Habitat change mediates the response of coral reef fish populations to terrestrial run-off

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ABSTRACT: Coastal fish populations are typically threatened by multiple human activities, including fishing pressure and run-off of terrestrial pollution. Linking multiple threats to their impacts on fish populations is challenging because the threats may influence a species directly, or indirectly, via its habitats and its interactions with other species. Here we examine spatial variation in abundance of coral reef fish across gradients of fishing pressure and turbidity in Fiji. We explicitly account for multiple pathways of influence to test the alternative hypotheses that (1) habitat moderates predation by providing shelter, so habitat loss only affects prey fish populations if there are abundant predators, (2) habitat change co-drives biomass of both prey and predator functional groups. We examined responses of 7 fish functional groups and found that habitat change co-drives both predator and prey responses to turbidity. Abundances of all functional groups were associated with changes in habitat cover; however, the responses of their habitats to turbidity were mixed. Planktivore and piscivore abundance were lower in areas of high turbidity, because cover of their preferred habitats was lower. Invertivore, browser and grazer abundance did not change strongly over the turbidity gradient, because different components of their habitats exhibited both increases and decreases with turbidity. The effects of turbidity on fish populations were minor in areas where fish populations were already depleted by fishing. These findings suggest that terrestrial run-off modifies the composition of reef fish communities indirectly by affecting the benthic habitats that reef fish use.

KEY WORDS: Coral reef fisheries · Integrated coastal management · Land-use change · Fiji · Trophic-cascade

INTRODUCTION

Coral reef fisheries support millions of livelihoods worldwide but are in general highly threatened (Burke et al. 2011). Reef fish, and the fisheries they support, are largely dependent on benthic habitats during at least some stages of their life histories (Jones et al. 2004, Wilson et al. 2008, Graham & Nash 2013, Rogers et al. 2014). The vulnerability of coral to human pressures like pollution (Fabricius et al. 2005)

means that management of reef fisheries must often extend beyond just managing fishing pressure (Caddy 2000, Weijerman et al. 2016). In particular, terrestrial run-off of nutrients and sediment may be a key driver of reef degradation in many regions (Fabricius et al. 2005, Burke et al. 2011, Kroon et al. 2014, Wenger et al. 2016) and thus may also impact reef fish (Houk et al. 2015). Therefore, where there is a strong link between human activities on land and the health of coral-reef ecosystems (Maina et al. 2012), fishery management is justified in extending its mandate to encompass catchments (Caddy 2000, Jupiter et al. in press a).

The link from terrestrial run-off to reef fish is challenging to document, because fish populations may respond both directly to terrestrial sediments (Wenger et al. 2015) and indirectly via changes in their habitats (Bejarano & Appeldoorn 2013, Gilby et al. 2016, Hamilton et al. in press), productivity (Roeger et al. 2016) or predation pressure (Almany 2004, Dulvy et al. 2004b). Fish typically use multiple habitats (e.g. Olds et al. 2016), and those habitats may show differential responses to terrestrial run-off. For instance, run-off of terrestrial sediments can carry nutrients that fertilize algal beds which are food for grazing fish (Fabricius et al. 2005), but it may also reduce benthic light and cause die-back of structurally complex corals that provide refuges from predation for grazing fish (Jones et al. 2004, Graham & Nash 2013, Rogers et al. 2014). The regulation of predation pressure by structural complexity is hypothesized to be an important control on trophic cascades (Salomon et al. 2010). Thus, the effects of terrestrial run-off on reef fish populations may be species and context dependent: abundance of small grazing fish species may be lower in high predation environments if structurally complex corals are degraded by run-off, whereas abundance of small grazing fish may increase in response to higher algal availability if predator biomass is low (Rogers et al. 2015).

Two approaches have proven useful to examine the context-dependency of fish responses to habitat change in field data. First, diverse coral reef fish communities can be aggregated into functional groups of species that are expected to show similar responses to habitat change and predator biomass (e.g. Jennings & Polunin 1997, Wilson et al. 2008). These functional groups can also be further partitioned by individual fish sizes to account for the decreasing vulnerability of larger individuals to predation (e.g. Mumby et al. 2006). Second, path analyses can be used to test alternative hypotheses about multiple causal linkages from terrestrial run-off to degrading

habitats and its effect on fish populations (Hamilton et al. 2017). For instance, previous analyses from Fiji have indicated that higher biomasses of invertivorous fish are associated with lower fishing pressure and more topologically complex reefs but show no response to biomass of predators (Wilson et al. 2008). However, to date such path analyses have not simultaneously addressed the roles of predation pressure, habitat change and terrestrial run-off in driving biomass of fish functional groups.

Here we examine multiple causal hypotheses for the interacting effects of fishing pressure and turbidity on a coral reef fish assemblages. We conducted our study in Fiji, across a gradient of turbidity that is driven by terrestrial run-off (Brown et al. 2017) and a gradient of fishing pressure. We compare alternative hypotheses for 4 general mechanisms linking run-off to fish biomass and abundance (Fig. 1): (Hypothesis A) Structurally complex reefs shelter prey fish from predation (Almany 2004), so loss of structurally complex reefs under more turbid conditions means prey fish will be more vulnerable to predation on more turbid reefs (moderation effect). If habitat moderates the role of predation, then pollution combined with removal of predators may 'cultivate' herbivore populations and provide for fisheries, even on degraded reefs (Brown & Trebilco 2014). (Hypothesis B) Predators exert top-down control on prey species, and predators are associated with particular habitats (e.g. Friedlander & Parrish 1998) that are affected by turbidity (mediation effect). If habitat has a mediating role on predation pressure, then the productivity of reef fisheries will depend on run-off independent of local fishing pressure. (Hypothesis C) Predator and prey biomass co-vary due to the responses of their habitats to turbidity. (Hypothesis D) Prey biomass is driven by coverage of its habitats and is independent of predator biomass.

METHODS

Overview

Our study focuses on catchments and reefs around the island of Vanua Levu, Fiji's second largest island, where a provincial-level integrated coastal management plan is being created for the 9 districts of Bua Province and adjacent customary fisheries management areas ('Qoliqoli') (Fiji Department of Environment 2011). Qoliqoli boundaries extend from the coast to the edge of barrier reef systems (Fig. 2). Informing the management plan requires historical
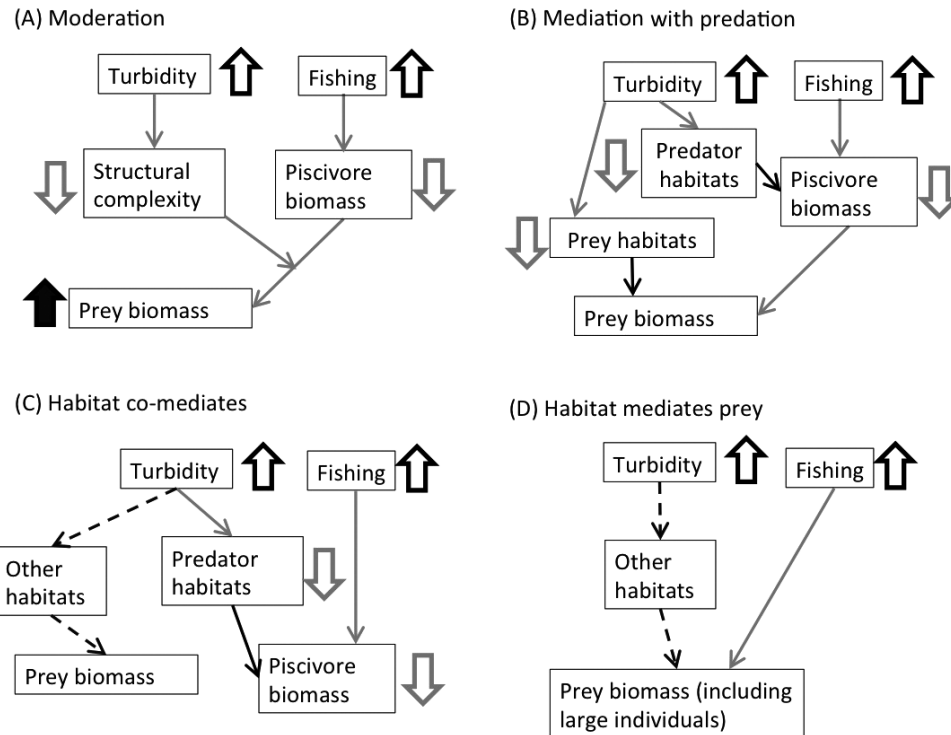
Fig. 1. Hypothesised influence of turbidity across a gradient of terrestrial run-off on biomass of a prey species. (A) Structural complexity moderates the effect of predators on prey, (B) predator habitats mediate the effects of predators on prey (fishing pressure is not pictured here, so the causal effect from turbidity to prey biomass is clear); (C) predator and prey covary due to covarying mediation effects of their habitats; (D) prey covary with turbidity due to changes in their habitats. Note that in (C) we analyse small individuals of each functional group (<13 cm), whereas (D) includes no predation effect, so we include individuals of all sizes. Boxes indicate variables; arrows connecting boxes indicate hypothesised effects; grey: negative effects; black: positive effects; dashed lines: effects that vary across functional groups (see Table 1). The box 'other habitats' varies across functional groups and may include structural complexity (Table 1). Wide arrows: hypothesised direction of effect; solid arrows: stronger effects than unfilled arrows. Not all variables without hypothesised directions depend on the functional group and habitats (Table 1); for clarity not all hypothesised interactions are pictured

context for how land-use change may have influenced fish populations. Historically, the northern side of Vanua Levu has been cleared, primarily for sugar cane, resulting in high erosions rates of both stream banks and hillslopes (Terry et al. 2008). Forests on the southern side are largely intact (Brown et al. 2017). The contrast in land-clearing north to south has resulted in a north-to-south water quality gradient, in addition to an inshore to offshore water quality gradient (Brown et al. 2017), thus providing an opportunity to use spatial contrasts to quantify the effects of turbidity associated with terrestrial run-off on fish biomass.

Modelling the gradient of turbidity

We used a previously developed Bayesian model of turbidity to estimate the gradient of turbidity across surveyed reefs (Brown et al. 2017). In brief, the model used satellite images from the medium resolution imaging spectrometer sensors on board the polar-orbiting Envisat environmental research satellite by the European Space Agency (Rast et al. 1999). Specifically we used a level 2 (derived) product that had been pre-processed to measure ocean turbidity. The gradient in satellite-measured turbidity was used as data for the Bayesian model, which fitted power relationships between the distance to river mouths and turbidity. The model allows for dispersion of sediments to vary by coastline, and thus accounts for the effect of the predominant south-easterly trade winds on sediment dispersal. Sediment yields were estimated using satellite-derived measures of forest cover in the catchments and literature values of erosion rates across different land-uses and wet-season rainfall (Brown et al. 2017). The Bayesian estimation then updated the estimates of sediment yields so that they are consistent with the turbidity gradient observed by the satellites. The Bayesian model provided an accurate fit to the satellite data and also independently predicts changes in benthic
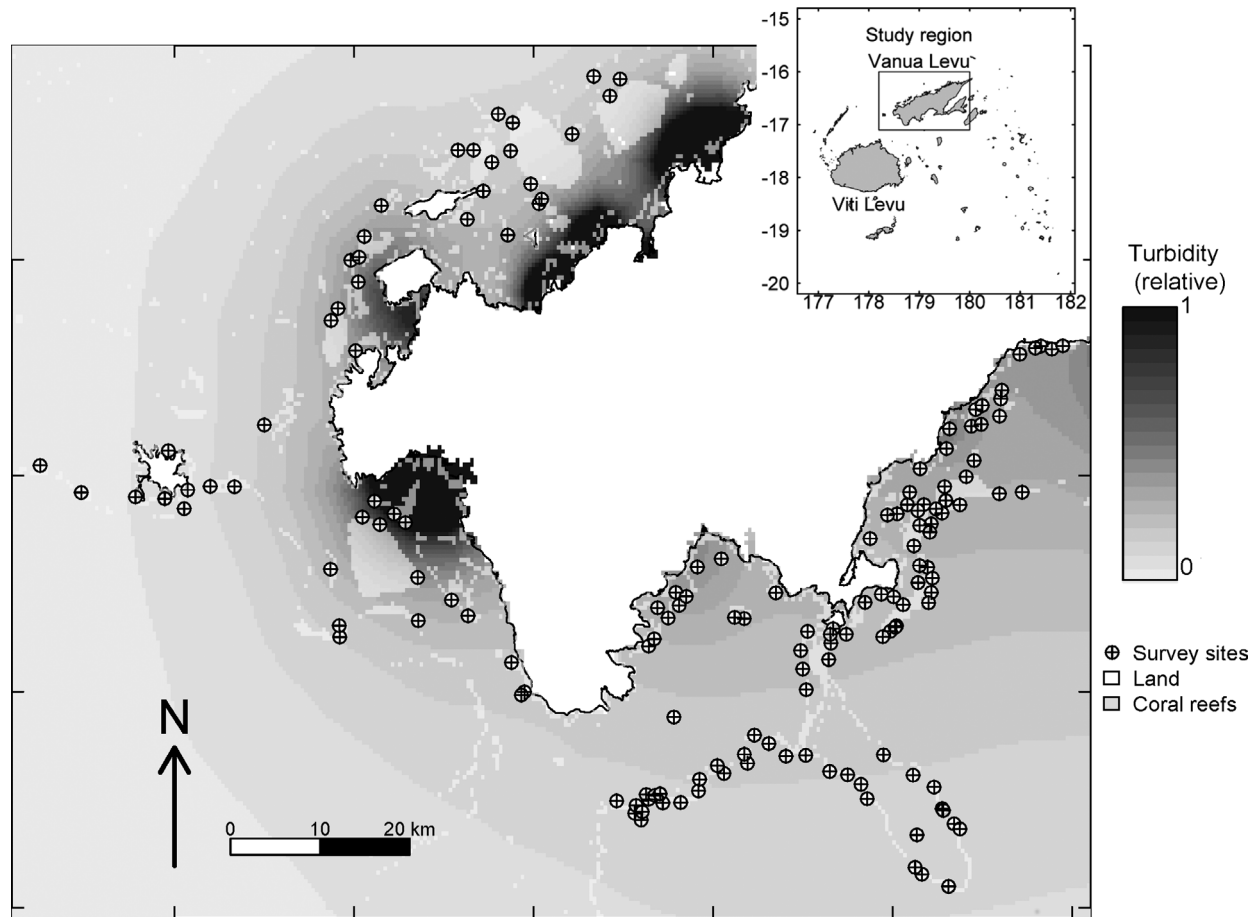
Fig. 2. Study region, study sites and the turbidity gradient (derived from run-off models developed in Brown et al. 2017). Turbidity values are scaled from 0 (minimum value) to 1 (maximum)

habitat types (Brown et al. 2017). We use outputs of the Bayesian model as a broad indicator of the turbidity gradient in our study region.

Fish and benthic habitat data

We used surveys of coral reef benthic habitats and fish counts conducted by the Wildlife Conservation Society at 166 sites. At each site, fish were counted along 2–6 replicate 5×50 m long transects, recording the species, its abundance and estimates of fish length. Length measurements were converted to biomasses using the standard length–weight ($L–W$) expression $W = aL^b$, with a and b parameter values preferentially selected from sites closest to Fiji, as per Jupiter et al. (2012). Following the fish surveys, point intercept surveys for benthic habitats were conducted along each transect, recording benthic categories at 0.5 m intervals according to a standard classification (adapted from Hill & Wilkinson (2004), see Table S1 in the Supplement; www.int-res.com/articles/suppl/ m576p055_supp.xls). Additionally, divers recorded a score of macro-habitat complexity on a 1–5 scale. These scores were normalised by observers prior to analysis (Obura & Grimsditch 2009).

For the purposes of our analysis we derived a further measure of structural complexity based on topologically complex coral life-forms that were presumed to provide fish shelter from predation. The coral life forms that formed our 'structured coral' habitat included: branching, corymbose, sub-massive and digitate corals (including *Acropora* and other genera) (Table S1). We also included a reef matrix category, which was made up of dead coral, reef pavement, crustose coralline algae and coralline algae.

We additionally created a continuous indicator of fishing pressure. While there are temporary fisheries closures in the region, most of these have not been actively enforced for a sufficient duration to act as appropriate controls for our hypothesis tests. Therefore, we needed an alternative indicator of fishing pressure. A useful indicator of fishing pressure from previous studies is mean parrotfish size, where larger

mean size indicates lower fishing pressure (Dulvy et al. 2004a). However, mean size of fish can also be influenced by habitat quality (Nash et al. 2016). To remove the effect of habitat from mean size, we therefore constructed a linear model regressing mean size against macro-complexity (a key habitat variable) and used the residuals from that model as the indicator of fishing pressure.

Fish species were grouped into functional groups for analysis based on earlier studies (MacNeil et al. 2015). The final functional groups were: piscivores, pisci-invertivores, browsers, herbivores, detritivores and planktivores (Table S2 in the Supplement). Parrotfish (family Scaridae) were not included in any functional group, to avoid confounding with the indicator of fishing pressure. Functional groups were chosen so that they were comparable to previous studies (e.g. Wilson et al. 2008) and to enable sufficient functional resolution to test the different hypotheses for how fish relate to their habitats (Table 1).

We classified the benthic categories into fish-relevant categories, based on prior hypotheses for how different fish functional groups relate to benthic habitat (Table 1).

Initially, we explored the response of benthic habitats to turbidity using Bayesian ordination and regression analysis (Hui et al. 2015). Bayesian ordination is a multivariate ordination technique that allows for response variables that are not normally distributed and also allows for the inclusion of fixed effects that constrain the ordination. Thus, we can quantify the response of benthic groups to turbidity directly, while accounting for unexplained correlations in the cover of benthic groups. We regressed benthic cover against turbidity assuming beta-distributed errors (the beta distribution takes values in 0–1) and accounted for between-group correlations using 2 latent variables. A small number (0.001) was added to benthic types with 0% cover to meet the assumptions of the beta distribution (Hui 2016). The macro-

Table 1. Habitat variables hypothesised to be related to each functional group and their hypothesised relationship to runoff-associated turbidity and justification. See Tables S1 & S2 in the Supplement for definitions of fish functional groups and habitat variables. Representative references for associations are also given

Habitat variables	Dependent fish groups and response	Justification for fish	Expected response to runoff-associated turbidity	Prior justification for turbidity response
Turf algae	Grazers + browsers + detritovores +	Food resource or substrate for food (e.g. Purcell & Bellwood 1993, Choat et al. 2002)	+	May replace empty space left by dead corals (e.g. Diaz-Pulido & McCook 2002, Golbuu et al. 2011)
Reef matrix	Grazers + browsers + pisci-invertivores + invertivores +	Substrate for food resource (e.g. McCormick 1995, Choat et al. 2002, Wainwright & Bellwood 2002)	+ or −	Response unclear; may increase in short-term due to coral and coralline algae loss, but decrease over longer term due to overgrowth by algae (Diaz-Pulido & McCook 2002)
Structured coral	All groups + (see text[a] for justification)	Provides refuge from predation	−	Corals die under highly turbid conditions and/or fail to grow (e.g. Birrell et al. 2005, Jupiter et al. 2008, Golbuu et al. 2011)
Macro-complexity	Piscivores + planktivores +	Affinity for structurally complex reefs may be driven by localised upwelling and locally high productivity[b]	−	Forms due to long-term growth of corals. May decline near to rivers due to lack of reef development (Kleypas 1996, Mallela et al. 2004) or erosion of dead corals
Rubble	Detritivores + pisci-invertivores + invertivores +	Substrate for food resource (Wainwright & Bellwood 2002)	+	Forms when corals die and break-up

[a]'Quantifying fish response to turbidity, fishing pressure and habitat change'
[b]This hypothesis was based on observational experience of our authorship team. We could find no specific reference to support this hypothesis; however, it reflects a common observation

complexity score was also included in the Bayesian ordination. Macro-complexity was measured on an ordinal scale, and we found that modelling it with normally distributed errors provided a more accurate fit to the data than using beta errors. We also fit a latent variable model without turbidity, so we could estimate the amount of covariation in benthic cover that is explained by turbidity. We used the boral package (Hui 2016) in the R programming language (R Development Core Team 2016) to implement the Bayesian ordination with 2 latent variables.

Quantifying fish responses to turbidity, fishing pressure and habitat change

We used structural equation models (SEMs) to test for the influence of turbidity on the biomass and abundance of several key functional groups of reef fish (Shipley 2000). Structural equation models enabled us to specify alternate mediating and moderating pathways for turbidity to influence fish biomass (Hamilton et al. in press).

We used linear functions for all relationships in the structural equation models. The response variable was different for the different fish functional groups. For abundant functional groups we modelled their response as ln(biomass ha^{-1}), because this met the normality assumptions of linear models. Biomass estimates for some functional groups contained many zero counts, for these groups we instead modelled abundances using generalised linear models (GLMs) with negative-binomial errors and a log-link function, which we found provided a superior fit to the data. We included an offset term in the abundance model to account for variation in survey area across sites.

For each fish functional group we specified *a priori* 4 or more SEMs for the relationships between turbidity, cover of benthic habitats and fish populations (Fig. 1). We compared alternative models using d-separation tests, where we take $p < 0.05$ as significant (Shipley 2000). For d-separation testing, a significant result indicates a poor model fit. A significant result indicates that there are significant associations between variables that were hypothesised *a priori* to be conditionally independent. The p-value was obtained from a chi-squared distribution, where the test statistic was calculated from the sum over the probabilities of each independence claim and the degrees of freedom was 2 times the number of independence claims (Shipley 2000). A non-significant d-separation test does not necessarily indicate that all hypothesised relationships are significant; therefore, we also

examined individual regression coefficients and their standard errors in all models that were supported ($p > 0.05$). All analyses were performed using the R programming language, using the packages piece-wiseSEM (Lefcheck 2016) and MASS for negative binomial GLMs (Venables & Ripley 2013).

The structural equation models for each functional group were designed to include relevant habitat variables for that group (Table 1). For each functional group we aimed to test 4 primary models that represented alternative hypotheses for the group's relationship with structural complexity (Table 1), turbidity, fishing pressure and predation (stylised representations of the 4 hypotheses for a generic functional group are given in Fig. 1). All models included effects of turbidity on cover of all of a functional group's habitats. Because piscivore biomass was explicitly included as a predictor, we initially tested the models using only small individuals for the response groups (<13 cm) and large individual piscivores (>20 cm) (Wilson et al. 2008). For several groups (pisci-invertivores and planktivores) there were too few sites with counts of small individuals to fit a model to small individuals only. For these groups we therefore ran path models where the response variable included individuals of all sizes; however, doing so precluded testing path models with predation effects.

For functional groups with sufficient sampling of small individuals we designed SEMs to represent the 4 primary hypotheses. Hypotheses A–C only included fishing pressure on predators and not prey fish, because the functional groups for prey fish included only small individuals. Hypothesis D included fishing pressure on prey fish, because the functional groups were expanded to include large individuals. We now describe these hypotheses and the ecological processes they represent.

First, we hypothesised a moderation effect whereby structural complexity reduced the vulnerability of the group to predation (e.g. Almany 2004) (Fig. 1A). Moderation was tested by allowing for an interaction between structural complexity and biomass of large piscivores, where the expectation was that the structural complexity would have a greater positive effect when predator biomass was higher (synergistic interaction between habitat cover and predator biomass). A moderation effect may occur if greater coverage of structural complex habitats provides greater access of prey individuals to refuges from predation (Rogers et al. 2014).

Second, we hypothesised that a functional group is directly affected by its habitats, as well as biomass of large piscivores, such that the group's response to tur-

bidity depended on the relative strengths of the predation and habitat effects (Fig. 1B). Specific reasons for fish biomass to co-vary with cover of different benthic habitats depend on the functional groups (Table 1) but may include foraging in specific habitats or habitat selection (e.g. Friedlander & Parrish 1998, Feary et al. 2007).

Third, we hypothesised that habitats mediate the effects of turbidity on both a functional group and its predators, so that both predators and the group would change linearly with turbidity (Fig. 1C). Justification for this hypothesis is similar to Hypothesis B, except that it assumes no statistically recognisable effect of predator biomass on prey biomass. Predator and prey biomass may be uncorrelated if predation pressure is too small to affect prey biomass, or there are non-linear effects such as the paradox of enrichment (Rosenzweig 1971).

Finally, where all of the initial 3 models showed poor fits to the data, we hypothesised that habitats alone would drive a functional groups' biomass or abundance and we removed piscivore biomass from the path analysis (Fig. 1D). In this final model we included individuals of all sizes. Justification for Hypothesis D is similar to C, except that by removing piscivores from the model, models are evaluated only on their ability to represent prey biomass, and not simultaneously prey and piscivore biomass.

We fitted similar models for all functional groups, except detritivores. We did not fit the models with structural complexity to detritivore abundance, because they are known to forage primarily in structurally simple habitats (Williamson et al. 2014). Further, none of the 4 hypotheses (A–D) were supported for detritivores, so we included an additional model for this group where there was a direct effect of turbidity on detritivore biomass. The exact specification of the models for each functional group was built around the 4 primary hypotheses, but additionally included key habitat variables where we had specific hypotheses to relate that habitat variable to a functional group's population (Table 1).

Where multiple habitat variables were included in the path models, we additionally had to account for relationships between habitat variables. In the SEMs we specified additional paths using the logic as follows. Component models for the macro-complexity score included relationships with the cover of structurally complex corals, because the macro-complexity score is higher with increased structural complexity. Component models for turf algae included a dependency on structurally complex corals, because corals settle and grow over

turfs in clear waters (e.g. McCook 2001). The Bayesian ordination also indicated 2 further correlations. The first was a negative correlation between cover of reef matrix and structurally complex corals and may represent an exposure gradient. The second was a negative correlation between cover of structurally complex corals and rubble, which may occur because rubble is formed by the break-up of dead corals.

Our final question was to compare the magnitudes of fishing and turbidity effects on fish populations. We thus calculated the total change in fish biomass/abundance from the most to the least turbid waters, assuming fishing pressure was set at its either its minimum, mean or maximum values using the method of Imai et al. (2010). For comparison, we calculated the total change in fish biomass/abundance from the highest to the lowest fishing pressure value assuming turbidity was set at its minimum, mean or maximum value. Log biomass was converted to natural units using the smearing estimate for Gaussian residuals given in Newman (1993).

RESULTS

Habitat change across the turbidity gradient

The Bayesian ordination indicated significant effects of turbidity on the cover of the benthic habitat types (Fig. 3A). More turbid sites were characterised by higher covers of unconsolidated sediment and turf algae (lower 95% credibility interval >0), whereas sites with relatively clear water possessed higher covers of coral, structurally complex coral, 'other biotic' (e.g. sponges and soft corals) reef matrix, and higher macro-complexity scores. Overall, we estimated that turbidity explained 63% of the variation in cover of benthic habitat types. Cover of macroalgae and rubble did not show significant responses to turbidity. Note that cover of macroalgae was low (range: 0–14%, median: 0.5%) compared to degraded reefs in other countries (e.g. De'ath & Fabricius 2010).

Cover of benthic habitat types were associated, even after accounting for turbidity, as indicated by the loadings of the habitats on the 2 latent variables (see Fig. 3B, benthic habitat variables that are close together are positively associated, whereas variables that are opposing are negatively associated). For instance, higher cover of structured coral was associated with lower cover of reef matrix.
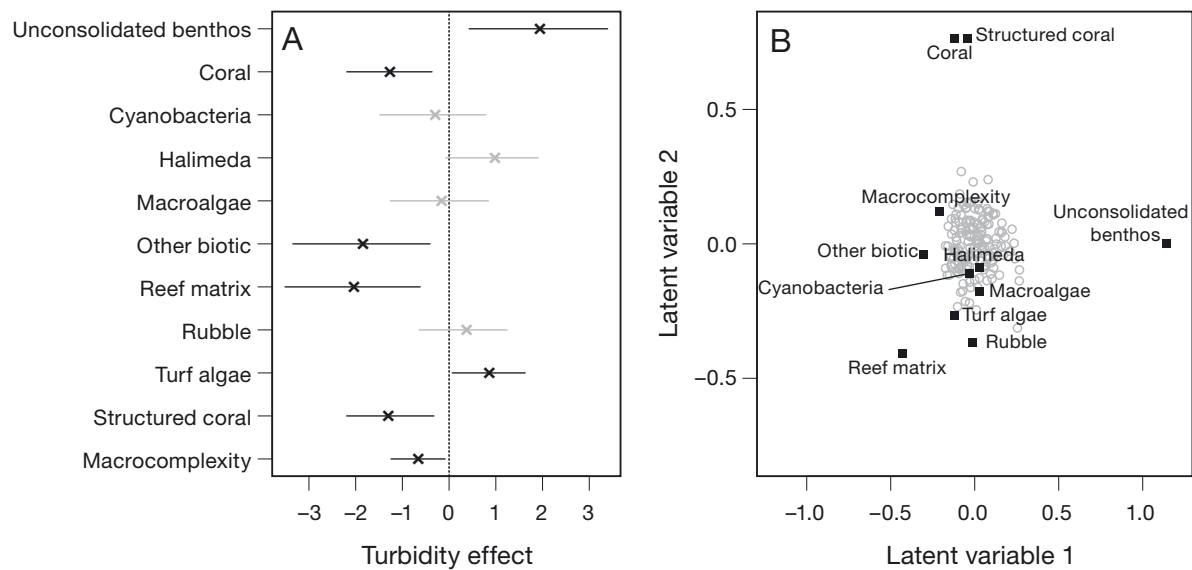
Fig. 3. Bayesian ordination of benthic habitats showing (A) the effect of turbidity on each benthic habitat type (crosses: medians; horizontal lines: 95% credibility intervals, intervals for black crosses do not overlap zero) and (B) ordination plot of the latent variables. Grey circles: site-level values on the 2 latent variables. Black squares: influence of each benthic habitat type. For instance, structurally complex coral and rubble tended be negatively associated (because their scores on the *y*-axis have opposite signs), even when the effect of turbidity was included

Responses of fish functional groups to turbidity and fishing

Across all functional groups, Hypotheses A–C generally were not supported by the data, whereas Hypothesis D was supported (Table 2). For piscivores, the models with effects of large predators on small piscivores (Hypotheses A–C) were supported by the d-separation tests (p > 0.05, Table 2). However, the estimated effect of predators on prey was weak (regression coefficient = 0.0036, standard error = 0.02), indicating there was no evidence for trophic cascades. None of the models A–D were supported for detritivores, because of a direct negative association between detritivore abundances and turbidity that could not be explained by any habitat associations (Table 2, Fig. 4).

Overall, the lack of predation effects in our analysis indicates that for the Fijian reefs, habitat was a more important driver spatial gradients of fish abundances/biomasses than predation. We find no evidence for a moderating effect of structurally complex habitats on predation pressure (Table 2).

Next we analysed the direction of change in fish abundance/biomass using only the path models that were able to explain the covariances among turbidity, habitat and fish populations (i.e. the non-significant models without predation effects in Table 2).

The indicator of fishing pressure was associated with lower abundances/biomasses for all functional groups (Fig. 4). All functional groups responded to turbidity except for pisci-invertivores (at least one significant path from turbidity to abundance/biomass—Fig. 4); however, their responses were mediated by different habitats. Lower piscivore biomass and planktivore abundances were associated with higher turbidity values (Figs. 4 & 5). The response of piscivores to turbidity was mediated by declining macro-complexity. The net effect of turbidity was small on most functional groups, aside from planktivores and piscivores. The total effect of turbidity on invertivore, browser and grazer groups was weak because the effect of turbidity on their habitats was both positive and negative (Fig. 4). Detritivores increased slightly under more turbid conditions, due to an increase in turf algae—a foraging habitat.

The fishing pressure indicator was associated with greater changes in the biomass/abundance of more functional groups across its range than the effect of turbidity (Fig. 5). Fishing pressure also masked the effects of turbidity; when fishing pressure was moderate to high, the effect of turbidity was small (Fig. 5), because fish biomass was depleted. The effect of fishing on planktivores and piscivores was also smaller under high turbidity, because fish biomass was simultaneously depleted by high turbidity (Fig. 5).

Table 2. Results for the path models testing alternative hypotheses (A–D) for the role of fishing, predation and habitat in each functional group's biomass or abundance. The number of independence claims gives the number of variable pairs hypothesised to be conditionally independent, and the *C*-statistic gives the test statistic used to obtain the p-value from the chi-squared distribution (Shipley 2000). Significant p-values (<0.05) indicate that a given path model did not adequately explain covariation of the data. Models for corresponding hypotheses are given by letters, where A is a moderation effect, B is mediation of turbidity effects via habitat with top-down predation pressure, C is a mediation effect of habitat that co-drives predator and prey biomass and D is a mediation effect of habitat on the target functional group only. Model D for planktivores and detritivores included a direct effect of turbidity. WQ: water quality

Model	Response variable	No. of independence claims	*C*-statistic	p
Piscivores				
A	Abundance small ind.	9	18.1	0.45
B	Abundance small ind.	4	8.2	0.418
C	Abundance small ind.	5	9.72	0.465
D	Biomass all ind.	4	2.1	0.717
Invertivores				
A	Log(biomass) small ind.	17	68.5	0.001
B	Log(biomass) small ind.	11	51.7	0.001
C	Log(biomass) small ind.	12	56.6	0.001
D	Log(biomass) all ind.	4	7.29	0.505
Browsers				
A	Abundance small ind.	13	64.5	<0.001
B	Abundance small ind.	11	53.1	0.001
C	Abundance small ind.	10	46.2	0.001
D	Abundance all ind.	4	6.5	0.61
Grazers				
A	Abundance small ind.	18	78.0	<0.001
B	Abundance small ind.	11	44.5	0.003
C	Abundance small ind.	12	47.8	0.003
D	Biomass all ind.	4	12.9	0.12
Detritivores				
B	Abundance small ind.	13	83.2	<0.001
C	Abundance small ind.	14	88.6	<0.001
D	Abundance large and small ind.	4	55	<0.001
D + effect of WQ	Abundance large and small ind.	3	0.29	>0.99
Pisci-invertivores				
D		5	13.7	0.19
Planktivores				
D		3	5.2	0.52

DISCUSSION

We tested multiple structural models for the interactive effects of turbidity from sediment run-off and fishing pressure on multiple fish functional groups around the reefs of Vanua Levu, Fiji. We found little evidence for models that included top-down effects of predators on prey biomass. We also found no evidence from our analysis of spatial associations that structural complexity would regulate trophic cascades (Salomon et al. 2010) or that overfishing combined with nutrient enrichment would cultivate pop-

ulations of herbivorous fish on degraded reefs (reviewed in Brown & Trebilco 2014). The strongest support was found for models that included a direct effect of fishing pressure on large fish and an effect of turbidity on most functional groups via the mediating effects of habitat. Our results add support to findings that fish populations and their habitats are sensitive to both overfishing and the impacts of pollution (Cheal et al. 2013). Further, the weakening effects of turbidity under higher fishing pressures suggested that fishing may mask the effects of pollution on fish populations. Thus, simultaneous management of catchments and fisheries is important for the conservation of Fiji's reef fish populations.

Several fish functional groups had both positive and negative associations with turbidity via the mediating effects of habitat. Thus, land-based run-off may not always simultaneously reduce biomass across an entire fish community (e.g. Jones et al. 2004, Bejarano & Appeldoorn 2013). Instead, run-off may alter the composition of reef communities. Reefs in highly turbid areas may still support some important fish functional roles and fisheries for some species, such as detritivores. However, we found that piscivorous fish were the most sensitive functional group to turbidity change. In Fiji, piscivorous fish have the highest sale value (Teh et al. 2009), so while highly turbid areas may still support food provisioning, their economic and cultural values may be degraded.

Piscivorous fish were found to have the greatest decline of any functional group across the gradient of turbidity due to their association with macro-complexity, which declined at higher turbidity. We hypothesised piscivorous fish would prefer higher macro-complexity, because macro-complexity would drive localised patches of high productivity, and therefore, food resources for piscivores. The decline
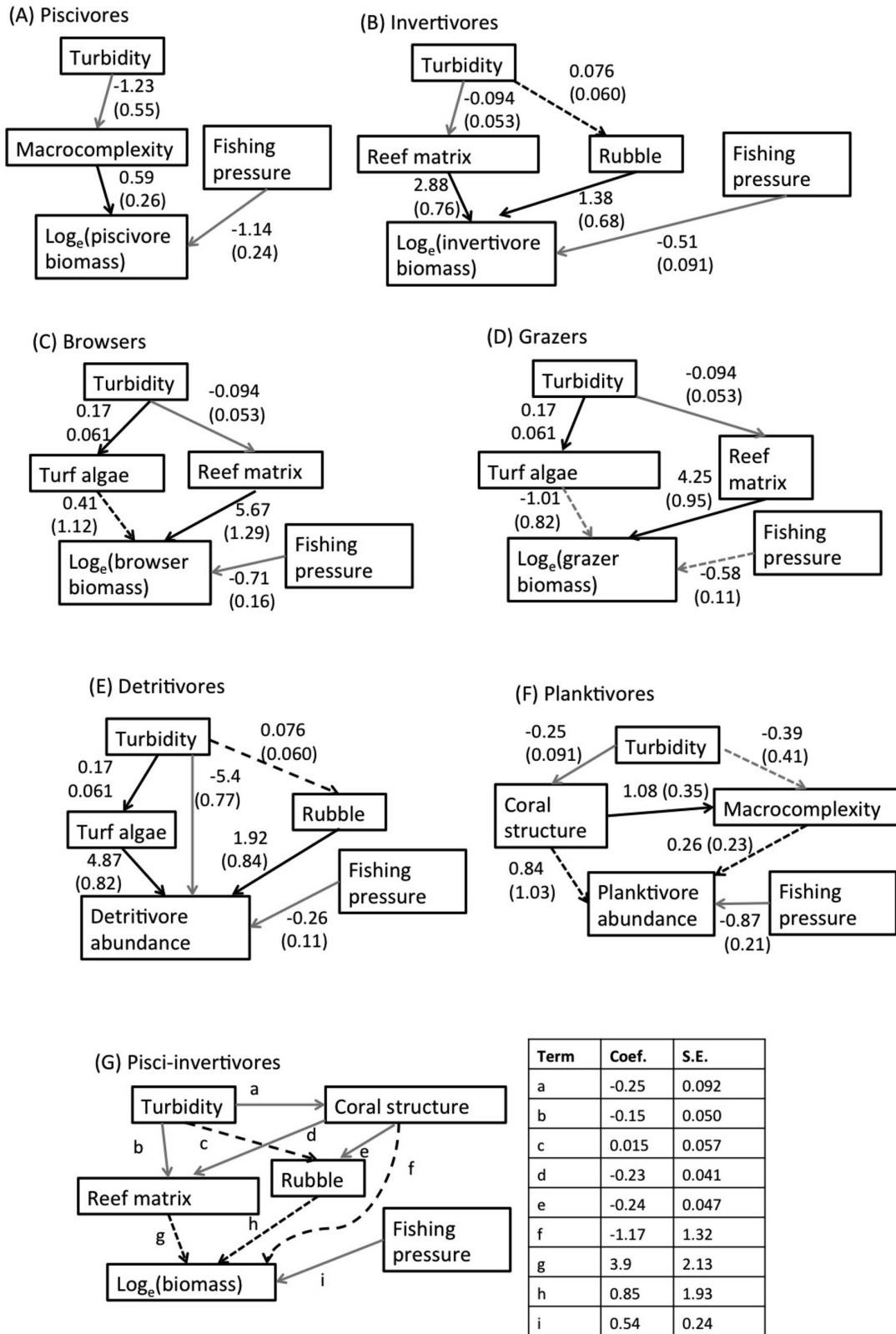
Fig. 4. Final structural equation models for (A) piscivores, (B) invertivores, (C) browsers, (D) grazers (E) detritivores, (F) planktivores and (G) pisci-invertivores. Model G is complex, so effects are given in the table. Grey arrows: negative effects; black arrows: positive effects; dashed arrows: effects included in the final model but where p > 0.05
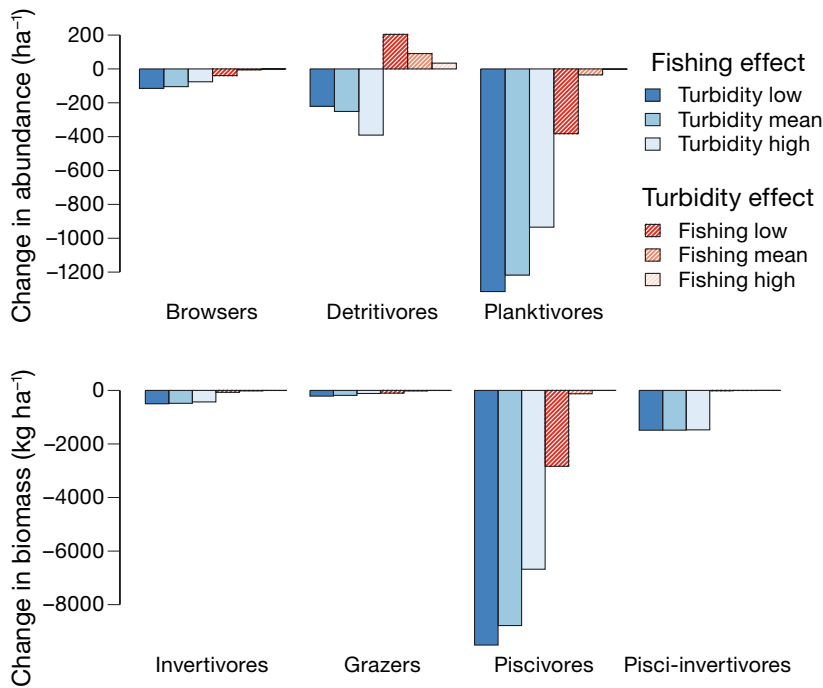
Fig. 5. Marginal effect of fishing (solid blue bars, shading indicates the turbidity level) and turbidity (striped red bars, shading indicates the fishing level) on fish abundance for functional groups where the response was (A) abundance counts and (B) biomass. Negative effects indicate a decline in biomass/abundance as fishing pressure or turbidity increase. Marginal effects were calculated across the full range of turbidity/fishing values

in macro-complexity at higher turbidity may be due to limited reef development in naturally turbid areas (Kleypas 1996, Mallela et al. 2004). Further tests of piscivore dependence on macro-complexity should seek comparison of piscivore biomass across sites with both high turbidity and high macro-complexity, such as on topographically complex rocky reefs. Our hypothesis predicts high piscivore biomass at high turbidity provided macro-complexity is high.

Comparison of effect sizes indicated that fishing was a stronger driver of fish biomass than turbidity in this region, and high fishing pressure could mask the effects of turbidity. This finding is consistent with other regions, where the effects of water quality on reef fish populations have generally been smaller than the effects of fishing pressure (Houk et al. 2015) and variation in the spatial arrangement of seascapes (Gilby et al. 2016). The effects of water quality on fish populations may be harder to detect than fishing effects, because change in water clarity can have detrimental but non-lethal, effects on individual fish (e.g. Wenger et al. 2012). Studies that measure the health of individuals are required for a more comprehensive evaluation of the effects of water quality change on coral reef fish and fisheries. For instance, terrestrial run-off can increase parasite loads on

fished species, decreasing their size and market value (Van Holt et al. 2012). The value of Vanua Levu's fisheries are likely primarily driven by fishing pressure, rather than turbidity, because land-clearing and associated run-off has historically been restricted to a few areas (Brown et al. 2017). However, future increases in land clearing are likely, and these may increase the extent of the most turbid waters and could become a dominant driver of fish biomass for inshore and lagoonal reefs in the longer term.

A challenge in studying the effects of turbidity gradients on fish populations is that turbidity is strongly associated with other major gradients in reef environments. For instance, nursery habitats for many reef fish are often associated with rivers (e.g. mangroves), so while the detrimental effects of turbidity may decrease further from shore, so will the availability of nursery habitats. Co-varying environmental gradients could potentially confound fish responses to turbidity with other environmental effects, like the effect nursery habitats on predation (Harborne et al. 2016). For Vanua Levu reefs, we were able to partially control for confounded environmental covariates by having contrasting water quality between northern and southern coastlines and limited proximity of all surveyed reefs to mangroves. However, a future research priority should be the analysis of fish responses to spatio-temporal gradients of pollution (e.g. Hughes et al. 2015). Temporal contrasts in turbidity would provide greater power to detect complex ecological changes, such as a moderating effect of turbid waters on trophic cascades.

We found little evidence that interactions among the fish community, such as trophic cascades or moderation, drove spatial variability in fish biomass. There is mixed evidence for trophic cascades on coral reefs (Dulvy et al. 2004b, Boaden & Kingsford 2015, Roff et al. 2016, Casey et al. 2017), with studies in Fiji generally finding weak or no top down control of reef fish species (Jennings & Polunin 1997, Wilson et al. 2008). Absence of trophic cascades manifesting in spatial contrasts also precludes us from detecting moderation effects in this study. This is surprising, because moderation effects are strong enough to manifest as spatial differences in abundances in other systems, such as when mangrove habitats pro-

vide nurseries for juvenile fish (Harborne et al. 2015). The lack of evidence for predation effects in our study most likely reflects extensive fishing of predatory fish across our study region. The detection of predation effects may therefore require control sites with no fishing pressure. Predation effects may also be hidden by a multitude of other processes governing reef fish dynamics (Jennings & Polunin 1997), including the effects of climate variability on recruitment (e.g. Cheal et al. 2007, Brown et al. 2016), productivity gradients (Williams et al. 2015), trophic redundancy (e.g. Roff et al. 2016, Casey et al. 2017) and competition between our functional groups other organisms, such as between grazing fish and sea urchins (Birkeland 1989). Further, abundance, a state variable, may be a poor indicator of predation rates, which is a rate variable. Thus, a priority for future studies of trophic cascades is to use temporal data to estimate productivity change across gradients of fishing pressure that include unfished sites.

Our analysis cannot exclude the possibility that moderation is an important driver of temporal dynamics of fish populations (Almany 2004). Moderation is commonly included in dynamic models of fish and their habitats (e.g. Walters et al. 1997), and if it is strong, it suggests that degraded reefs can support fisheries for prey populations if predators are also overfished (Rogers et al. 2015). Thus, we need further temporal studies of habitat complexity and fish biomass to untangle the importance of moderation in regulating predation, particularly on reefs degraded by pollution. Despite the shortcomings of spatial contrasts, we did find that the composition of benthic habitats was a more important driver of fish biomass than predation, supporting the dominant role of habitat and management of fisheries for all trophic levels in conserving coral reef fish populations.

One caveat to our analysis was unavailability of a direct measure of fishing pressure. Thus, we used a proximate indicator of fishing pressure. Use of such indicators is widespread; however, indicators may confound multiple ecological and economic gradients (Nash et al. 2016). Ideally, we would include a direct measure of fishing pressure, such as in studies that have analysed for trophic cascades by comparing inside and outside of no-take protected areas with varying degrees of protection (e.g. Casey et al. 2016). However, in Fiji, fisheries closures are not legally binding (Clarke & Jupiter 2010) or well enforced (Jupiter et al. in press b), and Vanua Levu's closures are not old enough to allow full recovery of fish biomass (MacNeil et al. 2015). We therefore used an indicator of fishing pressure that corrected for

habitat effects. The indicator could be improved by accounting for travel times from points of sale; however, field surveys to identify the location of fish buyers would be required (Maire et al. 2016). A more direct indicator of fishing pressure may give the analyst greater power to detect moderating effects of habitats on predation pressure.

We found fishing pressure and pollution from land-based run-off both affect coastal reef fish populations. Moderate to high fishing pressure masked the effects of habitat change on reef fish, meaning that the effects of pollution may often be difficult to detect. In locations with low fishing pressure, the response of reef fish to habitat change was variable, such that pollution modified the composition of reef fish communities. Our findings echo earlier calls for reef fish management to encompass both fisheries and linked catchments (Caddy 2000, Jupiter et al. 2017b). Management of catchments will help to sustain the composition of reef fish functional groups and the reef fisheries that are of greatest value for people.

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