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Examining the successional role of a pioneer species on post-disturbance coral reefs: Are they facilitators or short-term competitive dominants?

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Thesis

**EXAMINING THE SUCCESSIONAL ROLE OF A PIONEER SPECIES ON
POST-DISTURBANCE CORAL REEFS: ARE THEY FACILITATORS OR
SHORT-TERM COMPETITIVE DOMINANTS?**

by

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DEDICATION

I would like to dedicate this work to the two Myra Snows, Weck Bebb, Ashryn Castoris, Glori-BRUH, ? Nixon, Aspen Arryn, and the other Dungeons & Dragons characters that I played throughout this project, who helped keep me sane and make sure I took breaks from coral to occasionally consider other worlds and viewpoints.

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ABSTRACT

As coral reefs decline globally, there is an urgent need to understand recovery pathways and trajectories to both assess reef status and intervene with reef restoration efforts. However, the ecological role of various coral taxa on reef successional pathways is poorly understood. Building on terrestrial successional frameworks, it seems logical that weedy coral species may be placeholder species that quickly colonize cleared areas after a disturbance, but that are later replaced by more competitive, slower-growing species, leading to overall more biodiverse reefs. To test the competitive ability of a common pioneer species on Pacific reefs, *Montipora aequituberculata*, we tracked ~600 colonies across six equatorial islands through two time points (50 colonies per site per island), examining whether this species was more typically overgrown by other species over time, or whether *M. aequituberculata* was a more dominant competitor capable of overgrowing other reef taxa. Using photogrammetric data, we set out to answer questions about the fates of focal colonies and their place in the competitive hierarchy. Trajectories of area change of the focal colonies varied across islands, though they did not follow geographic patterns. Many of the changes in these post-disturbance reefs sometimes differed by site, even on the same island, and were not consistent within an archipelago. At an island scale, Howland (Phoenix Islands) and Flint (Line Islands) showed the

greatest growth of focal colonies, while Enderbury (Phoenix) and Millennium (Line) lost the most coral coverage of focal colonies. Interactions between the focal colony and other coral species were more consistent across islands, with the most common interactions being with other colonies of *M. aequituberculata* as well as common species of *Porites* and *Pocillopora*. There was a consistent trend of focal colonies mostly being overgrown by other colonies of *M. aequituberculata*: this conspecific replacement suggests that this species is capable of self-perpetuating as a primary space holder in lieu of other coral interactions. In contrast, most other coral species were commonly overgrown by the focal *M. aequituberculata*, suggesting that *M. aequituberculata* is a strong competitor when vying for groundcover. Indeed, *M. aequituberculata* may be able to dominate reefs post-disturbance until stress-tolerant species take over. Surprisingly however, we did not see a consistent pattern of species interaction, meaning that there was not a single coral taxon that universally overgrew *M. aequituberculata*, suggesting that *M. aequituberculata* is a generalist competitor and is not a specialized facilitator of any one competitively dominant taxa. Islands with similar species interaction patterns are not the same islands with similar growth or loss patterns, suggesting that site-level ecological complexity overrules any general patterns of geography or species interactions. This study is among the first to provide detailed species interactions in a successional framework, paving the way for future studies to do the same in the hopes that we can predict the trajectory of reefs based on the community composition.

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INTRODUCTION

Coral reefs are dynamic ecosystems that contain great biodiversity (Crisp et al., 2022) and provide many ecosystem services (Woodhead et al., 2019). There are myriad challenges facing reefs, namely climate change that increases risks of coral bleaching and ocean acidification (Brown 1997, Raven et al., 2005). Researchers are working to understand the dynamics that drive reef growth and recovery in hopes of gaining insights to help improve conservation and restoration efforts (Ferrari et al., 2021, Prach and Walker, 2011, Pulsford et al., 2016, Sandin et al., 2020, and many more).

The field of marine restoration ecology is a relatively young, growing field of study (Boström-Einarsson et al., 2020), often based on terrestrial analogues (Ferrari et al., 2021, Omori 2019). A review of coral restoration efforts found 221 papers on restorations, mostly focused on scientific advancement and the acceleration of reefs post-recovery (Boström-Einarsson et al., 2020). Both initial effort and tracked metrics of success usually focus on survivability of outplanted corals (Ferrari et al., 2021) though this is also the most time and effort intensive step. However, technology and understanding of the underlying biological processes is reducing the effort needed for growing or fragmenting corals for outplanting, and other techniques are now being used as well, such as larval enhancement and assisted evolution (Ferrari et al., 2021, Omori 2019, Suggett and van Oppen, 2022). These improvements to techniques can create positive feedback in conservation by both speeding up restoration efforts and more quickly allowing for data collection to inform future studies (Suggett and van Oppen, 2022).

In order to effectively protect and restore reefs in the face of climate change, it is important to understand the dynamics underlying the growth and organization of reefs. It is likely that there is a sequenced progression of coral taxa and community turnover, with common patterns of replacement and temporal dominance that change the short-term biodiversity of the reef as it approaches a stable, climax community. Successional dynamics such as those suggested by Frederic Clements have been described in many other ecosystems including grasslands (Clements 1904), boreal forests (Bergeron and Debuc, 1989, Taylor et al., 2020), tropical rainforests (Bazzaz and Pickett, 1980, Mo et al., 2013), marine intertidal ecosystems (Farrell 1991, Mayakun et al., 2022, Murray and Littler, 1978), however the successional progression of corals post-disturbance has not been well-described or field-tested (Steneck et al., 2019). Due to the complexity of coral reefs, successional trajectories on reefs are likely to be influenced by many factors including ocean basin, oceanographic context, and reef type (Mathews et al., 2021) which have a confounding influence on overall biodiversity. In addition to these factors, interspecific interactions between primary space holders (predominantly corals) will also influence whether a given taxa is a pioneer species, transitional species, or a climax species (Crook et al. 2016). Further, the mechanisms of transitions vary from competition to facilitation (Prach and Walker, 2011), but these interactions are not well described between taxa, nor have they been well-grounded by environmental context (Koffel et al., 2018). While data on interspecific competition, aggression rankings, and dominance hierarchies exist (Connell et al., 2004; Horwitz et al., 2017), for some taxa there are still

debates (Darling et al., 2012), and there is less literature looking at the overall succession on reef communities.

While there is less information on succession and recovery on reefs, there is work in this area. It has been shown that the beginning stage of recovery or restoration often determines much of the trajectory a reef will follow after a disturbance. Survival of larval recruits (Adjeroud et al., 2016) or transplanted coral (Shaish et al., 2010) will often drive these patterns, as they will determine the starting spatial and population dynamics of the reef, and these are often the metrics that are used to measure the success of restoration efforts (Ferrari et al., 2021). Recovery is influenced by the spatial dynamics of the corals on the reef; more dense clumps of coral can cause greater cascades of positive feedback during the recovery phases on the reef (Doropoulos et al., 2022, Huntington et al., 2017), though this has been found to be dependent on herbivory levels (Brito-Millán et al., 2019), and the dominance patterns and interactions of species that colonize disturbed reefs will drive early population dynamics (Alvarez-Filip et al., 2013) which will affect the function of the reefs. Growth of quick growing, easily fragmented corals in recovery and restoration will quickly establish a three-dimensional structure that attracts fish and other reef visitors (Shaish et al., 2010), starting feed-back systems.

Knowing about dominance can also help with understanding ecological succession on reefs, the patterns of change as successive waves of coral gain greater abundance on reefs before being replaced by new taxa (Pratch and Walker, 2011). Building dominance hierarchies to better understand which corals win in competitions for space and resources is important, as these hierarchies are one of the main drivers of coral

reef function (Alvarez-Filip et al., 2013). Dominance and competition are generally viewed through the lens of competition strategies, where species are typically classified as weedy, competitive, or stress tolerant, based on the life strategy patterns used terrestrially (Adjeroud et al., 2016). The biodiversity of the coral reefs in the Pacific are higher than those generally found in the Caribbean Atlantic reefs (Stehli and Wells, 1971). Between the equatorial currents, both the corals and the fish are found with higher numbers and diversity than the Atlantic, with more than twice the coral biodiversity associated with Pacific reefs than Atlantic ones (Stehli and Wells, 1971). This greater biodiversity leads to more complicated webs of interaction between the corals on a reef, creating more difficulty in understanding the competition between species.

The central Pacific basin is home to many islands, seamounts, atolls, and other coral reefs. Two island groups in the area are the Phoenix Islands, straddling the equator, and the Southern Line Islands, which are slightly farther south, though still above the Tropic of Capricorn. Within the basin is the Phoenix Islands Protected Area (PIPA), a Marine Protected Area in the waters of the nation of Kiribati. It is home to reefs that are largely unimpacted by human actions, allowing them to be studied to learn more about coral reef dynamics (Obura & Mangubhai, 2011, Rotjan et al., 2014). The area of the central Pacific that includes PIPA as well as our other islands, suffered a major mortality event in 2002 and a bleaching event in 2010 (Obura and Mangubhai, 2011, Vargas-Angel et al., 2011).

In this study, we used reefs surrounding six uninhabited islands in the central Pacific, three in the Phoenix Islands and three in the Southern Line Islands, as a natural

laboratory to study *Montipora aequituberculata*, an encrusting or laminar coral that often creates overlapping plates; it is common throughout the central Pacific (Veron and Stafford-Smith, 2002). *M. aequituberculata* has generally been classified as a weedy coral due to its fast growth rate and strong colonization, but this classification is now being debated (Darling et al., 2012), leading to a need for more information on where this taxon falls in dominance hierarchies of reefs. By visiting the same sites over time, we track the growth of individual colonies of the focal species, as well as the overgrowth of, or cover lost to, other species. Because of the mortality and bleaching events, these reefs are in a recovery phase. We can track if these species tend to grow and smother nearby corals, acting as a competitively dominant coral and therefore reducing biodiversity, or if it acts as a space holding, easily overgrown, facilitator coral that successionaly gives way to other species. This allows us to determine if *M. aequituberculata* is a successionaly dominant or facilitator species. Adding to the knowledge of reef succession and recovery will help inform restoration efforts, hopefully leading to more successful projects focused on protecting coral as climate change continues.

METHODS

Study Sites

Data was collected from six islands in the Central Pacific: two islands in PIPA: Enderbury and Nikumaroro, as well as nearby islands Howland (in the US PRIMNM), and Millennium, Vostok, and Flint in the Southern Line Islands (Figure 1). Two sites at each island were used; Each site was visited twice, varying years apart. The islands in PIPA were visited 3 years apart, in 2012 and 2015. Millennium, Flint, and Vostok were

visited 4 years apart, in 2013 and 2017, and Howland was visited a year apart, in 2017 and 2018 (Figure 2).

Data Collection in the Field

Image collection has been described in Sandin et al. (2020) but is explained here as well. 10 m x 10 m plots at each site were defined and marked on the first year of the survey using GPS points and steel pins. At each timepoint, the plot was confirmed using GPS and the boundaries were marked using dive weights; at each marker depth measurements were collected to define the plane of projection. The distances between markers were measured, and along with additional scale bars, were used to provide scale.

Images are collected using a pair of Nikon D7000 16.2-megapixel DSLR cameras that are mounted to a fixed frame. One camera has an 18mm length lens with a wide view angle to allow high overlap (>80%) between images. The other camera has a 55mm lens to capture higher resolution images to help with identification and detailed study. The cameras are set to take a photo each second while a diver swims above the reef. By keeping a constant speed (~5- 7 m/min) and height (1.5 m) above the reef, sufficient image coverage of the reef can be obtained by having the diver swim a grid pattern over the plot, first in the x direction, then the y. This swim pattern creates about 2500 images per camera per plot, allowing for photogrammetric reconstruction in the lab.

Photogrammetry

To study how the focal species, *M. aequituberculata*, interacted with other species over time, 2D orthoprojections were created for each year using Structure from Motion

software. The methods of creating the models have been described before (Sandin et al., 2020, McNamara et al., 2019), but are briefly described below.

Field-collected images were loaded into Agisoft Metashape (Agisoft LLC., St. Petersburg, Russia) to create a dense point cloud 3D model that was formed by stitching together hundreds of reef images, matching points across pictures, to form a scaled 3D model of the seafloor. This model was then imported to Viscore (Petrovic et al., 2014), where color correction, scaling, and depth information could be added. Once models for both years had been created for a site, they were lined up visually, by overlaying the two models and using landmarks to ensure scale and orientation were the same in both maps. The 3D models were then orthoprojected into a 2D image and exported, along with a scaled grid (Figure 3).

Data Extraction

Once the 2D image of the reef had been exported, Photoshop (Version 21.2.4) was used to digitize and track species identity of coral colonies. Each year 25 colonies from the focal species were chosen, for a total of 50 per site, by randomly laying down 25 points within the overlapped reef area between years. The nearest colony to each point was then found and marked as a Colony of Interest. The two sites at Nikumaroro did not have 25 colonies each year, so as many focal colonies as could be found were used. This gave a total of 573 focal colonies across 6 islands. Colonies were traced in one of two ways. Either a new layer was created in the Photoshop document, and the randomly chosen colonies were traced around the perimeter of the colony to capture the size and shape of the colonies before being imported to TagLab, or colonies were traced in

TagLab (v2022.04.21). Colonies traced in TagLab were traced with the 4-click segmentation tool and then the edges were refined with the editing tools. Once the focal colonies had been traced, the same location in the other year was investigated, by overlaying the layer with traced colonies over the other year's projection. Any coral colonies that were in the space of the focal colony were traced. This could include the same focal colony that survived across years, as well as any other colonies that interacted with the focal colony (colonies that were overgrown by or grew over the focal colonies). Hand-tracing focal and interacting colonies required a lot of manual effort, and a group of Boston University undergraduate students greatly contributed to this effort. Quality control was carried out by checking work as it was prepared for importation into TagLab for cleanup and identification, ensuring that no colonies were missed. Taxonomic identifications were assigned to each colony using reference images.

Looking Forward and Backward in Time

Once the focal colonies had been identified, the colonies were compared between years using TagLab, which calculated the area (cm²) of each colony (both focal and interacting) in each year and assigned a colony fate for surviving colonies as either having “grown” or “shrunk.” If the colony was only present in year two, it was assigned a fate of “born,” if a colony was only present in year one, it was assigned a fate of “died.” In addition, we examined what replaced a focal colony in year two when a colony shrank or died, thereby gaining insight into the community dynamics surrounding focal colony area loss (forward in time). However, we also examined focal colonies that grew or were born in year two and examined which primary space holders were displaced by the focal

colony in order to enable that growth (looking backward in time). In essence, 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 small scale (Figure 4).

Assumptions of the Approach

This approach assumes that common species are common everywhere and that common species have similar abundances and proportions everywhere. These assumptions are rarely if ever true and would need to be measured at the relevant scales to determine the accuracy of the assumptions.

Data Analysis

Overall expansion or shrinking of colonies was noted as change in area. Where there was growth between years, colonies that were overgrown were noted. The ID and total colony area, as well as the amount of area overgrown by the focal colony were collected. Where there was a loss of cover of a focal colony, the overgrowing colony's species ID, total area, and area of overgrowth were observed. After colonies were IDed, spatial information was collected, and used to create a virtual map of all colonies at each site. Using these models, we collected information on species composition and prevalence, as well as distributions and survivability across time. Data were imported into R (version 3.6.1) for analysis and statistics; graph creation was done in R, Origin Pro (version 2021b), and Adobe InDesign (version 17.2.1).

RESULTS

Patterns of Community Composition

To investigate the interactions of the focal colonies with other species of coral, we examined the number of other species that interacted with focal colonies (Figure 5A) and the taxonomic composition of those colonies (Figure 5B). Each *M. aequituberculata* colony only associated with a few other species of coral, ranging from three to nine taxa (Figure 5A), with an average of six species per site. The average size of each focal colony was 559.04 cm² with a median of 132.76 cm², leaving an average exposed edge perimeter of 84.6 cm for interactions with multiple neighbors. However, we found that there were only three common co-associated species with focal colonies; the largest of these consisted of other colonies of *M. aequituberculata*, followed by the *Pocillopora verrucosa* complex (green), and small colonies of massive *Porites spp.* (yellow) (Figure 5B). Of the 12 sites across six islands, general patterns of co-associated taxa were found together across all islands, though not at all sites (Tables 1 & 2).

Focal Colony Morphometrics Over Space and Time

To investigate how colonies of interest morphometrically changed, we examined how focal colony area changed by island and by site across both years. We found that location influenced the amount and direction of colony area change over time (Figure 6, panels A and C; Tables 3 and 4). Howland and Flint grew between years, in contrast to Enderbury and Millennium, which both lost more than 60,000 cm² of colony area. In

general, there was an overall pattern of greater negative change in area, compared to relatively insignificant amounts of colony area gain (Figure 6, panel C). These losses in colony area are further amplified because Enderbury and Millennium both had the largest initial area. While these patterns are noticeable at the island scale, it is clear that there are differences between sites at each island (Figure 6, panels B and D).

We investigated how focal colonies of *M. aequituberculata* changed over time by comparing their areas across years (Figure 7). It was found that, in general, surface areas of focal colonies in year two were smaller than year one (Figures 6 & 7). The largest colonies found anywhere in the second year were approximately 25% of the size of the largest colonies tracked across islands in the first year (Figure 7A). Using a simple linear regression (black line, Figure 7A), we found that this area loss was significant ($F(1,611) = 8.078$, $p = 0.005$), though the correlation was weak ($R^2 = 0.013$), suggesting that the area of a focal colony in the first year was at best a weak predictor of area in the second year. While we found a weak correlation of area loss based on starting size, we did not find an overall pattern that suggests the majority of colonies were shrinking or dying (Figure 7A, inset), suggesting that the correlation is driven by the few largest Enderbury and Millennium colonies and not by biologically relevant factors. A Kruskal Wallis rank sum test showed no statistically significant difference between the number of coral colonies that had each fate (born, died, grew, shrank) ($H(3) = 1.94$, $p = 0.585$).

Using multiple regression ($F(11,601) = 9.076$, $p = 4.22e-15$, R^2 of 0.14), we also considered whether the difference between islands could drive the change in area. The only islands that had a significant effect on the final area of their colonies were Flint ($\beta =$

182.37, $p = 0.005$) and Nikumaroro ($\beta = -128.05$, $p = 0.04$). There seemed to be a combined effect of the island a colony was found at and its starting area on the second measured area at Flint ($\beta = 0.41$, $p = 0.009$), Nikumaroro ($\beta = 0.65$, $p = 0.005$), and Howland ($\beta = 1.07$, $p < 0.001$).

The general trend across colonies was negative growth, or a loss of tissue. Larger colonies had larger losses in area between surveys across most islands (Figure 7). Flint Island, however, demonstrated higher growth and less overall loss between years ($F(6,606) = 663.5$, $p < 2.2e-16$, R^2 of 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 ($r(627) = -0.52$, $p = 2.2e-16$). The regression shows that for every cm of starting area, the colony would lose 0.95 cm by the second year (Table 5). The largest changes did not all come from the islands with the largest period between surveys (Figure 7B). Howland, with the shortest time between visits, did have only small amounts of change, but it also had smaller colonies to start with. To investigate whether there was an effect of time between visits, we also looked at the adjusted, proportional change (Figure 7B). The data were adjusted by dividing the change in area by the years between visits. We also proportionalized the area change based on the starting area, as larger colonies inherently have more area to lose. Howland had a different, positive pattern of change relative to the other islands ($F(11,601) = 61.2$, $p < 2.2e-16$, $R^2 = 0.528$) ($\beta = 137.12$, $p < 0.001$) when using multiple regressors of starting area and island. However, Howland did show much more variability in the changes in area that were found, reflected in the much larger confidence interval.

Once again, the simple regression seems to be driven by the largest colonies at Enderbury and Millennium. While the other islands all had a negative adjusted change, Flint showed negligible change, and Howland saw a positive change in area. This can be driven by two mechanisms, adjusting for the time between years, and also area changes based on starting area. This can have effects on size effects related to breakage of plating colonies of *M. aequituberculata*. The regression using the adjusted proportional change was weaker than the earlier regression which does not take the time between visits into account. Therefore, the time between visits and the breakage of larger colonies were not the main drivers of the patterns seen.

Although there was no major difference in fates across all colonies (Figure 7A inset), we wanted to determine if there were any island-level changes that could have been masked by the overall trend. As such, we looked at the fates of the focal colonies, and how they changed over time per island. We found that all islands experienced all fates (Figure 8), but there was no significant difference in colony fate by island ($H(5) = 5$, $p = 0.416$).

*The Role of *M. aequituberculata* in Ecological Succession Over Space and Time*

To see if there were patterns indicative of competition or facilitation (succession) between focal colonies and their neighbors, we used spatial data from TagLab to plot the locations of focal colonies and interacting colonies over time (Figures 9-14). We grouped the interacting colonies by their life strategy (weedy, competitive, or stress-tolerant), and investigated their ability to overgrow focal colonies with which they interacted. We

found that focal colonies were significantly overgrown by stress-tolerant species (X^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, though this pattern was not driven by any single coral taxa. Specifically, looking at two of the most common stress tolerant corals, *Favia stelligera* and *P. lobata/lutea*, we found no statistical evidence of facilitation or competition ($(X^2$ (4, N = 767) = 39.45, $p = 5.62e-8$, Pearson's post hoc residual = -0.071, $p = 0.943$ and residual = 0.075, $p = 0.075$ respectively), meaning that these particular species did not selectively overgrow, or get overgrown, by the focal taxa. We also calculated the probability that the focal taxa would win in a competition with stress tolerant species in our observations, and the probability was 0.487. All these data suggest that the focal taxon was an equal competitor to *F. stelligera* or *P. lobata/lutea* on these time scales; these coral taxa may together comprise a guild at this successional stage.

We found a pattern suggesting that *M. aequituberculata* is capable of outcompeting the guild of competitive species (X^2 (2, 303) = -28.815, $p < 0.001$, Pearson's post hoc residual = 5.356, $p < 0.001$), which is also seen when focusing specifically on the competitive *Pocillopora* complex ($(X^2$ (4, N = 767) = 39.45, $p = 5.62e-8$, Pearson's post hoc residual = 5.529, $p < 0.001$). This suggests that *M. aequituberculata* is a stronger competitor than other traditionally competitive species, with a dominance probability of 0.818. Other colonies of *M. aequituberculata* were the species most often found overgrowing the focal colonies ($(X^2$ (4, N = 767) = 39.45, $p = 5.62e-8$, Pearson's post hoc residual = -4.30, $p < 0.001$), suggesting that there is turnover

of this taxa over time, but that this taxa is capable of maintaining its position as a primary placeholder on these timescales. If we do not include these intraspecies interactions with other colonies of *M. aequituberculata* due to colony turnover, there is no difference in competitive dominance with the guild of weedy species ($X^2(2, 303) = -28.815$, $p < 0.001$, Pearson's post hoc residual = -1.21, $p = 0.227$) and the dominance probability is 0.444, though this may be due to the small number of non-*M. aequituberculata* weedy colonies included in the analysis ($n = 18$). We also investigated the number of species that overgrew or were overgrown by focal colonies at each site, to see 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 taxa ($X^2(11, 127) = 3.28$, $p = 0.986$), however the majority of sites had more species of coral overgrowing focal colonies than species being overgrown.

After looking at the overall patterns of overgrowth and overgrowing, we focused specifically on which colonies were taking space from focal colonies on an island scale (Figure 15). Looking at these overgrowing colonies, we find a similar pattern at Enderbury, Millennium, and Flint, the easternmost islands in both archipelagos, with *M. aequituberculata* (either the focal colony or a replacement colony) as the dominant taxa in year two. Although Nikumaroro and Vostok have a similar number of surviving colonies compared to other sites, they do not show the same prevalence of *M. aequituberculata*. Enderbury, Nikumaroro, and Vostok also have greater species diversity replacing focal colonies between years compared to the other islands: Enderbury showed

the greatest biodiversity overall, but Nikumaroro and Vostok had a higher abundance of multiple taxa. In comparison, Flint showed the least biodiversity in overgrowers. In contrast to all the other islands, Howland stayed the steadiest, and had the greatest number of surviving focal colonies, with very little taxonomic turnover. While there are clearly island-scale patterns, basic geographic inferences (N/S, E/W, equatorial boundaries, etc.) do not explain the fates of focal colonies.

To more extensively investigate the change in primary space holding (groundcover) associated with 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 space holders (Figure 16). Changes in groundcover were mostly consistent with our other findings: most focal colonies lost area over time with the exception of Howland and Flint, and the two taxa that had the most area change were *M. aequituberculata* and the *Porites* complex (Figure 16). There were no species that were found consistently taking over large areas of space. Notably, none of the corals we found that are generally classified as competitive species showed the expected pattern of growth (Darling 2012): all lost area coverage, suggesting that *M. aequituberculata* may be more competitive than previously appreciated.

DISCUSSION

Ecological succession is the replacement of taxa in a predictable pattern from initial colonizers to stable dominant species over time (Clementsian) (Clements, 1904, Prach and Walker, 2011) or to stable communities that change with regular disturbance (Tolerance Theory) (Connell & Slatyer, 1977). This species replacement can influence the physical structure of coral reefs and the diversity and abundance of all the other taxa that use these structure (Richardson et al., 2017). As a common, fast-growing, dominant species on Pacific reefs, *Montipora aequituberculata* and its interactions have the ability to shape the structure and ecological function of the reefs it inhabits, but it remains unclear how *M. aequituberculata* fits into reef successional trajectory. The main contributions of this thesis are to place *M. aequituberculata* into successional context using a novel experimental approach. We found many lines of evidence to support that *M. aequituberculata* can effectively compete against many reef taxa but is subordinate to stress-tolerant coral species in a post-disturbance environmental context. Our novel approach of looking into temporal dynamics from past-future, and future-past, provides a tool for similarly assessing additional reef taxa.

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), though in certain reefs, they have been classified as a dominant species (Jasmine et al., 2009). More recently, in the last decade or so, there has been discussion that *Montipora* should instead be considered a competitive taxa, due to its ability to

overgrow other corals, even traditionally stress-tolerant taxa such as *Porites*, due to both growth rate and *Montipora*'s ability to use physical attacks such as mesenterial filaments (Darling et al., 2012, Darling et al., 2013, Evensen et al., 2015), in some cases even taking over entire reefs after disturbances (Crane et al., 2016). Using photogrammetric data, we developed a novel analytical pipeline to track colonies not only forward in time as they grow and are overgrown, but also looking backward in time to see what used to exist and was displaced. In this way, we determined whether *M. aequituberculata* functioned as a weak competitor that quickly colonized an area, acting as a damper of biodiversity, or if it acted as a weedy, facilitator species by growing quickly but being easily overgrown by most other species, leading to an overall rise in biodiversity.

Attempting to classify the competitive dominance of *M. aequituberculata* on the reef, we found that *M. aequituberculata* was a dominant competitor among other taxa typically categorized as competitive, however, *M. aequituberculata* was unable to compete successfully against stress-tolerant species. *M. aequituberculata* consistently overgrew other competitive genera such as *Pocillopora*, and overall, other competitive taxa lost groundcover when in competition with *M. aequituberculata*. Other studies have shown that plating *Montipora* recover faster from physical damage compared to acroporids (Hall 2001), which could lead to greater competitive ability compared to species that are slower to grow and recover. Interestingly, there is less to support that *M. aequituberculata* is strong competition when faced with weedy species, though this may be due to a lack of weedy colonies found interacting with the focal taxa.

However, when *M. aequituberculata* interacted with slower-growing, more resilient stress-tolerant species, it was unable to successfully compete. Following the interactions of focal colonies with the most common stress-tolerant species (*Porites* complex and *F. stelligera*), our results suggest that neither coral has the upper hand in competition, but overall, the focal taxa yield space to stress-tolerant species when they interact. We found that stress-tolerant corals were the most common interactors with the focal colonies and that they generally won in competitions with *M. aequituberculata*. In areas of recent disturbance, *M. aequituberculata* can grow quickly and take over reefs (Crane et al., 2016), but does not appear to be as tolerant to chronic or repeated stress as other corals. Regardless of whether the focal taxon is competitive or weedy, it is more susceptible to routine disturbance and stress than it is to other corals.

Competition for space is critical on a reef (Chadwick and Morrow, 2011), and species interactions depend on environmental context (Connell et al., 2004, Johnston et al., 2020), and the outcome of competitive interactions can have an impact on reef diversity (Chadwick and Morrow, 2011). Competitive dominants may reduce or eliminate the reproductive stock of weaker species on a reef or reduce recruitment of larva (Dubinsky and Stabler, 2011). Environmental variables can affect the competitive ability of corals, either directly or indirectly, changing interspecific outcomes. For example, ocean acidification did not affect the competitive ability of *M. aequituberculata* in a direct confrontation but did reduce the growth rate of *M. aequituberculata* (Evensen et al., 2015, 2021). Reducing growth rate could lead to the decline of *M. aequituberculata* on reefs, which would result in a possible shift to more stress-tolerant, massive, and less

structurally complex corals and could, over time, reduce the surface complexity of the reef, removing the ability of the reef to provide shelter for fishes and other organisms that rely on the rugosity of the reef for habitat and safety.

From our investigation into the morphometrics of the focal colonies of *M. aequituberculata* and the changes over time, we found that larger colonies were more likely to lose surface area, compared to smaller colonies. This finding is consistent with other studies that investigated size effects on growth and survival (Hughes and Jackson, 1985, Shenkar et al., 2005, Brandt 2009, van Woesik et al., 2012, Kodera et al., 2020). Plating corals like *M. aequituberculata* are more susceptible to breakage and mechanical damage than massive or encrusting corals but are less susceptible to total mortality from physical damage (Hughes and Jackson, 1985). In addition, outcomes are size-dependent; for example, Kodera et al. (2020) found that larger colonies are less likely to suffer total mortality, but are more likely to lose surface area, which is consistent with our findings.

This paradigm of “the larger you are, the harder you fall” is accurate partially because larger colonies simply have more area to lose, although that is not the only reason for differential size effects. van Woesik et al. (2012) found that colony growth form, as well as the height to diameter ratio, impacted survivorship in environments of high thermal stress. Shenkar et al. (2005) found that a smaller size appeared to be advantageous for colonies in bleaching paradigms in the Mediterranean, and Brandt (2009) found a similar pattern for some Caribbean corals. Smaller corals had greater survivorship than larger ones, and partial mortality led to a smaller overall average colony size as thermal stress was biased toward larger colonies. These findings suggest

that over time, as thermal stresses and greater physical damage from stronger storms and human actions increase (De'ath et al., 2012), coral dynamics could be skewed toward smaller, more encrusting, or low-profile corals. If that happens, larger, late successional species could lose their competitive edge, changing the competitive and successional dynamics of reefs, affecting not only the corals themselves, but also the ecosystem services that the reefs offer to the organisms that rely on them, including humans.

Site, island, and archipelago patterns were tracked across this study to investigate different spatial scales. Understanding the scale at which different biological patterns exist can help make generalizations about habitat and inform conservation decisions (Concepcion et al., 2014, Toonan et al., 2011). Looking at the site scale, some patterns of competition were more common within an island than others. While investigating which species successfully outcompeted the focal taxa at each island (Figure 15), I observed that patterns of competition at sites within an island were similar, which could be due to similar biodiversity given the relatively small distance between sites. However, looking at the island scale, the islands with the most similar patterns of species competition were not the most geographically similar. For example, Enderbury (Phoenix Islands) can be visually grouped together with Millennium and Flint (Line Islands) as having similar patterns of competition. These islands are not the closest to each other, but they are the most easterly islands of their island chains. This set of easterly islands having similar patterns could be due to the bulk flow of the South Equatorial Current which flows westward between about five and 15 degrees South (Britannica) and has been implicated in the westward dispersal of some coral larvae (Wood et al., 2014).

Looking at gain and loss of surface area (Figure 6) we found inconsistent patterns at different spatial scales. At the island scale, the sites that lost the most area (Enderbury and Millennium) were not neighbors, although they are both eastern islands in their chains. Howland and Flint show the greatest growth and survivorship of the focal colonies, and are found in different island chains, with different positioning: equatorial (Howland) and farthest South (Flint). Some of these patterns are driven by specific sites on an island, where even at the smallest scale we have - sites - there are major differences. Aston et al. (2019) documented that hard corals as a group can vary in their cover around a single island, with changes on the sub-kilometer scale being predictable in the absence of local anthropogenic stressors, similar to our data. This could suggest that large-scale or global drivers can be drowned out by local stressors as drivers of survivorship and decline. However, much of the literature suggests the opposite: that regional, large-scale stressors tend to show the larger effect (Darling et al., 2010, Doropoulos et al., 2022, Ginter et al., 2019, Hughes et al., 2018), though storms have been shown to drive patterns at some reefs in the Great Barrier Reef (Lam et al., 2018). Sandin et al (2020) have also suggested that using simple oceanographic variables are not sufficient for making demographic predictions; instead, it seems that differences in life strategies may lend complexity and flexibility to coral responses to stressors. Our data support this idea, and it is clear that *M. aequituberculata* acts as a strong competitor in some conditions and as a weaker competitor in others.

Patterns of *M. aequituberculata* interactions with the number of interacting taxa were similar across all sites, islands, and archipelagos (Figures 9-14). There were no

differences at any site in how many species overgrew or were overgrown by the focal colonies. While we and many others have shown that competitive hierarchies can be circumstance dependent (Crane et al., 2016, Darling et al., 2012, Darling et al., 2013, Evensen et al., 2015, Jasmine et al., 2009), those changes do not appear to overwhelm hierarchies on a regional scale. By looking at the number of species alone, *M. aequituberculata* would likely be categorized as a neutral competitor, but other metrics are more revealing (see competitive dominance section- above), though none of them are sufficiently explained by spatial patterns at an island or archipelago scale.

Classifying the general competitive strategy of a coral taxa is complex, as strategy will always be contextualized to environmental context (Connell et al., 2004, Evensen 2015, Johnston et al., 2020), which is influenced by biodiversity, environmental conditions, and recent history (Doropoulos et al., 2022). *M. aequituberculata* was most frequent near human disturbed habitats and villages in Ulithi Atoll, Yap State, Federated States of Micronesia (Crane et al., 2016). Our findings do not show that *M. aequituberculata* are able to dominate traditionally stress-tolerant species, however, some research has found that the taxon is a dominant species even in disturbed environments (Evensen et al., 2015). On post disturbance reefs, *M. aequituberculata* was able to quickly establish itself and dominate on reefs, sometimes creating thickets of *M. aequituberculata* to the complete exclusion of other species at Palmyra atoll in the Line Islands and Ulithi Atoll, Yap State, in the Federated States of Micronesia (Williams et al., 2013, Crane et al., 2016). However, we did not observe that trajectory at any of our sites.

While the sites that we surveyed are all considered to be in recovery post-disturbance, most were showing decline in the coverage of *M. aequituberculata*, suggesting that this species does not maintain dominant cover, though these corals are clearly important primary spaceholders post-disturbance. We found that half our sites were losing coverage of the species (Figure 6), with a few possible reasons. It is possible that the *M. aequituberculata* is being replaced by other corals, either by facilitating the growth of other species or by being overgrown by later successional species that are able to competitively dominate the focal taxa, as is suggested by various succession models. It is also possible that the *M. aequituberculata* is dying off due to environmental factors being suboptimal for the species, leading to the death of the focal taxa with no replacement. We only found one island that showed that colonies of *M. aequituberculata* were consistently growing. Finally, some of the decline in area coverage that we observed may be caused by differential responses to types of stress. Literature suggests that while plating *Montipora* regenerate better than other taxa from physical damage such as breakage (Hall 2001), they are more susceptible to disease, which can be compounded by weather events (Haapkyla et al., 2013) or other environmental stressors, and ocean acidification and temperature changes can affect growth and survivability as well. Some successional theories also suggest that these different stress-responses could be the main drivers of visible succession patterns (Connell & Slatyer, 1977)

Reefs in post-disturbance recovery are typically associated with high CCA cover (Whitman et al., 2020), which begs the question of whether *M. aequituberculata* abundance is linked with CCA association. *Montipora* is usually shown to have

preference for larval settlement on crustose coralline algae (CCA) (Heyward & Negri, 1999), however in one study *M. aequituberculata* larvae did not seem to settle in response to cues from CCA that many other corals do (Whitman et al., 2020).

Understanding how these data can be reconciled could help inform the beginning stages of *Montipora* settlement and growth. Using the technique that we have pioneered in this paper could help to elucidate if *M. aequituberculata* shows preference for settlement on CCA in large scale natural experiments. If there is a preference toward settling in CCA, then more investigation into the mechanisms of this preference should be investigated.

Our data support the direction of the field to recognize *Montipora* as a competitive genus against most corals, though not against stress-tolerant species. We have provided support for the view that *M. aequituberculata* is a strong competitor in many cases on the reef (Figures 9-14, Competition Chi Squares, Dominance Probabilities). Going forward, this technique can be used to start investigating their facilitation potential. To test the hypothesis that *M. aequituberculata* facilitates species such as *Porites* and *Pocillopora* complexes, we could use the created mosaics to investigate their population abundance across the reef to determine if they are the most common corals at our sites. If they are the most abundant taxa on the reef, their ability to consistently overgrow *M. aequituberculata* is most likely random chance. If the *Porites* and *Pocillopora* complexes are not the most common taxa on the reef, but are the most common overgrowers of *M. aequituberculata*, it may be because their growth is being facilitated by the presence of *M. aequituberculata*. The second way to test this hypothesis would be to use our method to look backward in time. For a given taxa such as *Porites*,

we can test the hypothesis that *M. aequituberculata* facilitates its growth. To do this we can investigate the identification of spaceholders that were overgrown, similar to what we have done in this paper. By looking at how often the taxa overgrows *M. aequituberculata* versus other corals, other organisms, or empty space could provide insight into the relationship with *M. aequituberculata*. If the *Porites* colonies are more likely to overgrow the *M. aequituberculata* than other corals or empty space, it would support the hypothesis that *M. aequituberculata* is acting as a facilitator. If, however, the taxa will overgrow empty space and other coral as often as it overgrows the *M. aequituberculata*, it may simply be a stronger competitor and the hypothesis should be rejected. This approach could help tease apart more of the competitive and successional trajectories of reefs and help to begin an investigation into which coral taxa may act as facilitators, and how the expected environmental changes could change these paradigms.

Patterns of competitive interactions between organisms can be used to help understand biodiversity and successional changes on a reef (Prach and Walker, 2011), as well as what, if any stable communities could be expected. By teasing apart these interactions, we can better map the dynamics of coral reefs, with the goal of predicting how they may change over time, which is critical as reef degradation is occurring globally (Bruno and Valdivia, 2016). This knowledge can elucidate successional dynamics that shape a reef's biodiversity and resilience, as well as help direct conservation and restoration efforts. Understanding these dynamics of the reef can help us determine which reefs are likely still healthy and which are showing signs of decline. Knowing which reefs are most at risk or conversely, most likely to respond to

intervention, can help direct the efforts of conservationists when creating protected areas or making restoration plans. There have already been instances of groups using the life strategy makeup of reefs and their morphologic makeup to inform the sites being targeted for conservation (Edinger and Risk, 2000). The more information we have on the “normal” trajectories of reefs, the better informed these decisions can be, leading to larger gains.

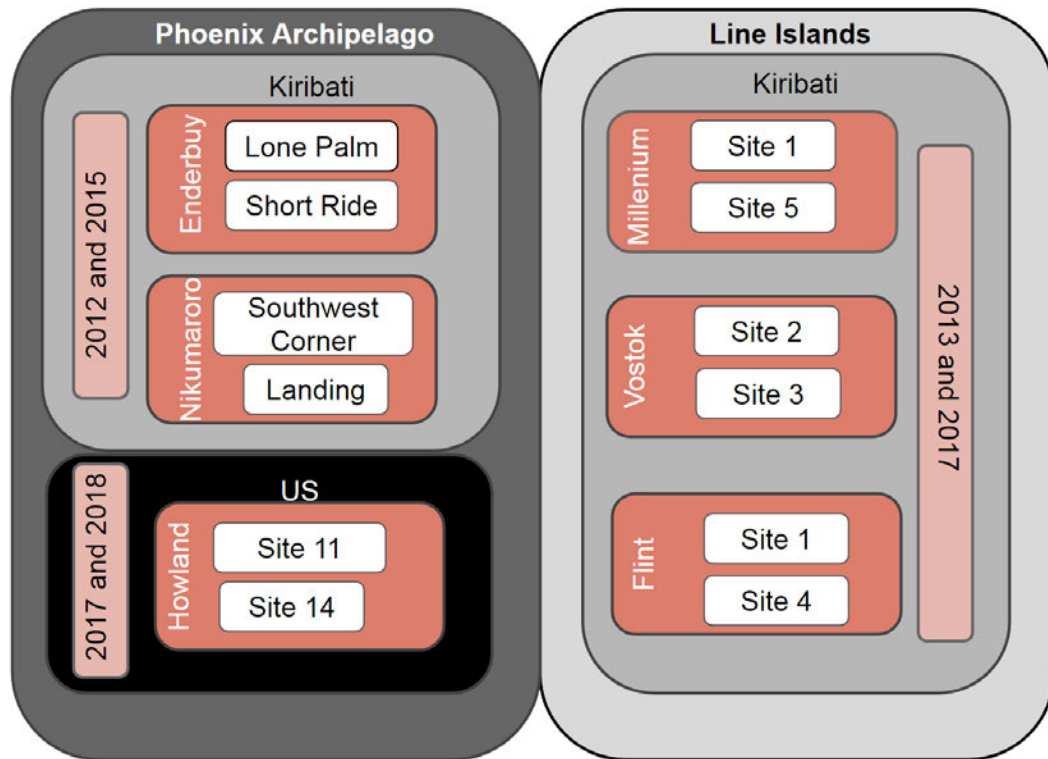


Figure 1. The schematic of the sites used. Sites on the left are in the Phoenix Archipelago and islands on the right are in the Line Islands. The years on the side indicate the years that data was collected.

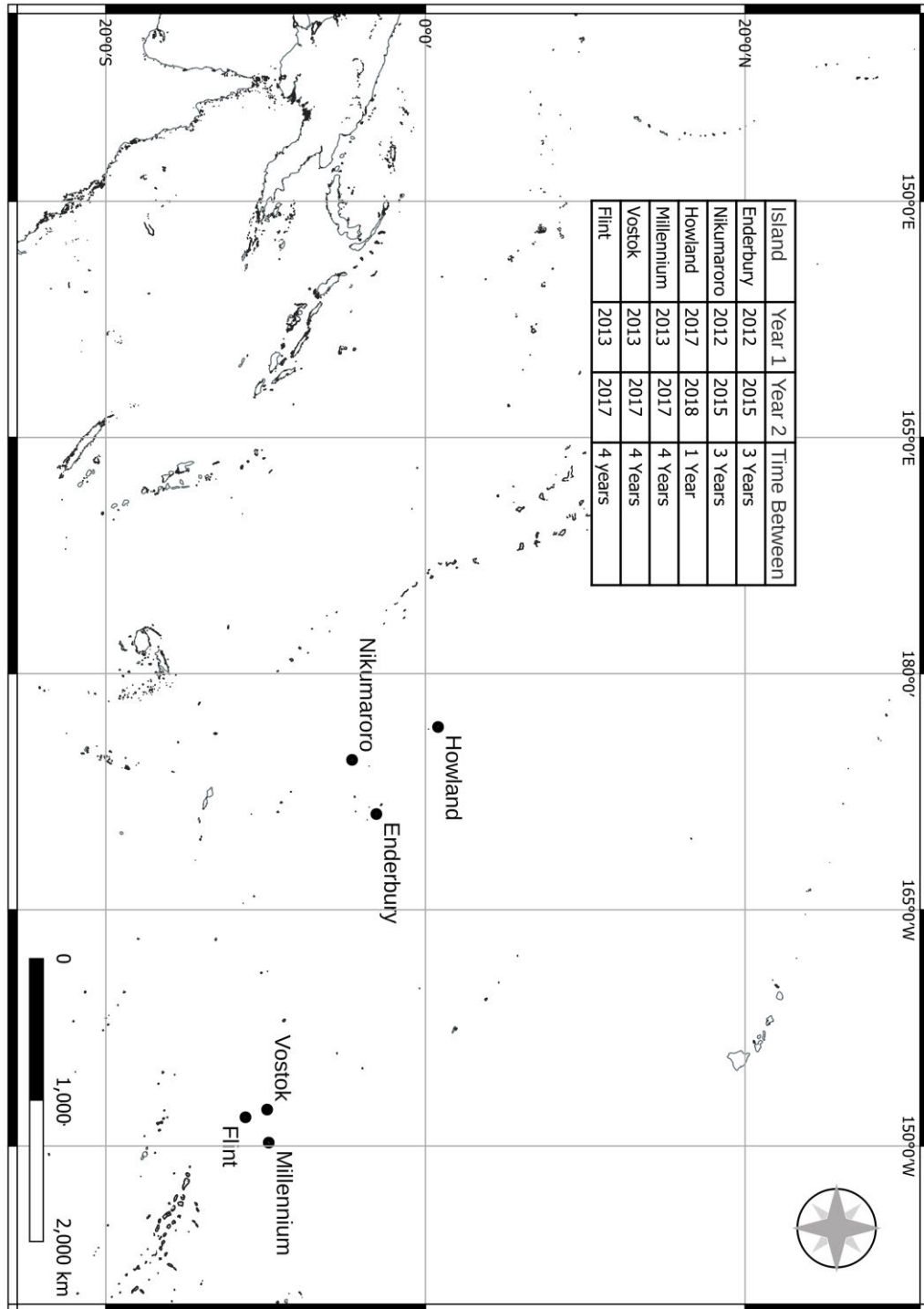


Figure 2. A map of the study sites used in this study. This map shows the locations of the six islands used in this study. Enderbury, Nikumaroro, and Howland are islands in the Phoenix Islands and Vostok, Flint, and Millennium are part of the Line Islands.

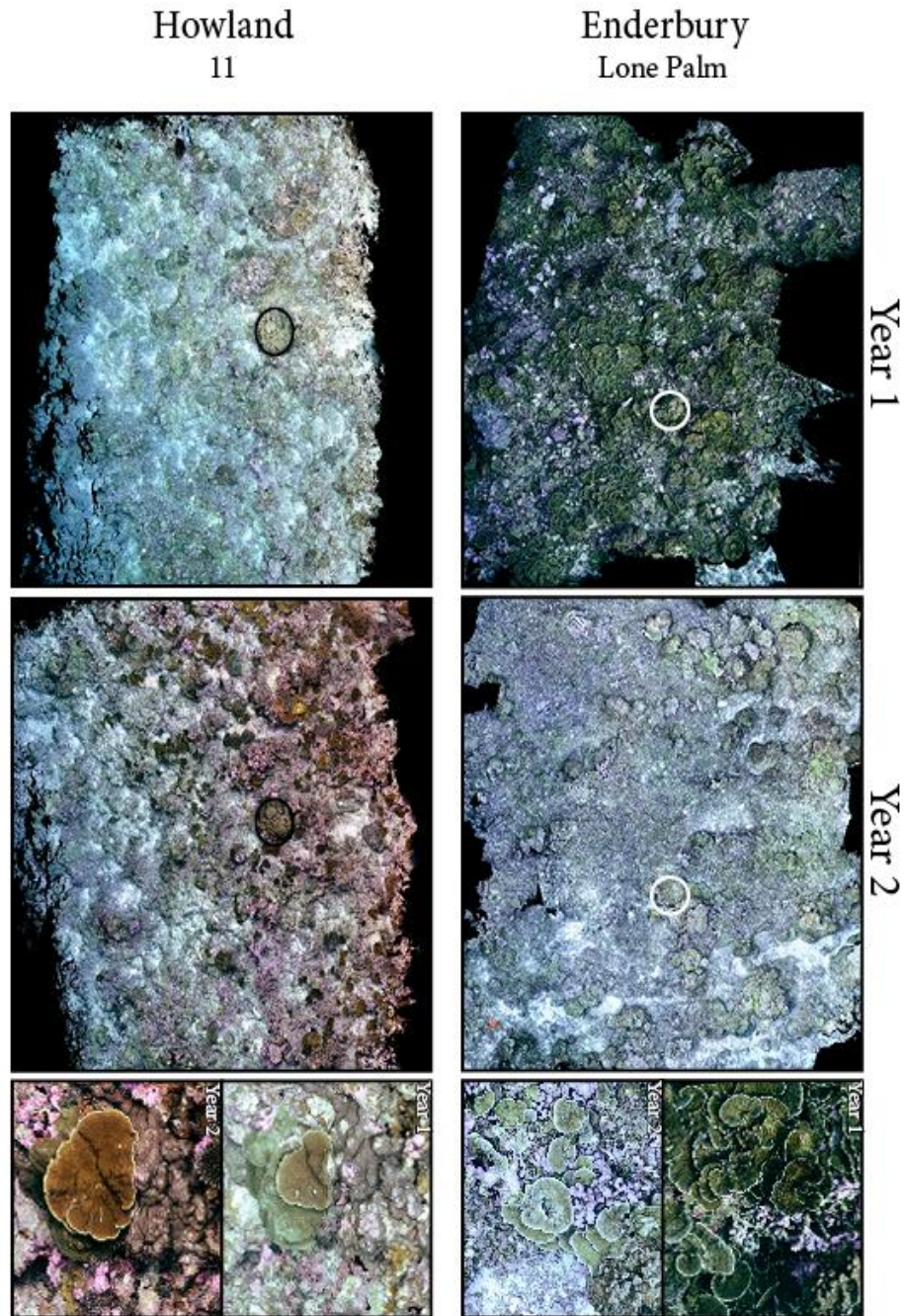


Figure 3. This figure shows examples of a site that declined between years (Enderbury) and a site that showed growth (Howland). Each site has the orthoprojected mosaics that were used on the left, as well as zoomed in examples of colonies on the right. The circles show a colony that can be found in both years as a point of orientation.

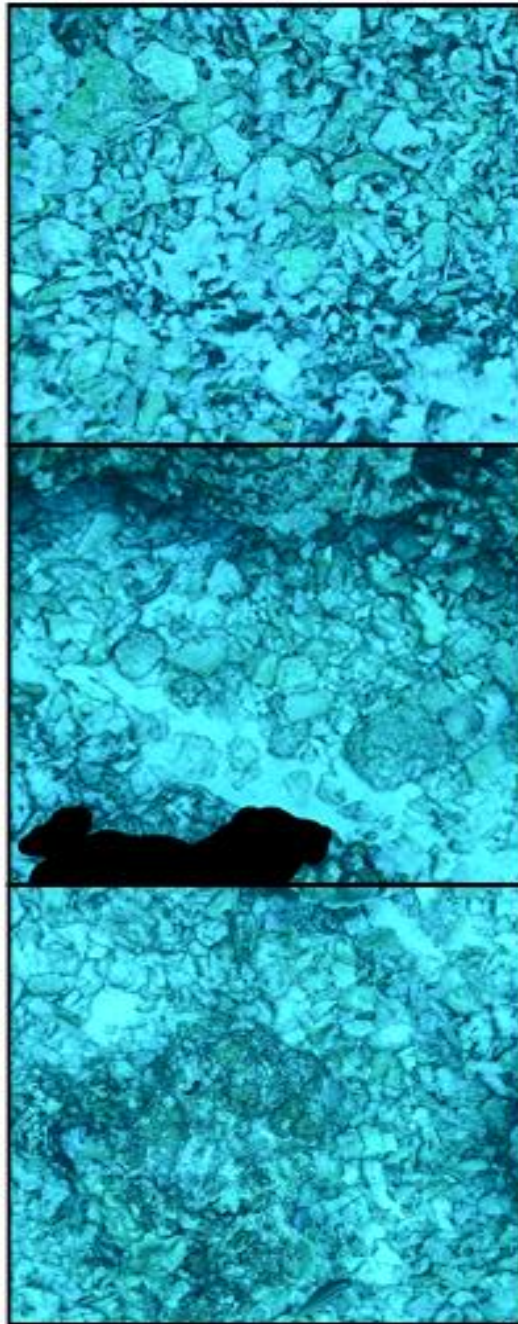


Figure 4. Examples of “Open Space”. For this analysis, Open Space refers to any non-living-coral groundcover. This includes coral rubble, sand patches, turf algae and sponges, and other algae and encrusting organisms.

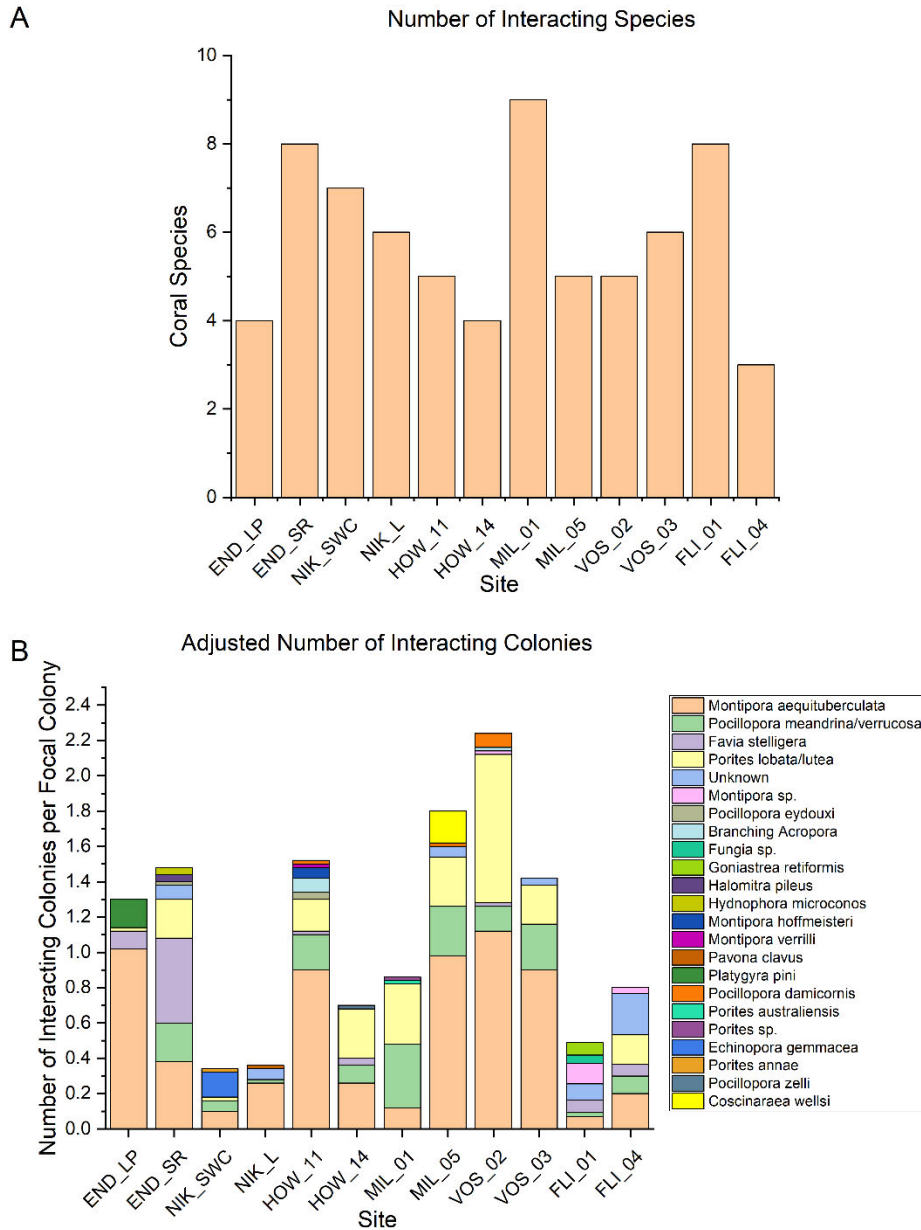


Figure 5. Species interacting with the focal colonies. This figure shows the species of coral that the colonies of interest interacted with at each site. **Panel A** shows the number of coral species that interacted with the focal colonies in any year, either overgrowing focal colonies or being overgrown by them. A chi square test found no differences across sites ($X^2(11, 12) = 3.88, p = 0.973$), islands ($X^2(5,6) = 1, p = 0.962$), or archipelagos ($X^2(1,2) = 0.310, p = 0.578$). **Panel B** shows the number of colonies of each species that interacted with the focal colonies across both years adjusted to the number of focal colonies used to account for the fact that there were too few colonies at the Nikumaroro sites to reach the target number of colonies. All sites had focal colonies interacting with other colonies of *M. aequituberculata*, and most had colonies of the *Porites* and *Pocillopora* complexes.

Table 1. This table shows what species the focal colonies interacted with at each site. A 1 indicates that the species was found interacting with one of the focal colonies in one or both years. *M. aequituberculata* and a *Porites* complex of *P. lobata* and *P. lutea* were found at all sites, and almost all had colonies of the *Pocillopora* complex of *P. meandrina* and *P. verrucosa*. The majority of other species were relatively uncommon.

	END _LP	END _SR	NIK L	NIK SWC	MI L 01	MI L 05	HOW _11	HOW _14	VOS _02	VOS _03	FLI _01	FLI _04	Total Sites
<i>Montipora aequituberculata</i>	1	1	1	1	1	1	1	1	1	1	1	1	12
<i>Porites lobata/lutea</i>	1	1	1	1	1	1	1	1	1	1	1	1	12
<i>Pocillopora meandrina/verrucosa</i>		1	1	1	1	1	1	1	1	1	1	1	11
<i>Unknown</i>		1	1	1		1	1	1		1		1	8
<i>Favia stelligera</i>	1	1	1	1	1	1					1		7
<i>Pocillopora damicornis</i>					1			1		1	1		4
<i>Branching Acropora</i>					1						1		2
<i>Goniastrea retiformis</i>	1			1									2
<i>Montipora hoffmeisteri</i>					1						1		2
<i>Pocillopora eydouxi</i>		1			1								2
<i>Coscinaraea wellsi</i>										1			1
<i>Echinopora gemmacea</i>							1						1
<i>Fungia sp.</i>				1									1
<i>Halomitra pileus</i>		1											1
<i>Hydnophora microconos</i>		1											1
<i>Montipora sp.</i>				1									1
<i>Montipora verrilli</i>					1								1
<i>Pavona clavus</i>								1					1

<i>Platygyra pini</i>	1												1
<i>Pocillopora zelli</i>						1							1
<i>Porites annae</i>							1						1
<i>Porites australiensis</i>									1				1
<i>Porites sp.</i>									1				1
Total Species/site	5	8	5	8	9	6	6	6	5	6	7	4	

Table 2. This table shows the number of colonies of each species of coral that interacts with the colonies of interest at that site across both years. Most species were relatively uncommon, with only a few colonies total across all sites.

	END LP	END SR	NIK L	NIK SWC	MI L 01	MI L 05	HOW 11	HOW 14	VOS 02	VOS 03	FLI 01	FLI 04	Total 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>Favia stelligera</i>	8	28	1	3	1	2					1		44
<i>Unknown</i>		2	8	4		1	1	1		4		2	23
<i>Coscinaraea wellsi</i>										12			12
<i>Pocillopora damicornis</i>					1			2		1	4		8
<i>Echinopora gemmacea</i>							7						7
<i>Branching Acropora</i>					4						1		5
<i>Montipora sp.</i>				5									5
<i>Goniastrea retiformis</i>	1			3									4
<i>Montipora hoffmeisteri</i>					2						1		3
<i>Platygyra pini</i>	3												3
<i>Fungia sp.</i>				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
<i>Porites sp.</i>									1				1
Total Colonies	73	67	21	22	82	41	18	19	50	106	111	75	685

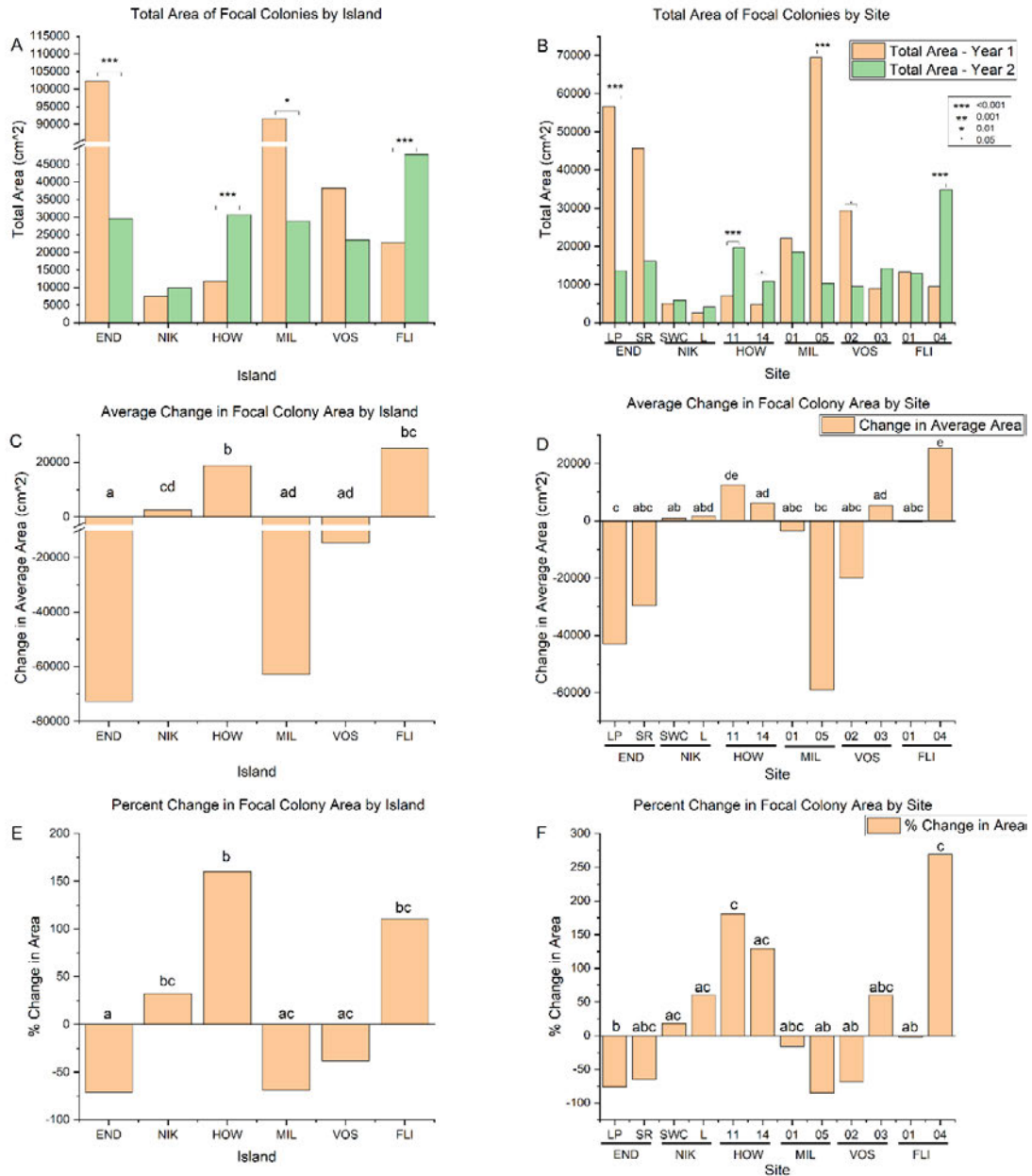


Figure 6. Investigating the change in area of focal colonies over time. This graph looks at how the areas of focal colonies at different islands change across time. **Panel A** shows the total area of the focal colonies in each year by island. **Panel B** shows the total area of the focal colonies in each year by site. The changes at most islands are driven by a single site. **Panel C** shows the change in the average area of focal colonies between years by island and **Panel D** shows the same by site. **Panel E** shows the percent change in the area of focal colonies at each island between years, and **Panel F** shows the percent change at each site. Flint is the only island where there are different patterns in percent change between sites. Wilcoxon tests were used for panels A and B. *** < 0.001, ** = 0.001, * = 0.01, • = 0.05. Panels C through G used Kruskal Wallis tests followed by Dunn tests, visualized by letters demarcating the groups of similarity.

Table 3. Statistics for Wilcoxon tests by Island. Bolded numbers indicate statistical significance.

Island	W	P value
Enderbury	4823.5	1.99e-05
Nikumaroro	3147	0.05
Howland	8428.5	8.60e-08
Millennium	2067	0.001
Vostok	4287	0.28
Flint	6508.5	6.63e-05

Table 4. Statistics for Wilcoxon tests by Site. Bolded numbers indicate statistical significance.

Island	Site	W	P value
Enderbury	Lone Palm	886	2.58e-05
	Short Ride	1569.5	0.08
Nikumaroro	Landing	580	0.05
	South West Corner	1024.5	0.38
Howland	Site 11	2059	3.88e-07
	Site 14	2193	0.005
Millennium	Site 01	1367	0.39
	Site 05	1182	0.0005
Vostok	Site 02	927	0.02
	Site 03	1254	0.26
Flint	Site 01	1179	0.88
	Site 04	2048	3.80e-08

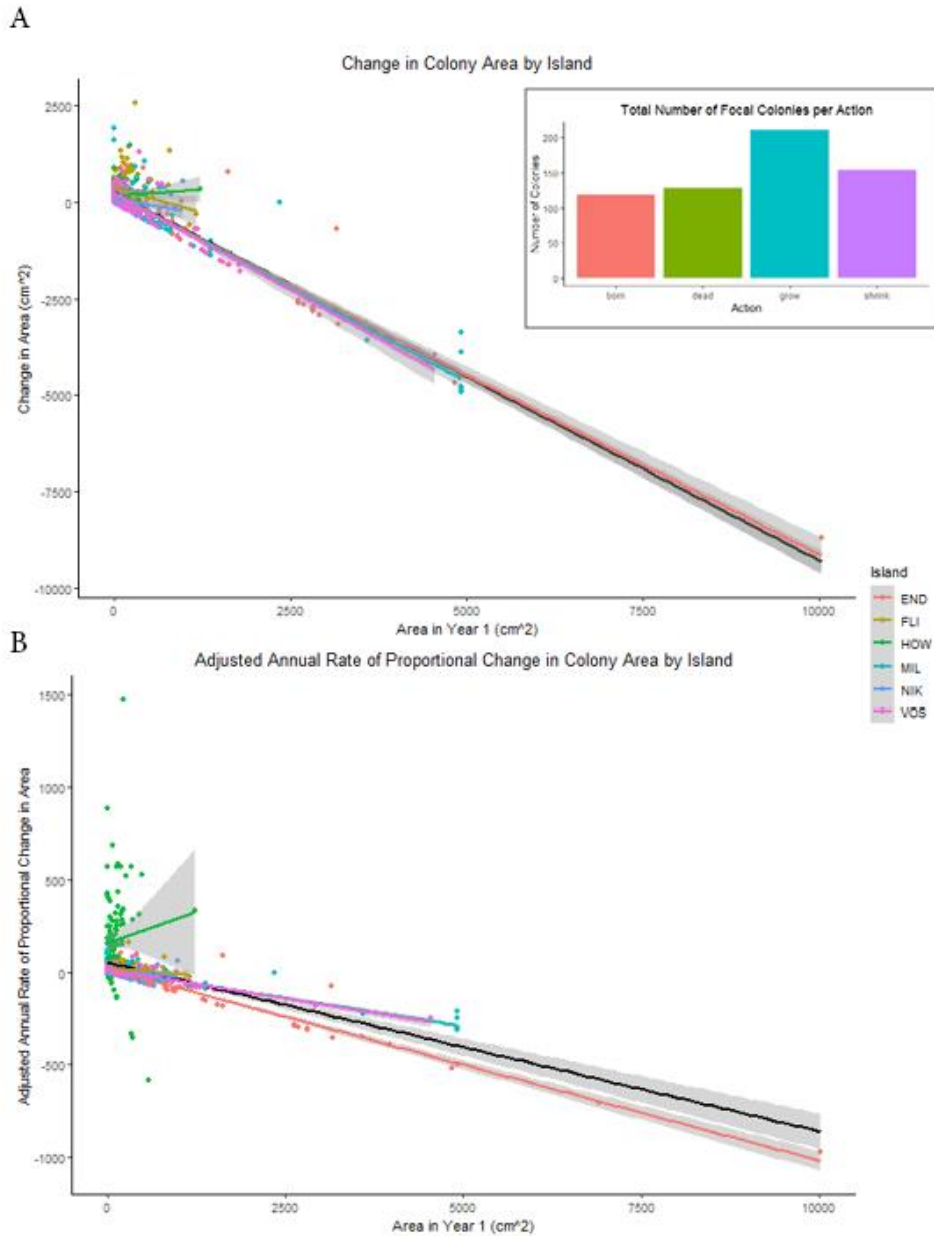


Figure 7. Panel A: Change in focal colony area based on starting colony size in year 1. Enderbury, Millennium, and Vostok all have similar regressions, and are driven by a small number of large colonies. The inset is of the total number of focal colonies of each fate summed across islands. **Panel B:** The adjusted proportional change in focal colonies. This graph plots the change in area of focal colonies proportional to their starting area and normalized by the number of years between visits. For both plots, multiple linear regressions were run using Island and Area in Year One as the regressors, plotted in the color of the corresponding island. A simple regression is plotted as a black line. Regressions are plotted with a 95% CI. A Kruskal Wallis test was used to compare the fates of colonies across all islands and found no difference between the fates of colonies.

Table 5. Regression statistics for Figure 7A multiple regression

Coefficient	Estimate	Standard Error	T Value	Pr(> t)
Intercept	200.52	16.9	5.42	8.55e-08
Area 1	-0.94	0.02	-58.85	<2e-16
Flint	269.79	51.93	5.20	2.79e-07
Howland	74.20	51.08	1.45	0.15
Millennium	4.03	48.86	0.08	0.93
Nikumaroro	-70.32	56.97	-1.23	0.22
Vostok	20.90	51.76	0.40	0.69

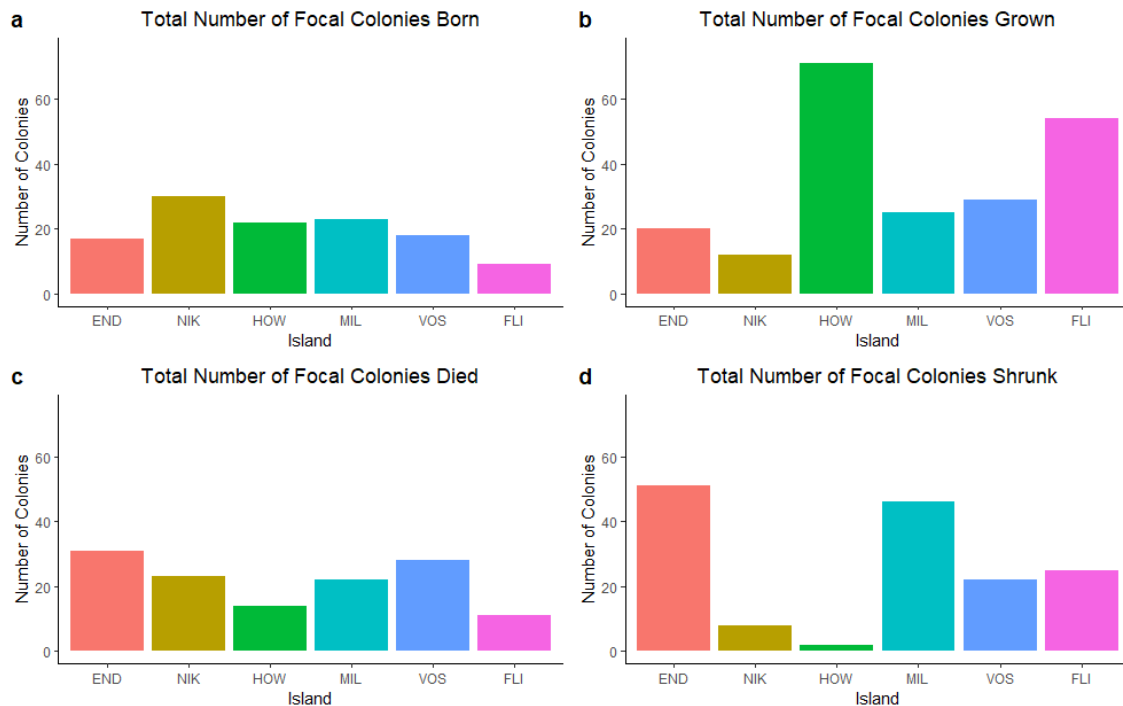


Figure 8. The fates of the focal colonies tracked across years. Colonies born were only found in the second year, colonies that died were only found in the first year, and colonies that were in both years either grew or shrunk based on the change in surface area between visits. Patterns of growing and shrinking match with the patterns found in previous figures. Kruskal-Wallis tests found no difference between the number of colonies with a certain fate across islands for any of the fates. $n=100$ for all sites but Nikumaroro, which is $n=73$.

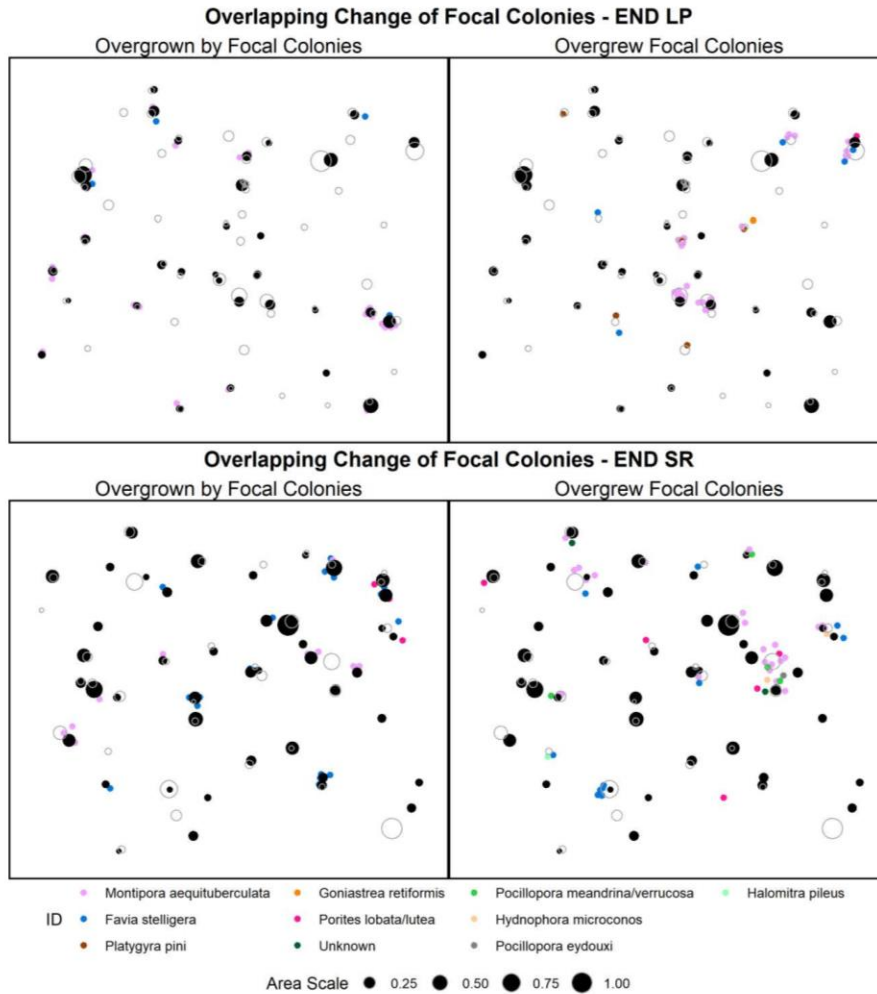


Figure 9. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies. At Enderbury sites, multiple colonies took space from the focal colonies they overgrew.

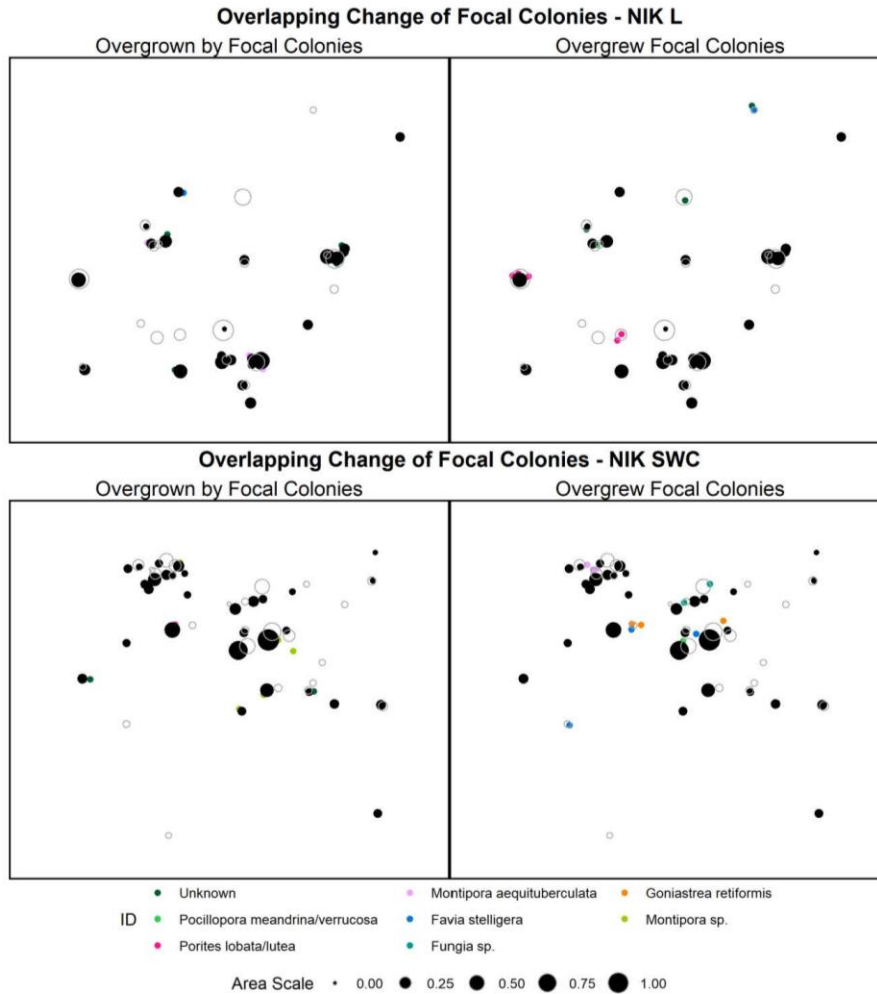


Figure 10. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies. At Nikumaroro sites, there were few interactions with other colonies of coral. Even with the small number of interactions, there were still more overgrown focal colonies than ones that overgrew other species.

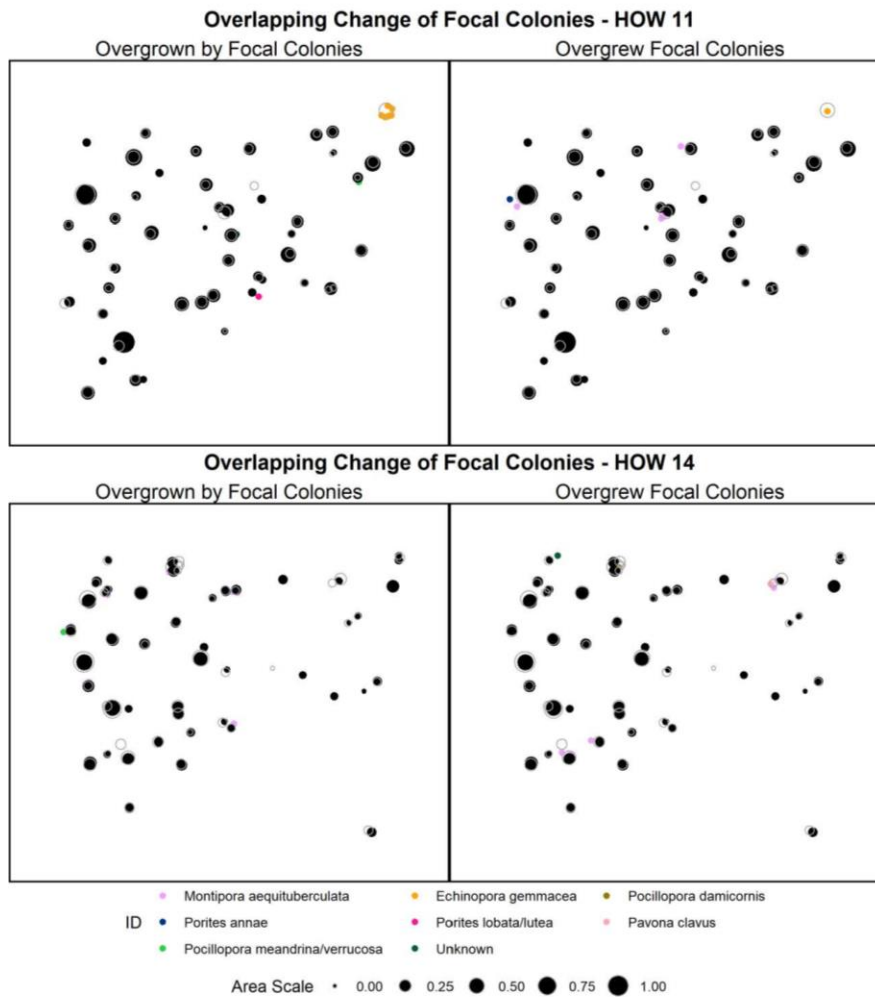


Figure 11. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies. At Howland sites, there were few interactions with other colonies. However, at this island, the scarcity of interactions is due to the fact that most of the colonies survived, and many of them grew, leaving little room for other species to gain ground space.

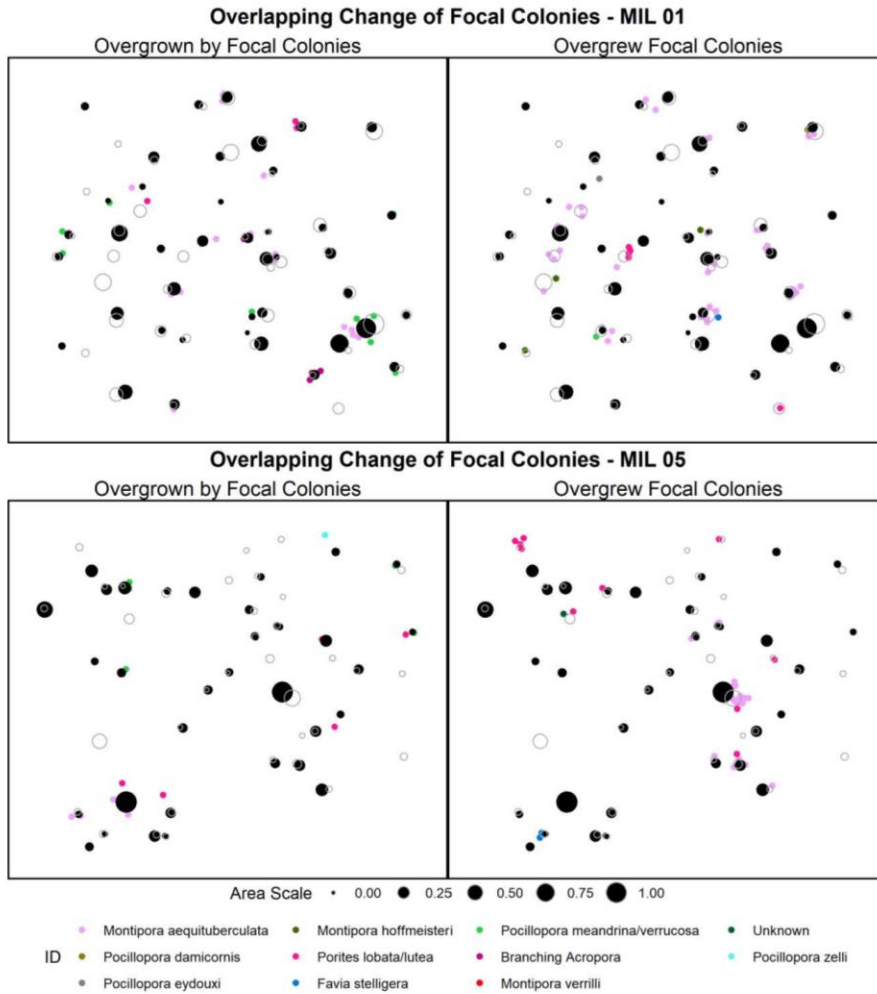


Figure 12. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies. At Millennium sites, there was a range of interactions found. At Site One, most of the interactions in both directions were with other colonies of *M. aequituberculata*, while there was more variation in species at Site Five.

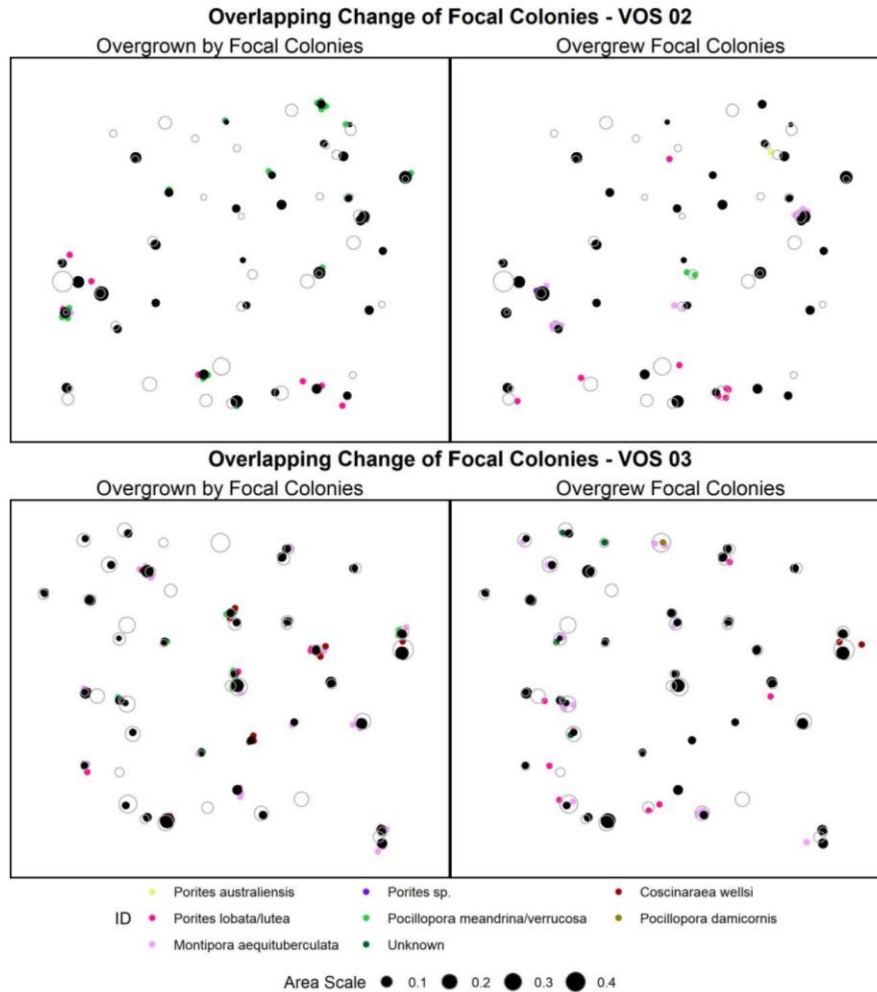


Figure 13. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies. At Vostok sites, there was a large variety of interactions. While many of the colonies at Site 2 died, there were still many instances of interaction in both directions. At Site 3, there was more survivability, with some focal colonies overgrowing four or five other colonies.

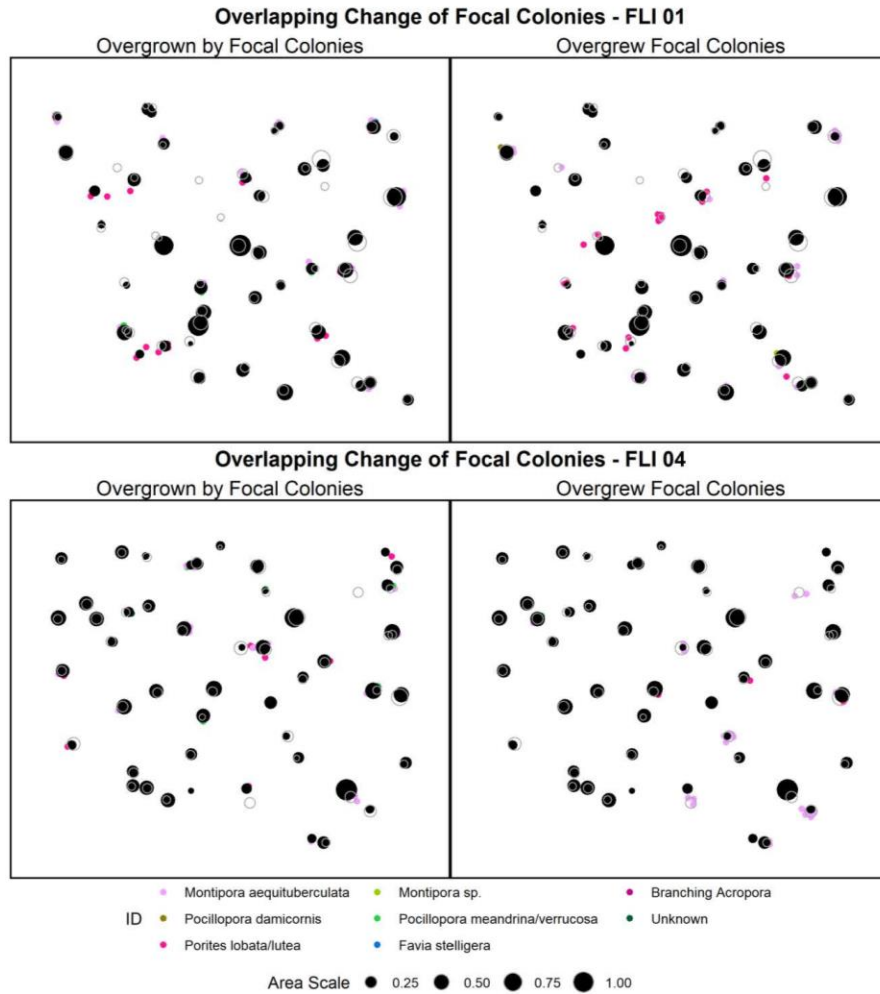


Figure 14. The interactions of focal colonies with surrounding colonies. The size and center location of focal colonies the first year is shown with the grey circle, and the colony in the second year is marked with the black dots. Colored dots on the left mark the location and species of colonies that were overgrown by the focal colonies, and colored dots on the right mark the location and species of colonies that overgrew the focal colonies.

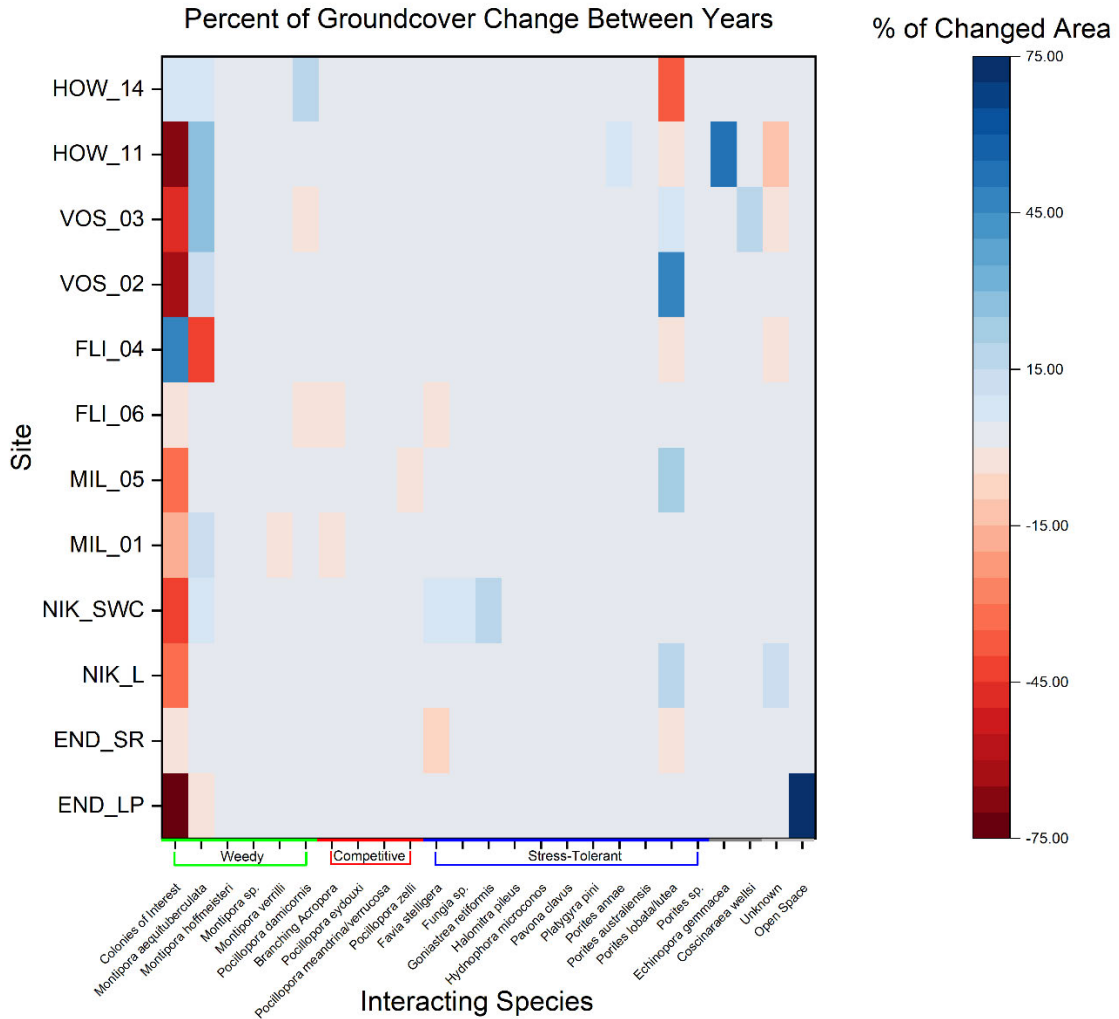


Figure 16. The change in groundcover area at different sites. The percent of changed area is calculated as the difference in percentage of pixels of change in each year. Reds signify overall loss of area of that species and blues represent gain. Paler colors show smaller amounts of change. Species along the x axis are organized by the competitive strategies in Darling (2012). Green are weedy species, red are competitive, blue are stress-tolerant, dark grey are unclassified and light grey do not have classifications.

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CURRICULUM VITAE

