Behavioural shifts of Diadema savignyi and their impact on coral communities around Rapa Nui

By Nathan Doorenbos

n.j.doorenbos@students.uu.nl

Solis ID: 4686675

under the supervision of Alexandre Génin

Abstract

A complex system of feedbacks between species and their surroundings often generates ecosystems at relatively stable states. Perturbations in such a system can lead to regime shifts especially in cases of bistability. Here the behavioural shifts of the sea urchin *Diadema savignyi* were first determined empirically at Rapa Nui. After which scenarios were created in a cellular automaton model to test whether these shifts were important to consider in the ecosystem, namely by testing the impact of herbivory pressure on the total covers of corals and algae. In bare dominated microhabitats, a doubled foraging rate as well as spatial aggregation were observed for urchins. These behaviour switches did not lead to evident changes in the model. However a scenario in which urchins also forage on coral recruits did show a decrease in coral cover as urchin density increased. Empirically around the island it was proposed increased pressures from human activities or wave exposure reduced the recruitment rates of corals to such an extent that urchin grazing may have led to barren seascapes at certain sites.

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Introduction

Ecosystems are held in relative stability due to the many feedbacks present between biotic and abiotic elements within these systems (Cuddington et al., 2009). However, as anthropogenic activities occur in natural habitats, their impacts may destabilise the ecosystem and lead to regime shifts, a particular case of critical transitions (Scheffer et al., 2001). These often-rapid shifts occur on multiple trophic levels and can be linked to external factors or shifts within the system's dynamics (Andersen et al., 2009). Some examples of regime shifts include the transformation of freshwater ecosystems by the introduction of beavers or the change in vegetation due to fires.

Shifts have been observed in coral reef communities, one such example being the abrupt change from coral to macroalgae-dominated Jamaican coasts during the 1980s (Hughes, 1994). In this case, the reefs had been victim of overfishing since the 1960s, of extensive damage from a hurricane in 1980, and later of a 99% die-off of most *Diadema antillarum* urchins. These elements favoured the establishment of macroalgae which expanded from 4 to 92% cover between 1977 and 1993 while coral cover declined from 52 to 3% (Hughes, 1994). Other alternative states can occur with new dominances of soft-corals, sponges, corallimorpharians or sea urchin barrens. These shifts commonly occurred after the disturbance of the coral community, either natural or man-induced (Norström et al., 2009). Furthermore, theoretical models suggest that human activities can induce losses of coral reef resilience which could lead to phase-shifts (Mumby, 2009). In these cases, other species with higher recruitment rates can populate the area previously covered in hard corals, thus limiting coral recovery (Kuffner et al., 2006). Herbivory presence has therefore been identified as a key element in coral community resilience as they control the recruitment and expansion of these other species through grazing (Andrew, 1993).

It remains difficult to predict shifts in coral communities as they result from a combination of factors. Indeed, these shifts often follow reef destruction from natural disasters or pollution events which cannot be predicted (Hughes, 1994; Norström et al., 2009; Scheffer et al., 2001). Furthermore, due to the variety of species in coral communities, understanding the feedbacks between different species can be arduous. Especially due to the current poor understanding of regulatory mechanisms and feedbacks in marine ecosystem dynamics (Scheffer et al., 2009). While individual feedback mechanisms may not cause a shift to another state, feedbacks which may be deemed unimportant could in weakened reefs lead to destabilization (van de Leemput et al., 2016). It is then important to expand the understanding of herbivory feedbacks within coral communities as their presence can provide resilience in the aftermath of reef disturbances.

Coral communities of Rapa Nui

Easter Island, also known as Rapa Nui in Polynesian, is an isolated island that lies about 3700 km west of the Chilean mainland and 2000 km east of the Pitcairn islands, its closest inhabited neighbour (Friedlander et al., 2013). Three submarine volcanos give it its triangular shape (Fig 1) (Vezzoli & Acocella, 2009). In part due to its remoteness, endemic marine species account for 75% of the total aquatic biomass even though they account only between 12 and 35% of the species within various groups (Friedlander et al., 2013). Rapa Nui, however, exhibits 5-10 times less biodiversity and is considered depauperate compared to other Eastern pacific islands with the most similar coral communities, (Glynn et al., 2007; Randall & Cea, 2011). At Salas y Gómez, an uninhabited islet 390 km away from Rapa Nui, apex predators account for 41% of the fish biomass, whereas it is only 2% for Rapa Nui, most likely due to past and ongoing overfishing of these species (Friedlander et al., 2013; Morales et al., 2019; Petit et al., 2021).
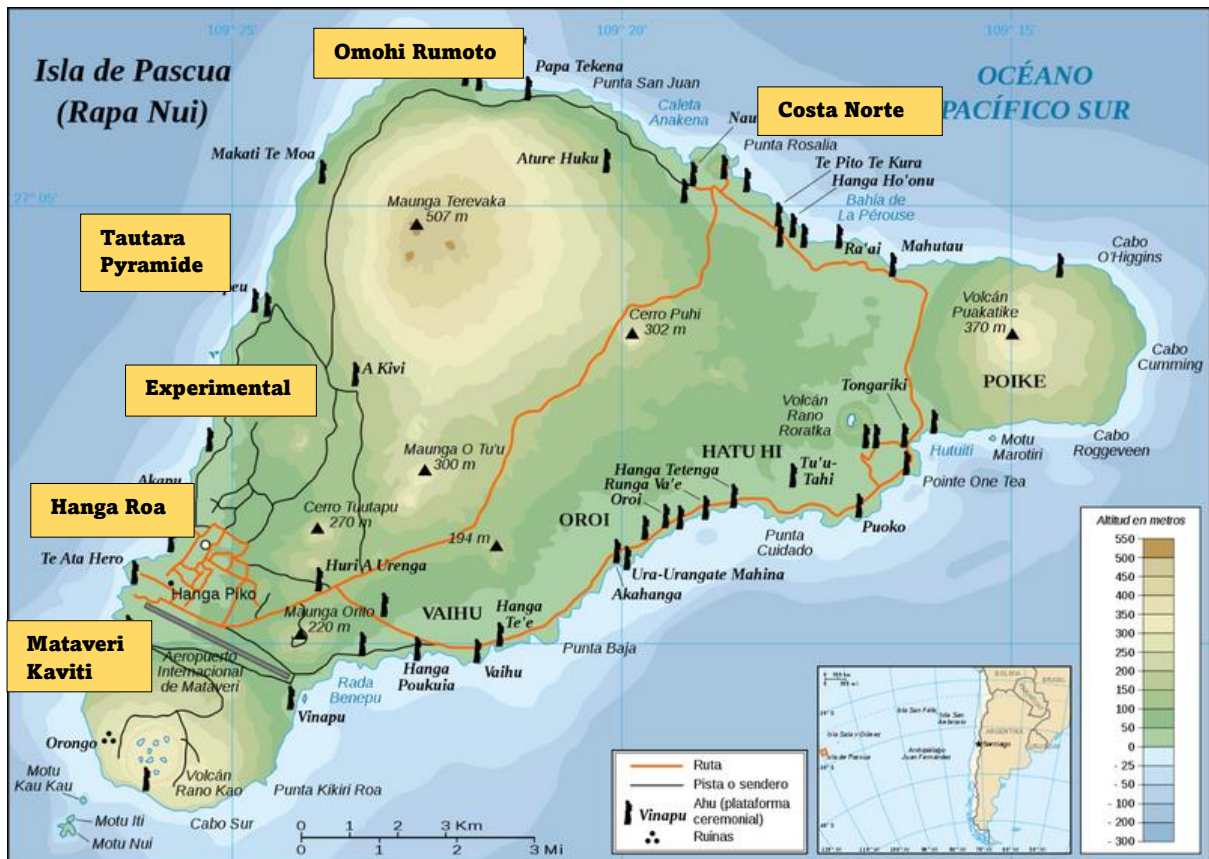
Figure 1: Topographic map of Rapa Nui with added locations where data was taken (Rapa Nui, 2019).

The coral reef communities at Rapa Nui dominate the depths from 7 to 50 meters with mostly the hard coral species *Porites lobata* and *Pocillopora verrucosa* (Fig 2) (Glynn et al., 2007)*. Porites* which often accounts for most of the live coral can attain colony sizes of 1-3 m, ten times larger than *Pocillopora*. Other coral species are also found growing in coral communities albeit at lower frequencies such as the *Pocillopora eydouxi*. Macroalgae also populate the shallows although in most places at low abundance (Wieters et al., 2014). The benthic community at Rapa Nui is further composed of macro-invertebrates of which the Echinodermata phyla is the most diverse, a group that includes among others, starfish, and sea urchins (Friedlander et al., 2013). Of this group, the two most common mobile species are the herbivore sea urchin *Diadema savignyi* and the coral-eating gastropod *Coralliophila violacea.* When looking at fish biomass at different trophic levels, Friedlander et al. found that these were equally divided between herbivores, planktivores, and carnivores (2013). However herbivorous fish were not found to significantly reduce algal growth due to their low abundance (Glynn et al., 2003), suggesting that urchins are most likely the dominant herbivore in the communities of Rapa Nui. *D. Savignyi* appears to be the key herbivore as it dominates the shallow reefs between depths of 5 to 20 m (Hinojosa et al., 2021; Wieters et al., 2014).

Furthermore, as Rapa Nui is famous for its culture, in recent years the number of tourists has increased, with at least three times as many between 2002 and 2014 causing waste treatment issues as waste is commonly disposed in the ocean (Figueroa & Rotarou, 2016). This is detrimental to its coastal ecosystems to which overfishing was added when they began exporting fish to the mainland (Zylich et al., 2014).
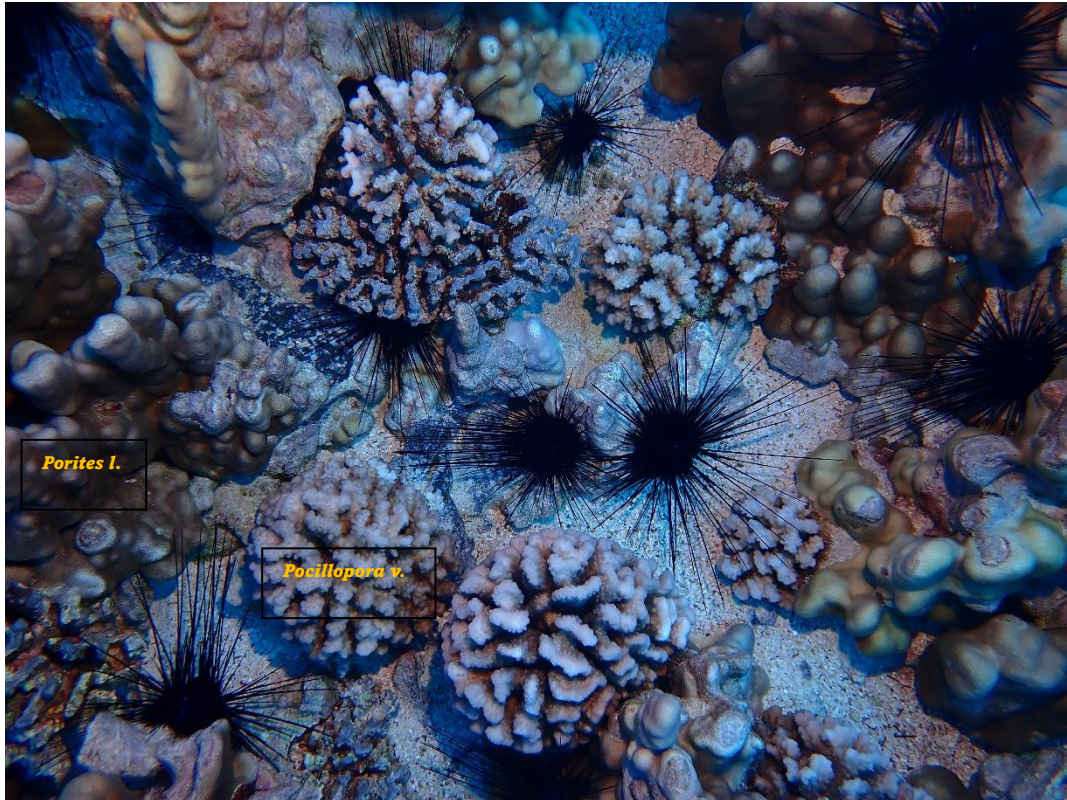
Figure 2: Community photo taken at Rapa Nui showing D. savignyi urchins among Porites l. and Pocillopora v. coral communities (Wieters field data, 2022).

Regime shifts and sea urchin behaviours at Rapa Nui

In the mid-1980s the shallow waters around Rapa Nui transitioned from a dominance of macroalgae, notably *Sargassum*, to a coral dominated seascape (Hubbard & Garcia, 2003). While this shift was observed, the causes remain unknown due to a lack in data before this event. Nonetheless, both coral and macroalgae dominated states are observed at Rapa Nui with rarely a combination of both, suggesting the possibility of shifting dynamics between the two.

Sea urchins are herbivore marine invertebrates, often characterised by their spines (The Editors of Encyclopaedia, 2022). They move using either their tube feet or spines and live primarily on hard ocean floors. The majority forage for algae or other food sources which they scrape using a mouth system situated under their body. They can be important in shaping ecosystems as they can reduce large areas of kelp forests or other algae in the right conditions (Myhre & Acevedo-Gutiérrez, 2007; Do Hung Dang et al., 2020). The control of urchins on abundances of algae comes from their density, but also their foraging behaviour. A bottom-up approach in macroalgae control was further found by Smith et al., indeed in the absence of aquatic herbivores, macroalgae spread to the detriment of corals and coralline algae (2010).

Sea urchins have also been found to exhibit shifts in their behaviour, switching between passive and active eating (Karatayev et al., 2021; Smith & Tinker, 2022). Passive grazing here refers to a detritivore diet and the consumption of dead algae, in this situation urchins possess low foraging and consumption rates. In contrast, active eating refers to a higher foraging rate with increased consumption, namely feeding on live algae. A higher consumption rate is then required to compensate for the increased energy required by moving more (Lauzon-Guay & Scheibling, 2007). The causes for

these shifts are complex, Smith & Tinker (2022) found that both biotic and abiotic factors may be involved. They argue that a marine heatwave may have switched urchin behaviour due to linked metabolic responses (Rasher et al., 2020). Another example was observed in the relation between shelter availability and species presence as shelters offer to some urchins species the ability to hide from predators (Andrew, 1993). Aggregation was also observed for *Diadema savignyi* in French Polynesia where the urchins could be split into two states, a first with low density occupation of crevices and a second in which large amounts of individuals were grouped together (Han, 2016). Time of day can also contribute to urchin behavioural shifts, however at Rapa Nui the *D. savignyi* have been observed at similar rates in both diurnal and nocturnal surveys, which differs from other diadema urchin species which strictly forage at night (Zapata-Hernández et al., 2021).

It is thus complex to predict behavioural switches in sea urchins, especially as distinct species exhibit contradicting behaviours (Han, 2016). These switches in behaviour can nonetheless be important to consider since Karatayev et al. (2021) found that the inclusion of their behavioural feedbacks led to better performing models. Therefore as their behavioural switches can have important consequences on ecosystem dynamics it is important to understand them and study how they impact coral communities namely with regards to coral reef restoration in which they could be a key actor. In this project the impact of these switches was studied using the communities of Rapa Nui as application. To do so we first investigate how urchin behaviour is affected by environmental factors, then investigate how these changes in behaviour can impact ecosystem dynamics.

This project was broken down into two main research questions:

1) How does sea urchin foraging behaviour vary with respect to the microhabitat in which they reside in the Rapa Nui coral communities?

    a. How do urchin foraging rates change in relation to their microhabitat?

    b. Does urchin abundance vary according to the microhabitat?

    c. How are sea urchins spatially distributed in different microhabitats?

2) What are the impacts on the coral community of switches in the behaviour of sea urchins in the case of Rapa Nui and how does this compare to observations?

This research was performed in two components following the research questions. In a first empirical part, different ecological variables were measured and analysed to identify how the foraging behaviour of sea urchins was impacted by the local habitat it was found in. *D. savignyi* grazing rates were first investigated in both coral and bare dominated microhabitats. Next urchin densities were measured while evaluating the presence of different biotic or abiotic features. After which, sea urchin spatial distribution in different microhabitat types were estimated. In a theoretical second component, the empirical data results from the former sections were used to test whether considering these would alter predictions of a spatially-explicit model of coral communities.
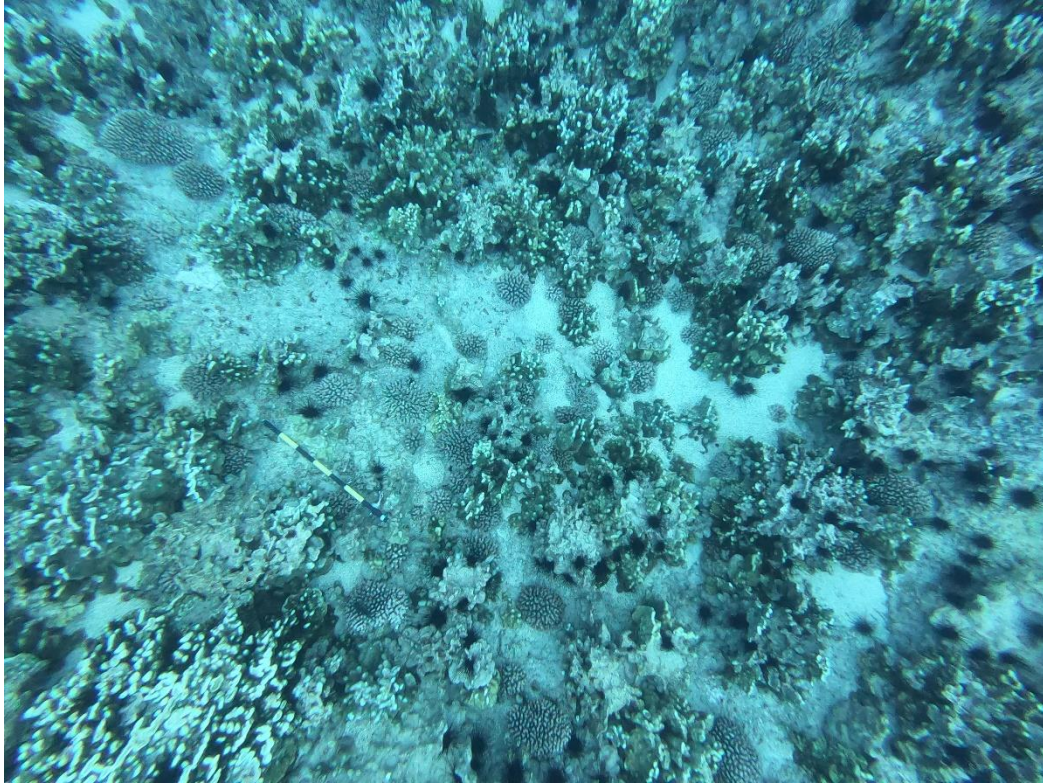
Figure 4: Example of a calibration image captured by a subtidal buoyant camera in a coral dominated microhabitat at the 'Experimental' site.

Figure 3: Example of a calibration image from a subtidal buoyant camera of a bare dominated microhabitat at the 'Mataveri' site.

Methods

Data on urchin behaviour

Foraging rates

In a first part of the quantitative analysis, the differences in displacement velocities of the sea urchins were measured according to their immediate environment. To do so, video data was obtained by E. Wieter's lab in November 2022 at either of two types of microhabitats available, namely within dense coral patches (Fig 3) or within mainly bare areas (Fig 4). Two locations around the island were chosen, one that dominated by corals but hosts a mosaic of large coral and bare microhabitats (site "Experimental", -27.1363324, -109.4295760), and a second dominated by macroalgae that hosts a mosaic of macroalgal and bare patches (site "Mataveri", -27.164907, -109.444554) (Fig 1).

Downward-facing Gopro Hero 6 cameras were stationarily moored approximately 5m above the seafloor, so that they would capture a view of approximately 4*3 m² area of seafloor from above. These subtidal buoyant cameras were set to record images at one-minute intervals for over 2 hours to create a timelapse of the seafloor. At the 'Experimental' location, 8 replicates were distributed across coral-dominated continuous habitat and another 8 in were distributed outside in adjacent mostly bare habitat. At 'Mataveri' only 4 repetitions were produced in bare microhabitats, as urchins avoid and are not found within macroalgae dominated microhabitats (Wieters, unpublished data).

A regularly marked (every 10cm) meter-long pole on the seafloor was used to calibrate distances from the images. Due to the rocking movement of the cameras while filming, a form of stabilisation was required to retrieve the movement rates of sea urchins. This was done using Hugin, a panorama stitching software (d'Angelo Pablo et al., 2022) which uses correspondence points between images to reposition and transform images, so they align. For each video, a section of just over 30 minutes was randomly selected, and each image was then aligned by the software which gave the transformation parameters of each image. The larger these values, the more did the images differ from the reference image (with the pole). To reduce errors in distances, 10 images with the smallest transformations parameters were kept of which the first and last had a 30min interval. Next, in Imagej (Schindelin et al., 2012), each video was calibrated using the reference image with the pole and then 10 randomly-chosen urchins were tracked over time using the manual tracking plugin. The total Euclidian distances travelled in those 30 minutes were then recorded. As foraging rate is assumed to be proportional to movement rate this could find a difference between bare and coral microhabitats.

Urchin biomass

The reference image from each video was also used to measure individual sizes (test diameter) of ten urchins selected at random to determine their average sizes. In a previous field trip in 2013 urchins had been measured and weighted to establish a weight and size relationship. It had been previously noted that the conversion from individual urchin size s_u in cm to biomass m_u in grams followed the relationship (Génin et al., 2023)

$$ln(m_u) = -0.55 + 2.88 ln\,(s_u). \qquad (1)$$

This relationship between size and weight was then used to obtain an average individual urchin mass used in this project.

Covers of microhabitats and urchin abundances

To obtain information on urchin abundance relative to the microhabitats found around the island, a set of photo transects was used. These transects were obtained by attaching a Gopro Hero 9 camera under a boat taking images vertically every half-second (E. Wieters' lab work, Nov. 2022 field campaign). Also attached under the boat was an echosounder which provided depth information. Different sections were surveyed around the island's coast. Due to triangular shape of the island, it was assumed that external factors such as wave exposure regimes would be similar along each side and thus the coastline was split into three sections, the north coast, the west coast, and the south coast. The increased wave exposure on the south coast appeared to reduce visibility and coral presence, so only the north and west coast were analysed. Different sections were surveyed along the western coast and the northwestern coast, hereafter named Mataveri-Kaviti (MK), Hanga Roa (HR), Tautara-Pyramide (TP), Omohi-Rumoto (OR) and Costa Norte (N) (Figure 1). For each location, between 50 and 100 images were randomly selected, this was higher for Costa Norte as it spanned a larger section of the coastline. Using R studio, each image depth was collected from a database file as the depths and photos were stored separately. The depths d obtained and the camera's field of view ϕ were then used in a trigonometric conversion to compute the size s in meters:

$$s = 2d \tan\left(\frac{\phi}{2}\right)$$

In our case the fields of view were $\phi_h = 87°$ horizontally and $\phi_v = 71°$ vertically (GoPro Community, 2021) producing the horizontal and vertical extents of each image. As all images had dimensions of 2592x1944 pixels, a conversion between pixels and meters was computed to calibrate the images. Using this, a grid with cells of 1x1m quadrats was overlaid on each image using Matlab (The Mathworks, 2021). A square region of 5 by 5 meters was further delimited using coloured points to standardize data collection to those 25 quadrats (Fig 5). We did not analyse images for which the seafloor shallower than 5 meters and those that were not clear enough, mostly at deeper depths (approximately above 12 m). To measure cover, a point-intercept sampling technique was used and for every 36 grid intersections the underlying cover type was classified into one of the following types: *Porites lobata, Pocillopora verrucosa,* algae, sand, rock, boulders, urchins, crustose coralline algae (CCA) or unknown. In each quadrat, the number of sea urchins was recorded. In case an urchin was on a grid line, it was visually determined which cell most of its body was found. However when split in half, the urchin was assigned to the cell below or to the right to avoid counting the same individual twice.

Urchin aggregation

Counting urchins per square meter cell allowed for an analysis of urchin aggregation according to their microhabitat. For each image when the cover was at least 80% coral or 80% bare rock we assumed it to be in either a coral or a bare patch. Then different probability distributions were fitted to the empirical data using the 'fitdist' function in Rstudio to determine which probability distributions would fit the data best. For the bare dominated data, sites at which no urchins were observed were excluded as these would indicate the absence of urchins at that location and which would not add an indication as to the aggregation.
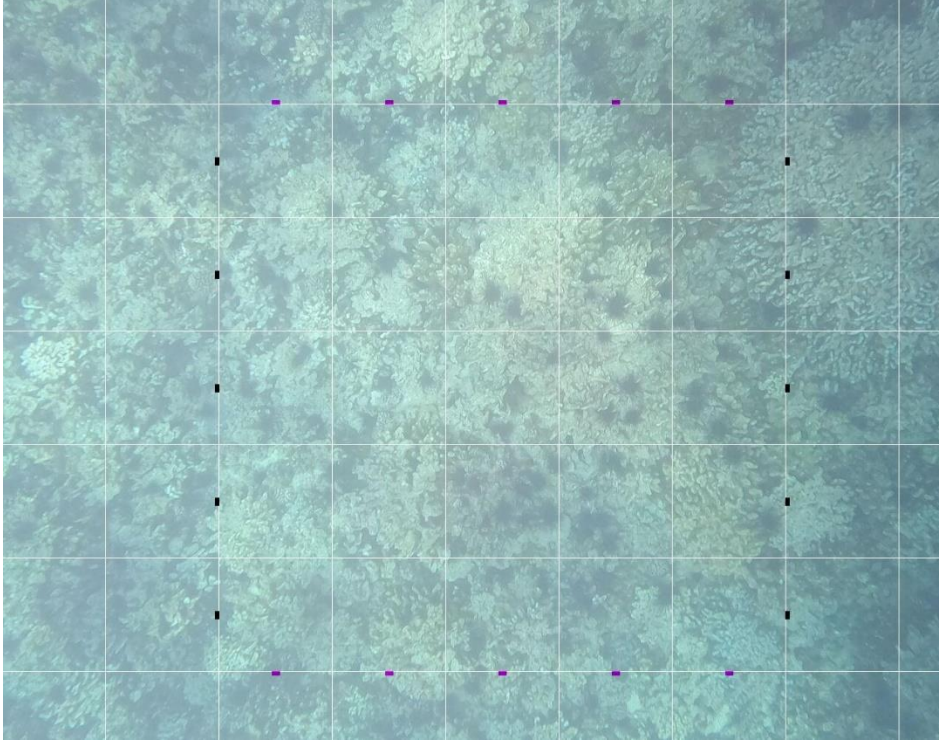
Figure 5: Example of photo transect image of a coral dominated patch on the north coast of Rapa Nui. Showing the square meter grid that had been added to record urchin density and cover data.

Model

Base model

A fully-parametrized and spatially-explicit model was created by Génin et al. (2023) which represents the coral reef communities of Rapa Nui. This model is a stochastic cellular automaton which describes the seafloor as a 2D lattice for which each cell is in one of three states describing its cover: coral, algae, or bare rock. To simplify mechanisms, cells relate to areas of about 20 cm². This is so that coral colony expansion for instance is modelled as something that spans multiple cells. At each time step, the state of each cell can change according to different transition probability equations. These equations describe the changes in the cover of coral and algae due to natural processes, namely their reproduction, lateral expansion and mortality. Some of these transitions depend on the neighbourhood of a given cell in the model. The states of the 4 neighbouring cells are thus considered and described by q_x where x is either a, b, or c for algae, bare and coral.

Two transition equations express the increase in algal cover of either organism, firstly the shift from bare to algae cover is defined by

$$P_{b \to a} = r_a(\alpha + (1-\alpha)\rho_a) + l_a q_a \qquad (2)$$

where r_a is the recruitment rate of the algae growing from spores which here is multiplied by the number of spores in the water column $\alpha + (1-\alpha)\rho_a$. ρ_a represents the density of algal cells in the landscape and α indicates the proportion of spores in the water column originating from outside of the landscape. Lastly, l_a describes the lateral growth of algae.

Secondly, coral establishment can be described as

$$P_{b \to c} = r_c \qquad (3)$$

where the recruitment rate is captured by r_c. Mortality is described by cells returning to the bare state. For the 'algae' state, this can be described by

$$P_{a \to b} = m_a + h_u g(\theta_c q_c + \theta_b q_b) \qquad (4)$$

where m_a describes the base mortality rate of algal cells, h_u the density of urchins in kg.m^{-2}, g is their foraging rate in m^2.kg^{-1} and θ_c and θ_b describe the preference for urchins to be in coral or bare areas, respectively. The values for theta had been determined by Génin et al. (2023) from 13 surveys done between 2013 and 2019 where urchin numbers had been registered as well as the microhabitat on which the quadrat had been placed. The average biomass per microhabitat were computed and the preference of urchins was calculated dividing the average biomass of a microhabitat by the general average biomass. A theta value of 1 would signify that the average biomass in a microhabitat is similar to that of the overall seascape. Finally, the mortality of coral cells is described by m_c as in

$$P_{c \to b} = m_c. \qquad (5)$$

Model simulations were run to investigate the effects of the different alterations to the system. For each run the system would be allowed to reach equilibrium by running it for half a million timesteps, then the next 2000 steps had their values averaged to reduce the impact of small perturbations in the data. The model was run varying the average urchin density in the model to characterize different levels of herbivory pressure.

Scenario creation

We altered the above 'baseline' model to consider the foraging behaviour of urchins, and its possible shift with environmental cues. Different scenarios were created to express individual behaviour switches and finally the different switches were combined in an 'all' scenario.

First, we used the video data to consider the different foraging rate of urchins in bare area relative to coral patches in a 'dual foraging' scenario. When determining the grazing pressure by sea urchins, different foraging rates g (Eq 4) were assigned to cells of coral or bare states. From the data only the displacement rates could be determined, however we assumed that urchin displacements and foraging rates are proportional to each another. Therefore the ratio between displacement rates was applied to the foraging rates that had been obtained in exclusion experiments (Génin et al., 2023). In scenario, sea urchins were assigned the foraging rate g_b if located in bare cells and the rate g_c to those in coral cells. g_b corresponded to the original g parameter in the formulation of the original model above (Eq 4), and g_c was adjusted using the ratio of displacement rate in bare to coral area, i.e. $g_b = r g_c$ (here $r = 2$ see Results section).

This transformed (Eq 4) to obtain the following equation

$$P_{a \to b} = m_a + h_u(g_c \theta_c q_c + g_b \theta_b q_b). \qquad (6)$$

Secondly, to consider the spatial aggregation of urchins in bare areas as observed in Figure 6, the distribution of sea urchins in different microhabitats was altered for urchins located in bare areas creating the 'aggregated' scenario. In the original model, the density of urchins h_u is fixed and constant for the whole lattice. Here, we let h_u vary over space, so that each cell in a bare state would at each time step have an urchin density drawn from the probability distribution as measured in 25 m² areas (see Methods above). This was multiplied by the average urchin density in the lattice h_u divided by the
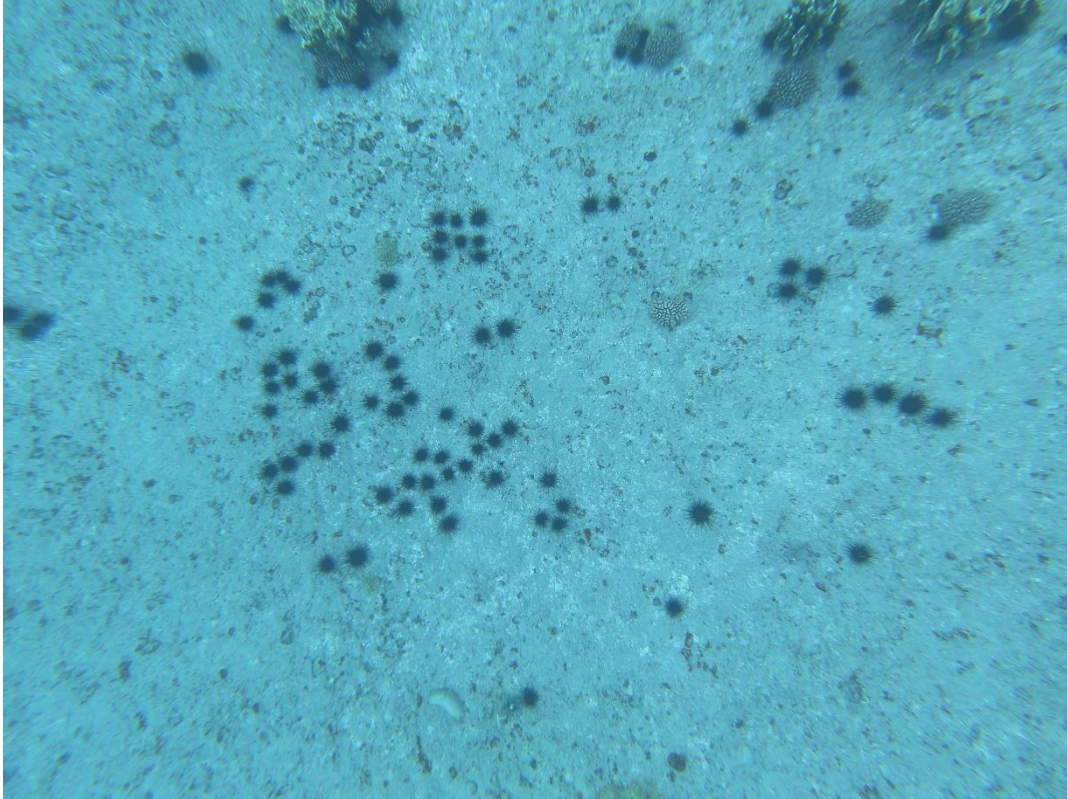
Figure 6: Illustration of urchin aggregation in bare dominated microhabitats. Image taken from a subtidal buoyant camera at the ''Experimental' site in November 2022.

average urchin density in bare spaces so that on average the bare cells would have as density h_u. This allowed h_u to vary spatially in a realistic way, with many urchin densities in cells close to zero, and a few at high densities. Urchins in coral cells were here assumed to follow a homogeneous distribution so h_u was kept constant for all coral cells in the lattice.

Thirdly, while Diadema urchins are known benefiting coral recruitment processes such as by reducing algal abundance, at high densities they have also been found to reduce recruit numbers as well as increasing the mortality of small coral fragments (Do Hung Dang et al., 2020; Qiu et al., 2014). An 'omnivory' scenario was proposed in which urchins were assumed to consume coral recruits at the same rate as they would forage for algae. The same rate was assumed due to the detritivore aspect of their diet. This was done by adding a term to equation (2) which gave:

$$P_{b \to c} = r_c\big(1 - h_u g(\theta_c q_c + \theta_b q_b)\big). \qquad (7)$$

We ran model simulations with the model in its original form, then added independently each of the above alterations ('dual foraging', 'aggregation' or 'omnivory') to investigate the effect of each aspect of urchin behaviour. We then combined all alterations to investigate their overall effect.

For each scenario, simulations were run on a 50 by 50 grid in which the initial cover of algae and coral were set at either 20 or 80% to investigate whether different initial configurations would lead to different final equilibrium states (i.e. alternative stable states). Simulations were run along a gradient of urchin density h_u, namely for number densities of 0.0, 1.8, 3.7, 5.5, 7.3, 9.2, 11, or 13 indiv.m^{-2} and final covers were averaged. For each scenario, this allowed the creation of bifurcation diagrams illustrating the equilibrium states of each cover type depending on the urchin density.

By running model simulations based on the altered model, we investigated whether the changes in urchin behaviour strongly altered the response of coral communities to variations in urchin density. We assessed how this new model compares in terms of presence of regime shifts or bistability. These comparisons will determine whether including the urchin behavioural shifts could significantly impact the dynamics of the whole community.

Model parametrization

The parameters used were previously obtained through experimental results and surveys gathered over the last 20 years (work done by A. Génin, 2023). The results of which have been listed in the following table.

Table 1: Parameters and their values used in the stochastic cellular automaton model. Variables with asterisk were determined from empirical data in this research, the others by Génin et al. (2023)

Variable	Description	Value used
r_a	Algal recruitment rate	1.79 wk^{-1}
l_a	Algal lateral growth rate	0.03 wk^{-1}
α	External portion of algal spores	0.01
ρ_a	Density of algae in the landscape	0.0181
r_c	Coral recruitment rate	1.31 x 10^{-3} wk^{-1}
m_a	Algal mortality rate	0.079 wk^{-1}
h_u	Urchin density	0, 2, 8 or 16 indiv.m^{-2}
g	Urchin grazing rate	0.19 m^2 wk^{-1}
θ_b, θ_c	Urchin preference of microhabitat	0.97, 1.03 (unitless)
m_c	Coral mortality	0.0001 wk^{-1}
g_c *	Urchin grazing rate in a coral microhabitat	0.19 m^2 wk^{-1}
g_b *	Urchin grazing rate in a bare microhabitat	0.38 m^2 wk^{-1}

Comparison of model and empirical data.

The photo transects were used to plot coral and algae covers against urchin density, giving an indication of the ecosystem's state on both western and northern coasts of Rapa Nui. The model had been parametrized based on empirical data from Rapa Nui, so the covers obtained from the models and the empirical data from the island were then compared. This was done to assess to what extent the model represents the ecosystem dynamics and suggest how it may be improved.
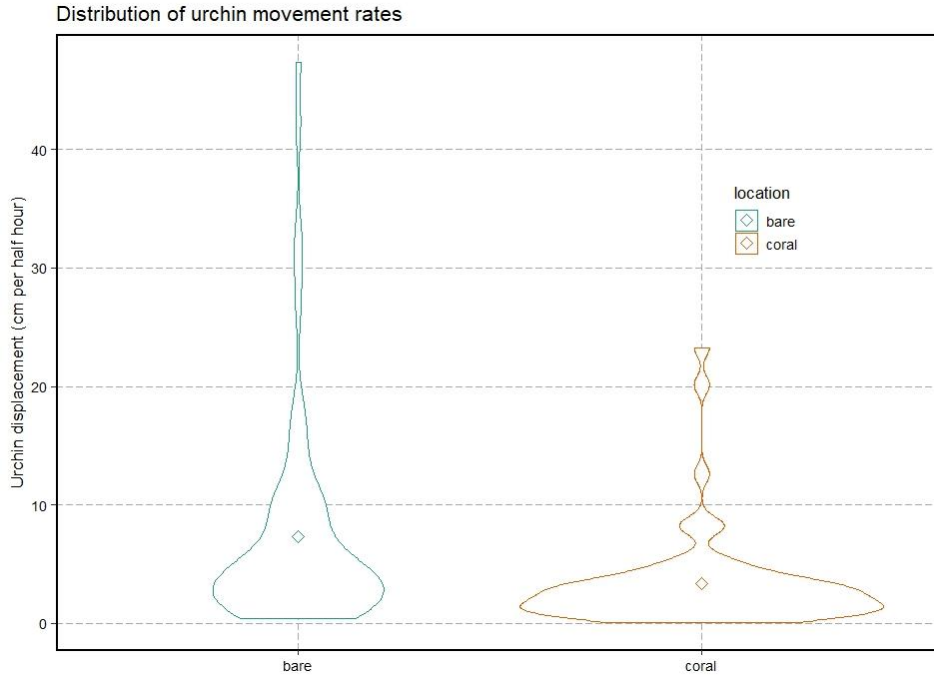
Figure 7. Violin plot of the observed displacement rates of *D. savignyi* in bare or coral areas obtained from the subtidal buoyant cameras.

Results

Empirical data analysis

Foraging rates

The change in microhabitat between the two types of microhabitats surveyed showed a change in the displacement rates of the *D. savignyi*. On average we obtained a rate of $d_b = 14$ cm.h^{-1} for foraging displacement in bare areas and $d_c = 7$ cm.h^{-1} in coral seascapes. So a ratio $r = 2$ was obtained as urchins travelled half as much in the coral microhabitats than in bare microhabitats (Fig 2). For the model alteration this created the 'dual foraging' scenario in which urchins were assigned foraging rates of $g_b = 0.38$ kg.m^{-2} or $g_c = 0.19$ kg.m^{-2} for bare or coral cells respectively. In bare patches lone sea urchins were also observed to join aggregations of sea urchins after which they would stop moving. The resulting average displacements in both types of seascapes showed large variances (Fig 7).

Urchin biomass

The average urchin body size was obtained for urchins for both microhabitats, finding as size $s_b = 5.9 \pm 1.4$ cm in the bare seascape and $s_c = 5.1 \pm 1.2$ cm in the coral seascape. Showing a slightly larger average size in bare areas albeit with a large standard deviation. The biomass would next be computed using the average individual urchin size of $s_u = 5.5 \pm 1.4$ cm. Which using the relationship from (Eq 1) produced an average individual urchin biomass of $m_u = 78$ g.
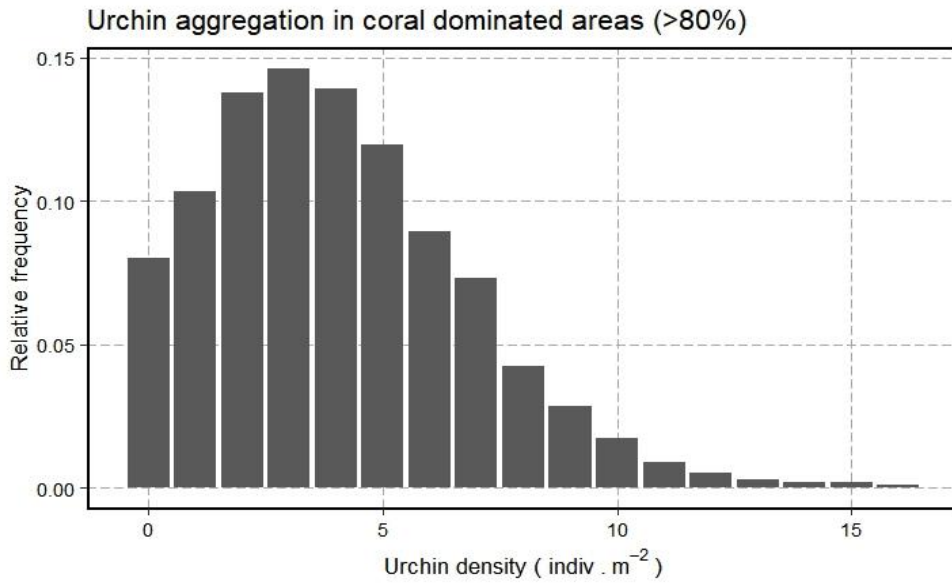
Figure 9: Distribution of urchin numbers per square meter in areas with at least 80% coral cover.
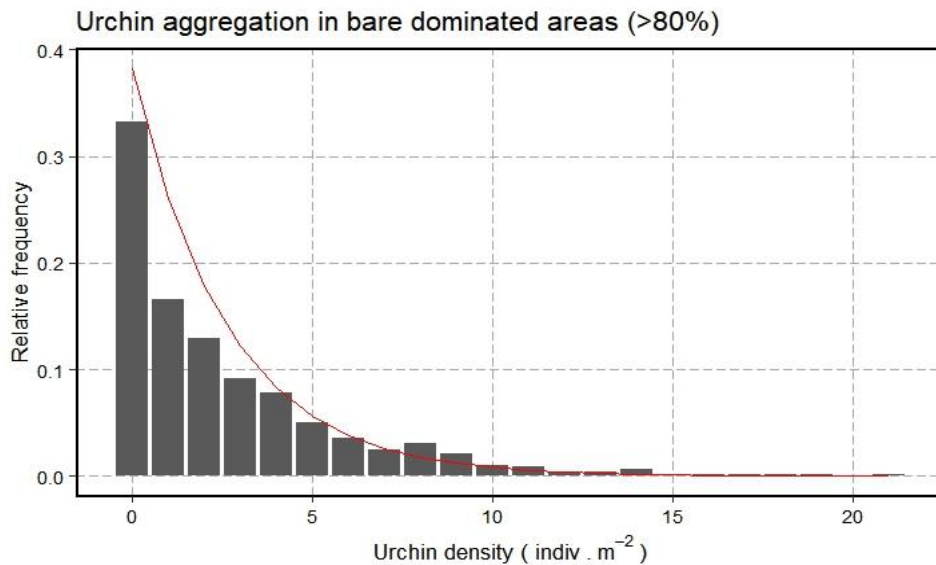

Figure 8: Distribution of sea urchins densities in areas with at least 80% bare cover. The red line shows the exponential fit of the data.

Urchin aggregation

The spatial distribution of sea urchins was found to vary between coral-rich and coral-poor microhabitats. In areas where coral occupied over 80% of the area a homogeneous distribution was observed (Fig 8). Here the urchin density followed a truncated normal distribution as the densities are always zero or above with average urchin density in a coral dominated habitat at $\overline{h_c} = 3$ indiv.m^{-2}.

On the other hand in mainly bare microhabitats, the urchin population was well-described by an exponential distribution the linear regression of its log transform obtained an R value of R = 0.95, and as p-value p = 3.5 e^{-14}. A rate of $\lambda = -0.30$ was found such that the probability of having a density of urchins x is given by $e^{-0.30x}$. Such distribution is highly skewed, which is consistent with a high occurrence of empty cells and occasional high densities (Fig 9), reflecting the aggregation of urchins in space.
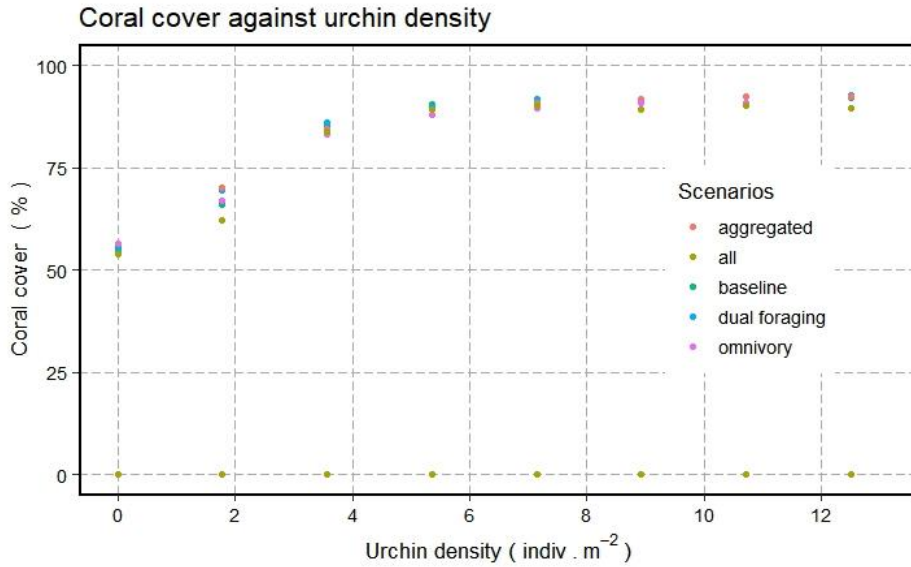
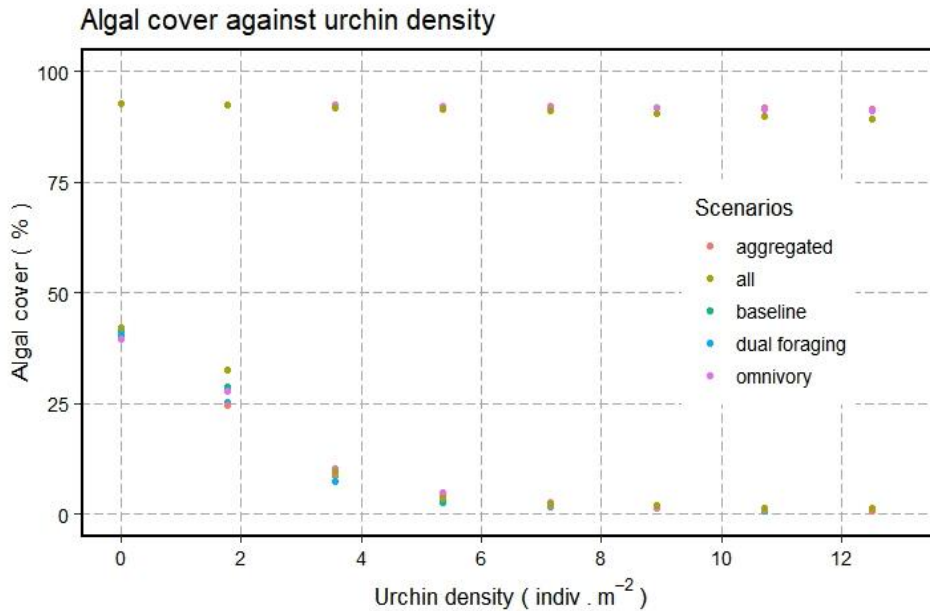Figure 11. Bifurcation diagram of coral cover against urchin density for all scenarios tested.

Figure 10. Bifurcation diagram of algae cover against urchin density for all scenarios tested.

Model

General model results

The model was run to evaluate the percentage cover for cells of each state (algae, coral, or bare) along gradients of urchin densities and different scenarios.

For all model variations, we observed two alternative stable states with either high cover of algae and low cover of coral, or vice-versa. The high-algae state was characterized by a cover of algae around 95% (Fig 11) where coral was absent, regardless of the urchin density h_u and the urchin behaviour scenarios, and bare areas within 7 to 11% cover (Fig 12). The low-algae state was characterized by a low, but variable cover of algae, from about 40 to 1% as h_u went from zero to 13 urchins m^{-2} (Fig 11). A high coral cover (above 50% for all values of h_u) (Fig 10), and a variable cover of bare area (from 4
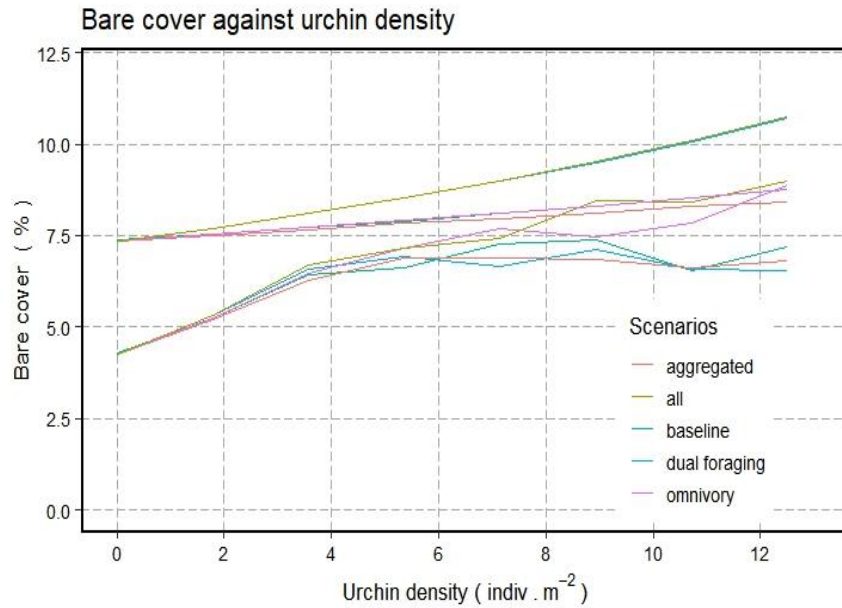
16

Figure 12. Bifurcation diagram of bare cover against urchin density for all scenarios tested.

to 8%) (Fig 12) were also observed in the low-algae state. The type of urchin behaviour did not seem to affect overall the above results, as all models followed the same response to urchin densities (Figure 5 and 6).

Comparison between the scenarios

Taking a closer look at the different scenarios we observed some variations. First looking at the high cover state of corals (Fig 15), the scenarios all seem to follow similar logistic growth curves albeit with differences in their growth. We observed that for both 'aggregated' and 'dual foraging' scenarios the coral cover increased at lower urchin densities than in the other scenarios, their rates of change also peaked at lower urchin densities (Fig 13). At higher urchin densities these scenarios converge towards the baseline scenario which appears to converge towards 92% above 12 indiv.m^{-2}. The omnivory scenario appeared to rise similarly to the baseline scenario but showed a peak coverage of 91% at 9 indiv.m^{-2} after which it declined. The combined scenario diverged the most from the baseline at low densities as the shift towards high coverage had its inflection point at a higher urchin density, it was also noted that the combined scenario showed the sharpest rate of change peak.

Next, the low cover state of algae as seen in Fig 11 showed that the different scenarios behaved similarly but opposite in the decline of algal cover as the urchin density increased. At higher urchin densities the algal cover is negligible however did not disappear like the low cover state of corals.
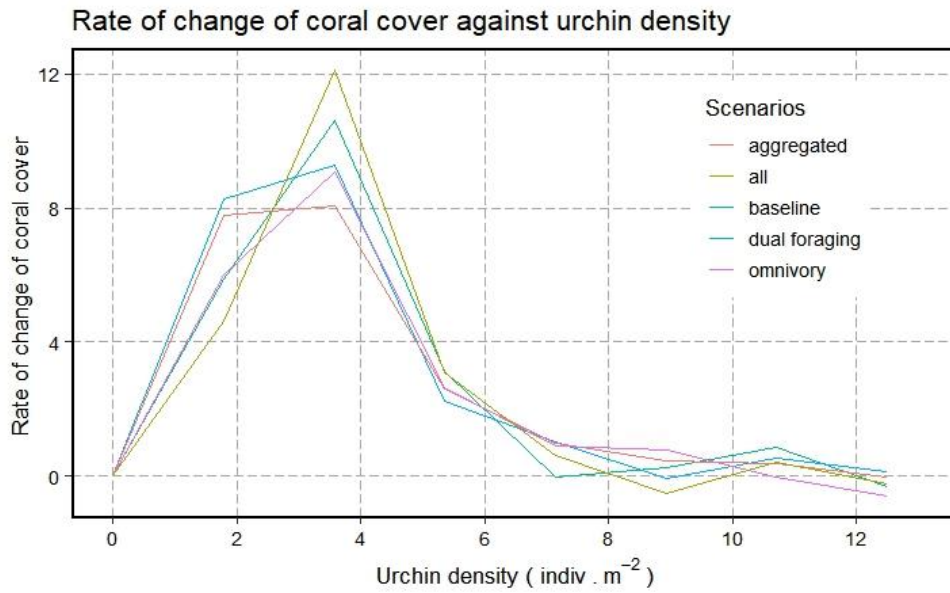
Figure 13 Rate of change of the coral cover plotted against urchin density h_u for all scenarios.
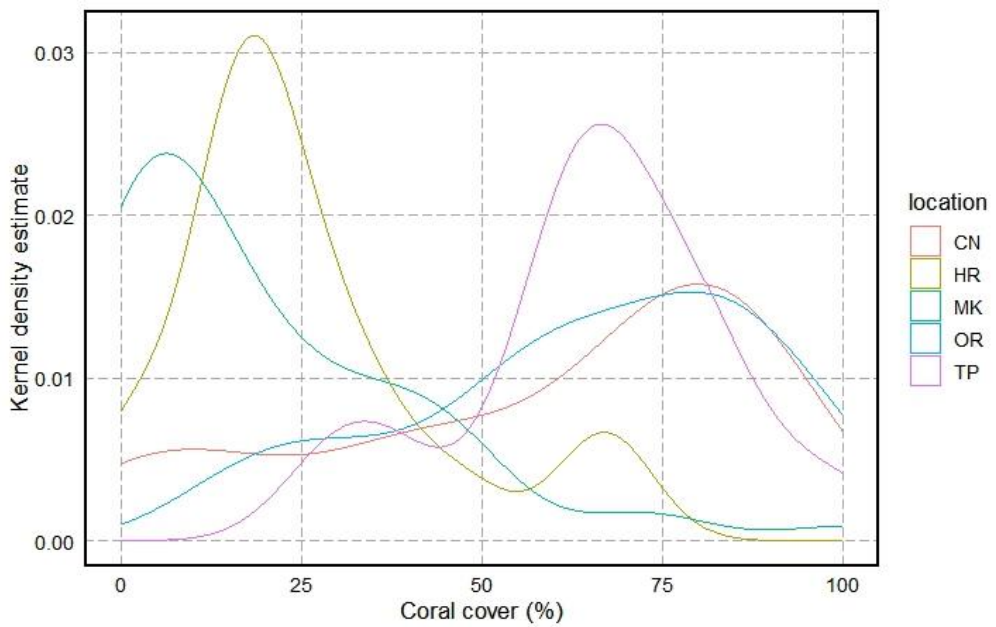

Figure 14: Kernel density estimate of coral cover at different locations along the coast of Rapa Nui.
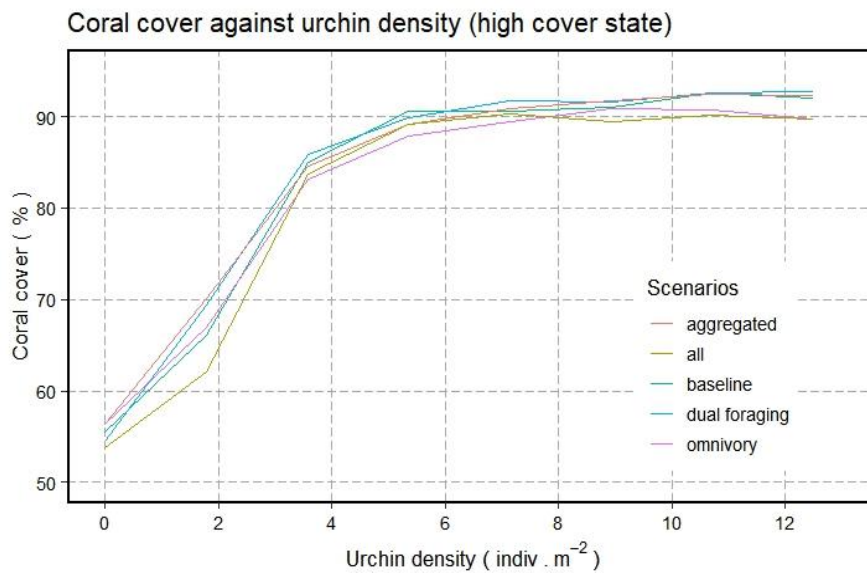

Figure 15 High coral cover state plotted against the herbivory pressure under different scenarios.
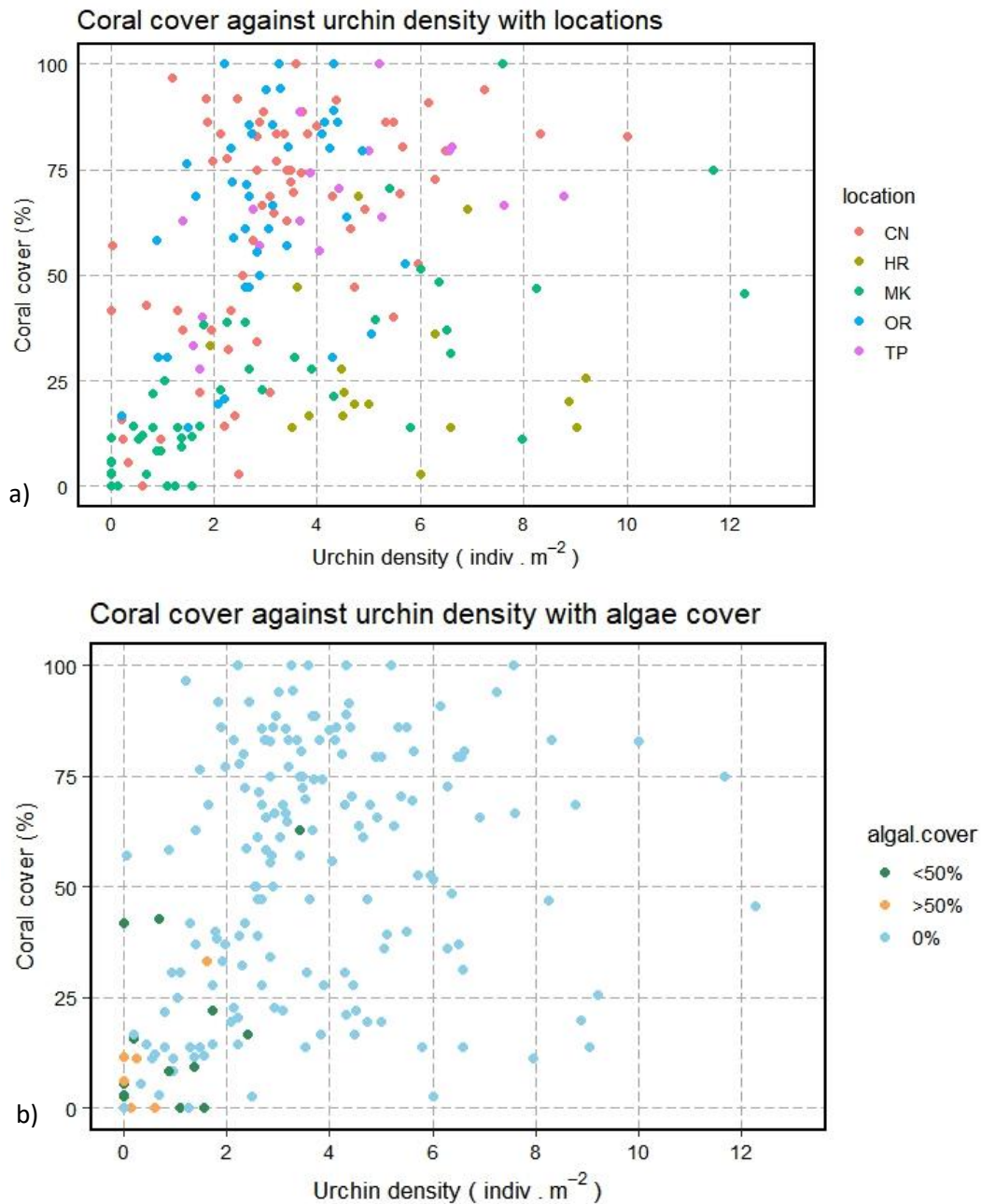
Figure 16. Empirical coral cover results plotted against the urchin density in the area. a) showing the location of the surveyed area and b) showing the algal cover of the same area.

Analysis of empirical data and comparison with the model

The photo transects generated information as to the spatial distribution of *D. savignyi* relative to the microhabitat. They also provided data that quantified the various seafloor covers for different sites on the north and eastern coasts of Rapa Nui. Various cover types were registered when analysing the images however it was at times difficult to differentiate between bare rocks, CCA, or boulders therefore only the coverages of algae and corals were analysed, while the other coverages were considered bare (CCA and boulders) or were excluded (sand, urchin and unknown).
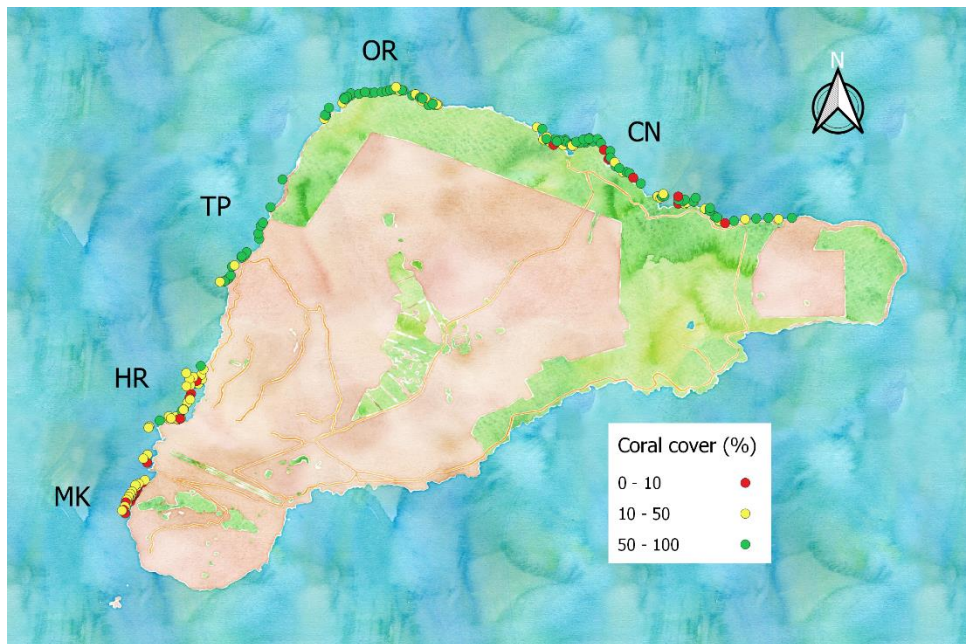
Figure 17. Map of Rapa Nui showing he survey locations and a visualisation of coral cover percentages around the island (created in QGIS).

From the coral cover against sea urchin density we could identify 2 modes (Fig 14), the first near 80% coral cover was observed mainly for the three northernmost locations surveyed (CN, OR and TP) although also observed at HR. A second mode of around 25% coral cover was also observed especially at HR. Although a third mode could be proposed at 0% coral cover especially for urchin densities below 2 indiv.m^{-2} (Fig 16a).

Algae was observed at all locations however only accounted for a small share of the total cover and was only dominant at sites with low urchin densities (Fig 16b). Bare areas were present at high frequency at many of the surveyed sites, this could be observed in Figure 16b as many sites marked by blue dots showed no algal cover and only bare coral and algal states were considered.

Geographically around Rapa Nui (Fig 17), we found that high coral coverage sites were primarily on the north coast (CN) and at Omohi-Rumoto (OR) on the northwestern coast. Low coverage of coral was mainly observed near Hanga Roa (HR) and Mataveri-Kaviti (MK) further south on the west coast. However all locations contained sites with high and low coverage of coral communities. On the west coast however the Tautara-Pyramide (TP) sites showed higher coverages in coral than at locations further south on the same coast.

The empirical data however contrasted with the model output especially with regards to bare rock. Indeed while the model only finds up to about 10% of bare cells, around Rapa Nui a third mode was observed with coral cover in a bare dominated seascape. Furthermore, the high cover state of algae showed no correlation between urchin density and algae cover while no high cover of algae was observed in the empirical data for high urchin densities.

Discussion

Urchin behaviour results interpretation

The behaviour of *D. savignyi* was shown to vary according to differences in biotic and abiotic changes in their habitat. Namely with regards to the presence or absence of coral communities and algae in its vicinity. Urchins located within coral microhabitats were found to be distributed homogeneously and with half the foraging rates of urchins in bare microhabitats. Coral communities offer protection for sea urchins from predators and strong currents as their complex structure includes crevices which serve as shelters (Zapata-Hernández et al., 2021). Being in a sheltered environment likely reduced the need of these urchins to travel large distances to feed as they remain protected from predators. These urchins most likely expressed a behaviour of passive grazing as these coral communities sustain high numbers of slow-moving urchins. Urchins in bare microhabitats showed more signs of an active eating behaviour due to their increased mobility needed to find food sources (Lauzon-Guay & Scheibling, 2007). In this microhabitat urchins sought safety by aggregating in numbers as they were left exposed to currents and predators. This behaviour has been proven effective at French Polynesia where their aggregation reduced mortality rates (Han, 2016). The accuracy of the empirical data was limited due to the movement of the subtidal cameras as well as the small numbers of urchins observed by those in bare microhabitats.

Scenario results interpretation

In general, individual shifts in the behaviour of sea urchins showed little impact on the overall dynamics in the ecosystem. Differences in final cover were small and could be explained by the stochastic nature of the model. This was especially the case for both the 'aggregated' and 'dual foraging' scenarios which considered either heterogeneous densities or increased herbivory in bare areas. These showed negligible differences from the 'baseline' scenario results which may be explained by the low proportion of cells in a bare state which at equilibrium accounted for 5 to 12% of the total cover at 13 urchins m^{-2}. In other words, as these effects are only effective in bare areas, and those were very little in the simulation outputs, our alteration of the model had overall little effect. The 'omnivory' scenario diverged the most from the 'baseline' namely at high urchin densities where the reduction in coral reproduction showed a negative trend in coral cover at high urchin densities. This was expected as it impeded the lateral expansion of coral communities in the lattice. However, it is worth noting that the effect was quantitatively very small, as even for high coral covers, only a reduction in coral cover of a few percents could be observed. Under realistic urchin densities, it is thus likely that this effect has a small amplitude. Finally the 'all' scenario diverged the most from the 'baseline' which was expected as it accounted for the most modifications in the model. However, the increase in bare area at higher urchin densities was significantly higher than the 'omnivory' scenario alone. This suggests that given an increase in bare areas within the seascape, urchin behaviours linked to these microhabitats became more important with regards to maintaining bare patches.

Comparison with empirical data and literature

Both the model output and the empirical data agree on the multimodality of coral covers and thus the multimodality of various seascapes. The two modes of either high algae cover, or high coral cover obtained by the model were also observed in the empirical data. The shift between the two modes occurs at an urchin density of about 2-4 indiv.m^{-2} in the empirical data as below this density corals are rarely observed at high densities. This was also observed in the model outputs. Low urchin densities are thus required for large macroalgae patches to establish. On the contrary for coral communities to dominate the seascape, urchin densities above 2 per square meter are required at Rapa Nui.

Coral coverage on the north coast showed similar results with most sites dominated by coral coverage. This could be explained by a similar wave exposure along the coast. However on the western coast three modes were observed. Increased wave exposure at the southernmost part of the west coast can explain the low cover of corals observed there. However wave exposure alone could not explain the differences in coral cover between HR and TP sites, the latter of which showed coral coverages like the northern coast. Similar urchin densities were furthermore found at these two locations. Pressures such as pollution or eutrophication from waste disposal would be more important around Hanga-Roa. Since these pressures affect coral recruitment negatively this could help explain the increased frequency of bare patches.

The proposed 'omnivory' scenario showed a decline in coral coverage due to urchins feeding on coral recruits however the observed coral coverage cannot be reflected by urchin omnivory alone. High densities of Diadema urchins have also been shown to physically damage hard coral communities of which principally recruits and small fragments (Do Hung Dang et al., 2020; Qiu et al., 2014). Such pressures would not vary much between similar geographic locations as we expect natural external factors to be similar. We can suggest that the combination of human pressures at Hanga Roa and the high density of urchins led to a situation unsuitable for coral establishment causing a bare dominated seascape at that location. Due to increased tourism at Easter Island added pressures from fishing and waste disposal could cause a decline in coral cover at other locations especially after disruptions to coral communities for instance from bleaching events (Figueroa & Rotarou, 2016; Zylich et al., 2014).

Future direction

Furthermore large disruptive events such as storms or heatwaves were not included in this model, these have the capacity to reduce coral coverage (Hughes, 1994). Such a disruption could create a bare microhabitat in which the high urchin densities may impede algae and coral communities from establishing. In a future study, the inclusion of such disruptions could indicate the importance of sea urchins in coral community recovery as currently the coral communities could only reduce due to their low mortality rate. Finally, the photo transects offer a snapshot in time of the shallow seafloor composition at Rapa Nui. A repetition of these surveys over time would further allow an understanding of the impacts by biotic and abiotic factors on coral community dynamics.

Conclusion

In this project, the shifting behaviour of *D. savignyi* sea urchins were studied with respect to their microhabitat. These urchins were observed to aggregate and forage twice as fast in bare dominated microhabitats compared to those dominated by corals in which they were more abundant. Around the island of Rapa Nui, three modes were found when analysing the empirical coral coverage at locations on the north and west coasts. These consisted in either coral or algae dominated microhabitats and a third showing a mix of bare and coral coverage. As main herbivory pressure, an urchin density of about 2 indiv.m^{-2} was observed as the minimum for coral communities to dominate the seascapes. Although on the southernmost section of the west coast bare dominated seascapes were observed likely in response to increased wave exposure and human settlement pressures. Testing various behaviour shifts by these urchins in a stochastic cellular automaton model showed little impact of the increased foraging or aggregation in bare microhabitats likely due to the lack of bare cells in the model as large die-off events were not considered. However the 'omnivory' scenario showed that for high densities of urchins, their bio eroding impact on coral communities could decrease overall coral coverage in the seascape. In future studies, a larger timeframe of empirical data as to the geographical coverage of different microhabitats would allow for a better understanding of the impact of urchins on the coral communities at Rapa Nui.

Acknowledgements

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