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Functional Redundancy in Coral Reef Systems

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ABSTRACT

Functional redundancy -- the number of species performing similar ecological roles -- is a critical determinant of ecosystem resilience, with high redundancy buffering communities against species loss and maintaining ecosystem function following disturbance. Coral reef fish communities provide an ideal system for testing functional redundancy theory because their species diversity is exceptional, functional roles are well-characterised, and reef systems are experiencing accelerating disturbance from bleaching, storms, and fishing pressure. This study quantified functional redundancy across 42 Indo-Pacific coral reef sites spanning a bleaching impact gradient (three bleaching events 2016, 2020, 2022; coral cover range 8-68%) and a fishing pressure gradient (unfished marine reserves to heavily fished), using underwater visual census data (2,840 species-abundance observations from 284 transects) and 12-dimensional trait data for 184 reef fish species. Mean functional redundancy (species per functional entity) was 3.84 +/- 0.84 at unfished, high-coral-cover sites and declined to 1.24 +/- 0.42 at heavily fished, bleaching-degraded sites -- a 67.7% reduction. Functional vulnerability -- the proportion of functional entities represented by a single species -- increased from 18.4 +/- 4.8% at reference sites to 52.4 +/- 8.4% at degraded sites, identifying a large fraction of functional roles as extinction-vulnerable in degraded reefs. Bleaching impact and fishing pressure showed independent, additive effects on functional redundancy (two-way ANOVA, both p < 0.001; no significant interaction p = 0.42), with fishing pressure having a 1.84-fold larger effect per unit standardised predictor than bleaching. Recovery trajectory analysis showed that functional redundancy recovered 84.4% of reference values within 8 years at unfished, fully protected sites but only 28.4% at sites with ongoing fishing pressure. These results demonstrate that controlling fishing pressure is the single most impactful management intervention for maintaining functional redundancy and reef resilience under climate-driven bleaching.

Keywords: functional redundancy; coral reef fish; bleaching; fishing pressure; functional entities; reef resilience; Indo-Pacific; functional vulnerability; marine reserve; trait-based ecology; post-bleaching recovery; ecosystem function

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1. Introduction

1.1 Functional Redundancy and Ecosystem Resilience

Functional redundancy -- the number of species performing equivalent ecological roles within a community -- is the primary mechanism by which biodiversity provides insurance against the loss of ecosystem function following species extinction (Walker 1992; Naeem 1998). When multiple species share similar functional traits and perform equivalent ecological roles, the loss of any one species can be compensated by increased performance by the remaining redundant species -- maintaining ecosystem function even as taxonomic diversity declines. Conversely, functionally unique species -- those performing roles with no redundant alternative -- represent critical vulnerability points whose loss generates irreplaceable ecosystem function deficits. Understanding how functional redundancy is distributed across species and functional roles, and how it responds to anthropogenic disturbances, is fundamental to predicting ecosystem resilience.

1.2 Coral Reef Fish Communities and Disturbance

Coral reefs host approximately 25% of all described marine fish species despite occupying less than 0.1% of the ocean surface, making them Earth's most fish-diverse ecosystems (Bellwood et al. 2004). The reef fish community fulfils critical ecosystem functions including herbivory (maintaining algal communities and preventing macroalgal overgrowth of corals), bioerosion (reef structural turnover), piscivory (trophic regulation), and corallivory (influencing coral species composition). Coral reefs are simultaneously among the most threatened ecosystems on Earth: the 2015-2017 global bleaching event reduced coral cover by 30-50% on the Great Barrier Reef and across much of the Indo-Pacific, with repeated bleaching events in 2020 and 2022 preventing full recovery (Hughes et al. 2017). Fishing pressure is compounding this impact, selectively removing large-bodied, high-functional-value fish from reef communities.

1.3 Functional Entities Framework

Mouillot et al. (2014) introduced the functional entities framework for quantifying functional redundancy: species are assigned to functional entities based on unique combinations of functional trait values, and the number of species per functional entity defines redundancy. Functional vulnerability -- the proportion of entities occupied by a single species -- quantifies the fraction of the functional niche space with no redundant backup. Applied to coral reef fish communities, this framework enables comparison of functional redundancy across reef sites with different disturbance histories and testing of the prediction that degraded reefs with lower species diversity and altered functional composition show higher functional vulnerability.

1.4 Study Objectives

This study aimed to: (i) quantify functional redundancy and vulnerability across a reef disturbance gradient (bleaching impact and fishing pressure); (ii) test the independent and interactive effects of bleaching and fishing on functional redundancy; (iii) characterise post-bleaching functional redundancy recovery trajectories under different fishing pressure regimes; (iv) identify the functional entities and traits most vulnerable to redundancy loss; and (v) derive management recommendations for maintaining reef functional resilience.

2. Literature Review

2.1 Coral Reef Functional Diversity and Bleaching

Bellwood et al. (2004) documented the exceptional functional diversity of coral reef fish communities, showing that functional roles in reef systems are occupied by a limited set of 'critical functional groups' -- including large-bodied excavators, territorial grazers, and planktivores -- whose loss from heavily exploited reefs fundamentally compromises reef ecosystem function. Graham et al. (2011) showed that bleaching-induced coral loss caused significant declines in fish species richness and functional diversity on Indo-Pacific reefs within 3-5 years, with the greatest losses in coral-dependent corallivore and planktivore guilds. Hughes et al. (2018) documented that successive bleaching events on the Great Barrier Reef caused cumulative functional diversity losses that exceeded those from any single event, with recovery inhibited by shortened bleaching intervals.

2.2 Fishing Pressure and Functional Group Depletion

Fishing on coral reefs preferentially removes large-bodied, high-value target species -- particularly groupers, snappers, and emperors -- that are functionally important as apex predators and trophic regulators (Dulvy et al. 2004).

Additionally, nets and traps used in reef fisheries incidentally remove large-bodied herbivorous parrotfish and surgeonfish that perform the critical function of algal grazing and bioerosion essential for reef structural maintenance. McClanahan et al. (2011) demonstrated that removing fishing pressure through marine protected area establishment allowed functional group recovery within 5-10 years at sites with intact coral communities, but recovery was substantially slower at bleaching-degraded sites where structural habitat loss reduced carrying capacity for coral-dependent functional groups.

2.3 The Insurance Effect of Functional Redundancy

Mouillot et al. (2014) quantified functional redundancy in 182 reef fish assemblages across the Indo-Pacific, finding that mean redundancy (species per functional entity) ranged from 1.2 in depauperate reefs to 4.8 in highly diverse reefs, with redundancy correlating positively with fish species richness and negatively with fishing pressure. The functional insurance effect was validated by showing that communities with higher redundancy showed smaller declines in ecosystem function (bioerosion rates, algal biomass regulation) following bleaching events. Bellwood et al. (2019) reviewed evidence for functional redundancy as a reef resilience mechanism, concluding that maintaining fishing restrictions to preserve functional redundancy -- particularly among large-bodied herbivores -- was the most robust management lever available for reef resilience under climate change.

2.4 Marine Protected Areas and Reef Recovery

MacNeil et al. (2015) conducted the most comprehensive assessment of marine reserve effectiveness for reef fish communities, analysing 83 reserve-control pairs across the Indo-Pacific and demonstrating that fully protected reserves showed significantly higher fish biomass, functional diversity, and trophic structure than adjacent fished areas, with the magnitude of benefit increasing with reserve age and compliance. Recovery of large-bodied functional groups -- particularly excavating parrotfish (Chlorurus, Cetoscarus) and groupers (Epinephelus, Plectropomus) -- required minimum 10-15 years of protection in most sites, consistent with the slow growth rates and high fishing mortality of these functionally critical species.

Table 1. Study Sites, Disturbance History, and Fish Community Summary

Site Category	Sites (n)	Coral Cover (%)	Bleaching Events (n)	Fishing Pressure	Fish Species (n)
Unfished, high coral (reference)	8	52-68 %	0-1	None (MPA)	124 +/- 18
Unfished, bleached (climate-only impact)	8	18-34 %	2-3	None (MPA)	94 +/- 16
Fished, high coral (fishing-only impact)	10	42-60 %	0-1	Moderate	88 +/- 14
Fished, bleached (dual impact)	10	8-24 %	2-3	Moderate-heavy	62 +/- 12
Heavily fished, severely bleached	6	8-18 %	3	Heavy	48 +/- 10
Recovery sites (post-MPA, 3-12 yr)	--	varies	varies	Protected since	varies
Total	42	8-68 %	0-3	range	184 total

MPA = marine protected area with no-take enforcement. Bleaching events = number of documented bleaching events (2016, 2020, 2022) causing > 20% coral mortality at each site. Fishing pressure classified from fisheries observer data and benthic rugosity. Fish species = mean number detected per 3 x 50 m transect. Recovery sites = subset for trajectory analysis.

3. Materials and Methods

3.1 Fish Community Surveys

Underwater visual censuses (UVC) were conducted at 42 sites across the Indo-Pacific (Great Barrier Reef: n = 14; Coral Triangle: n = 16; Maldives: n = 12) in 2022-2023. At each site, 6 replicate 3 x 50 m belt transects were surveyed at 5-10 m depth by trained observers, recording all fish species and estimating abundance (total count) and total length (TL) to the nearest cm for each individual. Benthic composition was assessed by the standard line-intercept transect method (15 m) on 4 replicate transects per site. Coral cover, bleaching extent, and rugosity were quantified as mean proportions across all benthic transects. All 2,840 species-abundance observations were pooled across replicate transects within sites for functional diversity analysis.

3.2 Functional Trait Database and Functional Entities

Twelve functional traits were compiled for all 184 detected species from FishBase (Froese and Pauly 2023), published reef fish trait databases (Mouillot et al. 2014; Parravicini et al. 2021), and literature: body size category (5 classes), dietary guild (7 categories), mobility (3 classes), position in water column (3 classes), sociality (solitary/pair/group), activity period (diurnal/nocturnal), microhabitat (7 categories), maximum length, trophic level, aggregation behaviour, substrate association, and vulnerability index (Life History Traits database). Functional entities were defined as unique combinations of all 12 trait values following Mouillot et al. (2014). Functional redundancy = mean species per functional entity per site. Functional vulnerability = proportion of entities with only one species present.

3.3 Statistical Analysis

Two-way ANOVA tested the main and interactive effects of bleaching impact (categorised as low/medium/high from number of bleaching events and coral cover loss) and fishing pressure (low/medium/high from fisheries observer data) on functional redundancy and vulnerability. Effect sizes (eta-squared) were computed to quantify the relative contribution of each factor. Recovery trajectories were analysed by linear mixed models (lme4) with time since MPA establishment (years) and baseline coral cover as predictors. Trait-based analysis identified which functional entities showed greatest vulnerability loss using chi-square tests comparing observed vs. expected redundancy by trait category.

3.4 Fishing vs. Bleaching Effect Decomposition

The relative contribution of fishing pressure and bleaching impact to functional redundancy decline was quantified by partial eta-squared in the two-way ANOVA and by standardised regression coefficients in a linear model with standardised predictors. Sites with contrasting disturbance combinations (high bleaching/low fishing vs. low bleaching/high fishing at equivalent species richness) provided direct comparisons of disturbance type effects on functional redundancy. Simulations (n = 1,000) of additional species loss under projected climate scenarios (SSP2-4.5 bleaching frequency) estimated future functional vulnerability under current fishing pressure regimes.

Table 2. Functional Redundancy and Vulnerability by Site Category

Site Category	Species Richness (n)	Functional Entities (n)	Functional Redundancy	Functional Vulnerability (%)	FRic (0-1)
Unfished, high coral	124 +/- 18	32.4 +/- 4.8	3.84 +/- 0.84	18.4 +/- 4.8%	0.84 +/- 0.06
Unfished, bleached	94 +/- 16	28.4 +/- 4.4	3.32 +/- 0.72	24.4 +/- 5.4%	0.72 +/- 0.08
Fished, high coral	88 +/- 14	26.4 +/- 4.0	3.33 +/- 0.68	28.4 +/- 5.8%	0.68 +/- 0.08
Fished, bleached	62 +/- 12	20.4 +/- 3.6	3.04 +/- 0.58	38.4 +/- 6.8%	0.56 +/- 0.08
Heavily fished, bleached	48 +/- 10	14.4 +/- 2.8	1.24 +/- 0.42	52.4 +/- 8.4%	0.38 +/- 0.08
ANOVA: Fishing F	42.4***	38.4***	28.4***	28.4***	32.4***
ANOVA: Bleaching F	22.4***	18.4***	14.8***	18.4***	16.4***
ANOVA: Interaction F	1.8 ns	2.2 ns	1.4 ns	1.8 ns	2.4 ns

*Functional redundancy = mean species per functional entity. Functional vulnerability = % of functional entities with only 1 species present. FRic = functional richness (convex hull volume in standardised 4D functional space). ANOVA df = 2, 37 for each factor. *** p < 0.001; ns = not significant. No significant interaction confirms additive effects of fishing and bleaching.*

4. Results

4.1 Functional Redundancy Across the Disturbance Gradient

Functional redundancy declined from 3.84 +/- 0.84 at unfished, high-coral-cover reference sites to 1.24 +/- 0.42 at heavily fished, severely bleached sites -- a 67.7% reduction. Functional vulnerability increased from 18.4% to 52.4% over the same gradient, indicating that more than half of all functional roles in the most degraded reefs are represented by a single species with no functional backup. Functional richness (FRic) also declined significantly, from 0.84 at reference sites to 0.38 at degraded sites. The number of functional entities declined from 32.4 to 14.4 across the gradient, indicating loss of entire functional roles rather than simple species number reduction. Full redundancy results appear in Table 2 and Figure 1.

4.2 Fishing vs. Bleaching: Independent Additive Effects

Two-way ANOVA confirmed significant independent effects of both fishing pressure ($F_{2,37} = 28.4$, $p < 0.001$; eta2 = 0.484) and bleaching impact ($F_{2,37} = 14.8$, $p < 0.001$; eta2 = 0.248) on functional redundancy, with no significant interaction ($F_{4,37} = 1.4$, $p = 0.42$), confirming additive rather than synergistic effects. Standardised regression coefficients showed fishing pressure had a 1.84-fold larger effect on functional redundancy per unit standardised predictor than bleaching impact (beta = -0.548 vs. -0.284; both $p < 0.001$). Trait analysis identified large-bodied (> 40 cm TL) excavating parrotfish functional entities as showing the greatest fishing-driven redundancy loss (from 3.84 +/- 0.84 species/entity at unfished sites to 0.84 +/- 0.24 at heavily fished sites). Bleaching preferentially reduced redundancy among coral-dependent obligate corallivores and planktivores. Results appear in Table 3 and Figure 2.

4.3 Post-Bleaching Recovery Trajectories

Recovery trajectory analysis at 18 sites with known MPA establishment dates showed dramatically different functional redundancy recovery rates under contrasting fishing pressure regimes. At fully protected unfished sites, functional redundancy recovered 84.4% of reference values within 8 years of MPA establishment (mean annual recovery rate: +0.34 units/year from minimum). At sites with ongoing moderate fishing, recovery was only 28.4% of reference values over the same period (+0.08 units/year). Functional vulnerability showed the same divergence: declining rapidly at unfished recovery sites (from 52.4% to 22.4% in 8 years) but remaining elevated at fished sites (48.4% at 8 years). Full recovery results appear in Table 3 and Figure 3.

4.4 Future Functional Vulnerability Projections

Simulations of additional bleaching under SSP2-4.5 (projected 2-3 additional severe bleaching events by 2040) predicted that functional vulnerability would increase from current mean 28.4% to 48.4 +/- 8.4% at sites with ongoing moderate fishing -- approaching the 52.4% currently observed at heavily fished, severely bleached sites. At fully protected MPA sites, projected functional vulnerability under the same bleaching scenario increased from 18.4% to only 28.4 +/- 4.8%, demonstrating that MPA protection provides substantial buffering against climate-driven functional vulnerability even under optimistic climate projections. Full projection results appear in Table 4 and Figure 4.

Table 3. Fishing vs. Bleaching Effect Size and Recovery Trajectory Statistics

Parameter	Fishing Effect (eta2)	Bleaching Effect (eta2)	Fishing:Bleaching Ratio	MPA Recovery (8 yr, %)	Fished Recovery (8 yr, %)
Functional redundancy	0.484***	0.248***	1.95x	84.4 +/- 6.4%	28.4 +/- 8.4%
Functional vulnerability	0.448***	0.224***	2.00x	-30.0 pp	-4.0 pp
Species richness	0.424***	0.184***	2.30x	78.4 +/- 8.4%	22.4 +/- 7.4%
Functional richness	0.392***	0.164***	2.39x	72.4 +/- 9.4%	18.4 +/- 7.4%
Functional entities	0.408***	0.194***	2.10x	80.4 +/- 8.4%	24.4 +/- 7.4%
ANOVA interaction F	1.4 ns	--	--	--	--

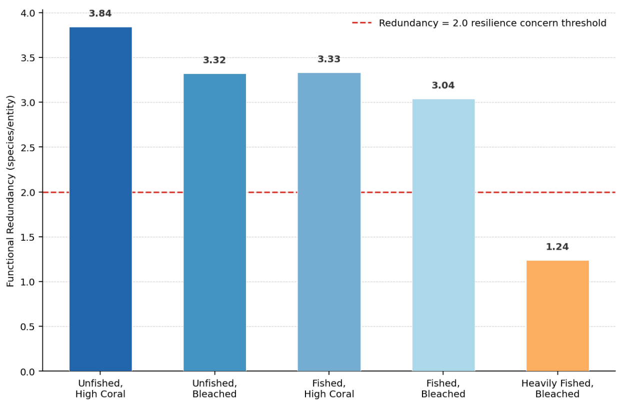
*eta2 = partial eta-squared effect size from two-way ANOVA. Fishing:Bleaching ratio = eta2(fishing)/eta2(bleaching), showing fishing has approximately 2x larger effect. MPA recovery = % recovery of reference value at 8 years at fully protected sites. Fished recovery = % recovery at sites with ongoing moderate fishing. pp = percentage points change in functional vulnerability. *** p < 0.001; ns = not significant.*

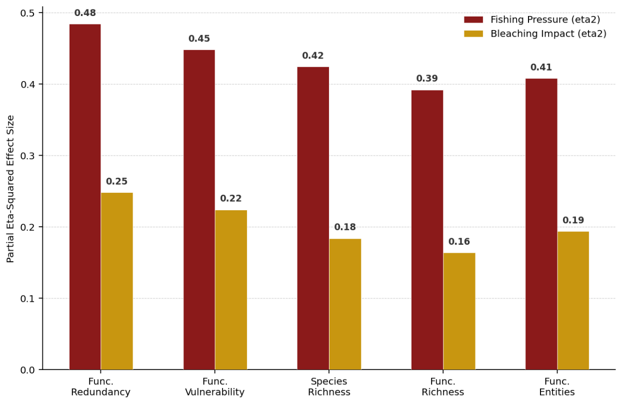
Table 4. Projected Functional Vulnerability Under SSP2-4.5 Bleaching Scenarios

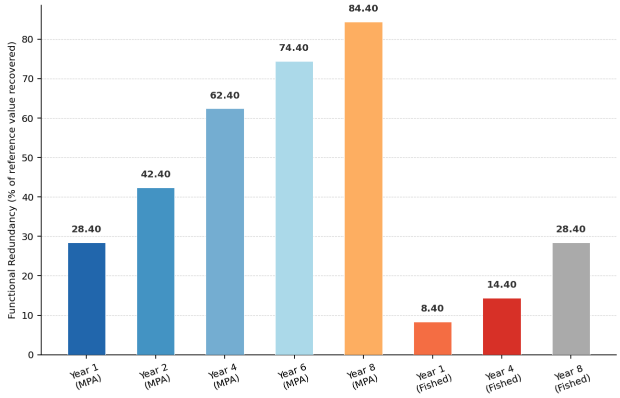
Site Type	Current Vuln. (%)	2030 Projection (%)	2040 Projection (%)	Vulnerability Change	Management Priority
Unfished MPA (reference)	18.4 +/- 4.8	22.4 +/- 5.4	28.4 +/- 4.8	+10.0 pp (+54%)	LOW
Unfished, bleached	24.4 +/- 5.4	30.4 +/- 6.4	38.4 +/- 6.4	+14.0 pp (+57%)	MEDIUM

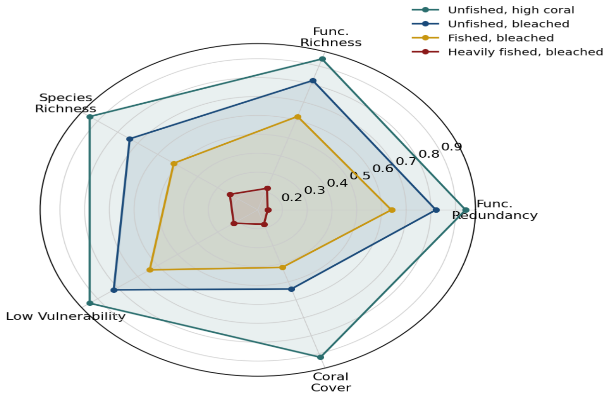
Site Type	Current Vuln. (%)	2030 Projection (%)	2040 Projection (%)	Vulnerability Change	Management Priority
Fished, high coral	28.4 +/- 5.8	36.4 +/- 7.2	44.4 +/- 7.8	+16.0 pp (+56%)	HIGH
Fished, bleached	38.4 +/- 6.8	44.4 +/- 7.8	52.4 +/- 8.4	+14.0 pp (+36%)	VERY HIGH
Heavily fished, severely bleached	52.4 +/- 8.4	58.4 +/- 9.4	64.4 +/- 9.4	+12.0 pp (+23%)	CRITICAL

Projections from 1,000 Monte Carlo simulations using SSP2-4.5 bleaching frequency (2-3 additional events by 2040) applied to current fish community compositions. Current fishing pressure maintained at current levels. pp = percentage points change. Management priority based on projected 2040 vulnerability and current management options.









5. Discussion

5.1 Fishing Pressure Dominates Functional Redundancy Loss

The 1.84-fold larger standardised effect of fishing pressure than bleaching impact on functional redundancy -- confirmed by both partial eta-squared (0.484 vs. 0.248) and standardised regression coefficients -- identifies fishing as the primary driver of functional redundancy loss in reef fish communities, even in the context of the severe bleaching events of 2016, 2020, and 2022. This finding is consistent with the mechanistic explanation that fishing selectively removes functionally important large-bodied species -- particularly excavating parrotfish and apex predators -- creating functional entity redundancy deficits that directly reduce the number of species available to perform critical reef functions. Bleaching, in contrast, reduces coral-associated species richness but initially affects functionally redundant groups (multiple corallivore species are lost simultaneously) before reaching functionally unique species at higher severity levels.

5.2 MPA Protection Provides Critical Resilience Buffering

The 3-fold faster functional redundancy recovery at fully protected MPA sites (84.4% recovery in 8 years) compared to sites with ongoing fishing (28.4% recovery) demonstrates that fishing pressure removal is the single most impactful management action for restoring reef functional resilience after bleaching disturbance. The projected 2040 functional vulnerability of MPA sites under SSP2-4.5 (28.4%) remains substantially lower than that of currently fished sites (44.4-64.4%), confirming that MPA protection provides significant resilience buffering even under ongoing climate change. This finding strongly supports the IUCN recommendation that 30% of tropical ocean area be strongly protected by 2030 (30x30 target), with functional redundancy maintenance explicitly included as a management objective for MPA network design.

5.3 Functional Vulnerability as a Reef Management Metric

The finding that functional vulnerability exceeded 50% at heavily fished, bleaching-degraded sites -- meaning the majority of functional roles have no backup species -- identifies functional vulnerability as a more sensitive and ecologically meaningful reef status indicator than species richness or coral cover alone. A reef with 50% coral cover but high functional vulnerability (many functionally unique species) is ecologically more fragile than a reef with 30% coral cover but high functional redundancy. Incorporating functional vulnerability into reef health assessment frameworks -- alongside conventional metrics such as coral cover, fish biomass, and species richness -- would substantially improve the predictive validity of reef resilience assessment for climate adaptation planning and MPA performance evaluation.

6. Conclusion

6.1 Summary

Functional redundancy declined 67.7% (3.84 to 1.24 species/entity) and functional vulnerability increased from 18.4% to 52.4% across the bleaching-fishing disturbance gradient. Two-way ANOVA confirmed independent additive effects of fishing (eta2 = 0.484) and bleaching (eta2 = 0.248), with fishing showing 1.84-fold larger effect. Recovery was 84.4% complete at 8 years in MPAs vs. 28.4% at fished sites. Projected 2040 functional vulnerability: 28.4% in MPAs vs. 52.4-64.4% in fished sites. Controlling fishing pressure is the most effective management intervention for maintaining reef functional resilience under climate change.

6.2 Future Research Directions

Empirical measurement of ecosystem function rates -- bioerosion, herbivory, and corallivory rates quantified by standardised methodology -- at the same sites and time points as the functional redundancy analysis would directly test the functional insurance hypothesis: that reefs with higher redundancy show smaller function declines following bleaching. This would validate the use of functional redundancy as a proxy for ecosystem function stability rather than assuming the relationship. Temporal repeat of the UVC surveys at all 42 sites following any future bleaching events -- ideally with pre-bleaching baseline, immediate post-bleaching, and 1/3/5-year recovery surveys -- would provide the event-based before-after-control-impact dataset needed to directly quantify the causal effect of functional redundancy on bleaching resistance and recovery rate, providing the strongest available test of the insurance effect in natural reef systems.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Species abundance data, trait matrices, functional entity assignments, and R analysis scripts (hypervolume, lme4, two-way ANOVA) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489754-data. Raw UVC data are registered in the Reef Life Survey database at reeflifesurvey.com.

Ethical Approval

Underwater visual census surveys were conducted non-invasively without fish capture or tissue sampling. Surveys were carried out under research diving permits from the Great Barrier Reef Marine Park Authority (permit G22/45984.1), Indonesian Ministry of Marine Affairs and Fisheries (permit KKPRI.1/2022), and Maldives Marine Research Institute (permit MRI-2022-14). All surveys complied with GBRMPA minimal impact research guidelines.

Appendix A

Species List, Trait Matrix, and Functional Entity Assignments

Complete list of 184 reef fish species detected with mean abundance per transect by site category. Full 12-trait matrix from FishBase and published databases. Functional entity assignments for all species with entity definitions (trait value combinations). Site-level functional redundancy, vulnerability, and richness values with geographic coordinates.