

Marine Benthic Communities and Their Effect on Coral Reef Resilience

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Abstract

Coral reefs are subject to recurrent thermal stress from the El Niño – Southern Oscillation, yet post-disturbance recovery and resistance to stress vary widely. This study attempts to test whether variation in benthic communities in terms of diversity and beneficial/non-beneficial taxa will alter coral resistance (bleaching-period loss) and recovery (24-month regrowth) on Mo’orea, French Polynesia. In terms of datasets, this study will use MCR LTER quadrat records from 2005 to the present day across six island-wide sites subdivided into multiple habitats. In terms of the benthos, two indicators were used/derived: first, Shannon’s diversity index, and also a mechanistic Helper Index that weighs non-coral taxa based on their relationship with coral reefs and whether or not they help polyp settlement. Ultimately, recovery and loss responses were generally not explained by benthic or nutrient terms, suggesting the need for additional covariates, a more complex model, and a larger data set across more sites to avoid pseudoreplication. Overall, there appears to be little correlation between benthic indicators and reef resilience, though further investigation may be needed.

Keywords: reef, benthos, Mo’orea, resilience, El Niño

1. Introduction

Coral reefs are some of the most biodiverse and productive ecosystems on earth, often deemed as the ‘rainforests of the sea’, but they remain extremely sensitive to even the slightest of climate-driven disturbances [1]. The heating and cooling cycles of El Niño and La Niña intensify coral stress, and especially during extreme heating, corals are massively threatened [2]. During the heating cycle of El Niño, elevated sea surface temperatures can trigger mass coral bleaching, destroying reef communities and resulting in major biodiversity losses [3]. While the effect of temperature on coral resilience is well documented [4], recovery after extreme heating is influenced by a spectrum of other variables that remain less understood.

Other than thermal stress, there are a variety of other variables at play, influencing coral recovery after El Niño events. Sedimentation is impactful as it can smother light availability for coral, essential for zooxanthellae to perform photosynthesis and provide vital organic molecules to the coral polyps [5]. Meanwhile, eutrophication, often indicated by elevated chlorophyll a levels, can promote algal blooms (Harmful), intensifying coral–algae competition (Evidence). These stressors, especially when taken into consideration in the context of extreme heating and competition for space and resources, can favor opportunistic species that compete with corals. Thus, determining the impact of these organisms present in the benthos is critical to explain variability in coral resilience.

Among these factors, benthic communities are instrumental in supporting coral reefs and their surrounding community. Certain benthic taxa hinder coral resilience by directly competing for space, overgrowing coral surfaces, or modifying microbial environments. For example, turf algae [8], *Lobophora variegata* (Long-Term), and *Dictyota* spp. [10] populations can expand during bleaching events, suppressing coral recruitment and slowing recovery. In contrast, some benthic organisms facilitate coral resilience. Crustose coralline algae [11] are able to stabilize reef substrates and provide settlement cues for coral polyps [12], while calcareous algae such as *Halimeda* spp. can contribute to substrate consolidation and benthic complexity [10], creating favorable conditions for regrowth. Thus, the benthos functions variably as both a barrier and an ally for corals.

Recent resilience-based management (RBM) frameworks focus on emphasizing the need for ecological indicators to capture these recovery dynamics locally [13]. As such, the focus of this study on Mo’orea, French Polynesia, is critical to be used as a model to assess coral resilience. Across 6 Long-Term Ecological Research sites along the coast of Mo’orea, and a multitude of survey depths. The long-term monitoring at Mo’orea has been able to

document various extreme El Niño events and later coral recovery, making it possible to investigate whether benthic structure, along with other previously mentioned stressors, drives recovery and coral resilience.

This study aims to examine the effects of benthic community structure on coral resilience across two El Niño-associated events at the local level: 2009-10 and 2015–16. These events have an overlap with the global Niño Index, corroborating local climate anomaly identification (EI) derived from Copernicus satellite data.

By evaluating the effect of benthic community composition in relation to other environmental stressors such as sedimentation and eutrophication, this study addresses a key research gap: although coral resilience has been widely studied in terms of temperature stress, fewer studies have systematically examined how the broader benthic community influences coral outcomes under multi-stressor conditions. A more complete understanding of these interactions is essential, as benthic assemblages may either amplify or mitigate the effects of heating events. By bridging this gap, the results of this study will contribute to frameworks that predict coral responses to future disturbances, aiding both local and global reef management strategies.

2. Methodology

This study is based on data from the coral reef ecosystems off the coast of Mo’orea, French Polynesia, where the Mo’orea Coral Reef Long-Term Ecological Research (MCR LTER) program has had consistent annual surveys since 2005. The data spans six permanent monitoring sites throughout the perimeter of the island, each divided into data from three habitats – back reef (2m depth), fringing reef (6m depth), and forereef (10 and 17m depth). These sites have records of reef conditions and benthic composition across multiple disturbance events, including the two focal El Niño heating events in 2010 and 2015-16 that this study focuses on. These events were chosen due to the fact that they are well documented in the thermal stress episodes they spurred on, alongside the fact that these events overlap with the benthic, coral, and satellite data both temporally and spatially. Thus, event-specific analysis rather than calendar-year aggregation was determined to be the best course of action to demonstrate resilience and recovery.

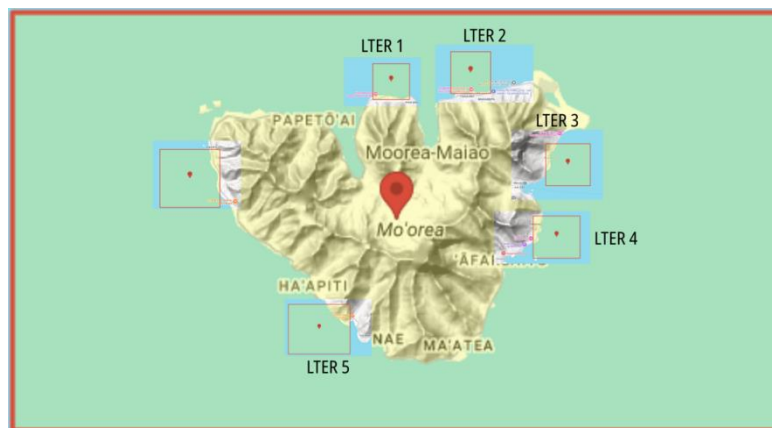


Figure 1. Mo’orea, French Polynesia alongside the six LTER data collection sites

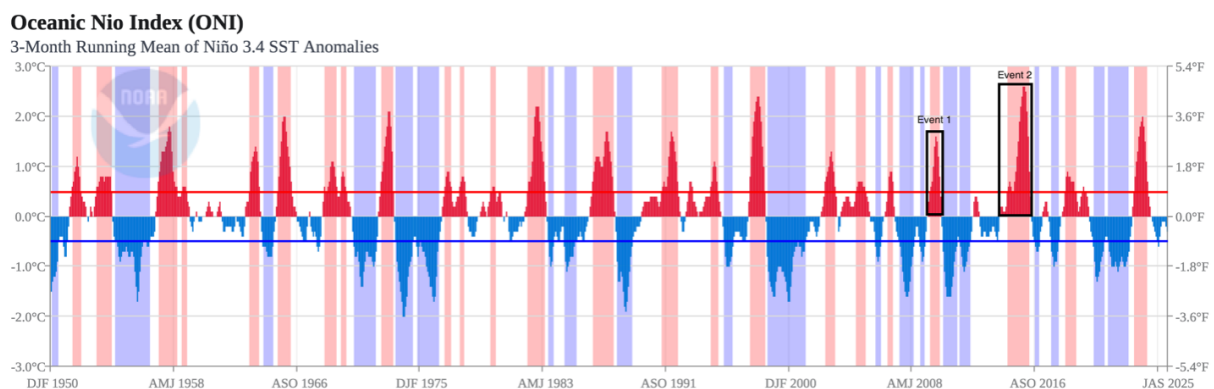


Figure 2. Global SST oscillations along selected event timeframes (El Niño / Southern)

Coral cover and benthic community composition were collected from the MCR LTER annual photo-quadrat surveys of 0.5 m by 0.5 m, with percentage cover estimates of scleratinian corals, algal groups, invertebrates, and substrate types. In terms of resilience, coral cover was used directly in determining loss and also as a baseline to determine recovery two years after disturbances. In terms of temperature, specifically degree heating weeks (DHW), data were sourced from the Copernicus Marine Service and their satellite sea surface temperature (SST) data, which records temperatures at a depth of 20cm at 0.05 x 0.05 degree horizontal grid resolution (~ 5 x 5 km). As such, these sources of data allow for an evaluation of coral resilience in the face of multiple compounding stressors, contextualizing results within benthic community frameworks.

Meanwhile, the effect of benthic communities was quantified by both Shannon’s index to capture overall diversity and a “helper index” based on the many species documented at Mo’orea and their ecological roles as a positive or negative contributor to coral health.

Resilience was defined using two metrics as previously mentioned: resistance to bleaching and recovery following the heating event. Coral loss was calculated as the decline from the coral cover in the 90 days preceding the event to the minimum coral cover value observed during the entire period of the event. Recovery is measured as the regrowth 24 months after the event onset relative to the pre-event baseline and event minima. By using event-specific windows for the baseline, decline, and recovery, the approach combatted the annual data collection that was sparse in terms of more concentrated data collection, avoiding the temporal distortions associated with annual aggregation. Additionally, the metrics for resilience were first calculated at the quadrat level, then averaged to site x event in order to prevent pseudo-replication from covariates such as degree heating weeks.

$$Loss = \frac{C_{pre} - C_{min}}{C_{pre}}$$

C_{pre} = coral cover 90 days before event

C_{min} = minimum observed coral cover during event

$$Recovery_{24} = \frac{C_t - C_{min}}{C_{pre} - C_{min}}$$

C_t = coral cover 24 months after event end

Just as important is the task of characterizing benthic community predictors, and once again, two indices were derived from the MCR LTER photo-quadrat data. Firstly, Shannon’s index was computed using the vegan package in R, which provided a value that represented the species evenness and richness of the non-coral benthic community. Additionally, a self-created Helper index (see appendix for all values assigned) was also created to represent the effect different organisms had on the coral, specifically in terms of polyp growth and larval settlement. This index assigned each benthic organism a weight of +1, -1, or 0 depending on its effect on coral recovery (positive, negative, neutral, respectively). For example, crustose coralline algae were classified as +1 due to their being the favored benthic cover for coral settlement and growth (Crustose), while fleshy macroalgae were classified as -1 as they compete with coral for space and light [17]. Afterwards, the relative covers of all the taxa were multiplied by these weights and summed to produce a helper score, which was then z-scored in order to compare values across sites and the 2010 and 2015-16 events. Although preliminary investigations used intermediate weights such as ±0.5, they were quickly dropped due to their subjective nature in terms of weighing the effects of different organisms on reef growth; thus, the ±1/0 scheme was ultimately more defensible and easier to interpret.

Finally, environmental covariates were aligned to the event windows. The thermal stress was quantified by DHW, which was a measure of continuous thermal stress and its severity across the events. The DHW chosen was to be the maximum of each event in order to provide a benchmark of comparison between the severity of thermal stress and subsequent coral cover loss.

Table 1. Data sources used in study

Data Type:	Temporal/Spatial Coverage:	Source:
Benthic Community Composition	Across 6 LTER sites measured in-situ from 2005-present	https://search-ucsb-1.dataone.org/view/https%3A%2F%2Fpasta.lternet.edu%2Fpackage%2Fmetadata%2Feml%2Fknb-lter-mcr%2F8%2F38

Coral Cover	Across 6 LTER sites measured in-situ from 2005-present	https://portal.edirepository.org/nis/mapbrowse?scope=knb-lter-mcr&identifier=4&revision=42
Sea Surface Temperature and Degree Heating Weeks	Satellite data from the Copernicus Marine Service measured ex-situ from 1982-present	https://data.marine.copernicus.eu/product/SST_GLO_SST_L4_REP_OBSERVATIONS_010_024/download

Statistical analyses were then undertaken to evaluate the effects of benthic community composition on coral resilience, while incorporating covariates of temperature, sedimentation, and nutrient conditions. For the analytical framework, ordinary least squares (OLS) regression was used with the site by event averages as the units of replication so that all data analyzed remains independent.

For resistance, the primary model included the helper index and a nutrient proxy (hydrogen percentage in macroalgal tissue). DHW and the Helper × DHW interaction were removed because only one post-disturbance window was analyzed (the 2015–16 event), and the 2010 El Niño window was not modeled; with a single event window, thermal stress (DHW) could not be validly assessed. This model tested whether benthic community structure buffered against disturbance and whether nutrient availability modified coral response. For recovery, the model incorporated the same Helper term, while Dry Weight × C:N was used to represent carbon and nitrogen impacts on post-event coral growth and settlement. We retained a single nutrient proxy per model for ecological interpretability (e.g., C:N as a common indicator of nitrogen enrichment, DW to weight biomass exposure) and excluded alternative nutrient indices that lacked clear ecological justification in this context.

The analysis was performed in RStudio using the packages: tidyverse, vegan, and lubridate. Separate datasets were first imported for benthic composition, DHW, and nutrient measurements, and each dataset was time-matched to the event windows of 2010 and 2015–2016. These windows were defined by pre-event (one year prior), heating (start to end of El Niño period), and recovery (24 months after event onset) phases. DHW maxima were calculated using NOAA Coral Reef Watch 5 km data for each event period, summarizing the highest accumulated thermal stress value. Each event’s benthic and temperature data were combined into a unified dataframe through site, depth, and quadrat identifiers, ensuring temporal alignment across datasets.

Table 2. Code for all models run alongside additional details

Scale	Resilience Component	Benthic Index	Response	Nutrient / Stoichiometry Term(s)	Full Model Definition
Site-Event	Resistance (Loss)	Helper	Loss	H	lm_resist1 <- Loss ~ Helper + DHW_max + Helper:DHW_max + H
Site-Event	Resistance (Loss)	Helper	Loss	C	lm_resist2 <- Loss ~ Helper + DHW_max + Helper:DHW_max + C
Site-Event	Resistance (Loss)	Helper	Loss	N	lm_resist3 <- Loss ~ Helper + DHW_max + Helper:DHW_max + N
Site-Event	Resistance (Loss)	Helper	Loss	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_resist4 <- Loss ~ Helper + DHW_max + Helper:DHW_max + Dry_Weight*CN_ratio
Site-Event	Recovery (Recov24)	Helper	Recov 24	H	lm_recov1 <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + H
Site-Event	Recovery (Recov24)	Helper	Recov 24	C	lm_recov2 <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + C
Site-Event	Recovery (Recov24)	Helper	Recov 24	N	lm_recov3 <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + N
Site-Event	Recovery (Recov24)	Helper	Recov 24	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_recov4 <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + Dry_Weight*CN_ratio
Site-Event	Resistance (Loss)	Shannon	Loss	H	lm_shannon_resist1 <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + H
Site-Event	Resistance (Loss)	Shannon	Loss	C	lm_shannon_resist2 <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + C
Site-Event	Resistance (Loss)	Shannon	Loss	N	lm_shannon_resist3 <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + N

Site-Event	Resistance (Loss)	Shannon	Loss	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_shannon_resist4 <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + Dry_Weight×CN_ratio
Site-Event	Recovery (Recov24)	Shannon	Recov24	H	lm_shannon_recov1 <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + H
Site-Event	Recovery (Recov24)	Shannon	Recov24	C	lm_shannon_recov2 <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + C
Site-Event	Recovery (Recov24)	Shannon	Recov24	N	lm_shannon_recov3 <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + N
Site-Event	Recovery (Recov24)	Shannon	Recov24	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_shannon_recov4 <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + Dry_Weight×CN_ratio
Transect-Event	Resistance (Loss)	Helper	Loss	H	lm_resist1a <- Loss ~ Helper + DHW_max + Helper:DHW_max + H
Transect-Event	Resistance (Loss)	Helper	Loss	C	lm_resist2a <- Loss ~ Helper + DHW_max + Helper:DHW_max + C
Transect-Event	Resistance (Loss)	Helper	Loss	N	lm_resist3a <- Loss ~ Helper + DHW_max + Helper:DHW_max + N
Transect-Event	Resistance (Loss)	Helper	Loss	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_resist4a <- Loss ~ Helper + DHW_max + Helper:DHW_max + Dry_Weight×CN_ratio
Transect-Event	Recovery (Recov24)	Helper	Recov24	H	lm_recov1a <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + H
Transect-Event	Recovery (Recov24)	Helper	Recov24	C	lm_recov2a <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + C
Transect-Event	Recovery (Recov24)	Helper	Recov24	N	lm_recov3a <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + N
Transect-Event	Recovery (Recov24)	Helper	Recov24	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_recov4a <- Recov24 ~ Helper + DHW_max + Helper:DHW_max + Dry_Weight×CN_ratio
Transect-Event	Resistance (Loss)	Shannon	Loss	H	lm_shannon_resist1a <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + H
Transect-Event	Resistance (Loss)	Shannon	Loss	C	lm_shannon_resist2a <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + C
Transect-Event	Resistance (Loss)	Shannon	Loss	N	lm_shannon_resist3a <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + N
Transect-Event	Resistance (Loss)	Shannon	Loss	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_shannon_resist4a <- Loss ~ Shannon + DHW_max + Shannon:DHW_max + Dry_Weight×CN_ratio
Transect-Event	Recovery (Recov24)	Shannon	Recov24	H	lm_shannon_recov1a <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + H
Transect-Event	Recovery (Recov24)	Shannon	Recov24	C	lm_shannon_recov2a <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + C
Transect-Event	Recovery (Recov24)	Shannon	Recov24	N	lm_shannon_recov3a <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + N
Transect-Event	Recovery (Recov24)	Shannon	Recov24	Dry_Weight, CN_ratio, Dry_Weight×CN_ratio	lm_shannon_recov4a <- Recov24 ~ Shannon + DHW_max + Shannon:DHW_max + Dry_Weight×CN_ratio

3. Results and Discussion

In total, sixteen linear models were run using RStudio to assess the impact of benthic community composition on reef resilience during the 2010 and 2015-16 El Niño events. Models tested either the Helper index or Shannon’s diversity index as proxies to benthic communities and their effect on reef resilience, paired with nutrient parameters of C, N, H, and C: N ratios as covariates. Additionally, two sections of models were run, at the site-event level (n=6) and at the transect-event level (n=30), to highlight spatial differences.

However, there was incomplete overlap between nutrient and thermal data, meaning that DHW_max was missing for one of the El Niño events, leading to NA values across models. As such, temperature could not be tested as a variable. Although there are thus limitations in inferring thermal stress, there are still examinations of how benthic and nutrient characteristics relate to coral loss and recovery.

3.1 Site-Event Level Models

Table 3. Site-event level model summaries

Index	Response (Resilience Component)	Nutrient Stoichiometry Term(s)	Significant Predictors ($p < 0.05$)	Adjusted R ²	Interpretation
Helper	Loss (Resistance)	H	Helper (-8.19, $p = 0.0089$); H (+0.30, $p = 0.0049$)	0.92	Higher Helper → less loss; higher H → greater loss. Strong fit but over-inflated by low n.
Helper	Loss	C	None	0.02	Weak fit; no clear trend.
Helper	Loss	N	None	-0.64	Negative Adj R ² → model cannot fit (low sample size).
Helper	Loss	Dry Weight × C:N	None	-0.75	Over-parameterized; no signal.
Helper	Recov24 (Recovery)	H	None (Helper $p \approx 0.083$)	0.48	Slight trend of higher Helper → faster recovery.
Helper	Recov24	C	None (Helper $p \approx 0.09$)	0.45	Same direction as H; not significant.
Helper	Recov24	N	None	0.30	Low explanatory power.
Helper	Recov24	Dry Weight × C:N	None	0.61	High R ² but statistically invalid (df = 1).
Shannon	Loss	H	None	0.42	Slight positive Shannon effect; nonsignificant.
Shannon	Loss	C	Shannon ($p = 0.10$)	0.49	Weak, marginal diversity effect.
Shannon	Loss	N	None	0.31	No relationship.
Shannon	Loss	Dry Weight × C:N	None	0.36	Overfit; no trend.
Shannon	Recov24	H - Dry Weight × C:N	None	< 0	All recovery models nonsignificant; negative Adj R ² = poor fit.

At the site-event level, the model using helper index and hydrogen had the strongest correlation with an R2 of 0.95 (adjusted to 0.92 at $p=0.011$). The helper index had a negative slope of -8.19 initially suggesting that higher benthic taxa that benefitted coral led to less coral loss during extreme heating in El Niño years. On the surface level, hydrogen, a proxy for nutrient enrichment showed a slight positive correlation with coral loss at a slope of 0.3, which meant that nutrient levels could have led to more stress susceptibility and possibly algal or microbial growth.

However, the model only has a sample size of $n=6$, like all other site-event level models, which is relatively small, alongside the low degrees of freedom ($df=3$), possibly meaning that the small sample could not reliably fit data due to undersampling. In small- n regressions, adjusted R2 penalizes model complexity and when the penalties exceed the explained variance, the adjusted R2 becomes negative, which illustrates statistical invalidity.

Looking at other site-event level models using C, N, or C:N ratios, there was inconsistent effects with $p>0.24$ and adjusted R2 values close or below zero, highlighting excess noise and not ecological patterns.

Then, models that used Shannon’s Index had a similar direction of slopes between 0.59-0.79 and an adjusted R2 of 0.31-0.49. All together, this implies that community diversity may very weakly correspond to coral loss, though not as strongly as the helper index.

Moving on to recovery models, there are weaker fits but still consistent trends in slope direction. The Helper + H model produced a positive relationship with a slope of 15.4 and an R² of 0.69, indicating a possible trend that reefs with more positive benthic organisms may recover faster post-disturbance. Hydrogen had a negative slope of -0.33; however, given the low explanatory power and inconsistency across models, this effect cannot be considered significant. Later models accounting for recovery also returned negative adjusted R² values (e.g., -0.74 for C:N models), suggesting that these models are statistically invalid and should not be interpreted further. This highlights the need for greater replication or alternative predictors to construct a robust recovery model.

3.2 Transect-Event Level Models

Table 4. Transect-event level model summaries

Index	Response (Resilience Component)	Nutrient Stoichiometry Term(s)	Significant Predictors ($p < 0.05$)	Adjusted R ²	Interpretation
Helper	Loss (Resistance)	H	H (+0.18, $p = 0.021$)	0.16	Higher H → greater loss; nutrient stress reduces resistance.
Helper	Loss	C	None	0.02	Weak fit; no trend.
Helper	Loss	N	None	0.01	Weak fit.
Helper	Loss	Dry Weight × C:N	Helper (+4.59, $p = 0.033$); Dry Weight (-0.002, $p = 0.032$); C:N (-0.13, $p = 0.008$)	0.30	Strongest model; Helper improves resistance; low C:N → greater loss.
Helper	Recov24 (Recovery)	H	Helper (+10.3, $p = 0.033$); H (-0.31, $p = 0.041$)	0.11	Positive benthic effect; nutrient enrichment slows recovery.
Helper	Recov24	C - N - Dry Weight × C:N	None	0.03-0.09	Nonsignificant; weak fits.
Shannon	Loss (Resistance)	H	Shannon (+0.48, $p = 0.016$)	0.29	Greater diversity → less coral loss.
Shannon	Loss	C	Shannon (+0.57, $p = 0.0035$)	0.29	Consistent positive diversity effect.
Shannon	Loss	N	Shannon (+0.61, $p = 0.004$)	0.21	Robust diversity-resistance relationship.
Shannon	Loss	Dry Weight × C:N	Shannon (+0.51, $p = 0.023$); C:N (-0.09, $p = 0.056$)	0.32	Strongest Shannon fit; diversity and nutrient balance matter.
Shannon	Recov24 (Recovery)	H - C - N - Dry Weight × C:N	None (C:N $p \approx 0.099$)	-0.08	No significant recovery effects; slight nutrient signal.

To increase replication, models were replicated at the transect-event level, where $n=30$. However, due to the fact that nutrient data is site-specific, not transect-specific, there was pseudoreplication. As such, statistically significant nutrient effects must be considered as descriptive.

In terms of loss, the Helper + H model showed a positive hydrogen slope of +0.18 and a modest negative helper slope of -2.5, consistent with trends seen in previous site-event level models, though with a relatively low adjusted R² value of 0.16. For the Dry Weight × C:N interactions, the model achieved a slightly better fit ($R^2 = 0.4$), with helper positively associated with loss (slope = 4.59) and C:N showing a negative relationship (-0.13). However, given the moderate fit and limited replication, these relationships should be interpreted cautiously, as they do not provide sufficient statistical support to infer causal ecological mechanisms.

In Shannon’s index model for loss, diversity continued to show a positive correlation to resilience with slopes ranging from 0.48 to 0.61 and R² of 0.26 to 0.41. Thus, suggesting that benthic diversity and positive benthic compositions were more resistant to bleaching.

Looking into recovery-based models, none reached statistical significance with a $p>0.15$. Helper slopes remained positive from 8.1 to 10.3, but adjusted R² were close to zero or negative, signalling coral recovery may not be influenced by those factors, or that it is a highly complex process, and such a simplified model is not well designed enough to capture the relationships between recovery and other covariates.

Collectively, this indicates that while benthic structure correlates strongly with immediate coral resistance, it does not reliably predict longer-term recovery across transects, likely due to additional post-disturbance processes (recruitment, hydrodynamics, larval supply) not captured here. No significant correlations were achieved with coral recovery, whereas moderate relationships were observed for coral loss, suggesting that structural and nutrient-related factors may play a greater role in determining initial vulnerability rather than subsequent

regeneration potential. This distinction underscores that drivers of resistance and recovery may operate on different spatial and temporal scales.

3.3 Limitations

- 1. Model design:** Models used in the investigation were linear models which are simple in design and may not capture complex ecological processes well.
- 2. Missing thermal data:** DHW_max was unavailable for the 2010 event, preventing direct modeling of heat stress which could be solved by investigation on a larger scale with more datasets.
- 3. Low sample size:** Site-event models ($n = 6$) produced spuriously high R^2 and negative adjusted R^2 values, confirming that these are **overfitted and unreliable** fits rather than genuine explanatory strength.
- 4. Pseudoreplication:** Transect-level models reused site-level nutrient data, artificially inflating sample independence and reducing ecological validity.
- 5. Temporal mismatch:** Nutrient measurements may not align perfectly with bleaching peaks, weakening causal inference.

4. Conclusion

Across some models, most notably `lm_resist1`, both the helper and Shannon's indices revealed similar ecological directions: Reefs that have more complex and mutualistic benthic communities resisted bleaching better. However, the helper index consistently outperformed Shannon's index in both R^2 and slope. This is hypothesized to be because Shannon's diversity only captures community richness and evenness, but fails to highlight beneficial or competitive taxa, unlike the helper index. As such, the helper index is more mechanistic as an indicator of benefits to coral resilience. Thus, coral resilience may be instead linked to more/less beneficial taxa, and not species diversity alone.

This analysis supports the hypothesis that benthic community composition affects coral resistance, as both ecological indices correlated positively with coral resilience. Nutrient availability was largely inconclusive caused by the small sample size, as H ranged from positive to negative, despite some negative correlation at the transect-event level analysis regarding C: N ratios.

While benthic composition appears central to short-term resistance (loss), it was less predictive of recovery, indicating that longer-term resilience depends on additional ecological and physical processes.

Statistically, the presence of negative adjusted R^2 values highlights difficulties in achieving valid conclusions with limited replication, demonstrating the need for consistent sampling across smaller time intervals and better event coverage (more study sites and events) to increase sample size.

In conclusion, this study reveals that reef resilience is driven by a multitude of factors, not only temperature, but also benthic diversity and biogeochemical conditions (nutrient availability). By integrating benthic indices like the helper index into earlier-mentioned RBM frameworks, scientists and conservationists could improve predictions and responses to thermal stress and future climate conditions, provided that analyses have more robust spatial and temporal replication.

5. Conflicts of Interest

The author declares that they have no conflict of interest.

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