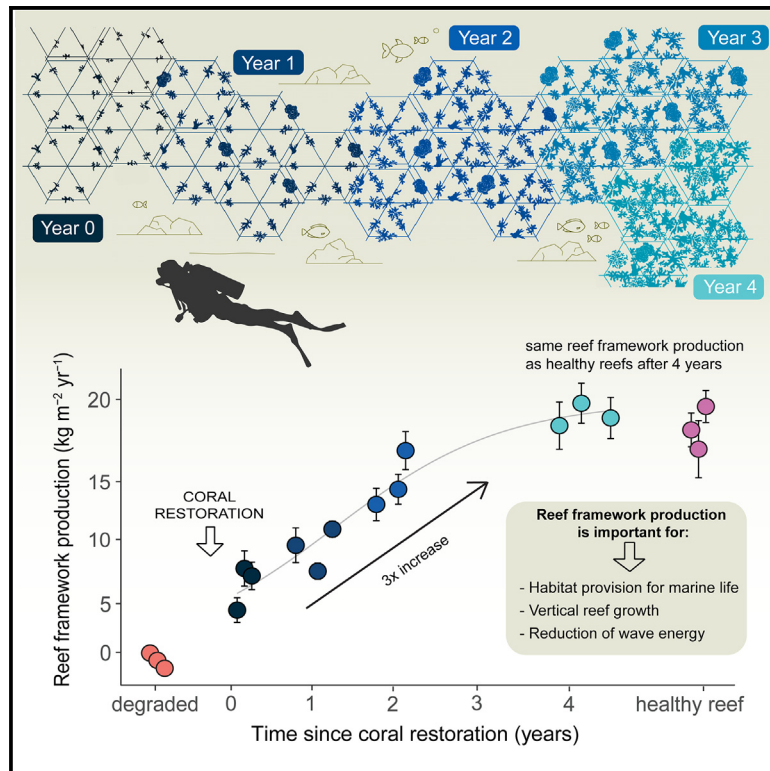


Current Biology

Coral restoration can drive rapid reef carbonate budget recovery

Graphical abstract



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In brief

Lange et al. demonstrate that coral reef restoration can recover important ecosystem functions such as reef carbonate production, structural complexity, and vertical reef accretion potential within 4 years. However, coral communities at restoration sites differ from healthy reefs due to preferential use of branching corals for transplantation.

Highlights

- Reef restoration drives rapid recovery of coral cover and carbonate production
- Net carbonate budgets at restoration sites resemble healthy reefs within 4 years
- Reef structure recovery is important for vertical reef growth and habitat provision
- Coral community composition differs due to preferential use of branching corals



Report

Coral restoration can drive rapid reef carbonate budget recovery

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SUMMARY

Restoration is increasingly seen as a necessary tool to reverse ecological decline across terrestrial and marine ecosystems.^{1,2} Considering the unprecedented loss of coral cover and associated reef ecosystem services, active coral restoration is gaining traction in local management strategies and has recently seen major increases in scale. However, the extent to which coral restoration may restore key reef functions is poorly understood.^{3,4} Carbonate budgets, defined as the balance between calcium carbonate production and erosion, influence a reef's ability to provide important geo-ecological functions including structural complexity, reef framework production, and vertical accretion.⁵ Here we present the first assessment of reef carbonate budget trajectories at restoration sites. The study was conducted at one of the world's largest coral restoration programs, which transplants healthy coral fragments onto hexagonal metal frames to consolidate degraded rubble fields.⁶ Within 4 years, fast coral growth supports a rapid recovery of coral cover (from $17\% \pm 2\%$ to $56\% \pm 4\%$), substrate rugosity (from 1.3 ± 0.1 to 1.7 ± 0.1) and carbonate production (from 7.2 ± 1.6 to $20.7 \pm 2.2 \text{ kg m}^{-2} \text{ yr}^{-1}$). Four years after coral transplantation, net carbonate budgets have tripled and are indistinguishable from healthy control sites (19.1 ± 3.1 and $18.7 \pm 2.2 \text{ kg m}^{-2} \text{ yr}^{-1}$, respectively). However, taxa-level contributions to carbonate production differ between restored and healthy reefs due to the preferential use of branching corals for transplantation. While longer observation times are necessary to observe any self-organization ability of restored reefs (natural recruitment, resilience to thermal stress), we demonstrate the potential of large-scale, well-managed coral restoration projects to recover important ecosystem functions within only 4 years.

RESULTS

The Society for Ecological Restoration (SER) defines “restoration” as any activity undertaken to assist recovery of a degraded ecosystem, with the goal of achieving substantial ecosystem recovery relative to an appropriate reference model.¹ This study aimed to assess the extent to which coral reef restoration sites can recover native reef communities and geo-ecological functions (e.g., structural complexity, carbonate production, and vertical reef accretion). It was conducted at the Mars Coral Reef Restoration Program in South Sulawesi, Indonesia (www.buildingcoral.com), one of the largest reef restoration projects worldwide.⁷ The project uses coral transplantation and substrate addition—the world's most widely used coral restoration methods^{3,4}—in attempts to restore reefs that were damaged by blast fishing 30–40 years ago. Despite the high availability of coral larvae,⁸ these degraded areas have shown no signs of recovery due to the dominance of mobile rubble, which inhibits coral juvenile survival.⁹ A continuous

network of interconnected “Reef Stars” (hexagonal sand-coated steel structures) consolidates mobile rubble and provides a three-dimensional structure for out-planting locally sourced coral fragments.^{6,10} In time, restoration sites are expected to recover the structure and functions of nearby undisturbed reefs through natural ecological processes (i.e., coral growth and coral recruitment). However, the time frames over which full recovery can take place are unclear. To quantify the magnitude and recovery trajectory of reef carbonate budgets at reef restoration sites, we conducted ReefBudget surveys¹¹ (<https://geography.exeter.ac.uk/reefbudget/>) on 12 sites that were restored a few months to 4 years ago (space-for-time substitution), as well as on 3 degraded and 3 healthy reefs that were used as reference sites (Figure 1).

Coral restoration recovers reef carbonate budgets within 4 years

Transplantation of coral fragments inherently results in immediate increases in coral cover (5-fold), structural complexity



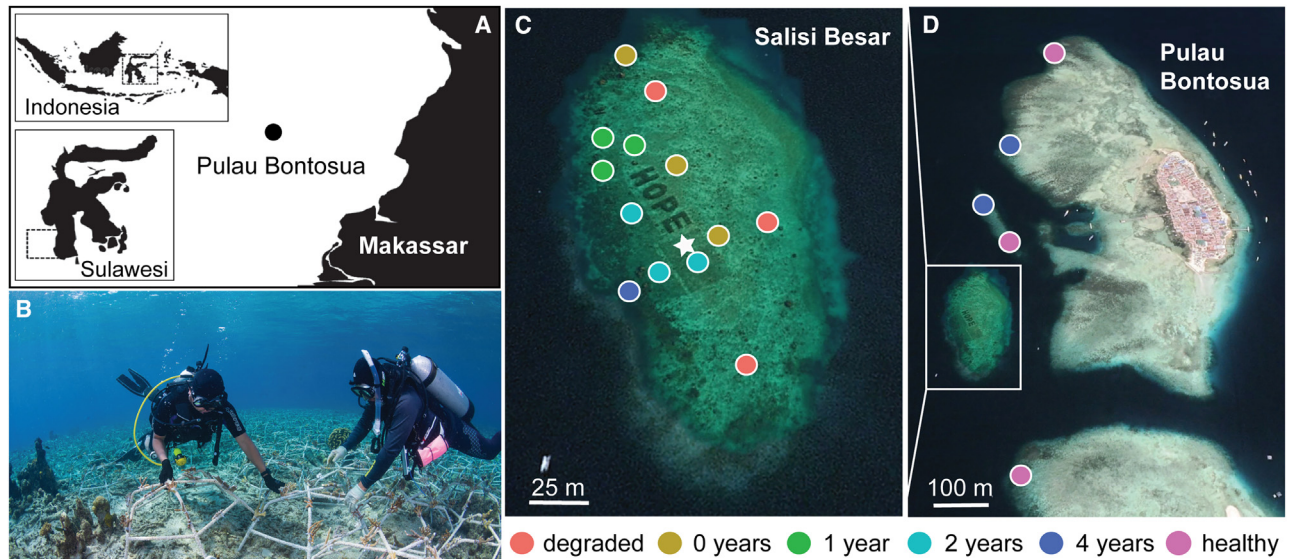


Figure 1. Location of study sites

(A) Pulau Bontosua in the Spermonde Archipelago, South Sulawesi, Indonesia (adapted from Smith et al. ⁶).

(B) Reef star installation on Salisi Besar.

(C and D) (C) Most restoration sites are located on Salisi Besar, (D) while some mature restoration and healthy control sites are located slightly further away (max 1 km distance). Restoration status of sites is color coded (degraded, 0-, 1-, 2-, and 4-year post-transplantation, healthy) and the star indicates the location of coral growth measurements (see Figure S3).

Satellite imagery from Google Earth Pro V 7.3.2.5776 (28 July 2023); Image: 2023 CNES/Airbus. Photo in (B): Indo-Pacific Films.

(1.2-fold), coral colony abundance (7-fold), and gross carbonate production (10-fold) at restoration sites compared to degraded control areas (Figures 2A–2D). Four years after coral transplantation, coral cover, average colony size, and carbonate production rates have tripled, and restoration sites are indistinguishable from proximal healthy reefs in all investigated parameters (Figure 2; Table S1). Four-year-old restoration sites are therefore referred to as “mature” throughout the rest of the paper. Net reef carbonate budgets change from net negative at degraded sites to net positive directly after coral transplantation, triple over the next 4 years, and reach levels equivalent to those quantified for proximal healthy reefs (Figure 2F). These changes are driven almost entirely by gross carbonate production increases, because gross erosion rates do not differ across sites (Figure 2E). Vertical potential accretion rates calculated from carbonate budget data are $18.0 \pm 0.5 \text{ mm yr}^{-1}$ at mature restoration sites (branching coral dominated) and $13.8 \pm 0.77 \text{ mm yr}^{-1}$ at healthy reefs (mixed species composition).

Coral community compositions on restoration sites and healthy reefs differ

Although gross carbonate production rates at mature restoration sites and healthy reefs are similar, the community composition and therefore coral genera contributions to total coral carbonate production differ. Due to their high cover and fast growth, *Acropora* (arborescent, corymbose, and tabular) dominate carbonate production at all sites (81% directly after transplantation, 53%–54% after 1–4 years and at healthy sites). Restoration sites additionally have high contributions by branching *Pocillopora* (8%–17%) and *Stylophora* (13%–26%), but low abundances of other morphotypes. Conversely, on

healthy reefs 33% of carbonate production derives from sub-massive, massive, encrusting, plating, and solitary morphotypes, including *Isopora* (12%), *Porites* (5%), and other massive corals (7%) (Figure 3A). On a community level, magnitudes and contributions to total carbonate production differ significantly between restoration sites and healthy reefs (PERMANOVA $F_{4,55} = 8.78$, $p = 0.001$; pairwise Adonis: $p_{adj} < 0.05$). Reefs 0-, 1-, and 2-years post-transplantation are dominated by branching *Stylophora*, *Acropora*, and *Pocillopora*, whereas healthy reefs are characterized by high carbonate production from a wider range of coral genera and morphologies and variability within and among sites is larger (Figure 3B). Mature restoration sites overlap with both healthy and more recently restored sites, reflecting their overall high total coral carbonate production but different genera contributions compared to healthy reefs. Similar patterns are visible in the benthic community composition, suggesting a gradual, yet still incomplete, succession toward healthy reef communities (Figure S1A). Coral genera diversity and evenness, however, are not significantly different between healthy reefs and mature restoration sites (Figures S2B and S2C).

Carbonate production is driven by the abundance and size of coral colonies. Size-frequency distributions of different morphotypes show that recently restored sites are characterized by high abundances of small *Acropora* colonies and other branching corals, whereas colonies at mature restoration sites and healthy reefs are generally larger (Figures 4 and S2) and therefore produce more calcium carbonate. Healthy reefs are furthermore characterized by high abundances of massive, encrusting, and other morphotypes, which are comparatively rare at all restoration sites (Figure 4).

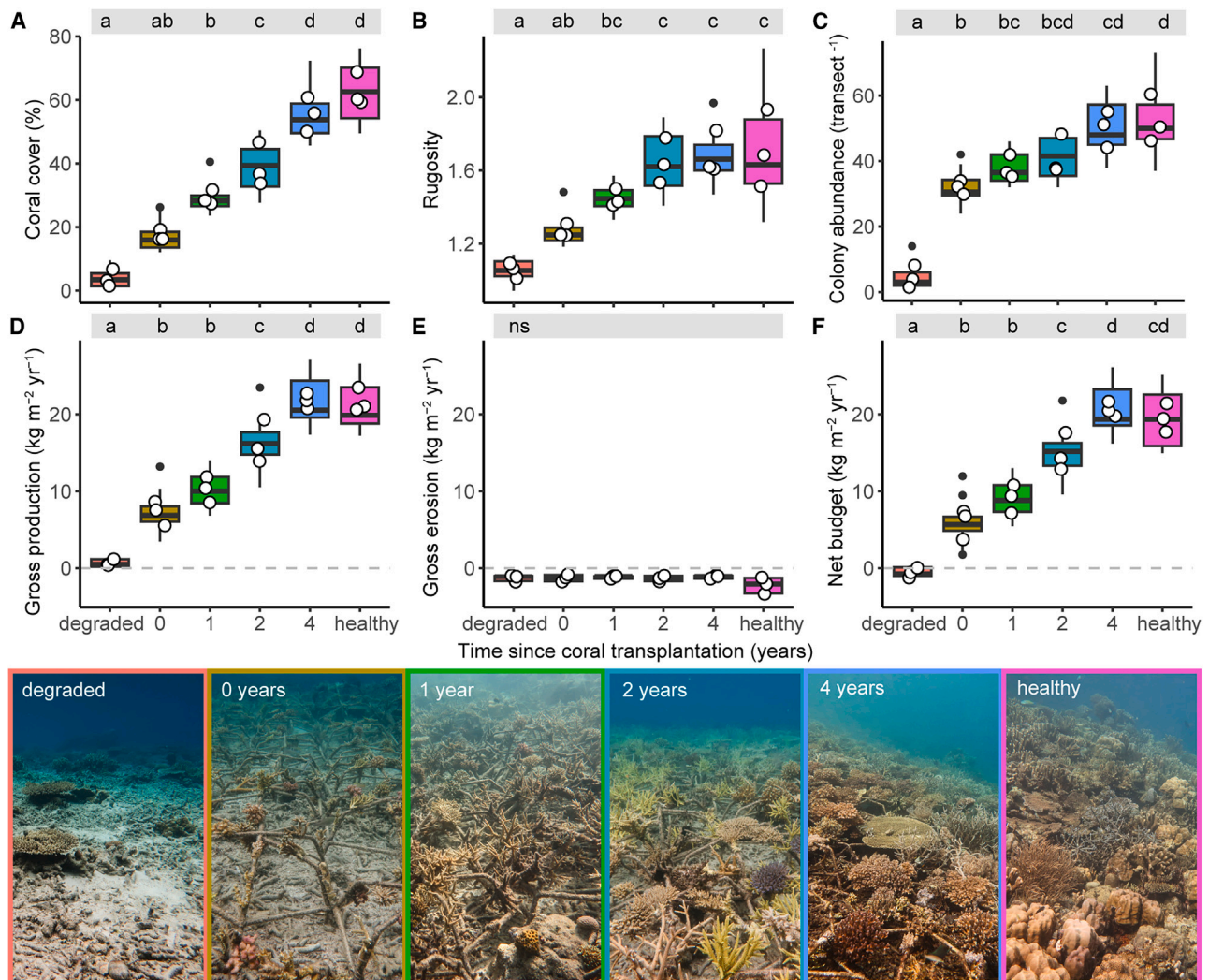


Figure 2. Recovery of coral restoration sites

Comparison of (A) coral cover, (B) substrate rugosity, (C) colony abundance, (D) gross carbonate production, (E) gross carbonate erosion, and (F) net carbonate budgets on degraded reefs, restoration sites (0-, 1-, 2-, and 4-year post-transplantation) and healthy reefs. Boxplots depict median values, 25th/75th percentiles (box), 5th/95th percentiles (whiskers), and outliers (points) of transect-level data. Empty circles represent mean values at site level ($n = 3$ per group). Different letters in gray boxes signify significant differences between groups, derived from linear mixed-effect models with restoration “status” as fixed and “site” as random factors (results in Table S1) and Tukey post hoc tests. The bottom row depicts representative photographs of surveyed restoration sites as well as degraded and healthy controls.

DISCUSSION

Coral restoration supports high reef framework production

Net carbonate budgets of mature restoration sites in our study ($20.6 \pm 0.6 \text{ kg m}^{-2} \text{ yr}^{-1}$) are among the highest rates reported for reefs globally (mean \pm SE: $3.3 \pm 0.2 \text{ kg m}^{-2} \text{ yr}^{-1}$, range: -7.4 – $19.9 \text{ kg m}^{-2} \text{ yr}^{-1}$; summarized in Lange et al.¹²). The fact that these match net budgets on nearby healthy reefs indicates that this is not an artifact of the restoration, but rather shows that restoration can drive rapid recovery of carbonate production. The comparatively high net carbonate budgets are a function of high coral cover and fast coral growth rates, as well as low rates of bioerosion at the study sites. Coral cover

at mature restoration sites ($56\% \pm 3\%$) and healthy control sites ($63\% \pm 3\%$) is relatively high compared to reefs situated closer to the Sulawesi mainland (range: $\sim 10\%$ – 50% ^{8,13,14}) and other Indo-Pacific reefs (mean \pm SE: $22.1\% \pm 0.7\%$ ¹⁵). However, much of the coral carbonate production is not driven by high coral cover, but by high local growth rates. Fast coral growth in the Spermonde Archipelago (Figure S3), and Indonesia in general,^{13,16,17} is most likely facilitated by favorable local conditions in temperature, light, and water quality.¹⁸ We found especially high growth rates for corymbose *Acropora* ($12.0 \pm 2.2 \text{ cm yr}^{-1}$), which dominate both restored and healthy reef communities and provide critical habitat complexity due to their table-like morphology. The calculated low rates of bioerosion reflect a low biomass of parrotfishes on both restoration sites (110 ± 4

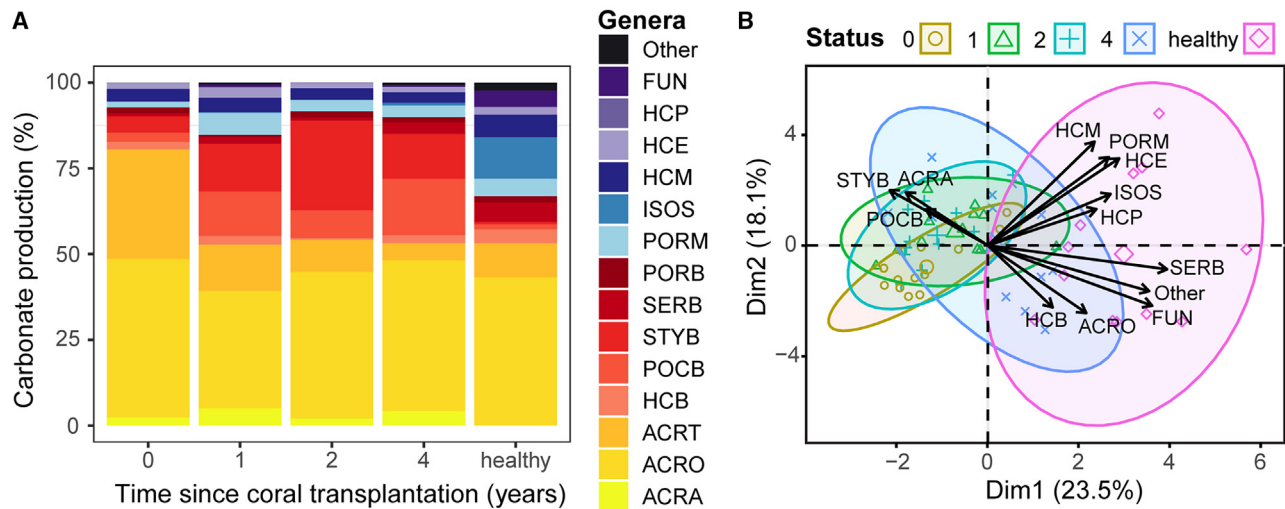


Figure 3. Coral genera carbonate production

(A) Contributions to total carbonate production by coral genera and morphotype (yellows: *Acroporids*; reds: *Pocilloporids* and other branching corals; blues: massive and submassive corals; purples: encrusting, plating, and solitary corals).

(B) (Dis)similarities in coral carbonate production between sites projected onto a two-dimensional space using principal component analysis (PCA). Sites are colored according to restoration status (degraded, 0-, 1-, 2-, and 4-year post-transplantation, healthy) and vectors represent coral genera significantly driving the displayed differences between sites (at $p < 0.05$). For differences in benthic community composition and coral genera diversity see Figure S1.

Abbreviations: ACRA, *Acropora* arborescent; ACRO, *Acropora* corymbose; ACRT, *Acropora* table; HCB, Other branching; POCB, *Pocillopora* branching; STYB, *Stylophora* branching; SERB, *Seriatopora* branching; PORB, *Porites* branching; PORM, *Porites* massive; ISOS, *Isopora* submassive; HCM, Other (sub)massive hard coral; HCE, hard coral encrusting; HCP, hard coral plating; FUN, *Fungia* and other solitary taxa; Other, foliose/columnar morphotypes.

to $186 \pm 50 \text{ kg ha}^{-1}$) and healthy reefs ($243 \pm 29 \text{ kg ha}^{-1}$), caused by high fishing pressure across the Spermonde Archipelago.¹⁹ Parrotfishes are key agents of reef erosion in most regions,²⁰ as they scrape or excavate the reef surface in search of microscopic algae and cyanobacteria.²¹ Besides acting as bioeroders, parrotfishes also remove turf algae, clear substrate for new coral recruitment, and contribute to sediment production and transport.²² The small number and body size of parrotfish at the study sites therefore does not aid overall ecosystem resilience despite promoting high net carbonate budgets.²² Sea urchins, which can also be locally important drivers of bioerosion,^{23,24} are rare across both restoration sites ($0.03 \pm 0.02 \text{ ind. m}^{-2}$) and healthy reefs ($0.14 \pm 0.13 \text{ ind. m}^{-2}$) and contribute little to gross erosion rates. Due to overall low bioerosion and low contributions by crustose coralline algae, the net carbonate budgets at the study sites thus almost entirely reflect coral carbonate production.

Coral restoration leads to differences in coral communities

Despite slightly lower coral cover, coral carbonate production rates on mature restoration sites exceed those at some healthy sites due to the higher percentage of fast-growing *Acropora*, *Pocillopora*, and *Stylophora*. The preferential use of branching coral genera in restoration programs is a common practice worldwide.³ Apart from the logistical advantages (easy fragmentation and attachment to substrates), fast-growing branching corals provide the most immediate gains in terms of coral cover, structural complexity, and carbonate production. On the other hand, the resulting reef may be less diverse in terms of biodiversity and habitat provision compared to natural reefs, which harbor more massive corals and large-scale framework structures. A

fundamental goal of reef restoration is thus to create ecological conditions that will foster subsequent natural coral recruitment and recovery (i.e., self-organization ability) by providing suitable substrate and seeding stocks.⁴ However, the timescales over which this may happen on restoration sites (and whether it will happen) remain unclear. What our data show is that at least in the first 4 years post-transplantation, recovery of coral cover and carbonate production was driven almost exclusively by the growth of transplanted coral fragments instead of natural recruitment; this is demonstrated by the fast and continuous increase in colony size (Figure S2) but limited increase in colony abundance (Figure 2) and species diversity (Figure S1). This means that although certain reef functions have been recovered at restoration sites, full recovery of reef communities and ecological functioning has not yet been achieved. Although colony sizes at mature restoration sites suggest fecundity of transplanted corals and a previous study found natural recruitment on and below Reef Stars on the neighboring island (Pulau Badi),¹⁰ we observed little new recruitment to Reef Stars in this study (although no targeted observations were conducted). Reef Stars may not provide the best substrate for new settlers as they are quickly overgrown by turf algae and cyanobacteria. Crustose coralline algae, which often induce coral settlement,²⁵ were not observed on Reef Stars (0% cover on reefs 0–2 years post-transplantation), and even on healthy reefs the occurrence is very low ($5.8\% \pm 1.3\%$). What we did observe, however, is that the space below Reef Stars at mature restoration sites has partly infilled with consolidated coral rubble, which may provide suitable hard substrate for natural recruitment in the near future. In any case, restoration sites may serve as seeding sites for adjacent degraded areas, so investigating the reproductive status of transplanted corals is

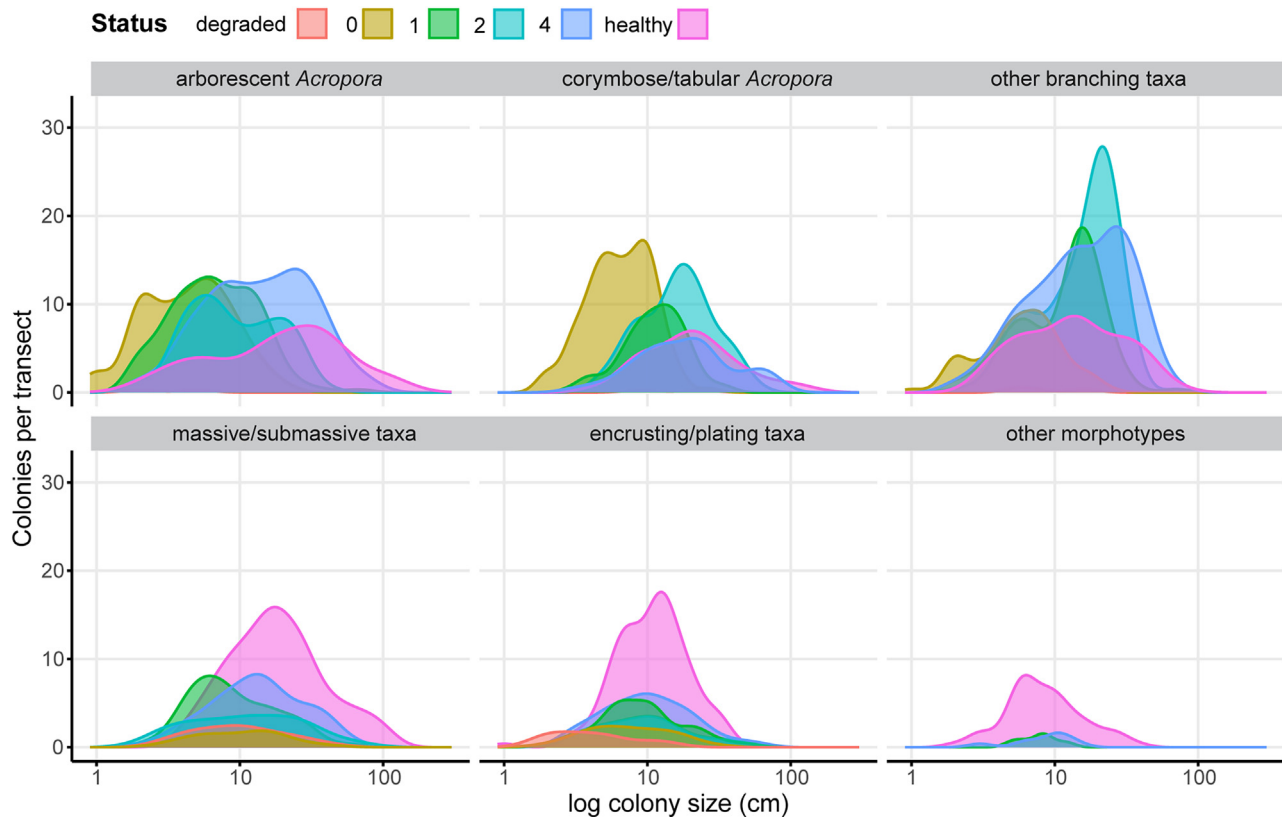


Figure 4. Coral colony size distribution

Size-frequency plots of coral colonies at degraded reefs, restoration sites (0-, 1-, 2-, and 4-year post-transplantation), and healthy reefs. Genera are grouped into dominant morphotypes (arborescent *Acropora*, corymbose/tabular *Acropora*, other branching taxa, massive/submassive taxa, encrusting/plating taxa, and other morphotypes). X axes were \log_{10} -transformed to better display frequencies across the whole size range. For comparison of average colony sizes and skewness of colony size distributions see [Figure S2](#).

suggested as a priority for future work. As the Mars restoration program is committed to full ecosystem restoration,⁶ the project is now incorporating additional substrates (e.g., concrete structures) and coral genera (e.g., slow-growing massive corals) to restore the native community composition.

Coral restoration supports vertical reef accretion

A major question surrounding all restoration efforts relates to their ability to translate increasing carbonate production rates into sustained vertical reef accretion, which is critical for enabling reefs to track rising sea levels. Sea-level rise (SLR) and storm waves increase the risk of coastal flooding, which poses a significant threat to coastal communities and is exacerbated by climate change.²⁶ This is of particular concern in East and Southeast Asia, where coastlines support 71% of the global coastal population within 10 m elevation above sea level, and where future *relative* SLR may be exceptionally high due to human-induced subsidence ($>20 \text{ mm yr}^{-1}$ ²⁷). Coral reefs serve as natural breakwaters by reducing wave energy reaching the coast by up to 97%,²⁸ a service that is threatened by ongoing and projected future reef decline.²⁹ One desired outcome of reef restoration should therefore be to support vertical reef framework accretion in order to enhance coastal protection.^{30,31} Two recent modeling studies have explored this question for northern

Caribbean reefs. In the US Virgin Islands, transplantation of *Acropora palmata* is projected to mitigate the most extreme impacts of coastal flooding by reversing projected trajectories of reef erosion and allowing reefs to keep pace with the $\sim 0.5 \text{ m}$ of SLR expected by 2100.³² Coral restoration targets for Cheeca Reef in the Florida reef tract on the other hand are not likely to support sufficient reef accretion rates under severe future bleaching predictions, although in this case restoration was projected to at least delay the switch from positive to negative carbonate budgets.³³ Overall, long-term reef accretion in the Caribbean is marginal due to low rates of carbonate production and high rates of bioerosion. In contrast, we have shown that net carbonate budgets in the Spermonde Archipelago are comparatively high, and restoration sites can recover healthy carbonate production rates—and therefore reef accretion rates—within only 4 years. Indeed, vertical potential accretion rates calculated for mature restoration sites are 30% higher than those for healthy reefs due to the dominance of branching corals that typically support higher framework accretion rates compared to mixed assemblages.³⁴

Vertical accretion rates in our study are generally high compared to regional means elsewhere (mean \pm SD Indian Ocean: $2.01 \pm 2.33 \text{ mm yr}^{-1}$; Caribbean: $1.87 \pm 2.16 \text{ mm yr}^{-1}$ ³⁴), although consistent with long-term accretion rates calculated from shallow

water branching- and tabular coral-dominated Indo-Pacific reef deposits (10–20 mm yr⁻¹³⁵). It is important to note that calculated rates are maximum potential accretion rates, which do not factor for episodic physical framework removal, and that the use of metal frames initially disconnects carbonate production from vertical accretion of the actual reef surface. However, we observed that transplanted corals grow both upward and downward, eventually fusing with the reef surface, and that live and dead coral fragments accumulate and consolidate within the Reef Stars. At our study sites it is thus reasonable to hypothesize that physical breakage of corals by storms will initially contribute material to rapidly infill the open steel structures, and thereby quickly raise the reef surface to the top of Reef Stars, but subsequent framework removal will ultimately lead to lower long-term accretion rates. However, even assuming 50% of produced carbonate is lost through physical removal, long-term accretion rates would still closely track regional SLR projections of 8 mm yr⁻¹ under an intermediate Shared Socio-economic Pathway (SSP) scenario (0.59 m total SLR by 2100, SSP2-4.5), although they may not track high-emission scenario projections (13 mm yr⁻¹, 0.81 m by 2100 under SSP5-8.5).³⁶ As in-field data on the links between restoration and vertical accretion remain limited at best, ongoing monitoring of changes in vertical substrate elevation at these and other sites would be very valuable given the relevance for coastal protection.

Restoring reefs in a warming world

A major challenge facing global efforts to restore coral reefs is the ongoing increase in frequency and severity of climate-related stressors. For example, record high sea-surface temperatures in late 2023 led to widespread coral beaching and mortality across the Caribbean and Eastern Tropical Pacific, initiating the relocation of thousands of nursery corals in Florida to avoid total mortality.^{37,38} Marine heat waves like this will become common events in coming decades³⁹ and current projections predict high-frequency severe bleaching by 2040–2050,⁴⁰ threatening the long-term success of reef restoration, especially when transplanting thermally sensitive coral taxa.⁴¹ There are several ways in which coral reef restoration might be deployed strategically in a warming world to accompany critical reductions in carbon emissions. For instance, restoration might be prioritized to take place in thermal refugia areas, where transplanted corals are less likely to encounter lethal environmental conditions in the near future.⁴² This approach was taken in the studied restoration program; the west coast of South Sulawesi is a potential thermal refuge due to regional patterns of wave-generated heat fluxes, which is expected to lead to lower bleaching risk relative to areas that experience less thermal variability.⁴³ In line with expectations, only minor bleaching was observed in the area in 2015, despite water temperatures exceeding 30°C.¹⁰ Other restoration projects aim to enhance thermal resistance through “assisted evolution”, prioritizing the transplantation of thermally tolerant genotypes.⁴⁴ Even without assisted evolution there is some emerging evidence that coral thermal tolerance can increase naturally, suggesting adaptation potential of natural and restored coral populations to future thermal stress.⁴⁵ Whether this thermal tolerance increase can keep pace with ocean warming will depend on global action on reducing carbon emissions.⁴⁵ To maximize the success of reef restoration in an uncertain future, species selection should therefore balance ecosystem value against the risk of future extinction,

which is most likely achieved by transplanting locally common species of a wide range of phenotypes.⁴⁶ Finally, restoration projects should aim to reduce direct anthropogenic stressors by ensuring local stewardship, which increases awareness and provides protection for restoration sites and nearby healthy reefs alike. As such, it is of utmost importance to carefully choose sites suitable for reef restoration and integrate social-ecological frameworks into restoration efforts.^{47,48}

Conclusions

In conclusion, this study demonstrates that commonly deployed coral reef restoration techniques (coral transplantation and substrate addition) can recover net carbonate budgets and therefore vertical reef accretion potential in short periods of time. Scaling up reef restoration continues to be a challenge and coral restoration does not negate the need for strong reductions in carbon emissions, especially given the higher heat sensitivity of branching corals commonly used for transplantation. Nevertheless, our findings suggest that large-scale and multidimensional reef restoration programs offer short-term options to recover some important ecosystem functions and thereby increase the reef’s resilience to local (e.g., fishing) and global stressors (e.g., sea-level rise).

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND SUBJECT DETAILS
 - Study sites and restoration method
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 - Coral growth and density
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.02.009>.

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AUTHOR CONTRIBUTIONS

Conceptualization, I.D.L. and T.A.C.L.; methodology, I.D.L. and C.T.P.; investigation, I.D.L., P.B.M., M.E.P., and I.; formal analysis, I.D.L.; writing – original draft, I.D.L.; writing – review & editing, I.D.L., T.B.R., C.T.P., and T.A.C.L.; project administration, T.B.R., P.B.M., M.E.P., and T.A.C.L.; funding acquisition, I.D.L., T.B.R., C.T.P., and T.A.C.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Results of ReefBudget surveys	This study	https://github.com/InesLange/reef-restoration-carbonate-budgets/blob/main/data/MARRS_ReefBudget.csv
Benthic community composition	This study	https://github.com/InesLange/reef-restoration-carbonate-budgets/blob/main/data/MARRS_benthic.csv
Coral colony sizes	This study	https://github.com/InesLange/reef-restoration-carbonate-budgets/blob/main/data/MARRS_colonysize.csv
Coral growth rates and skeletal densities	This study	https://github.com/InesLange/reef-restoration-carbonate-budgets/blob/main/data/MARRS_coralgrowth.csv
Calcification rates used for ReefBudget analyses	This study	https://github.com/InesLange/reef-restoration-carbonate-budgets/blob/main/data/MARRS_calcification_rates.xlsx
Software and algorithms		
ReefBudget methodology	Perry et al. ¹¹	https://www.exeter.ac.uk/research/projects/geography/reefbudget/
R software	R Core Team ⁴⁹	https://www.r-project.org/
R package <i>vegan</i>	Oksanen et al. ⁵⁰	https://CRAN.R-project.org/package=vegan
R package <i>tidyverse</i>	Wickham et al. ⁵¹	https://doi.org/10.21105/joss.01686
R package <i>lme4</i>	Bates et al. ⁵²	https://doi.org/10.18637/jss.v067.i01
R package <i>emmeans</i>	Lenth ⁵³	https://CRAN.R-project.org/package=emmeans
R package <i>ape</i>	Paradis and Schliep ⁵⁴	https://doi.org/10.1093/bioinformatics/bty633
R package <i>FactoMineR</i>	Lê et al. ⁵⁵	https://doi.org/10.18637/jss.v025.i01
R package <i>factoextra</i>	Kassambara and Mundt ⁵⁶	https://CRAN.R-project.org/package=factoextra
R package <i>pairwiseAdonis</i>	Martinez ⁵⁷	https://github.com/pmartinezarbizu/pairwiseAdonis

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Dr Ines Lange (i.lange@exeter.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

All data and original code supporting the findings in this paper are publicly available on GitHub (<https://github.com/InesLange/reef-restoration-carbonate-budgets>). Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study sites and restoration method

To date, the Mars Coral Reef Restoration Program (www.buildingcoral.com), has restored >4 ha of reef across two neighboring islands in the Spermonde Archipelago, South Sulawesi (and >8 ha across Indonesia in total). Restoration is defined as an activity undertaken to assist recovery of a degraded ecosystem¹ and in this case involves the installation of interconnected hexagonal, sand-coated metal frames termed “Reef Stars”, to which 10–15 coral fragments are attached with cable ties. The transplanted corals are harvested from nearby dedicated collection sites and represent a mixed assemblage of branching coral genera which match the natural local reef communities (*Acropora*, *Pocillopora*, *Stylophora*, *Isopora*, *Porites*, *Hydnophora*, *Montipora*). Reef stars are arranged in blocks of ~50 × 20 m, which receive regular maintenance (brushing of metal frames to remove turf algae, replacement of dead

coral fragments) in the months following transplantation. Over time, restoration sites are expected to recover the structure and functions of nearby undisturbed reefs through natural coral recruitment and the provision of diverse habitats for fish and invertebrate communities. The long-term funding of a dedicated restoration management team, in combination with involvement of the local island community, is critical for the success of this project.

This study was conducted on shallow reefs (2–3 m depth) around Pulau Bontosua in September 2022 and May 2023 (Figure S1A). To assess the recovery trajectory of restoration sites, we surveyed sites where Reef Star installation took place at different points in time between 2018 and 2023 (space-for-time substitution), as well as degraded and healthy reference sites. No coral bleaching or other major disturbance was observed at the study sites in this time frame. The focus area of current restoration efforts is Salisi Besar, which enabled us to survey three replicate sites each within areas transplanted with Reef Stars 1–3 months prior to surveys in 2023 (0 years), in 2022 (1 year) and in 2021 (2 years) in close proximity to one another (Figure S1B). Reef Star installations paused in 2020 due to COVID restrictions, so our analysis could not include restoration sites three years post-transplantation. Sites that were restored in 2018–2019 (4 years) and healthy control sites were located across a wider area (max 1 km distance; Figure S1C), as these habitats are not available in high enough replication on Salisi Besar. Spatial autocorrelation analysis therefore indicates a clustering of sites with high coral cover and net carbonate budgets (Moran's $I = 0.05$, $p = 0.03$), which however represents an artifact of site availability and has a very weak effect compared to time since coral transplantation. The proximity of mature restoration sites to healthy reefs might furthermore suggest that recovery at these sites could have been faster compared to recently restored sites, which however is not supported by our data (linear increase of coral cover and carbonate production over the first two years).

METHOD DETAILS

Carbonate budgets

Reef carbonate budgets were quantified at all 18 sites using the Indo-Pacific ReefBudget methodology¹¹ (available at <https://geography.exeter.ac.uk/reefbudget/>). At each site, data was collected by the same experienced observer (IDL) along four replicate transects (10 m long) placed within restoration sites or degraded/healthy controls. If the size of the restored area did not allow the placement of four consecutive transects, one or two of them were placed parallel to the other transects at a minimum distance of 5 m to better represent the whole restoration site. For substrate composition, the distance (in cm) covered by each benthic group beneath the 10 m guide transect line was measured using a separate flexible tape, following the reef contour. Recorded groups included scleractinian corals to the genus and morphological level e.g., *Acropora* tabular, *Porites* massive etc.; crustose coralline algae (CCA); turf algae; fleshy macroalgae; non-encrusting coralline algae (e.g., *Halimeda* spp.); sediment; rubble; sponges and other benthic organisms. Distances of benthic categories were collected as a function of the true three-dimensional surface of the reefs, including cover on overhangs and vertical surfaces, and thus exceed linear transect length. The cumulative total reef surface was divided by linear distance (10 m) to yield rugosity, a measure for structural complexity of the reef substrate.⁵⁸ Survey data was entered into the ReefBudget spreadsheets which use the morphology and size of individual coral colonies in combination with genera/morphotype-specific calcification rates to estimate total annual coral carbonate production (Coral G with $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). Cover of CCA was multiplied by an average Indo-Pacific calcification rate to estimate CCA carbonate production (CCA G) and was added to Coral G to yield Gross Production G. Endolithic bioerosion by macroborers (e.g., sponges, polychaetes, bivalves) and microborers (e.g., algae, fungi) were taken into account by multiplying published bioerosion rates with the available substrate along each transect (all benthic categories except sand) to yield annual endolithic erosion (Macro G and Micro G). Sea urchin abundance and test-size was determined in belt transects along the same transect lines (40 × 5 m) and their contribution to erosion calculated using published taxa- and size-specific erosion rates (Urchin G). Parrotfish abundance and size (to nearest cm) was quantified along the first transect line (50 × 5 m) by two experienced observers (PBM & MEP). Bioerosion for each observed parrotfish was calculated using species- and size-specific erosion rate data to yield site-specific annual erosion by fish (Parrotfish G). Erosion by macro- and microbioeroders was summed at transect-level, while fish and urchin erosion were factored in as site average values, to yield Gross Erosion G, which was subtracted from Gross Production G to yield the net carbonate budget (Net G). Rates of net carbonate production at each site were converted to maximum vertical reef accretion potential rates (RAP_{max} , mm yr^{-1} , sensu³⁴), using framework porosity values of 60% for branching dominated (mature restoration sites) and 50% for mixed assemblages (healthy reefs).

We suggest that carbonate budgets can be a useful tool for the quantification of geo-ecological functions provided by restoration sites, offering detailed insights into total carbonate production and contributions by different coral genera. However, its application in other restoration projects may require careful adaptation to smaller spatial scales, as only a limited number of restoration programs match the size of the Mars Reef Restoration Project in South Sulawesi. To assess carbonate production in smaller restoration areas, we propose measuring colony sizes within specific planar areas or on restoration modules, rather than along transect lines.

Coral growth and density

To increase the accuracy of carbonate budgets, we integrated local growth rates of coral colonies (quantified using photogrammetry and 3D modeling⁵⁹), and their skeletal densities (quantified using the Archimedes principle⁶⁰). In September 2022, 60 colonies of the genera-morphotypes arborescent *Acropora*, corymbose *Acropora*, branching *Hydnophora*, submassive *Isopora*, branching *Pocillopora*, branching *Porites*, branching *Stylophora* and branching *Seriatopora* ($n = 7\text{--}10/\text{genera}$) were tagged and photographed in an area on Salisi Besar that was restored one year prior (Figure 1). These genera are the most common corals used for restoration and also dominate local healthy reef communities. Photographs were taken from multiple angles around each coral colony covering

all aspects of the surface using a Canon Powershot G7X in an underwater housing (automatic underwater setting, no zoom, no flash) and a foldable ruler as a size reference. Sites were re-visited in May 2023 and while some colonies were found dead ($n = 13$), we were able to replicate models for 47 colonies. Additionally, a small fragment was collected from each colony for skeletal density analysis.

Using Agisoft Metashape professional (v1.8.4), 3D models were constructed, scaled and exported as .ply following the workflow described in Lange and Perry.⁵⁹ Dense point clouds of the same colony in subsequent years were then aligned in the software CloudCompare (v2.12.4) and isolated from the surrounding reef area by cutting around the colonies' peripheries. The alignment of point clouds was conducted manually using the Reef Star structure as reference. After models were aligned and isolated, the 'Compute cloud/cloud distance' command was used to display distances between models on a scalar field. For branching morphotypes, maximum linear extension was measured by measuring distances between branch tips ($n = 10$) using the 'Point picking' tool. For corymbose *Acropora*, colonies were divided into 'table-like' and 'cushion-like' growth, as linear growth rates (and skeletal densities) differed significantly (Figure S3). For submassive *Isopora*, average distances between colony surfaces were extracted by fitting a Gaussian model to the scalar field. Linear growth over the 8-month study period was translated to annual extension rates by dividing the measured distances by the number of days between surveys and multiplying by 365.

Collected coral fragments were sprayed with a water hose to remove all tissue, soaked in sodium hypochlorite solution (household bleach) to remove remaining organic material, rinsed, and dried. Bulk density of coral fragments was acquired using the Archimedes principle following Bucher et al.⁶⁰ After obtaining the dry weight of clean coral skeleton, a thin coating of paraffin wax (Paraplast X-TRA) was applied to each piece of coral by quickly dipping it into a pot of molten wax (in water bath at 74°C–79°C) and shaking off the excess. Waxed skeleton fragments were allowed to cool for a few minutes before being weighed dry and suspended in water. The density of the fresh water in the aquarium below the scale was determined by weighing a stainless-steel cube of known density (see Lange et al.⁶¹ for more details).

Measured growth rates and skeletal densities were integrated into ReefBudget sheets together with published growth rates from Indonesia for other genera-morphotypes. If no local or regional data were available, averages over all Indo-Pacific data were utilized.

Colony size structure

To examine differences in the size structure of coral communities between restoration sites and healthy reefs, colony sizes of all measured corals were extracted from the ReefBudget dataset. Abundance per transect and average colony size were calculated for all corals. To plot size frequency distributions of different morphotypes, corals were then grouped into 'arborescent *Acropora*', 'corymbose/tabular *Acropora*', 'other branching taxa' (mainly *Pocillopora*, *Stylophora*, some *Seriatopora*, *Porites*, *Hydnophora*), 'massive and submassive taxa' (mainly *Porites*, some *Goniastrea*, *Favites*, *Galaxea*), 'encrusting/plating taxa' and 'other morphotypes' (mainly free-living). Due to the nature of ReefBudget data collection, colony sizes represent colony contour lengths, rather than planar colony area or diameter used in other studies,^{62–64} and depict lengths of continuous live coral tissue cover (as in^{61,65}) and not estimates of total colony size connected by a shared skeleton (as in⁶⁴) or maximum size of coral colonies. A total of 2,611 colony sizes were recorded across all morphotypes and sites.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses were conducted in R version 4.3.1⁴⁹ using packages *vegan*,⁵⁰ and *tidyverse*.⁵¹ As sites with different histories of restoration were surveyed at the same time instead of repeatedly visiting the same sites, all datapoints are independent ($n = 6$ groups, $n = 3$ sites per group, $n = 4$ transects per site). Transect-level coral cover, rugosity, Gross Production G, Gross Erosion G and Net G, as well as genera diversity, total coral colony abundance and mean colony size were compared among degraded, healthy and restored sites of different years using linear mixed effects models (package *lme4*)⁵² with restoration status as fixed factor and site as random factor (total sample size $n = 72$, results in Table S1; Figures S1 and S2). Results of Tukey posthoc tests (package *emmeans*)⁵³ are depicted in Figures 2, S1 and S2 (different letters signify statistical differences at $p < 0.5$). Spatial autocorrelation of coral cover and net carbonate budgets was tested using Moran's I (package *ape*)⁵⁴.

Differences in genera contribution to Coral G were explored via principal component analysis (PCA) using packages *FactoMineR*⁵⁵ and *factoextra*⁵⁶ and differences between groups were tested via Permutational Multivariate Analysis of Variance (PERMANOVA) in packages *vegan* and *pairwiseAdonis*.⁵⁷ Group dispersion was tested via Permutational Multivariate Analysis of Dispersion (PERMDISP: $F_{5,55} = 2.0$, $p > 0.05$), and the non-significant result indicates that PERMANOVA pairwise differences between sites are entirely due to differences between groups.

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Supplemental Information

**Coral restoration can drive rapid
reef carbonate budget recovery**

Ines D. Lange, Tries B. Razak, Chris T. Perry, Permas B. Maulana, Mochyudho E. Prasetya, Irwan, and Timothy AC. Lamont

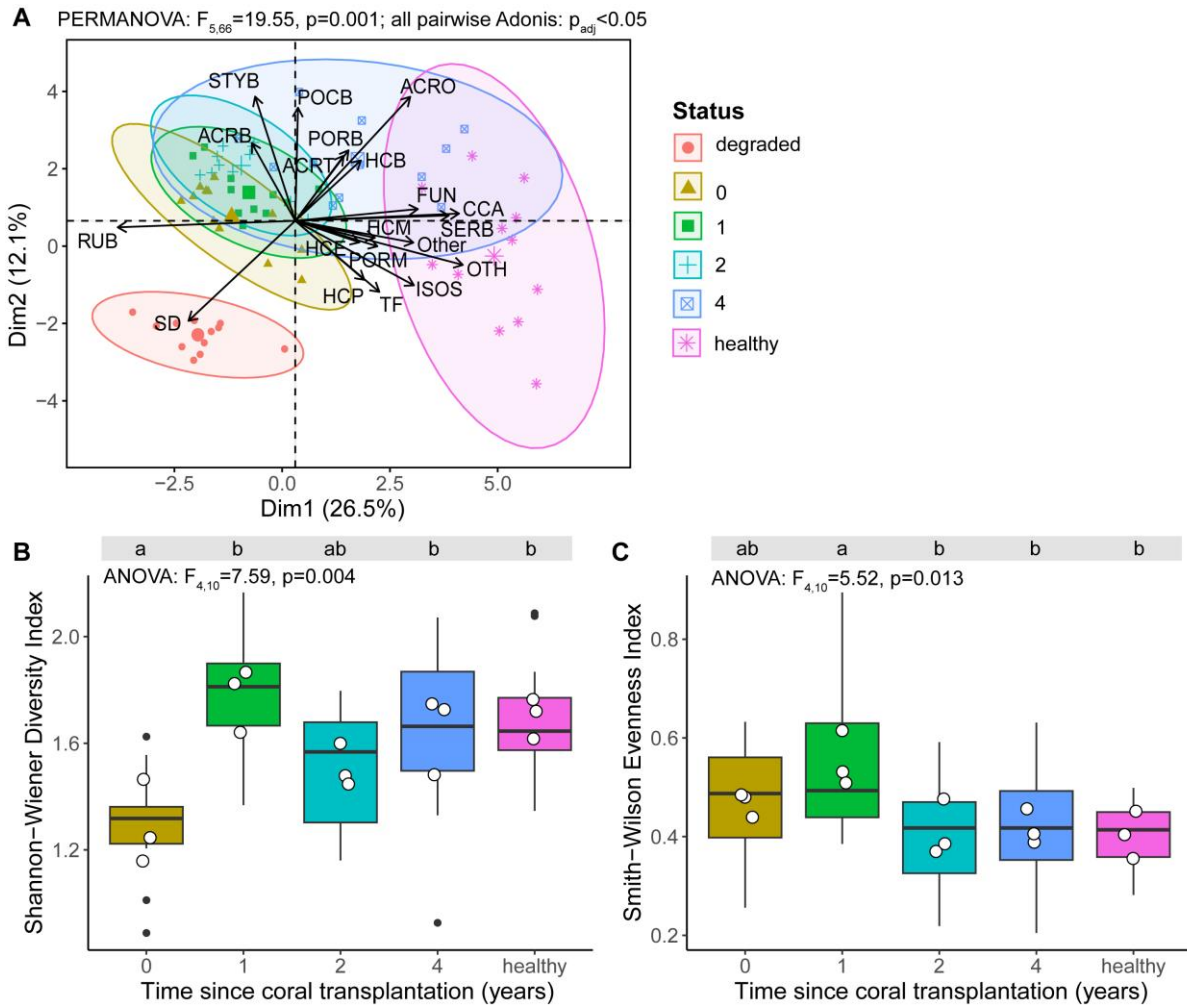


Figure S1. Benthic community composition and coral diversity, related to Figure 3. A) (Dis)similarities in benthic community composition (% cover) between sites projected onto a two-dimensional space using principal component analysis (PCA). Sites are coloured according to restoration status (degraded, years post-transplantation, healthy) and vectors represent benthic groups significantly driving the displayed differences between sites (at $p<0.05$). B) Shannon-Wiener diversity index (genera richness and evenness) and C) Smith-Wilson evenness index (evenness) comparing the diversity of coral communities on restoration sites (0-, 1-, 2- & 4-years post-transplantation) and healthy reefs. Boxplots depict median values, 25th/75th percentiles (box), 5th/95th percentiles (whiskers) and outliers (points) derived from transect-level data. Empty circles represent mean values at site-level ($n=3$ per group). Different letters in grey boxes signify significant differences between groups, derived from site-level one-way ANOVAs and Tukey post hoc tests. Abbreviations in alphabetical order: ACRB-*Acropora* arborescent, ACRO-*Acropora* corymbose, ACRT-*Acropora* table, CCA-Crustose coralline algae, FUN-*Fungia* and other solitary taxa, HCB-Other branching, HCE-Hard coral encrusting, HCM-Hard coral (sub)massive (except *Porites* and *Isopora*), HCP-Hard coral plating, ISOS-*Isopora* submassive, Other-foliose/columnar morphotypes, OTH-Other benthic categories, POCB-*Pocillopora* branching, PORB-*Porites* branching, PORM-*Porites* massive, RUB-Rubble, SERB-*Seriatopora* branching, SD-Sand, STYB-*Stylophora* branching, TF-Turf algae.

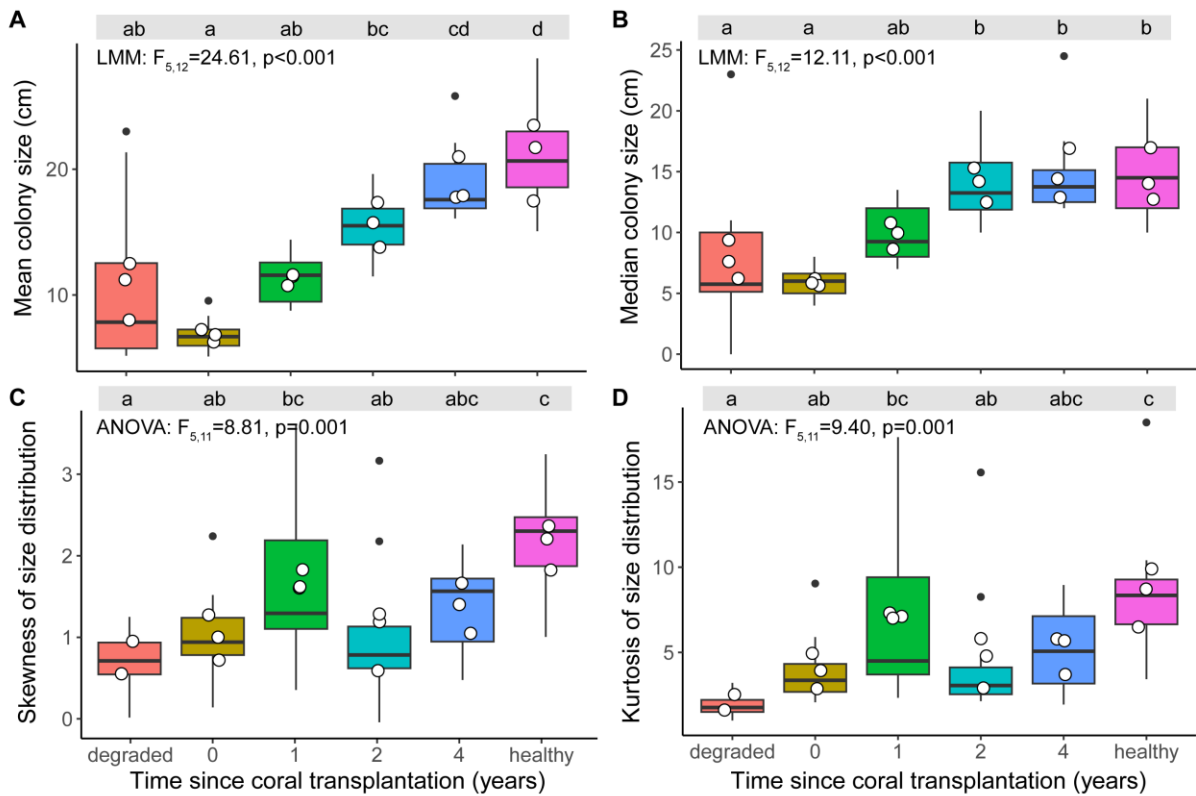


Figure S2. Coral colony size distribution, related to Figure 4. Comparison of A) mean colony size (cm), B) median colony size (cm), C) skewness of size distribution and D) kurtosis of size distribution on degraded reefs, restoration sites (0-, 1-, 2- & 4-years post-transplantation) and healthy reefs. Boxplots depict median values, 25th/75th percentiles (box), 5th/95th percentiles (whiskers) and outliers (points) derived from transect-level data. Empty circles represent mean values at site-level (n=3 per group). Different letters in grey boxes signify significant differences between groups, derived from linear mixed-effect models (LMM) with restoration 'status' as fixed and 'site' as random factor or from site-level one-way ANOVAs if LMMs suggested a singular fit.

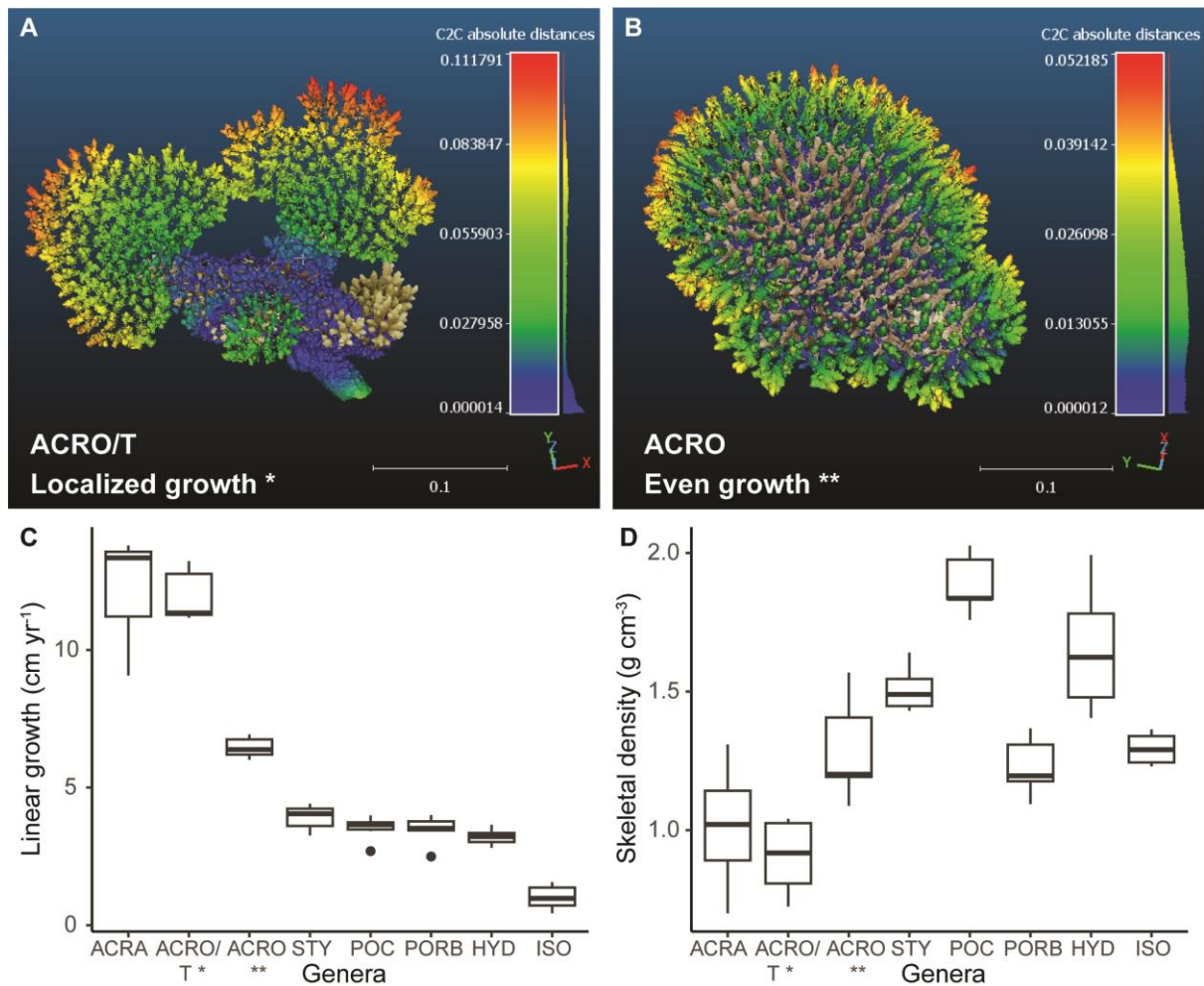


Figure S3. Local coral growth rates and skeletal densities related to STAR Method Coral growth and density. Linear growth rates were quantified using photogrammetry and 3D model comparison (following Lange & Perry^{S1}). Corymbose *Acropora* colonies displayed either A) high localized growth to form table-like morphologies or B) moderate growth in all directions. The two growth forms are therefore evaluated independently (* localized growth, ** even growth). Comparison of C) growth rates of all investigated taxa and D) skeletal densities quantified using the Archimedes principle (following Bucher^{S2}). Abbreviations: ACRA-*Acropora* arborescent, ACRO/T-*Acropora* corymbose & table-like, ACRO-*Acropora* corymbose, STY-*Stylophora* branching, POC-*Pocillopora* branching, PORB-*Porites* branching, HYD-*Hydnophora* branching, ISO-*Isopora* submassive.

Status	Coral cover (%)	Rugosity	Colonies (ind/trans)	Colony size (cm)	Production (kg m ⁻² yr ⁻¹)	Erosion (kg m ⁻² yr ⁻¹)	Net Budget (kg m ⁻² yr ⁻¹)
degraded	3.8±1.5	1.06±0.02	4.4±2.0	10.5±1.7	0.7±0.2	1.3±0.2	-0.6±0.4
0 years	17.2±1.0	1.27±0.02	32.0±1.2	6.9±0.4	7.2±0.9	1.3±0.3	6.0±1.1
1 year	29.1±1.3	1.45±0.03	37.8±2.0	11.2±0.3	10.3±1.0	1.2±0.1	9.1±1.1
2 years	39.1±3.9	1.65±0.07	41.2±3.4	15.7±1.0	16.3±1.6	1.3±0.2	14.9±1.4
4 years	55.5±3.1	1.68±0.07	50.1±3.3	18.7±1.0	21.8±0.6	1.1±0.1	20.6±0.6
healthy	62.8±3.0	1.71±0.12	52.2±4.2	20.7±1.9	21.7±0.9	2.2±0.6	19.5±1.1
LMM results	F _{5,12} =78.2, p<0.001	F _{5,12} =16.0, p<0.001	F _{5,12} = 36.5, p<0.001	F _{5,12} =24.6, p<0.001	F _{5,12} =77.5, p<0.001	ns	F _{5,12} =69.5, p<0.001

Table S1. Statistical analysis of restoration site recovery, related to Figure 2. Comparison of coral cover (%), rugosity, colony abundance (individuals per transect), average colony size (cm), gross carbonate production, gross carbonate erosion and net carbonate budgets (in kg CaCO₃ m⁻² yr⁻¹) on degraded reefs, restoration sites (0-, 1-, 2- & 4-years post-transplantation) and healthy reefs (n = 3 each). Values are mean ± SEM and the last row presents results of linear mixed effects models (LMM) analysing each metric with restoration 'status' as fixed and 'site' as random factor; see Figures 1 and S3 for Tukey posthoc results.

Supplemental References

- S1 Lange, I.D., and Perry, C.T. (2020). A quick, easy and non-invasive method to quantify coral growth rates using photogrammetry and 3D model comparisons. *Methods in Ecology and Evolution* 11, 714-726. 10.1111/2041-210x.13388.
- S2 Bucher, D.J., Harriott, V.J., and Roberts, L.G. (1998). Skeletal micro-density, porosity and bulk density of acroporid corals. *Journal of experimental marine biology and ecology* 228, 117-136.