El Niño-driven phase shift to algal dominance on Isla del Caño's coral reefs: Implications for urgent restoration (#116823)

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El Niño-driven phase shift to algal dominance on Isla del Caño's coral reefs: Implications for urgent restoration

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Background. Coral reefs at Isla del Caño, Costa Rica, have largely retained coral cover and high biodiversity during recent El Niño events that caused global bleaching, leading to suggestions of resilience. Supporting ecosystem services, including marine tourism and biodiversity, evaluating the impact of the 2023–24 El Niño is essential for guiding management and ensuring reef persistence. **Methods.** Reef surveys were conducted at nine sites in the Reserva Biológica de Isla del Caño and northern Corcovado. Benthic cover and coral health were assessed at eight sites from February 2024 to January 2025, with additional surveys at Chorro and Cueva in 2019–2020. Coral Reef Watch sea surface temperature (SST) data (1985–2025; CoralTemp V3.1) were used to calculate long-term SST trends, Degree Heating Weeks (DHW) and bleaching threshold exceedances; beta regression assessed temperature effects on coral cover. Benthic composition was recorded using point- and line-intercept transects. Coral diversity, abundance, and health were assessed via belt transects. Bayesian beta regression estimated bleaching prevalence by site and taxa and coral taxa proportions . SIMPER identified contributors to benthic composition change. Principal Component Analysis (PCA) examined community shifts: during bleaching (March–July 2024), after bleaching (August–December 2024), and latest (January–February 2025). Zero-inflated beta regression and generalized additive models (GAMs) tracked coral and algal cover. An Ecological Restoration Feasibility Index integrated PCA loadings, coral cover, and ecological weights to rank sites by recovery potential. **Results.** SST increased significantly over 40 years (~0.23°C/decade), with the 2023–24 El Niño recording peak SST (31.2°C). Bleaching threshold exceedance days increased, while cool days declined. Twelve coral taxa were recorded; *Pocillopora* spp. and *Porites lobata* were present at all sites. Coral diversity was highest at Cueva and Ancla and lowest at San Josecito. Bleaching prevalence was highest in *Pocillopora* spp.. SIMPER and PCA revealed a shift from coral to algal dominance: turf algae increased by 70.62%, dead coral declined 80.71%, and coral cover fell 40.44%. Major coral declines occurred at several sites alongside turf algae increases . Coral cover peaked at 7–8 m depth and was higher at warmer sites, though other factors were influential. Chorro and Esquina had the highest recovery potential; Ancla, San Josecito, and Barco Profundo the lowest.

Conclusion. There is urgent need to develop and implement a coral reef restoration strategy for Isla del Caño that addresses site-specific conditions, integrates tourism management, and promotes long-term resilience. Under continued climate change, localized, targeted restoration will be essential to maintain the ecological function of these historically resilient but increasingly vulnerable reefs in Costa Rica’s Tropical Eastern Pacific.

El Niño-Driven Phase Shift to Algal Dominance on Isla del Caño's Coral Reefs: Implications for Urgent Restoration

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Abstract

Background. Coral reefs at Isla del Caño, Costa Rica, have largely retained coral cover and high biodiversity during recent El Niño events that caused global bleaching, leading to suggestions of climatic resilience. As these reefs support key ecosystem services, including marine tourism and biodiversity conservation, evaluating the impact of the 2023–24 El Niño is essential for guiding management and ensuring reef persistence.

Methods. Reef surveys were conducted from 2019 to 2024 at nine sites in the Reserva Biológica de Isla del Caño and northern Corcovado. Benthic cover and coral health were assessed at eight sites from February 2024 to January 2025, with additional surveys at Chorro and Cueva in 2019–2020. Coral Reef Watch sea surface temperature (SST) data (1985–2025; CoralTemp V3.1) were used to calculate long-term SST trends and Degree Heating Weeks (DHW). Linear regression quantified SST increases and bleaching threshold exceedances; beta regression assessed temperature effects on coral cover. Benthic composition was recorded using point-intercept, line-intercept, and quadrat surveys. Coral diversity, abundance, and health were assessed via belt transects. Bayesian beta regression estimated bleaching prevalence by site and taxa. SIMPER identified contributors to benthic composition change. Principal Component Analysis (PCA) examined community shifts across three periods: during bleaching (March–July 2024), after bleaching (August–December 2024), and latest (January–February 2025). Zero-inflated beta regression and generalized additive models (GAMs) tracked coral and algal cover. Multivariate beta regression analyzed changes in coral taxa proportions. An Ecological Restoration Feasibility Index integrated PCA loadings, coral cover, and ecological weights to rank sites by recovery potential.

Results. SST increased significantly over 40 years (~0.23°C/decade), with the 2023–24 El Niño recording peak SST (31.2°C). Bleaching threshold exceedance days increased, while cool days declined. Twelve coral taxa were recorded; *Pocillopora* spp. and *Porites lobata* were present at all sites. Coral diversity was highest at Cueva and Ancla and lowest at San Josecito. Estimated baseline bleaching prevalence was ~23%, highest in *Pocillopora* spp. (33.9%). SIMPER and PCA revealed a shift from coral to algal dominance: turf algae increased by 70.62%, dead coral declined 80.71%, and coral cover fell 40.44%. Major coral declines were statistically significant at Ancla, Esquina, and Tina. Bayesian regression confirmed coral decline at Chorro, Cueva, Tina, and Ancla, alongside turf algae increases. Coral cover peaked at 7–8 m depth and was higher at warmer sites, though non-temperature related factors were influential. Chorro and Esquina had the highest recovery potential; Ancla, San Josecito, and Barco Profundo the lowest.

Conclusion. There is urgent need to develop and implement a coral reef restoration strategy for Isla del Caño that addresses site-specific conditions, integrates tourism management, and promotes long-term resilience. Under continued climate change, localized, targeted restoration will be essential to maintain the ecological function of these historically resilient but increasingly vulnerable reefs in Costa Rica's Tropical Eastern Pacific.

Introduction

Coral reefs are vital yet sensitive ecosystems that have experienced 50% global loss of coral cover over the last three decades (IPBES et al., 2019). Warm water reefs continue to face the unprecedented human-driven threat of global warming, repeatedly overshooting target temperatures and exceeding critical tipping point thresholds (Armstrong McKay et al., 2022; Intergovernmental Panel On Climate Change (Ipcc), 2023; IPCC, 2018). Breaching tipping points can result in irreversible shifts away from coral dominance to algal dominance (Klein et al., 2024), reducing biodiversity (Barlow et al., 2018), compromised ecosystem functioning and threatened livelihoods (Sing Wong et al., 2022). Coral reef collapse, involving functional extinction, typically occurs with 10% coral cover or less, and is associated with low taxa diversity and limited ecological interactions (Armstrong McKay et al., 2022; Darling et al., 2019). Widespread coral mortality, and shifts towards ecosystem collapse, occur primarily during El Niño events, which compound warming ocean temperatures and drive mass coral bleaching. Corresponding to the increasing frequency of El Niño Southern Oscillation (ENSO) events (Claar et al., 2018; Heron et al., 2016), there has been a significant increase in the extent of mass coral bleaching over the past 50 years (Virgen-Urcelay & Donner, 2023). The most recent El Niño (2023-24) drove the fourth global mass bleaching event with projected widespread coral mortality (Reimer et al., 2024), underscoring the urgent need for local coral reef monitoring and targeted restoration strategies (Hein et al., 2021; Shaver et al., 2022; Suggett et al., 2024).

Periods of abnormally warm water associated with ENSO have variably driven coral declines in the Costa Rican Tropical Eastern Pacific (TEP), including Isla del Caño (Alvarado et al., 2020; Cortés et al., 2010; Guzmán et al., 1987; Guzman & Cortés, 2007; Jiménez et al., 2001). Isla del Caño, located in the south Pacific coast of Costa Rica near the Osa Peninsula, was designated a protected area (Biological Reserve) in 1978. The Isla del Caño Biological Reserve, IUCN category I Wilderness Area for the long-term protection of ecological integrity (Dudley, 2008), was subsequently expanded to include 55km^2 of marine area (SINAC, 2009). Isla del Caño reportedly harbors the highest coral species richness in Costa Rica (Cortés et al., 2010; Salas et al., 2016) and is proposed as a unique biodiversity hot spot that has garnered dependence of an extensive local dive industry (ACOSA-TNC-UCI-ELAP, 2008; BIOMARCC-SINAC-GIZ, 2016; Naranjo-Arriola, 2021). With their protected status, high ecological and socio-economic importance, the biodiverse reefs of Isla del Caño are an key contributors to Costa Rica's ~~Tropical Eastern Pacific (TEP)~~, and purported to be resilient to climate change (Friedlander et al., 2022).

The 1982-83 El Niño impacted Isla del Caño, causing 50% coral mortality overall, virtually eliminating populations of *Gardineroseris planulata*, *Porites panamensis*, and *Pocillopora* spp. in shallow reef zones, causing a shift to CCA dominance in many reef areas (Guzmán et al., 1987). Subsequent El Niño events, however, have had a lesser impact on the coral communities at Isla del Caño. For example, though globally SSTs were reported to be higher in the 1998 coral bleaching compared to the 1983 event (Wilkinson, 1999), coral mortality ~~at~~ was minimal at Isla del Caño at just 5% (Guzman & Cortés, 2001). However, coral recovery was not observed between the mid 1980s and 1998, with coral cover across all reef habitats reported to be approximately 10% (Guzman & Cortés, 2001). The survival of corals in the 1998 bleaching event, including *Pocillopora* spp., that were impacted in previous thermal events, was suggested to be due to greater tolerance, acclimatization, marine protected area status (Alvarado et al., 2020) or due to localised cooling from upwellings (Green et al., 2019). However, MPA status does not protect coral reefs from global warming-associated bleaching (Johnson, Dick, & Pincheira-Donoso, 2022) impacts have a limited role in exasperating climate-change-scale impacts (Johnson, Dick, & Pincheira-Donoso, 2022), suggesting other factors drove apparent local resilience or refugia status of Isla del Caño's reefs. Similarly, despite the 2015-16 El Niño being a significant global-scale bleaching event (Eakin et al., 2019) that drove losses of 50 to 75% coral cover at Isla del Cocos and Golfo Dulce in the Costa Rican ~~TEP~~, coral mortality was minimal at Isla del Caño, with less than a 4% decrease in coral cover (Alvarado et al., 2020). Consistently, coral cover of 30.3% was reported between 2016 and 2017 (Naranjo-Arriola, 2021). Whilst Friedlander et al. (2022) report coral cover of coral reef areas to be approximately 20% in 2019, ecological monitoring of Isla del Caño as part of Costa Rica's National Ecological Monitoring Programme (Programa Nacional de Monitoreo Ecológico; PRONAMEC) (SINAC, 2016) reported coral cover between December 2015 and September 2023 to range from 23.2% to over 70% across five reef sites (SINAC, 2023). The PRONAMEC protocol states a healthy reef to have between 30 and 70% coral cover, and a more than 11% reduction in coral cover and >21% increase in algal cover warrants "comprehensive management measures to reduce impacts" (SINAC, 2016)p. 23). Additionally, rocky reefs at Isla del Cano, are considered healthy with up to 40% turf algae, and a more than 21% change considered problematic (SINAC-UNA, 2021)(p. 39). However, it is unknown whether the reefs of Isla del Caño retained coral cover and their purported resilience during the 2023-24 El Niño.

In response to increasingly frequent and extreme climate events, such as El Niño, and significant coral die-offs, coral reef restoration efforts are accelerating worldwide (Boström-Einarsson et al., 2020; Edwards et al., 2024; Suggett et al., 2025), with the general aim of improving the ecological state. Whilst coral reef restoration projects have flourished along Costa Rica's coastlines (Alvarado et al., 2025), they have not, as yet, been established at Isla del Caño, with the exception of a small-scale trial in response to the coral loss of the 1982-83 El Niño (Guzmán, 1991). The lack of restoration at Isla del Caño is likely historically due, in part, to a lack of need given the minimal coral declines reported for recent El Niño events (Guzmán et al., 1987; Jiménez et al., 2001) and the resilient status assigned to the coral communities (Alvarado et al., 2020; Friedlander et al., 2022). Given the increasing threat of climate change to coral reef stability (Armstrong McKay et al., 2022; Intergovernmental Panel On Climate Change (Ipcc), 2023) and the 2023-24 El Niño mass bleaching event (Reimer et al., 2024), restoration interventions are likely increasingly needed at Isla del Caño. To determine the necessity and feasibility of restoration efforts or resilience strategies at Isla del Caño, a fine-scale information on the impact of warming events is needed (Suggett et al., 2025) coupled with a detailed assessment of the current health status of the reef communities (SINAC-GIZ, 2020). With such information, if need for coral reef restoration intervention is identified a strategic plan for locally targeted interventions can be developed (Kleypas et al., 2021; Shaver et al., 2022; SINAC-GIZ, 2020; Suggett et al., 2024), in line with local technical and ethical guidelines (Alvarado et al., 2025; SINAC-GIZ, 2020).

The aims of this study are to quantify health dynamics of Isla del Caño's coral reef communities in response to the 2023-24 El Niño event, identify potential drivers of change and to assess the need and feasibility of coral reef restoration interventions.

Materials & Methods

Sea surface temperature

Daily sea surface temperature (SST) data for Isla del Caño (8°42'59"N 83°53'06"W) were obtained from Coral Reef Watch 5 km Heat Stress Product (1985–2025; CoralTemp V3.1) (Heron et al., 2015; Skirving et al., 2020). The Maximum of Monthly Means of climatological SST (MMM) was computed for 1985–1990 and 1993, excluding 1991–1992 due to anomalies caused by the Mt. Pinatubo eruption (Heron et al., 2016). Degree Heating Weeks (DHW), indicative of thermal stress accumulation, were calculated as days exceeding MMM + 0.5°C, using a 12-week rolling sum and dividing this by 7 to express thermal stress in °C-weeks (Liu et al., 2003, 2018). MMM + 0.5°C was used instead of MMM + 1°C to increase the sensitivity for capturing localized bleaching events (Lachs et al., 2023). A linear regression model was used to assess the long-term SST trends, with date as the predictor, and the slope estimate was used to calculate annual and decadal warming. The influence of ENSO on SST variability was also explored using linear regression, using date and Oceanic Niño Index (ONI) as the predictor variable. Diagnostic residual vs. time and normal Q-Q plots indicated that heteroscedasticity and outliers had minimal impact on the model. The change in annual frequency of days breaching bleaching and cooling thresholds between 1985 and 2025 were explored using linear regression models. The bleaching threshold was defined as MMM + 0.5°C and the cooling threshold was defined as the climatological monthly mean (1985–1990 and 1993) minus 0.5°C.

Study area, survey methods and environmental parameters

Between 2019 and 2024, nine coral community sites were surveyed within the Reserva Biológica de Isla del Caño (8°42'45.70"N 83°53'23.20" W) and northern Corcovado within the Osa Conservation Area (ACOSA), Costa Rica (Table S1; Fig. 1). Of the investigated coral communities, which ranged in depth from <2m to 16m (Table S1), eight sites were surveyed for benthic cover and coral health between February 2024 and February 2025, including Ancla, Barco Somero, Barco Profundo, Cueva de Tiburones "Cueva", Esquina, Este Intermedio, San

Josecito, and Tina (Fig. 1). A ninth site, Chorro, was additionally surveyed for benthic cover in 2019, 2020 and both Chorro and Cueva in 2021 (Table S2).

Benthic cover was recorded using variable, but comparable, methods, including the categories: live coral (coral), sand, rubble, rock, crustose coraline algae (CCA), recently dead coral (dead coral), turf algae, *Caulerpa*, cyanobacteria, and macroalgae. For surveys in 2019 (n=3), 2020 (n=3) and 2021 (n=6 per site), three haphazardly laid 10m point intercept transects were used, recording the benthic cover category every 20cm (SINAC, 2021). Surveys conducted in February and March 2024 used 1x1m quadrats to record the proportion of each benthic category over three 30m (San Josecito) and three 10m transects (Barco Somero, and Cueva; Table S2). For the remainder of the surveys, line intercept transects were conducted, recording substrate categories every 10cm (in April 2024), and then the continuous 10m line for three or six transects at each site (Tn=270 transects; Table S2). Coral diversity, abundance and health were recorded from April 2024 using three or six 1x10m belt transects, separated by 5m. Corals were identified to genus, or species when possible, and categorized as healthy, pale, partially bleached (patches), mostly bleached (>50% of the colony) and bleached (whole colony). An individual coral colony was defined as having distinct area of tissue, meaning that multiple colonies could arise from a coral undergoing partial mortality. Benthic cover data were converted into proportions, enabling comparison of data collected using different survey methods. Total coral abundance, the abundance of each coral taxa, total bleaching prevalence and bleaching prevalence per species were calculated for each belt transect. Temperature loggers (ONSET HOBO MX2202) were deployed at Ancla (15m), Barco Profundo (16m), Barco Somero (11m) and Tina (8m), though remained temporarily and variably functional between April and August 2024.

Fieldwork was conducted under permit numbers: SINAC-ACOSA-DT-PI-R-006-2019, SINAC-ACOSA-DASP-PI-R-067-2021, SINAC-ACOSA-D-PI-R-013-2023, SINAC-ACOSA-DR-PI-R-024-2024.

Data analysis

All analyses were conducted in R (R Core Team, 2021) and are summarized in the supplementary section (Table S3). Bayesian models were implemented in *brms* (Bürkner, 2017) using Stan (Carpenter et al., 2017) Hamiltonian Monte Carlo (HMC) sampling via the No-U-Turn Sampler (NUTS). Unless otherwise stated, models were fit with four chains of 4,000 iterations each (2,000 warm-up), using an adapt_delta of 0.99 for convergence and four cores for parallel computation. Model convergence was confirmed using R-hat values (≈1.00) and effective sample sizes (Bulk_ESS, Tail_ESS). Posterior predictive checks and leave-one-out cross-validation (LOO) were used to assess model fit and predictive accuracy. Proportion data (e.g., coral cover, bleaching prevalence) were bounded between 0.0001 and 0.9999 to avoid boundary issues. Continuous predictors such as date were standardized using z-scores (e.g., z_date) to improve numerical stability and allow comparability of effect sizes. Models involving proportional data were fitted using beta or zero-inflated beta (ZIB) distributions using a logit link for the mean and an identity link for zero inflation, where applicable. Structural zeros were handled by introducing zero-inflation components or explicit structural zero indicators, especially for bleaching and coral taxa models. All p-values for non-Bayesian tests were Bonferroni-adjusted where appropriate.

Coral bleaching prevalence and taxa-specific models

Site-level variation in bleaching prevalence was modelled at the site level using a Bayesian beta regression with logit link and a random intercept for site. The model included an intercept-only fixed effect and a random intercept for site, allowing for site-specific variability in bleaching prevalence and improving estimation (hierarchical structure). Logit-scale intercept was used to estimate a baseline bleaching prevalence through inverse logit transformation. A multivariate ZIB regression model was used to analyze bleaching prevalence among different coral genera, incorporating structural zeros to account for sites where certain coral species were absent. The response variables included bleaching prevalence for coral taxon categories of *Pocillopora, Porites, Pavona, Psammocora*, and Other corals, with each modelled as a function of their respective structural zeros and those of other genera. A hierarchical random intercept for site was included to account for spatial variation.

Coral diversity

The Shannon Diversity Index was computed using total abundance of 13 coral taxa, including an “Other” category with the *vegan* package. Rows with missing species count values were removed. Due to significant deviations from normality and variance homogeneity (Shapiro-Wilk and Levene’s $p < 0.05$), Kruskal-Wallis tests were conducted to determine differences in taxa abundance among sites. Dunn’s post-hoc tests (Bonferroni-adjusted) were performed to identify pairwise differences between sites.

Benthic composition shifts

Shifts in benthic composition were assessed using Similarity Percentage (SIMPER) analysis (*vegan*) conducted on “During Bleaching” (March to end of September 2024) and “After Disturbance” (December 2024 to February 2025) time periods. Ecologically relevant benthic variables were included; coral cover, macroalgae, turf, CCA, cyanobacteria, bleached coral and dead coral. SIMPER was performed at two levels: (1) across all sites combined to evaluate broad-scale compositional changes and (2) separately for each site to highlight site-specific patterns. Both analyses used 100 permutations to ensure robust estimates. Variables were ranked based on their contribution to compositional differences, and their mean before and after values were extracted to evaluate temporal trends. To avoid artificial inflation of change, missing values were replaced with the mean for the time period at that site, or the global mean if the variable was entirely absent. Percentage change and p-values were used to identify the strongest drivers of composition shifts.

Temporal trends in coral Cover and benthic covariates

To assess temporal changes in coral cover, several Bayesian ZIB regression models were fitted and compared using leave-one-out cross-validation (LOO). Models were implemented in brms with a logit link for the beta mean and an identity link for the zero-inflation component, appropriate for proportional data with excess zeros. All models included random intercepts by site, with variations in the treatment of time as a predictor. The candidate models included a linear model with time as a fixed effect and informative priors, a similar linear model with different prior structure, a second-order polynomial model to capture potential non-linear trajectories, and a polynomial model with random slopes by site to account for site-specific temporal variation.

Model performance was evaluated using LOO cross-validation, which estimates out-of-sample predictive accuracy via the expected log predictive density (ELPD). Models were ranked by ELPD, with differences of less than 2 units indicating similar predictive performance. The linear model had the highest predictive accuracy (ELPD difference = 0.0), with the simpler linear model performing nearly identically (ELPD difference = –0.3, SE = 0.3). The polynomial model without random slopes performed slightly worse (ELPD difference = –1.0, SE = 0.7), while the polynomial model with random slopes had the lowest predictive score (ELPD difference = –1.1, SE = 1.4). These results indicate that adding polynomial terms or random slopes did not improve predictive power and that coral cover trends over time were best explained by a linear relationship.

Given this, site-specific coral cover trends were assessed using simple linear regressions of coral cover over scaled date (z_date) for each site. This approach provided a robust and interpretable measure of the direction and magnitude of coral cover change at each location. While more complex models offered the potential to capture non-linear or heterogeneous responses, the linear approach proved more parsimonious and better suited to the available temporal resolution across sites

A second-degree polynomial regression was used to assess the nonlinear relationship between coral cover and depth. This approach captures potential curvature in coral response to depth, accounting for biological or environmental thresholds. Model fit and coefficients were evaluated using standard regression diagnostics, and results were visualized with a fitted polynomial trend and confidence intervals.

Temporal trends in benthic cover for algal groups (macroalgae, *Caulerpa*, turf algae, cyanobacteria, and CCA) were analyzed using Generalized additive models (GAMs) with beta error distribution and logit link. GAMs allowed flexibility in capturing potential nonlinear trends while controlling for site-level random effects. Penalized smoothing in mgcv allowed interpretability while avoiding overfitting. Models were fitted using REML, and diagnostics (residual checks, smooth term significance) were conducted to ensure model validity. A linear model was used to assess the relationship between coral cover and turf algae while accounting for site and temporal effects. Coral cover was modeled as a function of turf algae cover, site, and standardized time (z_date). The model was fitted using ordinary least squares regression, with model assumptions checked via residual diagnostics.

Coral cover and local temperature

HOBO logger data from four locations: Barco Profundo, Barco Somero, Tina, and Ancla was used to evaluate differences in local temperature conditions across sites. Raw temperature data were processed to calculate monthly mean, maximum, and minimum temperatures per site. All values were aggregated at monthly resolution after cleaning and aligning timestamps to ensure maximum overlap in sampling dates among sites. A one-way ANOVA was conducted separately for mean, max, and min monthly temperature data to test for differences among sites. Tukey's Honest Significant Difference (HSD) post hoc tests were performed to identify pairwise differences. All comparisons were adjusted for family-wise error rate, and significance was determined at $\alpha = 0.05$. A beta regression model was used to analyze the effects of temperature and site on coral cover. The initial model included mean, minimum, and maximum temperature as predictors but was refined based on statistical significance and model performance. Minimum and maximum temperature were removed due to their non-significant effects ($p = 0.585$ and $p = 0.429$, respectively), resulting in a final model with mean temperature and site as predictors. The beta regression framework, with a logit link function for the mean and an identity link for the precision parameter (φ), was chosen to account for heteroscedasticity and the bounded distribution of coral cover. Maximum likelihood estimation (BFGS optimization) was applied, and model performance was assessed using pseudo R^2.

Temporal trends in coral taxa

Temporal trends in the proportional cover of *Pocillopora, Porites, Pavona, Psammocora*, and Other corals were modelled using a multivariate beta regression model with random slopes. This allowed proportional data to be modelled while accounting for variation in coral cover (random intercept) and divergent temporal trends among sites (random slope for z_date). Alternative models were tested to determine the best structure. Model comparison showed that the random slopes model provided a better balance between complexity and interpretability than more parameter-rich interaction models, which increased uncertainty without improving fit. Models were implemented in *brms*, and convergence was confirmed through standard diagnostics.

Multivariate Benthic Analysis

Principal Component Analyses (PCAs) were performed to explore multivariate gradients of key benthic parameters. An initial, full model PCA was conducted including biological and benthic variables, as well as total coral cover and the abundance each of *Pocillopora* spp., *Porites* spp., *Pavona* spp., *Psammocora* spp., and other coral, and environmental parameters. Variables with minimal influence on components were then removed from the analysis, including pH, salinity, phosphate, and oxygen. In the first two PCA analyses, *Caulerpa* and dead coral contributed to PC1 but were absent in the latest analysis. Their exclusion was not due to methodological differences but rather reflects an ecological transition where these components were no longer present in the dataset.

PCAs were run on three datasets—(i) During Bleaching (all survey data up to July), (ii) After Bleaching (August to December 2024), and (iii) the Latest dataset (January or February 2025) for all sites—to capture potential shifts post-La Niña rains and landslide events. Each PCA used standardized variables (mean = 0, SD = 1), and *prcomp* in R was employed with centring and scaling. Zero-variance variables were removed, and incomplete cases were filtered out. PCA loadings were used to identify which benthic or environmental variables contributed most strongly to disparities among sites. To assess temporal trends in benthic community composition, PCA loadings were extracted and standardized to facilitate direct comparison and site scores were compared across the three time periods. Key benthic variables structuring PC1 were examined to identify benthic community composition shifts. All variables were transformed to z-scores (mean = 0, SD = 1) before PCA to prevent biases from differences in magnitude or measurement units. Only variables present in all three PCA results were included, excluding those filtered out due to low variance or collinearity. PC1 orientations were aligned across time periods to ensure consistent interpretation, with eigenvectors adjusted by multiplying by -1 when necessary.

Ecological Recovery Feasibility Index

The Ecological Recovery Feasibility Index was developed to assess the restoration potential of reef sites by integrating PCA loadings, expert-defined ecological impact directions, and site-level benthic composition. Ecological impact directions were assigned based on expected influences on reef resilience: coral cover and CCA received positive weights as they promote reef stability and coral recruitment (Tebben et al., 2015), while turf algae, cyanobacteria, and bleaching were assigned negative weights (Ford et al., 2018). Shannon diversity was included to account for the potential benefits of species richness on ecosystem function and resilience (Nyström et al., 2008). PCA loadings were calculated from the latest benthic survey data (January and February 2025) to capture the relative importance of each variable in site differentiation, and all variables were standardized (z-score) to ensure comparability. Weighted contributions were then calculated by multiplying each standardized value by its respective composite weight and ecological impact direction. Final feasibility scores were obtained by summing the weighted contributions for each site. This approach prioritizes coral cover as the primary determinant of restoration potential while ensuring that other ecological factors are appropriately weighted, providing a robust ranking of sites based on their likelihood of supporting natural reef recovery.

Results

SST at Isla del Caño

SST increased significantly over the 40-year period (1985–2025) at Isla del Caño ($R^2 = 0.095$; $F_{(1, 14642)} = 1544$, $p = 2.2e\text{-}16$; Fig. 2) and the MMM was calculated to be 29.08°C based on the highest monthly mean SST (1985–1990 and 1993). The estimated rate of SST increase was approximately 0.23°C per decade, equating to a 0.92°C warming over the 40-year period (Fig. 2). Incorporating the ONI into the regression model significantly improved the fit ($R^2 = 0.28$; $F_{(2, 14606)} = 2872$, $p = 2.2e\text{-}16$), confirming that ENSO as a strong predictor of SST and modulator of SST anomalies. El Niño periods are visible in the Isla del Caño SST record, with peaks or clustered peaks in SST and DHW most prominent in 1997-98, 2010, 2014-17, 2020 and 2023-24 (Fig. 2). The triple peaks of DHW during the 2023-24 El Niño reached 1.6-fold higher than the peak of the 2016 event, and 2-fold greater than the peak of 1998 (Fig. 2). The highest SST was also recorded during the 2023-24 El Niño, reaching 31.2°C, with peaks in 1998 and 2016 remaining below 31°C (Fig. 2).

Linear regression models indicate that the annual frequency of days breaching the bleaching threshold (MMM + 0.5°C) has significantly increased through time (Fig. 3), with an estimated additional 2.07 bleaching days per year ($F_{(1, 39)} = 12.94$; $p = 0.0009$; $R^2 = 0.23$). Conversely, that the frequency of cool days has significantly decreased, by approximately 0.72 days per year ($F_{(1, 39)} = 17.62$; $p = 0.0002$; $R^2 = 0.29$). Years prior to 2012 predominantly experienced frequent cool days, including in El Niño years when warm (bleaching) days were also frequent, including 1998 and 2010 (Fig. 3). After 2012, the frequency of cool days is markedly less, with not substantial cool periods occurring since 2021. Warm days were most frequent in 2023, amounting to two thirds of the year with no cool days (Fig. 3).

Local impacts, bleaching prevalence and coral susceptibility

Severe, mortality-inducing coral bleaching was observed at Isla del Caño from 2023 and throughout 2024 (Fig. 3), prior to the study period (Table S1). Numerous corals were observed as bleached in early 2024 and progressed to a state of partial or complete mortality by May 2024 (Fig. 3 and 4), suggesting that the 2024 to 2025 survey data span the tail-end of an extreme bleaching event (Fig. 2). However, occasionally corals were photographed severely bleached and subsequently recovered (Fig. 6). Additionally, in late November 2024 during the rainy season, a series of landslides occurred on Isla del Caño (Fig. S1a and b), with a significant amount of sediment washed onto reef sites (particularly Cueva and Ancla; S1c). During this time the Biological Reserve was closed to the public due to unsafe conditions, and it is unclear exactly when the landslides occurred and the immediate extent of the sediment plumes. Crown of thorns starfish were also observed sporadically at several sites, including predating on massive coral species (Fig. S2).

There was a baseline bleaching prevalence of approximately 23% across all surveys, as calculated through logit transformation (–1.17; 95% credible interval –1.54 –0.79), with significant variation in bleaching prevalence among sites (the beta regression with logit link; SD 0.48; 95% CI: 0.22, 0.91) and moderately low within site variability (phi 1.94; 95% CI 1.61 – 2.32). Ancla, Barco Profundo, and Chorro demonstrated increasing bleaching prevalence through time (Fig. 7), whilst decreasing prevalence was observed at San Josecito. The remaining sites, Barco Somero, Tina, Cueva, Este Intermedio and Esquina had approximately constant bleaching prevalence through time (Fig. 7).

Baseline bleaching prevalence varied among coral genera. Model (ZIB) estimates indicate that *Pocillopora* spp. exhibited the highest bleaching prevalence at 33.9%, followed by Porites, *Psammocora* spp., and *Pavona* spp., while Other corals exhibited minimal bleaching at just 0.25% (Table 1). The estimated standard deviation of site-level variation in bleaching prevalence was highest for *Porites lobata* (SD = 0.19), suggesting greater among-site variability than other taxa, and was lowest for Other corals (SD = 0.08). *Pocillopora* spp.*, Psammocora* spp. and *Pavona* spp. exhibited intermediate variability. The dispersion parameter (phi) estimates suggest moderate consistency in bleaching prevalence for most genera, while *Pavona* spp. showed moderate dispersion and Other coral had high dispersion of Other corals, indicating close to zero bleaching in this group across all sites (Table 1). Zero-inflation was negligible across all coral taxa (Table 1), confirming a close match between observed data and model expectations.

Coral Diversity

A total of 12 coral taxa were observed and identified at Isla del Caño, including *Pocillopora spp., Porites lobata, Pavona clavus, Pavona gigantea, Pavona varians, Pavona maldiviensis, Pavona chiriquiensis, Pavona frondidera, Psammacora stellata, Psammacora profundacella, Tubastraea coccinea* and *Gardineroseris planulata*. *Pocillopora* spp. and *Porites lobata* were present at all sites, and *Pavona clavus* and *Pavona gigantea* were present at all sites except Este Intermedio and San Josecito, respectively. *Gardineroseris planulata* was the rarest coral taxon, observed only at Ancla, Barco Somero and Cueva (Table S4).

Shannon Diversity Index varied significantly among sites (Kruskal-Wallis test: $\chi^2 = 92.623$, df = 8, $p < 2.2e-16$; Fig. 8), with Cueva exhibiting the highest mean Shannon Index (1.28 ± 0.43), followed by Ancla (1.14 ± 0.39) and Barco Somero (0.90 ± 0.44). San Josecito had the lowest diversity (0.12 ± 0.16), with Este Intermedio also showing relatively low values (0.43 ± 0.31). Post-hoc Dunn's test confirmed significant differences among sites (Table S5). For instance, Cueva had significantly higher diversity than San Josecito (p adj. = 6.30E-12), Este Intermedio (p adj. = 0.000002), and Esquina (p adj. = 0.02). Ancla also had significantly higher diversity than San Josecito (p adj. = 2.94E-12) and Este Intermedio (p adj. = 2.99E-06) (Table S5).

Drivers of community composition change

The SIMPER analysis identified key contributors to benthic composition changes across sites between the "During Bleaching" (March to August 2024) and "After Disturbance" (December 2024 to February 2025) periods (Tables 2 and 3). Turf algae and dead coral were the dominant drivers of overall change, with turf increasing by 70.62% ($p = 0.010$) and dead coral decreasing by 81.30% ($p = 0.010$; Table 2). Coral cover declined significantly by 40.42% ($p = 0.010$), from a mean of 19.33% to 11.46%. CCA increased modestly by 13.0%, though not significantly ($p = 0.347$). Macroalgae and cyanobacteria declined by 34.96% ($p = 0.069$) and 74.37% ($p = 0.010$), respectively. Bleaching contributed to compositional shifts, increasing by 35.30%, but was not significant ($p = 0.881$).

Site-level patterns revealed strong declines in coral cover at several locations (Table 3). Tina experienced a 52.44% decline ($p = 0.010$), while Ancla and Esquina showed declines of 46.0% ($p = 0.040$) and 50.56% ($p = 0.010$), respectively. Coral cover also declined at Barco Somero (−8.4%) and Este Intermedio (−45.34%), though these were not significant (Table 3). Turf algae increased at Ancla, Barco Profundo, Chorro, Cueva, and Esquina, with changes ranging from 43.2% to 336.7%, but was only significant at Cueva ($p = 0.010$), Barco Profundo ($p = 0.010$), and San Josecito ($p = 0.030$; Table 3). Macroalgae declined at most sites and was a significant contributor to benthic change at Barco Somero, Tina, Barco Profundo, San Josecito, and Este Intermedio (Table 3). Dead coral nearly disappeared at San Josecito, declining by 99.75% ($p = 0.010$), and declined significantly at Cueva (−97.1%, $p = 0.010$), Chorro (−29.8%, $p = 0.277$), and Este Intermedio (−97.64%, $p = 0.010$). The mean percentage coral cover after disturbance was lowest at Barco Profundo (3.52%) and highest at Chorro (16.86%) (Table S6). Four sites had less than 10% coral cover after disturbance (Cueva, Barco Profundo, Ancla, and San Josecito), while Esquina had 10.59% and Este Intermedio 11.12%.

Temporal changes in coral cover

The initial proportion of coral cover varied among sites, with Tina exhibiting the highest mean cover at 55% (SD ± 0.09, $n = 3$) in mid-April 2024, and Barco Profundo the lowest, with less than 1% (SD ± 0.115, $n = 3$; Fig. 9). Consistent with patterns identified in the SIMPER analysis, the Bayesian ZIB regression model revealed a general decline in coral cover over time. The best-supported model included a fixed linear effect of time and a random intercept for site. This model estimated a significant negative linear effect (Estimate = –0.19, 95% CI: –0.29 to –0.08), indicating a consistent decline in coral cover across the study period. The overall baseline coral cover was estimated at approximately 11.4% (Intercept = –2.05, 95% CI: –2.45 to –1.66), with moderate variation among sites (SD = 0.53, 95% CI: 0.28–0.98). There was no evidence of substantial zero-inflation (zi = 0.00, 95% CI: 0.00–0.01), suggesting that complete coral absence was rare. Linear regressions exploring site-level variability in coral trajectories highlighted the strongest significant decline in coral cover at Cueva (slope = –0.059, SE = 0.014, $p < 0.001$; Fig. 9), followed by Chorro (–0.022, SE = 0.008, $p = 0.009$) and Tina (–0.199, SE = 0.085, $p = 0.024$). Declines at Este Intermedio (–0.137, $p = 0.096$), Esquina (–0.131, $p = 0.204$), Ancla (–0.079, $p = 0.204$), and Barco Profundo (–0.046, $p = 0.277$) were not statistically significant. San Josecito and Barco Somero non-significant negative trends (–0.050, $p = 0.287$; 0.012, $p = 0.858$, respectively).

Temporal trends in algal cover

GAMs used to assess temporal trends in algal cover demonstrated a significant non-linear temporal trend in macroalgae (edf = 5.012, $p = 0.0055$) with site-level variability (edf = 5.299, $p = 0.0013$), with an adjusted R^2 of 0.0139. *Caulerpa* exhibited a weaker temporal pattern (edf = 1.746, $p = 0.0113$), though site effects were negligible ($p = 0.8621$). Turf algae displayed a strong temporal trend (edf = 1.665, $p < 0.0001$) without a site effect ($p = 0.88$), explaining 33% of deviance. Cyanobacteria and CCA showed no significant temporal trends ($p = 0.187$ and $p = 0.48$, respectively), although CCA exhibited significant site-level variation (edf = 7.120, $p < 0.0001$).

A linear model exploring the relationship between coral cover and turf algae demonstrated a significant negative association ($\beta = -0.131$, SE = 0.039, $t = -3.40$, $p = 0.00081$), indicating that higher turf algae cover corresponded with lower coral cover. Site effects were significant at Barco Profundo ($\beta = -0.087$, SE = 0.034, $t = -2.53$, $p = 0.012$) and Tina ($\beta = 0.059$, SE = 0.030, $t = 1.98$, $p = 0.049$), highlighting site-specific differences in coral cover. Temporal trends were not significant ($\beta = -0.035$, SE = 0.033, $t = -1.08$, $p = 0.282$; Fig. S3).

Depth and site temperature and coral cover

The polynomial regression model of overall coral cover and depth revealed a significant curvilinear decline in coral cover with depth ($F_{(2, 267)} = 18.6$, $p < 0.001$), explaining approximately 12.2% of the variance ($R^2 = 0.122$). Coral cover initially increased with depth, reaching a peak at 7 to 8 meters, before declining at greater depths. The first-order depth term was moderately significant ($\beta = –0.306$, SE = 0.123, $p = 0.013$), while the second-order term was strongly significant ($\beta = –0.681$, SE = 0.123, $p < 0.001$), indicating an accelerated decline in coral cover at deeper sites.

Mean monthly temperatures differed significantly among the four sites (ANOVA: $F_{(3,10)} = 8.39$, $p = 0.0044$), whereas no significant differences were detected for maximum ($F_{(3,10)} = 0.281$, $p = 0.838$) or minimum temperature ($F_{(3,10)} = 2.95$, $p = 0.085$). Post hoc comparisons revealed that Tina had significantly higher mean temperatures than both Ancla (difference = +1.12 °C, $p = 0.023$) and Barco Profundo (+1.63 °C, $p = 0.0035$; Table S7). No other pairwise comparisons were statistically significant. Coral cover was significantly influenced by mean temperature and varied across sites. Mean temperature had a positive effect (Estimate = 0.877, SE = 0.275, z = 3.187, p = 0.0014), indicating higher coral cover at warmer sites. The model explained 32.91% of the variation in coral cover (Pseudo $R^2 = 0.3291$), suggesting that while temperature influenced coral cover, site-specific factors played a substantial role in shaping spatial patterns. The precision parameter ($\varphi = 5.542$, SE = 1.058, $p < 0.0001$) indicated low dispersion.

Temporal Trends in the proportion cover of each coral taxa

The multivariate beta regression model with random slopes indicated variability in coral cover trends among sites. Posterior estimates showed no strong overall trends in the proportion cover of each coral taxa through time, though site-level differences may be driving variation in coral composition over time, as indicated by site-level variation in coral proportion changes (Table S7).

Shift from coral to algal dominance

PCA were used to assess changes in reef structure across three sequential time points: During bleaching (March to July 2024), After bleaching (August to December 2024), and the latest period (January to February 2025). Each PCA captured a high proportion of total variance in reef composition and collectively indicate shifts in community structure from coral dominance toward turf algae dominance at most sites (Fig. 10). While some sites have stabilized with remaining coral cover, others have continued to degrade, with San Josecito experiencing a near-total collapse. *Pocillopora* spp. was more predominant at shallow sites and was associated with high bleaching prevalence (Fig. 10). *Pavona* spp. and *Psammocora* spp. were initially associated with deeper reefs (Cueva and Ancla; Fig. 10a), they lost prominence as turf algae and bleaching increased (Fig. 10b and c). Similarly, *Porites* spp., while less strongly associated with deep sites, also reduced in dominance as turf and bleaching increased (Fig. 10). The disappearance of dead coral by the Latest Data PCA (Fig. 10c) suggests that sites initially characterized by recent mortality have transitioned to a different state, likely dominated by algal overgrowth.

During Bleaching (March to late July 2024):

The first four principal components (PCs) of survey data from March to late July 2024 explained 80.62% of the total variance, with PC1 (30.89%) and PC2 (21.62%) as the dominant axes (Fig. 10). PC1 primarily reflected a depth-related gradient, with deeper sites associated with *Pavona* spp. (0.405), *Psammacora* spp. (0.35), and depth (0.42), contrasting with sites experiencing high bleaching (-0.38) and recent coral mortality (-0.303). Ancla, Cueva, and Barco Profundo aligned with deeper reefs, while San Josecito exhibited extreme bleaching and coral mortality. PC2 distinguished sites based on benthic structure, with *Pocillopora* spp. (0.36) and dead coral (0.29) positively associated, and turf algae (-0.405) and macroalgae (-0.313) negatively loading. San Josecito had the highest positive score, while Barco Somero had the most negative, followed by Este Intermedio and Tina, suggesting high turf cover and low coral cover in those sites. PC3 (16.9%) explained site variance based on *Caulerpa* (0.61) and depth (0.23), contrasting with coral cover (-0.345) and turf algae (-0.250). Deeper sites such as Barco Profundo and Chorro clustered with higher CCA, while Tina and Esquina exhibited higher coral cover.

After Bleaching (August to December 2024):
The PCA for August to December 2024 distinguished sites with high bleaching prevalence, turf algae, and coral loss from deeper sites, explaining 81.41% of the total variance among the first four PCs (PC1 28.42%, PC2 22.04%, PC3 15.15%, and PC4 15.80%; Fig. 10). PC1 separated deeper sites with higher coral cover (such as Barco Profundo and Cueva) from sites with high turf algae (0.416) and macroalgae (0.359), reduced *Porites* spp. (-0.44) and total coral cover (-0.329). PC2 differentiated sites based on depth (0.397) and *Psammocora* spp. (0.407) with high bleaching prevalence (-0.468) and *Pocillopora* spp. (-0.336). San Josecito and Tina exhibited strong bleaching and coral loss, whilst Barco Somero and Cueva aligned with more coral dominance. PC3 captured site differences in *Pavona* spp. (0.542) and CCA (-0.484) and PC4 reflected variation in *Porites* spp. (-0.395) and macroalgae (-0.402).

Latest (January and February 2025): The PCA for the latest data demonstrated a strong gradient distinguishing coral-dominated and algal-dominated reef sites (Fig. 10). The first four PCs explained 88.92% of the total variance, with PC1 (34.58%) and PC2 (23.56%) as the dominant axes. PC1 primarily reflected a coral-to-algae gradient, with coral cover (-0.426) and *Porites* spp. (-0.391) negatively associated, and turf algae (0.347), macroalgae (0.279), and depth (0.366) positively associated. Barco Somero and Esquina aligned with remaining coral cover, while Barco Profundo, Cueva and San Josecito were aligned with algal dominance. PC2 contrasted *Pavona* spp. (0.486) and *Psammocora* spp. (0.335) with *Pocillopora* spp. (-0.398) and bleached coral (-0.387), further highlighting site-level differences. PC3 (17.82%) showed high positive loadings for rock (0.487) and CCA (0.478) and negative for coral (-0.391), whereas PC4 captured differences in *Porites* spp. (-0.491) and depth (0.382). San Josecito exhibited a substantial decline, with low coral cover (-0.43), high turf algae encroachment (0.35), and persistent post-bleaching impacts.

Changes in PC1 loadings over time revealed a steady decline in total coral cover, coinciding with an increasing influence of turf algae. Coral-associated variables, including total coral, *Pocillopora* spp., *Porites* spp., and *Psammacora* spp., contributed less to PC1 in the latest period, indicating a continued decline in coral dominance. Turf algae increased in importance post-bleaching and became the strongest structuring variable in the most recent analysis, reinforcing a transition towards algal-dominated states. Bleached coral initially played a key role in explaining community variation but declined in influence in later analyses, suggesting either coral mortality or stabilization of post-disturbance conditions.

Ecological Recovery Feasibility Index

The ecological recovery feasibility index, which prioritizes coral cover and ecologically relevant PCA loadings (Fig. 11), revealed significant variation in reef restoration potential across sites. Chorro (21.18) and Esquina (12.89) exhibited the highest feasibility scores, indicating favorable conditions for coral recovery. Este Intermedio (5.49) and Tina (4.56) showed moderate restoration potential, suggesting a balance between coral persistence and algal encroachment. Cueva (3.15) and Barco Somero (3.11) also ranked positively but with lower scores, likely influenced by higher macroalgae and cyanobacteria cover. Conversely, Ancla (-10.41), San Josecito (-14.26), and Barco Profundo (-25.72) ranked lowest, suggesting degraded reef conditions that may hinder self-recovery. These results highlight that sites with higher feasibility scores tend to maintain greater coral cover and lower turf and cyanobacteria prevalence, whereas low-ranking sites are characterized by persistent algal dominance.

Discussion

Climate change driven ocean warming is more frequently pushing coral reefs beyond their thermal limits and causing extensive coral loss and ecosystem collapse (Armstrong McKay et al., 2022; Bland et al., 2018; Pearce-Kelly et al., 2025). During the 2023-24 El Niño, Isla del Caño's coral communities underwent a shift from coral to stabilized turf algal dominance, with coral losses the highest at Ancla, Esquina, and Tina, and reef collapse documented at San Josecito, on the north of the Osa Peninsula. Coral reef destabilization of a biodiverse and resilient reef system (Alvarado et al., 2020; Friedlander et al., 2022; Glynn, Mones, et al., 2017; Romero-Torres et al., 2020) was driven by the 2023-24 El Niño event that saw the highest recorded SST (31.2C), on top of 4 decades of recorded temperature increase and reduced cooling. Thermal bleaching drove widespread coral mortality, with species- and site- specific variability, with deeper reefs initially providing refuge and subsequently experiencing mortality, potentially driven by landslide-associated sedimentation. Coral bleaching prevalence and associated declines in cover were site-dependent and drove a shift in coral species dominance from *Pocillopora* spp. towards massive taxa, broadly consistent with reported susceptibilities (Palmer et al., 2010). The phase shift to algal dominance highlights the urgent need for a reactive, science-led and innovative coral reef restoration strategy, collaboratively developed among all local stakeholders (Kleypas et al., 2021).

The 2023-24 El Niño broke historical SST at Isla del Caño

The 2023-24 El Niño event recorded the highest SST in 40 years at Isla del Caño, with a triple-peaked DHW anomaly surpassing previous bleaching events suggestive of a coral reef critical environmental threshold breach (Pearce-Kelly et al., 2025). The long-term warming SST trend for the area surrounding Isla del Caño is consistent with global climate change and ENSO-induced variability (IPCC, 2023). The estimated 0.92C increase in Isla del Caño's SST over the 40-year period from 1985 to 2025 is slightly above the global average, reported at 0.7C over a similar period (Samset et al., 2023), and highlights the thermal threat to local reef-building corals

(Coles & Jokiel, 1977). The SST records for Isla del Caño correspond with the El Niño events documented to affect coral reefs of Costa Rica's TEP since the 1980s (Alvarado et al., 2020; Cortés et al., 2010; Cortés & Jiménez, 2003; Guzmán et al., 1987; Jiménez et al., 2001), including the 2023/2024 El Niño, representing the fourth global mass bleaching event (Reimer et al., 2024). Whilst Isla del Caño's coral communities have previously escaped devastation from thermal anomalies (Alvarado et al., 2020; Jiménez et al., 2001), with the exception of 1983 El Niño, suggesting local resilience (Alvarado et al., 2020; Friedlander et al., 2022; Guzman & Cortés, 2007; Romero-Torres et al., 2020), examination of four decades of SSTs show that thermal events locally were not prolonged or extreme. Calculations of local DHW and the frequency of warmer and cooler days demonstrates that, rather than being home to resilient corals, Isla del Caño had sufficient cool days to offset the effects of El Niño at a local scale. Comparatively, the 2023-24 El Niño recorded the highest temperature and lowest frequency of cool days, making it the most extreme thermal event at Isla del Caño for 40 years. While extreme cooling events can cause coral die-off, as documented for reefs of Costa Rica's north Pacific (Palmer et al., 2022), cool periods are vital for reducing bleaching impact and aiding reef recovery (Green et al., 2019). The prolonged warming in the absence of cooling indicates a potential loss of climate variability that may have previously served as a buffer against extreme warming events (Pearce-Kelly et al., 2025; Trew & Maclean, 2021). Such a shift will likely lead to the lengthy natural coral reef recovery processes (Guzman & Cortés, 2007) being outpaced at Isla del Caño, likely cementing a shift to algal dominated reefs (Nyström et al., 2012; Pearce-Kelly et al., 2025).

Coral to algal dominance and alternative stable state

Highly impacted coral reefs undergo regime shifts to dominance of non-calcifying organisms, such as turf algae (Folke et al., 2004), and is indicative of a breach of tipping point threshold (Pearce-Kelly et al., 2025). Whist the definition and frequency to actual coral-algal phase shifts is debated (Bruno et al., 2009; Crisp et al., 2022), extensive coral declines driven by environmental stressors and/or disturbance events (Leggat et al., 2019) lead to reef restructuring (Stuart-Smith et al., 2018) and degradation (Bland et al., 2018; Nyström et al., 2012) with reduced biodiversity, presenting a threat to coral reef persistence (Pearce-Kelly et al., 2025).

Coral cover measured at reef sites at Isla del Caño and Corcovado declined by over 40% and algal cover increased by more than 70% through the 2023-24 El Niño event, breaching the PRONAMEC guidelines of acceptable system variability and indicating that the requirement of *"comprehensive management measures to reduce impacts, such as sedimentation, stress from tourism or fishing, sewage quality, among others"* (SINAC, 2016). Additionally, the most recent benthic surveys (January and February 2025) indicate that six of the nine sites have approximately 10% coral cover or less, consistent with levels associated with ecosystem collapse and loss of function (Armstrong McKay et al., 2022; Darling et al., 2019; Pearce-Kelly et al., 2025) and indicating widespread reef degradation (Bland et al., 2018; Norström et al., 2009) and a shift to algal dominance (Dudgeon et al., 2010; Norström et al., 2009). With reef sites surveyed from the tail-end of the thermal anomaly (Reimer et al., 2024), the documented 40% loss of coral cover is likely a gross underestimate, with severe bleaching observed locally since 2023. The progressive shift in reef composition, and the absence of recovery, signifies coral reef degradation and the establishment of an alternative stable state at many sites, with reduced structural complexity and algal dominance (Fung et al., 2011). With reduced complexity, the alternative stable state likely has reduced ecosystem function and is likely to be reinforced by positive feedback loops whereby algal dominance persists and suppresses coral growth and recruitment (Eddy et al., 2021; Norström et al., 2009). The benthic community composition shift at Isla del Caño suggests a significant digression from its previously reported status as a biodiversity hotspot (Cortés et al., 2010; Friedlander et al., 2022; Glynn, Alvarado, et al., 2017) which is likely to negatively impact on tourism (Sing Wong et al., 2022).

Site variation in benthic composition temporal trends

The phase shift to algal dominance varied among reef sites, highlighting the role of local characteristics in buffering or promoting reef degradation (Winslow et al., 2024). This variability provides insight into potential reef refugia and resilience factors. During the tail-end of the thermal bleaching event, shallow reefs such as San Josecito, Tina, and Este Intermedio showed early signs of degradation, with high bleaching prevalence, coral mortality, and the predominance of *Pocillopora* spp., which is characteristic of shallow TEP reefs (Glynn, Alvarado, et al., 2017). In contrast, deeper reefs such as Ancla, Cueva, and Barco Profundo appeared more structurally intact, despite having lower overall coral cover, potentially due to the significantly cooler mean water temperature. These deeper reefs initially retained complexity through the presence of *Pavona* and *Psammocora*, potentially offering some depth-related bleaching refugia, such as cooler water (Muir et al., 2017). However, while deeper sites were slower to degrade, they were not immune to long-term change, highlighting the extent of and speed of disturbance impacts (Ostrander et al., 2000).

Some sites showed a more gradual transition, retaining coral cover for longer before shifting toward an algal-dominated state. Esquina and Este Intermedio initially maintained higher coral cover, which may have delayed their degradation. However, by the latest surveys, both exhibited increasing alignment with turf algal cover, reinforcing the trend of gradual but persistent decline. Chorro and Tina, which had some of the highest coral cover early on, experienced steady losses, with turf algae progressively replacing coral as the dominant benthic component. Barco Somero showed signs of decline but followed a less extreme trajectory than other sites; while turf algae increased, it did not reach the dominance levels observed at San Josecito or Barco Profundo, suggesting that localized conditions or initial community composition may have influenced degradation dynamics (Norström et al., 2009). SIMPER analysis supports these patterns, identifying turf algae as the primary contributor to site-level dissimilarity over time, with increases particularly at Ancla, Cueva, and Barco Profundo, which are more characteristic of rocky reefs (SINAC-UNA, 2021). Coral cover declined significantly at Ancla and San Josecito, while dead coral decreased across most sites—likely reflecting overgrowth and erosion of coral skeletons following earlier mortality (Romanó De Orte et al., 2021). Although bleaching was visually prevalent in 2023, its statistical contribution to post-disturbance dissimilarity was low, suggesting that most mortality occurred prior to the 2025 survey period and was no longer a dominant structuring feature (Ostrander et al., 2000). These results quantitatively reinforce observed temporal trends in benthic structure and indicate that, despite differences in timing and severity, reef sites are converging toward a simplified, turf-dominated state (Dudgeon et al., 2010; Fung et al., 2011). The most substantial site-level changes were observed at San Josecito, Ancla, Barco Profundo, and Cueva, where significant coral loss, turf proliferation, and reductions in macroalgae and cyanobacteria occurred. These benthic shifts breach the levels of permissible variation described in SINAC PRONAMEC, indicating that management measures are required, though the action recommended is only to determine the cause, with no reactive measures suggested (SINAC, 2016; SINAC-UNA, 2021) (p. 39).

The impact of the landslides in November 2024 likely operated synergistically with the preceding bleaching event to cause further reef degradation (Good & Bahr, 2021), particularly at several nearby sites of Cueva and Ancla. For example, the proliferation of turf algae prior to the landslides would have promoted sediment adhesion to substrate and inhibits coral recruitment (Fourney & Figueiredo, 2017). By November 2024, the thermal stress anomaly had already significantly affected deeper reef sites, including Cueva and Ancla, which previously provided some thermal refuge. The coral loss and increasing algal cover, albeit to a lesser extent than in the shallower reefs. Intensive sedimentation from the landslides would have further stressed coral communities by reducing light availability for photosynthesis, impairing coral immunity (Sheridan et al., 2014), and increasing the energetic cost of sediment removal (Erftemeijer et al., 2012), essentially smothering the corals. It is also likely that the influx of nutrients associated with the fine sediment provided promoted the proliferation of turf algae and collectively they developed a thick matt over the available substrate (Vermeij et al., 2010).

The disappearance of dead coral as a structuring variable in the latest surveys suggests that the active phase of coral mortality had passed, with reefs now stabilizing in an algal-dominated state. This reflects a loss of structural complexity, as coral skeletons that once provided habitat and settlement space for coral recruits were overgrown. The increasing dominance of turf algae suggests that many sites have crossed a tipping point toward an alternative stable state, including tourist sites of Ancla, Cueva and Barco Profundo (BIOMARCC-SINAC-GIZ, 2016; Naranjo-Arriola, 2021).

Species-specific patterns

While benthic trends clearly show a system-wide shift toward algal dominance, species-level data offer insights into differential vulnerability and community restructuring. The genus *Pocillopora*, dominant at many shallow sites at Isla del Caño and Corcovado (Cortés & Jiménez, 1996, 2003), including San Josecito and Tina, exhibited the highest bleaching prevalence, consistent with its high thermal sensitivity (Marshall & Baird, 2000; Palmer et al., 2010). The decline in *Pocillopora* spp. drove early structural loss at these shallower sites, whereas deeper sites, such as Cueva and Barco Profundo, initially retained *Pavona* spp. and *Porites lobata*, which are considered more thermally tolerant (Glynn et al., 2001; Palmer, 2018b; Palmer et al., 2010). However, the persistence of *Pavona* spp. and *Porites* spp., is partially an artifact of the survey methods. These genera showed signs of decline, particularly *Pavona* spp., suggesting breaches of their damage thresholds, defined as the point at which accumulated physiological stress exceeds a coral's capacity for repair, triggering irreversible damage, including tissue loss (Palmer, 2018a). This led to extensive partial mortality of massive coral colonies, causing fragmentation and an increased count of coral colony abundance - artificially inflated colony counts for massive species. Thus, the apparent stability of these taxa likely reflects the persistence of remnants rather than functional resilience. Similarly, no significant changes in proportional taxonomic abundance were observed through time, even for *Pavona clavus*, which local knowledge and observations indicate has dramatically declines, likely because most mortality occurred prior the surveys, which were conducted after the peak of the thermal anomaly (Reimer et al., 2024). This highlights a limitation of the predominantly post-bleaching survey window, highlights that the findings of coral loss are likely a gross underestimate and reinforces the need for continuous monitoring to capture real-time community shifts (Obura et al., 2019).

Only 12 coral taxa were recorded in coral reef surveys (2024 to 2025), a reduction from the 22 species historically reported at Isla del Caño (Cortés & Guzman, 1998; Guzman & Cortés, 2001). Whilst our surveys grouped all *Pocillopora* spp. together, due to difficulties with identification to species level in the field (Johnston et al., 2018), the findings suggest a general loss of coral diversity at Isla del Caño, threatening long term resilience (Folke et al., 2004; Nyström et al., 2000). Particularly, *Porites panamensis* was absent, which may be locally extirpated, and *Gardineroseris planulata* was rare, with only occasional small colonies observed. Crown-of-thorns starfish (*Acanthaster planci*) were observed preying on surviving coral, including *Porites lobata*. This represents a shift in feeding behavior from a preference for *Pocillopora* spp., as has been previously noted in the TEP after coral mortality events (Guzman & Cortés, n.d.). The combined impacts of bleaching, sedimentation, and predation appear to have driven an ecological simplification, with turf algae expanding into vacated space and reef composition increasingly shaped by loss rather than resilience.

The low Ecological Recovery Feasibility and the urgent need for coral reef restoration

The more than 11% reduction in coral cover and >21% increase in algal cover, according to the governing body of Isla del Caño, warrants "comprehensive management measures to reduce impacts" (SINAC, 2016)p. 23). The need for urgent targeted reef restoration is underscored by the dramatic decline in coral cover and simplification of community composition at Isla del Caño and northern Corcovado, and the related limited ecological recovery feasibility (Kleypas et al., 2021; Suggett et al., 2024). The ecological recovery feasibility index offers a viable initial framework for evaluating relative reef recovery potential that can be applied locally and refined for more accurate indication of reef health as data become available (Obura et al., 2019). Currently, by integrating benthic composition, science-informed ecological directions and PCA-derived loadings, the index provides a transparent site-specific tool for triage-based restoration decisions. The variation in ecological reef recovery feasibility among sites highlights the need for, and importance of, developing a targeted approach and tailored interventions to restoring ecological reef function at the degraded sites of Isla del Caño and Corcovado (Kleypas et al., 2021; Shaver et al., 2022). The ecological reef recovery Index indicates that several sites have limited potential for natural recovery, particularly San Josecito, Ancla, and Barco Profundo, highlighting the necessity of reactive restoration (Hein et al., 2021; Kleypas et al., 2021). While sites such as Chorro and Esquina demonstrated comparatively higher ecological recovery potential, all surveyed locations remain vulnerable to escalating climate stress and impaired coral recruitment, suggesting that passive recovery is increasingly unlikely to restore ecosystem function without direct intervention (Hein et al., 2021; Pearce-Kelly et al., 2025). Proactive reef management across all sites is essential, given the accelerating frequency and severity of thermal stress events and limited coral adaptation capacity (Alvarado et al., 2025; Kleypas et al., 2021; Pearce-Kelly et al., 2025).

A wide array of coral reef restoration methods has been implemented or proposed to sustain reef structure and function in the face of climate change (Suggett & Van Oppen, 2022). Coral gardening—propagating fragments in nurseries and outplanting them to degraded sites—remains the most widely applied method and has shown moderate success in increasing local coral cover, particularly for fast-growing species like *Pocillopora* and *Acropora* spp. (Boström-Einarsson et al., 2020; Shaver et al., 2022). In Costa Rica, restoration efforts have rapidly expanded over the past decade, employing floating nurseries (trees and ropes), benthic structures (A-frames, tables, spiders), and outplanting of both branching and massive species (Alvarado et al., 2025). Reported growth rates (~6–9 cm/year) and survival rates (60–90%) in Costa Rica are encouraging, although these efforts remain vulnerable to thermal anomalies and algae overgrowth if not paired with resilience-enhancing actions (Alvarado et al., 2025). More experimental approaches, including those aimed at increasing resilience—such as larval enhancement, cryopreservation, microbiome manipulation, assisted evolution— as well as reef shading, and artificial upwelling, offer long-term potential to improve coral stress tolerance and restoration success (Barshis et al., 2013; Bay et al., 2023; Suggett et al., 2024). However, many of these methods are typically expensive (Schmidt-Roach et al., 2025), technologically complex, largely limited to pilot-scale trials in high-income nations (Bayraktarov et al., 2020; McLeod et al., 2022), and lack conclusive evidence of their long term efficacy in terms of increased reef resilience (Pearce-Kelly et al., 2025). Additionally, the implementation requires specialized infrastructure, ongoing technical support, and considerable investment—resources that are often unavailable in low- and middle-income countries (LMICs) where coral restoration efforts are often dependent on donations (Alvarado et al., 2025; Bayraktarov et al., 2020). In Costa Rica, where restoration is largely driven by community-based organizations, NGOs, and the Coral Restoration Consortium (Alvarado et al., 2025) that operate under the SINAC framework (SINAC-GIZ, 2020), lower-cost, scalable methods such as nursery propagation and strategic site protection remain the most feasible strategies. Integrating achievable methods to increase coral reef resilience, however, are essential for the persistence of Costa Rica's coral reefs (Kleypas et al., 2021).

Variations in coral immune function—including antioxidant enzyme activity and phenoloxidase production—play an important role in the maintenance and return to health (Palmer et al., 2008, 2010), including during thermal stress (Barshis et al., 2013; Palmer, 2018b). Understanding the variable health dynamics of local coral species through environmental fluctuations, as per the damage threshold hypothesis (Palmer, 2018a), potentially presents a more accessible and lower cost option for increasing the resilience of reefs during the restoration process, whilst addressing the call to refine tools for effective screening (Klepac et al., 2024). Therefore, integrating immune profiling into coral selection for nurseries may increase the probability that restored populations can persist under future thermal regimes (Palmer, 2018a).

Alongside ecological interventions, effective integration with government and stakeholders is essential for coral reef restoration (Alvarado et al., 2025; Kleypas et al., 2021; Shaver et al., 2022). This is perhaps especially the case for protected areas, like Isla del Caño (SINAC, 2009), that are also essential for local tourism (BIOMARCC-SINAC-GIZ, 2016; Naranjo-Arriola, 2021). Managing human pressures on vulnerable systems is critical for their survival (Andrello et al., 2022), with dive tourism impact including coral damage and pollutants, resulting in increased disease prevalence (Lamb et al., 2014). Coral damage linked to tourism activity has been observed at high-use dive and snorkel sites at Isla del Caño, such as Ancla, Barco Profundo, Cueva, and Esquina (Naranjo-Arriola, 2021), suggesting that temporary access restrictions to sensitive sites, redistributing use across a wider range of reef areas, and enhancing diver and guide training or pre-dive briefings could help mitigate further degradation of vulnerable areas while preserving socio-economic benefits (ACOSA-TNC-UCI-ELAP, 2008). Given the dependence of local tourism on the health of the reefs at Isla del Caño and Corcovado, and the support of conservation through tourism-based donations, continued dialogue and collaboration among conservation organization, local government and dive operators is essential for ensuring reef recovery and long-term persistence (Alvarado et al., 2025; Kleypas et al., 2021).

Conclusions

Isla del Caño's coral reef communities—historically considered climate-resilient—underwent a significant, El Niño-driven shift from coral to algal dominance in 2024, with coral cover declining by over 40% and turf algae increasing by more than 70%. Although the temporal scope of coral reef monitoring was constrained to one year following the peaks of the 2023–24 El Niño event for most reef sites, and therefore potentially underestimates the scale of coral loss. These results mark a critical ecological transition, suggesting that the resilience observed in past decades has been eroded under accelerating climate pressures.

By integrating long-term temperature trends, bleaching thresholds, and benthic community dynamics across nine sites, we provide a comprehensive and site-specific temporal assessment of reef degradation at Isla del Caño and one site in north Corcovado. The development of an Ecological Recovery Feasibility Index offers a novel, site-level tool for prioritizing reactive intervention. This simple tool enables triage-based conservation planning and can be applied to other regions and developed as additional information becomes available, such as coral recruitment rates, larval connectivity, more granular temperature data and herbivore density and diversity.

Passive recovery is unlikely to restore reef integrity at Isla del Caño and Corcovado, and urgent restoration is required to regain ecosystem function and mitigate further ecosystem collapse. Whilst global and national efforts to reduce climate impacts are ongoing, targeted, science-driven restoration aimed at increasing reef resilience is essential at Isla del Caño and Corcovado. Coral reef restoration activities must be developed and executed in collaboration with key stakeholders of this important biological reserve, including government, conservation organizations, scientists and dive tour operators.

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Figure Legends

Figure 1: The location of the nine coral community sites surrounding Isla del Caño and north Osa Peninsula (Corcovado).

Figure 2: Daily SST, MMM and DHW for 5km at Isla del Caño over a 40-year period (1985 to 2025). SST trendline shown in white.

Figure 3. Annual frequency (days) of thermal events at Isla del Caño 8°42'59"N 83°53'06"W based on NOAA Coral Reef Watch SST data (1985–2025). Warm events are defined as days when SST exceeds the bleaching threshold (MMM + 0.5°C). Cool events are defined as days when SST is below the monthly mean minus 0.5°C.

Figure 4: *Porites lobata* colony at San Josecito at approximately 1m on a) 22nd February 2024 and b) 30th May 2024.

Figure 5: *Pocillopora* spp. colony at San Josecito at approximately 1m on a) 28th January 2024 and b) 22nd February 2024 and c) 30th May 2024.

Figure 6: A time series of a *Porites lobata* colony at Barco Somero, photographed as healthy (2019), severely bleached (2023) and healthy, though with receded tissues in 2025.

Figure 7: The proportion of bleached corals at each site recorded during the study period. The blue line represents the fitted regression line from the linear model, and the shaded area around the line indicates the 95% confidence interval of the fitted values.

Figure 8: Shannon Index of coral species diversity among reef sites for the full study period. Ancla n=18, Barco Profundo n=24, Barco Somero n=24, Chorro n=48, Cueva n=18, Esquina n=24, Este Intermedio n=18, San Josecito n=27, Tina n=33.

Figure 9: Proportion of coral cover at each site through time. The blue line represents the fitted regression line from the linear model, and the shaded area around the line indicates the 95% confidence interval of the fitted values. Ancla n=24, Barco Profundo n=24, Barco Somero n=24, Chorro n=54, Cueva n=26, Esquina n=24, Este Intermedio n=24, San Josecito n=27, Tina n=39.

Figure 10: Principal Component Analysis (PCA) of reef site composition across different time periods. (A) During Bleaching: March to July 2024, (B) After Bleaching: August to December 2024 and (C) Latest Data: January to February 2024. Arrows indicate PCA loadings, representing the contribution of environmental and benthic variables to site differentiation

Figure 11: Ecological restoration feasibility index

Tables

Table 1: Bleaching Prevalence and Variability Estimates for Coral Genera from the Zero-Inflated Beta (ZIB) Model (95% CI)

Coral Genus	Bleaching Prevalence (%)	Site-Level Variation (SD)	Dispersion (phi)	Zero Inflation (zi)
Pocillopora spp.	33.9 (24.4 - 44.9)	0.13 (NA)	0.82 (0.68 - 0.97)	0.00 (0.00 - 0.02)
Porites lobata	24.0 (16.3 - 34.0)	0.19 (0.01 - 0.51)	1.08 (0.90 - 1.27)	0.00 (0.00 - 0.02)
Psammocora spp.	15.6 (10.2 - 22.6)	0.10 (NA)	0.92 (0.73 - 1.14)	0.00 (0.00 - 0.02)
Pavona spp.	10.1 (6.7 - 15.2)	0.10 (NA)	1.61 (1.21 - 2.08)	0.00 (0.00 - 0.02)
Other corals	0.25 (0.16 - 0.37)	0.08 (0.00 - 0.24)	105.63 (75.51 - 140.02)	0.00 (0.00 - 0.02)

Table 2: Key contributors to overall benthic composition change (SIMPER)

Variable	Average Contribution	Consistency Ratio	Mean Before	Mean After	Cumulative Contribution	% Change	P-Value
Turf	0.1598	1.466	0.337	0.575	0.332	70.62	0.0099
Bleached	0.1101	1.282	0.192	0.26	0.561	35.42	0.8811
coral	0.0821	1.094	0.193	0.115	0.732	-40.41	0.0099
CCA	0.062	0.785	0.094	0.106	0.861	12.77	0.3465
Dead coral	0.0455	0.571	0.093	0.017	0.955	-81.72	0.0099
Macroalgae	0.0125	0.532	0.017	0.011	0.981	-35.29	0.0693
Cyanobacteria	0.009	0.563	0.016	0.004	1.0	-75.0	0.0099

Table 3: Key drivers of substrate change at each site, based on significance (SIMPER)

Site	Variable	Cumulative Contribution	% Change	P-Value
Ancla	Turf	0.42	70.78	0.069
	CCA	0.607	195.96	0.455

	Coral	0.783	-53.99	0.04*
Barco Profundo	Turf	0.445	203.81	0.01*
	Bleached	0.735	676.25	0.04*
	CCA	0.821	211.5	0.257
Barco Somero	Macroalgae	0.279	-99.59	0.01*
	Turf	0.476	29.25	0.802
	Bleached	0.638	-13.76	1.0
Chorro	Turf	0.31	38.01	0.267
	Bleached	0.56	42.05	0.871
	Coral	0.704	28.07	0.436
Cueva	Turf	0.425	91.87	0.01*
	CCA	0.623	-22.71	0.693
	Bleached	0.762	-49.54	0.02*
Esquina	Turf	0.367	44.12	0.02*
	Coral	0.585	-50.55	0.01*
	Bleached	0.79	83.73	0.693
Este Intermedio	Turf	0.313	59.57	0.257
	Bleached	0.553	54.61	0.97
	Dead coral	0.711	-97.64	0.01*
San Josecito	Turf	0.399	344.03	0.03*
	Dead coral	0.748	-99.75	0.01*
	Bleached	0.915	-57.96	0.04*
Tina	Turf	0.329	62.26	0.277
	Coral	0.621	-48.02	0.01*
	Bleached	0.887	9.66	0.663

* indicates statistical significance.

Figure 1

Map of coral community monitoring sites at Isla del Caño and northern Corcovado

The location of the nine coral community sites surrounding Isla del Caño and north Osa Peninsula (Corcovado) .

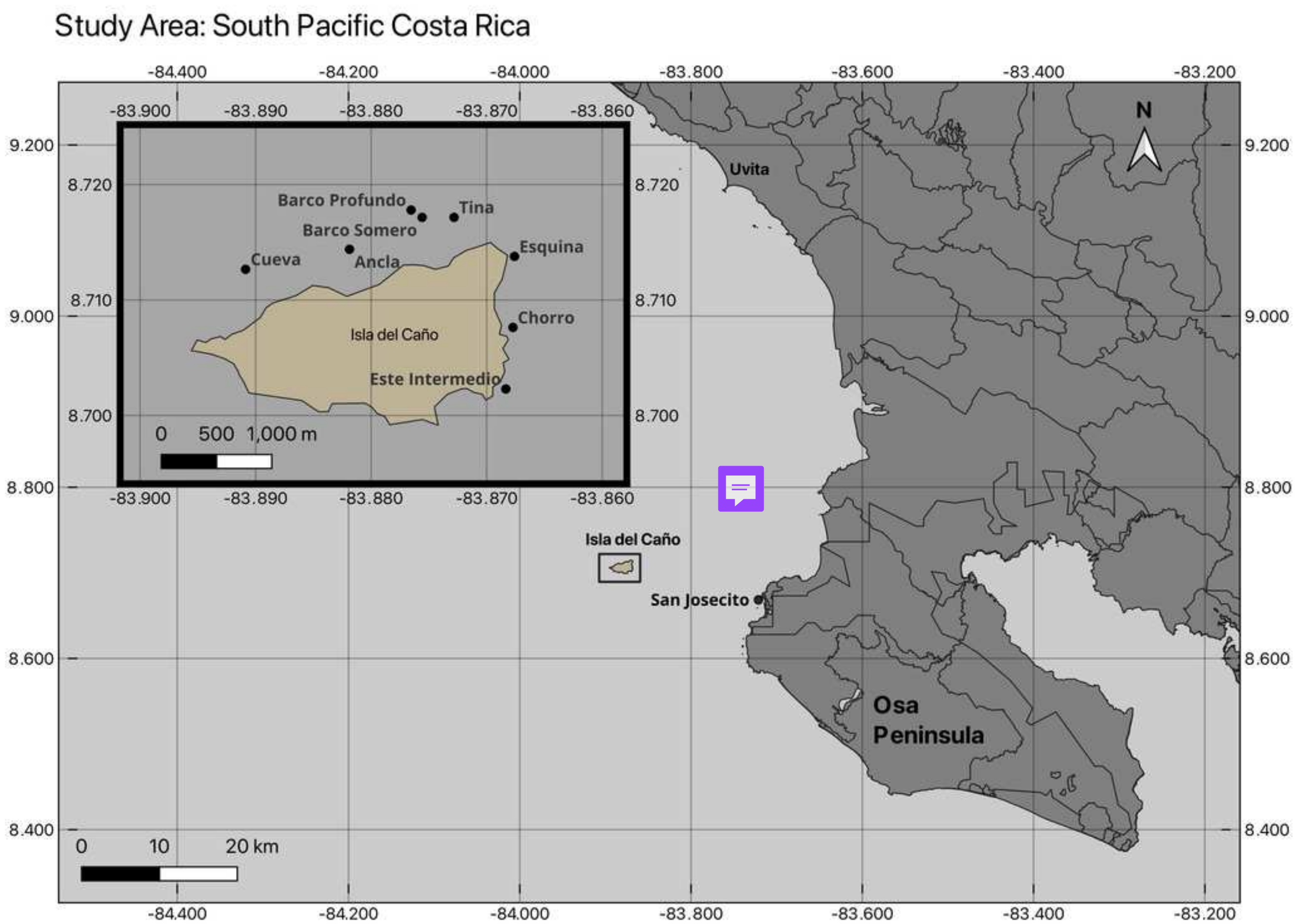

Figure 2

Daily SST, MMM, and DHW at Isla del Caño (1985–2025)

Figure 2: Daily SST, MMM and DHW for 5km at Isla del Ca ñ o over a 40-year period (1985 to 2025). SST trendline shown in white.

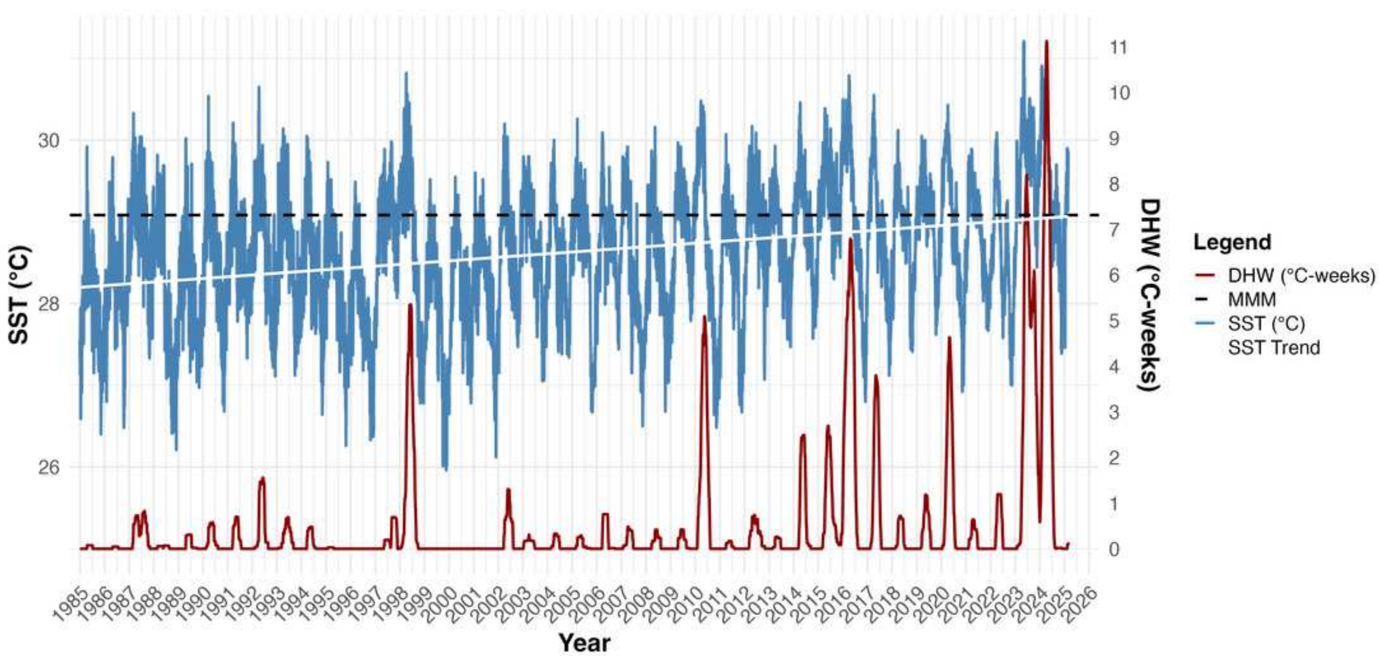

Figure 3

Annual frequency of warm and cool thermal events at Isla del Caño (1985–2025)

Annual frequency (days) of thermal events at Isla del Caño 8°42'59"N 83°53'06"W based on NOAA Coral Reef Watch SST data (1985–2025). Warm events are defined as days when SST exceeds the bleaching threshold (MMM + 0.5°C). Cool events are defined as days when SST is below the monthly mean minus 0.5°C.

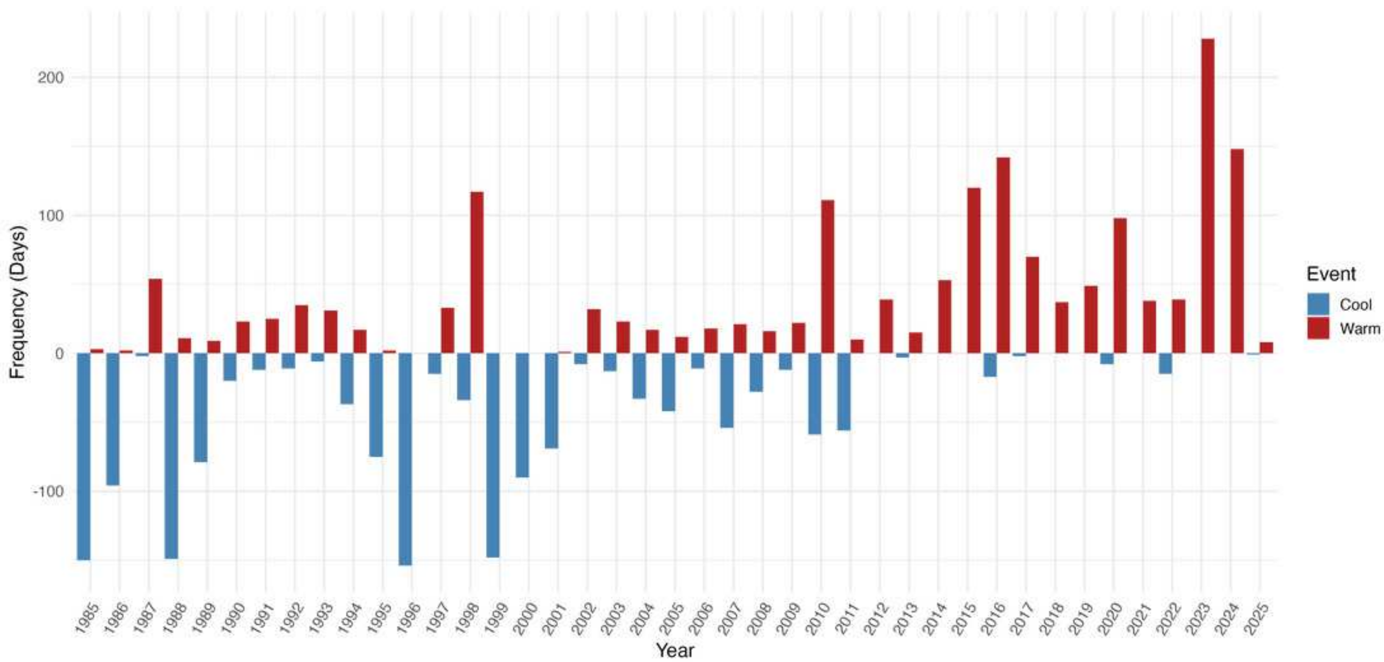

Figure 4

Porites lobata colony at San Josecito at ~1 m depth on a) 22 February 2024 and b) 30 May 2024

Porites lobata colony at San Josecito at approximately 1m on a) 22 nd February 2024 and b) 30 th May 2024.

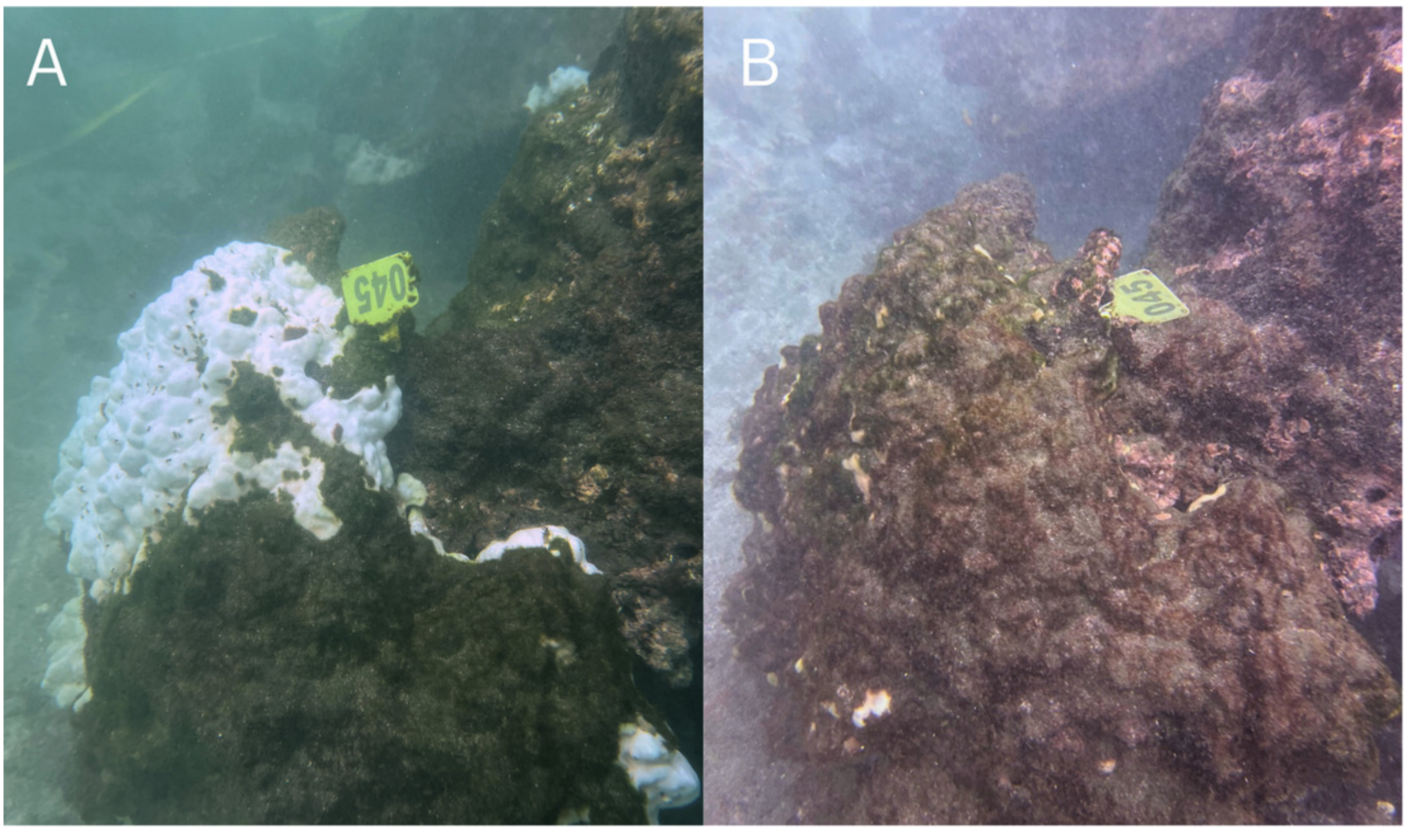

Figure 5

The change in health of a *Pocillopora* spp. colony at San Josecito between January and May 2024

Pocillopora spp. colony at San Josecito at approximately 1m on a) 28 th January 2024 and b) 22 nd February 2024 and c) 30 th May 2024.

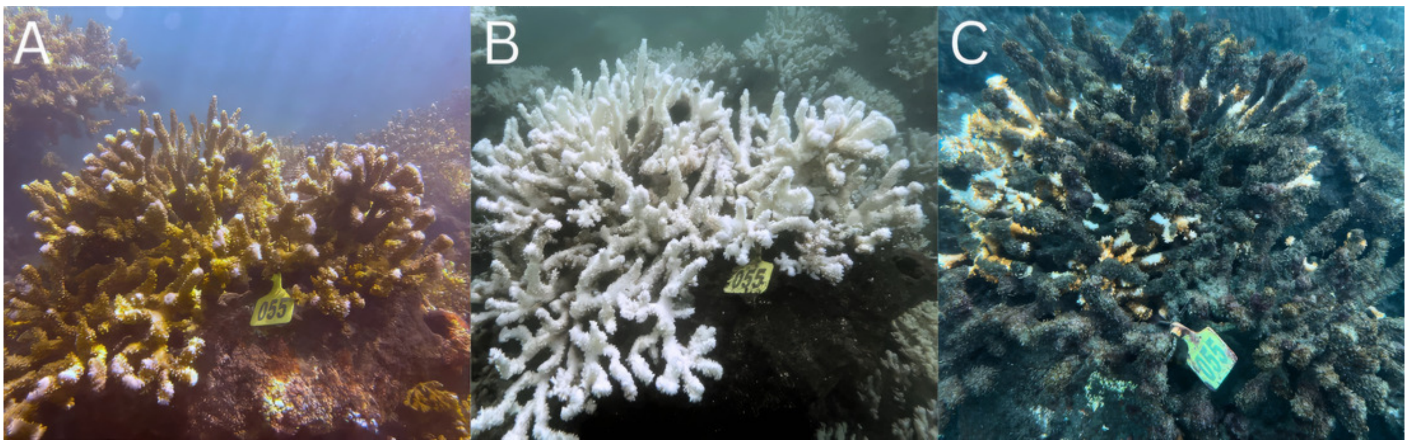

Figure 6

A time series of a *Porites lobata* colony at Barco Somero, photographed in different health states

A time series of a *Porites lobata* colony at Barco Somero, photographed as healthy (2019), severely bleached (2023) and healthy, though with receded tissues in 2025.

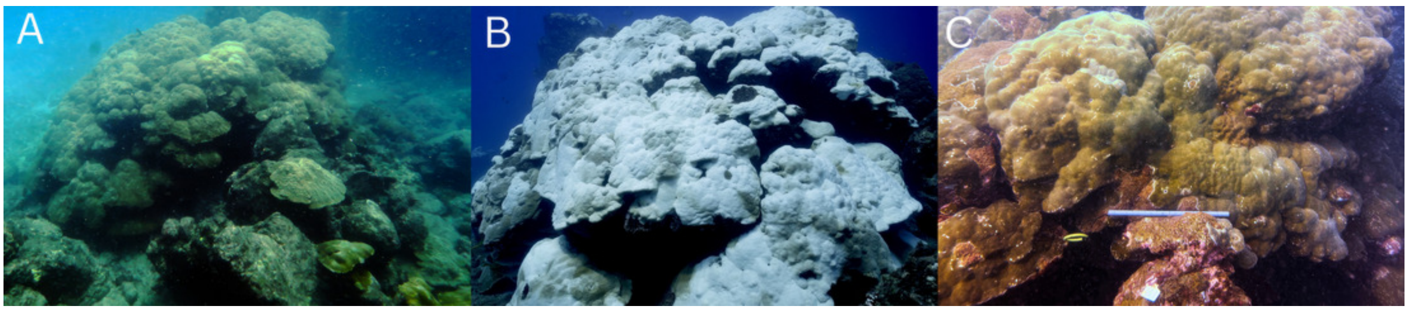

Figure 7

The proportion of bleached corals at each site recorded during the study period.

The proportion of bleached corals at each site recorded during the study period. The blue line represents the fitted regression line from the linear model, and the shaded area around the line indicates the 95% confidence interval of the fitted values.

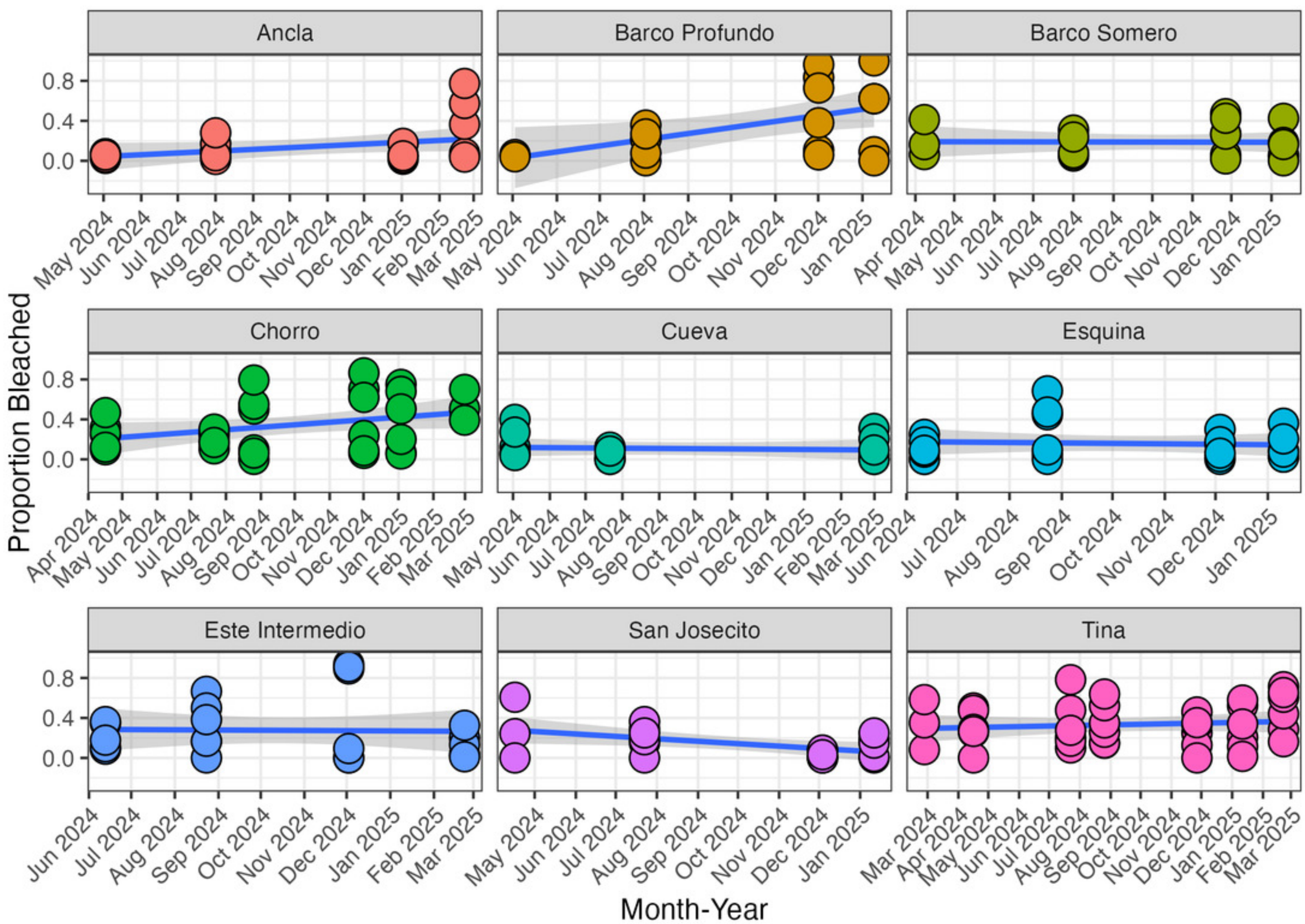

Figure 8

Shannon Index of coral species diversity among reef sites

Shannon Index of coral species diversity among reef sites for the full study period. Ancla n=18, Barco Profundo n=24, Barco Somero n=24, Chorro n=48, Cueva n=18, Esquina n=24, Este Intermedio n=18, San Josecito n=27, Tina n=33.

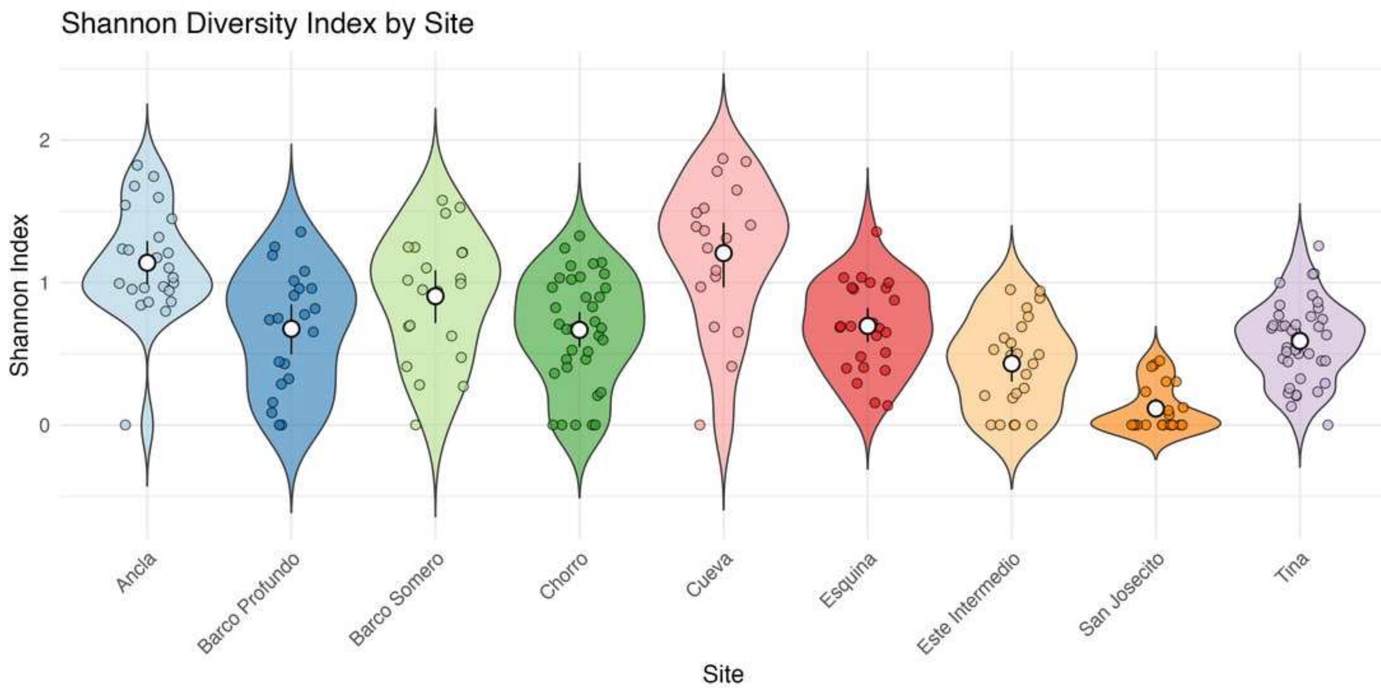

Figure 9

Proportion of coral cover at each site through time.

Proportion of coral cover at each site through time. The blue line represents the fitted regression line from the linear model, and the shaded area around the line indicates the 95% confidence interval of the fitted values. Ancla n=24, Barco Profundo n=24, Barco Somero n=24, Chorro n=54, Cueva n=26, Esquina n=24, Este Intermedio n=24, San Josecito n=27, Tina n=39.

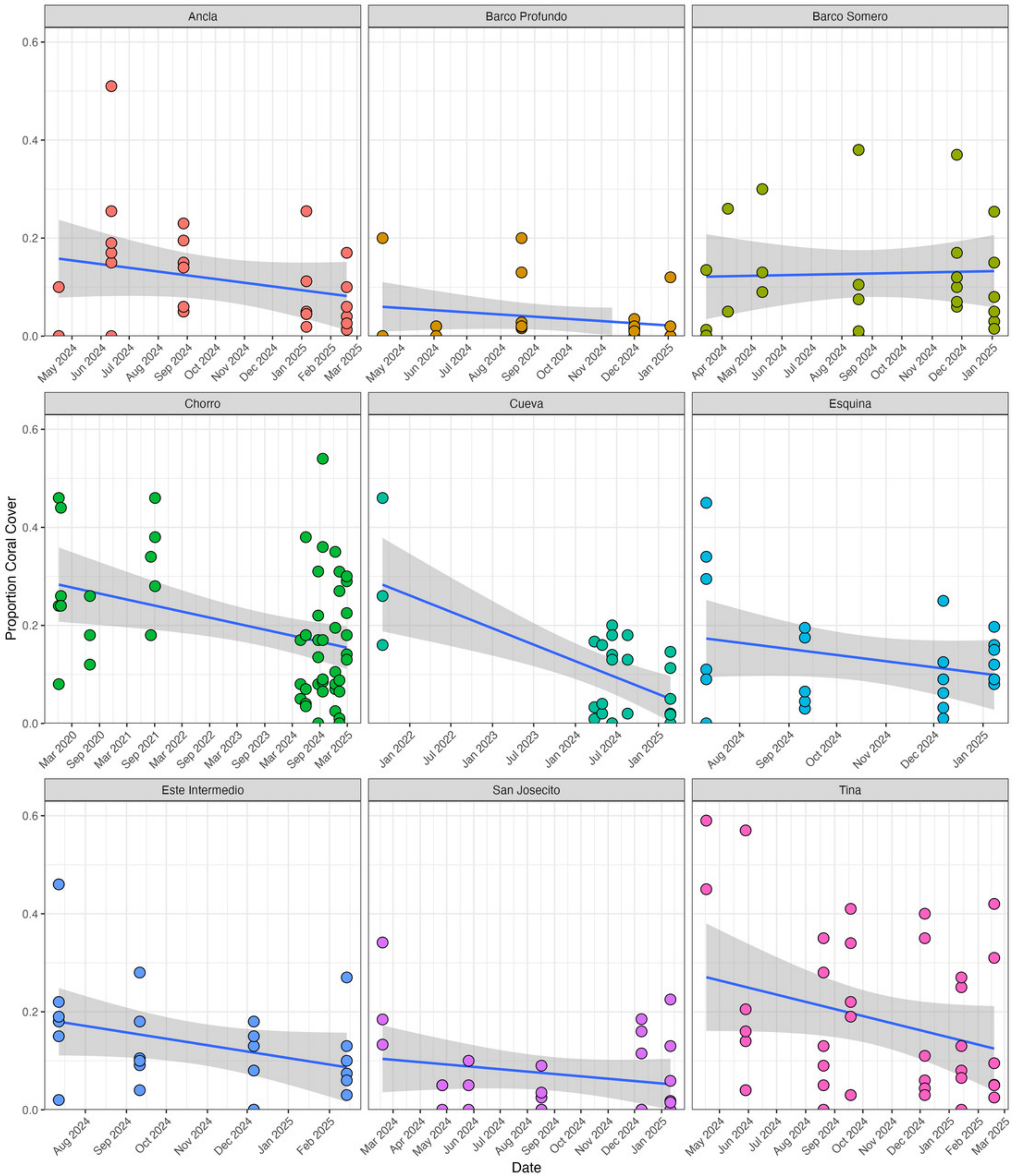
Ancla
Barco Profundo
Barco Somero
Chorro
Cueva
Esquina
Este Intermedio
San Josecito
Tina
Proportion Coral Cover
Date
0.0
0.2
0.4
0.6

Figure 10

Principal Component Analysis (PCA) of reef site composition across different time periods.

Principal Component Analysis (PCA) of reef site composition across different time periods. During Bleaching: March to July 2024 , After Bleaching: August to December 2024 and Latest Data: January to February 2024. Arrows indicate PCA loadings , representing the contribution of environmental and benthic variables to site differentiation

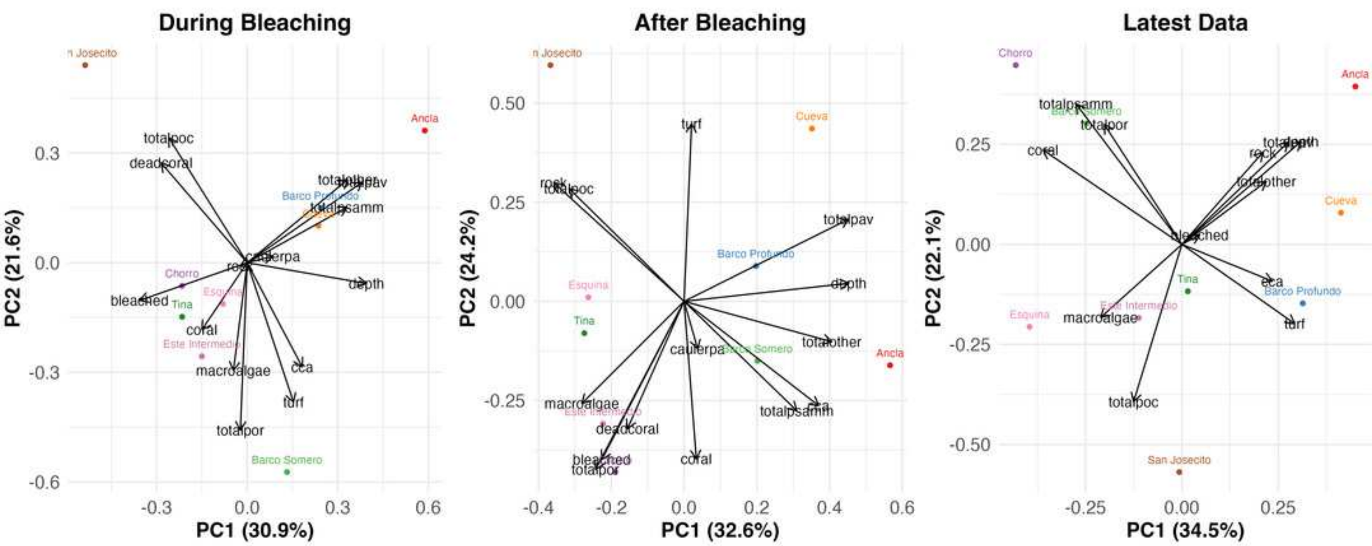

Figure 11

Ecological restoration feasibility index for coral reef sites at Isla del Caño

Ecological restoration feasibility index ranks the relative potential for passive recovery across reef sites at Isla del Caño. The index integrates site-level coral cover, benthic composition, and principal component loadings. Sites with lower scores (e.g., San Josecito, Ancla, Barco Profundo) exhibit minimal recovery potential and high degradation, indicating urgent need for active intervention. Higher scores (e.g., Chorro, Esquina) suggest greater potential for natural recovery under current conditions.