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Habitat discontinuities form strong barriers to gene flow among mangrove populations, despite the capacity for long-distance dispersal

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Abstract

Aim: Mangrove forests are among the world's most important ecosystems but are declining rapidly worldwide. Effective conservation management requires a better understanding of the patterns and drivers of gene flow across a range of spatial scales. Despite the capacity for long-distance propagule dispersal, field studies suggest that mangrove propagules tend not to disperse far from the release point, which has important implications for the impact of habitat discontinuities on gene flow. We use a comprehensive seascape genomics approach to investigate this concept in the world's most widely distributed mangrove species, *Avicennia marina*.

Location: Twenty-one sites along 2,400 km of Western Australian coastline.

Methods: We used 6,162 neutral SNP loci and a hierarchical sampling design to investigate patterns of gene flow and structuring among 21 populations of *A. marina*. We combined these data with GIS spatial analyses in a regression model to test the relative influence of habitat continuity and geographic distance on patterns of genetic differentiation.

Results: We found a complex pattern of gene flow; broadscale isolation-by-distance, disrupted by strong genetic discontinuities that coincided with gaps in mangrove distribution. These genetic discontinuities formed seven discrete subpopulations with negligible evidence for recent migration among them. The regression model combining marine geographic distance and habitat continuity as explanatory variables best fit the data, explaining 86% of the total genetic variation.

Main Conclusions: Our results validate previous assertions that propagule dispersal in *A. marina* is spatially limited and demonstrate that significant gaps in mangrove distribution present strong barriers to stepping-stone gene flow in this species. This reiterates that dispersive life history features cannot be assumed to lead to widespread connectivity and demonstrates that effective management of these important ecosystem builders should prioritize restoring habitat continuity and minimizing further fragmentation.

KEYWORDS

Avicennia marina, genotyping-by-sequencing, habitat discontinuities, mangrove, marine connectivity, propagule dispersal, seascape genomics

1 | INTRODUCTION

Understanding patterns of gene flow and connectivity among populations has long been a central theme in molecular ecology and evolutionary biology (Nei, 1972), and more recently, has become an important basis for conservation management (Allendorf, Hohenlohe, & Luikart, 2010; DeSalle & Amato, 2004). Gene flow maintains genetic diversity, which is critical for population resilience and persistence following environmental change, and such connectivity provides recruitment sources for the recovery of populations following major disturbances (Allendorf, Luikart, & Aitken, 2013; Frankham, Ballou, & Briscoe, 2002). With increasing pressures on natural populations from anthropogenic and climate disturbances, knowledge of population connectivity is vital for identifying vulnerable populations and informing management actions at appropriate spatial scales.

The extent of connectivity is initially dependent on the dispersal ability of the organism in question. This makes investigating connectivity in marine systems particularly challenging because dispersal is often facilitated through movements of larvae or propagules in ocean currents and is difficult to track directly (Cowen & Sponaugle, 2009). Genetic data provide an excellent indirect alternative, where spatial patterns of genetic variation can be used to infer connectivity among populations (Hellberg, Burton, Neigel, & Palumbi, 2002). Traditional genetic approaches have been limited by assuming homogeneous environments for equal dispersal over a given geographic distance, when a number of factors may bias the direction or ease of dispersal among populations (Balkenhol, Cushman, Storfer, & Waits, 2016). In a seascape context, factors such as coastal topography, physical oceanography, habitat continuity, selection or historical events may influence dispersal and limit connectivity, even in species with highly dispersive life stages (Cowen & Sponaugle, 2009; Selkoe et al., 2016). For example, oceanographic circulation can bias the strength and direction of larval dispersal in corals (Foster et al., 2012; Thomas et al., 2015) and habitat continuity is vital to maintaining connectivity in reef fish (Gonzalez, Knutsen, & Jorde, 2016; Johansson, Banks, Glunt, Hassel-Finnegan, & Buonaccorsi, 2008; Riginos & Nachman, 2001). Quantitative integration of population genetics with marine ecology, oceanography or geography, known as seascape genetics, is a rapidly growing field that allows powerful insight into the complexities of marine connectivity beyond traditional genetic models (reviewed in Selkoe et al., 2016). Seascape genetics studies to date have largely focussed on species with pelagic larval dispersal, particularly fish (Liggins, Treml, Possingham, & Riginos,2016; Saenz-Agudelo et al., 2015; Saha et al., 2015; Selkoe et al., 2010), corals (Foster et al., 2012; Thomas et al., 2015) and other invertebrates (Benestan et al., 2016; Giles, Saenz-Agudelo, Hussey, Ravasi, & Berumen, 2015; Selkoe et al., 2010; Silva & Gardner, 2016; Teske, Sandoval-Castillo, Van Sebille, Waters, & Beheregaray, 2016). With the exception of kelp stands (Alberto et al., 2011; Fraser, Thiel, Spencer, & Waters, 2010), relatively little attention has been paid to groups with non-larval propagules, such as mangroves.

Mangrove forests are among the most productive and biologically important ecosystems in the world (Giri et al., 2011), providing a wealth of services that uniquely bridge marine and terrestrial processes (Alongi, 2012; Nagelkerken et al., 2008; Rog, Clarke, & Cook, 2017). Dispersal in mangroves is also a combination of aquatic and terrestrial processes; propagules are dispersed by water, while pollination occurs *via* flying insects (Hutchings & Saenger, 1987). While insect pollination largely operates within populations, buoyant mangrove propagules remain viable for extended periods in water, such that they have the potential to drift in ocean currents (Tomlinson, 1986). Propagule dispersal, therefore, could be expected to result in high levels of population connectivity and little genetic structure over large distances. However, as for many marine species with the capacity for long-distance dispersal (LDD), genetic studies have demonstrated patterns of isolation-by-distance (IBD) and subpopulation structuring in several species (Cerón-Souza, Bermingham, McMillan, & Jones, 2012; Dodd & Afzal Rafii, 2002; Mori, Zucchi, & Souza, 2015; Wee et al., 2014), indicating that propagule dispersal in mangroves is more constrained than previously thought. More than half of the world's mangrove forests have been lost in the last 50 years due to both natural and anthropogenic causes (Giri et al., 2011), and as these ecosystems become smaller and more fragmented, a better understanding of the factors limiting connectivity is critical to their recovery and future preservation.

Avicennia marina (Forskk.) Vierh. is the most widely distributed mangrove species worldwide, and this is considered due to LDD of buoyant propagules, coupled with tolerance to a wide range of environmental conditions (Crisp, Daniel, & Tortell, 1990; Duke, 1990; Duke, Benzie, Goodall, & Ballment, 1998). However, field studies have suggested that LDD in *A. marina* is rare and instead, that the majority of propagules disperse less than 1 km from their release point and rarely over 10 km (Clarke, 1993). This has led to the prediction that habitat discontinuities should present major barriers to gene flow among populations (Clarke, 1993; Duke et al., 1998), although this has never been tested. Genetic studies to date have found evidence of structuring at global scales (Arnaud-Haond et al., 2006; Duke et al., 1998; Maguire, Saenger, Baverstock, & Henry, 2000) and panmixis at local scales between neighbouring estuaries (Hermansen, Roberts, Toben, Minchinton, & Ayre, 2015; Melville & Burchett, 2002); however, little work has been done at intermediate scales, which are most relevant to conservation management. Moreover, these studies have been limited by low numbers of markers and older molecular technologies; more comprehensive investigations of connectivity in *A. marina* are clearly needed.

The naturally patchy distribution of *A. marina* along the Western Australian coastline presents an ideal opportunity to use seascape genomics to resolve long-standing questions of connectivity, particularly the impact of habitat discontinuities on gene flow. Here, we employed genotyping-by-sequencing (GBS) to generate a high-resolution SNP dataset to assess patterns of genomic variation in a hierarchical sampling design of 21 populations that incorporated local, regional and broad spatial scales along approximately 2,400 km of coastline. We then used GIS data to quantify the mangrove

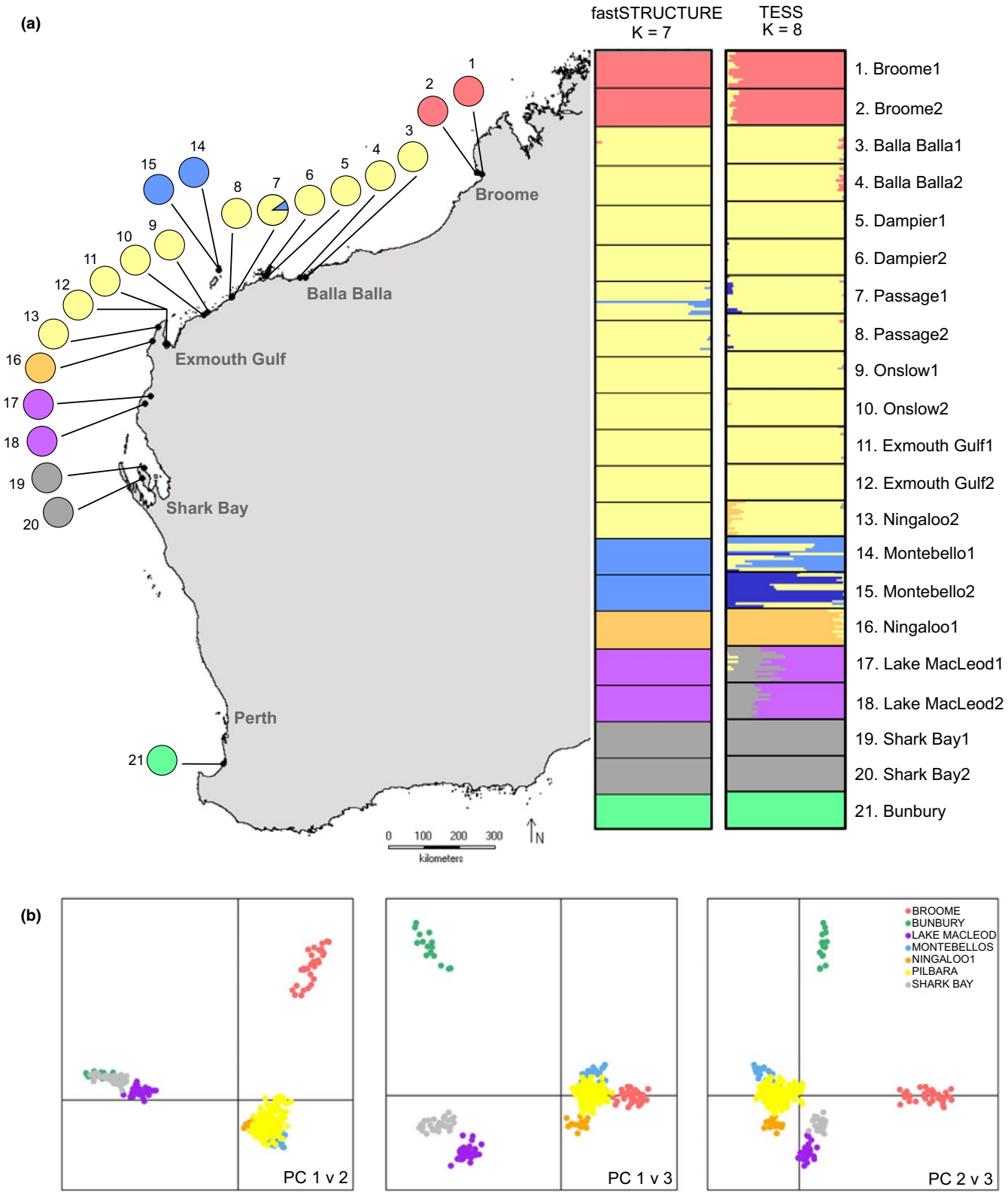

FIGURE 1 Clustering analyses of genomic variation for 21 sampled sites of *Avicennia marina* along the Western Australian coastline. (a) FastStructure (K = 7) and Tess (K = 8) results: for each analysis, the bar plot shows each individual represented by a horizontal bar that is partitioned into the proportion of its affinity to each genetic cluster by differential colouration. Individuals are arranged in population and cluster order for clarity. The map indicates the average proportions of assignment to each genetic cluster for each sampled site from FastStructure, represented in pie charts to show the geographic pattern of genomic variation. (b) Principal coordinate analysis for genomic variation across the first three axes coloured according to the seven FastStructure clusters [Colour figure can be viewed at wileyonlinelibrary.com]

distribution across this range and performed regression analyses to test the relative contributions of geographic distance and habitat continuity in explaining patterns of genetic variation. If LDD is extensive, we would expect no differentiation across the sampled range, regardless of distance or habitat continuity. If dispersal is limited by geographic distance alone, we would expect to see a strong pattern of IBD, and if habitat discontinuities do present a barrier to dispersal, we would expect them to coincide with sharp genetic discontinuities, forming discrete subpopulations.

2 | METHODS

2.1 | Sampling design and collection

A total of 21 sites were sampled in a hierarchical design from 11 locations along the Western Australian coastline (Figure 1). Sampling focussed on the Pilbara region for local-regional scales: seven locations were sampled approximately 100 km apart, with paired sites (3–40 km apart) nested within each location. Four additional locations were sampled for a broader perspective: to the north in Broome, and further south in Lake MacLeod, Shark Bay and Bunbury. Paired sites were also sampled for each of these locations except for Bunbury, which exists as an isolated stand. The southward flowing Holloway and Leeuwin Currents are the major currents operating along this stretch of coastline (Appendix S1) during the Autumn (April-Jun) fruiting period of *A. marina* in Western Australia (Duke, 1990). Within each site, fresh leaves were collected from 16 non-adjacent trees with a minimum sampling distance of 5-10 m. Leaf material was freeze-dried prior to DNA extraction.

2.2 | Genotyping-by-sequencing library preparation, de novo assembly and filtering

DNA was extracted using the Invisorb DNA Plant HTS 96 Kit (Stratec Molecular, Germany). Genotyping-by-sequencing included all 336 samples, plus 24 replicate samples for a total of 360 samples. Replicates had the same DNA source but were barcoded and processed independently. Samples were sent to the Australian Cancer Research Foundation's Biomolecular Research Facility (ACRF BRF; Canberra, Australia) for GBS library preparation and sequencing. Library preparation followed Elshire et al. (2011). Briefly, genomic DNA was digested with the *Pst*I restriction enzyme and fragments were ligated with uniquely barcoded adaptor pairs. Following PCR and quantification, the samples were pooled in an equimolar manner. Amplicons of 250–450 bp were extracted from agarose gel and sequenced for 75 bp, paired-end reads in a single lane of a NextSeq500 Illumina sequencer.

FastQC software (http://www.bioinformatics.bbsrc.ac.uk/projects/fastqc) found high sequence quality (average Phred scores of 37 per base and 38 per sequence). Sequences were then demultiplexed and filtered using the *process_radtags* pipeline in Stacks v1.37 (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013). Sequences were trimmed to 75 bp and options to clean data (*-c*), rescue barcodes (*-r*) and discard reads with low-quality scores (*-q*) were applied with default values. Due to low read recovery (<75,000 reads), four samples were discarded from further analysis.

Assembly, SNP calling and filtering methods are detailed in Appendix S2. Briefly, without a reference genome for *A. marina*, the demultiplexed data were assembled *de novo* and genotyped using the *denovo_map.pl* pipeline in Stacks. We followed the method of Mastretta-Yanes et al. (2014) using replicate pairs to determine the most suitable running parameters (*-m* = 5; *-M* = 2; *-n* = 2) for *de novo* assembly. To avoid linkage, we applied the *write_single_snp* option in the *populations* component of Stacks to produce a single SNP for each locus, resulting in a total of 43,491 SNPs. The data were filtered further in Tassel v5.2.21 (Bradbury et al., 2007) (maf = 0.02; min taxa = 0.1; min snps = 0.2; min het = 0.05; max het = 0.95), reducing the dataset to 6,502 SNPs. Analyses of population genetic structure often rely on assumptions of neutrality so we used BayPass v2.1 (Gautier, 2015) as a final filtering step to identify loci that may be influenced by selection. We used modified running parameters for consistency among runs (*-nval* = 100,000; *-burnin* = 10,000; *-npilot* = 30; *-pilotlength* = 2,000). Across three independent runs, 340 outlier loci identified at the 1% threshold, representing both directional (123) and balancing selection (217), were removed from further analysis. The final neutral dataset of 6,162 SNPs was converted to other program-specific input files using PGDSpider v2.1.0.0 (Lischer & Excoffier, 2012).

2.3 | Genomic diversity and population structure

To thoroughly investigate genetic structuring, we used several clustering methods that operate at the individual level but have differing assumptions. First, Bayesian analysis implemented in FastStructure (Raj, Stephens, & Pritchard, 2014) was used to detect *K* genetic clusters, without any priors regarding population identity or geographic location. The upper *K* limit was set to the number of populations plus one, and the *chooseK.py* function was used to infer the most likely value(s) of *K*. Discrete clustering patterns can be confounded with patterns of IBD (Meirmans, 2012), so we also used a spatially explicit Bayesian alternative, implemented in Tess v2.3.1 (Durand, Jay, Gaggiotti, & François, 2009). Tess assumes spatial autocorrelation in the data and accounts for the geographic distribution of samples in the clustering model. The program was run using the CAR admixture model, performing 100 iterations for each *K* value (again, K_{max} was the number of populations plus one), with 50,000 sweeps, a burnin of 10,000 and the default spatial interaction parameter. The most likely value(s) of *K* was determined by stabilization in the deviance information criterion across K_{max}. Finally, genetic structure was also assessed using principal coordinates analysis (PCoA) because this multivariate method does not rely on any particular evolutionary model and is therefore free of the more strict assumptions made by FastStructure and Tess (Jombart, Pontier, & Dufour, 2009). PCoA was performed in *R* (*R* Development Core Team, 2008) using the Adegenet package v.2.0.1 (Jombart, 2008).

Population differentiation (pairwise F_{ST}) was estimated using ARLEQUIN v35.2.2 (Excoffier, Laval, & Schneider, 2005) and visualized using the program's *R*-lequin functions. Analysis of Molecular Variance (AMOVA) was also performed in ARLEQUIN to partition the total genetic variation within and among groupings based on the results of the clustering analyses, as well as within and between sites and locations, as per the hierarchical sampling design. Genetic diversity was assessed using the HIERFSTAT package v0.04-22 (Goudet, 2005) in *R* to estimate allelic richness (A_R) and expected heterozygosity (H_E), while GENALEX v6.501 (Peakall & Smouse, 2006) was used to calculate the percentage of polymorphic loci.

Finally, contemporary migration rates and individual ancestries were estimated among the FASTSTRUCTURE clusters using BAYESASS v3.0 (Wilson & Rannala, 2003). To balance sample sizes, we randomly subset 50 samples from the Pilbara cluster (see Results). Preliminary runs ensured the mixing parameters were appropriate (20-60% acceptance) and five full runs (*-i* = 10,000,000; *-b* = 1,000,000; *-n* = 1,000) were performed with differing starting seeds. Convergence of parameter estimates was assessed by examination of trace files in TRACER v1.6 (http://tree.bio.ed.ac.uk/software/tracer/) and the best run was determined by Bayesian deviance using the *calculateDeviance.R* script from Meirmans (2014).

2.4 | Seascape effects on gene flow

To map the spatial extent of *A. marina* along the sampled range, we compiled existing mangrove GIS layers from remote sensing analysis. These mapping data were then used in FRAGSTATS v4.2.1 (http://www.umass.edu/landeco/research/fragstats/fragstats.html) to calculate three spatial metrics to represent mangrove habitat continuity: the proportion of gridcells between site pairs that had mangrove present (PROP); connectance index (CONNECT) for the proportion of joinings among all patches, given the total number of patches, over a threshold of 15 km; and coefficient of variation for the Euclidean nearest neighbour (ENN_CV) for the relative variability around the mean distances between nearest neighbouring patches. For the first two metrics, high values represent high levels of mangrove habitat continuity between paired sites, while high values of ENN_CV represent higher patch dispersion, indicative of lower habitat continuity. Details of GIS layers and FRAGSTATS analyses are given in Appendix S3.

To assess IBD, marine geographic distance (hereafter referred to as simply "geographic distance") between all pairwise site combinations was calculated as the shortest distance by water using the MARMAP v.0.9.6 (Pante & Simon-Bouhet, 2013) *R* package. Geographic distances were not log transformed because the coastal sampling design essentially followed a one-dimensional model (Rousset, 1997).

We used partial Mantel tests and multiple matrix regression with replication (MMRR; Wang, 2013) to determine whether geographic distance or habitat continuity better explained patterns of genetic differentiation in *A. marina*. Preliminary testing indicated that the three continuity metrics were highly correlated but the PROP metric performed the strongest and conformed to normality and homoscedasticity better than the CONNECT or ENN_CV measures so this metric was included in the model to represent habitat continuity. There was no collinearity between the geographic distance and habitat continuity metrics. Prior to analysis, the distance matrices were standardized to have a mean of zero and standard deviation of one. Simple and partial Mantel testing was done using IBDWS (http://ibdws.sdsu.edu/). To avoid potential issues with inflated Type I error rates, partial Mantel tests were interpreted based on a more stringent significance threshold of 0.005 (Cushman, Wasserman, Landguth, & Shirk, 2013). MMRR was implemented in *R* using the functions provided by Wang (2013) and run with 10,000 permutations.

3 | RESULTS

3.1 | Genomic diversity and population structure

Similar patterns of genetic clustering were found across the three analytic methods used. FASTSTRUCTURE identified seven genetic clusters that showed geographical structure (Figure 1a). The four broad locations each formed separate clusters, pairing sites within Broome, Lake MacLeod, Shark Bay and Bunbury, with a fifth cluster for the Montebello Islands. Along the Pilbara mainland, all sites and locations formed a single, large genetic cluster, with the exception of the southernmost Ningaloo site, which formed the seventh cluster. These clusters were highly distinct, the only admixture occurring between the Montebellos cluster and one of the sites at Passage. The TESS results were similar, finding the same seven clusters and an additional eighth cluster splitting the sites at the Montebellos into two separate clusters (Figure 1a). These Montebellos clusters were highly admixed with the Pilbara cluster. There was also some admixture between the Shark Bay and Lake MacLeod clusters. Finally, the PCoA showed four major clusters across the first three axes. The first axis primarily separated the Broome and Pilbara sites in the north from the Lake MacLeod, Shark Bay and Bunbury sites in the south (Figure 1b). The second axis largely split Broome from the Pilbara, and the third axis largely separated the Bunbury site from all others. Within these major clusters, further separation can be seen between the Lake MacLeod and Shark Bay sites, and the Pilbara sites were not randomly overlapped to indicate a single, homogeneous group but instead showed a geographic progression, indicative of a pattern of IBD, while the southernmost Ningaloo site and the Montebellos sites were slightly offset from the Pilbara cluster.

Pairwise differentiation ranged between 0.014 and 0.467, with a global value of 0.174 (Figure 2, Appendix S4). The greatest values largely occurred between pairwise comparisons of the Bunbury site with all others (mean = 0.389 ± 0.008) but also in comparisons with Broome, Montebello Islands and the southernmost Ningaloo site. The lowest values occurred between paired sites within locations, particularly in the Broome and Pilbara clusters (F_{ST} < 0.05 for all pairwise comparisons). Exceptions were moderate values found between paired sites within each of the Ningaloo and Montebello Island locations, with F_{ST} values of 0.147 and 0.156, respectively.

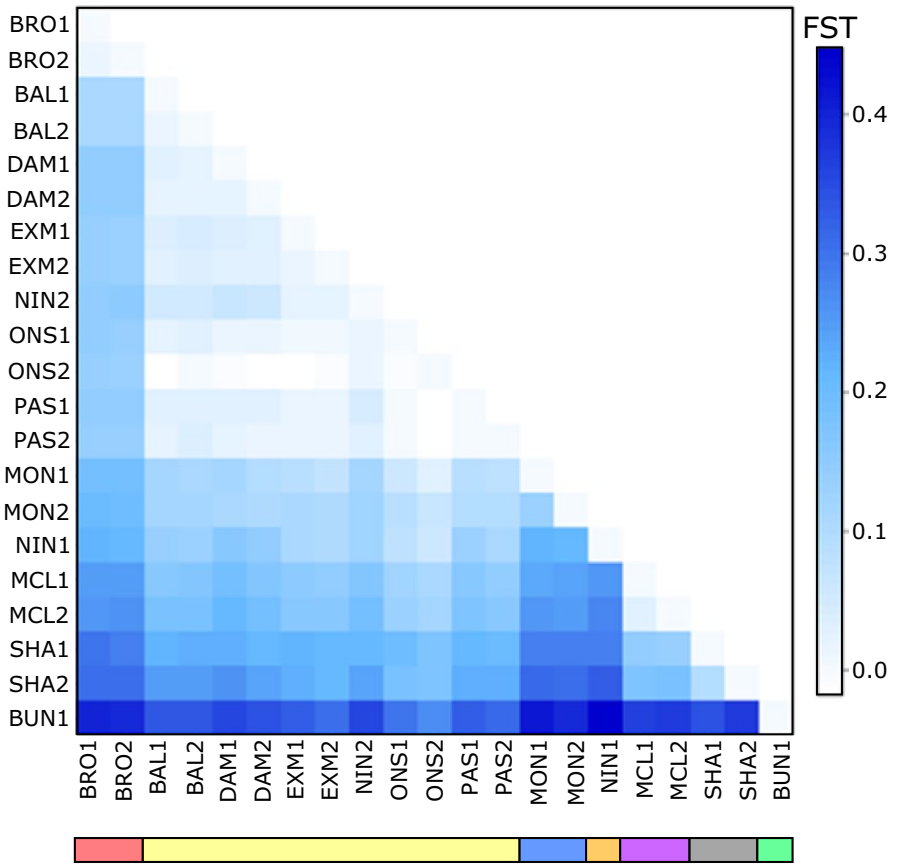

FIGURE 2 Heatmap of pairwise F_{ST} among all 21 sites sampled for *Avicennia marina* along the Western Australian coastline. Populations are ordered by genetic clusters identified by FastStructure, as indicated by the coloured bar [Colour figure can be viewed at wileyonlinelibrary.com]

Based on the hierarchical sampling design, AMOVA partitioned 11.3% of the total genetic variation among locations, with 3.7% among sites within locations and 85% within sites. Based on the seven genetic clusters from FastStructure, AMOVA found variation among clusters accounted for 15.4% of the total genetic variation, 2.9% among sites within clusters and 81.7% within sites. Finally, genetic diversity varied among sites and was positively correlated with latitude, (e.g., H_E; $p < 0.001$, $r = 0.92$), with particularly low diversity in the southernmost Bunbury site (Table 1). Excluding Bunbury, which is an outlier in terms of both diversity and latitude, the correlation between expected heterozygosity and latitude retained this strong pattern ($p < 0.001$, $r = 0.86$).

BayesAss inferred low rates of recent gene flow among the seven FastStructure clusters. The results were highly consistent among runs and all estimated values for migration had 95% confidence intervals that included zero. Four individuals were assigned with ancestry to a differing cluster: two Passage individuals were identified as second-generation migrants from the Montebellos, one Montebellos individual was a second-generation migrant from the Pilbara cluster and one individual from the northern Ningaloo cluster was identified as a second-generation migrant from the southern Ningaloo cluster.

3.2 | Seascape effects on gene flow

Habitat mapping along the Western Australian coastline found a highly continuous mangrove distribution along the Pilbara coastline, with large gaps between Balla Balla and Broome, Exmouth Gulf and Shark Bay, and between Shark Bay and Bunbury (Appendix S1). There was also a noticeable gap in mangrove habitat between the two Ningaloo sites.

Mantel testing and MMRR found that geographic distance and habitat continuity were both important predictors of genetic distance in the expected directions; genetic differentiation significantly increased with increasing geographic distance and significantly decreased with increasing habitat continuity. Individual Mantel tests were therefore highly significant ($p < 0.001$) for each explanatory variable separately ($r^2_{(geog)} = 0.69$, $r^2_{(habitat)} = -0.62$), and both remained highly significant after accounting for each other in partial Mantel testing ($p < 0.001$, $r^2_{(geog|habitat)} = 0.62$, $r^2_{(habitat|geog)} = -0.53$). These results were supported by the combined model implemented with MMRR, finding geographic distance ($\beta_{(geog)} = 0.56$) and habitat continuity ($\beta_{(habitat)} = -0.48$) were similarly important in explaining patterns of genetic differentiation ($p < 0.001$). Both factors together explained 86% of the genetic variability in *A. marina*. Moreover, exclusion of the outlier Bunbury population found that these highly significant relationships were maintained in all cases, with the combined regression model still explaining a substantial 78% of the total genetic variation.

The relationships among geographic distance, habitat continuity and genetic structure are complex, so we provide Figure 3 to illustrate each explanatory variable against genetic

TABLE 1 Estimates of genomic diversity across 21 sites of *Avicennia marina* along the Western Australian coastline. Locations are listed in order of increasing latitude to highlight the pattern of decreasing genetic diversity

Location-site	Site code	Latitude	Longitude	*P*	N_A	H_E
Broome 1	BRO1	−17.95	122.25	56.2	1.23 ± 0.003	0.236 ± 0.003
Broome 2	BRO2	−17.99	122.37	53.3	1.22 ± 0.003	0.230 ± 0.003
Montebellos 1	MON1	−20.49	115.52	36.6	1.18 ± 0.003	0.188 ± 0.003
Montebellos 2	MON2	−20.48	115.52	40.9	1.18 ± 0.003	0.179 ± 0.003
Dampier 1	DAM1	−20.59	116.79	44.6	1.21 ± 0.003	0.213 ± 0.003
Dampier 2	DAM2	−20.64	116.75	48.0	1.21 ± 0.003	0.216 ± 0.003
Balla Balla 1	BAL1	−20.67	117.63	49.6	1.21 ± 0.003	0.213 ± 0.003
Balla Balla 2	BAL2	−20.67	117.78	54.6	1.21 ± 0.003	0.214 ± 0.003
Passage 1	PAS1	−21.16	115.87	50.3	1.21 ± 0.003	0.217 ± 0.003
Passage 2	PAS2	−21.19	115.86	56.2	1.21 ± 0.003	0.215 ± 0.003
Onslow 1	ONS1	−21.65	115.13	57.4	1.21 ± 0.003	0.212 ± 0.003
Onslow 2	ONS2	−21.58	115.24	55.6	1.21 ± 0.003	0.213 ± 0.003
Ningaloo 1	NIN1	−22.32	113.81	28.1	1.17 ± 0.003	0.174 ± 0.004
Ningaloo 2	NIN2	−21.97	113.94	44.2	1.21 ± 0.003	0.213 ± 0.003
Exmouth 1	EXM1	−22.41	114.19	50.3	1.20 ± 0.003	0.203 ± 0.003
Exmouth 2	EXM2	−22.41	114.14	50.6	1.20 ± 0.003	0.203 ± 0.003
Lake MacLeod 1	MCL1	−23.97	113.61	33.4	1.15 ± 0.003	0.158 ± 0.003
Lake MacLeod 2	MCL2	−23.77	113.76	30.7	1.16 ± 0.003	0.161 ± 0.003
Shark Bay 1	SHA1	−25.91	113.53	31.0	1.14 ± 0.003	0.144 ± 0.003
Shark Bay 2	SHA2	−25.63	113.58	26.9	1.13 ± 0.003	0.135 ± 0.003
Bunbury 1	BUN1	−33.32	115.65	13.9	1.09 ± 0.003	0.085 ± 0.003
MEAN ± SE				43.44 ± 2.65	1.19 ± 0.010	0.190 ± 0.010

Note. H_E: expected heterozygosity; N_A: allelic richness; *P*: percent polymorphic loci.

distance, coloured by whether data points represent within- or between-cluster pairs (based on FastStructure). Genetic distance did not cline smoothly with geographic distance; instead, the plot revealed distinct groupings of data points (Figure 3a). These groupings highlight two major deviations from the IBD model: (a) inconsistencies at the same spatial scales, where within-cluster genetic differentiation was substantially lower than neighbouring, between-cluster site pairs at the same spatial scale (black *versus* green or pink, blue *versus* yellow); and (b) inconsistencies across different spatial scales, where between-cluster pairs exhibited similar levels of genetic differentiation, despite occurring over different spatial scales (blue *versus* pink or green). The importance of habitat continuity can be seen in Figure 3b, where the inconsistencies mentioned above are explained when habitat continuity is taken into account. The most prominent example is that all data points in the 75%–100% habitat continuity range were all within-cluster pairs, compared to the spatially similar but genetically more differentiated inter-clustal pairs that were associated with poorer (50%–75%) habitat continuity. Similarly, other inconsistencies either overlap (pink, blue) or separate (yellow, blue) to explain genetic differentiation when taking habitat continuity into account.

4 | DISCUSSION

Our research revealed a complex pattern of gene flow in Western Australian *A. marina*; broadscale IBD, disrupted by strong genetic discontinuities that coincided with gaps in mangrove habitat. Our comprehensive analysis fills a large gap in knowledge of connectivity at intermediate spatial scales and supports predictions that habitat discontinuities may present barriers to dispersal. These results reiterate that dispersive life history features do not necessarily lead to widespread connectivity in complex marine systems and provide an informed basis for effective mangrove conservation.

4.1 | Seascape effects of gene flow and connectivity

We detected strong population structuring in Western Australian *A. marina*, reflecting poor connectivity across the sampled range. Seven distinct genetic clusters were consistently identified among several analyses, indicating a robust genetic signal in our data. Negligible contemporary migration and high differentiation among clusters suggest that they are effectively isolated from contemporary gene flow and have been for some time. Significant IBD across the whole sampled range, therefore, likely reflects the species' colonization history, rather than ongoing contemporary gene flow. This

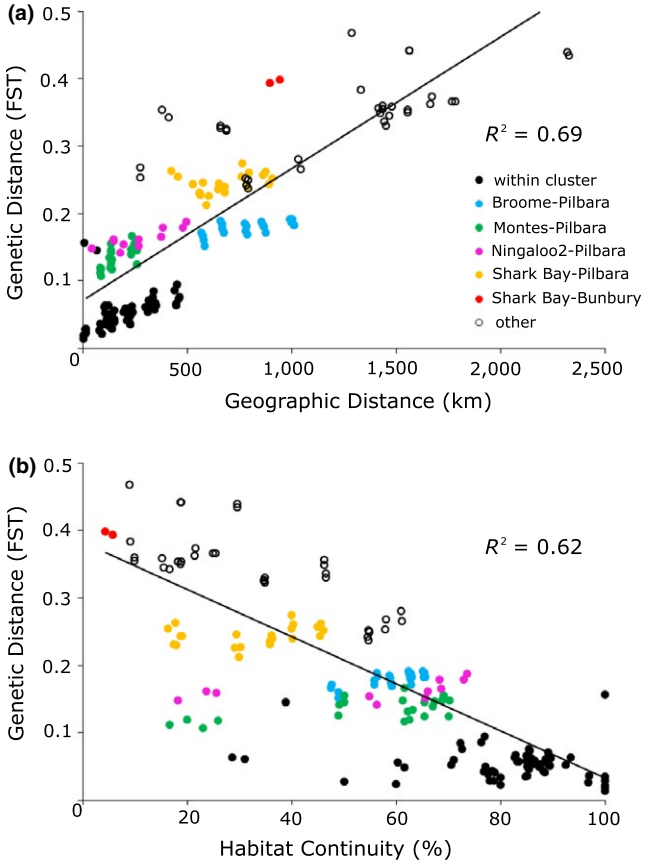

FIGURE 3 Relationships between genetic differentiation and (a) marine geographic distance or (b) habitat continuity for all pairwise population comparisons in Western Australian *Avicennia marina*. Data points are coloured according to FastStructure results with black points showing all pairwise comparisons within genetic clusters and all other solid colours indicating pairwise comparisons between neighbouring genetic clusters. Open circles indicate pairwise comparisons between non-neighbouring genetic clusters [Colour figure can be viewed at wileyonlinelibrary.com]

is exemplified by the landlocked Lake MacLeod sites that have been separated from the Indian Ocean, and therefore access for propagule dispersal, for approximately 6,000 years (Russell, 2004), and yet do not deviate from the IBD pattern. Likewise, the strong correlation of genetic diversity with latitude is consistent with patterns of lower diversity towards edges of the species' ranges in Asia and Africa, which have been attributed to founder events and bottlenecks through their colonization history (Arnaud-Haond et al., 2006; De Ryck et al., 2016; Maguire et al., 2000). And while not explicitly tested in this study, the hierarchical association of the Shark Bay, Lake MacLeod and Bunbury clusters in the PCoA lends support to hypotheses for colonization of the disjunct Bunbury population by propagule dispersal *via* an intensified Leeuwin current in the Holocene, rather than contraction of a once more widespread distribution of *A. marina* in southwestern Australia (Semeniuk, Tauss, & Unno, 2000).

At both local and broad spatial scales, levels of differentiation in this study are consistent with previous studies of *A. marina*, finding negligible differentiation between paired sites, similar to neighbouring estuaries in Eastern Australia (Hermansen et al., 2015; Melville & Burchett, 2002), and high differentiation among sites separated by 1,000+ km, similar to that found among Asian, African and Australian populations (Arnaud-Haond et al., 2006; De Ryck et al., 2016; Maguire et al., 2000). However, the range of intermediate spatial scales in our study demonstrates that the subpopulation structuring found in previous studies is not simply a consequence of dispersal limitation across oceans but can occur across much shorter distances along single coastlines. This adds to growing evidence of limited gene flow and significant population structure in mangroves (Cerón-Souza et al., 2012; Dodd & Afzal Rafii, 2002; Mori et al., 2015; Wee et al., 2014) and refutes traditional thinking that LDD and widespread connectivity are typical for these species.

The substantial contrast in partitioning of genetic variation within and among clusters indicates strong barriers to gene flow among clusters but high gene flow within them. Moreover, spatial inconsistencies in the size and distribution of these clusters demonstrate that geographic distance is not the only limiting factor to gene flow. We found a more complex model, combining geographic distance and habitat continuity, explained 86% of the total genetic variation across the sampled range. IBD within the large Pilbara cluster suggests that propagule dispersal is largely limited to adjacent populations and that connectivity among more distant populations is facilitated through multi-generational, stepping-stone dispersal. It follows then that abrupt genetic discontinuities coincided with habitat discontinuities, demonstrating that gaps in mangrove distribution can act as strong barriers to gene flow by disrupting this stepping-stone process. This explains how gene flow can be extensive across the 600 km stretch of relatively continuous habitat within the Pilbara cluster, while being highly restricted among clusters over shorter distances when the intervening landscape lacks stepping-stone populations. These results validate predictions by Clarke (1993) and Duke et al. (1998) that habitat discontinuities in the natural range of *A. marina* may present barriers to gene flow and add to growing knowledge of the importance of habitat continuity in maintaining connectivity for many marine species, even those with highly dispersive features (Fraser et al., 2010; Gonzalez et al., 2016; Johansson et al., 2008; Pinsky, Palumbi, Andréfouët, & Purkis, 2012).

4.2 | Factors affecting dispersal in *Avicennia marina*

Taken together, our seascape genomics analysis indicates that propagule dispersal is limited in *A. marina*, such that habitat discontinuities of just several 10's of kilometres can disrupt population connectivity. This is consistent with field observations in South Australia that *A. marina* propagules largely strand within 1 km of parents, and rarely over 10 km (Clarke, 1993). More detailed field studies in other mangrove species have shown that the majority of propagules typically strand within tens of metres of their release point due to physical barriers, particularly dense root systems and fallen debris, as well as low energy hydrodynamic features. As a result, proportionately few propagules are likely to reach outer currents for wider

oceanographic dispersal (Hamilton, Osman, & Feller, 2017; Sousa, Kennedy, Mitchell, & Ordóñez, 2007; Van Der Stocken et al., 2015). While *A. marina* propagules can remain viable in water for up to five months, the obligate dispersal phase is approximately one week (Clarke, 1993), which, combined with crypto-vivipary, favours rapid settlement close to the release point. Thus, rather than a means for regular, widespread dispersal, the buoyancy and viability of *A. marina* propagules in water probably represent features that facilitate opportunistic LDD in the rare event that propagules may reach outer ocean currents.

Indeed, our data do show some evidence for occasional LDD up to 100 km. The slight admixture and second-generation migrants detected between the Montebellos and Passage, is indicative of sporadic gene flow across the 60-85 km oceanic gap between them. The inclusion of the northern Ningaloo site in the large Pilbara cluster is also suggestive of LDD, given the lack of stepping-stones around the Exmouth peninsula and the 100 km distance across the Exmouth Gulf to the nearest stand. Both potential cases for LDD are consistent with the strength and direction of currents operating on the northwest shelf at the time when *A. marina* propagules would be dispersing (Feng, Colberg, Slawinski, Berry, & Babcock, 2016). Future work would greatly benefit from oceanographic modelling incorporating stepping-stone dispersal at a resolution that explores the influence of nearshore hydrodynamic processes on propagule retention and the opportunity for wider dispersal of mangrove propagules.

Alternate explanations for these genetic patterns should also be considered. Given that genetic data can only reveal successful dispersal and survival to reproduction, it is possible that propagule dispersal may be more spatially extensive but with strong selection impacting the recruitment of less suitable genotypes from more distant locations. This seems unlikely, based on field observations of limited propagule movement (Clarke, 1993; Hamilton et al., 2017; Van Der Stocken et al., 2015); however, selective processes are likely to influence the success of occasional LDD events that do occur. This is particularly true in temperate populations towards the edges of the species' range, including the Bunbury population, where the timing of flowering and fruiting varies substantially from that in tropical latitudes (Duke, 1990). The outlier loci filtered from the current dataset may present an interesting opportunity for further research on selection and adaptive processes in *A. marina*. Another consideration is subspecific divergence within the sampled range. *Avicennia marina* subsp. *eucalyptifolia* is described across northern Australia, overlapping with Western Australian *A. marina* subsp. *marina* between the Pilbara and Kimberley regions (Duke, 1991; Everett, 1994). These purported subspecies differ in leaf morphology and are readily described in mangrove literature (Duke, 2006); however, evidence for their genetic differentiation is limited by low numbers of loci, disjunct sampling and evidence of gene exchange when in sympatry (Duke et al., 1998; Maguire et al., 2000). Our sampling included equal proportions of each subspecies at the Exmouth and Ningaloo sites and these individuals clustered tightly by site rather than morphotype, with no indication of genome-wide differentiation between them. This further questions the validity of these subspecies and demonstrates that subspecific differentiation is not driving the patterns of genetic structuring seen in this study.

4.3 | Implications for mangrove management

Our findings have important implications regarding the management of *A. marina* both locally and worldwide. Poor connectivity among the genetic clusters identified in this study indicates that each of these subpopulations should be treated as separate management units in Western Australia. Without external sources for reliable recruitment, the smaller clusters, especially those with lower genetic diversity, have a limited capacity to recover from disturbance or adapt to environmental change. More broadly, in the midst of global concerns about mangrove decline (Duke et al., 2007; Polidoro et al., 2010; Sandilyan & Kathiresan, 2014), our results provide some spatial context for conservation planning of *A. marina* in other regions. While context is required when predicting connectivity in locations with differing oceanographic or topographic conditions, the knowledge that habitat discontinuities greater than several 10's of kilometres may significantly obstruct connectivity is valuable in assessing the conservation status of a given stand, delimiting management units across a broader range, or identifying appropriate stock for restoration actions in other parts of the species' range.

Our study is particularly timely with respect to the sudden and extensive dieback of mangroves across 1,000 km in northern Australia, of which *A. marina* is a dominant species (Duke et al., 2017). Mangrove propagules are recalcitrant due to vivipary and do not persist in the seed bank (Friess et al., 2012). Thus, population recovery and persistence are dependent on seasonal propagule production. Our results demonstrate that LDD should not be relied upon to supply recruits and that natural recovery will be highly dependent on the distance to the nearest sources of propagules. And because new gaps in mangrove forest can be rapidly replaced by saltmarsh expansion (Friess et al., 2012), recovery of large gaps may require active intervention. Should fragmentation persist long term, subsequent alterations to genetic connectivity and population dynamics will greatly impact the resilience of these populations to further environmental change. Given the important role that mangroves can play in mitigating the impacts of climate change (Murdiyarso et al., 2015), conservation efforts worldwide are critical and should prioritize the restoration of habitat continuity in degraded sites and minimize further fragmentation to maintain connectivity and population resilience.

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DATA ACCESSIBILITY

Genotype data are available on the Dryad repository at https://doi.org/10.5061/dryad.cr0c8c7.

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BIOSKETCH

The authors work as a multidisciplinary team with shared research interests in evolutionary biology and conservation for Western Australian marine and terrestrial ecosystems.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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