



# Examining the successional role of *Montipora aequituberculata* on remote, post-disturbance equatorial reefs

Brenna Stallings<sup>1,\*</sup>, Clinton Edwards<sup>2</sup>, Nicole Pedersen<sup>2</sup>, Tyler Chidsey<sup>1</sup>,  
Ethan Deyle<sup>1</sup>, Les Kaufman<sup>1</sup>, Peter Gawne<sup>3,4</sup>, Sangeeta Mangubhai<sup>5</sup>,  
Stuart Sandin<sup>2</sup>, Randi Rotjan<sup>1,6</sup>

<sup>1</sup>Boston University, Boston, MA 02215, USA

<sup>2</sup>Scripps Institution of Oceanography, UC San Diego, La Jolla, CA 92093, USA

<sup>3</sup>New England Aquarium, Boston, MA 02110, USA

<sup>4</sup>University of Massachusetts Boston, Boston, MA 02125, USA

<sup>5</sup>Talanoa Consulting, Suva, Fiji

<sup>6</sup>Blue Nature Alliance, Arlington, VA 20301, USA

**ABSTRACT:** Corals are dying globally at unprecedented rates and scales, and we are fast losing our ability to study the ecological dynamics of healthy, successional mature reef communities. Insight into species-specific competitive dynamics is a necessary tool for assessing reef growth patterns and trajectory. Based on terrestrial successional frameworks, it is currently assumed that fast-growing corals catalyze post-disturbance regrowth and are eventually replaced by competitive, slower-growing species. To test this hypothesis, we assessed the fate of a dynamic, fast-growing, common Pacific coral, *Montipora aequituberculata*, through photogrammetric analysis of repeated large-area imaging. We used this technology to track ~600 colonies across 6 equatorial islands spanning 2 time points, examining whether colonies of *M. aequituberculata* were more typically overgrown by other species or able to maintain space and prevent overgrowth by other taxa. To accomplish this goal, we examined temporal dynamics from past-to-future and future-to-past, a new approach for addressing these questions. We found that *M. aequituberculata* colonies are competitively dominant against ruderal and other competitive taxa but will yield space to stress-tolerant taxa on post-disturbance reefs. Interestingly, we found that *M. aequituberculata*'s island-scale interaction patterns — whether colonies successfully overgrew or were overgrown by other benthic taxa — did not necessarily correspond with *M. aequituberculata*'s island-scale growth or loss patterns, highlighting local, site-level ecological complexity. Detailed examination of species interactions across spatial scales helps provide a mechanistic understanding of benthic community changes. Understanding and predicting these changes is useful for projecting reef recovery patterns, paving the way toward improved ecological interventions in a changing world.

**KEY WORDS:** Coral reefs · Competition · Succession · Photomosaics · Photogrammetry · Recovery · *Montipora aequituberculata*

## 1. INTRODUCTION

Successional dynamics have been described in many ecosystems, including grasslands (Clements 1904), boreal forests (Bergeron & Dubuc 1988, Taylor et al. 2020), tropical rainforests (Bazzaz & Pickett

1980, Mo et al. 2013), and marine intertidal ecosystems (Murray & Littler 1978, Farrell 1991, Mayakun et al. 2022). However, despite this long history, the patterns of successional progression in coral reef benthic communities post disturbance have not been well described or field tested (Ohba et al. 2008, Sandin &

Sala 2012, Horwitz et al. 2017, Steneck et al. 2019). Coral reefs are dynamic, diverse, species-rich ecosystems (Crisp et al. 2022) that experience rapid, episodic change driven by disturbances such as wave action, storms, predation, and disease (Nyström et al. 2000). These disturbances are disruptive but also create opportunities, leading to dynamic turnover of species at a site and shaping the composition and resilience of communities over time. Post-disturbance dynamics emerge as ecological succession, which is a sequenced progression of taxa and community turnover exhibiting patterns of replacement and temporal dominance that change through waves of taxonomic replacement (Prach & Walker 2011).

To understand patterns of ecological succession on reefs, the interaction dynamics (e.g. dominance of any given taxon compared to another on the scale of individuals or populations, sometimes context-dependent) must be understood. Researchers often look at coral species interactions over time to determine which species will dominate in a given interaction pair (Sheppard 1979, Dai 1990, Evensen et al. 2015). Classically, disturbance–recovery patterns on coral reefs are intermittent and localized, enabling fast larval recruitment and initiation of ecological succession processes (Alvarez-Filip et al. 2013, Adjeroud et al. 2016). However, climate change has fundamentally altered disturbance–recovery patterns via increased storm frequency and intensity, mortality-inducing high thermal stress events, and major disease and predation outbreaks (e.g. Richmond 1993, Rogers 1993, Gouezo et al. 2015, and others) thereby making it more difficult to predict community transition probabilities and possible successional trajectories on a reef (Haapkylä et al. 2013, Gouezo et al. 2015, Mari et al. 2017, Johnston et al. 2020).

The study of altered successional dynamics in an era of global change is an emerging discipline across both terrestrial and marine ecosystems (Gouezo et al. 2015, Catullo et al. 2019, Heberling et al. 2019, Johnston et al. 2020). Many mechanisms of ecological transition are context-dependent (Prach & Walker 2011) and are not well described across taxa (Koffel et al. 2018). Although there has been foundational work on coral species interactions (Connell et al. 2004, Horwitz et al. 2017), there are still debates about how to functionally classify corals *in situ* (Darling et al. 2012) and varied methods to study their interactions (Sandin et al. 2020, George et al. 2021, Olinger et al. 2021, Doropoulos et al. 2022). Furthermore, many taxa are understudied, leading to an incomplete understanding of species interactions and growth dynamics in natural communities. As such, there is a renewed urgency in studying the dynamics

that drive reef growth, recovery, and succession in remote, uninhabited locations that still have remnants of natural dynamics, to gain insights needed to craft conservation strategies (e.g. Prach & Walker 2011, Pulsford et al. 2016, Sandin et al. 2020, Ferrari et al. 2021).

Remote, uninhabited equatorial coral reefs are some of the most intact, resilient reef ecosystems currently remaining (Sandin et al. 2008). One common coral found on central Pacific reefs is *Montipora aequituberculata* (Veron 2000), which is typically classified as plating (e.g. Browne 2012, Browne et al. 2013, Evensen et al. 2015), although it can also be found in encrusting, foliose, and laminar forms (Veron 2000). In Okinawa, Japan, and Moorea, French Polynesia, *M. aequituberculata* has been observed to spatially outcompete *Porites lutea* corals using mesenterial filaments, regardless of  $p\text{CO}_2$  levels (Evensen et al. 2015). In contrast, however, another study found that all tracked *M. aequituberculata* colonies ( $n = 34$  corals) in Kiritimati (Christmas) Island, Kiribati, experienced mortality following an extreme thermal event compared to full survival of *Porites lobata* colonies (McDevitt-Irwin et al. 2019). Thus, *M. aequituberculata* can be robust (Evensen et al. 2015) and vulnerable (McDevitt-Irwin et al. 2019) in different environmental contexts in addition to being common (Veron 2000) and fast-growing (Browne 2012). As such, *M. aequituberculata* is an interesting coral to examine in terms of successional trajectories and species turnover.

The outcome of species interactions post disturbance can shape subsequent community trajectories (Adjeroud et al. 2016). As species compete for newly available open space, the outcomes of these interactions drive patterns in early successional stages of recovery (Alvarez-Filip et al. 2013, McNamara et al. 2019). Not all fast-colonizing species have the same characteristics, and thus different species can influence the trajectory of reef recovery by influencing reef community dynamics (Harrison & Booth 2007), which will in turn affect reef function. Survival of larval recruits (Adjeroud et al. 2016) or transplanted coral (Shaish et al. 2010) can vary strongly on a local scale and will determine the starting spatial and population dynamics of the reef. The opportunity to study these types of ecological dynamics on relatively intact reefs is increasingly important as reefs experience altered biological communities as a result of global change (Elma et al. 2023, van Woessik & Schlesinger 2023, Datta et al. 2024).

In this study, we leveraged the opportunities provided by little-disturbed Pacific islands to study competition and hierarchy dynamics in coral communities, with a focus on *M. aequituberculata*. We

examined competitive hierarchies of *M. aequituberculata* within community networks (Sutherland 1974, Jackson & Buss 1975, Buss & Jackson 1979) across scales: within and across sites on reefs, islands, and archipelagos. To do so, we first tracked whether *M. aequituberculata* overgrew or was overgrown by nearby corals to test whether it acts as a competitive dominant or a temporary spaceholder that facilitates the growth of other species. By visiting the same sites over time and using large-area imagery (Edwards et al. 2023), we tracked the growth of *M. aequituberculata* as well as space lost (or gained) relative to neighboring corals. In essence, we asked which community spaceholders were able to displace focal colonies versus which community spaceholders were able to be displaced by focal colonies. We followed the successional definition of Grime (1977), who placed species along 3 axes that are considered ruderal (weedy), competitive, and stress-tolerant. This allowed us to determine if *M. aequituberculata* is a successional competitive or facilitative species to help sequence successional progressions.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

We observed community and successional dynamics on coral islands and atolls in the central Pacific; specifically, on 2 archipelagos: (1) Phoenix Islands (near the equator) and (2) Southern Line Islands (nearer the Tropic of Capricorn). Within the Phoenix Islands, we collected data from Howland (in the Pacific Islands Heritage Marine National Monument, formerly 'Pacific Remote Islands Marine National Monument'; Federal Register 2025), Enderbury, and Nikumaroro (in the Kiribati Phoenix Islands). In the Southern Line Islands, we collected data from Millennium, Vostok, and Flint (Fig. 1). Two sites at each island were used, and each site was visited twice (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m753p037\\_suppl.pdf](http://www.int-res.com/articles/suppl/m753p037_suppl.pdf)). All sampling was conducted between 2012 and 2018, with the duration between the first and second time points ( $t_1$  and  $t_2$ , respectively) differing across sites as follows: the Kiribati Phoenix Islands were visited in 2012 and

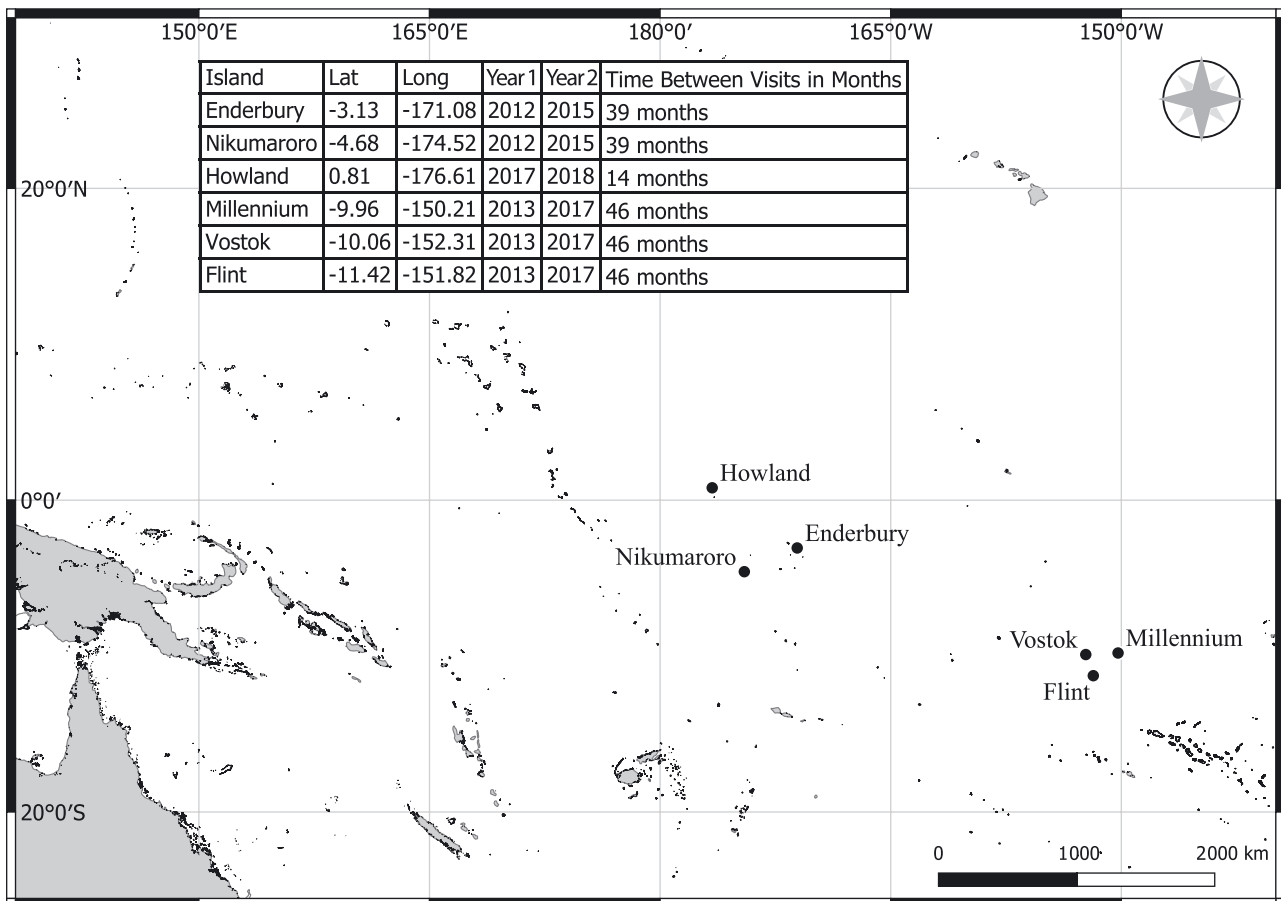


Fig. 1. The 6 islands used in this study: Enderbury, Nikumaroro, and Howland are islands in the Phoenix Islands; Vostok, Flint, and Millennium are part of the Line Islands

2015 (39 mo apart); the Southern Line Islands were visited in 2013 and 2017 (46 mo apart); and Howland was visited in 2017 and 2018 (14 mo apart) (Fig. S1). Other than global climate influences, the Phoenix and Southern Line Islands have been protected from local human disturbance during their period of full closure (Fig. 1), although waters in the Kiribati Phoenix Islands were reopened to human activity in 2023 (Kittinger et al. 2024). When protected, these living laboratories enabled the study of coral reef dynamics without local anthropogenic influence (Obura & Mangubhai 2011, Rotjan et al. 2014). Both archipelagos suffered major mortality from thermal stress and subsequent bleaching in 2002, 2010, and 2015 (Obura & Mangubhai 2011, Vargas-Ángel et al. 2011, Brainard et al. 2018, Fox et al. 2021), causing the damaged reefs to be in a recovery phase, while still protected, during our study (2012–2018).

## 2.2. Large-area imaging overview

To study competitive dynamics between *Montipora* and neighboring taxa, we implemented an approach known as large-area imaging (Edwards et al. 2023). This approach uses highly overlapping imagery collected in the field to create 3D models, from which orthoprojections (e.g. 2D planar projections) of sites can also be created using photogrammetric software. Time-series models from each site were co-registered, allowing changes in coral size to be tracked through time in a spatially explicit manner and with a high degree of precision (Fig. 2, Fig. S2).

## 2.3. Image collection

Using SCUBA, 10 × 10 m plots were established at ~10 m depth on the fore reef at each location. As sites were repeatedly visited, we marked each site using GPS at the left center mark of the plot directly above permanently installed steel pins on the seafloor to aid in plot relocation. Images were collected by SCUBA divers using a pair of Nikon D7000 16.2-megapixel DSLR cameras mounted to a fixed frame (Sandin et al. 2023). We used 2 cameras to simultaneously capture 2 different fields of view at different focal lengths but in the same frame. One camera had an 18 mm length lens with a wide view angle to allow high overlap (>80%) between images; these images were used to create the 3D models. The other camera had a 55 mm lens to capture higher resolution images, which were not used to make the 3D models but instead to facilitate detailed analysis of taxonomic identification and

precise definition of colony borders. The cameras were set to take 1 photo s<sup>-1</sup> while a diver swam a lawn-mower pattern above the reef. The diver swam along the x-axis of the plot, turned and swam about 1 m along the y-axis, then turned and swam another pass along the x-axis. After covering the entire plot, the same pattern was used but while swimming along the y-axis, creating a crisscross pattern. By keeping a constant speed (~5–7 m min<sup>-1</sup>) and height (1.5 m) above the reef, ~2500 images were collected per camera with sufficient image overlap (at least 10 images of each benthic point on the reef) to allow generation of a 3D model. To provide scale and orientation with respect to the sea surface (see Section 2.4), scale bars (marked PVC and dive weights) were deployed within the plot during imaging, and depth measurements were collected at 6 additional markers also deployed inside the plot.

Additional details on underwater setup and image capture are described in other papers that followed the same protocols (Fox et al. 2019, Kodera et al. 2020, Sandin et al. 2023).

## 2.4. Model creation

The software Metashape (Agisoft) was used to create a dense point-cloud 3D model following the protocols described in Sandin et al. (2023). Point clouds were then imported into Viscore (Petrovic et al. 2014), where the 3D models were color-corrected, scaled, and oriented using depth information (Sandin et al. 2020, Cook et al. 2023). Models were then co-registered in Viscore using landmarks including permanently installed markers as well as natural landmarks such as distinctive rock and coral formations. The 3D models were then orthorectified and exported from Viscore at a resolution of 1 mm pixel<sup>-1</sup>. Exporting 2D map views directly from co-registered 3D dense point clouds ensures precise global alignment and eliminates local distortion associated with blending found in orthophotomosaic images (Naughton et al. 2015, Edwards et al. 2023) (Fig. 2). We measured our natural landmarks and installed benthic markers across years and found that the same distances measured between time points had less than 2 mm of error.

## 2.5. Data extraction

To ensure that we could examine the fate of colonies from each time point (noting that some colonies in  $t_1$  might not exist in  $t_2$  and vice versa), we randomly

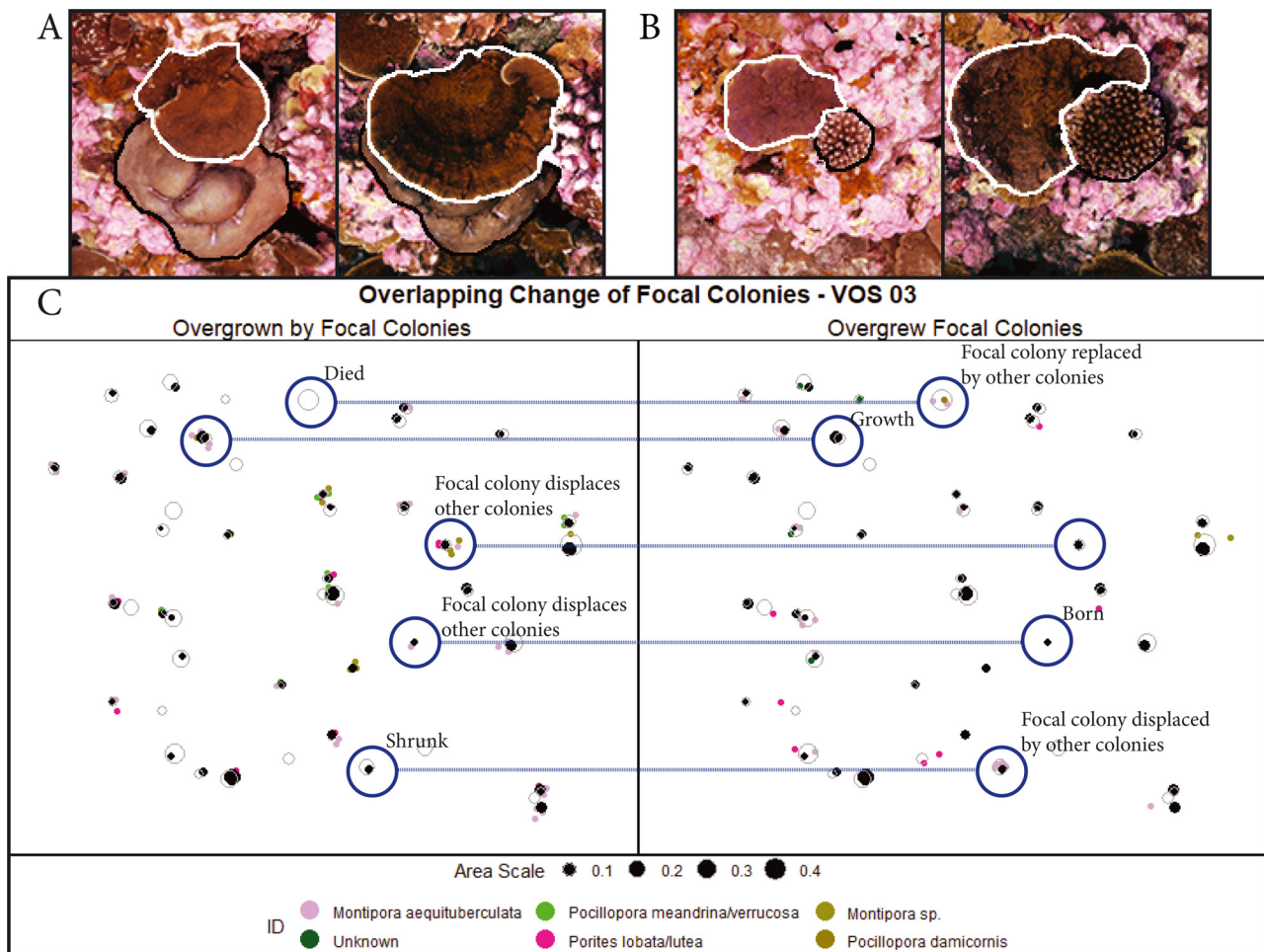


Fig. 2. Example of a colony of *Montipora aequituberculata* (A) overgrowing another coral and (B) being overgrown by another coral. Left images: first visit; right images: same corals the following visit. The colonies have been outlined for emphasis: white: focal colony; black: interacting colony. (C) Example of the interactions of focal colonies with surrounding colonies. Gray circle: size and central location of focal colonies the first year; black dots: the colony in the second year. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies; colored dots on the right mark the location and species of colonies that overgrew the focal colonies. Representative colonies have been marked in both years. Similar graphs for the other islands can be found in the Supplement (Figs. S6–S11)

selected 25 focal colonies of *Montipora aequituberculata* at each time point, for a total of 50 colonies per site. To achieve random selection, we generated 25 points within the overlapped reef area between years and selected the colony of *M. aequituberculata* closest to each point to mark as a focal colony. The 2 sites at Nikumaroro did not have 50 colonies each, so all available colonies were used ( $n = 73$ ).

We used TagLab (v.2022.04.21) to track the planar area of focal colonies and their neighbors (via digital segmentation) on the orthoprojected reef images (Table S2). Once each colony was segmented, the colony was located in the (co-registered) subsequent time point and again segmented to derive planar estimates of colony size at each time point (Fig. 2). Col-

onies whose absolute change in area was positive in the second time point were considered to have grown, while those whose area was smaller were considered to have shrunk. As such, this depiction integrates over any growth or shrinkage a colony might have experienced during the sampling interval to express an absolute value of areal change. If the colony was only present in one of the time points, it was assigned a fate of 'born' (area  $t_1 = 0$ ) or 'died' (area  $t_2 = 0$ ). Taxonomic identification was assigned to each colony using reference images. To ensure that all relevant colonies were completely digitized, we initiated a quality-control protocol whereby at least 2 people thoroughly checked the segmentation of colonies and their interacting partners.

## 2.6. Looking forward and backward in time

To determine potential taxonomic patterns of spatial competition, we next recorded changes in area between focal and neighboring colonies. Where there was a loss of area of a focal colony (or if a colony died), the species and area of the neighboring colonies were recorded as well as the area of the focal colony overgrown by that neighbor. Conversely, if a focal colony grew or was born in the second time point, the species and area of the neighboring colonies were recorded as well as the area of neighboring colonies that were overgrown by the focal coral (detailed in Section 2.7). It is important to note that selecting focal colonies (detailed in Section 2.3) from both time points was necessary to enable analysis both forward and backward in time and allowed us to capture corals that were 'born' after the first visit. Finally, neighboring colonies were assigned a life history strategy of weedy, competitive, or stress-tolerant as defined in Darling et al. (2012) (Table S3).

## 2.7. Data analysis

To consider colony size change over time in relation to initial colony starting size, we calculated the proportional change of colony area from  $t_1$  to  $t_2$  using the following formula:  $(\text{area in } t_2) / (\text{area in } t_1)$ . We then accounted for the time between visits by dividing the data by the number of months between visits to create normalized comparisons.

To place focal colony interactions in the context of the overall reef community, we calculated benthic community composition using Coral Point Count (v.4.1, 2006). We randomly placed 100 points on each site's orthoprojection each year and identified benthic cover to coral species or general category (sponge, macroalgae, coralline algae, unknown live cover, and other cover) as appropriate.

Data, including area measurements for colonies in each time point, taxonomic identity, and location, were imported into R (v.3.6.1; R Core Team 2021) as .csv files for analysis. Data were found largely to violate assumptions of normality, so non-parametric statistical tests were used on comparisons of means. To determine whether species interacting with focal colonies of *M. aequituberculata* were consistent, we used  $\chi^2$  goodness-of-fit tests to determine whether the observed number of interacting species was consistent across all 12 sites. Additionally, we calculated whether various taxa were more likely to overgrow or be overgrown by focal colonies using another  $\chi^2$  goodness-of-

fit test by comparing the ratio of overgrown colonies to the colonies that overgrew *M. aequituberculata*, followed by Pearson's post hoc tests to verify significance. To investigate areal change in colonies across time points at a site, we used Wilcoxon tests to compare the area in  $t_1$  to that in  $t_2$ . To investigate the growth rates and fate of *M. aequituberculata* colonies, we compared the change in area at each island and also examined the number of colonies that were recruited (born), died, grew, or shrank, using a Kruskal-Wallis test followed by Dunn's multiple comparison tests. To investigate how the starting size of colonies affected size trajectory (change in area) over time, we used multiple regressions and Spearman's rank correlation to regress starting size by area change for focal colonies across each island. Normalized fold change was calculated as follows:  $[(\text{area in Year 2}) / (\text{area in Year 1})] / (\text{months between visits})$ . To create dominance hierarchies, we compared the number of times each interacting species successfully overgrew or was overgrown by *M. aequituberculata* using binomial regressions (bbmle, v.1.0.25; Bolker & R Core Team 2022) and calculated the percentage of 'wins' of *M. aequituberculata* as the probability that *M. aequituberculata* would be dominant. To calculate the area gained or lost between focal colonies and their interacting partners, PNG files containing the segmented coral information were imported into R. These files allow for the colonies between years to be more closely examined while keeping the spatial relationship between years provided by TagLab. Using these images as the base, pixels that contained focal colonies in one year but not the other were found, representing the areas that focal colonies gained or lost. By identifying interacting corals found in these spaces and the amount of area that was exchanged, we were able to determine how much area *M. aequituberculata* gained on or ceded to other species on the reef. Focusing on only these sections, the percentage of area that was lost or gained to each species or empty space was calculated.

## 3. RESULTS

### 3.1. Patterns of community composition

The benthic cover at each of the study sites was characterized by relatively high live coral cover, which ranged from 52 to 96% of the benthos, with an average of 84% (Fig. 3A,B). To more closely examine the coral assemblage composition, we estimated the relative abundance of coral taxa (Fig. 3C,D) and found that richness and abundance varied by site, ranging from 4 (Nikumaroro and Flint) to 11 taxa

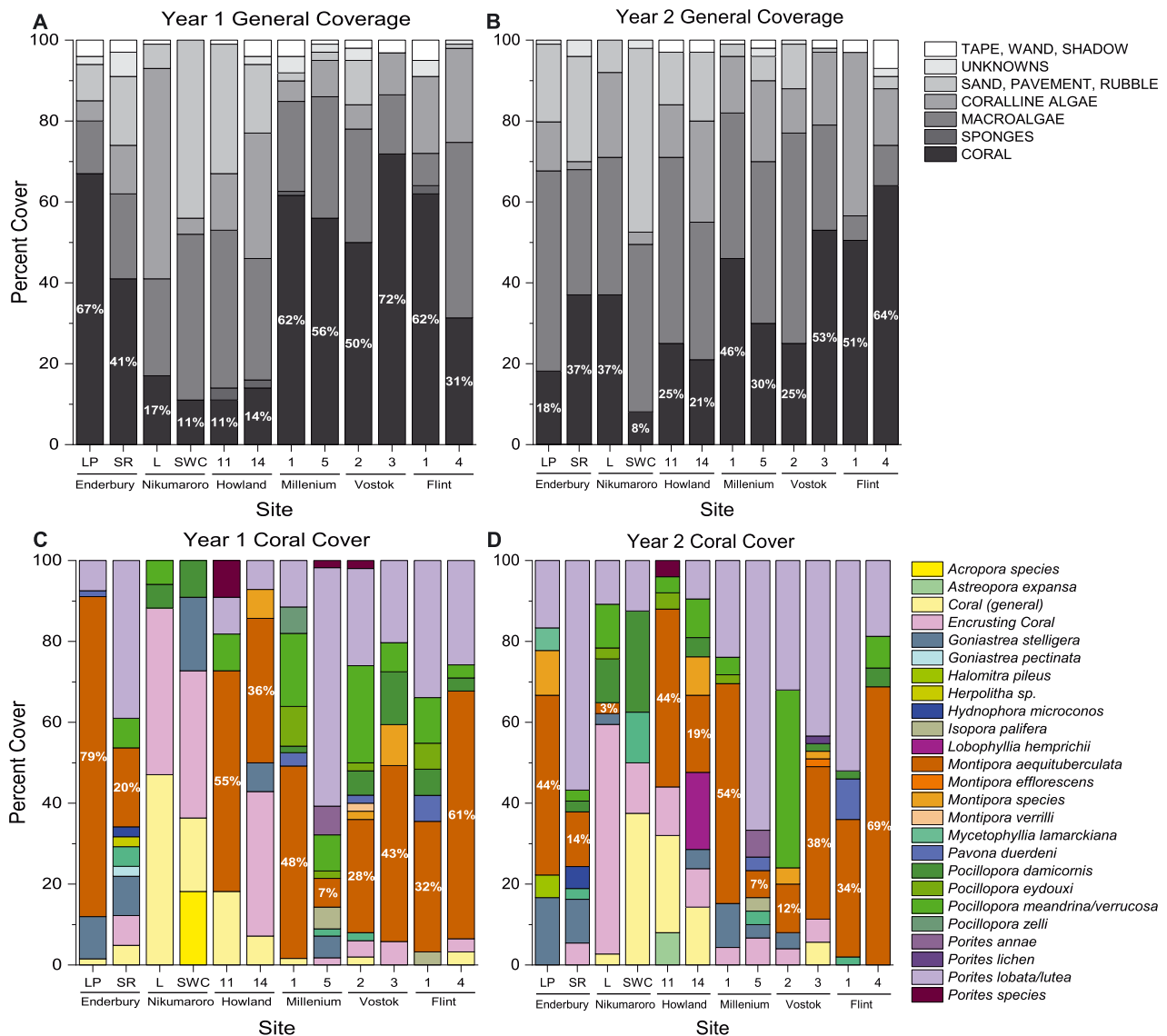


Fig. 3. Live coverage at sites showing the calculated percent cover of different classification categories, including both live and abiotic cover. Percent cover in (A) Year 1 and (B) Year 2 at each site, with the amount of coral cover shown in white on its corresponding bar. (C,D) Relative abundance of coral species at each site in each year, with the relative percent cover of the focal species *Montipora aequituberculata* in white on the corresponding bar. (C) Calculated relative abundance of corals at each site in Year 1; (D) relative abundance in Year 2

(Vostok Site 2). In addition, we found that the most common genera were *Porites*, *Montipora*, and *Pocillopora*, respectively, although assemblage structure varied by site (Fig. 3). Our primary species of interest, *Montipora aequituberculata*, ranged from 0 to 80%, with an average of 13%.

To investigate the interactions of focal colonies with other coral species, we examined the number of other species that replaced the area originally held by *M. aequituberculata* or were being replaced by them (Fig. S3A). We found that each *M. aequituberculata*

colony interacted with 3–9 other taxa (Fig. S3A), with an average of  $6.25 \pm 0.4$  coral taxa interacting with *M. aequituberculata* colonies per site. The average size of each focal colony was  $559.0 \text{ cm}^2$ . We investigated the taxonomic composition of neighboring colonies (Fig. S3B, Table 1) and found that only 3 interacting species were common — other colonies of *M. aequituberculata*, *Pocillopora verrucosa* complex, and small colonies of massive *Porites* spp. (Fig. S3B). *Montipora* and *Porites* were found to be the most abundant genera by coverage (Fig. S3B), so the most common

Table 1. Number of colonies of each species of coral that interact with the colonies of interest at that site across both years. END: Enderbury; NIKL Nikumaroro; HOW: Howland; MIL: Millennium; VOS: Vostok; FLI: Flint. Abbreviations and numbers after island names are site indicators. Green shading indicates the highest colony counts found; dark green indicates more than 25 colonies of a species interacting with the focal colonies at a site. The color scale in the last column indicates how common each species was across all sites; green: most common interacting partners; red: least common

	END LP	END SR	NIK L	NIK SWC	MIL 01	MIL 05	HOW 11	HOW 14	VOS 02	VOS 03	FLI 01	FLI 04	Total at all sites
<i>Montipora aequituberculata</i>	60	20	6	3	54	15	5	13	17	58	56	49	356
<i>Porites lobata/lutea</i>	1	9	5	1	8	16	1	1	15	17	41	11	126
<i>Pocillopora meandrina/verrucosa</i>		4	1	1	10	6	3	1	16	14	7	13	76
<i>Goniastrea stelligera</i>	8	28	1	3	1	2					1		44
Unknown		2	8	4		1	1	1		4		2	23
<i>Montipora</i> spp.				5					10				15
<i>Pocillopora damicornis</i>					1			2		1	4		8
<i>Echinopora gemmacea</i>							7						7
<i>Branching Acropora</i>					4						1		5
<i>Goniastrea retiformis</i>	1			3									4
<i>Montipora hoffmeisteri</i>					2						1		3
<i>Platygyra pini</i>	3												3
<i>Porites</i> spp.									1	2			3
<i>Fungia</i> spp.				2									2
<i>Hydnophora microconos</i>		2											2
<i>Pocillopora eydouxi</i>		1			1								2
<i>Halomitra pileus</i>		1											1
<i>Montipora verrilli</i>					1								1
<i>Pavona clavus</i>								1					1
<i>Pocillopora zelli</i>						1							1
<i>Porites annae</i>							1						1
<i>Porites australiensis</i>									1				1
<b>Total colonies</b>	<b>73</b>	<b>67</b>	<b>21</b>	<b>22</b>	<b>82</b>	<b>41</b>	<b>18</b>	<b>19</b>	<b>50</b>	<b>106</b>	<b>111</b>	<b>75</b>	<b>685</b>



associations were with the most common genera. Of the 12 sites across 6 islands, the same general patterns of co-associated taxa were found at most, although not all, sites (Table 1).

### 3.2. Focal colony morphometrics over space and time

To investigate how colonies of interest changed morphometrically, we examined how focal colony area changed by island and site across time points. We found that location influenced the amount and direction of colony area change over time (Fig. 4A,C, Tables S4 & S5). At Howland and Flint, total cover of focal *M. aequituberculata* as well as the average colony size grew between years, in contrast to Enderbury and Millennium. In general, there was an overall pattern of loss seen across islands in both total and average colony area of *M. aequituberculata* during the observed time intervals (Fig. 4C), with appreciable variability between sites at each island (Fig. 4B,D).

We investigated how individual colonies of *M. aequituberculata* changed over time by comparing areas across time points (Fig. S4) and found that in general, planar areas of focal colonies in  $t_2$  were smaller than in  $t_1$  (Fig. 4, Fig. S4). The largest colonies found anywhere in  $t_2$  were approximately 25% of the size of the largest colonies tracked across islands from  $t_1$  (Fig. S4A); this area loss was significant ( $F_{1,611} = 8.078$ ,  $p = 0.005$ ), although the relationship was weak ( $R^2 = 0.013$ ). However, at the same time, the majority of other large focal colonies were not found to be shrinking or dying (Fig. S4A, inset), thereby indicating that loss is driven by the few largest colonies which were found principally on 2 islands—Enderbury and Millennium. We examined overall coral fate (born, died, grew, shrank) and found no statistically significant difference in the number of colonies with each fate (Kruskal-Wallis  $H_3 = 1.94$ ,  $p = 0.585$ ), whether we examined all colonies together (Fig. S4A, inset) or looked at the data separated by island (Fig. S5;  $H_5 = 5$ ,  $p = 0.416$ ). Using multiple regression ( $F_{11,601} = 9.076$ ,  $p < 0.0001$ ,  $r^2 = 0.14$ ), we also considered whether differences at the island level could drive area changes and found that the only islands with a significant effect were Flint ( $\beta = 182.37$ ,  $p = 0.005$ ) and Nikumaroro ( $\beta = -128.05$ ,  $p = 0.04$ ).

The general trend across colonies was negative growth (i.e. a loss of tissue). Larger colonies had larger losses in area between surveys across most islands (Fig. 4, Fig. S4); we looked at planar area loss

both in terms of absolute area lost (Fig. 4) and in terms of relative loss once corrected for starting size (Fig. S4). Flint Island, however, demonstrated relatively higher growth and less overall loss between time points relative to colonies from the other islands ( $F_{6,606} = 269.8$ ,  $p < 0.0001$ ,  $r^2 = 0.867$ ). To assess the relationship between the starting area and the change in area of the focal *M. aequituberculata* coral colonies, we used Spearman's rank correlation and found a negative correlation ( $r_{627} = -0.94$ ,  $p < 0.0001$ ).

To investigate whether there was an effect of time between visits, we looked at the adjusted, proportional change (Fig. S4B). The data were adjusted by dividing the change in area by the months between visits; we also proportionalized the area change based on the starting area, as larger colonies inherently have more area to lose. Howland and Flint had a different, more negative relationship between starting size and proportional size change ( $F_{11,478} = 18.89$ ,  $p < 0.0001$ ,  $r^2 = 0.303$ ) ( $\beta = -3.056 \times 10^{-4}$ ,  $p < 0.001$ ) and ( $\beta = -1.556 \times 10^{-4}$ ,  $p = 0.004$ ), respectively. Howland and Flint also had the most overall growth of colonies (Fig. 4). This suggests that the overall growth of *M. aequituberculata* coral colonies is driven by colonies that started smaller and grew, rather than by initially large colonies. To investigate whether this pattern was mechanistically driven by time between visits or by starting area, we noted regression strength. We found that the adjusted proportional change was weaker than regressions that did not take time between visits and proportionalized size changes into account. Therefore, time between visits and colony size were not the main drivers of the patterns seen.

We also investigated the growth of individual *M. aequituberculata* colonies and calculated growth rates by focusing only on the subset of colonies that grew (Fig. 5A). We compared growth rates between islands after correcting for the number of months between visits (Fig. 5B) and found an average growth rate of  $9 \text{ cm}^2 \text{ mo}^{-1}$  and an average linear growth rate of about  $6 \text{ mm mo}^{-1}$ , although many colonies showed rates of  $1 \text{ cm mo}^{-1}$ . The islands with significantly higher linear growth were found in the Phoenix Islands (Kruskal-Wallis  $H_{11} = 116.11$ ,  $p < 0.001$ ). We calculated the proportional change of the growing colonies to determine if there was a relationship between the starting size of colonies and their growth (Fig. 6) and found that in general, smaller colonies have higher proportional changes while larger colonies have relatively small changes in area. This suggests that there may be a starting size effect of growth.

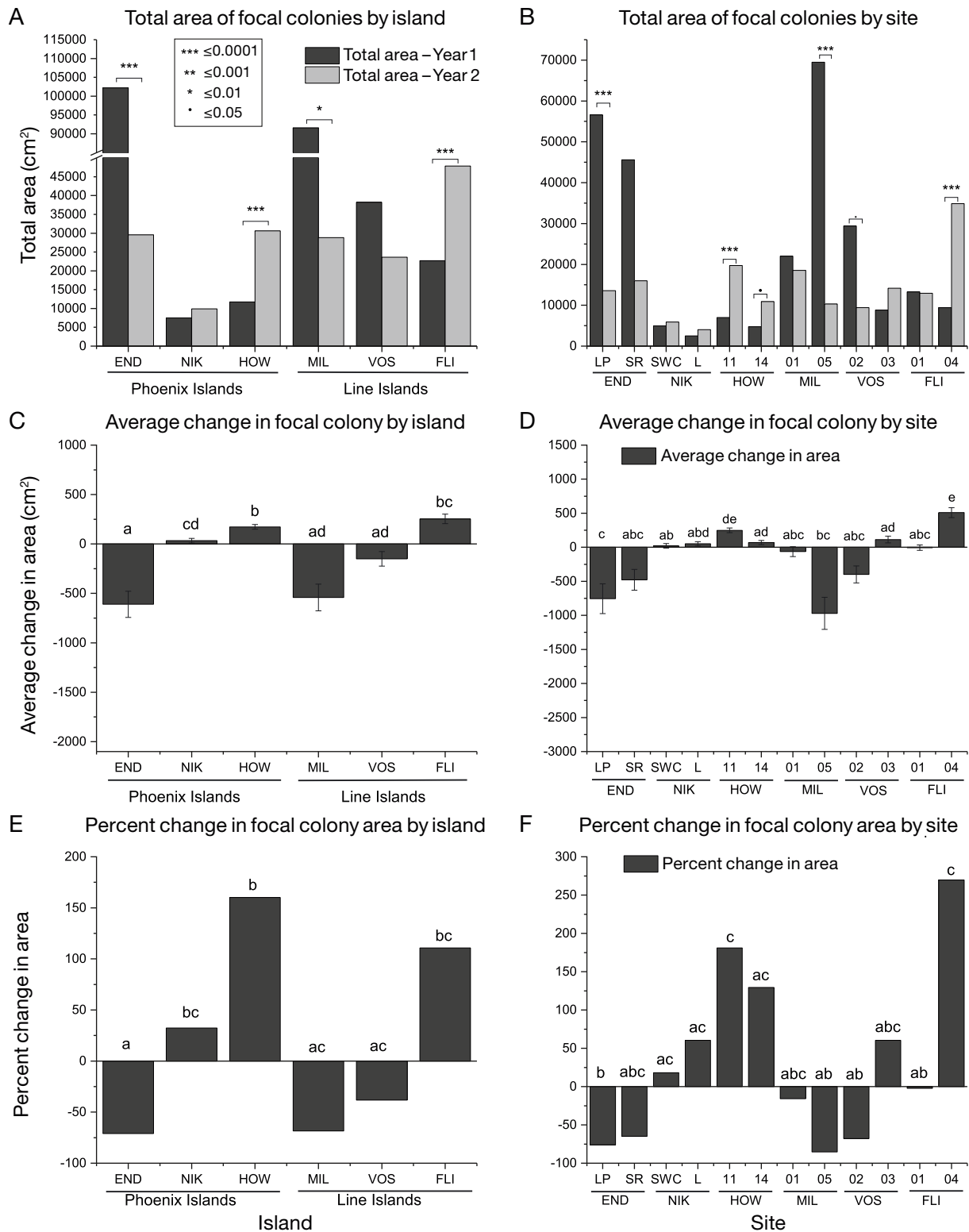


Fig. 4. Total area of the focal colonies in each year by (A) island and (B) site. The changes at most islands are driven by a single site. Change in average area of focal colonies between years by (C) island and (D) site. Percent change in the area of focal colonies at each island between (E) years and (F) sites. Wilcoxon tests were used for (A) and (B): \*\*\* $p \leq 0.0001$ , \*\* $p \leq 0.001$ , \* $p \leq 0.01$ ,  $\cdot p \leq 0.05$ . Kruskal-Wallis tests followed by Dunn tests were used in (C–F), visualized by letters demarcating the groups of similarity. END: Enderbury; NIK: Nikumaroro; HOW: Howland; MIL: Millenium; VOS:Vostok; FLI: Flint

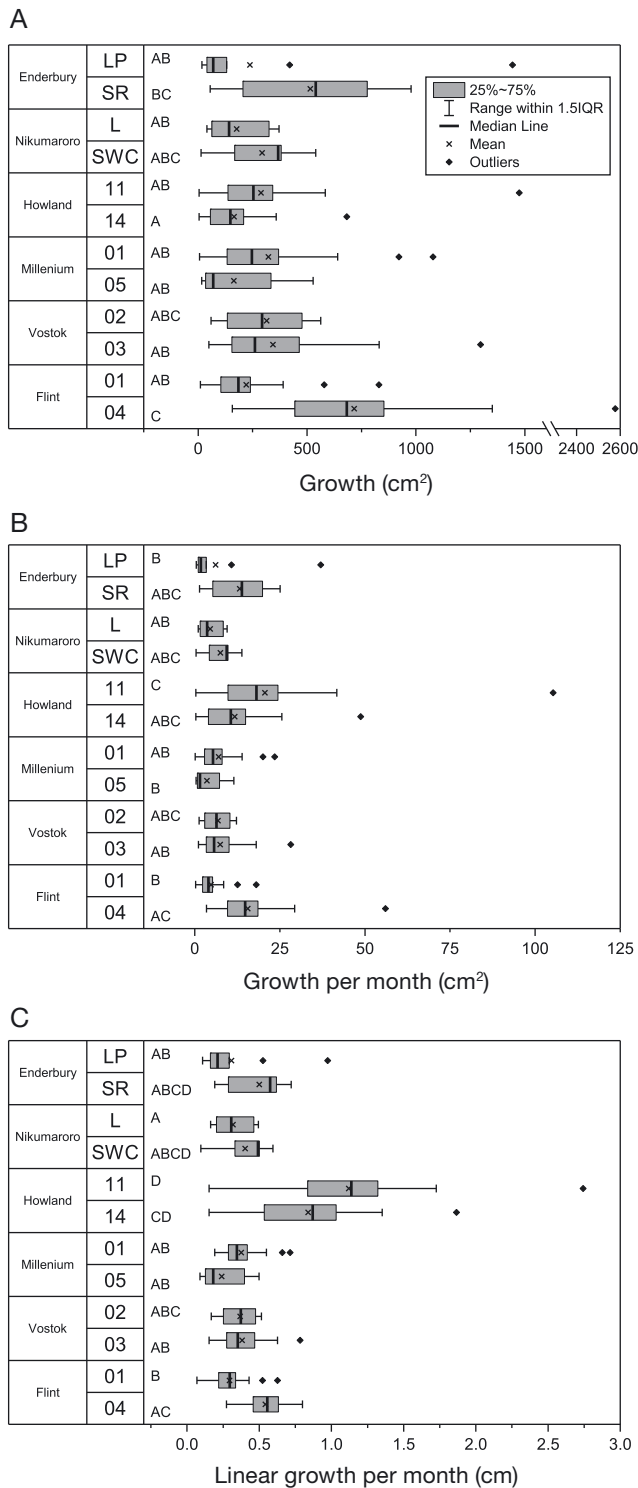


Fig. 5. The growth rate of focal colonies of *Montipora aequituberculata* at the study sites and islands. (A) Total growth rate (cm<sup>2</sup>) for focal colonies that exhibited positive growth. (B) Growth adjusted for the number of months between visits. (C) Linear growth adjusted for the number of months between visits. Left-aligned letters represent statistical groupings from a Dunn post-hoc test

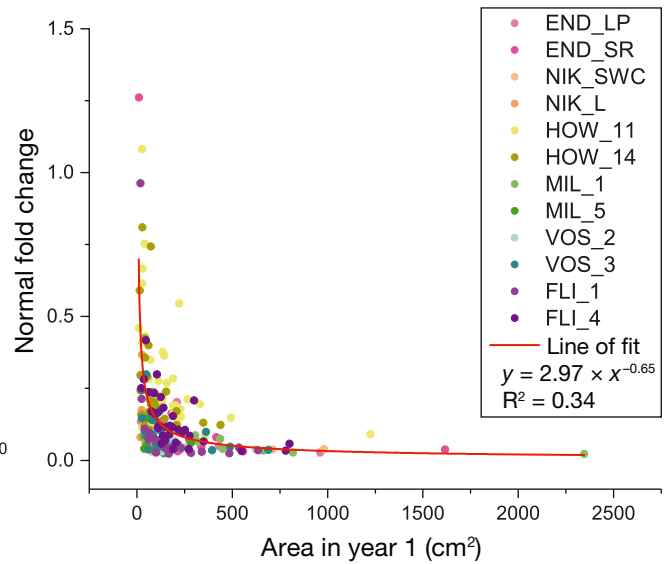


Fig. 6. Fold change of *Montipora aequituberculata* colonies of different starting sizes graphed relative to the fold change of their growth between visits. Normalized fold change was calculated as follows: (area in Year 2 / area in Year 1) / (months between visits). END:× Enderbury; NIK: Nikumaroro; HOW: Howland; MIL: Millenium; VOS: Vostok; FLI: Flint

### 3.3. Role of *M. aequituberculata* in ecological succession

To determine if there were patterns indicative of competition or facilitation between focal colonies and their neighbors, we used spatial data from TagLab to plot the locations of focal colonies and interacting colonies over time (Figs. S6–S11). We grouped the interacting colonies by their life history strategy (weedy, competitive, or stress-tolerant), and investigated their ability to overgrow focal colonies.

#### 3.3.1. Interaction with weedy species

*M. aequituberculata* commonly overgrew itself ( $\chi^2_4 = 39.45$ ,  $n = 767$ ,  $p < 0.0001$ ), Pearson's post hoc residual =  $-4.30$ ,  $p < 0.001$ ), noting that while there is colony turnover over time, the species maintains its position as a primary placeholder on these time scales. Other than such intraspecies colony turnover, there is no difference in competitive dominance within the guild of weedy species ( $\chi^2_{2,303} = -28.815$ ,  $p < 0.001$ , Pearson's post hoc residual =  $-1.21$ ,  $p = 0.227$ ) and the dominance probability is 0.444, although this may be due to the small number of non-*M. aequituberculata* weedy colonies included in the analysis ( $n = 18$ ).

### 3.3.2. Interaction with competitive species

We found a pattern suggesting that *M. aequituberculata* can outcompete the guild of competitive species ( $\chi^2_{2,303} = -28.815$ ,  $p < 0.001$ , Pearson's post hoc residual = 5.356,  $p < 0.001$ ), including the competitive *Pocillopora* complex ( $\chi^2_4 = 39.45$ ,  $n = 767$ ,  $p < 0.0001$ ), Pearson's post hoc residual = 5.529,  $p < 0.001$ ). This suggests that *M. aequituberculata* is a stronger competitor than other species that are traditionally thought of as 'competitive', with a dominance probability of 0.818.

### 3.3.3. Interaction with stress-tolerant species

We found that focal colonies were significantly overgrown by stress-tolerant species ( $\chi^2_{2,303} = -28.815$ ,  $p < 0.001$ , Pearson's post hoc residual = -4.5,  $p < 0.001$ ), suggesting that *M. aequituberculata* are comparatively less competitive and/or more vulnerable to stress, although this pattern was not driven by any single coral taxon. Specifically, looking at 2 of the most common stress-tolerant corals, *Goniastrea stelligera* and *Porites lobata/lutea*, we found no statistical evidence that these particular species selectively overgrew, or were overgrown by, the focal taxa ( $\chi^2_4 = 39.45$ ,  $n = 767$ ,  $p < 0.0001$ ; Pearson's post hoc residual = -0.071,  $p = 0.943$  and residual = 0.075,  $p = 0.075$ , respectively). Correspondingly, we also found no strong evidence that the focal taxa would win in a competition with stress-tolerant species (only 48.7% probability of 'winning' any spatial competition). Together, these data suggest that *M. aequituberculata* is an equal competitor for space with *G. stelligera* or *P. lobata/lutea* on these time scales.

### 3.3.4. Effects on focal colony coverage

We also investigated the number of species that overgrew or were overgrown by focal colonies at each site to determine if there was support for the idea that *M. aequituberculata* was more often overgrown by other taxa. No site had any statistical differences in overall number of species that either were overgrown or overgrew the focal taxon ( $\chi^2_{11,127} = 3.28$ ,  $p = 0.986$ ); however, most sites had more species of coral overgrowing focal colonies than species being overgrown.

To more extensively investigate the change in focal colonies over time, we looked at the margins of focal colonies and calculated the percentage change in area that was overgrown by other species as well as

the percentage change in area that the focal colonies took from other primary spaceholders (Fig. 7). Most focal colonies lost area over time apart from those on Howland and Flint, and the 2 taxa that had the most area change were *M. aequituberculata* and the *Porites* complex (Fig. 7). No species consistently took over large areas of space. Notably, none of the competitively classified corals (Darling et al. 2012) showed the expected pattern of growth: all lost area coverage to focal colonies, indicating the competitive abilities of *M. aequituberculata*.

## 4. DISCUSSION

Classifying the general competitive strategy of coral taxa on a reef is complex and contextualized to space, time, and specific environment (Connell et al. 2004, Evensen et al. 2015, Johnston et al. 2020, Doropoulos et al. 2022). As a common species on Pacific reefs (Veron 2000, Jasmine et al. 2009), *Montipora aequituberculata* has the potential to influence reef structure and ecological function (Piller & Riegl 2003, Crane et al. 2016, McWilliam et al. 2020). Especially in the context of reef recovery and restoration decisions, it is critical to understand the successional patterns and competitive hierarchies of common corals such as *M. aequituberculata*, which are taxa that are likely to play key roles in benthic dynamics. As such, the main contributions of this paper are to place *M. aequituberculata* into a successional context (competitive or facilitative) using a novel analytical approach looking both forward and backward in time to examine whether community spaceholders were able to displace focal colonies or be displaced by focal colonies. These temporal dynamics measure the fate of *M. aequituberculata* colonies and the surrounding benthos from past-to-future and future-to-past, which is a new approach for addressing these questions. We hypothesized that *M. aequituberculata* would outcompete weedy species, and by looking forward in time to see what *M. aequituberculata* was able to overgrow, we indeed found evidence to support this hypothesis. We also found that *M. aequituberculata* was an effective competitor across a diverse suite of other taxa. However, this competitive status is not ubiquitous. When looking back in time at the colonies that overgrew *M. aequituberculata*, we found evidence that *M. aequituberculata* can be subordinate to stress-tolerant corals in post-disturbance environments, pointing to the complexity of interactions. As *M. aequituberculata* is a highly dynamic species, it makes sense that it can both hold and yield space in different

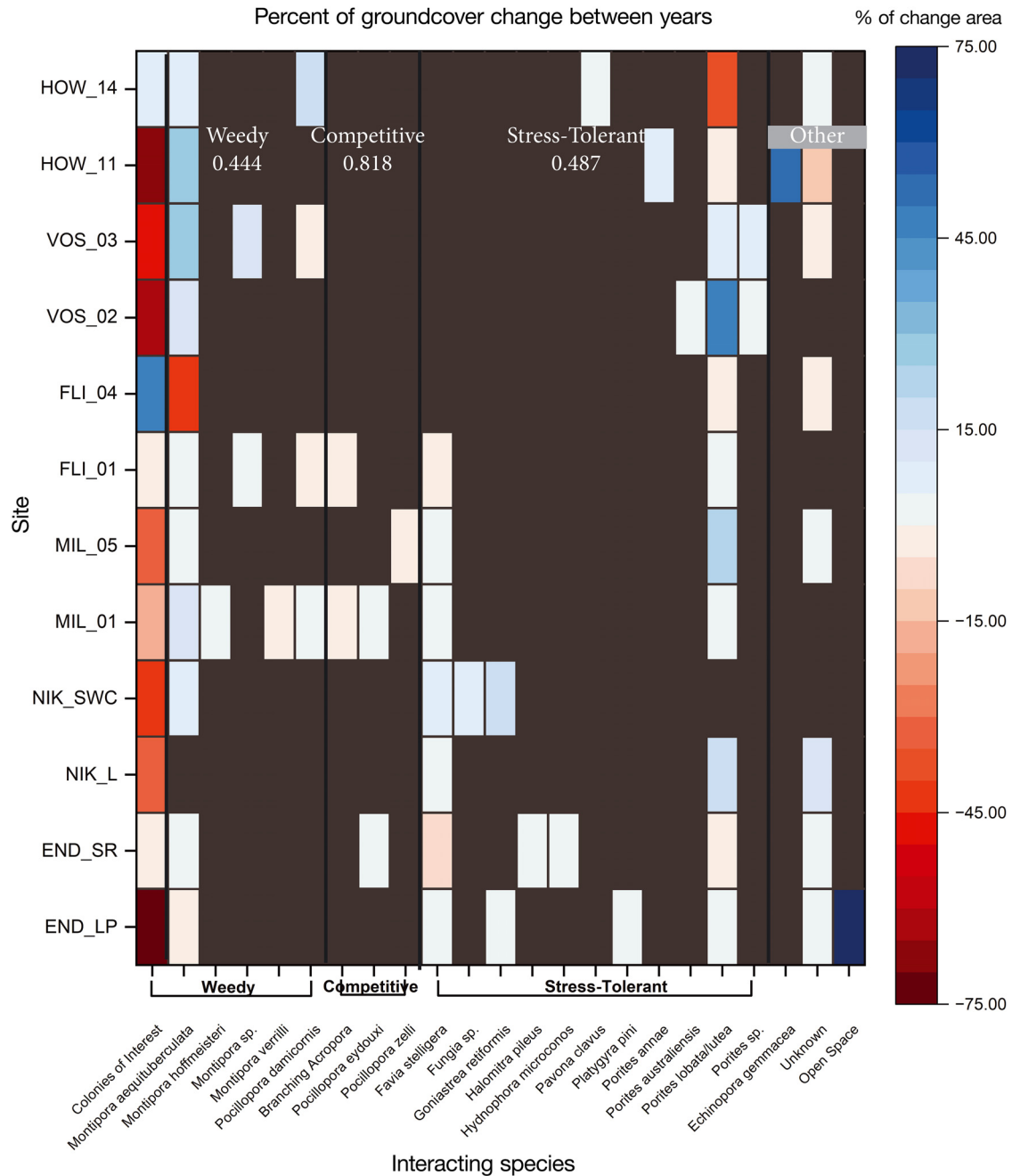


Fig. 7. Change in groundcover area at different sites calculated as the difference in percentage of pixels of change in each year. Reds: overall loss of area of that species; blues: gain. Paler colors show smaller amounts of change. Species along the x-axis are organized by the competitive strategies in Darling et al. (2012). The number under the classification name is the chance that *Montipora aequituberculata* overgrows a group. The first column shows the changes in the focal colonies, which have more change as we investigated the entire perimeter of the colonies. The remaining columns show the percent area of the sections of colonies perimeters that interacted with *M. aequituberculata*. END: Enderbury; NIK: Nikumaroro; HOW: Howland; MIL: Millenium; VOS: Vostok; FLI: Flint

contexts; the detailed understanding provided here enables better predictions of interaction patterns. Specifically, careful examination of interactions between taxa and resulting changes in coral planar area demonstrates the nuance of context-dependency on a

reef scale, which has important utility in understanding reef recovery and, by extension, can be used in reef restoration applications. However, even with nuanced differences between sites, our data overall support the re-classification of *M. aequituberculata* as a

competitive species on contemporary, post-disturbance Pacific reefs. In addition, despite the reef-scale differences, we found that competitive hierarchies appear to be relatively consistent on a regional scale.

#### 4.1. Competitive classification

As indicated above, *M. aequituberculata* was a surprisingly successful competitor in the majority of interactions with coral species previously classified as competitive. Specifically, we found that *M. aequituberculata* consistently overgrew other competitive genera (Fig. 7), including *Pocillopora*: a fast-growing, competitive genus with many coral species that can become dominant placeholders and protect their space with sweeper tentacles (Connell et al. 2004, Darling et al. 2012). Historically, *Montipora* species have generally been classified as weedy or ruderal due to their high growth rates, quick colonization, and fragile growth forms (Sheppard 1979, Dai 1990, Edinger & Risk 2000, Connell et al. 2004, Rachello-Dolmen & Cleary 2007). However, in the last decade or so, there has been increased discussion of whether *Montipora* should be considered a competitive taxon due to its ability to overgrow other corals and its ability to use physical attacks with mesenterial filaments (Darling et al. 2012, 2013, Evensen et al. 2015). It has been established that in areas of recent disturbance, *M. aequituberculata* can grow quickly and dominate benthic habitat (Crane et al. 2016), although its tolerance to chronic or repeated stress is unclear (Evensen et al. 2015, Crane et al. 2016). In our study, we found that *M. aequituberculata* successfully overgrew other competitive taxa, including *Pocillopora* spp. and *Acropora* spp. (Fig. 7). Given the totality of these findings, *M. aequituberculata* should be considered a competitive coral, particularly in the context of reefs undergoing the early phases of recovery.

Post-disturbance reefs are subject to rapid ecological change, as species are actively re-establishing populations and communities in newly available space, a process that can be highly stochastic (Connell et al. 2004). On post-disturbance reefs, *M. aequituberculata* can quickly establish and dominate available space, as observed in this study (Fig. 3). However, it has been previously documented that *M. aequituberculata* can sometimes create thickets that exclude other species; for example, on shallow reefs at Palmyra Atoll in the Line Islands and Ulithi Atoll in the Federated States of Micronesia (Williams et al. 2013, Crane et al. 2016). We did not observe that benthic trajectory, perhaps because our sites were

generally deeper or did not lose all coral cover during disturbances, allowing other taxa to gain or keep footholds in the area before *M. aequituberculata* was able to dominate completely. Therefore, the ability of *M. aequituberculata* to become a dominant spaceholder likely depends on available space, time of colonization, and diversity of existing and competing taxa in the wake of a disturbance.

Although *M. aequituberculata* was a successful competitor against other competitive and weedy coral species (Fig. 7) (Sheppard 1979, Dai 1990, Evensen et al. 2015, Crane et al. 2016), it was vulnerable to overgrowth by slow-growing, stress-tolerant corals (Fig. 7, Fig. S12). For example, when *M. aequituberculata* interacted with the most common stress-tolerant species (*Porites* complex and *Goniastrea stelligera*), neither coral had the upper hand in individual competitions, but overall, *M. aequituberculata* yielded space. As a result, we found that most sites lost *M. aequituberculata* cover to stress-tolerant corals over time.

To examine whether these patterns of competitive dominance or subordination were consistent, we investigated interactions across different spatial scales (site, island, archipelago). We found that patterns of *M. aequituberculata* interactions were similar across all scales (Figs. S3, S6–S11). There were no differences in the diversity of taxa overgrowing or overgrown by the focal colonies at any site. While we and many others have shown that competitive hierarchies can be circumstance-dependent (Jasmine et al. 2009, Darling et al. 2012, 2013, Evensen et al. 2015, Crane et al. 2016, Olinger et al. 2021), those changes do not appear to overwhelm hierarchies on a regional scale.

#### 4.2. Growth and survival

To validate the outcomes of competitive interactions of *M. aequituberculata*, we examined the growth and survival rates of focal colonies, asking whether colony size, community composition, or a combination thereof influenced colony fate. We found that larger colonies were more likely to lose planar area (Fig. 6) compared to smaller colonies, which is consistent with other studies that investigated size effects on growth and survival, both in the context of disturbance and competition (Hughes & Jackson 1985, Shenkar et al. 2005, Brandt 2009, van Woesik et al. 2012, Cresswell et al. 2020, Kodera et al. 2020, Madin et al. 2020). In general, plating or foliose corals like *M. aequituberculata* are more susceptible to breakage and damage than massive or encrusting corals, but these corals are commonly able to survive

physical damage and re-grow (Hughes & Jackson 1985). Nonetheless, survival outcomes for fragile growth-form colonies are still size-dependent; for example, Kodera et al. (2020) found that larger colonies of *Pocillopora* species are less likely to suffer total mortality but are more likely to lose planar area, which is consistent with our findings (Fig. 6) and reflects that larger colonies may have more area to lose or biomass to subdivide.

Previously, van Woesik et al. (2012) and Ferrari et al. (2016) have shown that colony growth form as well as the height-to-diameter ratio impacted survivorship in environments of high thermal stress. For example, it has been shown that smaller colonies have higher survival post bleaching (Shenkar et al. 2005, Brandt 2009), suggesting that after repeated disturbance, coral dynamics could skew toward smaller, more encrusting, or low-profile corals. In our study, smaller colonies had higher growth rates (Fig. 6), consistent with many (Hughes & Connell 1987, Kodera et al. 2020) but not all (Madin et al. 2020) other findings. As such, the demographics of surviving *M. aequituberculata* colonies would likely shift to smaller, faster growing colonies, potentially buffering the decline of cover on the reef, as also suggested by Madin et al. (2008) and Dornelas et al. (2017). Taken together, these findings suggest that larger colonies may have higher survival overall, but smaller surviving colonies would replace benthic cover more quickly.

We examined the overall growth rate on these remote, uninhabited reefs, and measured a linear growth rate of  $7 \text{ cm yr}^{-1}$ , averaged to  $6 \text{ mm mo}^{-1}$ , which is slightly higher than other published accounts that found a linear growth rate of up to  $2\text{--}5.8 \text{ cm yr}^{-1}$  (Browne 2012). Our average growth rates are largely driven by growth on Howland Island (Fig. 5); if Howland corals are removed from the analysis, our measured average linear growth rate is  $4 \text{ mm mo}^{-1}$ , or  $4.8 \text{ cm yr}^{-1}$ . This range of growth rates is similar to other work, such as on *Acropora* species, which have reported wide ranges in growth rates across sites and studies within the same species (e.g. Stimson 1996 and Bessey et al. 2018 with *Acropora spicifera*). These findings again suggest that local dynamics of time and place can strongly influence coral growth; these dynamics may include disturbance, season, general reef biodiversity, or other factors (Smith et al. 2008, Browne 2012, Haapkylä et al. 2013, Pratchett et al. 2015, Huntington et al. 2017).

Given that coral growth and species interactions vary based on environmental context, we investigated whether *M. aequituberculata* corals exhibited the same relative area at different spatial scales (defined

here as site, island, archipelago) and found inconsistent patterns (Fig. 4). Aston et al. (2019) documented that hard corals can vary in cover around a single island, with changes on the sub-km scale being predictable in the absence of local anthropogenic stressors, similar to our data (Fig. 3). This could suggest that local stressors are the main drivers of survivorship and decline at the local level, although much of the literature suggests the opposite: that regional, large-scale stressors tend to show the larger effect (Darling et al. 2010, Hughes et al. 2018, Gintert et al. 2019, Doropoulos et al. 2022), which may be related to time since the last major disturbance. Sandin et al. (2020) also suggested that simple oceanographic variables are insufficient for making demographic predictions; instead, it seems that differences in life history strategies may lend complexity and flexibility to coral stress responses. Our data support this idea, as *M. aequituberculata* clearly grows faster in some conditions (e.g. Howland Island; Fig. 5) and slower in others.

While it is apparent that *M. aequituberculata* is an important early successional coral placeholder (Fig. 7, Darling et al. 2012), it does not maintain consistent coral cover throughout the recovery period of a reef. All the sites surveyed were in a recovery phase 2–7 yr post disturbance and half of our sites showed a decline of *M. aequituberculata* coverage with species turnover (Figs. 4 & 7), noting that there was one site (Enderbury's Lone Palm) where *M. aequituberculata* was lost without replacement. Species turnover may have been facilitated by *M. aequituberculata* holding temporary space; in these cases, we would expect that slower-growing, stress-tolerant species (e.g. *Porites*) would reach a turnover point where overgrowth is possible post recovery, thereby leading to natural declines in *M. aequituberculata*. However, the possibility remains that *M. aequituberculata* declines are due to other environmental factors, such as bleaching or disease, which can be compounded by weather events (Haapkylä et al. 2013, Baird et al. 2017).

### 4.3. Conclusions

At a time when corals are dying globally at unprecedented rates and scales (IPCC 2023), the natural ecological dynamics of healthy, successional mature coral reef communities are becoming harder to study as these communities become rarer. Insights into species-specific competitive dynamics are necessary for assessing reef growth patterns and trajectory and may potentially be useful for outplanting and restoration efforts. Specifically, examining how a specific coral

species (in this case, *M. aequituberculata*) can support or inhibit the growth of other taxa may have implications for outplanting decisions (e.g. what species to outplant, what size, etc.). In this study, we asked both which community spaceholders were able to displace focal colonies and which community spaceholders were able to be displaced by focal colonies, thereby examining competition and successional processes on a colony scale. This study shows that *M. aequituberculata* is competitive against weedy and other competitive taxa but it will yield to stress-tolerant taxa in a post-recovery context. Exploring possible drivers for these dynamics, we found that islands with similar species interactions did not exhibit similar growth or loss patterns, highlighting site-level ecological complexity. The careful examination of shifting community composition, and underlying mechanisms thereof, is critical for understanding the widespread post-disturbance world and predicting the future fate of individual coral species in a changing world.

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