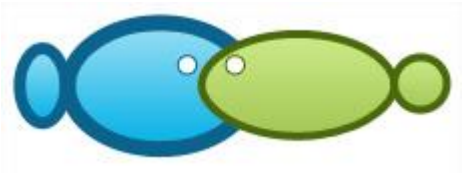

Management zoning drives reef fish communities structure revealed by environmental DNA in Nui Chua National Park, Vietnam

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Abstract. Environmental DNA (eDNA) metabarcoding provides a sensitive approach for assessing marine biodiversity; however, its ability to resolve ecological variation across small-scale management units in tropical coral reefs remains insufficiently explored. COI-based eDNA metabarcoding was employed to evaluate spatial patterns in reef fish assemblages across a final dataset of 13 sites in Nui Chua National Park (south-central Viet Nam), encompassing strictly protected zone (SPZ; n = 7) and human-use zone (HUZ; n = 6). High-throughput Illumina sequencing and downstream bioinformatic processing recovered 130 fish operational taxonomic units (OTUs), representing 56 families and 97 genera. Of these 121 OTUs (93.08%) were resolved to species level, while the remaining OTUs were assigned to higher taxonomic levels. Reef-associated taxa dominated the assemblage, whereas freshwater species constituted a minor component, likely reflecting background eDNA transport. Alpha diversity metrics did not differ significantly between management zones. In contrast, community composition differed significantly between zones, independent of dispersion effects. Beta-diversity partitioning showed that this divergence was primarily driven by species turnover rather than nestedness. Protected reefs exhibited higher exclusive richness and supported significant indicator taxa, whereas no indicator species were detected in the human-use zone. Overall, eDNA metabarcoding revealed turnover-driven restructuring of reef fish assemblages across contrasting management regimes, underscoring its utility for fine-scale ecological assessment and monitoring of tropical coral reef biodiversity.

Key Words: COI metabarcoding, coral reef fish assemblages, environmental DNA (eDNA), marine biodiversity, marine zoning.

Introduction. Coral reef ecosystems are among the most biodiverse habitats on Earth, providing essential ecosystem services such as coastal protection, fisheries production, and tourism. To safeguard these services, marine spatial planning often employs management units, such as marine protected areas (MPAs), to mitigate anthropogenic pressures. The effectiveness of such conservation strategies depends heavily on the availability of robust biodiversity data to support adaptive management. Despite their importance, accurately assessing reef fish assemblages remains challenging due to the structural complexity and high spatial heterogeneity of reef environments (Tkachenko et al 2023).

Traditionally, underwater visual census (UVC) and diver-based methods have served as the primary tools for reef fish monitoring. These approaches are nonetheless constrained by environmental conditions, observer expertise, and systematic biases against cryptic, nocturnal, or rare species (Polanco-Fernández et al 2021; Malik et al 2025). Consequently, visual surveys alone may underestimate total fish diversity and overlook functionally important or conservation-relevant taxa (Açıkbaş et al 2024; Muenzel et al 2024).

Environmental DNA (eDNA) metabarcoding has emerged as a complementary, non-invasive approach to overcome these limitations. By analyzing genetic material shed by organisms into the surrounding environment, eDNA enables the detection of a broad taxonomic spectrum, including species that are difficult to observe directly (Thomsen & Willerslev 2015; Goldberg et al 2016). Numerous studies have demonstrated that eDNA metabarcoding can recover a broader taxonomic spectrum and refine community

assessments, particularly by improving detection of cryptic, rare, or behaviorally elusive taxa (Polanco-Fernández et al 2021; Gösser et al 2023; Muenzel et al 2024).

In the Indo-Pacific region, applications of eDNA metabarcoding have consistently demonstrated sensitivity to broad patterns of spatial and ecological structuring in reef fish assemblages across management gradients or in MPAs (Gelis et al 2021; Bautista et al 2023; Gösser et al 2023; Malik et al 2025; Molina & Tabugo 2025; Tabugo et al 2025). Several studies indicate that eDNA can detect taxa that are infrequently documented by conventional reef survey approaches (Gelis et al 2021; Malik et al 2025) including cryptic, low-abundance, or conservation-relevant species (Bautista et al 2023), highlighting its complementary value within reef biodiversity assessments. In some cases, eDNA surveys have also provided first regional records of reef-associated taxa within specific protected areas (Bautista et al 2023), underscoring its utility for improving baseline biodiversity knowledge at local and national scales. Collectively, these findings highlight the capacity of eDNA metabarcoding to characterize reef fish assemblages beyond visually conspicuous components and to support comparative analyses across spatial management contexts.

Despite these advancements worldwide and across the Indo-Pacific, Vietnam faces a significant knowledge gap. The application of eDNA metabarcoding in Vietnamese marine national parks remains in its infancy, with limited implementation relative to global and regional applications. Biodiversity assessments in Vietnam still rely almost exclusively on traditional diver-based or gear-based methods (Nguyen & Mai 2020), with existing metabarcoding efforts largely limited to freshwater systems or localized sponge-based surveys (Durand et al 2022; Turon et al 2020).

This gap is notably pronounced in Nui Chua National Park, a key marine biodiversity hotspot located in Khanh Hoa Province, where coral reef ecosystems are of paramount conservation priority. Although previous conventional surveys have recorded 347 marine fish species across the park and its adjacent areas, including 68 species listed as threatened or near-threatened on the IUCN Red List and Vietnam Red Data Book (Nui Chua National Park Management Board 2024), the full capacity of eDNA to characterize these assemblages remains unexplored. There is a critical need to evaluate whether eDNA can resolve ecologically meaningful differences across the park's management zones to better inform conservation efforts.

Therefore, this study utilizes COI-based eDNA metabarcoding to evaluate reef fish communities across two contrasting management zones in Nui Chua National Park. By doing so, we aim to achieve the following: (i) characterize the taxonomic composition of reef fish assemblages detected by eDNA, including cryptic and rarely observed taxa; (ii) quantify differences in alpha and beta diversity between strictly protected and human-use zones; and (iii) assess the ability of eDNA metabarcoding to identify zone-associated taxa and patterns of species turnover relevant to marine spatial management.

Material and Method

Study area and water sampling. The study followed a stratified sampling design to evaluate the ecological responses of fish assemblages to marine zones. Fieldwork was conducted during the dry season in May 2024 to minimize confounding variables, such as terrestrial runoff and seasonal climatic variation. A total of 14 reef sites (Figure 1) were initially surveyed across two contrasting management regimes: a strictly protected "no-take" core zone (SPZ; n = 7), where extractive activities are prohibited, and an adjacent human-use buffer zone (HUZ; n = 7), where regulated activities including snorkeling, diving, and small-scale traditional fisheries are permitted (Le 2024).

At each station, triplicate 1 L surface seawater samples were collected at depths of 1-3 m using sterile polypropylene bottles, with site locations documented using a handheld GPS. To prevent cross-contamination and maintain sample integrity, field personnel utilized disposable gloves and decontaminated all sampling equipment with 10% bleach followed by a deionized water rinse between sites. Immediately following collection, seawater was filtered at a field station through 0.22 µm Sterivex cartridges (Millipore, Merck) using a sterile syringe, following the protocols of Cowart et al (2022).

Residual water was expelled from each cartridge, and 2 mL of ATL lysis buffer (Qiagen, Germany) was injected for DNA stabilization. The preserved cartridges were then sealed, transported on ice, and stored at -40°C until laboratory processing.

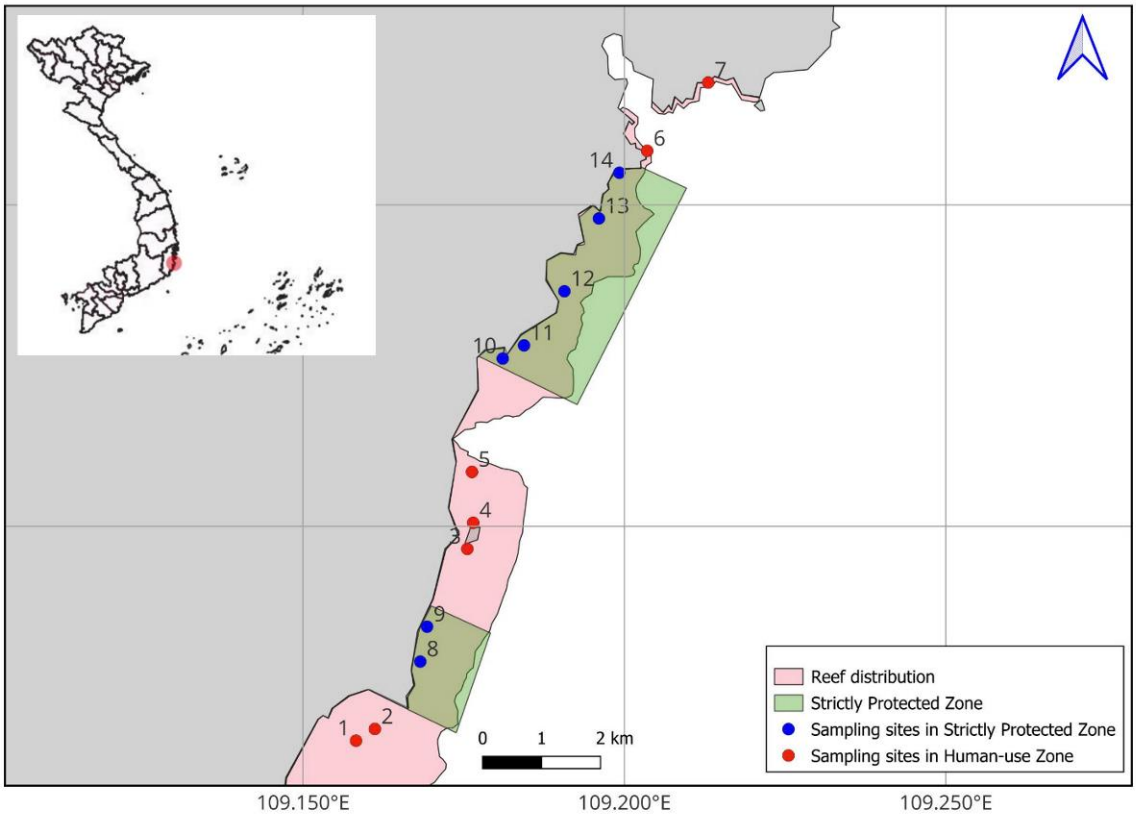

Figure 1. Spatial distribution of the 14 eDNA sampling sites in Nui Chua National Park. Reefs are shown with pink. The strictly protected zone (light green) and human-use zone are shown, with sampling sites marked in blue and red, respectively.

eDNA extraction. Environmental DNA captured on Sterivex™ filters was extracted using the QIAGEN DNeasy Blood & Tissue Kit (Qiagen, Germany) following Cowart et al (2022). Cartridges were surface-sterilized, incubated with Proteinase K at 56°C for 24 h. The lysate was recovered and mixed with Buffer AL and ethanol (1:1), at a 2:1 ratio relative to the lysate, and loaded onto DNeasy spin columns for binding and washing. DNA was eluted twice using preheated Buffer AE (56°C). DNA extraction quality was verified via 1.5% gel electrophoresis, and quantified using a Qubit fluorometer (Thermo Fisher, USA). Blank-filter controls were processed alongside samples to monitor potential contamination. Samples exhibiting PCR inhibition were treated using a OneStep PCR Inhibitor Removal Kit (Zymo Research, USA). All purified extracts were stored at -20°C prior to downstream analysis.

PCR amplification and Library preparation. Metabarcoding libraries were prepared using a two-step PCR amplicon workflow following Illumina dual-indexing practices (Illumina 2013; Leray et al 2013; Glenn et al 2019). The first PCR (PCR1) amplified the targeted COI fragment using mlCOIintF and jgCOIR primers (Leray et al 2013) modified with iTru overhangs (Glenn et al 2019). Each 10 µL reaction contained 1× HotStart GoTaq master mix, 0.3 µM of each primer, 0.2 mg mL^{-1} BSA, and 1 µL of eDNA template. Thermocycling comprised 95°C for 7 min; 35 cycles of 95°C for 30 s, 46°C for 30 s, and 72°C for 30 s; and a final extension at 72°C for 5 min. Amplicons were verified on 1.5% agarose gels, yielding the expected ~430 bp product. Triplicate reactions were pooled and purified using KAPA Pure beads (1.2×).

The second PCR (PCR2) attached dual iTru5/iTru7 indices and full Illumina adapters following the dual-indexing strategy described in Glenn et al (2019) and

Illumina (2013). Indexing reactions (25 µL) consisted of 1× HotStart GoTaq mix, 0.3 µM of each index primer, 0.2 mg mL^{-1} BSA, and 2 µL of purified PCR1 product. Indexing PCR was performed under the following conditions: 95°C for 5 min; 8 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 30 s; and a final extension at 72°C for 5 min. Indexed products (~499 bp) were checked by gel electrophoresis and purified using KAPA Pure beads (0.8×). Final libraries were quantified using a Qubit™ dsDNA HS assay and pooled equimolarly prior to sequencing on an Illumina MiSeq platform (2x250 bp) at the Genomic Core Lab, Texas A & M University Corpus Christi (USA).

Bioinformatics and statistical analyses

Sequence processing and taxonomic assignment. Raw MiSeq reads were processed in an Ubuntu Linux environment (v24.04.3 LTS). Quality filtering and trimming were first conducted using Fastp v0.23.4 (Chen et al 2018) to remove low-quality bases and reads. Quality-controlled paired-end reads were subsequently merged, dereplicated, and chimera-checked using VSEARCH v2.27 (Rognes et al 2016). Sequences were then clustered into operational taxonomic units (OTUs) using a ≥97% sequence identity threshold and a minimum alignment length of ≥250 bp. A custom reference database was constructed from fish mitochondrial genome sequences retrieved from NCBI (https://www.ncbi.nlm.nih.gov/home/genomes/) and BOLD (https://boldsystems.org/). Representative OTU sequences were taxonomically assigned using BLASTn v2.12.0+ (https://www.ncbi.nlm.nih.gov/books/NBK571452/) against this curated database. OTUs identified as non-fish taxa or detected in negative controls were removed from downstream analyses.

Downstream ecological and statistical analyses. All subsequent ecological analyses and statistical processing were conducted in the RStudio environment v4.3.3 (R Core Team 2024), including data reshaping using the tidyr package and visualization implemented in ggplot2 (Wickham 2016).

Fish taxonomic composition: the curated OTU table was aggregated at the species, genus, and family levels to describe fish community composition, following established frameworks for marine eDNA studies (Jeunen et al 2019; Stat et al 2017). Relative taxon abundance and distribution across samples were explored using hierarchical clustering based on community dissimilarities and stacked bar plots. Detected taxa were further categorized by habitat association and salinity preference, with ecological traits and distributional information compiled from FishBase (Froese & Pauly 2025) and regional references on fish distributions in Vietnam (Kimura et al 2019; Prokofiev 2021; Tran et al 2023), and adjacent regions (Randall & Lim 2000).

Alpha diversity: variation in local diversity between management zones was evaluated using species richness, the Shannon diversity index (Shannon 1948), and the Simpson diversity index (Simpson 1949), calculated using the vegan package v2.6-10 (Oksanen et al 2025). Statistical significance of differences in alpha diversity metrics between zones was assessed using non-parametric Wilcoxon rank-sum tests (Wilcoxon 1945).

Beta diversity and multivariate analyses: community differentiation across management zones was assessed based on Bray-Curtis dissimilarities (Bray & Curtis 1957). Differences in community structure were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001), while multivariate homogeneity of group dispersions was evaluated using PERMDISP (Anderson 2006). Both analyses were implemented using the adonis2 and betadisper functions in the vegan package (Oksanen et al 2025). Community relationships were examined using Principal Coordinates Analysis (PcoA) (Hotelling 1933). In addition, total beta diversity was partitioned into turnover and nestedness components following the Baselga (2010) framework, implemented via the betapart package (Baselga & Orme 2012).

Indicator taxa and SIMPER analyses: indicator species analysis was conducted using the IndVal.g method with 999 permutations, implemented via the multipatt function in the indicspecies package (De Cáceres & Legendre 2009). This approach

extends the original IndVal index (Dufrêne & Legendre 1997) by accounting for unequal group sizes. To complement this analysis, Similarity Percentage (SIMPER) analysis (Clarke 1993) was conducted using the vegan package to quantify the contribution of individual taxa to Bray-Curtis dissimilarities between management zones and to highlight taxa associated with assemblage divergence.

Results and Discussion

Sequencing output and data summary. High DNA concentrations were successfully recovered from all processed samples; however, one sample from the HUZ (site 4) failed to amplify during the initial PCR. Consequently, the final dataset of 13 samples (SPZ = 7; HUZ = 6) were retained. High-throughput Illumina sequencing of the COI gene yielded approximately 6.3 million raw paired-end reads, which were bioinformatically filtered to 1.1 million high-quality sequences retained for downstream analyses.

Using a 97% identity threshold, the dataset was resolved into 1,145 OTUs. After filtering for fish taxa, 130 OTUs remained, predominantly comprising Actinopterygii (126 OTUs) and a minor representation of Chondrichthyes (4 OTUs). In total, these OTUs represented 56 families and 97 genera (Table 1). Taxonomic assignment achieved high resolution, with 93.08% (121/130) of fish OTUs identified to the species level corresponding to 97 genera within 56 families. The remaining nine OTUs (6.92%) were assigned to higher taxonomic ranks, including the families Atherinidae, Ophichthidae, Pomacentridae, and Tripterygiidae, and the genera *Eviota*, *Favonigobius*, *Gobionellus*, *Scarus*, and *Enneapterygius*. To further resolve ecological patterns, the identified taxa were categorized based on habitat affiliation (Table 2).

Table 1

Summary of filtering, taxonomic richness, and zone-specific distribution of fish taxa detected via eDNA

Category	*Total count*	*Strictly protected zone (n = 7)*	*Human-use zone (n = 6)*	*Shared*
Total OTUs	130	50	18	62
Actinopterygii	126	48	18	60
Chondrichthyes	4	2	0	2
Families	56	16	2	38
Genera	97	31	15	51
Species	121	47	17	57

Table 2

Fish taxa detected by eDNA at 97% similarity sequence and classified by habitat affiliation

No.	*Family*	*Taxa*	*Reef-associated*	*Non-reef-associated*	
				Marine/ brackish	*Fresh water only*
Class: Actinopterygii					
1	Acanthuridae	*Acanthurus nigricauda*	☑		
2		*Acanthurus triostegus*	☑		
3		*Ctenochaetus striatus*	☑		
4	Alepocephalidae	*Rouleina attrita*		☑	
5	Ambassidae	*Ambassis gymnocephalus*		☑	
6	Apogonidae	*Apogon crassiceps*	☑		
7		*Apogon semiornatus*	☑		
8		*Cheilodipterus isostigma*	☑		
9		*Ostorhinchus cyanosoma*	☑		
10		*Taeniamia buruensis*	☑		
11	Argentinidae	*Argentina kagoshimae*		☑	

12	Atherinidae	*Atherinomorus lacunosus*	☑		
13		*Hypoatherina temminckii*	☑		
14	Bathylagidae	*Pseudobathylagus milleri*		☑	
15	Blenniidae	*Salarias fasciatus*	☑		
16	Bothidae	*Crossorhombus azureus*		☑	
17	Callionymidae	*Callionymus planus*		☑	
18		*Synchiropus lateralis*		☑	
19	Carangidae	*Decapterus macrosoma*	☑		
20		*Selar crumenophthalmus*	☑		
21		*Selaroides leptolepis*	☑		
22	Channidae	*Channa gachua*			☑
23	Cichlidae	*Hypselecara temporalis*			☑
24		*Pterophyllum altum*			☑
25		*Pterophyllum scalare*			☑
26	Cobitidae	*Lepidocephalichthys berdmorei*			☑
27	Congridae	*Conger cinereus*	☑		
28	Dorosomatidae	*Clupanodon thrissa*		☑	
29		*Sardinella jussieu*		☑	
30	Ehiravidae	*Sundasalanx mekongensis*			☑
31	Engraulidae	*Stolephorus insularis*		☑	
32	Epinephelidae	*Cromileptes altivelis*	☑		
33		*Epinephelus lanceolatus*	☑		
34		*Epinephelus merra*	☑		
35	Gastromyzontidae	*Pseudogastromyzon fasciatus*			☑
36	Gempylidae	*Promethichthys prometheus*		☑	
37	Gerreidae	*Gerres oyena*	☑		
38	Gobiidae	*Asterropteryx semipunctata*	☑		
39		*Bathygobius fuscus*		☑	
40		*Boleophthalmus boddarti*		☑	
41		*Eviota sigillata*	☑		
42		*Eviota storthynx*	☑		
43		*Eviota zebrina*	☑		
44		*Favonigobius gymnauchen*	☑		
45		*Favonigobius reichei*		☑	
46		*Gobiopterus chuno*		☑	
47		*Priolepis semidoliata*	☑		
48	Gobionidae	*Sarcocheilichthys hainanensis*			☑
49	Labridae	*Cheilinus chlorourus*	☑		
50		*Cheilinus trilobatus*	☑		
51		*Cheilio inermis*	☑		
52		*Cirrhilabrus brunneus*	☑		
53		*Halichoeres argus*	☑		
54		*Halichoeres margaritaceus*	☑		
55		*Stethojulis bandanensis*	☑		
56		*Stethojulis trilineata*	☑		
57		*Thalassoma jansenii*	☑		
58		*Thalassoma quinquevittatum*	☑		
59		*Xyrichtys martinicensis*	☑		
60	Leiognathidae	*Gazza minuta*		☑	
61		*Photolateralis stercorarius*	☑		
62		*Photopectoralis bindus*		☑	
63	Lethrinidae	*Lethrinus nebulosus*	☑		
64	Melamphaidae	*Scopelogadus bispinosus*		☑	
65	Monacanthidae	*Paraluteres prionurus*	☑		
66		*Pervagor janthinosoma*	☑		
67	Muraenidae	*Echidna nebulosa*	☑		
68		*Echidna polyzona*	☑		
69		*Gymnothorax chilospilus*	☑		
70		*Gymnothorax fimbriatus*	☑		

71		*Gymnothorax flavimarginatus*	☑		
72		*Gymnothorax pindae*	☑		
73		*Gymnothorax thyrsoideus*	☑		
74		*Gymnothorax undulatus*	☑		
75		*Uropterygius concolor*	☑		
76	Myctophidae	*Hygophum reinhardtii*		☑	
77	Nemacheilidae	*Traccatichthys pulcher*		☑	
78		*Traccatichthys taeniatus*			☑
79	Nemichthyidae	*Avocettina infans*		☑	
80	Nemipteridae	*Nemipterus furcosus*	☑		
81		*Scolopsis monogramma*	☑		
82	Ophichthidae	*Schismorhynchus labialis*	☑		
83	Opisthoproctidae	*Opisthoproctus soleatus*		☑	
84	Polymixiidae	*Polymixia japonica*		☑	
85	Pomacentridae	*Abudefduf septemfasciatus*	☑		
86		*Abudefduf vaigiensis*	☑		
87		*Chrysiptera biocellata*	☑		
88		*Chrysiptera brownriggii*	☑		
89		*Chrysiptera talboti*	☑		
90		*Neoglyphidodon melas*	☑		
91		*Plectroglyphidodon leucozonus*	☑		
92		*Pomacentrus chrysurus*	☑		
93	Pseudochromidae	*Congrogadus subducens*	☑		
94		*Labracinus cyclophthalmus*	☑		
95	Salangidae	*Salanx ariakensis*		☑	
96	Sciaenidae	*Argyrosomus japonicus*		☑	
97		*Johnius carouna*		☑	
98		*Pennahia aneus*		☑	
99		*Protonibea diacanthus*		☑	
100	Scopelarchidae	*Scopelarchus guentheri*		☑	
101	Scorpaenidae	*Parascorpaena aurita*	☑		
102		*Sebastapistes fowleri*	☑		
103	Siganidae	*Siganus spinus*	☑		
104	Sillaginidae	*Sillago aeolus*		☑	
105	Sphyraenidae	*Sphyraena japonica*		☑	
106	Synanceiidae	*Minous monodactylus*		☑	
107	Synodontidae	*Saurida nebulosa*	☑		
108		*Trachinocephalus myops*	☑		
109	Tetraodontidae	*Arothron hispidus*	☑		
110		*Dichotomyctere ocellatus*		☑	
111		*Lagocephalus gloveri*		☑	
112		*Lagocephalus spadiceus*		☑	
113		*Lagocephalus wheeleri*		☑	
114	Trichiuridae	*Trichiurus brevis*		☑	
115		*Trichiurus lepturus*		☑	
116	Tripterygiidae	*Helcogramma fuscipectoris*		☑	
117	Uranoscopidae	*Uranoscopus japonicus*		☑	
Class: Chondrichthyes					
118	Dasyatidae	*Pastinachus sephen*	☑		
119	Rhinidae	*Rhina ancylostomus*	☑		
120	Rhinochimaeridae	*Harriotta raleighana*		☑	
121	Triakidae	*Hemitriakis japanica*		☑	
		Total	70	42	9
		Percentage	57.85%	34.71%	7.44%

The high proportion of species-level assignments highlights the effectiveness of COI-based eDNA metabarcoding for resolving reef-associated fish assemblages in tropical marine systems. Comparable levels of taxonomic resolution have been reported from Indo-Pacific reef environments, reflecting the relatively good coverage of common reef

fishes in COI reference databases. The small proportion of OTUs assigned only to higher taxonomic ranks likely reflect gaps in regional reference libraries (Stat et al 2017), and to a lesser extent, potential primer bias (Elbrecht & Leese 2015), rather than limitations of the sequencing approach itself (Taberlet et al 2018). These results underscore the value of expanding regional barcode databases and adopting multi-marker strategies to further improve taxonomic resolution in future eDNA surveys (Stat et al 2017), particularly for understudied coral reef systems along the south-central Vietnamese coast.

Fish community composition, habitat associations, and spatial structure. Based on ecological classification, reef-associated fishes constituted the dominant component of the eDNA assemblage, accounting for 57.85% (70 species) of detected taxa, followed by marine-brackish non-reef species (34.71%, 42 species), while freshwater taxa represented a minor fraction (7.44%, 9 species) (Table 2). This pattern suggests that the molecular signal predominantly reflects local benthic and demersal reef communities, with limited contribution from transient pelagic or offshore assemblages. Given that sampling was conducted directly within coral reef habitats, the predominance of reef-associated taxa is consistent with the expected structure of the local species pool rather than being driven primarily by methodological artefacts of eDNA metabarcoding. Similar patterns have been documented across tropical reef systems, where seawater eDNA reliably captures the dominant structural components of reef fish communities even under constrained sampling effort or logistical limitations (Açıkbaş et al 2024; Gelis et al 2021). Freshwater-associated taxa (e.g., Cichlidae and Channidae) were consistently detected at low read abundance and are interpreted as background signals rather than indicators of true habitat occupancy, a common feature of coastal eDNA surveys attributed to hydrological transport and land-based runoff, rather than the presence of established freshwater assemblages within marine habitats (Turon et al 2020).

At the family level, three families - Gerreidae (24.35%), Labridae (20.17%), and Pomacentridae (13.47%) - together accounted for more than half of all assigned reads (Figure 2A). Gerreidae was the most abundant family overall and contributed a higher proportion of reads in the SPZ than in the HUZ, whereas Labridae contributed more strongly in the HUZ with pronounced dominance at several human-use sites (e.g., sites 1, 3 and 5, Figure 2A). Pomacentridae remained a major component in both zones but was slightly more abundant in the SPZ and showed a marked local peak at Site 2 in the HUZ (> 40%) (Figure 2A).

Secondary families further differentiated assemblage composition between management zones. Polymixiidae was strongly associated with the SPZ, while Gobiidae showed higher representation in the HUZ, and Muraenidae was moderately enriched in SPZ. Trichiuridae contributed only marginally to overall read abundance and was restricted to a limited number of sites (e.g., Sites 7 and 14, Figure 2A). Collectively, these patterns reflect greater site-to-site variability in the HUZ compared with a more even family-level composition in the SPZ, consistent with spatial heterogeneity associated with management regime.

At finer taxonomic resolution, species-level patterns broadly mirrored family-level distributions (Figure 2B). Consistent with family-level patterns, a small number of species accounted for a substantial proportion of reads, with *Gerres oyena* (24.35%), *Halichoeres margaritaceus* (12.83%), and *Polymixia japonica* (9.73%) representing the most abundant taxa overall. *G. oyena* was detected across all sites and contributed a higher proportion of reads in the SPZ, whereas *H. margaritaceus* was strongly associated with the HUZ, reaching local dominance at several human-use sites (e.g., Sites 1, 3, and 5; Figure 2B).

Several species showed contrasting zone associations. *Plectroglyphidodon leucozonus* and *Cheilinus chlorourus* were relatively enriched in the SPZ, whereas *Chrysiptera talboti* displayed broadly comparable contributions across zones. *P. japonica* was strongly associated with SPZ sites and was nearly absent from the HUZ, consistent with its benthic affinity. By contrast, strong site-level dominance in the HUZ was restricted to a small number of taxa, most notably *Gobiopterus chuno*, which locally dominated a single HUZ site (Site 7; Figure 2B). Other species, including *Acanthurus*

triostegus and *Ambassis gymnocephalus*, were detected more frequently in the HUZ but consistently occurred at low relative abundance.

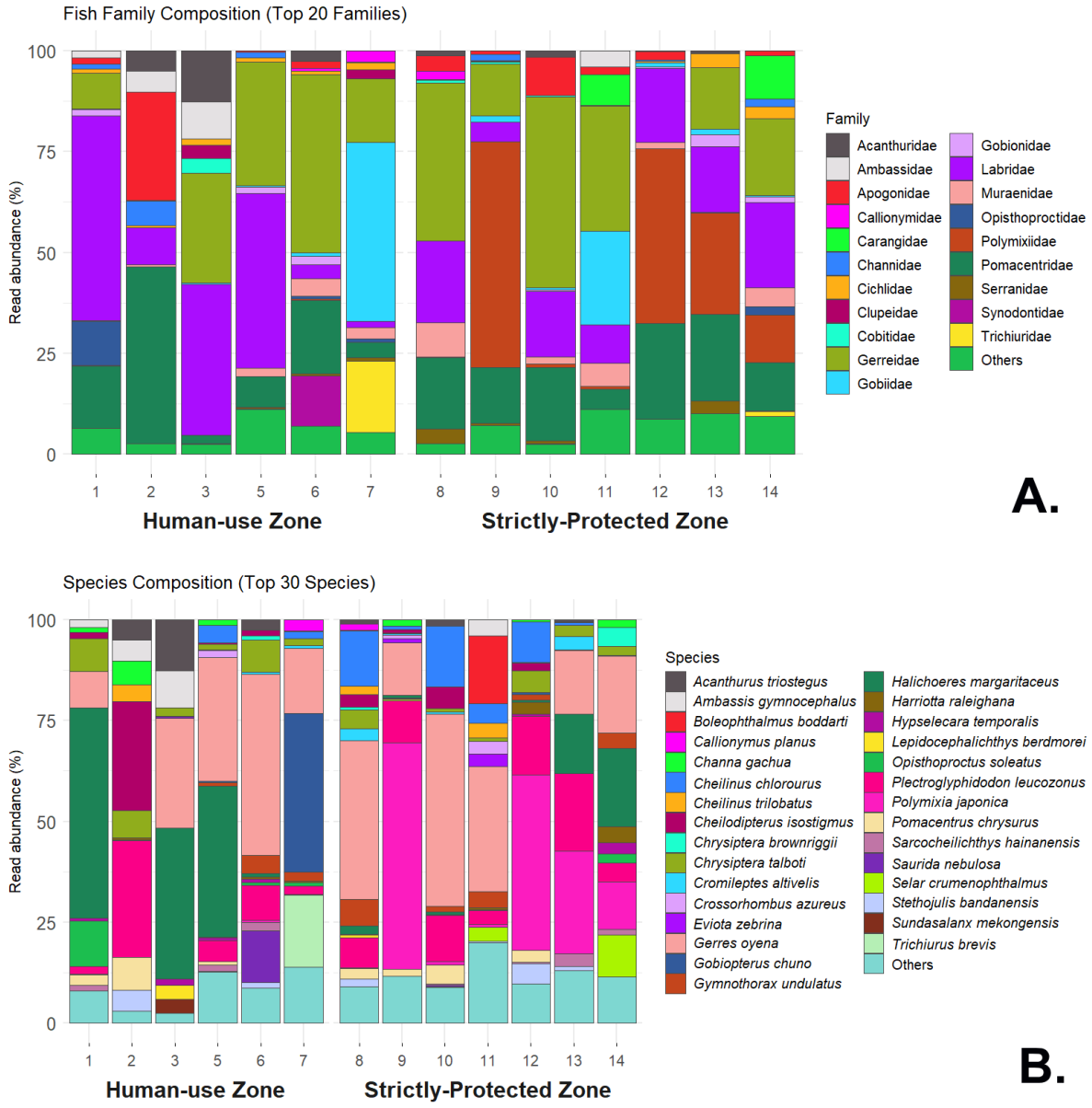

Figure 2. Community composition of fish detected across eDNA samples at family and species levels in Nui Chua National Park. Proportional read abundance of the top 20 families (A), and the top 30 species (B) detected from all eDNA samples, separated by management zone. Rare taxa are pooled as "Others". The combined figure provides an overview of community composition at coarse (family) and fine (species) taxonomic resolutions (one sample from the human-use zone (HUZ; site 4) failed PCR amplification and was therefore excluded from all downstream analyses and figures)

Across both zones, the "Others" category consistently represented a substantial fraction of reads, reflecting a background assemblage of low-abundance taxa. Among these, sequences assigned to Chondrichthyes comprised only a minor proportion of total reads; nevertheless, the detection of families such as Dasyatidae and Rhinidae indicates the presence of higher trophic-level elasmobranchs within the study area, despite their low relative representation in the eDNA dataset.

In addition, eDNA metabarcoding detected several rare and conservation-priority taxa, with most records originating from the SPZ and all represented by low read counts (< 27 reads). These included the chondrichthyan species *Pastinachus sephen* (Vulnerable, VU-A2d; Site 12-SPZ and Site 6-HUZ) and *Rhina ancylostomus* (Critically

Endangered, CR-A2bd; Site 12-SPZ), as well as the benthopelagic actinopterygian *Argyrosomus japonicus* (Endangered, EN-A2bd; Site 12-SPZ). The detection of these taxa, even at low read abundance, highlights the capacity of eDNA surveys to capture signals of conservation-relevant species that may be overlooked by conventional monitoring approaches.

Although several non-reef coastal and estuarine species were detected, the species-level assemblage was dominated by reef-associated taxa characteristic of Indo-Pacific coral reef systems (e.g., *H. margaritaceus*, *P. leucozonus*, *C. chlorourus*, *C. talboti*, and *A. triostegus*) as well as reef-adjacent or reef-slope–associated taxa (e.g., *P. japonica* and elasmobranchs such as *P. sephen* and *R. ancylostomus*), consistent with the reef-based sampling design. Moreover, the detection of multiple rare and conservation-priority taxa at very low read abundance, particularly within the strictly protected zone, highlights the capacity of eDNA metabarcoding to complement UVC methods. Such taxa, including elasmobranchs and benthopelagic species, are likely to be underestimated by visual surveys due to their low densities, cryptic behavior, or limited detectability under variable field conditions. This advantage is especially relevant in Vietnam and other data-limited regions, where logistical constraints, restricted survey effort, and variable underwater visibility can substantially limit the effectiveness of conventional monitoring approaches (Malik et al 2025; Turon et al 2020).

Alpha and Beta diversity patterns. Alpha diversity metrics indicated no statistically significant difference between the two management regimes. Mean species richness was slightly higher in the SPZ (29.86±8.21) than the HUZ (27.00±7.29), but this difference was not statistically significant (Wilcoxon test, p = 0.57). Shannon (*H'*: 2.10±0.19 vs. 2.16±0.37; p = 1.00), and Simpson (*D*: 0.77±0.06 vs. 0.79±0.07; p = 0.83) indices similarly indicated comparable within-sample diversity and evenness between zones (Figure 3).

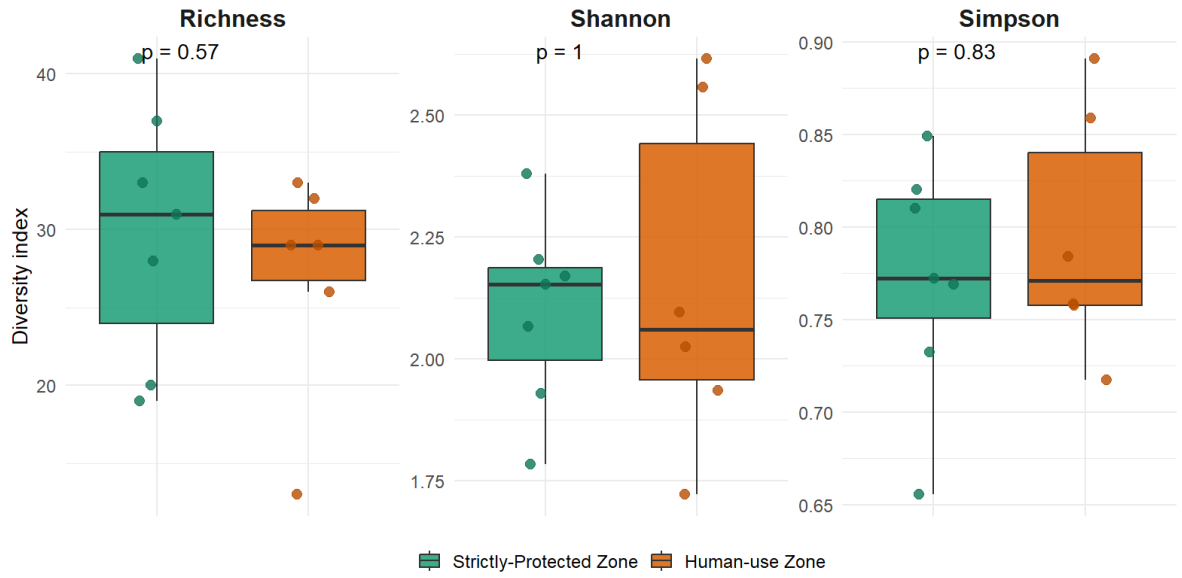

Figure 3. Comparison of alpha diversity indices for fish communities between management zones. Boxplots display species richness, Shannon diversity, and Simpson diversity for the strictly protected zone (green) and the human-use zone (orange). Points represent individual sampling replicates, and p-values (Wilcoxon rank-sum test) indicate no significant differences between the two zones (p > 0.05).

In contrast, beta diversity analyses revealed a significant but moderate separation in community composition between the two management zones. PERMANOVA based on Bray-Curtis dissimilarities indicated distinct clustering of samples (R^2 = 0.178, F = 2.380, p = 0.006). A non-significant PERMDISP result (F = 0.0892, p = 0.778) indicated that this pattern reflected differences in community centroids rather than heterogeneity in

multivariate dispersion. This separation was visually supported by principal coordinates analysis (PCoA; Figure 4), where samples from SPZ and HUZ were primarily distributed along the first axis, which explained 25.5% of the total variance. Partitioning of total beta diversity (βSOR = 0.855) indicated that most compositional variation was attributable to species turnover (βSIM = 0.818) with a comparatively minor contribution from nestedness (βSNE = 0.037).

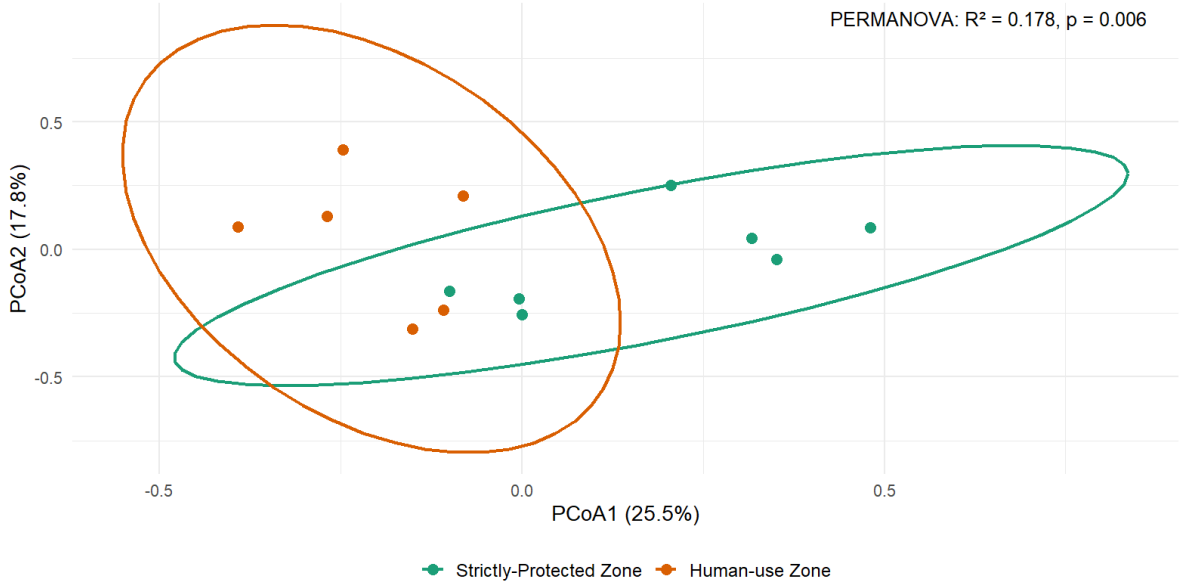

Figure 4. Principal Coordinates Analysis (PCoA) based on Bray-Curtis dissimilarity of fish community composition between two management zones. Points represent sites; ellipses indicate 95% confidence intervals.

Together, these findings indicate that local-scale alpha diversity metrics alone did not capture the spatial structuring of reef fish assemblages across management zones. Instead, community differentiation was expressed primarily at the multivariate level, driven by species turnover rather than systematic changes in richness or evenness. Similar turnover-dominated patterns have been reported from coral reef systems across management and disturbance gradients, underscoring the limited sensitivity of univariate diversity metrics for detecting ecologically meaningful change (Gelis et al 2021; Jaquier et al 2024).

Community divergence and taxon-specific responses to spatial management. Community divergence between management zones was evident across multiple taxonomic levels, with consistent differences in taxonomic richness, taxon-habitat associations, and community composition between the SPZ and the HUZ. A comparison of taxonomic richness and overlap across the two management zones (SPZ vs. HUZ) showed consistently higher diversity in the protected area across all taxonomic levels (Table 1). At the family level, a total of 56 families were detected, with protected sites recording 54 families compared to 40 families in human-use sites, of which 38 families were shared between zones. At the genus level, 97 genera were identified overall, with 82 genera detected in protected sites and 66 in human-use sites, resulting in 51 shared genera. At the species level, 121 species were recorded, with protected sites yielding 104 species compared to 74 species in human-use sites, and 57 species shared between zones. Consistent with these patterns, the SPZ exhibited higher exclusive richness (47 unique species) than the HUZ (17 unique species).

Indicator value analysis (IndVal.g, α = 0.05) identified significant indicator taxa exclusively for the SPZ. At the species level, *Stethojulis bandanensis* (IndVal = 0.903, p = 0.016) and *Cheilodipterus isostigmus* (IndVal = 0.897, p = 0.021) were strongly associated with protected reefs. Concordant patterns were detected at higher taxonomic

resolution, with the genera *Stethojulis* (IndVal = 0.982, p = 0.004) and *Cheilodipterus* (IndVal = 0.897, p = 0.019) also showed significant associations with the SPZ. No indicator taxa were detected for the HUZ at any taxonomic level, suggesting weaker or less consistent taxon–habitat associations in this zone.

SIMPER analysis showed that between-zone dissimilarity was primarily driven by reef-associated taxa, led by *H. margaritaceus* (6.88%; ratio = 1.55), *G. oyena* (4.75%; ratio = 1.46), and *P. leucozonus* (4.25%; ratio = 1.60). *P. japonica* contributed to overall dissimilarity (5.49%) but with more variable contributions (ratio = 1.04). At the family level, Labridae, Gerreidae, and Polymixiidae together accounted for over 22% of total dissimilarity.

Zoning emerged as a key factor shaping reef fish community structure within Nui Chua National Park. Although local-scale alpha diversity metrics (e.g., richness and evenness) did not differ significantly between the SPZ and the HUZ, clear differentiation was evident at the multivariate level, indicating that spatial management effects were expressed primarily through changes in community composition rather than overall diversity. Partitioning of beta diversity showed that this divergence was dominated by species turnover rather than nestedness, suggesting that zoning influences reef fish communities through species replacement rather than uniform gains or losses of taxa.

Assemblages in strictly protected reefs were characterized by higher taxonomic exclusivity and stronger taxon-habitat associations, whereas communities in human-use areas appeared more compositionally variable. The presence of multiple indicator species and genera in protected reefs, contrasted with the absence of robust indicator taxa in the HUZ, suggests greater ecological consistency under reduced disturbance. Similar asymmetries in indicator patterns have been documented in other reef systems, where protected areas maintain more stable community identities despite comparable levels of local diversity (Gelis et al 2021; Malik et al 2025).

Compositional divergence between zones was further structured by a limited number of taxa contributing disproportionately to community dissimilarity. Such concentration of influence among a limited number of taxa is consistent with the descriptive outcomes of SIMPER analyses, which frequently identify a small subset of taxa contributing disproportionately to Bray-Curtis dissimilarity in metabarcoding datasets (Kumar et al 2022). When considered alongside the dominance of species turnover in beta-diversity partitioning, this pattern supports a turnover-driven restructuring of reef fish communities rather than diffuse changes across entire assemblages (Gösser et al 2023).

Beyond community-level structure, the exclusive detection of several conservation-priority taxa in strictly protected reefs adds an important conservation dimension to the findings. Although low read counts require cautious interpretation, previous studies have shown that rare or low-frequency eDNA detections can reliably flag the presence of elusive or low-density species in reef environments (Açıkbaş et al 2024; Malik et al 2025). In this context, eDNA metabarcoding provides a valuable complement to conventional surveys by extending detectability beyond visually conspicuous taxa.

Overall, the results indicate that zoning in Nui Chua National Park shapes reef fish communities primarily through compositional turnover and taxon-specific associations rather than changes in local diversity. This pattern aligns with the central premise of the study-that spatial management influences the identity and structure of reef fish assemblages detectable by environmental DNA - and supports the use of eDNA as a sensitive and scalable tool for assessing spatial structuring of reef fish communities in tropical marine protected areas.

Management implications and strategic recommendations. The results indicate that strictly protected zones support reef fish assemblages with greater compositional consistency and stronger taxon-habitat associations, whereas human-use areas exhibit higher spatial variability. Given that species turnover was the dominant component of beta diversity, management strategies should emphasize the maintenance of habitat integrity and the reduction of localized disturbances that may disproportionately affect reef-associated specialists. In this context, the integration of eDNA-based monitoring into

routine management frameworks offers a sensitive tool for detecting early compositional shifts that may not be captured by traditional richness-based metrics. Such molecular approaches can complement existing survey methods and provide timely information to support adaptive zoning and conservation strategies.

Limitations and future directions. Despite the strong performance of eDNA metabarcoding in resolving reef fish assemblages, several methodological and ecological considerations warrant attention. Incomplete regional reference databases remain a challenge for Indo-Pacific fishes, resulting in a small proportion of OTUs being assigned only to higher taxonomic ranks. In addition, the detection of low-level non-marine signals (e.g., Cichlidae) highlights the influence of hydrodynamic transport and land-based runoff, processes that can redistribute eDNA beyond the immediate habitat of origin (Turon et al 2020).

Future research would benefit from multi-marker strategies combining COI with 12S MiFish primers to broaden taxonomic coverage and reduce primer bias (Kumar et al 2022; Gösser et al 2023; Tabugo et al 2025). Integrating physical oceanographic data will further improve interpretation of eDNA transport and retention. Finally, coupling eDNA with UVC or baited remote underwater video surveys will provide complementary insights into both molecular detection and functional biomass, strengthening the ecological basis for adaptive management of Vietnam's marine protected areas.

Conclusions. This study demonstrates that COI-based eDNA metabarcoding can recover a highly resolved reef fish assemblage in Nui Chua National Park and detect clear zoning-related patterns in community structure. Although local-scale alpha diversity metrics were comparable between the strictly protected and human-use zones, multivariate analyses revealed significant compositional divergence, driven primarily by species turnover rather than nestedness. Protected reefs supported greater exclusive richness and stronger taxon-habitat associations, reflected by the presence of significant indicator taxa detected only in the strictly protected zone. Between-zone dissimilarity was shaped disproportionately by a limited subset of reef-associated taxa, consistent with turnover-driven restructuring across management regimes. In addition, low-abundance detections of conservation-priority taxa, predominantly from protected sites, underscore the potential of eDNA surveys to complement conventional monitoring by flagging rare or low-detectability species. Together, these findings indicate that zoning in Nui Chua National Park influences reef fish communities chiefly through shifts in species composition and taxon-specific responses, highlighting the value of integrating eDNA into monitoring frameworks to support adaptive management of Viet Nam's tropical marine protected areas.

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