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Coral settlement and recruitment responses to reef fish foraging and trait diversity

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Abstract

The process of coral recruitment is crucial to the healthy functioning of coral reef ecosystems, as well as recovery following disturbances. Fishes are key modulators of this process by feeding on algae and other benthic taxa that compete with corals for benthic space. However, foraging strategies within reef fish assemblages are highly diverse and the effect of foraging diversity on coral recruitment success remains poorly understood. Here, we test how the foraging traits of reef fishes affect coral settlement and juvenile success at Lizard Island, Great Barrier Reef. Using a multi-model inference approach incorporating six metrics of fish assemblage foraging diversity (foraging rates, trait richness, trait evenness, trait divergence, herbivore abundance, and benthic invertivore abundance), we found that herbivore abundance had positive effects on both coral settlement and recruitment success. However, foraging trait diversity had a negative effect on coral settlement but not on recruitment. Coral settlement was higher at sites with less trait diverse fish assemblages, specifically in trait divergence and richness. Moreover, these two trait diversity metrics were stronger predictors of coral settlement success compared to herbivore abundance. Our findings provide evidence that impacts mediated by fish foraging on coral juveniles can potentially be harmful during settlement, but the space-clearing effect overall remains advantageous. We show here that the variation of fish biodiversity across reefs can be a partial driver to spatially uneven patterns of coral recruitment and reef recovery.

Introduction

In recent years, massive thermal bleaching and tropical cyclones associated with climate change have affected coral reefs worldwide with increasing frequency and severity (Hughes et

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al. 2017, 2018; Eakin et al. 2019; Skirving et al. 2019). The recovery of coral populations and assemblages after these disturbances is dependent on the recruitment of corals, which have been highly heterogeneous across space, both at local and regional scales (Roff and Mumby 2012; Holbrook et al. 2018; Hughes et al. 2019; Mellin et al. 2019). Comparisons between coral recruitment outcomes under grazing conditions point to fish assemblages as an important determinant of recovery trajectories due to the suppression of benthic competitors with corals through their foraging (Korzen et al. 2011; Graham et al. 2015; Kuempel and Altieri 2017). Here, we further examine how variation and diversity in fish assemblages affect coral settlement and recruitment success.

Dynamics at the early life stages of coral settlement and recruitment are critical bottlenecks in the recovery of reef coral assemblages from disturbances (Ritson-Williams et al. 2009; Adjeroud et al. 2017). Both the settlement of planktonic larvae and their recruitment to the juvenile stage are marked by high mortality rates (Vermeij and Sandin 2008). Successful coral settlement requires optimum water flow conditions as well as available substrate space (Chadwick and Morrow 2011; Hata et al. 2017), whereas factors for recruitment success involve not only competition with other benthic organisms but also light availability and avoiding predation (Doropoulos et al. 2016). Coral juveniles not only have to land upon available space during settlement but also must survive within that space post-settlement to reach the life stage of recruitment.

Algae are prevalent competitors for space and resources in both coral settlement and recruitment. They are able to proliferate quickly in response to space availability, as demonstrated by rapid colonisation of algae following massive coral community mortalities

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(McCook et al. 2001; Kuffner et al. 2006; Diaz-Pulido et al. 2010). Because of this opportunistic growth, algae can dominate coral reefs by inhibiting coral replenishment (Hughes 1994; McClanahan et al. 2001; Rogers and Miller 2006; Bruno et al. 2009; Bozec et al. 2019). The ability of reefs to suppress algae overgrowth has largely been attributed to foraging by herbivorous reef fishes (Graham et al. 2013; Kuempel and Altieri 2017; Manikandan et al. 2017; Dajka et al. 2019), which collectively have been estimated to consume up to 65% of net primary productivity on a reef (Polunin and Klumpp 1992). By suppressing the standing biomass of algae, herbivorous fishes are often considered indirect facilitators of coral settlement and recruitment (Bellwood et al. 2006; Hughes et al. 2007; Chong-Seng et al. 2014; Doropoulos et al. 2017).

The foraging impact from fishes on the benthic assemblage is mediated by their behavioural and physical characteristics (functional traits). Not all bites are equal, and trait-driven variation in foraging impacts can be assessed at two scales: among species and among assemblages. Foraging impacts among species vary according to traits such as food selectivity, jaw morphology, and biting mode, which are often summarised in functional groupings especially for herbivorous fishes (Mantyka and Bellwood 2007; Green and Bellwood 2009; Michael et al. 2013; Streit et al. 2015, 2019). However, other benthic taxa (e.g. sponges) also compete with corals and point to the need to consider the effects of other benthic foragers on coral settlement and survival (Elliott et al. 2016; Madduppa et al. 2017). It is not yet clear what, if any, effect invertivores have on coral settlement and recruitment. Demersal invertivorous fishes may lend a similar effect as herbivores to corals by suppressing other benthic competitors, such as sponges and soft corals.

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Foraging impacts vary with species traits, therefore impacts delivered collectively by a fish assemblage also vary according to the distribution and composition of these traits (Cheal et al. 2010). The species and trait composition of fish assemblages vary widely across space in coral reefs, depending on structural complexity of the habitat and environmental gradients (Cheal et al. 2012; Darling et al. 2017; Richardson et al. 2017; Bach et al. 2019). The trait variation within an assemblage results in highly differentiated strategies between species (trait complementarity) or similar overlapping strategies (trait redundancy). Foraging trait complementarity between specialist species has been shown to be most effective at reducing algal cover for coral juveniles (Burkepile and Hay 2008, 2011). It is unclear how variation in fish assemblage foraging-relevant traits links with spatial patterns in coral recruitment. Furthermore, trait diversity effects in foraging impacts on coral juveniles have not yet been assessed outside of more simplistic approaches that assess effects related to functional groupings as a proxy of traits (Brandl et al. 2019).

Here, we test an overarching hypothesis that spatial variation in fish assemblage trait diversity links positively with variation in coral settlement and subsequent recruitment to the juvenile population. Specifically, we test whether greater herbivore abundance, benthic forager abundance, and foraging rates facilitate coral settlement and recruitment. Given previous findings on positive species diversity effects on herbivory (Burkepile and Hay 2008; Rasher et al. 2013) in addition to the positive scaling of trait richness with species richness, we also hypothesise that assemblages that are more trait diverse promote coral settlement and recruitment.

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Materials and methods

Study location

We conducted our study at seven sites (1.4–3.7 m depth) representative of the variation in topography and abiotic substrate within a no-take marine national park zone at Lizard Island (14°40′ S, 145°28′ E) in the northern Great Barrier Reef, Australia (Figure 1). Recent coral mortalities from thermal bleaching and cyclone damage observed at the island (Madin et al. 2018; Hughes et al. 2019) made this an opportune time and location to investigate coral settlement and recruitment dynamics post-disturbance. Data collection took place during early austral summer surrounding the annual spawning event, from November-January. Coral data were collected in 2018-19 and 2019-20, and fish assemblage data were collected in 2019-20.

Remote underwater videos

We obtained fish assemblage and bite data from unbaited remote underwater videos (RUVs), using an adaptation of baited remote underwater video methods (Langlois et al. 2018). At each site, we deployed a single waterproof camera (GoPro Hero4 Session on a wide setting) in acrylic housing on an abiotic substrate. We placed markers at a 2 m radius from the camera lens, establishing a sampling area of approximately 4 sq m with a camera field of view measuring 118º. Deployment lasted for a total of 45 minutes at each site, with the first 15 minutes omitted from processing to avoid diver and boat presence influencing observations.

We processed videos in two iterations, the first to count and identify individual fish within the marked sampling area to species level or lowest possible taxon when possible, and the second to enumerate foraging rates. Observation records where we could not identify to the genus level with certainty were omitted from analysis. To reduce potential bias of double counting resident fish, we identified recurring individuals if one of the same species and relative size had been

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previously observed in the same video area with similar behaviours. For bite data, we recorded total bites and length class of the individual fish biting. We used visual estimation for fish length classifications (< 5 cm, 5–9 cm, 10–19 cm, 20-29 cm, and so on in 10 cm intervals inclusive). We then recorded total in-frame occurrence time for all species at the site observed biting at least once, regardless of the behaviour during the occurrence. Unlike processing for fish assemblage structure, this bite observation did not distinguish between individuals.

Coral settlement and recruitment

To quantify coral settlement, we sampled settling coral spat using experimental substrates in the summers of 2018-19 and 2019-20. In both years, six unglazed clay tiles (11 × 11 cm) were deployed horizontally onto permanent mountings installed at each site (n = 42). We deployed tiles one week before predicted coral spawning to allow for establishment of biofilms and crustose coralline algae that reflect the natural conditions of available hard substrate on a reef (Heyward and Negri 1999). We collected tiles after two months and subsequently bleached and dried them for inspection under dissection microscope to enumerate coral spat.

We counted coral recruits *in situ* aided by georeferenced orthomosaic reconstructions of 100 m^2 reef areas ("reef records") at each site. Recruits were defined as new colonies which were not fragments of previous colonies and had ≤ 5 cm in diameter (Bak and Engel 1979). These orthomosaics were produced from photogrammetric models following the pipeline of Pizarro et al. (2017) as adapted by Torres-Pulliza et al. (2020). We divided orthomosaics into quadrants for each site (n = 28), which were then annotated *in situ* with location and identification for all

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recruit and adult coral colonies. We identified recruits in 2019 by comparing annotation changes from 2018.

Fish assemblage predictor variables

We compiled six foraging traits for the fish species observed in RUVs. These traits were selected to represent assemblage diversity with respect to foraging ecology, interactions with substrate, substrate impact, and foraging range (Table 1). We extracted trophic and diet data from FishBase using the rfishbase R package (version 3.0.4; Boettiger et al., 2012). For the traits of water column position of foraging (benthic, demersal, pelagic/mid-water), we allocated values based on FishBase diet information. If a majority of food items within the diet were specified to be benthic substrata or zoobenthos, we assigned a category of benthic foraging. Where diets consisted of a minority food items found on the benthos, we classified as demersal. Exclusive planktivores and piscivores we assigned as mid-water/pelagic foragers. Foraging mode groupings were based on the classifications outlined by Green and Bellwood (2009), Cheal et al. (2010), and Stuart-Smith et al. (2013). Details on assigning foraging mode categories are described in the supplementary material.

Following classification of fish species functional groupings, we calculated the relative abundance of herbivores and benthic foragers (i.e. benthic-foraging detritivores, omnivores, and invertivores) for assemblages at each site.

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Trait diversity analysis

To assess and compare the foraging trait diversity of fish assemblages, we generated three complementary indices of 1) trait richness via the trait onion peeling index (TOP; Fontana et al. 2016), 2) trait evenness, and 3) trait divergence (see Villéger et al. 2008) from a global trait space. TOP quantifies the volume of the trait space filled by the assemblage, where higher measures indicate that the assemblage occupies more trait space and hence more trait rich. This metric is equivalent to convex hull volumes calculated by sequentially eliminating species at vertices, hence "onion peels" of convex hulls (Fontana et al. 2016; Legras et al. 2018). Trait evenness describes the variation in distance in the trait space between adjacent species, where higher measures of evenness mean that the abundance of species within an assemblage are more equally distributed throughout the trait space. Lastly, trait divergence measures the distribution of an assemblage relative to the trait space centroid and extremes. Higher trait divergence values reflect greater trait differentiation between species and therefore indicates an assemblage with very little trait overlaps or redundancy. Both evenness and divergence are weighted by species abundance.

Construction of the trait space was performed using Principal Coordinates Analysis (PCoA) based on Gower dissimilarities between all species observed in our study according to the six foraging traits (Villéger et al. 2008; Laliberté and Legendre 2010). The resulting principal coordinates represent new synthetic "traits" where multiple collinear traits are combined and represented by different axes. Ordered factor traits were handled using the Podani method (Podani 1999) and Cailliez corrections to conform the matrix to Euclidean space, which prevents the generation of negative eigenvalues during scaling (Legendre and Legendre 2012).

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The resulting trait indices are orthogonal, and so correlation between any of these measures should not be due to mathematical artefacts but rather to characteristics of the assemblages (Mason et al. 2005). Dissimilarity calculations, trait space construction, trait evenness, and trait divergence calculations were all performed with the FD R package (Laliberté et al. 2014). TOP was calculated using code provided in Fontana et al. (2016).

Calculation of site-level foraging rates

We standardised bite counts by the total observation time for each species to give bite rates (bites min^{-1}) for each length class at each site. As our goal was to calculate a foraging rate at the site-level from total bites observed, we did not standardize by number of biting fish. Bite rates were then aggregated by length class. To factor the difference in foraging impacts (i.e. substrate removal) due to trophic group, foraging mode, and water column position traits (Purcell and Bellwood 1993; Green and Bellwood 2009; Burkepile and Hay 2010; Hoey and Bellwood 2011), we calculated a species trait-based coefficient to scale bite rates (details in Supplementary Material). To factor the difference in foraging impacts due to differences in fish size (and hence bite sizes, see Adam et al. 2018; Hoey 2018), we scaled bite rates by the median length for individuals of each length class (e.g. 7.5 cm for length class 5–10 cm). We then obtained a foraging rate (bites-cm min^{-1}) for each site following Equation 1, where S_i is the trait-based coefficient for species *i*, L_{il} is the median length for individuals in length class *l* of species *i*, and B_{il} the bite rate by length class and species for each study site. We refer to bite rates as foraging rates (in bites-cm min^{-1}) after this scaling. Given the utility of this foraging rate for relative comparison and not for an objective quantity, we then scaled foraging rates by

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their standard deviation to place it on a common effect size scale with other explanatory variables for ease of interpretation, as they were indices or proportions constrained between 0 and 1.

Equation 1

$$\text{ForagingRate} = \sum_{i}\left(S_i \sum_{l} L_{il} B_{il}\right)$$

Statistical modelling

We modelled coral settlement and recruitment through spat and recruit counts respectively as functions of six predictors that captured realised and potential foraging impact. Foraging rates represented realised foraging impacts while trait richness (TOP), evenness (TEve), divergence (TDiv), herbivore abundance (Herb), and benthic forager abundance (Benthic) represented potential foraging impacts. Site was included as a random intercept term to account for non-independence in same-site coral abundances (Equation 2 and 3). To determine the most parsimonious effect structure that captures settlement and recruitment patterns, we used a multi-model inference approach for the response variables of coral spats and recruits. We fitted a global generalised linear mixed model with negative binomial errors and log link function for each response variable using the lme4 package (version 1.1-23, Bates et al., 2015). The global model for coral recruits (Equation 3) also included coral spat abundance from the previous year (i.e. 2018-19) as an explanatory covariate to account for the effect of settlement on recruit abundances the year following. All above analyses were conducted in R 4.0.0 (R Core Team 2020).

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Equation 2

$$\text{CoralSpat}_{ij} \sim \text{ForagingRate}_j + \text{TDiv}_j + \text{TEve}_j + \text{TOP}_j + \text{Herbivore}_j + \text{Benthic}_j + (1|\text{Site}_j)$$

Equation 3

$$\text{CoralRecruit}_{ijt} \sim \text{CoralSpat}_{j,t\text{-}1} + \text{ForagingRate}_{jt} + \text{TDiv}_{jt} + \text{TEve}_{jt} + \text{TOP}_j + \text{Herbivore}_j + \text{Benthic}_j + (1|\text{Site}_j)$$

From these models, we constructed two sets of candidate models that varied in the combination of potential foraging impact fixed effects. We fitted null models with only site as a random effect for model comparison. We also fitted a second null model for coral recruitment with 2018 spat as a fixed effect and site as a random intercept term. We ranked all candidates by Akaike Information Criterion values corrected for small sample sizes (AICc) for model selection (Burnham and Anderson 2002). Selection of the optimum coral spat and recruit models was based on the lowest AICc value (MuMIn package; Bartoń 2020). We also calculated AICc weights as estimates of the probability that each model is the optimum candidate. If top-ranked models were within a difference of 2 AICc, we selected the candidate with a greater AICc weighting.

Results

We identified a total of 624 individual fish from 104 species from a total 3.5 hours of video recordings. Fish abundance across the seven study sites ranged from 37 individuals at Turtle Beach to 210 at Southeast, with an overall mean of 89 ± 66 individuals SD. The 104 species observed were dominated by herbivores (33%) and invertivores (29%). Overall the relative abundance of herbivores was 32.5% ± 17.6% SD and ranged from 8.1% in Turtle Beach to

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62.4% in Southeast (Figure 2). Relative abundance of benthic foragers had a similar mean of 37.2% ± 7.56% SD (Figure 2).

Trait space and trait diversity metrics

The resulting four-dimensional global trait space captured 22.8% of the variation (i.e. proportional sum of eigenvalues; Figure S1a). Our validation of preserved trait space dissimilarities in the Mantel test returned a significant strong correlation ($r = 0.801$, $p < 0.01$; Figure S1b). Detritivores and corallivores were located toward the centre of the trait space in the first two dimensions (Figure S2 in Supplementary Material) while herbivores clustered tightly in the lower left corner and invertivores in the upper middle corner. In contrast, large differences in trait richness in the third and fourth dimensions were driven by solitary species with small active ranges and schooling species with large active ranges (Figure S3). Trait richness was relatively similar across sites apart from a notable outlier in Southeast (TOP = 0.55), ranging from 0.25 at Vicki's to 0.34 at Lagoon (Figure 2). Southeast was primarily influenced by trait extreme species in all four dimensions (Figure 3.1), resulting in the lowest trait evenness measures (TEve = 0.71) and greatest trait divergence (TDiv = 0.91). In contrast, the assemblage at North Reef was abundant in centrally clustered species and hence the least trait divergent (TDiv = 0.71; Figure 2).

Foraging rates

Only 35 fish species were observed biting the substrata. Resulting trait-weighted coefficients ranged from 0.05 for suction-feeding planktivores to 3.67 for excavator herbivores (Table S1).

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Five dominant biting species contributed to more than 50% of the total foraging rates observed at sites: *Ctenochaetus striatus* (15.4%), *Chlorurus spilurus* (12.6%), *Hemigymnus melapterus* (8.9%), *Chlorurus microrhinos* (8.6%), and *Acanthurus nigrofuscus* (7.6%). Herbivores, mainly excavators and algal croppers, were the most intense foragers especially at the sites Corner Beach, North Reef, and Vicki's, even though they were not the most prevalent (Figure 3).

Coral settlement and recruitment

Mean total spat abundance across sites was 21.29 spats in 2018-19 and 29 spats in 2019-20. Coral settlement was consistently low at Lagoon, Southeast, and Corner Beach (Figures 4-5), ranging from 3-18 total spats in 2018-19 and 8-14 in 2019-20. Coral recruitment was low at Lagoon (4.00 colonies ± 4.00 SD) and Turtle Beach (8.25 colonies ± 12.53 SD; Figures 4-5). Both coral settlement and recruitment in 2019-20 were highest at North Reef, where there was an average of 13.83 spats per settlement tile ± 6.52 SD (total of 83 spats) and 57.25 recruit colonies per site quadrant ± 21.69 SD (Figures 4-5).

Optimum predictors of coral settlement and recruitment

The fixed effect structure that best explained variation in coral settlement consisted of foraging rate, trait divergence, TOP, and herbivore abundance (Table 2). Although we identified strong negative correlation (r = -0.85) between herbivore abundances and trait evenness in pairwise checks, trait evenness performed drastically poorly as a predictor of coral settlement. The candidate model that only differed from the optimum coral settlement model in replacing

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herbivore abundance with evenness (foraging rates + TDiv + TOP + TEve) performed far worse (ΔAICc = 6.21; Table 2). Interestingly, coral settlement and recruitment did not share any similarities in their optimum fixed effect structures. The model that best explained coral recruitment (i.e. foraging rates + herbivore abundance) was in fact the worst-performing for coral settlement, resulting in a ranking lower than that of the null model (Table 2).

For both settlement and recruitment models, fish assemblage variables representing potential foraging impact were stronger predictors of success than observed foraging rates. Herbivore abundance had a strong positive effect on both coral settlement and recruitment, but this effect was greater and more precise for recruits (4.01 ± 0.98 SE; Table 3; Figure 5). Conversely, foraging rate showed little to no effect on either coral spat or recruits (Table 3; Figures 4-5). Foraging rates in the coral settlement model was estimated as a weak negative predictor, but this does not appear to fit higher spat counts at North Reef and Resort (Figure 4). The effect of foraging rates on coral recruitment was even smaller, with little to no effect (0.24 ± 0.30 SE, Table 3; Figure 5). Trait divergence was the strongest predictor of coral settlement success with a large negative effect and appeared to best explain variation in spat counts (-7.69 ± 2.31 SE; Table 3; Figure 4). Trait richness also had a negative effect on coral settlement but like foraging rates, it too did not capture higher spat counts at North Reef and Resort (Figure 4).

Discussion

Our results add nuance to the potential role of fish assemblages in coral settlement and recruitment success. Previous studies have suggested that fish assemblages aid reef recovery by facilitating coral juvenile success through their foraging impacts (Bellwood et al. 2006;

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Hughes et al. 2007; Cheal et al. 2010; Adam et al. 2011; Rasher et al. 2012). We found that coral settlement and recruitment both responded positively to herbivore abundance, but there was little evidence to support effects of benthic forager abundance or foraging rates. We detected an effect of trait diversity of fish assemblages on coral settlement, specifically trait divergence and richness. Of the two trait diversity metrics, divergence best explained the variation in coral settlement patterns (Figure 4; Table 3). Our findings of fish foraging impacts reveals that while herbivore abundance remains an important predictor for both coral settlement and recruitment success, settlement is highest where assemblages with fewer specialist traits occur.

While the modelled positive effects of herbivore abundance aligned with our initial prediction, we did not anticipate lower predictive power than trait diversity metrics for settlement compared with its performance in the recruitment model. This suggests that coral settlement may be highly sensitive to differences in trait diversity than herbivore abundance. One potential explanation for the differing response to trait diversity in coral settlement to recruitment may be due to recruits having greater energetic stores to overcome or compensate for sub-optimal growth conditions (Ritson-Williams et al. 2009; Doropoulos et al. 2012). This ability to withstand a certain period of sub-lethal inhibition by algae or even deleterious bites from fish is a likely reason for a spectrum of foraging impacts that can result in similar recruitment outcomes.

We detected overall stronger effects from assemblage diversity predictors, which represent potential foraging impact, rather than observed foraging rates (Table 3). From both a theoretical and behavioural standpoint, co-occurrence does not necessitate biotic interaction,

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and so we couldn't assume all present fish observed were actively foraging in the area (Blanchet et al. 2020). As such, we expected foraging rates to have had greater effect sizes than assemblage diversity metrics. The lack of predictive power in observed foraging rates may be due to highly clustered distributions of foraging sessions, selective patchy foraging across space, or the influence of gregarious foraging behaviours (Hoey and Bellwood 2009; Michael et al. 2013; Streit et al. 2019), resulting in a poor representation of the foraging occurring across each study site. Hence, we advocate inclusion of both bite observations and assemblage diversity metrics to better capture site-level foraging impacts from reef fish assemblages in future studies.

Settlement success in this study was lower with fish assemblages that had higher trait divergence (Figure 4b) i.e. more specialists, even when high herbivore abundances were accounted for. This result was in contrast with our hypothesis, and somewhat counterintuitive, because many centrally located detritivores are conventionally considered reducers of algal turf sediment load rather than effective substrate-clearing foragers (Purcell and Bellwood 1993; Tebbett et al. 2017). One possible reason for the sensitivity to trait differences in settlement is that trait specialist herbivores have an initial harmful effect on spat. Our findings suggest that beneficial foraging impacts declined when some specialists were present, possibly due to direct consumption of spat. Spat survival can be negatively correlated to the biomass of grazing fishes (especially parrotfishes) or their feeding scars (Mumby 2009; Baria et al. 2010; Penin et al. 2011; Trapon et al. 2013a, 2013b).

Excavating and scraping parrotfishes, two feeding modes that are located in the outer extremes of the trait space (Figure 2), have been suggested to be the most disruptive to coral settlement

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success due to incidental grazing of recently settled corals (Mumby 2009; Trapon et al. 2013b). These grazing fish are one reason settlement success is often greater in structurally complex areas with small crevices where spat can be protected (Nozawa 2012; Brandl et al. 2014; Doropoulos et al. 2016; Gallagher and Doropoulos 2017). Conversely, Brandl et al. (2014) reported facilitative foraging impacts from *Siganus* spp., a group of crevice feeding algal croppers that are also trait specialists in our study. The abundance of algal croppers was also high at the site with the highest spat counts even though our methods cannot ascertain effects from species or groups (North Reef; Figure 2). While fewer excavators or scrapers is a likely explanation for increased settlement, we do acknowledge that our study design does not factor how fish foraging impacts on corals may vary in different topographical surroundings. And indeed, studies do argue that foraging benefits to coral juveniles from abundant herbivores overall outweigh these risks of incidental grazing mortality (Bozec et al. 2015; Graham et al. 2015).

In this study, we emphasise the importance of top-down effects from fish assemblages on coral juvenile success. While herbivore abundance remains an important predictor, not all herbivores lend the same facilitative foraging impacts to coral spat and recruits. Especially for coral settlement, it is a less predictive, “broad stroke” metric compared to trait divergence, which captures the sensitivity of spat to specialist foragers. This sensitivity to highly trait differentiated fish assemblages puts forth one possible mechanism behind the spatial heterogeneity of coral recovery, as these specialists preferentially feed at reef slopes and crests (Hoey and Bellwood 2008; Carlson et al. 2017). While previous studies have emphasised focusing on fishery management of species that lend the greatest foraging impacts, we show

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here that management that prioritises a biodiverse assemblage with high herbivore abundance can facilitate coral recovery best.

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Data availability

The associated research data and analysis code can be found in GitHub (https://github.com/cherfychow/FishTraitxCoralRec).

Conflict of interest statement

The authors of this paper declare that there is no conflict of interest.

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Figure legends

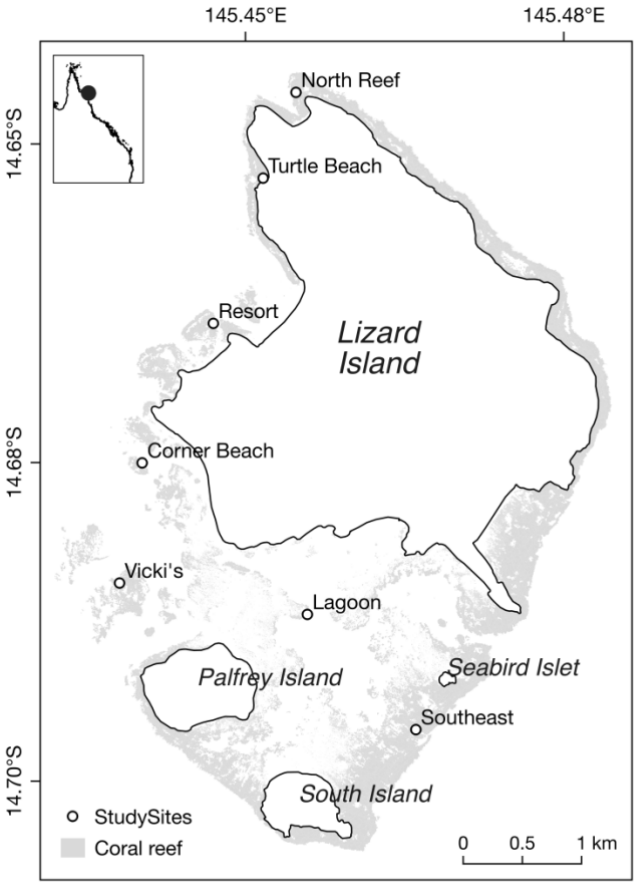

Figure 1. Map of study site locations around Lizard Island. The coral reef area is shown shaded in light grey. Spatial data for reef and coastline boundaries were sourced from the Great Barrier Reef Marine Park Authority Geoportal (GBRMPA 2020) and Roelfsema et al. (2014).

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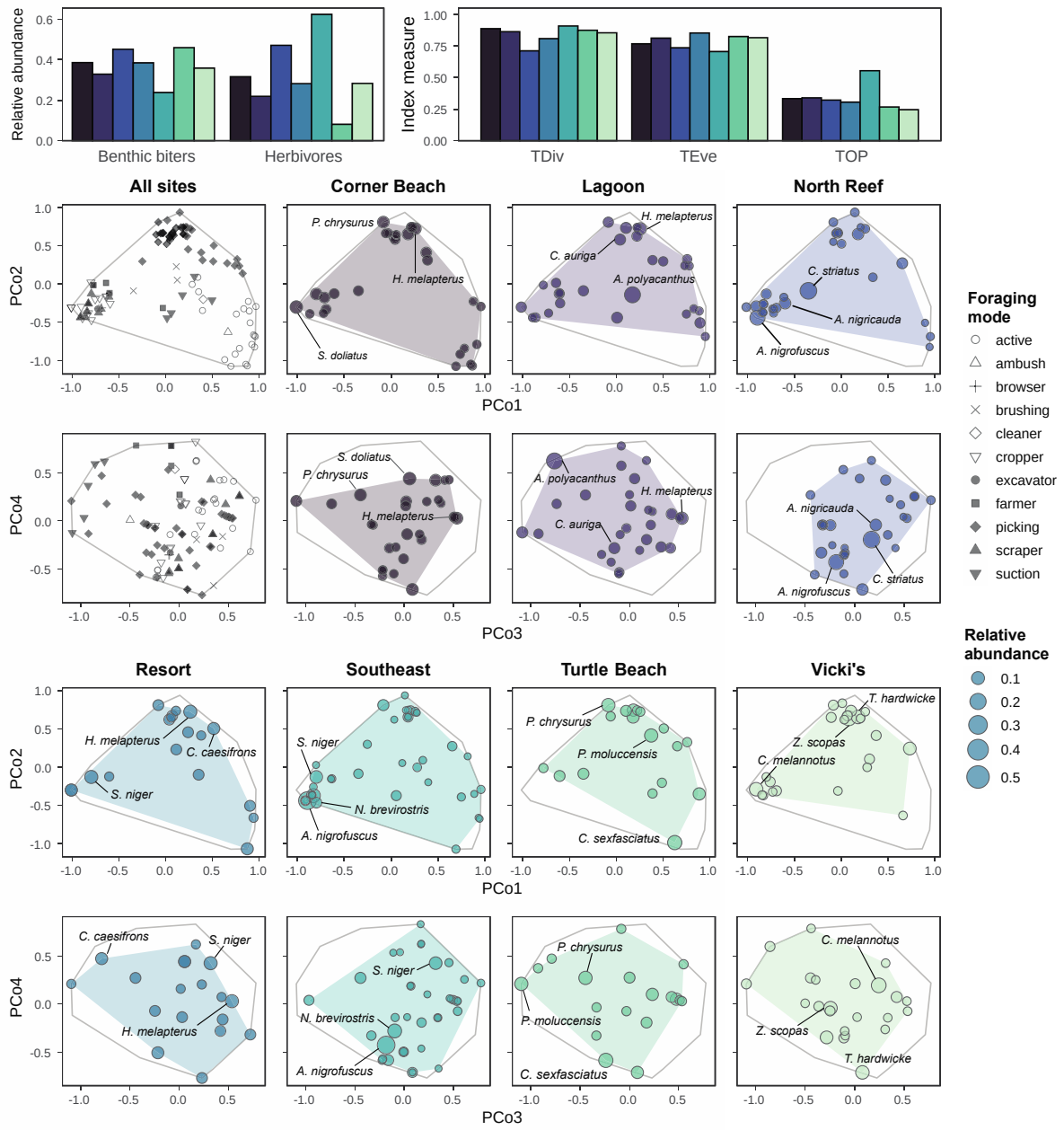

Figure 2. Trait diversity of fish assemblages at the site-level. The bar graphs (top) shows the measures for relative fish abundance (top left) and trait diversity indices (top right) for each site: benthic biters, herbivores, trait divergence (TDiv), trait evenness (TEve), and trait onion peeling index (TOP). These three facets of trait diversity relate to the volume of the occupied trait space (TOP), the regularity of species distributed within the space (TEve), and the dispersion of the assemblage from the center of the trait space (TDiv). The array shown is a

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representation of assemblages according to the functional traits of species. Species are represented by circles, with varying sizes by relative abundance. Distance between circles represents trait dissimilarity between species. The trait space occupied by the assemblage is shaded to represent TOP. For comparison, the reef-level trait space (i.e. all sites, representing TOP = 1) is shown as a grey outline.

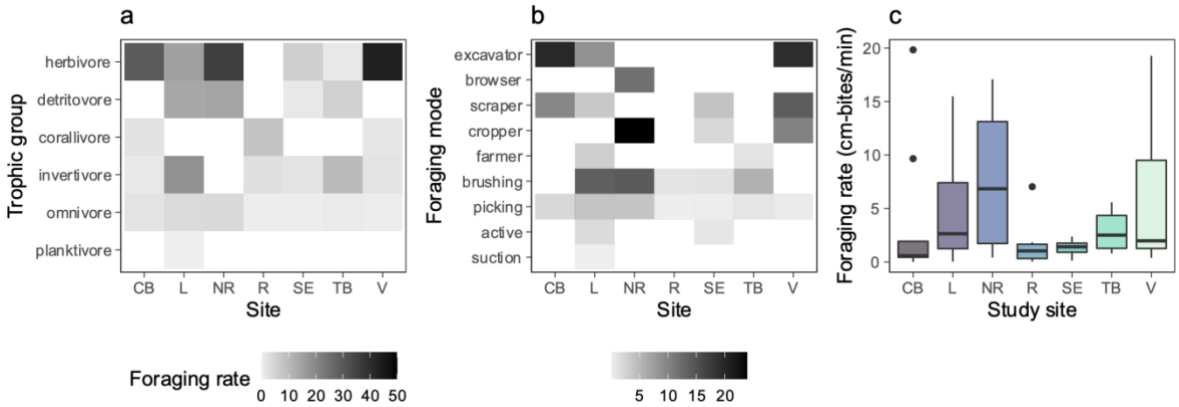

Figure 3. Observed foraging rates at each study site, Corner Beach (CB), Lagoon (L), North Reef (NR), Resort (R), Southeast (SE), Turtle Beach (TB), Vicki's (V). Foraging rates (cm bites min^{-1}) are grouped according to contributions by trophic group (a) and foraging mode (b). Both panels (a) and (b) represent foraging rates by shading, where darker shading represents higher feeding rates and vice versa. Note differences in scales as foraging rates range from 0.03-43.4 (a) and 0.03–23.9 (b). White represents absent groups from sites. Overall foraging rate distributions for species in each site are shown in (c).

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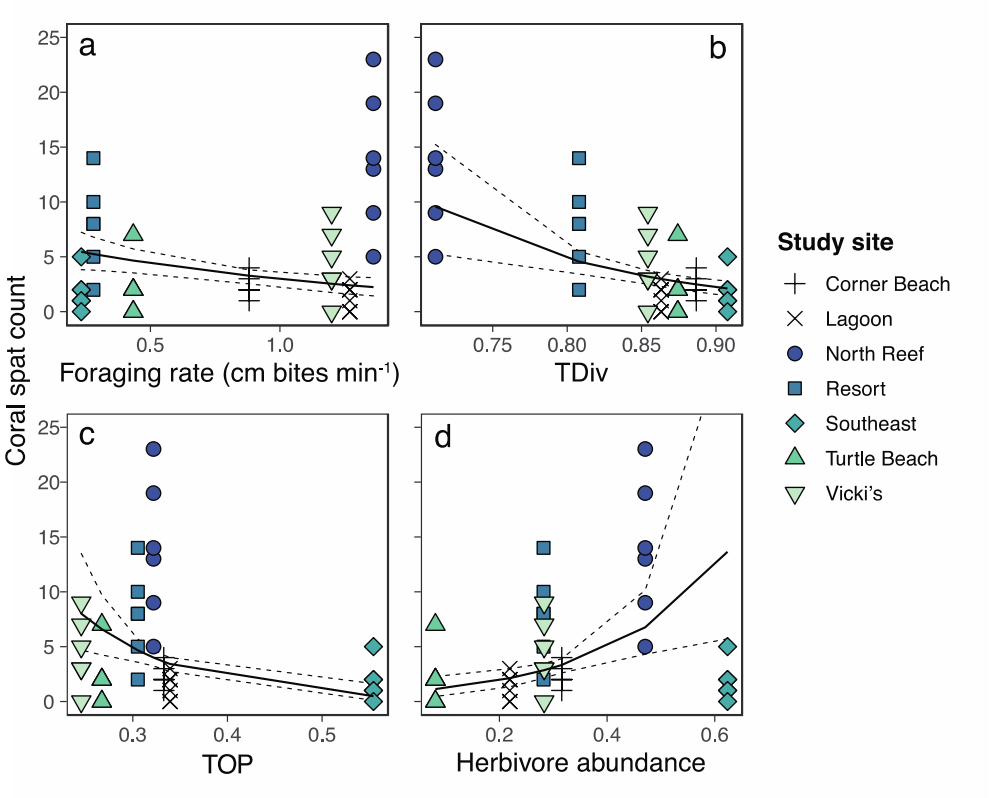

Figure 4. Partial predictions for the optimum model relating coral settlement with fish assemblages. This model includes the fixed effects of (a) foraging rate of fishes (cm bites min^{-1}), (b) trait divergence, (c) trait richness (TOP), and (d) relative abundance of herbivorous fish. Foraging rate was scaled by its range. Coral spat were counted from six settlement tiles at seven sites (n = 42). Each tile is shown in various shapes and colors by site. Partial predictions from the model for each parameter are represented by black lines with bootstrapped confidence intervals (from 999 simulations) shown with dashed lines.

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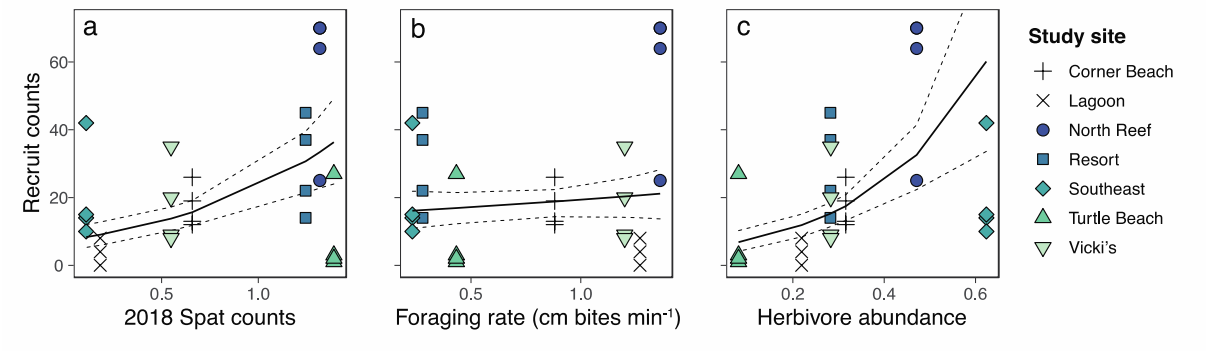

Figure 5. Partial predictions for the optimum coral recruitment model. This model included the fixed effects of (a) spat abundances from 2018, (b) scaled foraging rate of fishes (cm bites min^{-1}), and (c) relative abundance of herbivorous fish. Both spat counts and foraging rate were scaled by their range. Coral recruits were counted from four quadrants of a photomosaic for each site (n = 28) and are shown in various shapes and colours by site. Partial predictions for each parameter are represented by black lines with bootstrapped confidence intervals (from 999 simulations) shown with dashed lines.

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Tables

Table 1. Traits used to quantify the functional diversity of reef fish assemblages in regard to feeding ecology, substrate interaction, and delivery of feeding functions. Values were extracted or derived from various databases and literature.

Trait	Type	Levels/units	Source
Functional group	Factor	Herbivore, detritivore, planktivore, cleaner, omnivore, invertivore, piscivore	1, 2, 3
Foraging mode	Factor	Excavator, cropper, scraper, browser, brusher, picker, farmer, suction feeder, ambush feeder, active feeder	1, 4, 5
Trophic level	Continuous	2.0–5.0	1
Water column position of feeding	Factor	Pelagic, demersal, benthic	1
Residency/Range	Ordered factor	Index of residency and active range, 1-5 with 1 representing highly territorial species and 5 for wide-ranging pelagic species	1, 7-11
Schooling	Ordered factor	Index of schooling behaviours during feeding from 1-4, with 1 representing solitary species to 4 being species forming large shoals or schools	1, 6

1. Pauly and Froese 2019
2. Stuart-Smith et al. 2013
3. Brandl and Bellwood 2014
4. Green and Bellwood 2009
5. Purcell and Bellwood 1993
6. Randall et al. 1996
7. Meyer and Holland 2005
8. Meyer et al. 2010
9. Welsh and Bellwood 2012
10. Pillans et al. 2014
11. Davis et al. 2015

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Table 2. Ranking of candidate models for coral spat and recruit models. Site is included in every candidate as a random intercept term, represented as (1|Site). Fixed effect structures vary in fish assemblage diversity variables of trait divergence (TDiv), trait evenness (TEve), trait richness (TOP), herbivore abundance (Herb), and benthic biter abundance (Benthic). All candidates include foraging rates (For) and, for recruit models, spat counts from 2018. Model candidates were ranked according to their AICc values. Top-ranked models are bolded for emphasis. Candidates that failed to converge were omitted.

Models	**AICc**	**ΔAICc**	**Weight**	**mR^2**
Coral settlement				
For + TDiv + TOP + Herb + (1|Site)	**202.68**	—	**0.582**	**0.639**
For + TDiv + TEve + TOP + Herb + (1|Site)	205.69	3.01	0.129	0.638
For + TDiv + TOP + Herb + Benthic + (1|Site)	205.70	3.02	0.129	0.638
For + TDiv + TEve + TOP + Benthic + (1|Site)	206.14	3.46	0.103	0.634
For + TDiv + TEve + TOP + (1|Site)	208.89	6.21	0.026	0.566
For + TDiv + TEve + TOP + Herb + Benthic + (1|Site)	208.95	6.27	0.025	0.638
(1|Site)	213.20	10.52	0.003	0
For + Herb + (1|Site)	217.48	14.8	0	0.069
Coral recruitment				
Spat2018 + For + Herb + (1|Site)	**222.52**	—	**0.560**	**0.538**
Spat2018 + For + Herb + Benthic + (1|Site)	225.63	3.11	0.118	0.546
Spat2018 + For + TDiv + TOP + Herb + (1|Site)	225.69	3.17	0.115	0.64
Spat2018 + For + TEve + TDiv + TOP + (1|Site)	225.99	3.68	0.089	0.537
Spat2018 + For + TDiv + Herb + (1|Site)	226.20	4.03	0.075	0.625
Spat2018 + For + TEve + TDiv + TOP + Herb + Benthic + (1|Site)	229.82	7.30	0.015	0.647
Spat2018 + For + TDiv + TOP + Herb + Benthic + (1|Site)	229.82	7.30	0.015	0.647
Spat2018 + For + TEve + TDiv + TOP + Benthic + (1|Site)	229.82	7.30	0.015	0.647

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Table 3. Parameter estimates of selected models exploring the relationship of coral juveniles with fish assemblage foraging rates, trait divergence (TDiv), trait richness (trait onion peeling index, TOP), and herbivore abundance. Effect estimates are shown with their respective standard error and coefficient of variation. Estimates marked with asterisks (*) are significant ($p < 0.01$).

Parameter	Effect estimate		CV
Coral settlement			
Intercept	9.94 ± 1.74	*	.175
ForagingRate	-0.79 ± 0.30	*	.380
TDiv	-7.69 ± 2.31	*	.300
TOP	-9.07 ± 3.32	*	.366
Herbivore	4.59 ± 1.82	*	.397

Parameter	Effect estimate		CV
Coral recruitment			
Intercept	0.48 ± 0.59		1.232
Spat2018	1.15 ± 0.32	*	.278
ForagingRate	0.24 ± 0.30		1.250
Herbivore	4.01 ± 0.98	*	.244