo Island	Malaysia Borneo I sland	0			1	1		. 1		D	1	1 1	0	c	. 1	1	1	1.7856	111.2258	44
Total Malay peninsula	Malaysia Malay peninsula Malaysia Pangkor Island	0			. 0) 0	1) 1) (1	0 0	1 0 0 0	0	c) 1) (1	1	4.4836 3.4903	103.2434 113.2964	32
Chagos+Maldives	Mauritius Chagos Archipelago Maldives	0) 0) 0	0) (0	0 0	0 0 0 0	0	c		· 0	· 0	-6.1826 3.3087	72.0954 72.8828	4
Marianas	Marianas Marshallislands	0) (0 0	0) (0	0	0 0	0	0) (0	0	18.4586 7.3955	145.4762 168.7661	16
Bangladesh	Rep. of Nauru Bangladesh	0) ()	0 0	0) (1 1		1	0	0 0	0	0	0 0	0	. 0	-0.5306 22.1882	166.9250 89.9635	36
Total Cambodia	Cambodia Cambodia Kaoh Tonsay Island	0) () () 0) 0	1) 1) (0	0 0	1 0 0 0	0	0) 1) (1	1	11.0144 10.4366	103.1383 104.3300	30
Brunei	Cambodia Koh Rong Island Brunei	0			0	0) (0	0	0 0	0	0) (0	0	10.7345 4.7287	103.2308 114.5873	4
China China Hainan Island	China Kalena Idaed	0			0	1				0	0	1 1	1	0		. 0	0	21.0922	110.2249	28
China Hainan Islanu	Comoros	0			0 0	1		, . , .		0	0	0 0	0	0) 1	1	0	-11.8300	43.4619	13
Total Comoros	Comoros Anjouan island Comoros GRANDE COMORES	0) 0) 0	1				0	0	o o o o	0	0		. 0		-12.1824	44.4350 43.3759	3
	Comoros Mwaliisland (Comoroislands)	0			0 0	0) (D	0	0 0	0	c) (0	0	-12.3326	43.7316	. 4
Fiji	Fiji France Mayotte	1) () 0) 0	0) (0	0	0 0 0 0	0	c) 1) (1	1	-18.0475 -12.7282	178.5993 45.1340	16
Total Mayotte	France Mayotte Grand-Terre Island (main)	0			0 0	0) (D	0	0 0	0	c) (0	0	-12.7858	45.1377	5
Guam	France Mayotte Pamanai Island Guam	0) (0 0	0) (0	0	0 0	0	0) (0	0	-12.7824 13.3345	45.2856 144.7673	11
India East	India East India Laccadive Island (36 islands)	0) 0) 0	0		1 1) 0		1	0	0 0 0 0	0	0) 1) (. 1	. 0	11.4385 10.5592	79.7921 72.6366	36
Total India West	India West	0) o	0) 1) 1		0	o 0	0 0	0	0) 1) 1	0	0	11.1097	76.0281	27
Total India Andaman island	India Middle Andaman island	0				0				o n	0	0 0	0	0		0	0	12.5046	92.7929	5
India Nicobar Islands	India Nicobar I slands	0			. 0	1) 1		0	0	0 0	0	c) 1	1	1	8.0595	93.3768	30
Japan Nansei-Shoto Kenya	Japan Nansei-Shoto Kenya	0) U	1) () (0	0	0 0	0	0) 1	1	. 0	-2.0785	40.9644	14
South Africa Sri Lanka	South A frica SriLanka	0		0 0 L 1	0 0	1) 0 11		0	0	0 0 0 0	0	0) 1) 1	0	1	-29.8636 8.1397	30.9904 79.8077	31
Taiwan Tanzania	Taiwan Tanzania	0			0 0	1		0 1		0	0	1 0	1	c	0 1	0	0	25.1166 -7.8357	121.4696 39.4314	30
Tanzania islands	Tanzania Mafia Island Tanzania Pemba J dawi	0) () (0 0	0) (0	0	0 0 0 n	0	0) (0	0	-7.8584	39.7559 39.7649	3
	Tanzania Zanzibar I sland Thailand Cost	0) (0	1) (0	0	0 0	0	0) (0	0	-6.1538	39.3354	7
Total Thailand	Thailand Thailand	0		1 1) '	. 0	1) 1) '		1	0	1 0	0	0) 1) '	1	1	8.3903	98.5292 98.7410	45
Tuvalu	Tuvalu	0) 0	0		0 0		0	0	0 0	0	0) (0	0	-8.5222	179.1938	4
viculatti	v estnam	0			0	1						0	0			0	1			

Appendix R-resolution Dataset (Data source: MRDH, POWO)