

REVIEW ARTICLE

Global meta-analysis highlights recovery of animal functional diversity in restored coastal ecosystems

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Abstract

Introduction: Coastal ecosystems have experienced widespread global degradation, prompting substantial investment in restoration. While structural recovery is well documented, whether restoration reestablishes the functional diversity (FD) of animal communities and how recovery unfolds through time remains poorly resolved.

Objectives: This study evaluates the recovery of fish and decapod FD in restored coastal habitats—seagrass meadows, mangrove forests, saltmarshes, and oyster reefs—relative to reference and unstructured baselines and determines whether recovery occurs immediately or follows temporal trajectories.

Methods: We synthesized 61 studies encompassing 355 fish and 136 decapod species. We quantified functional richness (FRic; presence-absence based) and four abundance-weighted FD metrics (functional evenness, divergence, dispersion, and Rao's Quadratic Entropy [Rao's Q]) alongside species richness. Log response ratios (lnRR) comparing restored with reference and unstructured sites were analyzed in relation to time-since-restoration (TSR).

Results: lnRR did not differ significantly from zero in 93% of restored-reference comparisons, suggesting restored habitats frequently supported functionally comparable communities from early stages. FRic showed similarity to reference systems irrespective of TSR. For fish in vegetated habitats, some abundance-weighted metrics (particularly functional dispersion and Rao's Q) showed positive temporal trends, reaching parity within 3–7 years. Decapods showed greater variability, but all metrics indicated early functional equivalence, consistent with rapid colonization. The absence of strong temporal trends in most comparisons suggests early functional recovery followed by stable trajectories.

Conclusion: FD of fish and decapod assemblages responds relatively rapidly to coastal habitat restoration, with many systems achieving early equivalence to reference conditions. Recovery varied by ecosystem: oyster reefs showed consistent early parity, while vegetated systems exhibited more gradual trajectories, underscoring ecosystem-specific expectations.

Implications for Practice: Coastal habitat restoration can deliver early functional returns for fish and decapod communities, although recovery pace and extent are ecosystem-dependent. Oyster reefs showed rapid functional recovery, while mangroves and saltmarshes followed more gradual trajectories for some metrics. Incorporating functional diversity metrics alongside species counts in monitoring can provide a more direct assessment of ecological roles and ecosystem function. Given variability among ecosystems and metrics, monitoring frameworks should adopt ecosystem-specific benchmarks and extended time frames rather than uniform expectations across coastal restoration contexts.

Key words: coastal restoration, crustacean, ecosystem function, fish, functional diversity, global meta-analysis, post-restoration recovery, trait-based ecology

Introduction

Coastal habitats such as mangrove forests, oyster reefs, saltmarshes, and seagrass meadows constitute some of the most dynamic and ecologically significant systems globally, supporting climate change mitigation, shoreline protection, fisheries production, and biodiversity (Barbier et al. 2011; Nagelkerken et al. 2015). Yet, these systems face mounting pressures from industrialization and urbanization, the loss of key biological and physical resources, and reduced resilience to climate change and sea level rise (Elliott et al. 2016; Waltham et al. 2020), resulting in significant declines in their extent and condition globally (Duarte et al. 2020). These losses have driven substantial upscaling of coastal habitat restoration efforts, particularly in response to the United Nations Decade on Ecosystem

Author contributions: JMM, MS, RMC conceptualized the study; JMM, MS conducted the literature review, data extraction; MS, JMM led data analyses with contributions from BLG, CJH, RMC; all authors interpreted results; JMM led the manuscript writing; all authors revised and approved the final manuscript.

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doi: 10.1111/rec.70501

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Restoration, the Kunming-Montreal Global Biodiversity Framework, and the European Union Nature Restoration Law (Maron et al. 2018; Duarte et al. 2020; Hering et al. 2023). As investments expand, so too does pressure to demonstrate that restoration delivers tangible ecosystem benefits, including enhanced fisheries productivity and biodiversity support (Zu Ermgassen et al. 2012; Young & Schwartz 2019).

A key aspect of evaluating restoration success lies in understanding how animal communities respond to restoration (Sievers et al. 2022), particularly fish and decapods. These groups serve critical ecological roles as prey, predators, and bioturbators, support commercial and recreational fisheries, and are sensitive indicators of habitat quality (Nagelkerken et al. 2015; Whitfield 2017). Animal recovery in restoration contexts is most commonly assessed using taxonomic metrics such as species abundance, richness, and community composition (Hale et al. 2019; Ning et al. 2021; Sievers et al. 2024). However, these may not fully capture underlying shifts in ecological functioning, as species composition can remain relatively stable even when ecosystem function shifts (Mouillot et al. 2013; Bellwood et al. 2019). Evaluating functional diversity (FD), the diversity of species traits and functions that influence ecosystem processes, offers a valuable complement, and its recovery is now increasingly recognized as a core restoration goal alongside taxonomic recovery (Hyndes et al. 2014; Gann et al. 2019; Lance-man et al. 2025).

Functional diversity metrics incorporate ecological traits of organisms (e.g. feeding mode, habitat use, mobility, and life history) to quantify the extent of functional roles represented in a community (Petchey & Gaston 2006; Mouillot et al. 2013). This approach moves beyond simply documenting species list to reveal functional gaps, redundancy and ecological capacity (Bellwood et al. 2019; Streit & Bellwood 2023). Key metrics include functional richness (FRic; range of trait values), functional dispersion (FDis; spread in trait space), functional evenness (FEve; regularity of trait spacing and abundances), functional divergence (FDiv; dominance of trait-distinct species), and Rao's Quadratic Entropy (Rao's Q), which integrates both abundance and pairwise trait dissimilarities (Rao 1982; Botta-Dukát 2005; Cornwell et al. 2006; Villéger et al. 2008; Mouchet et al. 2010). Together, these metrics can reveal whether restored habitats support the functional capacity needed for key ecosystem services, such as nutrient cycling, secondary production, and trophic support for fisheries, outcomes that may not be evident from species lists alone.

Evidence from studies suggests that functional recovery can follow a range of trajectories. Some systems achieve rapid equivalence with reference sites; for instance, restored seagrass meadows achieved invertebrate FD equivalent to reference sites within 3–15 months of eelgrass transplantation (Gagnon et al. 2023), while others recover more gradually (Lefcheck et al. 2017) or maintain persistent functional differences despite supporting comparable species richness (Wong & Dowd 2015; Ziegler et al. 2021). These contrasting patterns indicate that functional equivalence with reference systems may be achieved at different rates depending on the system, or in some cases may not occur within the typical

monitoring time frames. Distinguishing between immediate recovery and time-dependent community reorganization is therefore essential when interpreting FD responses in coastal ecosystem restoration.

Despite increasing emphasis on functional outcomes in restoration (Gann et al. 2019), broad scale synthesis of FD recovery across coastal ecosystems remains limited. Prior meta-analyses have examined coastal and marine restoration success using animal taxonomic metrics (Davenport et al. 2021; Smith & Castorani 2023; Sievers et al. 2024; Danovaro et al. 2025). Broadly, these studies show that restoration enhances faunal abundance, recruitment, and diversity relative to unstructured habitats, but responses are highly variable among taxa and are strongly mediated by habitat characteristics and time-since-restoration (TSR). Whether the functional dimensions of these communities follow similar or distinct trajectories remains unclear, and many studies rely on single time snapshots, that make it difficult to distinguish immediate functional recovery from systems requiring extended recovery periods (Carlucci et al. 2020; McLean et al. 2021). Furthermore, restoration outcomes are often evaluated against a single baseline, either unstructured habitats (e.g. bare sediment) or natural reference sites (Sievers et al. 2024). These baselines provide complementary information: unstructured comparisons demonstrate improvement over degraded conditions, while reference comparisons assess functional equivalence with natural ecosystems.

Here, we address these knowledge gaps through a quantitative synthesis examining FD recovery of fish and decapod assemblages across mangroves, oyster reefs, saltmarshes, and seagrass meadows, comparing restored sites to natural reference habitats and to unstructured habitats where data are available. Given the high mobility of fish and decapods, we anticipated that functional equivalence would be achievable within relatively short time frames in many systems, though the pace and trajectory of recovery were expected to vary by ecosystem type, faunal group, and functional metric. Building on the taxonomic framework of Sievers et al. (2024), we aim to: (1) quantify FD metrics in restored habitats relative to available baselines; and (2) determine whether functional recovery occurs immediately, not at all, or whether it follows temporal trajectories, estimating recovery time frames where patterns exist. Our findings will inform realistic expectations for restoration monitoring and outcomes, distinguish immediate from progressive recovery pathways, and advance understanding of how restored coastal ecosystems can deliver fisheries support and biodiversity conservation.

Methods

Conceptual Framework

We provide a conceptual framework to interpret potential trajectories of FD recovery in restored coastal ecosystems (Fig. 1), built around two complementary baseline comparisons: (1) comparison to unstructured habitats (e.g. bare sediment), which demonstrates functional improvement over degraded conditions, and (2) comparison to reference (natural) sites which assess whether restored systems achieve functional equivalence with natural ecosystems. FD metrics were expressed as log

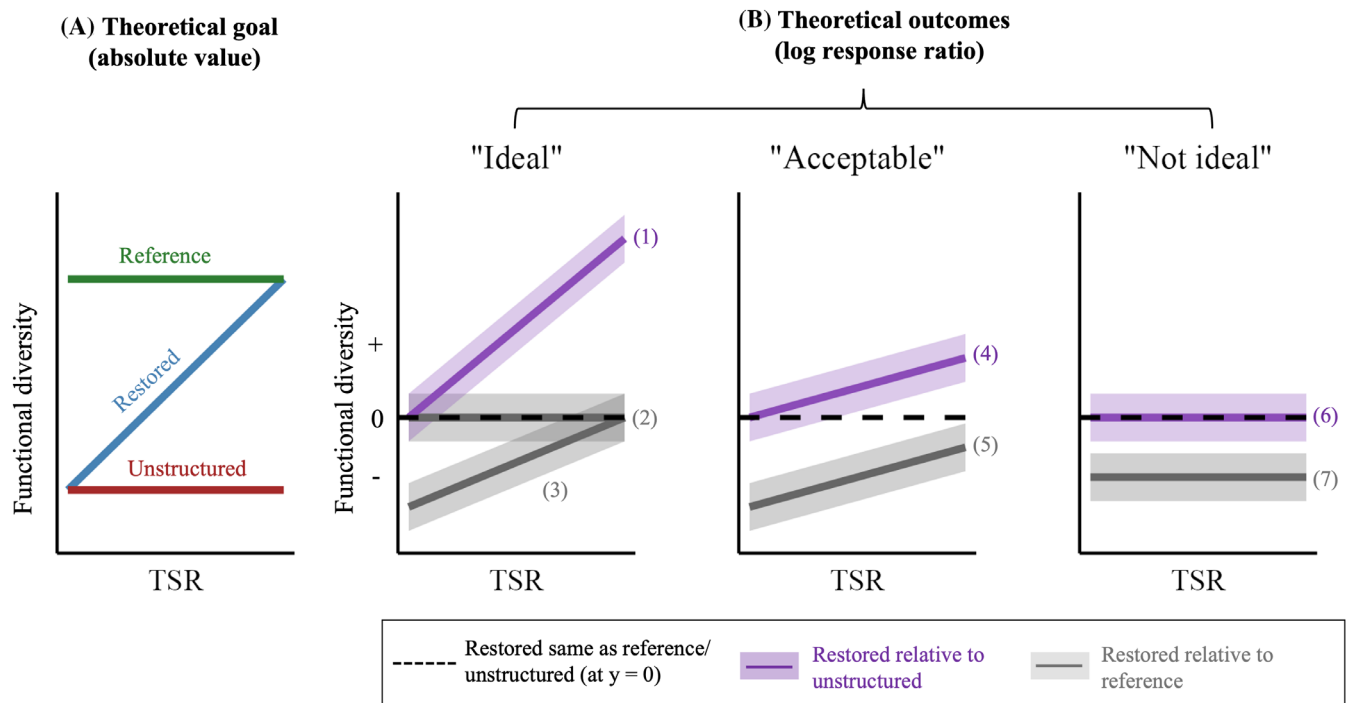


Figure 1. Conceptual framework illustrating theoretical goals and outcomes for functional diversity recovery following coastal habitat restoration. (A) The theoretical restoration goal in absolute terms, where restored habitats initially resemble unstructured conditions, increase in functional diversity through time, and ultimately converge on natural reference states. (B) Illustrative, hypothetical outcomes expressed as log response ratios (lnRRs) of restored habitats relative to unstructured (purple) or reference (gray) baselines across TSR, where values at $y = 0$ (dashed horizontal line) indicate functional equivalence, positive values (+) indicate higher functional diversity in restored habitats, and negative values (−) indicate lower functional diversity. Shaded ribbons represent uncertainty around each scenario trajectory, not around the dashed line. Numbered scenarios depict a range of possible recovery patterns and are intended as interpretive guides rather than categorical evaluations of success. Relative to unstructured baselines, restored sites may show rapid improvement (1), gradual gains (4), or no improvement over time (6). Relative to reference baselines, restored sites may achieve immediate functional equivalence (2), progressive recovery reaching parity (3), improvement without reaching parity (5), or persistent deficits with no upward trajectory (7). The framework focuses on recovery relative to reference parity and does not exhaustively depict all possible outcomes (e.g. persistent functional excess above reference levels). We categorize these responses as “Ideal,” “Acceptable,” and “Not Ideal” to provide a conceptual framework for interpreting trajectory shapes according to major theoretical expectations about recovery dynamics rather than formal reference data; they are intended to be indicative rather than prescriptive of all possible outcomes. Note that while relationships are shown as linear for clarity, actual recovery trajectories may be nonlinear.

response ratios (lnRR), where zero values indicate functional equivalence, positive values indicate higher FD in restored sites, and negative values indicate deficits relative to the baseline. Importantly, flat temporal trajectories (i.e. non-significant relationships with TSR) can reflect either immediate functional equivalence (if lnRR values remain near zero throughout), or a persistent deficit (if they remain below zero). The framework identifies seven potential recovery scenarios, which differ in both the pace of recovery and whether functional parity with reference ecosystems is ultimately achieved (Fig. 1).

An “Ideal” outcome captures restoration trajectories that achieve functional improvement over unstructured habitats rapidly (1), trajectories that are already stable at reference-equivalent values from early in the recovery process, indicating immediate functional parity (2), or where the deficit relative to reference sites steadily closes over time (3). An “Acceptable” outcome describes trajectories where functional improvement over unstructured habitats is still evident but occurs more gradually (4), and where the deficit relative to reference sites slowly

narrows over time but does not reach parity within the observed monitoring period, suggesting recovery is underway but likely incomplete on realistic restoration timescales (5). A “Not ideal” outcome describes flat trajectories that fail to demonstrate meaningful recovery under either baseline: FD in restored sites remains statistically indistinguishable from unstructured habitats (6), or remains persistently below reference levels with no evidence of closing that gap over time (7). Distinguishing these scenarios is important because a non-significant temporal trend alone cannot differentiate between rapid attainment of functional equivalence, a slow but genuine recovery trajectory, and a stalled or negligible one, each of which implies a different management response and a different expectation for how much further time or intervention a restored site may require.

Literature Search and Data Extraction

This study built upon the database and global synthesis of Sievers et al. (2024), which examined the benefits of coastal ecosystem

restoration for animal communities. We expanded our literature search to incorporate studies published between 2022 and 2024 using Institute for Scientific Information Web of Science and Scopus with the following search terms: TITLE (coast* OR saltmarsh OR “salt marsh” OR “tidal marsh” OR eelgrass OR seagrass* OR “sea grass” OR mangrove* OR mangal* OR oyster OR “oyster reef”) AND (restor* OR rehab*). We therefore focused on mangroves, oyster reefs, saltmarshes, and seagrass habitats and fish and decapods as our focal species as they are the most widely represented groups, are often the focus of restoration actions, and play key roles in ecosystem functioning, trophic interactions, and habitat structuring within restored coastal environments. As per Sievers et al. (2024) studies had to compare restored sites to either a reference (i.e. natural) or unstructured (e.g. bare sand or sediment) site (hereafter “Treatment”). Two additional criteria were implemented: (1) abundance reported at the species level, and (2) full species-level abundance data available for all community members. The complete screening process is summarized in a preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow diagram (Fig. 2).

Of the 160 studies included in Sievers et al. (2024), 120 focused on fish and decapods. After applying the updated

inclusion criteria and adding 25 newer studies, 61 studies were included in the analysis (full list in [Supplement S1](#)), encompassing 355 fish and 136 decapod species. Key study descriptors, including Treatment, study location, type of restored ecosystem, and the TSR (i.e. restored site age in years) were extracted from each study. Restored sites less than 1 year old are coded as TSR = 1, similarly those greater than 1 and less than 2 (where that information is provided) are coded TSR = 2, and so on. Where multiple TSR were available, all were retained for analysis.

Species Traits

We a priori identified five ecologically relevant traits for fish (feeding mode, trophic level, body shape, maximum length, and habitat) and seven for decapods (feeding mode, trophic level, body size, environment, development mode, mobility, and water column position) based on their relevance to FD and their role in shaping ecosystem functioning (Table S1). These traits fall into two broad categories: (1) trophic traits, which capture resource acquisition, habitat niche, and species contributions to ecosystem processes; and (2) response traits, which

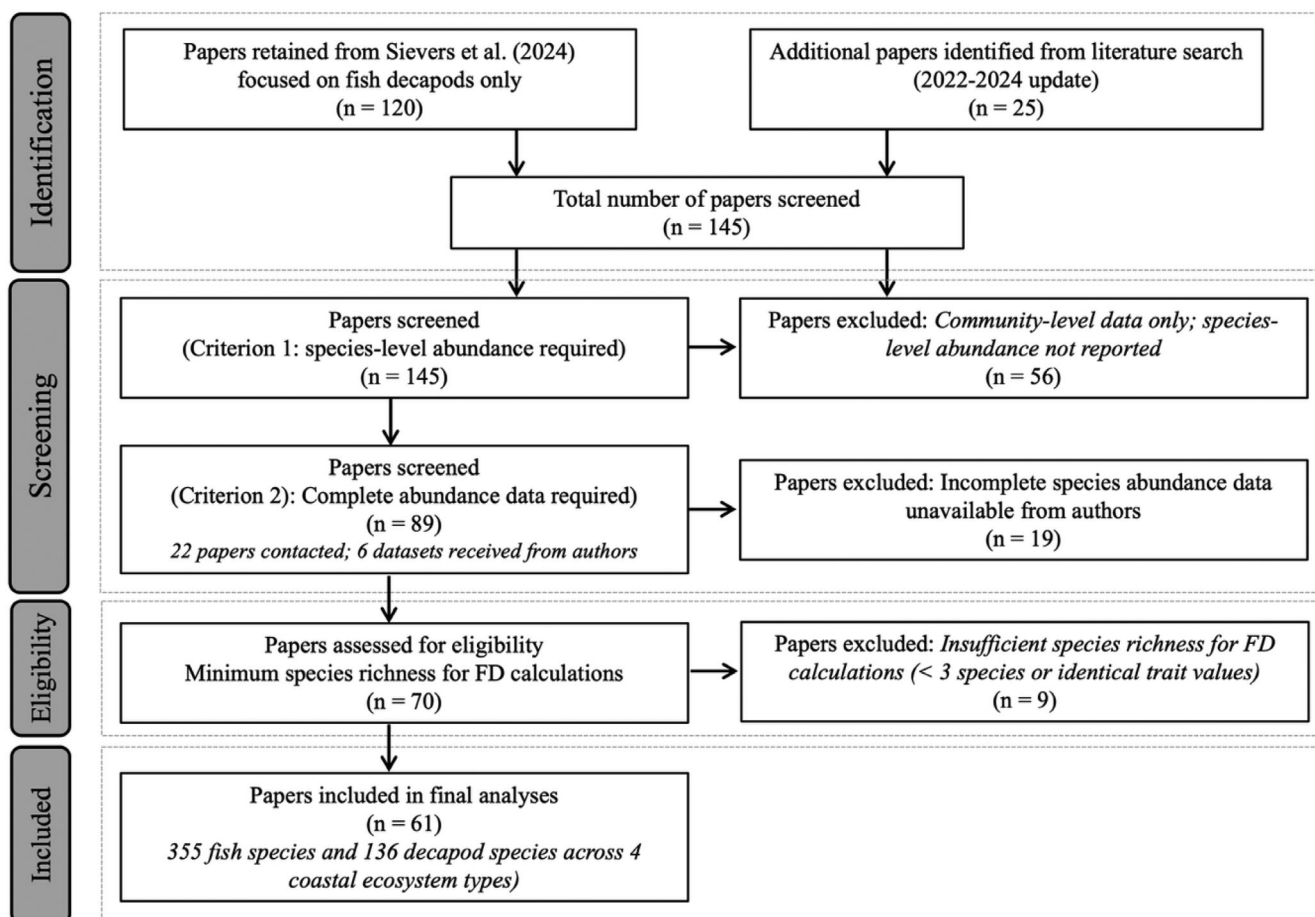


Figure 2. preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow diagram showing the procedure used for selection of studies for the systematic review and meta-analysis.

reflect how species respond to environmental variations, including dispersal ability, phenology, and reproductive strategies (Figs. S1 & S2). Trait selection was partly constrained by data availability, given the absence of a standardized methodology for trait selection (Miatta et al. 2021). Missing trait values were infilled using data from other species within the same genus already present in our species list to ensure consistency and avoid skewing the trait dataset. Fish traits were obtained from the FishBase database (Froese & Pauly 2025) while trait data for decapods were sourced from SeaLifeBase (Palomares & Pauly 2025), the World Register of Marine Species (WoRMS) (www.marinespecies.org), and the Smithsonian Environmental Research Center's National Estuarine and Marine Exotic Species Information System (NEMESIS) (Fofonoff et al. 2018).

Functional Diversity Metrics

We calculated five key FD metrics: FRic, FEve, FDiv, FDis, and Rao's Q (Table 1), calculated using the dbFD function from the FD package (Laliberté & Legendre 2010) in R (version 4.4.3). Trait values were standardized prior to analysis, and a Gower dissimilarity matrix was used to account for mixed trait types. To assess the relative change in FD in restored sites relative to reference and/or unstructured sites (paired within studies), we expressed these metrics as lnRR. This approach allowed us to quantify the extent and direction of FD shifts following habitat restoration, while accounting for important location effects (i.e. different species pools across locations). Traits with zero variance were excluded as they do not contribute to FD calculations. Communities with fewer than three species or fewer than two informative traits were flagged, and FD metrics were not

calculated for these subsets. This approach ensured that the minimum requirements for meaningful FD calculation were met. To handle potential issues with Euclidean distance matrices used in FD calculations, we implemented an adaptive approach testing different corrections (Cailliez, Lingoes, square root, and no correction) until a valid calculation was achieved. Cailliez correction consistently performed best and was applied for all valid cases.

Statistical Analyses

We analyzed fish and decapods separately, for each ecosystem with sufficient data ($n > 3$ paired sites). We refer to each unique combination of individual FD metric, faunal group (fish or decapods), ecosystem type, and Treatment (comparison to reference or unstructured sites) as a "dataset." Sufficient data comparing restored sites to unstructured sites only existed for oyster reefs; all ecosystem types had enough data to compare restored sites to reference sites. To examine how FD recovery varied with TSR, we fitted linear models with log-transformed TSR as the predictor for each FD metric and species richness. Log-transformed TSR was used to reduce the disproportionate influence of a few very high TSRs. We also examined Generalized Additive Models using the *mgcv* package (Wood 2011), which revealed near-identical trends (Figs. S3 & S5); therefore, we present and discuss linear models throughout. To account for potential non-independence of observations from multiple sites from the same studies, we used a mixed-effects modeling approach with the *lme4* package (Bates et al. 2015). For each dataset, we constructed models with the general form:

Table 1. Overview of the functional diversity metrics included in the analyses.

Metric	Description	Equation	Exemplar references
Rao's quadratic entropy (Rao's Q)	Mean dissimilarity among species weighted by species abundance.	$\text{Rao } Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j$ where p_i, p_j is the relative abundance of species i and j ; d_{ij} is the functional dissimilarity/distance between species i and j .	Botta-Dukát (2005)
Functional richness (FRic)	Value of the convex hull volume filled by the community.		Cornwell et al. (2006); Villéger et al. (2008)
Functional evenness (FEve)	Describes the evenness of abundance distribution in a functional trait space.	$\text{FEve} = \frac{\sum_{i=1}^{S-1} \min(\text{PEW}_i, (1/S-1)) - (1/S-1)}{1 - (1/S-1)}$ where PEW is the partial weighted evenness, S is the number of species.	Villéger et al. (2008)
Functional divergence (FDiv)	Relates to the extent to which high-abundance species are distributed toward the edges of trait space.	$\text{FDiv} = \frac{\Delta d + dG}{\Delta d + dG}$ where dG is the mean value of the Euclidean distance of each species.	Villéger et al. (2008)
Functional dispersion (FDis)	Mean distance of species (abundance-weighted) to the centroid of the trait space.		Laliberté and Legendre (2010)

$$\ln\text{RR.metric} \sim \log\text{TSR} + (1|\text{RefID}),$$

where $\ln\text{RR.metric}$ is the $\ln\text{RR}$ for the FD metric, $\log\text{TSR}$ is the log-transformed TSR in years and RefID is the study identifier included as a random effect to account for non-independence among sites from the same study. For datasets with limited study replication, simple linear models were used instead. Model selection between simple and mixed-effects approaches was based on the number of unique studies ($\text{RefID} > 1$), sample size ($n \geq 5$), and model convergence diagnostics. Residuals were inspected visually for homoscedasticity and approximate normality. For mixed-effects models, marginal r^2 values were calculated to quantify the variance explained by the fixed effect of $\log\text{TSR}$. Significance of TSR effects was assessed using t tests on slope coefficients, with $\alpha = 0.05$. Formal publication bias diagnostics could not be conducted as variance estimates were unavailable for the majority of individual effect sizes. This limitation is consistent with the broader meta-analytic literature on restored ecosystems where raw variance data are rarely reported (see also Sievers et al. 2024).

To determine the minimum TSR required for a positive impact on FD, we conducted two complementary analyses for each dataset:

- Zero-crossing analysis:** We identified the TSR at which the predicted effect size ($\ln\text{RR}$) transitioned from negative to positive (i.e. at $y = 0$). Crossing points and their corresponding 95% CI were calculated for each model, with parametric bootstrap methods (500 simulations) applied for mixed-effects models to ensure robust estimates.
- Positive effect threshold analysis:** We determined the minimum TSR at which the lower bound of the 95% CI for the predicted $\ln\text{RR}$ remained consistently positive, signifying a significantly higher FD value in restored sites compared to baseline sites.

We also examined whether FD metrics in restored sites differed from reference/control sites irrespective of TSR (i.e. whether mean $\ln\text{RR}$ were significantly different from zero) using one-sample, two-sided t tests to test the null hypothesis that mean $\ln\text{RR}$ differed from zero. The tests were conducted separately for each dataset. Finally, we conducted a fourth-corner analysis to assess associations between fish functional traits and TSR in restored habitats. The analysis focused on 136 sites classified as “Restored” or “After-Restored,” with a filtered abundance matrix of 338 fish species after removing those lacking complete trait data. Categorical trait variables (functional group, body shape, and habitat) were converted to binary format using one-hot encoding in the *fastDummies* package (Kaplan 2021) to enable independent evaluation of trait-environment relationships and improve interpretability. Continuous traits (trophic level and total length) were retained as-is. We applied the *traitglm* function from the *mvabund* package (Wang et al. 2012) using the “manyglm” method. Due to convergence issues, we implemented a manual fourth-corner approach by calculating species-level weighted means of

TSR (abundance-weighted across sites) and correlating these with trait values using Pearson’s correlation. Positive correlation values indicate greater abundance of a trait in older restoration sites, while negative values reflect association with younger sites. The decapod datasets did not converge for fourth-corner analyses and were therefore not included.

Results

Fish Functional Diversity

Relationships between fish FD and TSR were generally stable or positive, with effect sizes most often statistically indistinguishable from zero (Table S3a; Fig. 3). In oyster reefs, restored sites relative to unstructured habitats showed weak but positive temporal trends for FDis ($p = 0.067$) and Rao’s Q ($p = 0.056$) (Table S3a). These two metrics were initially comparable between restored and unstructured and became higher in restored sites following 2.6 years (Fig. 3). FRic, evenness, and divergence were consistently similar and showed no significant relationship with TSR between restored and unstructured sites (Table S3a; Fig. 3). No significant TSR relationships were detected for any metric in restored-reference comparisons for oyster reefs (all $p > 0.05$; Table S3a).

In saltmarsh, we found clear positive trajectories in two of the FD metrics (Fig. 3). TSR was positively associated with FDis ($p = 0.002$) and Rao’s Q ($p = 0.005$) (Table S3a). FDis was initially lower in recently restored sites compared to reference sites, and steadily increased, reaching parity with reference sites at 3.1 (1.1–5.4; 95% CI) years post-restoration. Rao’s Q quickly reached parity with reference sites at 2.8 (1–5.5) years post-restoration and exceeded these after 6.1 years (Fig. 3). All other metrics remained stable and on par with reference sites (Fig. 3) and showed no detectable TSR effects ($p > 0.05$) (Table S3a).

In mangroves, a positive TSR relationship was observed for Rao’s Q ($p < 0.001$) while FDiv showed a marginally positive trend ($p = 0.056$) (Table S3a). Functional divergence, dispersion, and Rao’s Q were significantly lower in restored sites initially and reached parity with reference sites at 3.5 (1.4–7), 6.8 (2–8.9), and 7.4 (3.0–8.4) years post-restoration, respectively (Fig. 3).

Mean $\ln\text{RR}$ for fish FD metrics were highly similar between restored sites and both reference and unstructured sites, with only 1 out of the 20 comparisons significantly different from zero (Table S2a; Fig. 3). This single metric was from restored oyster reefs, whereby mean FRic was significantly higher in restored sites compared to unstructured sites (mean $\ln\text{RR} = 0.417$, 95% CI = 0.065–0.768, $p = 0.029$). None of the metrics across ecosystems were significantly lower in restored sites (Table S2a; Fig. 3).

Similar to FD metrics, the mean $\ln\text{RR}$ s for fish species richness were generally not significantly different from zero, with one exception in oyster reefs relative to unstructured habitats, where species richness was significantly higher in restored sites (mean $\ln\text{RR} = 0.061$, 95% CI = 0.401–0.802, $p < 0.001$) (Table S2a; Fig. 3). TSR had no significant temporal trends in species richness for oyster reefs or saltmarshes ($p > 0.05$)

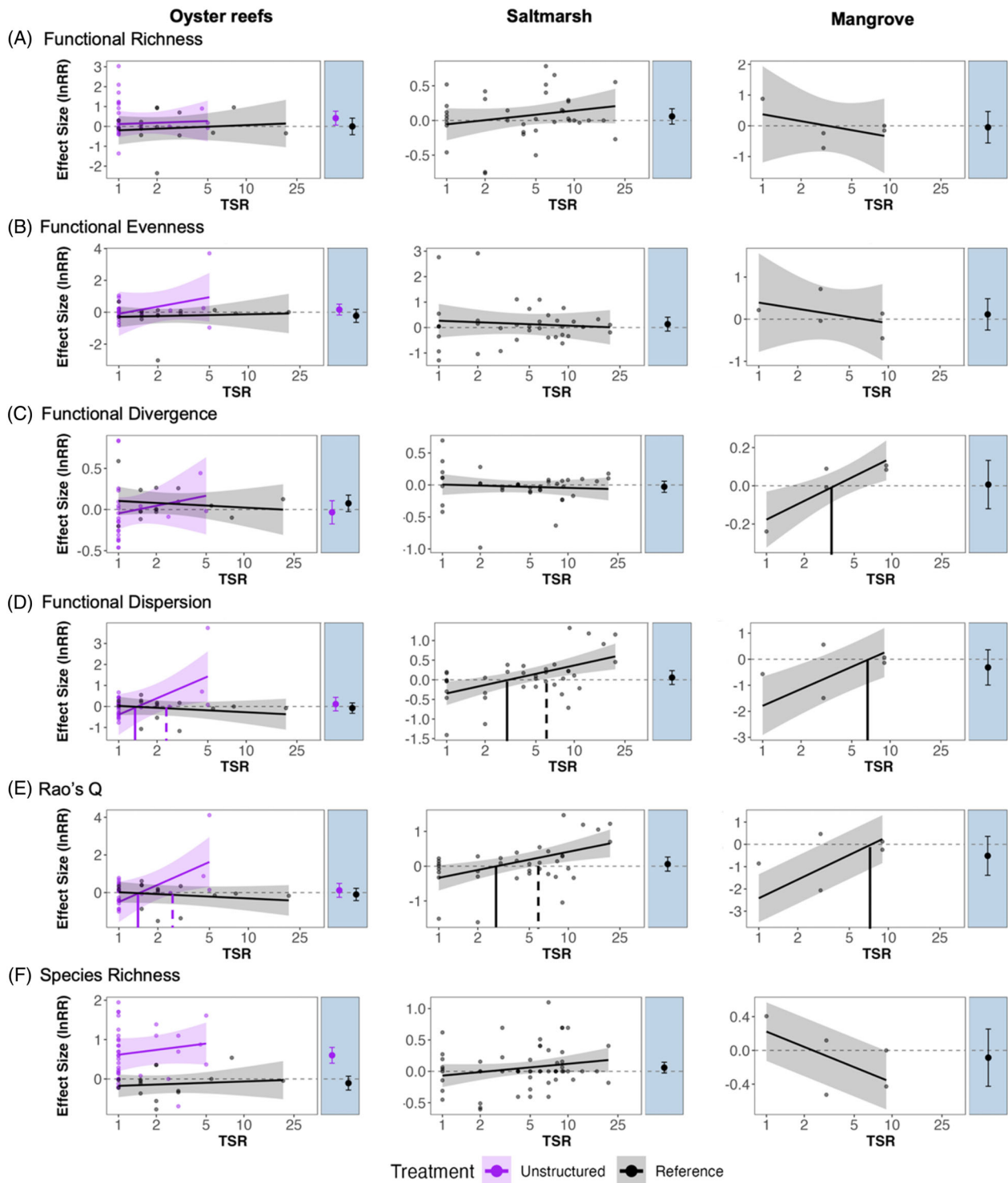


Figure 3. Fish functional diversity. Linear trends in log response ratios as a function of time-since-restoration (TSR) and overall log response ratio means (shaded blue region of each panel). Error ribbons and bars are 95% CIs. Dashed horizontal lines at $y = 0$ reflect where restored sites are equal to reference/unstructured sites. Vertical lines are provided for metrics with significant trends; solid vertical lines indicate where mean predictions cross $y = 0$, where applicable (i.e. the TSR where restored sites reach parity with reference/unstructured sites), and dashed vertical lines indicate where predictions are significantly higher than $y = 0$ (i.e. the TSR where restored sites are higher than reference/unstructured sites based on 95% CIs). Seagrass is excluded as insufficient data were available ($n < 3$ paired sites). See Figure S3 for Generalized Additive Models (GAM) outputs. (A) Functional richness. (B) Functional evenness. (C) Functional divergence. (D) Functional dispersion. (E) Rao's Q. (F) Species richness.

(Table S3a). In mangroves, however, a significant negative relationship between TSR and species richness was observed (slope = -0.262 , $p < 0.001$) (Table S3a). Species richness was strongly correlated with FRic ($r = 0.7$), but uncorrelated with other FD metrics ($r < 0.1$; Fig. S4).

Fourth-corner analysis identified trait-environment relationships associated with TSR across species traits. Among all traits assessed, only two showed notable associations with TSR: *benthopelagic* (habitat) was positively correlated, with species possessing the trait more common in older restoration sites, while *Trophic Level* was negatively correlated, indicating that species at higher trophic levels were more common at younger sites. The remaining traits showed weak or no clear relationship with TSR (Fig. 4).

Decapod Functional Diversity

TSR effects on decapod FD were generally weak, with no significant temporal trends detected across all ecosystems and metrics (Table S3b). The only marginal TSR relationship was observed for species richness in oyster reference habitats, which declined slightly with TSR (slope = -0.041 , $p = 0.070$) (Table S3b; Fig. 5). FD metrics for decapod communities were largely similar between restored sites and reference and unstructured sites across all metrics and ecosystems (Table S2b; Fig. 5). Notable exceptions occurred between restored and reference oyster reefs, where restored sites exhibited significantly higher mean lnRRs for FRic (mean lnRR = 0.068 , 95% CI = 0.014 – 0.123 , $p = 0.044$), Rao's Q (mean lnRR = 0.118 , 95% CI = 0.036 – 0.199 , $p = 0.025$), and species richness (mean lnRR = 0.034 , 95% CI = 0.004 – 0.065 , $p = 0.045$) (Table S2b; Fig. 5). Like for fishes, species richness was strongly correlated with FRic ($r = 0.9$), but uncorrelated with other FD metrics ($r < 0.15$; Fig. S6).

Discussion

Functional Diversity Responses and Temporal Dynamics

Across ecosystem types, restored habitats generally supported fish and decapod assemblages that were functionally comparable to reference sites, with 93% of comparisons indicating functional equivalence. This broad pattern suggests that restoration efforts are often effective in reinstating key functional attributes of these communities. Where temporal trends were detected, functional parity with reference sites was typically achieved within a few years (ranging 3–7 years). This indicates that restoration is not merely recovering species counts but also reinstating the functional roles that underpin ecosystem processes. This finding sits within a broader context of generally positive marine restoration outcomes spanning major coastal habitat types. Benefits to nekton communities often increase through time as restored habitats mature, although some responses can be immediate and taxon-specific rather than uniformly time-dependent (Davenport et al. 2021; Smith & Castorani 2023; Danovaro et al. 2025). While these studies assess restoration success through taxonomic rather than functional metrics, our

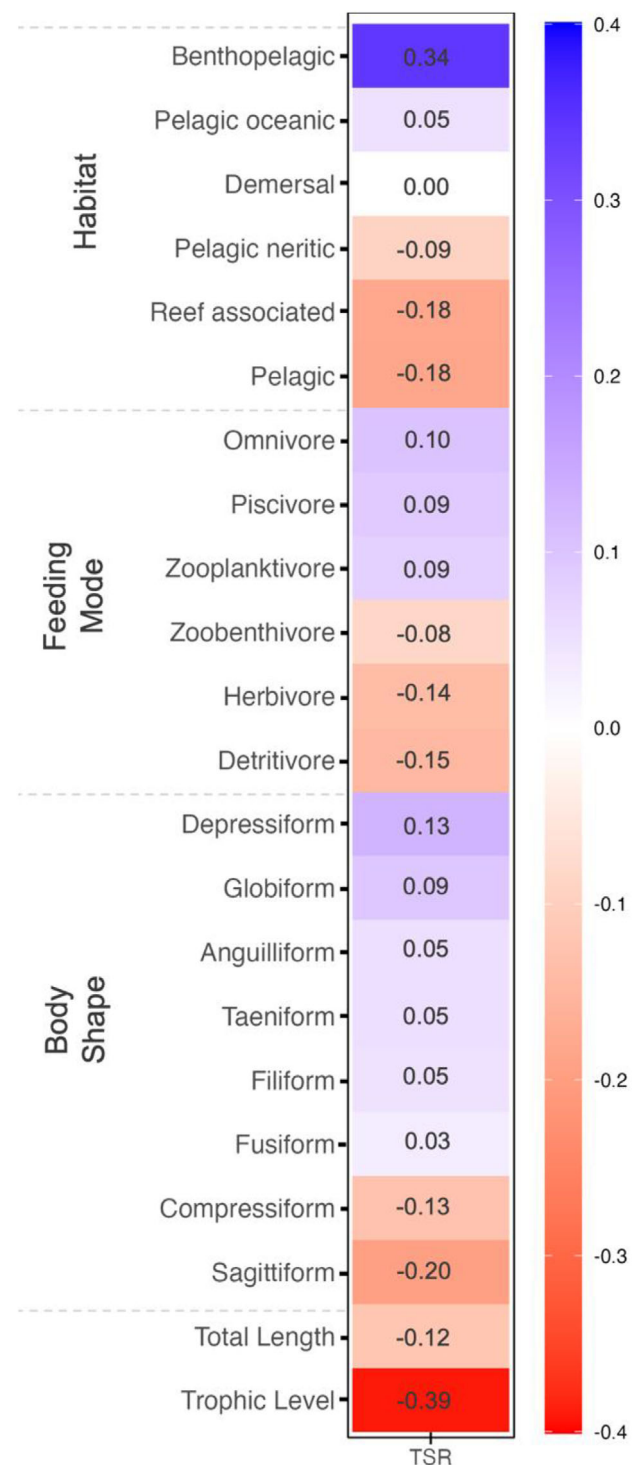


Figure 4. Relationships between fish functional traits and time-since-restoration (TSR) across restored sites ($n = 136$), based on fourth-corner analysis. The heatmap shows Pearson correlation coefficients between each trait and the species abundance-weighted mean TSR. Traits are grouped by category (habitat, feeding mode, body shape, and continuous traits: total length and trophic level), and ordered by strength of correlation within each category. Blue indicates positive correlations, red indicates negative correlations, and white indicates no relationship. Definitions of body shape traits are provided in Table S1.

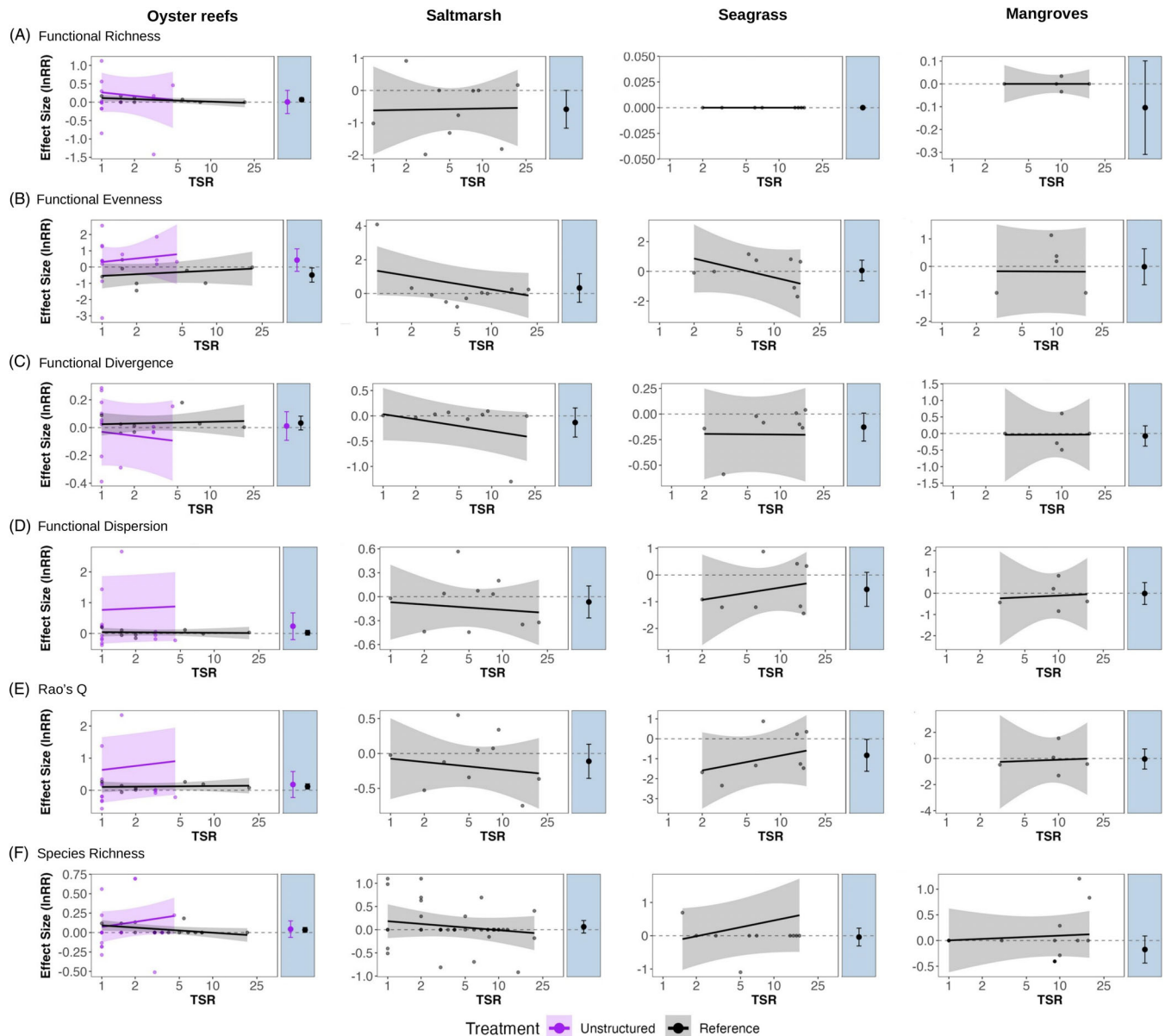


Figure 5. Decapod crustacean functional diversity. Linear trends in log response ratios as a function of time-since-restoration (TSR) and overall log response ratio means (shaded blue region of each panel). Error ribbons and bars are 95% CIs. Dashed horizontal lines at $y = 0$ reflect where restored sites are equal to reference/unstructured sites. No significant TSR trends were detected for decapods, and vertical lines are therefore not shown. See Figure S5 for Generalized Additive Models (GAM) outputs. (A) Functional richness. (B) Functional evenness. (C) Functional divergence. (D) Functional dispersion. (E) Rao's Q . (F) Species richness.

results complement their conclusions by demonstrating that restoration also recovers key functional attributes of associated animal communities. Broadly, these patterns of rapid functional equivalence and variable recovery trajectories map onto several of the recovery scenarios outlined in our conceptual framework. Immediate functional equivalence (scenario 2) was the most prevalent outcome, while progressive recovery reaching parity (scenario 3) was evident in saltmarsh and mangrove fish communities, where functional parity was achieved within 3–7 years. Rapid improvement relative to unstructured

baselines (scenario 1) was observed in oyster reefs. We considered all three of these scenarios to be an “ideal” outcome, and this variability by ecosystem type, response metric, taxonomic group, and TSR highlights the importance of considering ecosystem-specific and temporal variability when evaluating functional recovery.

The patterns of rapid functional recovery both contrast with, yet also complement, the slower taxonomic recovery trajectories documented in prior meta-analyses, where nekton abundance and richness on restored oyster reefs and saltmarshes often

continued accumulating over 8–13 years (Hollweg et al. 2020; Smith & Castorani 2023). The fact that functional equivalence can be achieved quickly, even where taxonomic composition is still shifting, suggests that the functional roles underpinning ecosystem processes may be reinstated before full species-level recovery is complete. This decoupling of functional and taxonomic recovery trajectories is consistent with the recognized disconnect between species richness and FD, where changes in one do not necessarily match changes in the other (Cadotte et al. 2011). From a restoration perspective, this result highlights the value of incorporating FD metrics alongside taxonomic measures when evaluating restoration success as taxonomic assessments alone may underestimate the degree to which ecological function has been recovered, particularly in the earlier stages of restoration.

Patterns of functional recovery differed among ecosystem types, likely reflecting contrasting modes of structural habitat development. In oyster reefs, the FD of fishes was similar between restored and reference sites, with little change over time and mean $\ln\text{RR}$ values consistently near zero. This pattern is consistent with scenario 2 of our conceptual framework, whereby restored sites achieve functional equivalence with reference habitats from early monitoring window rather than through gradual accumulation over time. These flat near-zero $\ln\text{RR}$ trajectories are indicative of immediate functional parity rather than a persistent functional deficit (scenario 7), supporting the interpretation of genuine equivalence rather than an artifact of insufficient statistical power. However, against unstructured baselines, FD_{Dis} and Rao's Q showed marginal positive trends with TSR, with restored sites becoming functionally richer than unstructured habitats after approximately 2.5 years. This result is more consistent with scenario 4 whereby functional gains over unstructured habitat continue to accrue as restored reefs mature. This two-scenario outcome is ecologically coherent: restored oyster reefs rapidly attain the functional characteristics of natural reference reefs, while simultaneously pulling further away from the functionally impoverished unstructured baseline. This pattern is consistent with Smith and Castorani (2023), who found that nekton abundance and richness on restored oyster reefs relative to unstructured habitats increased with reef age over an 8- to 9-year period, a temporal accumulation dynamic closely paralleling the scenario 4 trajectory, we observe here for fish FD. The rapid attainment of functional parity with reference sites likely reflects the immediate provision of complex three-dimensional structure inherent to oyster reef restoration, which typically involves deploying pre-formed materials (e.g. boulders and shells) that provide vertical relief, crevices, and heterogeneous surfaces from the outset (Humphries et al. 2011). These features immediately create a mosaic of microhabitats that offer shelter and feeding surfaces for fish, while simultaneously creating interstitial spaces that quickly support diverse decapod functional groups (Nestlerode et al. 2007; Grabowski et al. 2012). It should be noted, however, that this finding may be specific to restoration of oyster reefs into substrate-limited systems. In recruit-limited systems, or where alternative restoration approaches are used, functional recovery

trajectories may differ (Davenport et al. 2021; Smith & Castorani 2023).

In vegetated ecosystems such as mangroves and saltmarshes, a subset of FD metrics showed positive relationships with TSR, particularly for fish. In saltmarshes, FD_{Dis} and Rao's Q were initially lower in restored sites relative to reference sites and increased steadily with TSR, reaching parity approximately 3 years post-restoration. In mangroves, Rao's Q showed a significant positive TSR relationship, with restored sites reaching functional parity over a longer trajectory (7 years), while FD_{Div} showed a marginal positive trend. Notably, other FD metrics in both ecosystems remained statistically indistinguishable from reference sites throughout the monitoring window, suggesting that not all dimensions of FD follow the same recovery trajectory. Unlike the often structurally 'pre-assembled' oyster reef habitats, restoration in vegetated systems typically involves planting vegetation or modifying hydrology (Teutli-Hernández et al. 2019; Billah et al. 2022), meaning that critical features such as structural complexity, root systems, and canopy cover develop progressively over time (Bosire et al. 2008; Duarte et al. 2020). As these features mature, they alter habitat suitability for different functional groups, leading to gradual shifts in species composition, relative abundances and trait composition over time. The reestablishment of tidal connectivity and structural heterogeneity in saltmarshes, for example, creates microhabitats that facilitate colonization by species with diverse ecological strategies, while gradual vegetation regrowth in mangroves provide the refuge, nursery habitat, and foraging opportunities essential for supporting trait-diverse communities (Sheaves et al. 2015; Rezek et al. 2017). These patterns are most consistent with scenario 3 of our conceptual framework, which shows a progressive recovery over time trending toward parity with reference sites. The fact that several metrics reached or approached zero-crossing points suggests that fuller functional recovery in vegetated ecosystems may be achievable given sufficient time, although whether all metrics will ultimately reach equivalence remains uncertain given the temporal range of data currently available.

Decapod assemblages showed no significant temporal trends across any ecosystem type or metric, with functional composition remaining stable relative to both reference and unstructured baselines throughout the monitoring period. This pattern likely reflects the rapid colonization capacity of decapods (Pallas et al. 2006; Zhu et al. 2021) and their strong sensitivity to environmental features that are restored or available early, such as sediment type and shelter availability (Skilleter & Warren 2000; Pallas et al. 2006). The early availability of these key habitat features enables decapod communities to reestablish functional roles quickly and then stabilize, rather than showing gradual functional change with TSR that characterizes fish assemblages in vegetated systems. A similar pattern of rapid functional recovery driven by early colonization has been documented for crustaceans and other benthic invertebrates in restored ecosystems (Gagnon et al. 2023). For most ecosystems and metrics, mean $\ln\text{RR}$ values were statistically indistinguishable from zero, consistent with scenario 2, indicating early functional parity with reference sites established shortly after restoration. A

notable exception occurred in oyster reefs, where restored sites exhibited significantly higher mean $\ln\text{RR}$ than reference sites for FRic and Rao's Q . Rather than reflecting a deficit, this suggests that restored oyster reefs may in some cases support decapod assemblages that are functionally richer than reference reefs, likely a consequence of the dense interstitial habitat and high structural complexity provided by restoration materials, which concentrate diverse decapod functional groups beyond levels typical of natural reefs (Grabowski et al. 2012). Davenport et al. (2021) similarly found that restored oyster reefs more consistently enhanced nekton recruitment across taxonomic groups than natural reefs.

Together, the ecosystem- and taxon-specific patterns confirm that restoration does not follow a single functional recovery trajectory, and that the scenario framework provides a useful lens for identifying where and why deviations from the restoration goal occur. In relating patterns to the framework, we acknowledge the caution required in interpreting non-significant responses in $\ln\text{RR}$; these may not necessarily confirm ecological equivalence in data-limited ecosystems such as seagrass and mangroves, where wide CIs may reflect insufficient statistical power to detect real differences rather than actual functional parity. We return to this distinction in the [Limitations](#) section.

Trait-Based Mechanisms

Fourth-corner analyses offered a mechanistic view of the trait-level processes driving temporal patterns in fish FD. Among all fish traits assessed, only two showed notable associations with TSR. The relative abundance of benthopelagic species increased with TSR, suggesting that maturing habitats with increasing structural complexity progressively support species that exploit both benthic and pelagic zones. This pattern is consistent with the expectation that habitat structural development, such as vegetative growth, expands the range of available niches over time, facilitating the establishment of species with more generalized or mixed foraging strategies (Kitchingman et al. 2023; Ram et al. 2025). In contrast, trophic level showed a negative association with TSR, indicating a shift toward assemblages dominated by lower trophic level species, such as herbivores and detritivores, as restoration sites age. Rather than reflecting delayed arrival of higher trophic predators, this pattern may indicate increasing niche diversification as restored ecosystems mature, with expanding food and habitat opportunities favoring primary consumers (Lechêne et al. 2018; Soria-Barreto et al. 2023). Taken together, these trait-level shifts in fish mirror the progression of habitat structural development across restoration time, a connection that would benefit from more direct empirical investigation through concurrent monitoring of both structural and faunal attributes in future restoration studies.

Species Richness-Functional Diversity Relationships

Species richness was largely uncorrelated with most FD metrics, except for FRic . This pattern highlights an important distinction between metrics that capture the extent of trait space occupied (FRic) versus those that measure how species and their

abundances are distributed within that space (FDIs, evenness, divergence, and Rao's Q). The lack of correlation between species richness and abundance-weighted metrics indicates that changes in FD were primarily driven by shifts in species composition and relative abundances rather than increases in species number (Mason et al. 2005; Mouillot et al. 2013). In contrast, the coupling between species richness and FRic varied by taxon, where decapods exhibited stronger coupling ($r = 0.9$) than fish ($r = 0.7$), suggesting that FRic in decapod assemblages is more strongly driven by species accumulation. This result likely reflects the comparatively low functional differentiation among decapod species, combined with their rapid colonization capacity, facilitated by broad larval dispersal and relatively short generation periods (Sanvicente-Añorve et al. 2018). The weaker correlation in fish indicates that species additions or turnover sometimes involved functionally similar species, such that changes in species richness did not always translate proportionally into changes in FRic . These patterns highlight that the relationship between species richness and FD is neither universal nor straightforward, varying across both taxa and FD metrics (Mouchet et al. 2010). These findings confirm that species richness alone is an insufficient proxy for functional complexity in ecological communities, and that different FD metrics capture distinct aspects of community structure with different sensitivities to species turnover and abundance shifts (Villéger et al. 2008; Cadotte et al. 2011; Baker et al. 2021).

Limitations

While this study provides valuable insights into the functional recovery of fish and decapod communities in restored coastal habitats, several limitations deserve explicit acknowledgement. Data availability was uneven across ecosystem types, with mangrove and seagrass ecosystems notably lacking sufficient representation for certain metrics. This limited coverage constrains our ability to draw broad conclusions for these ecosystem types, and importantly, reported functional equivalence in these ecosystems should be interpreted with care. When sample sizes are small and CIs wide (e.g. in seagrass and mangroves), a non-significant $\ln\text{RR}$ does not necessarily confirm genuine ecological equivalence. It may instead reflect insufficient statistical power to detect actual differences. We thus cannot rule out meaningful functional differences in these systems where data representation was limited. Because $\ln\text{RR}$ standardizes differences across studies, our conclusions about functional equivalence should be interpreted as proportional convergence rather than equivalence in absolute functional trait space. For instance, communities with similar $\ln\text{RR}$ values may still differ in the size and structure of their trait space. Absolute functional values could therefore provide complementary insight into the recovery of functional roles.

TSR was the primary predictor we examined here; however, methodological and landscape-level factors, including restoration approach, restoration scale, and regional species pool composition likely contribute to the variation in outcomes observed across studies and highlight the complexity of design-dependent outcomes that a TSR-only analysis cannot fully capture. For

example, Davenport et al. (2021) demonstrated that reef characteristics such as size, vertical relief, and age can all influence nekton recruitment enhancement on restored oyster reefs in ways that vary by taxonomic group and tidal zone, underscoring that restoration design and physical context shape faunal outcomes beyond TSR alone. Many of these factors could not be systematically modeled in this study due to data paucity, consistent with constraints noted in Sievers et al. (2024) and the data limitations acknowledged above. Additionally, a considerable proportion of studies included in this analysis were conducted on time scales of less than 2 years, a pattern common across coastal restoration research more broadly (Bayraktarov et al. 2016). Short monitoring windows have been documented across multiple systems. For instance, mangrove restoration has a median post-restoration monitoring duration of 16 months, and seagrass restoration a median of 12 months, despite some individual studies extending far longer (van Katwijk et al. 2016; Gatt et al. 2022). Oyster reef studies show a similar pattern, with Smith and Castorani (2023) reported a median sampling time of just 1.5 years post-restoration. Davenport et al. (2021) similarly highlight significant data gaps beyond 6 years for subtidal reefs and beyond 8 years for intertidal reefs. The prevalence of short-term monitoring underscores the broader challenge of drawing long-term inference from existing oyster restoration studies and makes it difficult to assess whether early functional equivalence translates into sustained recovery over time. Future work should prioritize extended monitoring designs that reach well beyond a few years of post-restoration, and that capture a broader suite of contextual variables such as habitat structural complexity and connectivity.

The absence of raw species-level data in a number of studies meant they were excluded, potentially excluding ecologically relevant cases and narrowing the trait space represented. Similarly, formal publication bias diagnostics could not be conducted because variance estimates were unavailable for many individual effect sizes. These limitations highlight the need for greater data standardization and sharing in future restoration monitoring and output dissemination. Promising initiatives like the Mangrove Restoration Tracker Tool (Gatt et al. 2024) demonstrate how this gap can be addressed by supporting local practitioners with structured and standardized reporting frameworks, enabling practitioners to share information and learn from collective experiences. Enhanced data availability, both in terms of quantity and resolution, would also enable more rigorous investigation of additional determinants of FD outcomes, including restoration methodology, landscape-scale context, and broader seascape configuration across ecosystems.

In conclusion, our synthesis shows that coastal habitat restoration can support relatively rapid recovery of fish and decapod FD, with many restored systems showing early functional equivalence to reference habitats. However, recovery is not uniform across ecosystems, taxa or metrics, highlighting the need for ecosystem-specific expectations rather than assuming a single recovery trajectory. Collectively, these findings show the value of incorporating FD metrics alongside traditional taxonomic measures, offering a more direct window into the

ecological roles and processes that restoration aims to reinstate. As coastal restoration efforts continue to scale globally, understanding when and how functional equivalence is achieved will be essential for setting realistic targets, designing effective monitoring frameworks, and demonstrating the ecological returns of restoration investment.

Acknowledgments

MS was supported by an Australian Research Council (ARC) Discovery Early Career Researcher Award no. DE220100079. All authors declare no conflicts of interest. Data are available from the corresponding author upon reasonable request. Open access publishing facilitated by Griffith University, as part of the Wiley - Griffith University agreement via the Council of Australasian University Librarians.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Functional Traits for fish and decapod used in the analyses.

Table S2a. Mean ($\pm$ 95% CI) functional diversity responses for fish assemblages across ecosystems and treatments.

Table S2b. Mean ($\pm$ 95% CI) functional diversity responses for decapod assemblages across ecosystems and treatments.

Table S3a. Time-since-restoration (TSR) effects on functional diversity in fish assemblages across ecosystems.

Table S3b. Time-since-restoration (TSR) effects on functional diversity in decapod assemblages across ecosystems.

Figure S1. Summary of trait distributions for fish species ($n = 355$) recorded across study sites.

Figure S2. Summary of trait distributions for decapod species ($n = 136$) recorded across study sites.

Figure S3. Generalized Additive Models (GAMs) of fish log response ratios as a function of time-since-restoration (TSR) and overall log response ratio means.

Figure S4. Relationships between species richness and functional diversity (FD) metrics in fish communities across reference (red), restored (green), and unstructured (blue) sites.

Figure S5. Generalized Additive Models (GAMs) of decapod log response ratios as a function of time-since-restoration (TSR) and overall log response ratio means.

Figure S6. Relationships between species richness and functional diversity (FD) metrics in decapod communities across reference (red), restored (green), and unstructured (blue) sites.

Supplement S1. List of papers included in the meta-analysis.

Coordinating Editor: Valter Amaral

Received: 12 February, 2026; First decision: 25 March, 2026; Revised: 3 July, 2026; Accepted: 3 July, 2026