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Reef fish functional trait responses to wastewater-driven environmental gradients

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A B S T R A C T

Wastewater pollution is a persistent but understudied driver of coral reef degradation. Here, we investigate how reef fish assemblages respond to environmental gradients shaped by chronic wastewater exposure, combining trait-based analyses with long-term environmental data. We surveyed reef fish at seven sites along the leeward coast of San Andrés Island (Colombian Caribbean), quantifying variation in species richness, abundance, and eight functional traits. Environmental conditions were characterized using 13 years of water quality data, complemented by in situ measurements of benthic cover and algal nitrogen stable isotopes ($\delta^{15}N$). We calculated functional indices such as Functional Richness (FRic) and assessed trait–environment relationships. Impacted sites exhibited lower species richness and reduced FRic, driven by the absence of species occupying peripheral regions of functional space, including very mobile predators, demersal spawners, and small-bodied herbivores. Shifts in trait composition were explained by the combined influence of water quality variables and benthic composition (e.g. hard coral cover) along the pollution gradient. By demonstrating that wastewater exposure selectively erodes functional trait combinations underpinning key ecosystem processes, such as nutrient cycling, top–down control, and coral–fish mutualisms, this study highlights the importance of integrating functional metrics into reef monitoring and wastewater management strategies.

1. Introduction

Wastewater pollution is an escalating global threat to coastal ecosystems, fuelled by coastal population growth and urbanization coupled with inadequate sewage infrastructure (Vammen et al., 2015). Untreated or poorly treated wastewater releases excessive nutrients, organic matter, and pathogens into marine environments, triggering eutrophication, harmful algal blooms, habitat degradation, and hypoxic dead zones that severely impact marine biodiversity (Wear et al., 2021). Coral reefs are particularly vulnerable, as nutrient enrichment drives phase shifts from coral-to algae-dominated systems, reducing structural complexity and undermining resilience and ecosystem service provision (Naumann et al., 2015).

Fish assemblages are tightly linked to coral reef health and are crucial for maintaining key ecological processes such as herbivory, nutrient cycling, and trophic regulation (Villéger et al., 2017). Disturbances like wastewater pollution can shift fish community composition, but traditional taxonomy-based metrics, focused on species richness and abundance, may not clearly capture early signs of ecological degradation (McKinley and Johnston, 2010; Plazas-Gómez et al., 2025). Wastewater pollution can cause species to respond in distinct ways: while increased algal biomass may temporarily benefit herbivores and invertivores (Brown et al., 2017), species dependent on structurally complex coral habitats often experience severe declines (Wenger et al., 2015).

This limitation underscores the added value of functional approaches, which evaluate species according to their ecological roles and life-history traits (e.g., trophic level, body size, reproductive strategy), providing earlier and more sensitive signals of ecosystem degradation (Mouillot et al., 2013; Villéger et al., 2017). This approach has already

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proven effective in revealing patterns of fish responses to wastewater pollution and highlights functional erosion even in cases where species richness remains relatively stable (Plazas-Gómez et al., 2025). However, studies explicitly linking the functional structure of reef fish assemblages to different components and concentrations of wastewater remain scarce (Plass-Johnson et al., 2016).

The Caribbean Sea, where approximately 85% of wastewater is discharged untreated (Diez et al., 2019), and Colombia, ranking among the top 20 global contributors to nitrogen pollution in coastal waters (Tuholske et al., 2021), offers a compelling opportunity to address this gap. San Andrés Island (SAI), sited within one of the largest marine protected areas in the Western Hemisphere, the UNESCO-designated Seaflower Biosphere Reserve, faces escalating pressures from rapid, tourism-driven population growth and inadequate wastewater management (Navas-Camacho et al., 2019). As of 2022, a technical report estimated that 52.4% of the population on the northern side of the island was connected to a sewer system that discharges without treatment to a submarine outfall. The remainder rely on septic tanks, unlined cesspools, or discharge untreated wastewater directly into coastal waters (VEOLIA - Aguas del Archipiélago S.A. E.S.P., 2022).

Previous studies in SAI have documented the presence of wastewater in coastal waters and its potential impact on marine ecosystems (Diaz et al., 1995). Water quality assessments report biologically available nitrogen and phosphorus concentrations exceeding several times the recommended thresholds for coral reefs, and pathogenic bacteria levels surpassing legal limits for recreational waters (Gavio et al., 2010). Additionally, significant declines in coral reef health have been reported, with live coral cover decreasing from 26.9% in 1998 to 9.4% in 2014 (González-Gamboa et al., 2019), accompanied by increases in turf algal cover and reductions in coral recruitment (Navas-Camacho et al., 2019). Bioindicator species such as the sponge *Cliona delitrix*, often associated with eutrophicated conditions, have also become increasingly abundant (Chaves-Fonnegra et al., 2007). Declines in fish populations have been reported in connection with coral loss likely driven by wastewater inputs and overfishing (González-Gamboa et al., 2019); however, the mechanisms linking wastewater to shifts in fish functional structure remain poorly understood.

Here, we use SAI as a model system to explore how wastewater pollution shapes the functional trait composition and spatial distribution of reef fish assemblages. Specifically, we address two central questions: (1) How does a wastewater-driven environmental gradient alter the functional structure of reef fish assemblages? and (2) To what extent do spatial variations in environmental conditions correlate with the distribution of key functional fish traits across reef sites? To address the first question, we characterised the wastewater-driven environmental gradient using historical water-quality monitoring data, nutrient concentrations, microbial indicators, stable isotope signatures, and benthic habitat composition, and quantified changes in fish functional structure using complementary functional diversity indices. To address the second question, we examined trait–environment relationships using RLQ and Fourth Corner analyses, which integrate environmental variables, species abundances, and functional trait data to identify the strength and significance of the associations between environmental conditions and fish functional traits. By explicitly linking wastewater exposure to shifts in fish functional traits, this study highlights how wastewater-driven changes in fish functional structure may cascade into reduced nutrient cycling, weakened top-down control of algal growth, and impaired coral resilience, processes central to reef ecosystem health.

2. Methods

2.1. Study area and sampling design

San Andrés Island (SAI) is located in the Caribbean Sea, ~775 km northwest of mainland Colombia (12°32′N, 81°43′W). On the west coast, two major sewage sources discharge untreated wastewater directly into the ocean: the submarine outfall, which releases most of the island's effluent ~300 m offshore at 18 m depth, and multiple outlets around Cove Navy Bay (Fusalba-Carreño and Aguas-Meza, 2021). To capture the gradient of exposure, we surveyed seven reef sites at varying distances from these sources (Fig. 1, Supplementary Table S1). Bajo Bonito, located north of pollution sources with prevailing currents flowing southward (Espinosa-Ordoñez, 2023), was selected as a control site, along with Nirvana and Luna Verde, both located further from direct sewage exposure. Impacted sites were those closest to the sewage sources, particularly Casa Loft near the submarine outfall and Cove Navy near the outlets of the Bay. Wildlife and Schooner Bight are further away from sewage sources having an intermediate impact; notably, the latter is additionally affected by runoff from the nearby landfill. All sites were similar in habitat type (reef flats with hard and soft corals, hydrozoans, and algae), depth (~12–14 m), and distance from shore (~300 m), allowing for robust comparisons of fish assemblage responses to wastewater exposure.

2.2. Fish functional structure along a wastewater gradient

To address our first research question, we quantified changes in community functional structure using complementary functional diversity indices. These analyses were conducted across sites spanning a gradient of wastewater influence characterised using historical and in situ environmental measurements (see Section 2.4). During the dry season (09–22 February 2023), we conducted Underwater Visual Censuses (UVC) at seven sites between 09:00 and 12:00 h to standardize diel variation in fish activity. At each site, three 50 m × 5 m transects (250 m^2 each) were surveyed, separated by at least 10 m. All conspicuous fishes were identified to species, counted, and standardized to density (ind.•100 m^{-2}). Taxonomy followed Eschmeyer's Catalog of Fishes (Fricke et al., 2024). No permits were required for UVC fish counts.

To assess functional structure, we selected eight traits potentially associated with pollution-related disturbances: depth range, diet (e.g., herbivores, omnivores, fish-cephalopod feeders) home range (sedentary to very mobile), maximum body size, schooling behaviour (solitary to large groups), spawning strategy (demersal or pelagic), trophic level, and Vulnerability (Hadj-Hammou et al., 2021; McKinley and Johnston, 2010; Plazas-Gómez et al., 2025). Trait values were compiled from Quimbayo et al. (2021); each category definition is provided in Supplementary Table S2.

To visualise and compare the functional structure of fish assemblages across the wastewater-driven gradient, we constructed a multidimensional functional space using Principal Coordinate Analysis (PCoA) based on Gower distances calculated from a species × traits matrix containing the eight selected functional traits for all fish species recorded during underwater visual censuses. The resulting distance matrix quantified functional dissimilarity among species and served as the basis for constructing the multidimensional functional space. A four-dimensional space was selected as it exhibited one of the lowest mean absolute deviation values (0.32), indicating good congruence between trait-based distances and distances in the reduced space. The correlations of traits with axes are presented in Supplementary Table S3. For visualization we focus on the first two axes; full results are provided in Supplementary Fig. S1–3.

Functional diversity was quantified using three complementary indices calculated in multidimensional trait space: Functional Richness (FRic), Functional Divergence (FDiv), and Functional Identity (Fide). These indices describe distinct facets of community functional structure (Mouillot et al., 2013). FRic measures the volume of multidimensional trait space occupied by the species present in an assemblage and was calculated as the multidimensional volume of the convex hull encompassing species coordinates within the functional space. FRic therefore reflects the range of trait combinations represented within a community, with higher values indicating a broader diversity of functional traits.

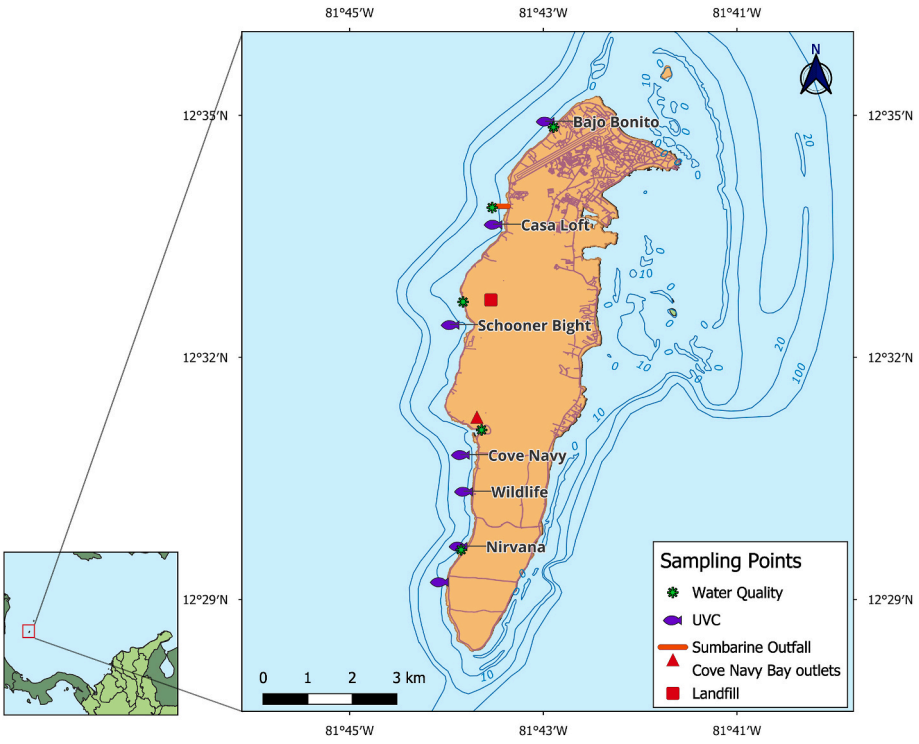

Fig. 1. Sampling sites in San Andrés Island. Fish silhouettes indicate Underwater Visual Census (UVC) sampling sites, while stars mark the locations of water quality sampling sites. Base Data:(DANE, 2018; INVEMAR, 2007).

FDiv quantifies the extent to which species abundances are distributed toward the margins of trait space rather than concentrated near its centre. FDiv was calculated from the abundance-weighted deviation of species relative to the centroid of the convex hull vertices defining the assemblage (Magneville et al., 2022). High FDiv values indicate that abundant species possess relatively extreme trait combinations, whereas low values indicate dominance by species with more average functional characteristics. FIde represents the abundance-weighted mean position of a community within the multidimensional trait space and corresponds to the community-weighted average trait composition (Mouillot et al., 2013). Changes in FIde reflect shifts in the dominant ecological strategies characterising assemblages. All indices were calculated using the alpha.fd.multidim function in the mFD package (version 1.0.6; Magneville et al., 2022), which computes multidimensional functional diversity metrics from species coordinates in a functional space and species abundance data.

2.3. Trait – environment relationships

To address our second research question, we assessed the relationships between environmental conditions and fish functional traits at the five sampling sites where historical water quality data were available (see section 2.4, Supplementary Table S4). Our analysis included 17 environmental variables: nine parameters monitored by REDCAM, Colombia's national monitoring network (REDCAM-INVEMAR, 2024), and local measurements comprising the nitrogen stable isotope ratio ($\delta^{15}N$) in macroalgae and the benthic cover composition (Supplementary Table S5).

We assessed trait–environment relationships using RLQ and Fourth-Corner analyses, which integrate environmental variables (R), species abundances (L), and species traits (Q) into a shared ordination space (Dray et al., 2014). Fourth-Corner tests with 49,999 permutations, corrected for false discovery rate (FDR), quantified the strength and significance of pairwise trait–environment associations. Standardized effect sizes were calculated to assess the magnitude and direction of these relationships. Analyses were implemented in R software (version 4.2.2; R Core Team, 2022) using the ade4 package (version 1.7-22; Dray and Dufour, 2007).

2.4. Spatial patterns of environmental variables

To characterise the wastewater-driven environmental gradient underlying both research questions, we compiled historical water quality data obtained from REDCAM, spanning 2007–2019, which covered nine indicators of wastewater pollution: total coliforms (TC), thermotolerant coliforms (TTC), faecal enterococci (FEC), dissolved oxygen (DO), nitrites (N-NO2), nitrates (N-NO3), orthophosphates (P-PO4), total suspended solids (TSS), and ammonia (N-NH4). Data were collected twice annually at five sites, and for analysis were assigned to the nearest fish sampling sites (Bajo Bonito, Casa Loft, Schooner Bight, Cove Navy, and Nirvana; Supplementary Table S1 and S4). We summarized long-term conditions as site-level means ± SE after confirming that no site or variable showed consistent increasing or decreasing trends over time (Supplementary Fig. S4). This approach assumes that chronic exposure to sublethal pollutant concentrations through bottom-up and direct effects drives fish assemblage responses more strongly than ephemeral pulse events (Smith et al., 1999).

We tested site-level differences in water quality using parametric or non-parametric approaches as appropriate (Supplementary Table S6). To further explore gradients, we performed a PCA on site-level means of the nine variables after standardization. The first two axes (PC1 = 67.6%; PC2 = 20.0%) were retained for visualization, and for visualization sites were ordered in a gradient of pollution based on the scores of the PC1 (Supplementary Fig. S5, Table S7).

To capture short-term wastewater signals, we measured $\delta^{15}N$ in macroalgae (*Dictyota* sp.) collected at five of the fish survey sites. Following collection, the holdfast region was removed and only algal thallus tissue was retained for analysis. Samples were carefully cleaned of epiphytes and debris, rinsed with freshwater to remove residual salt, dried with paper towels, wrapped in aluminum foil, and frozen at

−20°C. Samples were transported and maintained frozen until laboratory processing approximately three months later. Prior to analysis, samples were dried at 40°C for 72 h and subsequently pulverized to a fine powder. Samples were analysed for ^{15}N and ^{14}N using a Thermo Finnigan Delta Plus mass spectrometer (Thermo Fisher Scientific, Washington, DC, USA). Isotopic results are expressed in standard δ unit notation as:

$$\delta^{15}N(‰) = \left[\left(\frac{R\ sample}{R\ reference}\right) - 1\right] * 1000$$

where R is the ratio of ^{15}N to ^{14}N, relative to nitrogen in air.

At the same five sites, benthic cover was quantified using orthomosaic images generated using Agisoft-Metashape-Professional (v2.0.2, Drone Emotions Ltd., Albiate, Italy) from ~4500 photographs collected along one transect per site. Images were processed to create georeferenced mosaics, and benthic categories were annotated into seven groups: hard coral, soft coral, hydrozoan (*Millepora* spp.), algae, sponges, rock, and sand using TagLab (v 2.15, CNR-ISTI, Pisa, Italy). Final mosaics were standardized to 100 m^2 per site, and percent cover of each category was calculated using QGIS (v3.37, Open Source).

3. Results

3.1. Functional space description

The projected functional space summarized the distribution of reef fish based on ecological trait combinations, with the first two principal coordinate axes (PC1 and PC2) capturing the main functional gradients (Fig. 2A). All eight traits correlated significantly with at least one axis (Supplementary Table S3). PC1 primarily reflected body size, trophic level, diet, and spawning strategy, separating large-bodied pelagic-spawning predators (e.g., *Sphyraena barracuda*) at positive values from smaller-bodied, demersal spawners (e.g., *Stegastes diencaeus*) at negative values. PC2 represented schooling, diet, and home range, with sedentary, solitary invertebrate feeders (e.g., *Hypoplectrus randallorum*) at positive values, and very mobile, schooling herbivores, planktivores, and omnivores (e.g., *Melichthys niger*) at negative values. Together, the two axes delineated distinct functional niches within the assemblage.

3.2. Fish functional structure along a wastewater gradient

A clear gradient in species richness and FRic followed wastewater exposure (Fig. 2B). Control sites Nirvana and Bajo Bonito displayed the highest richness (42 and 38 species, respectively) and occupied greater proportions of functional space (FRic = 74.6% and 61.9%). Impacted sites showed lower richness and FRic: Casa Loft (32 species, 49.1%), Schooner Bight (27 species, 38.5%), and Cove Navy (21 species, 24.9%). Wildlife retained higher species richness and FRic (35 species, 43.1%) than heavily impacted sites.

Reduced FRic at impacted sites reflected the absence of particular functional groups (Fig. 2A and B). The contraction of the functional space was most pronounced among large, very mobile predators (e.g., *S. barracuda, Lutjanus cyanopterus*), which were absent from heavily impacted sites and accounted for much of the reduction of this index (Fig. 2B). Additionally, the loss of some small-solitary herbivores and demersal spawners (e.g., *Microspathodon chrysurus, Stegastes adustus*) was also observed in these sites. Wildlife's relatively high FRic was mainly due to the presence of *M. niger* and presence of small herbivore species.

Luna Verde deviated from this pattern, showing the lowest FRic (19.5%) despite its distance from sewage sources. This reduction stemmed from the absence of multiple higher-trophic-level invertebrate feeders that were still present at some impacted sites. However, unlike impacted sites, Luna Verde exhibited few low-trophic-level herbivores at negative PC1 values.

FDiv was relatively consistent across sites (0.725–0.883). Control sites Bajo Bonito (0.851) and Nirvana (0.852) showed slightly higher values than impacted sites such as Schooner Bight (0.810) and Cove Navy (0.725). Wildlife (0.883) and Casa Loft (0.876) had the highest FDiv values, reflecting relatively higher abundances of species located at the vertices of functional space, including *S. partitus* and *Azurina multilineata*.

FIde also varied across sites. Control sites Bajo Bonito, Nirvana, and Luna Verde showed lower FIde scores along PC2, driven by higher abundances of *Azurina cyanea* (Fig. 2B). Conversely, Cove Navy, where *A. cyanea* was scarce, presented higher FIde values along both axes. Schooner Bight showed the highest FIde scores across PC1 and PC2, reflecting greater densities of mobile invertebrate feeders (e.g., *Haemulon flavolineatum*) and planktivores (e.g., *Thalassoma bifasciatum*).

3.3. Trait – environment relationships

The RLQ analysis revealed strong correlations between fish traits and environmental conditions (Fig. 3A). The first axis (explaining 89.30% of variation) aligned positively with DO, hard and soft coral, and hydrozoan cover, and was associated with higher trophic levels, planktivores, and demersal spawners (e.g., *A. cyanea, A. multilineata*). Negative scores on this axis were linked to elevated nutrients, suspended sediments, and algae cover, and corresponded to omnivores and pelagic spawners (e.g., *S. partitus*). The second axis (8.87% of variation) reflected positive associations of herbivores and omnivores with faecal indicator bacteria (TTC, FEC, TC) and N-NH_4, whereas mobile invertebrate feeders with broader depth ranges (e.g., *H. adscensionis*) were negatively associated with nutrients, sponges, and rock cover. Traits such as maximum body size, home range, and vulnerability showed weak or near-zero correlations with measured environmental variables (Fig. 3A).

The Fourth-Corner analysis quantitatively supported these associations. Although no trait–environment pairs remained significant after FDR correction, several exhibited relatively high effect sizes and had significant unadjusted p-values (Fig. 3B–Supplementary Table S8). This likely reflects limited power due to the small number of sites (n = 5) and numerous predictors; therefore, the results should be interpreted with caution.

Among the clearest patterns, omnivores showed positive associations with bacterial indicators, particularly TC (ES = 1.81, p = 0.046). Planktivores were positively related to soft corals (ES = 1.73, p = 0.033) and hydrozoans (ES = 1.60, p = 0.042). Trophic level correlated positively with DO (ES = 1.83, p = 0.012) and soft corals (ES = 1.72, p = 0.038), and negatively with TC (ES = −1.86, p = 0.033). Very mobile species abundance was negatively related to N-NO_2 (ES = −1.00, p = 0.046).

Schooling behaviour displayed multiple associations: larger groups correlated with higher DO and coral cover, with medium schools positively linked to hydrozoans (ES = 1.88, p = 0.028) and large schools to sponge cover (ES = 1.78, p = 0.025). Negative relationships with N-NO_2 were consistent across small to large schools, whereas solitary species showed a positive association with this variable (ES = 0.98).

Other traits showed weaker or contrasting patterns. Sessile-invertebrate feeders tended to be negatively associated with N-NO_2 (ES = −1.86, p = 0.058). Spawning strategies diverged, with pelagic spawners positively related to N-NO_3 and algae cover, while demersal spawners showed negative associations. Vulnerability was negatively associated with bacterial indicators and N-NH_4 (ES < −1.41). Maximum body size showed moderate positive associations with rock cover and nitrogenous nutrients (ES = 1.08–1.39).

3.4. Spatial patterns of environmental variables

Significant spatial differences in water quality confirmed a wastewater pollution gradient across sites (Supplementary Table S6). Thermotolerant coliforms (TTC), total coliforms (TC), and dissolved oxygen

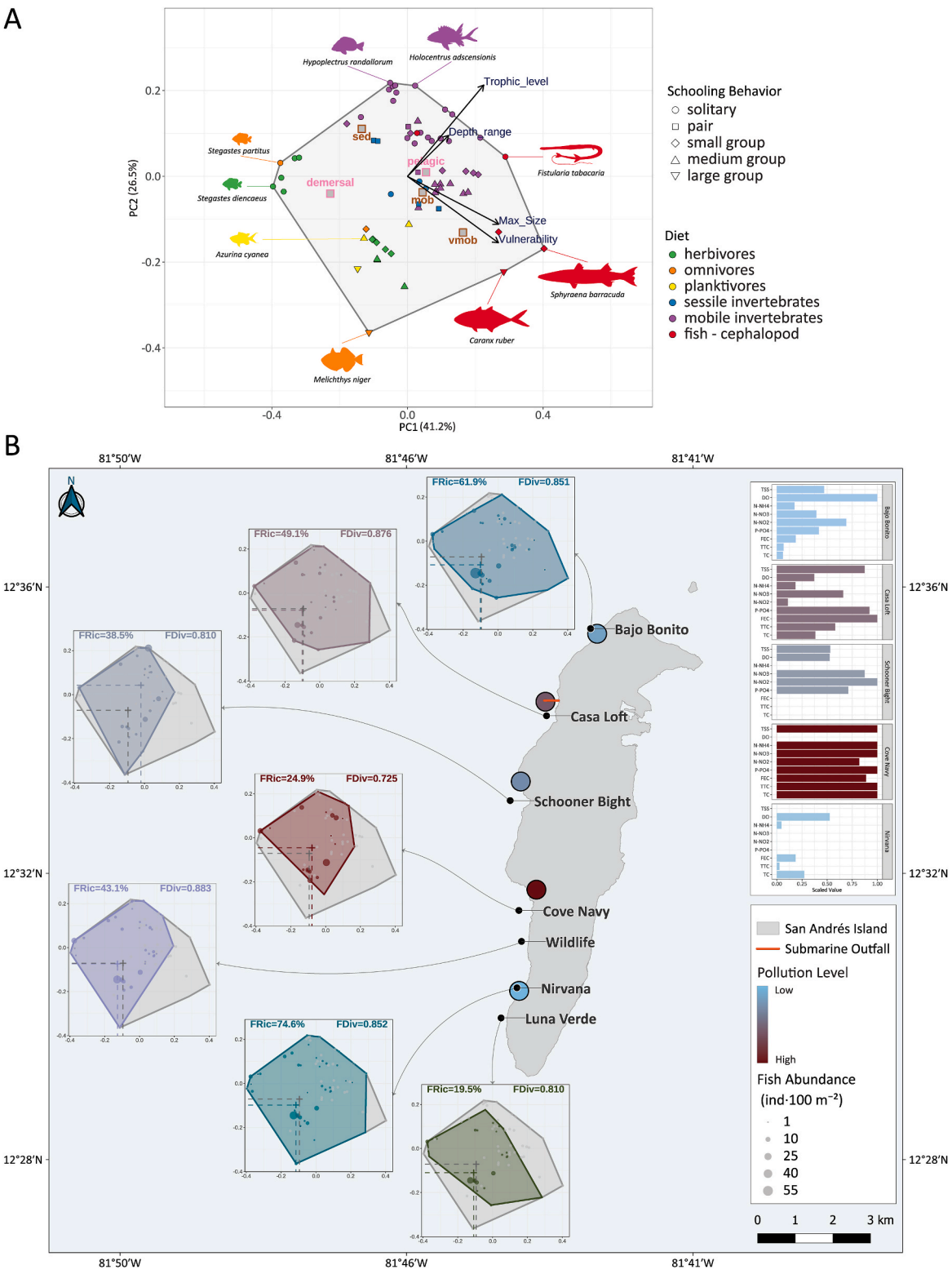

Fig. 2. (A) Principal Coordinate Analysis (PCoA) of reef fish species (dots) based on trait dissimilarities along the first two axes (PC1 and PC2). Percentages indicate the proportion of variation in the functional distance matrix represented by each axis. The grey convex hull represents the total functional space (FRic) of all surveyed species. Numerical traits (vulnerability, maximum body size, depth range, trophic level) are shown as vectors scaled to 40%. Categorical traits are depicted by shape (schooling), colour (diet), pink outlines (spawning strategy), and orange outlines (home range: sed = sedentary, mob = mobile, vmob = very mobile). Distances between points indicate functional dissimilarity. (B) Functional structure of reef fish assemblages across seven sites. The coloured bubbles represent each site's position along a continuous wastewater pollution gradient, with colours assigned according to PC1 scores from a PCA based on nine water-quality variables. Faceted bar plots display the scaled values of these same variables, illustrating their individual contributions to the overall pollution gradient. In each site's functional space, coloured dots indicate species presence (dot size ∝ abundance); grey dots are species absent at that site. Coloured convex hulls represent site-level FRic. Crosses and dashed lines indicate Functional Identity (FIde) relative to the global pool (grey). FDiv and FRic values per site are shown above each hull. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

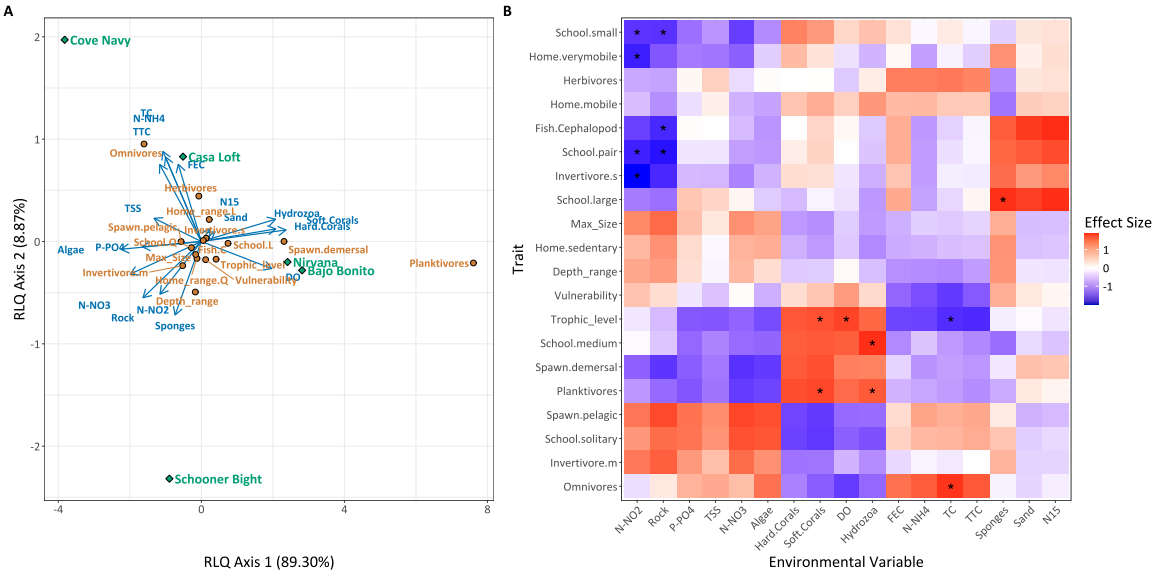

Fig. 3. (A) RLQ ordination plot showing relationships between environmental variables (blue vectors), species traits (orange points), and sites (green diamonds). Arrow length and direction indicate the strength and orientation of environmental variables. Trait positions reflect their associations with environmental gradients; ordinal traits are represented by linear (L) and quadratic (Q) terms. Environmental variables: DO = Dissolved Oxygen, FEC = Faecal Enterococci, TC = Total Coliforms, TTC = Thermotolerant Coliforms, N-NH_4 = Ammonia, N-NO_2 = Nitrite, N-NO_3 = Nitrate, P-PO_4 = Orthophosphates, TSS = Total Suspended Solids. (B) Fourth-Corner heatmap showing relationships between environmental variables (columns) and species traits (rows). Colours represent effect sizes (Std.Obs), with warm colours indicating positive and cool colours negative associations. Asterisks denote non-adjusted significant associations ($p < 0.05$). Categorical traits are displayed by category for clarity. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(DO) differed significantly among sites ($p < 0.05$), whereas differences in the remaining variables were not significant. The strongest wastewater signal occurred at Cove Navy and Casa Loft, which exhibited the highest mean TTC concentrations (336.5 ± 119.6 and 206.9 ± 114.3 MPN·100 ml^{-1}, respectively) and lower DO (5.86 ± 0.26 mg L^{-1} and 6.23 ± 0.18 mg L^{-1}, respectively) concentrations than control sites such as Nirvana (TTC: 31.84 ± 13.77 MPN·100 ml^{-1}, DO: 6.39 ± 0.27 mg L^{-1}). Schooner Bight displayed nutrient concentrations comparable to Casa Loft but lower bacterial loads (TTC: 23.68 ± 15.03 MPN·100 ml^{-1}). Although these patterns indicate increasing wastewater influence from control to impacted sites, post hoc analyses revealed that only Cove Navy differed significantly from all other sites (Supplementary Table S9). Total coliform concentrations were also highest at Cove Navy (454.5 ± 125.8 MPN·100 ml^{-1}), reinforcing its position as the most environmentally degraded site along the gradient (Supplementary Table S5).

Nitrogen stable isotope ratios ($\delta^{15}N$) varied across sites (Supplementary Table S5). Casa Loft recorded the highest value (>4‰), while all other sites ranged between 1.3 and 1.9‰, including Cove Navy, which despite elevated bacterial loads, displayed relatively low $\delta^{15}N$ values.

Benthic cover was dominated by algae across all sites (72–95%; Supplementary Table S5). Hard and soft corals were more abundant at control sites (up to ~7% hard coral and ~15% soft coral) and consistently lower at impacted sites (<2%). Sponge cover remained low (<1%) across all sites, and hydrozoans occurred in small patches at Bajo Bonito, Schooner Bight, and Nirvana (<0.21%) but were absent from Casa Loft and Cove Navy. Casa Loft also exhibited a comparatively high proportion of sandy bottom (11.54%), which distinguished it from the other sites (Supplementary Table S5).

4. Discussion

The functional structure of reef fish assemblages at SAI shifted markedly along the wastewater-driven environmental gradient. In impacted sites, the absence of large predators, small-bodied herbivores, and demersal spawners, groups still present at control sites, reflects a clear erosion of ecological roles, coupled with the dominance of opportunistic omnivores and mobile invertebrate feeders under higher nutrient and bacterial loads. These findings highlight the added value of functional indices like FRic for detecting early signs of ecological degradation and provide new evidence that wastewater pollution alters not only fish abundance and richness, but also the delivery of key ecological functions.

Although trait-environment correlation significance was largely limited to unadjusted p-values, the patterns observed are ecologically plausible and consistent with trait-mediated responses reported in other pollution-impacted reef systems (Johnston and Roberts, 2009; McKinley and Johnston, 2010; Plazas-Gómez et al., 2025). We also note that the use of adjusted p-values remains debated, as it can increase the risk of type II errors (false negatives), particularly when the goal is to identify patterns of ecological responses (Feise, 2002; Nakagawa, 2004). Therefore, we report unadjusted p-values alongside effect sizes and include their interpretation in the discussion below.

4.1. Ecological responses to wastewater impacts

Reef fish assemblages at SAI exhibited lower species richness and reduced FRic in impacted sites. These results contrast with earlier studies where wastewater pollution did not significantly affect richness (reviewed in McKinley and Johnston, 2010) but align with findings from other regions where impacted sites show lower FRic due to the loss of large predators and herbivores (reviewed in Plazas-Gómez et al., 2025). These context-dependent responses underscore the nuances of wastewater impacts and the value of a trait-based approach.

For example, nutrient enrichment can stimulate primary production, creating bottom-up effects that favour generalist species such as *S. partitus* and *T. bifasciatum* (Booth and Hixon, 1999; Dunkley et al., 2018). In systems dominated by such generalists, richness may remain stable or even increase under wastewater exposure, a pattern documented across marine, estuarine, and freshwater ecosystems (Naumann et al., 2015; Oczkowski and Nixon, 2008; Ribeiro et al., 2008). Still, the

loss of species with other trait combinations is reflected in indices such as FRic (Plazas-Gómez et al., 2025), reinforcing the interpretative power of functional approaches to reveal ecological dynamics not captured by taxonomic metrics.

Despite being an important trait, diet alone did not explain responses to wastewater. Both *A. cyanea* and *T. bifasciatum* are planktivores, yet only the latter dominated impacted sites. This contrast may reflect differences in spawning strategy, among other processes influencing recruitment and population persistence. As a demersal spawner, *A. cyanea* may face reproductive constraints under polluted conditions where sedimentation and organic matter reduce egg survival (Suthers and Frank, 1991; Wu, 2009), whereas the pelagic spawning of *T. bifasciatum* may provide an advantage. These cases underscore that trait combinations, rather than single traits, mediate species' success or exclusion in degraded reefs (Plazas-Gómez et al., 2025).

Luna Verde emerged as a notable exception to the wastewater-driven patterns. Although it recorded the lowest FRic, its FIde more closely resembled control sites than impacted ones (Fig. 2B). This means that the dominant trait combinations were similar to those of the control sites. For example, unlike wastewater-impacted sites where small-bodied herbivores were largely absent, Luna Verde retained these groups despite its low richness. Additionally, invertebrate feeders, present in most sites and dominant in impacted sites, were also absent in this area. This suggests that the mechanisms driving reduced FRic at Luna Verde differ from those at sewage-impacted sites, potentially reflecting other local stressors such as wave exposure, sedimentation, or fishing pressure. For instance, wave exposure has shown to reduce fish biomass and abundance (Friedlander et al., 2003), sedimentation can impair predation activity by reducing visibility (Ortega et al., 2020), and fishing can selectively filter larger fish (HAWKINS & ROBERTS, 2004). Regarding the latter, fishing gear was observed entangled in corals and rocks at this site.

4.2. Wastewater disproportionately affects top predators

Trophic level was negatively correlated with bacterial and nutrient concentrations, indicating that lower- and mid-trophic-level species were more abundant in polluted environments, while higher-trophic-level species were scarce or absent. Similar patterns have been reported in wastewater-impacted reefs globally, consistently identifying trophic level as a key response trait (Hadj-Hammou et al., 2021; Plazas-Gómez et al., 2025).

We observed that larger predators were absent from impacted sites; however, maximum body size did not correlate with any environmental variable. This likely reflects both the low abundance of large species overall and the presence of relatively large individuals spanning different trait combinations across sites. Still, the sensitivity of large predators to pollution is well established: turbidity and oxygen depletion can reduce predation efficiency and disproportionately affect species with high metabolic demands (Hess et al., 2019; Verberk et al., 2022), while nutrient enrichment can reduce energy transfer to higher trophic levels (Mor et al., 2022). Apex predators may also bioaccumulate persistent organic pollutants, leading to reproductive and physiological impairments (Lyons et al., 2025).

Large individuals are also vulnerable to fishing pressure, a stressor that can exacerbate the impact of wastewater on these species. Although fishing pressure is potentially similar across sites, limited information prevented us from accounting for this factor (Olmos-Pinzón, 2019).

Taken together, these provide mechanistic explanations of how wastewater reshapes reef trophic structure by excluding top predators. Given their role in exerting top-down control (Dale et al., 2011), their absence likely facilitated the proliferation of opportunistic species in impacted sites, leading to trait homogenization and reduced delivery of key functional services provided by reef fish.

4.3. Loss of fish functional services accelerates reef degradation

In this study, control sites showed higher coral and hydrozoan cover, while impacted sites had greater algae, sponge, and rock cover. Such shifts in benthic composition are typical of polluted reefs and are often associated with degraded reef condition and altered fish communities (Brodie et al., 2019). However, our results show that only a few benthic categories (e.g. soft corals and hydrozoans) displayed significant correlations with a limited number of fish traits, suggesting that benthic composition alone is not a reliable predictor of functional structure along the wastewater gradient.

Wastewater influence extends beyond physiological effects on corals, triggering cascading disruptions in fish communities that may reduce the delivery of key ecosystem functions. For example, the dominance of opportunistic omnivores at impacted sites, combined with the absence of specialized damselfishes (e.g. *S. diencaeus, S. adustus*), reduces beneficial coral–fish interactions such as coral oxygenation, nutrients cycling, sediment removal, and defence against predators (Johnson et al., 2011; Stier et al., 2025).

Additionally, butterflyfishes (*Chaetodon* spp.), largely absent from impacted sites, also play a functional role despite being corallivores. They can consume diseased coral tissue, recycle nutrients, and improve coral oxygenation (Stier et al., 2025). Their loss is concerning given ongoing outbreaks of stony coral tissue loss disease, which may be intensified by declining water quality (Estrada-Saldívar et al., 2021). Additionally, nutrient excretion by planktivores such as *A. cyanea* supports the growth of branching corals, enhancing reef structural complexity and morphological diversity (Stier et al., 2025). The decline of these interactions may reduce reef resilience, particularly in impacted sites where algal dominance is already established.

Importantly, fish–coral interactions are bi-directional. While reef fish support coral health through functions such as nutrient cycling and defence, benthic structure and live coral cover provide essential habitat and resources for fishes (Castaño et al., 2021; Johnson et al., 2011). Reductions in coral cover thus reinforce declines in fish functional diversity, creating a feedback loop of co-decline (Komyakova et al., 2013). This was evident at SAI, where reduced coral cover coincided with reduced FRic. Such dynamics underscore the intertwined nature of benthic habitat complexity and fish functional roles in sustaining reef resilience under pollution stress.

4.4. Interpreting variability in water quality indicators

Isotopic evidence provides context for the variability in water quality measurements. The elevated $\delta^{15}N$ value at Casa Loft (>4‰) reflects sustained wastewater exposure, whereas lower values at other sites (<2‰) match those from non-impacted reefs (Dailer et al., 2010). The low $\delta^{15}N$ at impacted sites, particularly Cove Navy, likely reflects untreated wastewater with relatively low $\delta^{15}N$ (Alldred et al., 2023) and the timing of sampling in the dry season, when reduced runoff, septic seepage, and groundwater inputs limit sewage-derived signals in algae (Sugimoto et al., 2016). This variability underscores how reef fish assemblages respond to chronic wastewater exposure despite fluctuating local water quality signals.

4.5. Recommendations for management and monitoring practices

This study addressed two central questions by showing how wastewater gradients restructure reef fish functional traits and identifying the environmental variables most strongly associated with these changes. Continued reef monitoring, particularly of water quality and fish abundance, is needed to capture seasonal and site-specific responses and to increase statistical power. Future research should also account for depth-related variability, as shallow reefs near sewage discharges may be more severely impacted.

The integration of functional traits with 13 years of water quality

data provided a rare, robust basis for establishing spatial gradients of chronic pollution. This temporal coverage allowed us to define a reliable gradient of wastewater impact for interpreting patterns in reef fish assemblages, a type of dataset that remains rare in many tropical reef regions.

Patterns in fish functional structure map closely to essential ecosystem functions offering actionable insights for management. We recommend that monitoring programs by regional authorities incorporate functional indicators, which are more sensitive than taxonomic metrics, to detect early signs of degradation, and identify vulnerable functional entities and derived ecosystem services (Mouillot et al., 2013; Villéger et al., 2017). Equally urgent is investment in wastewater treatment infrastructure: a centralized treatment plant, improved septic systems, and maintenance of existing facilities would reduce bacterial and nutrient inputs, alleviating stress on coastal ecosystems and artisanal fisheries.

Finally, management must consider the co-occurring impacts of wastewater, fishing pressure, and climate change, which can act synergistically to accelerate ecological degradation. Effective reef conservation will therefore require an integrated approach that improves water quality, regulates fisheries sustainably, and builds resilience to climate-driven impacts.

Declaration of generative AI in scientific writing

During the preparation of this work the authors used ChatGPT to improve readability of the document. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Ramón Alejandro Plazas-Gómez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Sonia Bejarano:** Conceptualization, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Camille Magneville:** Methodology, Supervision, Writing – original draft, Writing – review & editing. **Julian Prato-Valderrama:** Methodology, Validation, Writing – original draft, Writing – review & editing. **Adriana Santos-Martínez:** Investigation, Supervision, Writing – original draft, Writing – review & editing. **Sarah Zwicker:** Methodology, Writing – original draft, Writing – review & editing. **Marie Fujitani:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108208.

Data availability

The data generated for this study will be archived in PANGAEA and assigned a DOI upon acceptance. Water quality data and trait datasets were obtained from published sources cited in the manuscript.

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