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RESEARCH ARTICLE

Macroalgae exhibit diverse responses to human disturbances on coral reefs

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Abstract

Scientists and managers rely on indicator taxa such as coral and macroalgal cover to evaluate the effects of human disturbance on coral reefs, often assuming a universally positive relationship between local human disturbance and macroalgae. Despite evidence that macroalgae respond to local stressors in diverse ways, there have been few efforts to evaluate relationships between specific macroalgae taxa and local human-driven disturbance. Using genus-level monitoring data from 1205 sites in the Indian and Pacific Oceans, we assess whether macroalgae percent cover correlates with local human disturbance while accounting for factors that could obscure or confound relationships. Assessing macroalgae at genus level revealed that no genera were positively correlated with all human disturbance metrics. Instead, we found relationships between the division or genera of algae and specific human disturbances that were not detectable when pooling taxa into a single functional category, which is common to many analyses. The convention to use percent cover of macroalgae as an indication of local human disturbance therefore likely obscures signatures of local anthropogenic threats to reefs. Our limited understanding of relationships between human disturbance, macroalgae taxa, and their responses to human disturbances impedes the ability to diagnose and respond appropriately to these threats.

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KEYWORDS

coral reef health, coral reefs, Indian Ocean, local human disturbance, macroalgae, multiple stressors, Pacific Ocean

1 | INTRODUCTION

Coral reefs are a highly diverse habitats within the tropical and subtropical seascape and provide essential services to millions of people, even as anthropogenic stressors intensify (Williams et al., 2019). Changes in the relative abundance of indicator taxa are often used to evaluate the effects of disturbances and human stressors on coral reefs, two common indicators being macroalgae and coral cover. In general, high cover of macroalgae is considered indicative of degraded reefs while high cover of hard corals indicates healthy reefs (Bruno et al., 2009; Bruno et al., 2014; McCook, 1999; Vroom, 2011; Vroom et al., 2006). The perception that macroalgae cover is indicative of reef health is driven by the theory that local anthropogenic stressors can promote macroalgae proliferation through top-down or bottom-up processes (e.g., the Relative Dominance Model; Littler & Littler, 1984, 2007). However, macroalgae-dominated reefs are not necessarily unhealthy (Vroom, 2011; Vroom et al., 2006). Macroalgae support ecosystem functioning and services (Fulton et al., 2019), contributing to carbonate production and providing nursery habitat that supports adult fish populations (Sievers et al., 2020), including target species for tropical reef fisheries (Wilson et al., 2022). Moreover, while macroalgae and corals compete for space and macroalgae may impede coral recovery through shading, abrasion, or chemical defenses (Littler et al., 2006; Littler & Littler, 2007; Mumby et al., 2006), there are also positive interactions between corals and macroalgae. For example, macroalgae can provide refuge for corals from predation by the Crown-of-Thorns seastar, *Acanthaster planci* (Clements & Hay, 2017). Macroalgal canopies can also protect corals from bleaching by limiting exposure to high irradiance (Jompa & McCook, 1998; Smith et al., 2022).

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Macroalgae is a broad term that can encompass multiple taxa with different morphology, ecology, and biology. Consequently, comparisons of studies using the percent cover of macroalgae as a proxy for local human-driven degradation often find conflicting results. For example, Smith et al. (2016) reported a significant positive relationship between populated islands and macroalgal cover, concluding that human populations negatively affect reef health. Conversely, Bruno and Valdivia (2016) failed to find a relationship between human populations and macroalgal cover on reefs, concluding local signatures of degradation are being obscured by climate-driven stressors.

Differences in how macroalgae are defined may have confounded comparisons between studies. Smith et al. (2016), for example, included turf algae and excluded erect, calcifying algae such as *Halimeda*, while Bruno and Valdivia (2016) excluded turf algae but included *Halimeda* and other erect, calcifying taxa. Clearly, scientists define macroalgae inconsistently, and the nature of these definitions may obscure drivers of macroalgal cover.

Furthermore, environmental factors can influence macroalgal cover on reefs, such as exposure to wind and waves (Fabricius et al., 2023; Gove et al., 2015; Page-Albins et al., 2012), seasonality (Brown et al., 2018; Fulton et al., 2014), and sea surface temperature (SST; Graba-Landry et al., 2020; Tanaka et al., 2012). Studies endeavoring to assess links between local human disturbance and macroalgae cover should therefore consider these environmental factors in analyses. Macroalgae taxa also exhibit variability in their responses to local human and environmental stressors, including temperature (Anton et al., 2020; Fabricius et al., 2023), fishing pressure (Gilby et al., 2015), water pollution (Fabricius, 2005; McClanahan et al., 2004; McCook, 1999), and sedimentation (Fabricius, 2005; Harris et al., 2021). Research investigating these taxon-specific responses to local stressors are lacking for all but the most common macroalgae.

We re-examine the relationship between macroalgal cover and local human disturbance using data from 1205 sites in the Indian and Pacific Oceans collected between 2004 and 2020 (Figure 1). We define macroalgae as including erect calcifying genera but excluding turf or crustose algae (Bruno et al., 2009; Steneck, 1988; Tebbett & Bellwood, 2019). We use this definition to remain consistent with past studies (e.g., Bruno et al., 2009; Bruno & Valdivia, 2016; Steneck, 1988; Tebbett & Bellwood, 2019; Tebbett et al., 2023), and to make use of preexisting survey data in which turf algae was not identified consistently across surveys. The analyses test the hypothesis that macroalgal percent cover is correlated with local human disturbance when accounting for environmental factors that might have confounded the findings in previous studies (Bruno & Valdivia, 2016; Smith et al., 2016). For all sites and within six biogeographic realms (Costello et al., 2017; see Section 2), we determined the suite of human disturbance and environmental variables (Table S1) that best explain the genus-level macroalgae communities via canonical correspondence analysis (CCA) and stepwise ordination. Next, we fit permutational analysis of variance (PERMANOVA) models to estimate the effects of each variable on macroalgal communities. We then used Similarity Percentage Analysis (SIMPER) to determine the

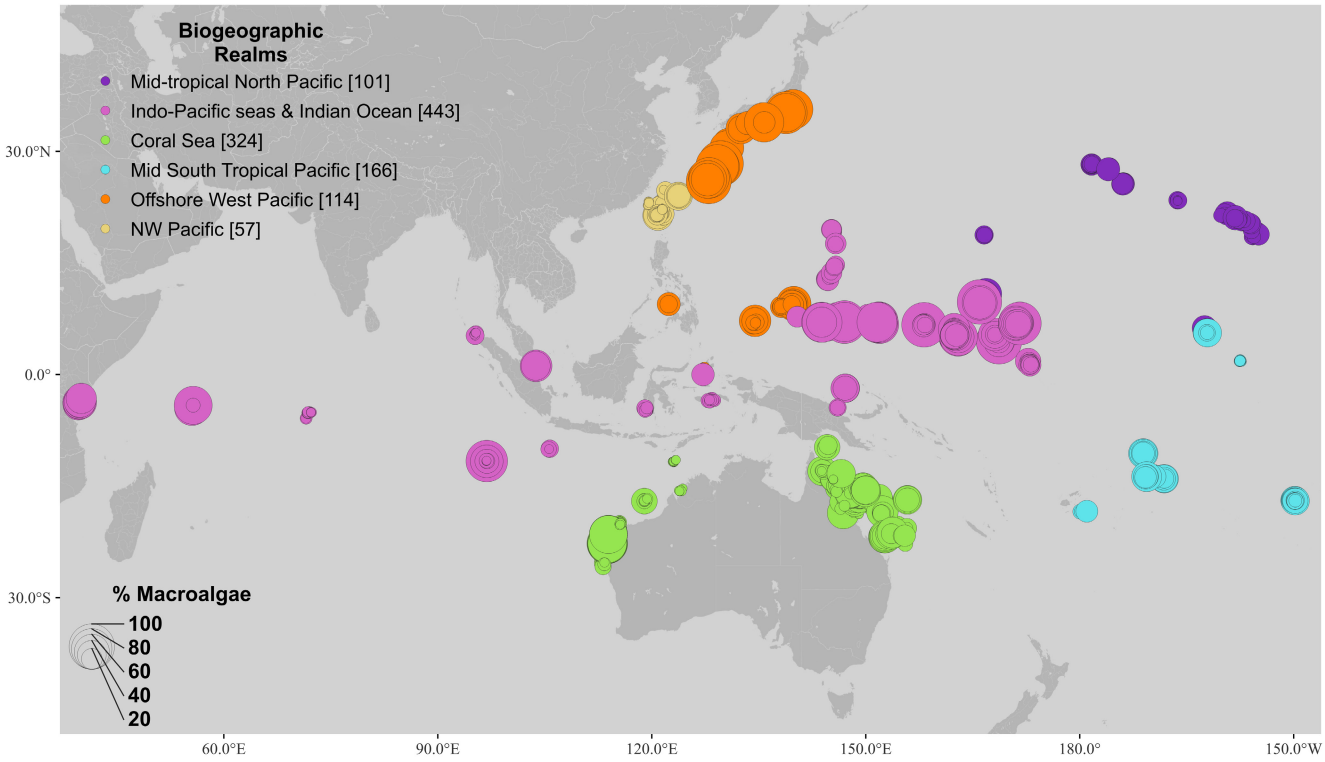

FIGURE 1 Map of 1205 study sites across the Indian and Pacific Oceans, by biogeographic realm (as described in Costello et al., 2017). The size of the points represents the total percent cover of macroalgae at each site. Map lines do not necessarily depict accepted national boundaries.

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taxa driving differences across biogeographic realms. Finally, we fit zero-inflated generalized linear mixed models (GLMMs) to quantify the relationships between local human disturbance and the common macroalgae genera and their divisions (red, green, brown).

2 | MATERIALS AND METHODS

We collated data from genus-level macroalgae benthic surveys conducted by the authors (Supporting Information: Data Sources) from 1205 individual tropical and subtropical coral reef study sites across the Indian and Pacific Oceans between 2004 and 2020, covering a period of 16 years. This dataset provides a snapshot of each site at a single time point and we did not investigate temporal changes in macroalgal communities. As discussed below, we considered temporal and methodological variables to account for differences across sites and surveys (Table S1). Of the 1205 sites, 1145 identified all macroalgae to the genus level, while 60 surveys only identified macroalgae of the genus *Halimeda*. We did not include these *Halimeda*-only surveys in the investigation of community drivers of macroalgae, but we included them in the genus-specific analyses described below. All statistical modeling, figures, and plots were done using R Statistical Software version 4.4.1 (R Core Team, 2021), R Studio version 2021.09.0 Build 351 (RStudio Team, 2020), the R package ggplot2 (Wickham, 2016), and InkScape (Inkscape Project, 2020). The R code is available on GitHub (https://github.com/secanno/Cannonetal2023_Macroalgae). We created the map in QGIS version 3.24 (QGIS Development Team, 2022) using a base map from OpenStreetMap (OpenStreetMap Foundation, 2021).

To limit the ability of confounding factors to obscure potential relationships between macroalgae and local human disturbance, we identified and calculated 45 site-specific variables (in addition to 15 variables representing human disturbance), representing drivers known to influence macroalgae growth and distribution at multiple resolutions. These variables encompassed eight categories: connectivity with other reefs, heat stress, human disturbance, methodological and site descriptive variables, net primary productivity, seasonality, storms, and wind and wave exposure. Because the estimates of these variables cover a wide geographic area, we conducted the analysis for the entire dataset, and also separated the sites into marine biogeographic realms (Costello et al., 2017) to test whether the macroalgae communities within realms were explained by different variables. One of the realms, the offshore Indian Ocean, included just 12 sites, which we added to the Indo-Pacific Seas and Indian Ocean realm. We also considered data contributors and the survey methodologies as explanatory variables to account for differences in site selection and sampling methodologies. Due to spatial constraints, we are unable to detail the methods and justifications for each of the 60 explanatory variables that we considered in the main text of the manuscript. Instead, Table S1 contains a table describing each variable, including its definition, source, spatial resolution, and justification for inclusion in the analysis.

We assessed multicollinearity during variable selection at two steps in the analysis. First, we used the R package Hmisc (Harrell, 2021) to calculate the Pearson's r correlation coefficients for all possible pairs of variables and eliminated any with r correlation values of greater than 0.7 within each of the eight covariate categories. When multiple variables were correlated within a given category, we chose those with the lowest summed Pearson's *r* coefficient, eliminating 33 variables (Table S2). Then, following Borcard et al. (2011), to select variables that best explained the macroalgae community compositions, we conducted CCA and stepwise variable selection using the R package vegan (Oksanen et al., 2020) for all sites combined and independently for each of the six realms. We addressed multicollinearity in this second step by eliminating any variables with a variable inflation factor (VIF) > 10 (Table 1; Borcard et al., 2011). We detail the variables selected by the CCAs and their VIF in Table S3.

Using the R package vegan (Oksanen et al., 2020), we ran SIMPER (999 permutations) to identify the macroalgae taxa driving differences across biogeographic realms. We also identified variables with strong correlations to macroalgal community composition with principal component analysis and by fitting seven PERMANOVAs: one for all the data combined and for each of the six realms independently. Each PERMANOVA included the variables selected by the CCA, excluding those with VIFs >10 (Table S3).

Last, we evaluated how local human disturbance, represented by variables detailed in Table S1, influenced the distribution of the most common genera of macroalgae. To estimate the effects of five categories of local human disturbance on the most common macroalgae taxa, their divisions, and for all macroalgae combined, we fit generalized linear mixed models using the R package glmmTMB (Bolker et al., 2009) for the following equation:

$$\begin{aligned}\text{Percent of Macroalgae} \sim\ & \text{cumulative human impact score} \\ & + \log(\text{population density}) + \text{NDVI} + \text{nutrients} + \text{market gravity} \\ & + (1|\text{Latitude: Longitude}).\end{aligned}$$

We considered each of the five human disturbance variables fixed effects, the interaction between latitude and longitude a random effect to account for spatial autocorrelation across sites. The most common genera were defined as those comprising more than 1% of the total macroalgae cover, either across the entire dataset or within one of the realms. The cumulative human impact score is a metric for local human disturbance that includes small-scale fishing pressure, coastal population, industrial development, tourism, and two types of water pollution (sedimentation and nitrogen from agriculture), while the normalized difference vegetation index (NDVI) is a proxy for nearby development. For more details, including methods and justifications for each of the model variables (see Table S1).

We compared zero and nonzero-inflated GLMM with gaussian and beta distributions. We selected zero-inflated beta regression models because they best met the assumptions that the residuals would exhibit homoscedasticity and be normally distributed, and that the data are not autocorrelated. The human population variable was log-transformed to meet the assumptions. We used diagnostic plots to test for normal distribution and equal variance of residuals with the R package DHARMA (Hartig, 2022), and Moran's tests

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TABLE 1 Variables that best explained macroalgal communities (canonical correspondence analysis [CCA] results) and had variable inflation factors of less than 10, shown with their pseudo-R^2 values (permutational analysis of variance [PERMANOVA] results). Values in bold are statistically significant at $\alpha = .05$, while those in italics are significant at $\alpha = .10$. Empty cells indicate that variables were not selected as best explaining the macroalgal communities by the CCA and were not included in the PERMANOVAs.

Variable type	Variable	All data	Mid-tropical N. Pacific	Indo-Pacific seas and Indian Ocean	Coral Sea	Mid-south tropical Pacific	Offshore West Pacific	NW Pacific
R^2 (full equation)		*.10*	*.05*	*.12*	*.21*	*.18*	*.07*	*.16*
Connectivity	Reef area (15 km)			**0.05**				
	Reef area (200 km)	**0.00**		**0.01**				
Human disturbance	Cumulative human impact	**0.01**						
	Fisheries management	**0.01**				**0.08**		**0.09**
	Normalized difference vegetation index	**0.00**		**0.02**		**0.02**	**0.03**	
	Nutrients (agriculture)	0.00	0.03		**0.04**			**0.04**
	Market gravity							
Methodology and sampling	Depth	**0.00**		**0.02**		**0.04**		
	Habitat	**0.02**						
	Latitude							
Net primary productivity (NPP)	Chl-a (kurtosis)	*0.00*		**0.01**	**0.02**			0.02
	NPP (SD)	0.00			**0.05**			
Seasonality	Month of survey (by sea surface temperature [SST])	**0.03**						
	Average photosynthetically -available radiation (PAR) (survey month)	0.00				**0.04**		
	mean SST (survey month)			**0.01**				
Storms	# Storms ≥ type 3	**0.00**	0.02		**0.01**			
	Cyclone score				**0.02**			
Heat stress	Max Degree Heating Weeks (DHW)	**0.00**						
	Maximum Monthly Mean (MMM)	0.00						
	SST_{SD}	**0.00**						
Wind and wave exposure	Aspect	0.00				0.00	0.01	
	Wave energy (mean)	**0.00**		**0.00**	**0.04**		**0.02**	
	Wind and wave exposure						0.01	0.01

to test for spatial autocorrelation with the package spdep (Bolker et al., 2009, Supporting Information S4). We also calculated the R^2 values (marginal R^2, which represents only the fixed effects, and conditional R^2, which measures the fit of the entire model) using the Nakagawa method (Nakagawa et al., 2017). Finally, to enable comparing the model results across taxa, we used the R package ggeffects to calculate the adjusted marginal effects for each of the explanatory variables (Lüdecke, 2018).

3 | RESULTS

Across these 1205 sites, we identified 96 genera of macroalgae and total macroalgae cover varied from zero to 88.2% per site, with a mean of 12.8% and a median of 6.8%. The calcified green algae *Halimeda* occurred at the most sites (68.2%).

Macroalgal community compositions differed across realms (Figure 2). The genus *Halimeda* was most common in all realms except for the offshore West Pacific and northwest Pacific, where *Lobophora*, a brown fleshy alga, was the most common taxa. We describe the most common taxa within each realm in detail in Table S5, and the full SIMPER results comparing all realms to each other in Table S6.

The drivers of spatial differences in macroalgal community compositions differed when considering the full model (containing all sites) or within each of the realms (Table 1; Table S7). A principal component analysis considering the potential drivers of macroalgae distribution (Table S1) found that the first three principal

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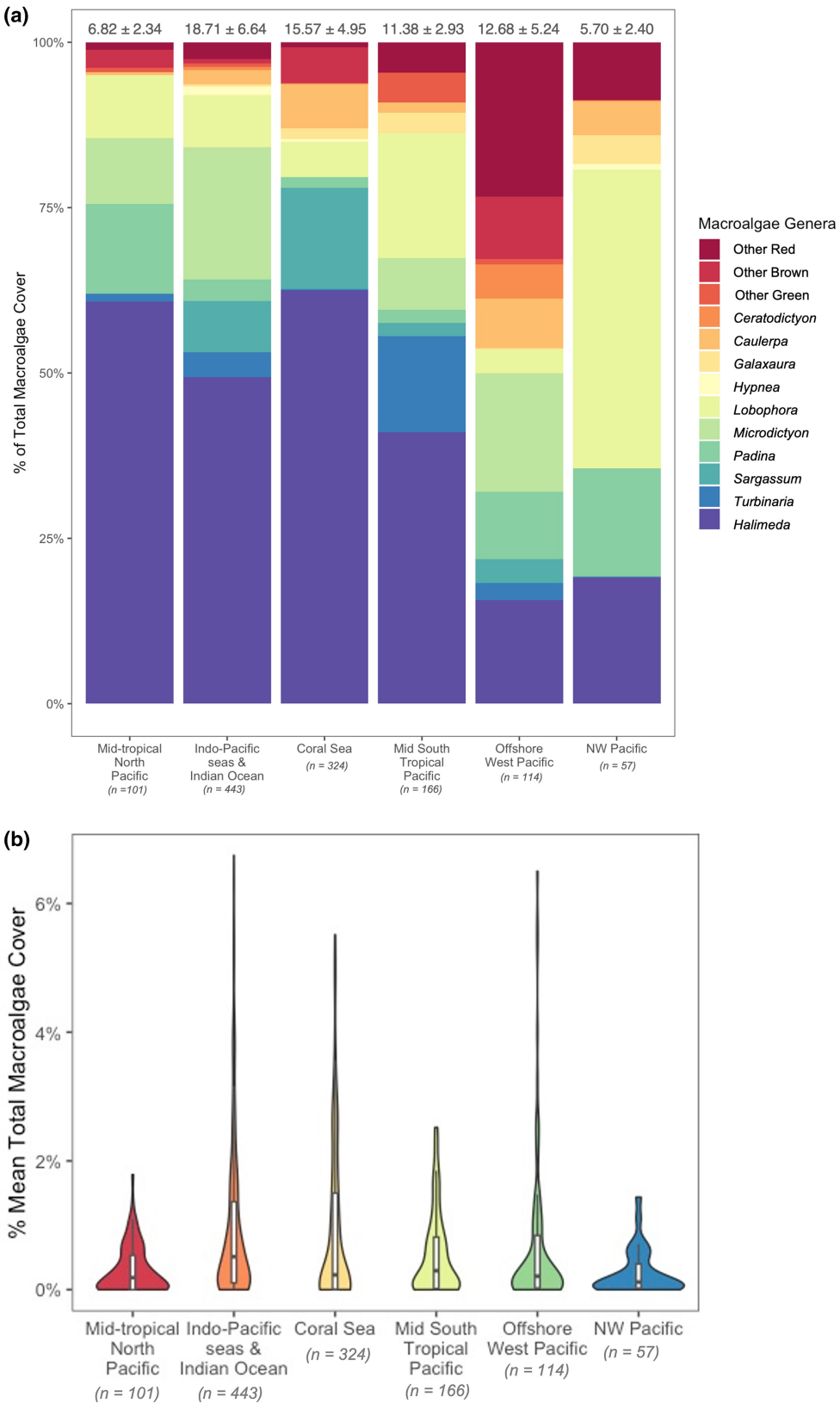

FIGURE 2 (a) Top 10 most common macroalgae taxa by biogeographic realm, with mean and standard deviation at the top of each bar. (b) Mean total macroalgae cover by site, grouped by biogeographic realms.

components accounted for 46.32% of the variation in macroalgal communities (Supporting Information S8). The full equations for all the PERMANOVAs were statistically significant with *p*-values <.01 for the model containing all sites, and models for each of the realms except the mid-tropical North Pacific, which was not significant ($p = .08$). The explanatory power of each model varied, and

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each of the independent variables had R^2 values less than .10. For all macroalgae combined, the PERMANOVA accounted for 10% of the variation in macroalgae percent cover across sites. The model for the Mid-Tropical North Pacific had the least explanatory power for variation in macroalgal community composition (R^2 = .05), while the model for sites in the Mid-South Tropical Pacific had the greatest (R^2 = .21).

The human disturbance metrics had the largest effects of all drivers contributing to the variation in macroalgal communities in all realms. Of these human disturbance indicators, the normalized difference vegetation index (NDVI, an indicator of development on land; see Section 2) and nutrients from agriculture had the greatest presence in the models, although nutrients were only significant in two of six models, while NDVI was significant in three of the six. Three of the models also included a categorical variable representing fisheries management (open-access, restricted, or closed/no access), which had greater explanatory power than the other human disturbance metrics (all of which had R^2 values less than .05). Of the biophysical indicators, mean wave energy was another common driver of macroalgae community composition and was significant in four of six models. Except for fisheries management, all the variables had R^2 values that were less than or equal to .05.

The relationships between the percent cover and each of the human disturbance metrics varied for different macroalgae genera (Figure 3) and divisions (Figure 4, Supporting Information S9). The adjusted estimates indicated weak relationships between the percent cover of total macroalgae and the human disturbance metrics (Supporting Information S10), with effect sizes that were all less than one. When investigating potential relationships by genera or division, however, some relationships between specific taxa and human disturbance became apparent that were not evident for all macroalgae combined. Similarly, when considering the division of macroalgae (red, green, or brown), relationships with human disturbance were less apparent than they were for specific macroalgae taxa. Percent cover of all algae had a negative relationship with three of five human disturbance variables. Within the brown macroalgae division, most taxa exhibited positive relationships with the log of the population density, and negative relationships with NDVI and nutrients from agriculture. Only two of the brown macroalgae genera exhibited strong relationships with the disturbance. The genus *Spatoglossum* was positively correlated with the cumulative human impact score (which includes sedimentation, nutrients from agriculture, tourism, industrial development, and small-scale fishery pressure; Andrello et al., 2021), log of population density, and market gravity, but was negatively correlated with NDVI and nutrients from agriculture. By contrast, *Dictyopteris* was positively correlated with the cumulative human impact score and NDVI, but negatively correlated with market gravity and nutrients from agriculture.

Similarly, both the green and red macroalgae taxa also demonstrated weak relationships with human disturbance when considered

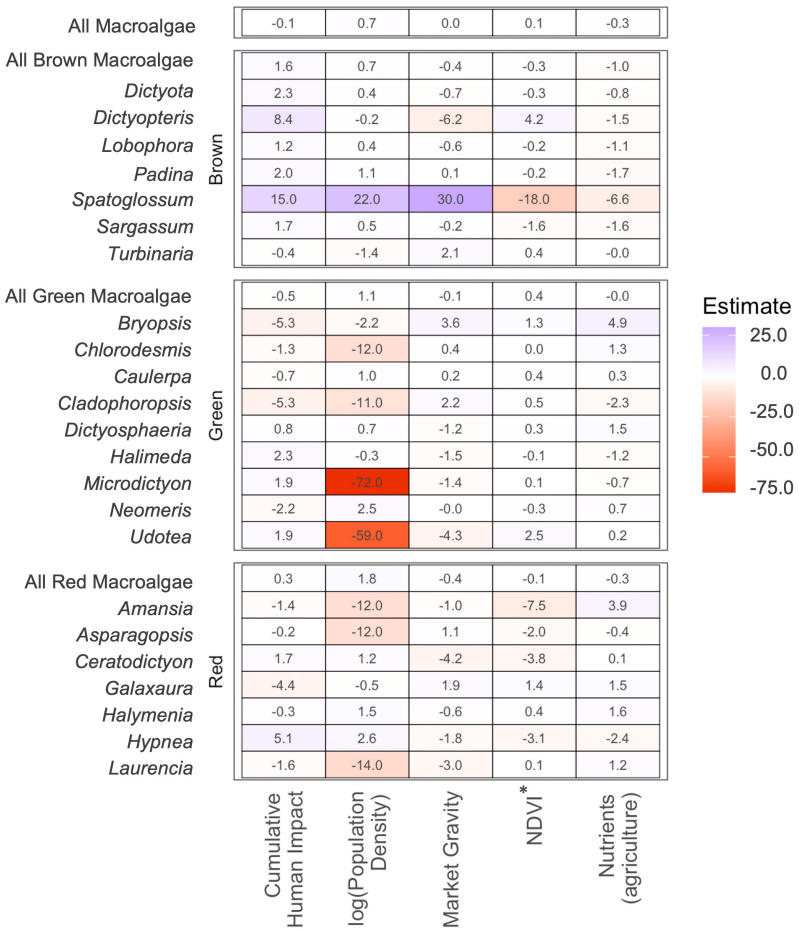

FIGURE 3 Estimated parameters for fixed effects from the generalized linear mixed models. *Estimates for normalized difference vegetation index have been multiplied by −1 to account for this variable's inverse relationship with disturbance.

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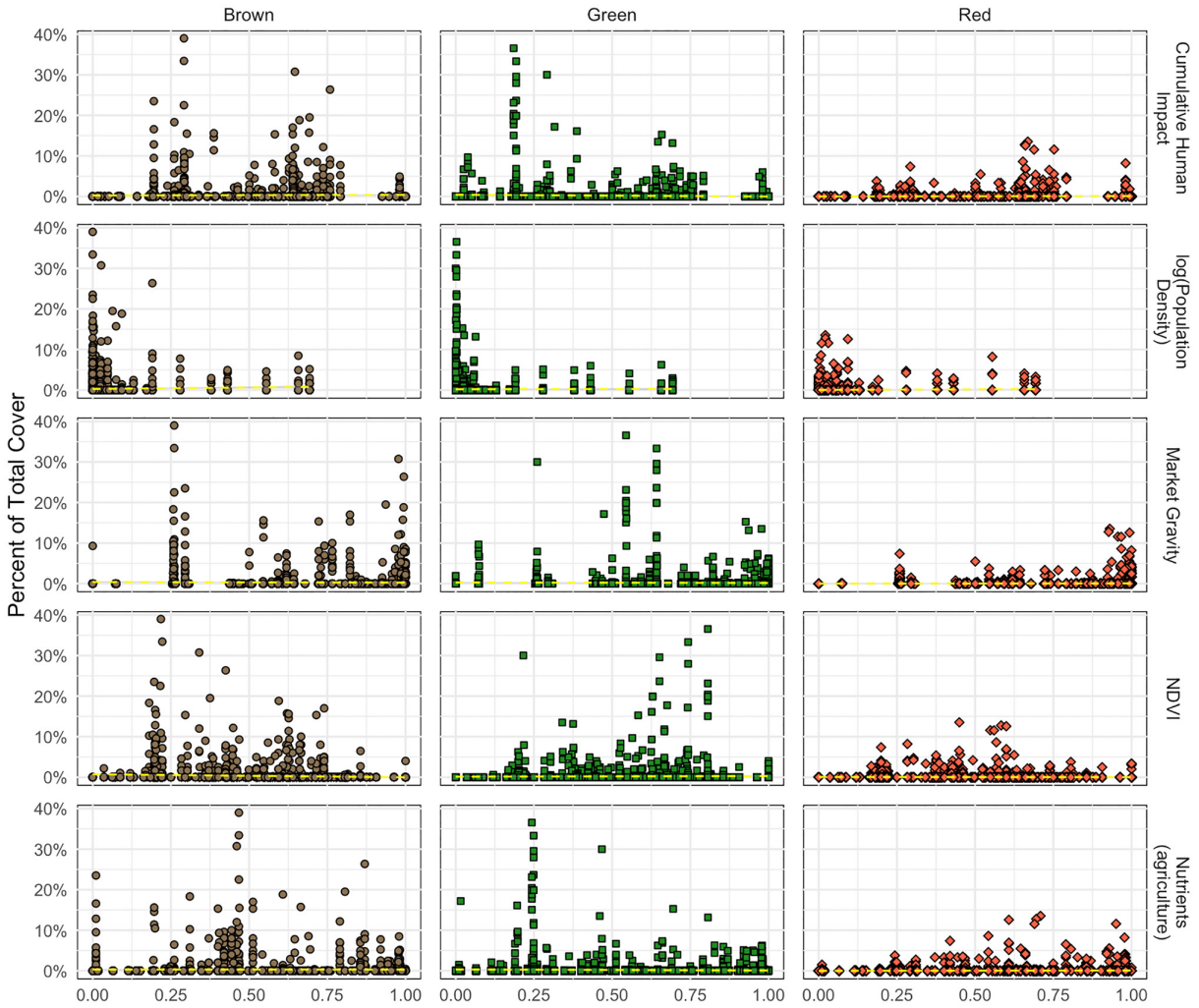

FIGURE 4 The percent cover of macroalgae genera grouped into three divisions (brown, green, and red), as they relate to five human disturbance variables. The dashed yellow line is the trendline. The disturbance variables have been normalized and range between zero and one (see Section 2).

by division, with specific taxa showing stronger positive or negative relationships. Most of the green macroalgae genera were negatively related to the log of the population density (*Microdictyon* and *Udotea* were strongly and negatively correlated) but were weakly related with the remaining human disturbance metrics. The red macroalgae taxa were also negatively related to the log of the population density and NDVI. By contrast, the red macroalgae genera *Ceratodictyon* and *Hypnea* were positively correlated with the population density, although these relationships were weak.

4 | DISCUSSION AND CONCLUSIONS

The percent cover of total macroalgae is not a robust indicator for local anthropogenic disturbance in the Indian and Pacific Oceans, for two main reasons: (1) the drivers of macroalgae communities are unclear, challenging to estimate, and differ across realms, and (2) different macroalgae genera and divisions have distinct and often opposite responses to diverse types of local human disturbance.

We find that multiple environmental factors, unrelated to local anthropogenic disturbance, influenced macroalgae community compositions (connectivity, wind and wave exposure, storms, net primary production, and seasonality). Accounting for these environmental factors is imperative if researchers and managers are to use macroalgae as an indicator of anthropogenic impact on reefs. Otherwise, researchers risk attributing observed patterns in macroalgal community composition to the wrong drivers. Furthermore, despite assessing 60 variables that could influence macroalgae communities, the most parsimonious models included few variables, and the PERMANOVAs all had R^2 values of less than .25. This indicates that the models were still unable to account for most of the variation in macroalgal communities and highlights the difficulty in identifying the drivers of ecological patterns (discussed further below).

In addition, the relative importance of the factors influencing macroalgal communities differed across the biogeographical realms. The CCA identified 17 variables influencing macroalgae distribution when considering all sites. However, each variable explained less than 3% of the variation and collectively, the full equation only accounted for

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10% of the variation. Many of these variables were selected only when considering all sites collectively, but not when examining the drivers of macroalgal communities by biogeographical realm. In the Coral Sea, the CCA identified six variables as best describing the variation in macroalgal communities, half of which (nutrients from agriculture, the kurtosis of chl-a, and the standard deviation of net primary productivity) are related to nutrients, and the other half were related to storms and exposure to wind and waves (number of storms greater than type 3, cyclone score, and mean wave energy). These variables collectively accounted for 21% of the variation across sites in the Coral Sea. In the mid-South Tropical Pacific, the PERMANOVA accounted for 18% of the variation, and fisheries management and development (represented by NDVI) were important for explaining variation in macroalgal communities, along with the depth of the surveys, photosynthetic radiation, and the aspect of the site. By contrast, the heat stress metrics were not important drivers of macroalgal communities, whether considering all sites collectively or within the biogeographic realms. Collectively, the CCAs and PERMANOVA results show that macroalgal communities are influenced by different factors depending on their location. Without accounting for these factors, studies that compare the percent cover of macroalgae across broad regions may obscure differences in community compositions, rather than revealing them.

The macroalgae genera we assessed also exhibited diverse and oftentimes opposing relationships with different metrics of human disturbance. Combining all macroalgae into a single category, or into divisions, obscured ecologically important relationships. In addition, the total macroalgae cover metric was uniformly weakly explained by each of the human disturbance variables. The cumulative human impact score did not have the strongest correlation with macroalgae cover. This is most likely because this metric is a conglomeration of multiple stressors, and our analysis clearly shows that many taxa respond more strongly to a specific anthropogenic stressor. Moreover, the percent cover of many taxa will increase in response to one stressor but decline when subjected to another, somewhat nullifying any response when responses from multiple stressors are combined. This indicates that taxon-specific responses to individual human pressures should be considered when evaluating local anthropogenic impacts on coral reefs.

The individual traits of the macroalgae genera may explain their relationships with the various disturbance metrics, each of which represents a different form of localized disturbance. The genus *Halimeda* was present at almost 70% of the sites and was the most common macroalga in our dataset. As the most common calcifying alga on tropical reefs globally, *Halimeda*, produce sediment on coral reefs and play an important role in reef accretion (Hillis-Colinvaux, 1980). Our results suggest that *Halimeda* cover will increase with increasing cumulative human impacts but will decline with increasing market gravity and nutrients from agriculture. While market gravity was designed as a metric for fishing pressure (Cinner et al., 2018), it incorporates human population size, and may therefore also reflect nutrient loading present in realms with high human populations. The weak but negative correlation with nutrients from agriculture, is in contrast with past findings showing that *Halimeda* growth is stimulated by nutrients (Delgado, 1994; Teichberg et al., 2013). Increasing market gravity might increase competition with other macroalgae taxa that would otherwise be kept in check by herbivory, which could explain the negative correlation. However, coral reef herbivores show low preferences for *Halimeda* and some species are chemically defended (Hay et al., 1988; Paul & Van Alstyne, 1988). Collectively, these results reveal a complex relationship between *Halimeda* and human disturbance; it is more likely to grow where nutrients are high, but not necessarily where there is high fishing pressure.

Complex relationships may also exist for other macroalgae taxa examined here, although confirming these relationships is not possible with the current data and will require further research as well as experiments that manipulate the extent of different stressors imposed on macroalgae taxa. For example, we found that canopy-forming brown algae, which provide important habitat for fish and support small-scale fisheries (Sievers et al., 2020; Wilson et al., 2022), exhibit diverse responses to disturbance. For example, blooms of *Turbinaria* have been linked to high nutrient concentrations on the Great Barrier Reef (McCook, 1999), which is consistent with our results from across the Indian and Pacific Oceans. *Sargassum* was one of the few taxa exhibiting a negative relationship with nutrients from agriculture, which aligns with past research (e.g., McClanahan et al., 2004). However, it is in direct opposition of the Relative Dominance Model (RDM), which posits that macroalgae cover on coral reefs is dictated by human disturbance acting through top-down (e.g., fishing pressure) or bottom-up (e.g., nutrients) processes (Littler & Littler, 1984, 2007).

While past research helps explain many of the relationships between specific macroalgae taxa and our human disturbance variables, we also found unexpected relationships. The morphology of *Turbinaria*, along with its chemical defenses, make it unpalatable to many herbivores (Bittick et al., 2010) and we would not anticipate an increase in percent cover with increasing fishing pressure (Davis, 2018). However, we found a positive correlation with market gravity. Other studies have also reported that macroalgae taxa often do not respond as predicted to stressors (McClanahan et al., 2004; McCook, 1999), again, underscoring how little these interactions are understood. Unfortunately, studies investigating taxa-specific interactions with human disturbance for tropical macroalgae are lacking for all but the most common taxa and often report conflicting results (Ramseyer et al., 2021). Existing studies are primarily motivated by negative interactions between corals and macroalgae (Fulton et al., 2019; Vroom, 2011). Furthermore, because of the RDM's predictions, studies are usually limited to investigating the effects of fishing pressure or nutrients (e.g., Adam et al., 2021; Holbrook et al., 2022).

Our results show that the lack of correlation between total macroalgal cover and local human disturbance may be in part because of the varied interactions between disturbance and individual macroalgae taxa. Signatures of human disturbance that were undetectable using total macroalgae cover may still be evident when identifying macroalgae at the genus level. In these cases, relying on the assumption that macroalgal percent cover correlates with local disturbance may lead to maladaptive interventions; for example, if managers

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assume that all macroalgae will respond similarly to enhanced herbivory despite evidence to the contrary (Kelly et al., 2016), or misidentify undisturbed reefs as degraded, this approach could lead to costly and ineffective management interventions.

For reef-building corals, research has greatly improved our understanding of diverse and complex responses to disturbance. Literature has documented differences in how corals respond to bleaching, for example, because of their morphology, heterotrophic feeding ability, physiology, and several other factors (Darling et al., 2012; Loya et al., 2001; Van Woesik et al., 2011). Yet, the focus on coral in the literature demonstrates that scientists have failed to consider how genera within diverse macroalgae assemblages may also respond to disturbance differently and what this means for ecosystem function (Fulton et al., 2019). Like reef-building coral communities, some taxa of macroalgae are susceptible to climate-driven stressors (Anton et al., 2020; Graba-Landry et al., 2020). Our limited understanding of the relationships between both human and climate disturbance and macroalgae taxa, and their importance in reef ecosystem functioning, impedes our ability to respond to the many threats facing coral reef ecosystems as a whole (Vroom, 2011).

This study builds on previous research that has called the RDM and the subsequent assertions that macroalgae is correlated with local human disturbance an oversimplification (Fulton et al., 2019; McCook, 1999; Vroom, 2011) with potentially negative implications for management (McCook, 1999; Vroom, 2011), and that has criticized the widespread reliance on macroalgae as an indicator of reef health or degradation (Bruno et al., 2009; Vroom, 2011). Despite these critiques, researchers and managers continue to use total macroalgae cover to provide proxy estimates on the health of coral reefs and how they are affected by people (Bruno & Valdivia, 2016; Smith et al., 2016). A key limitation to this and other research on macroalgae distribution (Keith et al., 2014; Tebbett et al., 2023) is the lack of available survey data identifying macroalgae at the genus level. Most of the survey data we analyzed were collected to investigate the status and/or health of coral reefs, and site selection may have excluded parts of the reef with higher macroalgae cover. In addition, the sampling was uneven across realms, and the reliance on large-scale, low-resolution global databases to calculate site-specific independent variables may have affected our ability to account for local drivers of macroalgal communities because of differences in scale. Despite these limitations, this study demonstrates that the links between macroalgae cover and human disturbance are uncertain, which undermines the usefulness of total macroalgae cover as a way of estimating local, human-driven degradation.

Strategic management of coral reefs is increasingly vital as the climate continues to warm (Darling et al., 2019). Evaluating how coral reefs are being affected by disturbance is an indispensable part of research and management, but the most common metrics used in that work are based on an oversimplified and poorly tested paradigm. We have shown here that total macroalgae cover does not correlate well with local human disturbance but that evaluating macroalgae cover at the genus level shows more promise as a management and assessment tool. Genus-level data might also provide greater understanding of the drivers of macroalgae and how they influence overall ecosystem functioning. Investments in further research on macroalgae at finer taxonomic resolutions, including genus-specific interactions with human-driven stressors, may be important for future coral reef conservation. In addition, as others have argued, testing long-standing paradigms in marine ecology will be increasingly necessary to make good predictions as climate change intensifies (Williams et al., 2019), demonstrating the need for enhanced monitoring to improve our ability to assess climate-driven changes in benthic communities. We hope that by demonstrating that total macroalgae cover is only weakly correlated with human disturbance and is not an effective way to estimate coral reef health in the Indian and Pacific Oceans, this work catalyzes much-needed consideration of how we define reef health and the effects of local human disturbance, especially under rapidly changing environmental conditions.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The full dataset is available at http://doi.org/10.5281/zenodo.7760495. The data from the Yap and Chuuk Outer Islands remain owned by communities in Yap and Chuuk, and the meta-data from these sites is not public. Please contact the data owners (listed in Supporting Information) for permission to use their data.

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