


# Scale dependence of environmental controls on the functional diversity of coral reef fish communities

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## Abstract

**Aim:** The functional composition of local assemblages is hypothesized to be controlled by hierarchical environmental filters, whereby the importance of different abiotic and biotic factors varies across both spatial scales and the different dimensions of functional diversity. We examine scale dependence in functional diversity–environment relationships with the ultimate aim of advancing models that predict the response of functional diversity to global change.

**Location:** Coral reefs surrounding 23 minimally disturbed central-western Pacific islands.

**Time period:** 2010–2015.

**Major taxa studied:** Coral reef fishes.

**Methods:** We surveyed 1,423 reef sites using a standardized monitoring protocol and classified the 547 taxa encountered based on traits related to resource use, body size and behaviour. For each fish community, we calculated species richness and three metrics of functional diversity: functional richness, functional redundancy and functional evenness. We then built nested models at three spatial scales to evaluate the predictive power of environmental conditions over each component of functional diversity.

**Results:** Climatic variables (e.g., primary productivity) and geomorphic context (e.g., bathymetric slope) were more important in predicting functional diversity at coarse spatial scales. In contrast, local measures of habitat quality, including benthic complexity, depth and hard coral cover, were generally most important at finer scales. All diversity metrics were better predicted at coarser scales, but which predictors were important varied among metrics.

**Main conclusions:** The observed scale dependence in environmental predictors of functional diversity generally matches models of hierarchical filters on functional community assembly. Contrary to expectation, however, functional evenness and functional redundancy, which incorporate information on biomass distributions, were not better predicted at finer spatial scales. Instead, broad-scale variation in environmental variables was most important in predicting all components of functional diversity. Furthermore, the distinct responses of each functional diversity metric to environmental variation indicate that each measures a unique dimension of reef-fish diversity, and environmental change may affect each differently.

## KEYWORDS

climate, ecosystem function, environmental gradient, functional evenness, functional redundancy, functional richness, habitat complexity, macroecology, species richness

## 1 | INTRODUCTION

Given continued declines in global biodiversity, interest in understanding how changes in biodiversity alter ecosystem processes and functions remains strong (Cardinale et al., 2012). Trait-based approaches to biodiversity measurement (i.e., functional diversity) may help to predict biodiversity responses to environmental change because species' traits mediate their resource and habitat requirements. Furthermore, functional diversity may be a better predictor of ecosystem function than taxonomically based measures of diversity because species' traits relate more directly to their function within a community than their taxonomic identity (Díaz & Cabido, 2001). Although functional diversity is increasingly recognized as a useful tool to study biodiversity, understanding the processes that determine the functional diversity of ecological communities remains a core challenge within community ecology (de Bello et al., 2013; Grime, 2006; McGill, Enquist, Weiher, & Westoby, 2006).

The functional diversity of a given community may be shaped by a combination of stochastic, dispersal and environmental factors, each of which may manifest at different scales (Keddy, 1992; McGill, 2010). Specifically, environmental conditions may act as hierarchical filters that serve to reduce the possible trait values present in a given community (de Bello et al., 2013; Sydenham, Moe, Totland, & Eldegard, 2015). Which environmental factor predominates in controlling diversity is likely to vary with scale (Cavender-Bares, Kozak, Fine, & Kembel, 2009). Factors that vary at larger spatial scales (e.g., climate) and affect diversity by filtering out species with unsuitable traits may be more prominent regionally, whereas factors that mediate biotic interactions (e.g., habitat complexity) and dispersal are thought primarily to matter locally (Cavender-Bares et al., 2009; de Bello et al., 2013; Hillebrand, Bennett, & Cadotte, 2008; Wiens, 1989). Thus, multiscale studies evaluating environment–diversity links are necessary to understand fully the processes regulating the functional diversity of ecological communities and predict responses under global change.

Furthermore, because functional diversity comprises several distinct dimensions, the relative importance of environmental controls and relevant spatial scale also may vary depending on which component is considered (Mouchet, Villéger, Mason, & Mouillot, 2010). Functional richness measures the total amount of trait variation in a community, and so it is expected to be related positively to species richness. Functional richness, therefore, may respond primarily to environmental filters at large spatial scales that control the presence or absence of trait values (i.e., species) in a community, such as broad-scale temperature regimes controlling requirements for thermal tolerance (Díaz, Cabido, & Casanoves, 1998; Grime, 2006). Functional redundancy measures the overlap in trait space amongst species or abundance; hence, it may be particularly sensitive to local-scale factors that facilitate coexistence or control the degree of competition amongst functionally similar individuals (Pillar et al., 2013). Functional evenness quantifies how evenly abundance or biomass is distributed across trait space and, therefore, is also expected to be most responsive to local-scale factors that control the dominance of certain (types

of) species (de Bello et al., 2013). Understanding how each component of functional diversity responds to environmental variation is crucial to predict the impacts of environmental change on biodiversity and overall ecosystem function.

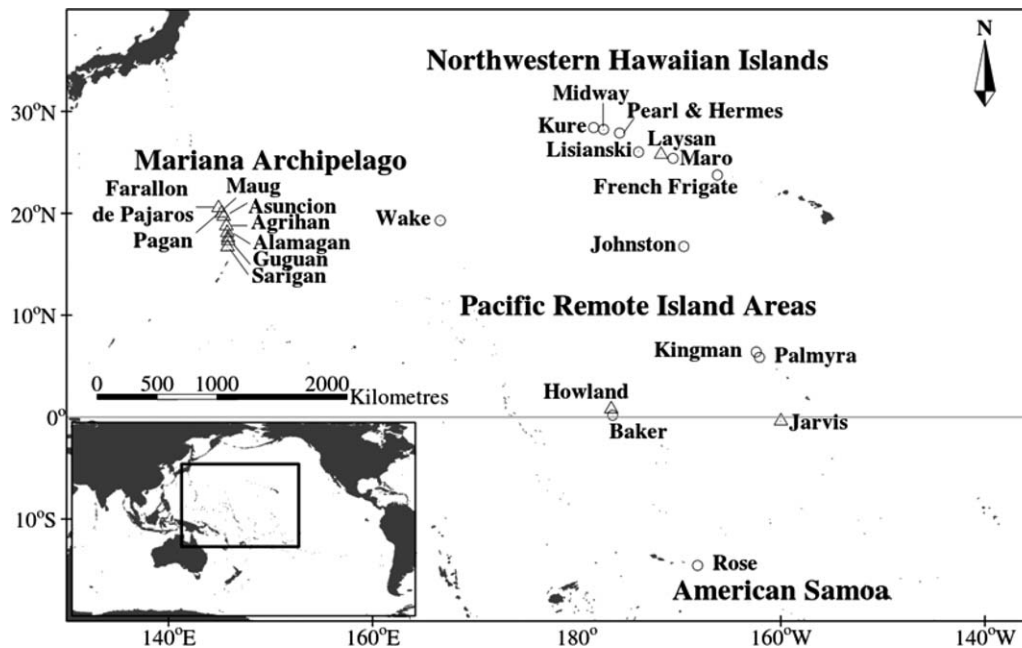
Consequently, we examined the extent to which different environmental factors predicted species richness and three dimensions of functional diversity (richness, redundancy and evenness) across multiple spatial scales (site, reef and island), using reef fishes as a model system. We expected to see greater variance and greater predictive power for richness-based measures of diversity (i.e., species richness and functional richness) at coarser spatial scales, and with environmental variables most related to climatic gradients or large-scale habitat complexity (e.g., temperature and bathymetric slope). Conversely, we hypothesized that biomass-weighted measures of functional diversity (functional redundancy and functional evenness) would be more sensitive to those environmental factors mediating biotic interactions (e.g., benthic complexity) or environmental energy (e.g., net primary productivity) and would be more variable and better predicted at finer spatial scales. Our study system comprised fish assemblages from near-pristine coral reefs spanning the central-western Pacific Ocean. Previous work on coral reef fish communities has found declines in species and functional richness in response to human disturbance (Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016; Halpern & Floeter, 2008; Micheli et al., 2014), although most studies focused on ecosystems with long histories of human degradation (Knowlton & Jackson, 2008). Importantly, our study provides a rare opportunity to examine scale-dependent controls over biodiversity in high-diversity ecosystems without the confounding effects of local human disturbance.

## 2 | METHODS

### 2.1 | Study location and survey data

This study centres on 23 Pacific islands, atolls and banks (hereafter islands; Figure 1), which span a wide range of oceanographic and environmental conditions (Supporting Information Appendix S1; Gove et al., 2016). The islands were surveyed from 2010 to 2015 by the U.S. National Atmospheric and Oceanographic Administration's Coral Reef Ecosystem Program and are part of one of the Pacific's largest standardized coral reef monitoring programmes (Coral Reef Ecosystem Program & Pacific Islands Fisheries Science Center, 2015). We focused our analysis on islands with minimal human disturbance (following the classification 'remote' given by Williams et al., 2011), in order to quantify the relationships between functional diversity and environmental variables without this potentially confounding factor. Briefly, an island was considered minimally disturbed if the level of human impact was extremely low to negligible based on local human population densities and distance to larger population centres (< 50 people within 100 km) and management status (e.g., no-take marine reserves).

The survey data consist of observations of individual fish made during underwater visual censuses by a small team of highly experienced scientific divers. Each island was surveyed biennially at randomized locations within hard-bottom reef habitat using a modified



**FIGURE 1** Location of 23 islands surveyed for coral reef fish communities across the central-western Pacific Ocean: islands ( $\Delta$ ) and atolls ( $\circ$ )

stationary point count method (Coral Reef Ecosystem Program & Pacific Islands Fisheries Science Center, 2015). On each dive, two scientific divers laid out a 30 m transect along the benthos, with each diver responsible for observing a non-overlapping 15-m-diameter cylinder along the transect. After a 5-min window during which a cylinder-specific species list was created, the survey divers recorded the abundance and estimated body length (total length) of all fishes within their cylinders. We constrained our study to include only surveys conducted within fore-reef habitat ( $n = 1,423$  sites), to limit differences in fish diversity amongst sites driven by habitat turnover. Furthermore, the behaviour of highly mobile sharks and jacks (Families Carcharhinidae and Carangidae) may in some locations be affected by diver presence, potentially biasing abundance estimates from underwater visual surveys (Richards, Williams, Nadon, & Zgliczynski, 2011). We therefore excluded these taxa from our analysis.

## 2.2 | Survey data treatment

We considered reef fish communities at three spatial scales: site, reef and island. We defined a site as the community of fishes sampled by a pair of divers during a single dive, consistent with the scale at which reef communities are typically surveyed and the scale at which fishes may respond to fine-scale benthic habitat features. We calculated reef-scale metrics by aggregating all survey sites on a 6 km  $\times$  6 km grid. This scale encompasses typical home range sizes of medium-bodied reef fishes (Green et al., 2015), and thus may better represent the scale at which fish respond to their environment at intermediate time scales. An island-scale observation was considered to be the aggregation of all sites on a given island in a given year into a single community, relating to the upper bound of a relatively contiguous reef system and encompassing from one to 12 'reefs' per island. We rarefied data at all three

scales using a Monte Carlo-based resampling technique with 1,000 random draws in order to control for the effects of bias associated with unequal sampling effort (detailed methods in Supporting Information Appendix S2, Figure S2.1–9; Walker, Poos, & Jackson, 2008). We rarefied site-scale data to  $n = 200$  individual fish/survey (henceforth 200n) because this allowed us to retain the majority of the sites in our analysis ( $n = 1,143/1,423$  sites), while still including enough fish to reduce the sensitivity of the diversity estimate to sample size; rarefactions with  $n = 500$  yielded comparable results (Supporting Information Appendix S2). Reef- and island-scale data were also rarefied to 200n for comparison with site-scale data. However, because rarefied metrics at these scales showed some sensitivity to sample size at 200n (Supporting Information Appendix S2), we also rarefied reef and island-scale metrics to  $n = 1,000$  fish/reef or island. All species richness and functional diversity measures reported in the remainder of the manuscript represent rarefied metrics.

## 2.3 | Functional traits data

Each coral reef fish species identified in the survey data was functionally classified based upon traits that relate to resource use or that mediate functional impact within the ecosystem (Table 1; Supporting Information Appendix S3). Following Green, Bellwood, and Choat (2009), resource use was categorized as a hierarchical classification of diet. Each species was assigned a fine-scale feeding group representing characteristics of prey type and feeding behaviour (e.g., scraper versus grazer, time of feeding activity, foraging microhabitat) nested within a coarser-scale trophic class. Functional impact categorization reflected schooling behaviour and body size. Following Kulbicki et al. (2011), each species was assigned to an ordinal schooling category ranging

TABLE 1 Functional traits used to estimate the functional diversity of Pacific coral reef fishes

Trait category	Trait	Trait levels	Variable type
Resource use	Coarse feeding group	Herbivore (HE), detritivore (DE), carnivore (CA), planktivore (PL), omnivore (OM)	Categorical
	Fine feeding group	HE: macro-algal browser, turf algal cropper, scraper, excavator; DE: detritivore; CA: diurnal piscivore, nocturnal piscivore, invertivore, corallivore, ectoparasite feeder, generalist; PL: diurnal planktivore, nocturnal planktivore; OM: benthic omnivore, pelagic omnivore	Categorical
Functional impact	Body size	Range = 2.9–800 cm, median = 55 cm	Ordered
	Schooling behaviour	1 (solitary), 2 (pairs), 3 (small groups up to 20), 4 (schools of 20–50), 5 (schools > 50)	Ordered

Note. Detailed descriptions of the functional trait categories, our species classification methodology and a full list of species' classifications are in the Supporting Information as Appendix S2.

from one to five. Body size was estimated as maximal total length for each species from FishBase (Froese & Pauly, 2014).

## 2.4 | Diversity metrics

For the rarefied communities at each site, reef and island, we quantified species richness (species count) and three distinct dimensions of functional diversity using continuous indices that accommodate both continuous and categorical traits (Supporting Information Appendix S4). As opposed to fixed functional groups, continuous indices retain information about the degree of similarity amongst species with different trait values (Villéger, Mason, & Moullot, 2008). To quantify functional richness, we computed Total\_MST (Moulton & Pimm, 1987); this metric is based on presence–absence data, and varies in value between zero and the number of species present less one. We chose to use Total\_MST as our measure of functional richness as opposed to other available indices because it does not suffer common limitations, such as requiring continuous data or imposing a hierarchical structure on the trait data. For functional redundancy, we computed *R* (Ricotta et al., 2016), which takes abundance or biomass into account and ranges from zero, when species show no functional overlap, to one, when all species in a community have identical trait values. For functional evenness, we computed FEve (Villéger et al., 2008), a minimum spanning tree (MST)-based metric that also varies from zero to one, with a value of one corresponding to a completely even distribution of abundance or biomass across trait space. Like *R*, FEve can take abundance or biomass into account (Supporting Information Appendix S4). We weighted *R* and FEve using biomass (instead of number of individuals) to best reflect the functional (versus demographic) response of the community to environmental variation (Villéger et al., 2008). The biomass for each species at each site, reef or island was estimated based on the observed body length of individuals counted during surveys and length–weight regressions compiled from published and Web-based sources (Froese & Pauly, 2014; Kulbicki, Guillemot, & Amand, 2005). We calculated species dissimilarity based on Gower distances (Podani, 1999) and for FEve computed average values for multiple equally parsimonious MST solutions to reduce sensitivity to species order (Supporting Information Appendix S4).

## 2.5 | Environmental variables

We selected nine environmental variables (Table 2; Supporting Information Appendix S5) that have been shown to affect reef fish species richness and community structure (Mellin, Bradshaw, Meekan, & Caley, 2010). These variables have previously been hypothesized to represent important controls on (taxonomic) diversity (Currie et al., 2004; Gaston, 2000) via effects on niche complexity, environmental energy, environmental stress, dispersal and the regional species pool (specific hypothesized effects of each environmental variable are provided in Supporting Information Appendix S5).

## 2.6 | Statistical analysis

Focusing on the survey data rarefied to 200n, we first used Pearson correlations to explore how the three functional diversity metrics related to species richness and to one another at each scale. Furthermore, we compared the mean and coefficient of variation of observed values across scales to examine at which scale each metric was most variable.

We next quantified how species richness and functional diversity metrics were predicted by environmental variables. All predictor variables were centred, and continuous variables were standardized before analysis (Schielzeth, 2010). Eighteen survey sites (of 1,143) were excluded from the site-scale analyses because of missing data for benthic complexity. At the site scale, we used mixed-effects models (setting random intercepts by island) to test the effects of all environmental variables on each diversity metric using the function *lmer* from the *lme4* package (Bates, Maechler, Bolker, & Walker, 2015) in R (R Development Core Team, 2015). Additionally, we compared the random-intercept mixed-effects model with one where slopes were also allowed to vary among islands for environmental variables that varied within islands (Supporting Information Appendix S6). Finally, because some environmental variables had low intra-island variability relative to inter-island variability, and treating island as a random effect would reduce the apparent effect of these variables, we also ran multiple linear regression models without the random effect of island using the *lm* function in R.

At the reef scale, we aggregated site-scale estimates of environmental variables and regressed these upon reef-scale diversity metrics

TABLE 2 Descriptions of covariates used in analyses of effects of environmental variables on functional diversity

Environmental covariate	Range in observed values (mean $\pm$ SD)	Data type	Variable description
Bathymetric slope ( $^{\circ}$ )	0.0–31.8 (10.7 $\pm$ 6.5)	Continuous	Slope of the bottom based on a global elevation model of the seafloor
Benthic complexity (m)	0.12–2.09 (0.62 $\pm$ 0.24)	Continuous	Mean substrate height, in situ site-scale complexity measurement
Biogeographical province	Hawaiian versus Central Pacific	Categorical	Biogeographical regions for reef fishes delineated based on reef fish community composition
Depth (m)	1.7–29.1 (14.6 $\pm$ 7.0)	Continuous	Depth of the water column
Geological type	Island versus atoll	Categorical	Primary geological make-up of the island
Hard coral cover (% cover)	0–70.8 (23.8 $\pm$ 15.6)	Continuous	Live Scleractinian coral cover, measured in situ
Net primary productivity (NPP; mg C m <sup>-2</sup> day <sup>-1</sup> )	263.5–995.1 day <sup>-1</sup> (541 $\pm$ 252)	Continuous	Inter-annual mean NPP (water column) 2003–2013 to characterize the long-term climatic average for a site
Reef area (km <sup>2</sup> )	1.8–1,653.0 km <sup>2</sup> (86.5 $\pm$ 232.2)	Continuous	Total amount of reef area within a 75 km radius of each survey site
Sea surface temperature (SST; $^{\circ}$ C)	18.6–26.6 (25.7 $\pm$ 1.8)	Continuous	Mean annual minimal SST 1982–2009 to characterize the long-term climatic average for a site

Full details of the data sources and methods for processing covariates is provided in the Supporting Information as Appendix S7.

(rarefied to 1,000n) using multiple linear regression. At the island scale, we again aggregated site-scale estimates of environmental variables for each island, then regressed these against the annual estimates of diversity metrics for each island (rarefied to 1,000n), while treating survey year as a random intercept.

Given a tight, curvilinear relationship between species richness and functional richness, environment–diversity models at each scale with functional richness as the response were repeated with  $\log_{10}$ -transformed species richness included among the predictors (Supporting Information Appendix S7). These models aimed to elucidate whether there was additional environmental control on functional richness beyond that mediated through changes in species richness.

For all models at each scale, we quantified explanatory power using the generalizable ‘variance explained’ derivation of  $R^2$  described by Nakagawa and Schielzeth (2013) and extended to models with random slopes by Johnson (2014) using the `r.squaredGLMM` function in the `MuMIn` package (Barton, 2015) in R, which can be decomposed into conditional ( $R^2_c$ ; variance explained by random effects plus fixed effects) and marginal ( $R^2_m$ ; fixed effects only) components when applied to mixed-effects models. We evaluated predictive power using cross-validated (leave-one-out) coefficients of determination ( $R^2_{cv}$ ; Arlot & Celisse, 2010). To make sure that differences in predictive power across scales were not an artefact of sample size (in terms of number of individuals sampled to which the metric was rarefied or number of environmental observations used to estimate local conditions) or overfitting (given the lower number of reefs and islands relative to sites), we also calculated bootstrapped ( $n = 100$  random draws)  $R^2_{cv}$  values based on the functional diversity metrics rarefied to 200n using one randomly selected observation for each environmental variable for each site, reef or island for  $n = 62$  observations (i.e., the lowest number of observations across scales). The number of sites or reefs drawn from an island were selected in proportion to the number available for each island–year combination.

We used an information theoretical approach based on multimodel inference to evaluate the relative importance of environmental variables at each scale (Burnham & Anderson, 2002). We examined models with all possible subsets of our explanatory variables using the function `dredge` in the `MuMIn` package in R. For the site-scale analyses, we used models including the random intercept by island. Following Cade (2015), we used weighted means of the absolute value of  $t$ -statistics across all subset models to assess variable importance. The  $t$ -statistic can be used as a measure of effect size within models because it is the parameter estimate divided by the standard error, with the strongest predictor in each model having the largest absolute value of the  $t$ -statistic. Model-specific statistics are multiplied by the corresponding model probability and then summed across subset models. In this way, the variables that were most important in predicting the given response (i.e., had the strongest effects in the more probable models) had the largest weighted mean  $t$ -statistics.

Finally, to determine whether the identity of the species traits included affected the observed environment–diversity relationships, we recalculated the importance of environmental variables in predicting functional diversity metrics using functional diversity metrics calculated with all possible subsets of three traits (to compare with those calculated with all four traits; Supporting Information Appendix S8). All code for statistical modelling is provided in Supporting Information Appendix S9.

### 3 | RESULTS

#### 3.1 | Diversity across scales

In total, 2,051,051 individual fishes were surveyed, representing 498 species and 49 taxa identified to genus or family only (hereafter collectively referred to as species; Supporting Information Table S3.1; Appendix S3). Rarefied species and rarefied functional richness both increased

**TABLE 3** Summary [mean and coefficient of variation (CV)] and model fit [explanatory ( $R^2$ ) and predictive ( $R^2_{cv}$ ) power] statistics of four diversity metrics across three spatial scales

Diversity metric	Site-scale analysis ( $n = 1,126$ sites at 200n)		Reef-scale analysis ( $n = 102$ at 200n, $n = 88$ at 1,000n)		Island year-scale analysis ( $n = 62$ at 200n, $n = 60$ at 1,000n)						
	Mean (CV), 200n	Full mixed-effects model, random intercept $R^2_c$ ( $R^2_m$ ), 200n	Full linear model $R^2$ , 200n	$R^2_{cv}$ , 200n	Full linear model $R^2$ , 1,000n	Full mixed-effects model, random intercept $R^2_c$ ( $R^2_m$ ), 1,000n					
Species richness	26.87 (0.36)	.48 (.19)	.41	.40	.56	.48	.27	41.54 (0.25)	.63 (.63)	.63	$R^2_{cv}$ 62 islyrs 200n, 1 env. obs./islyr
Functional richness	4.70 (0.26)	.51 (.21)	.42	.41	.60	.52	.33	5.78 (0.17)	.69 (.69)	.69	
Functional redundancy	0.45 (0.11)	.16 (.13)	.13	.11	.49	.40	.34	0.46 (0.06)	.70 (.65)	.58	
Functional evenness	0.34 (0.17)	.24 (.12)	.17	.15	.45	.27	-.01	0.30 (0.10)	.42 (.35)	.35	

env. obs. = environmental observation; islyr = island-year;  $n$  = number of observations;  $N$  = number of fish for rarefaction;  $R^2_c$  = conditional  $R^2$ ;  $R^2_m$  = marginal  $R^2$ . Note. At each scale, the cross-validated leave-one-out  $R^2_{cv}$  was calculated for the whole data set, as well as bootstrapped  $R^2_{cv}$  calculated based on data rarefied to 200n (individual fish) and resampled to the same number of observations across scales ( $n = 62$ ) to control for sample size and overfitting. Negative  $R^2_{cv}$  values may indicate overfitting, where model predictions for excluded data points performed poorer than using the mean value of the data.

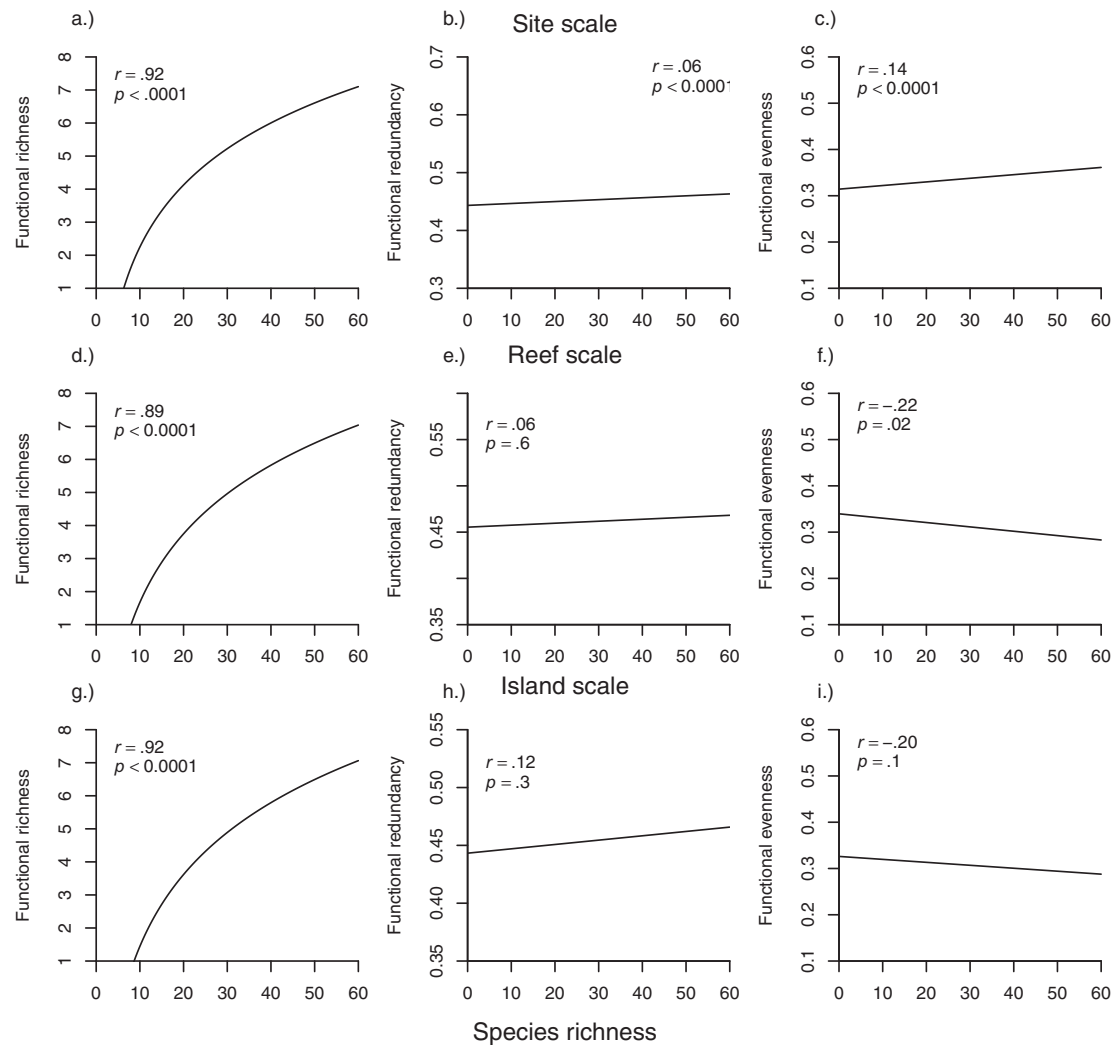
with spatial scale, but contrary to expectation these metrics were most variable at the site scale and least variable at the intermediate reef scale (Table 3). The mean value and variability of rarefied functional redundancy was similar across scales. In contrast, mean rarefied functional evenness decreased with increasing spatial scale; as expected, this metric also showed decreasing variability with increasing spatial scale.

The relationship between species richness and functional diversity varied substantially among the diversity metrics and across spatial scales. Functional richness exhibited a strong, positive correlation with  $\log_{10}$ -transformed species richness at all three spatial scales (Figure 2a, d, g), as expected. Functional redundancy showed a weak, positive correlation with untransformed species richness at the site scale, but the correlation was non-significant at both the reef and island scales (Figure 2b, e, h). Functional evenness showed a weak, positive relationship to species richness at the site scale, but showed weak, negative correlations with species richness at the reef and island scales (Figure 2c, f, i).

Relationships amongst the functional diversity metrics also varied across scales, although all were either weak or non-significant. Functional redundancy was not related to functional richness at any of the three scales (Figure 3a, d, g). In contrast, functional evenness showed a weak, positive correlation with functional richness at the site scale (Figure 3b), but showed non-significant negative correlations with functional richness at the reef and island scale (Figure 3e, h). Functional redundancy and functional evenness showed weak, negative relationships at the site and reef scales, but were unrelated at the island scale (Figure 3c, f, i).

### 3.2 | Scale dependence in predictability of diversity

For species richness, functional richness and functional redundancy, the explanatory power of environmental variables ( $R^2$  for linear models or  $R^2_m$  for mixed-effects models) was highest at the island scale and lowest at the site scale; explanatory power of functional evenness was similar at the reef and island scales (Table 3). The pattern of lower explanatory power at the site scale was especially true when considering  $R^2_m$  values of mixed-effects models, which assessed the variation explained by environmental variables after controlling for random effects. These low  $R^2_m$  values at the site scale may be somewhat misleading, however, because inter-island variation for some environmental variables [e.g., sea surface temperature (SST) or net primary productivity (NPP)] was high relative to intra-island variation and thus their true effects may have been masked by including island as a random effect. Furthermore, the  $R^2$  values for the linear models were similar to the  $R^2_c$  values for mixed-effects models with random intercepts, suggesting that the environmental variables we measured were good at capturing island-to-island differences in site-scale diversity metrics. Additionally, explanatory power ( $R^2_m$ ) was higher for more complex mixed-effects models including random slopes than for the random-intercept-only models, indicating that the effects of environmental variables on diversity may vary among islands (Supporting Information Appendix S6). When comparing across diversity metrics, the explanatory power of the models at the site and reef scales was highest for functional richness and species richness. At the island scale, it was highest for functional redundancy (Table 3).



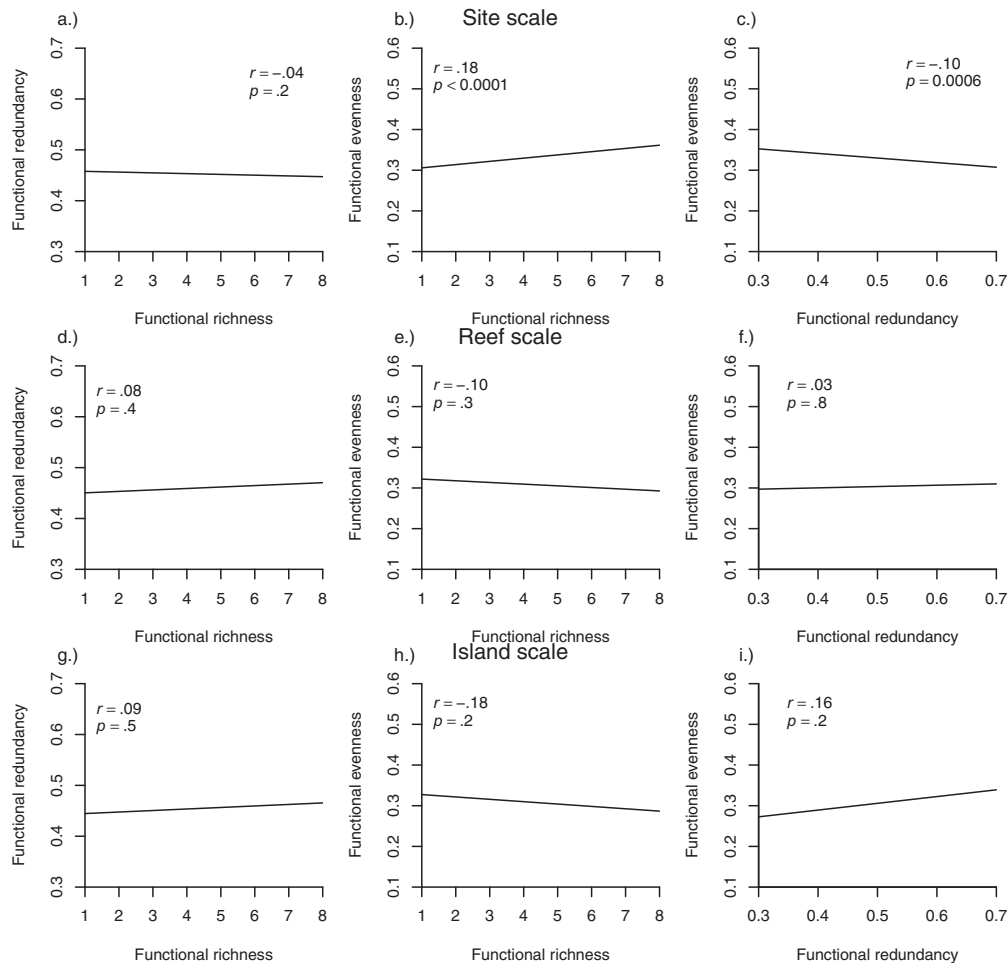
**FIGURE 2** Relationships between rarefied (to 200 fish/location) species richness and functional diversity metrics for Pacific coral reef fish communities at site (a–c), reef (d–f), and island (g–i) scales. Correlation coefficient ( $R$ ) and  $p$ -values are from Pearson correlations between each pair of variables. Correlation between species richness and functional richness at the site scale was run with  $\log_{10}$ -transformed species richness, but then back-transformed to plot the relationship between untransformed data

Controlling for sample size and overfitting (models with metrics rarefied to 200n, one environmental data point per observation, and bootstrapped to 62 observations across scales), predictive power ( $R_{CV}^2$ ) was highest at the island scale for species richness, functional richness and functional redundancy. For functional evenness, the predictive power was very low across scales. Additionally, for functional evenness at the coarser scales, 200n may not have sufficed to characterize functional evenness (Supporting Information Appendix S2), and the predictability of functional evenness was higher at the reef and island scale when rarefactions used 1,000n.

### 3.3 | Environmental predictors of diversity

The importance of environmental variables in predicting diversity varied depending on the diversity metric and spatial scale (Figure 4). For species and functional richness, each environmental variable, except SST, correlated with diversity at at least one spatial scale. At the site

scale, the most important predictors included depth and NPP, which had negative effects on both richness metrics, and benthic complexity and reef area, which had positive effects (Figure 4a–f). The importance of NPP increased at the two coarser scales, whereas depth and benthic complexity became unimportant in predicting either richness metric (Figure 4a–f). At the reef and island scales, species richness and functional richness declined with bathymetric slope and hard coral cover, increased with reef area, and were lower in the Hawaiian province and on islands when compared with atolls (Figure 4a–f). When species richness was included as a covariate in models of functional richness,  $\log_{10}$ -transformed species richness was by the far the most important predictor of functional richness across scales (Supporting Information Appendix S7, Figure S7.1). However, there was also a weak positive effect of SST on functional richness, as well as a negative effect of NPP at coarser scales. Moreover, functional richness declined faster with depth at the site scale and was lower on islands than atolls at the island scale than predicted by species richness alone.



**FIGURE 3** Pairwise relationships among rarefied (to 200 fish/location) functional diversity metrics of Pacific coral reef fish communities at site (a-c), reef (d-f), and island (g-i) scales. Correlation coefficient ( $R$ ) and  $p$ -values are from Pearson correlations between each pair of variables

For functional redundancy, SST was the most important predictor at the site scale, with functional redundancy declining with increasing SST (Figure 4g). Functional redundancy also declined with hard coral cover and increased with reef area and was higher on islands than atolls. At the reef scale, functional redundancy was positively related to NPP and negatively related to bathymetric slope (Figure 4h). Functional redundancy was also positively related to NPP at the island scale, as well as benthic complexity and depth, whereas SST had a negative effect (Figure 4i).

Functional evenness increased with hard coral cover at the site and reef scales and was higher in the Hawaiian province at these scales. Similar to other metrics, functional evenness also declined with depth at the site and reef scales. At the island scale, functional evenness increased with reef area and was higher on islands than atolls.

### 3.4 | Trait sensitivity

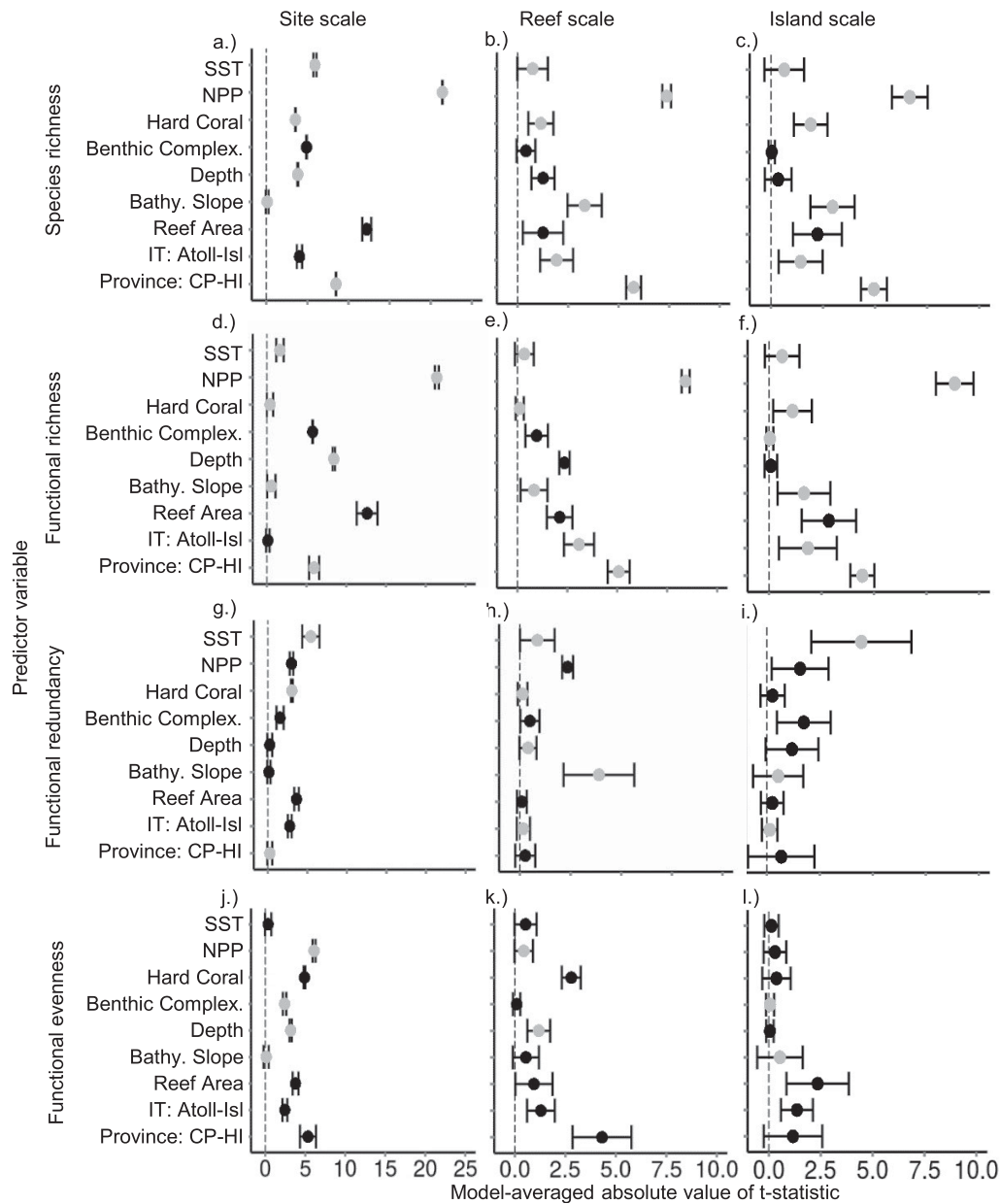
The importance of environmental variables in predicting functional richness was not highly dependent on the traits included, as the same sets of variables were generally important across models (Supporting

Information Figure S8.1). The negative effect of SST on functional redundancy was reduced whenever coarse-scale feeding group was excluded, suggesting that lower redundancy along this trait axis was important in driving lower overall functional redundancy at warmer sites and islands. The positive effect of NPP on functional redundancy at the island scale was reduced when either of the trophic traits was excluded, suggesting that redundancy in coarse- and fine-scale feeding groups drove the pattern in the four-trait model. For functional evenness, schooling behaviour and body size were important in driving effects of reef area and island type on functional evenness at the site scale. Coarse-scale feeding group and body size were important in driving the higher observed evenness in the Hawaiian province at the reef scale. Functional evenness was poorly predicted by environmental variables at the reef and island scales, however, in both the four-trait models and the reduced trait models.

## 4 | DISCUSSION

In concordance with hierarchical models of community assembly (McGill, 2010; Sydenham et al., 2015), we found evidence of scale





**FIGURE 4** Model-averaged absolute value of the  $t$ -statistics ( $\pm$  SD) for effects of environmental covariates on rarefied species richness (a-c), functional richness (d-f), functional redundancy (g-i), and functional evenness (j-l) across three spatial scales. Black dots represent weighted  $t$ -statistics of variables with positive influence on the response; grey dots indicate variables with negative influence. Bathym. = Bathymetric; CP = Central Pacific; Complex. = Complexity; HI = Hawaiian; IT = island type; NPP = net primary productivity; SST = sea surface temperature

dependence in the importance of environmental variables shaping the functional diversity of coral reef fish. Specifically, climatic factors and geomorphic context were more important in predicting functional diversity at coarser scales, whereas fine-scale measures of habitat quality (e.g., benthic complexity, depth, hard coral cover) were typically most important at smaller scales. These scale-dependent patterns suggest that both environmental filtering at large scales and biotic interactions at smaller scales are likely to shape the functional diversity of local reef fish communities.

Contrary to our predictions, however, all diversity metrics (with the possible exception functional evenness) were better predicted by the suite of environmental variables considered at the coarsest (island)

spatial scale. This greater predictive power at coarse scales met our expectation for the richness-related variables but not functional redundancy and evenness, which we hypothesized should respond at smaller scales given the importance of biotic interactions in mediating the relative biomass of individuals across functional space. Recent work on hierarchical filtering in bee assemblages likewise found that broad-scale climatic and landscape filters generally had a larger effect on functional community composition than local filters (Sydenham et al., 2015). Likewise, it has been suggested that broad-scale processes controlling larval dispersal to given reefs are stronger controls of reef community structure than local-scale processes that occur post-settlement (Sale, 2004). Another possible explanation for our counterintuitive results is

that our site-scale measurements represented too small a snapshot to characterize a reef community accurately, although presumably this is the scale at which individuals interact with fine-scale habitat features.

#### 4.1 | Environmental controls on diversity across scales

Across scales, climatic gradients in oceanic productivity emerged as one of the most important drivers of species richness, functional richness and functional redundancy. Contrary to the generally positive relationship between 'environmental energy' and species diversity observed at large spatial scales (Gaston, 2000), we found a negative relationship between NPP and richness diversity metrics. One explanation for this unexpected result is that the positive productivity–richness relationship observed at larger spatial scales is often attributed to increases in beta diversity with productivity (Steiner & Leibold, 2004), and by focusing on fore-reef sites only, we attempted to limit habitat heterogeneity across locations. Furthermore, benthic (versus water-column) productivity may represent a more relevant energy source pool for many reef fishes, and the observed negative relationship between depth and functional richness may be driven in part by lower benthic productivity at deeper reefs (Klump & McKinnon, 1989).

Surprisingly, SST was not an important predictor of functional richness or evenness, contrary to general expectations for species richness and functional diversity (Currie et al., 2004; McGill et al., 2006). In contrast, other studies on plant communities have found positive relationships between temperature and functional richness and negative effects of temperature on functional evenness (de Bello et al., 2013; Diaz et al., 1998). The negative relationship between SST and functional redundancy may indicate that cooler SSTs act as an environmental filter generally favouring species with similar traits. In our study, however, it was difficult to disentangle SST from biogeographical province completely, because the Hawaiian province experiences lower mean SST than the Central Pacific (mean  $\pm$  SD =  $24.4 \pm 1.2$  and  $28.0 \pm 0.4$  °C, respectively).

Like SST, reef area was to some extent confounded by biogeographical province, being generally higher in the Hawaiian province (mean log reef area within 75 km  $\pm$  SD =  $19.7 \pm 1.1$  km<sup>2</sup>) than the Central Pacific ( $16.8 \pm 1.4$  km<sup>2</sup>). However, through our use of model selection and model averaging, we were able to disentangle the positive effect of reef area on species richness, functional richness and functional evenness, despite opposing effects of province. Larger reef areas may be expected to increase reef fish richness through both evolutionary (e.g., higher speciation and lower extinction rates) and ecological (e.g., more individuals hypothesis) time-scale processes (Bellwood & Hughes, 2001). The lower fish species and functional richness and higher functional evenness observed in the Hawaiian province may also be the result of phylogenetic constraints, as historical climatologies and habitat availability have been suggested to be an important predictor of modern phylogenetic structure in reef fishes, and reef fish assemblages in the Hawaiian province generally show patterns of phylogenetic overdispersion compared with other Pacific provinces (Leprieur et al., 2016). As such, we may expect variation in the responses of reef fish communities to current and future environmental conditions

among biogeographical regions based on phylogenetic constraints characteristic of regional trait pools.

Interestingly, functional richness showed negative relationships with live coral cover. Although high coral cover is generally held to be an important indicator of reef health, relatively few species depend on live coral directly. Likewise, previous work has found no strong relationship between live coral cover and reef fish diversity while controlling for habitat complexity, as done here (Gratwicke & Speight, 2005). The effect of bleaching and coral loss are, however, expected to affect reef fishes over longer time scales through decreased reef complexity (Graham et al., 2007), which was an important predictor of higher reef fish species and functional richness in our study.

#### 4.2 | Sensitivity to trait choice

As with all functional diversity analyses, the patterns we observed are likely to depend on the traits we selected for our analyses. Through our trait sensitivity analysis, we found that whereas functional richness patterns appeared to be robust to the traits included, the effects of environmental gradients on functional redundancy seemed to be controlled by different traits across scales. Specifically, because the positive effect of NPP on overall functional redundancy at the island scale was mediated primarily through the two trophic traits, it suggests that impacts such as selective fishing based on trophic mode at coarser spatial scales may have the strongest impacts on overall functional redundancy, with possible cascading effects on the resilience of associated ecosystem functions to disturbance. Furthermore, as we used trophic categories and assigned traits to individuals based on species identity (rather than measuring intraspecific trait variation), we may have missed finer-scale differences in traits among sites in our analyses, possibly explaining why our functional diversity measures were best predicted at coarser scales. Moreover, depending on the specific ecosystem function considered in a study, the most relevant traits may vary. Body size may be particularly important when considering functions such as secondary production, whereas trophic mode may be more important for functions related to food web structure and grazing. The trait sensitivity analyses we performed allowed us to evaluate the robustness of our results to trait choice, while also providing insight into selective pressures on traits across scales.

#### 4.3 | Implications and conclusions

Different relationships between each dimension of diversity and environmental variables, together with the apparent lack of interdependence among some diversity dimensions (e.g., functional evenness versus all others at the island scale), suggest that each aspect of biodiversity responds differently to environmental variation or change. Among predicted consequences of changing atmospheric–ocean feedbacks under continued global warming are shifting ocean temperature and upwelling patterns in the tropical Pacific, which may alter large-scale productivity gradients (Collins et al., 2010) and ultimately shift functional diversity patterns even on reefs remote from human populations. Furthermore, climate-independent human impacts on coral reef

ecosystems may accelerate warming-related changes in functional diversity. Humans often simultaneously affect environmental conditions (via physical damage, pollution and sedimentation), taxonomic diversity (via overexploitation) and biomass (via harvest; Knowlton & Jackson, 2008), and these impacts may manifest at finer spatial scales than those at which the regional impacts of climate change manifest. Previous studies have indeed found declines in the functional richness of reef fishes with increasing local human population densities, which has ultimately been linked with declines in fish biomass and fisheries production (Duffy et al., 2016; Micheli et al., 2014; Mora et al., 2011). As we were examining islands remote from humans in this study, it is possible that patterns in scale dependence in environment–diversity relationships will be altered on human-populated islands as humans may drive finer-scale variation in key environmental gradients, such as NPP. Future work examining scale dependence in these relationships across human-impact gradients will be important for understanding how humans may modify the links between the environment and functional diversity of reef fishes and determining whether local human impacts will swamp out the importance of coarse-scale environmental variation.

Our analyses highlight the importance of considering scale in analyses of functional diversity. Additionally, by carefully controlling for common pitfalls associated with comparing patterns across scales (e.g., difference in sample size or overfitting), we can be confident that the scale dependence in our observed patterns is ecologically meaningful and not a statistical artefact. Although we focused on identifying the scale at which environmental conditions best predicted functional diversity, it will be equally important to determine at which scale each dimension of functional diversity is most relevant to ecosystem functioning (Loreau et al., 2001). Control and effect scales need not be the same. Functional evenness, for example, may respond most strongly to relatively coarsely scaled biophysical determinants, such as biogeographical province, island type and habitat area, but may be most relevant to ecosystem function at the much finer scales at which the biomass or number of individuals of different species may rebalance after disturbance (Hillebrand et al., 2008). Scale dependence of both impacts on and effects of each dimension of functional diversity therefore promises rich ground for further investigation.

## DATA ACCESSIBILITY

All fish survey data are available from NOAA's Coral Reef Ecosystem Program, Pacific Islands Fisheries Science Center; these data may be accessed by contacting [nmfs.pic.credinfo@noaa.gov](mailto:nmfs.pic.credinfo@noaa.gov). Environmental data were obtained from open access data products as described in Supporting Information Appendix S6.

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## BIOSKETCH

Our research team is focused on understanding how environmental variation and human activities affect the structure of marine communities across scales, and then linking these patterns to key ecosystem processes and functions. We are particularly interested in conducting research to predict the response of coral reefs and associated fisheries to global change and using these predictions to inform effective conservation and management practices.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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