Spatial distribution of benthic algae in the South China Sea: Responses to gradually changing environmental factors and ecological impacts on coral communities

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Abstract

Aim: In this study, we investigated whether environmental factors can effectively control the spatial distribution of various benthic algae and examined the critical ecological impacts of algae on corals across the South China Sea (SCS). Relationships between benthic algae and environmental factors were assessed, and potential ecological impacts of algae on coral communities were evaluated across spatial scales.

Location: A total of 104 sites at 12 coral reefs in four coral reef regions (CRRs) of the SCS (latitude range of 9–22° N).

Taxa: Turf algae, macroalgae (including fleshy macroalgae and Halimeda), crustose coralline algae (CCA), coral and juvenile coral.

Methods: Using diver-based surveys (2015–2018), we investigated four CRRs with different reef distance to mainland (RDM) across the SCS. We obtained field data on benthic algal composition and cover, coral cover and diversity, and juvenile coral density. We also measured and collected the environmental factors (including seawater environmental parameters and reef fish diversity).

Results: The cover of turf algae and CCA gradually decreased and increased, respectively, with an increase in RDM, which had a strong relationship with the gradually changing environmental factors. Random forest models suggested that nutrients, reef fish diversity, seawater transparency and temperature were the most important factors for predicting turf algae and CCA cover. Linear regression analyses showed a significant relationship between the turf algae, macroalgae, and CCA covers, and juvenile coral density.

Main conclusions: Our results showed that gradually changing environmental factors were correlated with the spatial distributions of turf algae and CCA. However, the natural biophysical relationships between macroalgae and environmental factors may be disrupted by turf algal overgrowth and nutrient subsidies. Increases in all benthic algal groups significantly impacted coral recruitment, highlighting the critical role of benthic algae in determining the recovery trajectory of the Indo-Pacific reefs that are threatened by human activities.

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1 | INTRODUCTION

Hard coral cover of most coral reefs has severely declined in the Anthropocene as a consequence of climate change and local environmental stressors (Hughes et al., 2017; Smith et al., 2016; Yu, 2012). Hard coral decline is frequently followed by an increase in the abundance of benthic algae, especially turf algae and macroalgae (Adjeroud et al., 2018; Graham et al., 2015). For example, following several mass bleaching events, coral cover in Seychelles reefs has declined by more than 90%, while the macroalgal cover has increased from 3% to 42% (Graham et al., 2015). Similarly, recurrent disturbances at Moorea Island have caused a decline in coral cover from 51% to 17%, along with an increase in turf algal cover from 16% to 50% (Adjeroud et al., 2018). On the contrary, calcifying algae such as crustose coralline algae (CCA) have decreased from 6.4% to 1% in degraded Caribbean reefs over the past 40 years (de Bakker et al., 2017).

In the short term, abrupt disturbances such as coral bleaching (Graham et al., 2015; Hughes et al., 2017) or outbreaks of crown-of-thorns starfish (Li et al., 2019) may induce regime shifts from coral to benthic algae dominance; conversely, in the long-term, nutrients, which exert bottom-up control, and herbivores, which impose top-down control, are important factors in the regulation of benthic algal communities (Benkwitt et al., 2019; Burkepile & Hay, 2006; Lapointe, 1997; Littler et al., 2006; Shantz et al., 2015). Factors such as seawater temperature, light conditions and wave energy that fluctuate seasonally and spatially can also control the abundance and composition of benthic algae (Brown et al., 2018; Cannon et al., 2019; Ferrari et al., 2012; Williams et al., 2013). Currently, nutrients and herbivores are becoming increasingly important for the development of coral reef ecosystems, because anthropogenic disturbances frequently lead to reef regime shifts owing to increasing nutrient contents and removal of key herbivores on a local scale (Lapointe, 1997; Stockwell et al., 2009). For instance, local nutrient enrichment has been shown to be responsible for the flourishing of macroalgae at Discovery Bay (Lapointe, 1997), and the addition of organic nutrients can quickly increase the cover of turf algae and frondose algae in field tests (McClanahan et al., 2005). Moreover, a local decrease in the abundance of herbivorous fish has been reported to result in rapid increases in macroalgal cover (Hughes et al., 2007; Humphries et al., 2020; Stockwell et al., 2009) and a decrease in CCA cover (Burkepile & Hay, 2006; O’Leary & McClanahan, 2010). The impacts of nutrients, herbivorous fish and other biophysical factors, such as temperature, light, wave energy and sediment on the distribution of benthic algae communities have been well studied in many reef regions, including in Kenya (Humphries et al., 2020; O’Leary & McClanahan, 2010; O’Leary et al., 2012), the Caribbean (Ferrari et al., 2012) and central Pacific islands (Cannon et al., 2019; Ford, Jouffray et al., 2020; Ford, Gove, et al., 2020; Williams et al., 2013, 2015). Notably, local human activities can disrupt the function of environmental factors in explaining the distributions of benthic algae and corals in the remote central Pacific islands (Ford, Jouffray, et al., 2020; Williams et al., 2015). However, it is not clear whether biophysical environmental factors will weaken or lose explanatory power with respect to the distribution of different benthic algae in reefs that are experiencing intense human activities at large spatial scales.

Coral reefs in the South China Sea (SCS) provide a unique opportunity to investigate the spatial distribution of benthic algae and explore their relationship with naturally changing environmental factors such as seawater nutrients, reef fish and other biophysical factors. Such coral reefs are distributed in areas ranging from uninhabited remote regions to crowded coastal regions across tropical latitudes ranging from ~4°N to ~24°N (Yu, 2012). Within the SCS, an increase in reef distance to mainland (RDM) can cause gradual decrease in seawater nutrient levels and an increase in reef fish abundance, temperature and light conditions (Guo et al., 2019; Li et al., 2011; Qin et al., 2020).

In contrast to fleshy turf algae and macroalgae, calcified CCA actively facilitates the recruitment of coral larvae and development of the reef framework (Gómez-Lemos et al., 2018; Harrington et al., 2004). Previous studies have shown that an increase in the abundance of turf algae and macroalgae can cause coral bleaching and mortality (Barott, Williams, et al., 2012; Brown et al., 2017; Liao et al., 2019) and hinder the settlement of coral larvae (Arnold et al., 2010; Birrell et al., 2008). Additionally, a mass decline in adult corals is associated with a collapse in larval recruitment (Hughes et al., 2019). Increases in the abundance of turf algae and macroalgae could, therefore, have significant negative effects on coral recruitment (Birrell et al., 2008). Understanding the ecological impacts of different benthic algae on coral communities and recruitment is crucial for accelerating the recovery of coral reef ecosystems.

Coral communities in the SCS, which are situated on the northern edge of the Coral Triangle, have dramatically declined over the past several decades (Yu, 2012). Live coral cover has declined by over 70% in the coastal reefs of the northern SCS over the last several decades (Liao et al., 2019; Yu et al., 2019; Zhao et al., 2012) as a consequence of coastal urbanization, coral harvesting, pollution, tourism, overfishing and destructive fishing (Hughes et al., 2013; Yu et al., 2019; Zhao et al., 2012). Similarly, live coral cover in the central SCS has declined from over 70% in the 1980s (Hughes et al., 2007) to 16% in 2015 (Chen et al., 2019), as a consequence of frequent human activities mainly overfishing, and destructive fishing, and recurrent natural events, such as coral bleaching, and outbreaks of crown-of-thorns starfish (Hughes et al., 2013; Li...
et al., 2015, 2017, 2019). Little is known about the spatial distribution of various algal functional groups and their ecological impacts on coral communities and recruitment in the SCS reefs. Field surveys into the potential ecological impacts of benthic algae on coral cover, diversity and recruitment may help reveal the role of various benthic algae in shaping the future coral community structure in the Indo-Pacific region.

In the present study, the main aims were to assess whether environmental factors (including seawater environmental parameters and reef fish diversity) across a large spatial scale can effectively control the biogeographical distribution of three main algal functional groups. We addressed three fundamental themes: (1) understanding the spatial distribution of benthic algae (turf algae, macroalgae including fleshy macroalgae and *Halimeda*, and CCA) with changes in geographic regions, zoned by RDM; (2) understanding whether and how the various benthic algae respond to the changes in surrounding environmental factors and their major predicting environmental factors; and (3) determining the potential ecological impacts of increasing benthic algal cover on coral cover, species diversity and juvenile coral density. We predicted that if the relationships between environmental factors and benthic algal groups are not disrupted by natural or anthropogenic factors, then the gradually changing environmental factors, with increasing RDM, could effectively predict the spatial distributions

**FIGURE 1** Maps of coral reefs investigated in the South China Sea. (a) Distribution of 12 coral reefs in four coral reef regions (CRRs) of the SCS (http://reefgis.reefbase.org/). Inshore coral reefs in the northern SCS: (b–d) coastal region, including Daya Bay (DYB), Xuwen Country (XW) and (e) Weizhou Island (WZI). Remote coral reefs in the central SCS: (f) the Xisha Islands, including North Reef (NR), Yongxing Island (YXI), East Island (EI), Huaguang Reef (HGR) and Langhua Reef (LHR). Remote coral reefs in the southern SCS: (g) the Nansha Islands, including Sanjiao Reef (SJR), Xian‘e Reef (XER) and Xinyi Reef (XYR). The hollow red dots in the Figure refer to the survey transects (N = 104). RDM: reef distance to mainland (China).
of algae. We also hypothesized that all benthic algae have significant ecological impacts on coral recruitment, regardless of how these algae respond to declines in coral cover. Consequently, control of turf algae or macroalgae will pose a great challenge for the natural recovery of Indo-Pacific reefs in the face of intensive human activities and rapid climate change.

2 | METHODS

2.1 | Study sites

This study was conducted on 12 coral reefs in four coral reef regions (CRRs) in the SCS during summer seasons from 2015 to 2018. Surveys were conducted in summer to obtain the optimum seawater temperature and transparency conditions for diving in inshore reefs and to avoid the impacts of typhoons and storms on remote reefs. The coral reefs were located in continental coastal regions (RDM < 1 km) and on Weizhou Island (RDM 40–50 km) in the northern SCS, on the Xisha Islands (RDM 200–400 km) in the central SCS, and on the Nansha Islands (RDM 1,000–1,200 km) in the southern SCS (Figure 1a; Table S1.1 in Appendix S1). The typical reef seascape for each CRR is shown in Figure S1.1 in Appendix S1. The three coastal coral reefs were located in Daya Bay (DYB), Xuwen County (XW) and Luhuitou Peninsula (LHT) (Figure 1b–d) and were investigated in September 2015, August 2015 and September 2017, respectively. Weizhou Island (WZI) is an inhabited volcanic island (408 people km\(^{-2}\); Figure 1e; Table S1.1 in Appendix S1), which was investigated in May 2018. We surveyed five coral reefs in the Xisha Islands, including the North Reef (NR), Yongxing Island (YXI), East Island (EI), Huaguang Reef (HGR) and Langhua Reef (LHR) (Figure 1f), which were investigated from May to July 2015. YXI is the largest coral island in terms of area (3.2 km\(^2\)) and human population (about 361 people km\(^{-2}\)) in the Xisha Islands, and it is a seabird habitat. EI is a sparsely inhabited coral island with high forest cover and abundant seabirds. The other three reefs, NR, LHR and HGR, belong to uninhabited subtidal atoll reefs with no outcropping land or sand cay. We also surveyed Sanjiao Reef (SJR), Xian’e Reef (XER) and Xinyi Reef (XYR) in the Nansha Islands from April to May 2016; these are uninhabited subtidal atoll reefs with no outcropping land or sand cays (Figure 1g; Table S1.1 in Appendix S1).

2.2 | Benthic community composition and coral recruitment

The photoquadrat method described by Preskitt et al., (2004) was used to determine the benthic community composition and cover in the surveyed reefs. At each coral reef, 4–12 transects (50 m long) were deployed at a depth of 2–6 m in coastal reefs and Weizhou Island and of 2–15 m in the Xisha Islands and the Nansha Islands (Table S1.2 in Appendix S1). At each transect (or site), a 50 m fiberglass measuring tape was fixed to the reef substrate, and sampling quadrats of 0.5 m × 0.5 m were randomly set along the tape. SCUBA divers used OLYMPUS TG-4 cameras to take over 20 photographs per quadrat in a vertical line from the reef substrate (about 0.6 m) for each sampling quadrat, and we set up 6 to 24 quadrats on each transect (Table S1.2 in Appendix S1). A total of 1,450 photoquadrats from 104 sites (one transect was done per site) across 12 reefs (Table S1.2 in Appendix S1) were used to calculate the benthic biotic and abiotic cover using Coral Point Count with Excel extensions (cpce version 4.1) software (Kohler & Gill, 2006). Briefly, this software was used to place 50 simple-random points on each photoquadrat, and benthos and substrate were identified beneath each point. Benthic communities were mainly defined as hard corals, benthic algae (turf algae, macroalgae, and CCA functional groups), and other benthic groups such as sponges, Milleporina, Helioporacea, Gorgonians and soft corals (Brown et al., 2017). Macroalgae were differentiated as fleshy macroalgae (e.g., Dictyota, Lobophora), Halimeda and other calcified macroalgae, while this study did not focus on the other calcified macroalgae. An abiotic substrate was defined as one consisting of rubble, sand, sediment, bare rock and dead coral. Hard coral and macroalgae genera were identified, and turf algae and CCA were identified to the level of functional groups.

The densities of juvenile corals were obtained from each of the above photoquadrats. Colonies with a maximum diameter of 1–5 cm were defined as juvenile corals, and asexual coral recruits were not considered as recruitment (Adjeroud et al., 2018; Birrell et al., 2008).

2.3 | Obtaining seawater environmental parameters and reef fish dataset

Seawater environmental parameters reflecting seawater quality were obtained from satellite and in situ investigation (details in Table S1.3 in Appendix S1). For each coral reef, the annual values in the period from 2014 to 2018 of sea surface temperature (SST), photosynthetically active radiation (PAR), chlorophyll \(\alpha\) (Chl-\(\alpha\)) and particulate organic carbon (POC) were obtained from satellite-derived datasets collected by NASA (monthly averaged MODIS-Aqua 4 km; https://giovanni.gsfc.nasa.gov). The significant height of combined wind waves and swell (SHWS) between 2014 and 2018 was extracted from the ERA5 reanalysis dataset (0.5° × 0.5° spatial resolution and hourly temporal resolution; https://cds.climate.copernicus.eu).

The in situ seawater environmental parameters, namely dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and seawater transparency, were measured from the seawater samples and sites. At the outer reef flat or slope of each reef, one shallow water site (2–4 m) and one deep water site (4–15 m) were randomly selected for collection of surface seawater samples, with three replicates for each site, using 250 ml Niskin bottles, and for measuring seawater transparency. DIN and SRP were measured using a continuous flow analyser (SEAL QuAAtro; SEAL Analytical.
Shanghai, China). Seawater transparency value in metres was measured using a Secchi disc (SD 30). Out of the various seawater environmental parameters, Chl-a, POC, DIN and SRP were used to indicate the reef nutrient level. The Chl-a threshold for eutrophication in coral reefs was in the range from 0.2 to 0.5 mg/m² (Bell et al., 2014; Guo et al., 2019).

The reef fish diversity, including species richness of herbivorous fish and total fish density, was derived from previous studies conducted between 2003 and 2018 in the regions or reefs we surveyed in this study (Table S1.4 and S1.5 in Appendix S1; Appendix S2). We re-analysed and integrated previously collected fish datasets. We further classified reef fish species into seven trophic levels (Jennings et al., 1995): herbivores, omnivores, invertebrate feeders and piscivores, invertebrate feeders, piscivores, planktivores and detritivores (https://www.fishbase.de/ and https://fishdb.sinica.edu.tw/) (Table S1.5 in Appendix S1; Appendix S2). The densities or biomass of each fish species were not reported in the previous studies. Thus, only the species richness of herbivorous fish and the total fish density were used to reflect the intensity of fish herbivory.

2.4 Statistical analyses

Differences in percentage covers of benthic algae (turf algae, macroalgae and CCA) and coral, number of coral genera, and juvenile coral densities among the four CRRs were quantified using Kruskal–Wallis tests followed by Student–Newman–Keuls (SNK) post hoc comparisons. Using Pearson correlation, we examined whether there was a positive or negative relationship between the seawater environmental parameters (SST, PAR, Chl-a, POC, DIN, SRP, SHWS and transparency) and RDM, as well as whether there was a positive relationship between species richness of herbivorous fish and total fish density with RDM. Then, to test the correlations among the environmental factors (seawater environmental parameters and reef fish diversity), CRRs and benthic algal cover (including macroalgae, fleshy macroalgae, Halimeda, turf algae and CCA), we carried out redundancy analysis (RDA) using canoco version 4.5 (Wageningen University & Research). Random forest models were used to assess the relative importance of each environmental factor in predicting the distribution of macroalgae, fleshy macroalgae, Halimeda, turf algae and CCA. In the processes, cover of each benthic algal type was divided into two levels, "<20%" and "≥20%." The relative importance of environmental factors was assessed using "mean decrease in Gini" in the randomForest function of the randomForest package (Liaw & Wiener, 2002) in R.

Linear regression was used to predict the relationship between the cover of benthic algae groups (including turf algae, macroalgae and CCA) and coral cover, coral species richness and juvenile coral density. Linear regression was also used to predict the relationship between both coral species richness and juvenile coral density and coral cover, and between coral species richness and juvenile coral density. Finally, using linear regression, we examined whether there was a negative relationship between turf algae, macroalgal cover and CCA cover, and between turf algae and macroalgal cover. The goodness of fit ($r^2$) was determined. Results were considered significant at $p < .05$. Statistical analyses were conducted using IBM spss Statistics 19 software, and in the R environment, ver. 4.0.3 (R Core Team, 2020).

3 RESULTS

3.1 Spatial distribution patterns of benthic algae

The cover of all benthic algae varied significantly among the four CRRs (all $p < .05$; Figure S1.2 and Table S1.6 in Appendix S1). Turf algal cover gradually decreased from 22% to 6% with increasing RDM from coastal reefs to the Nansha Islands; in contrast, macroalgal cover, which varied from 1% to 11%, did not change gradually with increasing RDM (Figure 2a,b). The macroalgal cover was highest in the Xisha Islands (11%), and there was no difference between coastal reefs and the Nansha Islands (Figure S1.2 in Appendix S1). CCA cover gradually increased from 2% to 18% from coastal reefs to the Nansha Islands (Figure 2c).

In coastal reefs, the benthic algal community was completely dominated by turf algae, accounting for 86% of benthic algal cover, and there was no Halimeda (Figure 3a,e). Turf algae were also the most abundant benthic algal group in Weizhou Island (46% of benthic algal cover), and no Halimeda was found there (Figure 3b,e). In contrast, the benthic algal community in the Xisha Islands was dominated by CCA (39%), and there was a high cover of turf algae (31%) and Halimeda (27%) (Figure 3c,e). In the NanSHA Islands, the benthic algal community was dominated by CCA (74%), and there were few Halimeda (1%) (Figure 3d,e).

3.2 Spatial distribution patterns of coral abundance, species richness and juvenile coral recruitment

The cover of hard coral varied significantly among the four CRRs ($p < .05$; Figure S1.3 and Table S1.6 in Appendix S1). However, coral cover did not change gradually with increasing RDM (Figure 4a), with the highest cover occurring in the Nansha Islands (20%) and coastal reefs (20%), followed by the Xisha Islands (19%) (Figure S1.3 in Appendix S1). The number of coral genera varied significantly among the four CRRs ($p = .021$) and gradually increased from 19 to 37 genera with increasing RDM from Weizhou Island to the Nansha Islands, with the highest numbers in the NanSHA Islands (36–40 genus), and the lowest number in Weizhou Island (19 genera) (Figure 4b; Figure S1.3 and Tables S1.6–S1.7 in Appendix S1). The density of juvenile corals also varied significantly among the four CRRs ($p = .021$) (Tables S1.6 in Appendix S1). However, the density of juvenile corals...
did not change gradually with increasing RDM (Figure 4c), with the highest density, of 26.3 ind/m$^2$, in the Nansha Islands. There was no difference among the regions of coastal reefs (6.0 ind/m$^2$), Weizhou Island (4.0 ind/m$^2$) and the Xisha Islands (8.4 ind/m$^2$) (Figure S1.3 in Appendix S1).

### 3.3 Relationships between seawater environmental parameters, herbivorous fish and RDM

Both the human population and anthropogenic disturbance gradually decreased with increasing RDM (Table S1.1 in Appendix S1). With increasing RDM, we observed an increase in SST, PAR, SHWS, transparency variables, number of herbivorous fish species and total fish density, whereas Chl-$a$, DIN, SRP and POC decreased (Tables S1.3–S1.5 in Appendix S1). All seawater environmental parameters and total fish density were significantly correlated with RDM (Pearson correlations: all $p < .05$; Table 1). However, the numbers of herbivorous fish species were not correlated with RDM (Pearson correlations: both $p > .05$; Table 1).

The Supporting Information in Appendix S3 provides detailed results of each seawater environmental parameters and reef fish distribution, diversity and trophic level across the SCS.

### 3.4 Relationships among seawater environmental parameters, herbivorous fish and benthic algal cover, and the main factors for predicting benthic algal distribution

The RDA found that DIN, SRP, POC and Chl-$a$, which reflected nutrient content, were positively correlated with turf algal cover and negatively correlated with CCA cover, but they were weakly correlated or not correlated with cover of macroalgae, *Halimeda* or fleshy macroalgae (Figure 5). The other seawater environmental parameters, SST, PAR, SHWS and transparency, were positively correlated with CCA cover and negatively correlated with turf algal cover, but weakly correlated or not correlated with the other macroalgae (Figure 5). Herbivorous fish species and total fish density were positively correlated with CCA cover and negatively correlated with turf algae; contrary to expectations, the number of herbivorous fish species was negatively correlated with macroalgae, *Halimeda* or fleshy macroalgal cover (Figure 5).

The turf algal cover was best predicted by DIN, with total fish density, SRP and seawater transparency also highly ranked (Figure 6a). Although the random forest models found that SHWS and DIN were the best predictors of cover of macroalgae, fleshy macroalgae or *Halimeda* (Figure 6b–d), the RDA showed a weak...
FIGURE 3  Compositions of algal functional groups in the four coral reef regions (CRRs). Different benthic algal composition in the four investigated CRRs: (a) coastal reefs (RDM < 1 km), (b) Weizhou Island (RDM 40–50 km), (c) the Xisha Islands (RDM 200–400 km), (d) the Nansha Islands (RDM 1000–1200 km). (e) Benthic algal compositions at individual sites of the surveyed CRRs with increasing RDM. Macroalgae were divided into fleshy macroalgae and Halimeda. CCA, crustose coralline algae; RDM, reef distance to mainland.

FIGURE 4  Variation in coral cover, diversity and recruitment at coral reefs in the South China Sea. (a) Hard coral covers, (b) number of coral genera and (c) juvenile coral densities in the four coral reef regions (CRRs). Each colour represents a CRR. Daya Bay (DYB), Weizhou Island (WZI), Xuwen County (XW), Luhuitou (LHT), North Reef (NR), Yongxing Island (YXI), East Island (EI), Huaguang Reef (HGR), Langhua Reef (LHR), Sanjiao Reef (SJR), Xian’er Reef (XER), Xinyi Reef (XYR); RDM: reef distance to mainland.
relationship or no relationship between all macroalgae and most environmental factors. Therefore, the ranking of the important factors was not used for predicting all macroalgal covers. Furthermore, CCA cover was best predicted by SST, with transparency, herbivorous fish species and DIN also highly ranked (Figure 6e).

3.5 Changes in coral abundance, species richness and juvenile recruitment with increasing benthic algal cover

We found a negative linear log-log relationship between coral and turf algal cover (linear regression, $r^2 = .11$, $p = .0010$; Figure 7a). We observed no significant linear relationships between coral cover and cover of macroalgae and CCA (Figure 7b,c). Similarly, a negative linear relationship between number of coral genera and turf algal cover was found ($r^2 = .16$, $p < .0001$; Figure 7d), but there was only a weak negative relationship between number of coral genera and macroalgal cover ($r^2 = .05$, $p = .0460$; Figure 7e), and no significant linear relationship between coral genus number and CCA cover (Figure 7f). We also identified negative linear relationships between the density of juvenile corals and covers of turf algae and macroalgae ($r^2 = .36$ and $r^2 = .15$, respectively; both $p < .0001$; Figure 7g,h). However, there was a positive relationship between the density of juvenile corals and CCA cover ($r^2 = .10$, $p = .0163$; Figure 7i).

Additionally, we observed that coral cover, number of coral genera and juvenile coral density were positively related ($r^2$ range of .26-.43, all $p < .0001$; Figure S1.4 in Appendix S1). Finally, we found a negative linear relationship between CCA and turf algal cover ($r^2 = .16$, $p < .0001$), but no significant linear relationship between both CCA and turf algal cover and that of macroalgae (Figure S1.5 in Appendix S1).

4 DISCUSSION

4.1 Seawater quality and herbivorous fish can effectively regulate the spatial distributions of turf algae and CCA

Our study revealed a gradual decrease in turf algae and increase in CCA with an increase in RDM. Further analyses showed that the spatial distributions of turf algae and CCA were better predicted by nutrients, seawater transparency, SST or herbivorous fish than other environmental factors. The ecological findings could enhance our understanding of the main drivers of regime shift processes between turf algae and CCA.

Most environmental factors were found to be correlated with turf algae. In particular, the nutrients DIN and SRP, total fish density and transparency were found to be the most important predictors of the spatial distribution of turf algae. Many studies have shown that changes in nutrient supply and/or the intensity of fish herbivory can significantly affect turf algal abundance (Fong et al., 2018;
Littler et al., 2006; McClanahan et al., 2005; Sura et al., 2019). For instance, Sura et al. (2019) found that turf algal height increased by 127% after nutrient addition, compared to that before nutrient addition. Moreover, the removal of herbivores increased the height of turf algae by 0.7 mm from an initial height of 1.4 mm, in the absence of sediment (Fong et al., 2018). Our study found a fourfold increase in turf algal cover with increasing nutrients and decreasing fish herbivory with decreasing RDM. This finding emphasizes the important role of nutrients and herbivorous fish in the regulation of the spatial distribution of turf algae. In addition to nutrients and herbivorous fish, light conditions, which are affected by seawater transparency, are an important factor in turf algal overgrowth (Brown et al., 2018; Ferrari et al., 2012; Hughes et al., 2007). Terrestrial sediments are responsible for the low transparency in inshore reefs of the SCS (Li et al., 2013; Zhao et al., 2013). Conversely, sediment loads on turf algae can provide nutrients to facilitate their growth (Fong et al., 2018; Goatley et al., 2016). It is interesting to note that we found a negative relationship between transparency and turf algal cover with increasing RDM. Therefore, we suggest that the gains in turf algal cover with increasing sediment, and hence decreasing transparency, exceeded any potential losses from lowering light conditions caused by sediments in the SCS reefs.

Most of the environmental factors were also correlated with CCA. However, CCA cover was best predicted by SST, followed by

**FIGURE 6** Results of random forest models showing the relative importance of seawater environmental parameters and reef fish diversity factors used to predict the cover of benthic algae. The relative importance of 10 environmental factors for predicting the cover of (a) turf algae, (b) macroalgae, (c) fleshy macroalgae, (d) *Halimeda* and (e) CCA. CCA, crustose coralline algae; Chl-*a*, chlorophyll *a*; DIN, dissolved inorganic nitrogen; PAR, photosynthetically active radiation; POC, particulate organic carbon; SHWS, significant height of combined wind waves and swell; SRP, soluble reactive phosphorus; SST, sea surface temperatures.
transparency, species richness of herbivorous fish and DIN. Previous studies have confirmed the positive effects of natural SST and seawater transparency on the distribution of CCA across spatial scales (Fabricius & De’ath, 2001; Ford, Gove, et al., 2020). These positive effects were also observed in our spatial surveys. Unlike natural factors, alteration of some environmental factors that are directly influenced by anthropogenic stressors, such as the exploitation of herbivorous fish and increase in nutrients and sedimentation, are causing sharp regime shifts in CCA dominated habitats (Burkepile & Hay, 2006; Fabricius & De’ath, 2001; Littler et al., 2006; O’Leary & McClanahan, 2010). Grazing herbivores are extremely important for CCA growth. The dominance of many CCA species is maintained by herbivores, which can effectively remove fleshy algae, although some parrotfish and sea urchins may consume CCA (Burkepile & Hay, 2006; O’Leary & McClanahan, 2010; O’Leary et al., 2012). Nevertheless, the positive effect of nutrients on CCA only occurs under conditions of a high level of herbivory (Littler et al., 2006); increasing nutrients will not benefit CCA growth in the absence of herbivorous fish (Burkepile & Hay, 2006). This finding was also supported by our data, which showed that even under the most nutrient-rich conditions, CCA cover was quite low in coastal reefs, where herbivorous fishes are scarce. Additionally, the high sedimentation rate (20.0–29.9 mg cm$^{-2}$ day$^{-1}$) (Li et al., 2013; Zhao et al., 2013) and low transparency (4.5–6.5 m in our survey) in coastal reefs could also reduce the abundance of CCA, while CCA in remote reefs of the SCS are unlikely to be affected by sediments (transparency was
15–25 m). The high sedimentation rate and the resulting low transparency were reported to be responsible for the gradient change in CCA cover in the Great Barrier Reef (Fabricius & De’ath, 2001). Laboratory experiment results also suggested that CCA photosynthetic activity and CCA survival were negatively affected by nutrient-rich sediments (Harrington et al., 2005). Furthermore, CCA have a low rate of growth. The maximum lateral growth rate was only 3–5 mm/month, even under fertilization (Matsuda, 1989; McClanahan et al., 2005; Smith, 1972), making the distribution of CCA largely indirectly controlled by other fast-growing turf algae or fleshy macroalgae (Littler et al., 2006).

4.2 Effective regulation of environmental factors influencing macroalgal distribution may be disturbed by the overgrowth of turf algae and nutrient subsidies

According to the RDA results, most environmental factors failed to reflect the spatial distribution of macroalgae, including fleshy macroalgae and *Halimeda*, indicating that the natural biophysical relationships between macroalgae and surrounding environmental factors have become decoupled in the SCS. We proposed two possible reasons: (1) the fast-growing turf algae may take over the macroalgae in inshore CRRs, where the human population pressures are the greatest; and (2) nutrient subsidies from atmospheric nitrogen deposition and seabird guano, which are hard to detect, may promote the flourishing of macroalgae in the remote reefs of the Xisha Islands.

According to the Relative Dominance Model (Littler et al., 2006), the inhabited coastal reefs and Weizhou Island are more likely to be dominated by foliose macroalgae, because of the high nutrient supply and low abundance of herbivores. However, in fact, macroalgal cover in the two CRRs was quite low, less than 8%. A possible explanation was that turf algae may take over from macroalgae under high human population pressures. Previous studies from the Indo-Pacific reefs also indicated that turf algae are generally dominant on the reefs with high human population, while macroalgae are relatively rare (Brown et al., 2017; Cannon et al., 2019; Smith et al., 2016). Reefs in the presence of local human populations generally had high nutrient content and low abundance of herbivores, which are conditions suitable for the growth of macroalgae. However, local human population pressures can disrupt the natural relationships between macroalgae and the environmental factors in the central Pacific (Ford, Jouffray, et al., 2020; Williams et al., 2015). Furthermore, even if grazing pressure is removed, the macroalgal growth rate in the Indo-Pacific could remain low (Roff & Mumby, 2012). This situation may provide an opportunity for the fast-growing turf algae to pre-empt the substrate or colonize the macroalgae. It has been demonstrated that turf algae can also overgrow macroalgae and hinder their recruitment by competition and by the formation of dense assemblages (Isaegus et al., 2004; Paine, 1990). Therefore, macroalgae could not dominate the inshore reefs of the SCS, despite the local population encountering suitable conditions for growth. However, the explanation about turf algae replacing macroalgae in inshore reefs lacks a historical baseline of algal cover before human disruption.

Macroalgae, mainly *Halimeda*, which accounts for 77% of the macroalgal cover, are most abundant in the oligotrophic Xisha Islands. Evidence of nutrient subsidies from atmospheric nitrogen deposition and seabirds may help to explain this anomaly. Chen et al. (2019) suggested that atmospheric nitrogen was the most likely potential source of nutrients for the promotion of macroalgal blooms in the Xisha Islands. In addition, nutrients from seabirds were found to promote the growth of *Halimeda* in the remote Chagos Archipelago of the central Indian Ocean (Benkwitt et al., 2019). The Xisha Islands are rich in seabird populations (Xu et al., 2016), and nutrient subsidies from seabirds, therefore, may promote the growth of *Halimeda*. The most dominant herbivorous fish in the Xisha Islands seem to prefer turf algae over macroalgae (Chen et al., 2019). In contrast, *Halimeda* or other macroalgae species were rarely observed in reefs of the Nansha Islands, possibly because of the extremely low nutrient levels, high fish herbivory and lack of nutrient subsidies from seabirds, since there is no land for seabirds to nest on subtidal atoll reefs.

Overall, the competitive overgrowth of turf algae on inhabited inshore reefs and nutrient subsidies in remote reefs may disrupt or decouple the natural relationships between macroalgae and surrounding environmental factors in the SCS, even when these environmental factors change with increasing RDM.

4.3 Response of benthic algae to reef degradation and their potential ecological impact on coral recruitment

Our results indicate a clear trend of increasing turf algal cover with the loss of coral cover. The increasing turf algal cover then establishes a negative feedback effect on coral recruitment. Several studies have shown negative effects of turf algal on adult corals and larval recruitment (Arnold et al., 2010; Barott, Williams, et al., 2012; Birrell et al., 2008). For example, turf algae caused the greatest damage to corals, including local coral tissue necrosis or discoloration, among a wide range of algal groups (Barott, Williams, et al., 2012; Brown et al., 2017; Liao et al., 2019). These impacts may be associated with the allelopathic and microbial mechanisms of turf algae that directly contact corals (Barott, Rodriguez-Mueller, et al., 2012; Rasher et al., 2011). Furthermore, data from field experiments (Arnold et al., 2010) indicate that a high turf algal cover could decrease the successful recruitment of juvenile corals. In turn, decreases in coral recruitment may be responsible for the loss of coral cover and species diversity (Figure S1.4 in Appendix S1). Although there is no definite evidence to support the contention that turf algae are the main cause of reef degradation, it is clear that a high turf algal cover could negatively influence the recovery of coral communities and may therefore determine the future structure of coral communities.
The replacement of live corals by macroalgae in degraded SCS reefs is less common and less geographically extensive. Therefore, we suggest that the negative ecological impacts of macroalgae on corals in the SCS are overestimated. This suggestion is supported by the results of studies on a global scale. Bruno et al. (2009) found only weak or no correlations between macroalgae and coral cover (all $R^2 < 0.10$); this finding was also supported by Smith et al. (2016). Only 1% of 963 reefs in the Indo-Pacific region are dominated by macroalgae, using a dominance threshold of $>50\%$ (Bruno et al., 2009). However, none of the reefs in the SCS were dominated by macroalgae, even using a much lower threshold of 25%. The extent of the negative effects of macroalgae on coral recruitment is affected by the abundance and species of macroalgae present (Díaz-Pulido et al., 2010; Hughes et al., 2007). Although macroalgal cover was lower in the SCS reefs (average of 6%, maximum $<18\%$), the non-dominant macroalgae were still negatively correlated with juvenile corals. Therefore, non-dominant macroalgae may also be a key obstacle to the recovery of many degraded reefs in the Indo-Pacific region.

Unexpectedly, CCA were not positively correlated with coral cover or genus diversity, which is consistent with the finding of Smith et al. (2016) but is contrary to the finding of Brown et al. (2017). A possible explanation for this observation is that the favourable effects of CCA on the coral cover and diversity may be offset by strong anthropogenic or natural disturbances, such as overfishing, destructive fishing, coral bleaching and outbreak of crown-of-thorns starfish in the SCS. Indeed, the positive effects of CCA on the recruitment process of coral larvae have been repeatedly confirmed (Gómez-Lemos et al., 2018; Harrington et al., 2004), and many species of CCA have been shown to induce coral larval settlement (Harrington et al., 2004). Furthermore, coral recruitment can also indirectly benefit from the high density of reef fish across large spatial scales, because of the positive effects of herbivorous fish on increasing CCA cover (O’Leary et al., 2012, 2013). This finding is also supported by our results. Coral reefs in the Nansha Islands, where the RDM is the largest and the reefs are the least affected by human activities, maintain the highest juvenile coral density, which may benefit from the high cover of CCA and high diversity of herbivorous fish. Therefore, the capacity of reefs to maintain high cover of CCA may be critical to the natural recovery of Indo-Pacific reefs.

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SUPPORTING INFORMATION

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