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Three competitors in three dimensions: photogrammetry reveals rapid overgrowth of coral during multispecies competition with sponges and algae

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ABSTRACT: Competition for limited space is an important driver of benthic community structure on coral reefs. Studies of coral–algae and coral–sponge interactions often show competitive dominance of algae and sponges over corals, but little is known about the outcomes when these groups compete in a multispecies context. Multispecies competition is increasingly common on Caribbean coral reefs as environmental degradation drives loss of reef-building corals and proliferation of alternative organisms such as algae and sponges. New methods are needed to understand multispecies competition, whose outcomes can differ widely from pairwise competition and range from coexistence to exclusion. In this study, we used 3D photogrammetry and image analyses to compare pairwise and multispecies competition on reefs in the US Virgin Islands. Sponges (*Desmapsamma anchorata, Aplysina cauliformis*) and macroalgae (*Lobophora variegata*) were attached to coral (*Porites astreoides*) and arranged to simulate multispecies (coral–sponge–algae) and pairwise (coral–sponge, coral–algae) competition. Photogrammetric 3D models were produced to measure surface area change of coral and sponges, and photographs were analyzed to measure sponge–coral, algae–coral, and algae–sponge overgrowth. Coral lost more surface area and was overgrown more rapidly by the sponge *D. anchorata* in multispecies treatments, when the sponge was also in contact with algae. Algae contact may confer a competitive advantage to the sponge *D. anchorata,* but not to *A. cauliformis*, underscoring the species-specificity of these interactions. This first application of photogrammetry to study competition showed meaningful losses of living coral that, combined with significant overgrowths by competitors detected from image analyses, exposed a novel outcome of multispecies competition.

KEY WORDS: Photogrammetry · Competition · Corals · Sponges · Algae

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1. INTRODUCTION

Caribbean coral reefs have deteriorated in past decades, mainly due to diseases, thermal stress, and overfishing (Ginsburg 1994, Hughes 1994, Aronson et al. 2002). On the most degraded reefs, loss of reef-building corals is coupled with increasing abundances of alternative, non-reef building taxa including algae, sponges, gorgonians, zoanthids, and cyanobacteria (Maliao et al. 2008, Norström et al. 2009, Brocke et al. 2015, de Bakker et al. 2017). Compared to corals, these groups grow faster and colonize more rapidly,

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especially when space becomes newly available after coral die-offs and when top-down trophic control is reduced by overfishing (Loh et al. 2015, Chaves-Fonnegra et al. 2018, Ladd et al. 2019). Non-reef builders such as algae and sponges are often competitively superior to corals, and can overgrow corals using tactics such as shading, smothering, and allelopathy (Aerts & van Soest 1997, Morrow et al. 2011, Loh et al. 2015). Colonization of newly vacant space by these groups can therefore lead to heightened competition with surrounding corals and further changes to benthic communities, meaning their spread is not only a response to but also a cause of coral mortality (Norström et al. 2009). Competition over limited space is a prominent factor structuring benthic reef communities, and the ability of coral reefs to recover may depend on whether corals can contend with faster-growing and more competitive groups (Dayton 1971, Connell 1983, Sandin & McNamara 2012).

Multispecies competition (i.e. among 3 or more competitors) can lead to unexpected winners and losers, and outcomes can be unpredictable based on the winners and losers of species pairs. Therefore, while many studies have examined pairwise coral–algae and to a lesser extent coral–sponge competition (McCook et al. 2001, Chaves-Fonnegra & Zea 2011, Barott et al. 2012), little is known about the winners and losers when corals, sponges, and algae compete in a multispecies context. In one of the few reports on multispecies interactions among these groups, González-Rivero et al. (2016) showed that sponge–algae interactions between the alga *Lobophora variegata* and the excavating sponge *Cliona tenuis* prevented sponges from taking over bleached *Orbicella* spp. corals following thermal stress in Belize. The disproportionate competitive superiority of *L. variegata* was probably due to absence of herbivores and appeared to indirectly benefit corals by preventing takeover by the sponge (González-Rivero et al. 2016). Multispecies competition can also lead to competitive intransitivities or networks, as recently reported among the scleractinian coral *Acropora cervicornis*, the sponge *Aplysina fistularis*, and the gorgonian *Erythropodium caribaeorum* in reefs in the Florida Keys (Ladd et al. 2019). In this case, patterns of overgrowth suggested no clear dominant winner, much like the game of 'rock–paper–scissors', where each member wins against one competitor and loses against another (Allesina & Levine 2011). These competitive networks structure coral reef communities and play an important role in maintaining biodiversity (Buss & Jackson 1979, Karlson & Jackson 1981, Sebens 1987).

Another type of multispecies interaction is one where 3 or more competitors are in direct contact with one another, hereafter referred to as local multispecies competition. This type of competition is common among corals, sponges, and algae on Caribbean reefs. A 2016 survey of 6 reef sites off St. Thomas, US Virgin Islands, revealed that of the 1200 coral colonies recorded, almost a quarter (n = 273) were in contact with both algae and sponges, in contrast to only 6% (n = 74) in contact with sponge alone (Brandt et al. 2019). When 3 competitors are neighboring or overlapping, outcomes can be highly variable, depending on the orientation of competitors (e.g. Buss & Jackson 1979) and the influence of one competitor on the dominance order of the other 2 competitors (e.g. Hiscox et al. 2017). If competitors are able to reciprocally suppress combative abilities or cause reversals over time in the dominance order of their rivals, this can lead to intransitively mediated coexistence of all members (Laird & Schamp 2008). The dominance of one competitor could also be amplified by the presence of multiple rivals. For example, some wood-decay fungi gain more space when flanked by 2 competitors than when interacting with only 1 competitor (Hiscox et al. 2017). In this case, the centrally located fungus likely responded to multiple competitors by producing multiple allelochemicals that amplified its competitive superiority (Hiscox et al. 2017). Such local interactions have been studied in cryptic reef habitats (Buss & Jackson 1979) but have yet to be investigated on the exposed surfaces of the reef, despite deteriorating coral cover and the rise of new superior competitors and strategies for maintaining space on the reef (Ladd et al. 2019).

It is challenging to quantify the growth of sessile benthic organisms with complex or plastic morphologies. The convention is to measure individual size or benthic cover on a 2-dimensional (2D) plane, but such metrics fail to capture the complex 3-dimensional (3D) structure of irregularly shaped organisms (Wulff 2012, Burns et al. 2016). Alternative methods such as foil-wrapping and wax-dipping have been used to measure surface area of individuals, but these methods are laborious and destructive and preclude repetitive measurements (Veal et al. 2010). With 3D photogrammetry, photorealistic 3D models can be made from photographs of an object taken from multiple perspectives, and this technique has gained popularity for measuring reef structural complexity and benthic composition (Burns et al. 2016, Ferrari et al. 2016). Continued improvement of photogrammetry in recent years has enabled generation

of models on smaller scales, for example of individual corals and sponges (Ferrari et al. 2017, Olinger et al. 2019). However, we are not aware of any existing applications of photogrammetry to study competitive interactions among individual organisms on the reef benthos.

The objective of this study was to compare competitive outcomes (i.e. growth of each competitor) between local multispecies coral–sponge–algae competition and pairwise coral–algae and coral–sponge competition. Our approach comprised a field experiment, where sponges (*Desmapsamma anchorata* or *Aplysina cauliformis*) and algae (*Lobophora variegata*) were attached to individual colonies of the coral *Porites astreoides* and arranged to simulate both multispecies (coral–sponge–algae) and pairwise (coral–sponge and coral–algae) competition. We analyzed a time series of photographs to measure linear overgrowth of sponge on coral, algae on coral, and algae on sponge. These planar photographs do not fully capture the growth of sponges and reef-building corals, which may expand vertically (e.g. changing from plate- to dome-shaped) when being overgrown as a way to compensate for lost ground (López-Victoria et al. 2006). To capture both the upwards and outwards growth of sponges and coral, we also used photogrammetry to generate 3D models and measure their surface area percent change in each competitive interaction.

2. MATERIALS AND METHODS

2.1. Experimental design

Experiments were conducted at 2 fringing reefs south of St. Thomas, US Virgin Islands: Flat Key (10–17 m depth) and Perseverance Bay (7–8 m depth). Two sites were chosen so that sufficient coral colony replicates across a range of reef environments could be used for the experiment. Both sites have similar coral cover and abundant sponges and macroalgae, but differ in distance to shore and exposure. The reef off Perseverance Bay is nearshore (<0.25 km) to the main island of St. Thomas, and its southeast facing orientation exposes it to strong winds and wave action. Flat Key is an uninhabited rock 3 km to the south of St. Thomas, and the reef on its northern edge is protected from the winds and waves that affect Perseverance Bay (Sabine et al. 2015).

Experiments were conducted using the coral *Porites astreoides*, the sponges *Desmapsamma anchorata* and *Aplysina cauliformis*, and the brown alga *Lobophora variegata*. We chose *P. astreoides* because this species is increasing in abundance and represents the main reef-building coral on many contemporary Caribbean reefs (Green et al. 2008). The 3 non-reef builders (sponges *D. anchorata* and *A. cauliformis*, and the alga *L. variegata*) were chosen because they are abundant and commonly observed overgrowing coral (Aerts & van Soest 1997, Jompa & McCook 2002, Easson et al. 2014). The encrusting sponge *D. anchorata* grows rapidly and produces allelopathic chemicals with antibacterial and larvicidal properties (Carballeira & Maldonado 1988, Osinga et al. 1999, McLean & Yoshioka 2008). The purple rope sponge *A. cauliformis* is structurally sturdy and unpalatable to spongivore predators (Pawlik et al. 2013, Loh & Pawlik 2014). The brown alga *L. variegata* has a leathery and tough morphology capable of shading and abrading coral tissue and also produces antibacterial compounds (Jompa & McCook 2002, Morrow et al. 2011).

In August 2016, 20 colonies of *P. astreoides* (mean diameter = 18 ± 8 cm SD, separated from one another by at least 5 m) were identified and mapped at each reef site. Fragments of the sponges *D. anchorata* and *A. cauliformis* were trimmed to a length equal to half of the perimeter of 1 coral colony, and then attached with nails to the perimeters of 10 colonies apiece. Fronds of the alga *L. variegata* were then attached with monofilament to the perimeters of all coral colonies and arranged to ensure that half of the perimeter was covered. On each coral colony, sponges and algae were oriented to create 4 treatments, where each quarter of the coral perimeter was covered with (1) sponge and algae (coral–sponge–algae, CSA), (2) only sponge (coral–sponge, CS), (3) only algae (coral–algae, CA), or (4) neither (coral only, C; Fig. 1). Each month, all colonies were photographed and organisms within a 10 cm perimeter were cleared from around the colony, including from the C (coral-only) treatment, whose purpose was to gauge the ability of coral to grow or hold captured space in the absence of direct competitors, either naturally occurring (e.g. turf algae, *Dictyota* spp.) or experimentally-added sponge and algae.

In September 2016, swells from Hurricane Matthew resulted in the loss of 6 experimental colonies, including 4 from Perseverance Bay (leaving 7 colonies with *A. cauliformis* and 9 colonies with *D. anchorata*), and 2 from Flat Key (leaving 8 with *A. cauliformis* and 10 with *D. anchorata*). The September hurricane also removed all *L. variegata*, and *L. variegata* was replaced in November 2016 by reapplying to the

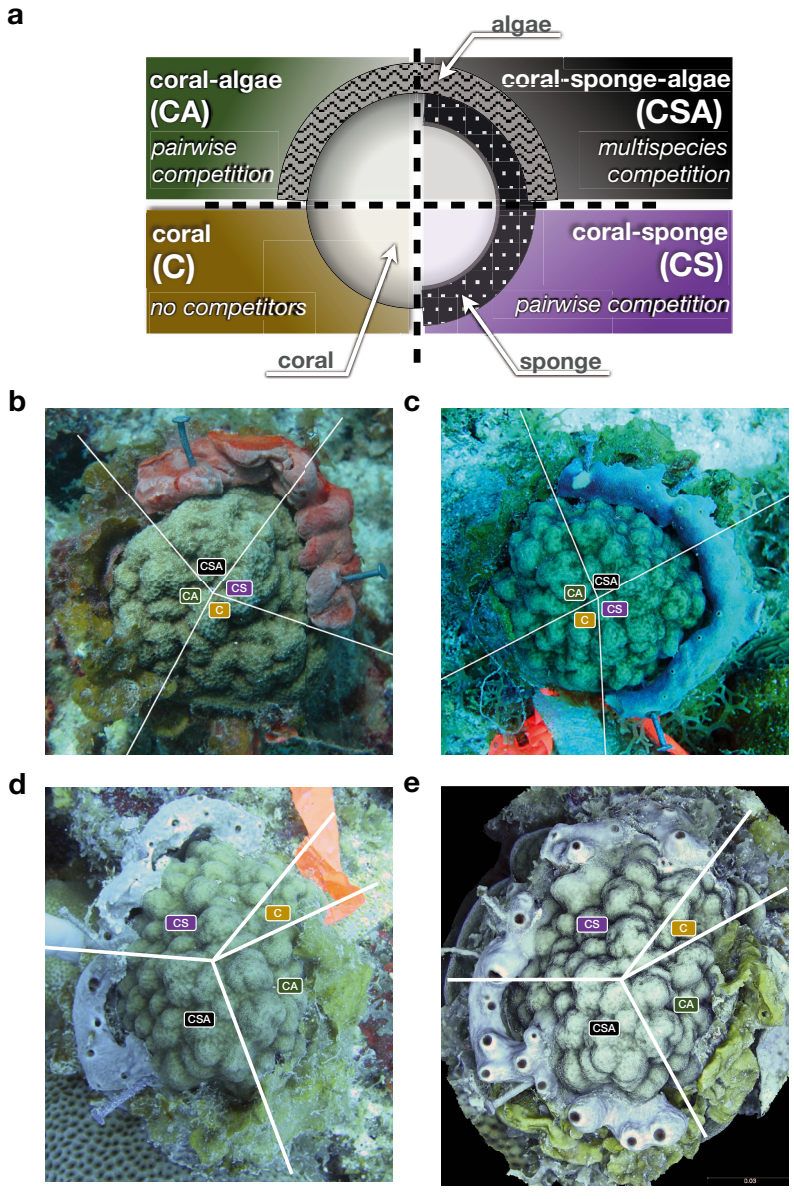

Fig. 1. Experimental colonies, showing orientation of competitors and 4 treatments from top-down perspective. (a) Schematic diagram of an experimental colony; photographs of characteristic colonies with both sponge species (b) *Desmapsamma anchorata* and (c) *Aplysina cauliformis* taken at the beginning of the experiment; (d) photograph from November 2016; and (e) 3D model from March 2017 of the same colony showing growth of *D. anchorata*

same half-perimeter of all remaining colonies. Data collection began in November 2016 after re-applying *L. variegata*, giving sponges ample time to heal in the 3 mo following the experimental setup in August when sponges were cut and affixed to coral colonies. A recent experiment observed healing within 1 mo for the slower-growing sponge species *A. cauliformis* (Brandt et al. 2019). For a detailed summary and timeline of the experiment, see Fig. 2.

2.2. Image analysis

Linear overgrowths of sponge on coral, algae on coral, and algae on sponge were measured from planar (top-down) photographs taken in November 2016 and January 2017 (duration: 62 d; Fig. 2), using the image analysis software ImageJ (Abràmoff et al. 2004). Prior to measurements, images were scaled according to a scale bar (a ruler) photographed along with the colony. To check that colony photographs from different timepoints were taken at similar angles, the distance between 2 distinct corallites was compared across photographs from each timepoint, ensuring a deviation of <3 mm. A distinct, centrally located corallite that was visible in the photographs from both timepoints was then used as the central point from which to draw all radiating lines to the competitors (sponge or algae) in each treatment. Care was taken to ensure lines were drawn at the same angle with respect to the coral colony at each timepoint, and then their lengths were measured. The length of line from the first timepoint was subtracted from that of the second timepoint to represent the lateral growth or retreat of the competitor during that time period. Sponge overgrowth of coral was measured in CSA and CS treatments, to compare multispecies and pairwise competition, respectively. Algae overgrowth of sponge was measured in CSA treatments, and algae overgrowth of coral was measured in CA treatments, in order to compare algae overgrowth of different competitors. We did not measure growth of coral from image analyses due to the many instances where coral perimeters were either obstructed by overgrowing competitors (in CSA, CS, and CA treatments), or not visible in the C treatments because of the mounded shape of most colonies. Coral growth was instead measured using photogrammetry as described below.

Eight colonies were omitted from the image analysis due to missing photographs at either timepoint. Analyses were conducted on the remaining 26 col-

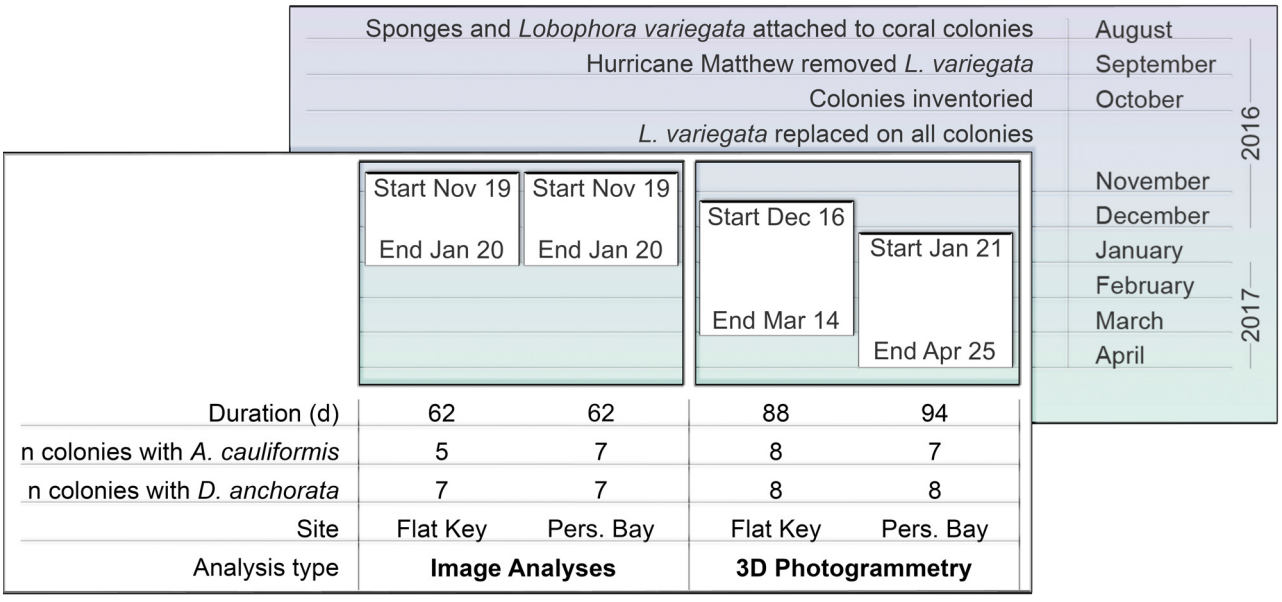

Fig. 2. Timeline and summary of experiments at Flat Key and Perseverance Bay, from setup to beginning of data collection in November. Boxes with dates denote the duration between sets of photographs from which measurements were derived for each analysis type and site. Also shown are the durations in days represented by those boxes and number of colony replicates with either sponge species (*Aplysina cauliformis* or *Desmapsamma anchorata*) included in the analyses

onies (n = 5 with *A. cauliformis* at Flat Key, n = 7 with *A. cauliformis* at Perseverance Bay, n = 7 with *D. anchorata* at Flat Key, n = 7 with *D. anchorata* at Perseverance Bay; Fig. 2).

For colonies for which all measurements were taken for each combination of competitor and treatment, the overall winner in each treatment quadrant was determined by applying the following rules. For pairwise CS and CA treatments, algae or sponge won when their overgrowth of coral was >0, and coral won when overgrowth was <0. For multispecies CSA treatments, algae won when algae overgrowth of sponge was >0 and greater than sponge overgrowth of coral, sponge won when sponge overgrowth of coral was >0 and greater than algae overgrowth of sponge, and coral won when both algae and sponge overgrowth were ≤0. Of the 26 colonies included in the image analyses, 3 were omitted due to at least 1 missing measurement of any combination of competitor and treatment, and this assessment of winners and losers was conducted on the remaining 23 colonies (n = 12 with *A. cauliformis*, n = 11 with *D. anchorata*).

2.3. Photogrammetry field methods

The change in surface area of sponge and coral competitors was measured from 3D models produced using photogrammetry. Photographs for 3D models were taken at Flat Key in December 2016 and March 2017 and Perseverance Bay in January 2017 and April 2017 (duration 91 ± 3 d; Fig. 2). Before photographing a colony, scale bars (2 each of either a ruler, dive knife, or metal disk or tag, all with length >4 cm) were placed nearby, and all flagging tape and fleshy algae in the immediate area (within ~0.5 m) was secured or removed. Divers used digital cameras to capture 50–60 photographs while completing 2 rotations and holding the camera at a distance of ~20 cm from the colony. The camera models used were Canon PowerShot G1 X Mark II (12.5 mm focal length, 4352 × 2904 resolution) and Canon PowerShot G12 (6.1 mm focal length, 3648 × 2432 resolution), in underwater housings set to standard point-and-shoot mode with flash disabled, and images were captured in .jpg format. During each rotation, divers took photographs at a rotation interval of no more than 20° to ensure sufficient overlap between images. On the first rotation, divers held the camera close to the bottom, pointing the lens perpendicular to the substrate, and took 30–40 photographs of the sides of the colony. On the second rotation, divers held the camera at a greater height off the bottom (20 cm to 1 m), angled the camera lens downward (~30°) and took 20–30 photographs of the top and sides of the colony. The resulting sets of photographs comprised images from every conceivable angle with large degree of overlap on a subject with strong camera geometry, to limit er-

ror in any dimension and optimize calibration. Three colonies were omitted from analyses of surface area percent change due to missing photograph sets at either timepoint. Analyses were conducted on the remaining 31 colonies (n = 8 with *A. cauliformis* at Flat Key, n = 7 with *A. cauliformis* at Perseverance Bay, n = 8 with *D. anchorata* at Flat Key, n = 8 with *D. anchorata* at Perseverance Bay); Fig. 2.

2.4. Photogrammetry processing

The software Agisoft PhotoScan Professional (v1.4.0) was used to make 3D models. The following is a brief description of the photogrammetry workflow in PhotoScan, which otherwise followed the methods in Olinger et al. (2019). First, photographs were aligned (high accuracy, pair preselection disabled, key point limit 40 000, tie point limit 10 000), and a sparse point cloud of tie-points was generated. 'Gradual selection' and 'optimize cameras' tools were then used to eliminate poor quality points and refine camera calibration parameters, respectively (Olinger et al. 2019). Final sparse point clouds had an average of 60 000 points. Next, a dense point cloud with an average of 5 million points was produced (high quality, depth filtering disabled). The dense clouds were visually inspected, and the 'manual selection' tool was used to select and remove extraneous points. A textured mesh with an average of 1 million faces was built using the dense cloud source data (mesh parameters: surface type arbitrary, face count high; texture parameters: mapping mode generic, blending mode average). The model was then scaled by placing 2 markers on either side of the object used as a scale bar, making a new scale bar in PhotoScan, and entering the known length of that object in the digital model. Two more markers were placed on the second scale bar, and this process was repeated in order to calculate error. The scale error was automatically calculated in PhotoScan from the 2 scale bars positioned in various oblique angles along *x*-, *y*-, and *z*-axes, and the average scale error (±SD) was 0.21 ± 0.16 mm. The average ground resolution (i.e. distance between pixels) was 0.09 ± 0.03 mm pixel^{-1}. The average time to process each 3D model was 2 h (macOS, 2.9 GHz Intel Core i7 processor, 16 GB RAM).

The textured mesh was exported out of PhotoScan, and into Autodesk Meshmixer (v3.4.35) and CloudCompare (v2.8.1) for further processing. First, the 'inspector' tool in Meshmixer was used to examine the mesh and repair or remove manifold edges, small holes, and extraneous mesh pieces that were artifacts of the reconstruction process. Manual selection was then used to trace the border around each competitor and extract the sponge and coral surface from the 3D mesh, and isolated competitors were saved as independent objects that preserved their original location with respect to the rest of the 3D model. For a single colony, the component pieces for the models generated at both timepoints were then imported into CloudCompare. The model from the first timepoint (made of its component coral and sponge pieces) was inspected in relation to the model from the second timepoint, and distinct coral polyps were used as reference points to manually, roughly align the models using the 'transform' tool. The 'fine register' tool in CloudCompare was then used to finely align the model from the second timepoint to the model in the first timepoint (fixed scale, theoretical overlap 50%). At this point, model alignment was checked to ensure that distinct corallites were overlapping in models from different timepoints, and this was the final check for any issues with scale. The 'split' tool in CloudCompare was then used to uniformly slice the models into the 4 treatment quadrants. The split was applied simultaneously to models from both timepoints and their component coral and sponge 3D objects, resulting in uniform separation of treatment quadrants across timepoints and individual competitors. The surface area of each competitor in each treatment quadrant at each timepoint was recorded using the 'measure mesh' tool in CloudCompare. This workflow from raw images to measurements in CloudCompare is summarized in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m657p109_supp.pdf. The percentage change in surface area of coral or sponge segments in each treatment quadrant was calculated by dividing the change in surface area by the initial surface area. Precision of the photogrammetric process was high, and measurements of coral surface area varied negligibly across meshes reconstructed from 10 photograph sets of the same coral colony (coefficient of variation = 1%).

2.5. Statistical analysis

Linear mixed effects models were used for all statistical analyses. Four sets of models were made for the 4 measured response variables: (1) overgrowth by sponge from image analyses, (2) overgrowth by algae from image analyses, (3) surface area percent change of sponge from photogrammetry, and (4) surface area percent change of coral from photogram-

metry. All models included nested random effects of site and colony. The fixed effects for overgrowth by sponges were treatment (CSA, CS), sponge species (*A. cauliformis, D. anchorata*), and the interaction between treatment and sponge species. The fixed effect for overgrowth by algae was the competitor it was overgrowing (*A. cauliformis*, *D. anchorata*, and *P. astreoides*). The fixed effects for sponge surface area percent change were treatment, sponge species, and the interaction between treatment and sponge species. The fixed effects for coral surface area percent change were treatment (CSA, CS, CA, C), sponge species, and the interaction between treatment and sponge species. Prior to analyses, we examined residual and Q–Q plots to confirm assumptions of homoscedasticity and normality. From this, we determined that assumptions were met for untransformed values of 3 response variables (sponge overgrowth, sponge surface area percent change, and coral surface area percent change) and for cube-root transformed values of algae overgrowth, the fourth response variable. The significance of each fixed effect (main effect or interaction) was evaluated using likelihood ratio tests of the model with the effect in question against the model without the effect in question. Significance within main effects and interactions was then determined from final mixed effects models containing all significant main effects and interactions through multiple contrasts from least square means (lsmeans). All statistical analyses were performed in R (v3.3.2; R Core Team 2016) using the packages 'lme4' (Bates et al. 2015) and 'lsmeans' (Lenth 2016).

3. RESULTS

The assessment of winners and losers in each combination of competitors revealed that outcomes of multispecies competition varied from those of pairwise competition and between colonies with *Aplysina cauliformis* and *Desmapsamma anchorata* (Fig. 3). In pairwise CS treatments, coral won most interactions when competing against *A. cauliformis* (n = 9 out of 12; 75%) and about half of the interactions against *D. anchorata* (n = 6 out of 11; 55%). However, in multispecies CSA treatments on colonies with *D. anchorata*, the sponge won 10 out of 11 interactions (~90%). These outcomes differed from CSA treatments on colonies with *A. cauliformis,* which showed approximately equal wins of algae and coral, but only a single win by *A. cauliformis* (Fig. 3).

Sponge overgrowth of coral differed significantly across treatments (χ^2_1 = 9.2, p = 0.003) and sponge species (χ^2_1 = 6.1, p = 0.013), and there was an interaction (χ^2_1 = 20.8, p < 0.001; Table 1). Overgrowth by *D. anchorata* in CSA treatments was significantly greater than in CS treatments (p = 0.001), and significantly greater than overgrowth by *A. cauliformis* in both CSA and CS treatments (p = 0.01 and 0.003, respectively; Fig. 4a). Algae overgrowth also differed significantly across the competitors it was overgrowing (χ^2_2 = 15.2, p = 0.001; Table 1), and algae overgrowth of *Porites astreoides* was significantly greater than overgrowth of *D. anchorata* (p = 0.001; Fig. 4b).

The change in sponge surface area was highly variable, ranging from (mean ± SE) −11.9 ± 9.7% for *A. cauliformis* to 20 ± 13.2% for *D. anchorata,* with both extremes occurring in CSA treatments. Sponge surface area change was not significantly different across treatments or sponge species, and there was no interaction (Table 1, Fig. 5a). In general, coral surface area change was negative, with the greatest loss (35.06 ± 8.0%) occurring in CSA treatments on colonies competing with *D. anchorata*. The greatest gain in coral surface area (7.06 ± 7.5%) occurred in C treatments on colonies competing with *A. cauliformis*. Coral surface area percent change differed significantly across treatments (χ^2_3 = 14.0, p = 0.003; Table 1), and there was a significant interaction between treatment and sponge species (χ^2_7 = 21.6, p = 0.003; Table 1). Post hoc tests revealed that coral lost significantly more surface area in CSA treatments on

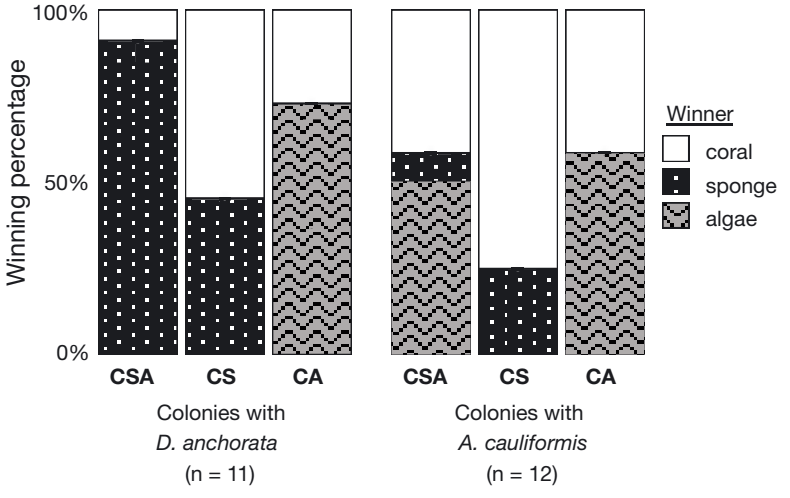

Fig. 3. Winning percentages for each competitor in each treatment (CSA: coral–sponge–algae; CS: coral–sponge; CA: coral–algae). Sponge species are *Desmapsamma anchorata* and *Aplysina cauliformis*

Table 1. Results from likelihood ratio tests for each response variable. Null models included only nested random effects of site and colony, given in R-specific notation (1|Site/Colony). The effect of interest in each model is shown in **bold**, and this effect was determined to be significant at $p < 0.05$. AIC: Akaike's information criterion; BIC: Bayesian information criterion

Response variable	Explanatory variables	df	AIC	BIC	logLik	Deviance	χ^2	χ^2 df	p
Overgrowth by sponge	(1|Site/Colony)	4	106.5	114.3	−49.2	98.5			
	Treatment + (1|Site/Colony)	5	99.3	109.1	−44.7	89.3	9.2	1	0.0025
	Sponge + (1|Site/Colony)	5	102.4	112.1	−46.2	92.4	6.1	1	0.0134
	Treatment×Sponge + (1|Site/Colony)	7	91.6	105.3	−38.8	77.6	20.8	3	0.0001
Overgrowth by algae	(1|Site/Colony)	4	53.8	61.1	−22.9	45.8			
	Competitor + (1|Site/Colony)	6	42.6	53.5	−15.3	30.6	15.2	2	0.0005
Sponge surface area percent change	(1|Site/Colony)	4	654.3	662.9	−323.2	646.3			
	Treatment + (1|Site/Colony)	5	655.9	666.6	−323.0	645.9	0.4	1	0.5201
	Sponge + (1|Site/Colony)	5	656.2	666.8	−323.1	646.2	0.1	1	0.7008
	Treatment×Sponge + (1|Site/Colony)	7	653.5	668.4	−319.8	639.5	6.8	3	0.0772
Coral surface area percent change	(1|Site/Colony)	4	1106.8	1117.8	−549.4	1098.8			
	Treatment + (1|Site/Colony)	7	1098.8	1118.1	−542.4	1084.8	14.0	3	0.0029
	Sponge + (1|Site/Colony)	5	1105.3	1119.1	−547.7	1095.3	3.5	1	0.0620
	Treatment×Sponge + (1|Site/Colony)	11	1099.2	1129.6	−538.6	1077.2	21.6	7	0.0030

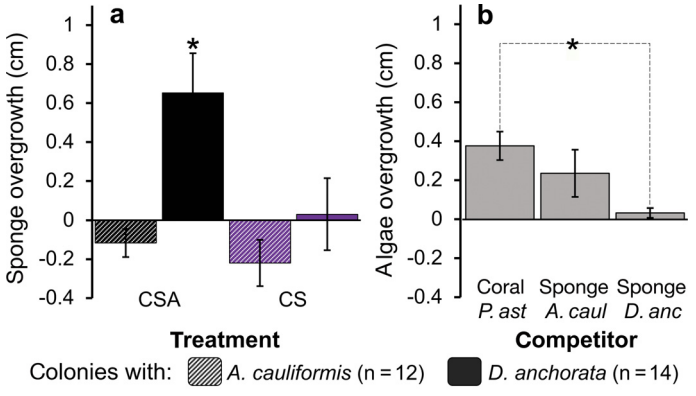

Fig. 4. Sponge and algae overgrowth measurements from image analyses. Error bars show standard errors, and asterisks denote significant differences from multiple comparisons. Colors represent the treatments specified in Fig. 1a. (a) Sponge overgrowth of coral during multispecies (coral–sponge–algae, CSA) and pairwise (coral–sponge, CS) competition. Negative values represent retreat by the sponge. (b) Algae overgrowth of competitors (coral *Porites astreoides*; sponges *Aplysina cauliformis* and *Desmapsamma anchorata*)

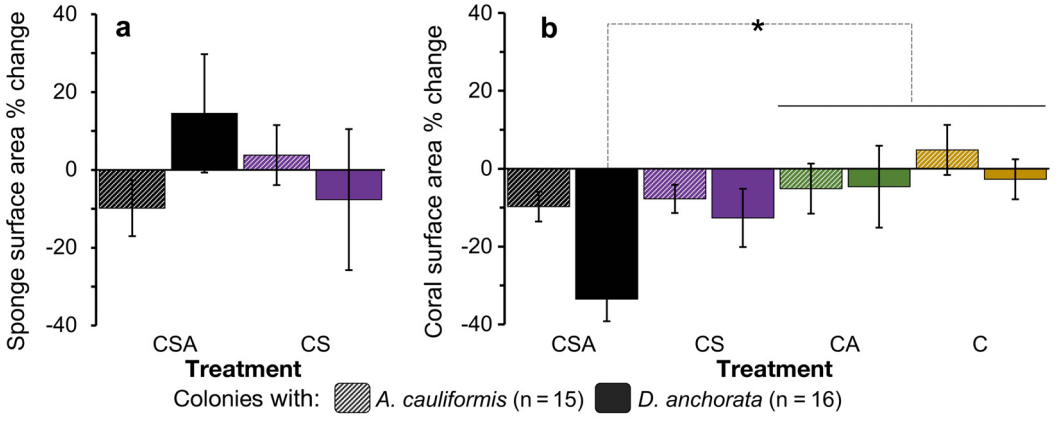

Fig. 5. Sponge (*Desmapsamma anchorata* and *Aplysina cauliformis*) and coral surface area percent change from 3D models. Error bars show standard errors, and asterisks denote significant differences from multiple comparisons. Colors represent the treatments specified in Fig. 1a. (a) Sponge surface area percent change during multispecies (coral–sponge–algae, CSA) and pairwise (coral–sponge, CS) competition. (b) Coral surface area percent change in all treatments (CA: coral–algae; C: coral only)

colonies with *D. anchorata*, compared to CA treatments on colonies with *D. anchorata* and *A. cauliformis* ($p = 0.024$ and 0.044, respectively) and C treatments on colonies with *D. anchorata* and *A. cauliformis* ($p = 0.031$ and 0.001, respectively; Fig. 5b). For tables and plots of coefficients from all mixed effects models, see Table S1 and Fig. S2.

4. DISCUSSION

Multispecies interactions are abundant on coral reefs, and studies of plants, phytoplankton, and wood fungi have shown that pairwise interactions are not reliable predictors of the outcomes of multispecies competition (Huisman & Weissing 2001, Weigelt et al. 2007, Hiscox et al. 2017). Our results are consistent with previous findings that competitive outcomes are distinct between multispecies and pairwise interactions. In the multispecies CSA treatment, *Porites astreoides* lost more surface area and was overgrown more rapidly by the sponge *Desmapsamma anchorata,* when the sponge was also in contact with the alga *Lobophora variegata*. This outcome is unexpected given the seemingly heightened competitive pressure faced by *D. anchorata* due to contact with algae in multispecies treatments. It is possible that contact with the alga conferred a competitive advantage to *D. anchorata* and improved the ability of the sponge to overgrow coral. If true, this algae–sponge facilitation appears to be species specific, as we did not find evidence of it on experimental colonies with the sponge *Aplysina cauliformis.*

D. anchorata was competitively superior to *P. astreoides* in multispecies treatments, but the ranking of these 2 species was unclear in pairwise CS treatments. For sessile reef fauna, not all species pairs have clear dominant and inferior competitors, and many species show reversals in which one overgrows the other (Buss & Jackson 1979). This definition of dominance, predicated on overgrowth, is not ideal when one species cannot overgrow another, such as the sponge (vs. algae) and coral (vs. sponge and algae) in our experiment. We therefore expand the definition of competitive dominance to include resistance to overgrowth of a competitor's pre-empted space. By this definition, our results show conflicting evidence for both inferiority and superiority of *D. anchorata* during pairwise competition with *P. astreoides*, with interesting implications in either case. We found that *D. anchorata* lost the majority of interactions, according to negligible overgrowth of *P. astreoides* in pairwise CS treatments. Such inferiority of *D. anchorata* suggests a competitive intransitivity among members engaged in pairwise competition, with *P. astreoides* > *D. anchorata* and *D. anchorata* > *L. variegata* through resistance to overgrowth, and *L. variegata* > *P. astreoides* through overgrowth. However, we also report substantial loss of coral surface area in pairwise CS treatments, suggesting competitive superiority of *D. anchorata* that is consistent with previous reports (Aerts & van Soest 1997) and indicative of a competitive hierarchy among members engaged in pairwise competition (*D. anchorata* > *L. variegata* > *P. astreoides*). Overall, the difference between pairwise and multispecies interactions involves either reversal or amplification of the rank order, resulting in an asymmetrical hierarchy with *D. anchorata* >> *P. astreoides* and *D. anchorata* > *L. variegata*, likely driven by coral overgrowth by *D. anchorata* that was either initiated or intensified by contact with *L. variegata.*

There are many possible mechanisms by which algae–sponge contact may have increased *D. anchorata* overgrowth of coral. One possibility is an exchange of nutrients and food resources. Nitrogenous waste produced by sponges can be an important source of nutrition for algae (Southwell et al. 2008). For example, nitrogen (N) supplied by sponges *Haliclona cymiforis* and *A. cauliformis* promoted growth and chlorophyll *a* production in the algae *Ceratodictyon spongiosum* and *Microdictyon marinum*, respectively (Davy et al. 2002, Easson et al. 2014). In exchange for sponge-derived N, algae may provide sponges with food in the form of dissolved organic carbon (DOC) photosynthate, a preferable food source for sponges (Rix et al. 2017). Contact-mediated exchanges of organic carbon and nitrogen between sponges and other autotrophs have been documented previously, for example between the red mangrove *Rhizophora mangle* and root-fouling sponges *Tedania ignis* and *H. implexiformis* (Ellison et al. 1996). Production of DOC by *L. variegata* (Haas et al. 2010) and consumption by *D. anchorata* (van Duyl et al. 2011) could alter the growth form of *D. anchorata.* For example, a readily available food source could liberate the sponge from needing to expend energy growing upwards for food capture, and the sponge could reallocate this energy towards lateral growth and improved basal stability.

L. variegata may also provide structural support to *D. anchorata*, and this is plausible considering the structural frailty of *D. anchorata* and rigidity of *L. variegata* (De Ruyter van Steveninck et al. 1988, Wulff 2012). Similar exchanges likely drive other sponge–alga associations: the rhodophyte *C. spon-*

giosum may provide skeletal reinforcement to its sponge associate *H. cymiforis* in exchange for sponge-derived nutrients (Davy et al. 2002). Other rhodophytes of the genus *Jania* (*J. adherens, J. capillacea*) are incorporated into and provide structural support to the sponges *Dysidea janiae* and *Strongylacidon griseum* (Rützler 1990). In what is likely a means of overcoming severe structural weakness, *D. anchorata* is commonly observed growing entangled around other sponges, octocorals, and hydrozoans (Calcinai et al. 2004, Wulff 2008, Mclean et al. 2015). If the physical structure of *D. anchorata* is reinforced by *L. variegata*, this could modify how the sponge grows, for example by allowing the sponge to divert energy from reinforcing its skeleton and towards competitive overgrowth of coral.

On healthy reefs, the growth of sponges and algae is controlled by a number of top-down and bottom-up factors, and human activities near many Caribbean reefs are interfering with these important controls, to the detriment of reef-building corals. This experiment was conducted on 2 overfished reefs that now support very low abundances of angelfish, parrotfish, and other spongivore and herbivore predators (Smith et al. 2015). Corals at these overfished sites likely face heightened competitive pressure from palatable sponges such as *D. anchorata* that at one time were kept to a minimum by sponge-eating fishes (Loh & Pawlik 2014), and algae such as *L. variegata* known to be strongly controlled by herbivore grazing (Carpenter 1986, Ferrari et al. 2012b). Had this experiment been carried out on reefs with abundant and diverse populations of fish predators able to graze *D. anchorata* and *L. variegata*, we may not have observed this novel outcome of multispecies competition. Both sites are also similarly impacted by terrestrial runoff, and accumulations of organic and carbonate sediment (Sabine et al. 2015), and such nutrient inputs are known to stimulate growth and amplify competitive dominance of algae and sponges over coral (Zea 1993). Seasonality can also influence competitive outcomes among these 3 groups, given the sensitivity of many benthic organisms to seasonal variations in water temperatures, sunlight, rainfall, and wind speed and direction (Duckworth & Battershill 2001, Chadwick & Morrow 2011, Ferrari et al. 2012b).

Coral overgrowth by the sponge was amplified only on colonies competing with *L. variegata* and *D. anchorata*, while coral overgrowth by the sponge *A. cauliformis* was negligible across treatments, regardless of contact with algae. The simplest explanation for this is that *A. cauliformis* grows much slower than *D. anchorata*, which may have prevented detection of *A. cauliformis* growth in the 2–3 mo experimental period. Another explanation is morphological differences between the 2 species. Sponge morphology governs the degree of spatial competition it can accommodate, and encrusting *D. anchorata* may be better equipped for spatial competition than the upright, rope-like *A. cauliformis* (Engel & Pawlik 2000). The allelochemicals produced by the 2 sponge species are also variable and may have affected competitive outcomes. A number of secondary metabolites have been extracted from *D. anchorata* with antibacterial and larvicidal properties that may be used for spatial competition (Carballeira & Maldonado 1988, Osinga et al. 1999, McLean & Yoshioka 2008). Conversely, the secondary metabolites produced by *A. cauliformis* may be more effective at deterring sponge predators than overgrowing competitors (Pawlik et al. 2013, Easson et al. 2014). Differences between *D. anchorata* and *A. cauliformis* may also explain why this algae-facilitated overgrowth only occurred in association with *D. anchorata*. For example, if *D. anchorata* benefitted from algae-derived food or structural support, *A. cauliformis* may not have derived the same benefit because of its sturdier structure and ability to gain energy from photosynthetic endosymbionts (Easson et al. 2014).

The species-specificity and context-dependence of competitive outcomes underscore the challenges inherent to experiments of multispecies competition where results can be variable and subject to even the slightest difference in starting conditions (Hiscox et al. 2017). The experimental design with 4 treatments on 1 colony was used to ensure uniform starting conditions and minimize the influence of external factors across treatment levels. There are limitations to this design, however, including the potential influence of surrounding treatment conditions and colony that had to be accounted for in the statistical analyses. Spatial orientation of competitors can also influence competitive outcomes (Buss & Jackson 1979), and our experiment examined only 1 combination of competitor positions during multispecies competition. It is therefore possible that other spatial orientations of *D. anchorata*, *L. variegata*, and *P. astreoides* could result in coral coexistence or other outcomes that differed from those observed herein. The duration of this experiment was fairly short, encompassing growth measurements collected in intervals of 2–3 mo, which is a brief period compared to some studies (e.g. 6 mo; Leong & Pawlik 2010), though still longer than oth-

ers (e.g. 16 d; River & Edmunds 2001). A final limitation of this experiment is the small sample size owing to logistical restraints and unintended loss of colonies before the start of data collection.

Despite the foregoing limitations, this study demonstrates the benefit of measuring change in coral surface area and lateral growth of overgrowing competitors using photogrammetric 3D models and traditional image analyses, respectively. In multispecies CSA treatments, the significant decrease in surface area of living coral tissue from 3D models corresponded to significantly greater overgrowth rates of *D. anchorata* measured from image analyses. Corals were the 'losers' in this interaction, with no indication that coral colonies compensated for lost ground, for example by growing upwards (López-Victoria et al. 2006). Interestingly, significant differences were reported for sponge overgrowth of coral but not sponge surface area change, probably because of high variability in measurements of the latter. *D. anchorata* overgrowth of coral was reduced in pairwise compared to multispecies treatments, but the sponge generally increased in height irrespective of competitive treatment and often formed characteristic branches that are known to be vulnerable to fragmentation (Wulff 2008). The larger base formed by greater overgrowth in multispecies treatments may reduce the risk of fragmentation and bolster the competitive advantage of *D. anchorata* over the coral that it is overgrowing. These differences between measurements of overgrowth and surface area highlight the value of measuring both using a combination of image analyses and photogrammetry. As 3D models become increasingly photorealistic, they can also be used for lateral measurements, with some advantages over analyses of single photographs, including the ability to collect measurements from several angles (e.g. planar and perpendicular to reef surface) and align viewports to ensure measurements are taken from the same angle. The investment of time needed to make 3D models may be justified considering the options to measure both lateral growth and surface area change of separate model components, using the novel workflow presented herein, without interrupting the subject being measured, making this an ideal process for time-series measurements.

The competitive inferiority of *P. astreoides* across all competitive treatments is consistent with other observations that species of *Porites* are poor competitors (Ladd et al. 2019), with competitive ability that diminishes with decreasing colony size (Ferrari et al. 2012a). Instead of competitive ability, the life history of small, 'weedy' *Porites* and *Siderastrea* favors tolerance to environmental stress, which is probably why these groups are now the dominant reef-builders on many Caribbean reefs (Green et al. 2008). On these same reefs, proliferation of alternative organisms (e.g. algae, sponges, zoanthids, gorgonians) will lead to more frequent interactions with weaker coral species (Ladd et al. 2019). For *Porites* spp., there may be a limit to tolerable competitive pressure, which when exceeded would negate any benefit of being tolerant to repetitive and severe disease, bleaching, and storm events. The algae–sponge facilitation proposed in this study may exacerbate the negative effect of competition. This facilitation may also act as a positive feedback favoring phase shifts from coral- to algae- or sponge-dominated reefs; for example, an increase in algae could lead to more algae–sponge interactions, more rapid sponge–coral overgrowth, further loss of coral cover, and subsequent algae colonization. Algae such as *L. variegata* are good colonizers and able to impair coral growth, but *L. variegata* does not overgrow coral as quickly as sponges such as *D. anchorata*, which are slower colonizers but can cause rapid coral mortality through overgrowth (Aerts & van Soest 1997, Lirman 2001, Nugues et al. 2004, Mumby et al. 2005, Box & Mumby 2007). This association of an efficient colonizer and rapid overgrower could add to the challenges faced by corals that remain on Caribbean reefs, especially if similar associations exist among other species of sponges and algae. Though only one of the myriad possible outcomes of multispecies competition, this proposed algae–sponge facilitation represents a previously unknown type of interaction that may be playing a role in ongoing restructuring of coral reef benthic communities.

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