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Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs

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Abstract

Anthropogenic activities such as land-use change, pollution and fishing impact the trophic structure of coral reef fishes, which can influence ecosystem health and function. Although these impacts may be ubiquitous, they are not consistent across the tropical Pacific Ocean. Using an extensive database of fish biomass sampled using underwater visual transects on coral reefs, we modelled the impact of human activities on food webs at Pacific-wide and regional (1,000s–10,000s km) scales. We found significantly lower biomass of sharks and carnivores, where there were higher densities of human populations (hereafter referred to as human activity); however, these patterns were not spatially consistent as there were significant differences in the trophic structures of fishes among biogeographic regions. Additionally, we found significant changes in the benthic structure of reef environments, notably a decline in coral cover where there was more human activity. Direct human impacts were the strongest in the upper part of the food web, where we found that in a majority of the Pacific, the biomass of reef sharks and carnivores were significantly and negatively associated with human activity. Finally, although human-induced stressors varied in strength and significance throughout the coral reef food web across the Pacific, socioeconomic variables explained more variation in reef fish trophic structure than habitat variables in a majority of the biogeographic regions. Notably, economic development (measured as GDP per capita) did not guarantee healthy reef ecosystems (high coral cover and greater fish biomass). Our results indicate that human activities are significantly shaping patterns of trophic structure of reef fishes in a spatially nonuniform manner across the Pacific Ocean, by altering processes that organize communities in both "top-down" (fishing of predators) and "bottom-up" (degradation of benthic communities) contexts.

KEYWORDS
biogeography, habitat, multiscale analysis, socioeconomic, spatial food webs, structural equation models

1 | INTRODUCTION

Human activities have introduced new types of disturbances into natural ecosystems that coincide with the growth and spread of our populations across the globe (Halpern et al., 2008; Mccauley et al., 2015). In marine systems, one ubiquitous example of these is fishing, which has contributed to declines in abundances of targeted fauna and shaped species interactions at global scales (Graham et al., 2017; Valdivia, Cox, & Bruno, 2017). At the same time, humans also influence marine environments through actions that can alter habitat complexity and nutrient flows (Mora et al., 2011; Valdivia et al., 2017). Such disturbances are overlaid on spatial variation in the biogeography of marine faunas, but how these two factors interact to determine the structure of marine ecosystems at regional (1,000s–10,000s km) and ocean basin scales is still unclear.

The coral reefs of the Pacific Ocean provide a good model to investigate the interaction of human activities, habitat and biogeography as structuring agents, due to the presence of large gradients in biodiversity and human activities at this scale (Kronen et al., 2012; Kulbicki et al., 2013; Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015; Williams, Baum et al., 2015; Wilson et al., 2008). There is good evidence that human activities can structure reef food webs in both a top-down and bottom-up manner (Bruno & Selig, 2007; De'ath, Fabricius, Sweatman, & Puotinen, 2012; Nadon et al., 2012; Williams, Gove, et al., 2015, Williams, Baum et al., 2015; Wilson et al., 2008). For example, the top-down impacts of fisheries on reefs initially tend to target large, often predatory fishes, at the top of the food chain and for some taxa that have high economic value, including sharks, fishing can have dramatic effects on populations at global scales (Darling & D'agata, 2017; Graham et al., 2017). These top-order predators have an important regulatory role in fish communities and their removal can elicit phenomena including mesopredator release, a situation where secondary consumers become highly abundant, resulting in trophic cascades, where changes occur in the structure and function of food webs at lower trophic levels (Barley, Meekan, & Meeuwig, 2017; Mumby et al., 2012; Ruppert, Travers, Smith, Fortin, & Meekan, 2013). Where fishing at higher trophic levels occurs at high intensity, "fishing down the food web" can occur where higher trophic groups are successively fished out so that the only remaining targets for capture are the smaller species that tend to be at the base of the trophic pyramid (Mumby et al., 2012).

Human activities in the coastal zones adjacent to reefs also drive coastal pollution that impact food webs in a bottom-up manner (Mora et al., 2011). For example, overgrazing, forest and mangrove removal and agriculture in water catchments alter the nitrogen cycle, introduce pollutants and increase rates of sedimentation on reefs. These activities on land ultimately degrade benthic communities, reducing the amount of coral cover and changing the structure and turnover of both benthic and fish assemblages (Bellwood, Hughes, Folke, & Nystrom, 2004; Mora, 2008; Mora et al., 2011). Additionally, the removal of mangrove habitats that act as nurseries for many marine fish species could potentially reduce the biomass of fish found on nearby coral reefs (Mumby et al., 2004). Overall, human-induced changes to reefs generally reduce reef resilience, ultimately decreasing the overall productivity and function of coral reef ecosystems (Mcclanahan et al., 2011). This can subsequently shift coral reef ecosystems to less productive alternate stable states to the detriment of many ecological processes and the human societies that depend on the reefs for ecological services (Bellwood et al., 2004; D'agata et al., 2016).

Although the importance of human activity as a structuring agent in coral reef ecosystems is well recognized (Jennings & Kaiser, 1998; Mccauley et al., 2013, 2015; Wilson et al., 2008), there has been little appreciation that this process is not uniform across broad spatial or temporal scales. Moreover, there is little understanding of how this phenomenon may interact with biogeographic patterns (i.e. biodiversity, community assemblage) to alter the susceptibility and resilience of reef systems. Notably, the amount and type of human impact will likely depend on wealth, culture, geographic location and prevalence of food-borne illnesses (e.g. ciguatoxins) (Kronen et al., 2012; Pinca et al., 2012). The susceptibility of reef ecosystems to anthropogenic disturbance will also vary due to changes in the environmental conditions, disturbance regimes, reef structure, coral cover, rugosity, identity, demography, connectivity and productivity of organisms inhabiting each reef (Anderson et al., 2008; Melbourne & Hastings, 2008; Mellin, Bradshaw, Meekan, & Caley, 2010; Mellin et al., 2016; Valdivia et al., 2017). Furthermore, many nations have in place management strategies to mitigate or reduce human influences that can operate with varying degrees of success (Gill et al., 2017; Robbins, Hisano, Connolly, & Choat, 2006). Understanding how these factors vary through space to influence trophic structure will ultimately help to design conservation and restoration strategies that better protect and restore coral reef ecosystems.

Here, we investigate spatial variability in human activities and habitat at both regional (~1–14 million km^2) and ocean basin scales (~37 million km^2) and document how this can impact the trophic structure of reef fish communities at locations spread across most of the tropical Pacific Ocean. Using structural equations and multivariate modelling approaches, three hypotheses involving the impact of human activity on coral reefs were tested: (1) human activity interacts with top predators (sharks) and coral cover to both directly and indirectly impact the trophic organization of reef fish communities; (2) spatial variability in human impacts and biogeography creates heterogeneity in the top-down and bottom-up processes structuring reef systems; and (3) human socioeconomic variables are the strongest predictors of the trophic structure of reef fish communities throughout the Pacific.

2 | MATERIALS AND METHODS

2.1 | Study region and distance-based diver surveys

Coral reefs throughout the Pacific Ocean were sampled using standardized underwater surveys. Surveys were conducted in 17 different countries and territories with 1,650 transects (50 m in length) with 4–6 sites per country and 24 transects per site on average from 2002 to 2007 (Figure 1). Transects were sampled in a stratified manner across four major reef types (fringing, intermediate, inner barrier and outer barrier reefs) within in each country. The locations of transects were selected using satellite imagery so that they were spaced about 0.5–3 km apart depending on the size and diversity of habitats found on the reef. To reduce interhabitat variability in our analysis of counts, our analysis here only included sites from outer reef slopes and excluded all sites where visibility was <10 m, giving a total sample size of 646 transects. Surveys were generally conducted along the 4–10 m depth contour (7.3 m average depth), but ranged between 1–20 m in depth on either side of the transect depending on the topography of the reef.

Counts of fish species included all reef sharks and 12 major families of teleosts including Acanthuridae, Balistidae, Chaetodontidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Serranidae, Siganidae and Zanclidae. Counts of species were conducted using a distance-sampling technique (Labrosse, Kulbucki, & Ferraris, 2002). Briefly, this involved two divers (one for each side of the transect), where each diver recorded the species, abundance, body length and distance to the transect line of each fish or group of fish on their side of the transect while swimming slowly down the line (Labrosse et al., 2002). Sources of error related to fish detectability and size estimates (which generally range within ~10% of actual size) have been explored in depth by Labrosse et al. (2002). For this study, all fish were counted within the range of visibility available to the diver, which is the maximum range of detection. Prior to analysis, all size data were grouped into five size classes (1–14, 15–24, 25–39, >40 cm and sharks; see Appendix S1 for more details). This approach allowed for the calculation of an appropriate width of transect for each size class, which is necessary to reduce well-known biases predominantly associated with body size (Fig. S1 and Table S1) (Bozec, Kulbicki, Laloe, Mou-Tham, & Gascuel, 2011; Kulbicki et al., 2010; Ward-Paige, Flemming, & Lotze, 2010). For example, the optimal transect width for detection of sharks on outer reef slopes was calculated to be 20 m (Fig. S1 and Table S1), a value consistent with earlier studies (Mccauley, Mclean, Bauer, Young, & Micheli, 2012; Robbins et al., 2006; Ward-Paige, Flemming, & Lotze, 2010). Like any survey method, visual transects will have biases associated with density estimates. For instance, visual transects biases might be created by fishes reacting to the presence of divers (Mccauley et al., 2012). However, this bias would be reduced by adjusting density estimates to the optimal transect width (Fig. S1 and Table S1). In addition, given that reef sharks are highly mobile and can demonstrate fidelity at a whole reef, but not at a transect scale (where transects were 0.5–3 km apart), (Field, Meekan, Speed, White, & Bradshaw, 2011; Vianna, Meekan, Bornovski, & Meeuwig, 2014), measurements of the biomass of sharks were summed at the reef level.

All fishes were classified into five trophic groups: sharks, carnivores, herbivores, corallivores and planktivores. The wet biomass of each individual was calculated using length–weight conversions available from the literature (Froese & Pauly, 2011; Kulbicki, Guillemot, & Amand, 2005; Kulbicki et al., 2011). Prior to analysis, the biomass of each group was first log-transformed and standardized (i.e. *z*-scores) to improve normality and to reduce the spread of values that can be extreme in some trophic groups (e.g. shark biomass with many zero counts and high counts) (Legendre & Legendre, 2012).

Finally, 28 benthic habitat parameters (e.g. % coral cover) were recorded using the medium scale approach (MSA; see Clua et al., 2006 for more details). In short, the MSA was implemented by using 20 quadrats (5 × 5 m), with 10 arranged on each side along the length of the 50 m transect. The benefit of this approach is that it generally provides an intermediate survey area of reef habitat (500 m^2) that generates data that are neither more variable when using smaller surveyed areas (e.g. line intercept transect; <100 m^2) or less variable when using broader surveys (e.g. landscape; >1,000 m^2) (Clua et al., 2006). These 28 characteristics were then averaged across the 20 quadrats for each transect and summarized into five categories (coral, turf algae, macroalgae, coralline crustose algae and other benthos; Table S2).

2.2 | Model covariates and subregions

Habitat, human activity and socioeconomic variables (Kronen et al., 2012) known or thought to influence the structure of reef food webs (Table S2) were compiled for the Pacific. Habitat variables including the per cent cover of live coral, macroalgae, turf algae, crustose coralline algae (hereafter CCA) and other benthic cover categories. These were subsequently arcsine transformed to conform to assumptions of continuity of variables used in the models. Other habitat variables included the average transect depth, habitat complexity (on a scale of 1–4 is a composite measure of the relief, coral cover and rugosity of the reef) and visibility during the survey (Tables S2 and S3).

Similar to earlier studies (Nadon et al., 2012; Ward-Paige, Mora, et al., 2010), human activity was estimated as the number of people

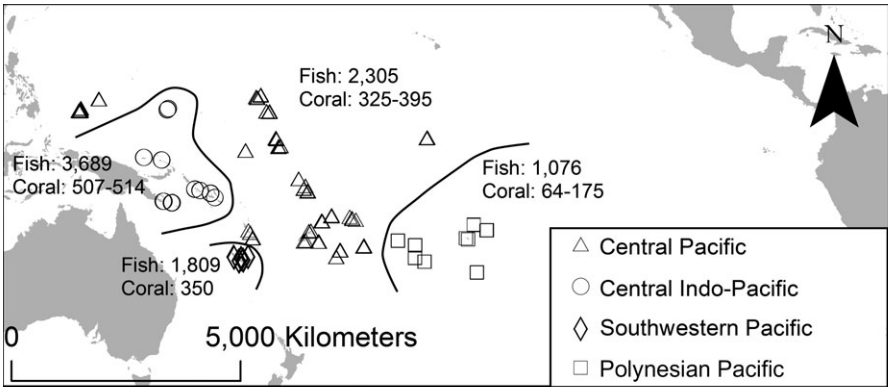

FIGURE 1 Study area throughout the Pacific Ocean. The sites (*n* = 63) where visual transects, habitat surveys and socioeconomic surveys were conducted are shown. The biogeographic classification and diversity estimates of fish communities are based on Kulbicki et al. (2013), and diversity estimates for coral are sourced from Veron et al. (2009) for each region. Sites were categorized into four regions

living within a given radius of the sampled reef sites. Here we used a 20 km buffer from the sampled site to estimate human activity, which was based on gridded population count data available from the Socioeconomic Data and Applications Center (SEDAC, 2005). Importantly, the 20 km radius included local villages sampled for socioeconomic data. Prior to analysis, these data were log-transformed to comply with model assumptions. Human activity is a proxy for many human-mediated environmental impacts on fish communities, including, but not limited to fishing, land use and pollution. To assess the type and degree of fishing-related activities, socioeconomic data were also gathered from local villages (see Kronen et al., 2012 for details). This included the size of the fishing grounds, the amount of sea life consumed per capita (invertebrates, fresh fish and canned fish), number of fishers, average size of household, gross domestic product per capita, the per cent of fishers that used ice for fishing catch (always or sometimes), source of primary income (fisheries, agriculture and salary) and the distance to marine protected areas (Tables S2 and S4) (IUCN & UNEP-WCMC, 2013). Prior to analysis, all of the predictors were standardized (i.e. *z*-scores) as they were recorded in different units (Legendre & Legendre, 2012). Finally, collinearity between human activity and all socioeconomic/habitat variables was assessed using Pearson's correlation. Most of the variables showed a low degree of collinearity ($r < .8$; results not shown) with only the consumption of fresh fish having a high correlation with human activity ($r > .8$; Table S5). Furthermore, the degree to which human activity is related to socioeconomic/habitat variables differed among regions and variables (Table S5).

Definitions of subregions were based on biogeographical patterns of similarity in species composition at the global scale (see Kulbicki et al., 2013 for details). Our study area included the biogeographic provinces of the central Pacific, central Indo-Pacific, southwest Pacific and Polynesian Pacific (Figure 1). Inclusion of these subregions ensured that similar communities of species were grouped within each region, enabling the analysis to control for variation in patterns of biodiversity at the largest spatial scale of our study. Additionally, species diversity observed at sites may have been an important covariable in our analysis that was related to biogeography. Consequently, relationships between the abundance, biomass, species diversity, mean size and human activity at our study sites were analysed using linear regression (Figs S2 and S3). Strong relationships between abundance, biomass and species diversity were found; however, relationships with mean size were less convincing (Fig. S2). Furthermore, it appeared that human activity in some regions (southwest Pacific and Polynesian Pacific; Fig. S3) may have had an impact on the species diversity we observed at our sites.

2.3 | Trophic and benthic structure comparisons

To investigate overall trends across a gradient of human activity, the biomass of sharks, carnivores, planktivores, corallivores and herbivorous fish were compared across three categories (related to the number of people that resided within a 20 km radius of our sites). These categories were low (≤100 inhabitants, $n = 40$), medium (101–1000, $n = 119$) and high (>1000, $n = 487$). Permutational multivariate analysis of variance using 1000 permutations (PERMANOVA) (Legendre & Anderson, 1999) was used to determine if the biomass of these groups of fishes differed significantly among categories. PERMANOVA was the preferred approach due to the nonparametric nature of the data and unbalanced design. In the same manner, benthic structure (e.g. live coral, turf algae) of transects was compared across the same gradient and tested for significant differences using PERMANOVA. Then grouping in trophic group biomass and benthic cover across the four biogeographic regions of the Pacific (as illustrated in Figure 1) were tested using PERMANOVA. PERMANOVA analyses, performed using the *adonis* function in the *vegan* library v. 2.4 in R software v. 3.2 (Oksanen et al., 2016).

Additionally, we tested for differences in individual trophic groups and benthic cover groups independent of other groups across human density categories and biogeographic regions using a one-way permuted ANOVA and adjusted for multiple comparisons using Bonferroni corrected *p* values with the *p.adjust* function in R software v. 3.2 (Legendre, 2007).

2.4 | Food web models

The impacts of human activity and the biomass of sharks and coral cover on the biomass of carnivorous and herbivorous fishes at our sites were investigated by creating a model of direct and indirect interactions using structural equation models (SEMs). This quantified the relative strength and significance of human activity on the biomass of sharks, carnivores, herbivores and coral cover (Grace, 2006) (see Appendix S2 for more details). Two habitat variables, depth and habitat complexity, were included that could also influence fish biomass in the SEMs. We then constructed SEMs based on interactions between the biomass of top-order predators (sharks), biomass of mesopredators (carnivores) and the most abundant group of lower level consumers (herbivores) to determine whether underlying interactions (such as mesopredator release or trophic cascades) could be detected in response to spatial variability in human activity and biogeography. This procedure was completed for reef fish communities both at the largest spatial scale of the study (most of the tropical Pacific Ocean) and within each biogeographic region.

Parameter estimation and testing of model fit for SEMs used the *lavaan* library v. 0.5 in R Software v. 3.2 (Rosseel, 2012). Maximum likelihood was used to estimate path coefficients and to examine whether coefficients were significantly different from zero using robust estimates of standard errors (Bentler & Dudgeon, 1996). Estimations of model fit were bootstrapped ($n = 1000$) and 95% confidence intervals were used to evaluate the overall fit of the final models (see Supporting Information for details). Standardized coefficients were used because the data in the models consisted of different units (coral cover, depth, habitat complexity and biomass) and we also needed to compare the magnitude of paths among several models. Finally, the amount of variation explained for each response (or endogenous variable in the SEMs) was determined using the formula $R^2 = 1 - V_e/V_o$, where V_e was the estimated variance and V_o

was the observed variance (see Arkema, Reed, & Schroeter, 2009 for details).

2.5 | Socioeconomic and habitat factors contributing to food web patterns

Changes in trophic structure that might be related to socioeconomic and habitat factors present at our sites (n = 63) across the Pacific and within our regions were explored using an analysis of the biomass of all trophic groups (shark, carnivore, planktivore, corallivore and herbivore). This involved a series of techniques including redundancy analysis (RDA), permutation tests (n = 1000) and variance partitioning (Legendre & Legendre, 2012; Peres-Neto, Legendre, Dray, & Borcard, 2006). These were applied to a subset of the data set used in the SEM analysis (n = 626 out of 646), as not all sites had socioeconomic data (two sites in Fiji: Nasaqalau and Nukunuku). Furthermore, one region (southwest Pacific) had a single value for the gross domestic product per capita, thus it was excluded as a covariate from the regional analysis in the southwest Pacific.

Socioeconomic and habitat predictors (Table S2) were first assessed for collinearity using variance inflation factors (VIF) and those producing a VIF > 10 were discarded (Borcard, Gillet, & Legendre, 2011). A forward selection procedure was then used to select for significant variables ($p < .05$) that explained variation in fish trophic structure for the overall Pacific and within each subregion (Dray, Legendre, & Blanchet, 2013). Permutation tests (n = 1,000) were used to determine the significance of the overall reduced model, axes of variation and predictors in the final model. A variance partitioning procedure was then used to determine the variance explained by predictors that were related to socioeconomic and habitat factors (Table S2) (Peres-Neto et al., 2006). Permutation testing (n = 1,000) was used to determine if the socioeconomic and habitat variables in the reduced model explained significant amounts of variation in patterns of fish trophic structure. We implemented RDA and variance partitioning using the *rda* and *varpart* functions in the *vegan* library v. 2.4 in R software v. 3.2 (Oksanen et al., 2016).

3 | RESULTS

3.1 | Trophic and benthic structure differences

The trophic structure of fish communities, in terms of the biomass of sharks, carnivores, planktivores, corallivores and herbivores, differed significantly across our gradient of human activity (PERMANOVA, n = 1000, $F_{1,644}$ = 15.37, $p < .001$; Figure 2) as did the benthic structure of reefs ($F_{1,644}$ = 12.92, $p < .001$; Figure 2). Generally, a higher overall biomass of fish was found at sites with low human activity along with significantly higher cover of live coral and lower amounts of turf algae (Table S6). Specifically, we found a significantly higher biomass of sharks and carnivores in the sites with low human activity (Table S6). We also observed significant differences in the biomass of trophic groups ($F_{1,644}$ = 7.59, $p < .001$) and benthic cover ($F_{1,644}$ = 7.76, $p < .001$; Figure 2) across biogeographic regions. Generally, there appeared to be a decline in overall biomass of fish from west (central Indo-Pacific) to east (Polynesian Pacific) and coral cover was lowest in the largest region, the central Pacific (Table S6).

3.2 | Food webs on Pacific reefs

Bootstrapped (n = 1,000) measures suggested that our models provided good fits to the data sets (Table S7). Variation explained by the models in shark biomass had a large range (1.9%–66.7%; Table 1) between Pacific-wide and regional scales. In contrast, smaller ranges in variation explained by the models for coral cover (5.6%–20.2%), herbivore biomass (15.6%–40.6%) and carnivore biomass (28.5%–54.1%) (Table 1).

SEMs indicated that changes in the trophic structure of reef fish communities were significantly linked with human activity in the Pacific-wide model (Table 2). While a significant and direct impact of human activity on shark biomass was detected, we could find no evidence that the biomass of carnivorous and herbivorous fishes lower down the food web were directly related to human activity (Table 2). However, there was evidence of a weak positive but indirect link between the biomass of herbivores and human activity ($0.030 = -0.19 \times -0.16$) and a weak negative indirect association between the biomass of carnivores and human activity ($-0.074 = -0.31 \times 0.24$). High coral cover was negatively related with the biomass of herbivores (Table 2). In contrast, there was no evidence that changes in coral cover in the Pacific-wide model were propagated up through the food web to alter the biomass of sharks or carnivores (Table 2).

While human activity played a role in structuring food webs of reef fishes in the Pacific-wide model, direct impacts varied dramatically across the Pacific Ocean and throughout the food web (Figure 3). The biomass of reef sharks was negatively and significantly related with human activity throughout all regions of the Pacific, with the strongest impact occurring in the southwestern Pacific (−0.64) and the weakest in the central Indo-Pacific (−0.14; Figure 3). In contrast, in only two regions (representing >85% of transects), the central and central Indo-Pacific, displayed a negative and significant direct impact on the amount of coral cover by human activity (Figure 3). Furthermore, carnivores were negatively and significantly related to human activity throughout the central and Polynesian Pacific (representing >83% of transects; Figure 3). Herbivores were only negatively and significantly related to human activity in the southwestern Pacific and the correlation was relatively strong (−0.62; Figure 3). In contrast, a weaker and significant positive interaction between herbivore biomass and human activity occurred in the central Indo-Pacific (Figure 3).

Generally, the biomass of sharks, carnivores and herbivores were positively correlated, with the exception of the Polynesian Pacific region, where shark biomass was negatively related to herbivore biomass (Figure 3). Furthermore, there was evidence that shark and carnivore biomass was positively correlated with the cover of live corals in the Polynesian Pacific and in the southwest Pacific (Figure 3). In both these regions, the amount of coral cover was not significantly linked to the human activity found on the reef, suggesting

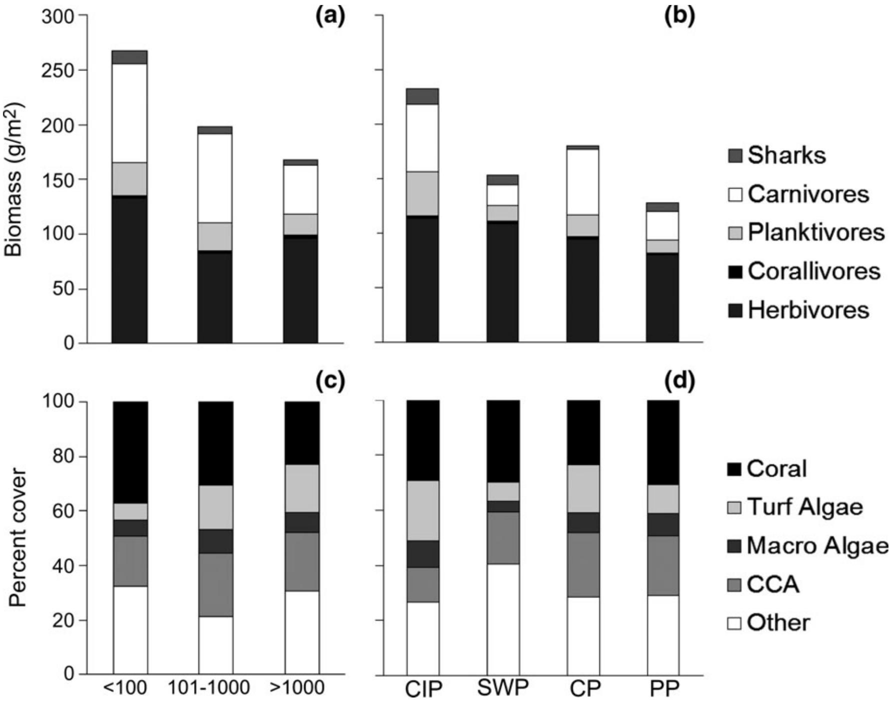

FIGURE 2 The mean observed (a, b) biomass of trophic groups (shark, carnivore, planktivore, corallivore and herbivore) and (c, d) per cent benthic cover at transects (coral, turf algae, macroalgae, crustose coralline algae [CCA] and other) across (a, c) human activity, low (<100), medium (101–1000) and high (>1000), and (b, d) four biogeographic regions (central Indo-Pacific [CIP], southwest Pacific [SWP], central Pacific [CP] and Polynesian Pacific [PP]) is shown

TABLE 1 The sample size (*n*) and variance explained by each structural equation model (for response variables) for the entire Pacific (All) and each biogeographical region: central Indo-Pacific (CIP), southwest Pacific (SWP), central Pacific (CP) and Polynesian Pacific (PP) as defined by Kulbicki et al. (2013)

		Variance explained (%)			
Model	Sample size (n)	Shark biomass	Carnivore biomass	Herbivore biomass	Coral cover
All	646	10.5	28.5	15.6	5.7
CIP	74	1.9	36.2	15.7	8.6
SWP	34	66.7	54.1	40.6	20.2
CP	476	12.9	34.5	30.4	5.6
PP	62	18.0	35.5	20.8	13.1

that this effect may occur independently of human modifications to the benthos (Figure 3). However, given the strength of relationships between coral cover and human activity (Table 2) and the amount of variation explained (Table 1), this link may be interpreted to be significant, but rather weak. There was also a significant and positive relationship between the abundance of lower trophic levels (carnivores and herbivores), coral cover and depth and habitat complexity (Table 2). The positive relationship between habitat variables and coral cover was likely a result of the gradients examined in our analysis, which included some transects deployed at relatively shallow (~2 m) depths (Table S3).

3.3 | Socioeconomic and habitat factors

We were able to explain 31.7% of variation (adjusted R^2) in trophic group structure of reef fishes across all of our sites in Pacific (Figure 4a and Table 3). The model, five axes of variation and all variables were significant ($p < .05$) by permutation analysis (n = 1,000). Finally, 10.6% of the explained variation was attributable to socioeconomic variables, whereas 14.2% of the variation was explained by habitat variables (Table 3). Furthermore, 6.9% of the explained variation was an interactive effect between socioeconomic and habitat variables (Table 3).

In the Pacific-wide model, a lower biomass of all trophic groups occurred alongside increased per capita consumption of canned fish, higher human activity and higher gross domestic product per capita (Figure 4a). Notably, shark biomass was most sensitive to these variables. In contrast, if the reported fishing grounds were much larger, which can be indicative of a larger reef size near the site or increased accessibility to more reef area, this appeared to be beneficial to shark biomass (Figure 4a). Furthermore, increased ice use, indicating a focus of fishers on catching fish for market, was related to increased shark biomass (Figure 4a). In contrast, habitat factors, such as coral cover, depth and habitat complexity, were most influential on lower level trophic groups (Figure 4a). Overall there was no clear separation in the position of different regional sites in the biplot (Figure 4a), indicating that there was an overlap in trophic structure, socioeconomic and habitat factors among all regions.

In 3 of the 4 comparisons within regions (central Indo-, southwest and Polynesian Pacific), socioeconomic factors explained 2–7 times more variation than habitat factors (Table 3 and Figure 4b, c, e). The only region that showed a distinctly different pattern was the central Pacific, where habitat (adjusted R^2 = 17.7%) explained marginally more variation than socioeconomic (adjusted R^2 = 14.3%) factors (Table 3 and Figure 4d). However, the interaction between habitat and socioeconomic variables accounted for 8.0% of variation explained (adjusted R^2; Table 3). Although variables selected by the

TABLE 2 The strength and significance of all interactions in structural equation models for the entire Pacific (All) and each subregion (central Indo-Pacific [CIP], southwest Pacific [SWP], central Pacific [CP] and Polynesian Pacific [PP])

Interaction		Region				
From	To	All	CIP	SWP	CP	PP
Human	Shark	−0.31***	−0.14*	−0.64***	−0.33***	−0.28*
	Carnivore				−0.19***	−0.34**
	Herbivore		0.12*	−0.62*		
	Coral	−0.19***	−0.29**		−0.14*	
Shark	Carnivore	0.24***		0.86***	0.23***	
	Herbivore	0.09*			0.14**	−0.37**
Coral	Shark			0.33**		0.30*
	Carnivore					0.46**
	Herbivore	−0.16***			−0.21***	
Depth	Shark					
	Carnivore	0.22***	0.42***		0.19***	
	Herbivore					0.34**
	Coral	0.15***		0.36*	0.19***	−0.31**
Habitat	Shark	0.11**			0.19***	
	Carnivore	0.33***	0.24*		0.39***	
	Herbivore	0.40***			0.54***	
Carnivore^a	Herbivore^a	0.31***	0.32*	0.49**	0.29***	0.25*
Habitat^a	Coral^a	0.28***	0.35**	0.40**	0.28***	0.52***
Habitat^a	Depth^a	0.24***	0.49***	0.54**	0.25***	
Human^a	Habitat^a	0.10**			0.13**	

For simplicity only significant values (*$p < .05$, **$p < .01$ and ***$p < .001$) are shown.
^{a}Interaction is in both directions.

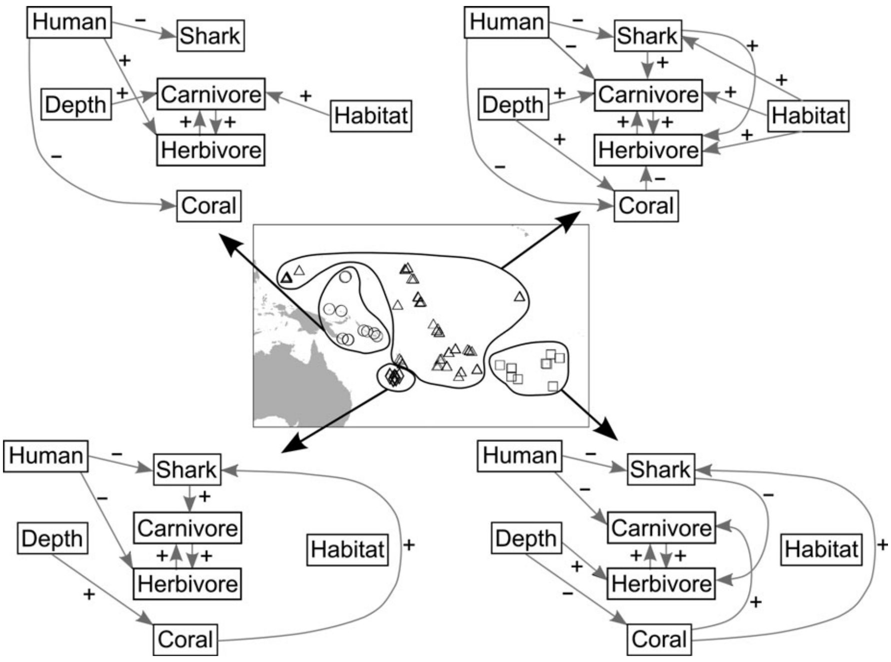

FIGURE 3 Spatial variability of significant ($p < .05$) interactions from regional structural equation models. The direction of significant interactions for the central Indo-Pacific (circles), central Pacific (triangles), southwest Pacific (diamonds) and Polynesian Pacific (squares) regions. Interactions that covary with habitat complexity are omitted for simplicity is shown

model differed among regions, human activity, canned fish consumption per capita, mean household size, mean transect depth and live coral cover were selected more frequently (in at least 3 out of 4 regions), compared to all other variables (Figure 4).

4 | DISCUSSION

Our study shows that the influence of humans on ecological processes operating at both the top and bottom of the food webs of coral reefs is both ubiquitous and spatially variable across the Pacific Ocean. These results imply that human activities may now overwhelm many natural structuring processes occurring within reef fish communities at both ends of the food chain. First, as human activity increased at our sites, there was an overall decrease in fish biomass. This was mainly attributed to a reduction in the biomass of sharks and carnivores, which was also accompanied by decreases in live coral cover (Figure 2), a result consistent with earlier work (Bellwood et al., 2004; Bruno & Selig, 2007; De'ath et al., 2012; Hughes et al., 2003; Nadon et al., 2012; Williams, Gove, et al., 2015, Williams, Baum et al., 2015). Second, at the uppermost end of the food web, the biomass of reef sharks was directly and negatively associated with human activity in the SEMs (Figure 3), a result reported by studies on Caribbean reefs (Ward-Paige, Mora, et al., 2010) and some of the more northerly Pacific reefs (Nadon et al., 2012). In the present study, this interaction was only uniform in terms of the significance and direction of impact, rather than strength across most of the Pacific Ocean. Finally, socioeconomic factors consistently predicted broad-scale spatial patterns of trophic structure better than the within-habitat factors that were included in our models. Although previous work has linked human activity to impacts on biodiversity across the Pacific (Mora et al., 2011), we are able to demonstrate that regional differences in activity have a wide range of impacts that appear to differ spatially and overwhelm many habitat-based or bottom-up processes to alter the trophic structure of reef ecosystems.

4.1 | Human activity as a structuring agent of Pacific reef fishes

There were strong, negative relationships between shark biomass and human activity; however, there were no significant direct relationships between the biomass of carnivorous or herbivorous fishes and human activity at the scale of the Pacific. In contrast, these relationships were present at regional scales, where we could identify significant links between either carnivore or herbivore biomass and human activity, but not both (Figure 3). In two regions (central and Polynesian Pacific) that comprised a majority of our sites, the biomass of sharks and carnivores were negatively and significantly impacted by human activities (Figure 3). Given that piscivores are a preferred target of many reef fisheries (Darling & D'agata, 2017; Dulvy, Freckleton, & Polunin, 2004; Mumby et al., 2012; Nadon et al., 2012; Robbins et al., 2006), this negative relationship with human activity (as a measure of fishing intensity) may be expected. Why this should vary among regions probably reflects the multispecific, artisanal and/or small-scale nature of coral reef fisheries (Kronen, Vunisea, Magron, & Mcardle, 2010; Kronen et al.,

TABLE 3 Summary of redundancy analysis (RDA) models explaining variation in trophic structure for the entire Pacific (All) and each subregion (central Indo-Pacific [CIP], southwest Pacific [SWP], central Pacific [CP] and Polynesian Pacific [PP]). The total adjusted R^2 and the amount of variation attributed to socioeconomic factors, habitat factors and the interaction between them for the biomass of trophic groups found at our sites are shown

	Variance explained (adjusted R^2)			
Model	Total	Socioeconomic	Habitat	Interaction
All	31.7***	10.6***	14.2***	6.9
CIP	48.5***	32.9***	14.0***	1.6
SWP	58.0***	40.6***	14.0***	3.5
CP	40.1***	14.3***	17.7***	8.0
PP	59.0***	35.8***	4.7**	18.4

Significance is denoted by $**p < .01$ and $***p < .001$.

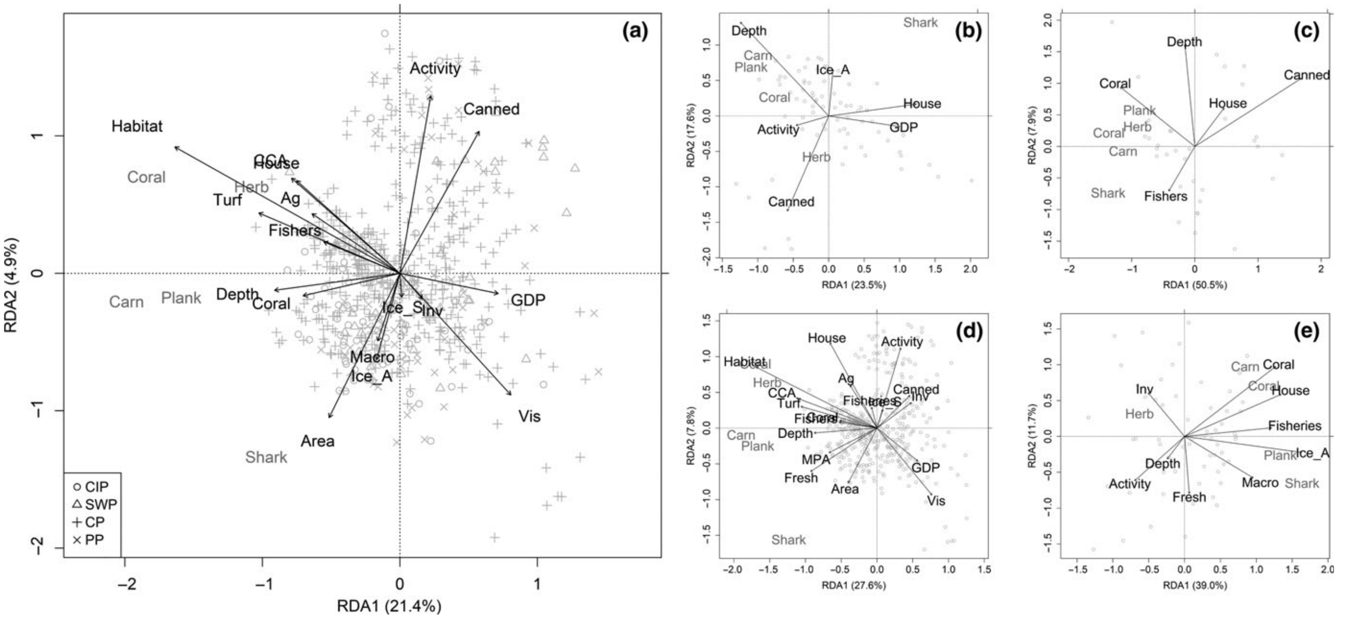

FIGURE 4 The reduced redundancy analysis (RDA) model for (a) all sample sites explaining 31.7% of variation (adjusted R^2) in the biomass of fish trophic groups. Also shown are the reduced models for the (b) central Indo-Pacific (CIP), (c) southwest Pacific (SWP), (d) central Pacific (CP) and (e) Polynesian Pacific (PP). Constraints or predictors are labelled in black and the trophic groups in grey. Variables are defined in Table S2

2012; Pinca et al., 2012), where differences in the key targets of fishing occur among regions as a result of the type of fishing practices and available resources. Additionally, in some regions certain species or families of fishes are avoided because of the risk of ciguatoxins (e.g. some herbivores and carnivores in the Polynesian Pacific), whereas in others, they are a common target of fisheries (Pinca et al., 2012).

In regions where overfishing is rife in coastal areas (Zeller, Harper, Zylich, & Pauly, 2015), humans may target species that are lower in the food web than in regions where reef fish assemblages remain largely intact (Mumby et al., 2012). The negative impacts of human activity on adjacent habitats such as mangroves that support fish biomass on reefs (Mumby et al., 2004) must also be considered; however, at present there is little information on these relationships in the Indo-Pacific, compared to the Caribbean (Faunce & Serafy, 2006; Nagelkerken et al., 2008). These same factors may similarly explain regional differences in the relationship between the biomass of herbivores and human activities. For example, in the southwest Pacific we found a direct and negative relationship between herbivore biomass and human activity, suggesting that humans likely target herbivores to the extent that they are having dramatic impacts on their biomass (Figure 3). These results confirm those of Carassou, Léopold, Guillemot, Wantiez, and Kulbicki (2013) who also indicated a negative effect of fishing on herbivore biomass in New Caledonia (SWP). In contrast, in the central Indo-Pacific, the biomass of herbivorous fishes was positively and significantly related to human activity. This demonstrates how human activity, a proxy for a range of human-mediated impacts, can have a direct and significant impact on trophic structure and that these effects may vary significantly across regions. This has major implications in the management of reef fish resources as similar sets of factors may have different effects depending on the region (Mora et al., 2011). It also challenges the generalization of results from local studies to broader scales, such as for instance the application of quotas for protected areas, which will likely vary geographically with taxonomic and productivity differences (Lester et al., 2009).

There was a positive relationship between live coral cover and the biomass of reef fishes and top-order predators such as sharks (Table 2, Figure 3), a phenomenon documented on reefs in the Indian and Pacific oceans as well as the Caribbean (Mcclanahan et al., 2011; Sandin et al., 2008; Valdivia et al., 2017). The generality of this pattern means that coral cover is often argued to be a proxy measure for the health of coral reef ecosystems (De'ath et al., 2012). Regardless of the mechanisms involved, our results suggest that bottom-up processes may potentially interact with the top predators to influence food web dynamics in some regions of the Pacific. How such effects might operate (i.e. in a synergistic, antagonistic or additive manner) is not clear (Darling & Côté, 2008; Hughes & Connell, 1999; Ruppert et al., 2013), although our study provides the first evidence that they may be detectable at very broad spatial scales of many thousands of kilometres.

4.2 | Habitat and socioeconomic drivers of trophic structure

Our SEMs demonstrated that regardless of region, increases in the biomass of all trophic groups of fishes was correlated with increased mean depth of the survey and habitat complexity (Table 2, Figure 3). Mean depth can yield higher estimates of fish biomass as there is generally more fish present on the deeper outer slope of reefs likely due to a combination of higher detectability, habitat complexity being greatest at intermediate depths and less fishing pressure. Furthermore, there is a long-recognized, positive relationship between habitat complexity (and heterogeneity) and fish biomass in reef systems (Pittman, Costa, & Battista, 2009; Wilson, NaJ, & Polunin, 2007). We also found that increases in mean transect depth could have both positive and negative relationships with cover of live coral (Table 2). Although coral cover generally declines with depth, the effects of disturbance events such as cyclones, bleaching and human activities also reduce with depth, with the outcome that coral may be more abundant at intermediate depths (Connell, 1997; Connell, Hughes, & Wallace, 1997). While SEMs demonstrate the importance of habitat to structuring fish communities, the impact of this variable may be mediated indirectly by human activities.

To ascertain whether human activities, habitat or the interaction between both affected trophic structure, variance partitioning using RDA was used to disentangle the relative contributions of these factors. Socioeconomic factors could explain 2–7 times more variation in trophic structure of reef fishes than within-habitat factors in three out of four of our regions (Table 3). Similar to the Pacific-wide SEM, this analysis found that mean depth, habitat complexity and live coral cover (among other habitat factors) were important predictors of trophic structure, particularly at lower trophic levels (Figure 4a). The analysis also identified the socioeconomic variables of GDP, human activity and canned fish consumption as strong negative correlates of fish biomass (Figure 4a). Canned fish is a luxury food item in the South Pacific, hence the higher GDP associated with this factor (Kronen et al., 2010). Higher GDP may allow the use of more sophisticated fishing techniques (e.g. fish finder, GPS) that enable fishing practices to be more effective and efficient. This reinforces the idea that economic development (in terms of GDP) does not necessarily guarantee the implementation of sustainable practices for resource management (Kronen et al., 2010). In contrast, we found that larger fishing grounds and ice use by fishers are positively correlated with shark and carnivore biomasses (Figure 4a). These factors may indicate that fishers travel to target valuable offshore species (tunas, mackerels, etc.) for market so that pressure on local reef fisheries is reduced.

At the regional level, higher mean household size, human activity and canned fish consumption were correlated with reduced fish biomass (Figure 4b–d), patterns consistent with previous studies that have in addition found negative correlations between human activity and the biomass of reef fishes (Bruno & Selig, 2007; Nadon et al., 2012; Williams, Gove, et al., 2015, Williams, Baum et al., 2015). However, it was notable in our study that the magnitude of impact of human activity as structuring agent on patterns of fish biomass could substantially outweigh habitat factors. The amount of variation attributable to an interaction between human activity and habitat was also less than that of each individual factor, except in the Polynesian Pacific (Table 3). In this region, an interaction between habitat and human factors may be important due to the lower frequency and severity of natural disturbance events such as cyclones and coral bleaching (Vincent et al., 2011). Ultimately, the combined direct and interactive impacts of socioeconomic factors accounted for the majority of the variation in trophic structure of fish communities throughout the Pacific.

4.3 | Limitations and uncertainties

Although our study provides evidence that human activities impacted both the top and bottom of the food web of coral reefs, the correlative nature of our work does not necessarily imply causality. In addition to human effects, we recognize that site differences, management, natural disturbances and temporal scale will also be important to the dynamics of reef food webs. These factors were taken into account in our study in a number of ways. Within countries, we only included surveys of outer reefs (i.e. one habitat) to control for interhabitat differences. Furthermore, we included cover of live coral, depth and habitat complexity in our models to account for potential habitat differences within reefs. In RDA models, we examined the effects of management regimes, such as distance to marine protected areas (MPAs), but could only find a significant relationship with the biomass of fish in the central Pacific (Figure 4d). This result is likely due to our sampling design not explicitly addressing comparisons of MPAs with adjacent fished areas, meaning we lacked statistical power to discern an effect.

The snapshot nature of the study also prevented the models accounting for temporal variability in fish communities that can arise from human activities, reef size, connectivity and recovery from disturbance (Anderson et al., 2008; Lamy, Galzin, Kulbicki, De Loma, & Claudet, 2016; Mellin et al., 2010; Ruppert et al., 2013). Loss of temporal resolution is an inevitable consequence of the spatial scale of our work (much of the tropical Pacific), although it is likely that the effect of such differences will be minimized by pooling data from many sites within or across regions.

Finally, trophic guild classifications can overlook hidden complexities, such as multiple trophic roles (apex vs. mesopredator) within some guilds such as sharks (Roff et al., 2016). This is less likely to have impacted our results since sharks that occupy true apex roles, such as great hammerhead (*Sphyrna mokarran*) and tiger (*Galeocerdo cuvier*) were very rare in our counts. Mesopredatory species such as the whitetip (*Triaenodon obesus*) and grey reef shark (*Carcharhinus amblyrhynchos*) accounted for nearly all the sharks commonly sighted by our study. Recent work shows that the categorizations used here can yield robust insights into the issue of human-mediated impacts, by capturing main species interactions and changes in trophic structure (Graham et al., 2017; Ruppert, Fortin, & Meekan, 2016). Moreover, finer division of guilds through the creation of more trophic groups also challenges the computational abilities of food web models.

4.4 | Structuring ecological processes and ecosystem function

Human activities can have dramatic impacts on the trophic structure of reef fish communities (Graham et al., 2017). Such changes can ultimately impact energy flow, which alters ecosystems processes that sustain healthy coral reef ecosystems (Mourier et al., 2016). We demonstrate that humans appear to be major contributors to declines of sharks and changes in the community structure of fishes throughout the Pacific. Moreover, our study suggests that benthic communities may also be adversely impacted by human activity, although this link was found to be relatively weak. Overall, human activities have shifted reefs towards benthic communities that have lower cover of live coral and a trophic structure of fishes with a relatively higher dominance of herbivores and a lower overall biomass in all trophic groups. Because the size of herbivores is related to the type and impact of their feeding on coral reef communities (Choat, 1991) and potentially the resilience of reef ecosystems (Bellwood et al., 2004), this suggests that human activity can impact the structure, resilience and function of coral reef ecosystems. This has implications for the future status of these reefs given that recent studies have shown that beyond a certain threshold of human activities (D'agata et al., 2016), the recovery towards communities found in pristine areas is no longer possible. We illustrate the spatial complexity of these impacts and note that no two regions in the Pacific appear to have similar human-mediated impacts, which supports our assertion that important structuring agents for coral reef ecosystems have effects that are not homogeneous at global scales. Consequently, the outcomes of conservation tools such as marine protected areas on the recovery of fish communities are unlikely to be consistent at all spatial scales across the Pacific.

Our study shows that there are now very few, if any, places in the tropical Pacific Ocean that are not impacted by human activities. Importantly, there were major differences in the response of reef food webs to human activity across the Pacific, implying that processes that structure reef food webs in both a top-down (e.g. shark removal) and bottom-up (e.g. benthic degradation) manner are affected to some degree by human activities. Furthermore, these processes act in different ways from one biogeographic region to the next or perhaps as a result of processes that differ due to regional species pools (Kulbicki, Mouillot, & Parravicini, 2015; Kulbicki et al., 2013). Nonetheless, our study found that socioeconomic factors, including indices of development and fisheries, accounted for most of the variation in the food web structure of reef fish communities across the Pacific. Of note, economic development does not appear to guarantee sustainable resource management. The spatial complexity of socioeconomic and habitat patterns described by our study must be taken into account in any attempt to restore coral reef ecosystems and manage human impacts. Adaptive management strategies that are tailored to this spatial variability are now urgently required given the challenges such as climate change and ocean acidification that now assail coral reef ecosystems.

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SUPPORTING INFORMATION

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

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