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Evidence of biological self-organization in spatial patterns of a common tropical alga

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Running head: Polygonal patterns of tropical algae

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Abstract

Tropical reef communities contain spatial patterns at multiple scales, observable from microscope and satellite alike. Many of the smaller-scale patterns are generated physiologically (e.g., skeletal structures of corals at <1-m scale) while some of the larger patterns have been attributed to scale-dependent feedbacks (e.g., spur-and-groove reefs at 10-100-m scales). In describing the spatial patterning of reef benthic communities at landscape levels, we uncovered unique spatial patterning among living marine algae. Populations of the calcifying green alga, *Halimeda*, were observed to form a consistent polygonal pattern at characteristic scale of 3-4 m. The pattern showed no clear evidence of having been formed through biologically created shifts in hydrodynamical conditions or related mechanisms. In considering the specifics of *Halimeda* growth patterns, a model of self-organization involving separation and patterned extension is proposed, a mechanism revealed in some geological pattern formation. This observation reinforces the diversity of pathways by which striking spatial patterns can occur in ecosystems.

Introduction

Coral reefs are renowned for their high species diversity and fascinate with myriad spatial patterns. The dominant framework builder is the namesake, the stony coral. Most reef-building corals are colonial, and the individual polyps construct intricate carbonate structures visible when the live tissue is removed from the underlying coral skeleton. In aggregate, the colonies formed from many polyps create a variety of skeletal morphologies that create the visible surface complexity on the reef. At a community scale, corals, along with calcifying algae, microbes, and other calcifying invertebrates, build structures that emerge as elaborate reef patterns, many visible from space (Eakin et al. 2010). The patterns created by the skeletons of corals and other calcifiers include geometrically striking formations, often creating bathymetric contours in subtidal habitats (Schlager and Purkis 2015; van der Kaaden et al. 2020). However, recent observations suggest that live tropical algae on coral reefs can also create regular patterns at spatial scales much larger than that of the individual 'plant' (or thallus), and until now, some of these patterns have been hidden in plain sight.

Among the most common groups of algae in tropical reef habitats is *Halimeda*, and the genus has been linked to spatial pattern formation in benthic habitats. *Halimeda* is one of the most common genera of algae in tropical waters and is known for its high rates of calcium carbonate production due to rapid growth rates and holocarpic reproduction (mortality following gamete release) (Hillis-Colinvaux 1980). Indeed, it has been estimated that *Halimeda* can produce up to 90% of the carbonate sand and sediment in tropical marine ecosystems (Rees et al. 2007). Surveys from across islands and atolls of the central Pacific, for example, reveal that species of *Halimeda* compose the vast majority of erect macroalgal coverage in forereef habitats, ranging from 0-99% of the macroalgal assemblage (and 0-32% of total benthic cover) (Smith et

al. 2016). The ubiquity of *Halimeda*, linked with its potential for rapid growth and carbonate production, may contribute to their role in creating other regular patterns in tropical waters such as the massive reticulated *Halimeda* bioherms described in Australia (McNeil et al. 2016). In habitats where *Halimeda* can grow prodigiously with abundant accumulation of carbonate skeletons, these carbonate piles themselves can promote accumulation of more material (including *Halimeda,* sediments, and the organisms using this habitat) through the reduction of local currents and promotion of nutritional delivery to the pile. With the dynamical process reinforcing the structure through countless algal generations, a geologically relevant structure can be formed, the bioherm. The bioherms that emerge through the material accumulation are large, with mounds or ridges spanning 10s to 100s of m across and in places covering 100s of km^2 (McNeil et al. 2016), and are created out of the dead skeletons of these algae.

Halimeda contributes as well to spatial patterns at smaller scales, linked to the natural history of an individual's growth. *Halimeda*, like other members of the order Bryopsidales, are siphonous in construction, composed of a single large, highly branched and multinucleated cell (coenocytic). *Halimeda* morphology consists of calcified disks or segments made up of interwoven siphons connected together with uncalcified joints allowing for flexion in aqueous environments (Hillis-Colinvaux 1980). Species tend to be either psammophytic, with one large holdfast as the attachment point, or rhizophytic, where individuals can sprawl or creep across the substrate with many small attachment points. Individuals of some species of *Halimeda* tend to grow linearly, following rhizoidal runners, though dislodged fragments can reattach to the benthos and continue to grow. Across sandy benthic habitats, linear arrays of live *Halimeda* have been noted in parallel rows separated by 10s of cm (Littler et al. 2007). Rhizoidal growth is

common across species of *Halimeda*, though to date no data have been reported of spatial patterning of the algal taxon across hard-bottom benthic habitats such as coral reefs.

Due to challenges of visibility and human perspective underwater, synoptic biological surveys of spatial patterns at intermediate spatial scales (m to 100 m scale) are relatively uncommon in benthic habitats. Rapid advances in imaging technology and computer engineering, however, are expanding the capacity of marine ecologists to visualize seascapes digitally. Analogous to the detailed landscape imagery provided by airborne and satellite image mosaics of terrestrial habitats, robust and systematic collections of underwater imagery can be combined into high-resolution large-area reconstructions of underwater habitats (Edwards et al. 2017). Technically, collecting sufficient imagery has not been the challenge; instead, concatenating the images into useable data at large scales has been the primary obstacle. Given the opacity of water, the imagery must be collected near to the benthos (within 0.25-4 m) in order to capture biological detail. As such, applications of remote sensing tools (e.g., satellite or aerial imagery) cannot provide resolution needed to identify taxonomy and borders of individual organisms or colonies (Naughton et al. 2015).

Having operationalized a workflow of large-area imaging for subtidal application, we have been studying the spatial ecology and demography of benthic organisms on coral reefs (Edwards et al. 2017; McNamara et al. 2019; Pedersen et al. 2019; Sandin et al. 2020). In the process of annotating the spatial distributions of organisms in these digital surrogates of 100 m^2 sections of fore reef habitats, we discovered unique patterning of the ubiquitous algal genus, *Halimeda* that we describe here.

Methods

This study was conducted using imagery collected at Palmyra Atoll in 2013 and 2014. Palmyra Atoll is a US Fish and Wildlife National Wildlife Refuge and supports functionally intact and robust coral reef communities that have received little to no impact since the brief US military occupation during WWII (Brainard et al. 2005; Sandin et al. 2008). As such, Palmyra serves as an important baseline to understand reef function and structure in the relative absence of local anthropogenic influence (Knowlton and Jackson 2008).

To map the distribution of benthic organisms, we used 2-dimensional (2D) orthoprojections (Lirman et al. 2007; Nicosevici et al. 2009) derived from 3-dimensional (3D) models generated via structure-from-motion (SfM). SfM uses multiple overlapping images to reconstruct natural scenes and generate highly accurate and detailed 3D and 2D models (Westoby et al. 2012). To generate 3D models and subsequent 2D orthoprojections, imagery was collected within 16 permanently marked 10m x 10m plots distributed along the 10-m isobath of Palmyra atoll, each plot surveyed annually. The image collection and orthoprojection process has been described at length elsewhere (Sandin et al. 2020) and will be described only briefly here. Images were collected with two cameras in a lawnmower pattern, with one camera using a lens with shorter focal length (18-mm) to ensure high overlap among images and the other camera using a lens with longer focal length (55-mm) to collect highly detailed imagery (sub-mm resolution) for identification of challenging borders or taxonomy. Scale bars and edge markers (markers individually linked to depth estimates) were deployed inside the plots and were used to establish scale and to define orientation of the plot with respect to the plane of the sea-surface (e.g., gravity), respectively.

3D models were generated using the SfM software Agisoft *Metashape* and were exported as dense point clouds into the software platform, *Viscore* (Petrovic et al. 2014). *Viscore* is a visualization and analytical platform that provides workflows enabling users to scale and orient models, spatially coregister models across replicate time points, and generate 2D orthoprojections of point clouds for internally accurate spatial mapping procedures (Sandin et al. 2020). Orthoprojections generated in *Viscore* were exported as high-resolution image files to the software platform, *TagLab* (Visual Computing Lab, CNR-ISTI; https://github.com/cnr-isti-vclab/TagLab). *Taglab* provides manual and machine-learning enhanced (not used here) image annotation tools. All patches of *Halimeda* larger than 1 cm diameter visible in the orthoprojections were annotated in *TagLab*, with identification facilitated by camera pose estimates provided by *Metashape* and the virtual point intercept tool in *Viscore* (Fox et al. 2019).

The distribution of *Halimeda* was characterized based upon visual assessment. The spatial distribution of *Halimeda* was inspected visually by contrasting the data layer containing all *Halimeda* annotations against a solid background (i.e., annotating all areas that did not contain *Halimeda* as solid black). Summary metrics of the size and shape of polygons were quantified from these visual products. The patterns of *Halimeda* are not perfect geometric shapes, given vagaries of growth and spatially inconsistent benthic features. To define shape characteristics, we report summaries of human annotations reflecting consensus geometric estimates. Four observers (authors xxx, xxx, xxx, and xxx) independently reviewed the orthoprojection from each plot, annotating linear patterns among *Halimeda* clusters. Features were defined as polygons when at least two observers annotated a complete polygon around a similar centroid (within 50 cm). For each such defined polygon, the number of sides and the

internal area of the polygon was recorded from each observer and the mean across observers of each geometric measurement was reported.

Results

Although not immediately obvious in an image-based map with natural coloring, when the data layer of *Halimeda* is isolated and visualized, a repeated polygonal pattern can be seen (Fig. 1). Many polygons are found to share edges, with vertices commonly connecting three polygons (Fig. 1). The *Halimeda* polygons are observed at multiple sites around Palmyra, clustered on the west-southwest shores of the island (Fig. 2); the trade winds and dominant swell energy come from the northeast. We have observed similar polygonal patterns at multiple time points at sites on Palmyra (Fig. 1) and on other reefs in the Line Islands and the Maldives (not presented here).

The geometry of the polygons showed elements of consistency. Within the five 100-m^2 plots that were hand-annotated, 21 polygons were identified commonly by at least two observers and of these features, 18 were assessed as polygons with 5 or 6 sides. The mean number of sides across polygons was 5.43 (0.51 standard deviation [SD]). The estimated area of these polygons was bounded between 2.9 and 22.7 m^2 (11.3 mean; 5.1 SD). If each polygon were approximated as a regular pentagon (i.e., 5-sided polygon with equal lengths of all sides), the mean side length would be 2.5 m (0.6 SD).

The commonness of polygonal features appears to be site-specific. When visualizing the distribution of *Halimeda* from an additional eleven 100-m^2 plots across Palmyra, only occasional polygonal features are apparent (Fig. S1). Note that the total coverage of *Halimeda* differs

significantly among the plots designated here as having and not having common polygons (n=5 and n=11, respectively). The mean percent cover of *Halimeda* in the 5 plots described in Fig. 2 is 5.8% compared to 15.7% for the other 11 plots (Welch two-sample *t*-test; $t = -3.61$, df=11.2, p<0.005).

Discussion

Structural patterns of coral reefs, as with most ecological systems, are linked to specifics of the physical environment (e.g., sunlight, wave energy), geology (e.g., coastal slope, island type), and myriad biological processes. In many cases, the linkage between the environment and the biological pattern is direct and linear, for example light-harvesting corals are found only in shallower, photic depths and reefs tend to build upon solid substrate. In such cases, we can refer to the biological structure as being 'forced' by the physical or geological conditions. Said another way, the external environment defines the spatial template that is then mirrored in the biological pattern. However, other biological patterns can emerge through internal nonlinear dynamics, including patterns that develop due to self-organization (Rietkerk and van de Koppel 2008). Spur-and-groove reef formation is one such example of self-organization, in which a relatively homogeneous shallow-water coastline can grow into a patterned array of finger reefs and small channels due to feedbacks between waterflow and rates of reef calcification and erosion (e.g., corals growing faster on promontories exposed to increased waterflow; Duce et al. 2020; Rogers et al. 2015). Not all forms of pattern formation, however, need be linked to creation of structural reef features and associated feedbacks with water flow. Through a visual assessment of the distribution of benthic organisms living on the surface layer of a coral reef, we have identified a consistent polygonal pattern of the macroalgal genus, *Halimeda*. We posit that

this patterning is the result of self-organization, and we consider further the dynamics likely to drive creation of this pattern.

In the case of the polygonal pattern, the formation either could be forced by a template in the environment external to *Halimeda* dynamics or could be the result of internal nonlinear dynamics that cause the pattern to emerge. In the first case, the forcing would necessarily require a spatial template from the environment that is the match of the polygonal pattern. One potential forcing template that could exist in the benthic environment would be a polygonal reef morphology, for example created by spacing of benthic competitors or topological contours. The pattern of *Halimeda* can be visualized relative to environmental features through inspection of 3D model outputs (Fig. S2-S6). When the polygonal patterns of *Halimeda* are overlain upon a map showing the distribution of other benthic taxa or upon a digital elevation model, we find no concordance of spatial patterns. There is no direct relationship between the reef morphology and the location of the *Halimeda* polygons. With no clear external template matching the polygonal pattern, the only remaining explanation for the formation of the polygons is via some type of nonlinear internal dynamics, or feedback processes, that drive emergence of the pattern.

Spatial patterns formed by biological feedbacks are not uncommon in nature, with prominent examples found in arid, savanna, and wetland ecosystems (Rietkerk and van de Koppel 2008). The spatial patterns in these well-known examples are formed by scale-dependent feedbacks in biological processes – local positive feedbacks activating growth and larger distance negative feedbacks inhibiting development. This mechanism is similar to the activator and inhibitor dynamics found in the pioneering work from Alan Turing on pattern formation in reaction diffusion systems (Turing 1990). Schlager and Purkis (2015) invoke the potential that the reticulate reef patterning observed among some Holocene reefs may have been formed by

such a system of activation and inhibition consistent with self-organization. It is quite plausible

that *Halimeda* bioherms are created similarly (McNeil et al. 2016), as the bioherm itself

promotes close-scale deposition of algal and other materials from slowed currents while at larger

distances the stronger currents prevent accumulation. More recently, phase separation via density

dependent dispersal, as is common in physical systems, has been put forward as a new self-

organization mechanism in ecological systems, in this case to explain observed patterns in

mussel beds (Liu et al. 2013).

The pattern in live *Halimeda* documented in this study occurs at a spatial scale that is

larger than the individual, the pattern appears to keep a consistent spacing (i.e., polygons with a

characteristic scale on the order of meters), and the pattern has a large-scale coherence in shape

(similar vertex structure; Fig. 1), all suggestive of self-organization. However, the polygonal

patterning of *Halimeda* can be viewed as something distinct from the *Halimeda* bioherm. First,

the *Halimeda* distributions described here are formed by the distribution of live algae while the

bioherm is composed largely of carbonate algal skeletons (with aggregation of other sediments

and materials). Further, the biological pattern observed here (Fig. 1) traces the outline of a

polygon at the scale of the organism, a scale much smaller than the 10s to 100s of m scale of the

bioherm. Further, the pattern of live *Halimeda* is not associated with any significant

topographical patterns (Fig. S2-S6), and the live tissue itself likely has no effect on local water

currents (i.e., defining patterns of activation and inhibition). The unique pattern of live *Halimeda*

without clear evidence of biophysical feedbacks suggests that the dynamical processes

generating the polygonal pattern are distinct from scale-dependent feedbacks between biological

growth and hydrodynamic processes.

The polygonal patterns of *Halimeda* resemble patterns found in polar geomorphic systems where stones and soil self-organize (Kessler and Werner 2003). While the detailed dynamics acting along the coral benthos are certainly different than those in polar stone-soil systems, we hypothesize that the basic feedback processes are likely similar. In these polar systems, larger stones organize into polygonal patterns within soil, and two feedback mechanisms govern the pattern generation – (i) stones and soil are sorted into separate regions by the upward swelling caused by annual frost heaving and (ii) physical bias causes stone piles to extend linearly along the major axis of the pile (Kessler and Werner 2003). Analogous mechanisms can be envisioned on reef habitats – (i) *Halimeda* and coral can sort as growth and subsequent buildup of *Halimeda* skeletal segments increases spatial separation and (ii) individual *Halimeda* plants expand linearly across the benthos through vegetative growth with lateral extension through rhizoidal runners (as in crabgrass or strawberries), as has been documented in soft sediment habitats (Littler et al. 2007). Additional physical and biological particulars would be required for a similar mechanism to generate polygons in *Halimeda* on a reef in comparison to what generates polygons among polar stones, yet the pattern similarity is striking.

We posit that the polygonal patterns of *Halimeda* may represent a novel example of ecological pattern formation that is not due to scale-dependent feedbacks between biological and physical mechanisms. While processes associated with phase separation cannot be ruled out, it would require a density dependent dispersal mechanism for *Halimeda* and modified mechanisms of polygon formation (the patterns of *Halimeda* form thin polygonal borders while the patterns described in examples of phase separation are often more space-filling) (Liu et al. 2013). Scale-dependent feedbacks could provide the framework for originating the pattern, but the scale-dependence would need to be mediated by chemical or microbial signals that have not yet been

found specific to this system. Further, we are not aware of examples of scale-dependent feedbacks forming polygons with thin borders.

The pattern of *Halimeda* was not ubiquitous, but instead is found across only about half of the sites surveyed on Palmyra atoll (Fig. S1). Interestingly, the sites with the pattern formation are those on the coasts opposite to the dominant swell with more limited total abundance of *Halimeda*, suggesting that the presence of the pattern itself may reflect elements of the island-scale environmental conditions. Additionally, the sites with polygonal patterning are those with less total algal cover, perhaps suggesting that more expansive *Halimeda* growth could swamp signals of patterned growth and distribution. Understanding the response of an ecosystem to changes in environmental forcing can sometimes require a clear picture of the pattern forming processes, as has been noted with pattern-forming termite mounds influencing ecosystem responses to aridification (Bonachela et al. 2015). A mathematical representation of the feedbacks that give rise to patterns in *Halimeda* may contribute to our system-level understanding of how coral reefs respond to changes in environmental forcing. Further, the introduction of a novel mechanism of self-organization in biological systems expands our view of how life can create unique patterns across natural landscapes.

Acknowledgements

Statement of authorship

S.A.S., C.B.E., and D.E.M. conceived the study and designed the methodology. All authors contributed to data collection and analysis. S.A.S. wrote the original draft and all author contributed to critical review and editing.

Data and code accessibility

All data are contained within the manuscript and the online supplement.

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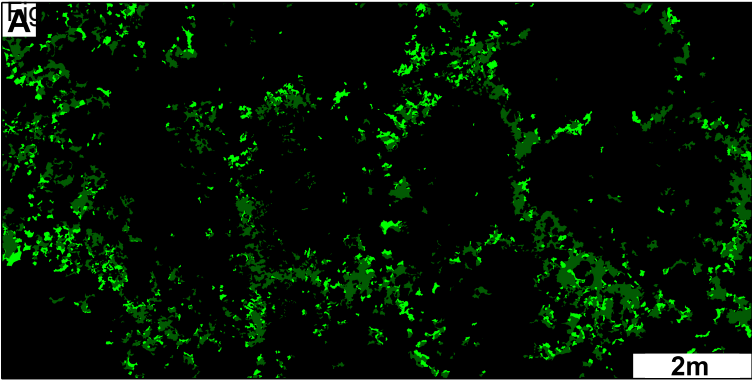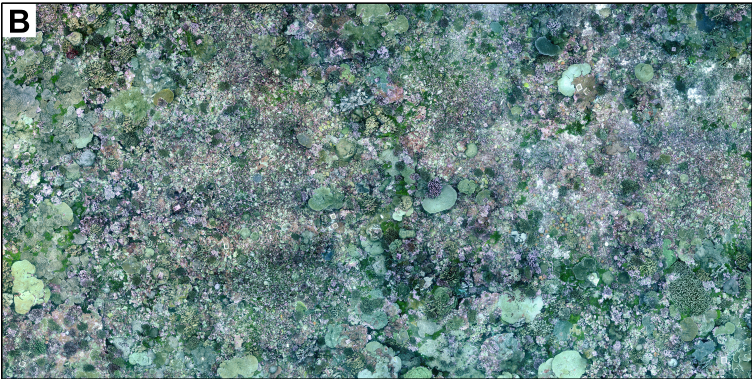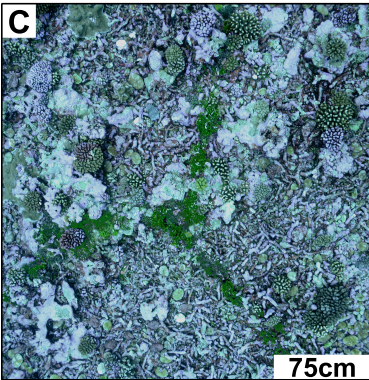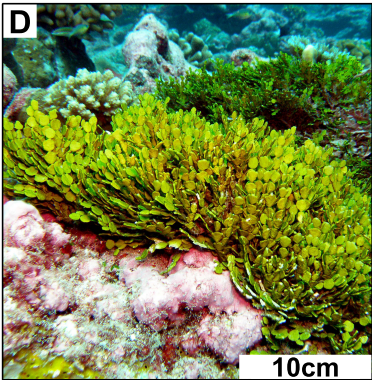on Underwater Networks & Systems:1-5.

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Figure captions

Figure 1. *Halimeda* growth on a central Pacific coral reef. (A) Large-area representations of coral reefs are made possible through the merging of information from ~5000 photographs, generating a 2-dimensional orthophotomosaic of a 20 m x 10 m reef area with high resolution. (B) By annotating *Halimeda* cover (in green) and viewing independently (against a black background), a distinct polygonal pattern is apparent at a characteristic spacing of 3-4 m. Note that two shades of green are used, representing *Halimeda* cover from two annual surveys (2013 and 2014); the pattern is largely consistent between sequential years. (C) When the distribution of *Halimeda* is viewed from above, linear growth with distinct star-like vertices (approximate 120° intersection angle) are noticeable. The patterning suggests spatial emergence at scales larger than the individual organism. (D) *Halimeda*, as seen in raw imagery, is a calcified, segmented group of tropical algae that competes for space with hard corals and other benthic taxa.

Figure 2. Spatial patterns of *Halimeda* at five 100 m^2 areas spanning the fore reef habitats (10 m depth) of Palmyra atoll (central Pacific) in 2013. The site locations are labeled in the island map and annotated orthophotomosaics are organized in corresponding, clockwise order, starting with FR9 in the top-left. Notably, in plots with more *Halimeda* coverage the polygonal pattern is less obvious (see data from additional sites in Fig. S1).

A 2m

B

C 75cm

D 10cm

Figure

FR9   FR13

5°54'–

FR3   FR5   FR4

5°52'–

162°6'   162°4'

Hawaii
Palmyra

N

1km
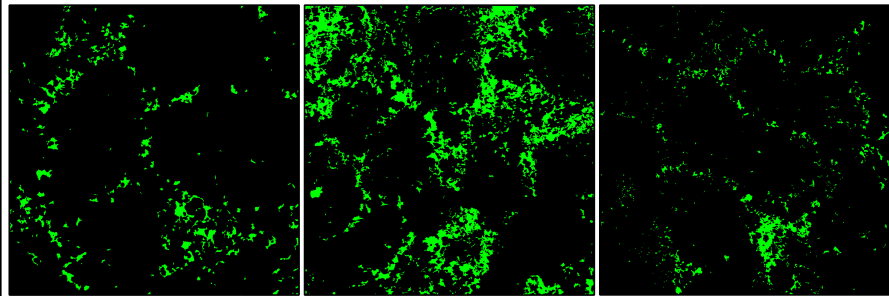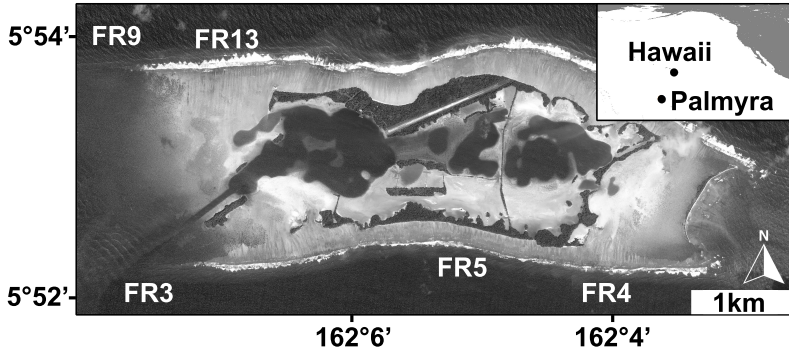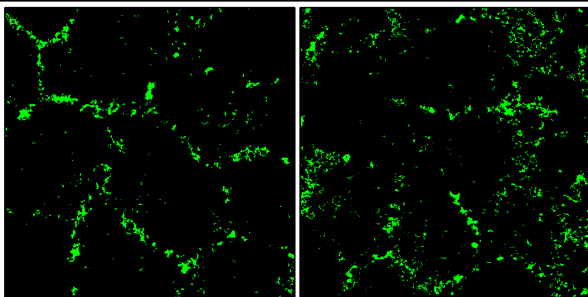
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Evidence of biological self-organization in spatial patterns of a common tropical alga

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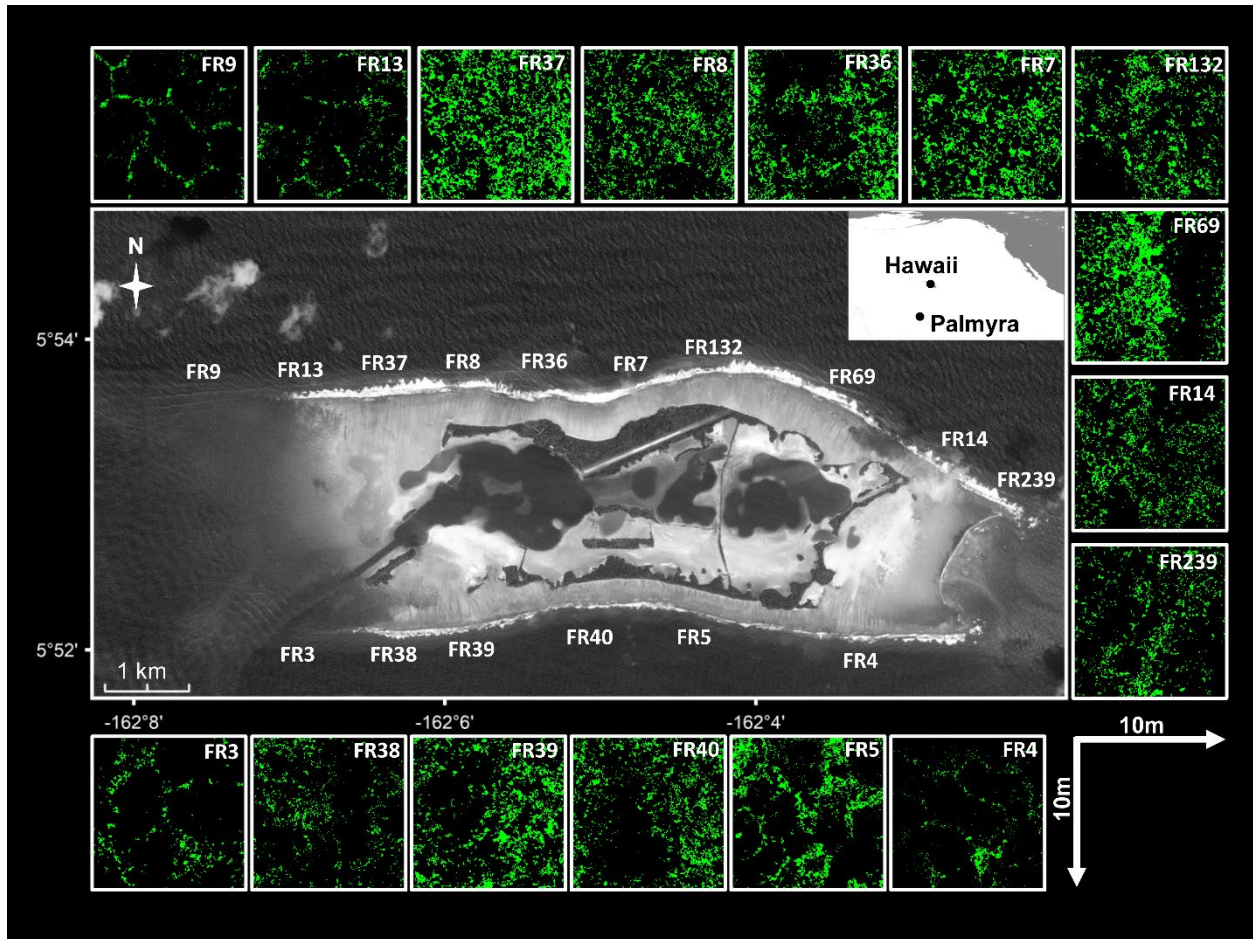
Figure S1. Spatial patterns of *Halimeda* as represented from orthophotomosaics from 16 100 m²

areas spanning the fore reef habitats (10 m depth) of Palmyra atoll (central Pacific) from

September 2013. Data presented here include data from Fig. 2, adding information from the

remainder of regularly surveyed sites from the fore reef. The polygonal pattern is clearly

observable across at least 5 of 16 plots, biased toward the west-southwest shores of the atoll.

Notably, the major swell energy reaches Palmyra from the northeast.
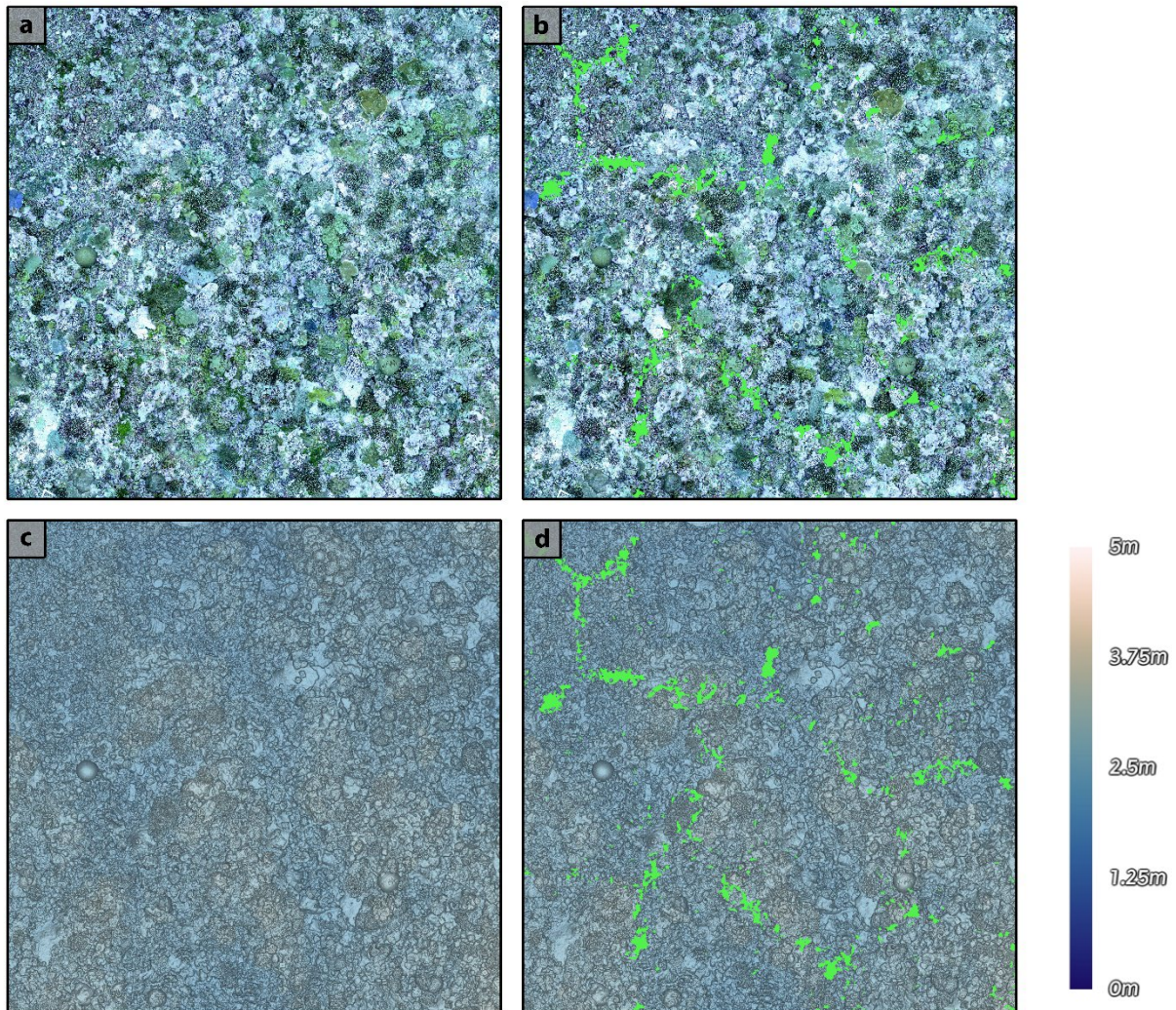
Figure S2. Spatial pattern of *Halimeda* (b,d) at FR9 from 100m^2 area represented on the orthophotomosaic (a-b) and digital elevation model (DEM) (c-d). Values of the DEM are the elevation relative to the greatest depth with the plot area.
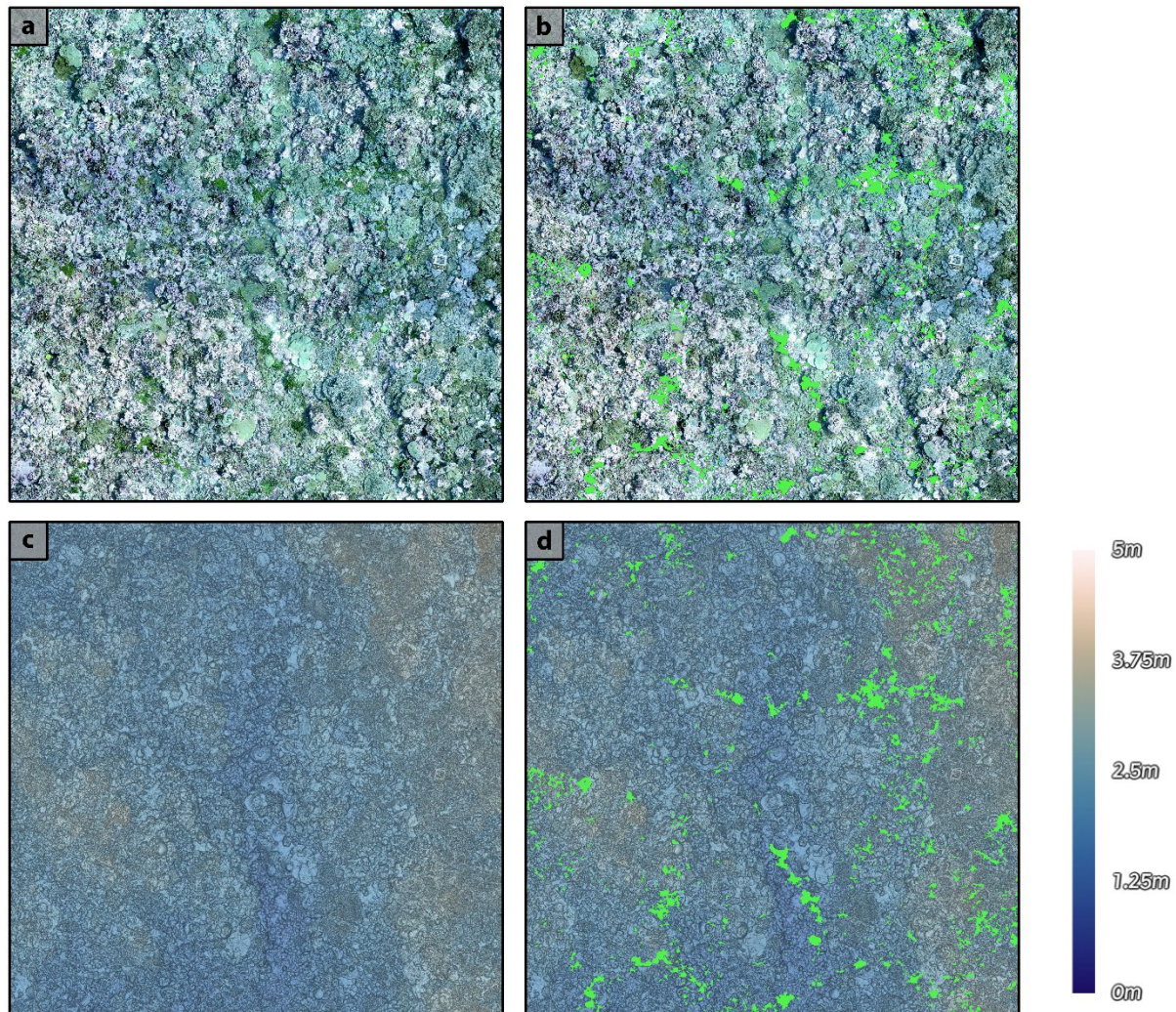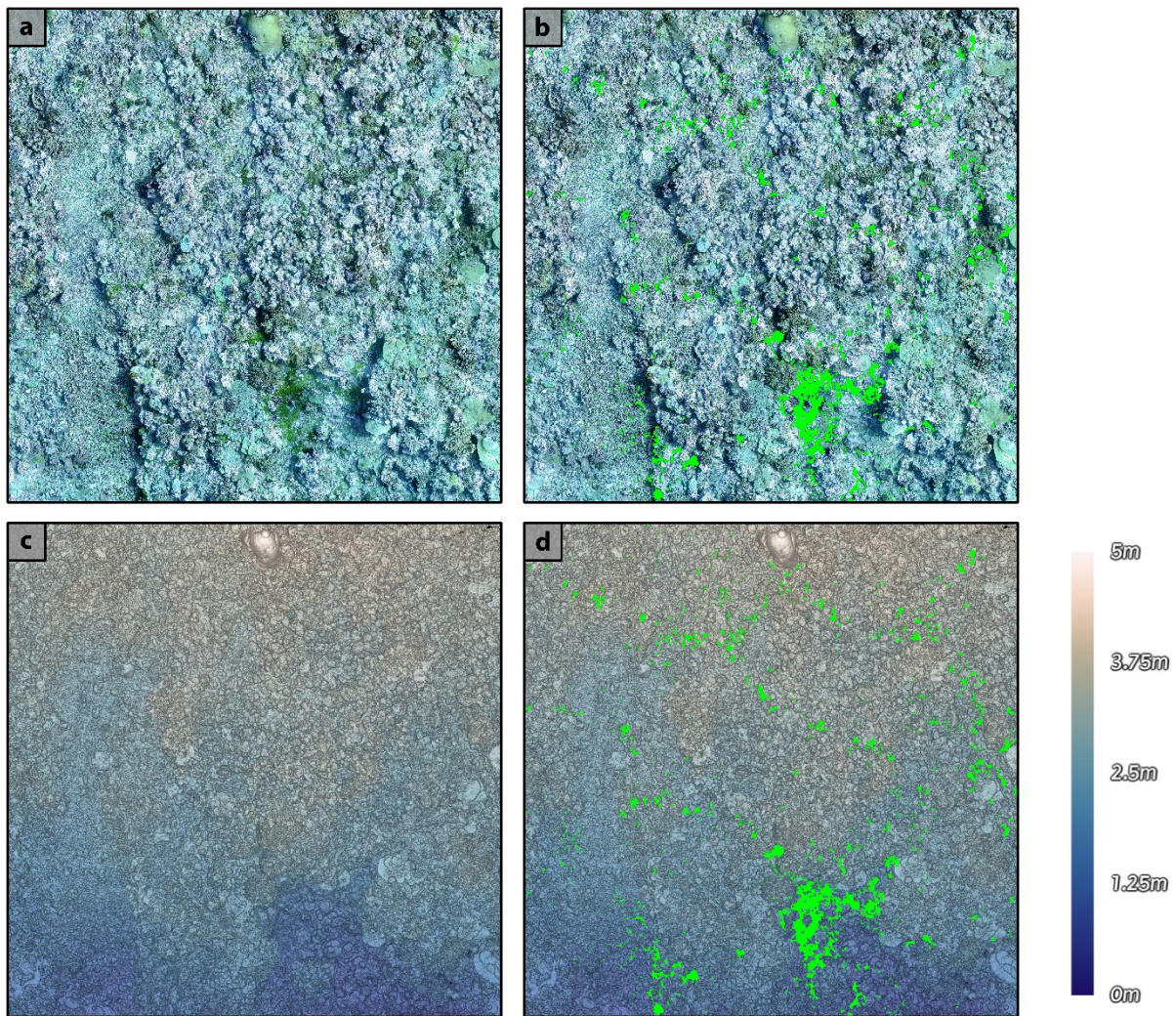
Figure S3. Spatial pattern of *Halimeda* (b,d) at FR13 from 100m^2 area represented on the orthophotomosaic (a-b) and digital elevation model (c-d). Values of the DEM are the elevation relative to the greatest depth with the plot area.

Figure S4. Spatial pattern of *Halimeda* (b,d) at FR4 from 100m^2 area represented on the orthophotomosaic (a-b) and digital elevation model (c-d). Values of the DEM are the elevation relative to the greatest depth with the plot area.
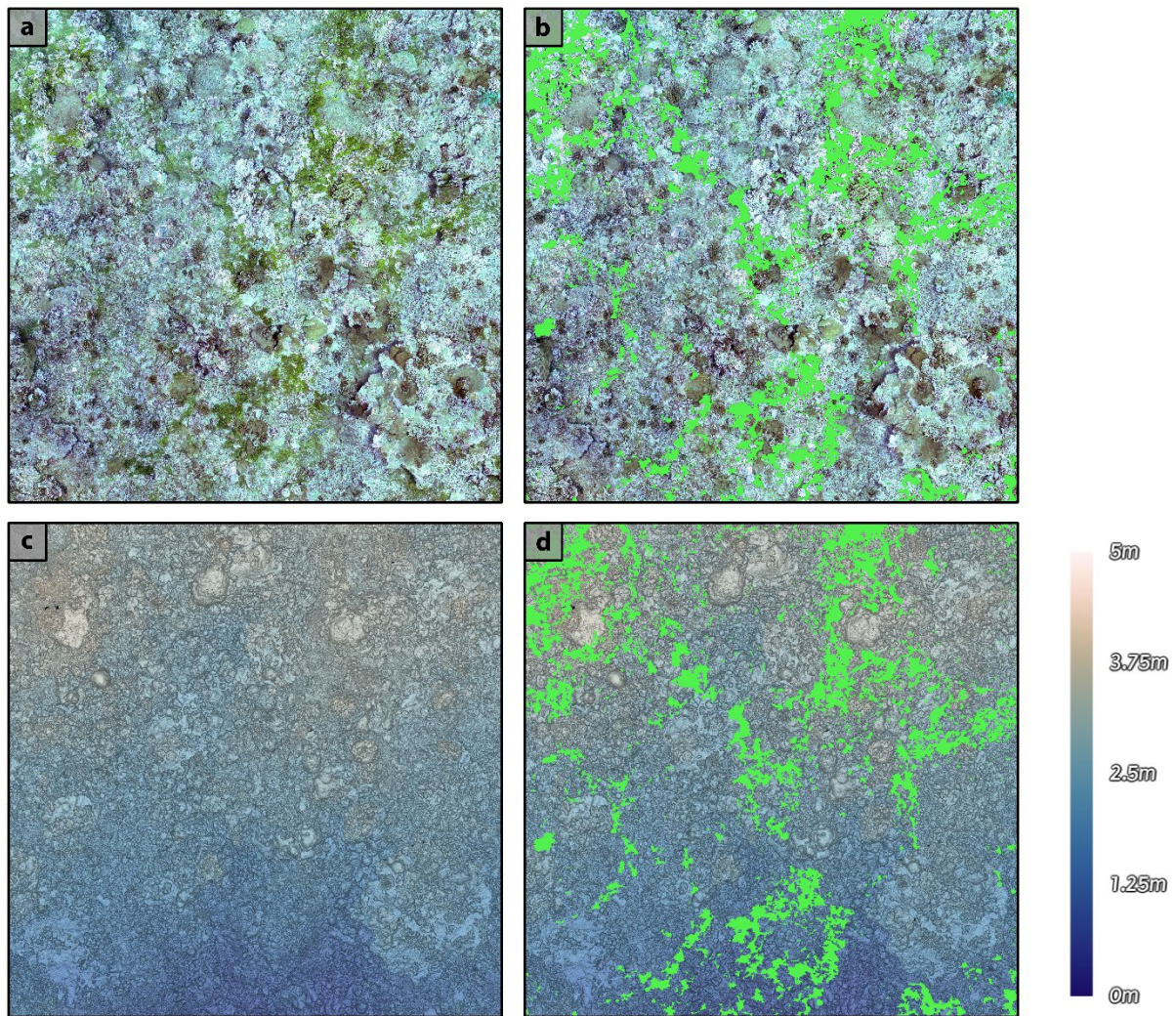
Figure S5. Spatial pattern of *Halimeda* (b,d) at FR5 from 100m² area represented on the orthophotomosaic (a-b) and digital elevation model (c-d). Values of the DEM are the elevation relative to the greatest depth with the plot area.
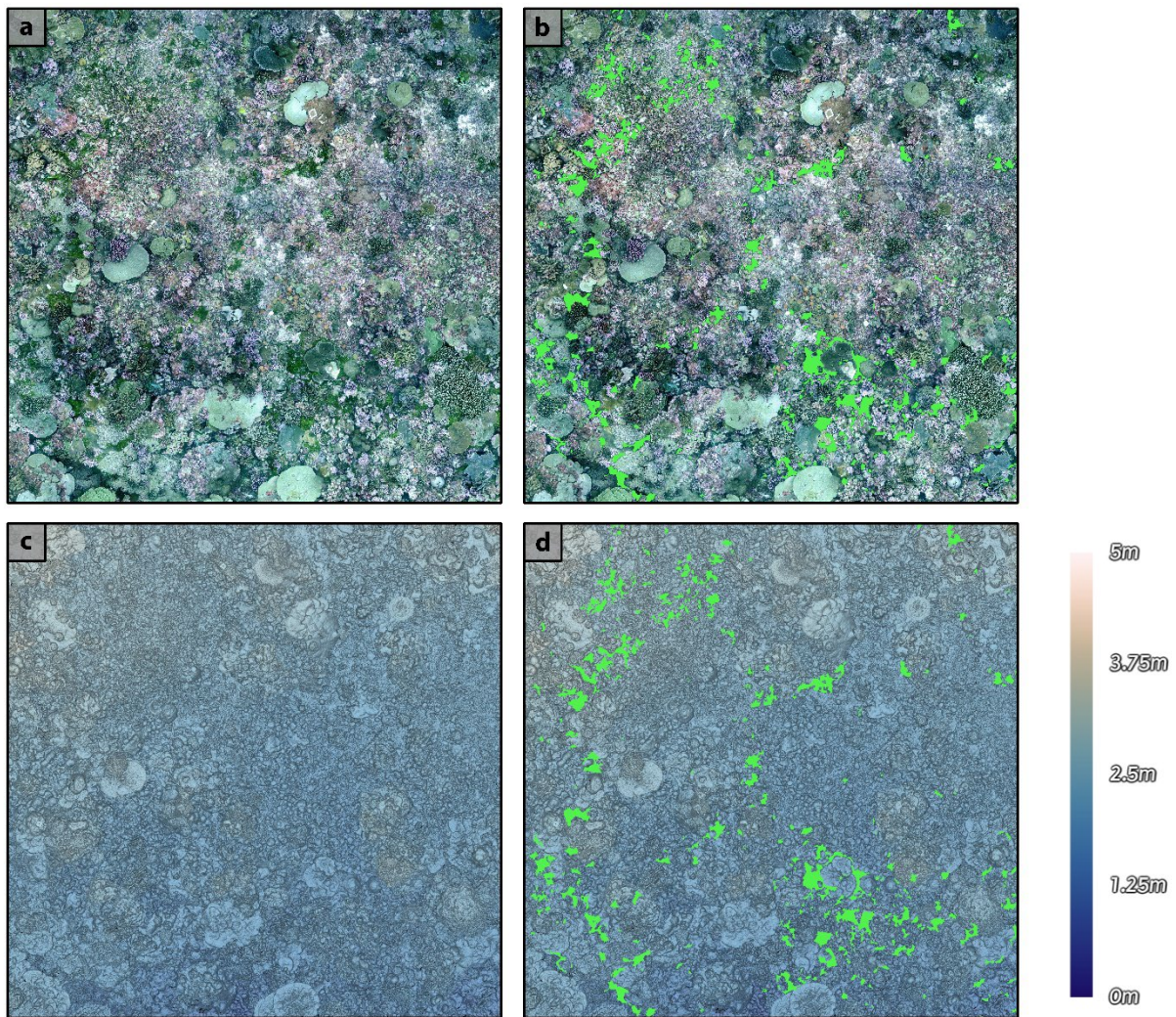
Figure S6. Spatial pattern of *Halimeda* (b,d) at FR3 from 100m² area represented on the orthophotomosaic (a-b) and digital elevation model (c-d). Values of the DEM are the elevation relative to the greatest depth with the plot area.