Coral Reefs
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RESEARCH

Habitat zonation of algal turf sediments and herbivores on two Caribbean coral reefs with comparison to the Great Barrier Reef

Sterling B. Tebbett[1,2] · Fiona E. Kelley[3] · Scott D. Ling[1] · Ryan S. McAndrews[2] · Micaiah N. Ocalvey[4] · Samuel E. Suleimán Ramos[5] · Tory J. Chase[3,4]

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Abstract Algal turfs represent the dominant benthic cover on most coral reefs globally, with the sediments they trap having a marked effect on reef functioning. Yet our quantitative understanding of these sediments remains poorly resolved for most regions. Despite habitat zonation representing one of the strongest ecological gradients on coral reefs, the distribution of turf-associated sediments across this gradient is unresolved beyond some sites on Australia's Great Barrier Reef (GBR), where reef crests are typified by the lowest sediment loads, shortest turf lengths, and highest herbivorous fish biomass. Here, we quantified the cross-habitat (flat, crest, and slope) distribution of turf length, sediment load, and key herbivores on two Caribbean reefs off Puerto Rico. Cross-habitat distribution of sediments was congruent with previous patterns on the GBR; sediment loads were lowest on the crest and highest on the flat, with a 1.7-fold difference between these habitats. Biomass of parrotfishes and surgeonfishes was inversely correlated with turf-bound sediments across habitats, peaking on the crest. Turf length was shortest on the crest at one reef, however, at the second reef, there was no difference in turf length across habitats, with shorter-than-expected turfs on the flat. The sea urchin, *Diadema antillarum*, was relatively abundant on the reef flat at this second reef, suggesting that this species may play a role in curtailing long sediment-laden algal turf development. This research extends the cross-habitat understanding of turf-associated sediments to the Caribbean, and suggests the role of urchins in these dynamics warrants specific investigation.

Keywords Ecosystem function · Habitat gradient · Herbivorous fishes · Long sediment-laden algal turfs · Puerto Rico · Sea urchin

Introduction

Declining coral cover on the world's reefs has led to the rise of alternative benthic organisms and transitions to different reef states (Bellwood et al. 2004; Hughes et al. 2017). Among the benthic states that develop following extensive loss of live coral, algal turf dominance has emerged as an increasingly omnipresent reef configuration (Smith et al. 2016; Tebbett et al. 2023b). On coral reefs, turfs are generally considered short (< 2 cm) multispecies assemblages of algae and cyanobacteria (Connell et al. 2014; Harris et al. 2015; Arjunwadkar et al. 2022). While variation in the cover of turfs is relatively well-quantified during standard coral reef monitoring practices, the composition and heterogeneity of turfs are often poorly documented, especially in terms of how much sediment they accumulate (reviewed in Connell et al. 2014; Tebbett and Bellwood 2019; Ladd et al. 2026). Turfs have a remarkable

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✉ Tory J. Chase
torychase@skidmore.edu

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Hobart 7001, Australia

[2] College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

[3] Department of Geography and the Environment, Villanova University, 800 Lancaster Ave, Villanova, PA 19085, USA

[4] Environmental Studies and Sciences Department, Skidmore College, 815 N Broadway, Saratoga Springs, NY 12866, USA

[5] Sociedad Ambiente Marino (SAM), San Juan, Puerto Rico

capacity to trap and retain sediments within their complex structure (Purcell 2000; Latrille et al. 2019), with these sediments shaping how turfs interact with key ecosystem processes (Goatley et al. 2016; Duran et al. 2019; Wakwella et al. 2020). For example, as sediment trapping increases in turfs, this has been linked to declines in key reef processes, such as herbivory (Bellwood and Fulton 2008; Goatley et al. 2016; Ng et al. 2021), coral settlement (Speare et al. 2019; Evans et al. 2020), and benthic productivity (Clausing et al. 2014; Tebbett et al. 2018a). Yet our understanding of fundamental patterns in turf sediments on coral reefs is constrained geographically, with the majority of research coming from the Indo-Pacific, especially Australia's Great Barrier Reef (GBR), where consistent patterns have been described for northern and central locations of this reef system (e.g. Purcell 2000; Gordon et al. 2016a; Tebbett et al. 2025). Extending this understanding to other geographic regions and contexts represents a fundamental research endeavour in evaluating the extent to which our understanding of turf sediment dynamics may be generalised.

Caribbean coral reefs have been typified by a longer history of net coral cover decline, and impaired resilience relative to many Indo-Pacific reefs (Roff and Mumby 2012; Roff 2021). Indeed, most Caribbean coral reefs are now characterised by low coral cover (generally $< 10\%$ cover) and high algal cover (Schutte et al. 2010; Tebbett et al. 2023a). This includes cover of long sediment-laden algal turfs (sensu Goatley et al. 2016; Ladd et al. 2026), also referred to as turf algal sediment mats (Roy 2004; Lacey et al. 2013; Duran et al. 2024). Research into the ecological effects of these long sediment-laden algal turfs in the Caribbean is increasing (e.g. Adam et al. 2018; Duran et al. 2019, 2024; Ladd et al. 2026; Speare et al. 2019), although quantitative evaluations of turf sediment loads remain limited. In this respect, cross-habitat variation represents one of the strongest and most important ecological gradients on reefs (Goreau 1959; Done 1983). Variation in key biophysical factors (e.g. light and hydrodynamics) is well known for driving marked differences in reef communities across typical coral reef habitat zones (e.g. the reef flat, crest, and slope) (Done 1983; Graus and Macintyre 1989). Likewise, research on GBR coral reefs has established that turf length and sediment load also vary distinctly across these habitats. Typically, the reef flat has the longest turfs and highest sediment loads, while the reef crest has the shortest turfs and lowest sediment loads (Purcell 2000; Goatley and Bellwood 2012; Gordon et al. 2016a; Tebbett et al. 2023c). Moreover, this cross-habitat pattern in turf sediment distributions has been closely linked to similar cross-habitat variability in the distribution and feeding rate of nominally herbivorous fishes (Goatley and Bellwood 2012). Whether this applies outside of the context of the GBR remains largely unexplored.

On coral reefs, herbivores are widely viewed as a critical group of reef organisms as they assimilate primary productivity and maintain low algal biomass in the process (Rasher et al. 2012; Steneck et al. 2018; Benkwitt et al. 2025). On one hand, the high productivity of turfs is known to support larger and more productive populations of nominally herbivorous fishes through bottom-up effects (Russ 2003; Benkwitt et al. 2025), while on the other hand, the feeding activity of herbivorous fishes maintains short productive algal turfs (sensu Goatley et al. 2016), that trap little sediment (McAndrews et al. 2019; Humphries et al. 2020). On Indo-Pacific reefs, increases in algal turf length are closely correlated with an elevated mass of sediments (e.g. Fong et al. 2018; Tebbett et al. 2024; Syafruddin et al. 2025), with the tight coupling between turf length and sediment mass likely mediated, at least in part, by herbivory dynamics (Goatley and Bellwood 2013; Tebbett and Bellwood 2019). These accumulated sediments are also known to mechanically disrupt feeding by nominally herbivorous fishes (Gordon et al. 2016b; Tebbett et al. 2020), as well as constrain benthic productivity (Tebbett et al. 2018a). This may explain why herbivorous fish abundance, biomass, and feeding rate are often highest on reef crest habitats on the GBR, and more broadly, where sediments are lowest and turf productivity is highest (Bouchon-Navaro and Harmelin-Vivien 1981; Lewis and Wainwright 1985; Russ 2003; Goatley and Bellwood 2012; Oakley-Cogan et al. 2020). However, the extent to which this may apply in the context of Caribbean reefs is unclear. In the Caribbean, sea urchins, especially *Diadema antillarum*, have historically played a major role in herbivory dynamics (Foster 1987; Carpenter 1990; Lessios 2016), especially when compared to the limited role of urchins on many GBR reefs (Sammarco 1985; Tebbett and Bellwood 2018). Given environmental contextual differences between GBR and Caribbean reefs, it may be that correlations between herbivore communities and turf sediment distributions differ on Caribbean reefs compared to those described previously for the GBR.

A thorough understanding of how established concepts and paradigms apply in different reef contexts is essential, as lessons learnt from one reef system do not necessarily apply to another (discussed in Ladd et al. 2026). Such an understanding is therefore critical if we are to develop robust knowledge about how coral reefs operate, especially with respect to omnipresent components and mediators of reefs such as turfs (Ladd et al. 2026). The present study therefore aimed to quantify the cross-habitat distribution of turf length, associated sediment loads, and herbivores in the Caribbean. To do this, we applied the same methods as previously applied on the GBR for quantifying turfs and the sediments they contain, across three habitat zones (reef flat, crest, and slope) on two reefs in Puerto Rico that exist in different environmental contexts. By focusing on reefs under markedly different, this can provide an insight into the extent to which turf sediment dynamics differ as reef context varies. Based on existing knowledge from the GBR (e.g. Purcell 2000; Goatley and Bellwood 2012; Gordon et al. 2016a), we hypothesised that turf length and accumulated sediment load would be highest on the flat and lowest on the crest, with this pattern correlating with the distribution of herbivores across the same habitat gradient.

Methods

Study Sites

Sampling for this study was conducted across the reef flat (1–2 m depth), crest (3–4 m), and slope (5–7 m) of two continuous reef sites in Puerto Rico, in June 2022 (during the wet season) (Fig. 1). La Palma reef site, La Parguera (17°57′30.32"N, 67° 3′21.00"W) is located 2.5 km from a mangrove-lined (chiefly *Rhizophora mangle*) shore, inside the La Parguera Natural Reserve, with potential terrestrial influences such as the outlet of the Rio Loco watershed (13.8 km to the east), and subsistence farming in the Lajas agricultural lands. Despite its reserve status, the La Parguera Natural Reserve is not completely closed to fishing, and has historically been subject to intense fishing pressure (Olson et al. 2019). Tamarindo reef site, Isla de Culebra (32 km off the coast of mainland Puerto Rico, 18°18′48.27"N, 65°19′26.44"W) is 38 m offshore (fringing reef) of Tamarindo Beach, a popular tourist destination and an out-planting site for *Acropora cervicorni*s, by Sociedad Ambiente Marino (SAM), a local coral restoration organization. This site falls within the Luis Peña Channel No-Take Natural Reserve, which has been closed to fishing since 1999 (Hernández-Delgado et al. 2006). Potential terrestrial influences associated with Tamarindo include a nearby non-enclosed, open-air dumping site / landfill (~ 275 m uphill) and local unpaved roads on Isle de Culebra. Both reef sampling sites are located adjacent to seagrass beds (a prominent feature of Caribbean seascapes [Harborne et al. 2006]) and are defined by low scleractinian coral cover (< ~ 5%) and low complexity reef benthos. Subsequently, it is likely that variations in anthropogenic (e.g. fishing, coastal populations, restoration activities, boating), oceanic (e.g. currents, waves), and terrestrial (e.g. runoff, coastal development, land-based pollution) influences differ between these two

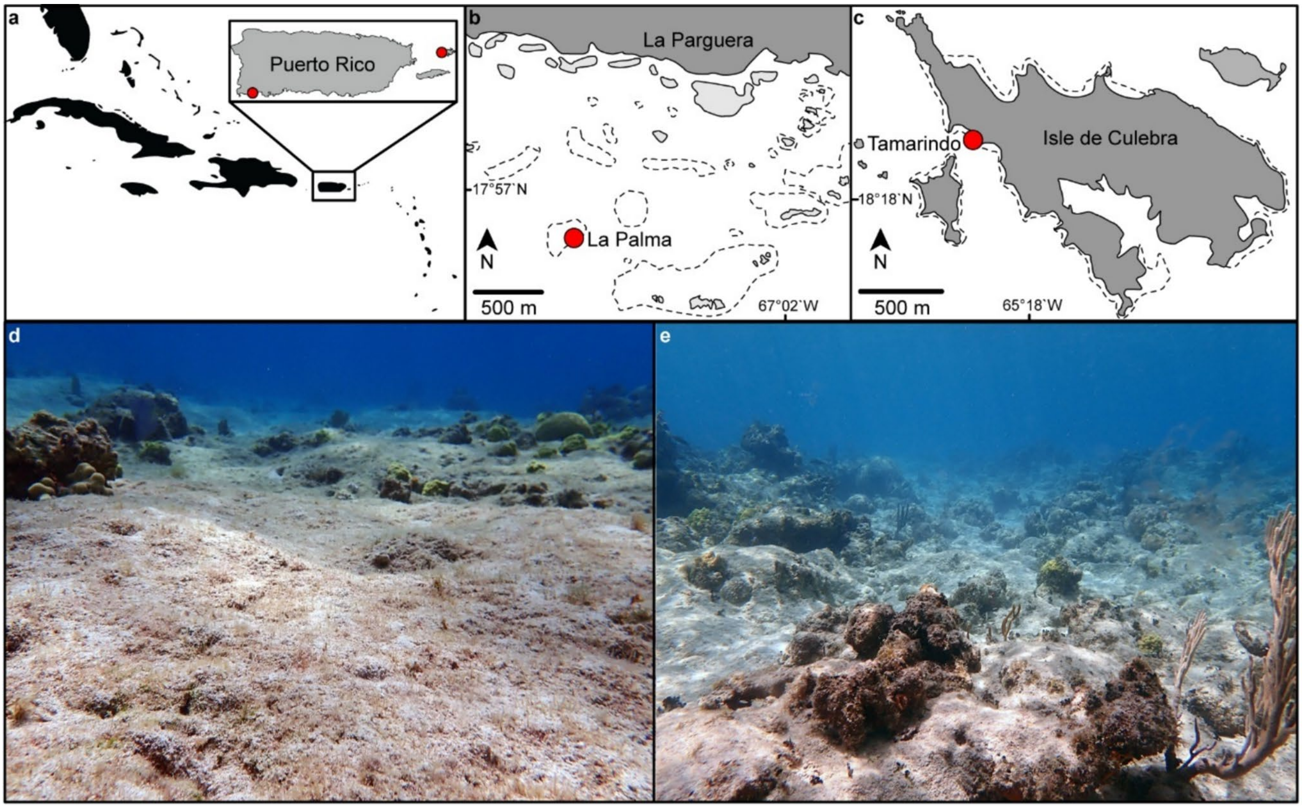

Fig. 1 **a** The location of Puerto Rico relative to the broader Caribbean archipelago, and two study sites (shown as red circles in the map inset). The study sites (red circles) at **b** La Palma reef, La Parguera, and **c** Tamarindo reef, Isle de Culebra (dashed lines show shallow reef extent in **b** and **c**). High cover of long sediment-laden algal turfs on the low-complexity **d** reef flat, and **e** reef slope at Tamarindo (photographs TJC)

sites (e.g. Orlando and Yee 2017; Otaño-Cruz et al. 2019; Ramos-Scharrón et al. 2024). The Caribbean long-spined sea urchin (*Diadema antillarium*) 2022 mass mortality event (Hylkema et al. 2023) spanned our sampling period, and there was evidence for urchin die-off along transects at both reef sites.

Surveys of herbivorous fishes and sea urchins

The abundance of nominal herbivores (surgeonfishes, parrotfishes, and sea urchins [*Diadema antillarium* and *Echinometra* spp.]) were quantified at our study sites due to their close interactions with turfs (Carpenter 1986; Adam et al. 2018; Duran et al. 2019). Fishes and sea urchins were quantified along four 30-m long belt transects in each habitat zone, at each site by a consistent diver (RSM). Fishes > 10 cm total length (TL) were identified to species, and counted in a 5-m wide belt as the transect tape was laid parallel to the reef crest. Fishes < 10 cm TL and sea urchins were subsequently counted in a 1-m wide belt by the diver during a return pass along the transect. It is important to note that given the nocturnal emergence of urchins, diurnal surveys are highly likely to represent conservative estimates of urchin abundance at these sites (e.g. Shulman 2020; Jones et al. 2026). The size of all fishes recorded > 10 cm TL were placed into 5 cm size categories, while fishes < 10 cm TL were placed into 2.5 cm size categories. Biomass of fishes was subsequently calculated using length–weight regression parameters (after Bouchon-Navaro 1997; Froese and Pauly 2025).

Algal turf sampling

At each site, turf length and sediments were sampled from suitable turf-covered surfaces. Suitable surfaces were approximately horizontal, relatively smooth (i.e. free of large sediment-retaining holes), free of encrusting organisms and macroalgae, and outside of the territory of farming damselfishes (following Tebbett et al. 2022). Replicate samples were spaced a minimum of ~ 2–3 m apart in all zones. Turf sediments were collected from within a 58 cm^2 area, delineated by a plastic ring, using an underwater vacuum sampler fitted with a plastic collection bag (following Tebbett et al. 2022). Following sediment collection, turf length was measured at ten haphazard locations within the 58 cm^2 sampling area, using the depth probe of vernier callipers. These length measurements were recorded by pushing the tips of the callipers into saltwater-resistant pressure-sensitive poster adhesive (Blu-Tack), with these measurements subsequently quantified using digital callipers (following Goatley and Bellwood 2013; Tebbett and Bellwood 2019). To quantify turfs across habitat zones, at each site, 34–38 patches of turf were sampled across the three habitat zones, with 10–15 samples per zone per site.

Sediment processing

Collected sediment samples were transferred to 9.4 L plastic containers and left to settle for 3 h, allowing particulate material > 10 µm to settle (Purcell 1996). Samples were subsequently decanted to remove excess water until they could be transferred into smaller 175- or 235-mL sample jars, leaving a minimum 3 h settling period between decants. To limit degradation of organic material within collected sediment, 10 mL of 4% buffered formaldehyde was added to the samples for transfer and storage back to the university lab, where they were stored in a Norlake Scientific freezer at −3°C. In the lab, thawed samples were initially wet sieved through a 2 mm Gilson sieve (ASTM E11), retaining all particulate material < 2 mm (sands, silts and clays; ISO 14688–1:2017). To remove salts, each sample was then rinsed three times with deionized water, leaving a minimum 3 h settling period between rinses. Samples were then dried in a Fisher Scientific oven to a constant mass at 55 °C. Total particulate mass of each sample was then measured using a Mettler Toledo balance (0.0001 g). Organic material was then removed from the samples by bleaching them using 35% trace metal grade hydrogen peroxide (H_2O_2) over a two-week period. During this time, samples were stirred and fresh H_2O_2 was added on a daily to semi-daily basis. Samples were then re-dried and weighed as above, yielding inorganic sediment mass. The inorganic sediment grain size distribution of each sample was then quantified by sieving dry sediments through a stack of five Gilson ATSM sieves, yielding six size categories: 2000–1000 µm (very coarse sand), 1000–500 µm (coarse sand), 500–250 µm (medium sand), 250–125 µm (fine sand), 125–63 µm (very fine sand), and < 63 µm (coarse silt or smaller) to align with previous research (e.g. Purcell 2000; Tebbett et al. 2018b). Each size class was individually weighed as described above.

Statistical analyses

We tested for differences in turf length and turf sediment mass across the two Puerto Rican sites and habitats, using separate generalised linear models (GLMs) for each metric. Turf length or total sediment mass were treated as the response variables, while site identity and habitat were treated as fixed effects in both cases. Additive models and models with an interaction term between fixed effects were fitted, and the most parsimonious model was selected based on the corrected Akaike Information Criterion (AICc) (Table S1). In both cases, the models were based on a Gamma distribution with log-link function. Post-hoc pairwise tests, based on a Tukey's adjustment, were conducted for models in which the interaction term was influential. Model fit and assumptions were examined using residual plots, and plots of simulated residuals, all of which were satisfactory. In addition, we examined the nature of the relationship between turf length and sediment mass across the two sites using a generalised linear mixed effects model (GLMM). In this case, turf length was treated as the response variable, sediment mass (logged) and site were treated as fixed effects, and habitat was treated as a random effect. This model was also based on a Gamma distribution with a log-link function, and all model fitting and checking procedures followed the details outlined above.

We also examined variation in the abundance and biomass of parrotfishes and surgeonfishes using separate GLMs for each taxon. In this case, abundance and biomass of parrotfishes and surgeonfishes were treated as response variables, and models were based on a negative binomial distribution with a log-link function (abundance models), or a Tweedie distribution with a log-link function (biomass models). As above, site and habitat were treated as fixed effects, and all model fitting and checking procedures followed those outlined above. Due to the nature of the urchin data (i.e. sparse data with absolute zeroes for multiple factor levels), variation in the abundance of the two major urchin taxa (*D. antillarum* and *Echinometra* spp.) across sites and habitats was explored graphically, based on their means and standard errors. All statistical analyses were conducted in the software R (version 4.4.1; R Core Team 2024), using the *Tidyverse* (Wickham et al. 2019), *glmmTMB* (Brooks et al. 2017), *emmeans* (Lenth 2020), *DHARMa* (Hartig 2020), and *AICcmodavg* (Mazerolle 2017) packages.

Results

Across both sites, turfs were largely characterised by long sediment-laden algal turfs, although the absolute length of turfs and the loads of sediments trapped varied between sites and among habitat zones (Fig. 1). The shortest turfs (5.4 ± 0.4 mm; GLM marginal mean ± SE) occurred on the reef crest at Tamarindo, while the longest turfs (9.4 ± 0.6 mm) occurred on the reef flat at Tamarindo, a 1.7-fold difference (Fig. 2a). However, a significant interaction between reef site and habitat was found, suggesting that cross-habitat patterns in turf length were not consistent at the two sites (Tables S1 and S2). Turfs were significantly longer on the flat compared to both the crest and slope at Tamarindo (GLM, $p < 0.001$ in both cases; Tables S2, S3), with no significant difference in turf length between the crest and slope at Tamarindo (GLM, $p = 0.146$; Table S3). In contrast, no significant differences in turf length were detected among any of the reef habitats at La Palma (Fig. 2a; Table S3).

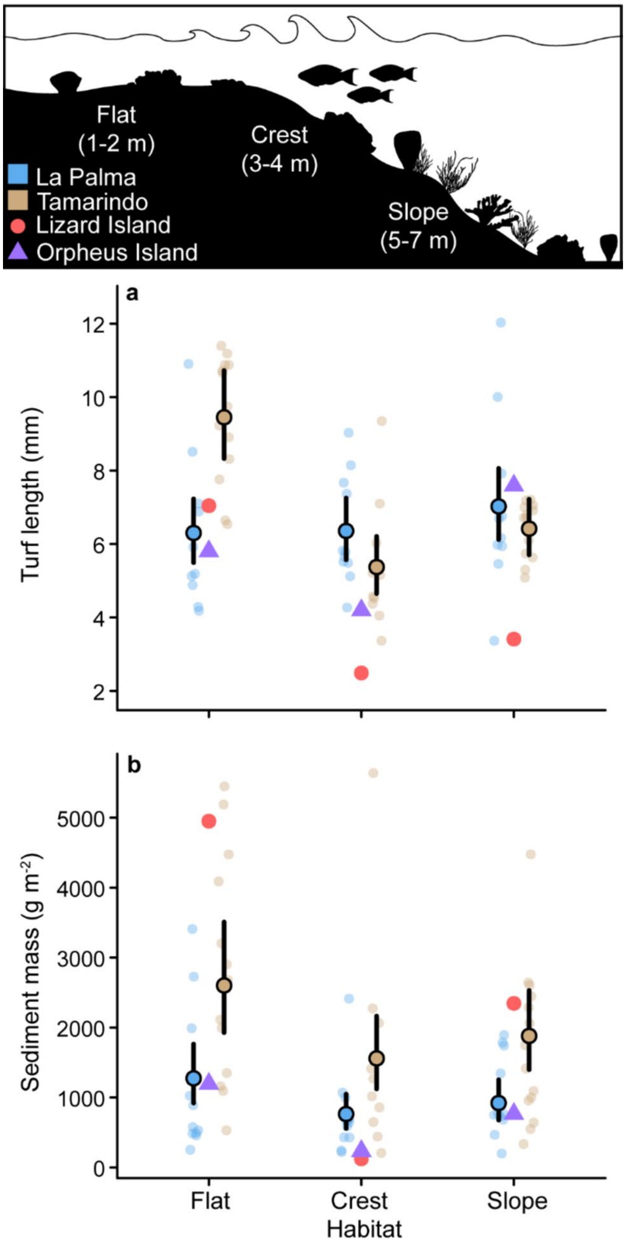

Fig. 2 Variation in **a** turf length, and **b** turf sediment load, across habitats at two Puerto Rican sites, La Palma reef and Tamarindo reef, in the Caribbean. The coloured circles and line ranges denote the predicted mean, and 95% confidence intervals, from generalised linear models, while the smaller semi-transparent circles are the raw data. For reference, the purple triangles and red circles show mean algal turf length and mean sediment load from similar cross-habitat studies conducted at Lizard Island (Purcell 2000) and Orpheus Island (Gordon et al. 2016a) on Australia's Great Barrier Reef

The mass of sediment contained in the turfs followed a consistent cross-habitat pattern at each reef site (Fig. 2b), with no influential interaction between habitat and site detected (Table S1). Turfs on the reef crest at both sites contained the lowest sediment loads (763.9 ± 123.0 and 1559.2 ± 260.3 g m^{-2} at La Palma and Tamarindo, respectively), while turfs on the flat at both sites contained the highest sediment loads (1274.4 ± 210.8 and 2601.2 ± 396.9 g m^{-2} at La Palma and Tamarindo, respectively; Fig. 2b). This 1.7-fold difference in sediment loads between reef crest and flat habitats was significant (GLM, $p < 0.05$; Table S2). Despite similarities in cross-habitat patterns of turf sediment distribution, the mass of sediments in turfs was also consistently higher, by twofold, at Tamarindo compared to La Palma ($p < 0.001$; Table S2). In general, the grain size distribution of sediments was coarser at La Palma compared to Tamarindo, with relatively more sediment in all sediment size classes between 250–2000 µm at La Palma, especially on the crest and slope (Fig. S1). In contrast, the 125–250 µm size class consistently contributed the most to the mass of sediments at Tamarindo (Fig. S1).

Although there was a difference in cross-habitat patterns of turf length at each site, and sediment mass was consistently higher at Tamarindo, examination of the relationship between turf length and sediment mass revealed that there was no significant difference in the length of turfs per unit mass of sediment between reef sites ($p = 0.067$, Table S1, Fig. 3). Instead, at both reef sites, there was a consistent, positive, significant relationship between turf length and sediment mass ($p < 0.001$; Table S2; Fig. 3).

The nominally herbivorous fish community was primarily composed of *Scarus taeniopterus*, *Acanthurus coeruleus*, and *Sparisoma viride*, with these three species accounting for 72% of all surveyed individuals, and 64% of biomass. Total abundance and biomass of parrotfishes and surgeonfishes, however, differed between locations and among habitats (Fig. 4). The abundance and biomass of parrotfishes and surgeonfishes was significantly higher at Tamarindo compared to La Palma (GLM, $p < 0.01$ in all cases; Tables S2, S3; Fig. 4). However, a significant interaction between habitat and location was found in the parrotfish abundance model, driven by the fact that there were no significant differences in abundance across habitats at Tamarindo, but there was at La Palma, where abundance was significantly higher on both the crest and flat compared to the slope ($p < 0.01$ in both cases; Tables S2, S3; Fig. 4a). Abundance of surgeonfishes was not significantly higher on the crest compared to the slope or flat at both locations (Fig. 4b; Table S2). For both parrotfishes and surgeonfishes, biomass peaked on the crest at both locations, with biomass of parrotfishes significantly higher (by 2.4-fold) on the crest, than on the slope ($p = 0.007$; Table S2; Fig. 4c) and biomass of surgeonfishes significantly higher (by 2.7-fold) on the crest, than the flat ($p < 0.02$; Table S2; Fig. 4d).

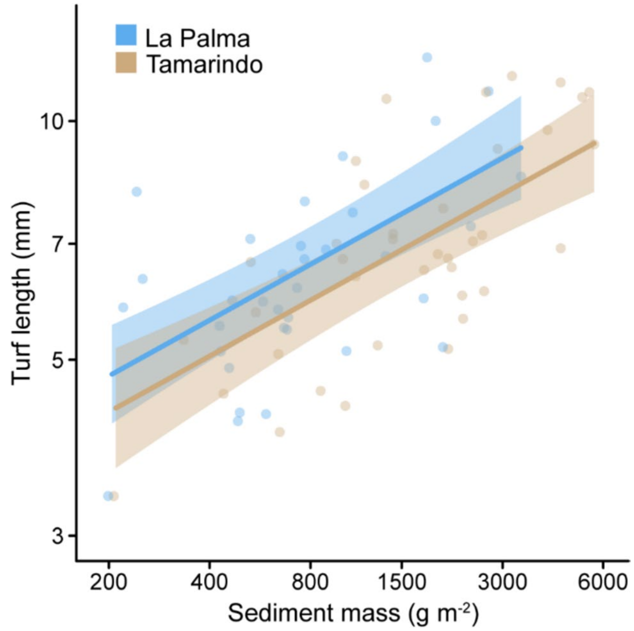

Fig. 3 The relationship between turf length and sediment load at two Puerto Rican sites, La Palma reef and Tamarindo reef, in the Caribbean. The coloured lines and shaded ribbons denote the mean predicted fits, and associated 95% confidence intervals, from a generalised linear mixed effects model. The coloured semi-transparent circles show the raw data. The x and y axes are on the $\log_{10}$ scale in both cases, showing the linear nature of the relationship on this scale (note the data itself has not been log transformed)

The abundance of sea urchins (*Diadema antillarum*, and *Echinometra* spp.) was highly variable among sites and habitats, with nil urchins documented in many cases (Fig. 5). *D. antillarum* densities were universally low, apart from on the reef flat at La Palma, where relatively high densities (0.32 ± 0.28 m^{-2}; mean ± SE) were recorded (Fig. 5a, b). Relatively high densities of *Echinometra* spp. were recorded on the reef flat at Tamarindo (2.19 ± 1.16 m^{-2}), and on the crest at La Palma (2.18 ± 0.52 m^{-2}) (Fig. 5d).

Discussion

By applying the same methods previously used on Indo-Pacific reefs, we evaluated cross-habitat patterns in turf length, associated sediments, and key herbivores at two Puerto Rican reefs in the Caribbean. We revealed that the cross-habitat pattern of turf sediment loads, previously described for reefs on the GBR (i.e. lowest on the crest and highest on the flat) (e.g. Purcell 2000; Gordon et al. 2016a), was conserved for the two Caribbean reefs (Fig. 6). Such congruent patterns suggest the biophysical drivers operating across this habitat gradient may be similarly structuring turf sediment dynamics across reefs even under different contexts (e.g. Schlaefer et al. 2022; Tebbett et al. 2023c). Indeed, the positive relationship between sediment load and turf length across the two Puerto Rican reefs is consistent with the relationship documented for other geographic locations, including the GBR, Australia (Purcell 2000; Tebbett et al. 2025), Dampier Archipelago, Australia (Tebbett et al. 2024), Ningaloo Reef, Australia (Pessarrodona et al. 2022), and Spermonde Archipelago, Indonesia (Syafruddin et al. 2025) (Fig. 6). Moreover, the cross-habitat distribution of herbivorous fish biomass followed expectations (e.g. Russ

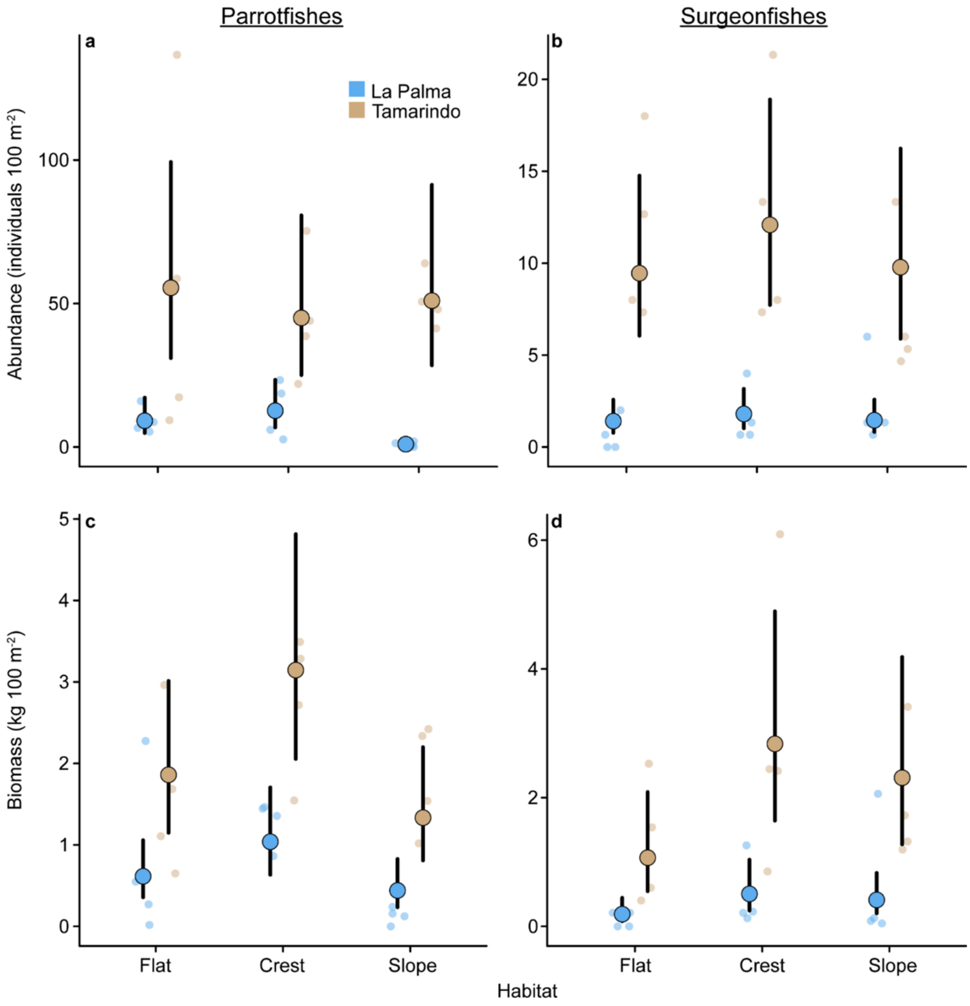

Fig. 4 Variation in the **a, b** abundance, and **c, d** biomass, of parrotfishes and surgeonfishes across habitats at two Puerto Rican reef sites in the Caribbean. The coloured circles and line ranges denote the predicted mean, and 95% confidence intervals, from generalised linear models, while the smaller semi-transparent circles are the raw data

2003; Fox and Bellwood 2007), in that it was highest on the reef crest for both parrotfishes and surgeonfishes, where turf sediment loads were lowest (Fig. 6). However, the cross-habitat pattern in turf length only aligned with expectations at Tamarindo reef (i.e. longest turfs on the flat, and shortest on the crest) (e.g. Purcell 2000; Gordon et al. 2016a), with La Palma's relatively short turf length on the flat driving a departure from expectations. Notably, the reef flat at La Palma was also the only location where relatively high densities of *D. antillarum* were recorded, with this correlation suggesting the capacity of *D. antillarum* to extensively graze algal communities (e.g. Carpenter 1986; Morrison 1988) may have shaped cross-habitat patterns in turf length at La Palma. Together, these results extend our understanding of cross-habitat turf sediment dynamics from the GBR to the Caribbean, and suggest that interactions between urchins and turf sediment dynamics warrant further investigation.

The consistent cross-habitat pattern in turf sediment loads on the Caribbean reefs examined, relative to previous research on the GBR, suggests that biophysical drivers, that operate across this gradient, may be structuring sediment loads in a unified manner. In this respect, hydrodynamics, especially wave-energy, are likely to be critical (Schlaefer et al. 2022; Tebbett et al. 2023c). Previous evidence has underscored the capacity for wave energy to limit sediment accumulation on the relatively high-energy reef crest, while dissipation of wave energy on the reef flat facilitates the deposition and accumulation of high sediment loads (Kench and Brander 2006; Tebbett et al. 2023c). While hydrodynamics may be a major driver shaping this consistent pattern, other contextual constraints, such as reef geomorphology, proximity to land, and exposure to riverine inputs, are likely to shape the absolute quantity of sediment accumulated on a reef and the magnitude of differences between habitats (Wolanski et al. 2005; Browne et al. 2013; Schlaefer et al. 2022).

The absolute quantity of sediment accumulated on the crest of the two reefs examined, as well as the magnitude of the difference in sediment loads between crest and flat habitats, differed from similar studies on the GBR. For example, at Lizard Island, a mid-shelf reef (30 km offshore) on the GBR, average turf sediment loads on the

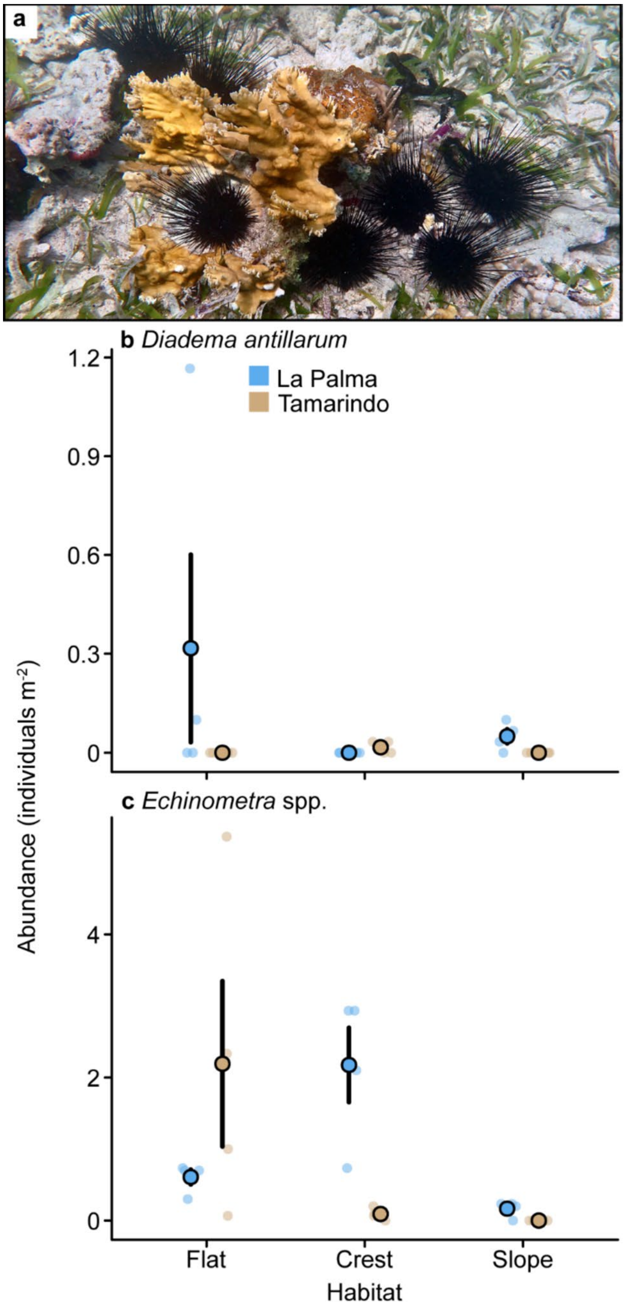

Fig. 5 **a** *Diadema antillarum* at the boarder of the reef flat and adjacent seagrass bed at La Palma, Puerto Rico. Variation in the abundance of **b** *D. antillarum*, and **c** *Echinometra* spp., across habitats at two Puerto Rican reefs in the Caribbean. The coloured circles and line ranges show the mean ± SE, while the smaller semi-transparent circles are the raw data

crest are ~ 123.5 g m^{-2}, while sediment loads on the flat are ~ 40-fold higher (Purcell 2000). In contrast, at La Palma and Tamarindo, average sediment loads on the crest were 763.9 and 1559.2 g m^{-2}, respectively, with loads on the flat only 1.7-fold higher. These high average sediment loads are directly comparable to those commonly encountered on more inshore and coastal reefs on the GBR (Tebbett et al. 2018b).

Lower turf sediment loads are generally found on reefs further offshore (Syafruddin et al. 2025; Tebbett et al. 2025), with this pattern produced by factors such as reduced terrestrial sediment inputs, as well as reduced sediment accumulation due to greater hydrodynamic exposure combined with export of sediment to deeper waters (Wolanski et al. 2003; Tebbett et al. 2023c). The lower sediment loads at La Palma compared to Tamarindo may be related to such factors as La Palma is located 2.48 km offshore, while Tamarindo is a nearshore fringing reef that is likely exposed to greater terrigenous sediment inputs (also see Ryan et al. 2008; Orlando and Yee 2017). Fringing reefs can also trap and accumulate more sediments, as cross-reef sediment movement can be limited by land (Schlaefer et al. 2022; Tebbett et al. 2023c). The sediment grain size distributions quantified at both sites also support these inferences. Higher quantities of fine sediment at Tamarindo likely reflect lower hydrodynamic energy and greater sediment deposition and accumulation, especially of terrigenous siliceous sediments, that are generally finer than reef-derived carbonate sediments (Storlazzi et al. 2009; Browne et al. 2013; Gordon et al. 2016a; Sartori et al. 2025).

The geomorphology of both La Palma and Tamarindo was relatively flat (pers obs TJC, RSM, SESR), and akin to the morphology of inshore reefs on the GBR (Done 1982; Browne et al. 2010). Such 'flatter' reef morphology can facilitate sediment accumulation (Duran et al. 2024; Sartori et al. 2025), and may explain the less pronounced differences in sediment loads between reef flat and crest habitats on these two Caribbean reefs, especially relative to Lizard Island. Indeed, the reef examined by Purcell (2000) at Lizard Island is characterised by a well-defined reef crest and relatively steep reef slope down to ~ 30 m depth. This means that at this Lizard Island reef, sediments are readily moved off the crest onto the flat or exported from the reef down the slope, where they are not readily resuspended and deposited back on the reef (Tebbett et al. 2023c). Therefore, while we document cross-habitat patterns in sediment distributions for two Caribbean reefs that are consistent with previous research from the GBR, differences in a reefs' environmental context may shape the absolute quantities of sediments that accumulate.

The divergence of cross-habitat patterns in turf length at La Palma from expectations based on past research is notable. In this respect, herbivorous fishes are known to structure turf communities on coral reefs via their grazing (Rasher et al. 2012; Fong et al. 2018; Humphries et al. 2020), with the low biomass of parrotfishes and surgeonfishes at La Palma potentially facilitating longer-than-expected turfs on the crest at this location. However, given the low biomass of herbivorous fishes at La Palma, this does not account for

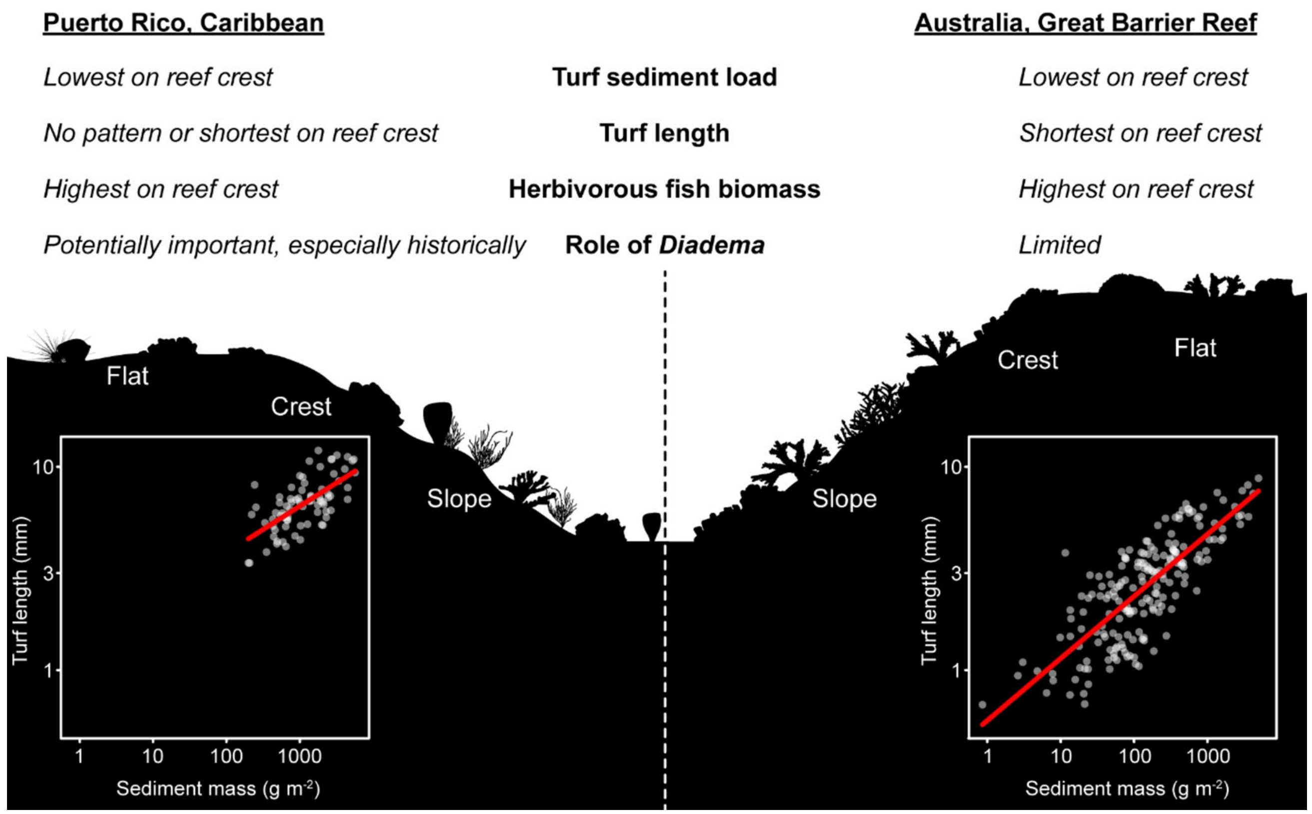

Fig. 6 Conceptual overview of key cross-habitat patterns quantified in the current study on two reefs off Puerto Rico, Caribbean, relative to previously documented cross-habitat patterns from reefs on Australia's Great Barrier Reef (GBR). The cross-habitat patterns for the GBR are based on previous results (Purcell 2000; Russ 2003; Fox and Bellwood 2007; Gordon et al. 2016a; Tebbett and Bellwood 2018). The inset in each reef profile shows the positive linear relationship (on a $\log_{10}$-$\log_{10}$ scale) between turf length and sediment mass found on reefs from each region. In this case, the turf length versus sediment mass data for the GBR were based on data reported in Tebbett et al. (2025), and were restricted to shallow reef crest/edge habitats

the shorter-than-expected turfs on the flat at this location. Instead, the shorter-than-expected turf length on the flat at La Palma may be the product of grazing by *D. antillarum*. This inference is based on the fact that this was the only area across all habitats and sites examined in which *D. antillarum* was relatively abundant. Moreover, the grazing impact of *D. antillarum* on Caribbean reefs is well-established, with experimental evidence suggesting this species has a greater impact on shallow-water algal communities than fishes (Carpenter 1986; Morrison 1988). Experimental re-introduction of *D. antillarum* to Caribbean reefs has revealed that *D. antillarum* grazing can drive transitions from long sediment-laden algal turfs to short productive algal turfs and crustose coralline algae (Williams 2022; cf Lacey et al. 2013). Evidence also suggests that the grazing impact of *D. antillarum* on algal communities is more uniformly distributed than *Echinometra* spp., which exhibit stronger localized or patchy grazing impacts even when at higher densities than *D. antillarum* (Sammarco 1982). Indeed, *Echinometra* spp. tend to graze over much smaller areas than *D. antillarum* and may be more cryptic as they substantially erode into the reef matrix while grazing (Griffin et al. 2003; Shulman 2020). Therefore, while *D. antillarum* densities appear to relate to shorter than expected turfs, the ecology of *Echinometra* spp. may explain why there was no apparent correlation in the data between high *Echinometra* spp. densities and shorter than expected turfs.

The potential for *D. antillarum* to play a role in shaping turf dynamics across the habitat gradient is interesting and emphasises a marked difference in the general functioning of reefs in the Caribbean versus the GBR. Historically, grazing by *D. antillarum* was a major process on many Caribbean reefs (Lessios 2016), with the extent of urchin grazing in this system differing markedly from the GBR, where urchin grazing is generally limited (Sammarco 1985; Tebbett and Bellwood 2018). However, the mass *D. antillarum* mortality event during the early 1980s in the Caribbean (Lessios 2016), as well as the more recent mass die-off event in 2022 (Hylkema et al. 2023), profoundly changed herbivory dynamics in the Caribbean. Indeed, our study encompassed the most recent mortality event, with evidence that the *D. antillarum* densities we report were already reduced from the densities (~ 1–2 m^{-2}) reported between 2011–2016 at Tamarindo (Rodríguez-Barreras et al. 2018). In this respect, future research that teases apart relationships between long sediment-laden algal turfs and *D. antillarum* in an experimental setting, could provide new insights into the increase of long sediment-laden algal turfs following the loss of *D. antillarum* from Caribbean reefs, and the potential to reverse such a reef condition if *D. antillarum* populations are rebuilt (cf. Lacey et al. 2013; Williams 2022). Exploring the sensitivity of *D. antillarum* grazing to increasing turf sediment loads and identifying if a threshold sediment load that impedes grazing exists, represents a key avenue for future research that may provide a mechanistic insight into past results (e.g. Lacey et al. 2013; Williams 2022). If *D. antillarum* grazing is less sensitive to increased sediments in turfs compared to fishes, then this could suggest that historic reductions in *D. antillarum* populations heralded the loss of a key function capable of maintaining short turfs, and/or reversing a long sediment-laden algal turf condition.

High turf sediment loads are known to constrain the feeding behaviour of nominally herbivorous fishes (Goatley and Bellwood 2012; Goatley et al. 2016; Gordon et al. 2016b), and potentially shape population sizes from the bottom-up by reducing turf productivity yields (Tebbett et al. 2018a, 2021). Indeed, abundance and biomass of herbivorous fish populations are well known for tracking the productivity of turf-based resources (e.g. Russ 2003; Tootell and Steele 2016; Benkwitt et al. 2025). As such, the higher biomass of parrotfishes and surgeonfishes on the reef crest at Tamarindo and La Palma, where turf sediment loads were lowest, aligns with expectations and previous patterns for the GBR (e.g. Russ 2003; Goatley and Bellwood 2012; Oakley-Cogan et al. 2020). However, the fact that biomass of both parrotfishes and surgeonfishes was higher at Tamarindo compared to La Palma, where absolute sediment loads were also higher, does not align with previous patterns. Such divergence from expectations may have been driven by a confounding effect of fishing. In this study system, the reef at La Palma has been exposed to intense fishing pressure (Olson et al. 2019), however, the reef at Tamarindo lies inside a no-take marine reserve, that has been closed to fishing since 1999 (Hernández-Delgado et al. 2006; Guarderas et al. 2011). Given that herbivorous fish populations have been shown to respond positively to fisheries closure inside this no-take marine reserve (Hernández-Delgado et al. 2006; Guarderas et al. 2011), this difference in fishing management/pressure likely explains the observed variations in herbivorous fish abundance and biomass between Tamarindo and La Palma reefs.

Overall, our study extends understanding of fundamental cross-habitat distribution patterns of turf sediments and herbivorous fishes to the Caribbean. Extending such knowledge to different geographic locations is critical in developing a more robust and general understanding of how reefs operate (Ladd et al. 2026), especially given the high cover of turfs on most coral reefs globally (Tebbett et al. 2023b). As coral cover continues to decline on reefs, our capacity to manage these systems will depend on our understanding of their functioning, and how this is either consistent or different under varying contexts (Bellwood et al. 2019; Ladd et al. 2026). In the case of turf sediments, cross-habitat distribution patterns appear to transcend broader biogeographic locations and environmental contexts. Going forward, further quantification of turf composition (both taxonomy and traits) and sediment loads, as well as experimental evaluation of mechanistic links between turfs and different groups of herbivores, reef geomorphology, and hydrodynamics, under different contexts, is essential to further our understanding of reef functioning.

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Author contributions TJC, SBT, and SESR conceived and designed the study; TJC and RSM performed the fieldwork; TJC, FEK, and MNO processed the samples and compiled the data; SBT analysed the data; SBT, SDL, and TJC conceived the figures and interpreted the results; SBT and TJC wrote the original manuscript; all authors reviewed and edited the final manuscript.

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Data availability The datasets generated during the current investigation have been uploaded as a supplementary material file accompanying the manuscript.

Declarations

Conflict of interest The authors declare no competing interest.

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