**Habitat, fishing and biodiversity controls on coral reef grazing function**

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Potential Journals:

* Global Ecology and Biogeography
* Ecology
* Functional Ecology (no reef herbivore papers since 2013)
* Ecological Applications
* Coral Reefs

**Keywords**

functional ecology, herbivory, coral reefs, fishing, bottom-up, top-down, biodiversity, grazing, benthic

**Abstract**

**Introduction**

Herbivory is crucial to ecosystem function and community structure, playing a key role in cycling nutrients (Metcalfe et al. 2014), regulating species diversity and productivity (Royo et al. 2010, Prieditis et al. 2017), and controlling habitat regime shifts (Zimov et al. 1995; Hughes et al. 2007; Keesing and Young 2014). Herbivory is generally measured at small-scales that quantifies individual behaviour and population sizes, yet anthropogenic pressures are impacting ecosystem processes including herbivory across large spatial scales. Therefore, fine-scale knowledge of herbivory must be combined with macroecology to generate patterns in herbivory impacts which are relevant at large spatial scales. Such understanding is particularly relevant for coral reef ecosystems, which are facing unrelenting human pressures (including climate change, overfishing and water pollution) and where herbivory is a key ecosystem function (Hughes et al. 2007; Ledlie et al. 2007; Cheal et al. 2010).

On tropical coral reefs, top-down control of algae and promotion of calcifying coral taxa are key functions primarily performed by a diverse guild of herbivorous fishes (Bellwood et al. 2004). Within this group, observations of grazers’ feeding morphology and behaviour have been used to categorise species into two distinct grazing functions: cropping and scraping (Bellwood and Choat 1990; Polunin et al. 1995; Green and Bellwood 2009). Cropping species graze filamentous turf algae, which promotes coral settlement and growth by maintaining cropped algal states (Arnold et al. 2010). Scraping species graze dead coral substrate to consume microscopic epiphytes and epilithic and endolithic phototrophs (Choat and Clements 2018). By removing detritus and epilithic algal matrix (EAM), scrapers promote coral recruitment by clearing settlement space (Bonaldo & Hoey 2014). Combined, cropping and scraping are considered essential functions which help sustain coral-dominated states (Bellwood et al. 2004).

Mature algae can proliferate in the absence of grazing pressure (Mumby et al. 2006; Burkepile and Hay 2008), and correlative analyses of fished reef ecosystems have provided evidence of grazing biomass thresholds below which reefs become algae dominated (Graham et al. 2015; Jouffray et al. 2015; Robinson et al. 2018). Herbivore populations are overexploited across the tropics (Edwards et al. 2014) which has compromised grazing functions on reefs which fail to maintain herbivore biomass thresholds (Bellwood et al. 2011, Graham et al. 2015, Robinson et al. 2018). However, fishing effects can be compounded by bottom-up influences on herbivore assemblages (Russ et al. 2015), whereby species-specific habitat associations produce spatial structuring of herbivore populations among different habitat types (Doropoulos et al. 2013) and benthic compositions (Gilmour et al. 2013; Heenan et al. 2016). Bottom-up control of fish populations may be particularly strong when fish rely on habitat for both structure and food, such as croppers which are generally small and particularly dependent on the reef matrix for shelter (REF). SENTENCE ON STUDY SIZES Thus, herbivore assemblage structure is mediated by both habitat composition and fishing intensity, yet grazing functions are not well resolved at macroecological scales.

Patterns in herbivore biomass are widely used to imply changes in herbivore functioning on coral reefs (Nash et al. 2016; Robinson et al. 2018). However, biomass data overlooks size- and species-specific differences in feeding rates and roles and so measures of grazing impacts can be improved by integrating information on feeding behaviours to estimate grazing rates (Bellwood and Choat 1990; Bellwood et al. 2003). Furthermore, though allometric grazing ~ body size relationships (Lokrantz et al. 2008; Nash et al. 2013) indicate that the functional role provided by larger species is disproportionately greater (Bonaldo and Bellwood 2008), grazing potential may also depend on community size structure. Because abundance decreases logarithmically with increasing body size, an assemblage of many small-bodied fish may be functionally equivalent to an assemblage of several large-bodied individuals (Munday and Jones 1998; Lokrantz et al. 2008). Indeed, size-selective exploitation which removes larger individuals (Robinson et al. 2017) and species (Taylor et al. 2014) has led to shifts in community size structure, but links between size distribution and grazing rate are unexplored. Irrespective of body size, assemblage-level grazing rates may also depend on species composition, whereby functional impact varies according to species’ relative abundances and interspecific variation in bite rates (Hoey and Bellwood 2008). Thus, the relationship between fishing pressure and grazing function is influenced by the species composition and size structure of the herbivore assemblage, which implies that habitat- or fishing-induced shifts in biomass distributions and assemblage compositions can result in a disproportionate loss of function, thereby causing biomass ~ function relationships to become decoupled. Despite the critical role of herbivory in determining benthic responses to disturbance (Nash et al. 2016), the direction and strength of biomass ~ function relationships under different habitat and fishing pressure remains unmeasured at large spatial scales.

Here, we combine underwater visual census (UVC) data with herbivore feeding observations across four regions in the Indo-Pacific to assess the drivers of herbivore functioning on coral reefs at a macroecological spatial scale (Fig. 1). Our large spatial scale analysis uses UVC data that was collected at reefs spanning a benthic gradient from coral to macroalgal dominance and a fishing gradient from open-access fisheries to no-take fishing zones and near-pristine wilderness areas (Graham and McClanahan 2013). We ask the questions: 1) How does fishing pressure and benthic composition influence the functioning of two major functional feeding groups (croppers and scrapers)? 2) Does grazing function scale consistently with herbivore biomass? 3) Does the composition and size structure of herbivore communities cause grazing function to decouple from grazing biomass?

**Methods**

*Survey methods*

Fish surveys were point counts of 7 m radius (Seychelles) or belt transects of 50 m length (Maldives, Chagos, GBR) conducted on hard-bottom reef slope habitat at 3-8 m depth. Surveys were designed to minimise diver avoidance or attracting fish. In point counts, large mobile species were censused before smaller territorial species. In belt transects, large mobile fish were surveyed in one direction for a 5 m transect width, and small site-attached species were recorded in the opposite direction for a 2 m transect width. For both survey types, all diurnal, non-cryptic (>8 cm) reef-associated fish were counted and sized to the nearest centimetre (total length, TL). TL measurements were calibrated by estimating the length of sections of PVC pipe and comparing it to their known length prior to data collection each day. All fish sizes (total length, cm) were then converted to body mass (grams) using published length ~ weight relationships (Froese and Pauly 2018), and standardised by survey area to give species-level biomass estimates that were comparable across datasets (kg ha-1). The UVC dataset included 101 herbivore species, with 11 species common to all four regions (Table S1). Although we combined two UVC methods to estimate fish biomass, point counts and belt transects give comparable biomass estimates (Samoilys and Carlos 2000). Observation error and bias were minimised because one observer (NAJG) performed all fish surveys.

Following fish surveys, benthic habitat composition was surveyed with eight 10 m line intercept transects (Seychelles), or 50 m point intercept (benthos recorded every 50 cm) transects (Maldives, Chagos Archipelago, and Great Barrier Reef). Taxa were grouped into broad functional groups (e.g. CCA, macroalgae, turf algae) and, if they were hard corals, identified to genus level. The structural complexity of the reef was visually estimated on a six-point scale, ranging from 0 (no vertical relief) to 5 (complex habitat with caves and overhangs) (Polunin and Roberts 1993), which correlates strongly with a range of other methods for capturing the structural complexity of coral reefs (Wilson et al. 2007)., except for benthic surveys in Seychelles (SW). Survey methods and site descriptions for each region are described in the Supplementary Material.

*Herbivore feeding observations*

Feeding observations of Indo-Pacific herbivores provided species-level estimates on bite rates and, for scrapers, bite volumes. Surveys were conducted in the Red Sea (AH), Indonesia (AH), and GBR (AH and AGL). We only analysed feeding observations for species observed in the UVC dataset (39). For each observed fish, we estimated the average feeding rate (bites per minute). For scrapers, we also estimated the average bite scar size. We define an individuals' functional impact by its feeding intensity (bite rate). By using in situ feeding observations that track fish forays, our approach accounts for variation in feeding frequency (the timing and distance of feeding forays) (Nash et al. 2013).

*Ecological variable processing*

Herbivore species were categorised as croppers or scrapers according to published diet observations (Froese & Pauly 2018) and observations of feeding behaviours (Green and Bellwood 2009). Croppers were defined as species feeding primarily on the epilithial algal matrix (EAM) including detritus, turf algae, and scrapers as species feeding primarily on exposed coral substrate (Choat et al. 2002; Howard Choat et al. 2004) (Table S1). By targeting live corals and removing larger portions of reef substrate, large ‘excavating’ scraper species also contribute to coral predation (Doropoulos et al. 2012) and bioerosion (Bellwood et al. 2011) but, because feeding observations did not record scar depth, we include these species in the scraper group and define scraping function as potential area grazed.

We defined grazing functions separately for each functional group, and used feeding observations to convert UVC biomass estimates into the total grazing potential of croppers and scrapers. We used a Bayesian hierarchical modelling framework that estimates species- and genera-level functional rates, which allowed us to estimate grazing rates for UVC species which were not observed in feeding surveys (63). Cropper function was quantified in terms of potential feeding intensity, measured as the total number of bites per minute and derived from a predictive model which accounted for species- and genera-specific bite rates (Eqs. 1,2)

 Eq. 1

 Eq. 2

We estimated the grazing rate of each cropper observed in UVCs, and used allometric relationships to convert bite rates into grams of carbon removed through EAM consumption (Marshell and Mumby 2015). Following Van Rooij et al. (Rooij et al. 1998), daily carbon intake was linked to body mass as

 Eq. 3

which we then divided by the predicted number of bites per day to produce an estimate of grams carbon consumed per minute by each cropper fish observed in UVCs. We summed estimates within each UVC replicate (i.e. point count or transect) and averaged across replicates to give site-level estimates of potential cropping function.

For scrapers, we defined the potential scraping function in terms of area of substrate removed per minute. Feeding observations provided estimates of bite rates, which we modelled as a function of body size (TL, cm) according to species- and genera-specific grazing rates, for gamma distributed errors (Eqs. 4, 5).

 Eq. 4

 Eq. 5

Scraping herbivores leave distinctive bite scars which represent the area of substrate removed in each bite. To account for potential differences in scraping action among species and across sizes, we used a second underwater feeding observation dataset of scraper bite areas. Scar area (cm2) was modelled as a function of body size (TL, cm), for Gamma distributed errors (Eqs. 6,7).

 Eq. 6

 Eq. 7

By including size (TL) as an explanatory covariate, our model accounted for scar area increasing with body size (Fig. S1a) and bite rates decreasing with body size (Fig. S1b). For each observed scraper in the UVC dataset, we estimated the expected bite rate and scar size according to its species identity and body size. Species which were not observed in feeding observations were assigned genera-level bite rates. These estimates were converted to area grazed per minute (bite rate \* scar size = area grazed) (m2 minute-1 hectare-1), summed within surveys and averaged to give site-level estimates of potential scraping function.

*Statistical modelling*

We modelled variation in herbivore functioning according to gradients in benthic habitat composition, exploitation pressure, and grazing assemblage biodiversity. Explanatory covariates were derived from fish and benthic surveys. First, to account for fishing effects ranging from the near-pristine Chagos archipelago to heavily-exploited reefs in Seychelles, we estimated total community biomass as a proxy for exploitation pressure. This proxy, hereafter fishable biomass, is highly sensitive to exploitation pressure and, in the Indian Ocean, is predicted by human population size, access to markets, and fisheries management (McClanahan et al. 2016). Reefs were also assigned a categorical fishing pressure covariate to distinguish between protected (i.e. no-take areas), exploited, and remote reefs. Second, benthic surveys provided site-level estimates of benthic composition. We estimated the site-level cover for four major habitat-forming groups (live hard coral, macroalgae, available substrate, and rubble), and structural complexity, by averaging across replicates at each site. To understand the range of benthic habitat types across the dataset, we categorised reefs according to their benthic regime, using a correlation-based PCA and K-means clustering (Jouffray et al. 2015). The optimal number of clusters was found using an elbow method with k=2-15 range, and then applied to the K-means clustering. For Seychelles reefs which were surveyed in multiple years, we estimated regimes at each site by averaging cover values over time. Third, we quantified compositional differences in grazing assemblages according to site-level alpha and beta diversity diversity. For alpha, we estimated rarefied species richness using coverage-based rarefaction curves which set estimates to the lowest sample coverage measured in the dataset (Chao and Jost 2012; Hsieh et al. 2016). For beta, we estimated the local contribution to beta diversity (LCBD) of each site, where higher values indicate sites which have unusually dissimilar compositions, relative to the full dataset (Legendre & De Cáceres 2013). Prior to statistical modelling, we scaled and centered all continuous covariates to a mean of zero and standard deviation of one, and converted the categorical fishing status covariate into two dummy variables (fished - protected, fished - pristine) (Schielzeth 2010).

We used multimodel inference to assess parameter effect sizes. For each function, we fitted a global linear mixed effects model with five benthic fixed effects (hard coral, macroalgae, sand, rubble and structural complexity) and four exploitation fixed effects (fishable biomass, pristine reef, protected reef and mean size), for gamma distributed errors (). Potential covariance among reefs in the same dataset and year was modelled using nested random intercept terms where, for each observation *i* at each reef *j* in dataset *k*:

[](https://www.codecogs.com/eqnedit.php?latex=grazing_%7Bijk%7D%20%3D%20A%20%2B%20B*hardcoral_%7Bijk%7D%20%2B%20C*macroalgae_%7Bijk%7D%20%2B%20D*sand_%7Bijk%7D%20%2B%20E*rubble_%7Bijk%7D%20%2B%20F*complexity_%7Bijk%7D%20%2B%20G*fishablebiomass_%7Bijk%7D%20%2B%20H*pristine.fished_%7Bijk%7D%20%2B%20I*fished.protected_%7Bijk%7D%20%2B%20%2B%20J*mean.size_%7Bijk%7D%20%2B%20reef_j%20%2B%20dataset_k%20%2B%20%5Cepsilon_%7Bijk%7D%250) Eq. 8

From the global model, we fitted all possible subset models (Bartoń 2013) and assessed their support using Akaike’s Information Criterion (AIC), where the top-ranked model had the lowest AIC score (Burnham and Anderson 2003). We visualised relative covariate effect sizes by extracting standardised t-values for all models within 7 AIC units of the top-ranked model and, for each model, rescaling t-values so that 1 is the strongest predictor in a given model, and weighing that value by the models’ AIC weight (Cade 2015). These scaled t-values represent the relative effect size of each covariate between 0 (unimportant) and 1 (important). Next we generated model predictions to visualise the effect of each covariate with scaled t-value > 0.4, excluding remaining fixed effects and random effects and correcting predictions by each models’ AIC weight, with prediction uncertainty represented by the AIC-weighted sample variance (Robinson et al. 2017). Our multi-model approach accounts for uncertainty in the ‘best’ fitted model when AIC scores indicate several models are equally valid (Burnham and Anderson 2003). We avoid potential biases in model-averaged coefficient sizes by presenting effect sizes as standardised t-values, which are more informative measures of covariate importance than sums of AIC weights (Cade 2015).

We examined the dependency of grazing function on grazing biomass, abundance and assemblage composition. For each function, we fitted a linear mixed effects model between function ~ biomass, with random intercepts of reef nested within dataset and gamma distributed errors. Deviation from 1:1 relationships (i.e. decoupling) was evaluated with R2 values, whereby high R2 indicated a tight correlation between function and biomass/abundance and low R2 indicated decoupling of function from biomass. We further investigated decoupling by fitting a global linear mixed effects model, for each observation *i* at reef (*j*) in dataset (*k*) (nested random intercepts) and gamma distributed errors:

[](https://www.codecogs.com/eqnedit.php?latex=grazing_%7Bijk%7D%20%3D%20A%20%2B%20B*biomass_%7Bijk%7D%20%2B%20C*abundance_%7Bijk%7D%20%2B%20D*rarefied.richness_%7Bijk%7D%20%2B%20E*LCBD_%7Bijk%7D%20%2B%20reef_j%20%2B%20dataset_k%20%2B%20%5Cepsilon_%7Bijk%7D%250) Eq. 9

This model allowed us to assess the influence of assemblage diversity and composition on function, while accounting for biomass and abundance effects. We fitted all subset models and weighed model support with AIC, and in this analysis, the top-ranked model was > 2 AIC units from other models, and thus covariate effect sizes and model predictions were interpreted directly from that model (Burnham and Anderson 2003).

All data were analysed in R (R Core Team 2018), using packages *iNext* (rarefaction; (Hsieh et al. 2016), *lme4* (linear mixed effect models; (Bates et al. 2015), *MuMIn* (multimodel inference; (Bartoń 2013), *rethinking* (Bayesian models; (McElreath 2017), and *vegan* (diversity estimates; (Oksanen et al. 2017).

**Results**

Visual census data were integrated with *in situ* feeding observations for 132 reefs in four Indo-Pacific archipelagos. For croppers, 9 species were assigned individual bite rates (32.9% of UVC biomass), and remaining species were assigned genera-specific (54.4%) or an average cropper bite rates (12.6%). Combined with biomass, bite rates corresponded with assemblage-level algal consumption rates ranging from 0.04 to 5.52 g ha-1 min-1, with grazing highest on GBR and Chagos reefs (Fig. S2a). Irrespective of region, algal consumption was maximised in complex habitats with high substrate availability and low macroalgal densities, while hard coral or rubble cover were weak influences (Fig. 2A, 3A). Algal consumption rates were unaffected by fishing intensity, with remote, protected and fished reefs hosting similar cropping function potential (Fig. 2A). Algal consumption did increase with average cropper size, indicating that reefs with cropper assemblages dominated by larger fishes had a higher grazing potential (Fig. 3B).

**Figure 2. Relative effect of benthic composition and fishing pressure on herbivore functioning for croppers (A) and scrapers (B).** Bars are relative effect size ratios of each covariate for top-ranking model sets (models ≤ 7 AIC units of top-ranked model), scaled to indicate very weak (0) or very important (1) drivers of grazing rates.

**Figure 3. Predicted effects of benthic and fishing drivers on cropper (A,B,C) and scraper (C,D) function.** Lines and points are herbivore functions as predicted by top model sets (≤ 7 AIC units from top-ranking model) holding other covariates to their means, with each model prediction weighted by its AIC weight and error represented as sample variance. All selected covariates had relative effect size ratios > 0.4 (Fig. 2). Decile rugs indicate the spread of observed data (in A, top rug is available substrate and bottom rug is macroalgae).

Feeding data were more highly resolved for scraping herbivores, with all fishes assigned size-based bite areas, and either species- (27 of 35 species, 80.9% of UVC) or genera-specific bite rates (19.1%). Potential area scraped was greatest on GBR reefs (> 1 m2 min-1 ha-1) and lowest on Maldives reefs (< 0.3 m2 min-1 ha-1) (Figure S3b). In contrast to croppers, scraping rates increased with structural complexity (Fig. 3C) but were relatively invariant across benthic cover covariates (Fig. 2B). Remote reefs had the greatest scraping rates, which were considerably lower on fished reefs than protected ones (Figs. 2B, 3D). After accounting for these coarse protection effects, scraping was only weakly associated with both fishable biomass and assemblage size structure (Fig. 2B).

Grazing biomass is often used as a proxy for grazing function. Here, cropping function was strongly and positively correlated with cropper biomass (R2 = 0.83, Fig. 4A), indicating that the drivers of biomass variation would match tightly to the modelled drivers of cropper function. Scraping function also increased with scraping biomass, but with greater levels of unexplained variation in area scraped (m2 min-1 ha-1) (R2 = 0.55) which occurred across the full biomass gradient and in all four regions (Fig. 4B). Such unexplained variation in grazing function, after accounting for biomass, indicates that turnover in the number and abundance of species among grazing assemblages can decouple function from biomass levels.

We found that the remaining variation in grazing rates was explained by biodiversity effects. For both groups, the addition of biodiversity covariates to grazing ~ biomass models improved predictive power (Table S3), indicating that decoupling of function from biomass was partially explained by differences in the identities and relative abundance of species among grazing assemblages. For croppers, grazing rates were moderately higher in speciose assemblages, and considerably lower for assemblages with high compositional dissimilarity (Fig. 5A,B). Scraping diversity relationships followed the same direction but changed in magnitude, with stronger richness effects and weaker composition effects (Fig. 5C,D). From the least to most speciose assemblages, richness effects corresponded with a 21% increase in algal consumption and 76% increase in area scraped. In contrast, grazing was reduced by 95% (croppers) and 17% (scrapers) at sites where compositional dissimilarity was highest.

**Figure 4. Association between grazing function and grazing biomass.** Reef-level estimates of cropper algal consumption (A) and scraper area grazed (B) plotted against UVC biomass, with shapes indicating regions and labels indicating marginal R2 from a linear model of function ~ biomass.

**Figure 5. Biodiversity effects on decoupling of herbivore function from herbivore biomass.** Lines are predicted effect of rarefied species richness (A,C) and beta diversity (LCBD) (B,D) on the grazing rates of croppers (blue) and scrapers (yellow), accounting for biomass and abundance effects, shaded with two standard errors and partial residuals shown as points.

**Discussion**

Herbivore functioning varied substantially across the Indo-Pacific in accordance with top-down (i.e. fishing pressure) and bottom-up (i.e. benthic habitat) drivers which were specific to each functional group. Small-bodied croppers were primarily controlled by bottom-up influences, with function maximised in complex habitats with high substrate availability and low macroalgae cover. Conversely, for larger scraping herbivores, function was maximised on remote reefs in the Chagos archipelago which have remained isolated from top-down fishing pressure. In fact, scraping function was only weakly associated with benthic habitat. After accounting for the strong dependency of grazing on fish biomass, we also identified biodiversity effects on grazing rates, thereby demonstrating that spatial variation in the number and relative abundance of species can alter grazing functions.

Cropping rates were primarily mediated by benthic habitat type, in particular structural complexity, macroalgae cover, and substrate availability. Our results emphasize the strong dependence of small-bodied reef fishes on benthic composition (Munday and Jones 1998; Wilson et al. 2010), and demonstrate that top-down fishing effects do not affect cropping function, likely because croppers are small-bodied and not targeted in many reef-associated fisheries (Hicks & McClanahan 2012). Strong relationships between benthic composition and the grazing function of small-bodied reef fish may reflect the importance of food availability, which has been shown to have stronger control on coral reef surgeonfishes than fishing pressure (Russ et al. 2018). For example, the decrease in function with increasing macroalgae is likely because turf algae are less accessible to croppers under macroalgal canopies (Roff et al. 2015) whereas, on reefs with high substrate availability and limited macroalgae, expansive and easily accessible turf mats tend to support large grazer populations (REF). Strong benthic effects imply that cropper functioning will respond more strongly to habitat disturbances, such as coral bleaching, habitat destruction or enrichment of algal communities, than to fishing. For example, disturbances which increase substrate availability for turf algal growth, such as coral mortality from heat stress (REF), might therefore be expected to stimulate an increase in cropping function. However, since structural complexity was also shown to be a strong driver, any positive rebound of cropping function may be negated if the disturbance also erodes structural complexity (REF).

Scraper function was strongly influenced by fishing pressure, which suppressed biomass levels far below those supported at remote wilderness reefs such as the Chagos Archipelago. Our results further indicate that selectivity for large-bodied scrapers has compromised scraping functions on coral reefs (Bellwood et al. 2011). This effect superseded influences of benthic and small-scale fishing protection, suggesting that 1) bottom-up control of scraping assemblages on reefs leads to minimal variation in their function and 2) small-scale fishing protection does not conserve wilderness levels of scraping function. Historical fishing effects (REF), movement of fish across reserve boundaries (REF), and low protection compliance (Bergseth et al. 2018) likely limited the effectiveness of these small MPAs, many of which are adjacent to fishing grounds.

Although biomass was the strongest predictor of herbivory function for both functional groups, unexplained variation in function ~ biomass relationships was attributable to biodiversity effects.

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Our findings are broadly consistent with recent coral reef studies which have demonstrated the positive effect of biodiversity on grazing rates (Lefcheck et al. 2019, Topor et al. 2019), and add to other studies which have linked biodiversity to ecosystem functioning at large scales (Duffy et al. 2015). The mechanisms underlying our results are, however, unclear. For coral reefs, small-scale experiments have demonstrated that biodiversity can enhance grazing function through feeding complementarity (Burkepile and Hay 2008, 2011), while feeding observations suggest that grazing intensity is strongest in high-diversity assemblages (Lefcheck et al. 2019). In these approaches, grazing is measured *in situ* as the pressure on the benthos, whereas here we integrate UVC data with Our definition of grazing function considers potential grazing rates in terms of aggregate bite rates and therefore, the diversity effects presented here act to promote grazing rates simply by raising the number of resident species. Richness effects can be confounded by abundance and sampling effort, though our analyses accounted for potentially spurious associations by using a rarefied richness estimate, including abundance and biomass in biodiversity models, and by capturing dataset-specific sampling correlations with a hierarchical random effects structure.

This is further supported by Lefcheck et al. (2019), who demonstrate that an increase in species, and high regional diversity increased grazing rates across a large spatial scale. The study found that herbivorous fish biomass and diversity both significantly predict grazing function, with biomass being the stronger predictor. However, their approach of ‘mass-standardising’ grazing rates inherently means that function will increase with body size, due to the way function is calculated. This means that their approach does not allow for any exploration of decoupling of function with biomass, like in the present study. While the two studies (Lefcheck and the present study) aim to link patterns in macroecology with herbivory ecosystem function, they explore the same question but from different approaches. While Lefcheck and colleagues use video footage to capture realised feeding rates at specific sites, our study aims to capture the “functional potential” of the entire herbivore community present. This method is coarser than measuring the bite rates of individual fish communities and might not capture regional differences in function, but it reflects the full extent of the fish diversity across reef habitats and makes use of widely available UVC data. This allows linking changes to functional groups with the wider fish community, and since UVC data is the most common form of long term monitoring data, has the potential to link temporal variations in ecosystem function with habitat changes. Finally, a recent meta-analysis looking at rates of browser macro-algal consumption illustrates the positive effect of diversity on function. This suggests that increased diversity results in possible functional complementarity that influences function independent of biomass (Topor et al., 2019).

This influence of biodiversity on function partially explained why herbivore function decoupled from herbivore biomass for the scraper functional group. Scraping functions were more highly resolved than croppers, with all fishes assigned species- or genera-level and size-specific bite rates and areas (Lokrantz et al. 2008) and therefore our estimate of scraping function was likely to be more sensitive to changes in species diversity. In contrast, changes in cropper diversity might be obscured by the high proportion of individual fishes assigned average grazing rates. Furthermore, by combining size-specific information of bite areas rather than simply using biomass as a determinant in calculations, our approach integrates allometric scaling relationships the relationship between function and size. Since this metric is currently lacking for cropper species, this could explain why we did not find any evidence of function decoupling from cropper function.

The random intercepts in our predictive models show that regional similarities in herbivore grazing rates were unexplained by benthic, fishing and biodiversity covariates, which is likely to be indicative of unmeasured processes that control grazing levels. For example, herbivore biomass variation (and thus grazing function) has been linked to differences in oceanic productivity (Heenan et al. 2016) and historic disturbance regimes (REF). Our definitions of grazing functions were also limited by our generalisation across species with similar functions but different feeding modes. For example, we were unable to account for differences in the morphology (REF), diet (e.g. detritivores or turf), and feeding behaviours of cropping species (REF). Furthermore, recent studies using underwater video observations have uncovered additional habitat-mediated effects on grazing communities, such as wave intensity (Bejarano et al. 2017) and primary productivity (REF), which were not measured here. However, these studies have typically focused on grazing intensity within benthic quadrats. Our approach of integrating grazing function with UVC data provides an assemblage-level estimate of grazing pressure could therefore be extended to examine effects of wave energy or seasonality of primary producers on grazing levels. Similarly, temporal analyses linking habitat suitability, primary productivity, and herbivory would greatly develop our understanding of how herbivory rates influence long-term changes in reef state.

Indeed, the modelling framework we used to generate grazing estimates is a significant improvement on the procedure employed by previous macroscale grazing studies (e.g. (Bellwood et al. 2011). By modelling genera- and species-specific bite rates from observations collected in several regions, we were able to leverage observational data in a hierarchical framework which predicts grazing rates of new, related species, given uncertainties in species, genera and body sizes. For example, we were able to assign bite rates to species observed in UVC but not observed in feeding surveys, with estimates that were informed by the feeding behaviour of closely related congeners. Such models could be further improved with additional feeding data on other herbivore species in different regions, and could even be developed to account for seasonality effects (REF) or temperature controls on grazing rates (Bruno et al. 2015) that might confound comparisons of grazing functioning across temperature regimes.

*8. Conclusion*

We stress that biomass was by far the most important predictor of scraping function, and recovery or protection of scraping biomass will help ensure scraping processes are functionally intact on degraded coral reefs (Williams et al. 2016).

**Acknowledgements**

Data? Grants?

**[Supplementary Material](https://github.com/jpwrobinson/grazing-gradients/blob/master/writing/ms/supp-material.pdf)**

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