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REPORT

Caribbean corals exhibit species-specific differences in competitive abilities with an aggressive encrusting alga, *Ramicrusta textilis*

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Abstract Caribbean coral cover has decreased substantially in recent decades, with much of the live coral being replaced by macroalgae. Encrusting red algae in the genus *Ramicrusta* have become abundant throughout the region and have demonstrated widespread harm to corals by overgrowing living tissue, causing colony mortality, and impairing coral recruitment. In this research, *Ramicrusta textilis* was identified by morpho-anatomy and DNA sequencing from nine sites around St. Thomas, US Virgin Islands, and 3D photogrammetry was used to measure the rate of algal growth on stony corals. 3D models of individual coral colonies (five species plus controls, $N = 72$) competing with *R. textilis* revealed differential competitive abilities among taxa, with *Siderastrea siderea* being the only species capable of inhibiting overgrowth by the alga (mean linear algal growth $-$ 1.1 mm yr^{-1}). Important reef building coral species such as *Orbicella annularis* and *Orbicella faveolata* were poor competitors (mean linear algal growth $+$ 15 mm yr^{-1} and $+$ 7.7 mm yr^{-1}, respectively), indicating that the emergence of the alga could have significant impacts on Caribbean coral reef species diversity, community composition, and structural complexity.

Keywords Ecology · Scleractinian · Coral–macroalgal competition · Photogrammetry · Peyssonneliaceae · DNA sequencing

Introduction

In recent decades, losses of coral cover have coincided with marked increases in macroalgae on Caribbean coral reefs (Hughes 1994; Gardner et al. 2003; McManus and Polsenberg 2004). Such substantial changes in community composition have raised concerns about the resilience of these valuable ecosystems (McClanahan et al. 2002; Hughes et al. 2007) because reductions in stony coral cover can have far-reaching impacts on coral reef ecosystem services (Wild et al. 2011). Persistent shifts from scleractinian coral to macroalgal cover have been linked to compounding reef degradation factors, such as reductions of herbivorous species and increases in nutrients, often in combination with widespread coral mortality events (Done 1992; Hughes et al. 2010).

While phase shifts from coral to fleshy algal species have been well documented (Done 1992; McManus et al. 2000; Hughes et al. 2010), shifts to encrusting algae are not as widely known. However, over the last decade, reports of abundant encrusting red algae in the genus *Ramicrusta* (family Peyssonneliaceae) have emerged throughout the Caribbean Sea (Pueschel and Saunders 2009; Ballantine and Ruiz 2013; Eckrich and Engel 2013; Edmunds et al. 2019). *Ramicrusta* spp. (hereinafter *Ramicrusta*) have been deemed a potentially severe threat to Caribbean coral reefs due to their rapid growth and strong ability to outcompete

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other benthic organisms; *Ramicrusta* overgrow a variety of reef species (Eckrich et al. 2011; Smith et al. 2018) and often quickly dominate the substratum as a highly abundant taxon (Slijkerman et al. 2011; Williams and García-Sais 2020). First described in the Caribbean by Pueschel and Saunders in 2009, three species of *Ramicrusta* have been identified in the region: *R. monensis* in Puerto Rico; *R. bonairensis* in Bonaire, the Lesser Antilles, and Puerto Rico (Ballantine et al. 2016); and *R. textilis* in Jamaica, Puerto Rico, and St. John (Pueschel and Saunders 2009; Ballantine and Ruiz 2013; Edmunds et al. 2019). Although *R. textilis* has been identified in the US Virgin Islands (USVI) in St. John, its presence in St. Thomas has yet to be confirmed.

In the USVI, *Ramicrusta* have expanded to over half of the 34 monitoring sites of the Territorial Coral Reef Monitoring Program (TCRMP) and have quickly become the most abundant benthic taxon at multiple locations (Smith et al. 2018). For example, Savana Island (8 m depth) and College Shoal East (30 m depth) exhibited high prevalence of *Ramicrusta* in 2016 (occurring in 98.25% and 87.30% of video clips, respectively) (Smith et al. 2018). Both sites are offshore with reduced land-based human impact, and College Shoal is a mesophotic reef within a no-take marine-protected area, suggesting that direct human disturbance is not a necessary driver of *Ramicrusta* abundance. However, reductions in coral cover may promote expansion of the algae. At Savana Island, the percent cover of *Ramicrusta* increased fivefold from 2005 to 2007, from 4.64% ± 1.28 SE to 20.2% ± 2.39, after loss of coral cover in the 2005 bleaching event (20.3% ± 4.73 to 13.1% ± 1.82) (Smith et al. 2018).

Ramicrusta are known to overgrow several species of corals in the Caribbean and cause colony mortality (Fig. 1; Eckrich and Engel 2013; Ruiz 2015; Smith et al. 2018). In addition, *Ramicrusta* may impair coral recruitment (Eckrich and Engel 2013; Bramanti et al. 2017; Wilson et al. 2020). Although the algae have the potential to negatively affect Caribbean coral populations, it remains uncertain which scleractinian species are most at risk. In Bonaire and Puerto Rico, *Porites astreoides, Porites porites,* and *Orbicella annularis* had over 30% of their colonies overgrown by *Ramicrusta*, while *Siderastrea siderea*, *Acropora palmata*, and *Agaricia* sp. were overgrown by the algae in a lower proportion (Eckrich and Engel 2013; Ruiz 2015). Despite nonsignificant differences in overgrowth rates of *Ramicrusta* among three coral species *(Millepora complanata, P. astreoides,* and *P. porites*) reported by Eckrich and Engel (2013), other coral taxa (e.g., *Orbicella* spp.) may be more vulnerable to *Ramicrusta* overgrowth. Coral taxa can have differential competitive abilities (Lirman 2001; Nugues et al. 2006; Swierts and Vermeij 2016), underscoring the importance of investigating species-specific competition with *Ramicrusta*.

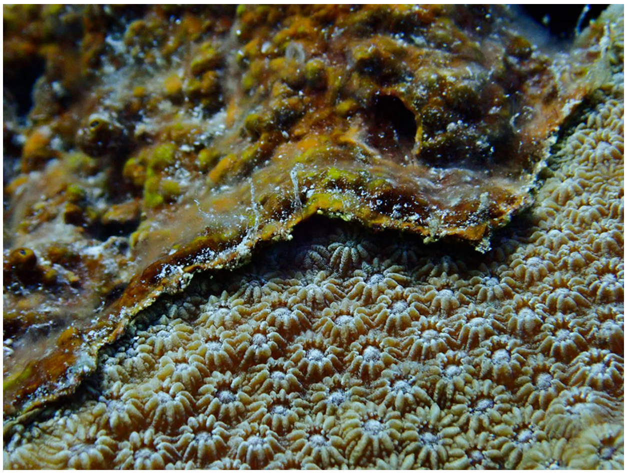

Fig. 1 Photograph of *Ramicrusta textilis* overgrowing a star coral (*Orbicella* sp.)

As shifts from coral to algal abundance have become more common on Caribbean reefs, there is a growing need to better understand the dynamics of coral–algal competition to predict ecological impacts and inform management decisions. Recently, advancements in imaging technology have made it possible for non-experts to measure the complex three-dimensional (3D) growth of sessile reef organisms with minimal training and affordable equipment (Gutiérrez-Heredia et al. 2015, 2016). 3D reconstruction of benthic organisms from underwater photographs has gained popularity as a method to capture more meaningful morphological changes (e.g., surface area and volume) because it is less field-intensive, less intrusive, and more informative than other approaches (Burns et al. 2015; Reichert et al. 2016) and mm-scale accuracy can be reasonably achieved (Holmes 2008; Ferrari et al. 2017; Olinger et al. 2019).

The goal of this research was to use 3D photogrammetry to explore variation in competitive interactions between massive Caribbean corals and *Ramicrusta.* Linear and areal growth rates of *Ramicrusta* were quantified from 3D models of individual coral colonies competing with the algae across: (1) coral taxa and (2) geographic location. Given the lack of information about *Ramicrusta* in the Caribbean, additional data were collected from all study sites to identify the species of *Ramicrusta* present in St. Thomas, examine *Ramicrusta*–coral interaction prevalence across location and coral species, and assess potential impacts of the algae on coral health.

Materials and methods

Overview

High-resolution 3D models of individual coral colonies were generated to measure the linear and areal expansion of *Ramicrusta* over time. Coral species with a massive morphology were selected for 3D modeling precision and selection of coral-like control substrates. Coral colonies were tagged and photographed in October 2018 and re-photographed 5 months later to calculate *Ramicrusta* growth rates using models of the same colony from two time points. To measure algal growth unhindered by coral competition, control replicates were photographed and modeled on dead coral or limestone pavement covered in *Ramicrusta* and a mixed epilithic algal community. Controls with a macro-morphology similar to massive coral colonies were selected to mimic the structure of the coral replicates. Two studies were conducted using this methodology to investigate algal overgrowth across coral taxa (Study 1) and geographic location (Study 2).

Study 1: Overgrowth across species

To evaluate species-specific differences in competition with *Ramicrusta*, algal growth rates were compared for five massive coral taxa that were most commonly competing with the algae in the USVI: *Orbicella faveolata, Orbicella annularis, Porites astreoides, Siderastrea siderea,* and *Pseudodiploria strigosa.* Four controls and four replicates of each of the selected coral species were marked at three representative study sites (Fig. 2; $N = 12$ controls and 12 colonies of each coral species).

Study 2: Overgrowth across location

Algal growth rates on *S. siderea* colonies and controls were compared across eight study sites (Fig. 2) to determine whether *Ramicrusta* competes more aggressively at different locations. *S. siderea* was chosen because the species was commonly found interacting with *Ramicrusta* at all study locations. Four controls and four replicates of *S. siderea* were marked at each site ($N = 32$ controls and 32 coral colonies). Data were collected at each site to assess benthic cover, community composition, coral health, and *Ramicrusta*–coral interaction prevalence (see below: Site characterization).

Study sites

All sites were located on the south side of St. Thomas, USVI, in proximity to the University of the Virgin Islands Center for Marine and Environmental Studies (Online Resource 1, Fig. 2). Each site was limited to a shallow depth range of six-to-nine meters to maximize the natural light necessary for 3D reconstruction. Fortuna Bay (FB), Savana Island (SI), and Flat Cay Windward (FW) were selected as Study 1 sites for species-specific overgrowth rates. FW and SI were also included as sites in Study 2 on location-specific overgrowth rates using separate replicates. Six additional locations were selected for Study 2: Flat Cay Leeward (FL), Buck Island (BI), Perseverance Bay (PB), Water Island (WI), Saba Island Windward (SW),

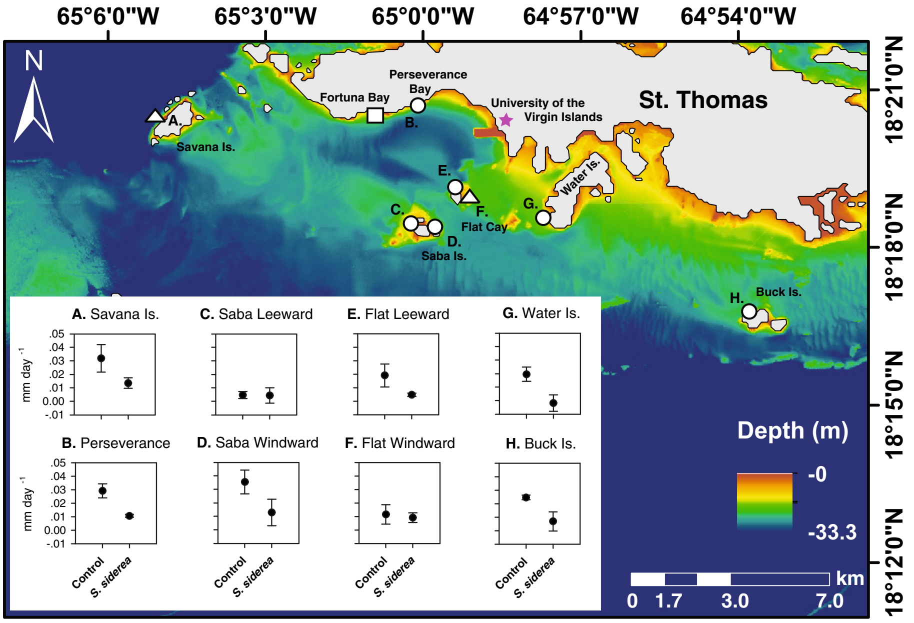

Fig. 2 Map of the southwest side of St. Thomas with study sites. Shape indicates which study corresponds to which sites (square = Study 1 only, triangle = Study 1 and Study 2, circle = Study 2 only). Gray areas show landmasses and color indicates depth. Inset shows average linear growth rates of *Ramicrusta textilis* (± SE) on controls and *Siderastrea siderea* colonies across sites from Study 2

and Saba Island Leeward (SL). Study 1 sites were selected for their high prevalence of coral–*Ramicrusta* interactions, allowing for sufficient replication of the five coral species. Study 2 sites were selected for their variation in *Ramicrusta* abundance (Table 2).

DNA sequencing

To identify the species of *Ramicrusta* present in the USVI and verify whether the same species was under investigation at each study site, representative samples of the algae were collected from each of the nine sites in April 2019 and placed in silica gel for DNA sequencing. Specimens were located near marked coral colonies at each study location. Between one and five samples were taken per site for a total of 23 specimens.

Specimen preparation, extraction, and sequencing were done at the University of North Carolina (UNC) Chapel Hill, following Gabrielson et al. (2011); amplification for *rbc*L followed Gabrielson et al. (2011); and amplification for *psb*A followed Adey et al. (2015). Forward and reverse sequence reactions were compiled and edited using Sequencher (Gene Codes Corporation, Ann Arbor, MI, USA), and consensus sequences were accessioned into GenBank.

Growth rates of *Ramicrusta*

Setup and data collection

Coral colonies and controls exhibiting *Ramicrusta* overgrowth were selected at each site in a confined area of approximately 900 m^2 via haphazard roving diver surveys. Healthy colonies with minimal interactions (e.g., low cover of tissue by fleshy macroalgae) were preferred, but not exclusively selected. The average maximum length of coral colonies included in Studies 1 and 2 was 19.5 cm (± 0.02 SE) and 16.4 cm (± 0.01), respectively. Replicates were at least 1 m apart at each site and within a 4-m depth range across sites, with the exception of SI, which is slightly deeper (Online Resource 1). Prior to photographing the replicates, divers carefully removed any benthic species that could interfere with the growth measurements (primarily *Dictyota* spp.) by hand and cleared the colony of sediment with brushes to ensure clear visibility of the coral–*Ramicrusta* border. A minimum of 60 photographs were taken 360° around each colony and from overhead, with minimal rotation between subsequent photographs to ensure overlap. Initial photographs for both studies were taken in October 2018, and final photographs were taken in March and April 2019 using a 12-megapixel Olympus Tough TG-5 digital camera.

Photogrammetry

All 3D reconstructions were created using Agisoft Metashape Professional following methodology similar to Olinger et al. (2019). After photograph alignment, the resulting 3D sparse point cloud was refined using the gradual selection and camera optimization tools. Final sparse point clouds were batch-processed to create high-quality dense point clouds using aggressive depth filtering, and a high-quality textured mesh was built with an unlimited face count. The textured meshes were scaled, keeping the error threshold below 1 mm. Final models were assessed for mesh quality at the *Ramicrusta* growth border before exporting. See supplementary material for an example of a finished model (Online Resource 2).

Ramicrusta growth was measured using CloudCompare software. For each replicate, two textured meshes (one from each time point) were finely aligned and superimposed using the point picking tool (Online Resource 3). A minimum of four static points (e.g., individual corallites) were matched across the two time points to align the meshes. The alignment error was limited to achieve 1-mm accuracy for all coral replicates; however, the error increased to 3 mm for some control replicates due to the lack of corallites. After aligning the meshes, the segmentation tool was used to isolate the longest "clean" subsection of the coral–*Ramicrusta* border. A clean border was defined as a clearly reconstructed area where *Ramicrusta* were overgrowing living coral tissue without any sediment, macroalgae, or blockages obscuring the competitive margin at either time point. A rectangular subsection was simultaneously segmented out of both meshes (Online Resource 3a) and analyzed for linear and areal *Ramicrusta* growth using the trace polyline and segmentation tools (Online Resource 3b; 3c). There was minimal vertical growth and change in total subsection area between time points, and an attempt was made to keep total subsection area similar among replicates.

Site characterization

At each of the nine study sites, divers assessed benthic cover and coral health along the same six 10-m transects located randomly on the reef near the study area. Benthic cover directly beneath each transect was recorded every 10 cm, and all biotic entries were identified to the lowest possible taxonomic level. To assess coral health, divers assessed as many corals as possible on the left side of 1-m belt transects, which ranged from 4 to 10 m length depending on coral density. Every living coral > 0.5 cm in maximum diameter was identified to the lowest possible taxonomic level. Corals were assessed in situ for interactions with *Ramicrusta* and signs of mortality, bleaching, and disease using a modified TCRMP protocol (Smith et al. 2018). *Ramicrusta* interactions were defined as living coral tissue visibly affected by a layer of *Ramicrusta* overgrowth (Fig. 1).

Statistical analyses

All statistical analyses were performed in R using the stats package; graphics were created using the ggplot2 package. An alpha level of 0.05 was set for all statistical tests. When post hoc tests were conducted with Bonferroni correction, P values were multiplied by the number of comparisons in the analysis. For ANOVA analyses, assumptions of homoscedasticity and normality were investigated.

Growth rates of Ramicrusta

Ramicrusta growth rate analyses were conducted on the two subsections corresponding to each replicate (one subsection from each time point). For each subsection pair, linear algal growth was calculated as the average of 15 measurements of linear extension across the advancing edge of *Ramicrusta*. This level of replication was selected to achieve a standard deviation below ± 0.0003 mm for average linear growth measurements on five test models. Areal algal growth was calculated as the percent surface area coverage of *Ramicrusta* in the subsection at the second time point minus the percent surface area coverage of *Ramicrusta* at the first time point. Both measures of *Ramicrusta* growth were calculated as a daily rate. Three replicates that could not be properly aligned or clearly measured were omitted from further analyses; one replicate each at PB, SW, and WI for Study 2. For Study 1, two-factor ANOVAs were used to determine the effect of species (control, *O. faveolata, O. annularis, P. astreoides, S. siderea,* and *P. strigosa*) and location (FB, SI, and FW) on the linear and areal growth rate of *Ramicrusta*. For Study 2, two-factor ANOVAs were performed to determine the effect of location (BI, FL, FW, PB, SI, SL, SW, and WI) and substratum (control and *S. siderea*) on the linear and areal growth rate of *Ramicrusta*.

Data validation

Using different sets of photographs from the same day, five replicate models of a single *S. siderea* colony were generated. A single-base model was paired with the replicate models to measure *R. textilis* growth using the above workflow. SE values for two sets of growth rates (five measurements on the replicate models testing 3D model variability and five measurements on the same model pair testing human measurement variability) were compared to the difference in average growth rate between two significantly different replicate groups (*S. siderea* and *O. faveolata*). The standard error values for the average linear (− 0.010 ± 0.0006 mm/d) and areal (− 0.099 ± 0.0100 percent/d, mean ± SE) validation growth rates were between one and two orders of magnitude smaller than the difference in average growth rate between the different replicate groups (+ 0.028 mm/d and + 0.158 percent/d, respectively). Therefore, the statistical differences in the data were due to ecologically relevant growth rates and not measurement variability associated with the 3D reconstruction process.

Ramicrusta interaction prevalence

Using the belt transect data, the prevalence of *Ramicrusta* interactions was calculated for each study site by dividing the number of corals with overgrowth by the total number of corals assessed. A two-way ANOVA was used to test the effect of coral species (*P. astreoides, S. siderea, P. porites, Agaricia agaricites, Siderastrea radians,* and *Orbicella franksi*) and location (FB, FL, and WI) on interaction prevalence. This subset of six coral species and three sites was used to omit data with a low count of coral colonies ($N < 10$ species per site). Data were squared to meet assumptions of homoscedasticity.

A single-factor ANOVA was used to separately test the effect of location (all sites) on interaction prevalence. In addition, a Kruskal–Wallis rank sum test was used on a subset of data to test the effect of abundant coral species with a total $N > 100$ across all sites (*P. astreoides, S. siderea, P. porites, A. agaricites, S. radians,* and *O. annularis*) on interaction prevalence. A one-way ANOVA was also used to separately test the effect of the five Study 1 coral species on interaction prevalence.

Relationship with coral health

A Pearson's Chi-square test of independence was conducted to examine the relationship between *Ramicrusta* interaction (presence/absence) and coral health status (healthy, diseased, bleached, old mortality, and recent mortality).

Results

DNA sequencing

Each of the 23 collected specimens was identified as *Ramicrusta textilis*, confirming that the same species was under investigation at all study sites. Collections ranged from 4.5 to 17.5 m depths. Field identification based on morpho-anatomy was confirmed by DNA sequencing of each specimen using the plastid-encoded *rbc*L gene (691 base pairs) and/or the *psb*A gene (850 base pairs). These gene sequences were identical to sequences obtained from topotype material of *R. textilis*. Sequences were deposited in GenBank (for the *rbc*L gene, KC130226; for the *psb*A gene KM360015) and are publicly available using accession numbers MT215139–MT215161 (https://www.ncbi.nlm.nih.gov/genbank/). All 23 sequences were identical to one another regardless of depth, morpho-anatomy, and substrate. All preserved specimens were deposited in the UNC Chapel Hill Herbarium (NCU 672,224–672,246).

Growth rates of *R. textilis*

Study 1: Overgrowth across species

Two-factor ANOVAs revealed clear differences in both linear and areal growth rates of *R. textilis* across coral species, but no significant difference across sites and no interaction (Table 1a). The linear growth rate of *R. textilis* on *S. siderea* was significantly slower than growth on all species except controls, and the linear growth rate of the alga on *O. annularis* colonies was significantly faster than growth on controls (Fig. 3). The areal growth rate of *R. textilis* on *S. siderea* was also significantly slower than on all other species (Online Resource 4). In addition, *S. siderea* was the only species that exhibited negative average overgrowth rates of *R. textilis* (recession of the algae over time). The alga grew approximately 2.5 times slower on *S. siderea* than on controls and about 4.2 (areal) to 6.7 (linear) times slower than on *O. annularis.* The rate of growth of *R. textilis* was about 1.7 (areal) to 2.6 (linear) times faster on *O. annularis* than on controls. The fastest average linear growth rate ± SE was + 0.039 ± 0.006 mm d^{-1} on *O. annularis* colonies, indicating that projected overgrowth on corals could reach nearly 1.5 cm yr^{-1} along advancing edges of growth.

Study 2: Overgrowth across location

Two-factor ANOVAs revealed significant differences in linear and areal growth rates of *R. textilis* across both substrata and site (Table 1a). Linear and areal growth rates of *R. textilis* occurred significantly faster on controls than on *S. siderea* colonies (Fig. 2; Online Resource 5). The post hoc analysis was unable to detect site-specific differences in linear growth rates; however, the areal growth rates of *R. textilis* were significantly slower at FW than at PB (Online Resource 5). Notably slow (and sometimes negative) growth rates of *R. textilis* on *S. siderea* were suspected to increase variability among the data, making it difficult to detect significant differences among sites. Therefore, to determine whether *R. textilis* growth rates vary by location, single-factor ANOVAs were conducted on control growth only. Results revealed a significant difference in areal growth rates across sites, but no significant difference in linear growth rates was detected despite mean growth rates that were up to 7 times different (Table 1a; Table 2; Fig. 2). A post hoc test with Bonferroni correction showed a significant difference in areal growth rate between PB and FL, FW, and SL as well as a significant difference between FW and SW. The fastest average linear growth was measured at SW and SI, and the fastest average areal growth was measured at PB; rapid growth rates were observed despite low cover of *R. textilis* at both PB and SW (Table 2).

R. textilis interaction prevalence

The two-factor ANOVA results indicated that *R. textilis* interaction prevalence did not differ across sites or coral species with no significant statistical interaction, but separate one-way analyses revealed significant differences across both location and taxa (Table 1c). Average interaction prevalence appeared to differ substantially across both sites and species, with means reaching over an order of magnitude in difference. Because the analysis was conducted on a subset of data, insufficient replication of coral species was suspected to be contributing to the results. To address this, single-factor analyses were conducted separately to assess interaction prevalence across all study locations. Results showed a significant effect of location on *R. textilis* interaction prevalence (Table 1c); prevalence was significantly greater at FW than at WI (Table 2). In addition, there was a significant difference in *R. textilis* interaction prevalence across coral species with a total sample size of $N > 100$ across sites, with a significantly lower interaction prevalence for *S. radians* than all other coral species (Table 1c, Fig. 4). Despite a total sample size of 220 *S. radians* across all sites, no *R. textilis* interactions were observed. *O. annularis* had the greatest recorded average interaction prevalence of all of the coral species, with 24% (± 5.3 SE) of the corals interacting with *R. textilis* across all sites (Fig. 4). When interaction prevalence was examined separately for the five coral species from Study 1, there was no significant effect. Similar to average growth rate observations, relatively high interaction prevalence co-occurred with low cover of *R. textilis* at some sites (e.g., SW; Table 2). Furthermore, extremely high interaction prevalence (55% and 64%) occurred with less than 1% cover of the alga on individual transects at SW.

Table 1 Results of two-way and one-way ANOVA analyses of *Ramicrusta textilis*: (a) growth rates (Study 1 and 2), (b) cover (all sites), and (c) interaction prevalence (subsets of belt transect data)

Effect		SS	df	MS	F	P
(a) Growth rates						
Study 1						
Linear	Species	0.009	5	0.002	5.29	< 0.001***
	Site	0.001	2	0.001	0.01	0.988
	Site x Species	0.005	10	0.001	1.32	0.244
	Residual error	0.029	54	0.001		
Areal	Species	0.407	5	0.081	7.59	< 0.001***
	Site	0.005	2	0.003	0.25	0.779
	Site x Species	0.088	10	0.009	0.82	0.612
	Residual Error	0.579	54	0.011		
Study 2						
Linear	Substrate	0.003	1	0.003	20.2	< 0.001***
	Site	0.002	7	0.001	2.32	0.042*
	Site x Substrate	0.001	7	0.001	0.92	0.500
	Residual Error	0.007	45	0.001		
Areal	Substrate	0.065	1	0.065	4.56	0.009**
	Site	0.314	7	0.045	3.14	0.038*
	Site x Substrate	0.124	7	0.018	1.24	0.304
	Residual error	0.643	45	0.014		
Control linear	Site	0.003	7	0.001	2.34	0.059
	Residual error	0.004	23	0.001		
Control areal	Site	0.274	722	0.039	5.69	< 0.001***
	Residual error	0.158	3	0.007		
(b) Cover						
	Site	207.1	8	25.89	29.5	< 0.001***
	Residual error	39.51	45	0.878		
(c) Interaction prevalence						
Two-way	Species	10,518,091	5	2,103,618	1.68	0.152
	Site	2,809,321	2	1,404,660	1.12	0.332
	Species x Site	11,434,260	10	1,143,426	0.91	0.528
	Residual error	82,796,011	66	1,254,485		
One-Way	Site	5729	8	716.2	3.04	0.010*
	Residual error	8966	38	235.9		
	Species (Study 1)	5866	4	1467	1.55	0.189
	Residual error	217,786	230	946.9		
Kruskal–Wallis	Species	($N > 100$)	6	H = 46.9		< 0.001***

Interaction prevalence for coral species with $N > 100$ analyzed using Kruskal–Wallis rank-sum test because data did not adhere to ANOVA assumptions. Significant effects denoted by asterisk(s). Refer to supplementary material for additional benthic cover and coral community composition data by site (Online Resources 6–10)

Relationship with coral health

The Pearson's Chi-square test of independence revealed a significant relationship between coral health status and *R. textilis* interaction (χ^2 (4, $N = 4671$) = 440.6, $P < 0.001$). Variables that contributed the most to the Chi-square statistic were corals with old mortality and healthy corals (both with and without an *R. textilis* interaction), followed by corals with recent mortality and an *R. textilis* interaction. For colonies with an *R. textilis* interaction, the observed frequency was significantly greater than the expected frequency for old and recent mortality, while the observed frequency was significantly less than the expected frequency for healthy corals (Fig. 5). Therefore, corals

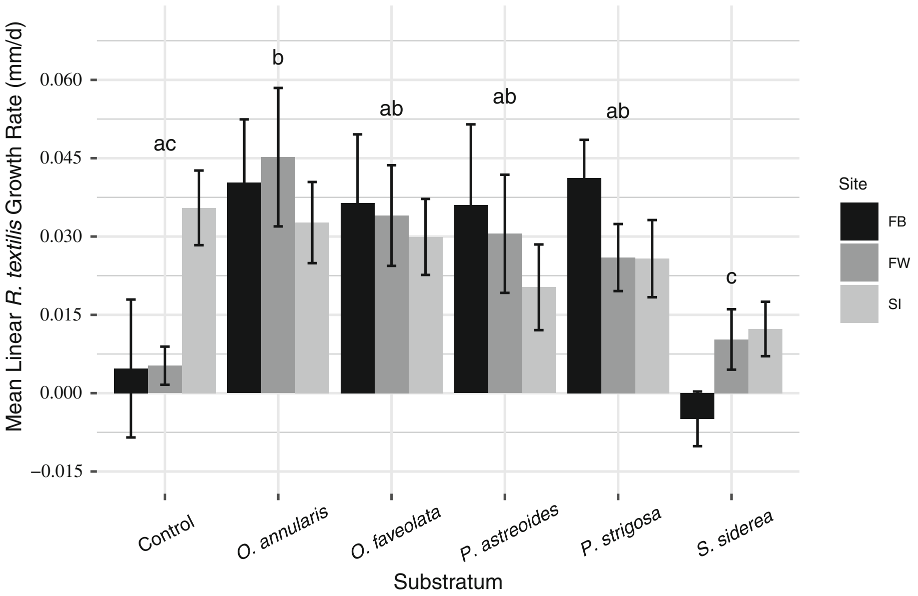

Fig. 3 Average linear growth rates of *Ramicrusta textilis* (± SE) by site and species. Study 1 site codes: FB = Fortuna Bay, FW = Flat Cay Windward, SI = Savana Island. Study 1 coral species: *Orbicella annularis, Orbicella faveolata, Porites astreoides, Pseudodiploria strigosa,* and *Siderastrea siderea.* Pairwise comparison results shown from Tukey's honestly significant difference post hoc test; substrata sharing a common letter have no significant difference

Table 2 *Ramicrusta textilis* cover, growth rates, and interaction prevalence by site (mean ± SE)

Site	Cover (%)	Linear growth (mm d^{-1})	Areal growth (% d^{-1})	Interaction prevalence (%)
BI	23 ± 3.8	0.016 ± 0.005	0.150 ± 0.046	27 ± 10
FL	2.7 ± 0.9	0.012 ± 0.005	0.052 ± 0.021	7.2 ± 4.0
FW	46 ± 5.9	0.010 ± 0.004	0.033 ± 0.028	34 ± 7.6
FB	6.5 ± 2.4	N/A	N/A	7.4 ± 0.8
PB	1.5 ± 0.5	0.021 ± 0.005	0.238 ± 0.031	11 ± 2.1
SL	7.2 ± 1.6	0.005 ± 0.003	0.066 ± 0.051	8.3 ± 1.8
SW	0.8 ± 0.8	0.023 ± 0.008	0.171 ± 0.046	28 ± 10
SI	19 ± 2.0	0.023 ± 0.006	0.208 ± 0.030	11 ± 3.9
WI	2.2 ± 0.9	0.010 ± 0.006	0.084 ± 0.087	2.5 ± 1.3

Site codes: BI = Buck Island, FB = Fortuna Bay, FL = Flat Cay Leeward, FW = Flat Cay Windward, PB = Perseverance Bay, SL = Saba Island Leeward, SW = Saba Island Windward, SI = Savana Island, WI = Water Island

with an interaction are more likely to have old and recent mortality and less likely to be healthy than corals without an interaction. The total observed frequency of all negative coral health parameters (bleaching, disease, and mortality) was also higher for coral colonies interacting with *R. textilis* than colonies without interactions (Fig. 5).

Discussion

Overgrowth rates of *R. textilis* can be strongly influenced by the coral species colonized by the algae. Although most coral taxa were poor competitors against the alga, *S. siderea* demonstrated a competitive ability to reverse overgrowth by *R. textilis.* Conversely, *O. annularis* was an exceptionally poor competitor with *R. textilis* in rate of overgrowth and the peak prevalence of interactions. Overall, *R. textilis* poses a severe threat to coral reefs in the USVI and potentially the greater Caribbean. The alga successfully outcompetes four of the five massive scleractinian species most commonly interacting with the alga in the region. Because these species include major reef-building taxa, it is possible that the emergence of *R. textilis* could have significant impacts on both coral species diversity and the structural complexity of reefs over time.

While only massive-shaped corals were targeted for this research, subtle differences in morphology could have contributed to the differential competitive abilities exhibited across species. Specifically, the lobed structure of *O. annularis* colonies could facilitate overgrowth by *R. textilis* by providing space that is favorable for the alga to establish. The alga generally grows from the base of each lobe upwards, presumably engulfing the living upper surface over time. The nonliving bases of *O. annularis* lobes are

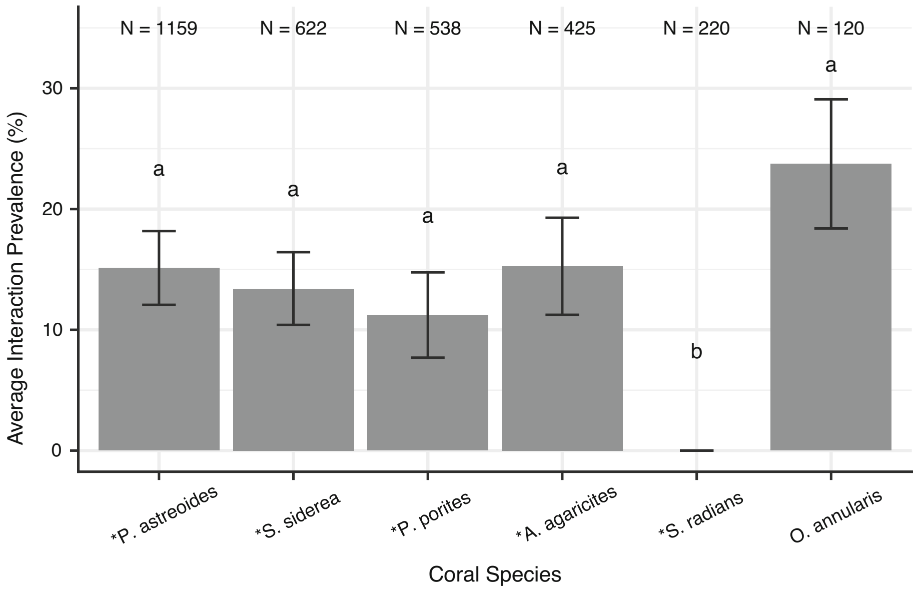

Fig. 4 Average interaction prevalence of *Ramicrusta textilis* (± SE) by coral species. Scleractinian species with total $N > 100$ across all sites are displayed. Asterisks indicate coral species that were included in the two-way ANOVA analysis across three sites (NOTE: *Orbicella franksi* also included in the two-way ANOVA, but not displayed because total $N < 100$ across all sites.) Pairwise comparison letters shown from Tukey's honestly significant difference post hoc test for one-way ANOVA across coral species with $N > 100$; coral species sharing a common letter have no significant difference. Coral species: *Porites astreoides, Siderastrea siderea, Porites porites, Agaricia agaricites, Siderastrea radians,* and *Orbicella annularis*

inaccessible to large grazers and contain few competitors, which could allow the alga to easily recruit on multiple lobes and aggressively overgrow the coral from multiple contact points. Furthermore, the vertical growth pattern of *O. annularis* inhibits its ability to overgrow *R. textilis*, unlike plating or encrusting species which can overgrow the alga horizontally. While these are plausible explanations for the enhanced susceptibility of *O. annularis*, species with the same morphological traits (namely hemispherical-massive *P. strigosa* and *S. siderea*) exhibited significant differences in competitive abilities against *R. textilis*, suggesting that morphology is not the primary factor influencing these competitive outcomes.

Differences in coral species-specific interaction prevalence with *R. textilis* were also evident, but did not necessarily reflect the differences in overgrowth rates among coral taxa. An analysis of interactions from the belt transect data indicated that *S. radians* was not susceptible to *R. textilis* overgrowth, with no *R. textilis* interactions observed on any of the colonies assessed. This could reflect a general robustness of corals in the family Siderastreidae to *R. textilis* interactions; however, differences in interaction prevalence among Study 1 coral taxa were not detected despite differences in the overgrowth rates on *O. annularis* and *S. siderea*. While *O. annularis* did exhibit generally higher interaction prevalence than other species, possibly because of the increased availability of contact points for the alga to establish on multiple lobes, *S. siderea* did not appear to interact with the alga less frequently than other taxa. Because *S. siderea* exhibited resistance to algal overgrowth, standoff interactions between *R. textilis* and *S. siderea* could have resulted in more prevalent interaction observations for this species. It is also possible that the initiation of interactions between corals and *R. textilis* does not depend on the competitive ability of the coral species, whereas overgrowth rates show a clear hierarchy.

R. textilis harms corals typically by overgrowing living tissue, but could also impact colony health less directly. Frequency analysis indicated that the presence of *R. textilis* on corals increases the likelihood that colonies also display signs of bleaching, disease, and mortality. Conversely, evidence of bleaching, disease, and mortality could increase the likelihood that a coral interacts with *R. textilis*. Regardless, signs of partially bleached tissue past the coral–algal margin were observed on multiple colonies throughout this research, which could be an indication of allelopathic capabilities of *R. textilis* and/or a result of coral stress. Competitive mechanisms in addition to overgrowth of *R. textilis* and its indirect impacts on coral health should be investigated (McCook et al. 2001); chemical interactions may be influenced by ecological and environmental factors such as coral species (Bonaldo and Hay 2014) and water flow (Brown and Carpenter 2015; Jorissen et al. 2016).

This research revealed that *R. textilis* is capable of aggressive growth and competition regardless of its

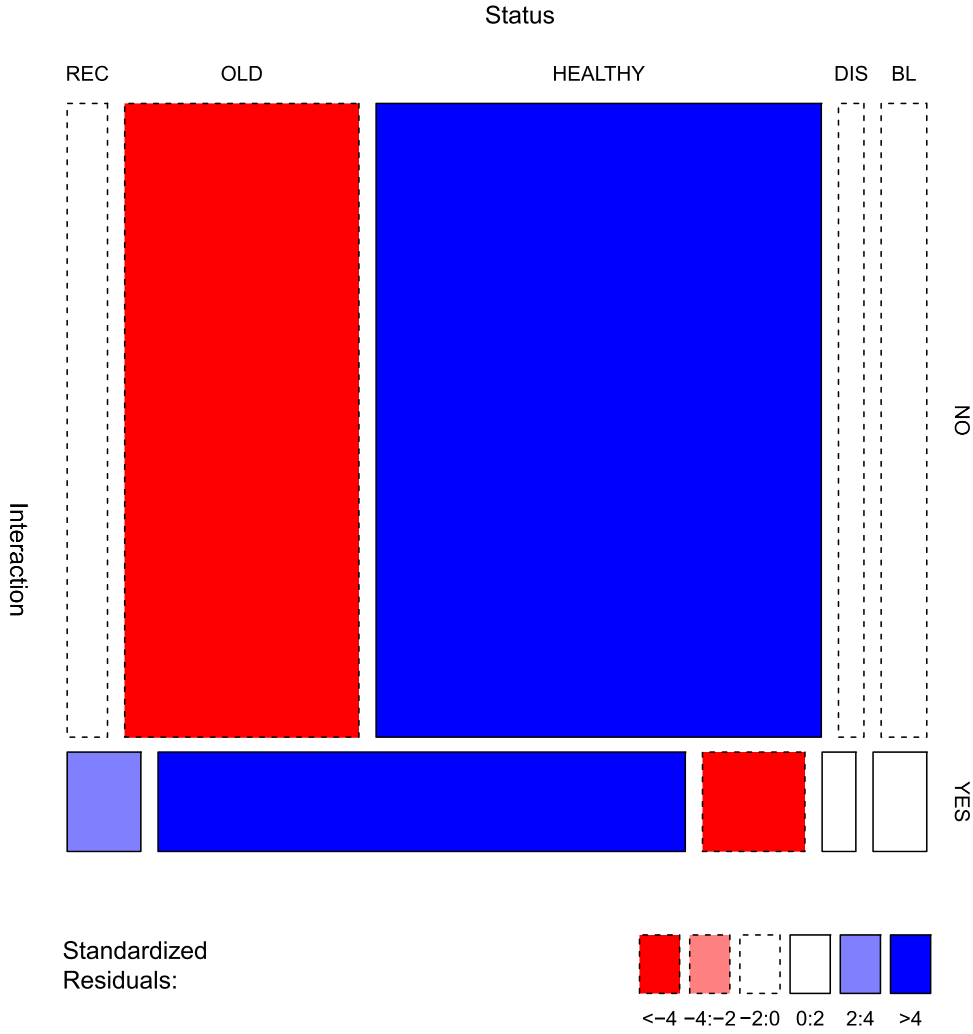

Fig. 5 Mosaic plot showing relationship between *Ramicrusta textilis* interaction (YES = interaction present, NO = interaction not present) and coral health status (BL = bleaching, DIS = disease, HEALTHY = no bleaching, disease or mortality observed, OLD = old coral mortality, REC = recent coral mortality). Blue color and solid outlines indicate frequency that is greater than expected, while red color and dashed outlines indicate frequency that is lower than expected. Color indicates significant result, and intensity of the color corresponds to magnitude of deviation from the expected frequency from Pearson Chi-square test of independence

abundance at a site. Some of the fastest average *R. textilis* growth was measured at PB despite the low average cover of the alga at this site (1.5%, Table 2). Furthermore, cases of extremely high interaction prevalence and moderate overgrowth rates co-occurred with very low cover of *R. textilis* at SW, suggesting that aggressive interaction and competition with corals occur even with a low abundance of the alga (< 1% average cover, Table 2). This could be a reflection of *R. textilis* recruitment preferences; it is possible that the alga establishes and/or grows more successfully near corals. Future studies could examine fine-scale spatial patterns of *R. textilis* occurrence and growth within coral reef patches to identify factors that may drive this pattern. Because *R. textilis* aggressively interacts with and overgrows corals regardless of its abundance, future research should also take care to focus on measurements in addition to percent coverage of the alga, such as growth rate and interaction prevalence.

This research has successfully expanded on the known physical characteristics of *Ramicrusta* in the USVI, confirming the presence of *R. textilis* in St. Thomas using DNA sequencing following its prior identification in St. John (Edmunds et al. 2019). Sequencing results indicate phenotypic differences in coloration (brown to red) and form (flat encrusting to flaky) may be attributed to external influences (e.g., light availability and water motion) rather than genetic variation at the species level, at least for the two plastid encoded markers that were sequenced. The depth range of *R. textilis* described in this research is 4.5–17.5 m, and average growth rates reached a maximum of + 0.04 mm d^{-1} and + 0.20 percent d^{-1} on *O. annularis* colonies. The maximum linear growth rate (+ 0.04 mm d^{-1}) was 50–67% slower than the average overgrowth rates reported by Eckrich and Engel (2013) (+ 0.06 to + 0.08 mm d^{-1}), which could indicate species-specific differences in the overgrowth rates of *R. textilis* (USVI) versus *R. bonairensis* (Bonaire). In making this comparison, it should be noted that the variability reported by Eckrich and Engel (2013) was greater than this study and sample sizes were smaller. Alternatively, these differences could be attributed to different study period lengths or simply reflect greater geographical variations in growth. As this was a 5-month study, seasonal variations in growth could influence competitive interactions and estimations of average growth rate (Renken et al. 2010).

While it still remains unknown whether the genus *Ramicrusta* is invasive to the Caribbean, a retrospective analysis of video surveys from the USVI revealed a low abundance of apparent *R. textilis* as early as 2003 (Smith et al. 2018), which precedes its original description by Pueschel and Saunders (2009). Considering that the alga was likely present in the Caribbean years before it was recognized and identified, *R. textilis* may be a cryptic native species that has only recently been documented due to its population expansion. Furthermore, a recent study reported *R. textilis* comprising up to 29% of the benthic cover and overgrowing living corals in the South China Sea (Nieder et al. 2019). This was the first report of the alga harming Pacific corals since the first description of the genus in 1981 (Zhang and Zhou 1981; Ballantine et al. 2016; Nieder et al. 2019). Because the species has similarly expanded and demonstrated harm to corals in a region where it is known to be native, it is possible that *R. textilis* is a competitive indigenous species that emerged in great abundance due to environmental change occurring over the last decade in the Caribbean and more recently in the Pacific.

A thorough understanding of coral interactions with *R. textilis* is imperative to recognizing the processes that currently shape benthic community structure on coral reefs and predicting future changes. Unchecked expansion of *R. textilis* across Caribbean reefs may exacerbate unfavorable coral community composition shifts from generalist taxa (e.g., *Orbicella* spp.) to stress-tolerant species (e.g., *Siderastrea* spp.), with potentially drastic reductions in coral species diversity due to the superior competitive abilities of the alga. These shifts could have far-reaching impacts on the basic ecological function of reefs and their ecosystem services. This underscores the importance of using informed management strategies to effectively mitigate *R. textilis* based on information about its ecology and physiology. It will also be important to evaluate the physiology of *R. textilis* under conditions that were not assessed in this research—particularly varying nutrients and temperature—and consider how the alga may respond to predicted environmental changes.

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Declarations

Conflict of interest statement On behalf of all authors, the corresponding author states that there is no conflict of interest.

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