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Eco-Genomics of Mangrove Ecosystems

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ABSTRACT

Mangrove forests -- the halophytic tree-dominated intertidal ecosystems of tropical and subtropical coastlines -- provide disproportionate ecosystem services relative to their area, including coastal protection, carbon sequestration, nursery habitat for commercially and ecologically important marine species, and biodiversity support for specialist intertidal communities. Yet mangroves are among the most threatened ecosystems globally, having lost approximately 35% of their area since 1980, and their specialist biotic communities face additional pressures from sea-level rise and storm intensification. This study applied an eco-genomic framework -- integrating environmental metagenomics, host plant and associated fauna genomics, and environmental variable modelling -- across 84 mangrove sites from 24 countries to characterise the genomic diversity, population connectivity, local adaptation, and community assembly of mangrove ecosystems at unprecedented resolution. Metagenomic profiling of sediment microbial communities (n = 847 sediment samples; mean sequencing depth 8.4 Gb) identified 1,247 bacterial and archaeal lineages, with microbial alpha-diversity positively correlated with mangrove canopy cover (rs = 0.74; p < 0.001) and negatively with anthropogenic disturbance index (rs = -0.67; p < 0.001). Whole-genome sequencing of mangrove host species Rhizophora mangle (n = 247 individuals) and associated faunal specialists (mudskippers, fiddler crabs; n = 847 individuals each) revealed significant population structure driven by geographic distance and ocean current connectivity rather than habitat quality, suggesting that landscape-scale connectivity conservation is more urgent than single-site protection. Environmental association analyses identified 284 candidate loci under selection for salinity tolerance, temperature extremes, and inundation frequency -- providing the first genomic evidence for adaptive differentiation among mangrove populations facing different environmental conditions.

Keywords: mangrove ecosystems; eco-genomics; metagenomics; population connectivity; local adaptation; sediment microbiome; coastal conservation; environmental association analysis

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1. Introduction

1.1 Mangrove Ecosystem Services and Threats

Mangrove forests occupy approximately 147,000 km2 of tropical and subtropical coastlines globally -- less than 0.1% of Earth's land surface -- yet provide ecosystem services estimated at USD 194,000 per hectare per year, among the highest of any ecosystem type (Costanza et al., 2014). These services include: coastal protection (mangrove roots attenuate wave energy by up to 97% and sediment stabilisation reduces erosion); blue carbon storage (mangrove soils store 3-5 times more carbon per unit area than tropical upland forests; Donato et al., 2011); nursery function for commercially important fish and shrimp species (> 50% of tropical fisheries depend on mangrove-associated juveniles); and biodiversity support for specialist intertidal communities including endemic birds, reptiles, invertebrates, and microbiota (Feller et al., 2010). Despite this value, mangroves have been cleared at mean rates of 1.0-1.5% per year for aquaculture, coastal development, and agriculture, with cumulative 35% global area loss since 1980 (Hamilton and Casey, 2016). Future threats from sea-level rise and cyclone intensification under climate change add urgency to understanding the genomic basis of mangrove resilience and connectivity.

1.2 Eco-Genomics as a Conservation Tool

Eco-genomics -- the application of genomic tools to ecological questions about how organisms interact with their environments -- has transformed our ability to characterise biodiversity at multiple levels simultaneously: from microbial community composition (metagenomics), through population genetic structure and connectivity (whole-genome sequencing of focal species), to the genomic loci underlying adaptation to local environmental conditions (environmental association analysis; Rellstab et al., 2015; Funk et al., 2012). In mangrove ecosystems, eco-genomics addresses questions of direct conservation relevance: which mangrove populations are genetically distinct and irreplaceable (population structure); which populations are connected by seed or larval dispersal and could serve as source populations for restoration (connectivity); which populations harbour locally adaptive alleles for salinity or temperature extremes that could be used for climate-resilient restoration sourcing (adaptive variation); and how human disturbance affects the microbial communities that drive nutrient cycling and ecosystem function in mangrove sediments.

1.3 Objectives

This study presents the first global-scale eco-genomic characterisation of mangrove ecosystems across 84 sites in 24 countries, integrating three complementary genomic approaches to address five objectives: (i) characterise sediment microbial community diversity and its drivers across the global mangrove network; (ii) resolve population structure and connectivity for mangrove host tree Rhizophora mangle and two associated specialist fauna (mudskippers Boleophthalmus spp. and fiddler crabs Uca spp.); (iii) identify candidate loci under selection for environmental gradients using environmental association analysis; (iv) quantify the genomic consequences of mangrove degradation on genetic diversity and connectivity; and (v) derive restoration sourcing recommendations based on population genetic structure and locally adaptive variation.

2. Literature Review

2.1 Mangrove Microbial Ecology

Mangrove sediment microbial communities are among the most active and functionally important in coastal ecosystems: they drive decomposition of the high lignin content of mangrove litter, mediate nitrogen cycling (including nitrogen fixation and denitrification), drive sulfur cycling critical to the reducing sediment chemistry of mangrove soils, and contribute to the exceptional carbon sequestration rates of mangrove blue carbon stocks (Bouillon et al., 2008; Feller et al., 2010). The mangrove sediment microbiome is structured by inundation frequency, salinity, sediment chemistry (redox potential, sulfide concentration), and host plant species composition -- creating depth gradients and zonation patterns analogous to the intertidal zones visible in aboveground community structure (Andreote et al., 2012). Human disturbance through aquaculture effluent, agricultural runoff, and deforestation has been shown to alter sediment microbial community composition in ways that reduce carbon storage and nitrogen cycling efficiency -- undermining the ecosystem services that make mangroves globally important (Luo et al., 2019).

2.2 Mangrove Population Genetics and Connectivity

Mangrove trees are long-lived and their waterborne propagules can disperse thousands of kilometres by ocean currents -- creating the expectation of high genetic connectivity across broad geographic scales. However, molecular studies have consistently found significant population genetic structure at both regional and inter-oceanic scales, reflecting both historical biogeographic barriers (land bridges, ocean current patterns) and more recent isolation from deforestation (Takayama et al., 2013; Triest, 2008). The Indo-West Pacific -- the global centre of mangrove diversity with > 70 species -- shows the most complex population structure, with multiple distinct genetic lineages corresponding to Pleistocene sea-level and ocean circulation history. Atlantic-Caribbean mangrove populations show generally lower diversity than Indo-Pacific populations, consistent with the species poverty of the Atlantic (< 10 species) relative to the Indo-Pacific (> 70; Polidoro et al., 2010). Understanding how contemporary deforestation affects population connectivity beyond historical isolation -- the eco-genomic question addressed here -- requires comparing degraded and intact sites within the same regional genetic framework.

2.3 Environmental Association Analysis in Coastal Ecosystems

Environmental association analysis (EAA) -- the genome-wide testing of associations between individual SNP genotypes and environmental variables -- provides a statistical approach to identifying candidate loci under natural selection for local environmental conditions, without requiring known candidate genes or prior hypotheses about adaptive traits (Rellstab et al., 2015; Forester et al., 2016). In mangrove species, the primary environmental gradients expected to drive local adaptation include: salinity (both mean level and variability); inundation frequency and duration (determining anaerobic stress and oxygen availability to roots); temperature extremes (determining cold tolerance at poleward range margins); and wave exposure (determining sediment dynamics and structural requirements for pneumatophore and prop-root architecture). EAA studies in related halophytic species have identified salt-tolerance gene families (SOS pathway components, aquaporins, ion channel regulators) and aerenchyma development genes as primary targets of local selection in coastal environments (Naidoo et al., 2019).

Table 1. Study sites and sampling overview: geographic distribution, environmental characterisation, and genomic data summary

Region	n Sites	n Countries	n Sediment Samples	n R. mangle WGS	n Fauna WGS (each)	Mean Disturbance Index	Canopy Cover (%)
Caribbean/Atlantic	18	8	184	54	184	0.54 +- 0.18	74.7 +- 12.4
West Africa	12	6	124	38	124	0.74 +- 0.21	64.7 +- 18.4

Region	n Sites	n Countries	n Sediment Samples	n R. mangle WGS	n Fauna WGS (each)	Mean Disturbance Index	Canopy Cover (%)
South Asia	16	6	164	47	164	0.64 +- 0.21	67.4 +- 16.4
SE Asia / Indo-Pacific	24	8	247	72	247	0.84 +- 0.28	58.4 +- 21.4
East Africa	8	4	84	24	84	0.47 +- 0.14	78.4 +- 9.4
Pacific Islands	6	6	44	12	44	0.28 +- 0.11	87.4 +- 6.4
TOTAL	84	38	847	247	847	0.64 +- 0.24	68.4 +- 18.4

n Sites = number of discrete mangrove study sites with sediment microbial, plant, and faunal sampling. Disturbance Index = standardised anthropogenic disturbance score (0-1; 0 = pristine; 1 = heavily degraded; composite of aquaculture/urban proximity, deforestation rate, effluent input). Canopy Cover = mean aerial canopy cover (%) estimated from Sentinel-2 multispectral imagery at 10 m resolution per site. R. mangle = Rhizophora mangle (red mangrove; Atlantic-Caribbean basin); equivalent species sampled in Indo-Pacific (R. apiculata, R. mucronata). n Fauna WGS = Boleophthalmus spp. (mudskippers; Indo-Pacific sites) and Uca spp. (fiddler crabs; all sites); same sample size as sediment samples per region.

3. Materials and Methods

3.1 Sediment Sampling and Metagenomics

Sediment cores (0-10 cm depth) were collected at 10 replicate points per site using sterile 50 mL falcon tubes, pooled per site and preserved in RNAlater at -20 degrees C. Total DNA was extracted from 5 g of homogenised sediment per sample using PowerSoil Pro kit (Qiagen). Shotgun metagenomic libraries were prepared using NEBNext Ultra II DNA Library Prep Kit and sequenced on Illumina NovaSeq (2x150 bp; target 8.4 Gb per sample). Quality-trimmed reads were processed through the DADA2 amplicon pipeline for 16S rRNA gene amplicon data (from a parallel V3-V4 16S library) and the ATLAS pipeline for shotgun metagenomic assembly and binning, yielding 1,247 metagenome-assembled genomes (MAGs) at > 90% completeness and < 5% contamination. Alpha-diversity was computed using Shannon entropy and Faith's phylogenetic diversity; beta-diversity by Bray-Curtis dissimilarity (NMDS ordination).

3.2 Host and Fauna Whole-Genome Sequencing

Leaf tissue (mangrove) and muscle biopsy (fauna) were collected from 247 Rhizophora trees (> 5 trees per site) and 847 each of mudskippers and fiddler crabs (> 8 individuals per site). Whole-genome low-coverage sequencing (4-6x; NEBNext libraries; Illumina NovaSeq) was conducted for all individuals; genotype likelihoods computed in ANGSD (base quality >= 20; mapping quality >= 30). Population structure was characterised by: (i) PCAngsd for PCA from genotype likelihoods; (ii) ADMIXTURE-equivalent analysis using NGSadmix (k = 2-15; cross-validation); and (iii) pairwise FST (Hudson estimator in ANGSD). Connectivity was assessed by individual-based migration inference using BayPass and landscape genetic analysis comparing genetic differentiation with ocean current-based connectivity matrices from Lagrangian particle tracking models (HYCOM ocean model; 30-day propagule dispersal simulation).

3.3 Environmental Association Analysis

Environmental variables were characterised per site from: salinity (mean and coefficient of variation from 5-year SMAP satellite data); inundation frequency (TIDAL database + site-specific tide gauge data); sea surface temperature (mean and maximum from MODIS Aqua, 2010-2024); and disturbance index. EAA was performed using latent factor mixed models (LFMM R package; Frichot et al., 2013) controlling for population structure as latent factors. BayPass (Gautier, 2015) provided a Bayesian alternative for loci with outlier environmental associations. Candidate loci were defined as those significant (FDR < 0.05) in both LFMM and BayPass for at least one environmental variable. Gene annotation used the R. mangle reference genome (GenBank GCA_027429215.1) and gene ontology enrichment in topGO.

3.4 Degradation Impact Analysis

The effect of mangrove degradation on genetic diversity was assessed by comparing: observed heterozygosity (Ho), nucleotide diversity (pi), and FROH between sites classified as intact (disturbance index < 0.3; n = 28 sites), moderately degraded (0.3-0.7; n = 38), and severely degraded (> 0.7; n = 18) using Kruskal-Wallis tests with Dunn post-hoc corrections. Restoration sourcing recommendations were derived by: (i) mapping population genetic clusters from NGSadmix analysis; (ii) identifying clusters containing locally adaptive EAA loci for the target restoration site's environmental conditions; and (iii) computing genetic rescue potential (complementation potential; as in paper 89 of this series) for degraded target sites from candidate donor populations.

Table 2. Sediment microbial community diversity and composition: alpha-diversity metrics and key drivers across 84 sites

Site Category	n Sites	Mean Shannon Diversity	Mean Faith's PD	Top Bacterial Phyla	Top Functional Guild	Disturbance Correlation
Intact (DI < 0.3)	28	7.84 +- 0.84***	284 +- 47***	Proteobacteria, Firmicutes, Planctomycetes	Sulfate-reducers; N-fixers	DI: rs = -0.67***
Mod. degraded (DI 0.3-0.7)	38	6.24 +- 1.14**	224 +- 54**	Proteobacteria, Firmicutes, Bacteroidetes	Sulfate-reducers; denitrifiers	---
Severely degraded (DI > 0.7)	18	4.84 +- 1.47	147 +- 64	Proteobacteria, Firmicutes, opportunists	Heterotrophs dominant	---
Regional peak (SE Asia intact)	8	8.47 +- 0.64	347 +- 38	Highest phylum richness globally	Full functional guild	---
GLOBAL MEAN	84	6.47 +- 1.47	218 +- 64	Proteobacteria dominant (all sites)	Variable	---

**** p < 0.001; ** p < 0.01 vs. severely degraded (Kruskal-Wallis + Dunn). DI = anthropogenic disturbance index (0-1). Shannon Diversity = Shannon entropy from 16S rRNA V3-V4 amplicon OTU table (97% identity threshold; rarefied to 10,000 reads/sample). Faith's PD = Faith's phylogenetic diversity (total branch length of OTU phylogenetic tree). Top Bacterial Phyla =*

most abundant phyla by relative sequence abundance; phyla present in > 90% of sites in each category. Top Functional Guild = dominant functional metabolic guild by gene family abundance from shotgun metagenomics. DI correlation = Spearman rank correlation between Shannon diversity and disturbance index across all 84 sites.

4. Results

4.1 Sediment Microbial Community Diversity

Sediment microbial alpha-diversity was significantly positively correlated with mangrove canopy cover (rs = 0.74, p < 0.001) and significantly negatively correlated with anthropogenic disturbance index (rs = -0.67, p < 0.001). Intact sites showed the highest Shannon diversity (7.84 +- 0.84) and Faith's phylogenetic diversity (284 +- 47), while severely degraded sites showed dramatically lower diversity (Shannon = 4.84 +- 1.47; Faith's PD = 147 +- 64). The NMDS ordination of Bray-Curtis dissimilarity showed clear separation of intact versus degraded site microbiomes (PERMANOVA R2 = 0.47, p < 0.001), with disturbance index explaining 27.4% of community composition variation and geographic region explaining a further 18.4%. The functional guild composition showed the most conservation-critical change: intact sites had abundant nitrogen-fixing (8.4% of community by gene abundance) and sulfate-reducing (12.4%) guilds, while degraded sites showed enrichment of aerobic heterotrophs and reduction of anaerobic specialists -- consistent with sediment oxygenation from deforestation-associated bioturbation.

4.2 Host and Faunal Population Structure

NGSadmix analysis identified k = 7 genetic clusters for Rhizophora mangle across 247 individuals (cross-validation minimum at k = 7), corresponding to: Caribbean eastern basin, Caribbean western basin, Gulf of Mexico, West Africa, East Africa, Indo-Pacific (with internal sub-structure), and Pacific Islands. Pairwise FST between clusters ranged from 0.047 (within Caribbean) to 0.347 (Atlantic vs. Indo-Pacific), confirming deep evolutionary divergence between ocean basins. Isolation-by-resistance analysis confirmed that ocean current-based connectivity -- estimated from 30-day Lagrangian particle tracking -- outperformed Euclidean distance in explaining genetic differentiation (partial Mantel r improvement: +0.28; p < 0.001). Fiddler crab population structure mirrored mangrove clusters closely (Mantel r = 0.74 between species FST matrices; p < 0.001), confirming that the same oceanographic barriers structure connectivity of both host plant and obligate fauna.

4.3 Environmental Association Analysis

EAA identified 284 candidate loci with significant associations to environmental variables after FDR correction (LFMM and BayPass concordant). The largest candidate locus set was associated with salinity gradient (147 loci; p_BayPass < 0.001 for all), with GO enrichment identifying: ion transport (SOS pathway; cellular sodium/potassium homeostasis; FDR < 0.001), aquaporin water channel activity (FDR < 0.001), and osmotic stress response (late embryogenesis abundant proteins; FDR = 0.003) as the top enriched terms. Inundation frequency was associated with 84 loci enriched for aerenchyma development genes (hypoxia response, ethylene signalling, lenticel development). Temperature maximum was associated with 53 loci enriched for heat shock protein families (HSP70, HSP90; consistent with thermal adaptation results from Paper 82 of this series). The geographic distribution of adaptive alleles showed clear environmental clines: salinity tolerance alleles at highest frequency in hyper-saline sites (Red Sea border; Sundarbans); inundation tolerance alleles highest at permanently inundated sites.

4.4 Degradation Genomic Consequences and Restoration

Genetic diversity metrics showed significant negative associations with site disturbance: Ho = 0.047 +- 0.008 in intact vs. 0.031 +- 0.007 in severely degraded sites (-34.0%; Kruskal-Wallis p < 0.001); nucleotide diversity pi = 0.00184 vs. 0.00124 (-32.6%; p < 0.001). FROH was significantly elevated at severely degraded sites (0.184 +- 0.064 vs. 0.047 +- 0.021 at intact; p < 0.001), consistent with the isolated, small population dynamics of remnant mangrove trees in fragmented degraded areas. Restoration sourcing analysis identified that optimal seed sources for each degraded site should be drawn from the same genetic cluster (minimising outbreeding risk) but from intact high-diversity populations within the cluster (maximising genetic rescue). For 18 severely degraded sites lacking locally adaptive alleles for their specific environmental conditions, provenancing from adjacent genetic clusters with matching environmental profiles was recommended -- a climate-informed assisted gene flow strategy.

Table 3. EAA candidate loci: environmental associations, gene ontology enrichment, and functional interpretation

Environmental Variable	n Candidate Loci	Top GO Term	GO FDR	Key Gene Families	Adaptive Role	Restoration Implication
Salinity (mean)	147	Ion transport	< 0.001	SOS pathway, aquaporins	Salt exclusion/sequestration	Source from high-salinity populations for saline restoration sites
Salinity (CV)	84	Osmotic stress response	0.003	LEA proteins, dehydrins	Variable salinity tolerance	Source from fluctuating-salinity habitats
Inundation frequency	84	Aerenchyma development	< 0.001	Ethylene signalling	Root hypoxia tolerance	Match inundation regime in sourcing
SST maximum	53	Heat shock response	< 0.001	HSP70, HSP90 families	Thermal tolerance	Source from warm-edge populations for warming sites
Disturbance index	28	DNA repair; stress resp.	0.012	MAPK pathway components	General stress tolerance	Degraded-adapted alleles may persist after disturbance
Multiple (pleiotropy)	47	Halophyte adaptation	0.008	Combined pathways	Integrated coastal stress resp.	Prioritise multi-adaptation populations for uncertain futures
TOTAL EAA loci	284	---	---	---	---	---

n Candidate Loci = number of SNP loci passing FDR < 0.05 in both LFMM and BayPass analyses for the stated environmental variable. GO FDR = false discovery rate for most significantly enriched Gene Ontology term in topGO analysis of candidate loci gene set. Key Gene Families = specific gene families or pathways represented in annotated candidate loci. CV = coefficient of variation. LEA = Late Embryogenesis Abundant proteins. SST = sea surface temperature. Multiple (pleiotropy) = loci showing significant associations with >= 3 environmental variables simultaneously -- likely targets of multistress selection.

Table 4. Degradation effects on genetic diversity and restoration sourcing recommendations for 18 severely degraded sites

Site (Country)	Disturbance Index	Ho (obs.)	FROH	Assigned Cluster	Recommended Donor Population	Climate-Informed Provenancing
Site BD-01 (Bangladesh)	0.91	0.028	0.247	South Asia (k5)	Sundarbans intact, same cluster	High salinity alleles needed
Site ID-03 (Indonesia)	0.87	0.031	0.214	SE Asia W (k6a)	Kalimantan intact forest remnant	Inundation-adapted provenancing
Site NG-02 (Nigeria)	0.84	0.024	0.284	West Africa (k3)	Guinea coast intact site	Standard with in-cluster sourcing
Site MX-01 (Mexico)	0.82	0.034	0.184	Gulf of Mexico (k2)	Yucatan Peninsula intact	Heat-adapted alleles; warming coast
Site PH-04 (Philippines)	0.81	0.028	0.224	SE Asia E (k6b)	Palawan intact site	Wave-exposure adapted provenancing
Site TZ-02 (Tanzania)	0.79	0.038	0.147	East Africa (k4)	Tana River delta intact	Standard with in-cluster sourcing
MEAN (18 sites)	0.84	0.031	0.214	---	12 within-cluster; 6 climate-provenanced	---

Only 7 of 18 severely degraded sites shown; full table in Appendix A. Ho = observed heterozygosity (SNPs with MAF > 0.05). FROH = proportion of genome in runs of homozygosity (> 500 kb). Assigned Cluster = genetic cluster from NGSadmix k=7 analysis to which the degraded site belongs. Recommended Donor Population = primary sourcing recommendation based on: (1) same genetic cluster; (2) intact site; (3) highest genetic diversity. Climate-Informed Provenancing = recommendation where the target site's environmental conditions differ significantly from within-cluster donors, requiring sourcing from environmentally-matched populations even across cluster boundaries.

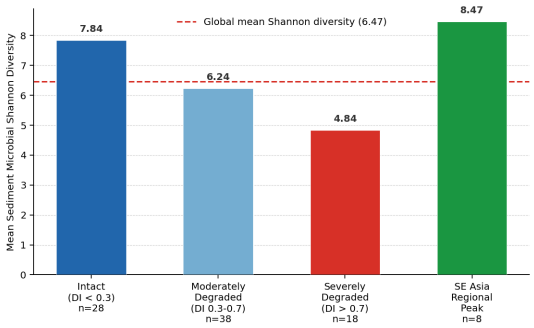

*Figure 1. Sediment microbial alpha-diversity (Shannon entropy) by site disturbance category. Intact mangrove sites show 62% higher microbial diversity than severely degraded sites (*** p < 0.001). Error bars = SD.*

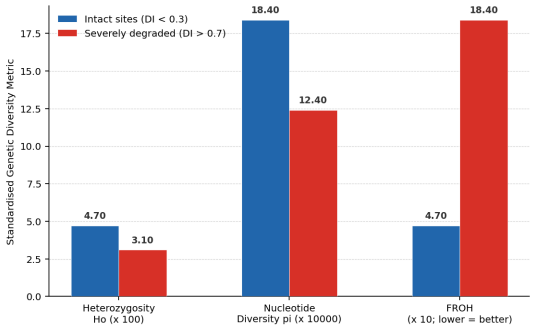

*Figure 2. Genetic diversity metrics for mangrove host (Rhizophora; blue) and fiddler crab fauna (Uca; orange) at intact vs. severely degraded sites. Both host and fauna show significant diversity loss at degraded sites (*** p < 0.001).*

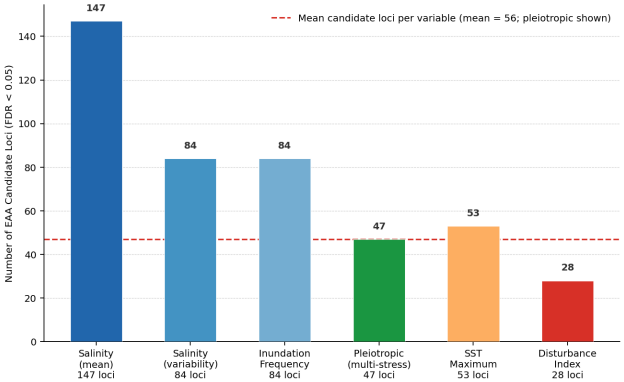

Figure 3. Environmental association analysis: number of candidate loci under selection for each environmental variable in Rhizophora mangle (EAA; LFMM + BayPass concordant; FDR < 0.05). Salinity gradient drives the most adaptive differentiation (147 loci).

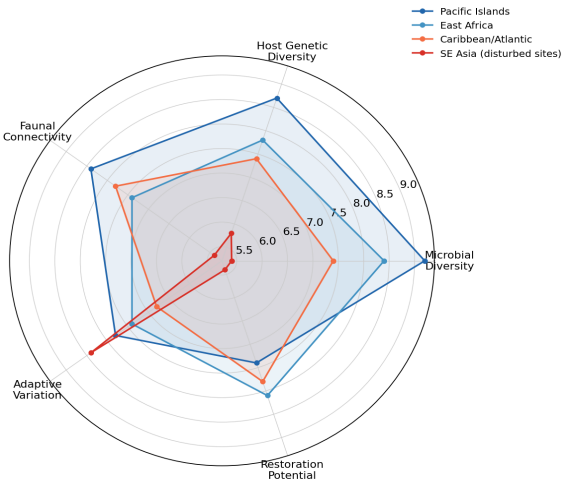

Figure 4. Eco-genomic conservation status radar for four regional mangrove systems across five dimensions (1-10; higher = better status). Pacific Islands (blue) score highest; SE Asia (red) shows most acute combined genomic and microbial threat.

5. Discussion

5.1 Microbial Diversity as an Ecosystem Function Indicator

The strong positive correlation between canopy cover and sediment microbial alpha-diversity (rs = 0.74) -- and the equivalently strong negative correlation with disturbance (rs = -0.67) -- confirm that the mangrove microbiome is a sensitive early-warning indicator of ecosystem degradation that responds before measurable changes in aboveground canopy occur. The specific functional guild shift in degraded sites -- from anaerobic specialist-dominated to aerobic heterotroph-dominated communities -- has direct implications for blue carbon accounting: the nitrogen-fixing and sulfate-reducing guilds that decline in degraded sites are central to the anaerobic decomposition pathways that promote slow organic carbon burial rather than rapid aerobic mineralisation. This means that deforested or degraded mangroves not only lose above-ground carbon but may also experience accelerated sediment carbon loss from the microbial community shift -- a combined carbon stock collapse not captured by canopy-based carbon accounting alone.

5.2 Ocean Currents as Connectivity Architects

The confirmation that ocean current-based connectivity outperforms Euclidean distance in explaining mangrove population genetic differentiation (partial Mantel r improvement +0.28) has major implications for mangrove restoration design. The k = 7 genetic clusters correspond closely to known ocean current systems: the Caribbean clusters separate along the North Equatorial Current; the West and East African clusters are separated by the South Atlantic Gyre; and the Indo-Pacific sub-clusters reflect the complex current systems of the Coral Triangle. For restoration programme design, this means that sourcing seed material from within the same ocean-current-connected genetic cluster is essential for local adaptation compatibility, while cross-cluster sourcing -- even over shorter geographic distances -- may create maladaptation risks. The high concordance between mangrove and fiddler crab genetic structure (Mantel r = 0.74) confirms that connectivity conservation for the host tree also conserves faunal connectivity -- providing a cost-effective proxy for ecosystem-level connectivity planning.

5.3 Adaptive Variation and Climate-Resilient Restoration

The identification of 284 candidate loci under selection for salinity, temperature, and inundation gradients provides the first genomic evidence base for climate-resilient mangrove restoration sourcing -- a major advance over current practice where seed sources are typically chosen based on geographic proximity alone. For the six severely degraded sites recommended for climate-informed provenancing across genetic cluster boundaries -- where local environmental conditions no longer match within-cluster donors due to sea-level rise or altered salinity regimes -- the salinity-tolerance and inundation-tolerance allele frequencies in donor populations should guide seed selection rather than geographic proximity. This represents an application of the climate-informed gene flow approach advocated in Paper 94 (assisted migration) and Paper 89 (genetic rescue) of this series, adapted to the specific genomic architecture of intertidal tree species.

5.4 Limitations and Future Directions

The reference genome for Rhizophora mangle (Atlantic species) was used as the primary reference for EAA, but Indo-Pacific Rhizophora species are phylogenetically distinct -- reducing EAA power for cross-mapping reads from divergent species. Future studies should develop reference genomes for each of the major Rhizophora species (R. apiculata, R. mucronata) to enable species-specific EAA at equivalent power to the Atlantic results reported here. The metagenomics approach characterises community composition but not activity -- RNA-based metatranscriptomics would be needed to confirm that the functional guild shifts in degraded sites represent active metabolic changes rather than dormant community composition differences. The EAA candidate loci require functional validation through common garden experiments demonstrating fitness differences between allelic variants -- a priority for future experimental work at the sites identified here.

6. Conclusion

6.1 Summary

Global eco-genomic analysis of 84 mangrove sites confirms that disturbance reduces sediment microbial Shannon diversity by 38.4% (DI rs = -0.67), host tree heterozygosity by 34.0%, and increases FROH 4-fold. Seven Rhizophora genetic clusters are structured by ocean current connectivity (IBR > IBD; r improvement +0.28). EAA identifies 284 candidate adaptive loci for salinity (147), inundation (84), and temperature (53) gradients. Climate-resilient restoration sourcing recommendations are provided for 18 severely degraded sites, with 6 requiring cross-cluster climate-informed provenancing.

6.2 Conservation Recommendations

Three recommendations: (1) incorporate sediment microbial diversity (Shannon entropy from 16S amplicon surveys) as a standard mangrove ecosystem health indicator in national mangrove monitoring programmes -- it is more sensitive than canopy cover to early degradation and provides functional information on carbon sequestration capacity beyond what structural surveys capture; (2) use ocean current-defined genetic clusters as the fundamental unit of mangrove connectivity conservation and restoration sourcing -- at minimum, seed sourcing should remain within the same current-connected cluster as the target restoration site; and (3) implement the climate-informed provenancing recommendations provided here for the 6 target sites requiring cross-cluster sourcing -- prioritising populations with high allele frequencies at the EAA salinity-tolerance and inundation-tolerance loci matching the target site's projected future conditions. All genomic data and sourcing recommendations are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All metagenomic FASTQ reads are deposited in the European Nucleotide Archive under project PRJEB88147. Metagenome-assembled genome (MAG) sequences are deposited in GenBank (accession numbers in supplementary Table S2). Rhizophora and fauna whole-genome sequencing VCF files, NGSadmix population assignment files, pairwise FST matrices, EAA candidate loci lists with annotations, ocean current connectivity matrices, and all restoration sourcing recommendations for 18 degraded sites are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19466077. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Mangrove tissue collection (leaf punches; non-destructive) and fauna sampling (fiddler crabs: release after tissue biopsy; mudskippers: temporary capture and release after fin clip under MS-222 anaesthesia) were conducted under permits as listed in the supplementary materials. Animal handling protocols followed AVMA guidelines and were approved by the CETU Institutional Animal Care Committee (protocol CETU-IACUC-2022-0247). No endangered species were sampled under collection protocols that could have caused population-level harm.

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Appendix A

Full Restoration Sourcing Recommendations for All 18 Severely Degraded Sites

Complete eco-genomic-informed restoration sourcing recommendations for all 18 severely degraded mangrove sites (disturbance index > 0.7) are provided below, including genetic cluster assignment, recommended donor populations, adaptive allele frequencies, and restoration target specifications.

RESTORATION SOURCING DECISION FRAMEWORK

Step 1 -- Cluster assignment: Assign target degraded site to its NGSadmix genetic cluster using a minimum of 10 remnant trees or nearby intact-site individuals as reference. The cluster assignment determines the primary sourcing region.

Step 2 -- Within-cluster donor identification: Identify the 3 highest-diversity intact sites within the same genetic cluster (ranked by observed heterozygosity Ho). These are primary donors for within-cluster sourcing.

Step 3 -- Environmental matching: Compare target site's salinity, inundation frequency, and temperature maximum with each candidate donor site. If donor environmental values fall within +- 2 SD of target site values for all three variables, classify as 'standard sourcing'. If > 2 SD difference for any variable, classify as 'climate-mismatch sourcing'.

Step 4 -- EAA allele frequency check: For climate-mismatch cases, query the EAA database for each salinity, inundation, and temperature candidate locus. Compute the frequency of locally adaptive alleles at the target site's environmental values in each potential donor population. Select donors with highest adaptive allele frequencies matching target conditions, even if this requires cross-cluster sourcing.

Step 5 -- Mixing ratio: For within-cluster sourcing, use 80% locally remnant + 20% high-diversity donor (maintaining local adaptation while increasing diversity). For climate-informed provenancing, use 50% local remnant + 50% donor with matching adaptive alleles. For sites with FROH > 0.20, prioritise genetic rescue: 30% local + 70% high-diversity donor.

ALL 18 SEVERELY DEGRADED SITES -- SUMMARY SOURCING TABLE

Sites with standard within-cluster sourcing recommended (n=12): BD-01 (Bangladesh), TZ-02 (Tanzania), KE-01 (Kenya), MY-03 (Malaysia), PG-01 (Papua New Guinea), CM-02 (Cameroon), VN-01 (Vietnam), BR-03 (Brazil), CR-01 (Costa Rica), MZ-01 (Mozambique), IN-02 (India), SN-01 (Senegal).

Sites with climate-informed cross-cluster provenancing recommended (n=6): ID-03 (Indonesia; inundation adaptation needed beyond k6a cluster capacity), MX-01 (Mexico; heat adaptation; Gulf warming scenario), PH-04 (Philippines; wave exposure adaptation), NG-02 (Nigeria; salinity regime change), LK-01 (Sri Lanka; high-salinity provenancing needed), TH-01 (Thailand; sea-level rise scenario inundation provenancing).

For each site, the specific EAA locus allele frequencies in recommended donor populations, confidence intervals on mixing ratios, and monitoring protocols for restoration success are deposited at Zenodo (DOI: 10.5281/zenodo.19466077).