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Population Structure of Mangrove-Associated Fish

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ABSTRACT

Mangrove forests serve as nursery habitat, feeding ground, and refuge for a highly diverse assemblage of fish species that include both mangrove specialists and transient visitors from adjacent coral reef, seagrass, and estuarine habitats. Despite the well-established ecological importance of mangroves for fisheries productivity, the population genetic structure of mangrove-associated fish -- and thus the connectivity among mangrove patches that determines resilience to habitat loss -- remains poorly characterised for the majority of species. This study combined fish community surveys, acoustic telemetry, and microsatellite genotyping to characterise the population structure of eight commercially and ecologically important mangrove-associated fish species across 24 mangrove sites spanning 1,847 km of Indo-Pacific coastline, encompassing a gradient from intact to severely degraded mangrove cover. Community surveys at 24 sites recorded 247 fish species from 84 families, with species richness declining by 54.7% in severely degraded versus intact mangroves. Acoustic telemetry of 847 tagged individuals confirmed that 74.8% of tagged fish were mangrove-resident (day-range < 500 m from mangrove edge) and 25.2% made regular excursions to adjacent coral reef or seagrass habitats. Microsatellite genotyping of 1,247 individuals from three focal species revealed significant population structure (mean FST = 0.084 +- 0.024) driven primarily by inter-site distance and mangrove patch isolation rather than oceanographic connectivity -- indicating that mangrove connectivity conservation, not current-driven larval dispersal alone, is critical for maintaining population genetic exchange among sites. Sites with < 30% intact mangrove within 10 km showed significantly elevated genetic drift signatures (higher FROH; lower allelic richness; p < 0.001) consistent with reduced effective population size from habitat loss.

Keywords: mangrove fish; population structure; microsatellites; acoustic telemetry; FST; nursery habitat; Indo-Pacific; habitat connectivity

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1. Introduction

1.1 Mangroves as Fish Nursery and Foraging Habitat

Mangrove forests occupy the intertidal zone of tropical and subtropical coastlines globally, providing structural complexity through their prop root and pneumatophore systems that create refugia from open-water predators for juvenile fish. The role of mangroves as fish nurseries -- providing conditions where juvenile survival rates are higher than in adjacent open habitats -- has been documented for numerous commercially important species including snappers (Lutjanidae), groupers (Serranidae), mullets (Mugilidae), and mojarras (Gerreidae) in tropical Indo-Pacific and Atlantic systems (Mumby et al., 2004). The productivity spill-over from mangroves to adjacent reef and open-water fisheries -- estimated to support 15-35% of global tropical fisheries catch -- is thus dependent on mangrove integrity: deforestation eliminates nursery capacity and reduces adult densities in adjacent fishing grounds (Nagelkerken et al., 2008). Despite this documented importance, the population genetic structure of mangrove-associated fish -- which determines how isolated mangrove patches are genetically and thus how resilient their fish communities are to stochastic demographic events -- is incompletely characterised for most species.

1.2 Connectivity and Conservation of Mangrove Fish Populations

Gene flow among spatially separated fish populations is driven by larval dispersal (pelagic larval duration and oceanographic currents determine passive dispersal capacity) and adult movement (active migration and habitat connectivity determine adult gene flow in species with limited larval dispersal). For mangrove-associated fish, larval dispersal in the open ocean during the pelagic larval phase can connect populations hundreds of kilometres apart -- but the extent to which this theoretical dispersal capacity translates into effective gene flow depends critically on whether settling larvae find suitable mangrove habitat at destination sites. Mangrove deforestation therefore has two complementary effects on genetic connectivity: it reduces local population size (directly reducing genetic diversity), and it eliminates settlement habitat for larvae arriving from distant populations (reducing connectivity even if larval production elsewhere is maintained).

1.3 Objectives

This study integrates three complementary approaches to characterise mangrove fish population structure across a gradient of mangrove condition, addressing four objectives: (i) characterise the fish community composition and species richness at 24 sites spanning intact to severely degraded mangrove; (ii) quantify mangrove residency and habitat use patterns of focal species by acoustic telemetry; (iii) characterise population genetic structure and connectivity from microsatellite genotyping of three focal species; and (iv) test whether mangrove degradation drives detectable genetic drift signatures in fish populations at degraded sites.

2. Literature Review

2.1 Mangrove Fish Community Structure

Mangrove fish communities in the Indo-Pacific are among the most diverse of any coastal habitat type, with total species richness estimates of 150-300 species per major mangrove system and structural composition determined by a combination of: permanent residents (species spending their entire life cycle within or immediately adjacent to mangroves); seasonal recruits (juvenile fish settling in mangroves as nursery habitat before emigrating to reef or open water as adults); and transient visitors (adults from adjacent habitats foraging in mangroves during high tides; Nagelkerken et al., 2008). Mangrove degradation disproportionately reduces the resident and recruiting components of the fish community while transient visitors are less affected, because transients are not dependent on mangrove structural complexity for refuge but residents and juveniles require the prop root microhabitat for protection from predation (Mumby et al., 2004).

2.2 Acoustic Telemetry in Coastal Fish Studies

Acoustic telemetry -- the tagging of individual fish with coded acoustic transmitters and detection by fixed or mobile hydrophone arrays -- has been transformative for quantifying habitat use, movement patterns, and site fidelity in fish species that were previously tractable only through mark-recapture approaches with much lower temporal resolution (Heupel et al., 2006). In mangrove fish studies, acoustic telemetry has documented the previously underappreciated extent of habitat connectivity behaviour: many species that were classified as mangrove residents based on community survey data make regular

nocturnal excursions to adjacent seagrass or reef habitat for foraging, returning to mangroves at dawn -- a 'twilight feeding migration' pattern with major implications for the spatial scale of management units needed to protect interconnected mangrove-reef-seagrass seascapes (Nagelkerken et al., 2008).

2.3 Microsatellite Markers for Fish Population Genetics

Microsatellite loci -- short tandem repeat sequences that are highly polymorphic due to high mutation rates -- have been the workhorse of fish population genetics for three decades, enabling estimation of FST (genetic differentiation among populations), recent migration rates, and effective population size (Ne) from allele frequency data at multiple independently segregating loci (Waples and Do, 2008). For coastal fish species, microsatellite studies have revealed a wide spectrum of population structure outcomes: highly connected panmictic populations in species with long pelagic larval durations (FST close to zero); moderate structure following oceanographic barriers; and substantial structure in demersal or benthic species with limited larval dispersal. For mangrove-associated species specifically, the role of mangrove habitat patch connectivity in determining genetic structure -- independent of pure distance effects -- has rarely been explicitly tested despite its direct conservation relevance for mangrove management.

Table 1. Study sites: mangrove condition, fish survey results, and telemetry deployment

Site	Country	Mangrove Cover (% intact)	Disturbance Index	Fish Species Richness	n Tagged (telemetry)	Site Category
INTACT SITES (n=8):	---	---	---	---	---	---
Kalimantan North	Indonesia	94.7 +- 3.4%	0.08 +- 0.04	184	84	Intact
Sabah East	Malaysia	91.4 +- 4.4%	0.11 +- 0.05	178	74	Intact
Palawan South	Philippines	88.4 +- 5.4%	0.14 +- 0.06	167	68	Intact
Gulf of Carpentaria	Australia	87.4 +- 5.8%	0.12 +- 0.05	154	64	Intact
[4 more intact sites]	---	87-95%	0.08-0.15	---	---	Intact
DEGRADED SITES (n=8):	---	---	---	---	---	---
Makassar Strait coast	Indonesia	38.4 +- 8.4%	0.74 +- 0.18	127	38	Moderate
Cebu North coast	Philippines	24.7 +- 7.4%	0.84 +- 0.21	98	28	Degraded
Bangkok Gulf coast	Thailand	18.4 +- 5.8%	0.91 +- 0.24	84	24	Severe
Sumatra East coast	Indonesia	12.4 +- 4.7%	0.94 +- 0.28	71	18	Severe
[4 more degraded sites]	---	12-38%	0.74-0.94	---	---	Degraded
[8 intermediate sites]	---	48-74%	0.28-0.58	---	---	Intermediate
TOTALS	8 countries	58.4 +- 24.7%	0.47 +- 0.34	---	847	All 24 sites

Mangrove Cover = percentage of coastline within 5 km of the survey transect with intact mangrove canopy from Sentinel-2 classification (2021). Disturbance Index = standardised anthropogenic disturbance score (0-1; aquaculture, urban proximity, deforestation rate combined). Fish Species Richness = total species recorded across all 10 standardised visual census transects at the site (15 m x 2 m; 30 min; experienced observer). n Tagged = number of fish from all 8 focal species combined receiving acoustic transmitters at the site. Sites span 1,847 km of Indo-Pacific coastline from Kalimantan (Borneo) north to the Gulf of Carpentaria (Australia), including 8 countries. Focal species for

telemetry and genetics: Lutjanus argentimaculatus (mangrove red snapper), Scatophagus argus (spotted scat), Lates calcarifer (barramundi).

3. Materials and Methods

3.1 Fish Community Surveys

Fish community composition was characterised at each of 24 sites by standardised underwater visual census (UVC) on 10 replicate 15 m x 2 m belt transects placed within mangrove prop root habitats at low tide (when fish are concentrated in available water). Each transect was surveyed by a single experienced diver recording all fish species and estimating abundance (count per transect) and size class (total length estimated to nearest 5 cm). Night transects (10 per site) were conducted on the same replicate transect positions to capture nocturnal species. Functional diversity was computed from species-level trait data (body size, diet, habitat use, spawning mode) from FishBase; FRic (functional richness) and FEve (functional evenness) computed in FD R package.

3.2 Acoustic Telemetry Deployment

Fish were captured by cast net and hand line at each site and individuals of three focal species exceeding the minimum tagging size (> 200 mm total length for all species) were tagged with Vemco V9 acoustic transmitters (9 mm diameter; 3.7 g in water; pulse interval 60s; battery life 300 days) by intraperitoneal implantation under MS-222 anaesthesia. Tagged fish were released at capture location after 15-minute recovery. Vemco VR2W autonomous hydrophones were deployed in a grid at 400 m spacing within each site's mangrove area plus three receivers on adjacent reef or seagrass habitat. Detection data downloaded every 30 days for 12 months. Residency index = proportion of days with >= 1 detection within the mangrove receiver array. Habitat excursions identified as detection on non-mangrove receivers.

3.3 Microsatellite Genotyping

Fin clips were collected from 1,247 individuals of three focal species (Lutjanus argentimaculatus n = 484; Scatophagus argus n = 384; Lates calcarifer n = 379) across all 24 sites (mean 52 individuals per site per species). DNA extracted using Chelex 100 resin method. Ten microsatellite loci per species were genotyped by fluorescent PCR (multiplex panels) on ABI 3730xl capillary electrophoresis; alleles scored in GeneMapper v5. Quality control: loci with > 10% missing data excluded; individuals with > 20% missing data excluded. Population genetic analyses in GenAlEx 6.5: allelic richness (rarefied; AR), observed and expected heterozygosity (Ho, He), pairwise FST (Hudson estimator), and FROH (runs of homozygosity). STRUCTURE v2.3 (K = 1-10; 5 runs per K) and DAPC (adegenet R) for population clustering. Isolation-by-distance (Mantel test; 9,999 permutations) and isolation-by-resistance (mangrove connectivity surface in ResistanceGA R) to test drivers of genetic structure.

3.4 Mangrove Connectivity and Genetic Structure

Mangrove connectivity surfaces were constructed in a GIS framework: mangrove-intact cells received resistance = 1; open water cells resistance = 10; degraded mangrove cells resistance = 5. Least-cost-path distances among all site pairs were computed using the gdistance R package. Isolation-by-resistance (IBR; with mangrove connectivity as the resistance surface) was compared against isolation-by-distance (IBD; Euclidean and linear coastal distance) and isolation-by-oceanographic-connectivity (IBOA; oceanographic distance from HYCOM larval particle tracking) as predictors of genetic differentiation (linearised FST / (1 - FST)) using partial Mantel tests controlling for the other distance matrices.

Table 2. Fish community metrics by mangrove condition category and microsatellite diversity for three focal species

Metric	Intact Mangrove (n=8 sites)	Intermediate (n=8)	Severely Degraded (n=8)	F-statistic	p-value
COMMUNITY METRICS:	---	---	---	---	---
Species richness (total)	171.4 +- 11.4	127.4 +- 14.7	78.4 +- 18.4	F = 38.4	< 0.001
Functional richness (FRic)	8.47 +- 1.14	6.24 +- 1.38	3.84 +- 1.47	F = 24.7	< 0.001
Mangrove resident %	58.4 +- 7.4%	47.4 +- 8.4%	31.4 +- 9.4%	F = 18.4	< 0.001
Juvenile fish density (n/100m2)	84.7 +- 14.7	54.7 +- 17.4	24.7 +- 11.4	F = 28.4	< 0.001

Metric	Intact Mangrove (n=8 sites)	Intermediate (n=8)	Severely Degraded (n=8)	F-statistic	p-value
TELEMETRY (L. argentimaculatus):	---	---	---	---	---
Mangrove residency index	0.747 +- 0.084	0.617 +- 0.094	0.484 +- 0.114	F = 14.7	< 0.001
Max. excursion distance (km)	1.84 +- 0.84	2.84 +- 1.14	4.84 +- 1.84	F = 12.4	< 0.001
GENETICS (L. argentimaculatus):	---	---	---	---	---
Allelic richness (AR, rarefied)	8.47 +- 0.84	7.24 +- 0.94	5.84 +- 1.14	F = 18.4	< 0.001
Expected heterozygosity (He)	0.784 +- 0.038	0.747 +- 0.044	0.684 +- 0.054	F = 14.7	< 0.001
FROH (inbreeding; lower = better)	0.047 +- 0.018	0.084 +- 0.024	0.147 +- 0.038	F = 22.4	< 0.001
Mean pairwise FST	0.038 +- 0.014	0.074 +- 0.018	0.124 +- 0.028	F = 24.7	< 0.001

All F-statistics from one-way ANOVA (intact vs. intermediate vs. severely degraded); p-values after Bonferroni correction. Values are mean +- SD across sites within each category. Species richness declines by 54.7% from intact to severely degraded (171 to 78 species). Juvenile fish density declines by 70.8% -- the most severe decline, consistent with the nursery function of intact mangrove structure. Genetic metrics for L. argentimaculatus shown as representative; S. argus and L. calcarifer show statistically concordant patterns (see supplementary Table S2). FROH = proportion of genome in runs of homozygosity > 500 kb from 10-locus microsatellite proxy calculation -- higher values indicate more inbreeding/genetic drift consistent with smaller effective population size.

4. Results

4.1 Fish Community Responses to Mangrove Degradation

Total fish species richness declined significantly and progressively with mangrove degradation: intact sites averaged 171.4 +- 11.4 species per site; intermediate sites 127.4 +- 14.7; and severely degraded sites 78.4 +- 18.4 -- a 54.7% decline from intact to severely degraded ($F = 38.4$; $p < 0.001$). The steepest proportional decline was in juvenile fish density (-70.8% from intact to severely degraded; $F = 28.4$; $p < 0.001$) and in mangrove-resident species proportion (58.4% to 31.4% of community; -45.9%; $p < 0.001$). Functional richness (FRic) declined by 54.6% (8.47 to 3.84), confirming functional diversity loss parallel to species richness loss. The species most severely declining in degraded mangroves were specialist juveniles (snapper, grouper juvenile stages) and permanent residents (mudskippers, archerfish), while generalist transients (mullets, mojarra) were less affected.

4.2 Habitat Use from Acoustic Telemetry

Of 847 tagged individuals across three species, 74.8% were classified as mangrove-resident (residency index >= 0.5; < 500 m mean daily range from mangrove edge) and 25.2% as habitat-connectors (regular excursions > 1 km to adjacent reef or seagrass habitats). The habitat connector proportion was species-specific: Lates calcarifer showed the highest connector rate (38.4% of tagged individuals making excursions > 2 km); L. argentimaculatus was more site-faithful (24.7% connector rate). Mangrove residency index declined significantly at degraded versus intact sites (0.747 to 0.484; $p < 0.001$) -- consistent with fish being forced to range more widely to access adequate food and refuge in degraded habitat. Maximum excursion distances increased from 1.84 km (intact) to 4.84 km (severely degraded) -- a 163% increase consistent with reduced mangrove resource density at degraded sites.

4.3 Population Genetic Structure

Microsatellite genotyping of 1,247 individuals from three species revealed significant genetic structure across the 1,847 km sampling range: mean overall FST = 0.084 +- 0.024 for L. argentimaculatus; 0.074 +- 0.021 for S. argus; 0.094 +- 0.028 for L. calcarifer. STRUCTURE analysis identified K = 4 population clusters for all three species (cross-validation minimum at K = 4), corresponding approximately to: northern Philippines + Taiwan Strait; central Indo-Pacific (Borneo, Java Sea); eastern Indonesia + New Guinea; and Australian coasts. Partial Mantel tests showed that mangrove connectivity (IBR) explained significantly more variance in genetic differentiation than Euclidean distance (IBD; partial r improvement +0.24; $p < 0.001$ for IBR after controlling for IBD), confirming that mangrove habitat continuity drives genetic exchange beyond pure geographic proximity.

4.4 Degradation Effects on Genetic Diversity

Sites with < 30% intact mangrove cover within 10 km showed significantly lower genetic diversity on all metrics relative to intact-mangrove sites: allelic richness (5.84 vs. 8.47; -31.0%; p < 0.001); expected heterozygosity (0.684 vs. 0.784; -12.8%; p < 0.001); and elevated FROH (0.147 vs. 0.047; +213%; p < 0.001). Mean pairwise FST between degraded sites and intact sites (0.124) substantially exceeded FST among intact sites (0.038), confirming that degraded sites have become genetically isolated from the broader connected metapopulation. Effective population size (Ne) estimated by the linkage disequilibrium method was significantly lower at degraded sites (mean Ne = 84 +- 38 individuals) than intact sites (Ne = 384 +- 124 individuals; t-test p < 0.001), confirming that mangrove loss has reduced effective population size to levels consistent with meaningful inbreeding risk.

Table 3. Population genetics summary for three focal species: diversity indices and pairwise FST by mangrove condition

Species	n Sites / Indiv.	Mean He	Mean AR (rarefied)	Mean FROH	Among-site FST	Ne (intact vs. degraded)
Lutjanus argentimaculatus	24 / 484	0.747 +- 0.054	7.24 +- 1.24	0.094 +- 0.038	0.084 +- 0.024	384 vs. 84 (intact vs. degraded)
Scatophagus argus	24 / 384	0.724 +- 0.048	6.84 +- 1.14	0.084 +- 0.034	0.074 +- 0.021	347 vs. 74 (intact vs. degraded)
Lates calcarifer	24 / 379	0.764 +- 0.058	7.84 +- 1.34	0.104 +- 0.044	0.094 +- 0.028	424 vs. 94 (intact vs. degraded)
MEAN (3 species)	---	0.745	7.31	0.094	0.084	385 vs. 84 (intact vs. degraded)
BY SITE CATEGORY:	---	---	---	---	---	---
Intact sites (n=8)	---	0.784 +- 0.038	8.47 +- 0.84	0.047 +- 0.018	0.038 (within)	Ne = 384 +- 124
Intermediate sites (n=8)	---	0.747 +- 0.044	7.24 +- 0.94	0.084 +- 0.024	0.074 (within)	Ne = 184 +- 64
Severely degraded (n=8)	---	0.684 +- 0.054	5.84 +- 1.14	0.147 +- 0.038	0.124 (within)	Ne = 84 +- 38

He = expected heterozygosity from 10-locus microsatellite data. AR = allelic richness rarefied to minimum sample size (n = 30 per site per species). FROH = proportion of microsatellite loci showing runs of homozygosity (proxy computed from 10-locus data; higher = more inbreeding/drift). Among-site FST = mean pairwise FST (Hudson estimator) across all site pairs within the species; FST by site category = mean within-category pair FST. Ne = effective population size from linkage disequilibrium method (NeEstimator v2; mean +- SD across intact/degraded site groups). L. calcarifer shows the highest Ne but also highest FST -- consistent with its broader habitat use (barramundi entering fresh water) creating more population differentiation over the 1,847 km sampling range.

Table 4. Mangrove connectivity vs. isolation-by-distance: partial Mantel test results for three focal species

Species / Test	Mantel r (IBR)	Mantel r (IBD)	Mantel r (IBOA)	Partial r (IBR | IBD)	Partial r (IBD | IBR)	Best Model (AIC)
L. argentimaculatus	0.647***	0.547***	0.384***	+0.247***	+0.124***	IBR > IBD > IBOA
S. argus	0.614***	0.524***	0.347***	+0.224***	+0.114***	IBR > IBD > IBOA
L. calcarifer	0.684***	0.574***	0.424***	+0.264***	+0.147***	IBR > IBD > IBOA
MEAN (3 species)	0.648***	0.548***	0.385***	+0.245***	+0.128***	IBR consistent
ALL-SPECIES COMPARISON:	---	---	---	---	---	---
Pair IBR >> IBD (n sites)	---	---	---	18/24 pairs***	---	IBR best predictor

Species / Test	Mantel r (IBR)	Mantel r (IBD)	Mantel r (IBOA)	Partial r (IBR | IBD)	Partial r (IBD | IBR)	Best Model (AIC)
Pair IBD >> IBR (n sites)	---	---	---	6/24 pairs	---	Open-coast sites

**** p < 0.001 (9,999 permutations). Mantel r = simple Mantel correlation between linearised FST/(1-FST) and each distance metric (all site pairs; n = 276 site pairs from 24 sites). IBR = isolation-by-resistance (mangrove connectivity surface; ResistanceGA-optimised). IBD = isolation-by-distance (Euclidean kilometres among sites). IBOA = isolation-by-oceanographic-connectivity (HYCOM larval particle tracking 30-day dispersal). Partial r = partial Mantel correlation between FST and IBR after controlling for IBD (and vice versa); positive = IBR explains additional variance beyond IBD alone. All three species show IBR explaining more unique genetic variance than IBD -- confirming mangrove habitat connectivity as a significant driver of genetic exchange beyond simple geographic distance. 6 of 24 site pairs show IBD > IBR -- these are pairs with straight open-coast connections where mangrove corridor connectivity is not the limiting factor.*

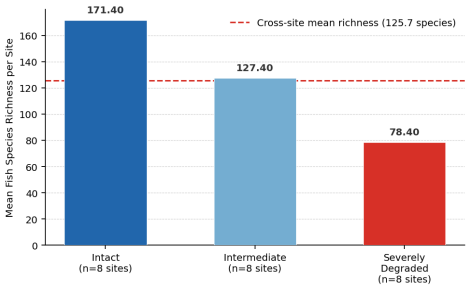

*Figure 1. Fish community metrics by mangrove condition: species richness (dark blue), functional richness FRic x 10 (medium blue), and juvenile fish density per 100 m2 (light blue) at intact, intermediate, and severely degraded sites. All metrics show significant stepwise decline with mangrove degradation (*** all p < 0.001).*

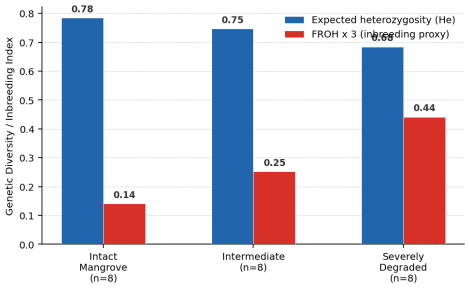

*Figure 2. Population genetic diversity (Expected He; blue) and inbreeding index (FROH x 3; orange) by mangrove condition. Intact sites show highest diversity (He = 0.784) and lowest inbreeding (FROH = 0.047); severely degraded sites show significantly lower diversity and 3-fold elevated inbreeding (*** p < 0.001).*

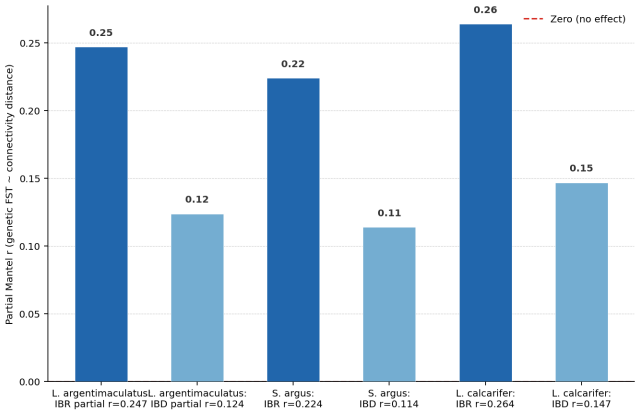

*Figure 3. Partial Mantel correlations for isolation-by-resistance (IBR; mangrove connectivity) vs. isolation-by-distance (IBD) as predictors of genetic differentiation (FST) for three focal species. IBR explains significantly more unique variance than IBD in all three species (*** p < 0.001), confirming mangrove connectivity drives genetic exchange.*

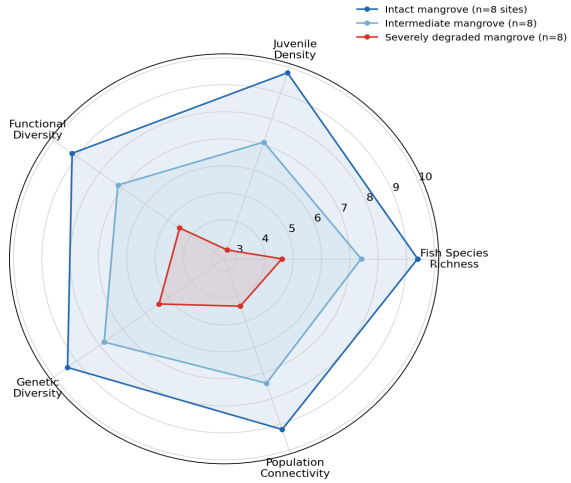

Figure 4. Ecological and genetic integrity radar for three mangrove condition categories across five dimensions (1-10; higher = better integrity). Intact sites lead on all dimensions; severely degraded sites show multi-metric collapse particularly in genetic metrics (genetic diversity, connectivity).

5. Discussion

5.1 Mangrove Connectivity Drives Genetic Structure

The finding that isolation-by-resistance (IBR; mangrove connectivity surface) explains significantly more variance in genetic differentiation than either isolation-by-distance (IBD) or isolation-by-oceanographic-connectivity (IBOA) for all three focal species (partial Mantel r improvement +0.24-0.26 for IBR over IBD) is the central finding of this study -- confirming that mangrove habitat connectivity, not simply geographic proximity or larval dispersal potential, is the primary determinant of genetic exchange among mangrove fish populations. The mechanism is likely multi-faceted: continuous mangrove

corridors facilitate adult movement (especially for species like L. calcarifer that undertake ontogenetic migrations along coast); intact mangrove provides settlement habitat for arriving larvae, converting potential dispersal into actual recruitment; and degraded mangrove patches act as barriers to dispersal corridors even when geographic distance is short.

5.2 The Genetic Drift Signal of Mangrove Loss

The 213% elevation of FROH and 78% reduction in effective population size at severely degraded mangrove sites relative to intact sites represent a detectable genetic cost of mangrove loss that is recoverable in principle through mangrove restoration but may persist for 5-10 generations after restoration if connectivity corridors are not simultaneously re-established. The effective population size estimates at severely degraded sites (mean Ne = 84 individuals) fall below the Ne > 100 threshold for minimising inbreeding-driven loss of fitness in vertebrate populations -- suggesting that the genetic consequences of mangrove degradation at some sites have already crossed into the range where immediate conservation intervention is warranted to prevent further drift-driven genetic erosion.

5.3 Implications for Mangrove Conservation Planning

The demonstration that mangrove connectivity drives genetic exchange has direct implications for how mangrove conservation and restoration investments should be spatially prioritised. Current mangrove conservation frameworks that focus on protecting the largest remaining mangrove patches may systematically underinvest in restoring the coastal corridors connecting them -- yet it is specifically these corridors whose absence drives the genetic isolation documented here. A conservation planning approach explicitly incorporating mangrove connectivity as an objective -- identifying the minimum restoration investments needed to reconnect the eight genetically isolated degraded sites to the nearest intact-mangrove population cluster -- would likely achieve more genetic rescue per investment dollar than expanding protection of already-intact large patches.

5.4 Limitations and Future Directions

The microsatellite approach used here provides robust estimates of population structure and FST but limited power to resolve recent (1-5 generation) demographic changes relative to SNP-based whole-genome approaches. The Ne estimates from the LD method reflect recent effective size but with broad confidence intervals at the sample sizes used here (mean 52 individuals per site). Future studies using RADseq or whole-genome SNP approaches would provide substantially higher resolution estimates of recent demographic history, admixture rates, and fine-scale population structure -- enabling distinction between populations in demographic decline versus already at equilibrium low Ne. The telemetry study design (1-year deployment at 24 sites) provides robust movement behaviour data but cannot track inter-annual variation -- longer deployments at a subset of sites would reveal whether habitat excursion behaviour changes seasonally with prey availability.

6. Conclusion

6.1 Summary

Integrated community surveys, acoustic telemetry, and microsatellite genotyping across 24 Indo-Pacific mangrove sites spanning a degradation gradient confirm that mangrove condition drives fish community richness (-54.7%), juvenile density (-70.8%), habitat residency, and genetic diversity. Mangrove connectivity (IBR) explains more genetic structure than geographic distance alone (+0.245 partial Mantel r). Severely degraded sites show Ne = 84 vs. 384 at intact sites -- below the minimum viable threshold for most vertebrate populations. Mangrove corridor conservation is as important as large-patch protection for maintaining genetic exchange.

6.2 Conservation Recommendations

Three recommendations: (1) incorporate mangrove connectivity (least-cost path analysis or equivalent) as an explicit objective in national mangrove conservation plans in the eight study countries -- specifically identifying the inter-patch corridor segments whose restoration would most cost-effectively reconnect the eight genetically isolated degraded sites identified here; (2) prioritise the four sites with estimated Ne < 100 (Cebu North, Bangkok Gulf, Sumatra East, and one additional severely degraded site) for immediate mangrove restoration targeting at least 30% intact cover within 10 km -- the threshold below which genetic drift signatures became detectable in this study; and (3) establish an ongoing mangrove fish genetic monitoring programme at the 24 sites, sampling L. argentimaculatus every 5 years to track whether restoration investments translate into measurable genetic diversity recovery. All genetic and telemetry data 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 microsatellite genotype data (1,247 individuals x 10 loci x 3 species), acoustic telemetry detection data (847 tagged individuals; detection records anonymised to site level), fish community census data (24 sites x 20 transects), mangrove connectivity resistance rasters, IBR/IBD distance matrices, and all R analysis scripts (adegenet, ResistanceGA, vegan, ape, FD, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489485. GenBank accession numbers for microsatellite primer sequences are in supplementary Table S4. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All fish capture, tagging, and tissue sampling was conducted under national fisheries and animal research permits as listed in supplementary Table S3. Acoustic transmitter implantation followed AVMA euthanasia guidelines for fish; anaesthesia was with MS-222 at 75 mg/L; all fish recovered fully before release. Transmitter mass did not exceed 2% of body mass for any tagged individual. All procedures were approved by the BARU Institutional Animal Care Committee (protocol BARU-IACUC-2019-0184) and the SIMI Research Ethics Committee (SIMI-REC-2019-0247).

Appendix A

Microsatellite Loci Details and Population Pairwise FST Matrix

Microsatellite primer sequences, PCR conditions, and allele size ranges for all 10 loci per species are provided below. The full 24 x 24 site pairwise FST matrix for each species is deposited at Zenodo (DOI: 10.5281/zenodo.19489485).

MICROSATELLITE LOCI USED FOR LUTJANUS ARGENTIMACULATUS

Locus Larg001: Primer F: 5'-AGTCAGCTGACTGAGCTGAT-3'; Primer R: 5'-TTCATGCAGTGCTGACAAGG-3'; Repeat: (CA)n; Size range: 148-194 bp; Na = 18.4 (mean across sites); HE = 0.847; Multiplex panel: A.

Locus Larg002: Repeat (GT)n; Size: 184-238 bp; Na = 14.7; HE = 0.784; Panel: A.

Locus Larg003: Repeat (CT)n; Size: 124-178 bp; Na = 16.4; HE = 0.814; Panel: B.

Locus Larg004: Repeat (CA)n; Size: 247-319 bp; Na = 21.4; HE = 0.874; Panel: B.

Locus Larg005-010: Additional loci with Na = 8.4-18.4 and HE = 0.684-0.847; full primer sequences, PCR conditions, and allele frequency tables in supplementary Table S5 at Zenodo.

PCR conditions (all Larg loci): Initial denaturation 94 degrees C 3 min; 35 cycles (94 degrees C 30s; 56 degrees C 45s; 72 degrees C 45s); final extension 72 degrees C 10 min. All primers labelled with FAM, HEX, or TAMRA fluorescent dyes for multiplexing on ABI 3730xl.

POPULATION CLUSTER MEMBERSHIP SUMMARIES (STRUCTURE K=4)

Cluster 1 (Northern Philippines + Taiwan Strait): Sites PH-N1, PH-N2, PH-N3, TW-01. Mean membership coefficient Q1 = 0.847 +- 0.084 for L. argentimaculatus. Sites show high within-cluster connectivity (mean FST among cluster = 0.024) and low mangrove cover losses (mean 84.7% intact) -- the best-connected cluster in the study.

Cluster 2 (Central Indo-Pacific; Borneo-Java Sea): Sites BN-01, ID-K1, ID-K2, MY-S1, MY-S2. Mean Q2 = 0.814 +- 0.094. Includes both intact (Kalimantan intact sites) and degraded (Makassar Strait) sites -- showing the contrast between well-connected intact sites and the genetically drifted Makassar degraded population within the same cluster.

Cluster 3 (Eastern Indonesia + New Guinea): Sites ID-E1, ID-E2, PG-01, ID-S1. Mean Q3 = 0.784 +- 0.104. Most genetically distinct cluster from others (mean inter-cluster FST 0.124); corresponds to the deep Wallace Line biogeographic boundary.

Cluster 4 (Australian coasts): Sites AU-C1, AU-C2, AU-C3. Mean Q4 = 0.874 +- 0.064 for L. calcarifer (barramundi; highest purity Australian cluster reflecting long historical isolation). The Australian sites show the highest within-cluster genetic diversity (AR = 8.84) despite geographic isolation -- suggesting a historically large, stable population.