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Local Human Impacts Disrupt Relationships Between Benthic Reef Assemblages and Environmental Predictors

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Human activities are changing ecosystems at an unprecedented rate, yet large-scale studies into how local human impacts alter natural systems and interact with other aspects of global change are still lacking. Here we provide empirical evidence that local human impacts fundamentally alter relationships between ecological communities and environmental drivers. Using tropical coral reefs as a study system, we investigated the influence of contrasting levels of local human impact using a spatially extensive dataset spanning 62 outer reefs around inhabited Pacific islands. We tested how local human impacts (low versus high determined using a threshold of 25 people km^{-2} reef) affected benthic community (i) structure, and (ii) relationships with environmental predictors using pre-defined models and model selection tools. Data on reef depth, benthic assemblages, and herbivorous fish communities were collected from field surveys. Additional data on thermal stress, storm exposure, and market gravity (a function of human population size and reef accessibility) were extracted from public repositories. Findings revealed that reefs subject to high local human impact were characterised by relatively more turf algae (>10% higher mean absolute coverage) and lower live coral cover (9% less mean absolute coverage) than reefs subject to low local human impact, but had similar macroalgal cover and coral morphological composition. Models based on spatio-physical predictors were significantly more accurate in explaining the variation of benthic assemblages at sites with low (mean adjusted-R^2 = 0.35) rather than high local human impact, where relationships became much weaker (mean adjusted-R^2 = 0.10). Model selection procedures also identified a distinct shift in the relative importance of different herbivorous fish functional groups in explaining benthic communities depending on the local human impact level. These results demonstrate that local human impacts alter natural systems and indicate that projecting climate change impacts may be particularly challenging at reefs close to higher human populations, where dependency and pressure on ecosystem services are highest.

Keywords: climate change, reef degradation, ecological reorganisation, ecological homogenisation, generalised additive models, model selection

INTRODUCTION

Humans have become a dominant force of planetary change (Steffen et al., 2007). Ecosystems worldwide are being fundamentally altered by climate change impacts against a diverse backdrop of local anthropogenic stressors. Our ability to reliably predict the future configuration of affected ecosystems requires a thorough understanding of interactions between these different stressor types (Williams et al., 2019). Increasing evidence indicates that ecosystems are being reorganised or homogenised into stress-tolerant or opportunistic communities, leading to novel systems that differ from their previous state in terms of their dominant constituents (Graham et al., 2014; Morse et al., 2014). Quantifying ecological reorganisation over broad scales remains challenging due to coarse taxonomic resolution inherent to large datasets that are necessary to address this topic. Nonetheless, this phenomenon may significantly alter a system's relationship with various environmental and climate change-related drivers (Côté and Darling, 2010; Williams G.J. et al., 2015). Understanding what role local human impacts play in driving ecological reorganisation and changing a system's relationship with its biophysical environment is thus pivotal to improving predictive models and informing local management (Robinson et al., 2018; Jouffray et al., 2019; Henderson et al., 2020).

Inherent high biodiversity and the presence of multiple stressors acting at local and global scales make tropical coral reefs a unique system to examine how local human impacts drive ecological states (Hoegh-Guldberg et al., 2007; Ban et al., 2014; Norström et al., 2016; Darling et al., 2019). Locally, rapidly expanding coastal development, sewage input, and agricultural practices are reducing water quality, whilst the modernisation of fishing gear and expedited market access are facilitating overexploitation of coastal fisheries resources (Fabricius et al., 2005; Brewer et al., 2012; Hamilton et al., 2012). Globally, the intensity and frequency of thermal anomalies, unusual weather patterns, and destructive storm events are increasing (Gattuso et al., 2015; van Hooidonk et al., 2016; IPCC, 2019), and recovery windows between stress events are narrowing (Riegl et al., 2013; Hughes et al., 2018). The productivity and provision of ecosystem services (e.g., Woodhead et al., 2019) of coral reef benthic communities differ depending on their composition (Ferrario et al., 2014; Rogers et al., 2018), underlining the importance of quantifying how communities are affected by global change. The widespread negative effects of climate change-related stressors are relatively well-understood. However, despite more than half the world's coral reefs being located within 30 min travel time from human populations (Maire et al., 2016), the role of local stressors remains somewhat contested. These local stressors can range greatly in their intensity depending on inherent factors such as human population density and the level of exploitation of, or reliance on, marine resources.

Higher human population densities have been linked to reductions in reef fish biomass and coral cover, and to increases in fleshy (turf and macro-) algal cover (Sandin et al., 2008; Williams I.D. et al., 2015; Heenan et al., 2016; Smith et al., 2016). However, coarse taxonomic resolution (inherent to large-scale datasets) can lead to the conclusion that there is no link between local stressors and reef condition (e.g., Bruno and Valdivia, 2016). This may be a particular issue in regions such as the tropical Pacific where species diversity is exceptionally high and fleshy macroalgae, frequently stated as principal alternative organisms on degraded reefs, do not play such a dominant role in benthic dynamics compared, for instance, to the Caribbean region (Roff and Mumby, 2012). Furthermore, reefs are increasingly existing in a partially degraded condition between distinct regimes (Mumby, 2017), likely having undergone ecological homogenisation resulting from the non-random removal of species with particular traits in response to environmental factors (McWilliam et al., 2020). In this case, coral cover can remain moderate but comprises a less diverse community of stress-tolerant and opportunistic types (Côté and Darling, 2010; van Woesik et al., 2011; Riegl et al., 2013). Ecological homogenisation is visible across reef habitat types, with inshore reefs that are naturally exposed to a more challenging environment (e.g., in terms of light, temperature, and sediment input) favouring a smaller species pool of stress-resistant corals compared to nearby outer reef habitats (Rogers, 1990; Browne et al., 2013; Williams et al., 2013; Schoepf et al., 2015; Morgan et al., 2016).

A recent study demonstrated that whilst sea surface temperature (SST), chlorophyll concentration, and wave energy have strong power in predicting benthic assemblages at remote reefs, this predictive power is lost or the relationships fundamentally altered at reefs closer to human populations (Williams G.J. et al., 2015). Considering the dominant role of humans in shaping ecosystems, factors associated with local anthropogenic impacts may have overtaken biophysical drivers in structuring these altered reefs. It has also been postulated that reorganisation toward a stress-tolerant coral community could increase resilience to climate change, assuming co-tolerance between local and climate change-related stressors (Côté and Darling, 2010), in line with the concept of "intrinsic resistance" (Darling and Côté, 2018). Indeed, coral richness does not translate into higher resilience to disturbances (Zhang et al., 2014). Better understanding and accounting for the role that local human impacts play in shaping benthic communities and their relationships with environmental drivers is important for developing theories, designing experiments, setting baselines, informing management, as well as optimising large-scale spatial predictive models for coral reef futures.

Here, we investigate how local human impacts affect coral reef benthic communities in the tropical Pacific. We start by classifying 62 island sites into two levels of local human impact (low versus high) using a set threshold of human population density informed by previous work (i.e., D'agata et al., 2014). We then ask whether the level of local human impact influences benthic community structure or the relationship between benthic community structure and spatio-physical explanatory drivers. Lastly, we examine the relative roles of ten biophysical parameters as drivers of benthic community structure under low versus high local human impact. We hypothesised that benthic community structure would be more related to spatio-physical drivers on reefs exposed to low local human impact compared to those with high local human impact, where we expect human-associated factors to have become more dominant. This approach allowed us to develop on the findings of Williams G.J. et al. (2015) by testing whether decoupling between reefs and biophysical drivers in the presence of humans was also detectable between different levels of local human impact.

MATERIALS AND METHODS

Study Area and Sampling Design

This study intended to build on work from Williams G.J. et al. (2015) by assessing in more detail how local population density, rather than human presence/absence, potentially decouples the relationship between reef benthos and larger-scale environmental drivers. To do so, we utilised a large-scale dataset that is unique in having both site-level ecological (fish and benthic) and socio-economic data (in particular human density per reef area at the site level), which is missing from other datasets that rely on global socioeconomic estimates for human population density, or in some cases district-level surveys. Fish and benthic communities at 62 reefs within 17 different Pacific Island countries and territories were surveyed once between 2003 and 2008 (see **Supplementary Figure 1** for map) as part of the Pacific Regional Oceanic and Coastal Fisheries Development Programme (PROCFish/C/CoFish) under the auspices of the Pacific Community (SPC). Importantly, all reefs were in close vicinity to, and used by, coastal human communities across a large range of intensities (e.g., relative human density ranged from 1.3 to 1705 humans km^{-2} reef). For site disturbance history, sampling dates and detailed sampling methodology, refer to **Supplementary Table 1** and Pinca et al. (2010). Though it is important to acknowledge that the sampling programme was not originally designed in a way to address macroecological questions or aggregate beyond the state/territory level, we did our best to account for the shortcomings in the design by including additional information such as observer bias (see section "Data Analyses" for details on environmental parameters included). Furthermore, while data may not be representative of the current-day scenario, it is the trends that are important for this study. Accordingly, we are confident that despite some inevitable compromising, this gave us the best possible dataset to look at the effects of site-specific human density.

Field Surveys

Underwater surveys covered outer (fore-) reefs, with on average nine (n = 3–47) joint fish-benthic 50 m transects measured at each site. Transect data were pooled within each site. Reef fish communities were measured using the variable distance-sampling underwater visual census method along transects (described in Labrosse et al., 2002). Data on abundance and size were recorded to species-level for herbivorous fish. Counts were converted to biomass (g m^{-2}) from established length-weight relationships (Kulbicki et al., 2005). Benthic cover data was obtained using the medium-scale approach described by Clua et al. (2006). This method is based on a semi-quantitative description of ten 25 m^2 (5 × 5 m) quadrats laid down on each side of the 50 m transect (i.e., 20 replicate quadrats/500 m^2 per transect). Surveyors first recorded abiotic and live coral substrates, i.e., sand, rubble, rocky slab, boulders, and hard coral — live, bleached, and long dead, with live coral divided into broad morphologies (e.g., branching, encrusting, massive). Each component was quickly estimated using a semi-quantitative scale ranging from 0 to 100% per quadrat, in units of 5%. Secondly, benthic groups (e.g., macroalgae–inclusive of calcified and fleshy types, turf algae, crustose coralline algae [CCA], sponges, cyanobacteria) growing over abiotic substrate such as long dead coral were recorded using the same semi-quantitative scale (**Table 1**).

Fishing grounds were initially delineated from information given by local fishers and quantified from satellite interpretations (similar to methods in Close and Hall, 2006; Léopold et al., 2014). Total reef area (km^2) within each fishing ground was then derived from reef areas quantified by the Millennium Coral Reef Mapping Project from satellite images (Andréfouët et al., 2006). Socioeconomic assessments determined total population within communities with access to the fishing ground, allowing subsequent calculation of human population relative to reef area (referred to as "relative human density"). Finfish landings for each site, determined from interviews with fishers, were extrapolated to total finfish catch per year per reef area ("relative fishing pressure") (see Pinca et al., 2010).

Data Analyses

Response Variables

As response variables, we selected the main benthic groups (i.e., those with a mean composition >10% of benthic community): dead coral (incorporating long dead coral, rubble, boulders, and pavement), live hard coral, and algal groups (differentiating turf algae, macroalgae, and CCA). We also assessed the proportional representation (within the live hard coral community) of the three most commonly observed morphological groups: branching, encrusting and massive morphologies. Pairwise relationship tests (*corvif* function–Zuur et al., 2009) established no collinearity among the response variables (correlation; $R^2 < 0.5$). **Table 1** provides an overview of the benthic variables and their ranges.

TABLE 1 | Benthic variables included in the models and their ranges.

Variable	Description	Range (%)
live hard coral	mean cover (%) of live hard coral	6.1–65.1
dead hard coral	mean cover (%) of dead hard coral; including rubble, boulders, and pavement. Dead hard coral may also include biotic groups (i.e., growing over the dead coral), which are further classified as additional categories below*	5.5–61.2
branching morphologies	proportion (%) of branching coral morphologies within live hard coral community	0.1–85.6
encrusting morphologies	proportion (%) of encrusting coral morphologies within live hard coral community	2.8–72.9
massive morphologies	proportion (%) of massive coral morphologies within live hard coral community	0.1–60.6
CCA	mean cover (%) of crustose coralline algae	0.2–43.5
macroalgae	mean cover (%) of macroalgae; inclusive of calcified and fleshy types	0.0–31.2
turf algae	mean cover (%) of turf algae	0.0–45.6

**not all categories are mutually exclusive–abiotic (e.g., dead coral, sand) and live coral substrates were recorded up to 100%, and biotic cover (e.g., algal groups) was recorded separately up to 100% (i.e., sum of substrate and biotic cover $\neq$100%).*

Model Predictors

We had to make a feasible choice of how to determine low versus high impact sites. Rather than choosing a completely arbitrary threshold, we selected one that was informed by previous findings by D'agata et al. (2014)–using boosted regression trees for the same dataset, the authors identified 25 people km^{-2} reef to be the threshold after which taxonomic diversity of parrotfishes significantly declined. We then ran a sensitivity analysis to demonstrate how robust our findings were (see section "Assumptions and Sensitivity Tests"). To compare reefs exposed to different disturbance regimes, we thus categorised all sites into those subject to low (i.e., $<$25 people km^{-2} reef; n = 29) and high (i.e., $>$25 people km^{-2} reef; n = 33) local human impact. Relative human density correlates with relative exploitation–i.e., relative human density was collinear (R^2 = 0.8) with fishing pressure (tonnes fish km^{-2} reef year^{-1}; **Table 2**). This threshold was also a median point and allowed similar sample sizes in each impact level (see **Supplementary Figure 2**). Relative human density also showed weak positive correlation with market gravity–an index combining the population size of nearby human settlements and their accessibility to reefs (Cinner and Maire, 2018; Cinner et al., 2018). However, we decided to base our study on relative human density as we had unique site-level data and we see this metric to be more directly linked to benthic communities in terms of human density-dependent sewage and agricultural run-off in addition to subsistence and artisanal fishing.

The selected biophysical predictors included a variety of factors that were either collected during field surveys or extracted from public data repositories (**Table 2**). Due to inherent differences in coral reefs across latitudinal scales (e.g., Hughes et al., 1999; Harriott and Banks, 2002), latitude was represented by degree distance from the equator without differentiating between north and south (0–23.9°). Degree heating weeks (DHW) data were extracted from the NOAA Coral Reef Thermal Anomaly Database (CoRTAD version 4 – Casey et al., 2012). Storm exposure was quantified from the NOAA IBTrACS-WMO data (Knapp et al., 2010a,b) within ArcMAP 10.4 (ESRI, 2011), where the number of storms (categories 1–5 on the Saffir-Simpson Hurricane Scale) passing within a 50 km radius of each site (Behrmann projection) was extracted. Storm exposure and DHW data were confined to 12 years prior to each respective site's survey date based on the premise that remote reefs can recover from acute disturbances within this timeframe (Sheppard et al., 2008; Gilmour et al., 2013). Reef depth, estimated during field surveys, was averaged over all transects at each site. Island relief refers to each site's geomorphology, and was classified into three categories: atoll, low-lying island, and high island based on available information (see **Supplementary Table 1** for references), and authors' knowledge. Island relief was included as a predictor due to its known influence on coral reef benthic and fish communities (Donaldson, 2002; Houk et al., 2015). Herbivorous fish from selected families (e.g., excluding herbivorous damselfish) encountered during visual surveys were classified into functional groups according to Heenan et al. (2016) (see **Supplementary Table 2**). Biomasses (g m^{-2}) of the following functional groups were then incorporated as predictors: browsers, grazers, detritivores, scrapers and small excavators, and large excavators and bioeroders. Market gravity (Cinner and Maire, 2018) was extracted for each site in QGIS (QGIS Development Team, 2019) and was incorporated as a continuous predictor.

Prior to model fitting, paired plots were assessed for collinearity between model terms. Strong collinearity ($R^2 > -0.9$) between latitude and DHW precluded their joint inclusion in subsequent models, and consequently latitude was selected because of its complete reef-specific dataset (DHW data limited to n = 55 sites). Multi-collinearity was also then tested using the generalised variance inflation factor (*GVIF*) function (*car* package—Fox and Weisberg, 2019) where values $>$3 suggest collinearity; as a result longitude was excluded from all models and the joint inclusion of browsers and scrapers was prohibited (i.e., individual best-fit models -see "Statistical Models" section- were constrained to contain only one or the other).

Statistical Models

All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019). Differences in benthic community structure between reefs exposed to low versus high local human impact level were tested using t-tests with appropriate variance structures depending on homogeneity of variance test outcomes. Due to surveyor discrepancies in recording turf algal cover, we created a random effect (*bias_score*)

TABLE 2 | Predictor descriptions and ranges at outer reefs.

Predictor	Description	Range
reef depth[a,b]	mean depth (m) of transects	3.9–10.5
degree heating weeks (DHW)	measure of cumulative thermal stress–sum of previous 12 weeks where thermal stress anomaly $\geq$1°C; value averaged over 12 years preceding survey; negatively collinear ($R^2 = -0.9$) with latitude; only available for $n = 55$ sites	0.6–3.5
latitude[a,b]	degrees (°) distance from equator (absolute value). Negatively collinear ($R^2 = -0.9$) with DHW	0.0–23.9
longitude	degrees (°) longitude on continuous scale (i.e., −175 counted as 185), included to account for distance from the Coral Triangle biodiversity hotspot	134.3–214.2 (i.e., −145.8)
storm exposure[a,b]	total number of storms (cat. 1 to 5 on the Saffir-Simpson Hurricane Scale) passing within 50 km of site within previous 12 years	0–14
relief[a,b]	3 classifications: 1 = atoll; 2 = low-lying island; 3 = high island	
browser biomass[b]	biomass (g m^{-2}) of browsers	0.1–58.5
detritivore biomass[b]	biomass (g m^{-2}) of detritivores	0.5–62.8
excavator biomass[b]	biomass (g m^{-2}) of large excavators and bioeroders	0.0–369.1
grazer biomass[b]	biomass (g m^{-2}) of grazers	1.1–161.0
scraper biomass[b]	biomass (g m^{-2}) of scrapers and small excavators	1.9–134.3
relative human density	number of people within communities of the primary/customary resource users (living adjacent to/accessing fishing grounds within the reef area) related to total reef area (people km^{-2} reef), positively collinear ($R^2 = 0.7$) with relative fishing pressure. Used to determine local human impact level	1.3–1705
relative fishing pressure	annual reef finfish catch (tonnes) km^{-2} reef year^{-1}; positively collinear ($R^2 = 0.8$) with relative human density	0.1–78.2
market gravity[b]	index that combines human population size and reef accessibility	0–1140

[a]predictor incorporated in spatio-physical models. [b]predictor used in model selection procedures. For sources of data, see main text.

to be incorporated within turf algae models (see **Supplementary Figure 3** for details). No surveyor-related discrepancies were evident for other benthic groups (see **Supplementary Figure 3**). To test how turf algal cover differed across the two local human impact levels we thus used a linear mixed effects model incorporating *bias_score* as a random effect. All hereon described models were run separately for sites predetermined to be exposed to either low or high local human impacts to explicitly test for decoupling of abiotic and biotic predictors under different disturbance regimes.

To test whether the level of local human impact influenced the relationship between benthic community structure and spatio-physical explanatory drivers, we developed a spatio-physical model (i.e., focussing on spatial and physical predictors only) that included storm exposure, reef depth, latitude, and island relief. To account for non-linear relationships between response variables and predictors, we applied generalised additive mixed effects models (GAMM) using the *gamm4* (Wood and Scheipl, 2014) and *lme4* packages. To account for possible spatial autocorrelation, ten unique island clusters (*cluster*) were identified and incorporated into models as a random effect (for details see **Supplementary Figure 4**). For turf algae models, *bias_score* was additionally included as a random effect. To avoid overfitting, the number of knots within models was limited to four. We retained the adjusted-R^2 (Adj-R^2) values from the model output to quantify each model's explanatory power. Adj-R^2 values for each response variable were then compared (by paired t-tests) to test overall differences in model performance in explaining benthic community structure under the two local human impact levels.

Lastly, to examine the relative roles of ten biophysical parameters as predictors of benthic community structure under low versus high local human impacts, we applied model selection techniques using the *MuMIn* package (Barton, 2016). From an initial model containing ten biophysical predictors (i.e., those included in the spatio-physical model as well as biomass of herbivorous fish functional groups, and market gravity–see **Table 2**), the dredge function was used to run all possible predictor combinations and rank models from best to worst based on Akaike weight. The function also returns a value between 0 and 1 for each predictor that reflects its relative importance (RI), representing the total Akaike weight of all models containing that predictor (i.e., higher values correspond to greater RI). Output models were restricted to comprising a maximum of four predictors. One sample (Niue) was removed from the model selection procedure due to a lack of data for market gravity (i.e., $n = 61$). Model selection was run separately for sites with low and high levels of local human impact, and all models incorporated the *uGamm* wrapper function to allow the inclusion of random effects consistent with spatio-physical model constructions. To assess incongruities between benthic communities exposed to different local human impact levels, we retained the best-fit model structures (i.e., all predictors included in models with Akaike weight >0.05) for each benthic response variable, as well as the RI of individual predictors.

Assumptions and Sensitivity Tests

All response variables were logit-transformed (appropriate for percentage data — Warton and Hui, 2011) using the *car* package, following adjustment using each respective variable's minimum value >0. All model predictors were standardised (z-scores) to allow comparisons between predictors with largely varying effect sizes and numeric values (Zuur et al., 2009). Model residuals were checked for the violation of model assumptions using the *gam.check* function (see **Supplementary Figure 5**). As part of a sensitivity analysis, spatio-physical models were additionally run using ±5 and ±10 humans km^{-2} reef as a threshold from which to categorise "low" and "high" impact sites, with consistent outcomes observed (see **Supplementary Table 3**). Furthermore, we repeated the same for a range of thresholds based on human density relative to outer reef area (as opposed to full reef area), again with consistent outcomes observed (see **Supplementary Table 4**).

RESULTS

Benthic Assemblages Under Contrasting Local Human Impacts

Benthic communities subject to high local human impact were associated with lower live hard coral cover (−9.2% mean absolute coverage; t-test: $p = 0.002$; **Figure 1A**). However, the relative contribution of different coral morphologies within the live hard coral community did not differ significantly with local human impact level (**Figure 1B**). The only algal group that differed significantly depending on the local impact level was turf algae, which was higher under high local human impact (+10.7% mean absolute coverage; linear mixed effects model: $p = 0.015$; **Figure 1C**).

Predictive Strength of Spatio-Physical Model

The pre-defined spatio-physical model exhibited relatively high power in explaining benthic assemblage variance at sites with low local human impacts (mean Adj-R^2 ± SE; 0.35 ± 0.09; **Figure 2**), but model performance was severely compromised when local human impacts were high (0.10 ± 0.04; paired t-test: $p = 0.01$). When considering only the substrate types and dominant morphological groups (i.e., without the algal groups) the mean adjusted-R^2 for sites with low local human impacts increases to 0.44 ± 0.06 but stays unchanged at sites with high local human impacts. When local human impacts were low, spatio-physical predictors explained a high proportion of the variance of live hard coral (Adj-$R^2 = 0.52$) and macroalgae (Adj-$R^2 = 0.59$) cover, and the relative contribution of branching (Adj-$R^2 = 0.64$) and massive (Adj-$R^2 = 0.50$) coral morphologies. Conversely, these variables were consistently poorly explained when local human impacts were high (Adj-R^2 = 0.00, 0.26, 0.17, 0.10, respectively). No variance in turf algae was explained by this model for reefs at either local human impact level. Significant differences in the power of the spatio-physical model in explaining benthic assemblage variance between "low" and "high" impact sites held constant when the threshold was moved ±5 and 10 humans km^{-2} reef (i.e., paired t-test: $p < 0.05$; **Supplementary Table 3**).

Relative Importance of Predictors

Best-fit models tailored for each individual benthic variable comprised distinctly different predictors depending on the level of local human impact (**Figure 3A**). Two of the predictors where discrepancies were most apparent were storm exposure and grazer biomass, which were only selected for best-fit models at sites with low and high local human impacts, respectively. Similarly, reef depth was selected as part of best-fit models for more response variables (live hard coral, branching morphologies, and macroalgae) at sites with low local human impacts. Further discrepancies under the two levels of local human impact were revealed by comparing the mean RI of each predictor (**Figures 3B,C**), as the RI trends for predictors almost reversed between low versus high local human impact sites. At sites with low local human impacts, the individual predictors with the highest RI in explaining benthic communities were storm exposure, scraper biomass, and island relief, followed by reef depth (**Figure 3B**). Contrastingly, apart from island relief which was on average the most important predictor, storm exposure, scraper biomass, and reef depth were among the least important predictors when local human impact was high (**Figure 3C**). For benthic communities exposed to high local human impact, biomass of grazers, detritivores, and browsers, as well as market gravity, ranked as the most important predictors of benthic community structure.

Individual relationships of best-fit predictors for each response variable further emphasised discrepancies between benthic communities and environmental predictors driven by local human impacts (for all plots see **Supplementary Figure 6**). A clear example of this discrepancy can be seen in coral compositional changes with increasing storm exposure. Whilst live hard coral cover remained unrelated to storm exposure under both local human impact levels (**Figure 4A**), the morphological composition was closely correlated with storm exposure at sites where local human impacts were low (**Figures 4B–D**). Specifically, with increasing storm exposure, the relative proportion of branching morphologies decreased significantly (**Figure 4B**), whereas encrusting (**Figure 4C**) and massive (**Figure 4D**) morphologies increased. No morphological changes with storm exposure were observed at sites with high local human impacts. Though these relationships appear primarily driven by few points at the higher end of storm exposure, they remained consistent when all reefs exposed to >10 storms were removed from the analysis–i.e., significant at "low" impact sites (branching coral $p = 0.02$; encrusting coral $p = 0.02$; massive coral $p = 0.03$), insignificant at "high" impact sites (all morphological growth forms $p > 0.05$), and no relationship for either impact level for total live hard coral cover ($p > 0.05$).

DISCUSSION

Under increasing climate change-associated stressors and local anthropogenic influence (Burke et al., 2011; Gattuso et al., 2015; IPCC, 2019), it is particularly important for researchers and planners to maximise the ability of models to predict ecosystem futures to allow appropriate mitigation strategies to be implemented. This study indicates that the role of local human impacts in changing coral reef ecological communities and their responses to environmental drivers should be accounted for. The results revealed that local human impacts influenced

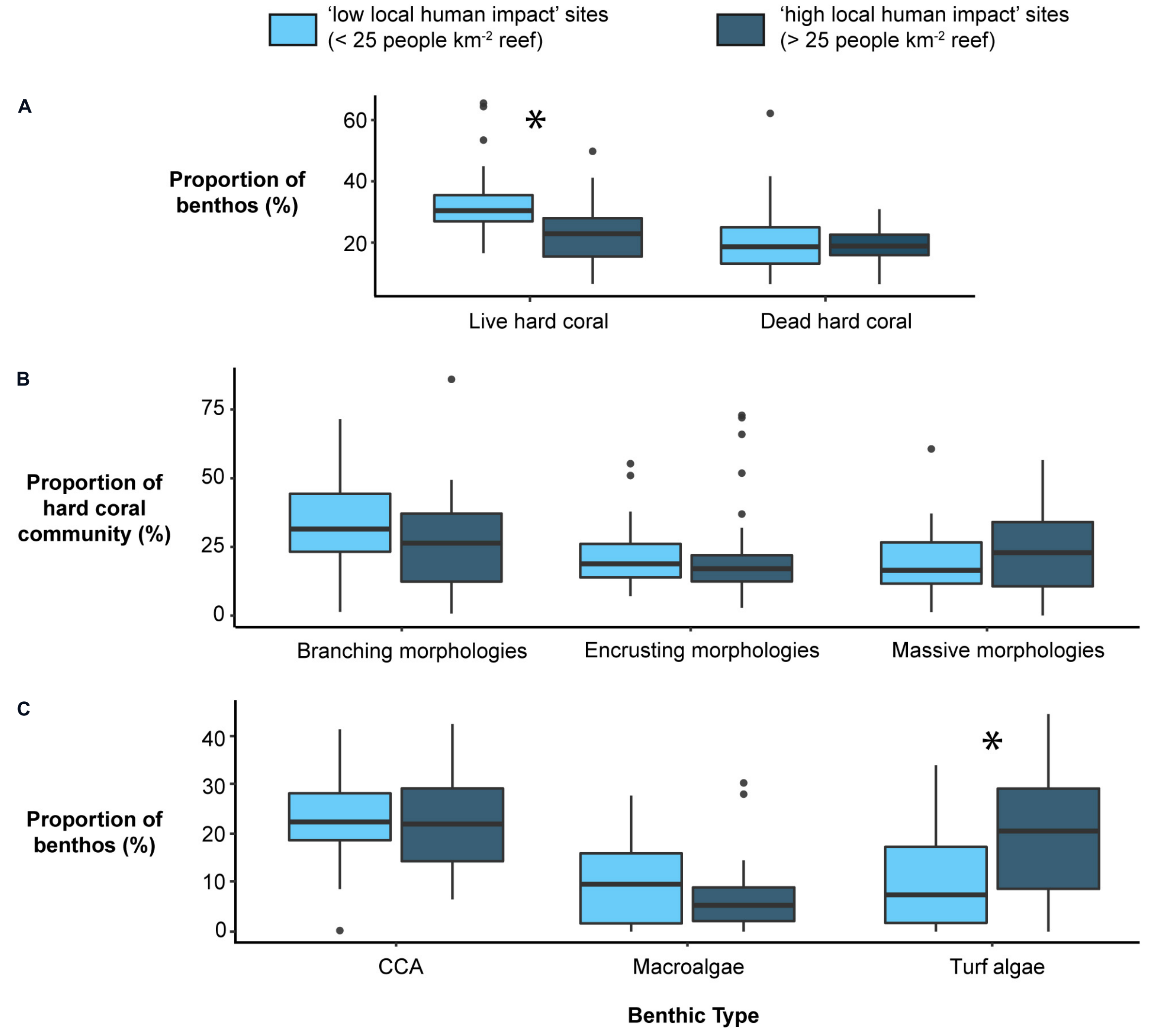


FIGURE 1 | Boxplots detailing **(A)** benthic cover (%) of substrate types (from left to right; live hard coral, dead hard coral), **(B)** the relative proportion (%) of the three most dominant morphologies in the live hard coral community (branching, encrusting, massive), and **(C)** benthic cover (%) of different algal groups (CCA, macroalgae, turf algae), at sites determined to have low or high local impacts. *Indicate significant differences ($p < 0.05$) in cover of the respective benthic variable between local impact levels according to two-sample *t*-tests, or for turf algae according to linear mixed effect models incorporating *bias_score* as a random effect (see section "Model Predictors").

both benthic community structure and relationships with biophysical predictors. Specifically, models based on spatio-physical predictors (i.e., reef depth, latitude, storm exposure, and relief) exhibited high power at explaining benthic assemblages under low local human impacts but were strongly compromised where local human impacts were high. Importantly, these outcomes remained similar when our threshold for human impacts, informed by previous work, was reduced or increased in the frame of a sensitivity analysis. Increasing sewage input, agricultural run-off, and sedimentation are potential changes associated with increasing human densities that reduce water quality and affect benthic communities (Fabricius, 2005; Fabricius et al., 2005; Ford et al., 2017). Furthermore, as fishing removes biomass of functionally important fish species, important top-down control of some benthic organisms is lost (Bellwood et al., 2004). These localised human impacts may homogenise benthic communities by driving ecological reorganisation that favours tolerant taxa (Darling et al., 2019). Our results indicate that this homogenisation may be occurring at Pacific Island reefs that are exposed to local human impacts, leading to novel systems that react fundamentally differently and unpredictably to environmental predictors compared to reefs less influenced by humans (Williams G.J. et al., 2015). In turn, we expect that local human impacts will influence responses of coral reefs to climate change-related stressors, and that reefs close to human populations will require context-specific management approaches to maximise their future sustainability and associated critical ecosystem services (Moberg and Folke, 1999).

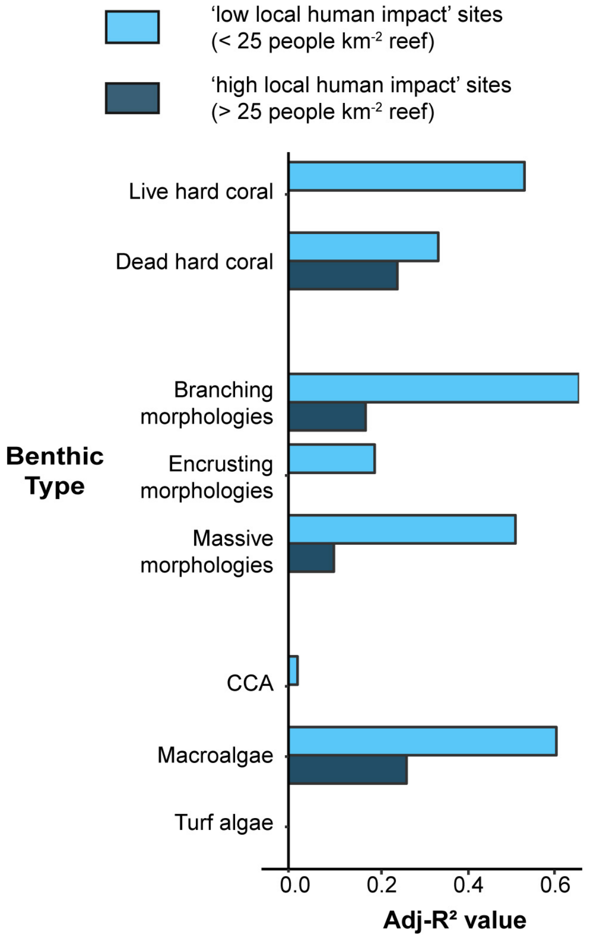
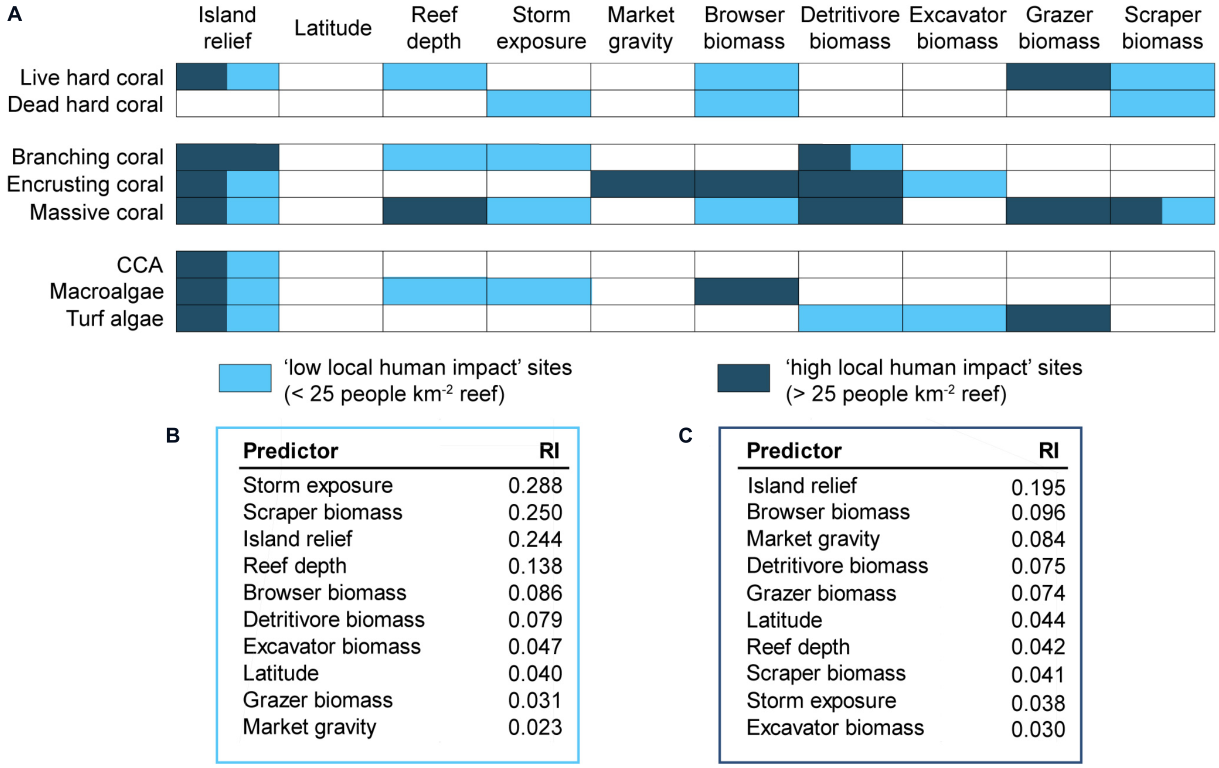


FIGURE 2 | Explanatory power (Adj-R^2) of the spatio-physical model (including the predictors storm exposure, reef depth, latitude, and island relief) in predicting individual benthic responses (live hard coral, dead hard coral, the proportion of branching, encrusting, and massive morphologies, and cover of algal groups CCA, macroalgae, and turf algae). Bars are absent where the Adj-R^2 value = 0.

The results emphasise the variation in benthic assemblages that exists among Pacific Island reefs exposed to different levels of local human impact. Benthic communities were not restricted to distinct regimes dominated by either hard corals or macroalgae, supporting previous studies from the Pacific (Bruno et al., 2009; Albert et al., 2012; Jouffray et al., 2015, 2019; Smith et al., 2016). In fact, macroalgae was the least common of all the algal groups, with turf algae and CCA more prominent on these outer reefs. Reefs at sites with higher local human impacts comprised significantly more turf algae and less live hard coral. Abundant and diverse outer reef coral communities (e.g., Ellis et al., 2017) have likely retained sensitive species, facilitating measurable differences (i.e., reductions in live hard coral cover) under higher local human impacts. Higher turf algae coverage at sites with more local human impacts provides further evidence that turf algae may become the dominant benthic group on degraded Pacific Island reefs (Jouffray et al., 2015; Smith et al., 2016; Tebbett and Bellwood, 2019). This may contrast with coral reef systems in the Caribbean, where macroalgae naturally play a more dominant role (Roff and Mumby, 2012). Furthermore, a signal of local human impact may have been detected if the data had distinguished macroalgae into fleshy/frondose and calcified types (e.g., Smith et al., 2016; Cannon et al., 2019). A similar link between human population size, hard coral cover, and turf algae has also recently been reported from sites in the Indian Ocean (Brown et al., 2017).

The spatio-physical models were weak in explaining the variance of benthic communities exposed to relatively more local human impacts. At these sites, model selection identified mostly local biotic controls or ecological features such as fish biomass and market gravity to be of highest RI. These results suggest that reefs altered by chronic local human impacts become decoupled from spatio-physical factors (Williams G.J. et al., 2015) and become more related to factors associated with human activities (e.g., market gravity) or local ecological features (e.g., biomass of functional groups of fish). Interestingly, this outcome contrasts to recent findings by Robinson et al. (2018) who did not detect decoupling at inhabited versus uninhabited reefs. Our different outcomes for decoupling could in part be explained by Robinson et al. (2018) combining (i) hard corals and CCA, and (ii) fleshy macroalgae and turf algae, each of which we found to exhibit different responses to local impacts (i.e., with higher local impacts hard coral cover decreased whereas CCA remained unchanged, turf algae increased whereas macroalgae remained unchanged). Model selection indicated that the specific spatio-physical predictors whose influence was most disrupted by local human impacts were storm exposure and reef depth. Storms can have mixed effects, benefitting reefs by alleviating thermal stress during warmer summer months but also causing physical destruction, particularly to delicate branching coral morphologies, leading to a higher proportion of more robust massive morphologies (Heron et al., 2005; Manzello et al., 2007). Accordingly, when local human impacts were low, coral communities comprised relatively less branching and more encrusting and massive morphologies at sites subject to more frequent storms. However, relationships between storm exposure and benthic assemblages were only observed at sites classified as having low local human impacts. Returning to the concept that local human impacts drive ecological reorganisation, we would expect reefs with less local human impacts to harbour a great diversity of species and morphologies, thus allowing for greater levels of ecological reorganisation in response to a stormier environment (i.e., favouring more robust morphologies). We anticipate that Pacific reefs would more likely display this phenomenon than Caribbean reefs due to a significantly larger initial species pool, with greater response diversity and functional redundancy affording a higher level of ecological insurance (Elmqvist et al., 2003; Bellwood et al., 2004; Nyström, 2006), and a loss of structurally complex coral species throughout most of the Caribbean over past decades (Alvarez-Filip et al., 2009). It would be interesting to test whether storm exposure results in more conspicuous negative impacts on coral cover (e.g., Gardner et al., 2005) in less diverse regions due to the limited capacity for ecological reorganisation to a tolerant community, even in



	Island relief	Latitude	Reef depth	Storm exposure	Market gravity	Browser biomass	Detritivore biomass	Excavator biomass	Grazer biomass	Scraper biomass
Live hard coral	⬛🟦		🟦			🟦			⬛	🟦
Dead hard coral				🟦		🟦				🟦
Branching coral	⬛		🟦	🟦			⬛🟦			
Encrusting coral	⬛🟦				⬛	⬛	⬛	🟦		
Massive coral	⬛🟦		⬛	🟦		🟦	⬛		⬛	⬛🟦
CCA	⬛🟦									
Macroalgae	⬛🟦		🟦	🟦		⬛				
Turf algae	⬛🟦						🟦	🟦	⬛	

🟦 ‘low local human impact’ sites (< 25 people km^{-2} reef)

⬛ ‘high local human impact’ sites (> 25 people km^{-2} reef)

B

Predictor	RI
Storm exposure	0.288
Scraper biomass	0.250
Island relief	0.244
Reef depth	0.138
Browser biomass	0.086
Detritivore biomass	0.079
Excavator biomass	0.047
Latitude	0.040
Grazer biomass	0.031
Market gravity	0.023

C

Predictor	RI
Island relief	0.195
Browser biomass	0.096
Market gravity	0.084
Detritivore biomass	0.075
Grazer biomass	0.074
Latitude	0.044
Reef depth	0.042
Scraper biomass	0.041
Storm exposure	0.038
Excavator biomass	0.030

FIGURE 3 | (A) Outcome of model selection procedures: coloured boxes indicate that the predictor was selected for best-fit models (i.e., those with Akaike weight >0.05) at sites subject to low and/or high levels of local impacts. The overall mean relative importance of each predictor (RI–based on total Akaike weight of all models including that predictor) in explaining the benthic response variables is shown separately for sites subject to **(B)** low and **(C)** high local impacts. Note: though model selection was limited to four predictors per model, all predictors included in models with Akaike weight >0.05 are shown meaning there may be more than four predictors shown within one impact level for a response variable. Model outputs for best-fit models are available in **Supplementary Table 5**.

sites with minimal local human impact. In terms of reef depth, benthic communities at sites with low local human impacts also exhibited a higher level of depth-structuring (particularly in terms of coral cover and composition, consistent with Huston, 1985) compared to those with high local human impacts. Island relief was also identified as being a strong predictor of benthic community structure (despite being found to be a weak predictor on central-western Pacific reefs – Robinson et al., 2018), and interestingly this role was maintained regardless of local human impact level. Importantly, when considering latitude–collinear with DHW/cumulative thermal stress–as an individual predictor, our results neither contradict nor confirm previous observations that local impacts exacerbate the sensitivity of coral communities to thermal stress (Wiedenmann et al., 2013; Ellis et al., 2019), instead highlighting a large variance among sites.

Thermal stress and the intensity of storms are projected to increase under future climate change scenarios (IPCC, 2019), with profound implications for coral reefs and adjacent ecosystems. Our findings suggest that while the effects of factors associated with climate change (e.g., storm exposure) on Pacific reef benthic assemblages may be reasonably well-predicted where local impacts are low, system responses become less predictable as local human impacts increase. In both marine and terrestrial systems, structural changes caused by local impacts have profoundly changed how ecosystems respond to natural stressors: for example, local stressors have affected how parts of Australia’s Great Barrier Reef have recovered from recent climate change impacts (MacNeil et al., 2019; Mellin et al., 2019) and habitat fragmentation and modification have exacerbated recent impacts of tropical and temperate forest fires (Brando et al., 2014; Alencar et al., 2015; Taylor et al., 2016). Because the effects of storms are strongly dependent not only on their intensity, but also the extent of the fetch, their frequency, and intrinsic reef properties such as topography (Lugo et al., 2000; Heron et al., 2005), this study incorporated all recorded storms (category 1–5 on the Saffir-Simpson Hurricane Scale) passing within 50 km of each site. We thus cannot deduce benthic community responses to increasing storm *intensity*, which is projected to occur (IPCC, 2019).

Functional groups of herbivorous fishes also emerged to be of contrasting RI depending on the level of local human impact, shifting from scrapers and small excavators at less impacted reefs to grazers at more impacted reefs. Browsers were of similar importance at reefs exposed to both local human impact levels, perhaps linked to the fact that their food source (macroalgae) remained constant regardless of local human impact level. Additional reasons for this could be that browsers have remained more resilient to fishing pressure than other herbivores, or

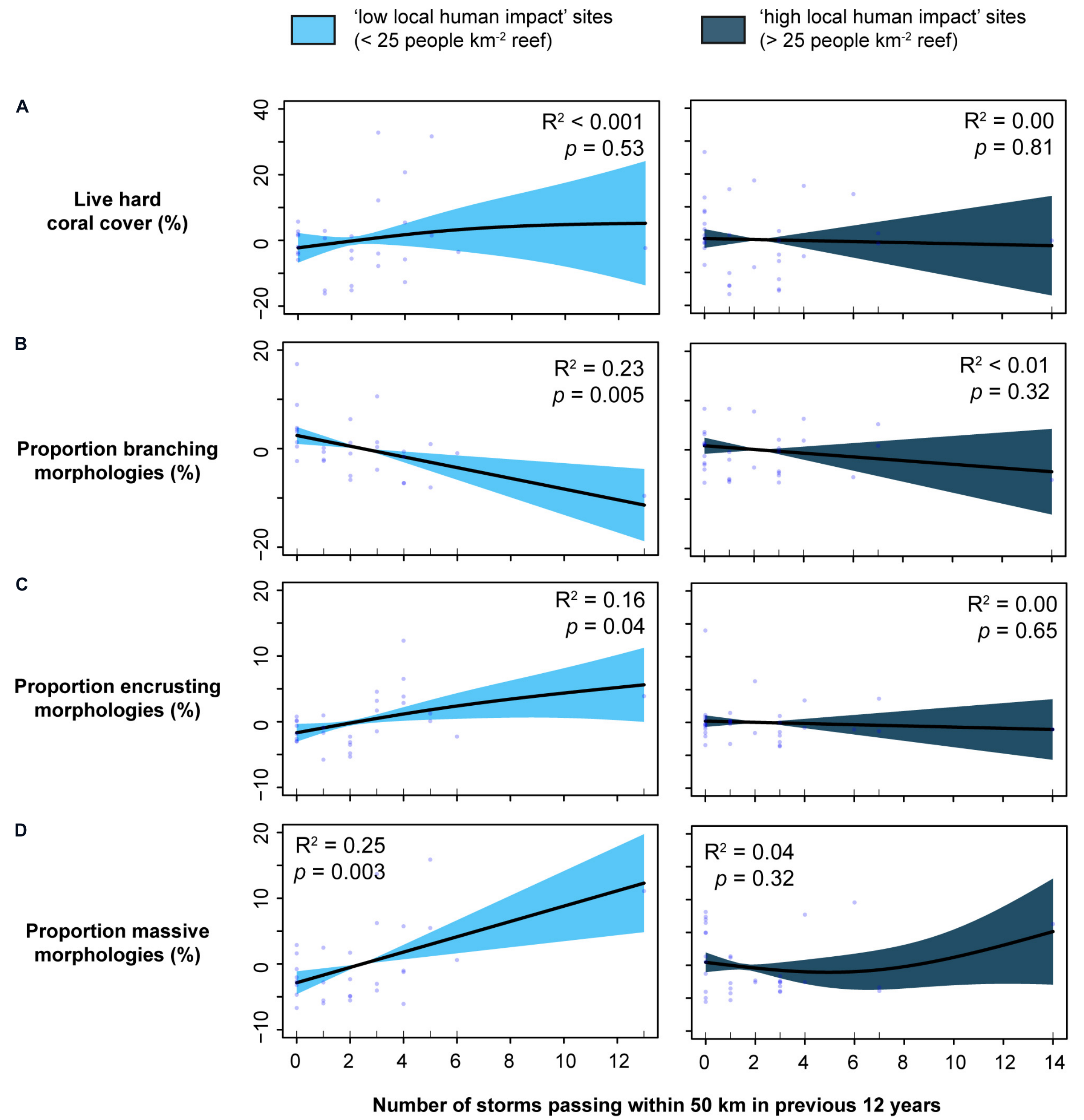


FIGURE 4 | Smoother plots of normalised residuals from generalised additive models with 95% confidence intervals (shaded areas) to exemplify discrepancies in response-predictor relationships between local impact levels, using storm exposure as an example. The plots represent the explanatory power of storm exposure in predicting **(A)** live hard coral cover, and the proportion of **(B)** branching, **(C)** encrusting, and **(D)** massive morphologies, separated for sites with low versus high local impacts. Refer to **Supplementary Figure 6** for all predictor-response plots from best-fit models.

that visual survey data does not accurately represent browser populations (for example some browser species are known to be particularly wary of divers–Kulbicki, 1998). Fish that act on turf algae and/or on surfaces available for coral settlement seem to be more sensitive to local human impacts, likely in response to benthic community shifts. Scrapers and small excavators clear substrate for calcifiers, justifying their higher RI in models focussed on less locally impacted reefs where live hard coral cover was higher and conditions for settlement and growth of juvenile corals were likely better (e.g., less nutrients, lower sedimentation). Contrastingly, grazers crop and maintain algal turfs, explaining their importance under higher local human impacts where turf algae were more dominant. These results align with findings in the Hawaiian Archipelago, where biomass of grazers and scrapers were the most important predictors of turf/macroalgal, and calcified regimes, respectively (Jouffray et al., 2015; see also Robinson et al., 2018). Though collinearity tests ruled out significant, potentially confounding relationships between biomass of different functional groups with individual abiotic predictors, it is important to acknowledge that fish communities themselves can be affected by various physical predictors (Williams I.D. et al., 2015; Samoilys et al., 2019), which could in turn influence benthic structure.

Other factors not included in these analyses are known to structure benthic assemblages, including chlorophyll, SSTs, and wave exposure (Gove et al., 2013, 2015; Williams et al., 2013; Robinson et al., 2018; Darling et al., 2019). Remotely sensed chlorophyll data captures offshore productivity, but we expected land-based input to dominate many of these reefs which are close to land, while the survey design (sometimes around the periphery of small islands/atolls) made wave exposure challenging to quantify. Additionally, wave exposure, mean SSTs, and climatological ranges can be relatively well-captured by latitude in the Pacific (Gove et al., 2013). Also, although this study goes into more detail than many similar large-scale analyses by evaluating coral growth forms, it is still limited in its ability to quantify ecological reorganisation, which would require higher resolution data (at least family or genus). This limitation can be overcome by broad-scale surveys refining the level at which hard coral communities are recorded, which will become easier with improvements in automated software tools. These results do however emphasise that even broad morphological groupings (i.e., branching, massive, encrusting morphologies) provide pertinent information on ecological changes and can improve model performance compared to when overall hard coral cover is considered (Gove et al., 2015).

Importantly, the threshold used in this study for determining low and high human impact, while informed by a previous study, was set *a priori* and thus does not allow defining a "carrying capacity" of human density–this would require a different survey design and analytical approach, and should be pursued in future studies. We would however suggest that although this metric is most applicable to areas where customary resource use is common practice, we anticipate that this threshold (25 humans km^{-2} reef) is highly relevant across the tropical Pacific (i.e., given that it is a median point in this dataset for which sites were selected due to being regionally representative of fished areas). Furthermore, the study design was not originally meant to address macroecological questions but was nonetheless the best available to study the questions we were interested in (with incorporation of appropriate secondary data on local environmental context). Again, future studies should address this by appropriate designs that allow for large-scale comparability and collect both ecological and socio-economic local data. Our findings indicate that island relief is a factor that should be considered in designing regional sampling programmes with comparable sites. Finally, we should aim to obtain context-specific information on factors associated with human population density (e.g., sewage treatment presence, farming and associated fertiliser-usage) that strengthens our ability to predict benthic communities under various levels of human population density and improve its use as a proxy of local human impact.

Our findings contribute to a better understanding of the role of local human impacts on highly diverse ecosystems such as tropical coral reefs. The results provide empirical evidence that local human impacts drive conspicuous changes in benthic community relationships with environmental predictors, with indications of ecological reorganisation. Even if decisive steps are taken to reduce fossil fuel emissions, most reefs will suffer long-term degradation from the effects of climate change by 2050, and >75% of reefs will experience annual severe bleaching (Frieler et al., 2013; van Hooidonk et al., 2016). Our results show that local human impacts can lead to increasingly unpredictable relationships between benthic communities and their physical environment, and that overlooking their role could pave the way to significant errors in future projections, potentially compromising mitigation efforts.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AF developed the study idea with close support from J-BJ, AN, BM, and SF. AF led the statistical analyses together with input from J-BJ, GW, and SF. BM and FM provided expertise on the original data. All authors provided support throughout the interpretation of the results and development of the manuscript and approve this final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.571115/full#supplementary-material

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