Effect of coral reef restoration on demersal biodiversity in Okinawa, Japan

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Global climate change is leading to damage and loss of coral reef ecosystems. On subtropical Okinawa Island in southwestern Japan, the prefectural government is working on coral reef restoration by outplanting coral colonies from family Acroporidae back to reefs after initially farming colonies inside protected nurseries. In this study we evaluated the ongoing restoration efforts by comparing outplanted locations with nearby control locations with no restoration activity. We examined 3 sites on the coast of Onna Village on the west coast of the island; each site included an outplanted and control location. We used 1) coral rubble sampling to evaluate and compare abundance and diversity of rubble cryptofauna; and 2) coral reef monitoring using photograph transects to track live coral coverage. Results showed that rubble shape had a positive correlation with the numbers of animals found within rubble themselves and may therefore constitute a reliable abundance predictor. Outplanted locations did not show differences with the controls in rubble cryptofauna abundance, but had significantly lower coral coverage. Differences between sites were significant, for both rubble cryptofauna and coral coverage.We recommend; 1) to evaluate outplanting colonies from more stress-resistant genera in place of *Acropora*, 2) to conduct regular surveys to monitor the situation closely, and 3) to establish conservation and sustainable practices that could aid restoration efforts, reducing coral mortality of both outplanted and native colonies.

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Abstract

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Introduction

Coral reefs in the Indo-Pacific are the most diverse marine ecosystems in the world (Hoeksema 2007). Okinawa Island is part of the Ryukyu Archipelago in southwestern Japan, whose high levels of marine biodiversity are connected with the presence of the warm Kuroshio Current that provides a favorable environment for more than 360 scleractinian coral species (Nishihira 2004). However, marine biodiversity in the Ryukyus, when compared to other regions in the Indo-Pacific, such as the Red Sea or the Great Barrier Reef, is still relatively understudied for numerous marine taxa (e.g. Fujii & Reimer 2011; Reimer et al. 2019). While there is abundant information on hard corals, fish, shellfish, large crustaceans, and other commercially important groups, other marine taxa have large research gaps (Roberts et al. 2002; Colin 2009; Reimer et al. 2019). Studies on ecological processes, conservation-related issues, and human impacts are also comparatively few (Reimer et al. 2019).

Biodiversity forms the basis of healthy ecosystems and their corresponding ecosystem services, and overall, biodiversity trends are negative in the world's ecosystems due to increasing anthropogenic pressures (Butchart et al. 2010). Because coral reefs have high biological diversity and provide fundamental ecosystem services, including fisheries and tourism, it is of strategic importance for administrations in subtropical and tropical regions locations, including Okinawa, to preserve their coral reef ecosystems. Despite this, coral reefs in the Ryukyus are under stress from a wide variety of global anthropogenic stressors, particularly temperature-induced bleaching caused by climate change (Nakano 2004a), aggravated by local stressors, such as overfishing, soil runoff, pollution, habitat loss and fragmentation (Nakano 2004b; Hongo & Yamano 2013; Reimer et al. 2015; Masucci & Reimer 2019, in press; Masucci et al. 2019; Reimer et al. 2019) with the result being a decline in overall ecosystem health. Realizing this, the Okinawa Prefectural Government has recently promoted efforts to mitigate the ongoing decline with a coral (Scleractinia) restoration program based in Onna Village on the west coast of Okinawa Island (Omori 2011; Omori et al. 2016).

Restoration in Okinawa

In Okinawa Prefecture, scleractinian corals have been reduced in both terms of coverage and diversity, with documented bleaching and high mortality rates for at least five decades, which have particularly affected branching coral genera such as *Acropora* and *Montipora*, which were once dominant in the Ryukyu Archipelago (Sakai & Nishihira 1986; Mori 1995; Loya et al. 2001; Omori 2011; van Woesik et al. 2011; Masucci et al. 2019). Restoration attempts have been carried out by local fishermen and dive centers since the end of the 1990s (Okubo & Onuma 2015), and restoration efforts have been coordinated and directed by the prefectural government from 2006 (Okubo & Onuma 2015; Omori et al. 2016).

The restoration approach chosen by Okinawa Prefecture includes the use of coral nurseries at Okinawa Island and Kume Island, where sexually and asexually produced colonies are grown and then outplanted to target areas on the reefs. Coral outplanting is still underway in Onna Village (Table 1, Fig. 1) on the west coast of Okinawa Main Island, and planned in the future for Kume Island (Masucci et al. 2019).

About 20 species of Acroporidae have been transplanted at the cost of 2000 Japanese yen (approx. 20 US$) per colony (Omori et al. 2016). With the final goal of coral reef ecosystem restoration, a rigorous assessment of the reef ecosystem beyond just live coral coverage is desirable as reef ecosystems are not only corals, and transplanting corals ideally should aid surrounding biological communities. Innovative assessment methods are critically needed in order to more accurately assess anthropogenic stress, coral reef health, and the success of these restoration efforts.

Additionally, although reef restoration is a developing field, there are relatively few comparative studies on how restored coral reef diversity compares with that of unmanipulated surrounding areas. For example, coral cryptofauna composed of metazoan organisms living in inter- and intra-skeletal structures of hard corals (Enochs 2011) are extremely important in maintaining trophic systems and hence coral reef functionality due to their capability to capture and recycle nutrients (Richter et al. 2001; Enochs 2011). Coral rubble cryptofauna have been used as proxies for benthic diversity, and studies have shown that many cryptic species live within rubble in different environments (Takada, Abe & Shibuno 2007; Enochs 2011; Takada et al. 2014) including coral nurseries (Wee et al. 2019). Rubble cryptofauna surveys can allow comparisons of the animal community living at each location in order to evaluate differences in biodiversity and examine the effects of coral restoration on these communities.

The aim of this study was to perform an assessment of the status of coral reef restoration efforts at Onna Village, Okinawa Island, by measuring the abundance and diversity of coral rubble cryptofauna, as well as coral coverage. Surveys and samplings were conducted at three different sites where *Acropora* spp. has been outplanted, which were compared with surveys and samplings at nearby control locations that had not been treated. We hypothesized there would be significant differences between outplanted locations and controls, with higher diversity and numbers of animals at outplanted locations.

Materials and methods

Sampling area and experimental design

Sampling was performed at three sites in Onna Village, with each site consisting of an outplanted (restored) location and a control location where no restoration had been performed (Table 1, Fig. 1). Maeganeku1 (26.44715° N, 127.79077° E) is located at the south side of the channel that connects Maeganeku Port to the outer reef while Maeganeku2 (26.453902° N, 127.79313° E) is located on the north side of the same channel. Manza (26.508497° N, 127.85287° E) is located at the north side of Cape Manzamo. Restoration (=outplanting of coral colonies raised in inner reef nurseries) activities started from 2012 at Maeganeku1, and from 2017 at Maeganeku2 and Manza (Onna Village Fisheries Cooperative, pers. comm.).

Fieldwork was performed in winter 2017, summer 2018, and winter 2019. Each season, we investigated the same 3 sites (for each site, one outplanted and one control location). For each location, three buckets (10 liters each) of coral rubble were collected (total n=3 buckets x 6 locations, 18 buckets per season).

Three buckets of coral rubble were collected from each location by SCUBA diving; at outplanted locations at the same depths as transplanted colonies (between 2 and 4 m) from the area immediately around transplanted colonies (e.g. within 2 m from the closest transplant), and from control locations at least 100 m from outplanted locations, at the same depths. Immediately after rubble collection buckets were sealed with lids to prevent mobile animals from escaping. Buckets were then transported back to Maeganeku Port, with the sorting process starting immediately after returning (with an hour after the end of each dive).

Images of collected coral rubble were taken immediately after sampling (Fig. S1). Each coral rubble fragment was then classified as “massive-submassive” or “branching-tabular” following the coral classification protocol from English, Wilkinson & Baker (1997). For each survey, the frequency of "branching-tabular" of the total rubble was calculated and correlated with collected rubble animal abundance and phyla diversity data.

Each cryptofauna specimen of size ≥1 mm was collected with tweezers or syringes and photographed with macro lenses (Sony SEL30M35 f/3.5 mounted on Sony a6x00 camera) and scales (Fig. S2). Each initially animal was identified to the phylum level, given a specimen number, and preserved in 99% ethanol. Studies at the phylum are suitable in describing ecosystem diversity and environmental impacts: Anderson et al. (2005) measured biodiversity (richness, total abundance and structural composition) of animals living in the kelp holdfasts considering major phyla community. Other applications of phylum-level diversity data include the study of human impacts or interventions on natural ecosystems. The loss of fine-scale species information is compensated by a reduction in noise variability from lower taxonomic levels, making this level suitable to monitor ecosystem responses to human intervention (Warwick 1993). Another key advantage is speed: monitoring at high taxonomic levels allows obtaining the results of a survey in shorter times, which is important when monitoring where considerable public investments are made. Further advantages of using phylum-level data include reduced operative costs (studies which use phylum-level identification can be up to 95% less expensive than those which employ species-level identification) for sorting and identification (Khan 2006). Taxonomic sufficiency of phylum-level data has been confirmed for a wide range of studies, for terrestrial (Souza et al. 2016), freshwater (Cabral et al. 2017) and marine (Anderson at al. 2005) ecosystems.

Additionally, collected rubble data were compared with more traditional approaches: during Winter 2019 sampling, coral coverage data were collected from all six locations via LIT (Line Intercept Transects; Beenaerts & Vanden Berghe 2005) (10 m each, for each location n=6 transects) at the same depth as outplanted coral colonies (2-4 m). Photographs were taken and analyzed to calculate the percentage coral coverage. Living corals were identified to genus level following to Veron (2000) except for families Merulinidae and Montastraeidae, for which we followed Huang et al. (2014).

Statistical analyses

Coral rubble

Statistical tests were performed using R software (version 3.6.0, R Development Core Team 2019). The effects Treatment (outplanted vs control) and Site factors on animal abundance were tested using 2-way ANOVA. Normality was tested with the Shapiro-Wilk test (Royston 1982), and homoscedasticity with Bartlett's test (Bartlett 1937). Since both assumptions were respected, no transformation of data was performed. The Tukey post-test (Yandell 1997) was performed on significant ANOVA results.

The effects of the Treatment and Site factors on phyla abundance was tested with PERMANOVA, using the adonis function from the Vegan package for R (version 2.5-2, Anderson 2001), with a Bray-Curtis distance and 9999 permutations. Correlation between rubble shape and animal abundance were tested using the Kendall's tau correlation coefficient (Kendall 1938).

To highlight correlation patterns between locations, phyla distribution and rubble shape Principal Component Analyses (PCA) were used, with the rda function from the Vegan package for R (version 2.5-2, Anderson 2001). Results were displayed as a biplot (scaling 2, Gabriel 1971) with phyla and "branching-tabular" frequency expressed as arrows and locations as labels.

Coral coverage

To test differences in coral coverage between the Site and Treatment factors, a 2-way ANOVA was performed. The assumptions of ANOVA were tested in the same way as for the rubble data. This time, data were not normally distributed. Therefore, before proceeding with ANOVA, they were normalized using a log+x transformation. After transformation, all data respected the aforementioned ANOVA assumptions.

To test differences in the coverage of the different coral genera, between different sites and treatments, PERMANOVA was performed (adonis function, Vegan package for R), using Bray-Curtis distance and 9999 permutations. To highlight correlation patterns between the coverage of different coral genera and Site and Treatment, Principal Component Analyses (PCA) were performed. The analyses and resulting biplot were generated with the same method as for coral rubble data.

Results

Rubble cryptofauna

Total abundance

A total of 2491 specimens were collected from coral rubble. Arthropoda was the most abundant phylum with 1272 specimens, followed by Mollusca (591) and Annelida (235). Maeganeku1 showed the highest abundance of animals with 1283 specimens, 685 in the outplanted location and 598 in the control location. Manza followed with a total of 681 specimens, 384 in the outplanted location and 297 in the control location. Maeganeku2 was the least numerous in terms of animal abundance (n=527) with 206 in the outplanted location and 321 in the control location. Treatment (Outplanted vs Control) did not significant affect total animal abundance (2-way Anova; $F=0.090$, $P=0.77$) (Fig. 2A). Conversely, Site had a significant effect (2-way Anova; $F=12.3$, $P<0.001$) (Fig. 2B). Maeganeku1 was significantly different in abundance of animals from Maeganeku2 (Tukey post-test; $P= 0.0013905$) and Manza (Tukey post-test; $P= 0.0073704$), while Manza and Maeganeku2 did not show any significant differences ($P= 0.6167673$). The effect of treatment was also not significant when analyzing data within the same season for both winter (1-way ANOVA; $F=0.002$; $P=0.96$) and summer (1-way ANOVA; $F=0.105$; $P=0.76$).

Abundances within phyla

Treatment did not have any significant effects of abundances within phyla (2-way PERMANOVA; total df=17, $R2=0.019$, $P=0.78$) (Fig. 3), while differences between Sites were statistically significant (2-way PERMANOVA; total df=17, $R2=0.37$, $P=0.0025$) (Table 2). Maeganeku1 was the most abundant for Annelida, Arthropoda, Chordata, and Nemertea. This location also had the highest number of unidentified specimens. Maeganeku2 had the lowest abundance for most phyla (6 out of 9) and also had the lowest number of unidentified specimens. However, it was the only site where Brachiopoda were found. Manza was the most numerous for Echinodermata, Nematoda, and Platyhelminthes. The effect of treatment was also not significant when analyzing data within the same season for both winter (1-way PERMANOVA; df = 11; $R2 =0.022$; $P=0.92$) and summer (1-way PERMANOVA; df = 5; $R2 = 0.107$; $P=0.89$).

Correlation with rubble shape

There was a strong positive correlation between the “branching-tabular” rubble shape and total abundance (Kendall's tau correlation coefficient =0.64; p=0.0002). The PCA biplot shows how rubble shape affects abundances within phyla (Fig. 4): Maeganeku1 was rich in "branching-tabular" rubble associated with higher levels of abundances for all phyla. Conversely, Maeganeku2, characterized by "massive-submassive" rubble shapes, showed less total abundance and low abundances within individual phyla.

Living coral community

Control locations showed a higher coral coverage (15.0% ± 11.8%) compared to outplanted locations (11.5% ± 9.8%) (Fig. 5A). This negative effect on coral coverage associated with outplanted sites was statistically significant (2-way ANOVA; F=4.487, P=0.0425). Even when only considering genus *Acropora*, the target taxa being actively transplanted, coverage was significantly higher in control locations (9.2% ± 8.7%) than in outplanted locations (3.4% ± 2.4%) (2-way ANOVA; F= 12.813, P= 0.00119) (Fig. 5B). Coverage between sites was also significantly different (2-way ANOVA; F= 35.062, P= 1.41e-08): Manza was the site with highest coral coverage with a mean of 25.6% (± 9.6%), and it differed significantly from Maeganeku1 (Tukey post-test; P= 0.0000031) and Maeganeku2 (Tukey post-test; P<0.001) (Fig. 5C). Maeganeku1 (8.0% ± 2.8%) and Maeganeku2 (6.1% ± 4.7%) did not show differences between each other in terms of coral coverage (Tukey post-test; P=0.1527080). When considering just genus *Acropora*, differences between sites were significant (2-way ANOVA; F= 6.758, P= 0.00378) (Fig. 5D). Manza had the highest *Acropora* coverage (10.5% ± 10%) and was significantly different from Maeganeku2 (3.5% ± 3.8%) (Tukey post-test; P= 0.0027093) but did not show significant differences with Maeganeku 1 (5.0% ± 3.0%) (Tukey post-test; P = 0.0967279). Maeganeku1 and Maeganeku2 did not show significant differences in their *Acropora* coverage (Tukey post-test; P = 0.3018441).

While some scleractinian coral genera showed higher mean coverages in the control treatment locations, notably *Acropora*, others had higher mean coverages for the outplanted treatment locations (Table 3). Overall, the coral community differed significantly between treatments (2-way PERMANOVA; R2= 0.06377, P= 0.0105) and sites (2-way PERMANOVA; R2= 0.15775, P= 0.0003). The PCA biplot (Fig. 6) highlights that *Acropora* and the control location at Manza were strongly associated, with other associations between locations and coral genera being weaker.

Discussion

Rubble cryptofauna

Coral restoration did not have any observable significant effect on rubble cryptofauna numbers or phylum diversity in this study. Conversely, sites significantly affected both cryptofauna abundance and its diversity at the phylum level. This might be explained by differences in environmental parameters (such as rubble shape, as well as wave action or fish abundance) and/or anthropogenic impact.

Sites with a higher frequency of branching-tabular rubble shapes were associated with higher levels of abundance and diversity. This result is in line with previous research that attributed differences in density of coral reef cryptofauna with the spatial complexity of the associated coral frameworks, either living or dead (Enochs 2011). Rubble shape is therefore important in determining total abundance and diversity of cryptofauna at the phylum level. This highlights the importance of rigorous pre-restoration assessments, as transplanting corals might change community composition beyond the corals themselves. In Okinawa Island, corals have been transplanted by private entities for decades (including fishermen and diving centers; Okubo & Onuma 2015) and, due to the lack of a centralized coordination until 2012, it is difficult to track whether appropriate assessments were made or not for different sites.

Seasonal effects were not tested as a factor in this study, due to the insufficient number of replicates (two winter seasons, one summer season). However, the analyses conducted within the same season (only summer replicates, only winter replicates) gave similar results to those of the full dataset (the restoration effort did not have significant effects on rubble diversity). Therefore, seasonal effects, if present, do not seem to lead to different conclusions when evaluating restoration using coral rubble cryptofauna. As monitoring of these sites will continue season by season over the coming years, additional data will be collected and allow to better define the role of seasonal variation in the abundance and diversity of rubble cryptofauna.

Living coral community

Control locations had a significantly higher living coral coverage. Perhaps more concerning is that, despite the fact that transplanted colonies were of genus *Acropora* (Omori et al. 2016), *Acropora* coverage was also significantly higher in the control locations. We propose two possible explanations for these results. Firstly, the restored areas were selected because of poor coral coverage conditions compared to the surrounding areas and the restoration efforts did not increase coral coverage enough to span this gap. For example, for Maeganeku2 and Manza the exact outplanted locations were chosen by the Okinawa Prefectural Government based on their low coral coverage, low sedimentation rate, low recruitment, low algal coverage, low wave energy, and suitable water temperatures (Onna Village Fisheries Cooperative, pers. comm.). Unfortunately, due to the lack of central coordination in the project in the initial phase, there are no quantitative data for pre-transplant assessments. Additionally, there is no information is available for Maeganeku1, as restoration here was started by the independent efforts of local fishermen (Okubo & Onuma 2015).

Secondly, it may be that the restoration efforts actually had negative effects on live coral coverage. Coral restoration programs do not always bring benefit to targeted reefs and can sometimes harm the pre-existing community (Edwards & Clark 1999; Casey, Connolly & Ainsworth 2015). Branching corals are quite fragile, and they can be easily broken during transplantation activities. In Okinawa, many boats do not employ buoys and thus boats are secured by anchoring on the seafloor, even in the same locations where the restoration and restoration-related monitoring are carried out. Fins, boots, and other tools used by divers during outplanting (see images 2.2. 1-10 and 2.2. 1-12 in Okinawa Prefecture 2017) may also damage pre-existing corals, and control locations are spared from these effects. An excessive accumulation of coral rubble can also impact living coral colonies (Rasser & Riegl 2002; Masucci et al. 2019). It is possible that an increase in rubble due to constant transplanting of colonies subject to high mortality could have damaged native colonies. This does not seem to be the case of this study, as there were no significant differences in rubble coverage (<5% for all locations) between treated and control locations. However, as rubble are not fixed to the substrate, and storms can potentially relocate them down the reef slope, it is possible that the present situation is not reflective of damage done by the same rubble in past years. The relevance of many of these issues along the west coast of Okinawa Island should be assessed in the future via rigorous pre-outplanting assessment combined with detailed monitoring of sites.

Regardless of pre-existing conditions, our results do not indicate that restoration efforts, which have lasted seven years in Maeganeku1, have led to improvements in the coral coverage of the restored areas when compared to control sites. At Maeganeku1 the situation may have been different until 2016 as survival rate for colonies transplanted after 2013 was reported to be exceeding the expected performance targets (over 40% at three years after transplantation; Omori et al. 2016). Subsequently, and before this study, in the summers of 2016 and 2017, the Ryukyu Island experienced two consecutive bleaching events, which had serious negative consequences on shallow water hard corals across the archipelago, particularly for branching/tabular species (Kayanne, Suzuki & Liu 2017; Masucci et al 2019).

Rubble cryptofauna vs Living coral community

The Site factor had a significant effect on both living coral coverage and coral rubble cryptofauna. However, while Manza had the highest coral and *Acropora* coverage, Maeganeku1 was the site with the highest rubble cryptofauna abundance. The Manza site, although having the highest coverage of *Acropora* (10.5 %), had a lower frequency of branching-tabular coral rubble, which may have been related to the healthier state of branching corals at this site, particularly *Acropora*. Both the data from rubble cryptofauna and from the living coral community (= coral coverage) highlighted how differences between different sites are larger than those between treatments (outplanted vs control locations). An important difference from our data is that cryptofauna showed no significant restoration effect, while coral coverage data indicated significantly lower coverages at restored sites. Thus, rubble data suggest comparatively better situations in the sites where corals were outplanted, and this could be related to the stable supply of branching rubble provided by the artificially outplanted *Acropora* colonies.

In summary, live coral coverage data and rubble agree in demonstrating the different environmental situations between sites, and also show that restoration does not appear to be working effectively towards ecosystem restoration. The two datasets can be considered complementary, as the information they give integrate well each other at different spatial scales and for different components of the coral reef community. Sampling coral rubble can provide a variety of data including abundances and diversity of cyptofaunal groups that are often overlooked when dealing with reef restoration, although rubble fauna data have been used before to study biodiversity in different environments (Takada et al. 2014) as well as in coral nurseries (Wee et al. 2019).

Conclusions

Overall, the data show that, as of 2019, restoration efforts have not contributed to measurably higher coral coverage or rubble cryptofauna abundance at the three sites we have examined on the west coast of Okinawa Island.

Going forward, a number of initiatives could be undertaken to improve the situation. Currently, fishing has not been restricted at the outplanted locations. Fish are known to have important roles in reef resilience (Cramer et al. 2017; Kuempel & Altieri 2017) and as well the act of fishing can negatively impact the coral community. As an example, at the surveyed locations, and especially in Maeganeku (1 & 2) we observed numerous damages to the benthic environment caused by anchors, fishing lines, and nets. Protecting the locations where restoration is underway could significantly help the coral community to recover, perhaps even independently from outplanting and restoration efforts. Especially when restoration results are uncertain, it is important to associate restoration activities with protection and conservation. Human activities are known to be changing the trophic structure of coral reef fishes in the Pacific (Ruppert at al. 2018). Conservation plans such as restricted fishing zones might help increasing the number of fishes, while at the same time helping to protect corals from further damage, with potential positive effects on the coral community at all levels of the trophic net (Topor et al. 2019).

It should be noted that the fact that the Okinawa Prefectural Government is working on improving the status of its coral reefs is without question a positive development, and the science from this project can help improve future restoration efforts. However, transplanted colonies are subject to the same impacts and stress factors as pre-existing native colonies. Coral reefs in the Ryukyu Archipelago have been affected by repeated bleaching events over the last decades (Nakano 2004a; Hongo & Yamano 2013). In 2016 and 2017 two consecutive bleaching events occurred, causing coral mortality across the archipelago (Kayanne et al. 2017; Masucci et al. 2019). Moreover, research conducted in Okinawa Island has highlighted how bleaching acts synergically with local anthropogenic stress factors such as excessive turbidity (Hongo & Yamano 2013). In this project efforts have focused on restoring *Acropora*, although this genus is, along with *Pocillopora*, one of the taxa most subject to thermal stress (Guest et al. 2012). Considering this and the adverse effect of rubble accumulation, in light of the unprecedented climate crisis that zooxanthellate corals have been facing in recent years, priority could be given to the restoration of massive and submassive coral taxa, as some of these are more resistant to bleaching and other anthropogenic stressors. Although massive and submassive coral growth is slower than that of *Acropora*, and their capacity to create complex three-dimensional environments is much more limited, their resistance could allow the retainment of at least part of the ecosystem benefits that reefs provide.

Additionally, heat resistant genotypes can be found within natural populations of coral species (Bay & Palumbi 2014), and research to this end is being pursued by the prefectural government (Zayasu, Satoh & Shinzato 2018). In the future these activities may provide critical opportunities for restoration.

Because reefs of Okinawa Island have been affected by decades of anthropogenic impacts, and natural coral populations have been decreasing (Hongo & Yamano 2013; Masucci & Reimer 2019, in press), we recommend that Okinawa Prefecture identifies areas where corals are still relatively healthy and apply stricter protection and conservation regulations and more detailed monitoring protocols. It is important to remember that restoration, even when successful, can provide ecosystem benefits estimated to be around six orders of magnitude lower than the amount of occurred damage (Okubo and Onuma 2015), and thus protection of existing healthy reefs should take priority over the restoration of damaged reefs (Abelson 2006). Among the sites considered in this study, Manza had the highest amount of living corals. Coastal construction and reclamation have been considered as the primary cause of coral mortality in Okinawa (Nakano 2004b), and coastal development and construction is ongoing, even in Onna Village (e.g. new parking lots and shopping mall under construction at Cape Manza Onna Village 2019). By combining restoration efforts with more effective environmental protection and more environmentally-aware development practices, Okinawa may be able to conserve its remaining coral reefs.

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Figure 1

Map of Okinawa and study area.

A) General view of Okinawa. B) Study sites in detail. Green = Control locations, yellow = Outplanted locations.

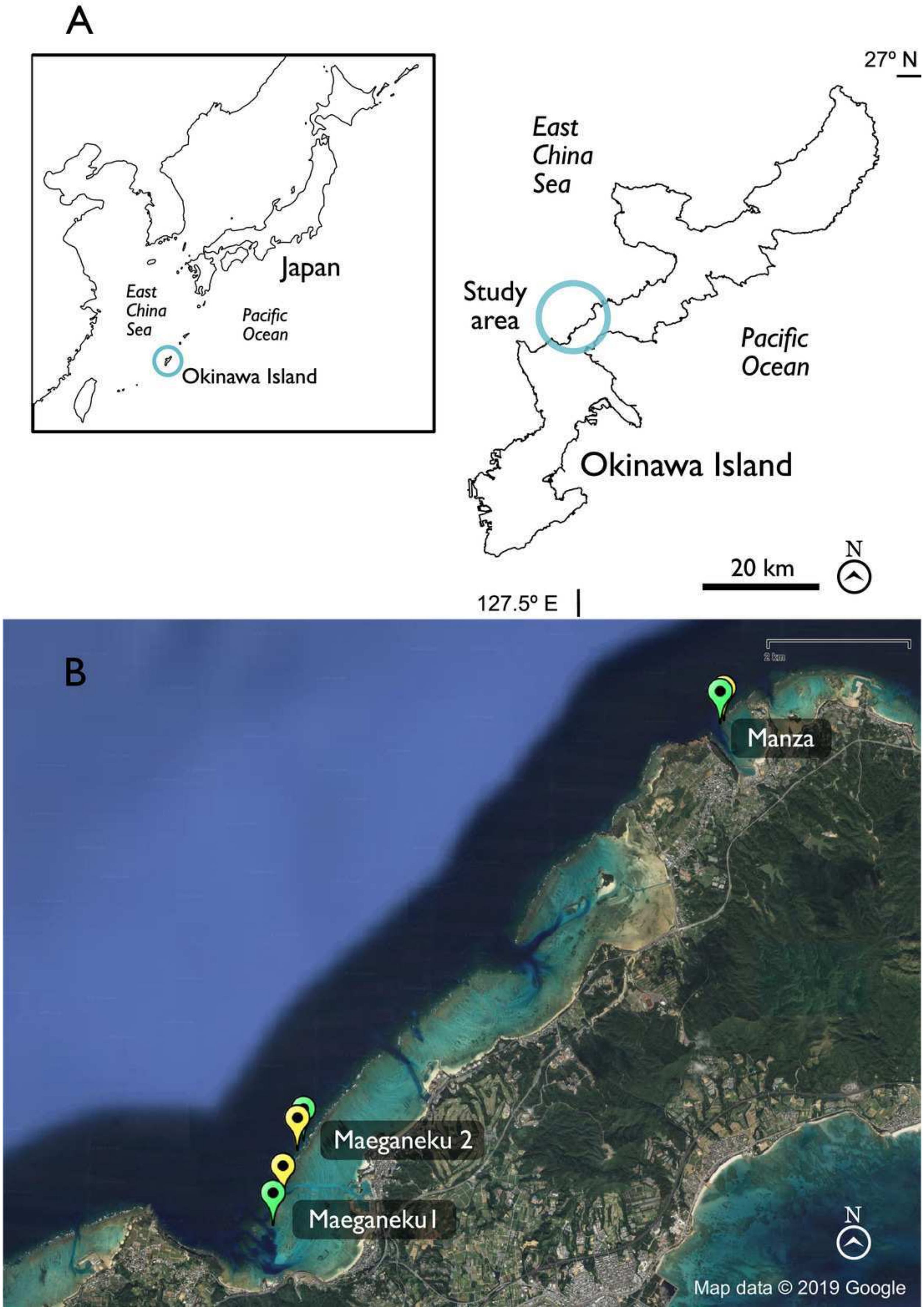
A
Japan
East China Sea
Pacific Ocean
Okinawa Island
27º N
East China Sea
Study area
Pacific Ocean
Okinawa Island
20 km
N
127.5º E
B
2 km
Manza
Maeganeku 2
Maeganeku1
N
Map data © 2019 Google

Figure 2

Mean animal abundances barplots.

Number of animals per (A) treatment and (B) sites. Error bars represents standard deviations. Error bars represent standard deviation, letters indicate statistical significances.

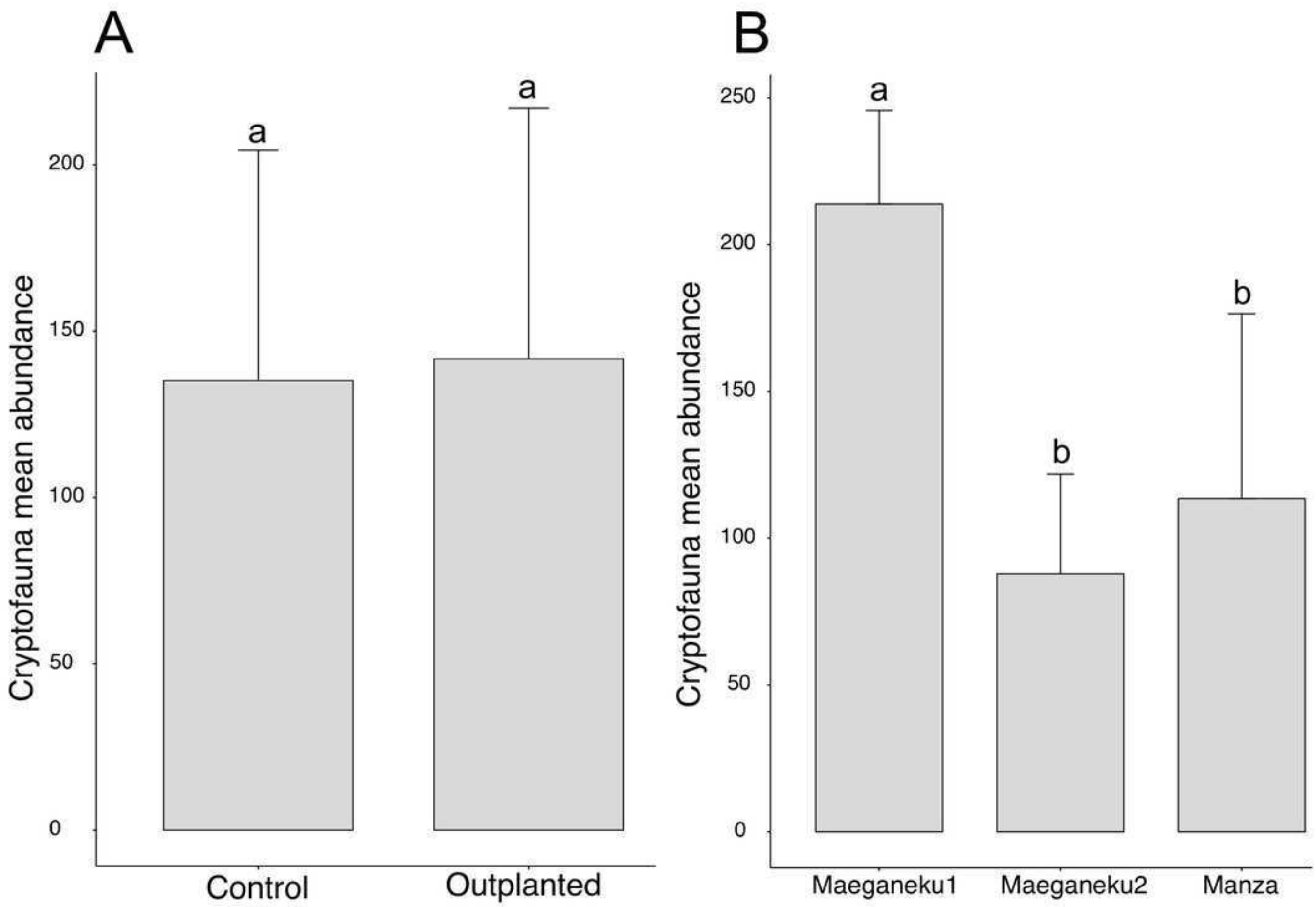

Figure 3

Abundances of different phyla within treatments.

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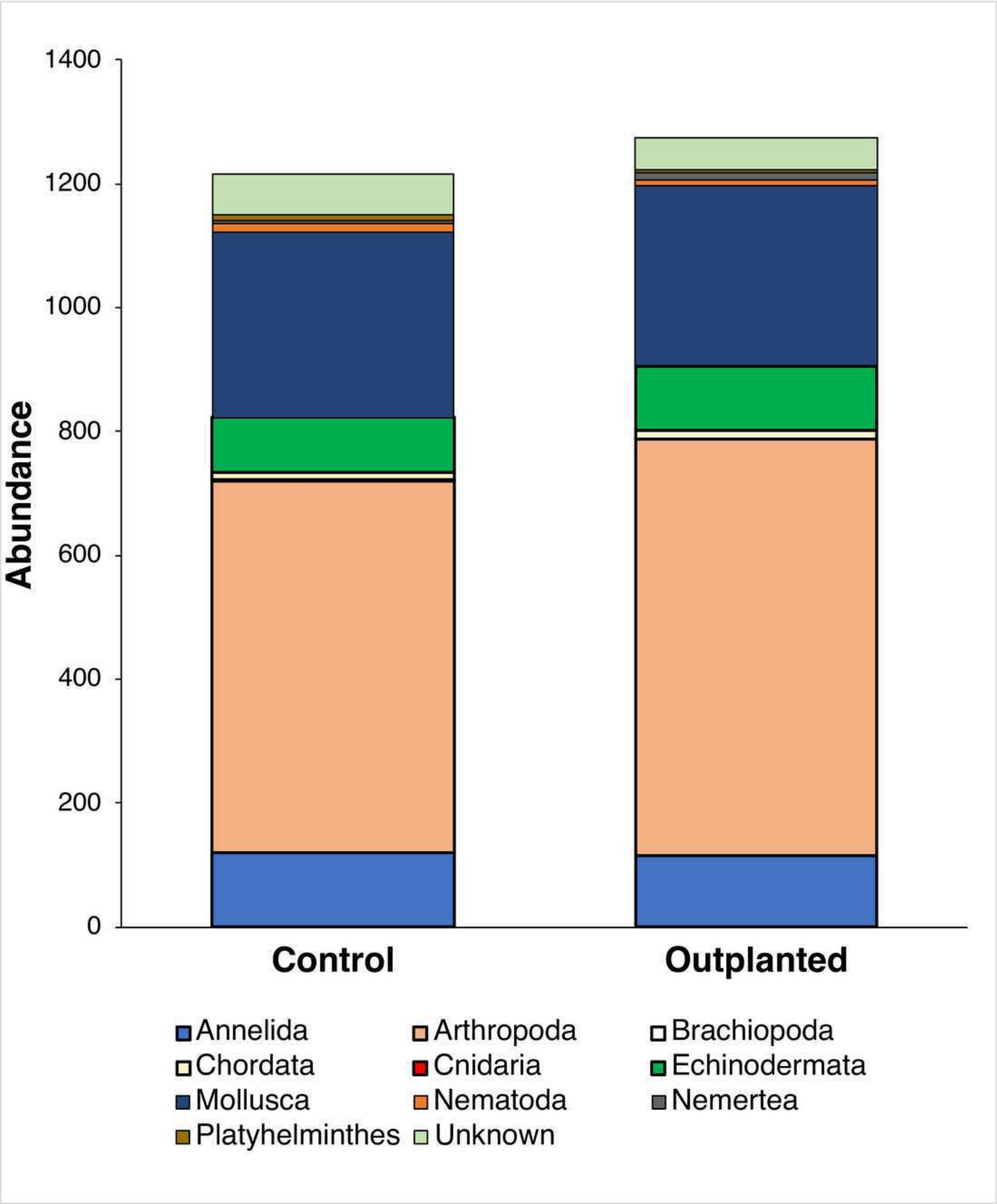
1400
1200
1000
800
600
400
200
0
Abundance
Control
Outplanted
Annelida
Arthropoda
Brachiopoda
Chordata
Cnidaria
Echinodermata
Mollusca
Nematoda
Nemertea
Platyhelminthes
Unknown

Figure 4

Principal Component Analyses biplot showing correlation between rubble shape and animal abundance at different locations.

Phyla and “branching-tabular” frequency expressed as arrows and locations as labels. Mae1Con = Maeganeku1 Control; Mae1Out = Maeganeku1 Outplanted; Mae2Con = Maeganeku2 Control; Mae2Out = Maeganeku2 Outplanted; ManCon = Manza Control; ManOut = ManzaOutplanted.

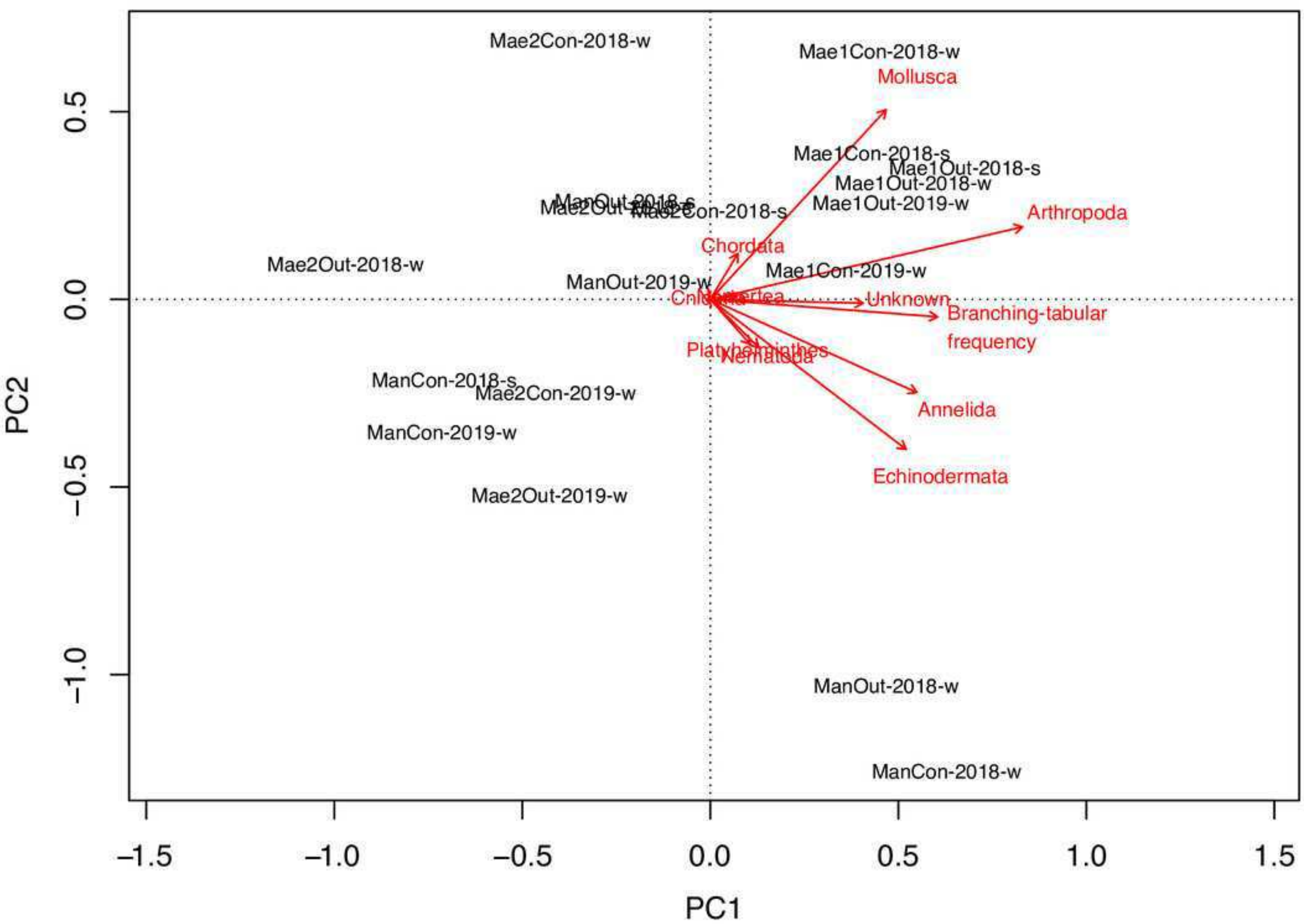

Figure 5

Mean coral cover (%) barplots.

(A) Total coral coverage at control and outplanted sites. B) *Acropora* coverage at control and outplanted sites. C) Total coral coverage at the three sites surveyed in this study. D) *Acropora* coverage at the three sites surveyed in this study. Error bars represent standard deviation, letters indicate statistical significances.

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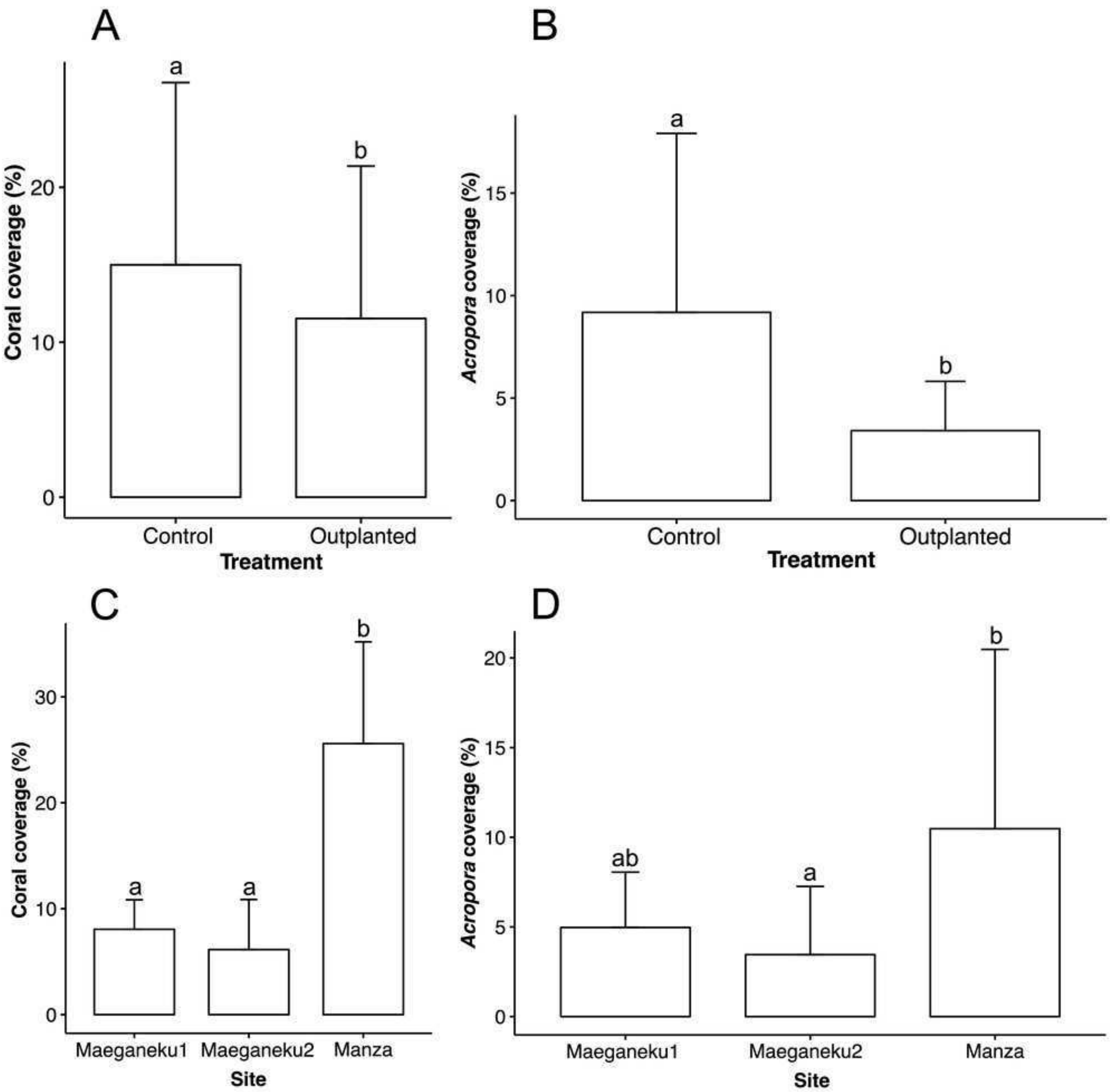
A
a
b
Coral coverage (%)
20
10
0
Control
Outplanted
Treatment
B
a
b
Acropora coverage (%)
15
10
5
0
Control
Outplanted
Treatment
C
b
a
a
30
Coral coverage (%)
20
10
0
Maeganeku1
Maeganeku2
Manza
Site
D
b
ab
a
20
15
Acropora coverage (%)
10
5
0
Maeganeku1
Maeganeku2
Manza
Site

Figure 6

Principal component analysis biplot showing correlation patterns between the coverage of different coral genera and Site and Treatment.

Corals genera expressed as arrows and locations as labels. Mae1Con = Maeganeku1 Control; Mae1Out = Maeganeku1 Outplanted; Mae2Con = Maeganeku2 Control; Mae2Out = Maeganeku2 Outplanted; ManCon = Manza Control; ManOut = ManzaOutplanted.

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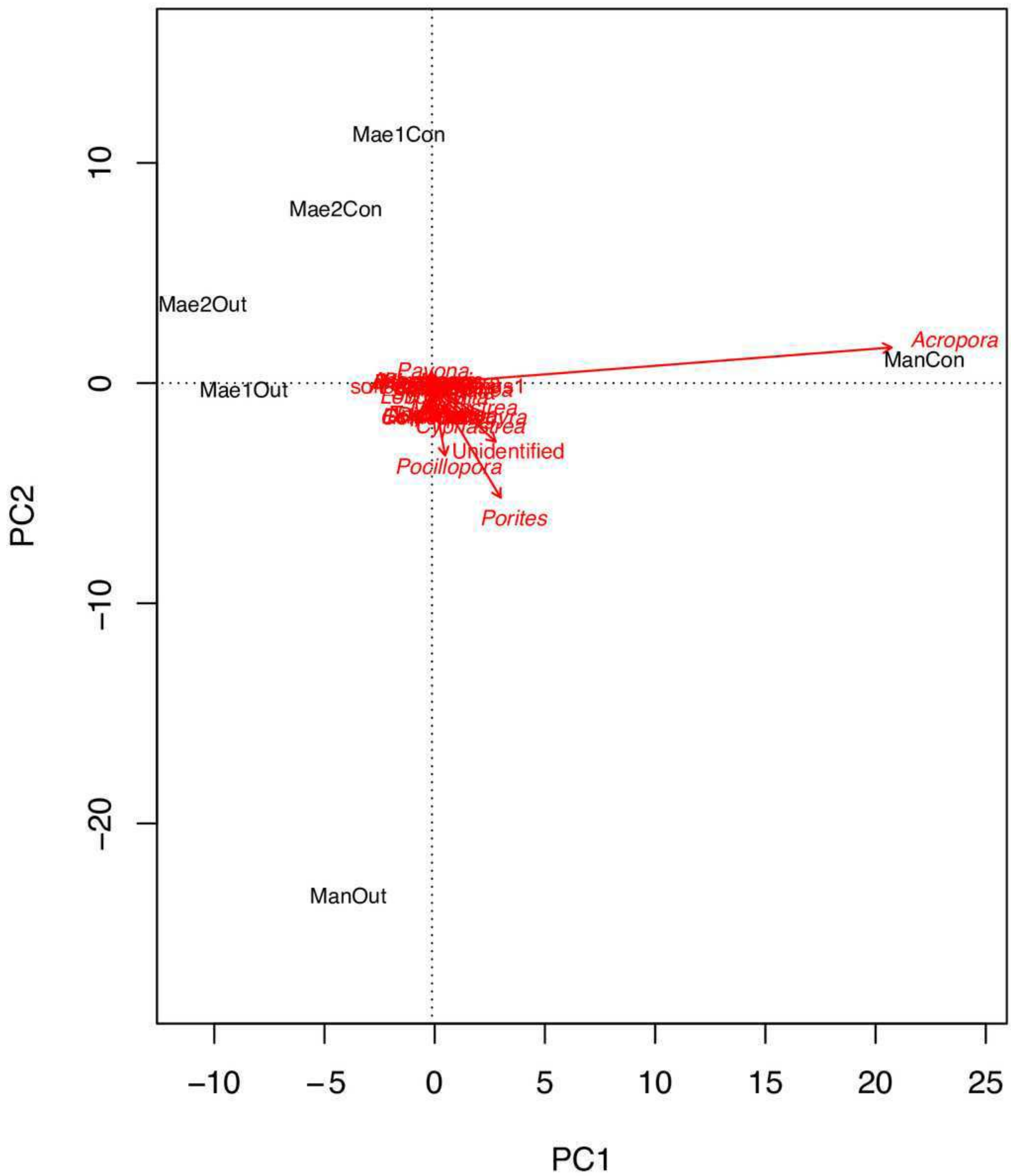
Mae1Con
Mae2Con
Mae2Out
Mae1Out
ManOut
ManCon
Acropora
Pavona
Unidentified
Pocillopora
Porites
PC1
PC2
−10
−5
0
5
10
15
20
25
10
0
−10
−20

Table 1 (on next page)

Latitude and longitude of locations in this study.

Location	Latitude and Longitude
Maeganeku Outplanted 1	26.44715, 127.79077
Maeganeku Control 1	26.443167, 127.788947
Maeganeku Outplanted 2	26.453902, 127.79313
Maeganeku Control 2	26.454056, 127.793351
Manza Outplanted	26.508497, 127.85287
Manza Control	26.506983, 127.85207

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Table 2(on next page)

Mean rubble cryptofauna phyla abundances per site (combined treatment and control).

	Maeganeku1		Maeganeku2		Manza	
	mean	sd	mean	sd	mean	sd
Annelida	16.2	7.8	8.2	5.5	14.8	17.0
Arthropoda	121.0	26.5	39.5	20.2	51.5	20.7
Brachiopoda	0.0	0.0	0.7	1.0	0.0	0.0
Chordata	2.3	2.2	1.2	1.2	0.5	1.2
Echinodermata	11.2	4.4	4.3	3.0	16.7	19.0
Mollusca	49.3	10.8	29.5	20.7	19.7	9.8
Nematoda	1.2	1.2	0.2	0.4	2.3	3.4
Nemertea	1.3	1.9	0.0	0.0	1.2	0.8
Platyhelminthes	0.8	0.4	0.2	0.4	1.7	3.1
Unidentified	10.5	6.7	4.0	2.8	5.2	5.4

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Table 3 (on next page)

Living coral community coverage divided per genus at control versus outplanted locations.

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Treatment	Control (%)	Outplanted (%)
Achantastrea	0.00	0.02
Acropora	9.18	3.41
Astreopora	0.38	0.27
Coeloseris	0.06	0.00
Cyphastrea	0.52	0.44
Echinopora	0.04	0.28
Dipsastrea	0.42	0.59
Favites	0.38	0.48
Galaxea	0.00	0.03
Goniastrea	0.33	0.18
Goniopora	0.00	0.28
Leptoria	0.04	0.34
Leptoseris	0.02	0.00
Lobophyllia	0.02	0.12
Montastrea	0.32	0.29
Montipora	0.01	0.19
Pachyseris	0.00	0.04
Pavona	0.22	0.00
Platygyra	0.47	0.34
Pocillopora	0.31	0.80
Porites	1.41	2.34
Psammocora	0.03	0.00
Symphyllia	0.09	0.09
Turbinaria	0.01	0.24
Unidentified	0.74	0.66

1

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