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Epilithic algal composition and the functioning of Anthropocene coral reefs

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ABSTRACT

Epilithic algae dominate cover on coral reefs globally, forming a critical ecological interface between the benthos and reef organisms. Yet, the drivers of epilithic algal composition, and how composition relates to the distribution of key taxa, remain unclear. We develop a novel metric, the Epilithic Algal Ratio, based on turf cover relative to total epilithic algae cover, and use this metric to assess cross-scale patterns. We reveal water quality and hydrodynamics as the key environmental drivers of the Epilithic Algal Ratio across the Great Barrier Reef (GBR), and reefs globally. On the GBR, the abundance of herbivorous fishes and juvenile corals were also related to the Epilithic Algal Ratio, suggesting that reefs with long-dense turfs support fewer herbivores and corals. Ultimately, epilithic algae represent the interface through which the effects of declining water quality, which impacts a third of reefs globally, can reverberate up through coral reefs, compromising their functioning.

1. Introduction

Scleractinian corals define coral reefs, yet these organisms themselves are often not the dominant benthic component on Anthropocene reefs (Smith et al., 2016; Tebbett et al., 2023b). Following precipitous declines in the size and abundance of corals globally, most reefs are now dominated by short epilithic algae (Pisapia et al., 2020; Souter et al., 2021; Tebbett et al., 2023a), despite widespread expectations that they would become dominated by fucalean and dictyotacean macroalgae (Bellwood et al., 2004; Hughes et al., 2010). Coral reefs are, in the words of Adey (1998), "*algal structured and mediated ecosystems*". As such, the functioning of coral reefs now, and in the future, is inextricably tied to the cover of epilithic algae (Harvey et al., 2021; Cornwall et al., 2023; Tebbett et al., 2023a). Understanding ecological relationships that define the composition of these algal forms, therefore represents a key opportunity for forecasting the capacity of coral reefs to sustain ecological functions and the services on which people depend.

High cover of epilithic algae on the world's reefs means that these algae form a critical interface where ecological processes and organisms interact with the benthos, many of which are crucial to reef functioning and resilience. Scleractinian corals (henceforth, corals) and nominally herbivorous fishes (henceforth herbivorous fishes) are both widely viewed as critical groups of organisms that play important roles in ecosystem functioning (Bellwood et al., 2004; Steneck et al., 2018; Robinson et al., 2023; Morais et al., 2024). Both juvenile corals and herbivorous fishes also closely associate with epilithic algae on reefs (Birrell et al., 2008; Rasher et al., 2012; Steneck et al., 2018). For example, the recruitment of new corals to reefs is key to regenerating coral populations post-disturbance (Holbrook et al., 2018; Evans et al., 2020), and when these corals settle, they interact directly with epilithic algae (Birrell et al., 2005; Speare et al., 2019). Herbivorous fishes act as major trophic conduits of on-reef primary productivity and are in near-continuous interactions with algae via their grazing activity (Choat et al., 2004; Adam et al., 2015; McAndrews et al., 2019). Given these close ecological associations, it is unsurprising that small-scale experimental studies have suggested that the composition of epilithic algae is critical in mediating important ecological processes, such as coral settlement (Birrell et al., 2005; Speare et al., 2019) and herbivory (Bellwood and Fulton, 2008; Goatley et al., 2016) on coral reefs.

The composition of epilithic algae and the terminology relating to it

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are relatively complex and intertwined with ecological processes. Here we use ‘epilithic algae’ as an inclusive term for both crustose coralline algae (CCA) and algal turfs (both groups grow over the surface of the reef benthos – hence ‘epilithic’). CCA are calcifying red algae in the order corallinales (Bittner et al., 2011; Dean et al., 2015). Algal turfs are commonly defined as short (<2 cm) multispecies assemblages of both algal and cyanobacteria taxa that are often filamentous in nature (Connell et al., 2014; Arjunwadkar et al., 2022). However, the terms used to define turfs can be varied. Historically, the term ‘epilithic algal community’ (EAC) was often used in the 1980s–90s to recognise that algal turfs were composed of a diverse community of algal/cyanobacteria taxa (e.g. Hatcher and Larkum, 1983; Russ, 1987). In the late 90s the term evolved into the ‘epilithic algal matrix’ (EAM) which was used to recognise that algal turfs were a matrix of components composed of the EAC as well as organic detritus, microbes, and inorganic sediment (Wilson and Bellwood, 1997). The terms short productive algal turfs (SPATs) and long sediment-laden algal turfs (LSATs) were developed in the mid-2010s to recognise that the EAM was highly heterogenous in terms of its structure (Goatley et al., 2016). Specifically, SPATs were considered short (~ < 3–5 mm) EAMs with low sediment loads, while LSATs (a term largely analogous to ‘turf algal sediment mats’ [e.g. Lacey et al., 2013; Shantz et al., 2015]) were considered long

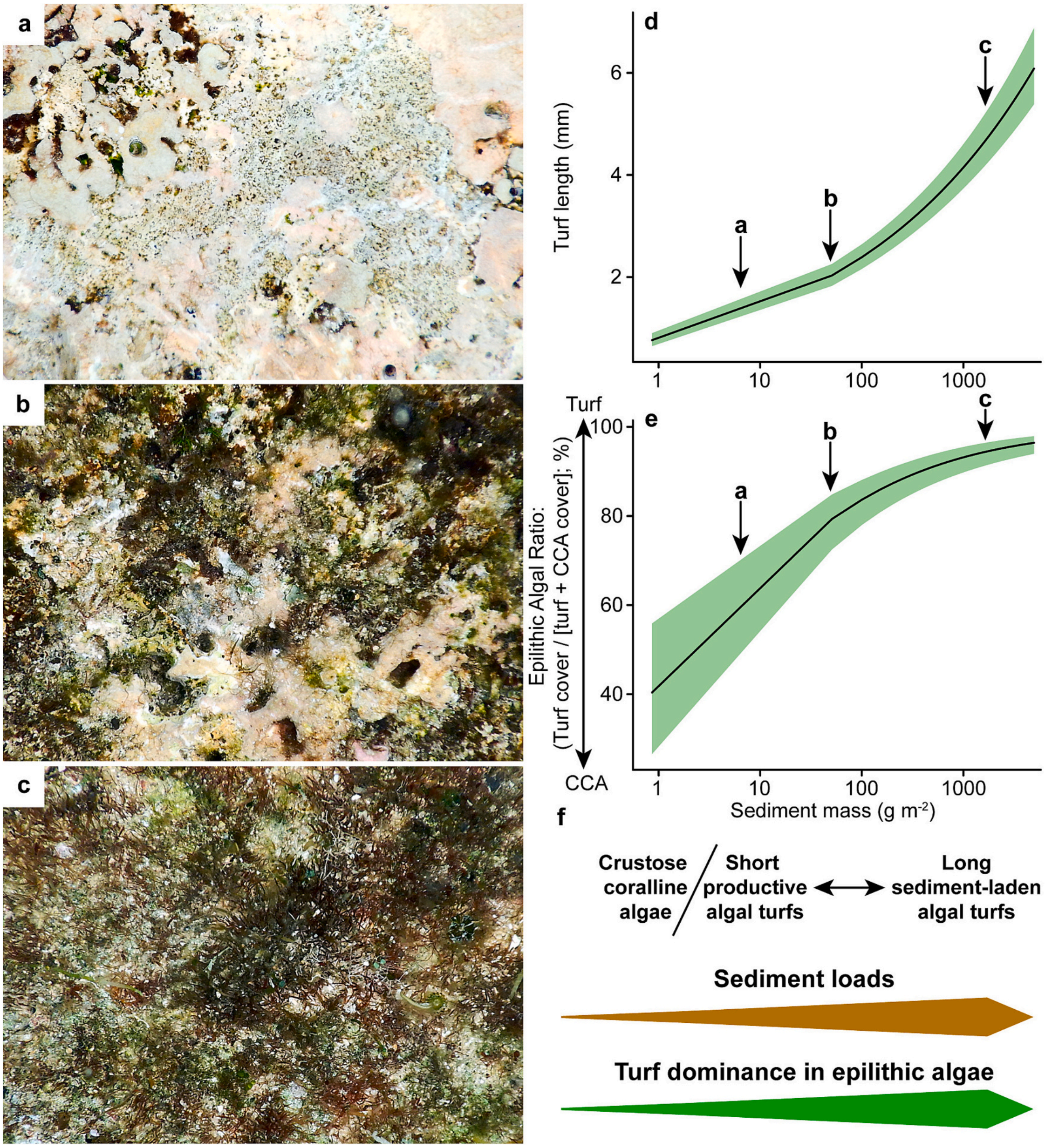

Fig. 1. The spectrum of epilithic algal compositions. Photographs from coral reefs on the Great Barrier Reef, Australia, showing various epilithic algae compositions: (a) predominantly crustose coralline algae (CCA) with some short productive algal turfs (SPATs), (b) SPATs and CCA, and (c) long sediment-laden algal turfs (LSATs). Note sediment has been removed in a-c to show turf composition, refer to Fig. S8 in the supplemental material for photographs showing areas of long dense turfs with sediments intact adjacent to areas with sediments removed. The relationships between turf sediment mass and (d) turf length as well as (e) the Epilithic Algal Ratio (i.e. turf cover/ [turf + crustose coralline algae (CCA) cover]). Black lines denote the mean predicted fit from generalised linear mixed effects models, and green ribbons denote the 95 % confidence intervals ($n = 190$ in both cases; refer to Fig. S4 in the supplemental material for a version with raw data). Note the arrows and letters in (d and e) show the position of photographs (a-c) on each relationship. Also note the x-axes are on the log10 scale in both cases. (f) A simplified conceptual overview of the spectrum of compositions in which epilithic algae exist. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(∼ > 5 mm) EAMs with high sediment loads (Tebbett and Bellwood, 2019, 2020).

Recently, it has become apparent that it is hard to strictly define SPATs and LSATs because of the fact that epilithic algae exist on a continuous spectrum from CCA through SPATs to LSATs (Fig. 1a-c; Tebbett et al., 2023a), with this spectrum potentially relating to how reefs function. Indeed, this spectrum of epilithic algal composition directly relates to sediment trapping, coral settlement, and herbivory (Steneck, 1997; Tebbett and Bellwood, 2019). CCA are critical to the functioning of reefs as they provide important settlement (Ricardo et al., 2021; Abdul Wahab et al., 2023) and grazing surfaces (Adam et al., 2015; Nicholson and Clements, 2020) for reef organisms, while also contributing to processes such as calcification and reef growth (Kench et al., 2022; Cornwall et al., 2023). In contrast, LSATs are unproductive and can suppress herbivorous fish feeding (Bellwood and Fulton, 2008; Goatley et al., 2016) and the settlement of benthic organisms, including corals (Birrell et al., 2005; Speare et al., 2019; Duran et al., 2024). Consequently, there is the potential that the composition of epilithic algae could predict how reefs function and, therefore, provide critical information about the condition of these systems.

Despite the ecological importance of epilithic algae, they are rarely considered and poorly quantified in coral reef ecological surveys (Cornwall et al., 2023; Tebbett et al., 2023a). As such, we have a limited understanding of the drivers underpinning epilithic algae composition across broad scales, and how variation in composition is connected to reef health at these spatial scales. To overcome this problem, we develop the Epilithic Algal Ratio (i.e. the cover of algal turf [numerator] relative to the sum total cover of algal turf and CCA [denominator]) based on detailed mm-scale quantification of algae. We then utilise a multi-scale approach to assess how key environmental drivers relate to the Epilithic Algal Ratio at the scale of the Great Barrier Reef (GBR) and across reefs globally. We also assess how the Epilithic Algal Ratio is related to the abundance of two ecologically important groups of reef organisms: juvenile corals and nominally herbivorous fishes. Ultimately, we highlight the cross-scale importance of hydrodynamics and water quality in shaping the Epilithic Algal Ratio and suggest that this ratio could hold the key to unravelling critical aspects of coral reef functioning.

2. Methods

2.1. The spectrum of algal compositions and development of the Epilithic Algal Ratio

To examine the extent to which epilithic algal composition varied along the spectrum from CCA through to LSATs, we quantified algal composition in relation to accumulated sediment loads at 19 locations in the northern GBR, Australia, in January/February 2021/2022 (Fig. S1). The 19 locations spanned a nearly 50 km-wide environmental gradient encompassing a broad swath of conditions, from turbid inner-shelf reefs to clear-water outer-shelf reefs (Fig. S1). At each location, epilithic algae were quantified at 10 haphazardly selected sampling sites, all in relatively shallow ∼2–3 m water in the 'reef crest/edge' habitat. All sampling sites were composed of flat, consolidated substratum, covered in short CCA/turfs, outside the territories of farming damselfishes, and free of large sediment-retaining pits, macroalgae, and encrusting organisms.

At each sampling site, we collected the sediment trapped in epilithic algae from within a 58 cm^2 PVC ring using a submersible electronic underwater vacuum sampler (following Tebbett et al., 2022). Collected sediments were subsequently processed to yield dry inorganic sediment mass (see Text S1 for full details). Following removal of sediments, the length of 10 haphazardly selected turf filaments from within the sampling ring were quantified using the depth probe of vernier callipers (following Tebbett and Bellwood, 2019). The ten measurements were averaged, yielding mean turf length for each sample. Finally, the sampled area was photographed using a Nikon Coolpix AW130 digital camera, and the cover/density of turf filaments and CCA was subsequently quantified from each photograph. This was achieved by overlaying 30 randomly stratified points over the sampling area in the software PhotoQuad (Trygonis and Sini, 2012) and recording if turf or CCA was present under each point. In situations where a turf filament was overlaying CCA, this point was classed as both turf and CCA.

We used separate generalised linear mixed-effects models (GLMMs) to examine if turf length and the Epilithic Algal Ratio (i.e. turf cover/[turf + CCA cover]) were related to the load of sediments trapped in epilithic algae. It is important to note that, in this case, the Epilithic Algal Ratio was calculated based on counts consisting of two categories (i.e. point counts of turf and CCA) which aligns with a binomial response. Inorganic sediment mass was treated as a continuous fixed effect (logged, scaled, and mean-centred), while reef location was treated as a random effect to account for any lack of spatial independence in the GLMMs. The relative distance of each location across the continental shelf was also fitted as a scaled and mean-centred continuous fixed effect to account for this environmental gradient in both models (see Table S1 for details of how this was calculated). The turf length model was based on a gaussian distribution with a log-link function, while the Epilithic Algal Ratio model was based on a binomial model with a logit-link function. Model fit and assumptions were examined via standard residual plots, and simulation-based model-checking procedures (package: *DHARMa*; Hartig, 2020), which suggested model fit was satisfactory and assumptions were met. In addition, we refitted the Epilithic Algal Ratio model with turf length as a continuous fixed effect (in place of inorganic sediment mass), to examine the relationship between these two metrics. This refitted model used all the same model fitting and checking procedures as above. All model fitting was performed in the software R (version 4.2.2; R Core Team, 2022) using the *glmmTMB* (Brooks et al., 2017) package.

2.2. Drivers of epilithic algae composition and upscaling

Our ability to scale up detailed, but relatively small-scale, quantitative measures of epilithic algae is currently limited because detailed quantification of epilithic algae (as above) is rare in standard coral reef ecological surveys (reviewed in Tebbett and Bellwood, 2019; Tebbett et al., 2023b). However, when broad scale ecological surveys of benthic cover are conducted on coral reefs, epilithic algae are often recorded as dichotomous categories (i.e. CCA or turf) (e.g. Smith et al., 2016; Aued et al., 2018; Fabricius et al., 2023). While dichotomous, these data may still reflect the spectrum of epilithic algal compositions by facilitating the calculation of the Epilithic Algal Ratio (as above).

Based on past research into the drivers of epilithic algal composition (Fabricius and De'ath, 2001; Tebbett et al., 2023c), one would expect that the Epilithic Algal Ratio would relate to environmental factors, such as water quality (i.e. turbidity and nutrient concentrations) and sediments/hydrodynamics. This is because turfs can be competitively successful over CCA under specific environmental conditions, such as enhanced sediment accumulation (Steneck, 1997). To explore how the composition of epilithic algae was related to environmental drivers at broad scales, we utilised ecological survey data at the scale of the GBR and on different reefs around the world. In all cases, ecological survey data calculated the planar benthic cover of CCA and turfs on the same surveys, allowing us to calculate the Epilithic Algal Ratio. It should be noted that, to the best of our knowledge, other encrusting macroalgae (such as peyssonnelioids which can be abundant in some contexts [e.g. Edmunds et al., 2023]) were discriminated from CCA in these data. However, given that epilithic algae in general, and CCA in particular, can be difficult to identify (e.g. Dean et al., 2015), there is always the potential for some level of misidentification when benthic data are collected on coral reefs.

For GBR-specific data, we used the dataset from the Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP) (Emslie et al., 2020). The LTMP data represent one of the most comprehensive and longest running coral reef monitoring programs in the world (Emslie et al., 2020). LTMP sampling is conducted between 6 and 9 m on a standard reef slope habitat, usually on the north-east flank of individual reefs, with three permanent sites at each reef, and five fixed 50 m transects at each site ($n = 15$ transects reef^{-1} year^{-1}). Fifty digital images were taken along each transect, and the cover of benthic components (including turf and CCA) was quantified in forty randomly selected images, by identifying benthic organisms to the lowest taxonomic resolution possible beneath five points in each image ($n = 200$ points transect^{-1}) (Jonker et al., 2020). As we were interested in exploring broad-scale relationships between the Epilithic Algal Ratio and environmental drivers, we relied on site-level mean cover of turf and CCA for each sampling year to calculate the ratio. To minimise low total cover of epilithic algae biasing calculation of the Epilithic Algal Ratio, we only included data where the mean sum total cover of turf and CCA was 10 % or more for a given reef in a given year ($n = 5$ observations <10 %). The GBR data covered a temporal sampling period of 1994–2023 and were available for up to 103 reefs with annual or biennial surveys ($n = 4441$ yearly site level average Epilithic Algal Ratio observations).

For the global data, we relied on a recently compiled global dataset of benthic cover on coral reefs (for all data sources see Tebbett et al., 2023a, 2023b). We used a subset of this dataset ($n = 7935$ turf and CCA cover estimates), based on ecological survey data in which CCA and turf were recorded as separate categories (following Tebbett et al., 2023b). In addition, we extended this dataset by including data derived from the AIMS LTMP on the GBR (as above), as well as the AIMS inshore marine monitoring program (MMP) ($n = 1859$). In the MMP, AIMS has quantified the benthic cover (including turf and CCA as separate categories) on 28 inshore reefs of the GBR since 2005, at both 2 and 5 m depth, also using the photo-quadrat method, as above (Jonker et al., 2020). However, in the MMP 40 images were taken and thirty-two randomly selected images were analysed ($n = 160$ points transect^{-1}). Our primary goal with this large ($n = 14{,}420$) compilation of ecological survey data was to explore spatial variation in the Epilithic Algal Ratio in relation to variation in key potential drivers. Therefore, we calculated average Epilithic Algal Ratio to the nearest 0.01 degrees of latitude and longitude, within the same habitats, in 3 m depth bins, across years. Average calculations were only based on benthic cover data that were collected using one of two planar methods (i.e. point intercept transects, or photo-quadrat transects), between 1995 and 2018 (a period which maximised temporal overlap between the datasets). Prior to averages being taken, this subset of data consisted of 11,708 observations (3518 from LTMP; 1373 from MMP; 6817 from the recently compiled global dataset). After averaging across the dataset, this resulted in 5099 average Epilithic Algal Ratio data points for analysis (again, to minimise bias, this dataset for analysis only included data where the sum total cover of turf and CCA was 10 % or more).

We considered how the Epilithic Algal Ratio was related to a suite of potential broad-scale environmental drivers at the scale of the GBR over space and time (seven predictors: sea surface temperature [SST], year of sampling, total cover of epilithic algae, significant wave height, chlorophyll-*a* concentration, kd490 [i.e. turbidity], photosynthetically active radiation [PAR]) and across different reefs globally over space (nine predictors: SST, total cover of epilithic algae, chlorophyll-*a* concentration, kd490, PAR, relative distance offshore, depth, biogeographic region, habitat). The selection of predictors was based on demonstrable justification of links to the nature of the epilithic algae on reefs, the availability of data on predictors at the scale being examined, and examination of collinearity between predictors (Figs. S2, S3). The predictors considered, their justification for inclusion, how they were calculated, and data sources, are outlined in Table S1. To examine the relative importance of the environmental drivers in predicting the Epilithic Algal Ratio, and to examine the nature of relationships between key drivers and the Epilithic Algal Ratio, we used an extreme Gradient Boosted Regression Tree (implemented via the *XGBoost* package; Chen and Guestrin, 2016). Gradient Boosted Regression Trees are a versatile machine learning technique that efficiently model nonlinearities and multilevel interactions in data that may not be suitable for traditional analysis (Elith et al., 2008). The algorithm used by XGBoost has been specifically designed to be efficient, flexible, and robust, and has been shown to outperform the algorithms used by other Gradient Boosted Regression Trees (Chen and Guestrin, 2016).

We analysed the GBR data, and the global data, separately in two XGBoost models. In both cases, Epilithic Algal Ratio was treated as the dependent variable and examined against the potential environmental drivers, which were constrained with monotonic trends where scatterplots suggested this was appropriate. Both models used a logistic objective loss function, due to the proportional nature of the Epilithic Algal Ratio (to fit the logistic function values of 0 and 1 were converted to 0.001 and 0.999, respectively). Initially, we performed two tuning steps on the XGBoost models prior to making predictions (following Morais and Bellwood, 2018). Firstly, models were repeatedly fitted with systematically varied combinations of model hyperparameters (learning rate, maximum tree depth, gamma, and subsampling rate), while all other hyperparameters were kept at their default values. We subsequently recorded the combination of hyperparameters that minimised the root mean square error (rmse). Secondly, models were repeatedly fit with combinations of hyperparameters that were randomly drawn from a uniform distribution bounded by the recorded hyperparameters from the first tuning step ±10 %. In both cases, the second tuning step mildly improved the rmse from 0.06016 to 0.05867 and from 0.144 to 0.143 for the GBR and global models, respectively. The final hyperparameters used were: learning rate = 0.227 and 0.097, maximum tree depth = 8 and 8, gamma = 0.008 and 0.158, and subsampling = 0.988 and 0.934, for the GBR and global models, respectively.

The accuracy and precision of the final XGBoost models were evaluated using a cross-validation procedure. Specifically, both the GBR and global datasets were split into training and testing datasets. The training datasets were based on 80 % of the data and were used to generate coefficients for prediction, while the testing datasets were based on 20 % of the data and were used to evaluate the predictions made using the training dataset. To examine accuracy, we calculated a bias metric by subtracting the predicted Epilithic Algal Ratio values from the XGBoost models from the actual value (an accurate model has a bias value close to zero). To examine precision, we used prediction R^2 values which were calculated by fitting a linear regression model between the raw data and the predicted values, and then recording the R^2 from this regression. These cross-validation steps were repeated 1000 times for both models. This process suggested that both models were precise, with mean bias estimates of −0.0007, and − 0.0005 for the GBR and global model, respectively.

Predictions of the Epilithic Algal Ratio were calculated based on our tuned and cross-validated XGBoost models across all explanatory variables. In all cases, we bootstrapped predictions for 1000 iterations to generate a distribution of predicted Epilithic Algal Ratios and subsequently sampled the mean and ± 95 % highest density intervals from these predictions. The relative importance of different environmental drivers in accounting for variation in the Epilithic Algal Ratio were assessed against the expected importance of variables given chance alone (i.e. if a variable only explained 14.3 % or 11.1 % or less of the variance explained by the GBR and global models, respectively, then this variable was deemed to be uninformative). All XGBoost modelling was performed in the software R (version 4.2.2; R Core Team, 2022), using the *XGBoost* (Chen et al., 2019) package.

2.3. The ecological importance of the Epilithic Algal Ratio on reefs

To explore relationships between two critical groups of reef organisms (juvenile corals and nominally herbivorous fishes) and epilithic algae on coral reefs across large spatial scales, we once again used data from the AIMS LTMP (Emslie et al., 2020). Importantly, under the LTMP, herbivorous fish abundance, juvenile coral abundance, and epilithic algal cover (CCA and turf) are quantified over the same areas of the reef, at the same times, ensuring tight spatial-temporal coupling that facilitates the exploration of relationships between different organisms. Specifically, along each transect, the abundance of key fishes and juvenile corals is surveyed using standardised underwater visual census methods. Fishes are surveyed along 50 m × 5 m belt transects and all herbivorous fishes are identified to species and their abundance is recorded (Emslie and Cheal, 2018). Juvenile corals (~5 mm to <50 mm) are identified to genus and counted along a 0.34 m × 5 m belt at the start of each transect (Jonker et al., 2020). The cover of turf and CCA are quantified using the photoquadrat method along 50 m transects (Jonker et al., 2020). As we were interested in exploring broad-scale relationships between the abundances of herbivorous fishes as well as juvenile corals with the cover and composition of epilithic algae, we relied on site-level means, for each sampling year.

To explore patterns in herbivorous fishes, we used data on the mean abundance (number of individuals 250 m^{-2}) of nominally herbivorous surgeonfishes and parrotfishes that associate with epilithic algae on coral reefs when feeding (i.e. scrapers, excavators, croppers, and detritivores but not browsers) (Cheal et al., 2012). The final dataset for herbivorous fishes included 103 individual reefs surveyed on multiple occasions between 1994 and 2023 ($n = 4396$). For juvenile corals, we used data on the total abundance (number of colonies m^{-2} of available substratum [i.e. the area of reef covered in turf and CCA following Jonker et al., 2019]) of Scleractinian juvenile coral colonies (not including solitary fungid corals). The final dataset for juvenile corals included data from 103 reefs surveyed on multiple occasions between 2007 and 2023 ($n = 3609$). Note the shorter temporal span for juvenile coral data is because monitoring of juvenile colony densities only commenced in 2007. For each respective herbivorous fish and juvenile coral abundance data point, we also compiled data on the average cover of epilithic algae (i.e. the total percentage of the reef benthos covered in turfs and CCA) and the average Epilithic Algal Ratio.

To explore the nature of relationships between the abundance of herbivorous fishes as well as juvenile corals and epilithic algae, we used separate generalised additive models (GAMs) with tweedie distributions and a log-link function. Specifically, the abundance of herbivorous fishes and juvenile corals were treated as response variables in separate GAMs. In both models, the Epilithic Algal Ratio and the percent cover of epilithic algae were fitted as continuous smoothed fixed effects. In addition, to account for any spatial and temporal lack of independence, we included relative distance across the shelf and relative distance along the GBR as smoothed interacting fixed effects (note these relative spatial factors account for spatial variability better than absolute latitude and longitude on the GBR [De'ath et al., 2012]), and sampling year (with separate splines for the northern, central, and southern regions of the GBR following De'ath et al., 2012) as smoothed continuous fixed effects in both models. In all cases, we used thin plate splines for the fixed effects, initially relying on the default level of knots. After fitting the GAMs, we checked that the number of knots used was sufficient by checking if *k* and the effective degrees of freedom *edf* were close to each other, while simultaneously considering the values of the *k*-index and simulated *P* value (Wood, 2017). Where this procedure suggested the number of knots was too restrictive, we increased *k* until it suggested enough knots had been used. In addition, we checked the models for concurvity among the fixed effects, temporal autocorrelation using residuals, and spatial autocorrelation using variograms of the residuals, all of which were satisfactory and/or no meaningful patterns were detected. Finally, we also examined standard residual plots and used simulation-based model-checking procedures (as above), which suggested model fit was satisfactory in all cases. All GAMs were undertaken in the software R (version 4.2.2; R Core Team, 2022), using the *mgcv* (Wood, 2017) and *gstat* (Gräler et al., 2016) packages.

3. Results

3.1. The spectrum of algal compositions and development of the Epilithic Algal Ratio

Using vacuum sediment sampling and turf measurements, we quantified the epilithic algae in detail across a ~ 50 km-wide environmental gradient on the GBR. This detailed quantification showed how epilithic algal composition varied on a spectrum from CCA with SPATs through to LSATs in relation to benthic sediment loads (Figs. 1, S1, S4, S5). Turf length was significantly ($p < 0.001$; Table S2) and positively related to sediment load across this broad gradient (Figs. 1d, S4). Likewise, the percentage cover of turf in epilithic algae cover (i.e. the Epilithic Algal Ratio) increased significantly as sediment load increased ($p < 0.001$; Table S2; Figs. 1e, S4); a similar relationship also existed between the Epilithic Algal Ratio and turf length ($p < 0.001$; Table S2; Fig. S6). The GLMMs also revealed that both turf length and the Epilithic Algal Ratio decreased with increasing relative distance offshore ($p < 0.001$; Table S2; Fig. S5). These relationships suggest that across the SPATs to LSATs spectrum, epilithic algal composition varies from CCA with short, sparse turfs, through to long, dense turfs with limited CCA cover (Fig. 1). Specifically, if the Epilithic Algal Ratio comprises high values (i.e. 100 % turfs), the composition of epilithic algae is likely to be closer to the LSATs end of the spectrum (Fig. 1d-f), while low values would reflect the CCA and SPATs end of the spectrum.

3.2. Drivers of epilithic algae composition and upscaling

To explore the key environmental drivers of the Epilithic Algal Ratio, we examined two datasets based on broad-scale ecological surveys of coral reef benthic cover. Specifically, we applied a machine learning technique (boosted regression trees) to assess the relative importance of environmental factors in shaping the Epilithic Algal Ratio at both regional (i.e. GBR; Fig. 2a) and global (Fig. 3a) scales. The model applied to the GBR-specific data explained the majority of spatial variation in the Epilithic Algal Ratio. Indeed, across 4441 observations (site × year), the mean precision (prediction R^2) of the boosted regression tree was 0.89. Turbidity (as quantified via kd490 – the rate at which light at 490 nm attenuates with depth), Chlorophyll-*a*, and significant wave height (i.e. the average height of the top 1/3 highest waves affecting the reef) emerged as key factors that disproportionately explained more variance (32 %, 28.6 %, and 16.6 %, respectively) than expected by chance alone (Fig. 2b). Model results revealed that high Epilithic Algal Ratios occurred when kd490 and chlorophyll-*a* concentrations were higher (Fig. 2c, d). By contrast, as significant wave height increased, the Epilithic Algal Ratio decreased (Fig. 2e). Notably, these three environmental factors are all closely related to the relative distance of reefs offshore (Figs. S2, S7), suggesting that this cross-shelf spatial gradient is one of the key spatial gradients over which the Epilithic Algal Ratio varies on the GBR (Fig. 2a).

At the global scale, the boosted regression tree again identified chlorophyll-*a*, in addition to total epilithic algae cover, relative distance offshore, and sea surface temperature (SST), as the key factors explaining more variation than expected by chance alone (Fig. 3b) (boosted regression tree mean $R^2 = 0.5$). Specifically, as both chlorophyll-*a* levels and the total cover of epilithic algae increased, the Epilithic Algal Ratio increased (Fig. 3c, d). In contrast, at sites in closer relative proximity to the open ocean (where hydrodynamic exposure and wave energy is likely to be higher [see Fig. S7 for a scatterplot of significant wave height values across the GBR]) and with higher SST, the Epilithic Algal Ratio was lower (Fig. 3e, f). Considering the results of the two boosted regression tree analyses together (Figs. 2, 3), reveals that low Epilithic Algal Ratios generally characterise offshore locations, especially in areas with higher water quality (i.e. clear water with low nutrient concentrations) and under more intense wave energy.

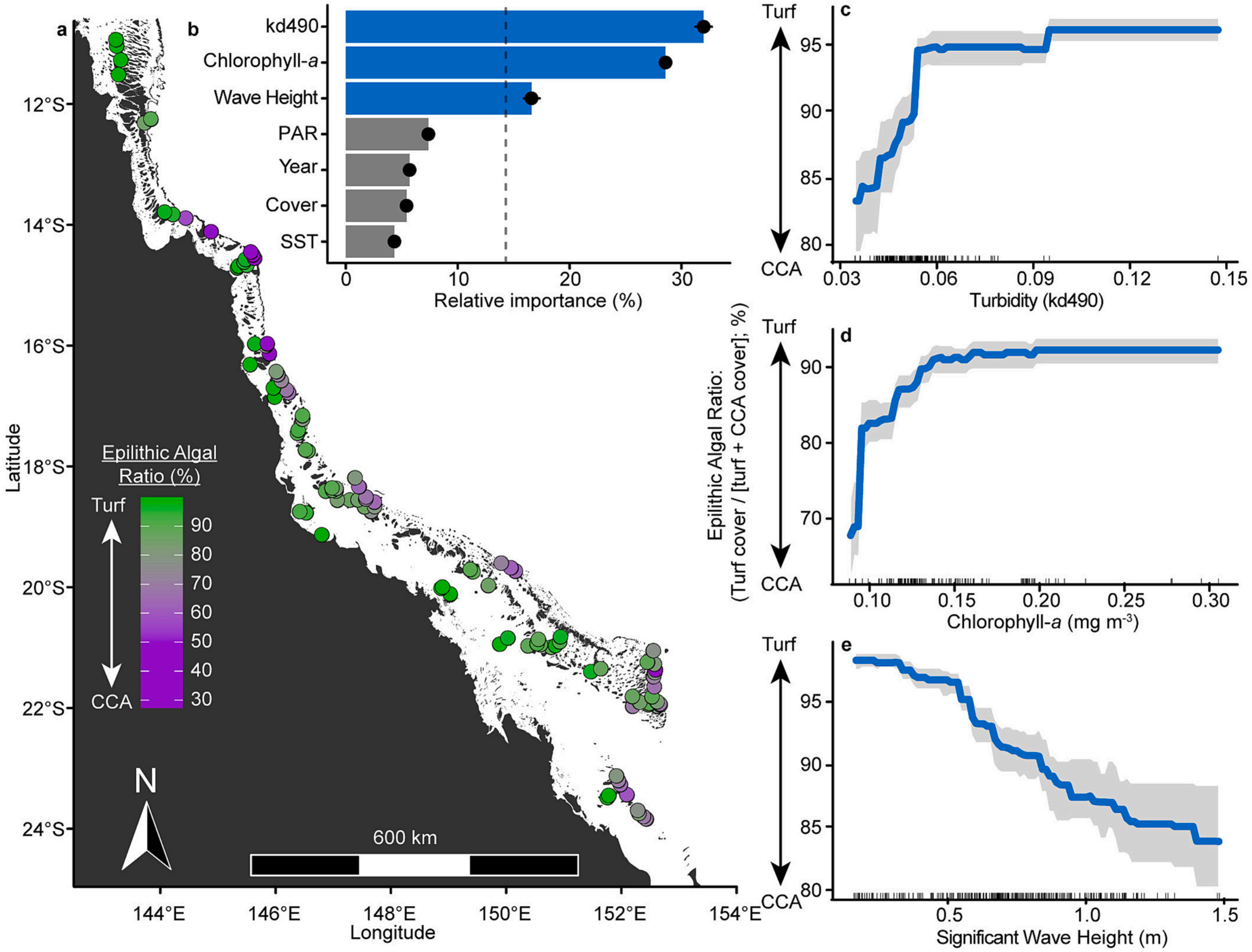

Fig. 2. Epilithic Algal Ratio distribution on the Great Barrier Reef and potential drivers. (a) Spatial variation in the mean Epilithic Algal Ratio (i.e. turf cover/[turf + crustose coralline algae (CCA) cover]) from 103 coral reefs on the Great Barrier Reef ($n = 4441$). (b) The relative importance of explanatory variables in accounting for spatial variation in the Epilithic Algal Ratio. Black dots indicate the mean relative importance value, while the range denotes the 95 % highest density intervals based on 1000 bootstrapped iterations. The vertical dashed line indicates the null expectation (i.e. the relative importance expected for each variable by chance), with blue bars denoting factors that explained more variation than expected. Partial dependency plots showing the relationship between the Epilithic Algal Ratio and the key explanatory variables of (c) turbidity measured via kd490, (d) chlorophyll-*a* concentration, and (e) significant wave height. The blue line denotes the mean predicted value, while the grey ribbon denotes the 95 % highest density intervals, based on an extreme gradient boosted regression tree model ($n = 1000$ model iterations). The ticks on the x-axes in (c)-(e) show the distribution of the raw data. Note the y-axes are on different scales. SST = sea surface temperature, PAR = photosynthetically active radiation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. *The ecological importance of the Epilithic Algal Ratio on reefs*

Model results revealed that the abundance of both juvenile corals and herbivorous fishes were strongly related to the Epilithic Algal Ratio (Fig. 4; Table S3) and the total cover of epilithic algae (Fig. 5; Table S3). The GAM for juvenile coral abundance showed that, as the Epilithic Algal Ratio increased (i.e. turfs progressively dominated over CCA in epilithic algae cover), the abundance of juvenile corals declined by approximately 37 % in a relationship significantly different from a flat line ($p < 0.001$; Table S3) (Fig. 4c). In addition, juvenile coral abundance remained high when total epilithic algae cover ranged from ~14–60 %, before declining by approximately half as epilithic algae cover increased beyond ~60 % (Fig. 5a). In terms of herbivorous fishes, their abundance increased gradually from an Epilithic Algal Ratio of ~11–64 %, with a distinct peak at 64 %, beyond which it declined steeply ($p < 0.001$; Table S3; Fig. 4d). Moreover, as the cover of epilithic algae increased, the abundance of herbivorous fishes more than doubled, increasing in a continuous relationship (Fig. 5b). These results suggest that reefs typified by a high Epilithic Algal Ratio are likely to support lower abundances of juvenile corals and herbivorous fishes compared to reefs typified by a low-moderate Epilithic Algal Ratio. The results also suggest that reefs with high cover of epilithic algae are likely to have lower juvenile coral abundances but support more herbivorous fishes.

4. Discussion

Together, CCA and turfs (i.e. epilithic algae) are often the most abundant benthic component on Anthropocene reefs globally (Smith et al., 2016; Tebbett et al., 2023b). Here, we show that these epilithic algae exist on a spectrum from CCA and short algal turfs (i.e. SPATs), through to long sediment-laden algal turfs (i.e. LSATs), and link this to the Epilithic Algal Ratio. By using the Epilithic Algal Ratio, and scaling-up inferences using broad-scale ecological survey data, we revealed that the composition of epilithic algae is primarily related to water quality (measured via chlorophyll-*a* concentration and kd490) and/or

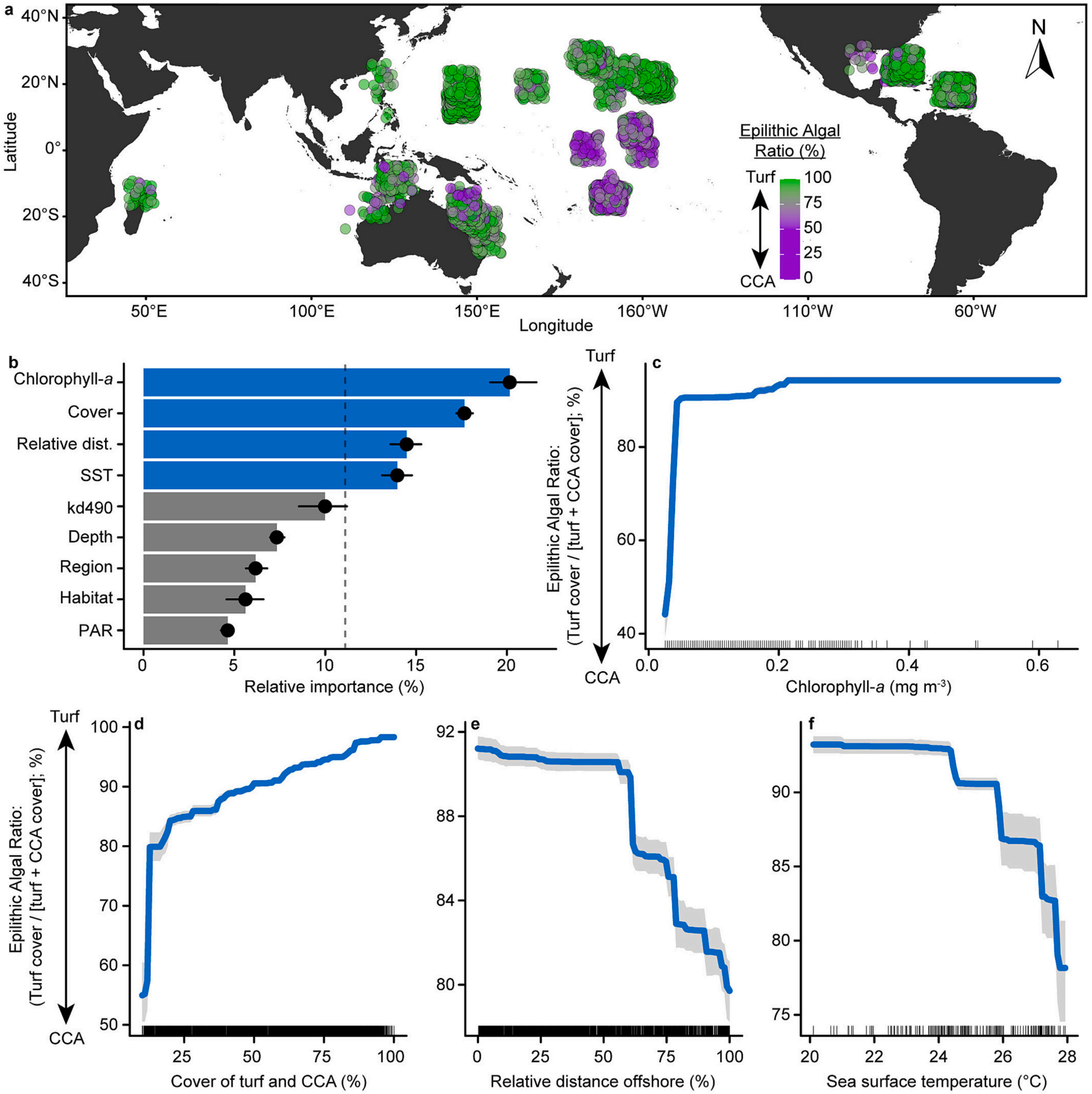

Fig. 3. Epilithic Algal Ratio at a global scale and potential drivers. (a) Spatial distribution of locations where the Epilithic Algal Ratio was examined across the world's coral reefs ($n = 5099$; note points are jittered to enhance clarity). (b) The relative importance of explanatory variables in explaining the Epilithic Algal Ratio (i.e. turf cover/ [turf + crustose coralline algae (CCA) cover]). Black dots indicate the mean relative importance value, while the range denotes the 95 % highest density intervals based on 1000 bootstrapped iterations. The vertical dashed line indicates the null expectation (i.e. the relative importance expected for each variable by chance), with blue bars denoting factors that explained more variation than expected. Partial dependency plots showing the relationship between the Epilithic Algal Ratio and the key explanatory variables of (c) chlorophyll-*a* concentration, (d) total epilithic algal cover, (e) the relative distance of each site between land and the open ocean, and (f) sea surface temperature (SST). The blue line denotes the mean predicted value, while the grey ribbon denotes the 95 % highest density intervals, based on an extreme gradient boosted regression tree model (n = 1000 model iterations). The ticks on the x-axes in (c)-(e) show the distribution of the raw data. Note the y-axes are on different scales. Dist. = distance, PAR = photosynthetically active radiation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hydrodynamics (measured via significant wave height or inferred from relative distance offshore) across every spatial scale considered. Importantly, we also revealed that the abundances of juvenile corals and herbivorous fishes were closely related to both the Epilithic Algal Ratio and total cover of epilithic algae on the GBR. Given the close relationships between these important reef organisms and epilithic algae on reefs, continuing to disentangle how these relationships underpin the functioning of coral reefs remains a pressing research endeavour. The urgency of this endeavour is heightened by the increasing stressors, such as intensifying climate change (Hughes et al., 2018) and declining water

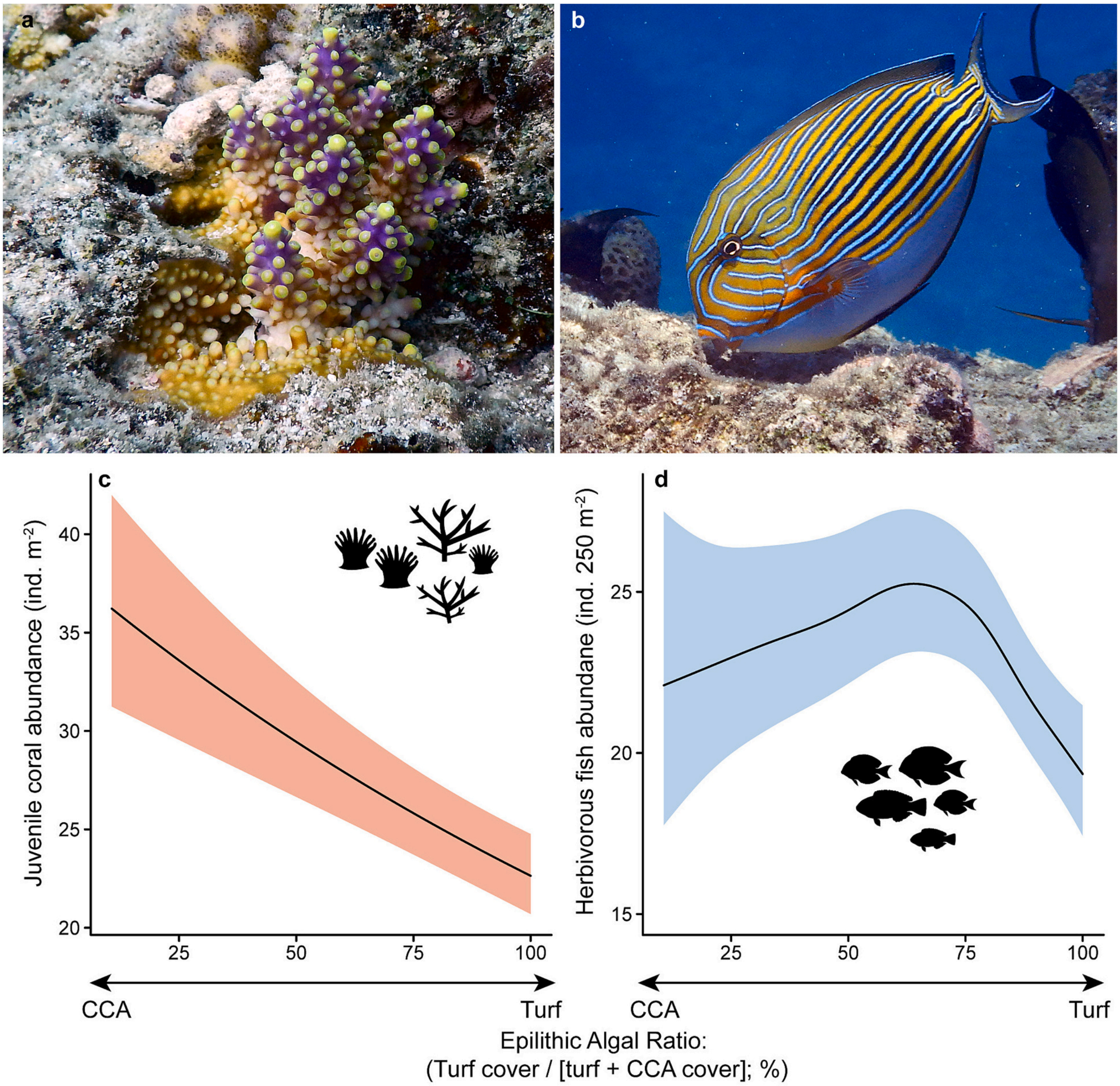

Fig. 4. Relationships between juvenile corals or herbivorous fishes and epilithic algal composition on the Great Barrier Reef. Both (a) juvenile corals and (b) herbivorous fishes closely associate with epilithic algae on reefs (photographs from Lizard Island, Australia; SB Tebbett). The relationships between (c) the abundance of juvenile corals ($n = 3609$) on available substrata, as well as (d) the abundance of nominally herbivorous fishes ($n = 4396$), with the Epilithic Algal Ratio, while all other covariates including total epilithic algae cover (Fig. 5) are held at their mean levels. Solid black lines denote the mean fit from generalised additive models, while shaded ribbons denote the 95 % confidence intervals.

quality (Andrello et al., 2022), which are reshaping coral reefs globally.

Research into the composition of epilithic algae on reefs, and its relation to physical drivers and ecological processes, has been stymied by the fact that these algae are often overlooked in reef monitoring, with detailed quantification requiring laborious in-situ methods (Connell et al., 2014; Tebbett et al., 2022). However, by correlating detailed data collected via such methods with the Epilithic Algal Ratio, our study suggests this ratio represents a useful proxy for epilithic algal composition. Indeed, compared to in-situ quantification (e.g. turf length measurements, sediment load quantification) the Epilithic Algal Ratio is an advantageous proxy in that it can be calculated ex-situ from photographs. In addition, the ratio is based on the cover of two benthic categories (CCA and turfs) that are often quantified in coral reef studies and monitoring programs. Therefore, the ratio can be calculated from historic data to examine epilithic algal composition in cases where in-situ quantification is no longer possible. By using broad-scale monitoring data, the ratio also facilitates the upscaling of studies on epilithic algal composition, as in our study, which can help disentangle how epilithic algal composition relate to physical drivers and ecological processes.

Across multiple spatial scales, we revealed that epilithic algal composition was primarily related to water quality (i.e. turbidity as measured by kd490 and nutrient concentrations as indicated by Chlorophyll-*a*) and hydrodynamic drivers. These cross-scale results directly align with past research showing that sediment accumulation in epilithic algae is dependent on sediment supply as well as hydrodynamic energy. The energy exerted by waves can clear sediment directly or facilitate sediment clearance by other organisms such as via the 'whiplash' effect of macroalgae (Reeves et al., 2018; Schlaefer et al., 2022; Tebbett et al., 2023c). Critically, sediment accumulation can be particularly detrimental to CCA on coral reefs (Fabricius and De'ath, 2001; Harrington

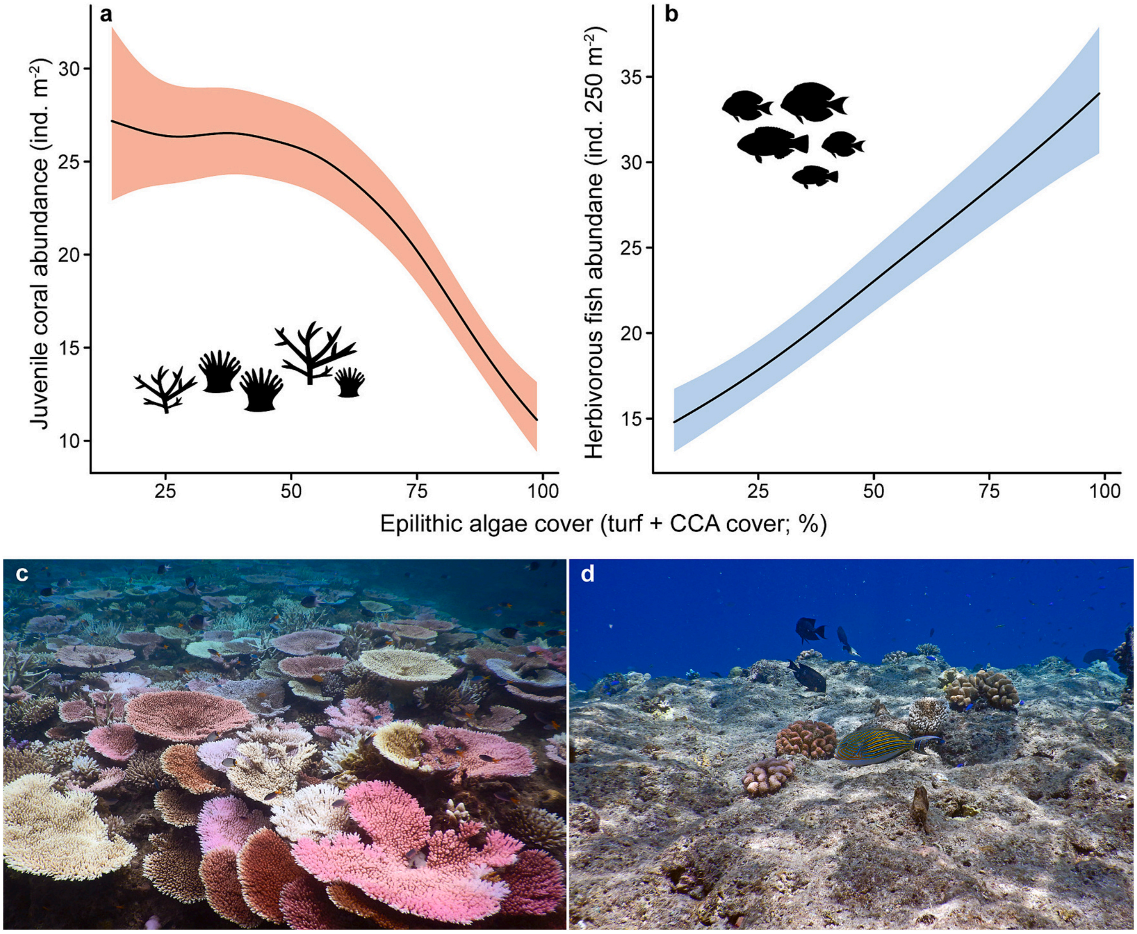

Fig. 5. Relationships between juvenile corals or herbivorous fishes and the cover of epilithic algae on the Great Barrier Reef. The relationships between (a) the abundance of juvenile corals (n = 3609) on available substrata, as well as (b) the abundance of nominally herbivorous fishes (n = 4396), with epilithic algae cover, while all other covariates including the Epilithic Algal Ratio (Fig. 4) are held at their mean levels. Solid black lines denote the mean fit from generalised additive models, while shaded ribbons denote the 95 % confidence intervals. (c) A reef with low cover of epilithic algae and high coral cover, showing the early stages of coral bleaching (i.e. fluorescing hard corals), and (d) a reef with high cover of epilithic algae following cumulative disturbance by cyclones and coral bleaching (photographs from South Direction Island and Lizard Island, Australia, respectively; SB Tebbett).

et al., 2005), while also facilitating the development of LSATs via the suppression of herbivory (Goatley et al., 2016). Previous research has also suggested that eutrophication and declining water quality can facilitate the spatial expansion and growth of turfs on reefs, allowing turfs to succeed over CCA (Albert et al., 2008; Rasher et al., 2012; Fong et al., 2018). Taken together, these lines of evidence suggest that declining water quality and sediment accumulation/hydrodynamics on reefs underpin the capacity of turfs to succeed over CCA (as in Steneck, 1997; Reeves et al., 2018), with epilithic algal composition likely to be dependent on the specific environmental context operating on a given reef.

The fact that potential drivers of the Epilithic Algal Ratio were generally conserved across multiple spatial scales in our study, and that our results aligned with those of previous studies (e.g. Fabricius and De'ath, 2001; Dean et al., 2015; Tebbett et al., 2023c), suggest our inferences are robust. However, it is important to note that these results represent the nature of the Epilithic Algal Ratio on average under these environmental conditions. Potential drivers of epilithic algal composition can be multifaceted, with their relative importance and magnitude likely to vary temporally and spatially (e.g. Tebbett et al., 2023c). Likewise, while the Epilithic Algal Ratio strongly correlates with the spectrum of epilithic algal composition spanning from CCA through to LSATs, it is only a proxy based on the cover of CCA and turfs (which includes both SPATs and LSATs). Therefore, while high Epilithic Algal Ratios are certainly indicative of LSATs, it does not necessarily guarantee that LSATs are present (this can only be confirmed with direct quantification). For example, local scale factors, such as reef complexity, could modify the exact composition of turfs, including in cases where a high Epilithic Algal Ratio is indicative of LSATs. Specifically, while turfs may dominate on a high-relief complex reef, sediment accumulation in these turfs is likely to be lower and more variable compared to on a low-relief reef (Tebbett et al., 2020; Duran et al., 2024). Therefore, while the Epilithic Algal Ratio represents a useful and versatile metric, especially for unpacking broad-scale relationships, its application in local-scale reef monitoring and management may be context specific. In this respect, evaluation of the Epilithic Algal Ratio may represent a useful initial broad-scale filter to identify reefs at risk of LSATs, and then these reefs could be evaluated in detail using more targeted in-situ measurements.

As for the Epilithic Algal Ratio, the density of juvenile corals represents a functionally informative metric of reef condition. Indeed, juvenile coral density can help predict future coral cover as juvenile coral density is positively related to coral cover in subsequent years (Evans et al., 2020; Morais et al., 2024). However, our data suggests that juvenile coral density is lower when epilithic algal cover is high and when the Epilithic Algal Ratio is high. Notably, the former relationship may simply reflect coral stock-recruitment relationships, with high epilithic algal cover invariably meaning lower coral cover and fewer corals to reproduce (Hughes et al., 2019). The latter relationship aligns with past research on smaller-scale correlations between juvenile coral densities and turf length (Ford et al., 2018; Steneck et al., 2018) and is supported by past experimental studies that revealed the potential mechanisms underpinning these correlations. Specifically, juvenile coral abundance is partially determined by the successful settlement and subsequent survival of coral larvae, with both processes being linked to epilithic algae composition (Birrell et al., 2005; Doropoulos et al., 2022; Ricardo et al., 2021).

Experimental research has revealed the importance of epilithic algal composition in coral settlement (Ricardo et al., 2021). CCA often produce positive settlement cues (Ritson-Williams et al., 2016; Abdul Wahab et al., 2023) while long, dense turfs, especially when laden with sediment, limit larval settlement (Birrell et al., 2005; Arnold et al., 2010; Speare et al., 2019). Moreover, these long, dense turfs are fierce competitors with settled corals and can compromise their post-settlement survival (Birrell et al., 2008; Arnold et al., 2010; Doropoulos et al., 2022). Taken together, these lines of evidence suggest that coral reefs with a high Epilithic Algal Ratio support fewer juvenile corals and, in turn, have reduced capacities to regenerate coral cover. In contrast, coral reefs with a low Epilithic Algal Ratio and low-moderate epilithic algae cover support higher juvenile coral densities, thus facilitating reef recovery. Therefore, while various factors may place constrains on juvenile coral abundance beyond epilithic algae, such as inherent variation in larval supply (Hughes et al., 2019), coral settlement success and survival is likely to be moderated, at least in part, by the Epilithic Algal Ratio (sensu Hughes et al., 2007).

It is important to note, however, that while the Epilithic Algal Ratio is likely to moderate juvenile coral densities, at least in part, corals themselves may also shape the Epilithic Algal Ratio. For example, as canopy-forming corals develop from juveniles to adults, they can overgrow and shade the underlying epilithic algae (Goatley and Belwood, 2011), with this shading filtering for algal taxa that tolerate these conditions (Connell, 2005; Fricke et al., 2014). As corals grow, they can also contribute to the complexity of the reef substratum (Graham and Nash, 2013). This is important because the capacity of turfs to trap sediments, and develop into LSATs, is related to the complexity of the reef, with low complexity reef environments typified by homogenous LSATs (Tebbett et al., 2020; Duran et al., 2024). Therefore, while the Epilithic Algal Ratio represents a proxy that is related to the abundance of juvenile corals, it can also shape, and be shaped by, various ecological processes on coral reefs.

The feeding activity of herbivorous fishes has long been viewed as a critical ecological process to support reefs' capacity to regenerate coral cover. Herbivory can facilitate reef recovery through the reduction of algal biomass, which opens up space for coral larvae to settle and lessens competition with newly settled corals (Bellwood et al., 2004; Hughes et al., 2007; Rasher et al., 2012). However, herbivorous fishes are inherently coupled with epilithic algae on coral reefs, through both top-down (i.e. fishes removing algae) and bottom-up (i.e. algae providing nutritional resources to fishes) mechanisms. Historically, research has primarily focused on the top-down mechanisms, and subsequently highlighted the importance of herbivores in maintaining reef resilience (e.g. Hughes et al., 2007; Mumby et al., 2007; Burkepile and Hay, 2008). Nevertheless, a growing body of literature has now revealed how the population sizes (Russ et al., 2015; Tootell and Steele, 2016; Robinson et al., 2019) and feeding behaviour (Bellwood and Fulton, 2008; Goatley et al., 2016; Tebbett et al., 2017) of herbivorous fishes are dependent on the availability and quality of nutritional resources through bottom-up mechanisms. Our results largely align with this latter perspective revealing a strong relationship between herbivorous fish abundance and epilithic algal cover as well as evidence for an Epilithic Algal Ratio that correlates with a high abundance of herbivorous fishes.

Our data revealed that, at the scale of the GBR, the abundance of herbivorous fishes is strongly and positively related to the cover of epilithic algae. This is suggestive of bottom-up processes operating, since higher cover of epilithic algae equates to greater resource availability (both algal and detrital resources), allowing the presence of more herbivorous fishes (also see Russ et al., 2015; Tootell and Steele, 2016). Similarly, epilithic algae typified by SPATs (i.e. moderate Epilithic Algal Ratios), rather than completely by CCA (low Epilithic Algal Ratios) or LSATs (high Epilithic Algal Ratios) is likely to be more productive and support better quality detritus (Tebbett et al., 2018; Tebbett and Bellwood, 2020). As such, surfaces covered in epilithic algae of this nature are preferentially fed on by many species of herbivorous reef fish (Tebbett and Bellwood, 2019; Nicholson and Clements, 2020), facilitating more abundant herbivorous fish communities, as indicated by our data.

The directionality of the relationship between herbivorous fish abundance and the Epilithic Algal Ratio is, however, difficult to determine due to the duality of this consumer-resource interaction. Indeed, the Epilithic Algal Ratio is a proxy of epilithic algal condition, which is both the result and cause of several variable and intertwined ecological processes. For example, many herbivorous fishes preferentially feed on turfs that are more productive with lower sediment loads (Bellwood and Fulton, 2008; Goatley et al., 2016). But the feeding activity of herbivorous fishes also results in short, low-sediment turfs that are more productive and more favourable to herbivores (Rasher et al., 2012; Tebbett et al., 2018). More productive turfs, in turn, can support larger populations of herbivorous fishes (Russ, 2003; Tootell and Steele, 2016), which can also exert greater feeding pressure on the benthos (Bennett et al., 2015). As such, the relationship between herbivorous fish abundance and the epilithic algal ratio that we describe is likely to be the result of both bottom-up (as in Russ, 2003; Tootell and Steele, 2016) and top-down (as in Rasher et al., 2012; Sheppard et al., 2023) processes. Importantly, while our results highlight that epilithic algae and herbivore populations are tightly coupled on reefs across broad spatial scales, the interactions between them are embedded in a broader environmental context bounded by key drivers such as runoff, primary production, sediment size, water quality parameters, and hydrodynamics (Fabricius et al., 2005; Bejarano et al., 2017; Smith et al., 2020; Tebbett et al., 2024). It is thus likely that these environmental drivers shape the nature of the epilithic algae on coral reefs and, ultimately, aspects of reef functioning.

Globally, the environmental context for reefs is rapidly changing. Among the suite of local stressors, declining water quality and sediment pollution are particularly pervasive, operating on a third of all reefs globally (Andrello et al., 2022). Our results suggest that such reefs, especially those with limited hydrodynamic activity, are likely to be typified by epilithic algae that have a high Epilithic Algal Ratio and are dominated by LSATs. Given the close relationships we document, previous experimental evidence of causal relationships (e.g. Bellwood and Fulton, 2008; Tebbett et al., 2017; Speare et al., 2019; Ricardo et al., 2021), and the fact both corals and herbivorous fishes are widely considered as critical to coral reef functioning (Bellwood et al., 2004; Brandl et al., 2019), it is likely that variation in the composition and cover of epilithic algae will shape the future of coral reef ecosystems. Importantly, geological evidence also suggests that reefs in the past, including prior incarnations of the GBR, have declined because of intensified sediment inputs, and changing hydrodynamic regimes (Webster et al., 2018; Dechnik et al., 2021). Could it be that, on these past reefs, sediments drove a transition to a high Epilithic Algal Ratio, resulting in turfs overgrowing CCA, and reduced recruitment of corals? Given the importance of corals and CCA in reef growth (Kench et al., 2022; Cornwall et al., 2023), such a scenario could potentially explain the failure of reefs to keep up with rising sea levels and ultimately ‘drown’. It could thus be argued that the Epilithic Algal Ratio holds the key to unravelling how the impacts of sediments reverberate up through coral reef ecosystems, determining the life or death of not just corals and fishes, but potentially reef systems.

Unfortunately, the capacity for today's coral reefs to grow is also being reshaped by the intensifying impacts of climate change, which are driving reductions in coral cover and concomitant increases in epilithic algal cover, globally (Kennedy et al., 2013; Hoegh-Guldberg et al., 2019;

Tebbett et al., 2023a). Although climate change undoubtedly remains the single largest stressor threatening the long-term functioning of reefs (Hughes et al., 2017; Hoegh-Guldberg et al., 2019), as epilithic algal composition is closely tied to water quality and sediment accumulation, enhanced local management of these stressors may help bolster reef resilience (MacNeil et al., 2019; Gove et al., 2023). Ultimately, on reefs of the past, reefs of today, and reefs of the future, turfs and CCA form a critical ecological interface. It is through this interface that the effects of declining water quality and increased sediment inputs may reverberate up through coral reef trophic webs, potentially compromising their resilience, functional integrity, and survival.

CRediT authorship contribution statement

Sterling B. Tebbett: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Michael J. Emslie:** Writing – review & editing, Investigation, Data curation. **Michelle J. Jonker:** Writing – review & editing, Investigation, Data curation. **Scott D. Ling:** Writing – review & editing, Conceptualization. **Morgan S. Pratchett:** Writing – review & editing, Conceptualization. **Alexandre C. Siqueira:** Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Angus A. Thompson:** Writing – review & editing, Investigation, Data curation. **Helen F. Yan:** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **David R. Bellwood:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.117322.

Data availability

Raw data from detailed turf quantification has been uploaded as a supplementary excel file. All other data are available from the corresponding author on reasonable request.

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